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**CALIBRAÇÃO PÓLEN-VEGETAÇÃO E RECONSTITUIÇÃO PALEOAMBIENTAL
DOS ÚLTIMOS 7.500 ANOS DE SEDIMENTO LACUSTRE NO ECÓTONO CERRADO-
CAATINGA (NE, BRASIL)**

FORTALEZA

2025

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ÚLTIMOS 7.500 ANOS DE SEDIMENTO LACUSTRE NO ECÓTONO
CERRADO-CAATINGA (NE, BRASIL)

Tese apresentada ao Programa de Pós-graduação em Ecologia e Recursos Naturais da Universidade Federal do Ceará, como requisito parcial à obtenção do grau de Doutor em Ecologia e Recursos Naturais. Área de Concentração: Ecologia e Recursos Naturais.

Orientadora: Profa. Dra. Marie-Pierre Ledru.
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RESUMO

No Brasil, a descrição da diversidade vegetal e da ampla variedade de grãos de pólen associados é fundamental para compreender a evolução das espécies e garantir estratégias eficazes de conservação. A identificação precisa é a chave para o sucesso de estudos palinológicos e para a interpretação consistente das mudanças na vegetação do passado. No entanto, enquanto os atlas polínicos brasileiros focam majoritariamente na Amazônia, Mata Atlântica e Cerrado, as informações sobre a Caatinga permanecem dispersas, o que dificulta o avanço da pesquisa na região. Para preencher essa lacuna, a presente tese investigou a história da vegetação no ecótono Cerrado-Caatinga no estado do Piauí por meio de uma abordagem integrada em três etapas fundamentais. Primeiramente, desenvolveu-se um Atlas Palinológico abrangente, composto por 398 espécies de 99 famílias, a partir de material do Herbário Prisco Bezerra (EAC), da Universidade Federal do Ceará (UFC). Este catálogo, que descreve 51 táxons pela primeira vez, inclui não apenas a morfologia polínica detalhada e fotomicrografias em vistas polares e equatoriais, mas também dados ecológicos como formas de vida, variando de ervas e lianas a arbustos e árvores, substratos e tipos de vegetação, servindo como base para futuras reconstituições ambientais. Essa base referencial permitiu caracterizar a chuva polínica moderna da Bacia do Rio Parnaíba através da análise de 41 amostras de sedimentos superficiais úmidos, comparadas a inventários botânicos publicados. Os resultados revelaram uma assinatura mista única, onde elementos do Cerrado, como os tipos *Astronium* e *Tapirira*, coexistem com táxons da Caatinga, como o tipo *Mimosa*. Análises multivariadas identificaram seis grupos florísticos específicos (*Tapirira-Astronium*, mixed, Melastomataceae-Combretaceae, *Borreria-Aspidosperma*, mixed woody-herbaceous, and *Mimosa-type*) e confirmaram que a temperatura média anual (MAT) é o principal vetor ambiental da variância observada. Além disso, o estudo demonstrou que as frequências de pólen arbóreo (AP) rastreiam com precisão a cobertura florestal, enquanto os tipos *Borreria* e Poaceae funcionam como indicadores robustos de abertura da paisagem. A comparação com registros glaciais revelou uma mudança florística drástica de períodos mais frios e úmidos para o clima atual mais quente, marcado pela escassez de táxons de ambientes mais úmidos. Por fim, a calibração entre os dados modernos e o registro sedimentar da Lagoa de Parnaíba possibilitou a reconstituição paleoambiental dos últimos ~7.500 anos, utilizando uma abordagem multi-proxy que incluiu pólen, macrocarvões e geoquímica orgânica. A análise de 112 amostras revelou cinco zonas de mudanças marcantes: inicialmente, entre 7490 e 7050 cal anos AP (Zona

PAR1), a região enfrentou aridez extrema e paisagens abertas dominadas por gramíneas, refletindo um Sistema de Monção da América do Sul (SASM) enfraquecido. Essa instabilidade resultou em um hiato sedimentar de quase quatro milênios (7050 – 3430 cal anos AP), sugerindo o ressecamento total do lago. O restabelecimento da bacia ocorreu no Holoceno Tardio, com a expansão florestal e o pico de consolidação arbórea entre 2050 e 1520 cal anos AP (PAR4), fase que coincide com as primeiras evidências de fogo antrópico. O período final, de 1510 cal anos AP ao presente, é marcado por máxima instabilidade, eutrofização e flutuações intensas no regime de fogo sob forte pressão humana. Em suma, esta tese estabelece um referencial essencial para a interpretação de registros fósseis e compreensão da dinâmica de ecossistemas de transição, destacando a vulnerabilidade do Nordeste brasileiro a futuras mudanças climáticas e à degradação ambiental.

Palavras-chave: Caatinga; catálogo polínico; Cerrado; chuva polínica; ecótono; paleoecologia.

ABSTRACT

In Brazil, the description of plant diversity and the wide variety of associated pollen grains is fundamental for understanding species evolution and ensuring effective conservation strategies. Accurate identification is key to the success of palynological studies and to the consistent interpretation of past vegetation changes. However, while Brazilian pollen atlases predominantly focus on the Amazon, Atlantic Forest, and Cerrado, information on the Caatinga remains scattered, hindering research progress in this region. To fill this gap, this thesis investigated the vegetation history of the Cerrado–Caatinga ecotone in the state of Piauí through an integrated approach structured in three main stages. First, a comprehensive Palynological Atlas was developed, comprising 398 species from 99 families, based on material from the Prisco Bezerra Herbarium (EAC) at the Federal University of Ceará (UFC). This catalog, which describes 51 taxa for the first time, includes not only detailed pollen morphology and photomicrographs in polar and equatorial views, but also ecological data such as life forms, ranging from herbs and lianas to shrubs and trees, as well as substrate types and vegetation categories, thereby providing a foundation for future environmental reconstructions. This reference framework enabled the characterization of modern pollen rain in the Parnaíba River Basin through the analysis of 41 surface wet sediment samples, compared with published botanical inventories. The results revealed a unique mixed signature, in which Cerrado elements, such as *Astronium* and *Tapirira* types, coexist with Caatinga taxa, such as the *Mimosa* type. Multivariate analyses identified six distinct floristic groups (*Tapirira-Astronium*, mixed, Melastomataceae-Combretaceae, *Borreria-Aspidosperma*, mixed woody-herbaceous, and *Mimosa*-type) and confirmed that mean annual temperature (MAT) is the main environmental driver of the observed variance. Furthermore, the study demonstrated that arboreal pollen (AP) frequencies accurately track forest cover, while *Borreria* and Poaceae types serve as robust indicators of landscape openness. Comparison with glacial records revealed a marked floristic shift from cooler and wetter periods to the current warmer climate, characterized by a scarcity of taxa associated with more humid environments. Finally, calibration between modern data and the sedimentary record from Lagoa de Parnaguá (Piauí) enabled the paleoenvironmental reconstruction of the last ~7,500 years using a multi-proxy approach that included pollen, macrocharcoal, and organic geochemistry. The analysis of 112 samples revealed five zones of significant change: initially, between 7,490 and 7,050 cal yr BP (Zone PAR1), the region experienced extreme aridity and open grass-dominated landscapes, reflecting a weakened South

American Monsoon System (SASM). This instability led to a sedimentary hiatus of nearly four millennia (7,050–3,430 cal yr BP), suggesting complete lake desiccation. Basin reestablishment occurred during the Late Holocene, with forest expansion and a peak in arboreal consolidation between 2,050 and 1,520 cal yr BP (PAR4), a phase that coincides with the earliest evidence of anthropogenic fire. The final period, from 1,510 cal yr BP to the present, is marked by maximum instability, eutrophication, and intense fluctuations in the fire regime under strong human pressure.

Keywords: Caatinga; Cerrado; ecotone; pollen catalog; pollen rain; paleoecology.

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1 CAPÍTULO I

1 INTRODUÇÃO GERAL

As mudanças climáticas do Quaternário, com destaque para as rápidas e pronunciadas variações do Holoceno (últimos ~11.700 anos), moldaram, globalmente, de forma decisiva a distribuição geográfica, a composição e as complexas interações que definem os ecossistemas contemporâneos (BENITO-GARZÓN; LEADLEY; FERNÁNDEZ-MANJARRÉS, 2014; MORAES *et al.*, 2022). Essas flutuações, longe de serem subjetivas, resultaram em intensas transições entre períodos úmidos e secos que reconfiguraram continuamente a paisagem global (CASSINO *et al.*, 2020; MONTADE *et al.*, 2014). As mudanças ambientais da era moderna, predominantemente as aceleradas pela ação humana, tornam urgente a necessidade de conhecermos a estrutura original dos ecossistemas (FLANTUA *et al.*, 2015)

A importância de saber a estrutura original dos ecossistemas advém da precisão de uma base essencial para a criação de estratégias de conservação e manejo sustentável eficazes, a qual necessita-se fundamentar na resistência e adaptação dos ecossistemas ao longo do tempo (JAMRICOVÁ *et al.*, 2017; WHITLOCK *et al.*, 2018). É precisamente neste contexto que a paleoecologia se revela uma disciplina indispensável, ao ser utilizado uma coleção de registros fósseis, como sedimentos lacustres, turfeiras e testemunhos de gelo, para a reconstituição detalhada das condições ecológicas de eras passadas, resultando assim em insights únicos para os dilemas ambientais do presente (FLANTUA *et al.*, 2015).

O crescente interesse em estudos sobre a paleoecologia vegetacional no Brasil, advém dessa necessidade de compreender como o meio ambiente se caracterizava quando a interferência humana era mínima ou inexistente (FLANTUA *et al.*, 2015). O Nordeste brasileiro desponta como uma prioridade crítica para a aplicação dessa premissa. A região é marcada por sistemas climáticos complexos, vegetação heterogênea e alta densidade populacional irregular, e com isso tem enfrentado intensa degradação do solo e de seus ecossistemas nas últimas décadas (BDIA, 2022; CASTRO, 2007; MARENCO *et al.*, 2018).

A crise ambiental é acentuada pela variabilidade climática natural, alta insolação, elevada evapotranspiração e chuvas irregulares, somada as projeções de mudanças climáticas globais que preveem a redução das chuvas e o agravamento da desertificação (IPCC, 2022). Essa combinação coloca a região em um estado de alta vulnerabilidade. Diante desse cenário de crise iminente, a paleoecologia apresenta-se como uma ferramenta indispensável, pois permite estabelecer um

padrão natural do ambiente e avaliar se a velocidade e a magnitude das mudanças atuais superam as registradas no passado geológico (BENITO-GARZÓN; LEADLEY; FERNÁNDEZ-MANJARRÉS, 2014).

Dentro da paleoecologia, a palinologia, estudo da morfologia dos grãos de pólen e esporos, se destaca como um dos métodos mais eficazes e confiáveis para inferir o passado de determinados ambientes devido à excelente conservação dos grãos de pólen que se depositaram em sedimentos (HYDE; WILLIAMS, 1945; TRAVERSE, 2007). A conservação adequada dos grãos de pólen é crucial para facilitar a identificação das espécies correspondentes e, assim, relacioná-los eficazmente ao ambiente de origem (ERDTMAN, 1952; SALGADO-LABOURIAU, 2007). Para que essa preservação ocorra, é necessário que o ambiente de depósito seja anóxico/anaeróbico (livre de oxigênio), como ocorre em lagos e turfeiras, pois o oxigênio acelera a degradação da esporopolenina, componente essencial da parede do grão de pólen (SALGADO-LABOURIAU, 2007). Os grãos de pólen possuem uma estrutura interna (intina) e uma camada externa (exina) composta por esporopolenina, que lhes confere resistência a patógenos, radiação e desidratação, preservando sua morfologia ao longo do tempo (BROOKS; SHAW, 1978; KNOX, 1984).

As características morfológicas dos grãos de pólen são geneticamente determinadas e permanecem constantes independentemente das variações ambientais, tornando-os uma ferramenta valiosa em estudos taxonômicos (MELHEM *et al.*, 2003). Sendo assim, cada planta apresenta uma característica morfológica distinta de pólen e a soma dos grãos identificados permite a reconstituição do ambiente que os produziu (HYDE; WILLIAMS, 1945). Para a correta identificação dos grãos e posterior interpretação paleoambiental, a palinologia se baseia no princípio da calibração, realizando trabalhos que catalogam a morfologia das espécies atuais (tipos polínicos modernos) (LORENTE *et al.*, 2017; SILVA *et al.*, 2014). Os grãos de pólen são assim objetos de estudo fundamentais nos trabalhos paleoecológicos pois, ao serem dispersados, podem se depositar em locais favoráveis à conservação (FERRAZ-VICENTINI; SALGADO-LABOURIAU, 1996; SALGADO-LABOURIAU, 1973). A comparação do material fóssil, depositados nos sedimentos, com esses catálogos palinológicos é o que permite uma identificação precisa dos tipos polínicos encontrados nos sedimentos, possibilitando a reconstituição paleoambiental dos eventos que ocorreram na região (BEHLING *et al.*, 2000; SALGADO-LABOURIAU, 2007).

Estudos sobre a chuva polínica moderna, definida como a deposição dos grãos de pólen em

superfícies, oferece uma assinatura polínica da composição vegetacional contemporânea associada e serve como base para inferências paleoecológicas sobre as mudanças climáticas (CASSINO *et al.*, 2020; CASSINO; MARTINHO; CAMINHA, 2018; FLANTUA *et al.*, 2015; XAVIER; ARAÚJO; LEDRU, 2022). O Nordeste brasileiro (NEB) tem ganhado destaque em trabalhos com intuito de conhecerem a assinatura polínica atual dos domínios fitogeográficos nordestinos. No entanto, os estudos ainda são limitados em comparação com outras regiões do país (BEHLING *et al.*, 2000; LEDRU *et al.*, 2022; SANTOS *et al.*, 2015).

As assinaturas polínicas atuais de uma vegetação combinada a materiais confiáveis de consulta para identificação dos grãos de pólen (como palinotecas e catálogos polínicos), apresentam-se como ferramentas imprescindíveis na reconstituição de paleoambientes (CASSINO; LEDRU, 2021; HAN *et al.*, 2020). Isso ocorre, pois, com esses dados, é possível realizar a “calibração” e interpretação do registro fóssil, estabelecendo assim as relações ecológicas e taxonômicas entre os tipos polínicos observados nas camadas sedimentares dos testemunhos e as comunidades vegetais que os produziram (DAWSON *et al.*, 2016; HAN *et al.*, 2020). Sendo assim, para reconstruir o passado de forma confiável a partir de grãos de pólen fóssil, é crucial entendermos primeiro como a vegetação, o clima e as atividades humanas influenciam a chuva polínica moderna (CASSINO; LEDRU, 2021; MONTADE *et al.*, 2016).

1.1 A complexidade do nordeste brasileiro

1.1.1 Contexto climático

O Nordeste brasileiro abrange cerca de 1.558.000 km² do território nacional e possui clima descrito como semiárido, tropical e quente. É caracterizado por uma grande variabilidade térmica e pluviométrica, com diferenças marcantes em sua distribuição espacial e temporal (IBGE, 2021). Devido a essa alta variabilidade podemos separar o Nordeste em três sub-regiões: o Norte, Oeste/Sudoeste, Leste/Central (Fig. 1). Na região Norte, devido a influência sazonal da Zona de Convergência Intertropical (ZCIT), o pico do período chuvoso ocorre durante fevereiro-maio com temperaturas médias anuais em torno de 26°C e precipitação média anual de 800 mm, embora esses valores apresentem variações locais (MARENCO *et al.*, 2018; MOURA *et al.*, 2019).

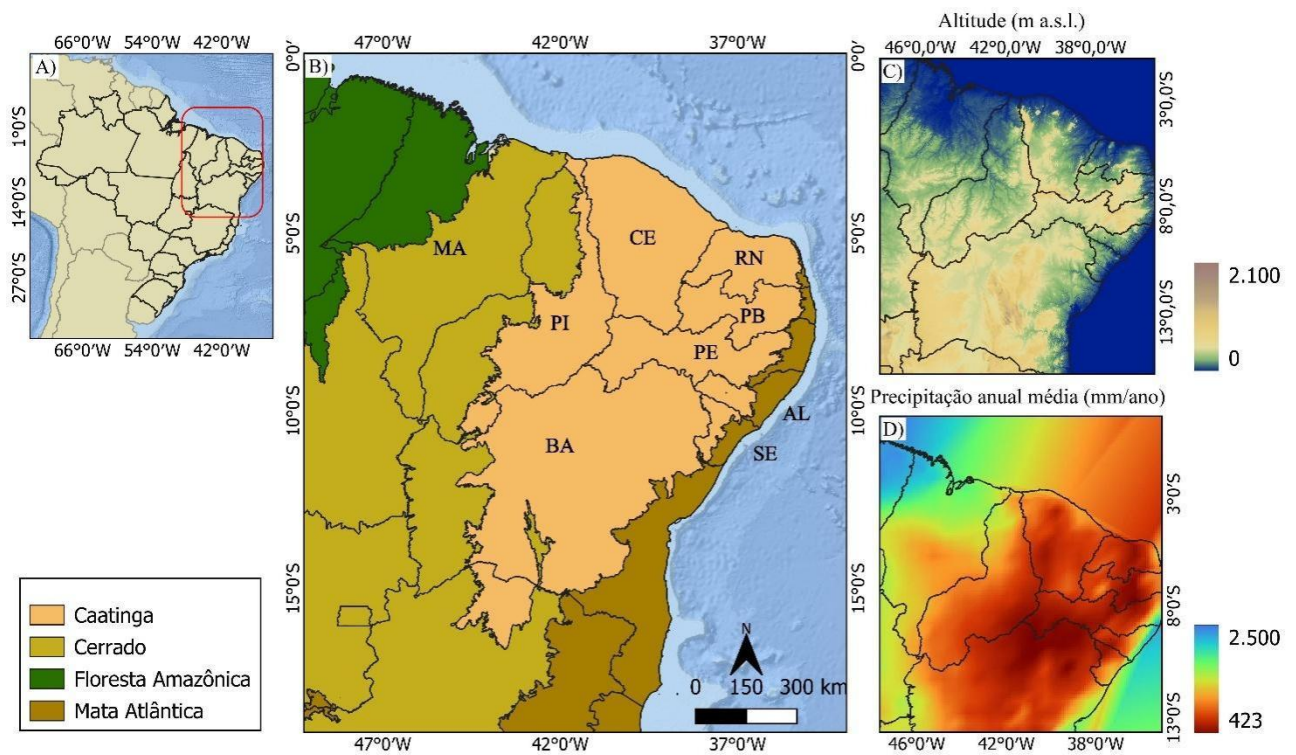


Fig. 1. (A) Localização do Nordeste brasileiro. (B) Mapa detalhado dos domínios fitogeográficos da região, destacando os estados que a compõem: Maranhão (MA), Piauí (PI), Ceará (CE), Rio Grande do Norte (RN), Paraíba (PB), Pernambuco (PE), Alagoas (AL), Sergipe (SE) e Bahia (BA). (C) Mapa de precipitação anual média. (D) Mapa hipsométrico mostrando as variações altitudinais (IBGE, 2023).

Enquanto isso, o clima no Oeste/Sudoeste é afetado pelo fluxo de umidade amazônico do Sistema de Monções da América do Sul (SMAS), consequentemente, a estação chuvosa ocorre de outubro a março, com precipitação média anual de 1.100mm, embora apresente amplitude que varia de 400 e 1800 mm dependendo da localidade (SILVA *et al.*, 2025). Na maior parte da região Leste/Central, também sob influência da ZCIT, a precipitação média anual é de 550 mm (com chuvas de fevereiro a maio), embora em áreas específicas esse valor possa atingir 2.000 mm (janeiro a julho). Para ambas as sub-regiões, a temperatura média anual situa-se em 24°C (MARENGO *et al.*, 2018; SILVA *et al.*, 2025). De modo geral, o Nordeste brasileiro é caracterizado por elevadas temperaturas, cujas médias climatológicas anuais costumam apresentar mínimas ao redor de 20°C e máximas que não ultrapassam os 32°C (INMET, 2020).

Episódios recorrentes de seca na região são profundamente conhecidos e amplamente documentados, sendo uma característica intrínseca de seu clima semiárido (CHIMELI; MUTTER; ROPELEWSKI, 2002). O episódio mais recente ocorreu entre 2010-2016, devido a uma combinação de fatores. O principal deles foi o aquecimento anômalo das águas superficiais do

Atlântico tropical norte, que favoreceu o deslocamento da ZCIT para latitudes mais ao norte, reduzindo drasticamente o transporte de umidade para o nordeste (MARENGO *et al.*, 2018; MEDEIROS; OLIVEIRA; TORRES, 2020). Esse fator interagiu com as oscilações do fenômeno ENSO (El Niño-Oscilação Sul) no Oceano Pacífico, e, a ocorrência da fase “La Niña” (fase fria, tipicamente pluviosa), como em 2012, não foi suficiente para reverter a condição seca imposta pelo Atlântico. O forte evento de “El Niño” (fase quente, tradicionalmente associada à seca no NEB), como em 2015-2016, contribuiu para o agravamento da estiagem (MARENGO *et al.*, 2018; MEDEIROS; OLIVEIRA; TORRES, 2020). Essa seca prolongada (2010-2016) é descrita como a seca mais severa e uma das mais longas registradas na região, com imensos impactos sociais e econômicos (MARENGO *et al.*, 2018).

Contudo, enquanto no período de 2010-2016 ficou demonstrada a extrema sensibilidade da região às oscilações oceânicas em escala interanual (MARENGO *et al.*, 2018), o estudo das variações multimilenares ao longo do Holoceno (~11.700 anos) mostra mudanças profundas, evidenciando a transição de um ambiente úmido para o semiárido atual. Durante o Holoceno Inferior (~11.700 a ~8.200 anos AP), as condições no Nordeste foram mais úmidas. Nessa época, a baixa insolação de verão no Hemisfério Sul manteve a posição média da ZCIT mais ao norte e enfraqueceu o Sistema de Monção da América do Sul (SMAS) (CRUZ *et al.*, 2009; UTIDA *et al.*, 2020). Esse enfraquecimento reduziu a descida de ar seco (subsidiência) sobre o Nordeste brasileiro, favorecendo as chuvas locais. Essa fase úmida foi observada até meados de 5.000 anos AP, período que contrasta diretamente com um clima mais seco na Amazônia ocidental e no sudoeste do país (VAN BREUKELLEN *et al.*, 2008; WANG *et al.*, 2007), evidenciando um padrão de dipolo leste-oeste na precipitação da América do Sul. Assim, a variação da umidade regional era, e permanece, controlada principalmente pela dinâmica integrada entre a oscilação da ZCIT e do SMAS, ambos modulados pela temperatura da superfície do Oceano Atlântico e pela insolação (MARENGO *et al.*, 2018; UTIDA *et al.*, 2020).

A mudança mais significativa que definiu a estrutura climática atual do Nordeste brasileiro ocorreu por volta de 4.200 anos AP, marcada por uma redução abrupta da precipitação (CRUZ *et al.*, 2009; UTIDA *et al.*, 2020). Esse evento foi impulsionado pelo aumento da insolação no Hemisfério Sul, o que aqueceu o continente e favoreceu a migração média da ZCIT para o sul. Contudo, esse mesmo aquecimento intensificou o Sistema de Monção da América do Sul (SMAS) na Amazônia e nos Andes. O fortalecimento da monção gerou uma forte subsidiência (descida de

ar seco) sobre o Nordeste, inibindo a formação de chuvas e consolidando a aridez regional, apesar da maior proximidade da ZCIT (CHIESSI *et al.*, 2021; VAN BREUKELEN *et al.*, 2008). Essa configuração histórica estabelecida em 4.200 anos AP não apenas moldou o clima semiárido, mas também tornou a região altamente sensível. Tal vulnerabilidade se manifesta na recorrência das secas atuais, cujos mecanismos de modulação, como o aquecimento do Atlântico e os deslocamentos da ZCIT, atuam agora em escalas interanuais e decadais, repetindo a lógica das grandes variações do passado (MARENGO *et al.*, 2018).

1.1.2 A vegetação nordestina

A fitofisionomia atual do Nordeste do Brasil (NEB) resulta de uma organização complexa e diversificada de domínios fitogeográficos, cuja delimitação é diretamente determinada pela extensão e pelo regime de precipitação local (Fig. 1). A paisagem do NEB é caracterizada pela presença dos biomas Floresta Amazônica, Mata Atlântica, Caatinga e o Cerrado, que se interconectam no território (ANDRADE-LIMA, 1966). A noroeste, a Floresta Amazônica se caracteriza como uma floresta tropical úmida, cuja estação chuvosa estende-se por sete meses (janeiro a julho), com precipitação média anual superior a 1800 mm (NASCIMENTO; BRAGA; ARAÚJO, 2017). Com características climáticas semelhantes, a Mata Atlântica acompanha a costa oriental do Nordeste, abrangendo uma área de 164.700 km² (10% da área do NEB), compartilha do mesmo perfil de floresta tropical úmida, mas apresenta um período chuvoso ligeiramente mais longo, de janeiro a agosto, e chuvas médias anuais acima de 1500 mm (CORREIA FILHO *et al.*, 2019).

A Caatinga (ou savana-estépica) domina as porções leste e central (Fig. 1), frequentemente descrita como uma floresta sazonalmente seca (FTSS), caracterizada pelo clima semiárido e quente, com precipitação média anual que varia entre 400 e 800 mm com estação chuvosa curta e variável (janeiro a maio, 5 meses) (INMET, 2020). É resistente a variabilidade interanual e as secas recorrentes, sendo um domínio independente de fogo devido à baixa frequência de descargas elétricas e a vegetação dispersa dificulta a queima contínua (PIVELLO *et al.*, 2021). Sua vegetação é composta por quatro subgrupos fitofisionômicos distintos: a Savana-Estépica Florestada (formação mais fechada, estruturada em dois estratos: um superior denso de nanofanerófitas decíduas, com troncos grossos e espinhosos, e um estrato inferior gramíneo-lenhoso de pouca expressão), Savana-Estépica Arborizada [compartilha as características do estrato superior esparsa

da Florestada, mas se diferencia por um estrato gramíneo-lenhoso inferior de relevante importância fisionômica, abrigando espécies endêmicas como o xique-xique (*Pilosocereus gounellei*) e o mandacaru (*Cereus jamacaru*), Savana-Estépica Parque [caracterizada por um arranjo de pequenas árvores e arbustos distribuídos de forma muito espaçada (*parkland*) sobre um denso tapete de herbáceas e gramíneas, com predominância de *Mimosa acutistipula* e *Auxemma onocalyx*] e, por último, Savana-Estépica Gramíneo-Lenhosa (também chamada de campo espinhoso, é marcada pela presença de um extenso tapete graminoso (principalmente o capim-panasco, *Aristida sp.*) mesclado por plantas lenhosas anãs e espinhosas, como os nanofanerófitos do gênero *Jatropha*) (VELOSO; FILHO; LIMA, 2012).

O Cerrado, conhecido como savana brasileira, é o segundo maior domínio do país e ocupa a região oeste/sudoeste do NEB, agindo como uma região de transição entre a Caatinga seca e o fluxo de umidade advindo da Amazônia (Fig 1). Caracterizado pelo clima tropical sazonal, a estação chuvosa costuma ser mais longa que a da Caatinga, de outubro a março (6 meses), e com precipitação média anual entre 1000 a 1800 mm (INMET, 2020). A vegetação do Cerrado possui fisionomias bastante diversas que vão desde formações florestais (matas de galeria e cerradão) e formações savânicas (Cerrado *sensu stricto* e veredas) até formações campestres abertas (campo limpo e campo rupestre) (RIBEIRO; WALTER, 2008). Diferentemente da Caatinga, o Cerrado é uma vegetação dependente de fogo, incêndios naturais são frequentes durante a mudança das estações (de seca para chuvosa), facilitados pela frequência de descargas elétricas e disponibilidade contínua de biomassa inflamável (GOMES; MIRANDA; BUSTAMANTE, 2018).

As espécies características do Cerrado nordestino se diferem das espécies do Cerrado da região central do Brasil. No Nordeste os gêneros mais comuns são: *Anacardium* (Anacardiaceae), *Bowdichia* e *Dimorphandra* (Fabaceae), *Curatella* (Dilleniaceae) e *Qualea* (Vochysiaceae) (VIEIRA *et al.*, 2019). Enquanto que no Cerrado central os gêneros mais observados são *Chamaecrista* e *Mimosa* (Fabaceae), *Croton* (Euphorbiaceae) e *Myrcia* (Myrtaceae) (MENDONÇA *et al.*, 2008). Devido a isso e outros fatores (dispersão geográfica, variabilidade climática, composição mista de espécies com influência da Caatinga e da Amazônia), o Cerrado nordestino é classificado como uma província periférica por divergir do Cerrado central (RATTER; RIBEIRO; BRIDGEWATER, 1997; VIEIRA *et al.*, 2019)

O NEB é uma região altamente vulnerável às mudanças climáticas, a combinação do aquecimento global com a intensa pressão antrópica (desmatamento e avanço das fronteiras

agrícolas) está provocando alterações significativas na estrutura dos ecossistemas (BDIA, 2022). Projeções futuras são alarmantes com secas prolongadas e extremas, aumento da atividade de incêndios e diminuição das chuvas. Até 2100 é esperado que as chuvas sejam reduzidas em mais de 54% da região com aumento das temperaturas acima de 4°C (IPCC, 2022; SALAZAR; NOBRE; OYAMA, 2007). Tais mudanças podem causar uma redução drástica da cobertura vegetal regional e uma severa perda de biodiversidade, colocando em risco os domínios singulares do NEB como o Cerrado e a Caatinga.

1.1.3 A bacia hidrográfica do Rio Parnaíba

A bacia hidrográfica do Rio Parnaíba (Fig. 2; 02°21'S - 11°06'S; 47°21'W - 39°44'W; BHRP) é reconhecida como uma das mais importantes da região nordeste do Brasil, sendo superada em destaque apenas pela bacia do rio São Francisco (ABREU; MUTTI; LIMA, 2019). Essa bacia atende a cerca de 4,15 milhões de habitantes e possui uma área territorial estimada em aproximadamente 331.000 km². Seu território abrange partes do Maranhão (19% da bacia) e do Ceará (4%), mas a sua maior porção encontra-se no Piauí (77% da bacia), englobando quase a totalidade (99%) da área desse estado (ABREU; MUTTI; LIMA, 2019; MOTTA; GONÇALVES, 2016).

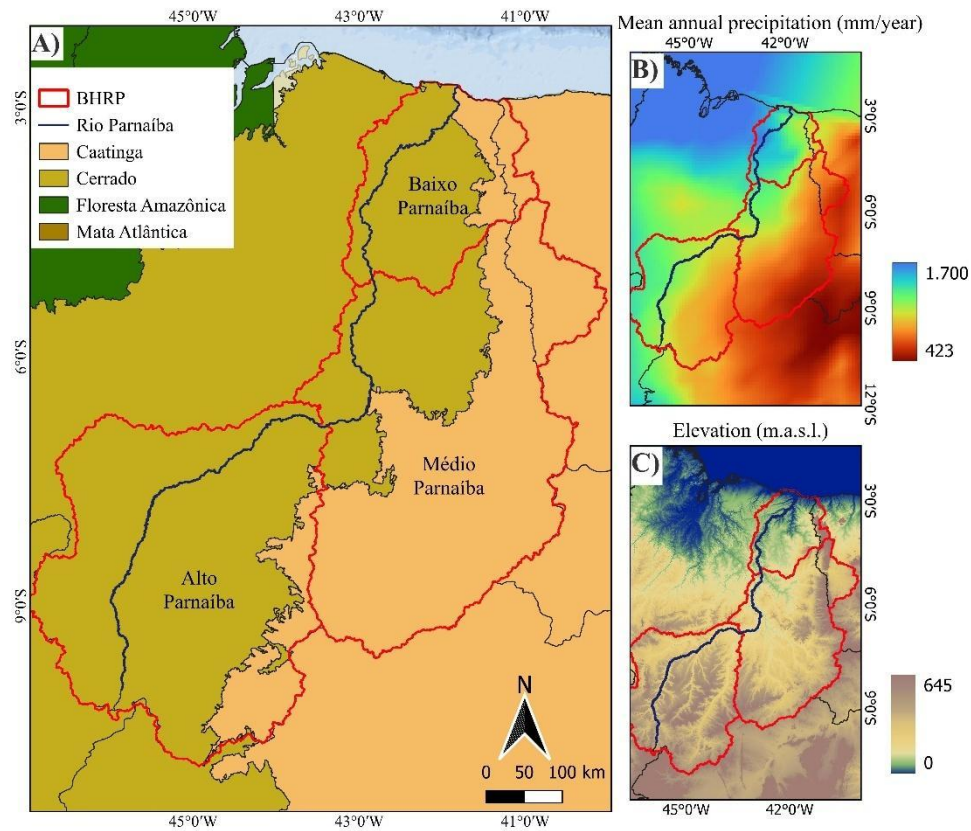


Fig. 2. (A) Localização da Bacia Hidrográfica do Rio Parnaíba (BHRP), incluindo suas principais sub-bacias, Alto, Médio e Baixo Parnaíba, o curso do Rio Parnaíba e a distribuição dos domínios fitogeográficos presentes na bacia. (B) Mapa de precipitação média anual. (C) Mapa hipsométrico indicando as variações altitudinais (IBGE, 2023).

O Rio Parnaíba, que dá o nome a bacia, possui extensão de aproximadamente 1.400 km (MOTTA; GONÇALVES, 2016). Ele nasce na Chapada das Mangabeiras, divisa entre o Piauí e o Tocantins e seu curso, seguindo do sul para o norte da bacia, separa os estados do Piauí e Maranhão desaguando, ao fim, no Oceano Atlântico onde forma um delta amplo e recortado, com três braços do rio na saída para o mar (GANDARA, 2013). Devido a sua extensa dimensão territorial e a grande heterogeneidade ambiental e hidrológica, a bacia é tradicionalmente dividida em três unidades fisiográficas: Alto, Médio e Baixo Parnaíba (PENNEREIRO, 2020).

Entre os principais afluentes, que, em sua maioria, são supridos por águas pluviais de escoamento superficial direto, destacam-se: Alto Parnaíba - Rios Balsas (MA, 525 km); Uruçuí Preto (PI, 270 km); e Gurgueia (PI, 532 km), sendo as sub-bacias do Alto Parnaíba e do Rio Balsas as que mais contribuem com a vazão do Parnaíba; Médio Parnaíba - Rios Canindé/Piauí (o Canindé é torrencial e intermitente em grande parte); e Poti (nasce no Ceará e deságua em Teresina/PI); Baixo Parnaíba - Rio Longá (perene no médio e baixo curso)(MOTTA; GONÇALVES, 2016;

PENEREIRO, 2020). Nessa última parte, o Parnaíba assume características de rio de planície com baixa velocidade de escoamento e presença notória de bancos de areia (MOTTA; GONÇALVES, 2016).

A BHRP possui grande importância quanto aos recursos hídricos subterrâneos, com sistemas aquíferos considerados de maior potencial do Nordeste (MMA, 2006; MOTTA; GONÇALVES, 2016). Os principais sistemas são Serra Grande, Cabeças e Poti-Piauí. Contudo, a exploração desses recursos apresenta desafios como o grande desperdício de água proveniente dos poços jorrantes no Vale do Gurgueia (Cabeças), que foram perfurados a partir da década de 1970 e estimam que o desperdício seja de 250 milhões de litros de água por dia (MMA, 2006; MOTTA; GONÇALVES, 2016).

O clima ao longo da BHRP é diversificado, sendo classificado de semiárido e subúmido, com temperatura média anual de 27,5 °C e precipitação média anual de 1.172 mm (CODEVASF, 2014; LIMA *et al.*, 2020). As estações são bem definidas, com um período chuvoso concentrado, 50-350 mm/mês, de 3 a 6 meses (novembro a abril) e uma estação seca prolongada podendo durar de 4 a 8 meses, com precipitação inferior a 100 mm/mês, a depender da região (ABREU; MUTTI; LIMA, 2019; IBGE, 2023). O principal sistema atmosférico associado à precipitação da bacia é a Zona de Convergência Intertropical (ZCIT), principalmente no litoral, e os Sistemas Convectivos de Mesoescala (SCM) no Sudoeste (ABREU; MUTTI; LIMA, 2019).

A vegetação e o relevo da BHRP possuem características ambientais diversificadas (ABREU; MUTTI; LIMA, 2019). Por exemplo, a vegetação no Alto Parnaíba é característica de Cerrado, enquanto o Médio compreende a zona transicional entre o Cerrado e a Caatinga; e o Baixo Parnaíba além do Cerrado e da Caatinga, também conta com a vegetação costeira no litoral (MOTTA; GONÇALVES, 2016; PENEREIRO, 2020). É estimado que 75% da vegetação nativa ainda cobrem a área da bacia mesmo com a grande pressão antrópica que a região vive atualmente devido a expansão das fronteiras agrícolas nos estados do Maranhão, Piauí, Tocantins e Bahia (também conhecidos como MATOPIBA) (CODEVASF, 2014; MOTTA; GONÇALVES, 2016).

Os solos da bacia são predominantemente os Latossolos Amarelos, Neossolos Quartzarênicos e Neossolos Litólicos (MOTTA; GONÇALVES, 2016). No Alto Parnaíba, os Latossolos são geralmente distróficos e ácidos, o que lhes confere uma fragilidade natural (FARINASSO *et al.*, 2006). Somada a essa característica, a intensa exploração agropecuária resultante do avanço da fronteira do MATOPIBA gerou um potencial erosivo excessivo em 41,82%

da área (FARINASSO et al., 2006). Esse cenário exige trabalhos imediatos de prevenção e estudos focados no manejo sustentável e no ordenamento da ocupação territorial.

1.2 Calibração palinológica

1.2.1 A importância dos catálogos palinológicos

Os atlas palinológicos reúnem descrições de grãos de pólen provenientes de fontes botânicas (herbário e campo) ou sedimentares (material fóssil), servindo como referência para a identificação de táxons ocorrentes em uma área de estudo (LORENTE *et al.*, 2017; SALGADO-LABOURIAU, 1973). Essas obras apresentam detalhes da morfologia polínica (como forma, tamanho, aberturas, ornamentação) que permitem a comparação sistemática com palinomorfos observados em diversas matrizes, a exemplo de sedimentos e mel (CASSINO, 2011; SILVA *et al.*, 2014). Na ausência desses referenciais, a determinação taxonômica dos grãos de pólen torna-se imprecisa, comprometendo a confiabilidade dos dados nas áreas onde a palinologia é aplicada (NOVAIS *et al.*, 2018).

A utilidade dos atlas palinológico é ampla, além da paleoecologia, áreas como taxonomia e filogenia vegetal, aeropalinologia (estudo das alergias) e palinologia forense se veem refém da necessidade desses materiais de referência (MOTOMURA *et al.*, 2021; ROWNEY *et al.*, 2021). No Brasil, podemos encontrar alguns atlas e catálogos palinológicos que auxiliam no estudo dos palinomorfos como por exemplo para a Amazônia (COLINVAUX; DE OLIVEIRA; PATIÑO, 1999), para o Cerrado (CASSINO; MEYER, 2011; SALGADO-LABOURIAU, 1973), de pólen e plantas utilizados por abelhas da Caatinga, do Cerrado e da Mata Atlântica (LORENTE *et al.*, 2017; SILVA *et al.*, 2014, 2020a), de esporos e grãos de pólen de plantas aquáticas do litoral do sudeste brasileiro (YBERT; BOVE; CARVALHO, 2017).

Cada tipo de vegetação possui um conjunto florístico singular, o que exige a criação de catálogos específicos para cada região (SILVA, 2007). Um atlas de Mata atlântica, por exemplo, terá representatividade limitada ao utilizá-lo para identificação de grãos de pólen oriundos de plantas da Caatinga. A lacuna de conhecimento prévio acerca dos tipos polínicos locais, torna as identificações uma tarefa difícil e imprecisa (CASSINO; MEYER, 2011; SILVA, 2007). O estudo de Silva (2007) sobre a Caatinga hiperxerófila de Canudos (Bahia) exemplifica esse aspecto, constituindo-se como a primeira grande contribuição para a caracterização morfológica dos grãos de pólen desse domínio, e ressaltando que, aproximadamente, um terço das espécies da Caatinga

são endêmicas.

O Cerrado, por sua vez, se mostra tão complexo quanto, sua grande extensão e biodiversidade estabelece áreas de transição, também chamados de ecótonos, com quase todos os tipos de vegetação brasileiros (MÉIO *et al.*, 2003; VIEIRA *et al.*, 2019). Esta característica transicional torna a elaboração de atlas palinológicos importante e desafiadora. O estudo de palinomorfos do Holoceno em uma vereda no Chapadão dos Gerais (Minas Gerais) destaca isso (CASSINO; MEYER, 2011). O trabalho revelou não apenas táxons de fitofisionomias típicos de Cerrado (campo sujo, mata de galeria, etc.), como também grãos de pólen de plantas característicos de outros domínios como a Caatinga (*Commiphora leptophloeos*) e a Mata atlântica (*Podocarpus*, *Drimys brasiliensis*).

Essas ocorrências confirmam que depósitos sedimentares em áreas de transição podem registrar uma palinoflora mais ampla com elementos característicos de vegetações vizinhas (CASSINO; MEYER, 2011). Sendo assim, um atlas focado apenas no “Cerrado típico” seria insuficiente para interpretar tais registros com confiabilidade. Conclui-se, portanto, que o desenvolvimento de catálogos detalhados para regiões de transição é fundamental, pois não só aprimora a precisão das reconstituições paleoambientais, como também fornecem dados valiosos para a ecologia e conservação dessas áreas complexas.

1.2.2 Chuva polínica moderna

O estudo de Behling *et al.* (2000) foi o precursor do intuito de conhecer a assinatura polínica existente atualmente no Nordeste brasileiro, no qual utilizou 15 amostras de superfície de diversos tipos de vegetação (Caatinga, restinga, Floresta Atlântica) para que os resultados fossem calibrados com um testemunho marinho. Isso demonstrou uma predominância de grãos de pólen de espécies herbáceas da Caatinga, exibindo assim a consequência da intensa atividade humana, e mapeou um gradiente de umidade ao longo da costa leste, onde esporos de samambaia (indicadores de umidade) aumentavam em direção ao sul.

Historicamente, a Caatinga é um domínio fitogeográfico carente de dados palinológicos modernos (Fig. 2) e isso limita as interpretações paleoclimáticas e de dinâmica das comunidades vegetais (LEDRU *et al.*, 2022). Com o passar do tempo novos estudos no NEB tem surgido, e a escassez de dados sobre a chuva polínica moderna da Caatinga foi parcialmente mitigada por estudos realizados na Estação Biológica de Canudos (Bahia), onde testaram diferentes coletores.

No uso de coletores naturais, foi validado o uso de bromélias e tapetes de musgos como armadilhas de pólen, em ambos foi possível observar uma alta diversidade polínica e o predomínio de espécies zoófilas (91,4% nos musgos) (GOMES *et al.*, 2014; SANTOS *et al.*, 2015). Quando coletores artificiais (*Tauber*), foi possível observar uma concentração polínica anual elevada para um ambiente semiárido e conseguiu-se correlacionar o aumento da temperatura com a deposição de pólen de árvores/arbustos. Em comum, esses trabalhos identificaram e confirmaram um conjunto de táxons indicadores de Caatinga, como *Commiphora leptophloeos*, *Cereus jamacaru* e *Pilosocereus tuberculatus* (MAGALHÃES-E-SILVA; SANTOS, 2024).

Contudo, outros estudos aprofundaram a relação entre a assinatura polínica e a paisagem no Ceará. Montade *et al.* (2016) utilizou amostras de superfície em maciços montanhosos do Ceará para caracterizar diferentes tipos de vegetações presente nas florestas de altitude (Ombrófila densa, estacional semidecídua e decídua), confirmando que o aumento da precipitação de acordo com a altitude é o principal fator de controle da composição da vegetação. Enquanto isso, outra pesquisa utilizou reservatórios no mesmo estado para quantificar o impacto humano na vegetação (LEDRU *et al.*, 2022). O estudo desenvolveu um “escore de alteração” e concluiu que o semiárido está completamente impactado pelas ações antrópicas, sendo a dominação de *Mimosa tenuiflora* um indicativo do uso intensivo da terra (para cultivo ou pastagens) e sugerindo assim, um processo de desertificação fortemente relacionado à ação humana e independente do clima local (LEDRU *et al.*, 2022).

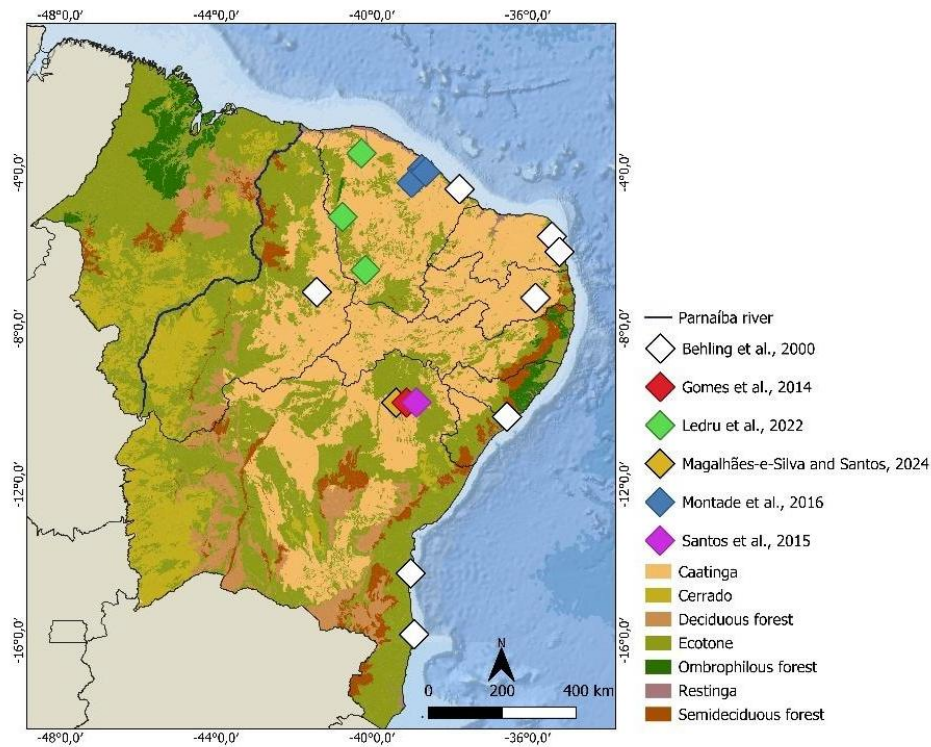


Fig. 2. Distribuição dos estudos de chuva polínica moderna realizados no Nordeste do Brasil até 2025 e localização do Rio Parnaíba (BDIA, 2022).

1.2.3 Paleocologia do Nordeste Brasileiro

Apesar da importância do NEB para a paleoecologia, a região ainda é marcada pela carência de dados paleoambientais. Devido ao clima semiárido que recobre aproximadamente 63% da região há a dificuldade em localizar lagos permanentes ou turfeiras em ambiente hidromórficos, o que resulta na má preservação das amostras (MORAES; DE OLIVEIRA; BEHLING, 2020; XAVIER; ARAÚJO; LEDRU, 2022). A pesquisa na região ainda é mais complexa devido a baixa resolução de muitos registros que tendem a se concentrar em regiões costeiras influenciadas pelo nível relativo do mar ou pela ZCIT, mascarando os sinais climáticos regionais (XAVIER *et al.*, 2024).

No entanto, mesmo com essas dificuldades, importantes resultados têm sido alcançados na reconstituição da história climática e vegetal da região. O início do Holoceno (~10.990-10.540 anos AP) (COHEN *et al.*, 2013) na região da Caatinga/Cerrado do Vale do Rio Icatu (Bahia) foi marcado por condições mais úmidas e temperaturas moderadas, o que favoreceu a expansão de uma floresta tropical de galeria rica em espécies (DE OLIVEIRA; BARRETO; SUGUIO, 1999). As conexões biogeográficas foram confirmadas por meio das análises palinológicas, que

registraram a migração dos táxons da Amazônia e Mata Atlântica para o vale do Rio Icatu por ~10.500 anos AP (DE OLIVEIRA; BARRETO; SUGUIO, 1999).

No Holoceno médio (~8.000-4.200 anos AP) (COHEN *et al.*, 2013), o litoral norte experimentou um elevado nível relativo do mar (RSL), resultando no *highstand* entre 5.500 e 5.020 anos AP que permitiu a dominância de vegetação de mangue (*Rhizophora*) (MORAES *et al.*, 2021a). Nesse período, o principal influenciador na distribuição da vegetação Amazonica/Cerrado foi a oscilação da intensidade do gradiente de umidade leste-oeste, em fase com a variabilidade do SASM (XAVIER *et al.*, 2026). O evento de seca em 4.200 anos AP é o marco climático mais proeminente do Holoceno, caracterizado por uma redução abrupta na precipitação, iniciando assim o processo de aridez do NEB (BENITO-GARZÓN; LEADLEY; FERNÁNDEZ-MANJARRÉS, 2014).

A severidade do evento foi tão marcante que resultou em amostras estéreis devido à oxidação na Chapada das Mesas (XAVIER *et al.*, 2024). Regionalmente, houve respostas diferenciadas: no Leste (Serra de Maranguape), a floresta ombrófila foi substituída por semidecídua (MONTADE *et al.*, 2014), no Icatu, ocorreu a expansão da Caatinga seca (DE OLIVEIRA; BARRETO; SUGUIO, 1999). O Holoceno Tardio (após 4.200 anos AP) é definido pela inversão do gradiente de umidade leste-oeste: a Caatinga se expandiu no Leste mais seco, enquanto o oeste/sudoeste se tornou mais úmido, favorecendo a expansão de Cerrado e Floresta Amazônica após ~2.600 anos, em sincronia com o aumento da convecção da monção (GUERRA *et al.*, 2024; XAVIER *et al.*, 2024).

A partir de 2.600 anos AP, os registros paleoecológicos demonstram um aumento acentuado na atividade antropogênica, observado por maior queima de biomassa e indicadores culturais (XAVIER *et al.*, 2026). A presença de palmeiras (*Orbignya* e *Mauritia*) e feijão (*Phaseolus*), junto com alta frequência de carvão, atesta forte influência ameríndia no leste do NEB (Catimbau, ~2.150-450 anos AP) (MORAES; DE OLIVEIRA; BEHLING, 2020). No Maranhão, registros arqueológicos únicos mostram a construção de vilas palafíticas após ~2.580 anos AP (MORAES *et al.*, 2022).

A chegada da colonização europeia após 1650 d.C. no Cerrado de Sete Cidades, marcou uma mudança expressiva nas práticas de uso da terra: de baixa queima (indígena) para incêndios extensivos e desmatamento (XAVIER; ARAÚJO; LEDRU, 2022). Em termos de conservação, os achados mostram que as formações florestais do NEB são particularmente vulneráveis a seca

extrema (GUERRA *et al.*, 2024; MONTADE *et al.*, 2014). No entanto, ao observar o caso de Sete Cidades, é possível destacar a importância que políticas modernas de proteção (como a criação do Parque Nacional) tem o poder de mitigar séculos de intensa exploração (XAVIER; ARAÚJO; LEDRU, 2022).

1.2.4 Presença humana no Nordeste

O NEB representa uma das áreas mais cruciais e controversas para o estudo do povoamento inicial na América do Sul (BUENO; DIAS, 2015). Os registros arqueológicos sugerem uma ocupação que se estende ao Pleistoceno final e Holoceno inicial, confrontando o antigo paradigma que limitava a presença humana na região a apenas ~3.000 anos AP (MELO, 2007). Pesquisas recentes refutaram essa visão de “vazio” demográfico, indicando que o povoamento dos sertões semiáridos começou em um contexto de maior umidade (MARTIN, 2013; MELO, 2007). Rotas de interiorização, como o Vale do Rio São Francisco, são consideradas eixos que conectaram o Nordeste à região central brasileira (DIAS; BUENO, 2014).

Há evidências de ocupação antiga que se distribuem em diversos estados: Na Bahia, sítios como Coribe e Toca do Manoal Latão apresentam datações superiores a 10.000 anos, enquanto que na Toca da Esperança sugere uma potencial ocupação humana no Pleistoceno médio (MARTIN, 2013). Em Pernambuco, a Furna do Estrago possui destaque devido a recuperação esqueléticas humanas datados em torno de 10.000 anos AP. No Rio Grande do Norte, região de Seridó, sítios como o Sítio do Alexandre (um cemitério pré-histórico) e outros revelam a presença de caçadores com tecnologia lítica refinada (pontas de projétil bifaciais) entre 9.400 e 9.410 anos BP (MARTIN, 2013). Na ocupação costeira, só se tem registros a partir de 8.000 anos AP, possivelmente devido a destruição dos vestígios pela elevação do mar pós-glaciação (BUENO; DIAS, 2015).

O sudeste do Piauí se encontra no centro do debate cronológico, principalmente a área do Parque Nacional da Serra da Capivara (PNSC), que concentra o maior número de sítios contendo arte rupestre na América (MELO, 2007). O Toca do Boqueirão da Pedra Furada, sítio de maior destaque, apresenta cronoestratigrafia que sugere ocupação a partir de 48.000 anos AP (MELO, 2007). Essas datações, associadas a carvões e indústrias sobre seixo, geraram intensa polêmica e ceticismo na comunidade científica internacional, que questiona a origem antrópica dos artefactos mais antigos (LOURDEAU, 2019; MELO, 2007). No entanto, o PNSC apresenta outras evidências robustas de antiguidade, como o Sítio do Meio, com datação de até 14.300 ± 400 anos AP, e a Toca

do Gordo do Garrincho, que forneceu crânios humanos fósseis cruciais para a paleoantropologia (LOURDEAU, 2019; MELO, 2007).

O Piauí é considerado como uma região de encruzilhada cultural, incluindo a tradição de pinturas rupestres (LOURDEAU, 2019; PESSIS; GUIDON, 2007). Há evidências de densificação da ocupação e expansão territorial das populações durante o Pleistoceno-Holoceno (BUENO; DIAS, 2015). Essas relações entre a tradição nordestina da Serra da Capivara e a subtradição Seridó no Rio Grande do Norte sugerem movimentos migratórios e interações culturais (MARTIN, 2013). Apesar das controvérsias, o conjunto de dados confirma o NEB como um laboratório essencial para a compreensão das múltiplas rotas e cronologias do povoamento sul-americano, embora a hipótese do "Archaic Gap" sugira um potencial despovoamento parcial durante o Holoceno Médio devido a estresses climáticos (BUENO; DIAS, 2015).

Ao sul do Piauí, encontra-se o município de Parnaguá, uma cidade história sendo considerada o segundo município mais antigo do estado, atrás apenas de Oeiras. A ocupação histórica do município remonta ao século XVII, contudo, ele está próximo de regiões do sul do Piauí (como a Serra da Capivara) com vastos e antigos registros arqueológicos que atestam a presença humana desde o Pleistoceno (com mais de 40.000 anos AP) (GUIDON, 1992). Nos registros mais recentes, Parnaguá era habitada por índios Pimenteiras, Cheréns e Acoroás, e começou a ser ocupada após a divisão em sesmarias pelo Governador de Pernambuco a partir de 1676 (IBGE, 2025). A fundação da Vila de Parnaguá em 1698, na margem ocidental da lagoa de mesmo nome, foi impulsionada pelas incursões dos índios Macoazes e Rodelleiros no sertão de Rodellas, e a povoação se tornou parte da Capitania do Piauí em 1751, e se tornou município apenas em 1935 (IBGE, 2025).

1.3 Justificativa e Objetivos

O Nordeste brasileiro (NEB) tem se mostrado, com o passar dos anos, ser uma região extremamente sensível às mudanças climáticas e à influência humana. Contudo, ainda é uma das regiões menos abordadas pela pesquisa paleoecológica. Dominado pela Caatinga semiárida, o NEB também apresenta formações florestais e micro-refúgios, como o Cerrado, que demonstram alta sensibilidade às variações climáticas, com recuperação lenta após secas extremas (MONTADE *et al.*, 2014). A urgência do presente estudo é reforçada pelo fator humano: o aumento acentuado da atividade antropogênica, a partir de 2.600 anos AP, tem dificultado as mudanças de alcance e a

migração de espécies necessárias para o ajuste dos ecossistemas frente a transição climática (Holoceno-Antropoceno) que é de maior magnitude do que as observadas em períodos passados (BENITO-GARZÓN; LEADLEY; FERNÁNDEZ-MANJARRÉS, 2014).

O estado do Piauí, inserido no NEB e que abrange grande parte da Bacia do Parnaíba, possui uma relevância ímpar principalmente devido a sua localização estratégica. O estado atua como uma zona de transição (ecótono) entre dois domínios fitogeográficos de grande importância, a Caatinga e o Cerrado, conferindo-lhe uma notável heterogeneidade vegetal (CASTRO, 2007). No entanto, a complexidade histórica ambiental e vegetal desta região ainda se encontra incompleta.

Adicionalmente, a necessidade de registros terrestres robustos é sublinhada pelas interpretações contraditórias geradas por estudos marinhos próximos (Fig. 3). Testemunhos coletados na foz do Parnaíba (ex: GeoB16205-4 e GB1248) divergiram significativamente sobre as rotas de intercâmbio biótico (Corredor litorâneo vs. Rota montanhosa) e os mecanismos de dispersão de pólen (*Podocarpus* associado à umidade/fluvial vs. *Podocarpus* associado a vento/seco) (BOUIMETARHAN *et al.*, 2018; PIACSEK *et al.*, 2021). Esta incerteza sobre os mecanismos de transporte de pólen e as rotas biogeográficas exige uma calibração detalhada em terra para validar as inferências paleoecológicas.

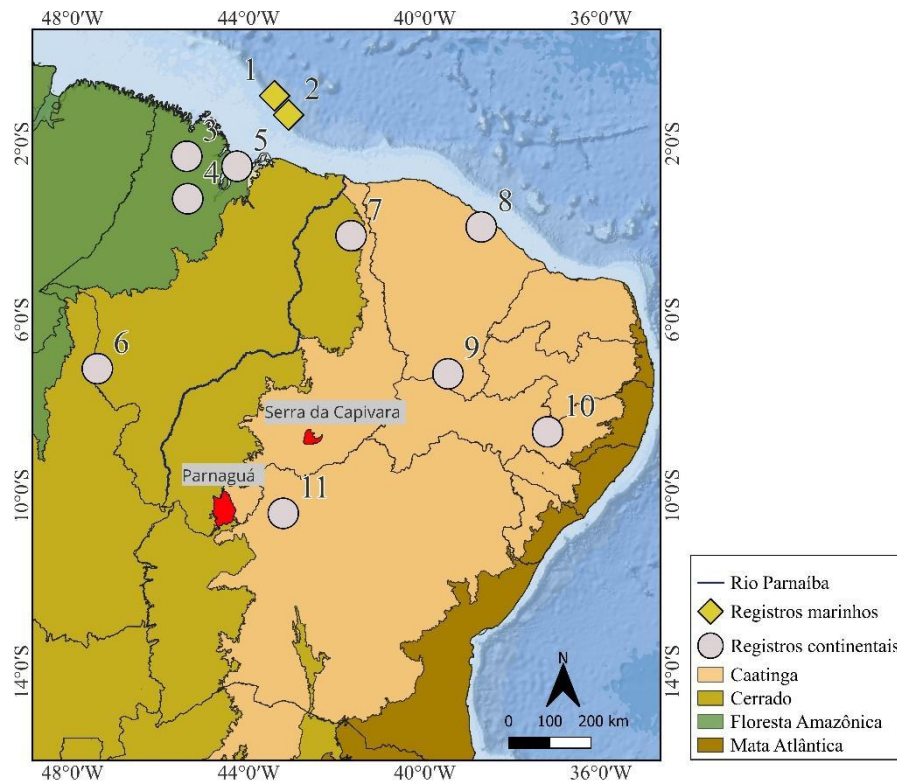


Fig. 3. Mapa dos biomas presentes no Nordeste brasileiro, com a localização dos estudos paleoecológicos de testemunhos marinhos (1. GeoB1248 (PIACSEK *et al.*, 2021); 2. GeoB16205-4 (BOUIMETARHAN *et al.*, 2018)) e continentais (3. Cabeludo (MORAES *et al.*, 2022); 4. Lago Formoso (MORAES *et al.*, 2021a); 5. Lago Caçó (LEDRU *et al.*, 2006); 6. Chapada das Mesas (XAVIER *et al.*, 2024); 7. Sete Cidades (XAVIER; ARAÚJO; LEDRU, 2022); 8. Serra de Maranguape (MONTADE *et al.*, 2014); 9. Araripe (GUERRA *et al.*, 2024); 10. Catimbau (MORAES; DE OLIVEIRA; BEHLING, 2020); 11. Icatu (DE OLIVEIRA; BARRETO; SUGUIO, 1999) no Nordeste brasileiro. O Parque Nacional da Serra da Capivara e o município de Parnaguá se encontram destacados em vermelho (IBGE, 2023).

O lago de Parnaguá, no Piauí, possui potencial de constituir um arquivo sedimentar de relevância ímpar devido à sua localização estratégica no centro do NEB (Fig. 3) e em uma área de ecótono entre os domínios fitogeográficos do Cerrado e da Caatinga. Sua posição geográfica garante que os sedimentos lacustres capturem um sinal polínico integrado da dinâmica de ambas as formações vegetais, permitindo quantificar as flutuações da linha de transição em resposta às forças climáticas. Ademais, por estar em uma região altamente sensível às variações da ZCIT, os dados de Parnaguá oferecem o potencial de fornecer um registro terrestre de alta resolução da história de umidade do NEB e da influência antrópica ao longo do tempo.

Conhecer os processos que moldaram as paisagens atuais e a dinâmica da flora piauiense é essencial para a formulação de estratégias eficazes de conservação e para a compreensão da vulnerabilidade dos ecossistemas. Neste contexto, o principal objetivo da presente tese é ampliar nosso conhecimento da história paleoambiental do Nordeste brasileiro e, mais especificamente,

investigar a história da vegetação do estado do Piauí por meio do desenvolvimento de um atlas palinológico, da análise da composição da chuva polínica atual e do estudo das mudanças vegetacionais ao longo dos últimos 7.500 anos com base em sedimentos datados.

Desta forma, esta tese se propõe a responder às seguintes perguntas:

1. Quais são as morfologias dos grãos de pólen dos táxons vegetais representativos da Caatinga e do Cerrado no Piauí?
2. Como a composição da chuva polínica moderna na Bacia do Parnaíba reflete e se correlaciona com a vegetação atual, e quais os papéis dos gradientes climáticos e edáficos nesta relação (vegetação-pólen)?
3. Como as flutuações da ZCIT e do SMAS modularam a vegetação do ecótono Cerrado-Caatinga através do tempo na região de Parnaguá?

Esta pesquisa é baseada em grãos de pólen de exsicatas depositados em herbário, em grãos de pólen de sedimentos superficiais de ambientes úmidos e de grãos de pólen e macro-carvões depositados em sedimento lacustre como bioindicadores paleoclimáticos e paleoambientais. Os três artigos apresentados a seguir, cada um com seus objetivos específicos, contribuem de forma complementar para que o objetivo principal da tese seja atingido.

Artigo 1. Capítulo II: A palynological atlas of the Cerrado-Caatinga ecotone in northeastern Brazil. Objetivo: Construir um atlas polínico que reunisse os táxons vegetais representados nos dois principais domínios fitogeográficos do estado do Piauí (Caatinga e Cerrado) para subsidiar futuros estudos paleoecológicos.

Artigo 2. Capítulo III: Modern pollen rain signatures along the Parnaíba river basin (northeastern Brazil). Objetivo: Caracterizar a assinatura polínica moderna e sua relação com a vegetação e com os gradientes edáficos na Bacia do Parnaíba.

Artigo 3. Capítulo IV: Vegetation responses in a climatic transition zone of northeastern Brazil over the last 7.500 years (Lagoa de Parnaguá, Piauí, Brazil)

Objetivo: Compreender a evolução temporal dos limites de influência da monção e como suas alterações impactaram a dinâmica ambiental da região semiárida.

2 CAPÍTULO II

A PALYNOLOGICAL ATLAS OF THE CERRADO-CAATINGA ECOTONE IN NORTHEASTERN BRAZIL

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A palynological atlas of the Cerrado-Caatinga ecotone in northeastern Brazil

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Abstract

Describing the diversity of Brazilian plant species, as well as the wide variety in the associated pollen grains, is crucial to understanding their evolution and ensuring effective conservation. The accurate identification of pollen is key to successful pollen studies and the consistent paleoecological interpretation of past vegetation changes. Pollen analysts usually identify plant taxa from reference collections built from herbaria material. In Brazil, pollen atlases primarily focus on three main vegetation domains, namely, the Amazon Forest, the Atlantic Forest, and the Cerrado, while information about Caatinga pollen taxa is dispersed across multiple studies; this significantly impedes efforts to further develop palynological research. To address this gap, we have developed a palynological atlas for the state of Piauí, covering the Caatinga and Cerrado regions along with their transitional zones. These domains encompass various vegetation types, including Caatinga (*stricto sensu*), Cerrado (*lato sensu*), dense shrubland, grassland, palm vegetation, riverine forest, seasonal deciduous and semi-deciduous forest, as well as valley-side marshes. We collected flower buds from specimens at the Herbarium Prisco Bezerra (EAC) at the Federal University of Ceará to build a pollen reference collection. The Atlas comprises 398 species from 99 families, with the most represented families being Asteraceae, Bignoniaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Malvaceae, Malpighiaceae, and Rubiaceae. Each species is accompanied by a description of its pollen grains, photos showing polar and equatorial views, and ecological details like life form (liana/scandent/vine, herb, subshrub, shrub or tree) substrate, and vegetation type to support further studies.

Key words

Brazil, identification, images, semi-arid, pollen

2.1. Introduction

Tropical ecosystems are well-known as biodiversity hotspots (Joly *et al.*, 2019; Oliveira *et al.*, 2019). Research into how these ecosystems have formed, as well as how they respond to environmental changes, is vital to future conservation and preservation efforts, which will become more and more relevant in light of ongoing climate warming (Salazar *et al.*, 2007). Pollen analysis is a robust tool for this type of research, and quaternary palynology can be leveraged to reconstruct past vegetation changes through time, from the centennial to orbital scale (Ledru *et al.*, 1998; Meyer *et al.*, 2014; Traverse, 2007).

Such studies are based on the relationship between pollen production at the plant source and pollen deposition in the sediment (Chevalier *et al.*, 2020). Pollen assemblages are then interpreted in terms of vegetation types, which can be distinguished based on specific factors, such as annual precipitation and soil type. Reconstructions of the vegetation associated with a certain time period from pollen samples are significantly influenced by knowledge of which pollen types belong to different vegetation types or specific landscapes (physiognomy) (Cassino and Ledru, 2021; Dawson *et al.*, 2016; Marchant *et al.*, 2009). The identification of pollen grains deposited in the sediment requires access to reference materials, which are built from the flora stored in herbaria.

The vegetation of northeastern Brazil responded rapidly to climate changes and human impacts during the Holocene, which impacted the composition and distribution of vegetation (Ledru *et al.*, 2006, 2022, 2020; Montade *et al.*, 2019; Xavier *et al.*, 2022). However, the reference materials relevant for pollen from northeastern Brazil remain scarce and unpublished, which substantially limits interpretations of fossil data.

At present, the published pollen atlas of Brazilian species focuses on the Amazon forest, Atlantic Forest and Cerrado biomes (Salgado-Labouriau, 1973; Colinvaux *et al.*, 1999; Lorente *et al.*, 2017). Although there are certain publications that describe Caatinga plant species, these studies primarily present the morphological description of a certain genus or vegetation type, or highlight species that are relevant to beekeeping (e.g., Dias *et al.*, 2022; Duarte *et al.*, 2021; Nascimento *et al.*, 2021; Peixoto *et al.*, 2022; Silva and Santos, 2009); as such, a far more comprehensive record of plant species is needed to further paleoecological research in northeastern Brazil.

Piauí, a Brazilian state located in the northeast of the country, includes several

archaeological and national parks that contribute to the preservation of native ecosystems and heritage (Cavalcante, 2019; Guidon, 1975). The vegetation in this area mainly falls under two phytogeographical domains, the Cerrado and the Caatinga, which are separated by transitional areas (CEPRO, 2019). Vegetation types (or physiognomies) within these two biomes are defined according to their form, structure, dominant growth forms, and potential seasonal changes, and range from open to closed vegetation (Ribeiro and Walter, 2008).

The Caatinga, a region exclusively distributed in Brazil, covers about 52.664 km² of the state of Piauí and is characterized by a hot semi-arid climate (Castro, 2007; IBGE, 2021; Peel *et al.*, 2007). This region experiences a mean annual temperature between 28-30°C, high evapotranspiration (between 1500-2000 mm/year), and a short rainy season (between 3-5 months) (Veloso *et al.*, 2012). The Caatinga region shows rich plant diversity (3.347 species) with a high number of endemic species (526). The region mainly comprises small trees up to 5 m in height (Queiroz *et al.*, 2018). The canopy does not form a continuous cover; as such, trees and shrubs in the Caatinga are typically characterized by slender trunks, often with thorns, and small or compound leaves that are shed during the dry season (Veloso *et al.*, 2012).

In the state of Piauí, the Cerrado covers an area of approximately 50.150 km² (Castro, 2007). This area is characterized by a variable climate that ranges from dry subhumid to humid-subhumid (Thorntwaite and Mather, 1955). The Cerrado is the only phytogeographical domain in Brazil that has direct contact with four other domains: the Amazon Forest; Atlantic Forest; Caatinga; and Pantanal. As a result, the flora in this region is influenced by the surrounding domains. For this reason, species from the Amazon and Atlantic forests are observed in the Cerrado (Méio *et al.*, 2003; Ratter and Oliveira-Filho, 1995; Vieira *et al.*, 2019). Despite demonstrating high species richness, the Cerrado is also one of the Brazilian domains most threatened by human activities (Coutinho, 2006; Myers *et al.*, 2000; Vieira *et al.*, 2022).

Here, we aimed to build a pollen atlas that would gather the plant taxa represented in the two main phytogeographical domains of the state of Piauí (the Caatinga and Cerrado) to support future paleoecological studies. The presented pollen atlas builds upon the atlases of the Cerrado domain located in central Brazil published by Salgado-Labouriau (1973), Cassino and Meyer (2011), and Escobar-Torrez *et al.* (2023).

2.2. Materials and Methods

2.2.1. Collection and processing of pollen material

The material underlying the presented research was collected from the Herbarium Prisco Bezerra (EAC) of the Department of Biology at the Federal University of Ceará. Prior to visiting the chosen herbarium, the speciesLink database - which contains information about all of the species deposited in herbaria worldwide - was consulted to determine which species we could expect the Herbarium Prisco Bezerra to contain (CRIA, 2023). When filtering the country and state section for Brazil and Piauí, the acronym 'EAC - Herbário Prisco Bezerra' was selected. Our data survey resulted in 513 genera with the status of 'accepted' in the system. After this stage, flower buds were collected prior to anthesis from duplicate specimens, whenever available, of the herbarium. These buds were stored in envelopes labeled with the scientific name, family, and herbarium code. The bud samples then underwent an acetolysis process, which represents a type of artificial fossilization of the pollen grains using an acid medium to better visualize the morphological characteristics. Briefly, samples were left in acetic acid for 24 hours, after which a 9/1 solution of acetic anhydride (9ml) and sulfuric acid (1ml) was added and boiled for three minutes to accelerate the reaction (Erdtman, 1960). The residue was washed in water and left in a 50% glycerin solution for 24 hours. Finally, the pollen grains were deposited on a glass slide – more specifically – mounted in glycerin gelatin and sealed with paraffin (Erdtman, 1960). The material was observed using a Zeiss AXIO Scope A1 optical microscope (Zeiss AG, Oberkochen, Germany) and photographed with a digital camera attached to the microscope. Pollen diameter measurements were performed using the ImageJ program (Schneider *et al.*, 2012). A label with the herbarium code was assigned to each reference taxon (EAC0033808).

The main morphological characteristics of the pollen grains, namely, size, format both in polar and equatorial views, and number of colpi and pores, were described according to specialized bibliographies, such as those of Erdtman (1952), Punt *et al.*, (2007) and Salgado-Labouriau (1973). The absence of a specific reference in the following material means that no study was found to describe the genus and, as such, the description is our own.

The pollen types are grouped into monocotyledons and dicotyledons and, within each group, plant families are organized according to Angiosperm Phylogeny Group IV (A.P.G., 2016) in alphabetical order as well as their corresponding species. Species names, life form, substrate and

vegetation type were verified by consulting of the Brazilian species database REFLORA (Reflora, 2023).

2.2.2. *Vegetation types of Piauí*

In the state of Piauí, 251,529 km² of land covers two significant phytogeographical domains: the Caatinga, which encompasses 37% of the State area; and the Cerrado, which covers 33% of the State area (Figure 2.1) (Oliveira *et al.*, 1998). Additionally, there are transition areas between these two domains which occupy 19% of the State area (Oliveira *et al.*, 1998). Descriptions of the vegetation type are based on the Reflora (2023) database and botanical surveys (Castro, 2007).

The Caatinga (*stricto sensu*) is a deciduous tropical forest that exists in the semi-arid climate of Northeastern Brazil. It is characterized by hills and plateaus with sparse vegetation, along with seasonal rivers (Rizzini, 1997; Veloso *et al.*, 2012). The most frequent plant species in this domain are *Aristida setifolia* Kunth (Poaceae), *Jatropha mollissima* (Pohl) Baill. (Euphorbiaceae), *Cereus albicaulis* (Britton & Rose) Luetzelb. (Cactaceae), and *Senegalia globosa* (Bocage & Miotto) L.P. Queiroz (Fabaceae) (Veloso *et al.*, 2012).

The Cerrado (*lato sensu*) consists of various vegetation types; for example, woody savanna (*cerradão*), savanna (Cerrado *stricto sensu*), and grassland (*campo sujo*) coexist with xerophytic plants (Ribeiro and Walter, 2008). The most characteristic species of this domain include *Caryocar coriaceum* Wittm. (Caryocaraceae) and *Parkia platycephala* Benth (Fabaceae, *Salvertia convallariodora* A.St.-Hil. (Vochysiaceae) (Veloso *et al.*, 2012). The grassland portion of the Cerrado is mainly characterized by an uninterrupted carpet of grasses and low-growing dicotyledonous subshrubs, with a notable absence of trees and robust shrubs, e.g., notable species include *Mikania officinalis* Mart. (Asteraceae) and *Ancistrotropis firmula* (Mart. ex Benth.) A. Delgado (Fabaceae).

Castro (2007) describes the seasonal semi-deciduous forest of Piauí as "Mata de Babaçu" or "Mata Dicótilo-Palmacea" due to the frequency of mixed palm trees (palm vegetation/*palmeiral*) and dicotyledonous broadleaf plants such as *Handroanthus impetiginosus* (Mart. ex DC.) Mattos (Bignoniaceae) and *Attalea speciosa* Mart. Ex Spreng. (*Babaçu*) (Arecaceae). The seasonal deciduous forest typically shows dense arboreal structure in which the canopies of tree individuals intertwine, along with the shedding of leaves during the dry period (Castro, 2007). The most

common species observed in this deciduous forest are *Anadenanthera colubrina* var. *cebil* (Vell.) Brenan and *Apuleia leiocarpa* (Vogel) J.F. Macbr. (Fabaceae) (Veloso *et al.*, 2012).

The transition areas between the Caatinga and Cerrado often involve dense shrubland (*Carrasco in Portuguese*) (Araújo and Martins, 1999). The *Carrasco* is characterized by dense shrubby xerophytic vegetation with abundant vines and a discontinuous canopy with sparse emerging trees (e.g., *Justicia triloba* (Lindau) E.C.O. Chagas & Costa-Lima and *Lepidagathis montana* (Nees) Kameyama) (Acanthaceae)) (Araújo and Martins, 1999).

The vegetation occurring in humid areas, e.g., near rivers and lakes, is commonly referred to as aquatic vegetation or riverine forest (Veloso *et al.*, 2012). Aquatic vegetation can be observed in both flowing (lotic) and still (lentic) aquatic environments. It comprises floating plants, rooted plants with leaves that float on the water's surface, and plants with submerged leaves. Some common plants in the aquatic vegetation of this area are *Echinodorus palaefolius* and *Limnocharis laforestii*, both of which belong to the Alismataceae family. Riverine forests are generally rich and diverse in species (Veloso *et al.*, 2012). Another type of humid vegetation that is typical of the Cerrado is the savanna palm swamps (*veredas in Portuguese*). Valley-side marshes are characterized by shallow depressions in which water accumulates; this results in damp and saturated soils that are optimal for species like *Pontederia subovata* (Seub.) Lowden and *Xyris macrocephala* Vahl) (Veloso *et al.*, 2012). Pioneer vegetation formations can also be observed in both the Caatinga and the Cerrado.

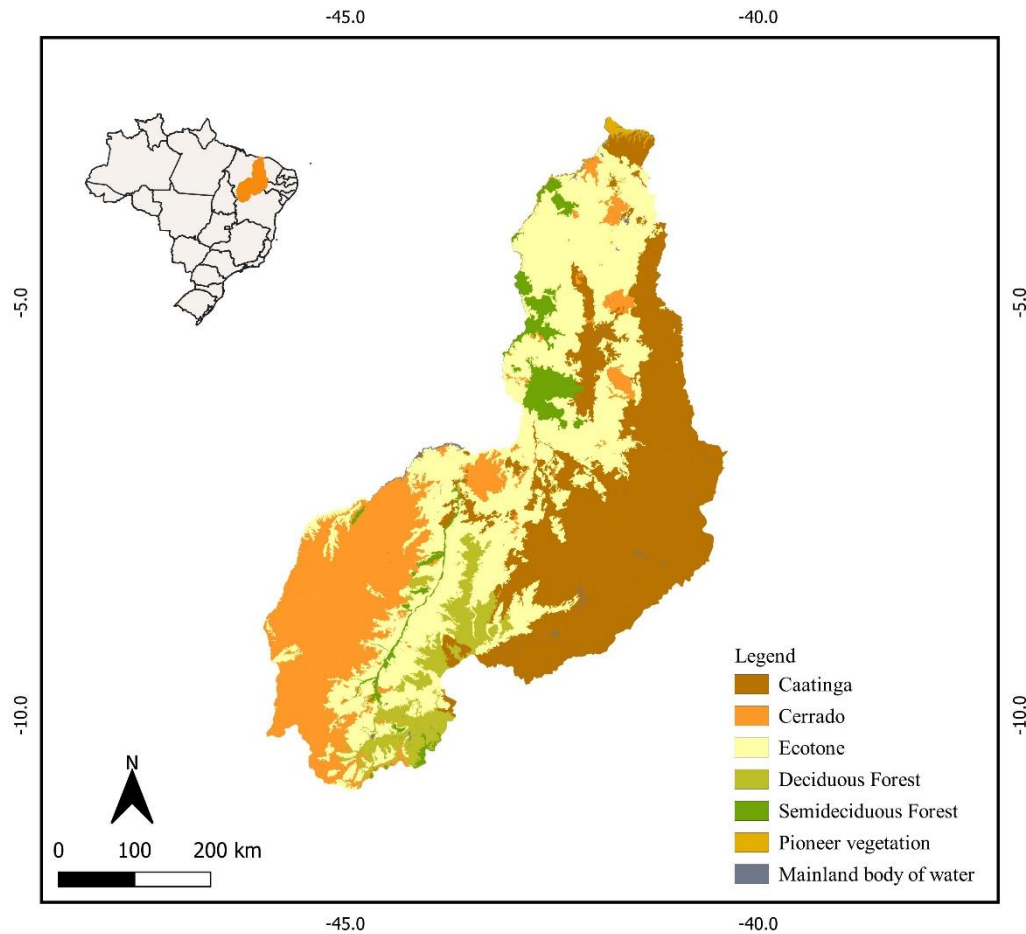


Figure 2.1. Map of Brazil showing the location of the State of Piauí (top left), and a map of the state of Piauí with the distribution of vegetation types denoted (Bdia, 2022).

2.3. Results

The presented pollen atlas illustrates and describes 398 species belonging to 388 genera and 99 families (Appendix). The pollen of various plants are described in the following order: order; family; species name; polar diameter (P); equatorial diameter (E) or simply diameter (D); morphological description of the pollen, and the potential reference for confirmation; life form; substrate; and the type of vegetation where the species is found (from Re flora database). The references used to validate the descriptions of pollen morphology are indicated in the Appendix. When no published description could be found, the acronym DMA (description made by the author) is used (Appendix).

3.1. Pollen descriptions

MONOCOTS

Order: ALISMATALES R. Br. ex Bercht. & J. Presl

Family: ALISMATACEAE Vent.

Species: *Echinodorus palaefolius* (Ness & Mart.) J.F. Macbr. (Plate I, 1,2)

Herbarium number: EAC0033808

Description: D: 30µm. Monad, apolar, medium-sized, circular, pantoporate, exine ornamentation: microechinate (Alves *et al.*, 2021).

Life form: herb

Substrate: aquatic

Vegetation type: aquatic vegetation, Caatinga (stricto sensu)

Species: *Limnocharis laforesti* Duchass. ex Griseb. (Plate I, 3,4,5,6)

Herbarium number: EAC0043549

Description : P: 16µm; E: 19µm. Monad, isopolar, small-sized, triporate, triangular (convex), rectangular, exine ornamentation: microechinate (Argue, 1973).

Life form: herb

Substrate: aquatic

Vegetation type: aquatic vegetation.

Order: LILIALES Perleb

Family: ALSTROEMERIACEAE Dumort.

Species: *Alstroemeria longistaminea* Mart. ex Schult. & Schult.f. (Plate I, 7,8)

Herbarium number: EAC0043560

Description: D: 91 µm. Monad, heteropolar, large-sized, prolate, monocolpate, elliptical, exine ornamentation: striate/reticulate (Sarwar *et al.*, 2010).

Life form: herb

Substrate: terrestrial

Vegetation type: grassland, Caatinga (stricto sensu).

Order: ALISMATALES R. Br. ex Bercht. & J. Presl

Family: ARACEAE Juss.

Species: *Spathiphyllum gardneri* Schott (Plate I, 9,10)

Catalog number: EAC0047232

Description: D: 21µm. Monad, isopolar, small-sized, inaperturate, circular, oblate, exine ornamentation: striate (Jiménez *et al.*, 2021).

Life form: herb

Substrate: terrestrial

Vegetation type: riverine forest.

Order: POALES Small

Family: BROMELIACEAE Juss.

Species: *Bromelia laciniosa* Mart. ex Schult. & Schult.f. (Plate I, 11,12)

Herbarium number: EAC0020699

Description: D: 45µm. Monad, heteropolar, medium-sized, monocolpate, suboblate, exine ornamentation: reticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Neoglaziovia variegata* (Arruda) Mez (Plate I, 13,14)

Herbarium number: EAC0019688

Description: D: 47µm. Monad, heteropolar, medium-sized, monocolpate, oblate, exine ornamentation: reticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Tillandsia loliacea* Mart. ex Schult. & Schult.f. (Plate I, 15,16,17,18)

Herbarium number: EAC0007570

Description: P: 27 µm; E:31. Monad, heteropolar, medium-sized, monocolpate with irregular contour, oblate, exine ornamentation: reticulate (de Oliveira Souza *et al.*, 2021).

Life form: herb

Substrate: epiphytic, rupicolous

Vegetation type: anthropic area, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Order: COMMELINALES Mirb. ex Bercht. & J. Presl

Family: COMMELINACEAE Mirb.

Species: *Commelina benghalensis* L. (Plate I, 19,20)

Herbarium number: EAC0022860

Description: D: 30 µm. Monad, heteropolar, medium-sized, monosulcate, circular, prolate, exine ornamentation: microechinate (Pradesh *et al.*, 2019).

Life form: herb

Substrate: rupicolous, terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Order: POALES Small

Family: CYPERACEAE Juss.

Species: *Cyperus articulatus* L. (Plate II, 1,2,3,4)

Herbarium number: EAC0056901

Description: P: 29µm; E: 30µm. Monad, isopolar, medium-sized, circular, suboblate, exine ornamentation: granulate (Sosam and Al-mayyahi, 2018).

Life form: herb

Substrate: aquatic

Vegetation type: valley-side marshes, Cerrado (lato sensu), riverine forest.

Species: *Cyperus metzii* (Hochst. ex Steud.) Mattf. & Kük. (Plate II, 5,6)

Herbarium number: EAC0011842

Description: D: 24µm. Monad, isopolar, small-sized, circular, suboblate, exine ornamentation: granulate (Sosam and Al-mayyahi, 2018).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), seasonal deciduous forest.

Order: ASPARAGALES Link**Family: IRIDACEAE Juss.****Species: *Cipura paludosa* Aubl. (Plate II, 7,8)**

Herbarium number: EAC0059374

Description: D: 47µm. Monad, heteropolar, medium-sized, monosulcate, oblate, exine ornamentation: reticulate (Goldblatt and Le Thomas, 1992).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, aquatic vegetation, Cerrado (lato sensu), grassland.

Species: *Nemastylis* sp. Nutt. (Plate II, 9,10)

Herbarium number: EAC0008036

DESCRIPTION: D: 50 μ m. Monad, heteropolar, large-sized, monosulcate, oblate, exine ornamentation: reticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Order: POALES Small**Family: POACEAE Barnhart****Species: *Andropogon fastigiatus* Sw. (Plate II, 11,12)**

Herbarium number: EAC0018578

Description: D: 30 μ m. Monad, apolar, medium-sized, monoporate, circular, exine ornamentation: scabrate (Guimarães *et al.*, 2018)

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu); grassland.

Species: *Aristida setifolia* Kunth. (Plate II, 13,14)

Herbarium number: EAC0018579

Description: D: 29 μ m. Monad, apolar, medium-sized, monoporate, circular, exine ornamentation: psilate (Leal *et al.*, 2011).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Dactyloctenium aegyptium* (L.) Willd. (Plate II, 15,16)

Herbarium number: EAC0056886

Description: D: 29µm. Monad, apolar, medium-sized, monoporate, circular, exine ornamentation: microechinate (Nazish and Althobaiti, 2022).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Eragrostis maypurensis* (Kunth) Steud. (Plate II, 17,18)

Herbarium number: EAC0008700

Description: D: 24µm. Monad, apolar, small-sized, monoporate, circular, exine ornamentation: microechinate (Guimarães *et al.*, 2018).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Lasiacis* sp. (Griseb.) Hitchc. (Plate II, 19,20)

Herbarium number: EAC0030700

Description: D: 24µm. Monad, apolar, small-sized, monoporate, subprolate, exine ornamentation: scabrate (Matos *et al.*, 2014).

Life form: herb, liana/scandent/vine, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Melinis repens* (Willd.) Zizka (Plate III, 1,2)

Herbarium number: EAC0008096

Description: D: 27 μ m. Monad, apolar, medium-sized, monoporate, circular, exine ornamentation: scabrate.

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu); Caatinga (stricto sensu), Grassland.

Species: *Setaria adhaerens* (Forssk.) Chiov. (Plate III, 3,4)

Herbarium number: EAC0011840

Description: D: 29 μ m. Monad, apolar, medium-sized, monoporate, prolate, exine ornamentation: areolate-microechinate (Morgado *et al.*, 2015).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Trachypogon spicatus* (L.f.) Kuntze. (Plate III, 5,6)

Herbarium number: EAC0008154

Description: D: 43 μ m. Monad, apolar, medium-sized, monoporate, prolate, exine ornamentation: microechinate (Radaeski and Bauermann, 2018)

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Order: COMMELINALES Mirb. ex Bercht. & J. Presl

Family: PONTEDERIACEAE Kunth

Species: *Heteranthera rotundifolia* (Kunth) Griseb. (Plate III, 7,8,9,10)

Herbarium number: EAC0056920

Description: D: 27 μ m. Monad, isopolar, medium-sized, dicolpate, perprolate, exine ornamentation: granulate (Ybert *et al.*, 2017a).

Life form: herb

Substrate: aquatic

Vegetation type: aquatic vegetation.

Species: *Pontederia subovata* (Seub.) Lowden. (Plate III, 11,12,13,14)

Herbarium number: EAC0042294

Description: D: 30 μ m. Monad, isopolar, medium-sized, dicolpate, perprolate, exine ornamentation: fossulate (Ybert *et al.*, 2017a).

Life form: herb

Substrate: aquatic

Vegetation type: aquatic vegetation, Caatinga (stricto sensu), Cerrado (lato sensu), valley-side marshes.

Order: POALES Small

Family: RAPATEACEAE Dumort.

Species: *Rapatea* sp. Aubl. (Plate III, 15,16)

Herbarium number: EAC0010743

Description: D: 39 μ m. Dyad, heteropolar, small-sized, monosulcate, suboblate, exine ornamentation: psilate.

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), valley-side marshes.

Order: LILIALES Perleb

Family: SMILACACEAE Vent.

Species: *Smilax sp.* L. (Plate III, 17,18,19,20)

Herbarium number: EAC0043171

Description: D: 18 μ m. Monad, isopolar, small-sized, inaperturate, circular, exine ornamentation echinate (Chen *et al.*, 2006).

Life form: liana/scandent/vine, shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Order: POALES Small

Family: XYRIDACEAE C.Agardh

Species: *Xyris macrocephala* Vahl (Plate IV, 1,2)

Herbarium number: EAC0043557

Description: D: 49 μ m. Monad, heteropolar, large-sized, circular, exine ornamentation: reticulate (da Luz *et al.*, 2015).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, aquatic vegetation, Cerrado (lato sensu), grassland valley-side marshes.

EUDICOTS, MAGNOLIIDS AND NYMPHAEALES

Order: LAMIALES Bromhead

Family: ACANTHACEAE Juss.

Species: *Dicliptera ciliaris* Juss. (Plate IV, 3,4,5,6)

Herbarium number: EAC0001645

Description: P: 41 μ m; E:71 μ m. Monad, isopolar, medium- to large-sized, lobate – 9, prolate, stephanocolporate, exine ornamentation: reticulate (Perveen and Qaiser, 2010).

Life form: herb

Substrate: rupicolous, terrestrial

Vegetation type: Caatinga (stricto sensu), riverine forest, seasonal semi-deciduous forest.

Species: *Justicia triloba* (Lindau) E.C.O.Chagas & Costa-Lima. (Plate IV, 7,8,9,10)

Herbarium number: EAC0005993

Description: P: 32 μ m; E: 28 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Kiel *et al.*, 2017).

Life form: shrub or vine

Substrate: rupicolous, terrestrial

Vegetation type: dense shrubland, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Lepidagathis montana* (Nees) Kameyama. (Plate IV, 11,12,13,14)

Herbarium number: EAC0043565

Description: P: 40 μ m; E: 80 μ m. Monad, isopolar, medium- to large-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Perveen and Qaiser, 2010).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, riverine forest.

Species: *Ruellia asperula* (Mart. ex Nees) Lindau. (Plate IV, 15,16)

Herbarium number: EAC0018367

Description: D: 102 μ m. Monad, isopolar, large-sized, triporate, circular, exine ornamentation: reticulate (Perveen and Qaiser, 2010).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), seasonal deciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: ACHARIACEAE Harms

Species: *Lindackeria ovata* (Benth.) Gilg. (Plate V, 1,2,3,4)

Herbarium number: EAC0026683

Description: P: 16.59 μ m; E: 19.42 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: psilate.

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: AMARANTHACEAE Juss.

Species: *Alternanthera brasiliana* (L.) Kuntze. (Plate V, 5,6)

Herbarium number: EAC0054827

Description: D: 13 μ m. Monad, apolar, small-sized, polyantoporate, without colpus membrane, spheroidal, exine ornamentation: granulate (Saensouk and Saensouk, 2022).

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu); grasslands, riverine forest.

Species: *Amaranthus viridis* L. (Plate V, 7,8)

Herbarium number: EAC0022883

Description: D: 20 μ m. Monad, apolar, small-sized, polyantoporate, without colpus membrane, spheroidal, exine ornamentation: granulate (Saensouk and Saensouk, 2022).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland.

Species: *Froelichia humboldtiana* (Roem. & Schult.) Seub. (Plate V, 9,10)

Herbarium number: EAC0018543

Description: D: 24 μ m. Monad, apolar, small-sized, pantoporate, without colpus membrane, semitectate, columellae freely visible, spheroidal, exine ornamentation: reticulate (Borsch, 1998).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Gomphrena leucocephala* Mart. (Plate V, 11,12)

Herbarium number: EAC0023512

Description: D: 20 μ m. Monad, apolar, small-sized, pantoporate, without colpus membrane, semitectate, columellae freely visible, spheroidal, exine ornamentation: reticulate (Borsch, 1998).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Xerosiphon angustiflorus* (Mart.) Pedersen. (Plate V, 13,14)

Herbarium number: EAC0018539

Description: D: 21µm. Monad, apolar, small-sized, pantoporate, without colpus membrane, spheroidal, exine ornamentation: reticulate (Borsch, 1998).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Order: SAPINDALES Juss. ex Bercht. & J. Presl

Family: ANACARDIACEAE R.Br.

Species: *Anacardium occidentale* L. (Plate V, 15,16,17,18)

Herbarium number: EAC0054979

Description: P: 37µm; E: 38µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Assis *et al.*, 2021).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Apterokarpos gardneri* (Engl.) Rizzini. (Plate VI, 1,2,3,4)

Herbarium number: EAC0047172

Description: P: 22µm; E: 25µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate-striate (Assis *et al.*, 2021).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Astronium fraxinifolium* Schott. (Plate VI, 5,6,7,8)

Herbarium number: EAC0058394

Description: P: 20 μ m; E: 25 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate-striate (Assis *et al.*, 2021).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Astronium urundeuva* (M.Allemão) Engl. (Plate VI, 9,10,11,12)

Herbarium number: EAC0045743

Description: P: 26 μ m; E: 27 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate-striate (Assis *et al.*, 2021).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Schinus sp.* L. (Plate VI, 13,14,15,16)

Herbarium number: EAC0044557

Description: P: 21 μ m; E: 23 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate-striate (Assis *et al.*, 2021).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Spondias tuberosa* Arruda. (Plate VI, 17,18,19,20)

Herbarium number: EAC0006044

Description: P: 26 μ m; E: 41 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate-striate (Assis *et al.*, 2021).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland.

Species: *Tapirira guianensis* Aubl. (Plate VII, 1,2,3,4)

Herbarium number: EAC0011051

Description: P: 16 μ m; E: 20 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate-striate (Assis *et al.*, 2021).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Order: MAGNOLIALES Bromhead

Family: ANNONACEAE Juss.

Species: *Annona leptopetala* (R.E.Fr.) H.Rainer. (Plate VII, 5,6)

Herbarium number: EAC0007479

Description: D: 38 μ m. Monad, isopolar, medium- to large-sized, inaperturate, spheroidal, exine ornamentation: reticulate (Doyle and Le Thomas, 2012).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Order: GENTIANALES Juss. ex Bercht. & J. Presl

Family: APOCYNACEAE Juss.

Species: *Aspidosperma pyriforme* Mart. & Zucc. (Plate VII, 7,8,9,10)

Herbarium number: EAC0049768

Description: P: 33 μ m; E: 41 μ m. Monad, isopolar, medium-sized, 5-6 colpi, circular, suboblate, exine ornamentation: psilate (Moreira *et al.*, 2004).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Himatanthus drasticus* (Mart.) Plumel. (Plate VII, 11,12,13,14)

Herbarium number: EAC0001788

Description: P: 38 μ m; E: 34 μ m. Monad, isopolar, medium-sized, tricolpate, circular, suboblate, exine ornamentation: psilate (Rodrigues *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation Type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest.

Species: *Mandevilla tenuifolia* (J.C.Mikan) Woodson. (Plate VII, 15,16,17,18)

Herbarium number: EAC0014851

Description: P: 47 μ m; E: 36 μ m. Monad, isopolar, medium-sized, tetraporate, circular, oblate-spheroidal, exine ornamentation: psilate (Rodrigues *et al.*, 2017).

Life form: liana/scandent/vine, subshrub

Substrate: rupicolous, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Odontadenia hypoglauca* Müll.Arg. (Plate VIII, 1,2)

Herbarium number: EAC0018429

Description: D: 41µm. Monad, isopolar, medium-sized, tetraporate, circular, exine ornamentation psilate (Rodrigues *et al.*, 2017).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Rhabdadenia biflora* (Jacq.) Müll.Arg. (Plate VIII, 3,4)

Herbarium number: EAC0023564

Description: D: 71µm. Monad, isopolar, large-sized, tetraporate, circular, subprolate, exine ornamentation: psilate (Moreira *et al.*, 2004).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Rhodocalyx rotundifolius* Müll.Arg. (Plate VIII, 5,6)

Herbarium number: EAC0003612

Description: D: 43µm. Monad, isopolar, medium-sized, tetraporate, circular, oblate, exine ornamentation: scabrate.

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Secondatia floribunda* A.DC. (Plate VIII, 7,8,9,10)

Herbarium number: EAC0055044

Description: P: 20 μ m; E: 16 μ m. Monad, isopolar, small-sized, triporate, triangular (convex), oblate, exine ornamentation: scabrate (Rodrigues *et al.*, 2017).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), grassland.

Species: *Tabernaemontana catharinensis* A.DC. (Plate VIII, 11,12,13,14)

Herbarium number: EAC0007592

Description: P: 31 μ m; E: 36 μ m. Monad, isopolar, medium-sized, tricolporate, circular, oblate, exine ornamentation: scabrate (Rodrigues *et al.*, 2017).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), seasonal semi-deciduous forest.

Order: AQUIFOLIALES Senft

Family: AQUIFOLIACEAE Bercht. & J.Presl

Species: *Ilex sp.* L. (Plate VIII, 15,16,17,18)

Herbarium number: EAC0048979

Description: P: 20 μ m; E: 20 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: clavate (Cruz-Barros *et al.*, 2006).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, valley-side marshes, Cerrado (lato sensu); grassland, riverine forest, seasonal semi-deciduous forest, Caatinga (stricto sensu).

Order: APIALES Nakai

Family: ARALIACEAE Juss.

Species: *Didymopanax sp.* Dec. & Planch. (Plate IX, 1,2,3,4)

Herbarium number: EAC0059647

Description: P: 19 μ m; E: 22 μ m. Monad, isopolar, small-sized, tricolporate, circular, subprolate, exine ornamentation: striate (Fiaschi *et al.*, 2010).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Order: PIPERALES Bercht. & J. Presl

Family: ARISTOLOCHIACEAE Juss.

Species: *Aristolochia gardneri* Duch. (Plate IX, 5,6,7,8)

Herbarium number: EAC0005179

Description: P: 52 μ m; E:58 μ m. Monad, isopolar, large-sized, circular, exine ornamentation: granulate (Freitas *et al.*, 2023).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Order: ASTERALES Link

Family: ASTERACEAE Giseke

Species: *Acanthospermum australe* (Loefl.) Kuntze. (Plate IX, 9,10,11,12)

Herbarium number: EAC0050635

Description: P: 17 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex),

oblate, exine ornamentation: echinate (Dias *et al.*, 2022).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Aspilia leucoglossa* Malme. (Plate IX, 13,14,15,16)

Herbarium number: EAC0009109

Description: P: 34 μ m; E: 29 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: echinate (Mabel *et al.*, 2014).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Blainvillea acmella* (L.) Philipson. (Plate IX, 17,18,19,20)

Herbarium number: EAC0050725

Description: P: 22 μ m; E: 21 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: echinate (Dias *et al.*, 2022).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Calea microphylla* (Gardner) Baker. (Plate X, 1,2,3,4)

Herbarium number: EAC0010025

Description: P: 24 μ m; E: 26 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: echinate (Stanski *et al.*, 2013).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Centratherum punctatum* Cass. (Plate X, 5,6,7,8)

Herbarium number: EAC0022880

Description: P: 29µm; E: 30µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), circular, exine ornamentation: echinate (Nascimento *et al.*, 2021).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, seasonal semi-deciduous forest.

Species: *Chresta martii* (DC.) H.Rob. (Plate X, 9,10,11,12)

Herbarium number: EAC0006864

Description: D: 33µm. Monad, isopolar, medium-sized with small pores, 3- porate, circular, exine ornamentation: echinate (Siniscalchi *et al.*, 2017).

Life form: subshrub

Substrate: rupicolous

Vegetation type: Caatinga (stricto sensu).

Species: *Chromolaena myriocephala* (Gardner) R.M.King & H.Robinson. (Plate X, 13,14,15,16)

Herbarium number: EAC0050629

Description: P: 39µm; E: 40µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex),

oblate-spheroidal, exine ornamentation: echinate (Mabel *et al.*, 2014).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Clibadium armanii* (Balb.) Sch.Bip. ex O.E.Schulz. (Plate X, 17,18,19,20)

Herbarium number: EAC0010626

Description: P: 18 μ m; E: 20 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), circular, exine ornamentation: echinate (Salamah *et al.*, 2019).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland, riverine forest.

Species: *Conocliniopsis prasiifolia* (DC.) R.M.King & H.Rob. (Plate XI, 1,2,3,4)

Herbarium number: EAC0003599

Description: P: 17 μ m; E: 17 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), circular, exine ornamentation: echinate (Lucas *et al.*, 2018)

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu). grassland.

Species: *Dasyphyllum sprengelianum* (Gardner) Cabrera. (Plate XI, 5,6,7,8)

Herbarium number: EAC0008679

Description: P: 35 μ m; E: 40 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microechinate (Urtubey and Tellería, 1998).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Eclipta prostrata* (L.) L. (Plate XI, 9,10,11,12)

Herbarium number: EAC0022837

Description: P: 20 μ m; E: 20 μ m. Monad, isopolar, small-size, tricolporate, triangular (convex), subprolate, exine ornamentation: echinate (Mabel *et al.*, 2014).

Life form: herb

Substrate: aquatic, terrestrial

Vegetation type: anthropic areas, aquatic vegetation.

Species: *Elephantopus mollis* Kunth. (Plate XI, 13,14)

Herbarium number: EAC0050652

Description: D: 29 μ m. Monad, isopolar, medium-sized, periporate, circular, exine ornamentation: microechinate (Mabel *et al.*, 2014).

Life form: herb

Substrate: rupicolous, terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Emilia* sp. (Cass.) Cass. (Plate XI, 15,16,17,18)

Herbarium number: EAC0022871

Description: P: 24 μ m; E: 25 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: echinate (Mabel *et al.*, 2014).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Fleischmannia remotifolia* (DC.) R.M.King & H.Rob. (Plate XII, 1,2,3,4)

Herbarium number: EAC0010038

Description: P: 17 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: echinate (Lorente *et al.*, 2017).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Lepidaploa arenaria* (Mart. ex DC.) H.Rob. (Plate XII, 5,6,7,8)

Herbarium number: EAC0012120

Description: P: 21 μ m; E: 21 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate-spheroidal, exine ornamentation: echinate (Mendonça *et al.*, 2007).

Life form: shrub

Substrate: terrestrial

Vegetation type: grassland, seasonal semi-deciduous forest.

Species: *Lepidaploa remotiflora* (Rich.) H.Rob. (Plate XII, 9,10,11,12)

Herbarium number: EAC0054885

Description: P: 30 μ m; E: 29 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate-spheroidal, exine ornamentation: echinate (Mendonça *et al.*, 2007).

Life form: shrub

Substrate: terrestrial

Vegetation type: grassland.

Species: *Lessingianthus coriaceus* (Less.) H.Rob. (Plate XII, 13,14,15,16)

Herbarium number: EAC0050647

Description: P: 51 μ m; E: 48 μ m. Monad, isopolar, medium- to large-sized, triporate, triangular (convex), oblate, exine ornamentation: echinate (Angulo and Dematteis, 2010).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Mikania officinalis* Mart. (Plate XII, 17,18,19,20)

Herbarium number: EAC0009130

Description: P: 23 μ m; E: 22 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: echinate (Mendonça and Gonçalves-Esteves, 2000).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Pectis brevipedunculata* (Gardner) Sch.Bip. (Plate 13, 1,2,3,4)

Herbarium number: EAC0018457

Description: P: 25 μ m; E: 24 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: echinate (Mendonça and Gonçalves-Esteves, 2000).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Species: *Pseudobrickellia brasiliensis* (Spreng.) R.M.King & H.Rob. (Plate 13, 5,6,7,8)

Herbarium number: EAC0012117

Description: P: 25µm; E: 22µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: echinate.

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Rolandra fruticose* (L.) Kuntze (Plate 13, 9,10)

Herbarium number: EAC0050760

Description: D: 34µm. Monad, isopolar, medium-sized, triporate, circular, exine ornamentation: echinate (Angulo *et al.*, 2018).

Life form: subshrub

Substrate: terrestrial

Vegetation type: valley-side marshes.

Species: *Stilpnopappus sp.* Mart. ex DC. (Plate 13, 11,12)

Herbarium number: EAC0006882

Description: D: 43µm. Monad, isopolar, medium-sized, triporate, hexangular, exine ornamentation: echinate (Carrizo *et al.*, 2013).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, valley-

side marshes.

Species: *Synedrella nodiflora* (L.) Gaertn. (Plate 13, 13,14,15,16)

Herbarium number: EAC0011268

Description: P: 21µm; E: 24µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: echinate (Mabel *et al.*, 2014).

Life form: herb, shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Tagetes minuta* L. (Plate 13, 17,18,19,20)

Herbarium number: EAC0043624

Description: P: 30µm; E: 34µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: echinate (Osman, 2011).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropics area.

Species: *Tilesia baccata* (L.) Pruski (Plate XIV, 1,2,3,4)

Herbarium number: EAC0054877

Description: P: 23µm; E: 22µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: echinate (Mendonça and Gonçalves-Esteves, 2000).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous

forest.

Species: *Trichogonia campestris* Gardner (Plate XIV, 5,6,7,8)

Herbarium number: EAC0055064

Description: P: 18 μ m; E: 17 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: echinate

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Trichospira verticillata* (L.) S.F.Blake (Plate XIV, 9,10)

Herbarium number: EAC0027103

Description: D: 24 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: echinate (Bolick, 1983).

Life form: herb

Substrate: terrestrial

Vegetation type: aquatic vegetation.

Species: *Vernonanthura brasiliiana* (L.) H.Rob. (Plate XIV, 11,12,13,14)

Herbarium number: EAC0054784

Description: P: 27 μ m; E: 31 μ m. Monad, isopolar, medium-sized, triporate, triangular (convex), suboblate, exine ornamentation: echinate (Nascimento *et al.*, 2021).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu); grassland, Caatinga (stricto sensu).

Order: LAMIALES Bromhead

Family: BIGNONIACEAE Juss.

Species: *Adenocalymma divaricatum* Miers (Plate XIV, 15,16)

Herbarium number: EAC0054762

Description: D: 53µm. Monad, apolar, large-sized, inaperturate, circular, exine ornamentation: reticulate (Bove, 1993).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), seasonal semi-deciduous forest.

Species: *Anemopaegma laeve* DC. (Plate XIV, 17,18)

Herbarium number: EAC0047041

Description: D: 56µm. Monad, apolar, large-sized, inaperturate, circular, exine ornamentation: reticulate (Bove, 1993).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Bignonia campanulata* Cham. (Plate XV, 1,2)

Herbarium number: EAC0022869

Description: D: 41µm. Monad, apolar, medium-sized, inaperturate, circular, exine ornamentation: reticulate (de Souza *et al.*, 2019).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: riverine forest.

Species: *Fridericia platyphylla* (Cham.) L.G.Lohmann (Plate XV, 3,4,5,6)

Herbarium number: EAC0006204

Description: P: 45µm; E: 47µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate (de Souza and Gasparino, 2014).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Handroanthus impetiginosus* (Mart. ex DC.) Mattos (Plate XV, 7,8,9,10)

Herbarium number: EAC0028748

Description: P: 39µm; E: 31µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (de Souza *et al.*, 2019)

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, seasonal deciduous forest.

Species: *Lundia helicocalyx* A.H.Gentry (Plate XV, 11,12,13,14)

Herbarium number: EAC0008049

Description: P: 39µm; E: 40µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (de Souza *et al.*, 2019).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Mansoa hirsute* DC. (Plate XV, 15,16)

Herbarium number: EAC0022894

Description: D: 49 μ m. Monad, apolar, medium-sized, inaperturate, circular, exine ornamentation: reticulate (Bove, 1993).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Pleonotoma melioides* (S.Moore) A.H.Gentry (Plate XVI, 1,2,3,4)

Herbarium number: EAC0046633

Description: P: 45 μ m; E: 43 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (de Souza *et al.*, 2019).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Stizophyllum perforatum* (Cham.) Miers (Plate XVI, 5,6,7,8)

Herbarium number: EAC0007454

Description: P: 38 μ m; E: 35 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (de Souza *et al.*, 2019).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: anthropic areas, seasonal deciduous forest.

Species: *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore (Plate XVI, 9,10,11,12)

Herbarium number: EAC0007644

Description: P: 56µm; E: 46µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (de Souza *et al.*, 2019).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), dense shrubland, seasonal deciduous forest.

Order: MALVALES Juss.

Family: BIXACEAE Kunth

Species: *Cochlospermum regium* (Mart. ex Schrank) Pilg. (Plate XVI, 13,14,15,16)

Herbarium number: EAC0006428

Description: P: 56µm; E: 46µm. Monad, isopolar, medium-sized, tricolporate, triangular (concave), subprolate, exine ornamentation: psilate (Keating, 1972).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Order: BORAGINALES Juss. ex Bercht. & J. Presl

Family: BORAGINACEAE Juss.

Species: *Euploca lagoensis* (Warm.) Diane & Hilger (Plate XVI, 17,18,19,20)

Herbarium number: EAC0040634

Description: P: 24µm; E: 37µm. monad, isopolar, small- to medium-sized, tricolporate, triangular (concave), subprolate, exine ornamentation: psilate (Dias *et al.*, 2022).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), valley-side marshes.

Species: *Heliotropium elongatum* (Lehm.) I.M.Johnst. (Plate XVII, 1,2,3,4)

Herbarium number: EAC0006860

Description: D: 41µm. Monad, isopolar, medium-sized, tricolporate, triangular, prolate, exine ornamentation: microreticulate (Landi *et al.*, 2021).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, aquatic vegetation, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Myriopus salzmännii* (DC.) Diane & Hilger (Plate XVII, 5,6,7,8)

Herbarium number: EAC0021673

Description: P: 17µm; E: 20µm. Monad, isopolar, small-sized, 6-colporate, 6-lobate, suboblate, exine ornamentation: psilate (Landi *et al.*, 2021).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), grassland, riverine forest.

Species: *Varronia leucocephala* (Moric.) J.S.Mill. (Plate XVII, 9,10,11,12)

Herbarium number: EAC0018053

Description: P: 72µm; E: 67µm. Monad, isopolar, large-sized, tricolporate, triangular (convex), circular, exine ornamentation: reticulate (Landi *et al.*, 2021).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Order: SAPINDALES Juss. ex Bercht. & J. Presl

Family: BURSERACEAE Kunth

Species: *Commiphora leptophloeos* (Mart.) J.B.Gillett (Plate XVII, 13,14,15,16)

Herbarium number: EAC0008063

Description: P: 27µm; E: 31µm. Monad, isopolar, medium-sized, tricolporate, subcircular, suboblate, exine ornamentation: perforate (Harley *et al.*, 2005).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: CACTACEAE Juss.

Species: *Cereus albicaulis* (Britton & Rose) Luetzelb. (Plate XVII, 17,18,19,20)

Herbarium number: EAC0020644

Description: P: 70µm; E: 30µm. Monad, isopolar, medium- to large-sized, tricolpate, circular, oblate, exine ornamentation: perforate (Santos *et al.*, 1997).

Life form: liana/scandent/vine, shrub, succulent

Substrate: terrestrial

Vegetation type: dense shrubland, Caatinga (stricto sensu).

Order: ROSALES Bercht. & J. Presl

Family: CANNABACEAE Martinov

Species: *Celtis* sp. L. (Plate XVIII, 1,2,3,4)

Herbarium number: EAC0011271

Description: P: 24µm; E: 20µm. Monad, isopolar, small-sized, triporate, triangular (convex), suboblate, exine ornamentation: psilate (Zarafshar *et al.*, 2010)

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Trema micranta* (L.) Blume (Plate XVIII, 5,6,7,8)

Herbarium number: EAC0018332

Description: P: 15 μ m; E: 13 μ m. Monad, isopolar, small-sized, diporate, triangular (convex), suboblate, exine ornamentation: scabrate (Cassino and Meyer, 2011).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: riverine forest, seasonal semi-deciduous forest.

Order: BRASSICALES Bromhead

Family: CAPPARACEAE Juss.

Species: *Cynophalla hastata* (Jacq.) J.Presl (Plate XVIII, 9,10,11,12)

Herbarium number: EAC0007574

Description: P: 22 μ m; E: 26 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), circular, exine ornamentation: scabrate.

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Mesocapparis lineata* (Dombey ex Pers.) Cornejo & Iltis (Plate XVIII, 13,14,15,16)

Herbarium number: EAC00047043

Description: P: 25 μ m; E: 32 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate.

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: seasonal semi-deciduous forest.

Species: *Neocalyptrocalyx longifolium* (Mart.) Cornejo & Iltis (Plate XVIII, 17,18,19,20)

Herbarium number: EAC0007581

Description: P: 25µm; E: 29µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate.

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: CARYOCARACEAE Voigt

Species: *Caryocar coriaceum* Wittm. (Plate XIX, 1,2,3,4)

Herbarium number: EAC0008817

Description: P: 47µm; E: 60µm. Monad, isopolar, medium- to large-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Order: CELASTRALES Link

Family: CELASTRACEAE R.Br.

Species: *Fraunhoferia multiflora* Mart. (Plate XIX, 5,6,7,8)

Herbarium number: EAC0048573

Description: P: 15µm; E: 19µm. Monad, isopolar, small-sized, tricolporate, triangular (convex),

circular, exine ornamentation: reticulate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Monteverdia erythroxylo* (Reissek) Biral (Plate XIX, 9,10,11,12)

Herbarium number: EAC0044546

Description: P: 25 μ m; E: 24 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), circular, exine ornamentation: reticulate (Perveen and Qaiser, 2008).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, dense shrubland, riverine forest.

Species: *Prionostemma asperum* (Lam.) Miers (Plate XIX, 13,14,15,16)

Herbarium number: EAC0028369

Description: P: 28 μ m; E: 28 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate.

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, riverine forest, seasonal semi-deciduous forest.

Species: *Salacia elliptica* (Mart.) G.Don (Plate XIX, 17,18,19,20)

Herbarium number: EAC00023513

Description: P: 23 μ m; E: 28 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular

(convex), subprolate, exine ornamentation: reticulate (Gonçalves-Esteves and Melhem, 2000).

Life form: liana/scandent/vine, shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), riverine forest, seasonal semideciduous forest.

Species: *Tontelea micrantha* (Mart.) A.C.Sm. (Plate XX, 1,2,3,4)

Herbarium number: EAC00012141

Description: P: 25µm; E: 25µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate (Gonçalves-Esteves and Melhem, 1998).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: CHRYSOBALANACEAE R.Br.

Species: *Chrysobalanus icaco* L. subsp. *icaco* (Plate XX, 5,6,7,8)

Herbarium number: EAC0054977

Description: P: 26µm; E: 27µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate (Heigl, 2021).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: pioneer vegetation.

Species: *Couepia grandiflora* (Mart. & Zucc.) Benth. (Plate XX, 9,10,11,12)

Herbarium number: EAC0010723

Description: P: 31µm; E: 25µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate (Ybert *et al.*, 2017b).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Exellodendron cordatum* (Hook.f.) Prance (Plate XX, 13,14,15,16)

Herbarium number: EAC0010644

Description: P: 28µm; E: 29µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Parinari campestris* Aubl. (Plate XX, 17,18,19,20)

Herbarium number: EAC0030813

Description: P: 32µm; E: 32µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: microscabrate (Leal *et al.*, 2011).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest.

Order: BRASSICALES Bromhead

Family: CLEOMACEAE Bercht. & J.Presl

Species: *Physostemon guianense* (Aubl.) Malme (Plate XXI, 1,2,3,4)

Herbarium number: EAC0001969

Description: P: 21 μ m; E: 33 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, riverine forest, Caatinga (stricto sensu).

Species: *Tarenaya microcarpa* (Ule) Soares Neto & Roalson (Plate XXI, 5,6,7,8)

Herbarium number: EAC0012205

Description: P: 19 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: echinate (Lorente *et al.*, 2017).

Life form: herb, subshrub

Substrate: rupicolous, terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: CLUSIACEAE Lindl.

Species: *Clusia panapanari* (Aubl.) Choisy (Plate XXI, 9,10,11,12)

Herbarium number: EAC0047228

Description: P: 16 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: microgranulate (Ybert *et al.*, 2017b).

Life form: shrub, tree

Substrate: hemiepiphytes, terrestrial

Vegetation type: dense shrubland.

Order: MYRTALES Juss. ex Bercht. & J. Presl

Family: COMBRETACEAE R.Br.

Species: *Combretum fruticosum* (Loefl.) Stuntz (Plate XXI, 13,14,15,16)

Herbarium number: EAC0052838

Description: P: 19µm; E: 25µm. Monad, isopolar, small-sized, stephanocolporate, 6-lobate, subprolate, exine ornamentation: scabrate (El Ghazali, 2016).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Combretum mellifluum* Eichler. (Plate XXI, 17,18,19,20)

Herbarium number: EAC0059635

Description: P: 20µm; E: 23µm. Monad, isopolar, small-sized, stephanocolporate, 6-lobate, subprolate, exine ornamentation scabrate (El Ghazali, 2016).

Life form: liana/scandent/vine, shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland dense, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Terminalia corrugata* (Ducke) Gere & Boatwr. (Plate XXII, 1,2,3,4)

Herbarium number: EAC0057743

Description: P: 21µm; E: 19µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblata, exine ornamentation: microechinate (El Ghazali, 2022).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Terminalia fagifolia* Mart. (Plate XXII, 5,6,7,8)

Herbarium number: EAC0056856

Description: P: 16 μ m; E: 19 μ m. Monad, isopolar, small-sized, 6-stephanocolporate, lobate, subprolate, exine ornamentation: microrugulate (El Ghazali, 2022).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest.

Order: OXALIDALES Bercht. & J. Presl**Family: CONNARACEAE R.Br.****Species: *Connarus suberosus* Planch. (Plate XXII, 9,10,11,12)**

Herbarium number: EAC0028301

Description: P: 22 μ m; E: 27 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Mondal, 1994).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu).

Species: *Rourea induta* Planch. (Plate XXII, 13,14,15,16)

Herbarium number: EAC0012137

Description: P: 22 μ m; E: 22 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Order: SOLANALES Juss. ex Bercht. & J. Presl

Family: CONVOLVULACEAE Juss.

Species: *Evolvulus anagalloides* Meisn. (Plate XXII, 17,18)

Herbarium number: EAC0052578

Description: D: 39 μ m. Monad, isopolar, medium-sized, periporate, circular, exine ornamentation: reticulate (Vasconcelos *et al.*, 2019).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Ipomoea brasiliana* (Choisy) Meisn. (Plate XXII, 19,20)

Herbarium number: EAC0058060

Description: D: 39 μ m. Monad, isopolar, medium-sized, periporate, circular, exine ornamentation: reticulate (Vasconcelos *et al.*, 2019).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Jacquemontia gracillima* (Choisy) Hallier f. (Plate XXIII, 1,2)

Herbarium number: EAC0063620

Description: D: 76 μ m. Monad, isopolar, large-sized, pericoporate, circular, exine ornamentation: baculate (Vasconcelos *et al.*, 2019).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Order: DILLENIALES DC. ex Bercht. & J. Presl

Family: DILLENiaceae Salisb.

Species: *Curatella americana* L. (Plate XXIII, 3,4,5,6)

Herbarium number: EAC0057130

Description: P: 29.39 μ m; E: 25.40 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Sosam and Al-mayyahi, 2018).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Species: *Davilla cearensis* Huber (Plate XXIII, 7,8,9,10)

Herbarium number: EAC0050722

Description: P: 24 μ m; E: 30 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Barth, 1962).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: grassland, seasonal semi-deciduous forest.

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: DROSERACEAE Salisb.

Species: *Drosera sessilifolia* A.St.-Hil. (Plate XXIII, 11,12,13,14)

Herbarium number: EAC0049799

Description: P: 52 μ m; E: 57 μ m. Tetrad, heteropolar, large-sized, triporate, triangular (convex), suboblata, exine ornamentation: baculate (Kuprianova, 1973).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland, palm vegetation, valley-side marshes.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: ERYTHROXYLACEAE Kunth

Species: *Erythroxylum squamatum* Sw. (Plate XXIII, 15,16,17,18)

Herbarium number: EAC0055196

Description: P: 31µm; E: 30µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Rodríguez *et al.*, 2002).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: EUPHORBIACEAE Juss.

Species: *Cnidoscolus bahianus* (Ule) Pax & K.Hoffm. (Plate XXIV, 1,2)

Herbarium number: EAC0041852

Description: D: 68µm. Monad, isopolar, large-sized, inaperturate, circular, exine ornamentation: reticulate (Punt, 1961).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest.

Species: *Croton pedicellatus* Kunth. (Plate XXIV, 3,4,5,6)

Herbarium number: EAC0050249

Description: D: 40µm. Monad, isopolar, medium-sized, inaperturate, circular, exine ornamentation: croton-type (de Souza *et al.*, 2020).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Dalechampia fernandesii* G.L. Webster (Plate XXIV, 7,8,9,10)

Herbarium number: EAC0012725

Description: P: 62 μ m; E: 82 μ m. Monad, isopolar, large-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Souza *et al.*, 2017).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland.

Species: *Ditaxis desertorum* (Müll.Arg.) Pax & K.Hoffm. (Plate XXIV, 11,12,13,14)

Herbarium number: EAC0062723

Description: P: 43 μ m; E: 45 μ m. Monad, isopolar, medium-sized, tricolporate, circular, oblate, exine ornamentation: reticulate (Souza *et al.*, 2017).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Euphorbia hirta* L. (Plate XXIV, 15,16,17,18)

Herbarium number: EAC0059385

Description: P: 18 μ m; E: 25 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (El-Ghazaly and Chaudhary, 1993).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Gymnanthes boticário* Esser, M.F.A.Lucena & M.Alves (Plate XXV, 1,2,3,4)

Herbarium number: EAC0010912

Description: P: 22 μ m; E: 23 μ m. Monad, isopolar, small-sized, tricolporate, lobate, subprolate, exine ornamentation: reticulate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, seasonal semi-deciduous forest.

Species: *Jatropha mollissima* (Pohl) Baill. (Plate XXV, 5,6)

Herbarium number: EAC0063586

Description: D: 128 μ m. Monad, apolar, large-sized, inaperturate, circular, exine ornamentation: croton-type (Tiwari *et al.*, 2014).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Manihot caerulescens* Pohl (Plate XXV, 7,8)

Herbarium number: EAC0007458

Description: D: 107 μ m. Monad, apolar, large-sized, inaperturate, circular, exine ornamentation: croton-type (Vieira *et al.*, 2012).

Life form: liana/scandent/vine, shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Microstachys glandulosa* (Mart. & Zucc.) F.Dietr. (Plate XXV, 9,10,11,12)

Herbarium number: EAC0007572

Description: P: 24.µm; E: 26µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Sakugawa *et al.*, 2019).

Life form: herb, subshrub.

Substrate: terrestrial.

Vegetation type: Cerrado (lato sensu); grassland.

Species: *Sapium argutum* (Müll.Arg.) Huber (Plate XXV, 13,14,15,16)

Herbarium number: EAC0056887

Description: P: 43µm; E: 41µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: rugulate (Corrêa *et al.*, 2010).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Tragia volubilis* L. (Plate XXV, 17,18,19,20)

Herbarium number: EAC0023505

Description: P: 22µm; E: 20µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblolate, exine ornamentation: reticulate (Santos *et al.*, 2019).

Life form: liana/scandent/vine, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu).

Order: FABALES Bromhead

Family: FABACEAE Juss.

Subfamily: CAESALPINIOIDEAE DC.

Species: *Cassia ferruginea* (Schrad.) Schrad. ex DC. (Plate XXVI, 1,2,3,4)

Herbarium number: EAC0053232

Description: P: 31 μ m; E: 42 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (concave), subprolate, exine ornamentation: microreticulate (Antonio-Domingues *et al.*, 2018a).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu); riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Cenostigma macrophyllum* Tul. (Plate XXVI, 5,6,7,8)

Herbarium number: EAC0020639

Description: P: 55 μ m; E: 49 μ m. Monad, isopolar, medium- to large-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Dias *et al.*, 2022).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, riverine forest.

Species: *Cenostigma pyramidale* (Tul.) Gagnon & G.P.Lewis (Plate XXVI, 9,10,11,12)

Herbarium number: EAC0048876

Description: P: 66 μ m; E: 65 μ m. Monad, isopolar, large-sized, tricolporate, circular, subprolate, exine ornamentation: reticulate (Dias *et al.*, 2022).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Chamaecrista duckeana* (P.Bezerra & Afr.Fern.) H.S.Irwin & Barneby (Plate XXVI, 13,14,15,16)

Herbarium number: EAC0008098

Description: P: 19 μ m; E: 33 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: psilate (Da Luz *et al.*, 2013).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Dimorphandra gardneriana* Tul. (Plate XXVI, 17,18,19,20)

Herbarium number: EAC0003570

Description: P: 21 μ m; E: 31 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate (Leal *et al.*, 2011).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Species: *Diptychandra aurantiaca* subsp. *epunctata* (Tul.) H.C.Lima *et al.* (Plate XXVII, 1,2,3,4)

Herbarium number: EAC0031166

Description: P: 48 μ m; E: 47 μ m. Tetrad, isopolar, medium-sized, tricolporate, circular, exine ornamentation: reticulate (Barata and Carreira, 2005).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Libidibia ferrea* (Mart. ex Tul.) L.P.Queiroz (Plate XXVII, 5,6,7,8)

Herbarium number: EAC0054898

Description: P: 55 μ m; E: 50 μ m. Monad, isopolar, large-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (Buril *et al.*, 2011).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Melanoxylon brauna* Schott (Plate XXVII, 9,10,11,12)

Herbarium number: EAC0043545

Description: P: 30 μ m; E: 34 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Senna cearensis* Afr.Fern. (Plate XXVII, 13,14,15,16)

Herbarium number: EAC0059231

Description: P: 30 μ m; E: 42 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate (Buril *et al.*, 2011).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Senna obtusifolia* (L.) H.S.Irwin & Barneby (Plate XXVII, 17,18,19,20)

Herbarium number: EAC0063593

Description: P: 32µm; E: 46µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate (Buril *et al.*, 2011).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), grassland.

Species: *Tachigali vulgaris* L.G.Silva & H.C.Lima (Plate XXVIII, 1,2,3,4)

Description: P: 23µm; E: 17µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Subfamily: CAESALPINIOIDEAE (MIMOSOID CLADE)

Species: *Anadenanthera colubrina* var. *cebil* (Vell.) Brenan (Plate XXVIII, 5,6)

Herbarium number: EAC0018422

Description: D: 36µm. Polyad, apolar, large-sized, inaperturate, circular, exine ornamentation: microreticulate (Caccavari, 2002).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Chloroleucon foliolosum* (Benth.) G.P.Lewis (Plate XXVIII, 7,8)

Herbarium number: EAC0059721

Description: D: 99µm. Polyad, apolar, large-sized, 5-porate, suboblate, exine ornamentation: psilate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Desmanthus virgatus* (L.) Willd. (Plate XXVIII, 9,10,11,12)

Herbarium number: EAC0022852

Description: P: 39µm. E: 40µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Buril *et al.*, 2010).

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Entada polystachya* (L.) DC. (Plate XXVIII, 13,14,15,16)

Herbarium number: EAC0006256

Description: P: 36µm; E: 37µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: granulate (Jumah, 1991).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: riverine forest, valley-side marshes.

Species: *Enterolobium contortisiliquum* (Vell.) Morong (Plate XXVIII, 17,18)

Herbarium number: EAC0016404

Description: D: 81µm. Polyad, apolar, large-sized, circular, exine ornamentation: psilate (Buril *et al.*, 2010).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest,

Species: *Inga laurina* (Sw.) Willd. (Plate XXVIII, 19,20)

Herbarium number: EAC0010706

Description: D: 69µm. Polyad, apolar, large-sized, circular, exine ornamentation: psilate (Antonio-Domingues *et al.*, 2018a).

Life form: tree

Substrate: terrestrial

Vegetation type: grassland, seasonal semi-deciduous forest.

Species: *Mimosa caesalpinifolia* Benth. (Plate XXIX, 1,2)

Herbarium number: EAC0063595

Description: D: 12µm. Tetrad, isopolar, small-sized, elipitical, oblate, exine ornamentation: psilate (Lima *et al.*, 2008).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), riverine forest.

Species: *Neptunia plena* (L.) Benth. (Plate XXIX, 3,4,5,6)

Herbarium number: EAC0059379

Description: P: 39 μ m; E: 54 μ m. Monad, isopolar, medium- to large-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: striate (Buriel *et al.*, 2010).

Life form: herb, subshrub

Substrate: aquatic, terrestrial

Vegetation type: anthropic areas, aquatic vegetation, Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Parkia platycephala* Benth. (Plate XXIX, 7,8)

Herbarium number: EAC0038923

Description: D: 121 μ m. Polyad, apolar, large-sized, apertures indiscernible, circular, exine ornamentation: psilate (Sorsa, 1969).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Piptadenia retusa* (Jacq.) P.G.Ribeiro, Seigler & Ebinger (Plate XXIX, 9,10,11,12)

Herbarium number: EAC0060000

Description: D: 25 μ m. Polyad, apolar, medium-sized, apertures indiscernible, circular, exine ornamentation: microreticulate (Lima *et al.*, 2008).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu).

Species: *Pithecellobium diversifolium* Benth. (Plate XXIX, 13,14)

Herbarium number: EAC0041357

Description: D: 67 μ m. Polyad, apolar, large-sized, apertures indiscernible, circular, exine ornamentation: psilate (Buriel *et al.*, 2010).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Pityrocarpa moniliformis* (Benth.) Luckow & R.W.Jobson (Plate XXX, 1,2,3,4)

Herbarium number: EAC0059161

Description: P: 17 μ m; E: 14 μ m. Polyad, apolar, small-sized, apertures indiscernible, circular, exine ornamentation: psilate (Buriel *et al.*, 2010).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, seasonal deciduous forest

Species: *Plathymenia reticulata* Benth. (Plate XXX, 5,6,7,8)

Herbarium number: EAC0063114

Description: P: 30 μ m; E: 29 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: rugulate (Sorsa, 1969).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal semideciduous forest.

Species: *Samanea saman* (Jacq.) Merr. (Plate XXX, 9,10)

Herbarium number: EAC0048511

Description: D: 99 μ m. Polyad, heteropolar, large-sized, apertures indiscernible, circular, exine ornamentation: psilate (Sorsa, 1969).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Senegalia globosa* (Bocage & Miotto) L.P.Queiroz (Plate XXX, 11,12)

Herbarium number: EAC0017036

Description: D: 43 μ m. Polyad, apolar, medium-sized, inaperturate, circular, exine ornamentation: psilate (Dias *et al.*, 2022).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Stryphnodendron coriaceum* Benth. (Plate XXX, 13,14)

Herbarium number: EAC0013310

Description: D: 52 μ m. Polyad, apolar, large-sized, apertures indiscernible, circular, exine ornamentation: psilate (da Luz *et al.*, 2013).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Zygia latifolia* (L.) Fawc. & Rendle (Plate XXX, 15,16)

Herbarium number: EAC0018689

Description: D: 57µm. Polyad, apolar, large-sized, inaperturate, circular, exine ornamentation: psilate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, valley-side marshes, seasonal deciduous forest, seasonal semi-deciduous forest.

Subfamily: CERCIDOIDEAE LPWG**Species: *Bauhinia acuruana* Moric. (Plate XXX, 17,18,19,20)**

Herbarium number: EAC0031345

Description: P: 93µm; E: 79µm. Monad, isopolar, large-sized, tricolpate, triangular (convex), circular, exine ornamentation: reticulate (Taia *et al.*, 2022).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Schnella glabra* (Jacq.) Dugand (Plate XXXI, 1,2,3,4)

Herbarium number: EAC0032202

Description: P: 30µm; E: 33µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate.

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu); palm vegetation, riverine forest.

Subfamily: DETARIOIDEAE Burmeist. emend. LPWG

Species: *Copaifera langsdorffii* Desf. (Plate XXXI, 5,6,7,8)

Herbarium number: EAC0059729

Description: P: 24 μ m; E: 25 μ m. Monad, isopolar, small-sized, tricolporate, triangular, oblate, exine ornamentation: perforate (Banks, 2003).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Cynometra bauhiniifolia* Benth. (Plate XXXI, 9,10,11,12)

Herbarium number: EAC0034204

Description: P: 20 μ m; E: 20 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Banks; Rico, 1999).

Life form: tree

Substrate: terrestrial

Vegetation type: valley-side marshes.

Species: *Hymenaea courbaril* L. (Plate XXXI, 13,14,15,16)

Herbarium number: EAC0012965

Description: P: 29 μ m; E: 26 μ m. Monad, isopolar, medium-sized, tricolporate, subcircular, subprolate. exine ornamentation: microreticulate (Soares *et al.*, 2021).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), riverine forest.

Species: *Peltogyne confertiflora* (Mart. ex Hayne) Benth. (Plate XXXI, 17,18,19,20)

Herbarium number: EAC0010040

Description: P: 49 μ m; E: 55 μ m. Monad, isopolar, medium- to large-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: gemmate (Lorente *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: riverine forest, seasonal semi-deciduous forest.

Subfamily: DIALIOIDEAE LPWG

Species: *Apuleia leiocarpa* (Vogel) J.F.Macbr. (Plate XXXII, 1,2,3,4)

Herbarium number: EAC0021665

Description: P: 19 μ m; E: 29 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: microreticulate (Zimmerman *et al.*, 2013).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Martiodendron mediterraneum* (Mart. ex Benth.) R.C.Koeppen (Plate XXXII, 5,6,7,8)

Herbarium number: EAC0007982

Description: P: 23 μ m; E: 28 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Silva *et al.*, 2005).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Poeppigia procera* var. *conferta* Benth. (Plate XXXII, 9,10,11,12)

Herbarium number: EAC0027452

Description: P: 15µm; E: 17µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: rugulate (Buril *et al.*, 2011).

Life form: shrub, subshrub, tree

Substrate: rupicolous, terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), dense shrubland.

Subfamily: FABOIDEAE (PAPILIONOIDEAE DC.)

Species: *Aeschynomene evenia* C.Wright & Sauvalle (Plate XXXII, 13,14,15,16)

Herbarium number: EAC0063596

Description: P: 11µm; E: 14µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: equinate (Antonio-Domingues *et al.*, 2018b).

Life form: herb, shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Species: *Amburana cearensis* (Allemão) A.C.Sm. (Plate XXXII, 17,18,19,20)

Herbarium number: EAC0006472

Description: P: 24µm; E: 29µm. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Buril *et al.*, 2011).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Ancistrotropis firmula* (Mart. ex Benth.) A.Delgado (Plate XXXIII, 1,2,3,4)

Herbarium number: EAC0012567

Description: P: 31µm; E: 44µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Nascimento *et al.*, 2021).

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland.

Species: *Andira cordata* Arroyo ex R.T.Penn. & H.C.Lima (Plate XXXIII, 5,6,7,8)

Herbarium number: EAC0047184

Description: P: 21µm; E: 25µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (da Luz *et al.*, 2013).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Arachis dardani* Krapov. & W.C.Greg. (Plate XXXIII, 9,10,11,12)

Herbarium number: EAC0055653

Description: P: 17µm; E: 31µm. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Chaturvedi *et al.*, 1990).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), seasonal deciduous forest.

Species: *Bionia tomentosa* (Benth.) L.P.Queiroz (Plate XXXIII, 13,14,15,16)

Herbarium number: EAC0011045

Description: P: 28 μ m; E: 28 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate.

Life form: shrub

Substrate: rupicolous, terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Bowdichia virgilioides* Kunth. (Plate XXXIII, 17,18,19,20)

Herbarium number: EAC0028647

Description: P: 29 μ m; E: 32 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: psilate (Ferguson and Stirton, 1993).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, riverine forest, seasonal semi-deciduous forest.

Species: *Cajanus cajan* (L.) Huth (Plate XXXIV, 1,2,3,4)

Herbarium number: EAC0022892

Description: P: 32 μ m; E: 34 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Srivastava, 1978).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Camptosema sp.* Hook. & Arn. (Plate XXXIV, 5,6,7,8)

Herbarium number: EAC006683A

Description: P: 26 μ m; E: 27 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblata, exine ornamentation: reticulate (Kavanagh and Ferguson, 1981).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: riverine forest.

Species: *Canavalia brasiliensis* Mart. ex Benth. (Plate XXXIV, 9,10,11,12)

Herbarium number: EAC0063580

Description: P: 72 μ m; E: 73 μ m. Monad, isopolar, large-sized, tricolporate, triangular, subprolate, exine ornamentation: reticulate (Buril *et al.*, 2011).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), palm vegetation, riverine forest, seasonal semi-deciduous forest.

Species: *Centrosema brasilianum* (L.) Benth. (Plate XXXIV, 13,14,15,16)

Herbarium number: EAC0063582

Description: P: 37 μ m; E: 34 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Buril *et al.*, 2011).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Clitoria guianensis* (Aubl.) Benth. (Plate XXXIV, 17,18,19,20)

Herbarium number: EAC0017585

Description: P: 41 μ m; E: 39 μ m. Monad, isopolar, medium-sized, inaperturate, circular, exine ornamentation: scabrate.

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Cranocarpus gracilis* Afr.Fern. & P.Bezerra (Plate XXXV, 1,2)

Herbarium number: EAC0031341

Description: D: 26 μ m. Monad, isopolar, medium-sized, pantoporate, circular, exine ornamentation: rugulate (Ferguson and Skvarla, 1979).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, seasonal deciduous forest.

Species: *Cratylia mollis* Mart. ex Benth. (Plate XXXV, 3,4,5,6)

Herbarium number: EAC0006455

Description: P: 32 μ m; E: 38 μ m. Monad, heteropolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: psilate (Kavanagh and Ferguson, 1981).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland.

Species: *Crotalaria incana* L. (Plate XXXV, 7,8,9,10)

Herbarium number: EAC0014095

Description: P: 20 μ m; E: 32 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Buril *et al.*, 2011).

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest.

Species: *Dahlstedtia araripensis* (Benth.) M.J.Silva & A.M.G.Azevedo (Plate XXXV, 11,12,13,14)

Herbarium number: EAC0029043

Description: P: 20 μ m; E: 16 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: perforate (Teixeira *et al.*, 2002).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest.

Species: *Dalbergia cearenses* Ducke (Plate XXXV, 15,16,17,18)

Herbarium number: EAC0062147

Description: P: 19 μ m; E: 23 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: perforate (da Luz *et al.*, 2013).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, seasonal deciduous forest.

Species: *Deguelia nitidula* (Benth.) A.M.G.Azevedo & R.A.Camargo (Plate XXXVI, 1,2,3,4)

Herbarium number: EAC0012600

Description: P: 22 μ m; E: 28 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate to prolate, exine ornamentation: psilate (Fontes *et al.*, 2020).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Dipteryx lacunifera* Ducke (Plate XXXVI, 5,6,7,8)

Herbarium number: EAC0049815

Description: P: 29 μ m; E: 31 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Discolobium hirtum* Benth. (Plate XXXVI, 9,10,11,12)

Herbarium number: EAC0054505

Description: P: 20 μ m; E: 26 μ m. monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Lattar *et al.*, 2020).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Eriosema crinitum* (Kunth) G.Don (Plate XXXVI, 13,14,15,16)

Herbarium number: EAC0009131

Description: P: 28 μ m; E: 34 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblata, exine ornamentation: rugulate (Oliveira *et al.*, 2019).

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland, riverine forest, valley-side marshes.

Species: *Galactia jussiaeana* Kunth (Plate XXXVI, 17,18,19,20)

Herbarium number: EAC0002828

Description: P: 19 μ m; E: 22 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: rugulate (da Luz *et al.*, 2013)

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Harpalyce brasiliiana* Benth. (Plate XXXVII, 1,2,3,4)

Herbarium number: EAC0050597

Description: P: 33 μ m; E: 37 μ m. Monad, isopolar, large-sized, tricolporate, triangular (convex), prolate, exine ornamentation: microrugulate (Dos Santos *et al.*, 2022).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Indigofera hirsuta* L. (Plate XXXVII, 5,6,7,8)

Herbarium number: EAC0059225

Description: P: 29 μ m; E: 33 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: microreticulate (Nascimento *et al.*, 2021).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu); Cerrado (lato sensu).

Species: *Leptolobium parvifolium* (Harms) Sch.Rodr. & A.M.G.Azevedo (Plate XXXVII, 9,10,11,12)

Herbarium number: EAC0008203

Description: P: 19 μ m; E: 19 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: microreticulate.

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Lonchocarpus sericeus* (Poir.) Kunth ex DC. (Plate XXXVII, 13,14,15,16)

Herbarium number: EAC0019737

Description: P: 23 μ m; E: 23 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), circular, exine ornamentation: microreticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Species: *Luetzelburgia auriculata* (Allemão) Ducke (Plate XXXVII, 17,18,19,20)

Herbarium number: EAC0028439

Description: P: 16 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Dos Santos *et al.*, 2022).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Machaerium acutifolium* Vogel (Plate XXXVIII, 1,2,3,4)

Herbarium number: EAC0028746

Description: P: 18 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: psilate (Leal *et al.*, 2011).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Macroptilium lathyroides* (L.) Urb. (Plate XXXVIII, 5,6,7,8)

Herbarium number: EAC0059405

Description: P: 25 μ m; E: 33 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Buriel *et al.*, 2011).

Life form: herb, liana/scandent/vine, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), riverine forest, seasonal semi-deciduous forest.

Species: *Macropsychanthus bicolor* (Benth.) L.P.Queiroz & Snak (Plate XXXVIII, 9,10,11,12)

Herbarium number: EAC0047182

Description: P: 48µm; E: 50µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: microperforate (Kavanagh and Ferguson, 1981).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland.

Species: *Muelleria moniliformis* L.f. (Plate XXXVIII, 13,14,15,16)

Herbarium number: EAC0021454

Description: P: 28µm; E: 29µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: valley-side marshes.

Species: *Nissolia vincentina* (Ker Gawl.) T.M.Moura & Fort-Perez (Plate XXXVIII, 17,18,19,20)

Herbarium number: EAC0006456

Description: P: 14µm; E: 19µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Lattar *et al.*, 2020).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal semideciduous forest.

Species: *Periandra coccinea* (Schrad.) Benth. (Plate XXXIX, 1,2,3,4)

Herbarium number: EAC0005770

Description: P: 40µm; E: 44µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: rugulate (da Luz *et al.*, 2013).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Platypodium elegans* Vogel (Plate XXXIX, 5,6,7,8)

Herbarium number: EAC0031170

Description: P: 15µm; E: 14µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: rugulate (Antonio-Domingues *et al.*, 2018a).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Poiretia punctata* (Willd.) Desv. (Plate XXXIX, 9,10,11,12)

Herbarium number: EAC0048065

Description: P: 21µm; E: 23µm. Monad, isopolar, small-sized, tricolporate, circular, prolate, exine ornamentation: psilate (Lattar *et al.*, 2020).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Pterocarpus villosus* (Mart. ex Benth.) Benth. (Plate XXXIX, 13,14,15,16)

Herbarium number: EAC0017065

Description: P: 16µm; E: 18µm. Monad, isopolar, medium-sized, tricolporate, circular, subprolate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Pterodon abruptus* (Moric.) Benth. (Plate XXXIX, 17,18,19,20)

Herbarium number: EAC0031171

Description: P: 29µm; E: 36µm. Monad, isopolar, medium-sized, tricolporate, circular, subprolate, exine ornamentation: rugulate.

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, riverine forest, seasonal deciduous forest.

Species: *Rhynchosia minima* (L.) DC. (Plate XL, 1,2,3,4)

Herbarium number: EAC0058784

Description: P: 29 μ m; E: 30 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (Oliveira *et al.*, 2019).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest, valley-side marshes.

Species: *Sesbania exasperata* Kunth (Plate XL, 5,6,7,8)

Herbarium number: EAC0047171

Description: P: 27 μ m; E: 26 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Buril *et al.*, 2011).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), grassland, riverine forest, valley-side marshes.

Species: *Soemmeringia semperflorens* Mart. (Plate XL, 9,10,11,12)

Herbarium number: EAC0006829

Description: P: 13 μ m; E: 13 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), dense shrubland, riverine forest, valley-side marshes.

Species: *Stylosanthes viscosa* (L.) Sw. (Plate XL, 13,14,15,16)

Herbarium number: EAC0048947

Description: P: 15 μ m; E: 33 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), perprolate, exine ornamentation: reticulate (Buriel *et al.*, 2011)

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Swartzia psilonema* Harms (Plate XL, 17,18,19,20)

Herbarium number: EAC0007988

Description: P: 30 μ m; E: 32 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Tephrosia cinerea* (L.) Pers. (Plate XLI, 1,2,3,4)

Herbarium number: EAC0059019

Description: P: 22 μ m; E: 22 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Buriel *et al.*, 2011).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Trischidium molle* (Benth.) H.E.Ireland (Plate XLI, 5,6,7,8)

Herbarium number: EAC0026119

Description: P: 19 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: areolate (Buriel *et al.*, 2011).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Vatairea macrocarpa* (Benth.) Ducke (Plate XLI, 9,10,11,12)

Herbarium number: EAC0054900

Description: P: 15 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Zornia sericea* Moric. (Plate XLI, 13,14,15,16)

Herbarium number: EAC0023511

Description: P: 22 μ m; E: 36 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (da Luz *et al.*, 2013).

Life form: subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Order: GENTIANALES Juss. ex Bercht. & J. Presl

Family: GENTIANACEAE Juss.

Species: *Schultesia pohliana* Progel (Plate XLI, 17,18)

Herbarium number: EAC0048506

Description: D: 52 μ m. Tetrad, apolar, large-sized, coaperturate, triangular, exine ornamentation: reticulate (Ybert *et al.*, 2017b).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland, riverine forest.

Order: LAMIALES Bromhead**Family: GESNERIACEAE Rich. & Juss.****Species: *Sinningia elatior* (Kunth) Chautems (Plate XLII, 1,2,3,4)**

Herbarium number: EAC0010625

Description: P: 19 μ m; E: 17 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate/reticulate (Ybert *et al.*, 2017b).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Order: LAURALES Juss. ex Bercht. & J. Presl**Family: HERNANDIACEAE Blume****Species: *Sparattanthelium botocudorum* Mart. (Plate XLII, 5,6)**

Herbarium number: EAC0012087

Description: D: 22 μ m. Monad, isopolar, small-sized, inaperturate, circular, exine ornamentation: echinate (Scherer *et al.*, 2011).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: anthropic areas, seasonal semi-deciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: HUMIRIACEAE A.Juss.

Species: *Humiria balsamifera* (Aubl.) A.St.-Hil. (Plate XLII, 7,8,9,10)

Herbarium number: EAC0028365

Description: P: 35µm; E: 35µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: scabrate (Ybert *et al.*, 2017b).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland, riverine forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: HYPERICACEAE Juss.

Species: *Vismia guianensis* (Aubl.) Choisy (Plate XLII, 11,12,13,14)

Herbarium number: EAC0054773

Description: P: 13µm; E: 13µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Ybert *et al.*, 2017b).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal semi-deciduous forest.

Order: ICACINALES Tiegh. ex Tiegh.

Family: ICACINACEAE Miers

Species: *Emmotum nitens* (Benth.) Miers (Plate XLII, 15,16,17,18)

Herbarium number: EAC0010645

Description: P: 11µm; E: 13µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: psilate (Carvalho, 1971).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu). grassland.

Order: ZYGOPHYLLALES Link

Family: KRAMERIACEAE Dumort.

Species: *Krameria tomentosa* A.St.-Hil. (Plate XLIII, 1,2,3,4)

Herbarium number: EAC0006429

Description: P: 31 μ m; E: 31 μ m. Monad, isopolar, medium-sized, triporate, circular, suboblate, exine ornamentation: striate (Simpson and Skvarla, 1981).

Life form: shrub, subshrub

Substrate: hemiparasitic, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, seasonal deciduous forest.

Order: LAMIALES Bromhead

Family: LAMIACEAE Martinov

Species: *Amasonia* sp. L.f. (Plate XLIII, 5,6,7,8)

Herbarium number: EAC0011824

Description: P: 55 μ m; E: 48 μ m. Monad, isopolar, medium- to large-sized, tricolpate, triangular (convex), subprolate, exine ornamentation: microechinate.

Life form: herb, shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Eriope crassipes* Benth. (Plate XLIII, 9,10,11,12)

Herbarium number: EAC0010717

DESCRIPTION: P: 31 μ m; E: 37 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, oblate, exine ornamentation: reticulate (Silva, 2007).

Life form: herb, subshrub

Substrate: rupicolous, terrestrial

Vegetation type: anthropic areas, grassland, seasonal semi-deciduous forest.

Species: *Hypenia salzmannii* (Benth.) Harley (Plate XLIII, 13,14,15,16)

Herbarium number: EAC0050731

Description: P: 37 μ m; E: 38 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, oblate, exine ornamentation: reticulate (Silva, 2007).

Life form: herb, shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Hyptidendron leucophyllum* (Pohl ex Benth.) Harley (Plate XLIII, 17,18,19,20)

Herbarium number: EAC0012128

Description: P: 31 μ m; E: 35 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, oblate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Hyptis crenata* Pohl ex Benth. (Plate XLIV, 1,2,3,4)

Herbarium number: EAC0062767

Description: P: 27 μ m; E: 34 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, oblate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland, palm vegetation, valley-side marshes.

Species: *Leonotis nepetifolia* (L.) R.Br. (Plate XLIV, 5,6,7,8)

Herbarium number: EAC0063679

Description: P: 29 μ m; E: 33 μ m. Monad, isopolar, medium-sized, tricolpate, triangular (convex), subprolate, exine ornamentation: reticulate (Halbritter, 2016).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, valley-side marshes.

Species: *Marsypianthes chamaedrys* (Vahl) Kuntze (Plate XLIV, 9,10,11,12)

Herbarium number: EAC0062838

Description: P: 35 μ m; E: 36 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, suboblate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest.

Species: *Mesosphaerum suaveolens* (L.) Kuntze (Plate XLIV, 13,14,15,16)

Herbarium number: EAC0063627

Description: P: 37 μ m; E: 37 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, oblate, exine ornamentation: reticulate.

Life form: herb, shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Ocimum gratissimum* L. (Plate XLIV, 17,18,19,20)

Herbarium number: EAC0064119

Description: P: 42 μ m; E: 38 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, suboblate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic area, riverine forest.

Species: *Rhaphiodon echinus* (Nees & Mart.) Schauer (Plate XLV, 1,2,3,4)

Herbarium number: EAC0005641

Description: P: 27 μ m; E: 28 μ m. Monad, isopolar, medium-sized, stephanocolpate, 6-lobate, oblate, exine ornamentation: reticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Vitex flavens* Kunth. (Plate XLV, 5,6,7,8)

Herbarium number: EAC0026173

Description: P: 23 μ m; E: 23 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Lorente *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Order: ERICALES Bercht. & J. Presl

Family: LECYTHIDACEAE A.Rich.

Species: *Eschweilera nana* (O.Berg) Miers (Plate XLV, 9,10,11,12)

Herbarium number: EAC0009976

Description: P: 22 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Moura *et al.*, 2004).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Lecythis pisonis* Cambess. (Plate XLV, 13,14,15,16)

Herbarium number: EAC0059912

Description: P: 22 μ m; E: 21 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Ybert *et al.*, 2017b).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas.

Order: CORNALES Link

Family: LOASACEAE Juss.

Species: *Aosa rupestris* (Gardner) Weigend (Plate XLV, 17,18,19,20)

Herbarium number: EAC0043616

Description: P: 13 μ m; E: 13 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: psilate.

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu).

Order: GENTIANALES Juss. ex Bercht. & J. Presl

Family: LOGANIACEAE R.Br. ex Mart.

Species: *Antonia ovata* Pohl. (Plate XLVI, 1,2,3,4)

Herbarium number: EAC0028298

Description: P: 17 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblata, exine ornamentation: microscabrate/perforate (Taylor *et al.*, 2011).

Life form: tree

Substrate: rupicolous, terrestrial

Vegetation type: Cerrado (lato sensu), grassland, riverine forest.

Species: *Mitreola petiolata* (J.F.Gmel.) Torr. & A.Gray (Plate XLVI, 5,6,7,8)

Herbarium number: EAC0010571

Description: P: 13 μ m; E: 13 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: perforate (Punt and Leenhouts, 1967).

Life form: herb

Substrate: terrestrial

Vegetation type: riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Strychnos araguaensis* Krukoff & Barneby (Plate XLVI, 9,10,11,12)

Herbarium number: EAC0008142

Description: P: 29µm; E: 32µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: riverine forest, seasonal semi-deciduous forest.

Order: SANTALALES R. Br. ex Bercht. & J. Presl**Family: LORANTHACEAE Juss.****Species: *Passovia pedunculata* (Jacq.) Kuijt (Plate XLVI, 13,14,15,16)**

Herbarium number: EAC0054229

Description: P: 31µm; E: 34µm. Monad, isopolar, medium-sized, tricolpate, triangular (straight), oblate, exine ornamentation: reticulate (Grímsson *et al.*, 2018).

Life form: herb

Substrate: hemiparasitic

Vegetation type: Cerrado (lato sensu), riverine forest, valley-side marshes.

Species: *Psittacanthus eucalyptifolius* (Kunth) G.Don (Plate XLVI, 17,18,19,20)

Herbarium number: EAC0013928

Description: P: 46µm; E: 56µm. Monad, isopolar, medium- to large-sized, tricolpate, triangular (concave), oblate, exine ornamentation: psilate (Grímsson *et al.*, 2018).

Life form: herb

Substrate: hemiparasitic

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, valley-side marshes.

Species: *Struthanthus polyanthus* (Mart.) Mart. (Plate XLVII, 1,2,3,4)

Herbarium number: EAC0007230

Description: P: 26 μ m; E: 35 μ m. Monad, isopolar, medium-sized, tricolpate, triangular (straight), oblate, exine ornamentation: psilate (Grímsson *et al.*, 2018).

Life form: herb

Substrate: hemiparasitic

Vegetation type: Cerrado (lato sensu), seasonal semi-deciduous forest.

Order: MYRTALES Juss. ex Bercht. & J. Presl

Family: LYTHRACEAE J.St.-Hil.

Species: *Ammannia maritima* (Aubl.) S.A.Graham, P.W.Inglis & T.B.Cavalc. (Plate XLVII, 5,6,7,8)

Herbarium number: EAC0023556

Description: P: 14 μ m; E: 19 μ m. Monad, isopolar, medium-sized, triangular, tricolporate, circular, exine ornamentation: microverrucate (Mahmoodi *et al.*, 2022).

Life form: shrub, subshrub

Substrate: aquatic

Vegetation type: aquatic vegetation.

Species: *Cuphea campestris* Mart. ex Koehne (Plate XLVII, 9,10,11,12)

Herbarium number: EAC0063629

Description: P: 28 μ m; E: 32 μ m. Monad, isopolar, medium-sized, tricolporate, circular, oblate, exine ornamentation: single striation on either side of the pore (Graham and Graham, 1968).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), grassland.

Species: *Cuphea laricoides* Koehne (Plate XLVII, 13,14,15,16)

Herbarium number: EAC0057244

Description: P: 18 μ m; E: 25 μ m. Monad, isopolar, small-sized, tricolporate, triangular, oblate, exine ornamentation: psilate (Facco *et al.*, 2021).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Diplusodon* sp. Pohl (Plate XLVII, 17,18,19,20)

Herbarium number: EAC0009974

Description: P: 72 μ m; E: 79 μ m. Monad, isopolar, large-sized, triporate, circular, suboblate, exine ornamentation: verrucate (Muller, 1981).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal deciduous forest.

Species: *Lafoensia replicata* Pohl (Plate XLVIII, 1,2,3,4)

Herbarium number: EAC0015557

Description: P: 34 μ m; E: 35 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: verrucate (Muller, 1981).

Life form: tree

Substrate: terrestrial

Vegetation type: riverine forest, seasonal semideciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: MALPIGHIACEAE Juss.

Species: *Amorimia rigida* (A.Juss.) W.R.Anderson (Plate XLVIII, 5,6)

Herbarium number: EAC0019708

Description: D: 39 μ m. Monad, isopolar, small-sized, pantoporate, circular, exine ornamentation: microscabrate.

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: seasonal deciduous forest.

Species: *Banisteriopsis stellaris* (Griseb.) B.Gates (Plate XLVIII, 7,8,9,10)

Herbarium number: EAC0054886

Description: D: 33 μ m. Monad, isopolar, small-sized, pantoporate, circular, exine ornamentation: microscabrate (Leal *et al.*, 2011).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Byrsonima crassifolia* (L.) Kunth (Plate XLVIII, 11,12,13,14)

Herbarium number: EAC0059497

Description: P: 14 μ m; E: 14 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: microreticulate (Gonçalves-Esteves *et al.*, 2007).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest.

Species: *Callaeum psilophyllum* (A.Juss.) D.M.Johnson (Plate XLVIII, 15,16,17,18)

Herbarium number: EAC0011656

Description: D: 38 μ m. Monad, apolar, small-sized, pantoporate, circular, exine ornamentation: scabrate.

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), riverine forest.

Species: *Camarea affinis* A.St.-Hil. (Plate XLIX, 1,2,3,4)

Herbarium number: EAC0009129

Description: D: 46 μ m. Monad, apolar, small-sized, pantoporate, circular, exine ornamentation: scabrate (Cassino and Meyer, 2011).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Dicella* sp. Griseb. (Plate XLIX, 5,6,7,8)

Herbarium number: EAC0026689

Description: P: 49 μ m; E: 37 μ m. Monad, apolar, medium-sized, 4-colporate, quadrangular, subprolate, exine ornamentation: psilate.

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: dense shrubland, Cerrado (lato sensu), riverine forest, seasonal semi-deciduous

forest.

Species: *Diplopterys pubipetala* (A.Juss.) W.R.Anderson & C.C.Davis (Plate XLIX, 9,10)

Herbarium number: EAC0024224

Description: D: 43 μ m. Monad, apolar, medium-sized, 7-porate, circular, exine ornamentation: rugulate with psilate areas (Belonsi and Gasparino, 2015).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu); riverine forest, seasonal semi-deciduous forest.

Species: *Glicophyllum latibracteolatum* (Nied.) R.F.Almeida (Plate XLIX, 11,12)

Herbarium number: EAC0059562

Description: D: 26 μ m. Monad, apolar, medium-sized, stephanoporate, circular, exine ornamentation: microscabrate (Leal *et al.*, 2011).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Heteropterys trichanthera* A.Juss. (Plate XLIX, 13,14,15,16)

Herbarium number: EAC0057238

Description: D: 57 μ m. Monad, apolar, medium-sized, pantocolporate, circular, exine ornamentation: scabrate (Gonçalves-Esteves *et al.*, 2007).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Peixotoa jussieuana* A.Juss. (Plate XLIX, 17,18)

Herbarium number: EAC0040846

Description: D: 67 μ m. Monad, apolar, medium-sized, stephanoporate, circular, exine ornamentation: microreticulate (Gonçalves-Esteves *et al.*, 2007).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Stigmaphyllon paralias* A.Juss. (Plate XLIX, 19,20)

Herbarium number: EAC0009487

Description: D: 51 μ m. Monad, apolar, large-sized, stephanoporate, circular, exine ornamentation: rugulate-psilate (Gonçalves-Esteves *et al.*, 2007).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Verrucularina sp.* Rauschert (Plate L, 1,2)

Herbarium number: EAC0047042

Description: D: 31 μ m. Monad, apolar, medium-sized, stephanoporate, circular, exine ornamentation: microscabrate.

Life form: shrub

Substrate: terrestrial

Vegetation type: grassland.

Order: MALVALES Juss.

Family: MALVACEAE Juss.

Species: *Apeiba tibourbou* Aubl. (Plate L, 3,4,5,6)

Herbarium number: EAC0011802

Description: P: 31 μ m; E: 31 μ m. Monad, isopolar, medium-sized, tricolporate, circular, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu); riverine forest.

Species: *Ayenia erecta* Mart. ex K.Schum. (Plate L, 7,8,9,10)

Herbarium number: EAC0009572

Description: P: 27 μ m; E: 29 μ m. Monad, isopolar, medium-sized, triporate, triangular (convex), suboblate, exine ornamentation: microreticulate (Saba and Santos, 2003).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland, seasonal deciduous forest.

Species: *Byttneria divaricata* Benth. (Plate L, 11,12,13,14)

Herbarium number: EAC0024213

Description: P: 20 μ m; E: 20 μ m. Monad, isopolar, small-sized, triporate, triangular (convex), suboblate, exine ornamentation: microreticulate (Lopes *et al.*, 2022).

Life form: shrub

Substrate: terrestrial

Vegetation type: riverine forest, valley-side marshes.

Species: *Cienfuegosia heterophylla* (Vent.) Garcke (Plate L, 15,16)

Herbarium number: EAC0022962

Description: D: 88µm. Monad, apolar, large-sized, periporate, circular, exine ornamentation: echinate (Fryxell, 1969).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Helicteres muscosa* Mart. (Plate LI, 1,2,3,4)

Herbarium number: EAC0034946

Description: D: 35µm. Monad, isopolar, small-sized, triporate, suboblate, exine ornamentation: microechinate (Lopes *et al.*, 2022).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland.

Species: *Luehea candicans* Mart. (Plate LI, 5,6,7,8)

Herbarium number: EAC0054507

Description: P: 35µm; E: 34µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Lopes *et al.*, 2022).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Malvastrum Americanum* (L.) Torr. (Plate LI, 9,10)

Herbarium number: EAC0006181

Description: D: 52µm. Monad, apolar, large-sized, circular, exine ornamentation: echinate (Germano *et al.*, 1997).

Life form: herb, shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Melochia tomentosa* L. (Plate LI, 11,12,13,14)

Herbarium number: EAC0055772

Description: P: 41µm; E: 43µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), circular, exine ornamentation: microreticulate (Silva *et al.*, 2020)

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu).

Species: *Pavonia glazioviana* Gürke (Plate LI, 15,16)

Herbarium number: EAC0054838

Description: D: 124µm. Monad, apolar, large-sized, periporate, circular, exine ornamentation: echinate (Nascimento *et al.*, 2021).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Pseudobombax longiflorum* (Mart.) A.Robyns (Plate LII, 1,2,3,4)

Herbarium number: EAC0047764

Description: P: 47 μ m; E: 52 μ m. Monad, isopolar, medium- to large-sized, tricolporate, triangular (concave), oblate, exine ornamentation: reticulate (Lopes *et al.*, 2022).

Life form: rupicolous, terrestrial

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland, seasonal semi-deciduous forest.

Species: *Sida cordifolia* L. (Plate LII, 5,6)

Herbarium number: EAC0022885

Description: D: 67 μ m. Monad, apolar, large-sized, periporate, circular, exine ornamentation: echinate (Leal *et al.*, 2011).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Sterculia foetida* L. (Plate LII, 7,8,9,10)

Herbarium number: EAC0018340

Description: P: 20 μ m; E: 20 μ m. Monad, isopolar, small-sized, tricolporate, triangular (concave), suboblate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Urena lobata* L. (Plate LII, 11,12)

Herbarium number: EAC0050650

Description: D: 120 μ m. Monad, apolar, large-size, periporate, circular, exine ornamentation:

echinate (Cruz-Barroz *et al.*, 2006).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Waltheria brachypetala* Turcz. (Plate LII, 13,14,15,16)

Herbarium number: EAC0054986

Description: P: 34 μ m; E: 37 μ m. Monad, isopolar, medium-sized, 4-porate, quadrangular, suboblate, exine ornamentation: reticulate (Saba and Santos, 2003).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Species: *Wissadula amplissima* (L.) R.E.Fr. (Plate LIII, 1,2)

Herbarium number: EAC0006449

Description: D: 65 μ m. Monad, apolar, large-sized, circular, apertures indiscernible, exine ornamentation: echinate (Christensen, 1986).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Order: ERICALES Bercht. & J. Presl

Family: MARCGRAVIACEAE Bercht. & J.Presl

Species: *Schwartzia adamantium* (Cambess.) Bedell ex Gir.-Cañas (Plate LIII, 3,4,5,6)

Herbarium number: EAC0010746

Description: P: 18 μ m; E: 20 μ m. Monad, isopolar, small-sized, tricolporate, triangular (concave), suboblate, exine ornamentation: psilate (Lorente *et al.*, 2017).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: grassland, riverine forest.

Order: MYRTALES Juss. ex Bercht. & J. Presl

Family: MELASTOMATACEAE Juss.

Species: *Clidemia biserrata* DC. (Plate LIII, 7,8,9,10)

Herbarium number: EAC0058301

Description: P: 15 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, lobate, subprolate, exine ornamentation: microreticulate (De Novais and Absy, 2013).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Henriettea* sp. DC. (Plate LIII, 11,12,13,14)

Herbarium number: EAC0011049

Description: P: 13 μ m; E: 13 μ m. Monad, isopolar, small-sized, tricolporate and tricolpate, triangular (convex), prolate, exine ornamentation: psilate (Fontes *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: valley-side marshes, riverine forest.

Species: *Macairea radula* (Bonpl.) DC. (Plate LIII, 15,16,17,18)

Herbarium number: EAC0011053

Description: P: 13µm; E: 12µm. Monad, isopolar, small-sized, tricolporate and tricolpate, 6-lobate, subprolate, exine ornamentation: scabrate.

Life form: shrub, subshrub, tree

Substrate: rupicolous, terrestrial

Vegetation type: Cerrado (lato sensu), grassland, riverine forest.

Species: *Marcetia sp* DC. (Plate LIV, 1,2,3,4)

Herbarium number: EAC0008708

Description: P: 16µm; E: 21µm. Monad, isopolar, small-sized, tricolporate and tricolpate, 6-lobate, prolate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: herb, shrub, subshrub

Substrate: rupicolous, terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Mouriri guianensis* Aubl. (Plate LIV, 5,6,7,8)

Herbarium number: EAC0003492

Description: P: 21µm; E: 24µm. Monad, isopolar, small-sized, tricolporate and tricolpate, 6-lobate, prolate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal deciduous forest, valley-side marshes.

Species: *Pterolepis polygonoides* (DC.) Triana (Plate LIV, 9,10,11,12)

Herbarium number: EAC0055059

Description: P: 16µm; E: 15µm. Monad, isopolar, small-sized, tricolporate and tricolpate, 6-lobate, prolate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Rhynchanthera serrulata* (L.C.Rich.) DC. (Plate LIV, 13,14,15,16)

Herbarium number: EAC0054775

Description: P: 19µm; E: 24µm. Monad, isopolar, small-sized, tricolporate and tricolpate, 6-lobate, subprolate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), valley-side marshes.

Species: *Tibouchina* sp. Aubl. (Plate LIV, 17,18,19,20)

Herbarium number: EAC0043535

Description: P: 17µm; E: 14µm. Monad, isopolar, small-sized, tricolporate and tricolpate, 6-lobate, subprolate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub, subshrub, tree

Substrate: rupicolous, terrestrial

Vegetation type: Cerrado (lato sensu), grassland, valley-side marshes.

Order: SAPINDALES Juss. ex Bercht. & J. Presl

Family: MELIACEAE Juss.

Species: *Melia azedarach* L. (Plate LV, 1,2,3,4)

Herbarium number: EAC0038576

Description: P: 31µm; E: 36µm. Monad, isopolar, medium-sized, 4-porate, quadrangular, circular, exine ornamentation: psilate (Liu *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Order: RANUNCULALES Juss. ex Bercht. & J. Presl

Family: MENISPERMACEAE Juss.

Species: *Cissampelos ovalifolia* DC. (Plate LV, 5,6,7,8)

Herbarium number: EAC0013946

Description: P: 14µm; E: 16µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate (Teixeira *et al.*, 2013).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), dense shrubland, grassland, riverine forest.

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: MICROTEACEAE Schäferh. & Borsch

Species: *Microtea* sp. Sw. (Plate LV, 9,10)

Herbarium number: EAC0050301

Description: D: 15µm. Monad, apolar, small-sized, periporate, circular, exine ornamentation: reticulate (Neves, 2006).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, valley-side marshes.

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: MOLLUGINACEAE Bartl.

Species: *Mollugo verticillata* L. (Plate LV, 11,12)

Herbarium number: EAC0055771

Description: D: 32µm. Monad, apolar, small-sized, pericollpate, circular, exine ornamentation: microequinate (Nascimento *et al.*, 2021).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), grassland.

Order: Rosales Bercht. & J. Presl

Family: MORACEAE Gaudich.

Species: *Brosimum gaudichaudii* Trécul (Plate LV, 13,14)

Herbarium number: EAC0042200

Description: D: 11µm. Monad, isopolar, small-sized, diporate, circular, exine ornamentation: psilate (Barth, 1976).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu).

Species: *Dorstenia cayapia* Vell. (Plate LV, 15,16)

Herbarium number: EAC0011844

Description: D: 15µm. Monad, apolar, small-sized, periporate, circular, exine ornamentation: granulate (Barth, 1976).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Maclura tinctoria* (L.) D.Don ex Steud. (Plate LV, 17,18)

Herbarium number: EAC0014383

Description: D: 13µm. Monad, apolar, small-sized, diporate, circular, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Order: MAGNOLIALES Bromhead

Family: MYRISTICACEAE R.Br.

Species: *Virola subsessilis* (Benth.) Warb. (Plate LVI, 1,2,3,4)

Herbarium number: EAC0009037

Description: P: 24µm; E: 29µm. Monad, apolar, small- to medium-sized, monocolpate, triangular (convex), perprolate, exine ornamentation: reticulate (Leal *et al.*, 2011).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Order: MYRTALES Juss. ex Bercht. & J. Presl

Family: MYRTACEAE Juss.

Species: *Campomanesia* sp. Ruiz et Pav. (Plate LVI, 5,6,7,8)

Herbarium number: EAC0005156

Description: P: 19µm; E: 20µm. Monad, apolar, small-sized, tricolpate, triangular (convex), oblate, exine ornamentation: perforate (Corrêa *et al.*, 2018).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Eugenia gracillima* Kiaersk. (Plate LVI, 9,10,11,12)

Herbarium number: EAC0059664

Description: P: 14µm; E: 16µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: perforate (Corrêa *et al.*, 2018).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Myrcia guianensis* (Aubl.) DC. (Plate LVI, 13,14,15,16)

Herbarium number: EAC0059633

Description: P: 18µm; E: 21µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: perforate (Corrêa *et al.*, 2018).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Psidium myrsinites* DC. (Plate LVI, 17,18,19,20)

Herbarium number: EAC0062919

Description: P: 16µm; E: 16µm. Monad, apolar, small-sized, tricolporate, triangular (convex), oblate, exine ornamentation: areolate (Corrêa *et al.*, 2018).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: NYCTAGINACEAE Juss.

Species: *Guapira opposita* (Vell.) Reitz (Plate LVII, 1,2,3,4)

Herbarium number: EAC0059939

Description: P: 45µm; E: 38µm. Monad, isopolar, small-sized, tricolpate, triangular (convex), suboblate, exine ornamentation: microechinate (Souza *et al.*, 2010).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, riverine forest, seasonal semi-deciduous forest.

Species: *Pisonia* sp. L. (Plate LVII, 5,6,7,8)

Herbarium number: EAC0010748

Description: P: 31µm; E: 24µm. Monad, isopolar, small- to medium-sized, tricolpate, suboblate, exine ornamentation: reticulate.

Life form: liana/scandent/vine, tree

Substrate: terrestrial

Vegetation type: seasonal deciduous forest, seasonal semi-deciduous forest.

Order: NYMPHAEALES Salisb. ex Bercht. & J. Presl

Family: NYMPHAEACEAE Salisb.

Species: *Nymphaea jamesoniana* Planch. (Plate LVII, 9,10,11,12)

Herbarium number: EAC0059450

Description: P: 35µm; E: 34µm. Dyad, heteropolar, medium-sized, zonosulcate, triangular

(convex), suboblate, exine ornamentation: psilate (Ybert *et al.*, 2017a).

Life form: herb

Substrate: aquatic

Vegetation type: aquatic vegetation.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: OCHNACEAE DC.

Species: *Ouratea castaneifolia* (DC.) Engl. (Plate LVII, 13,14,15,16)

Herbarium number: EAC0039869

Description: P: 17µm; E: 18µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Order: SANTALALES R. Br. ex Bercht. & J. Presl

Family: OLACACEAE R.Br.

Species: *Dulacia* sp. Vell. (Plate LVII, 17,18,19,20)

Herbarium number: EAC0032244

Description: P: 29µm; E: 29µm. Monad, isopolar, medium-sized, triporate, triangular (convex), oblate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: liana/scandent/vine, shrub, tree

Substrate: hemiparasitic, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), valley-side marshes, riverine forest, seasonal semi-deciduous forest.

Species: *Heisteria ovata* Benth. (Plate LVIII, 1,2,3,4)

Herbarium number: EAC0030872

Description: P: 13 μ m; E: 13 μ m. Monad, isopolar, small-sized, triporate, triangular (convex), suboblate, exine ornamentation: scabrate (Corrêa and Barros, 2011).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Ximenia coriacea* Engl. (Plate LVIII, 5,6,7,8)

Herbarium number: EAC0038158

Description: P: 13 μ m; E: 13 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub

Substrate: hemiparasitic, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Order: SANTALALES R. Br. ex Bercht. & J. Presl

Family: OPILIACEAE Valetton

Species: *Agonandra brasiliensis* Miers ex Benth. & Hook.f. (Plate LVIII, 9,10,11,12)

Herbarium number: EAC0042208

Description: P: 12 μ m; E: 14 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate.

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Order: OXALIDALES Bercht. & J. Presl

Family: OXALIDACEAE**Species: *Oxalis divaricata* Mart. ex Zucc. (Plate LVIII, 13,14,15,16)**

Herbarium number: EAC0032967

Description: P: 23 μ m; E: 28 μ m. Monad, isopolar, small-sized, tricolporate, triangular (concave), subprolate, exine ornamentation: microreticulate (Corrêa and Fonseca, 2015).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl**Family: PASSIFLORACEAE Juss. ex Roussel****Species: *Mitostemma brevifilis* Gontsch. (Plate LVIII, 17,18,19,20)**

Herbarium number: EAC0026680

Description: P: 34 μ m; E: 29 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Araújo *et al.*, 2020).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Passiflora cincinnata* Mast. (Plate LIX, 1,2,3,4)

Herbarium number: EAC0014033

Description: P: 58 μ m; E: 58 μ m. Monad, isopolar, small-sized, stephanocolpate, lobate, circular, exine ornamentation: reticulate (Mezzonato-Pires *et al.*, 2015).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-

deciduous forest.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: PHYLLANTHACEAE Martinov

Species: *Phyllanthus clausenii* Müll.Arg. (Plate LIX, 5,6,7,8)

Herbarium number: EAC009948

Description: P: 15µm; E: 14µm. Monad, isopolar, small-sized, 4-colporate, prolate, exine ornamentation: reticulate (Corrêa *et al.*, 2010).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland.

Order: PIPERALES Bercht. & J. Presl

Family: PIPERACEAE Giseke

Species: *Piper tuberculatum* Jacq. (Plate LIX, 9,10,11,12)

Herbarium number: EAC0046664

Description: D: 9µm. Monad, isopolar, small-sized, monosulcate, circular, exine ornamentation: microreticulate (Fontes *et al.*, 2020).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Order: LAMIALES Bromhead

Family: PLANTAGINACEAE Juss.

Species: *Angelonia cornigera* Hook.f. (Plate LIX, 13,14,15,16)

Herbarium number: EAC0018555

Description: P: 14µm; E: 14µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate.

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), grassland.

Species: *Bacopa angulata* (Benth.) Edwall (Plate LIX, 17,18,19,20)

Herbarium number: EAC0057705

Description: P: 12 μ m; E: 11 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (El-Husseini and Shamsou, 2002).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Stemodia maritima* L. (Plate LX, 1,2,3,4)

Herbarium number: EAC0007573

Description: P: 14 μ m; E: 14 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Nascimento *et al.*, 2021).

Life form: herb

Substrate: aquatic, terrestrial

Vegetation type: Caatinga (stricto sensu), grassland.

Species: *Tetraulacium veroniciforme* Turcz. (Plate LX, 5,6,7,8)

Herbarium number: EAC0018578

Description: P: 23 μ m; E: 29 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate.

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Order: FABALES Bromhead

Family: POLYGALACEAE Hoffmanns. & Link

Species: *Bredemeyera floribunda* Willd. (Plate LX, 9,10,11,12)

Herbarium number: EAC0054770

Description: P: 31 μ m; E: 32 μ m. Monad, isopolar, medium-sized, 10-stephanocolporate, circular, suboblate, exine ornamentation: psilate (Lorente *et al.*, 2017).

Life form: liana/scandent/vine, shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Species: *Monnina insignis* A.W.Benn. (Plate LX, 13,14,15,16)

Herbarium number: EAC0012741

Description: P: 33 μ m; E: 40 μ m. Monad, isopolar, medium-sized, stephanocolporate, circular, prolate, exine ornamentation: perforate (Picanço Leite *et al.*, 2015).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Polygala trichosperma* Jacq. (Plate LX, 17,18,19,20)

Herbarium number: EAC0050300

Description: P: 31 μ m; E: 28 μ m. Monad, isopolar, medium-sized, stephanocolporate, circular, suboblate, exine ornamentation: psilate (Simpson and Skvarla, 1981).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: grassland, seasonal semi-deciduous forest.

Species: *Securidaca coriacea* Bonpl. (Plate LXI, 1,2,3,4)

Herbarium number: EAC0006830

Description: P: 30µm; E: 29µm. Monad, isopolar, medium-sized, stephanocolporate, circular, suboblate, exine ornamentation: foveolate (Cruz-Barros *et al.*, 2005).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Order: CARYOPHYLLALES Juss. ex Bercht. & J. Presl

Family: POLYGONACEAE Juss.

Species: *Coccoloba mollis* Casar. (Plate LXI, 5,6,7,8)

Herbarium number: EAC0054771

Description: P: 21µm; E: 25µm. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Lucas *et al.*, 2010).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, seasonal deciduous forest, seasonal semi-deciduous forest.

Order: ROSALES Bercht. & J. Presl

Family: RHAMNACEAE Juss.

Species: *Colubrina cordifolia* Reissek (Plate LXI, 9,10,11,12)

Herbarium number: EAC0021303

Description: P: 22µm; E: 25µm. Monad, isopolar, small-sized, tricolporate, triangular (convex),

subprolate, exine ornamentation: scabrate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), dense shrubland.

Species: *Rhamnidium molle* Reissek (Plate LXI, 13,14,15,16)

Herbarium number: EAC0007372

Description: P: 18 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: RHIZOPHORACEAE Pers.

Species: *Rhizophora mangle* L. (Plate LXI, 17,18,19,20)

Herbarium number: EAC0021664

Description: P: 16 μ m; E: 18 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Mohd-Arrabe' and Talip, 2013).

Life form: tree

Substrate: aquatic, terrestrial

Vegetation type: aquatic vegetation.

Order: ROSALES Bercht. & J. Presl

Family: ROSACEAE Juss.

Species: *Eriobotrya japonica* (Thunb.) Lindl. (Plate LXII, 1,2,3,4)

Herbarium number: EAC0031286

Description: P: 14µm; E: 17µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: rugulate.

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, riverine forest.

Order: GENTIANALES Juss. ex Bercht. & J. Presl

Family: RUBIACEAE Juss.

Species: *Alibertia edulis* (Rich.) A.Rich. (Plate LXII, 5,6,7,8)

Herbarium number: EAC0027074

Description: P: 28µm; E: 26µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Fontes *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, grassland, riverine forest.

Species: *Borreria diacrodonta* L.M. Miguel & E.L. Cabral (Plate LXII, 9,10,11,12)

Herbarium number: EAC0022855

Description: P: 18µm; E: 19µm. Monad, isopolar, small-sized, 6-lobate, circular, oblate, exine ornamentation: perforate (Miguel *et al.*, 2018).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Chiococca alba* (L.) Hitchc. (Plate LXII, 13,14,15,16)

Herbarium number: EAC0063274

Description: P: 30µm; E: 31µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Leal *et al.*, 2011).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Chomelia obtusa* Cham. & Schltdl. (Plate LXII, 17,18,19,20)

Herbarium number: EAC0035664

Description: P: 26µm; E: 24µm. Monad, isopolar, small- to medium-sized, triporate, triangular (convex), suboblate, exine ornamentation: reticulate-retipilate (Dutra *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, grassland, riverine forest.

Species: *Coccocypselum lanceolatum* (Ruiz & Pav.) Pers. (Plate LXIII, 1,2,3,4)

Herbarium number: EAC0027079

Description: P: 44µm; E: 40µm. Monad, isopolar, medium-sized, triporate, triangular (convex), suboblate, exine ornamentation: reticulate-retipilate (Leal *et al.*, 2011; Schroeder *et al.*, 2019).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Species: *Cordia myrciifolia* (K.Schum.) C.H.Perss. & Delprete (Plate LXIII, 5,6,7,8)

Herbarium number: EAC0054878

Description: P: 27µm; E: 30µm. Monad, isopolar, medium-sized, triporate, triangular (convex),

suboblate, exine ornamentation: reticulate (Judkevich *et al.*, 2022).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Coussarea hydrangeifolia* (Benth.) Müll.Arg. (Plate LXIII, 9,10,11,12)

Herbarium number: EAC0061597

Description: P: 22µm; E: 22µm. Monad, apolar, small-sized, diporate, circular, oblate, exine ornamentation: microreticulate (Dutra *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest.

Species: *Coutarea hexandra* (Jacq.) K.Schum. (Plate LXIII, 13,14,15,16)

Herbarium number: EAC0027090

Description: P: 32µm; E: 32µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate-echinate (Dutra *et al.*, 2020)

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Declieuxia fruticosa* (Willd. ex Roem. & Schult.) Kuntze (Plate LXIII, 17,18,19,20)

Herbarium number: EAC0051401

Description: P: 34µm; E: 37µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: microreticulate (Leal *et al.*, 2011).

Life form: shrub, subshrub

Substrate: rupicolous, terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Faramea nitida* Benth. (Plate LXIV, 1,2,3,4)

Herbarium number: EAC0031369

Description: P: 28µm; E: 28µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (Dutra *et al.*, 2020).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Guettarda viburnoides* Cham. & Schltld. (Plate LXIV, 5,6)

Herbarium number: EAC0055696

Description: P: 27µm; E: 30µm. Monad, isopolar, medium-sized, triporate, triangular, suboblate, exine ornamentation: rugulate (Dutra *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), dense shrubland, grassland, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Hexasepalum apiculatum* (Willd.) Delprete & J.H.Kirkbr. (Plate LXIV, 7,8,9,10)

Herbarium number: EAC0035825

Description: P: 37 μ m; E: 37 μ m. Monad, isopolar, medium-sized, stephanocolporate, circular, oblate, exine ornamentation: echinate (Fader *et al.*, 2016).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland.

Species: *Machaonia acuminata* Bonpl. (Plate LXIV, 11,12,13,14)

Herbarium number: EAC0047286

Description: P: 23 μ m; E: 26 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest, valley-side marshes.

Species: *Mitracarpus baturitensis* Sucre (Plate LXIV, 15,16,17,18)

Herbarium number: EAC0018549

Description: P: 23 μ m; E: 25 μ m. Monad, isopolar, small-sized, stephanocolporate, lobate, subprolate, exine ornamentation: microreticulate (Dutra *et al.*, 2020).

Life form: herb

Substrate: rupicolous, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Palicourea veterinariorum* J.H.Kirkbr. (Plate LXV, 1,2)

Herbarium number: EAC0009063

Description: D: 55µm. Monad, apolar, large-sized, inaperturate, circular, exine ornamentation reticulate (Leal *et al.*, 2011).

Life form: shrub

Substrate: terrestrial

Vegetation type: riverine forest.

Species: *Perama hirsute* Aubl. (Plate LXV, 3,4,5,6)

Herbarium number: EAC0053592

Description: P: 37µm; E: 35µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: baculate (Rull, 2003).

Life form: herb

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Psyllocarpus* sp. Mart. ex Mart. & Zucc. (Plate LXV, 7,8,9,10)

Herbarium number: EAC0028089

Description: P: 33µm; E: 32µm. Monad, isopolar, medium-sized, stephanocolporate, lobate, subprolate, exine ornamentation: microreticulate (Do Carmo *et al.*, 2018).

Life form: herb, shrub, subshrub

Substrate: rupicolous, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Randia armata* (Sw.) DC. (Plate LXV, 11,12)

Herbarium number: EAC0055712

Description: P: 60µm. Tetrad, isopolar, small-sized, triporate, circular, exine ornamentation:

psilate (Dutra *et al.*, 2020).

Life form: liana/scandent/vine, shrub, tree

Substrate: rupicolous, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Richardia grandiflora* (Cham. & Schltdl.) Steud. (Plate LXV, 13,14,15,16)

Herbarium number: EAC0064234

Description: P: 36 μ m; E: 32 μ m. Monad, isopolar, medium-sized, stephanocolpate, lobate, oblate, exine ornamentation: echinate (Nascimento *et al.*, 2021).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, seasonal semi-deciduous forest.

Species: *Rudgea sp.* Salisb. (Plate LXVI, 1,2,3,4)

Herbarium number: EAC0030674

Description: P: 31 μ m; E: 28 μ m. Monad, isopolar, medium-sized, tricolporate, triangular, prolate, exine ornamentation: baculate (Dutra *et al.*, 2020).

Life form: shrub, subshrub, tree

Substrate: aquatic, terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Sabicea cinerea* Aubl. (Plate LXVI, 5,6,7,8)

Herbarium number: EAC0031327

Description: P: 58 μ m; E: 61 μ m. Monad, isopolar, large-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: seasonal semi-deciduous forest.

Species: *Simira gardneriana* M.R.V.Barbosa & Peixoto (Plate LXVI, 9,10,11,12)

Herbarium number: EAC0011058

Description: P: 29 μ m; E: 28 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (Dutra *et al.*, 2020).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Species: *Spermacoce confusa* Rendle (Plate LXVI, 13,14,15,16)

Herbarium number: EAC0022887

Description: P: 14 μ m; E: 14 μ m. Monad, isopolar, small-sized, stephanocolpate, triangular (convex), subprolate, exine ornamentation: psilate.

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), dense shrubland, grassland.

Species: *Spermacoce reflexa* (J.H.Kirkbr.) Govaerts (Plate LXVI, 17,18,19,20)

Herbarium number: EAC0027059

Description: P: 40µm; E: 33µm. Monad, isopolar, small-sized, stephanocolpate, lobate, subprolate, exine ornamentation: reticulate (Gonçalves-Esteves *et al.*, 2020).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, grassland.

Species: *Stachyarrhena sp.* Hook.f. (Plate LXVII, 1,2,3,4)

Herbarium number: EAC0047176

Description: P: 68µm; E: 67µm. Monad, isopolar, large-sized, tricolporate, triangular (convex), oblate, exine ornamentation: reticulate (Persson, 1993).

Life form: shrub, tree

Substrate: rupicolous, terrestrial

Vegetation type: grassland, riverine forest, valley-side marshes.

Species: *Staelia virgata* (Link ex Roem. & Schult.) K.Schum. (Plate LXVII, 5,6,7,8)

Herbarium number: EAC0027061

Description: P: 33µm; E: 30µm. Monad, isopolar, medium-sized, stephanocolporate, lobate, oblate, exine ornamentation: reticulate (Salas and Cabral, 2014).

Life form: herb, subshrub

Substrate: aquatic, rupicolous, terrestrial

Vegetation type: anthropic areas, aquatic vegetation, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, palm vegetation, seasonal semi-deciduous forest.

Species: *Tocoyena hispidula* Standl. (Plate LXVII, 9,10,11,12)

Herbarium number: EAC0047206

Description: P: 43µm; E: 41µm. Monad, isopolar, medium-sized, tricolporate, circular, suboblate, exine ornamentation: foveolate (Dutra *et al.*, 2020).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Warszewiczia schwackei* K.Schum. (Plate LXVII, 13,14,15,16)

Herbarium number: EAC0043526

Description: P: 13µm; E: 14µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: reticulate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: riverine forest, seasonal semi-deciduous forest.

Order: SAPINDALES Juss. ex Bercht. & J. Presl

Family: RUTACEAE Juss.

Species: *Ertela trifolia* (L.) Kuntze (Plate LXVII, 17,18,19,20)

Herbarium number: EAC0009686

Description: P: 45µm; E: 44µm. Monad, isopolar, medium-sized, tricolporate, circular, subprolate, exine ornamentation: reticulate.

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, seasonal semi-deciduous forest.

Species: *Esenbeckia pumila* Pohl (Plate LXVIII, 1,2,3,4)

Herbarium number: EAC0010624

Description: P: 24 μ m; E: 30 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Dutra and Gasparino, 2018)

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Pilocarpus trachylophus* Holmes (Plate LXVIII, 5,6,7,8)

Herbarium number: EAC0042197

Description: P: 24 μ m; E: 24 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolate, exine ornamentation: striate-reticulate (Dutra and Gasparino, 2018).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Spiranthera odoratissima* A.St.-Hil. (Plate LXVIII, 9,10,11,12)

Herbarium number: EAC0026668

Description: P: 60 μ m; E: 65 μ m. Monad, isopolar, large-sized, triporate, triangular (convex), suboblate, exine ornamentation: echinate (Morton and Kallunki, 1993).

Life form: shrub

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), grassland.

Species: *Zanthoxylum stelligerum* Turcz. (Plate LXVIII, 13,14,15,16)

Herbarium number: EAC0059657

Description: P: 16 μ m; E: 16 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: striate (Dutra and Gasparino, 2018).

Life form: tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: SALICACEAE Mirb.

Species: *Casearia grandiflora* Cambess. (Plate LXVIII, 17,18,19,20)

Herbarium number: EAC0011810

Description: P: 25 μ m; E: 30 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation psilate.

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, seasonal semi-deciduous forest.

Order: SAPINDALES Juss. ex Bercht. & J. Presl

Family: SAPINDACEAE Juss.

Species: *Cardiospermum anomalum* Cambess. (Plate LXIX, 1,2,3,4)

Herbarium number: EAC0009816

Description: P: 40 μ m; E: 42 μ m. Monad, isopolar, medium-sized, triporate, triangular (convex), oblate, exine ornamentation: reticulate (Nascimento *et al.*, 2021).

Life form: herb, subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, seasonal semi-deciduous forest.

Species: *Cupania sp. L.* (Plate LXIX, 5,6,7,8)

Herbarium number: EAC0054785

Description: P: 23 μ m; E: 28 μ m. Monad, isopolar, small- to medium-sized, triporate, triangular (convex), oblate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Magonia pubescens* A.St.-Hil. (Plate LXIX, 9,10)

Herbarium number: EAC0052658

Description: D: 49 μ m. Tetrad, isopolar, small-sized, trizonocolporate, triangular (convex), exine ornamentation: striate-reticulate (González *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Matayba sp.* Aubl. (Plate LXIX, 11,12,13,14)

Herbarium number: EAC0050768

Description: P: 18 μ m; E: 29 μ m. Monad, isopolar, small- to medium-sized, triporate, triangular (convex), oblate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Paullinia* sp. L. (Plate LXIX, 15,16,17,18)

Herbarium number: EAC0028267

Description: P: 26 μ m; E: 29 μ m. Monad, isopolar, medium-sized, triporate, triangular (convex), oblate, exine ornamentation: microreticulate (Silva *et al.*, 2014).

Life form: liana/scandent/vine, shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Sapindus saponaria* L. (Plate LXX, 1,2,3,4)

Herbarium number: EAC0060024

Description: P: 14 μ m; E: 19 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblato, exine ornamentation: microreticulate.

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, riverine forest, seasonal semi-deciduous forest.

Species: *Serjania glabrata* Kunth (Plate LXX, 5,6,7,8)

Herbarium number: EAC0027439

Description: P: 33 μ m; E: 35 μ m. Monad, isopolar, medium-sized, triporate, triangular (convex), suboblato, exine ornamentation: scabrate (Nascimento *et al.*, 2021).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), seasonal semi-deciduous forest.

Species: *Talisia* sp. Aubl. (Plate LXX, 9,10,11,12)

Herbarium number: EAC0030681

Description: P: 22 μ m; E: 23 μ m. Monad, isopolar, small-sized, triporate, triangular (convex), oblato, exine ornamentation: scabrate (Fontes *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Toulicia* sp. Aubl. (Plate LXX, 13,14,15,16)

Herbarium number: EAC0024251

Description: P: 19 μ m; E: 21 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), suboblato, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), palm vegetation, riverine forest, seasonal semi-deciduous forest, valley-side marshes.

Order: ERICALES Bercht. & J. Presl**Family: SAPOTACEAE Juss.****Species: *Chrysophyllum arenarium* Allemão (Plate LXX, 17,18,19,20)**

Herbarium number: EAC0063154

Description: P: 15 μ m; E: 15 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), prolata, exine ornamentation: psilate (Rull, 2003).

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Order: SAPINDALES Juss. ex Bercht. & J. Presl

Family: SIMAROUBACEAE DC.

Species: *Homalolepis ferruginea* (A.St.-Hil.) Devecchi & Pirani (Plate LXXI, 1,2,3,4)

Herbarium number: EAC0012156

Description: P: 18 μ m; E: 17 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Devecchi *et al.*, 2018).

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Homalolepis maiana* (Casar.) Devecchi & Pirani (Plate LXXI, 5,6,7,8)

Herbarium number: EAC0001005

Description: P: 28 μ m; E: 39 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Devecchi *et al.*, 2018).

Life form: tree

Substrate: terrestrial

Vegetation type: pioneer vegetation.

Order: SOLANALES Juss. ex Bercht. & J. Presl

Family: SOLANACEAE Adans.

Species: *Brunfelsia uniflora* (Pohl) D.Don (Plate LXXI, 9,10,11,12)

Herbarium number: EAC0039563

Description: P: 30 μ m; E: 29 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: rugulate (Silva *et al.*, 2014).

Life form: shrub

Substrate: terrestrial

Vegetation type: seasonal semi-deciduous forest.

Species: *Cestrum sp.* L. (Plate LXXI, 13,14,15,16)

Herbarium number: EAC0008145

Description: P: 25µm; E: 30µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblata, exine ornamentation: scabrate (Fontes *et al.*, 2020).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), grassland, palm vegetation, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Nicotiana glauca* Graham (Plate LXXI, 17,18,19,20)

Herbarium number: EAC0053834

Description: P: 22µm; E: 25µm. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate (Nascimento *et al.*, 2021).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas.

Species: *Schwenckia sp.* L. (Plate LXXII, 1,2,3,4)

Herbarium number: EAC0011836

Description: P: 18µm; E: 20µm. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Lorente *et al.*, 2017).

Life form: herb, liana/scandent/vine, shrub, subshrub

Substrate: aquatic, rupicolous, terrestrial

Vegetation type: anthropic areas, aquatic vegetation, Caatinga (stricto sensu), riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Species: *Solanum paniculatum* L. (Plate LXXII, 5,6,7,8)

Herbarium number: EAC0063652

Description: P: 28 μ m; E: 30 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate (Lorente *et al.*, 2017).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas.

Order: ERICALES Bercht. & J. Presl

Family: STYRACACEAE DC. & Spreng.

Species: *Styrax* sp. L. (Plate LXXII, 9,10,11,12)

Herbarium number: EAC0010740

Description: P: 28 μ m; E: 31.49 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: reticulate (Cassino and Meyer, 2011).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: TRIGONIACEAE A.Juss.

Species: *Trigonia* sp. Aubl. (Plate LXXII, 13,14,15,16)

Herbarium number: EAC0021675

Description: P: 26 μ m; E: 31 μ m. Monad, isopolar, medium-sized, 4-porate, quadrangular, oblate, exine ornamentation fossulate (Corrêa and Barros, 2011).

Life form: herb, liana/scandent/vine, shrub, subshrub, tree

Substrate: rupicolous, terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest, valley-side marshes.

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: TURNERACEAE Kunth ex DC.

Species: *Piriqueta plicata* Urb. (Plate LXXII, 17,18,19,20)

Herbarium number: EAC0010637

Description: P: 47 μ m; E: 42 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Matos *et al.*, 2014).

Life form: subshrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland.

Species: *Turnera blanchetiana* Urb. (Plate LXXIII, 1,2,3,4)

Herbarium number: EAC0055575

Description: P: 24 μ m; E: 26 μ m. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: reticulate (Matos *et al.*, 2014).

Life form: shrub, subshrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Order: ROSALES Bercht. & J. Presl

Family: URTICACEAE Juss.

Species: *Cecropia pachystachya* Trécul. (Plate LXXIII, 5,6,7,8)

Herbarium number: EAC0027717

Description: P: 8 μ m; E: 13 μ m. Monad, isopolar, small-sized, diporate, elliptical, prolate, exine ornamentation: psilate (Lorente *et al.*, 2017).

Life form: tree

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest.

Order: LAMIALES Bromhead

Family: VERBENACEAE J.St.-Hil.

Species: *Aloysia gratissima* (Gillies & Hook.) Tronc. var. *gratissima* (Plate LXXIII, 9,10,11,12)

Herbarium number: EAC0009079

Description: P: 19 μ m; E: 24 μ m. Monad, isopolar, small-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Nascimento *et al.*, 2021).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Cerrado (lato sensu), grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Species: *Lippia organoides* Kunth (Plate LXXIII, 13,14,15,16)

Herbarium number: EAC0061558

Description: P: 32 μ m; E: 32 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: microreticulate (Nascimento *et al.*, 2021).

Life form: shrub

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), dense shrubland, grassland, riverine forest, seasonal semi-deciduous forest.

Species: *Stachytarpheta lythrophylla* Schauer (Plate LXXIII, 17,18,19,20)

Herbarium number: EAC0045628

Description: D: 53µm. Monad, isopolar, large-sized, tricolporate, triangular, oblate, exine ornamentation: verrucate (Nascimento *et al.*, 2021).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Order: MALPIGHIALES Juss. ex Bercht. & J. Presl

Family: VIOLACEAE Batsch

Species: *Calyptrion* sp. Ging. (Plate LXXIV, 1,2,3,4)

Herbarium number: EAC0023559

Description: P: 25µm; E: 28µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: psilate (Mark *et al.*, 2012).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu), valley-side marshes, riverine forest.

Species: *Hybanthus* sp. Jacq. (Plate LXXIV, 5,6,7,8)

Herbarium number: EAC0008078

Description: P: 60µm; E: 69µm. Monad, isopolar, large-sized, tricolporate, triangular (convex), prolate, exine ornamentation: perforate/psilate (Mark *et al.*, 2012).

Life form: herb

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), grassland.

Species: *Pombalia calceolaria* (L.) Paula-Souza (Plate LXXIV, 9,10,11,12)

Herbarium number: EAC0059355

Description: P: 36µm; E: 35µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: granulate (Lorente *et al.*, 2017).

Life form: herb

Substrate: terrestrial

Vegetation type: anthropic areas, Caatinga (stricto sensu), Cerrado (lato sensu), riverine forest, seasonal semi-deciduous forest, valley-side marshes.

Order: VITALES Juss. ex Bercht. & J. Presl

Family: VITACEAE Juss.

Species: *Clematicissus simsiana* (Schult. & Schult.f.) Lombardi (Plate LXXIV, 13,14,15,16)

Herbarium number: EAC0063453

Description: P: 24µm; E: 26µm. Monad, isopolar, small- to medium-sized, tricolporate, triangular (convex), prolate, exine ornamentation: microreticulate (Cartaxo-Pinto *et al.*, 2017).

Life form: liana/scandent/vine

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, seasonal deciduous forest, seasonal semi-deciduous forest.

Order: MYRTALES Juss. ex Bercht. & J. Presl

Family: VOCHYSIACEAE A.St.-Hil.

Species: *Callisthene microphylla* Warm. (Plate LXXIV, 17,18,19,20)

Herbarium number: EAC0010913

Description: P: 33µm; E: 29µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: granulate (Barth and da Luz, 2014).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu).

Species: *Qualea parviflora* Mart. (Plate LXXV, 1,2,3,4)

Herbarium number: EAC0062859

Description: P: 25µm; E: 27µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), suboblate, exine ornamentation: perforate (Barth and da Luz, 2014).

Life form: shrub, tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Salvertia convallariodora* A.St.-Hil. (Plate LXXV, 5,6,7,8)

Herbarium number: EAC0050679

Description: P: 30µm; E: 29µm. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: scabrate.

Life form: tree

Substrate: terrestrial

Vegetation type: Cerrado (lato sensu).

Species: *Vochysia* sp. Aubl. (Plate LXXV, 9,10,11,12)

Herbarium number: EAC0028317

Description: P: 28 μ m; E: 31 μ m. Monad, isopolar, medium-sized, tricolporate, triangular (convex), subprolate, exine ornamentation: granulate (Lorente *et al.*, 2017).

Life form: shrub, subshrub, tree

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu), Cerrado (lato sensu), grassland, riverine forest, valley-side marshes.

Order: ZYGOPHYLLALES Link

Family: ZYGOPHYLLACEAE R.Br.

Species: *Kallstroemia tribuloides* (Mart.) Steud. (Plate LXXV, 13,14)

Herbarium number: EAC0011939

Description: D: 53 μ m. Monad, apolar, large-sized, pantoporate, circular, exine ornamentation: reticulate.

Life form: shrub

Substrate: terrestrial

Vegetation type: Caatinga (stricto sensu).

Data Availability

The ecological data presented in this article can be found in the Re flora database (<https://reflora.jbrj.gov.br/reflora/herbarioVirtual/>) which represents a virtual herbarium.

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Appendix A. Supplementary data

Supplementary data to this article can be found in the attachment.

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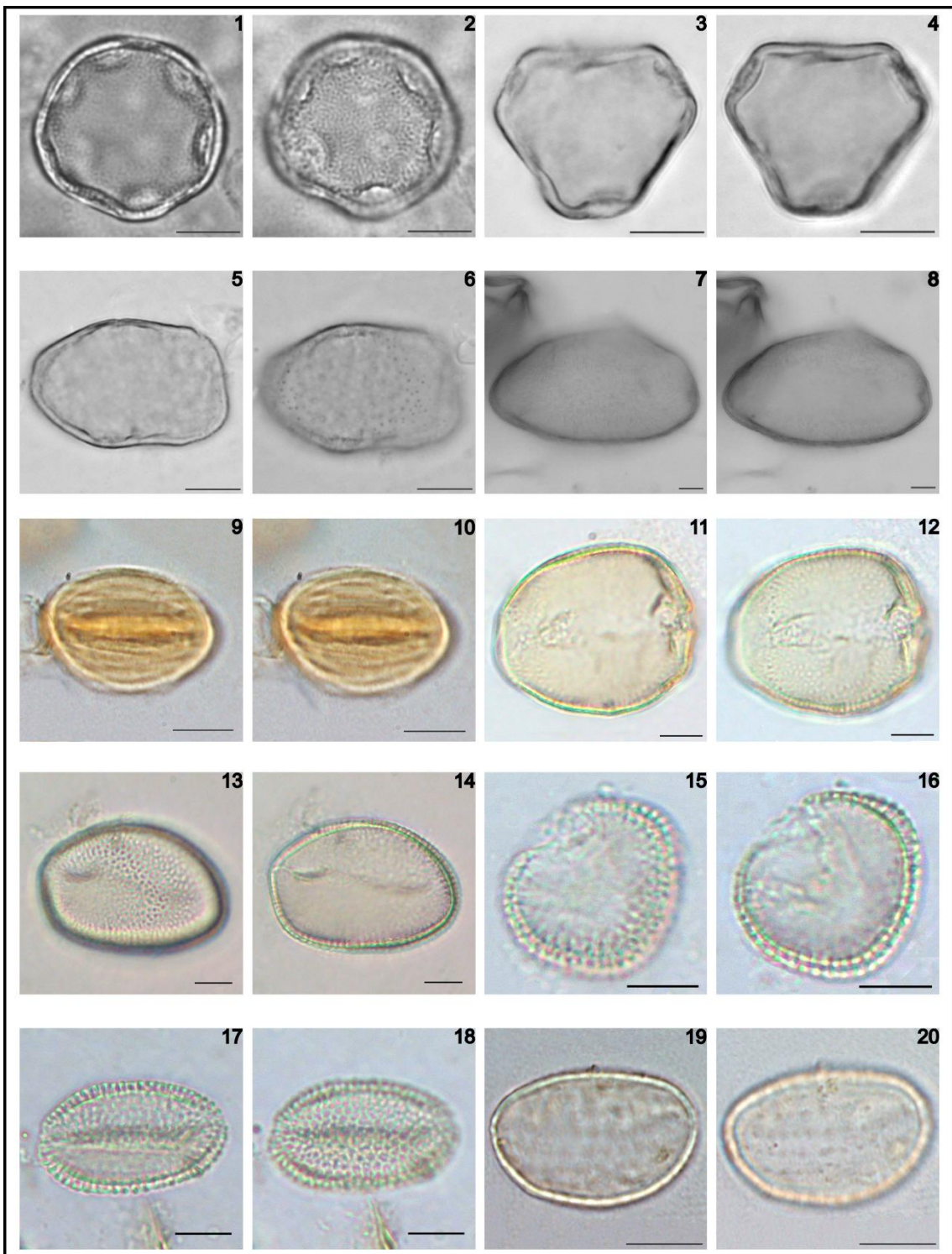


Plate I. Monocots. Alismataceae: *Echinodorus palaefolius* (1,2), *Limnocharis laforesti* (3,4,5,6); Alstroemeriaceae: *Alstroemeria longistaminea* (7,8); Araceae: *Spathiphyllum gardneri* (9,10); Bromeliaceae: *Bromelia laciniosa* (11,12), *Neoglaziovia variegata* (13,14), *Tillandsia loliacea* (15,16,17,18); Commelinaceae: *Commelina benghalensis* (19,20). Scale bars = 10 μ m.

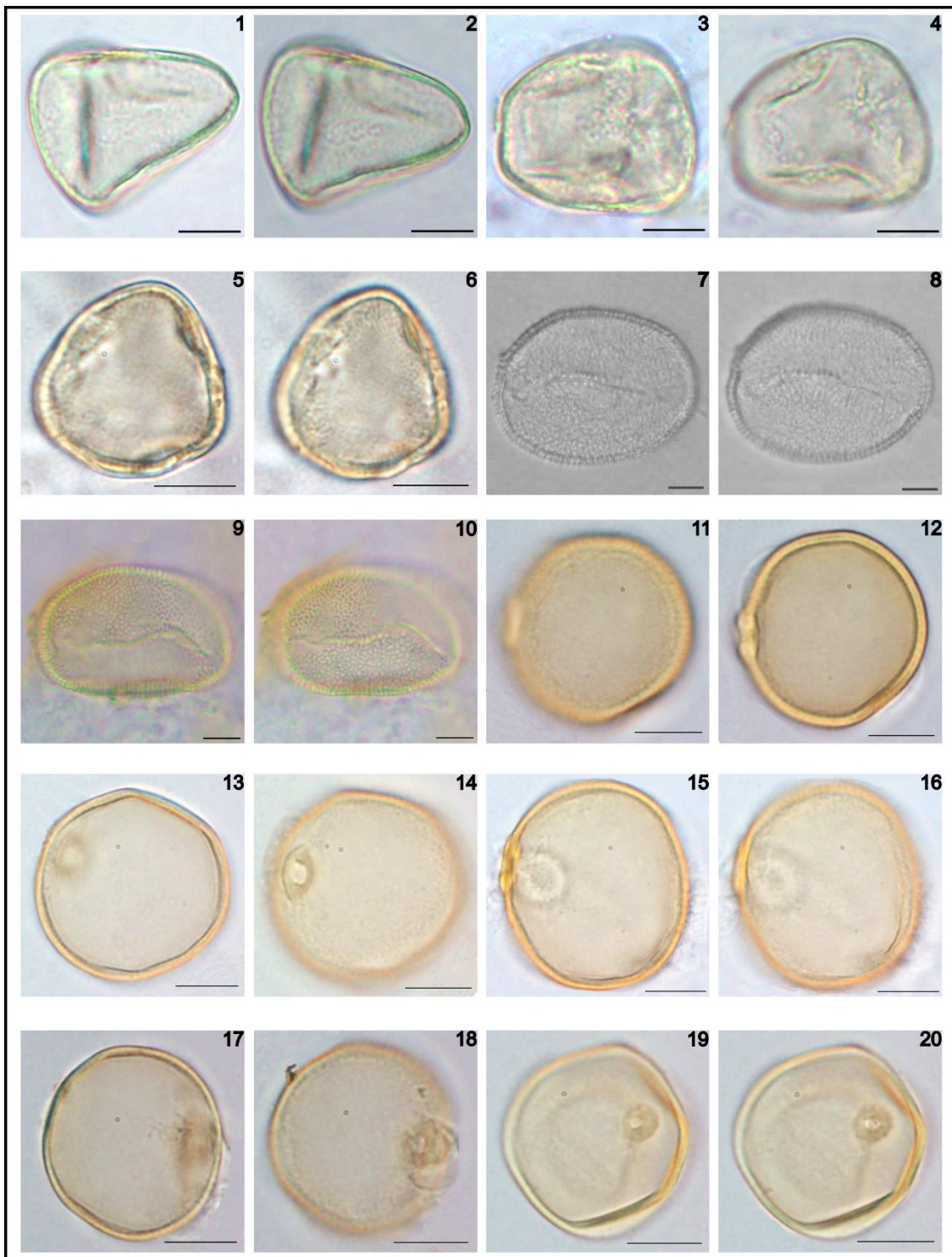


Plate II. Cyperaceae: *Cyperus articulatus* (1,2,3,4), *Cyperus metzii* (5,6); Iridaceae: *Cipura paludosa* (7,8), *Nemastylis* sp. (9,10); Poaceae: *Andropogon fastigiatus* (11,12), *Aristida setifolia* (13,14), *Dactyloctenium aegyptium* (15,16), *Eragrostis maypurensis* (17,18), *Lasiacis* sp. (19,20). Scale bars = 10 μ m.

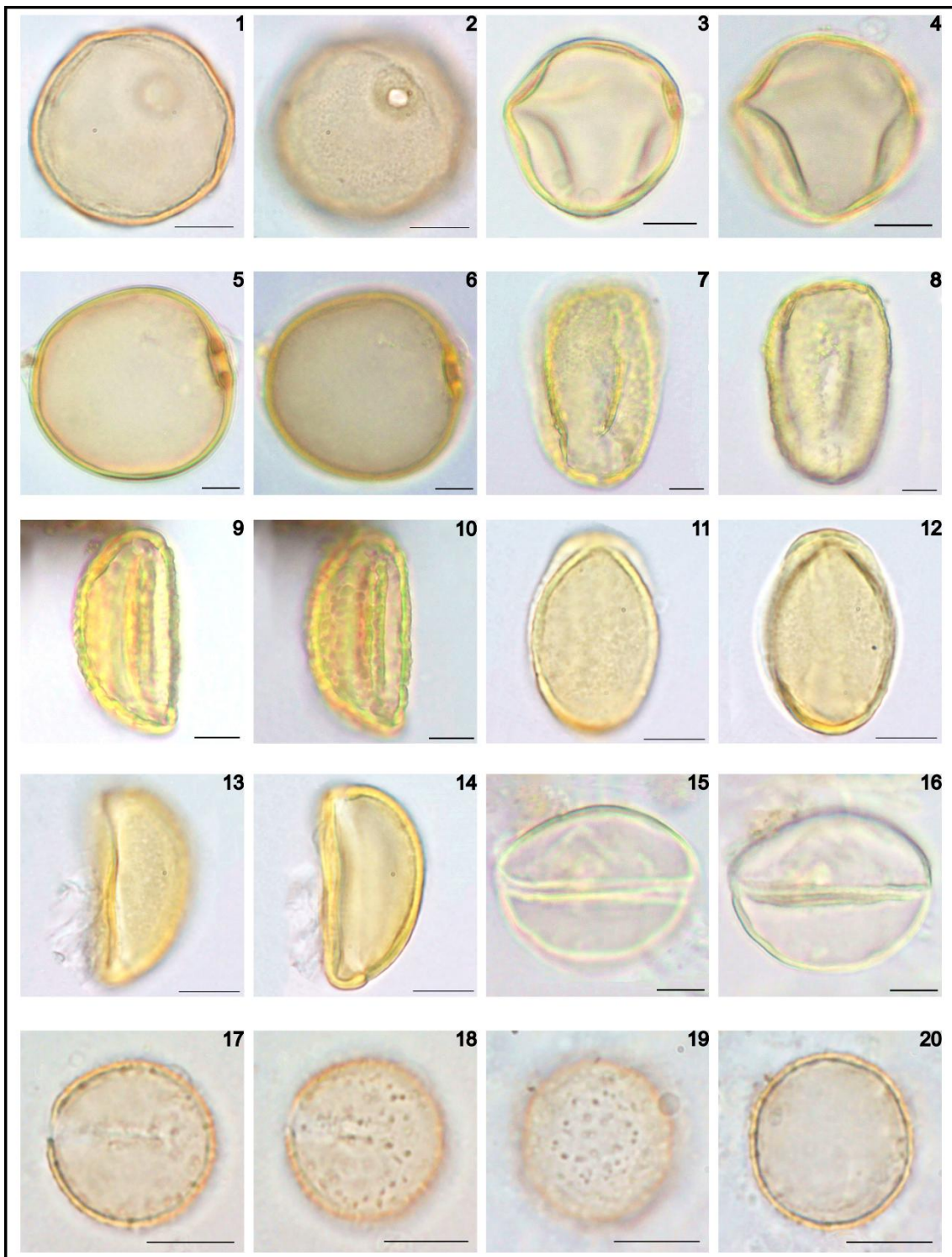


Plate III. Poaceae: *Melinis repens* (1,2), *Setaria adhaerens* (3,4), *Trachypogon spicatus* (5,6); Pontederiaceae: *Heteranthera rotundifolia* (7,8,9,10), *Pontederia subovata* (11,12,13,14); Rapateaceae: *Rapatea* sp. (15,16); Smilacaceae: *Smilax* sp. (17,18,19,20). Scale bars = 10 μ m.

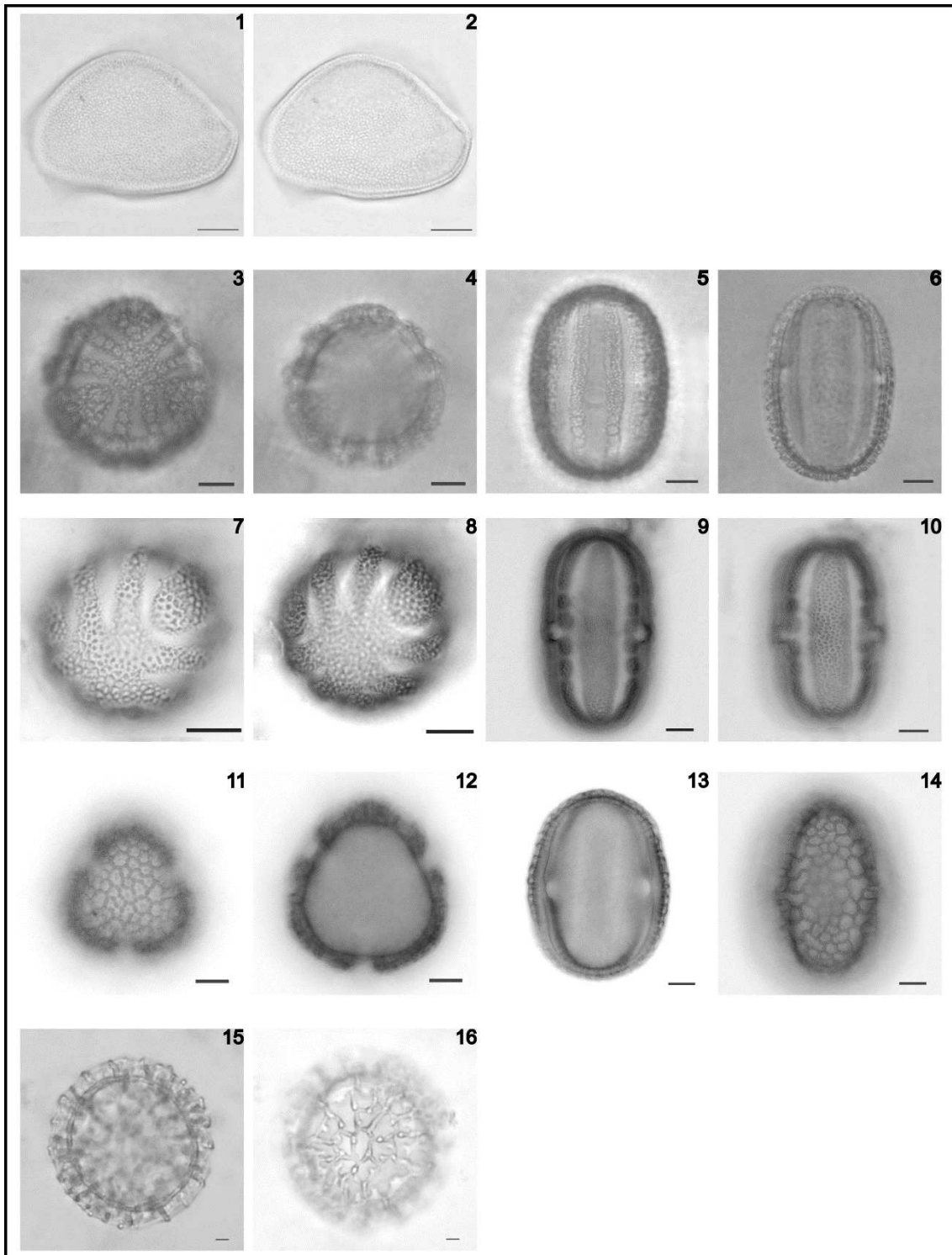


Plate IV. Xyridaceae: *Xyris macrocephala* (1,2). Eudicots. Acanthaceae: *Dicliptera ciliaris* (3,4,5,6), *Justicia triloba* (7,8,9,10), *Lepidagathis montana* (11,12,13,14), *Ruellia asperula* (15,16). Scale bars = 10 μ m.

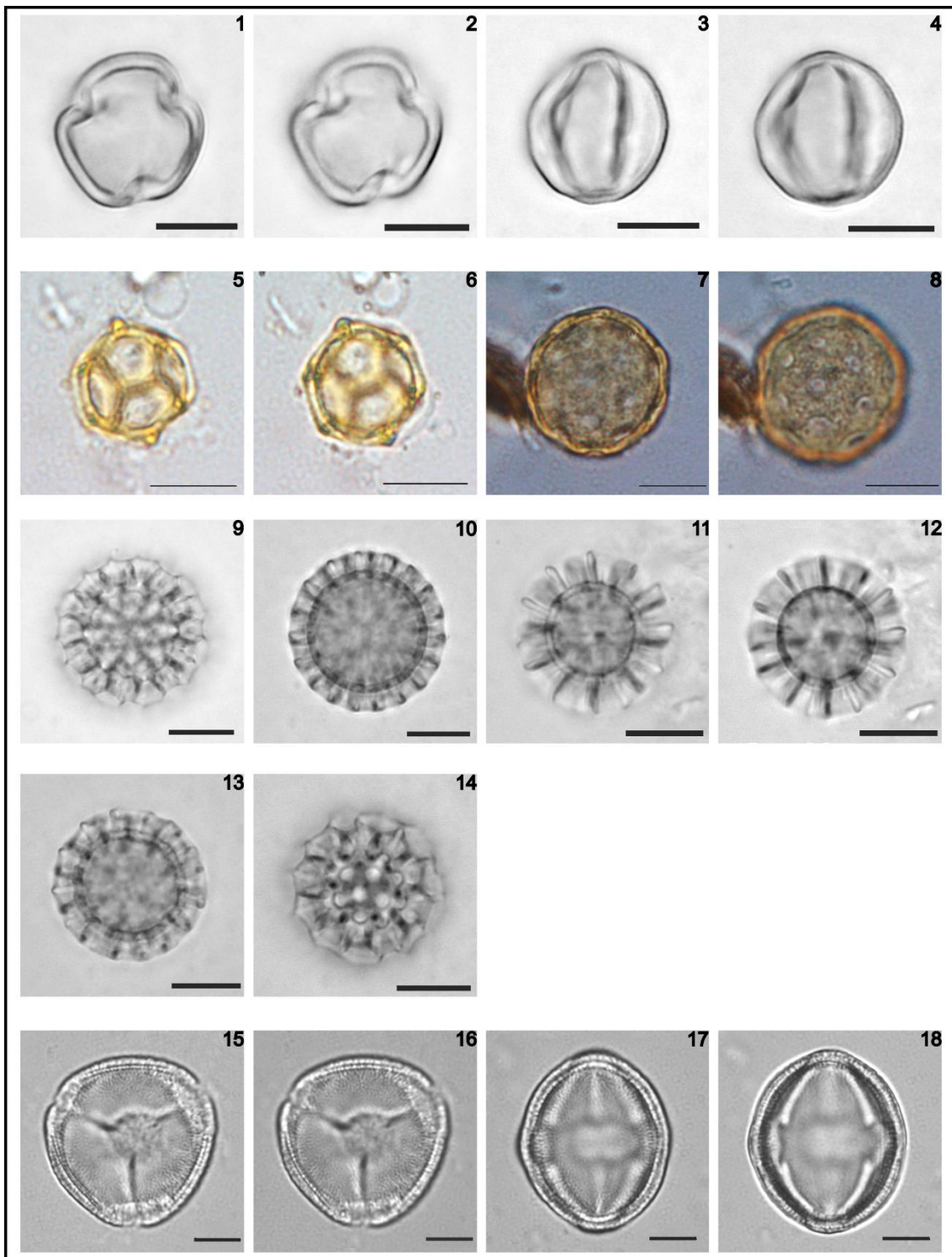


Plate V. Achariaceae: *Lindackeria ovata* (1,2,3,4); Amaranthaceae: *Alternanthera brasiliana* (5,6), *Amaranthus viridis* (7,8), *Froelichia humboldtiana* (9,10), *Gomphrena leucocephala* (11,12), *Xerosiphon angustiflorus* (13,14); Anacardiaceae: *Anacardium occidentale* (15,16,17,18). Scale bars = 10 μ m.

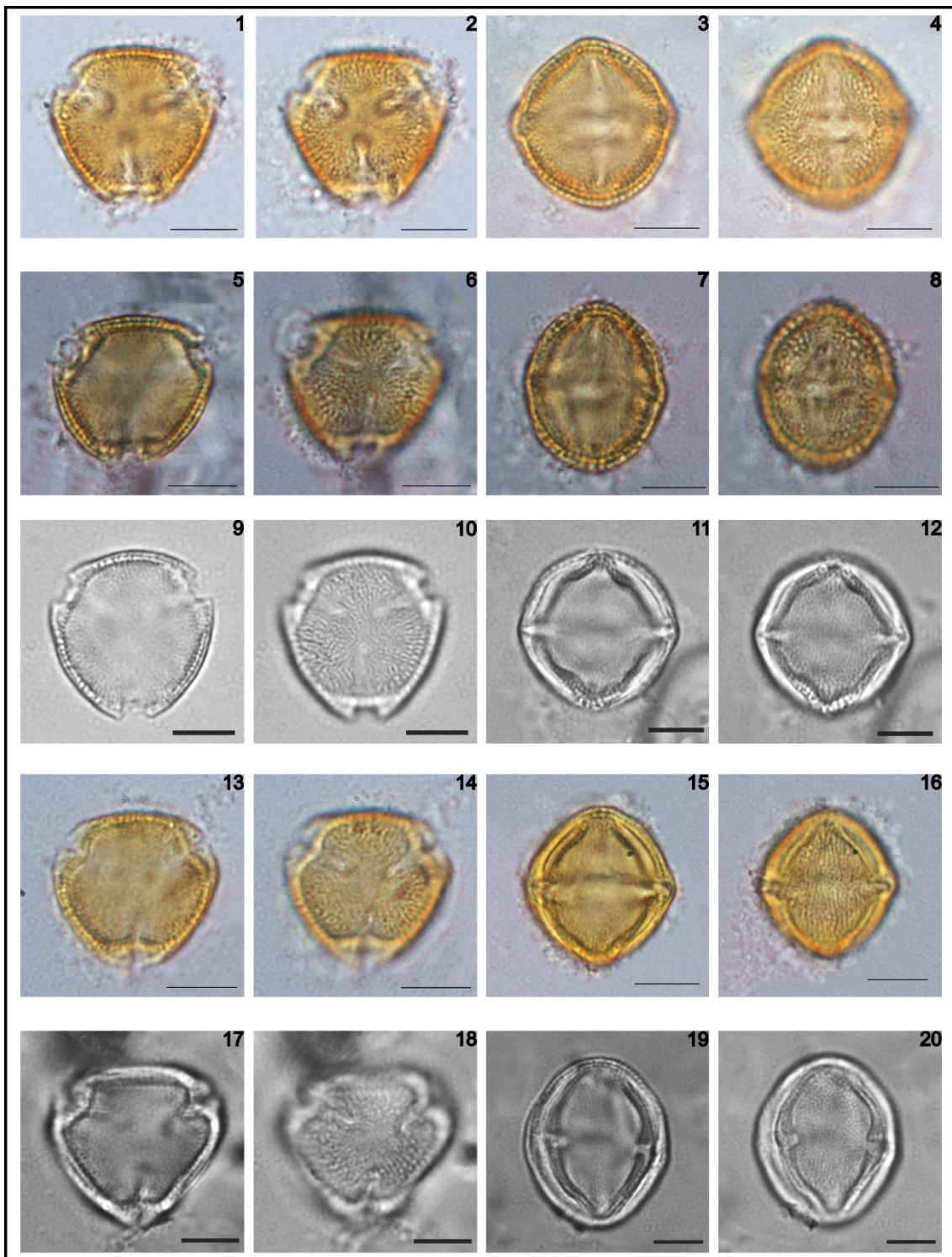


Plate VI. Anacardiaceae: *Apterokarpos gardneri* (1,2,3,4), *Astronium fraxinifolium* (5,6,7,8), *Astronium urundeuva* (9,10,11,12), *Schinus* sp. (13,14,15,16), *Spondias tuberosa* (17,18,19,20). Scale bars = 10 μ m.

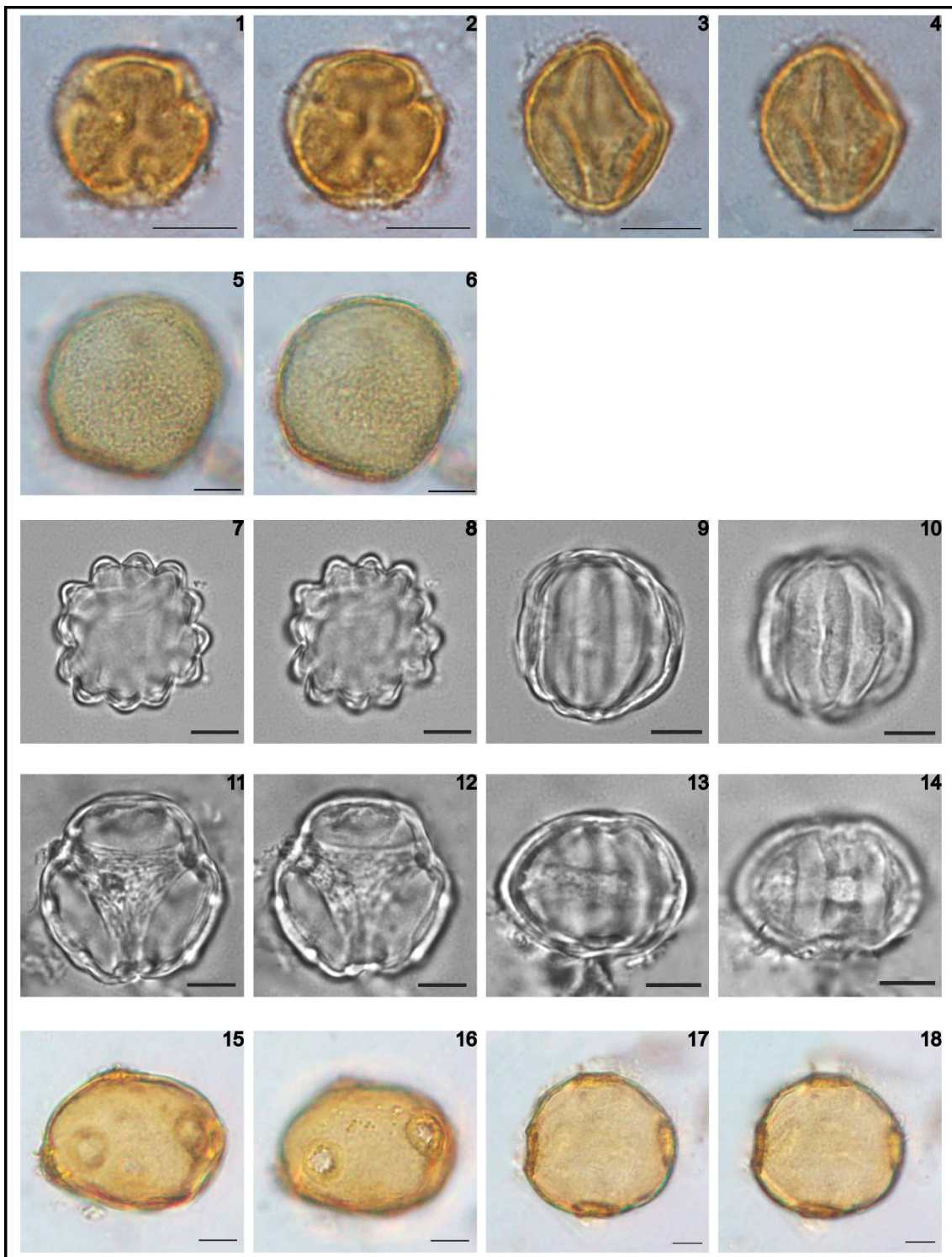


Plate VII. Anacardiaceae: *Tapirira guianensis* (1,2,3,4); Annonaceae: *Annona leptopetala* (5,6); Apocynaceae: *Aspidosperma pyriforme* (7,8,9,10), *Himatanthus drasticus* (11,12,13,14), *Mandevilla tenuifolia* (15,16,17,18). Scale bars = 10 μ m.

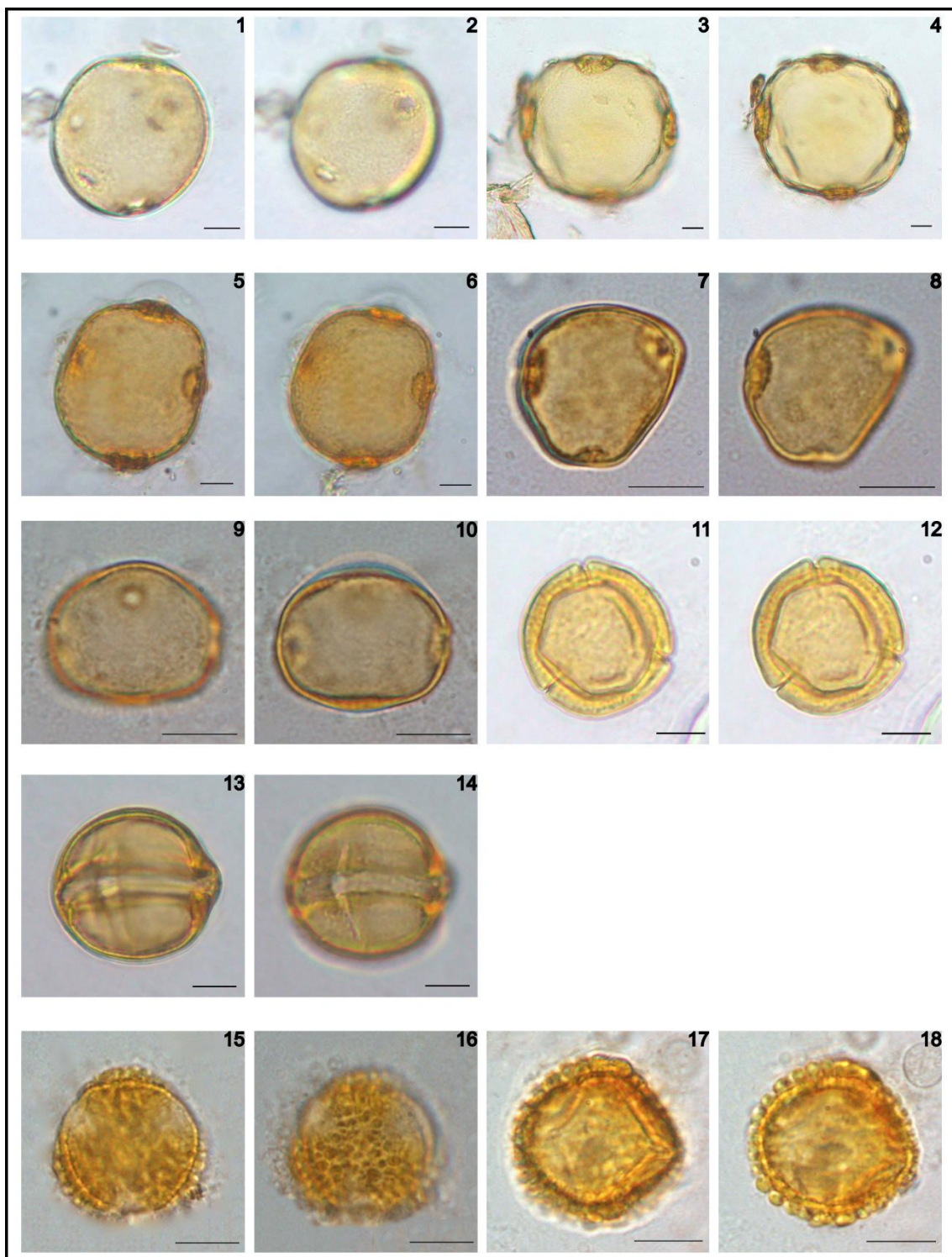


Plate VIII. Apocynaceae: *Odontadenia hypoglauca* (1,2), *Rhabdadenia biflora* (3,4), *Rhodocalyx rotundifolius* (5,6), *Secondatia floribunda* (7,8,9,10), *Tabernaemontana catharinensis* (11,12,13,14); Aquifoliaceae: *Ilex* sp. (15,16,17,18). Scale bars = 10 μ m.

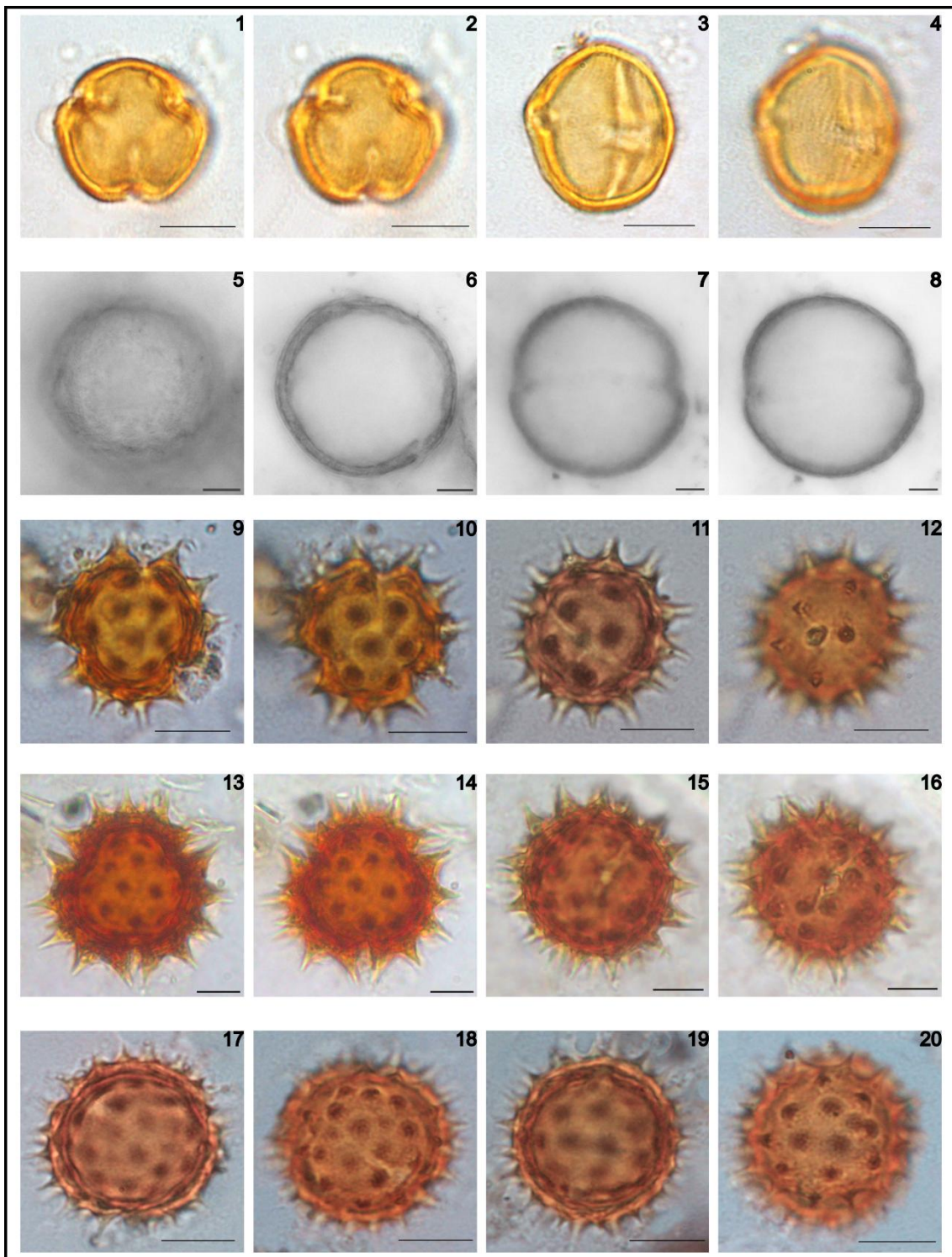


Plate IX. Araliaceae: *Didymopanax* sp. (1,2,3,4); Aristolochiaceae: *Aristolochia gardneri* (5,6,7,8); Asteraceae: *Acanthospermum australe* (9,10,11,12), *Aspilia leucoglossa* (13,14,15,16), *Blainvillea acmella* (17,18,19,20). Scale bars = 10 μ m.

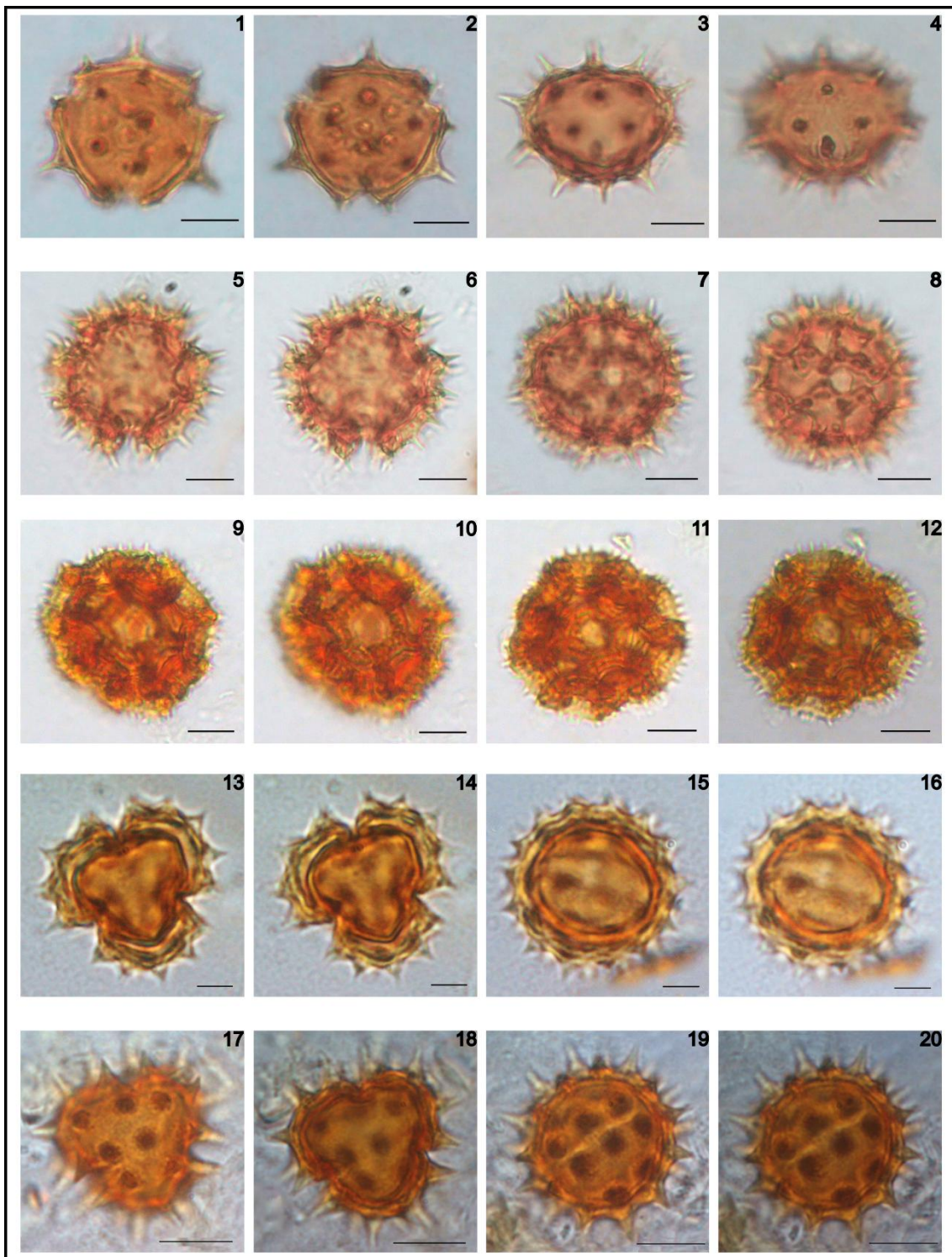


Plate X. Asteraceae: *Calea microphylla* (1,2,3,4), *Centratherum punctatum* (5,6,7,8), *Chresta martii* (9,10,11,12), *Chromolaena myriocephala* (13,14,15,16), *Clibadium armanii* (17,18,19,20). Scale bars = 10 μ m.

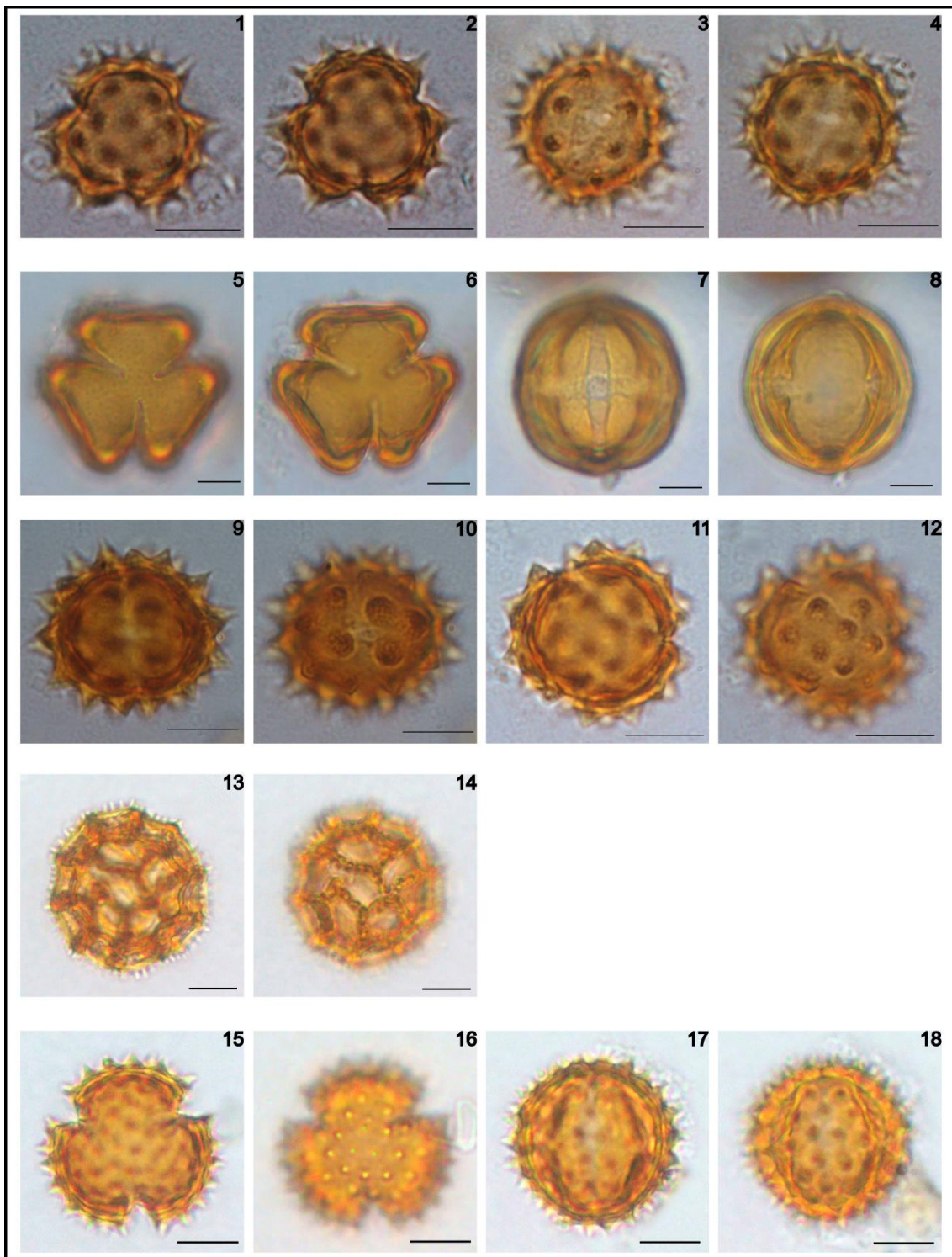


Plate XI. Asteraceae: *Conocliniopsis prasiifolia* (1,2,3,4), *Dasyphyllum sprengelianum* (5,6,7,8), *Eclipta prostrata* (9,10,11,12), *Elephantopus mollis* (13,14), *Emilia* sp. (15,16,17,18). Scale bars = 10 μ m.

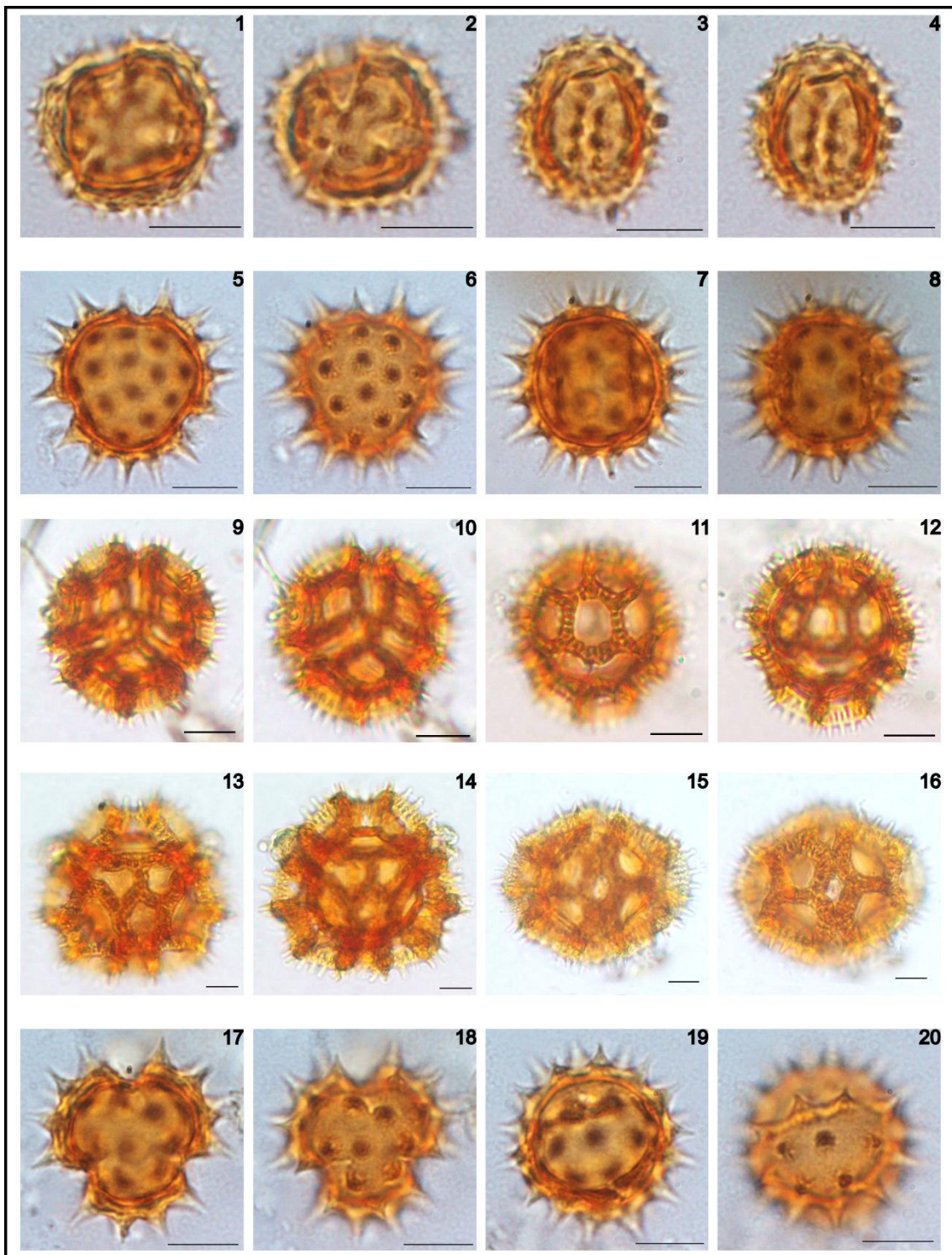


Plate XII. Asteraceae: *Fleischmannia remotifolia* (1,2,3,4), *Lepidaploa arenaria* (5,6,7,8), *Lepidaploa remotiflora* (9,10,11,12), *Lessingianthus coriaceus* (13,14,15,16), *Mikania officinalis* (17,18,19,20). Scale bars = 10 μ m.

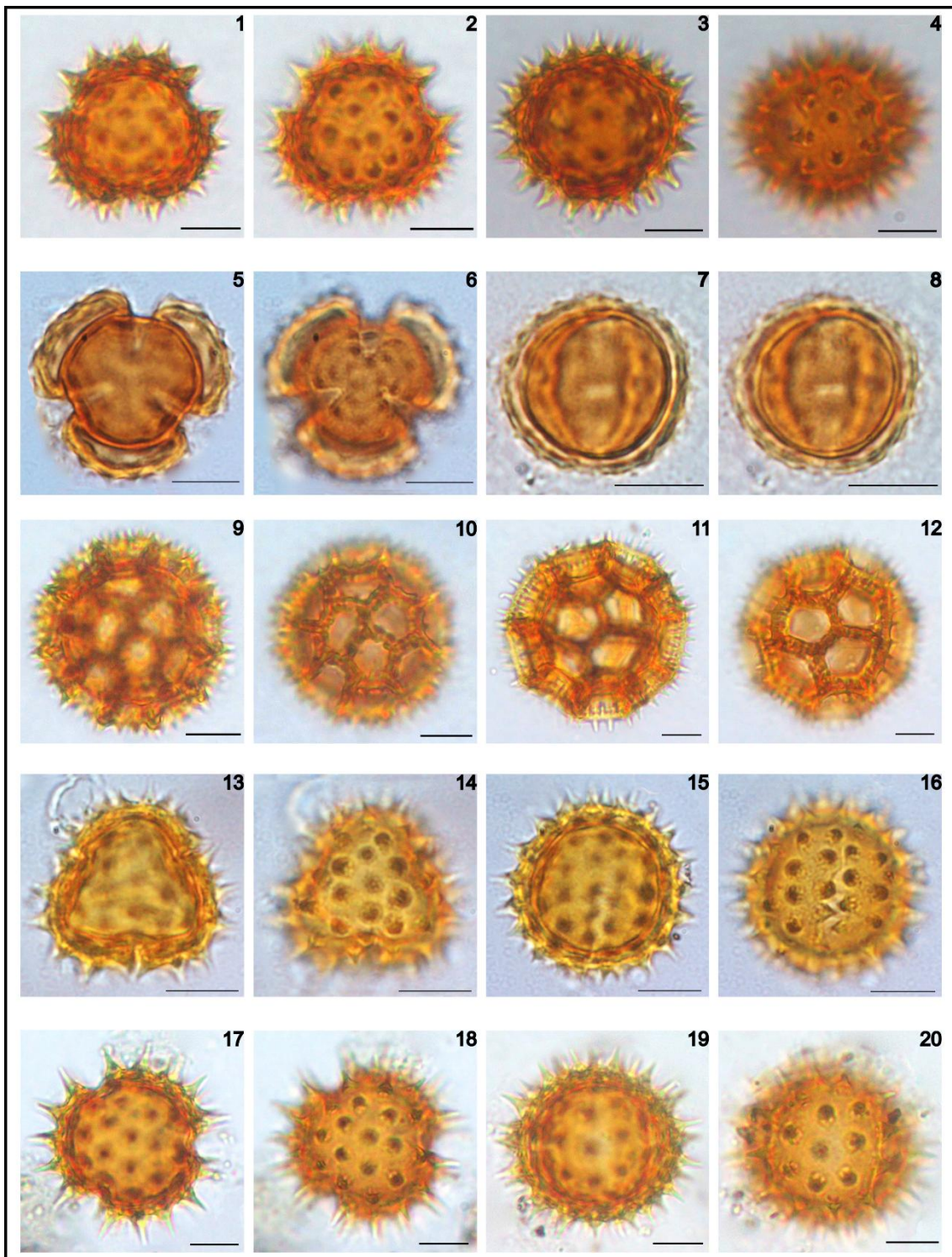


Plate XIII. Asteraceae: *Pectis brevipedunculata* (1,2,3,4), *Pseudobrickellia brasiliensis* (5,6,7,8), *Rolandra fruticosa* (9,10), *Stilpnopappus* sp. (11,12), *Synedrella nodiflora* (13,14,15,16), *Tagetes minuta* (17,18,19,20). Scale bars = 10 μ m.

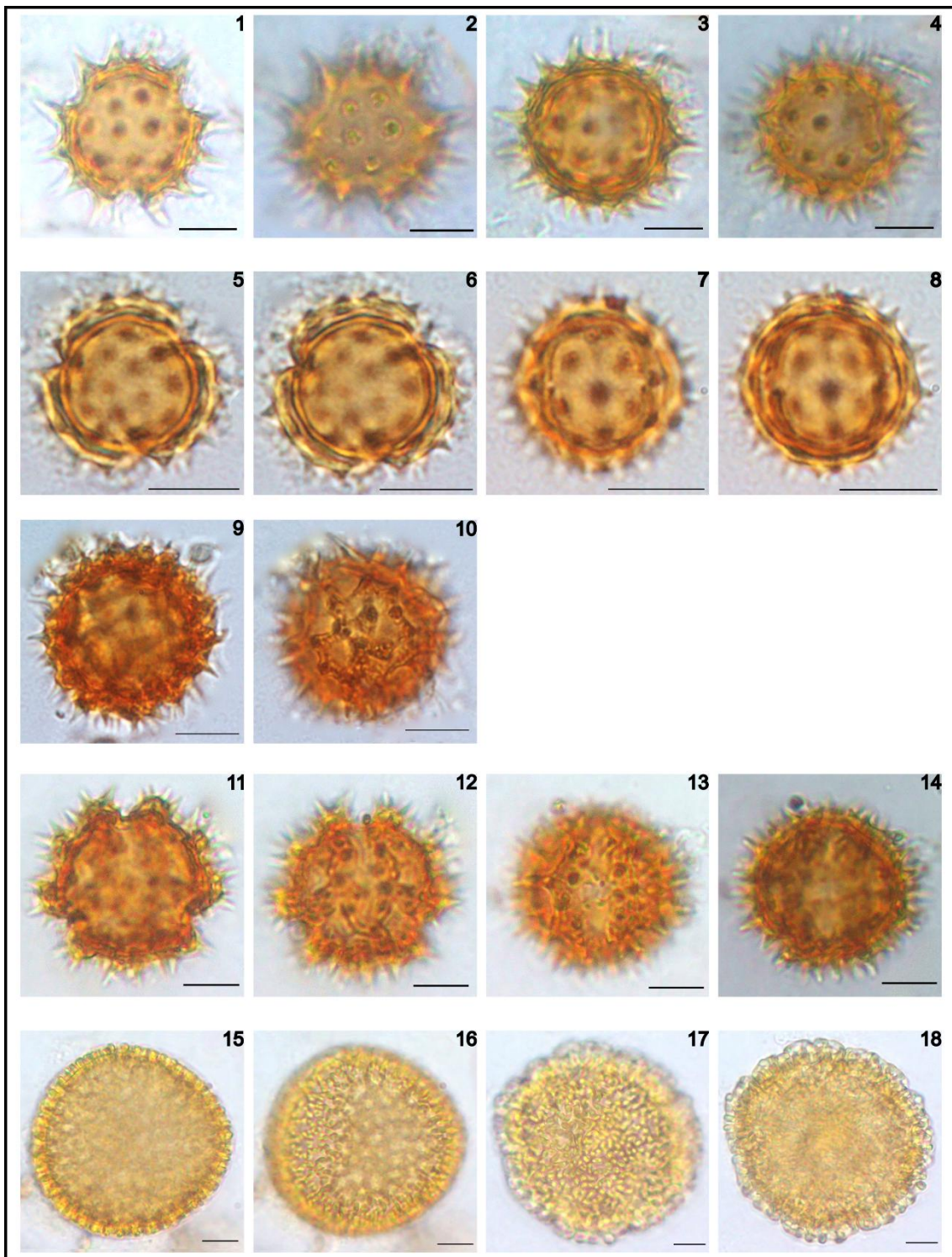


Plate XIV. Asteraceae: *Tilesia baccata* (1,2,3,4), *Trichogonia campestris* (5,6,7,8), *Trichospira verticillata* (9,10), *Vernonanthura brasiliiana* (11,12,13,14); Bignoniaceae: *Adenocalymma divaricatum* (15,16), *Anemopaegma laeve* (17,18). Scale bars = 10 μ m.

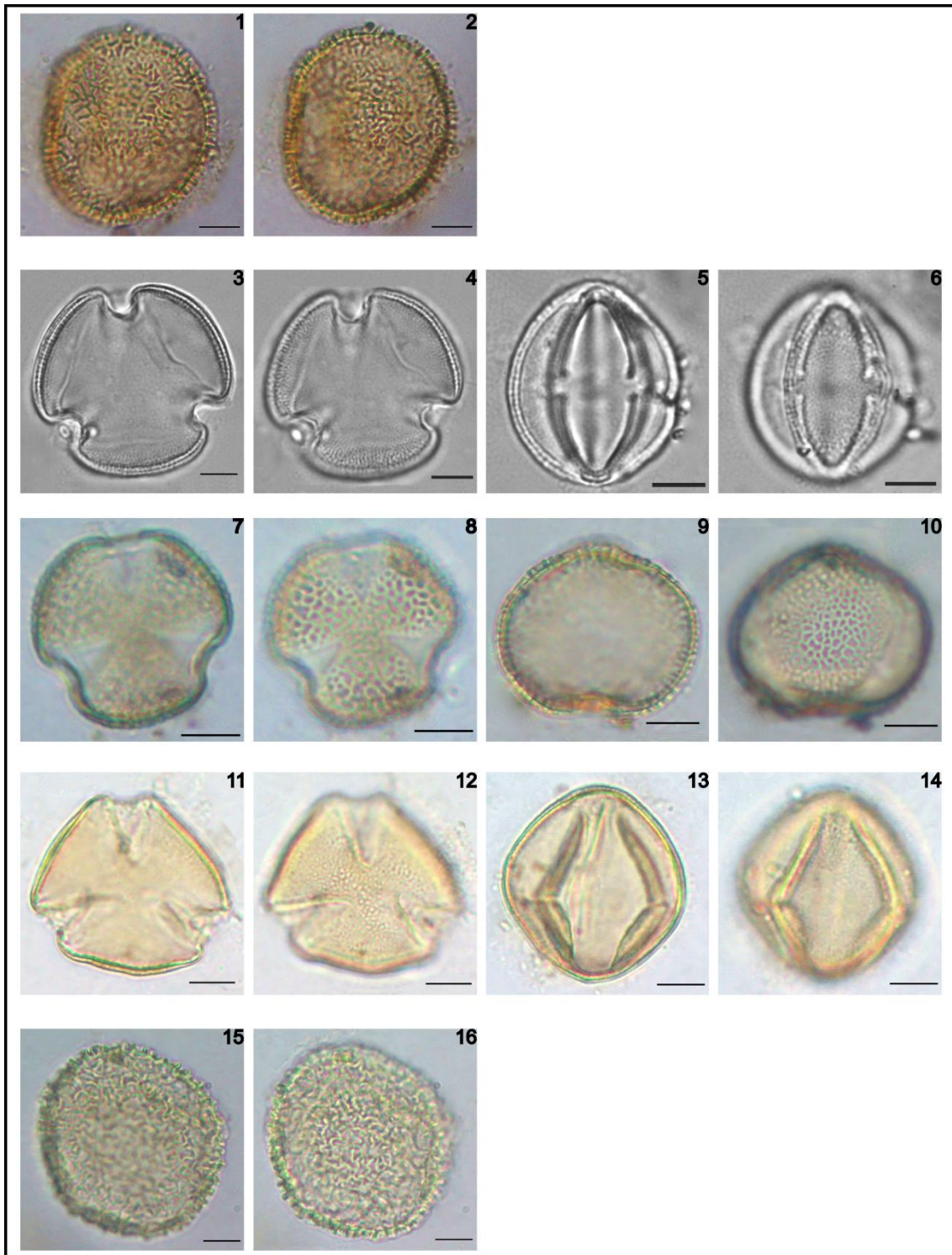


Plate XV. Bignoniaceae: *Bignonia campanulata* (1,2), *Fridericia platyphylla* (3,4,5,6), *Handroanthus impetiginosus* (7,8,9,10), *Lundia helicocalyx* (11,12,13,14); *Mansoa hirsute* (15,16). Scale bars = 10 μ m.

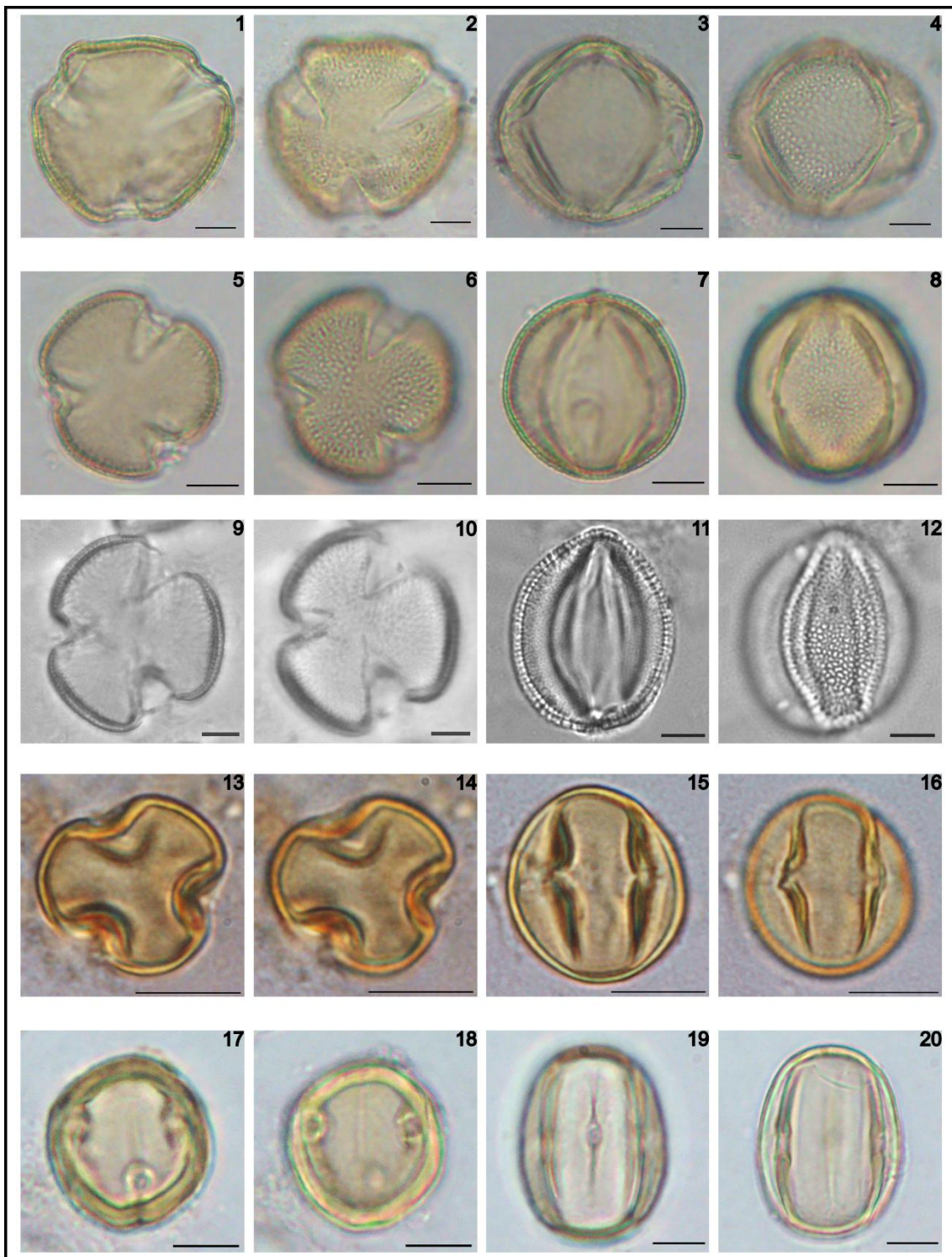


Plate XVI. Bignoniaceae: *Pleonotoma melioides* (1,2,3,4), *Stizophyllum perforatum* (5,6,7,8), *Tabebuia aurea* (9,10,11,12); Bixaceae: *Cochlospermum regium* (13,14,15,16); Boraginaceae: *Euploca lagoensis* (17,18,19,20). Scale bars = 10 μ m.

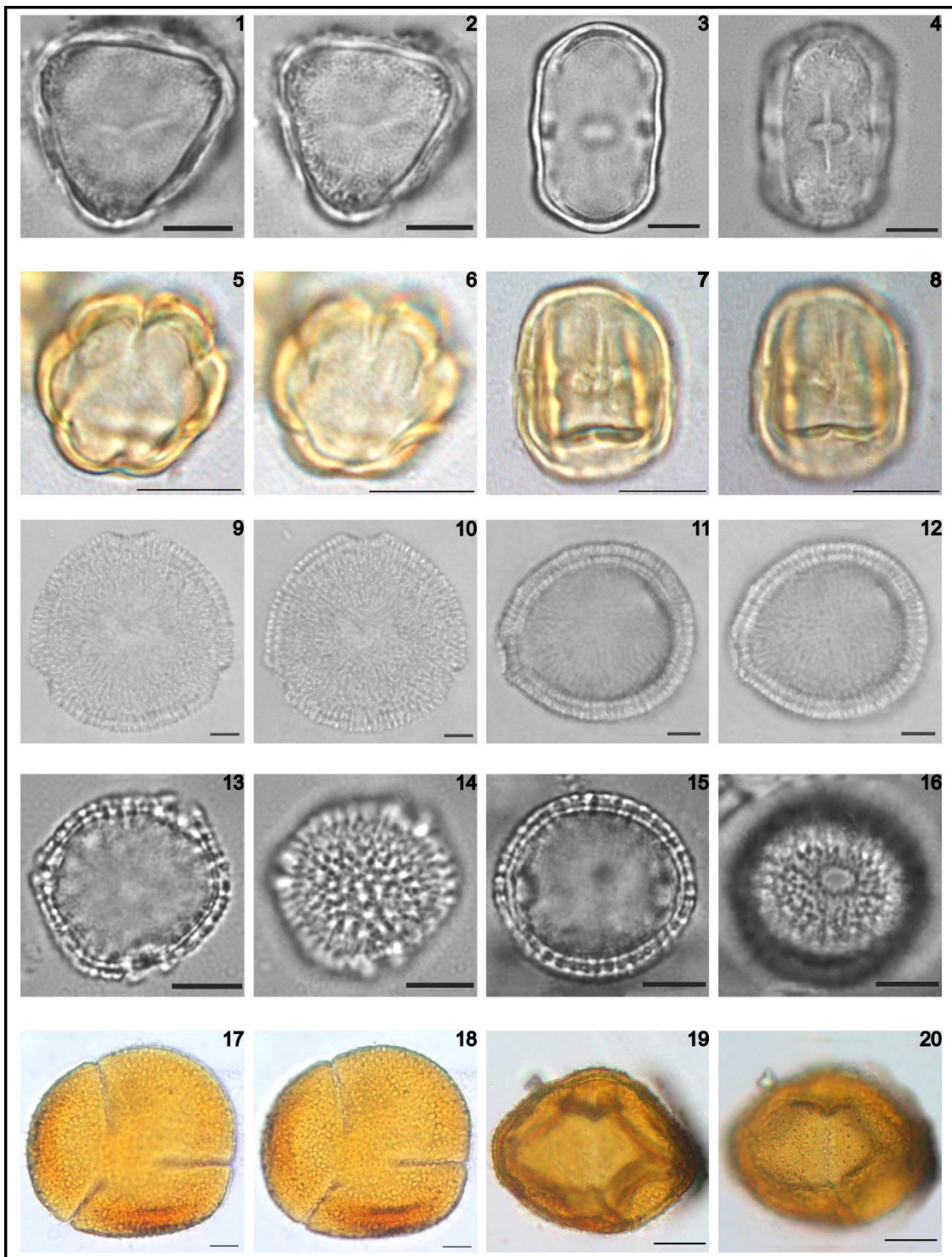


Plate XVII. Boraginaceae: *Heliotropium elongatum* (1,2,3,4), *Myriopus salzmannii* (5,6,7,8), *Varronia leucocephala* (9,10,11,12); Burseraceae: *Commiphora leptophloeos* (13,14,15,16); Cactaceae: *Cereus albicaulis* (17,18,19,20). Scale bars = 10 μ m.

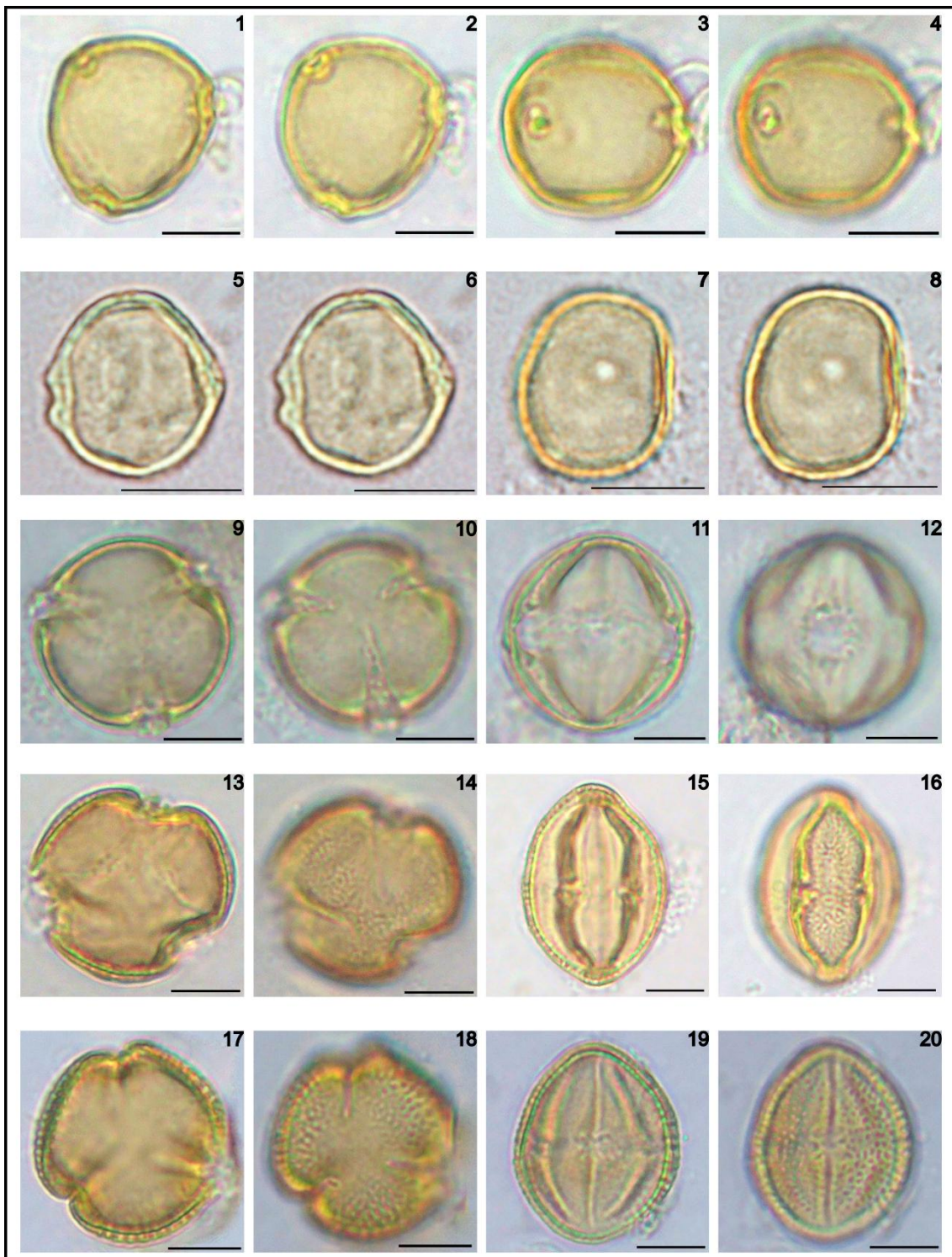


Plate XVIII. Cannabaceae: *Celtis* sp. (1,2,3,4), *Trema micranta* (5,6,7,8); Capparaceae: *Cynophalla hastata* (9,10,11,12), *Mesocapparis lineata* (13,14,15,16), *Neocalyptrocalyx longifolium* (17,18,19,20). Scale bars = 10 μ m.

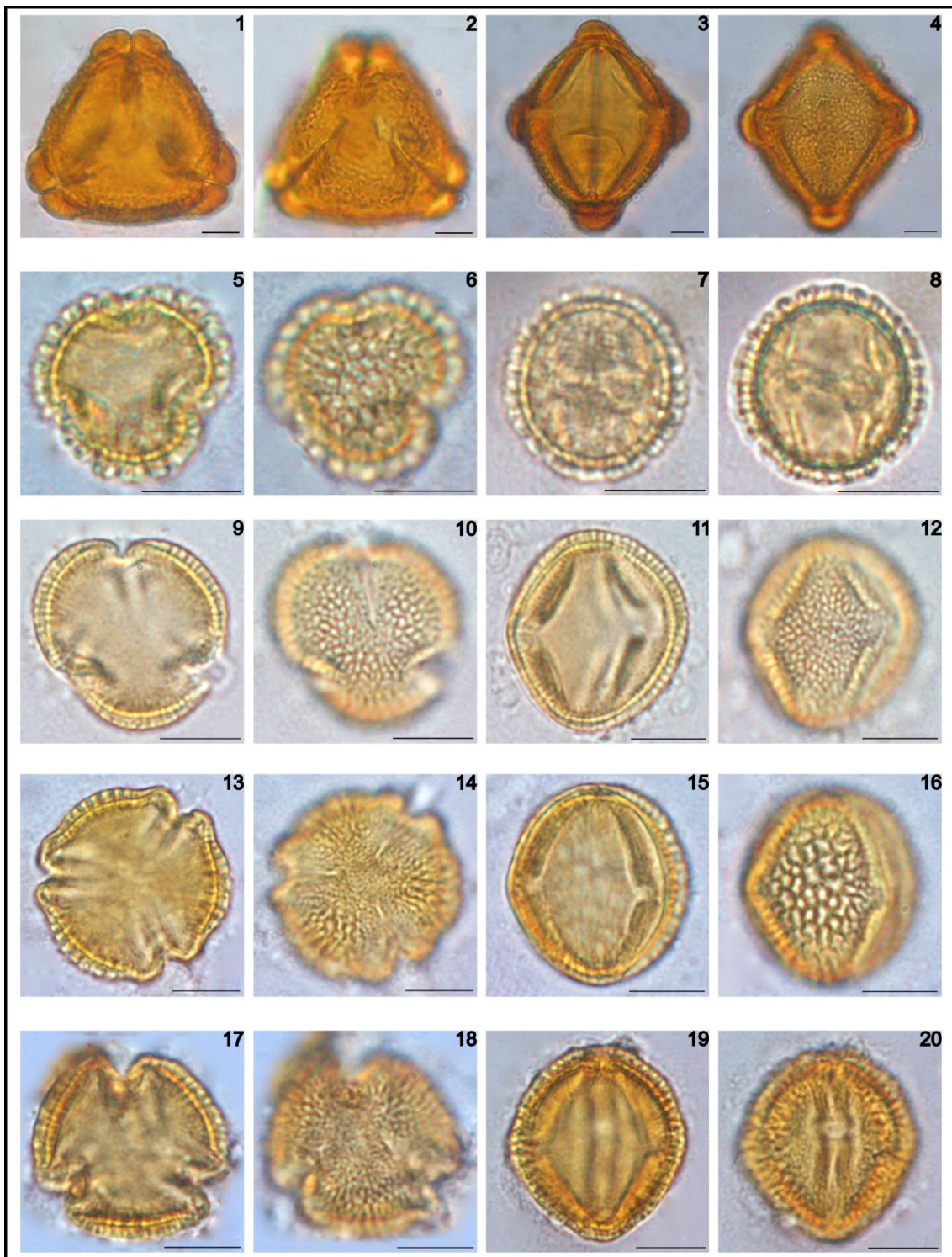


Plate XIX. Caryocaraceae: *Caryocar coriaceum* (1,2,3,4); Celastraceae: *Fraunhoferia multiflora* (5,6,7,8), *Monteverdia erythroxyla* (9,10,11,12), *Prionostemma asperum* (13,14,15,16), *Salacia elliptica* (17,18,19,20). Scale bars = 10 μ m.

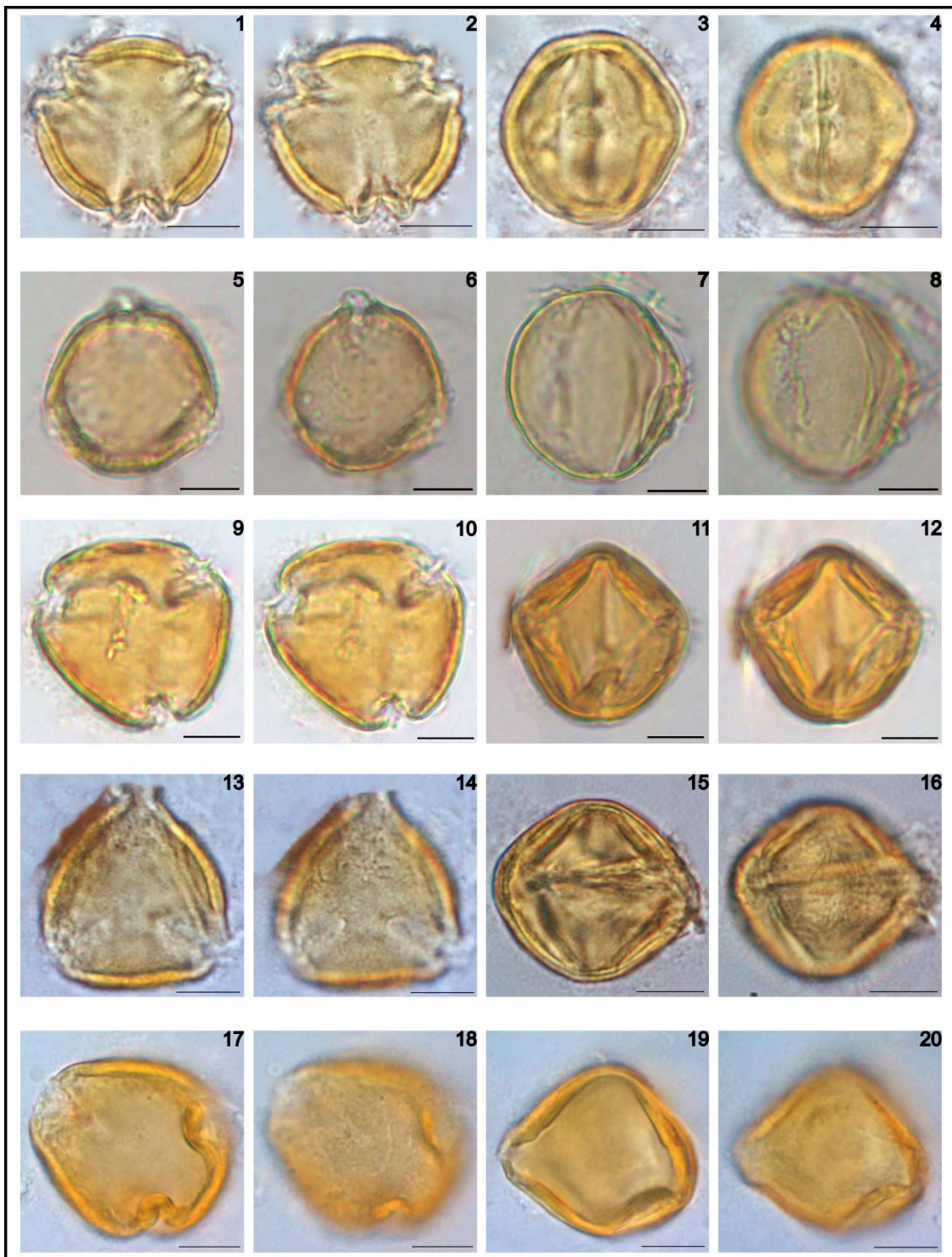


Plate XX. Celastraceae: *Tontelea micrantha* (1,2,3,4); Chrysobalanaceae: *Chrysobalanus icaco* (5,6,7,8), *Couepia grandiflora* (9,10,11,12), *Exellodendron cordatum* (13,14,15,16), *Parinari campestris* (17,18,19,20). Scale bars = 10 μ m.

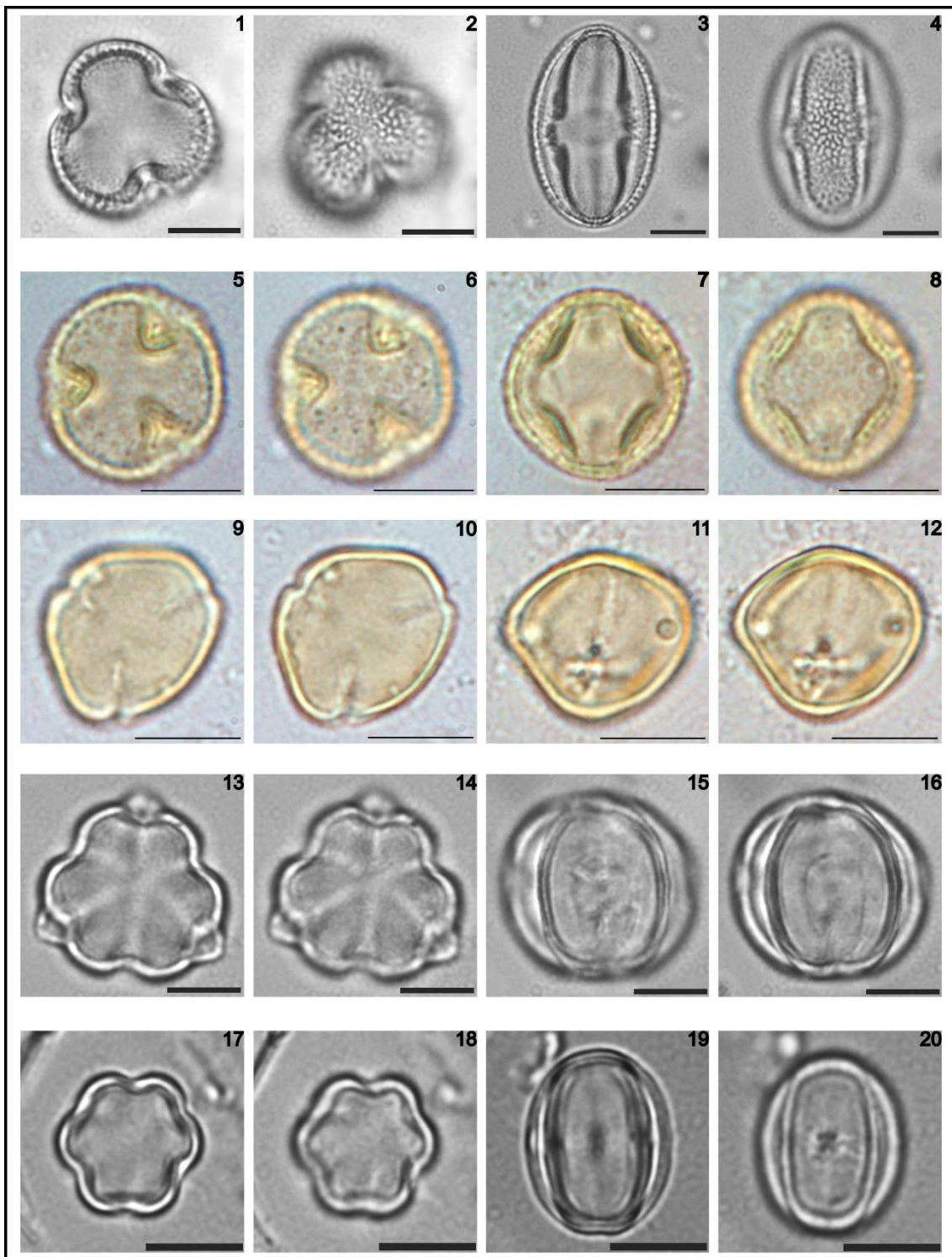


Plate XXI. Cleomaceae: *Physostemon guianense* (1,2,3,4), *Tarenaya microcarpa* (5,6,7,8); Clusiaceae: *Clusia panapanari* (9,10,11,12); Combretaceae: *Combretum fruticosum* (13,14,15,16), *Combretum mellifluum* (17,18,19,20). Scale bars = 10 μ m.

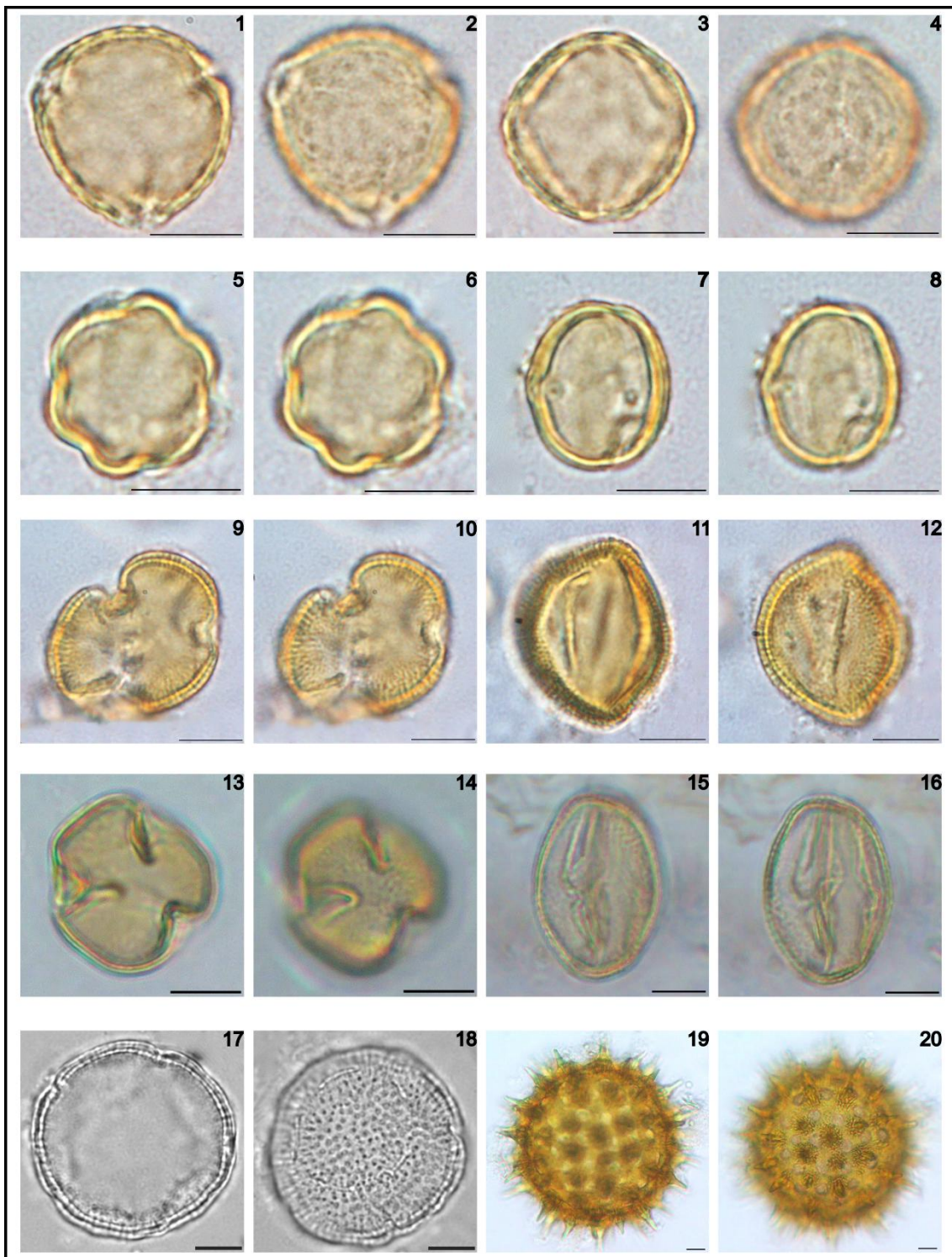


Plate XXII. Combretaceae: *Terminalia corrugata* (1,2,3,4), *Terminalia fagifolia* (5,6,7,8),
 Connaraceae: *Connarus suberosus* (9,10,11,12), *Rourea induta* (13,14,15,16); Convolvulaceae:
Evolvulus anagalloides (17,18), *Ipomoea brasiliana* (19,20). Scale bars = 10 μ m.

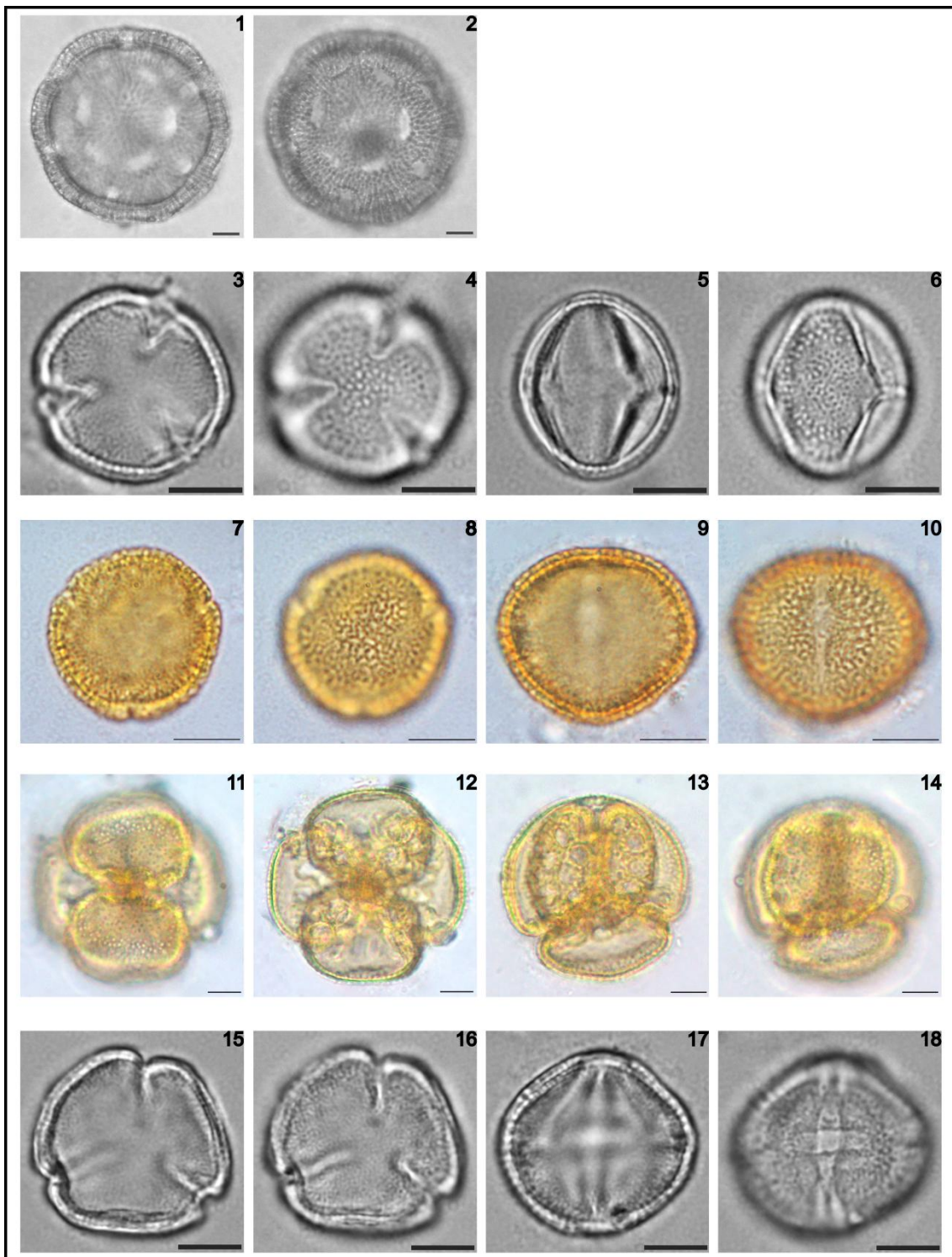


Plate XXIII. Convolvulaceae: *Jacquemontia gracillima* (1,2); Dilleniaceae: *Curatella americana* (3,4,5,6), *Davilla cearenses* (7,8,9,10); Droseraceae: *Drosera sessilifolia* (11,12,13,14); Erythroxylaceae: *Erythroxylum squamatum* (15,16,17,18). Scale bars = 10 μ m.

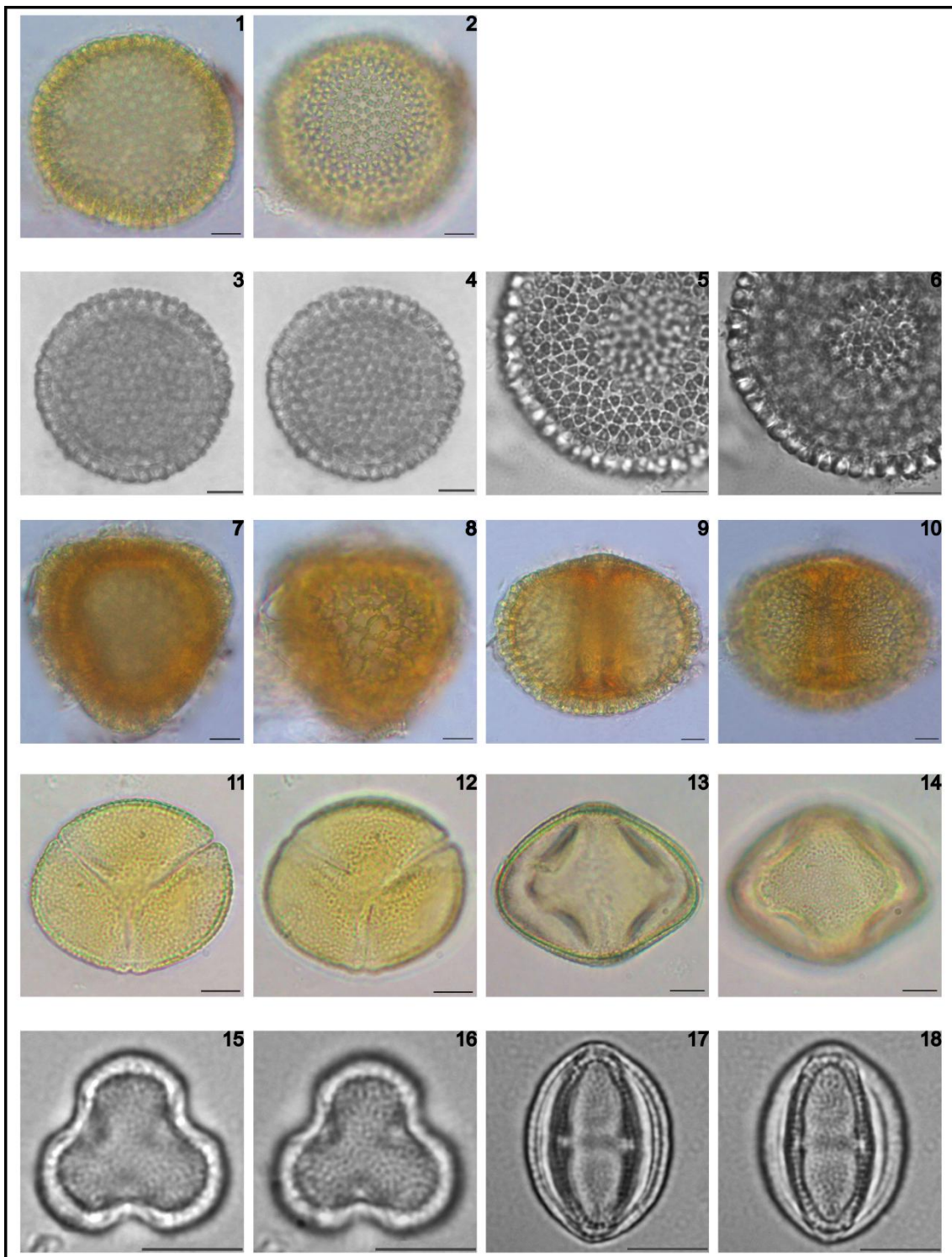


Plate XXIV. Euphorbiaceae: *Cnidoscolus bahianus* (1,2), *Croton pedicellatus* (3,4,5,6), *Dalechampia fernandesii* (7,8,9,10), *Ditaxis desertorum* (11,12,13,14), *Euphorbia hirta* (15,16,17,18). Scale bars = 10 μ m.

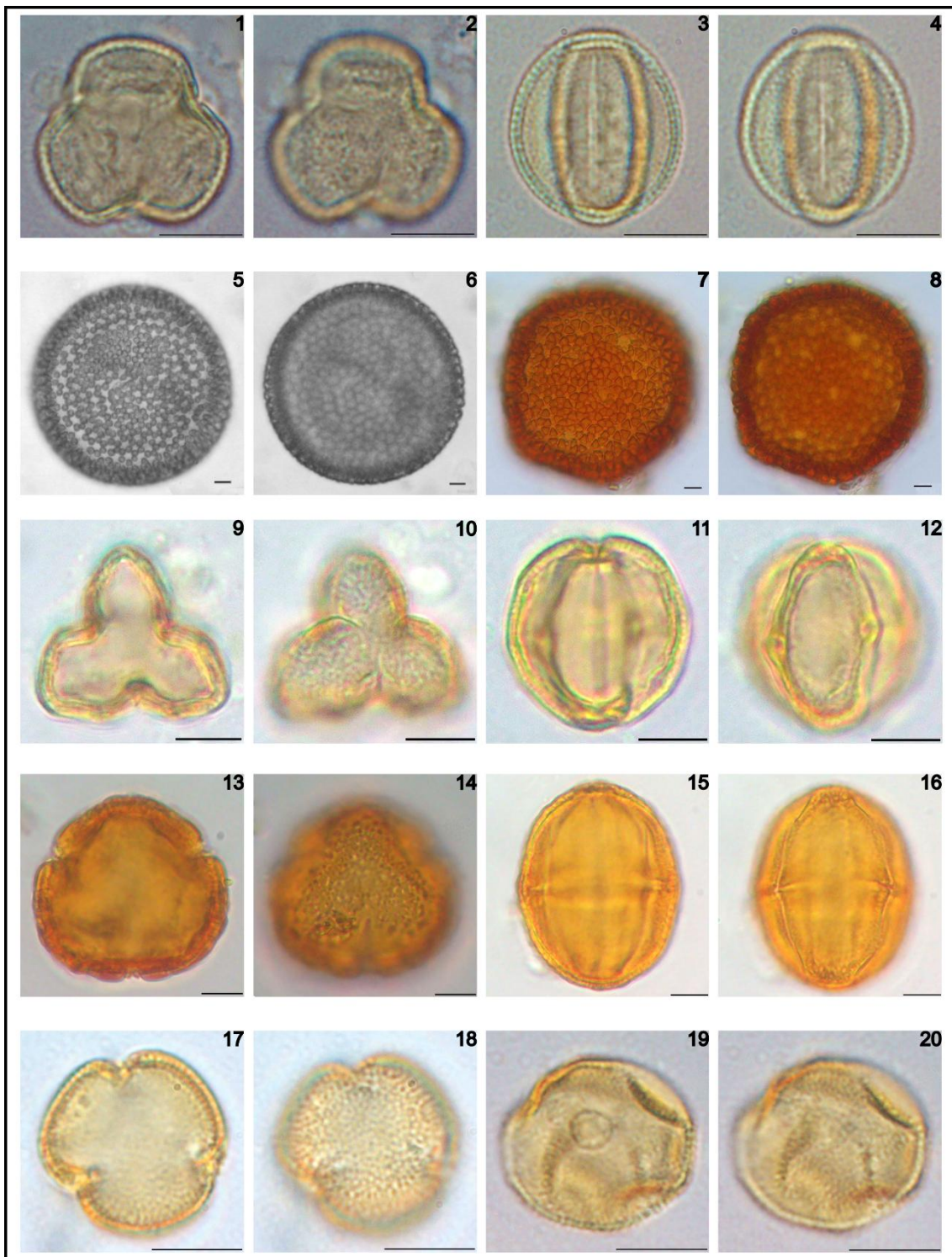


Plate XXV. Euphorbiaceae: *Gymnanthes boticário* (1,2,3,4), *Jatropha mollissima* (5,6), *Manihot caerulescens* (7,8), *Microstachys glandulosa* (9,10,11,12), *Sapium argutum* (13,14,15,16), *Tragia volubilis* (17,18,19,20). Scale bars = 10 μ m.

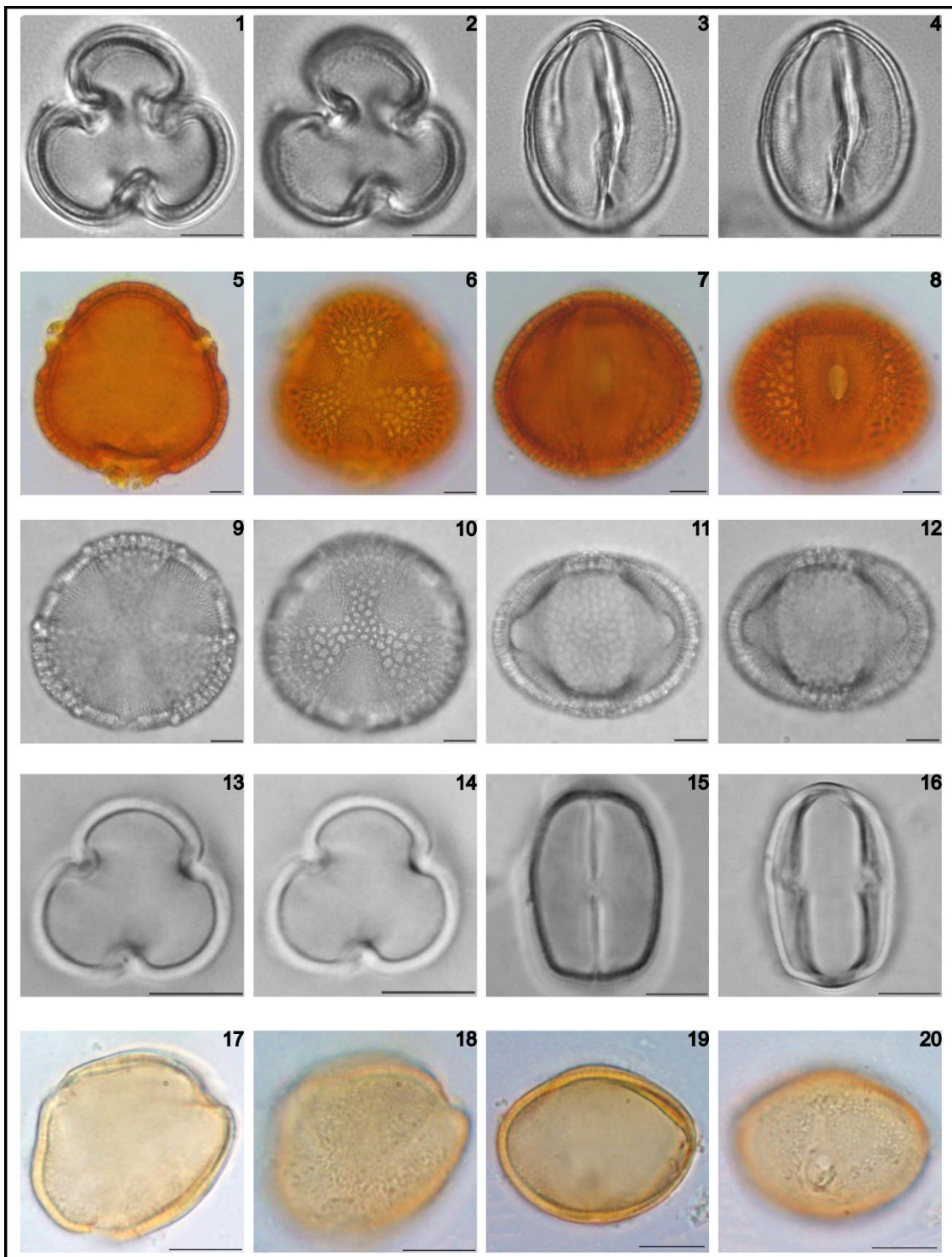


Plate XXVI. Fabaceae – Caesalpinioideae: *Cassia ferruginea* (1,2,3,4), *Cenostigma macrophyllum* (5,6,7,8), *Cenostigma pyramidale* (9,10,11,12), *Chamaecrista duckeana* (13,14,15,16), *Dimorphandra gardneriana* (17,18,19,20). Scale bars = 10 μ m.

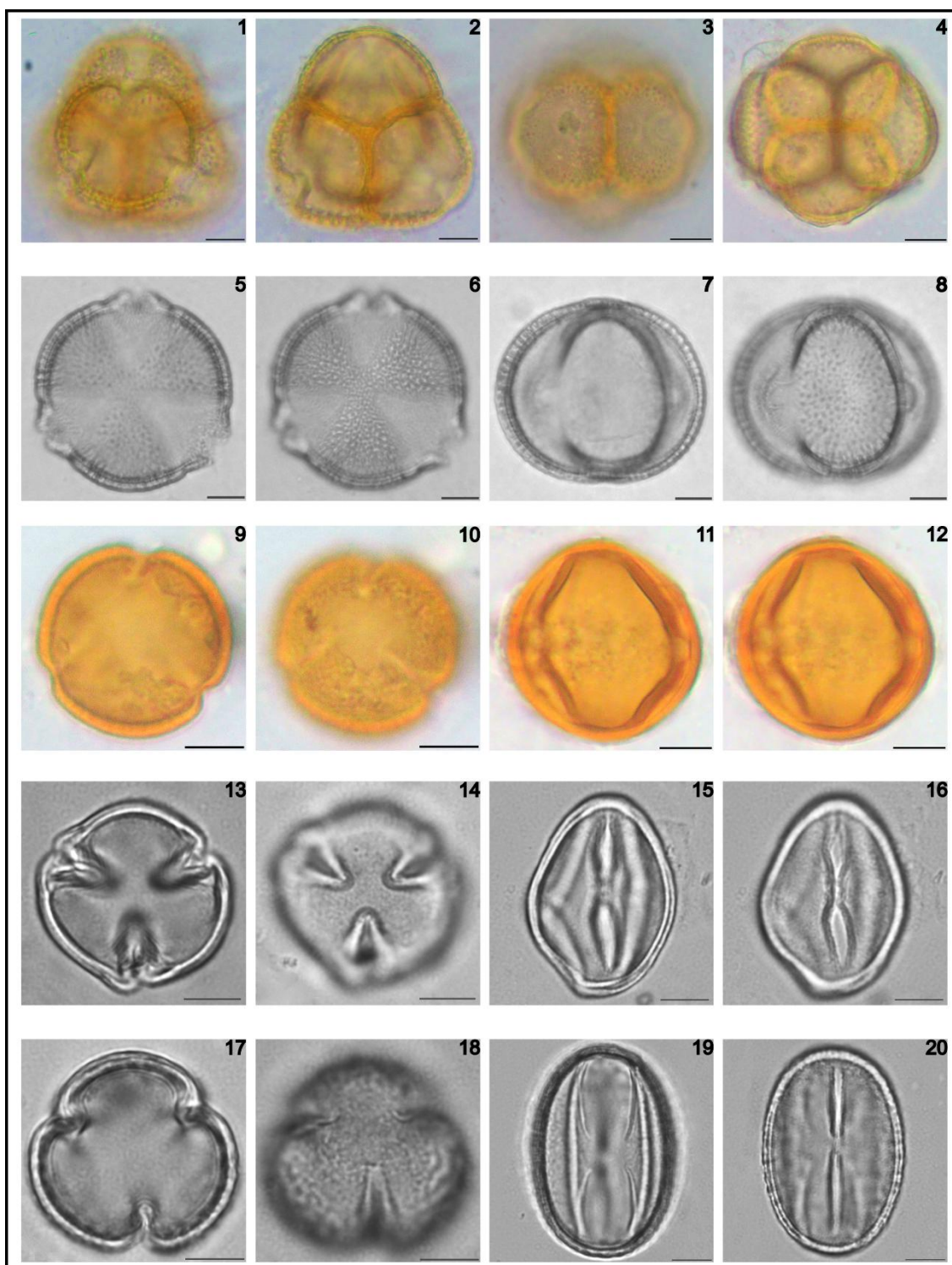


Plate XXVII. Fabaceae – Caesalpinioideae: *Diptychandra aurantiaca* (1,2,3,4), *Libidibia ferrea* (5,6,7,8), *Melanoxylon brauna* (9,10,11,12), *Senna cearensis* (13,14,15,16), *Senna obtusifolia* (17,18,19,20). Scale bars = 10 μ m.

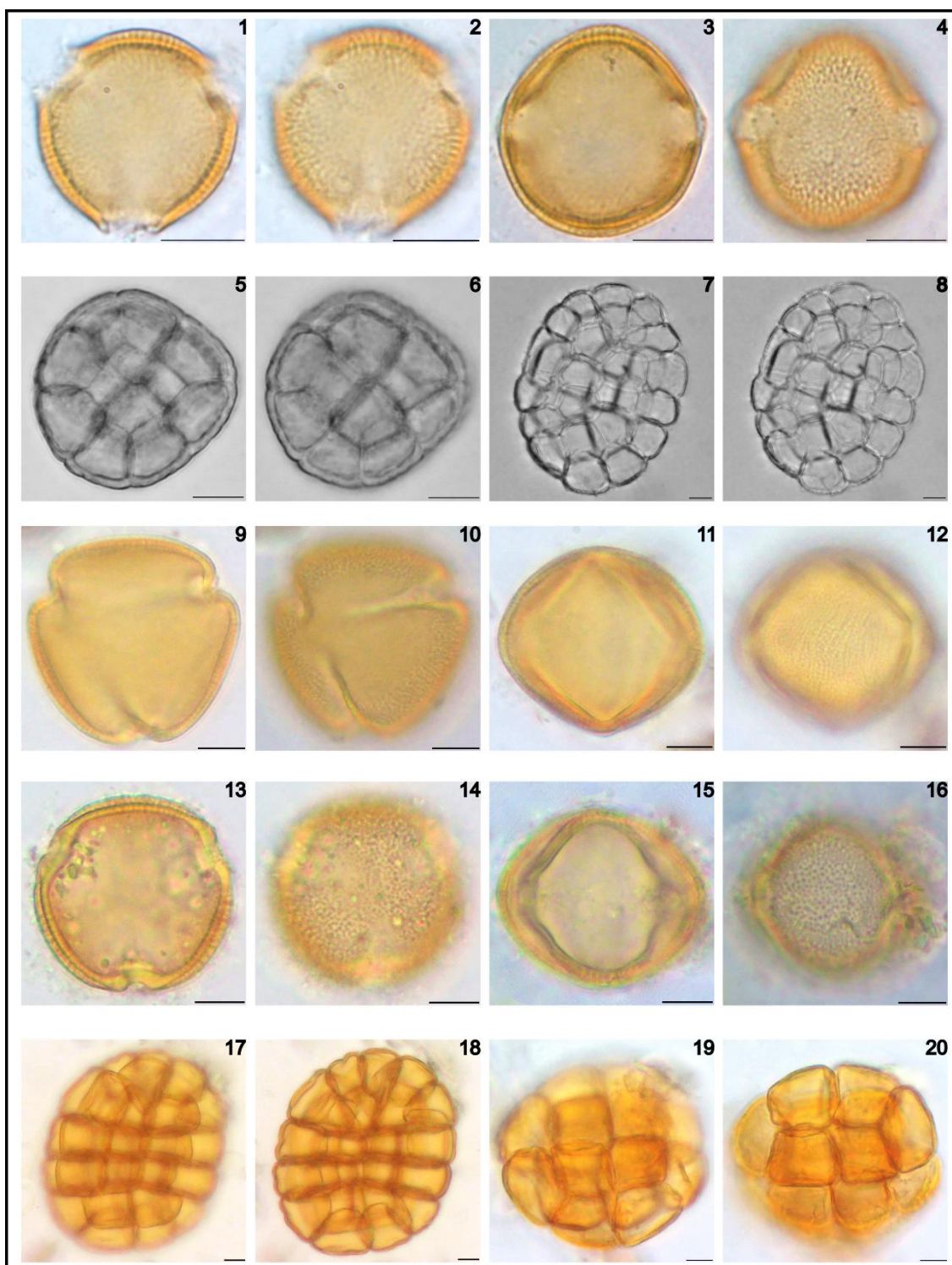


Plate XXVIII. Fabaceae – Caesalpinioideae: *Tachigali vulgaris* (1,2,3,4); Fabaceae – Caesalpinioideae (Mimosoid Clade): *Anadenanthera colubrina* (5,6), *Chloroleucon foliolosum* (7,8), *Desmanthus virgatus* (9,10,11,12), *Entada polystachya* (13,14,15,16), *Enterolobium contortisiliquum* (17,18), *Inga laurina* (19,20). Scale bars = 10 μ m.

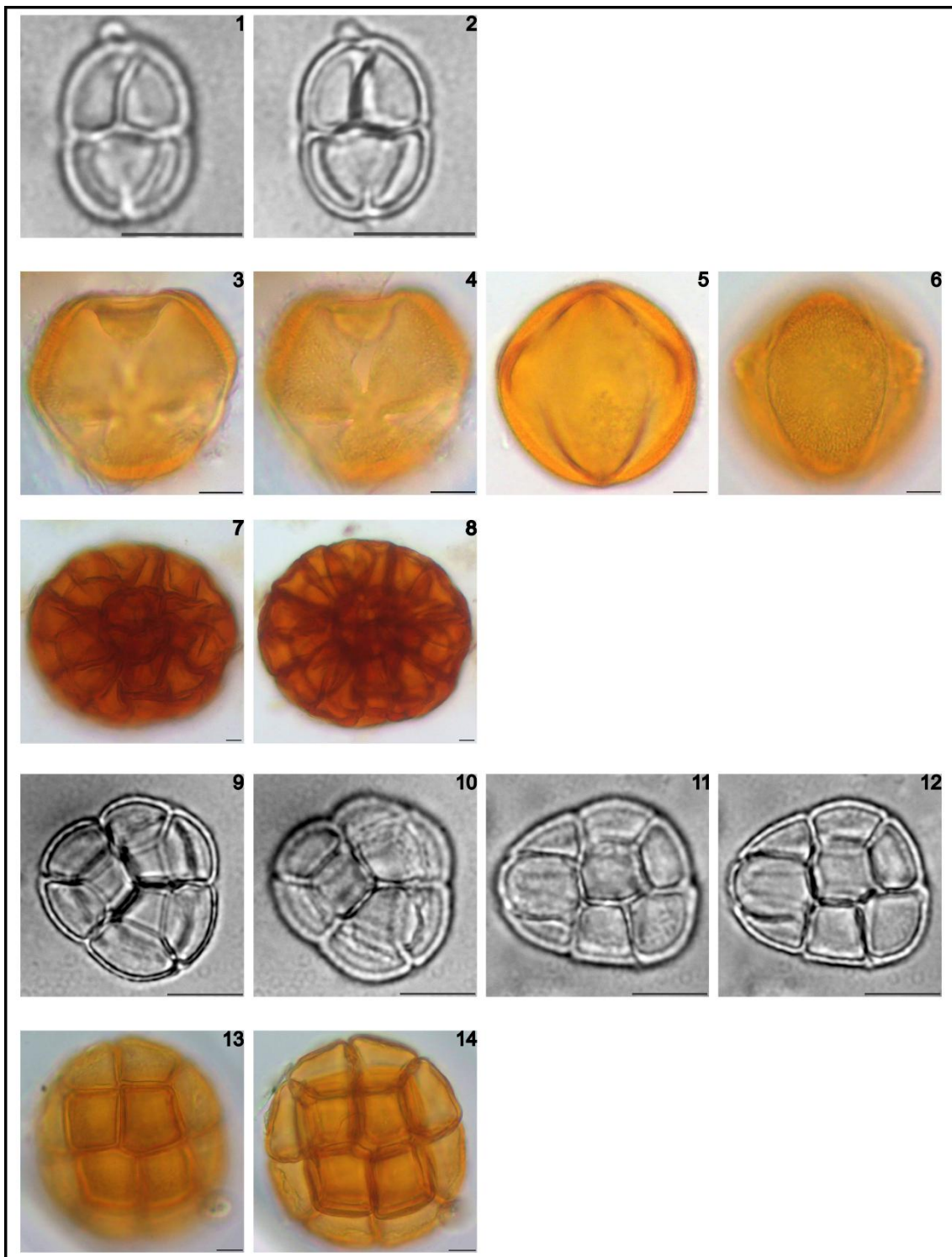


Plate XXIX. Fabaceae – Caesalpinioideae (Mimosoid Clade): *Mimosa caesalpinifolia* (1,2), *Neptunia plena* (3,4,5,6), *Parkia platycephala* (7,8), *Piptadenia retusa* (9,10,11,12), *Pithecellobium diversifolium* (13,14). Scale bars = 10 μ m.

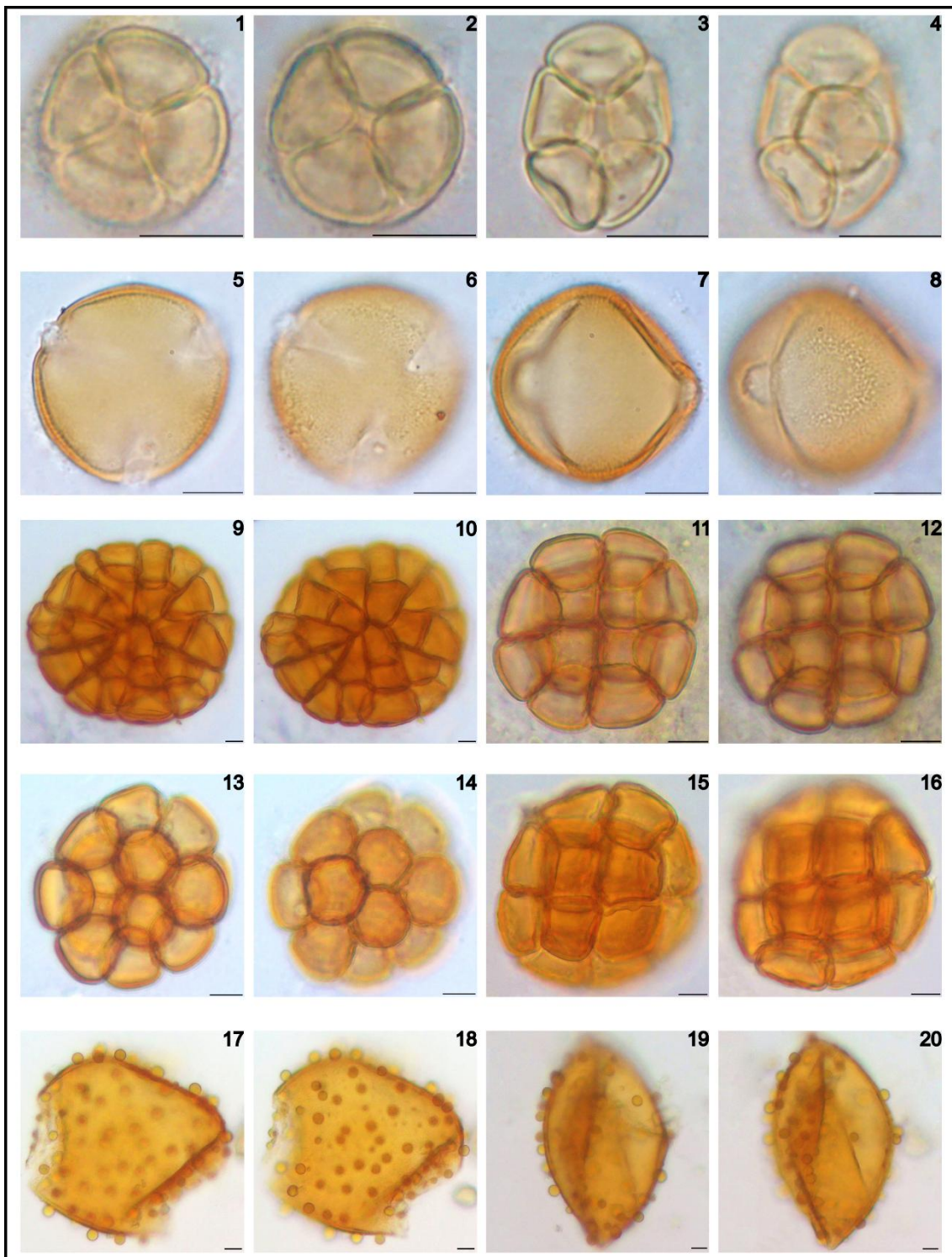


Plate XXX. Fabaceae – Caesalpinioideae (Mimosoid Clade): *Pityrocarpa moniliformis* (1,2,3,4), *Plathymenia reticulata* (5,6,7,8), *Samanea saman* (9,10), *Senegalia globosa* (11,12), *Stryphnodendron coriaceum* (13,14), *Zygia latifolia* (15,16); Fabaceae – Cercidoideae: *Bauhinia acuruana* (17,18,19,20). Scale bars = 10 μ m.

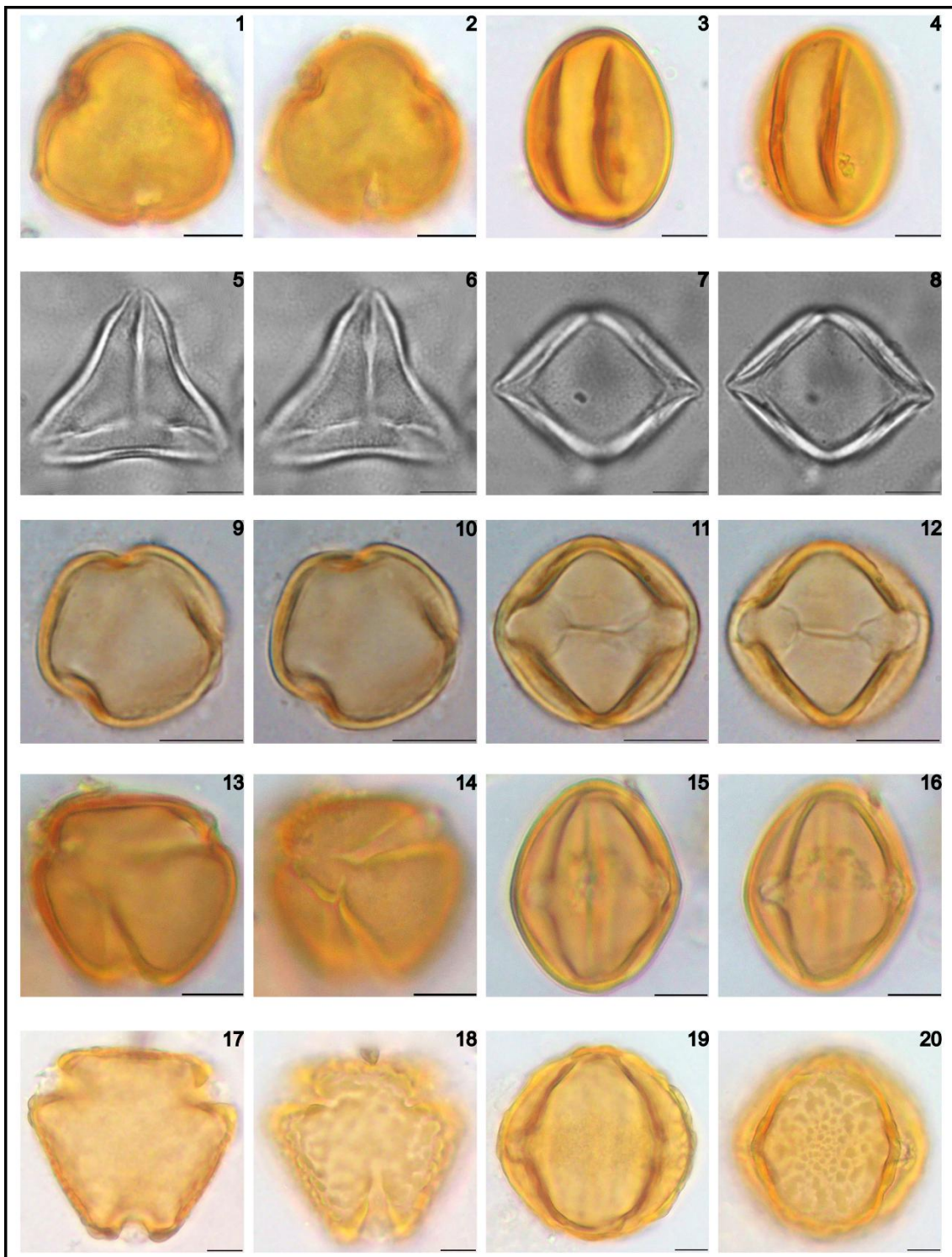


Plate XXXI. Fabaceae – Cercidoideae: *Schnella glabra* (1,2,3,4); Fabaceae – Detarioideae: *Copaifera langsdorffii* (5,6,7,8); *Cynometra bauhiniifolia* (9,10,11,12); *Hymenaea courbaril* (13,14,15,16), *Peltogyne confertiflora* (17,18,19,20). Scale bars = 10 μ m.

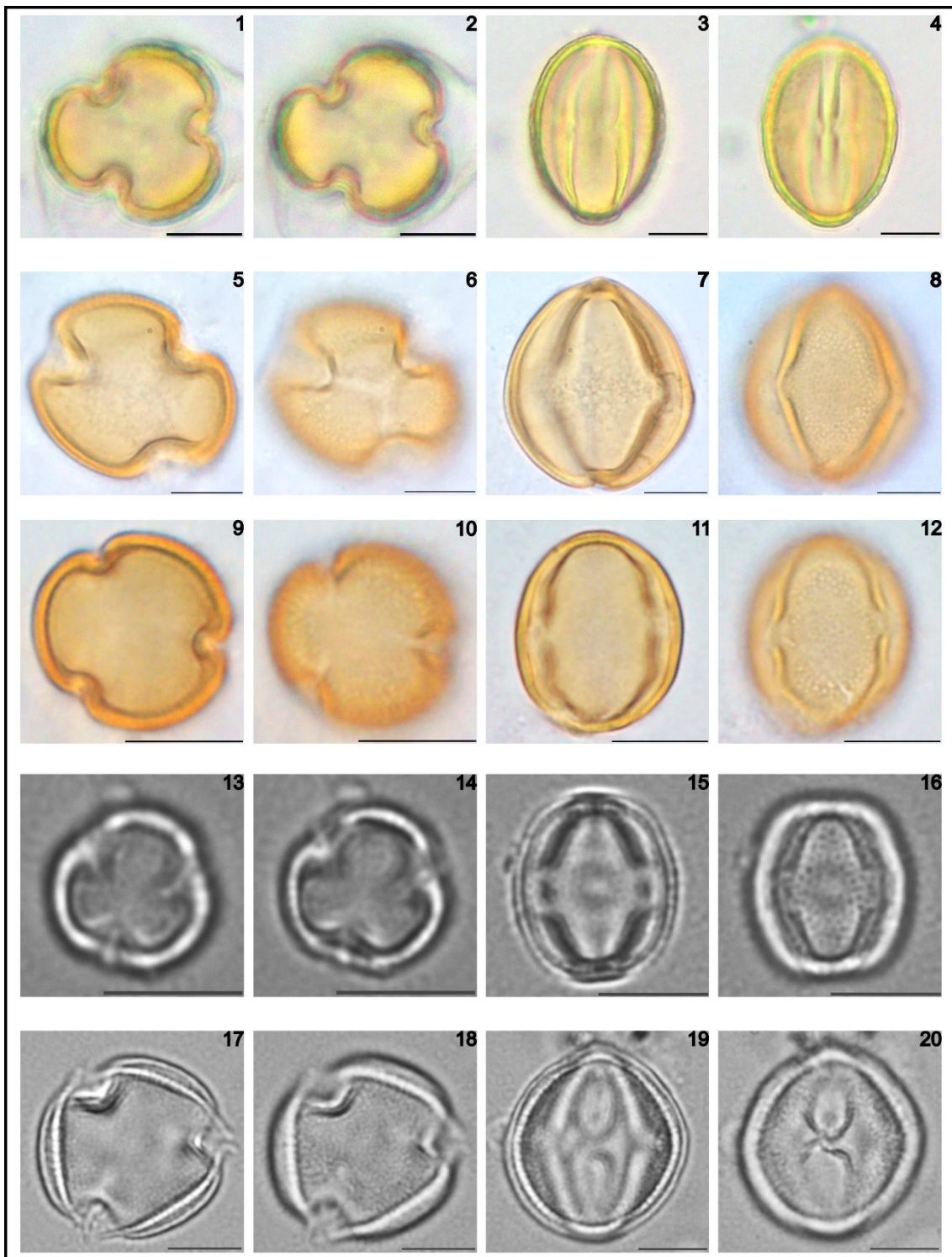


Plate XXXII. Fabaceae – Dialioideae: *Apuleia leiocarpa* (1,2,3,4), *Martiodendron mediterraneum* (5,6,7,8); *Poepigia procera* (9,10,11,12); Fabaceae – Faboideae: *Aeschynomene evenia* (13,14,15,16), *Amburana cearensis* (17,18,19,20). Scale bars = 10 μ m.

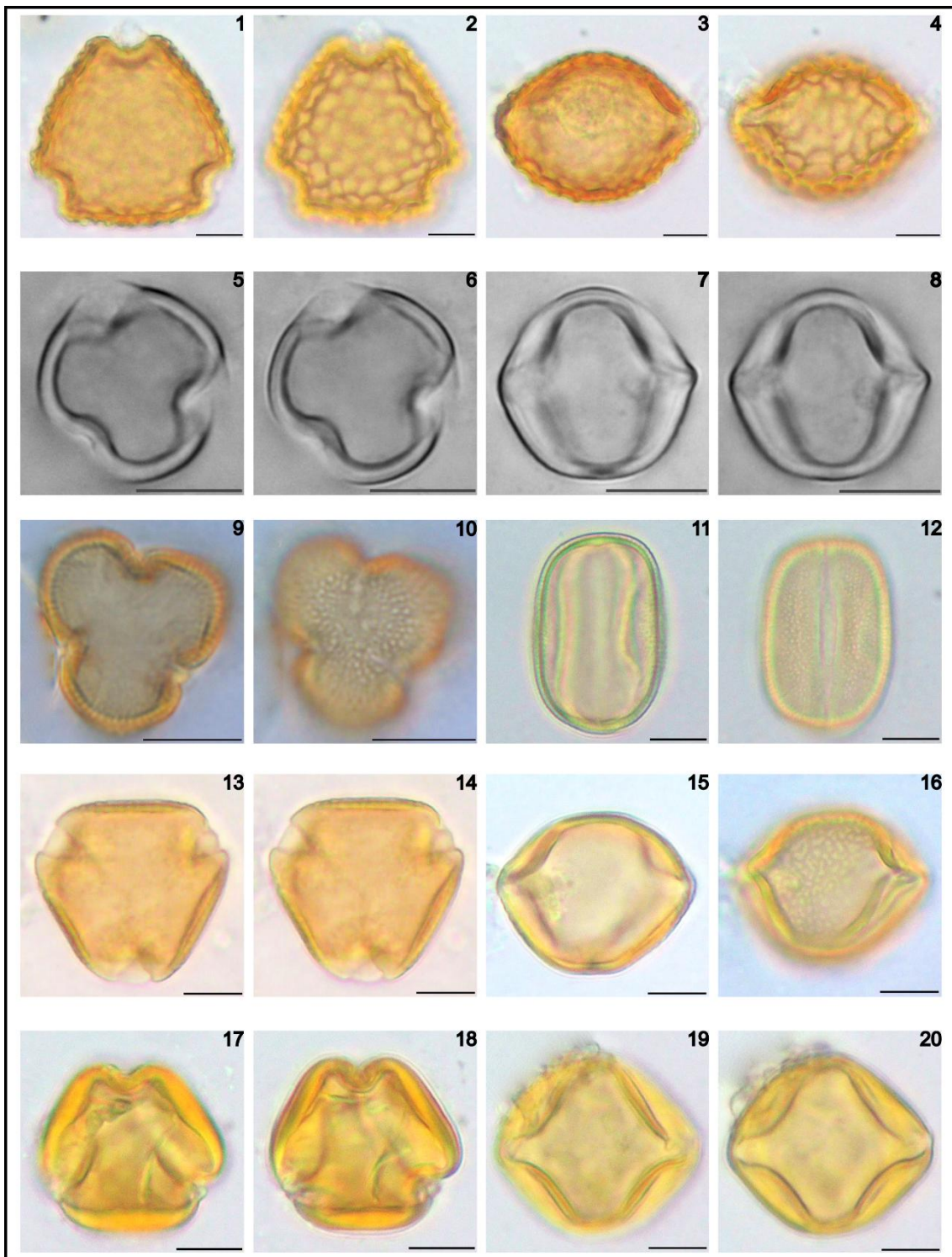


Plate XXXIII. Fabaceae – Faboideae: *Ancistrotropis firmula* (1,2,3,4), *Andira cordata* (5,6,7,8); *Arachis dardani* (9,10,11,12), *Bionia tomentosa* (13,14,15,16), *Bowdichia virgilioides* (17,18,19,20). Scale bars = 10 μ m.

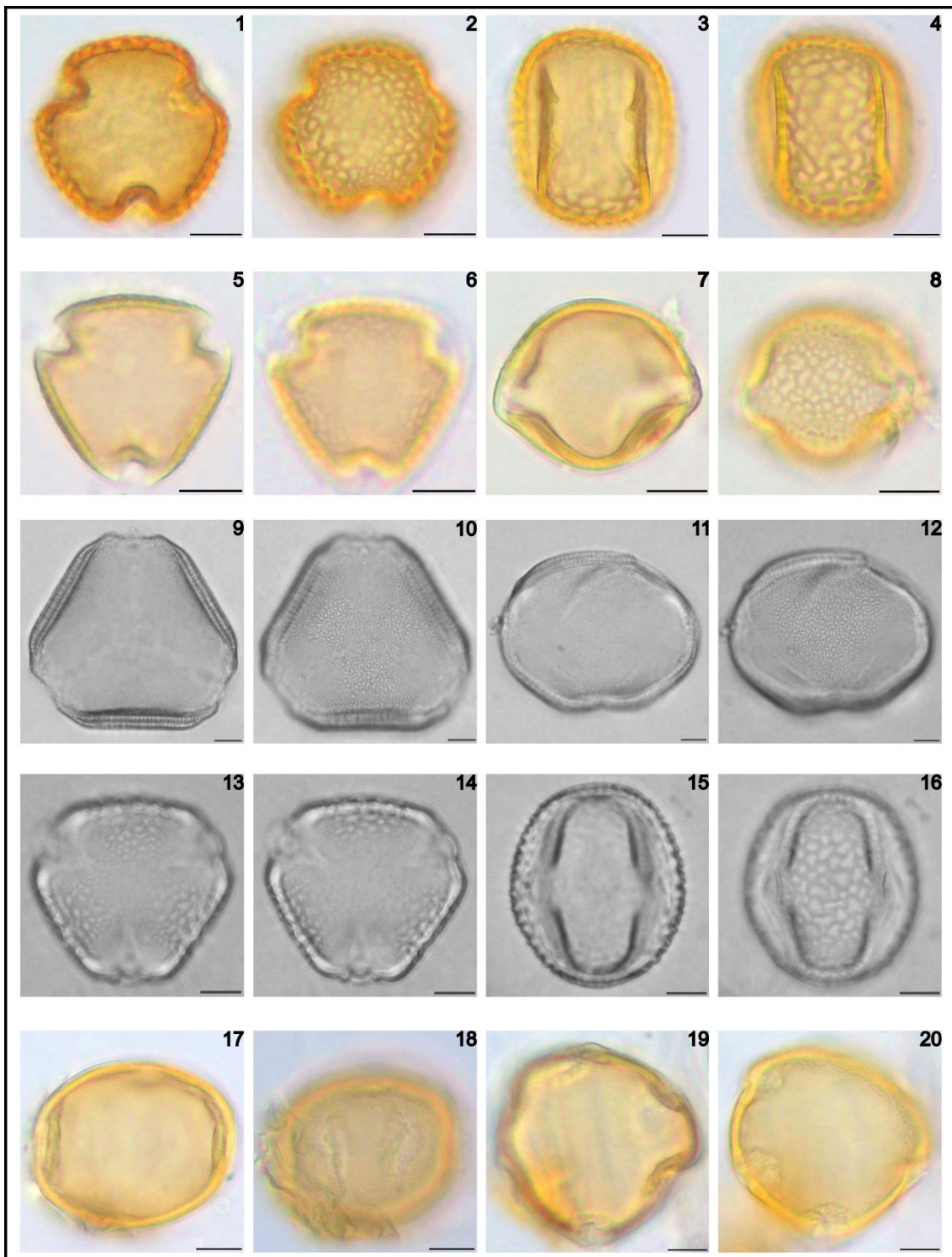


Plate XXXIV. Fabaceae – Faboideae: *Cajanus cajan* (1,2,3,4), *Camptosema sp.* (5,6,7,8); *Canavalia brasiliensis* (9,10,11,12), *Centrosema brasilianum* (13,14,15,16), *Clitoria guianensis* (17,18,19,20). Scale bars = 10 μ m.

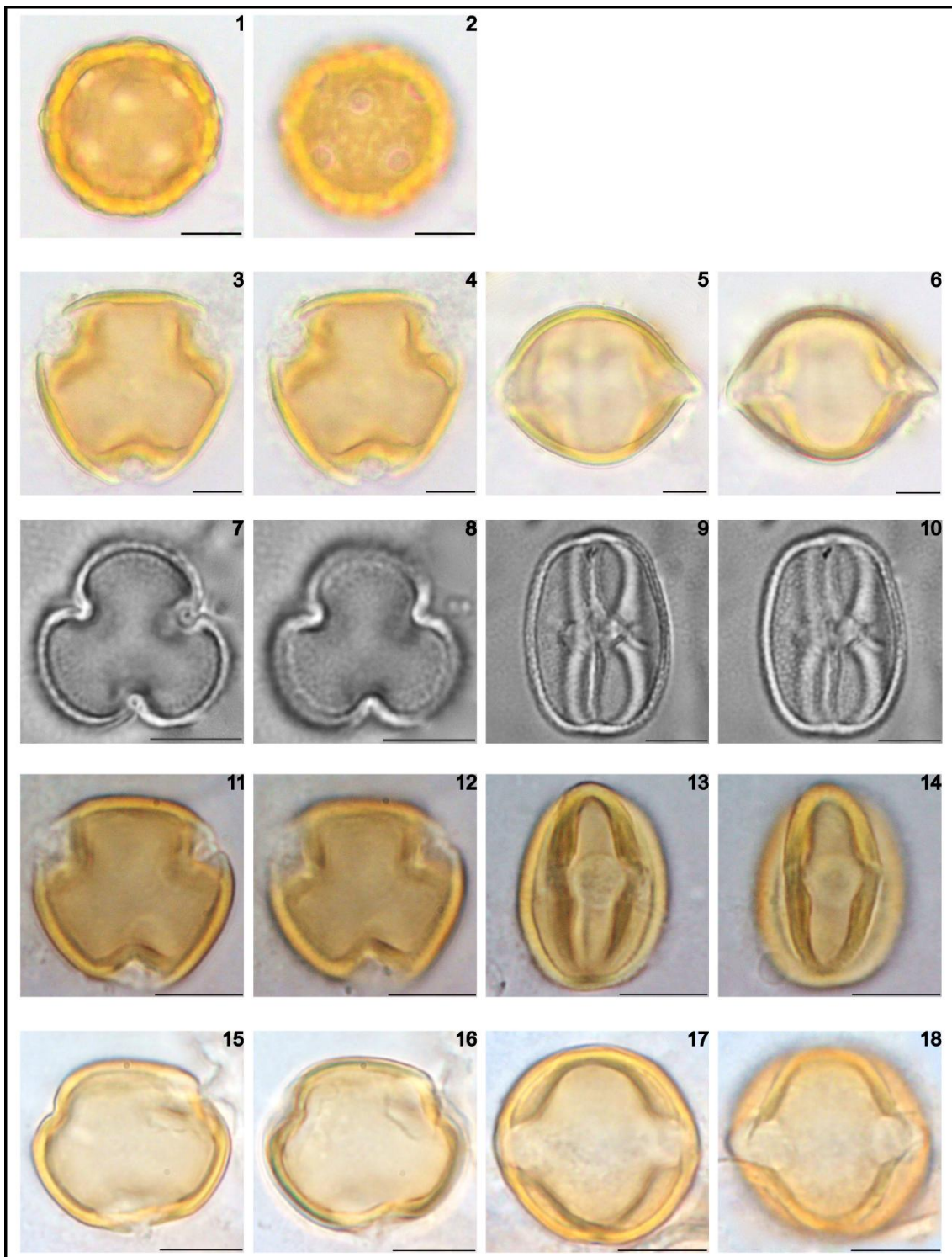


Plate XXXV. Fabaceae – Faboideae: *Cranocarpus gracilis* (1,2), *Cratyilia mollis* (3,4,5,6); *Crotalaria incana* (7,8,9,10), *Dahlstedtia araripensis* (11,12,13,14), *Dalbergia cearenses* (15,16,17,18). Scale bars = 10 μ m.

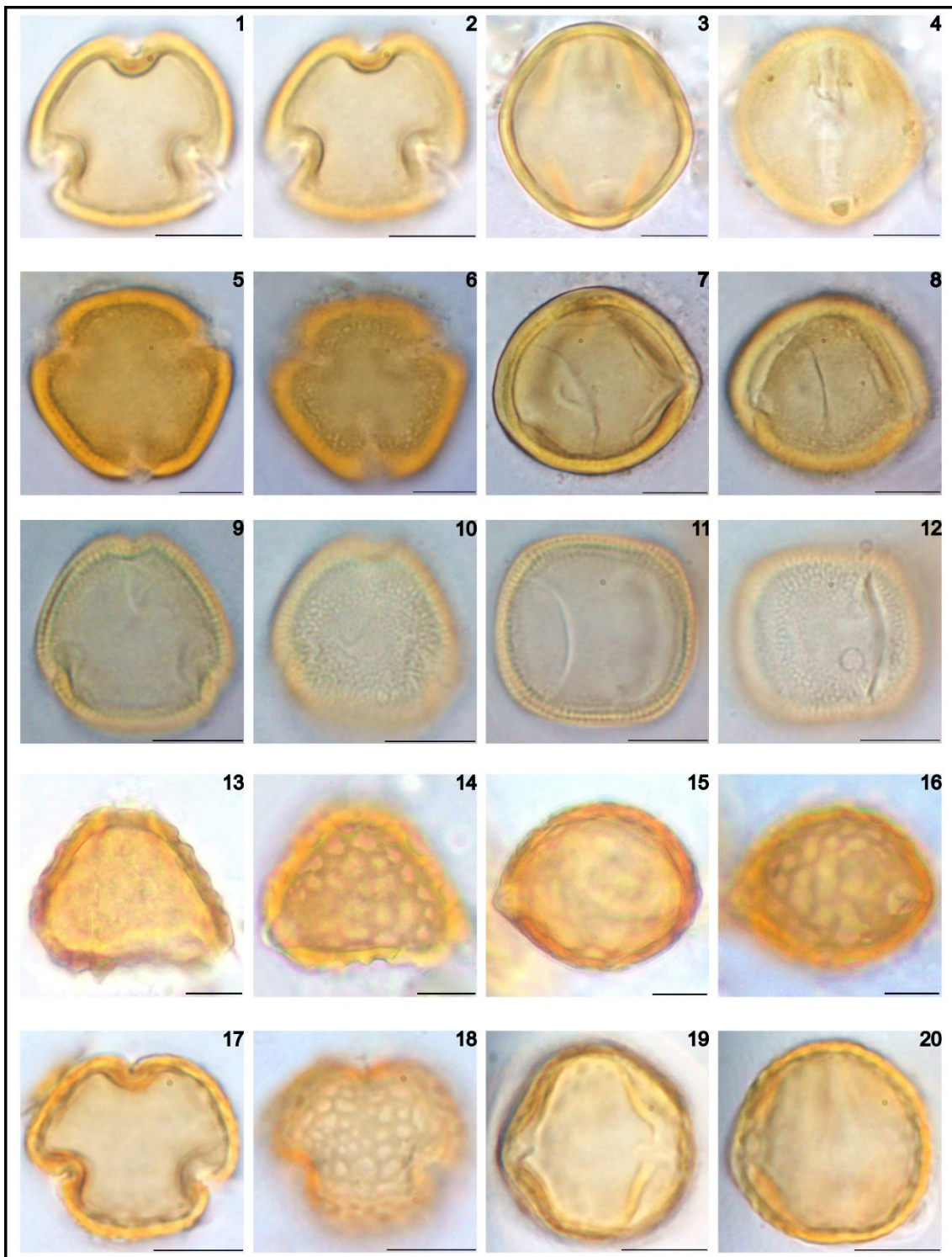


Plate XXXVI. Fabaceae – Faboideae: *Deguelia nitidula* (1,2,3,4), *Dipteryx lacunifera* (5,6,7,8); *Discolobium hirtum* (9,10,11,12), *Eriosema crinitum* (13,14,15,16), *Galactia jussiaeana* (17,18,19,20). Scale bars = 10 μ m.

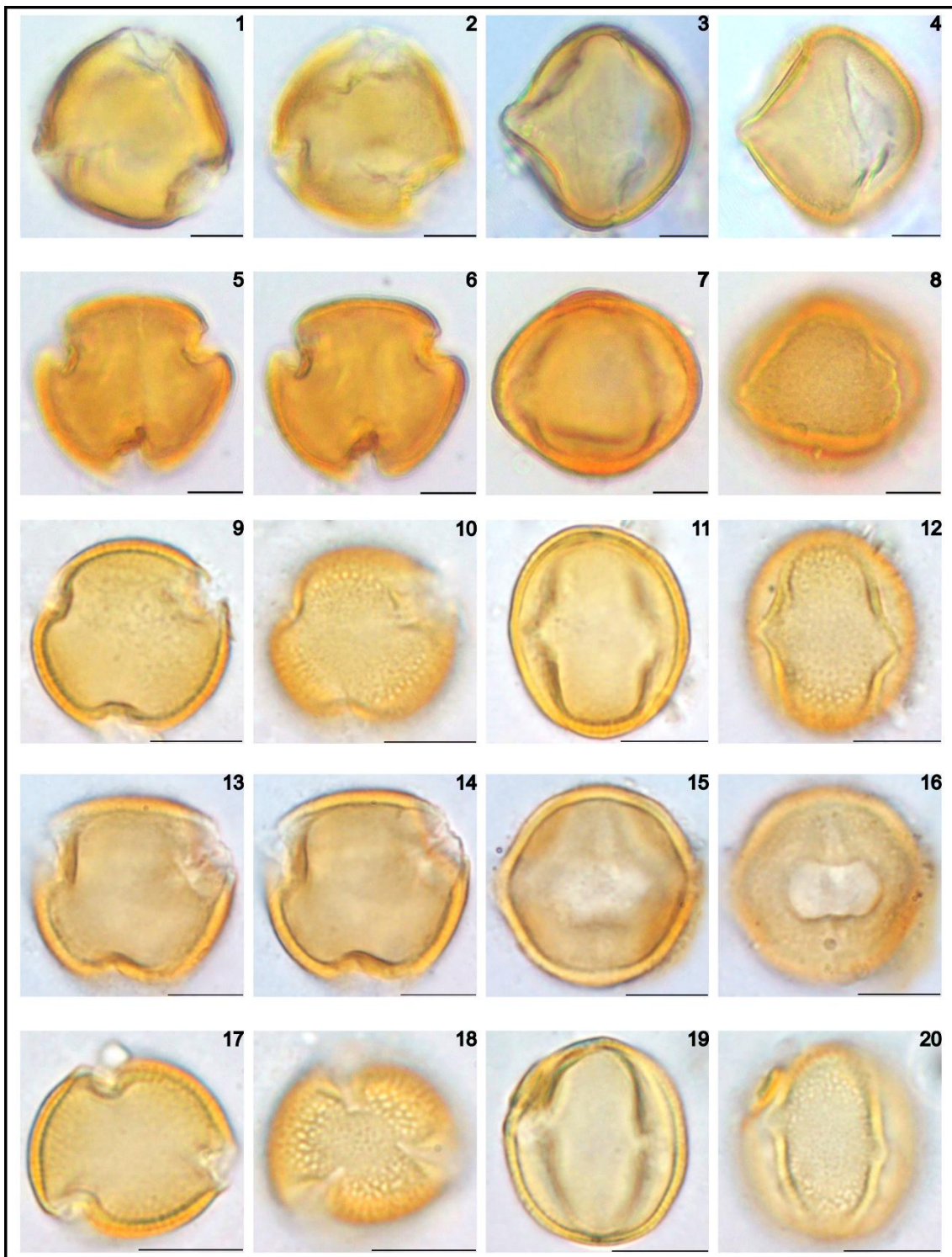


Plate XXXVII. Fabaceae – Faboideae: *Harpalyce brasiliiana* (1,2,3,4), *Indigofera hirsuta* (5,6,7,8); *Leptolobium parvifolium* (9,10,11,12), *Lonchocarpus sericeus* (13,14,15,16), *Luetzelburgia auriculata* (17,18,19,20). Scale bars = 10 μ m.

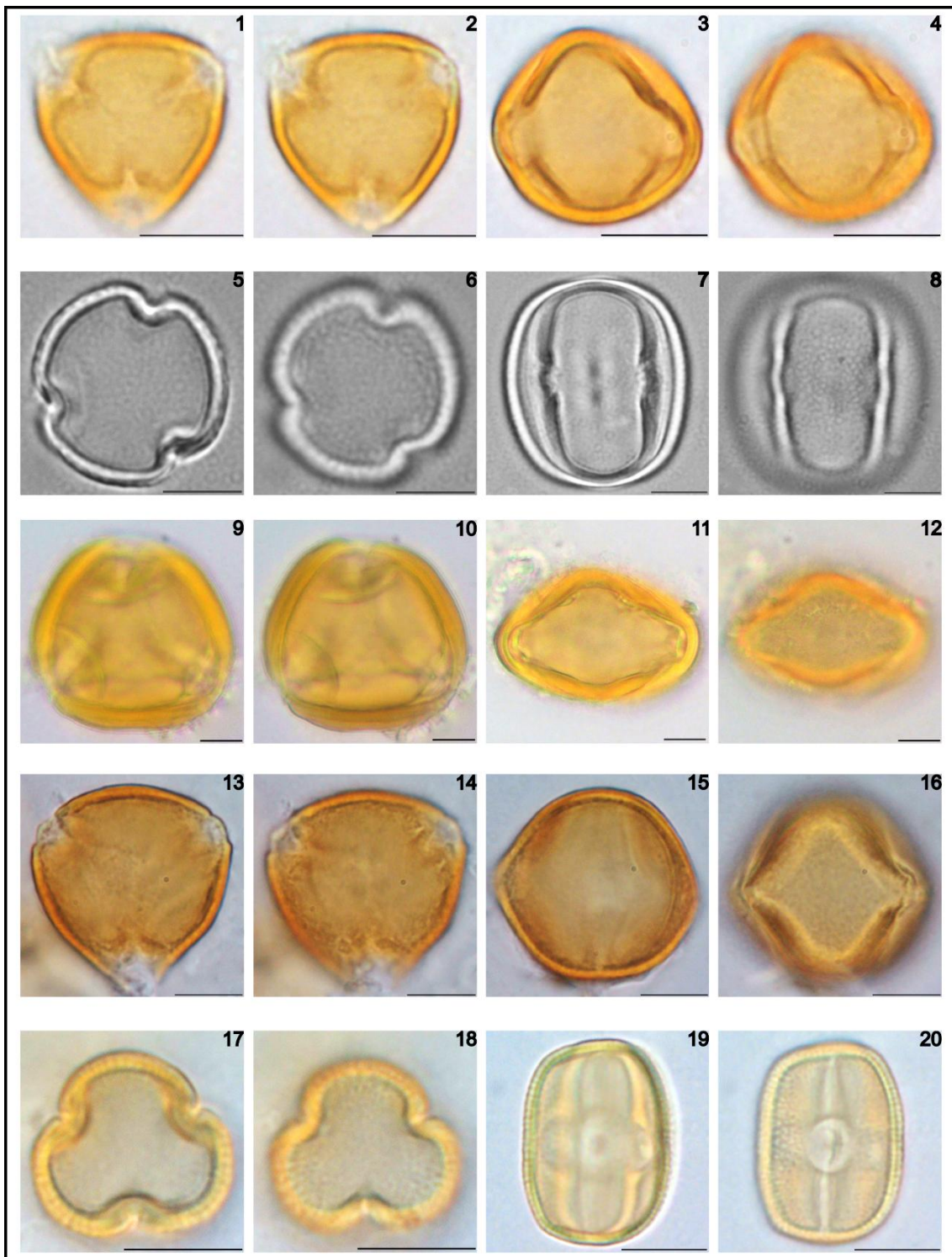


Plate XXXVIII. Fabaceae – Faboideae: *Machaerium acutifolium* (1,2,3,4), *Macroptilium lathyroides* (5,6,7,8); *Macropsychanthus bicolor* (9,10,11,12), *Muellera moniliformis* (13,14,15,16), *Nissolia vincentina* (17,18,19,20). Scale bars = 10 μ m.

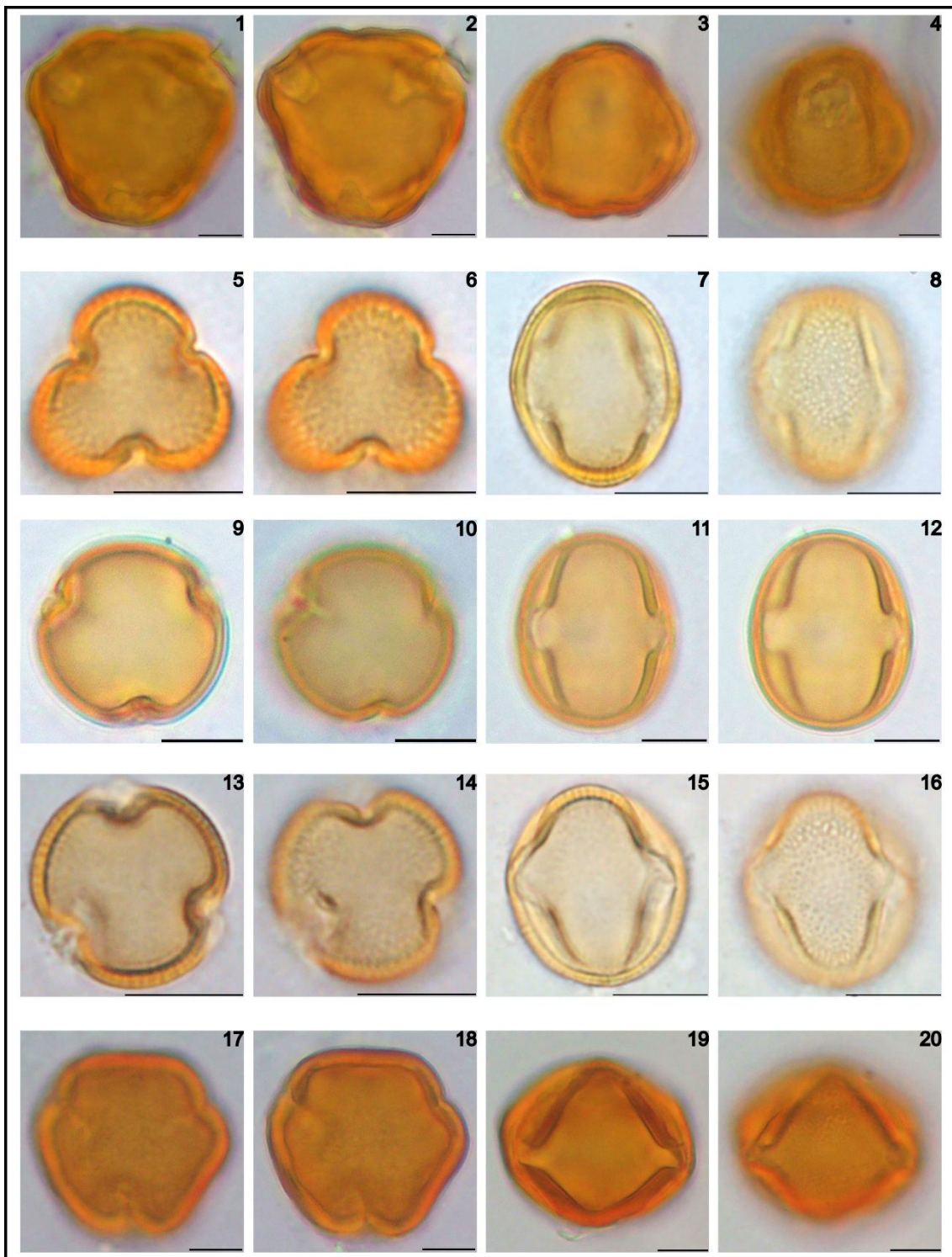


Plate XXXIX. Fabaceae – Faboideae: *Periandra coccinea* (1,2,3,4), *Platypodium elegans* (5,6,7,8); *Poiretia punctata* (9,10,11,12), *Pterocarpus villosus* (13,14,15,16), *Pterodon abruptus* (17,18,19,20). Scale bars = 10 μ m.

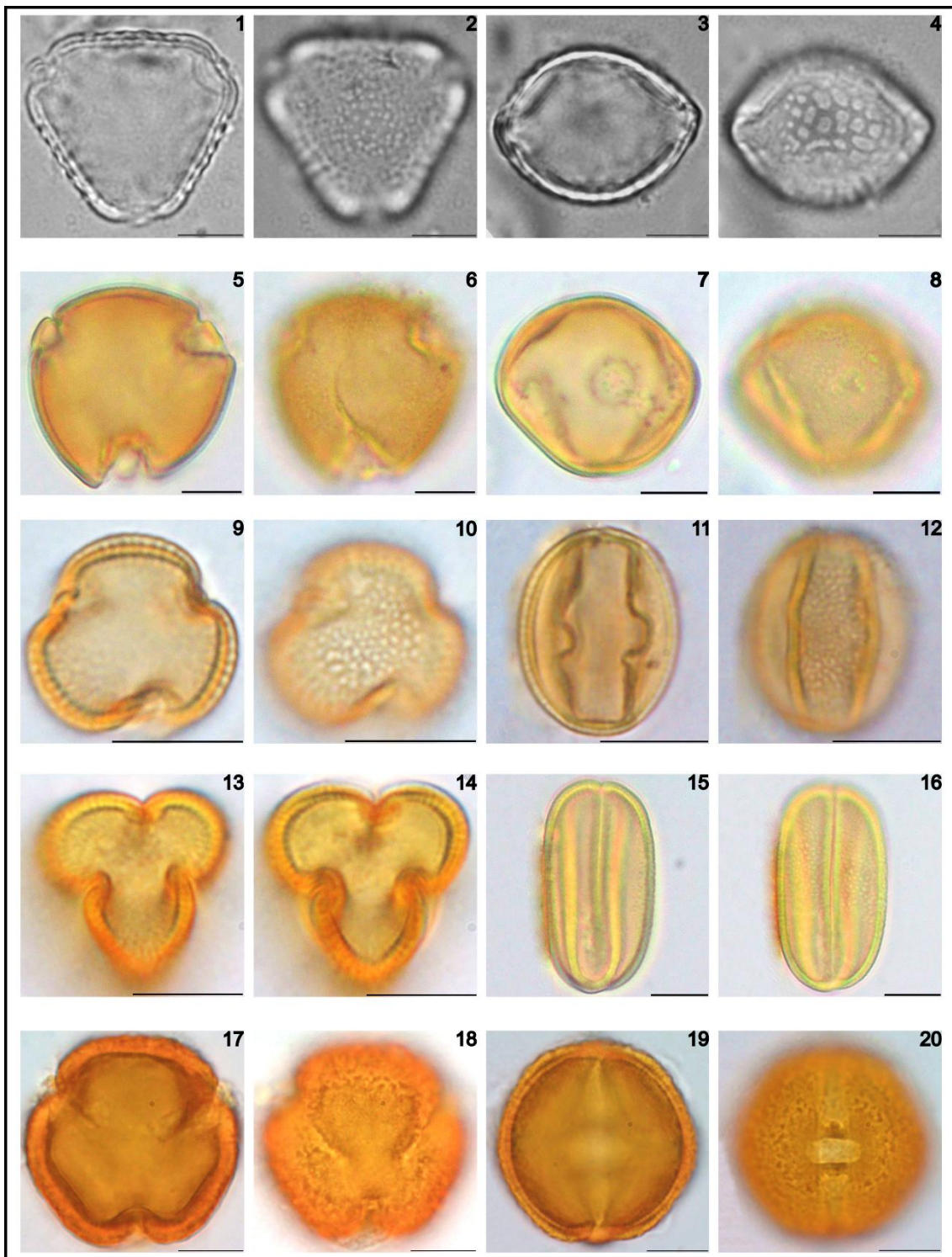


Plate XL. Fabaceae – Faboideae: *Rhynchosia minima* (1,2,3,4), *Sesbania exasperata* (5,6,7,8); *Soemmeringia semperflorens* (9,10,11,12), *Stylosanthes viscosa* (13,14,15,16), *Swartzia pylonema* (17,18,19,20). Scale bars = 10 μ m.

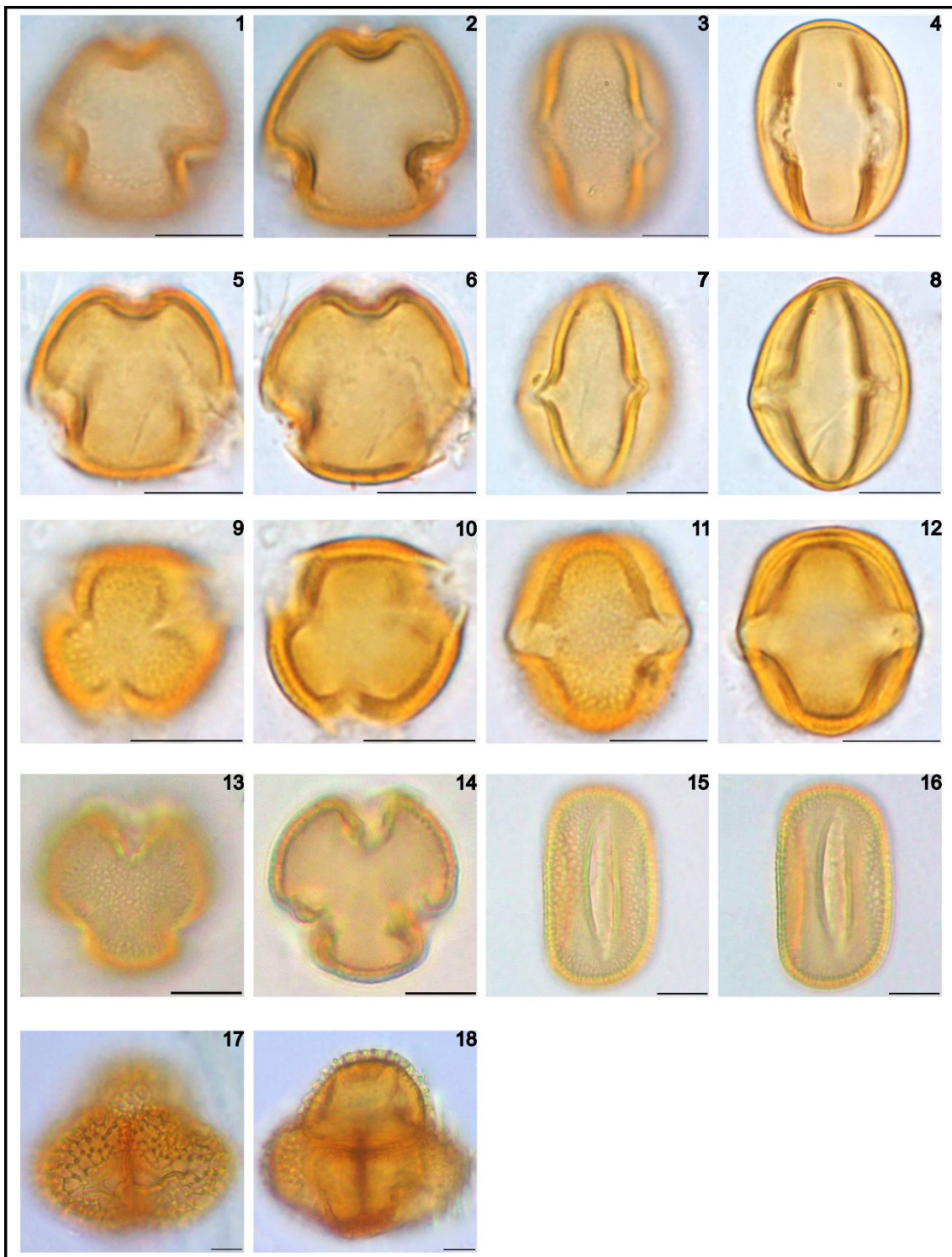


Plate XLI. Fabaceae – Faboideae: *Tephrosia cinerea* (1,2,3,4), *Trischidium molle* (5,6,7,8), *Vatairea macrocarpa* (9,10,11,12), *Zornia sericea* (13,14,15,16); Gentianaceae: *Schultesia pohliana* (17,18). Scale bars = 10 μ m.

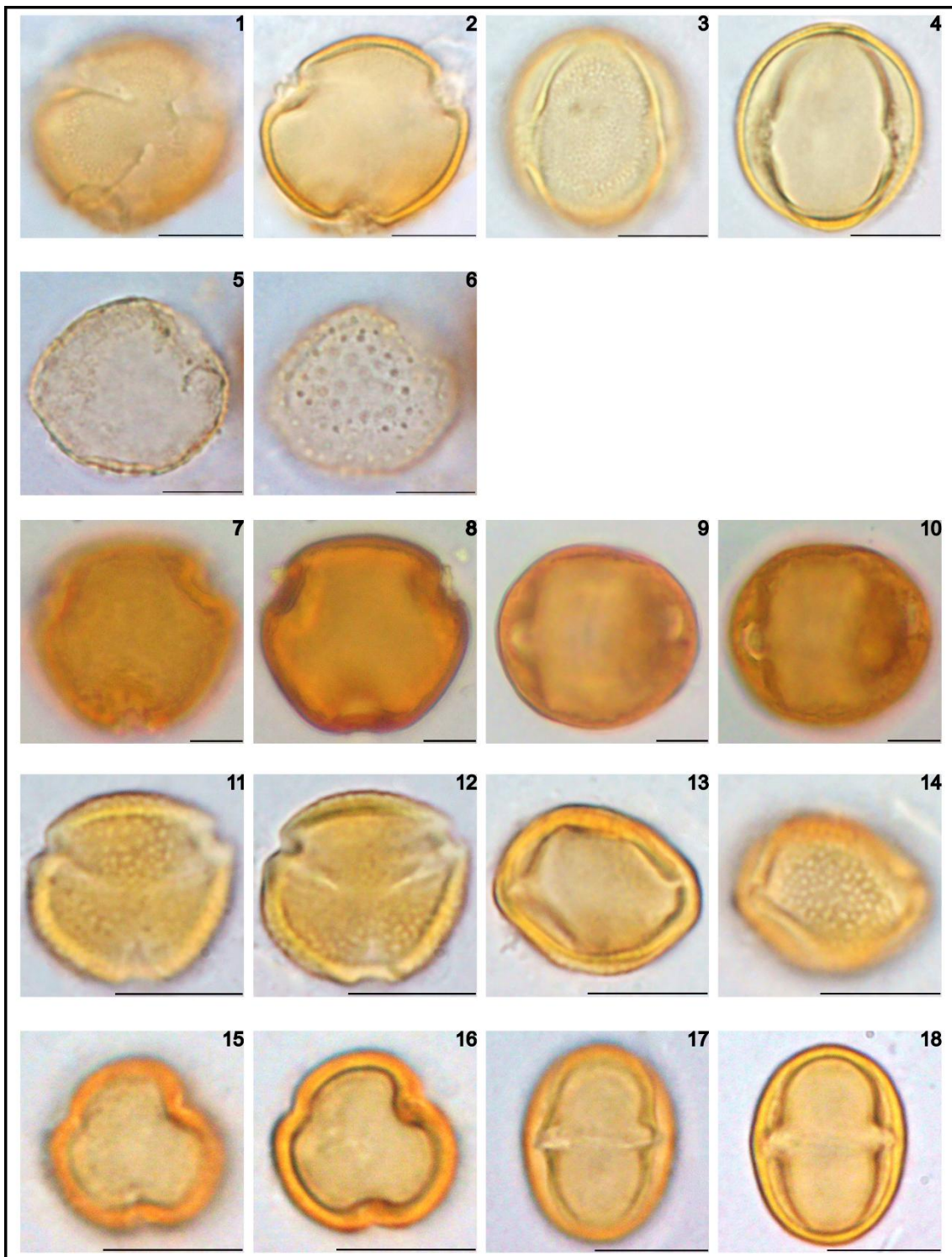


Plate XLII. Gesneriaceae: *Sinningia elatior* (1,2,3,4); Hernandiaceae: *Sparattanthelium botocudorum* (5,6); Humiriaceae: *Humiria balsamifera* (7,8,9,10); Hypericaceae: *Vismia guianensis* (11,12,13,14); Icacinaceae: *Emmotum nitens* (15,16,17,18). Scale bars = 10 μ m.

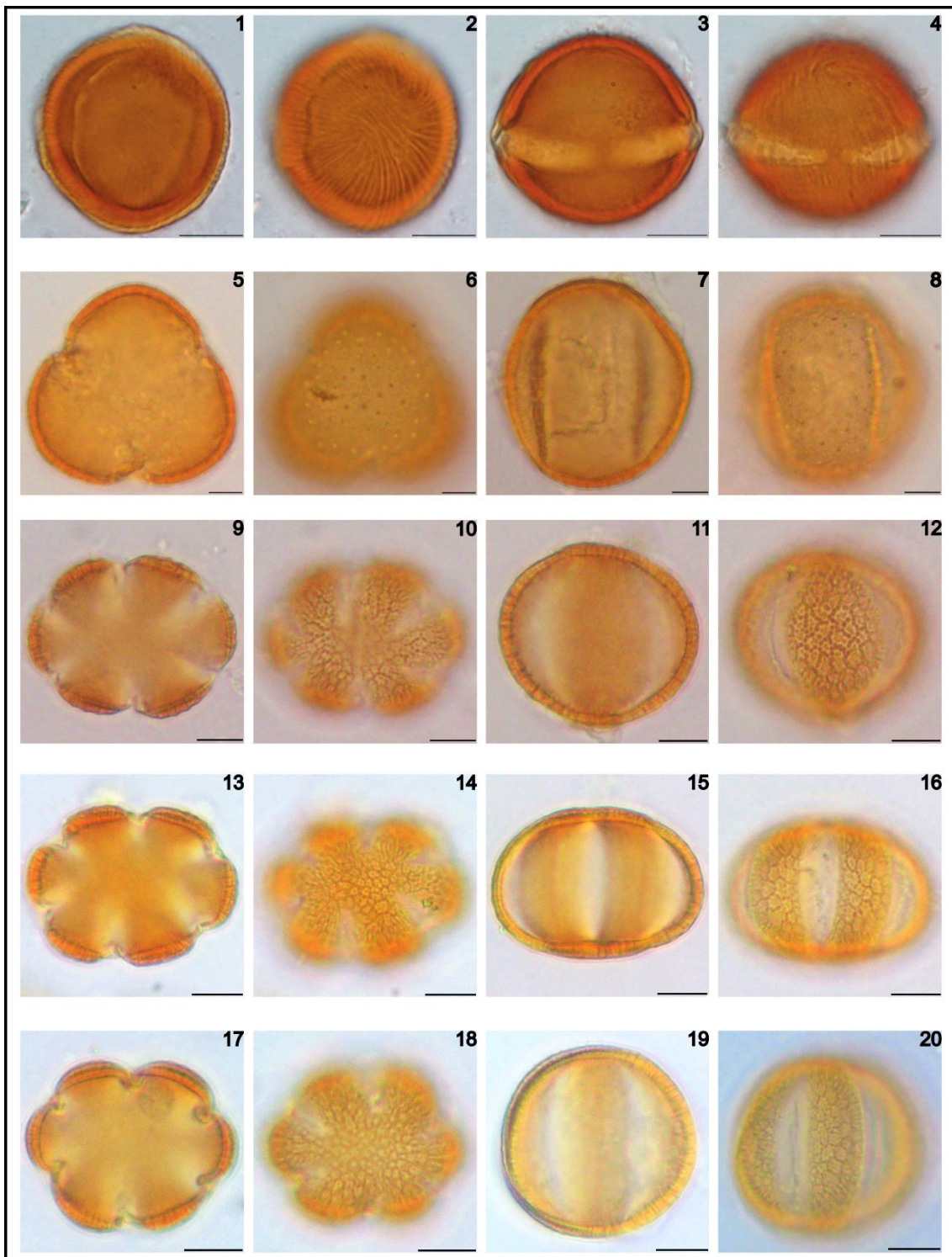


Plate XLIII. Krameriaceae: *Krameria tomentosa* (1,2,3,4); Lamiaceae: *Amasonia* sp. (5,6,7,8), *Eriope crassipes* (9,10,11,12), *Hyperia salzmännii* (13,14,15,16), *Hyptidendron leucophyllum* (17,18,19,20). Scale bars = 10 μ m.

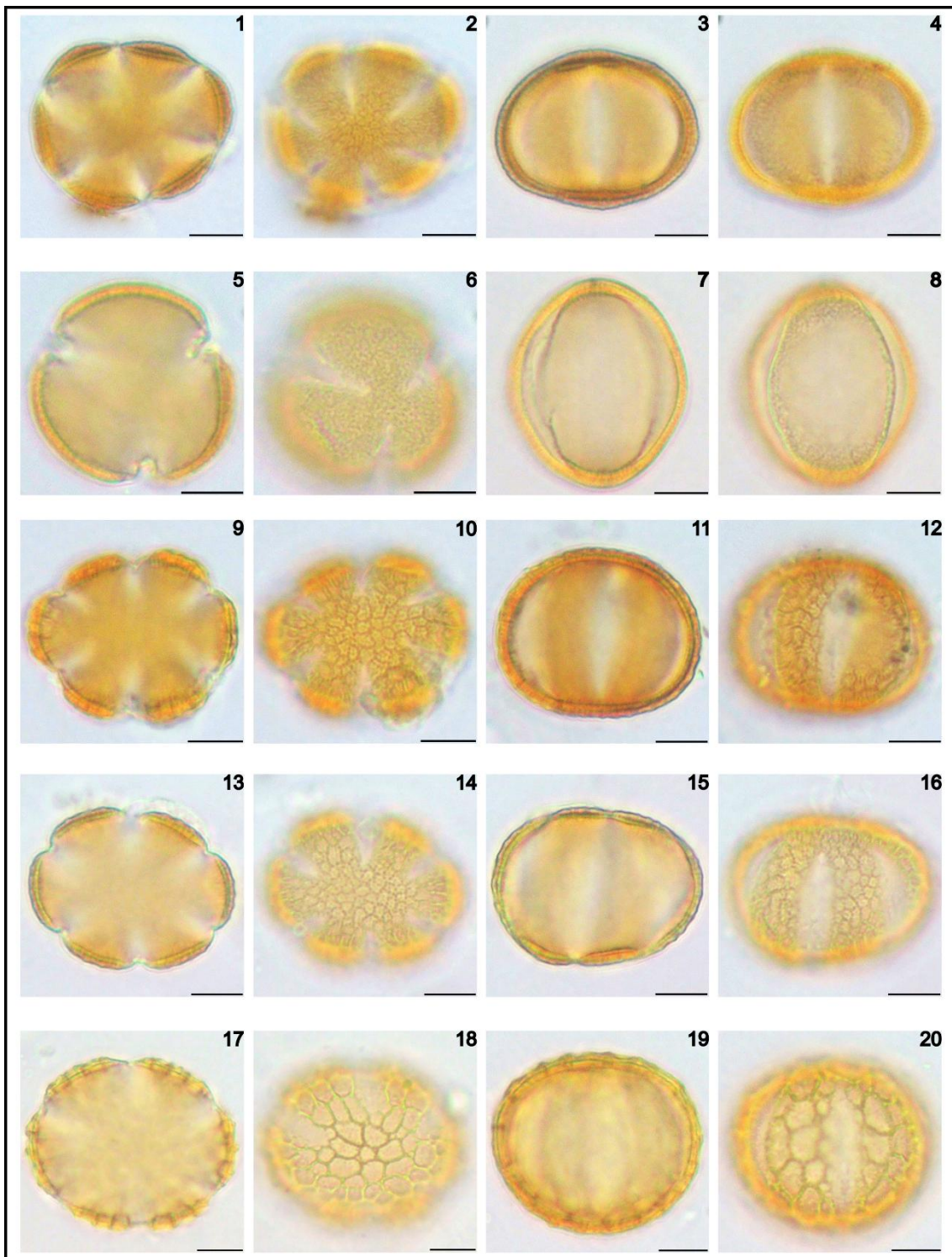


Plate XLIV. Lamiaceae: *Hyptis crenata* (1,2,3,4); *Leonotis nepetifolia* (5,6,7,8), *Marsypianthes chamaedrys* (9,10,11,12), *Mesosphaerum suaveolens* (13,14,15,16), *Ocimum gratissimum* (17,18,19,20). Scale bars = 10 μ m.

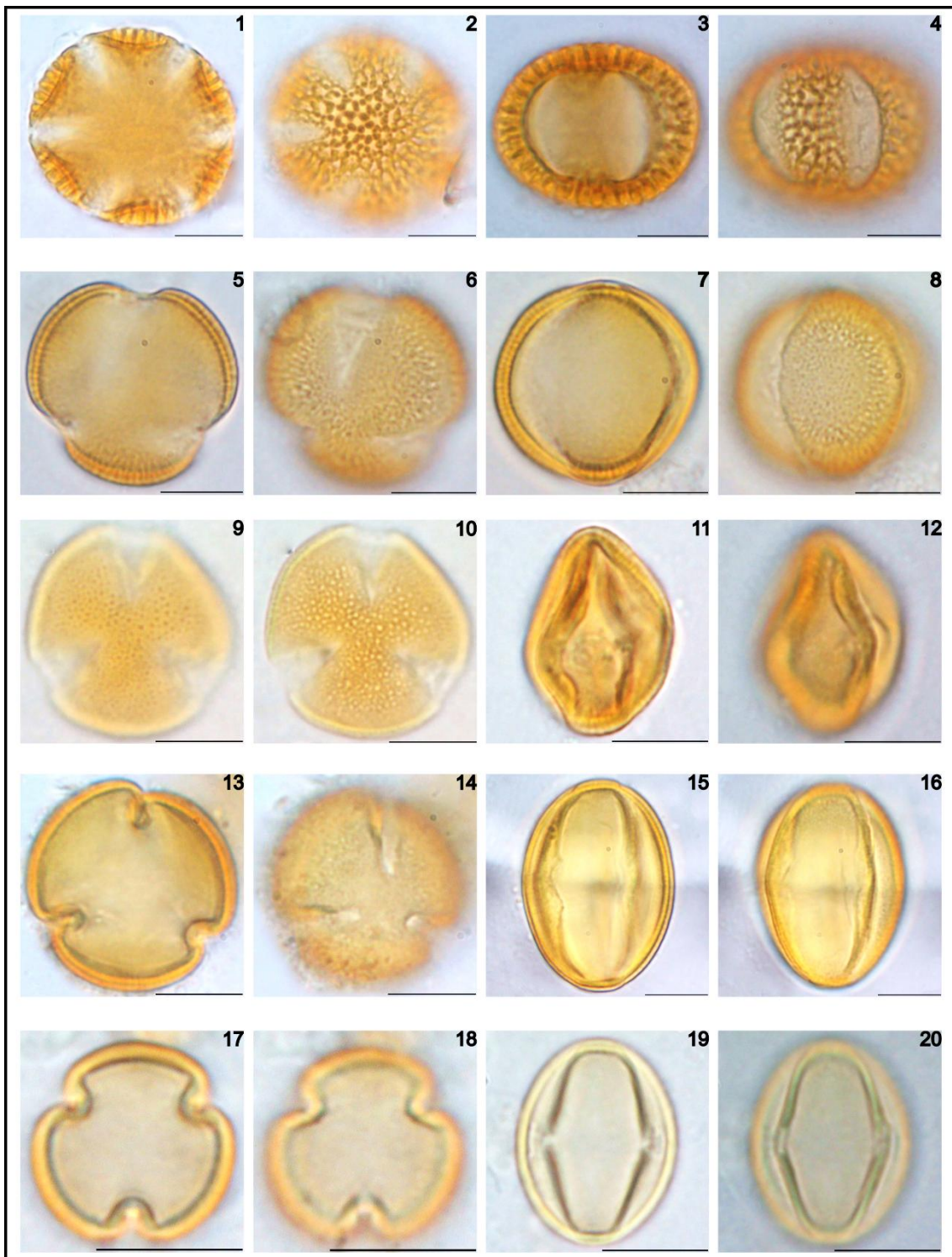


Plate XLV. Lamiaceae: *Rhapsiodon echinus* (1,2,3,4); *Vitex flavens* (5,6,7,8); Lecythidaceae: *Eschweilera nana* (9,10,11,12), *Lecythis pisonis* (13,14,15,16); Loasaceae: *Aosa rupestris* (17,18,19,20). Scale bars = 10 μ m.

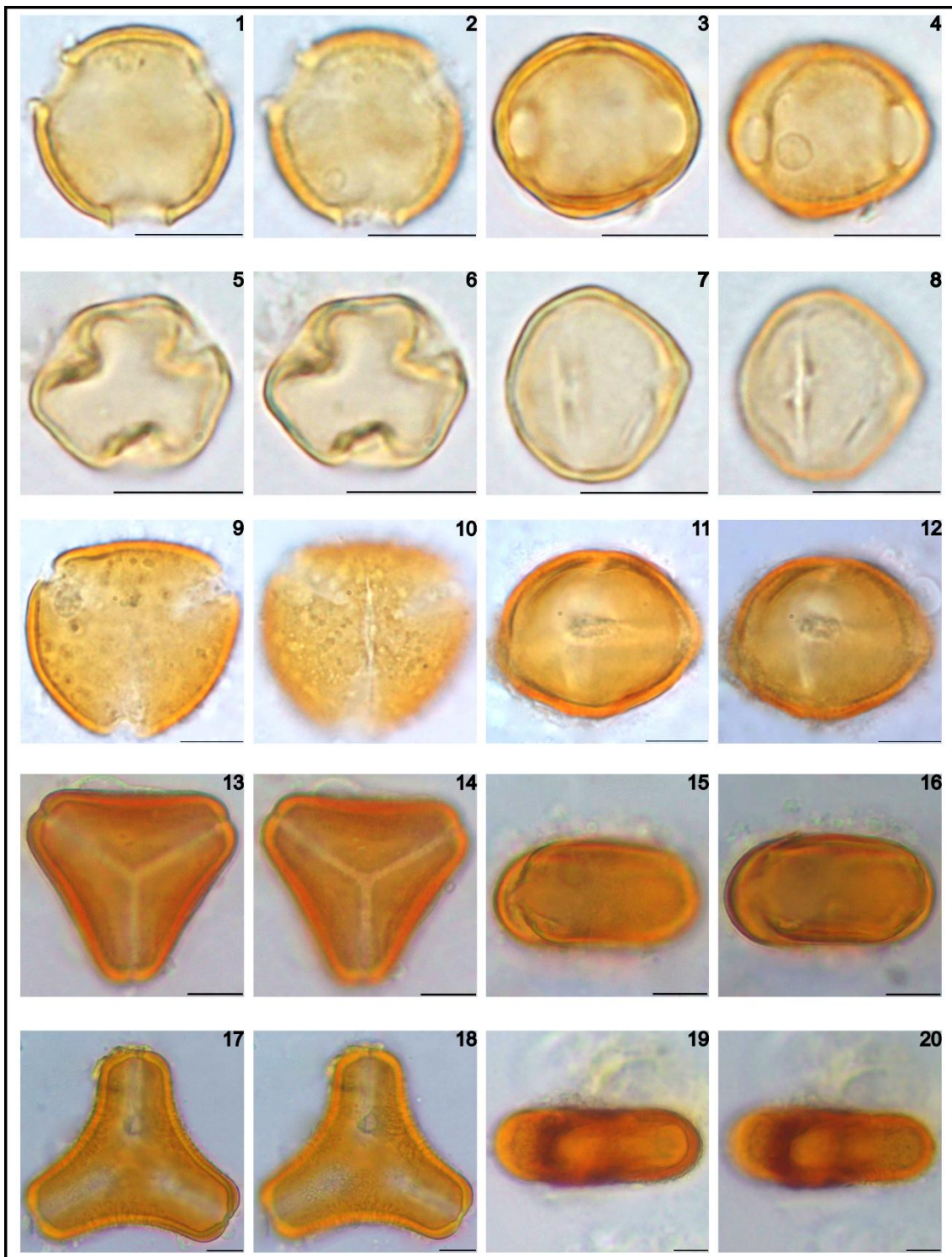


Plate XLVI. Loganiaceae: *Antonia ovata* (1,2,3,4), *Mitreola petiolata* (5,6,7,8), *Strychnos araguaensis* (9,10,11,12); Loranthaceae: *Passovia pedunculata* (13,14,15,16); *Psittacanthus eucalyptifolius* (17,18,19,20). Scale bars = 10 μ m.

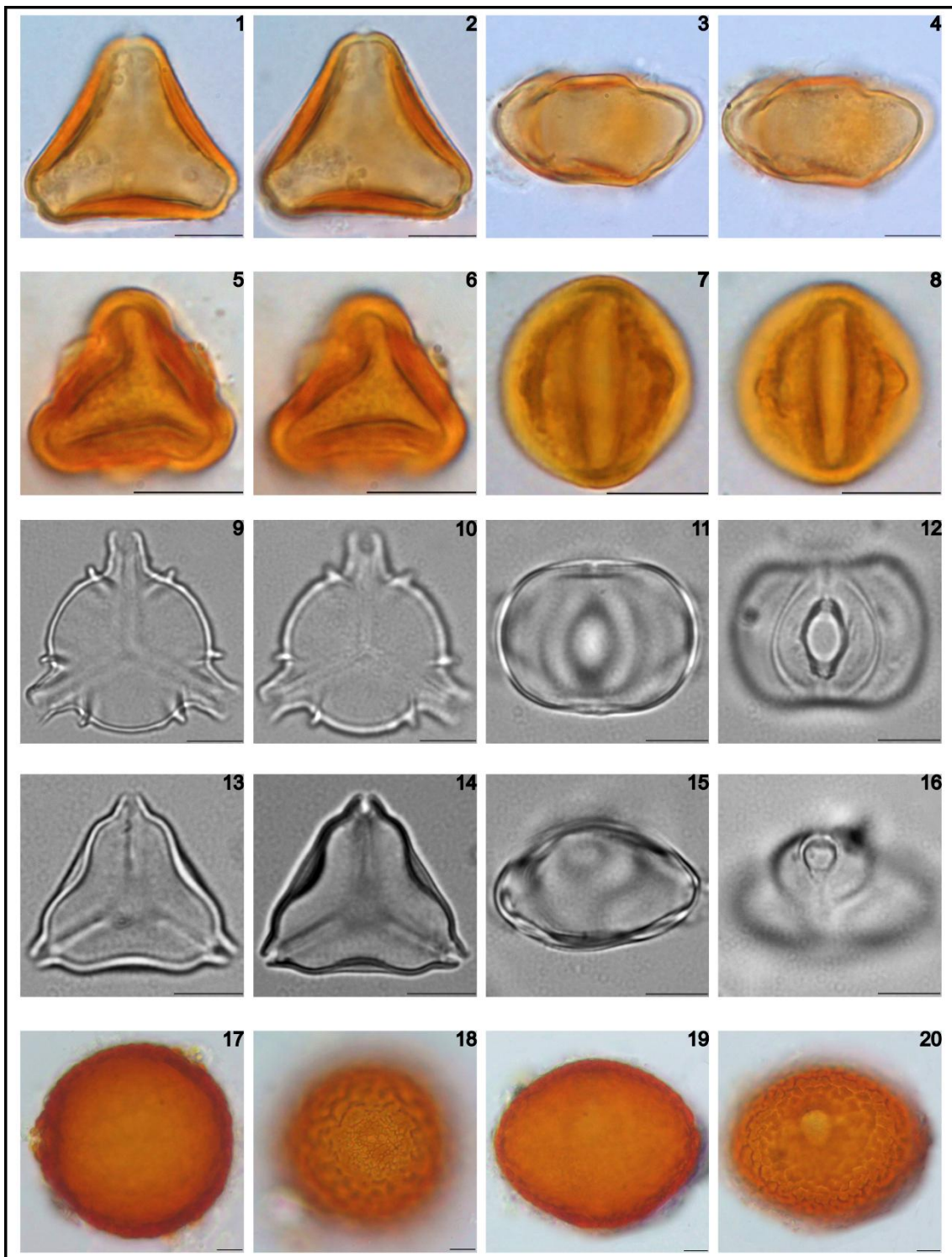


Plate XLVII. Loranthaceae: *Struthanthus polyanthus* (1,2,3,4); Lythraceae: *Ammannia maritima* (5,6,7,8), *Cuphea campestris* (9,10,11,12), *Cuphea laricoides* (13,14,15,16); *Diplusodon* sp. (17,18,19,20). Scale bars = 10 μ m.

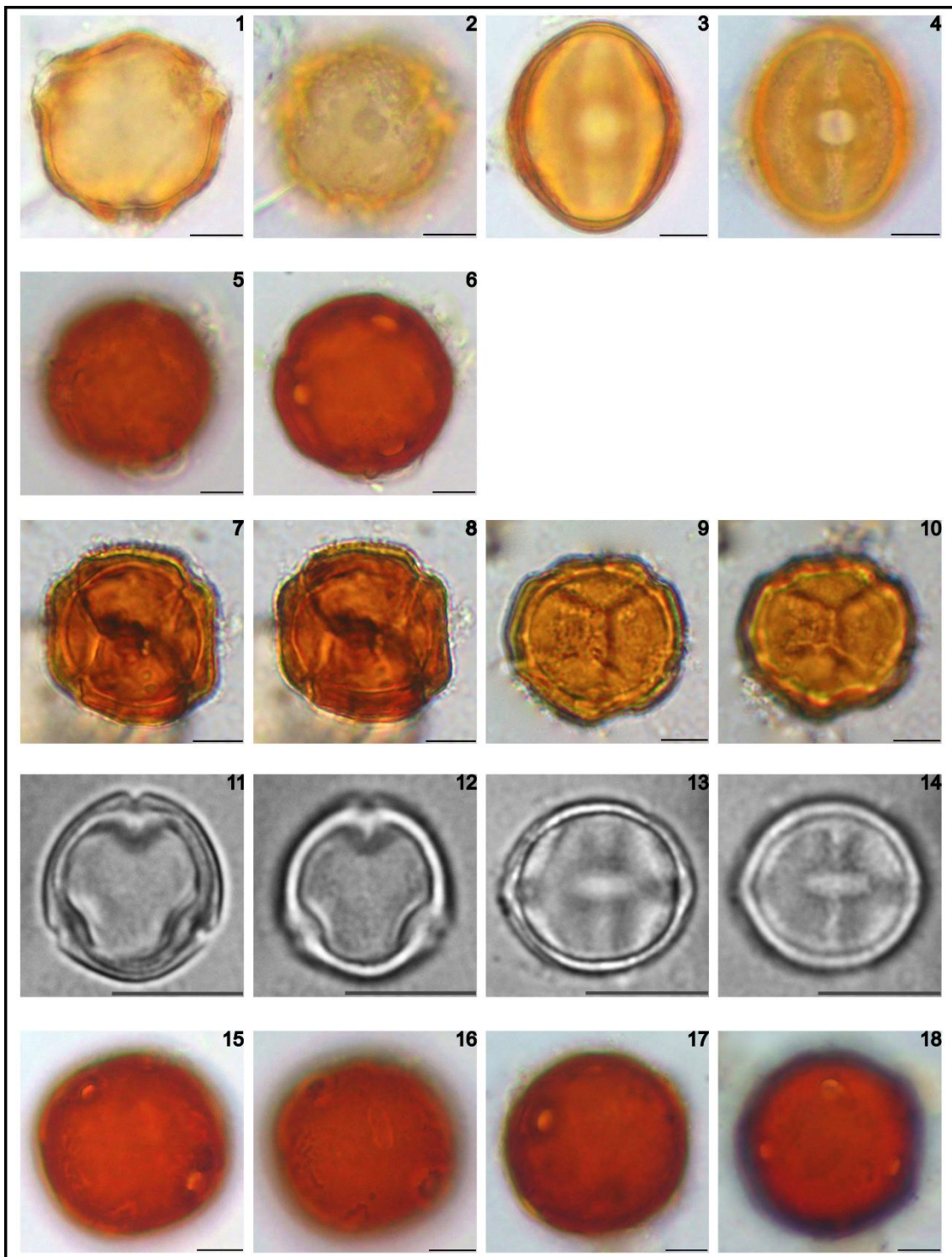


Plate XLVIII. Lythraceae: *Lafoensia replicata* (1,2,3,4); Malpighiaceae: *Amorimia rigida* (5,6), *Banisteriopsis stellaris* (7,8,9,10), *Byrsonima crassifolia* (11,12,13,14); *Callaeum psilophyllum* (15,16,17,18). Scale bars = 10 μ m.

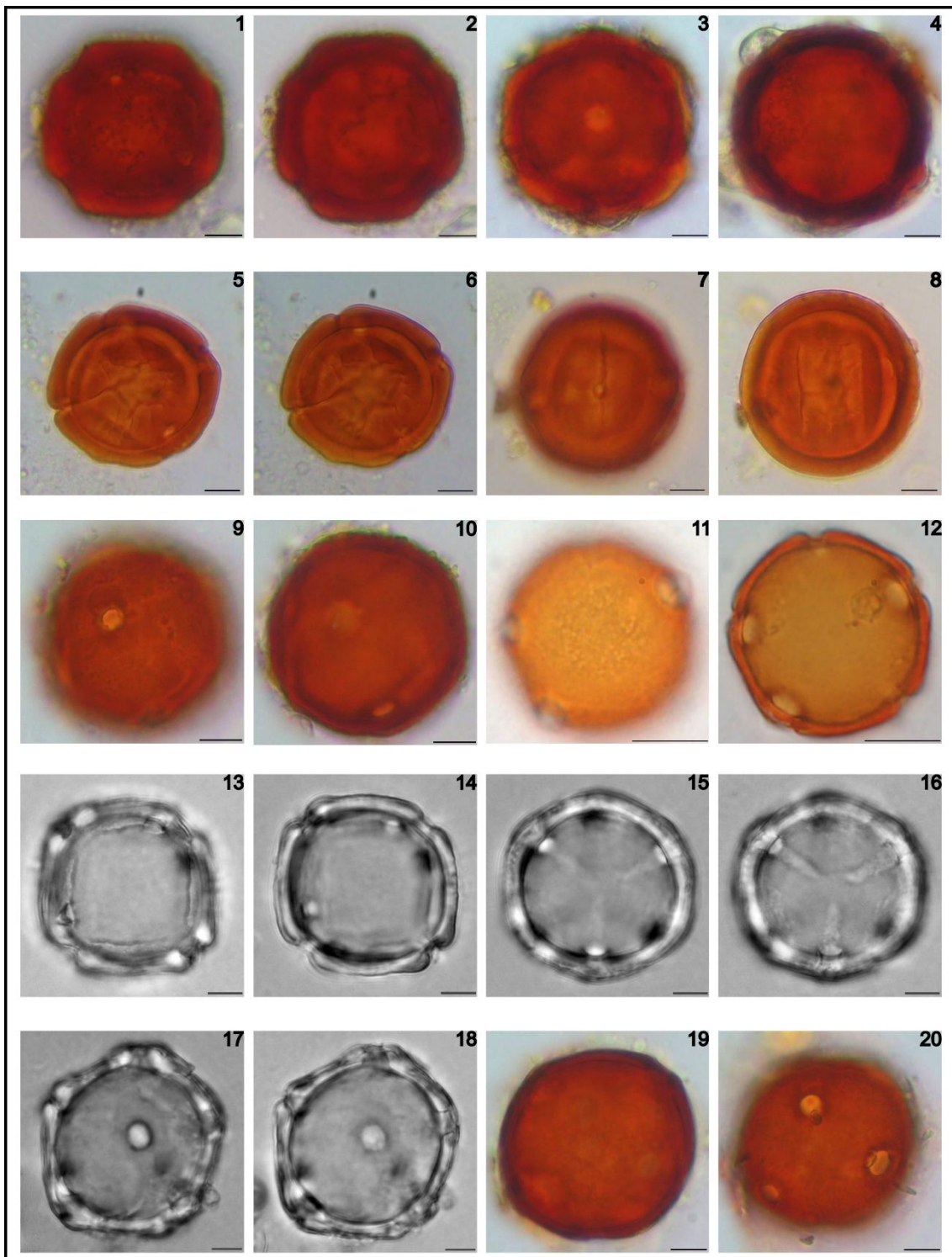


Plate XLIX. Malpighiaceae: *Camarea affinis* (1,2,3,4); *Dicella* sp. (5,6,7,8), *Diplopterys pubipetala* (9,10), *Glicophyllum latibracteolatum* (11,12), *Heteropterys trichanthera* (13,14,15,16), *Peixotoa jussieuana* (17,18), *Stigmaphyllon paralias* (19,20). Scale bars = 10 μ m.

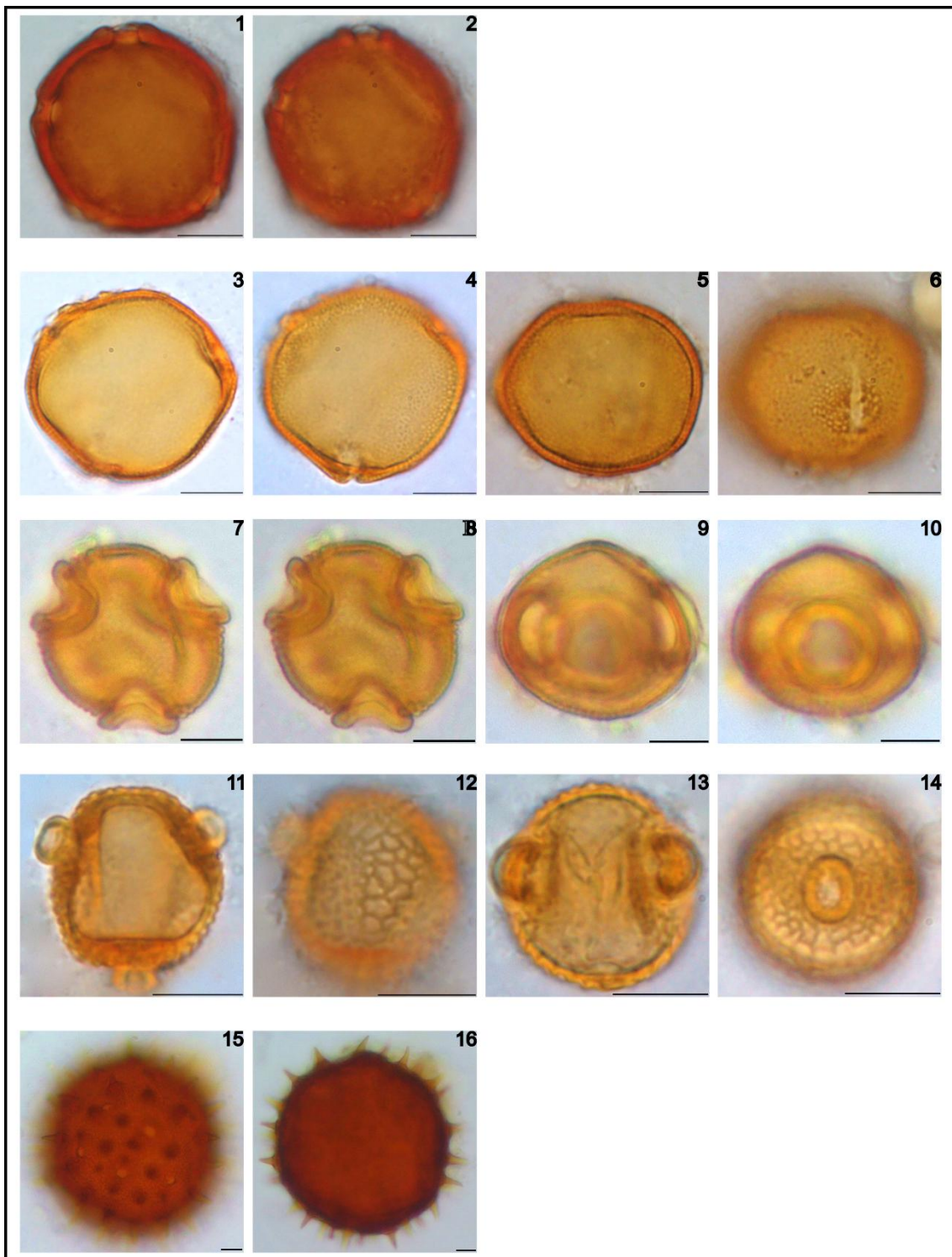


Plate L. Malpighiaceae: *Verrucularina* sp. (1,2); Malvaceae: *Apeiba tibourbou* (3,4,5,6), *Ayenia erecta* (7,8,9,10), *Byttneria divaricata* (11,12,13,14); *Cienfuegosia heterophylla* (15,16). Scale bars = 10 μ m.

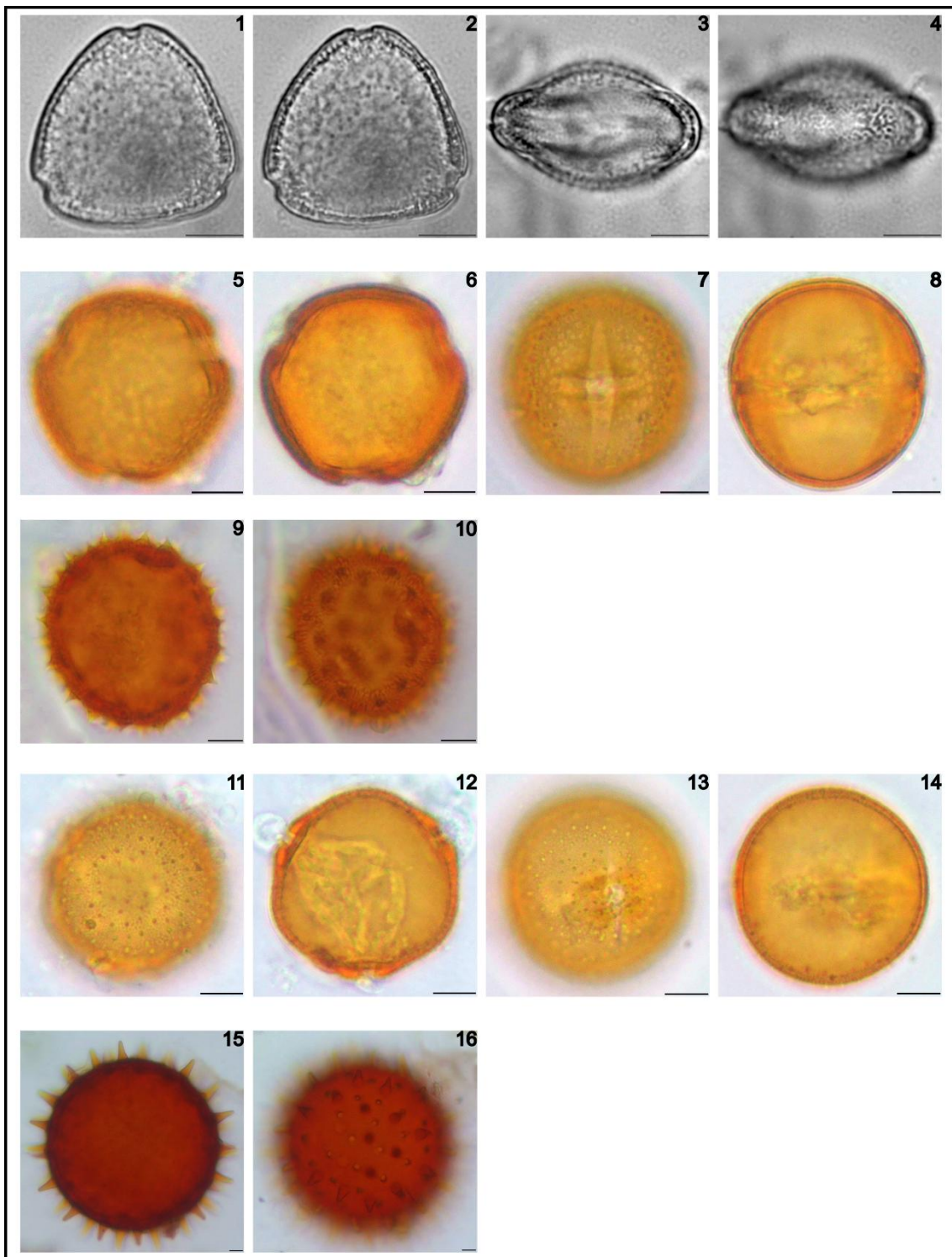


Plate LI. Malvaceae: *Helicteres muscosa* (1,2,3,4), *Luehea candicans* (5,6,7,8), *Malvastrum americanum* (9,10), *Melochia tomentosa* (11,12,13,14), *Pavonia glazioviana* (15,16). Scale bars = 10 μ m.

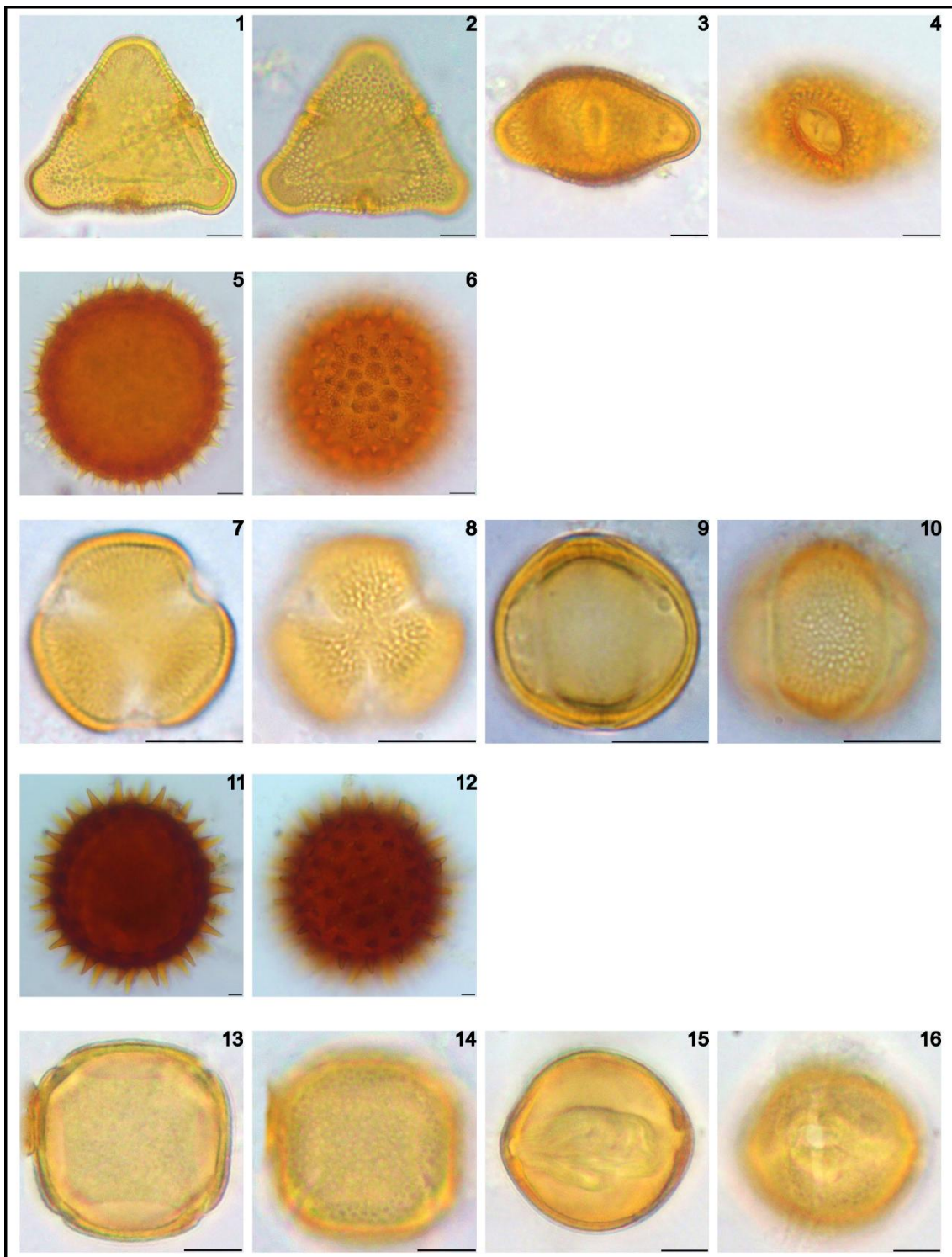


Plate LII. Malvaceae: *Pseudobombax longiflorum* (1,2,3,4), *Sida cordifolia* (5,6), *Sterculia foetida* (7,8,9,10), *Urena lobata* (11,12), *Waltheria brachypetala* (13,14,15,16). Scale bars = 10 μ m.

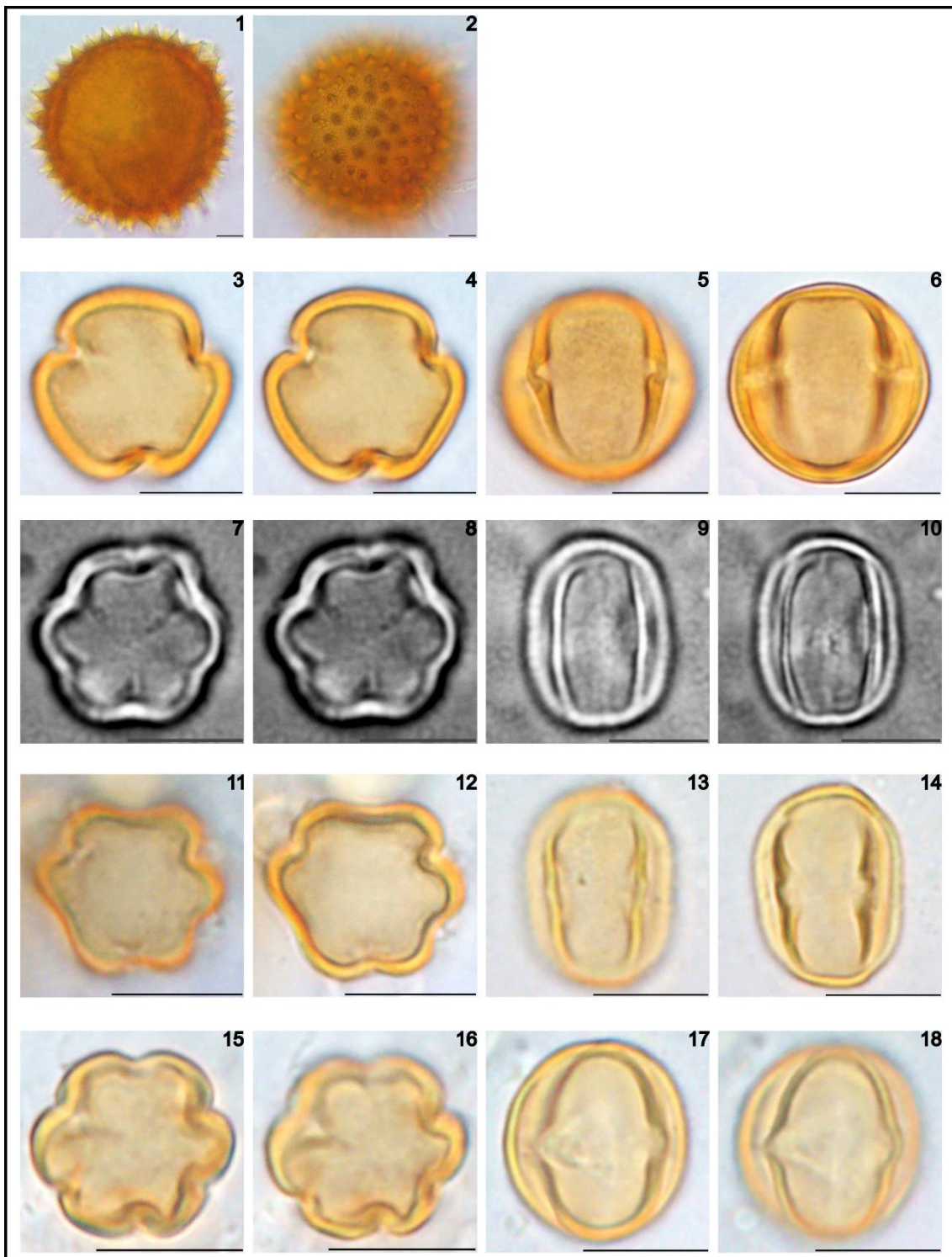


Plate LIII. Malvaceae: *Wissadula amplissima* (1,2); Marcgraviaceae: *Schwartzia adamantium* (3,4,5,6); Melastomataceae: *Clidemia biserrata* (7,8,9,10), *Henriettea* sp. (11,12,13,14), *Macairea radula* (15,16,17,18). Scale bars = 10 μ m.

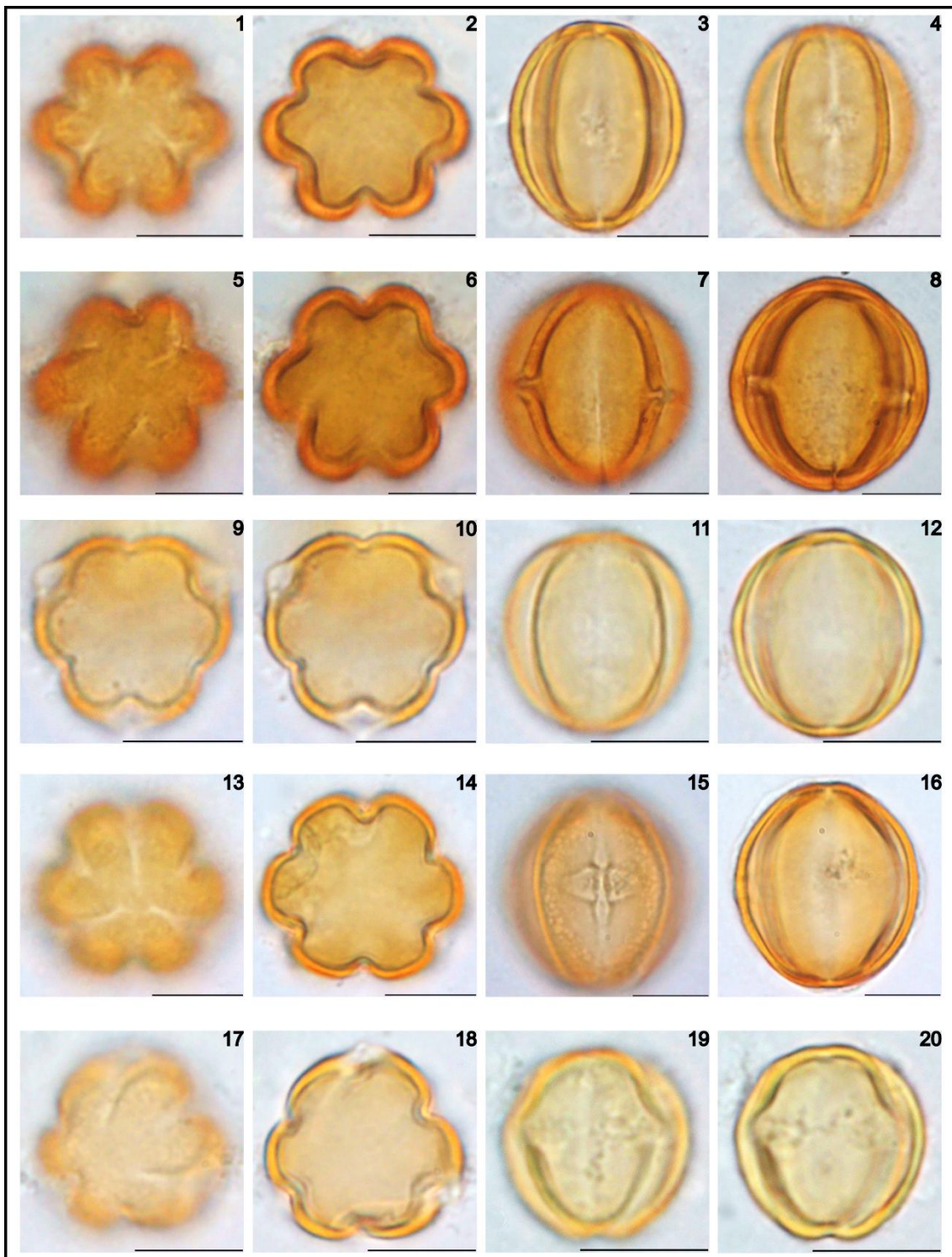


Plate LIV. Melastomataceae: *Marcetia* sp. (1,2,3,4), *Mouriri guianensis* (5,6,7,8); *Pterolepis polygonoides* (9,10,11,12), *Rhynchanthera serrulata* (13,14,15,16), *Tibouchina* sp. (17,18,19,20). Scale bars = 10 μ m.

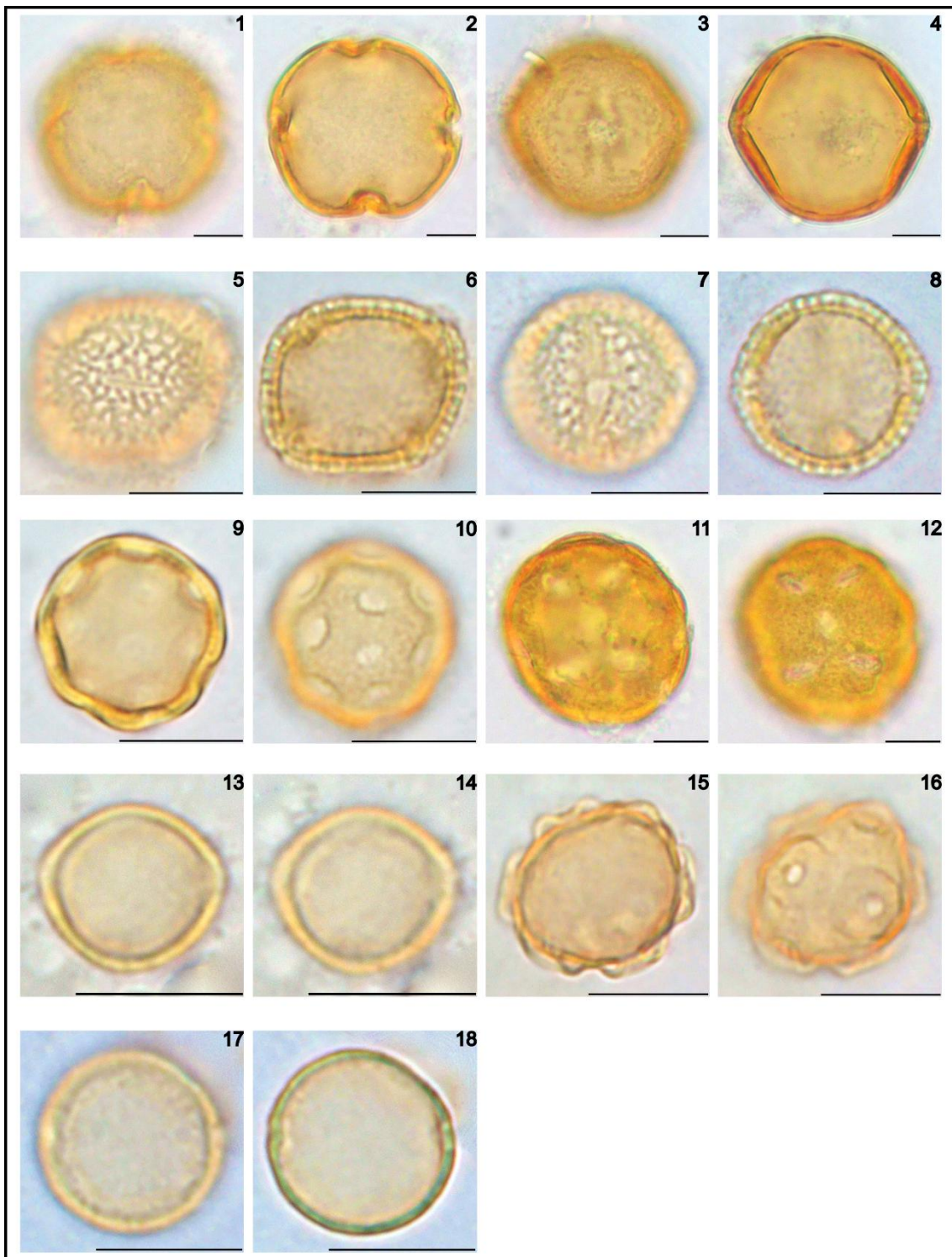


Plate LV. Meliaceae: *Melia azedarach* (1,2,3,4); Menispermaceae: *Cissampelos ovalifolia* (5,6,7,8); Microteaceae: *Microtea sp.* (9,10); Molluginaceae: *Mollugo verticillata* (11,12); Moraceae: *Brosimum gaudichaudii*. (13,14); *Dorstenia cayapia* (15,16); *Maclura tinctoria* (17,18). Scale bars = 10 μ m.

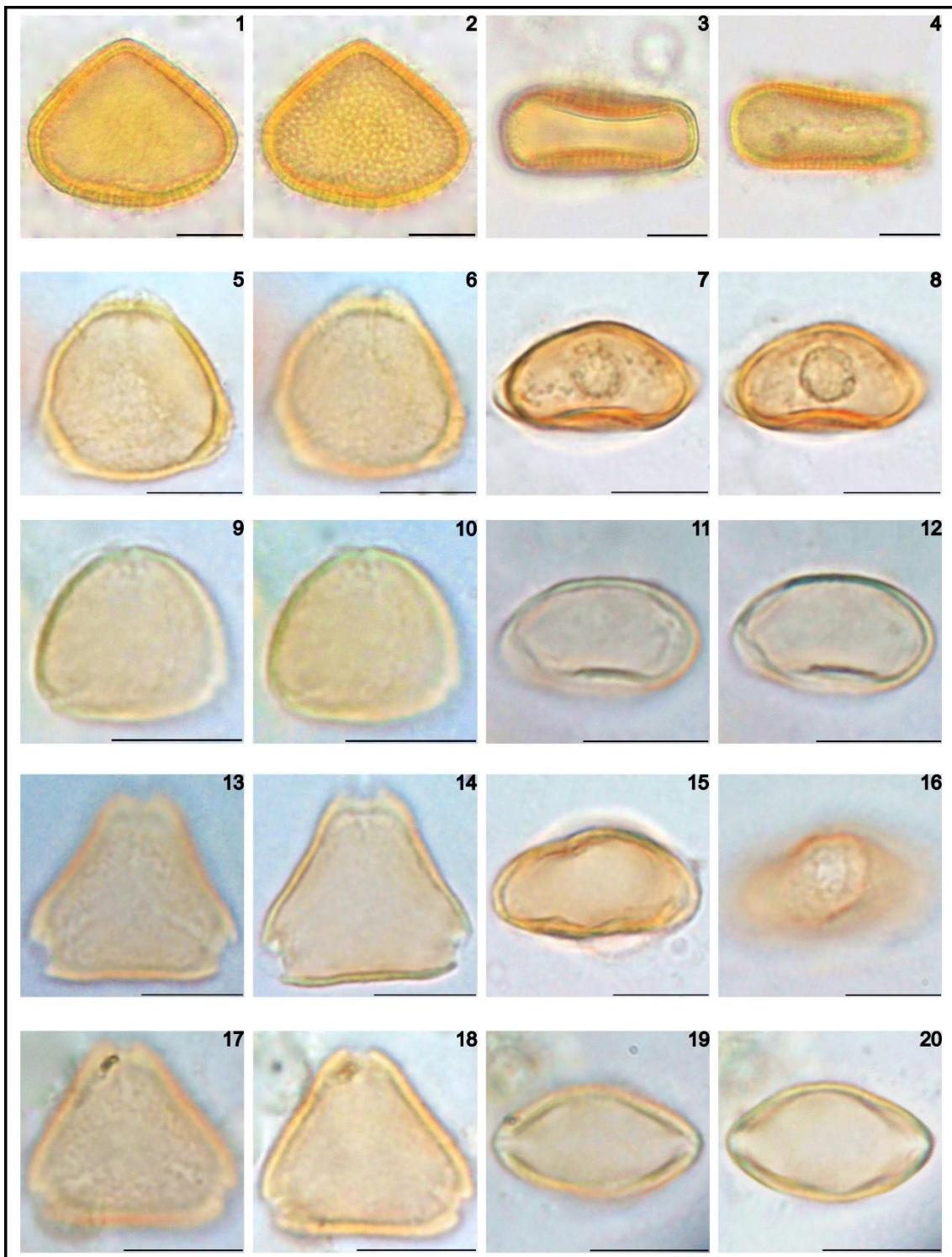


Plate LVI. Myristicaceae: *Virola subsessilis* (1,2,3,4); Myrtaceae: *Campomanesia* sp. (5,6,7,8); *Eugenia gracillima* (9,10,11,12), *Myrcia guianensis* (13,14,15,16), *Psidium myrsinites* (17,18,19,20). Scale bars = 10 μ m.

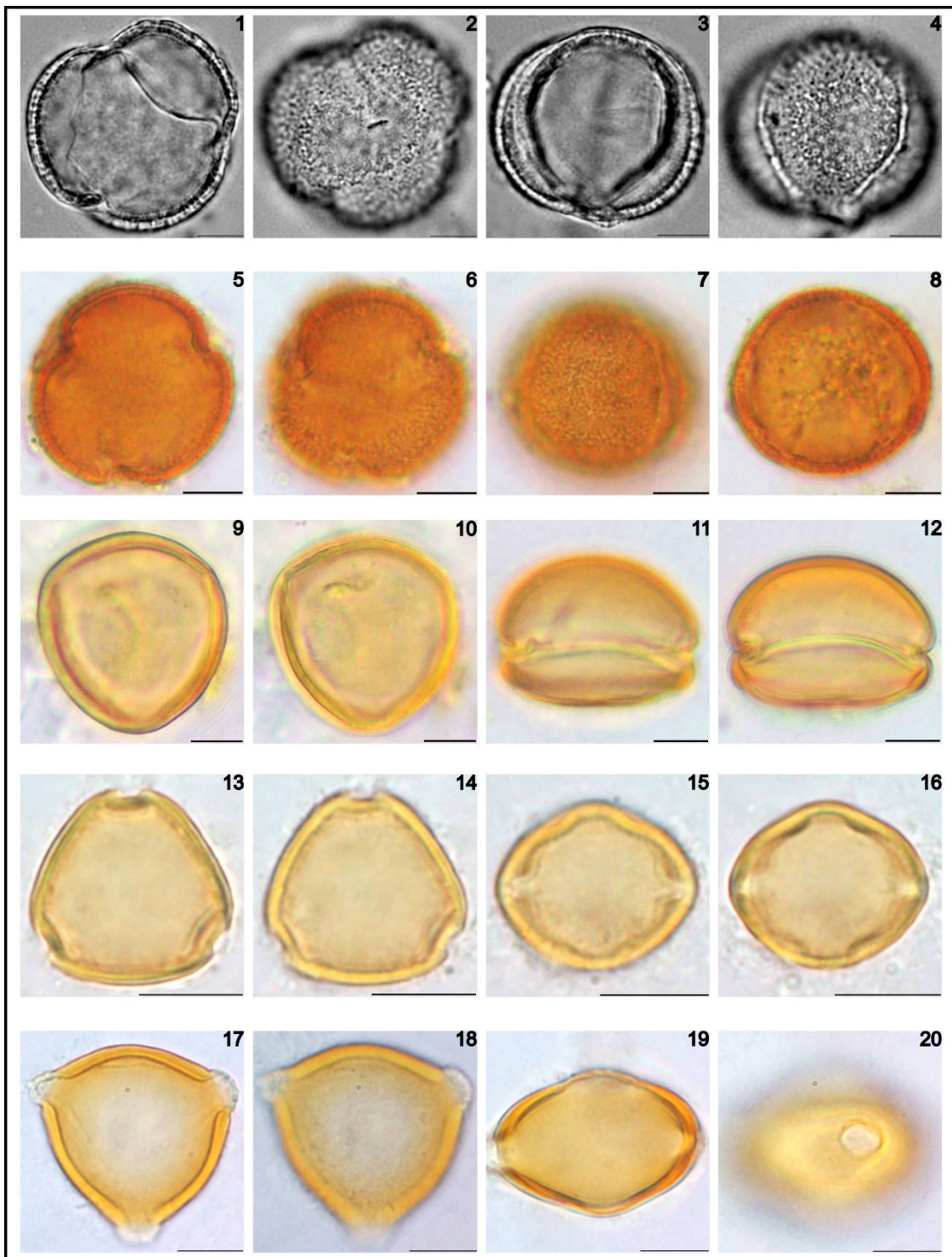


Plate LVII. Nyctaginaceae: *Guapira opposita* (1,2,3,4), *Pisonia sp.* (5,6,7,8); Nymphaeaceae: *Nymphaea jamesoniana* (9,10,11,12); Ochnaceae: *Ouratea castaneifolia* (13,14,15,16); Olacaceae: *Dulacia sp.* (17,18,19,20). Scale bars = 10 μ m.

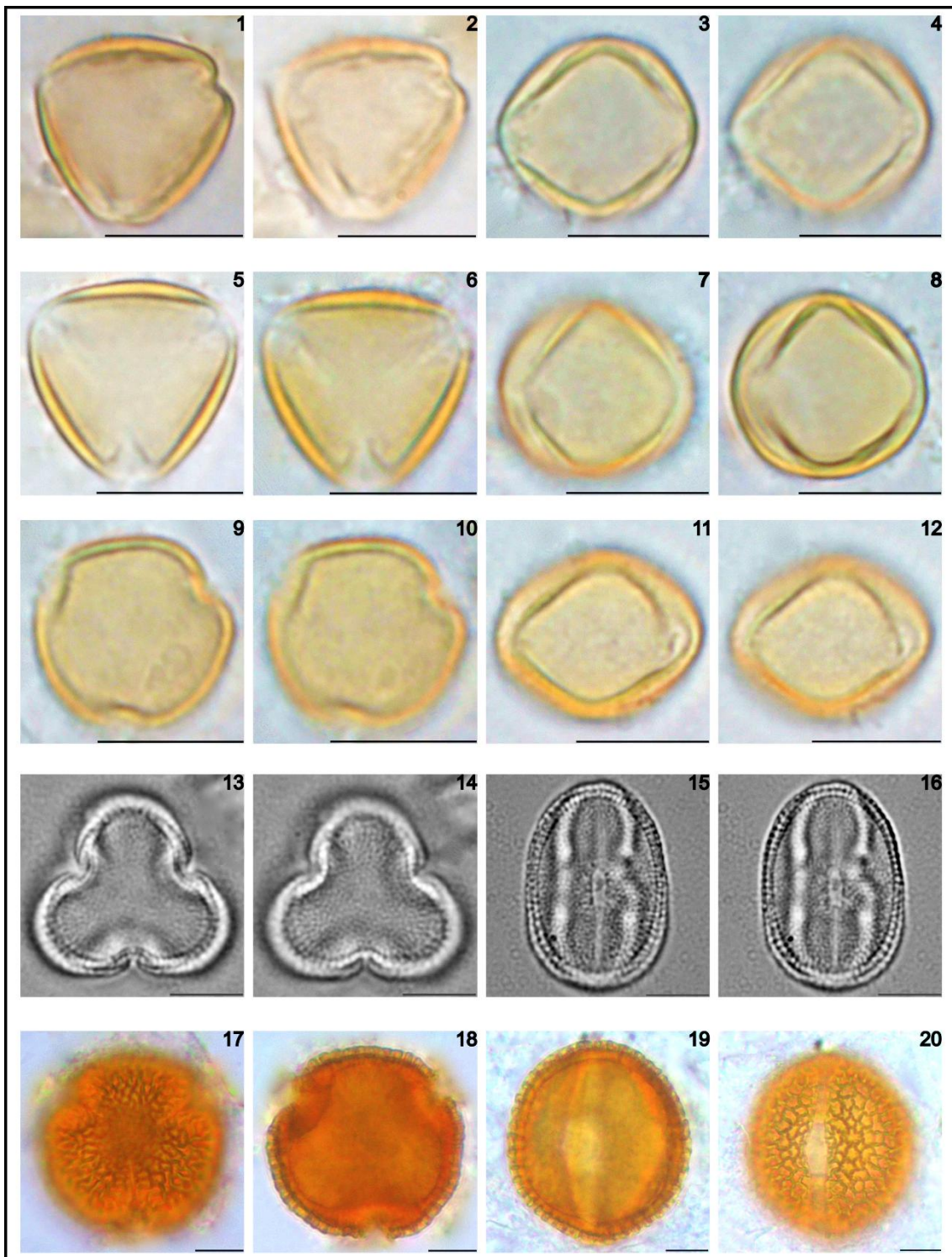


Plate LVIII. Olacaceae: *Heisteria ovata* (1,2,3,4), *Ximenia coriacea* (5,6,7,8); Opiliaceae: *Agonandra brasiliensis* (9,10,11,12); Oxalidaceae: *Oxalis divaricata* (13,14,15,16); Passifloraceae: *Mitostemma brevifilis* (17,18,19,20). Scale bars = 10 μ m.

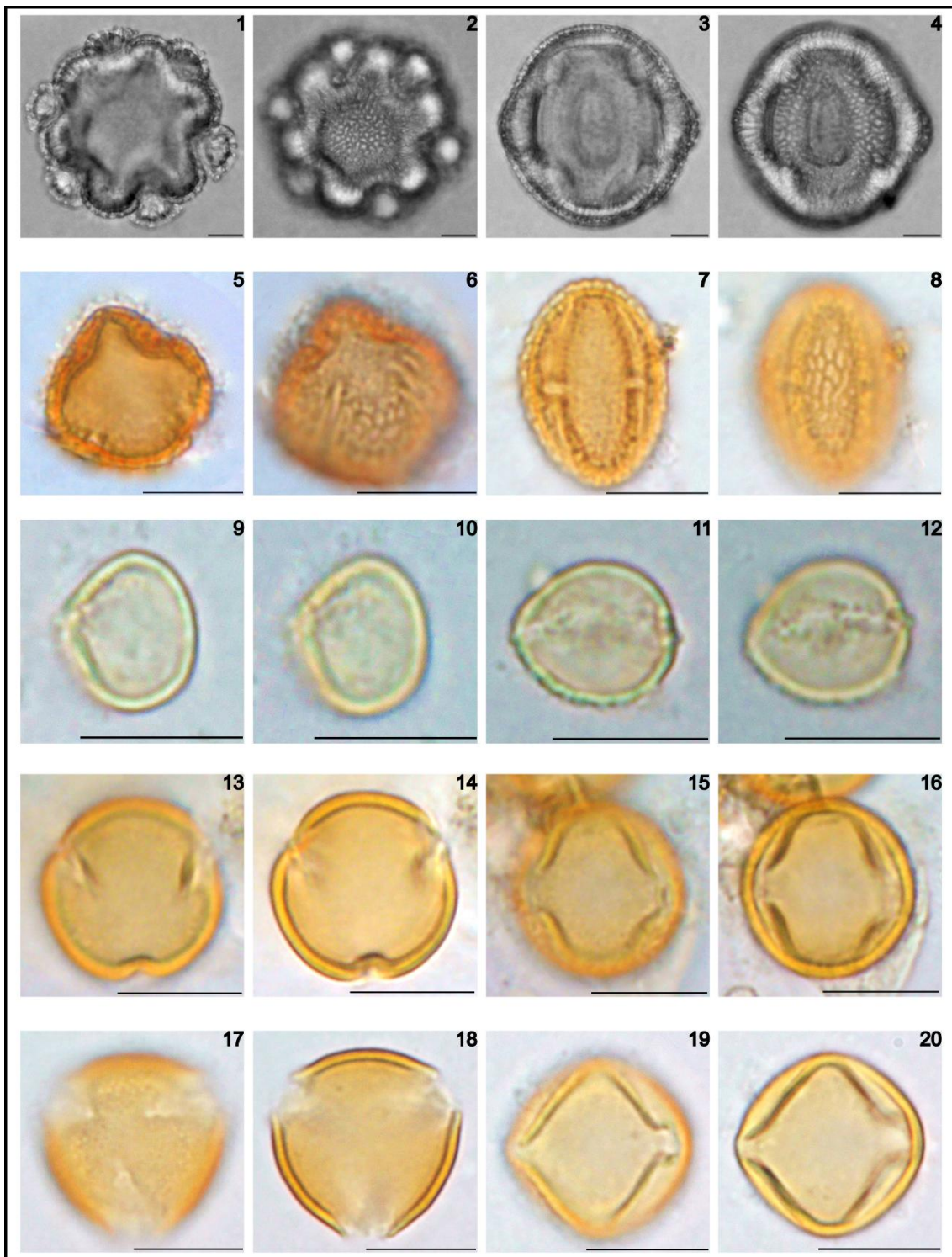


Plate LIX. Passifloraceae: *Passiflora cincinnata* (1,2,3,4); Phyllanthaceae: *Phyllanthus clausseii* (5,6,7,8); Piperaceae: *Piper tuberculatum* (9,10,11,12); Plantaginaceae: *Angelonia cornigera* (13,14,15,16), *Bacopa angulata* (17,18,19,20). Scale bars = 10 μ m.

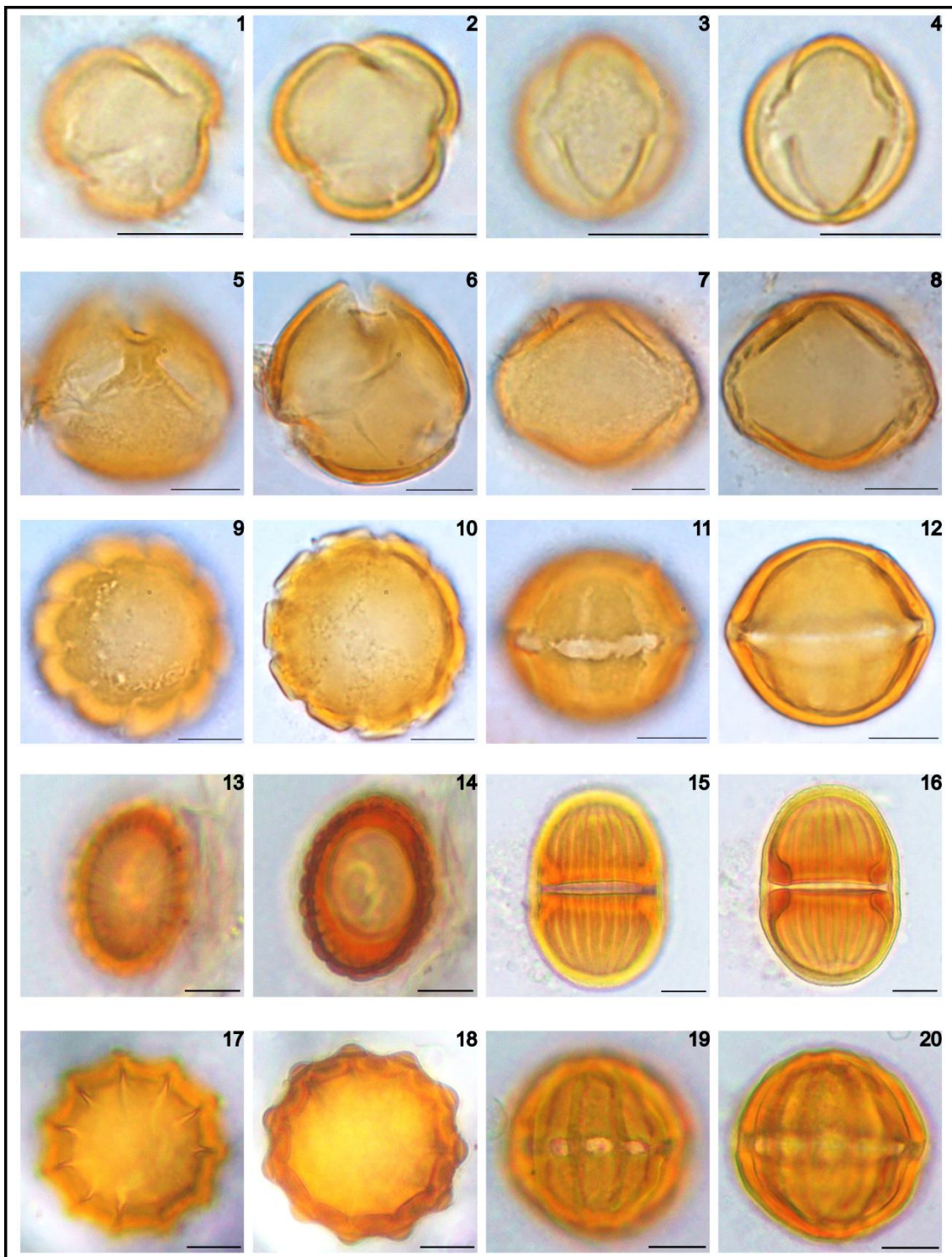


Plate LX. Plantaginaceae: *Stemodia maritima* (1,2,3,4), *Tetraulacium veroniciforme* (5,6,7,8); Polygalaceae: *Bredemeyera floribunda* (9,10,11,12), *Monnina insignis* (13,14,15,16), *Polygala trichosperma* (17,18,19,20). Scale bars = 10 μ m.

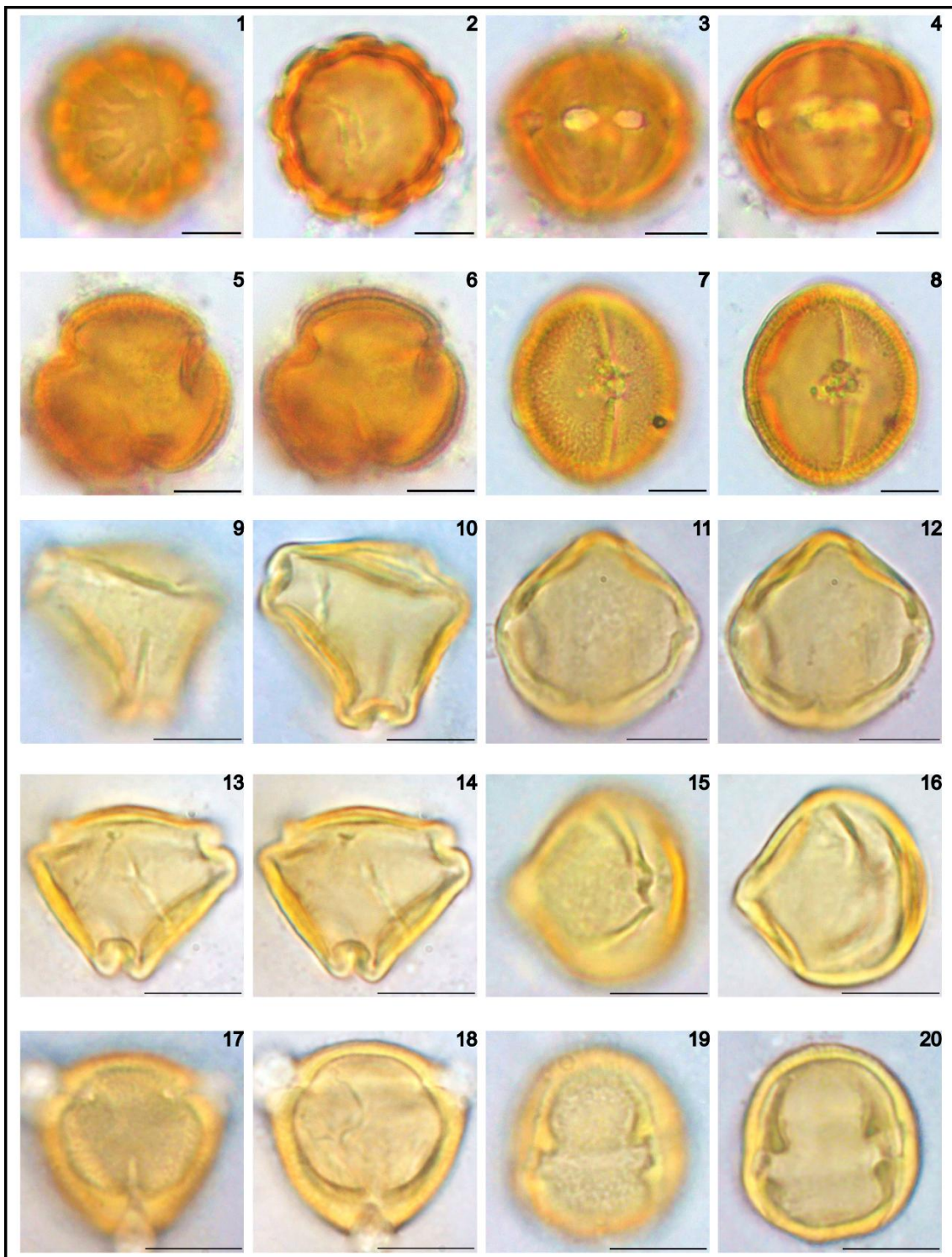


Plate LXI. Polygalaceae: *Securidaca coriacea* (1,2,3,4); Polygonaceae: *Coccoloba mollis* (5,6,7,8); Rhamnaceae: *Colubrina cordifolia* (9,10,11,12), *Rhamnidium molle* (13,14,15,16); Rhizophoraceae: *Rhizophora mangle* (17,18,19,20). Scale bars = 10 μ m.

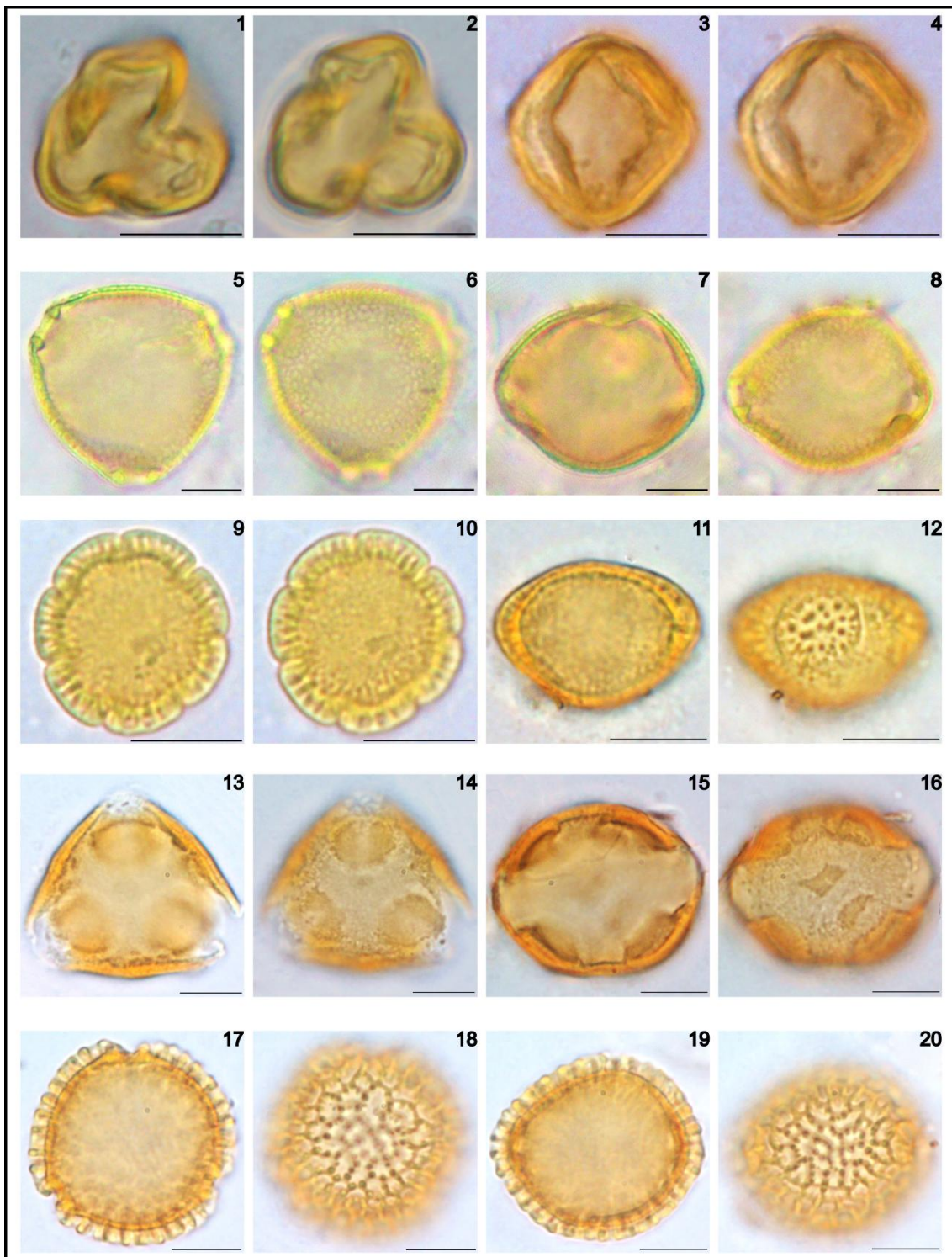


Plate LXII. Rosaceae: *Eriobotrya japonica* (1,2,3,4); Rubiaceae: *Alibertia edulis* (5,6,7,8); *Borreria diacrodonta* (9,10,11,12), *Chiococca alba* (13,14,15,16), *Chomelia obtusa* (17,18,19,20). Scale bars = 10 μm .

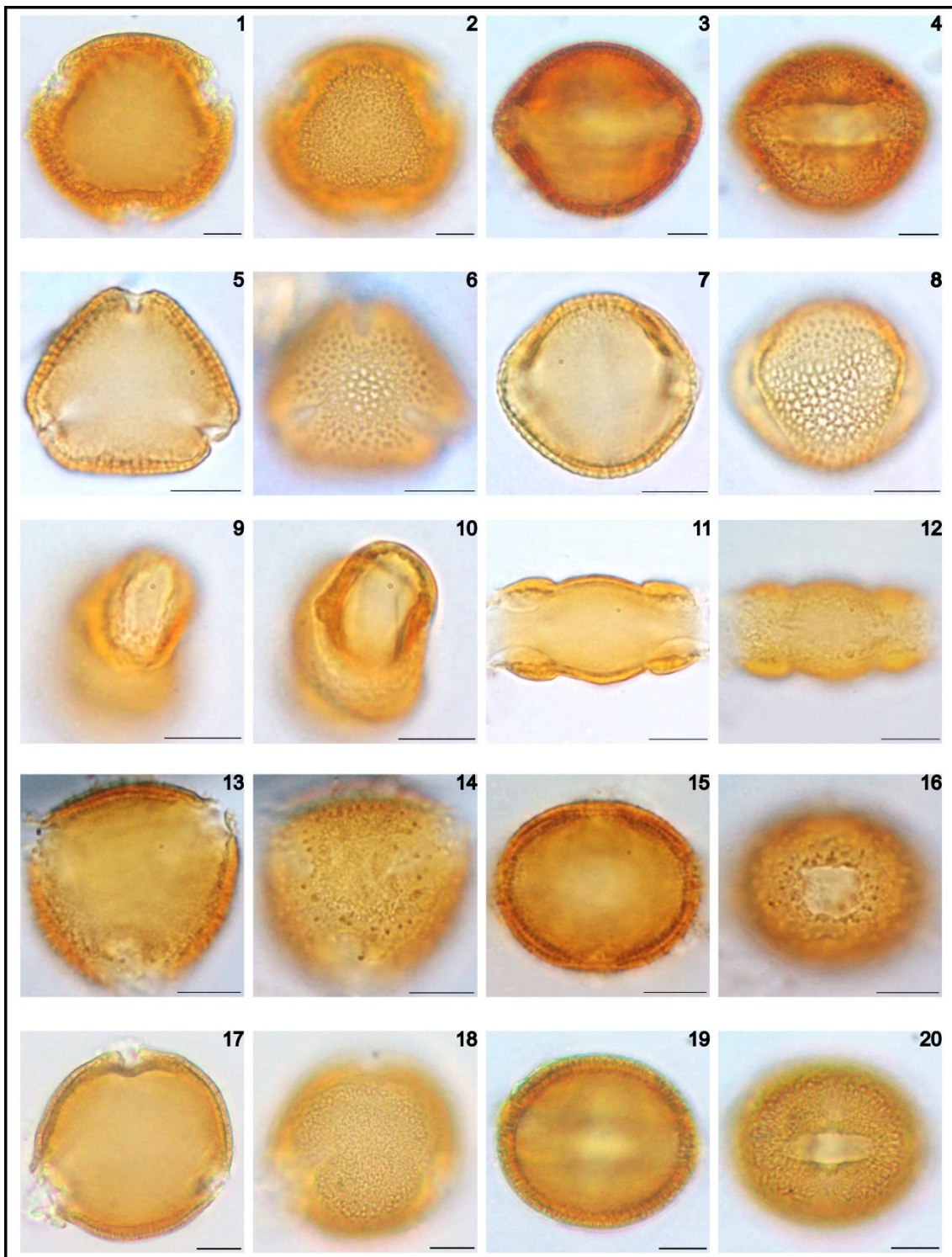


Plate LXIII. Rubiaceae: *Coccocypselum lanceolatum* (1,2,3,4), *Cordia myrciifolia* (5,6,7,8), *Coussarea hydrangeifolia* (9,10,11,12), *Coutarea hexandra* (13,14,15,16), *Declieuxia fruticosa* (17,18,19,20). Scale bars = 10 μ m.

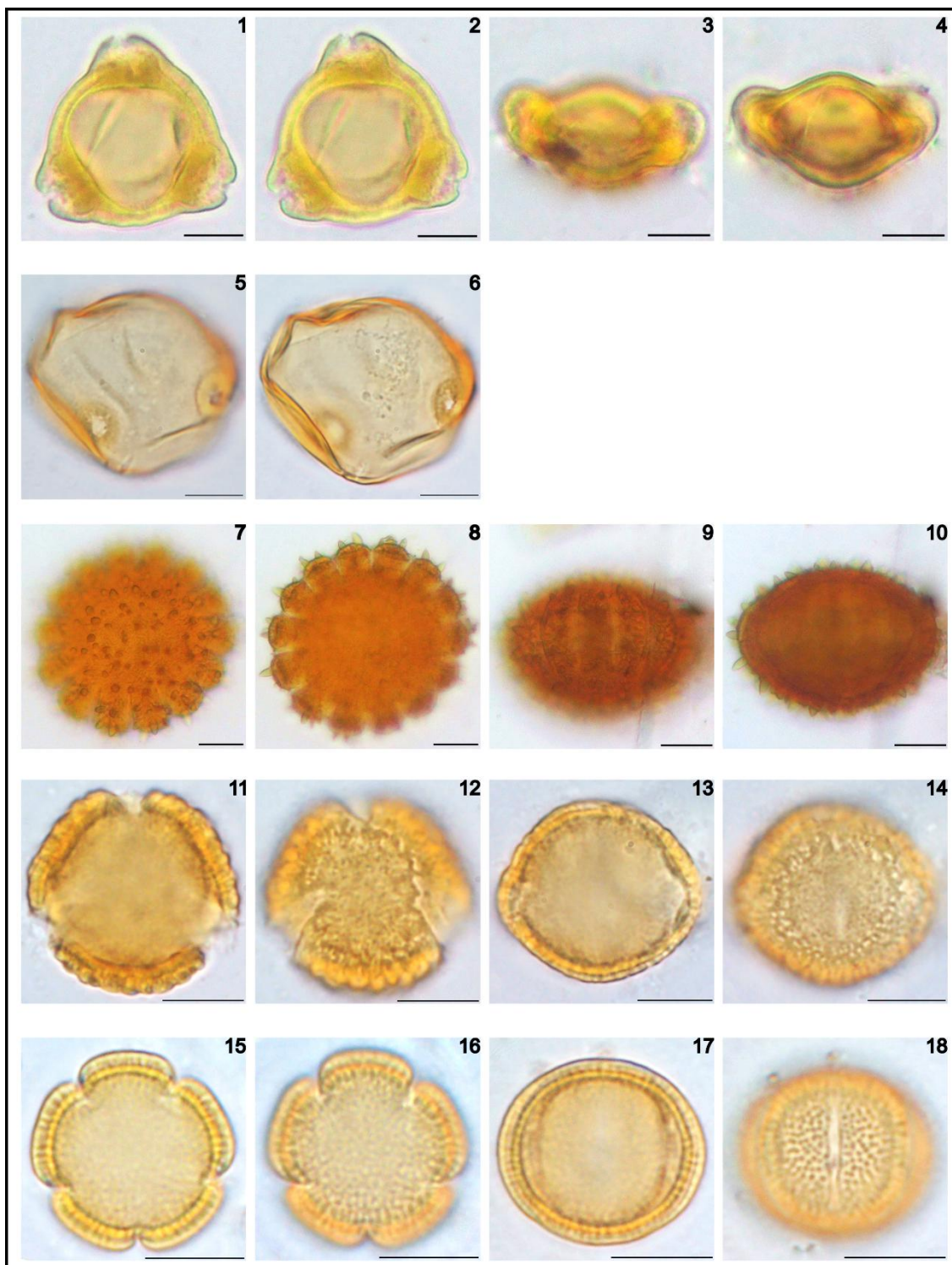


Plate LXIV. Rubiaceae: *Faramaea nitida* (1,2,3,4), *Guettarda viburnoides* (5,6), *Hexasepalum apiculatum* (7,8,9,10), *Machaonia acuminata* (11,12,13,14), *Mitracarpus baturitensis* (15,16,17,18). Scale bars = 10 μ m.

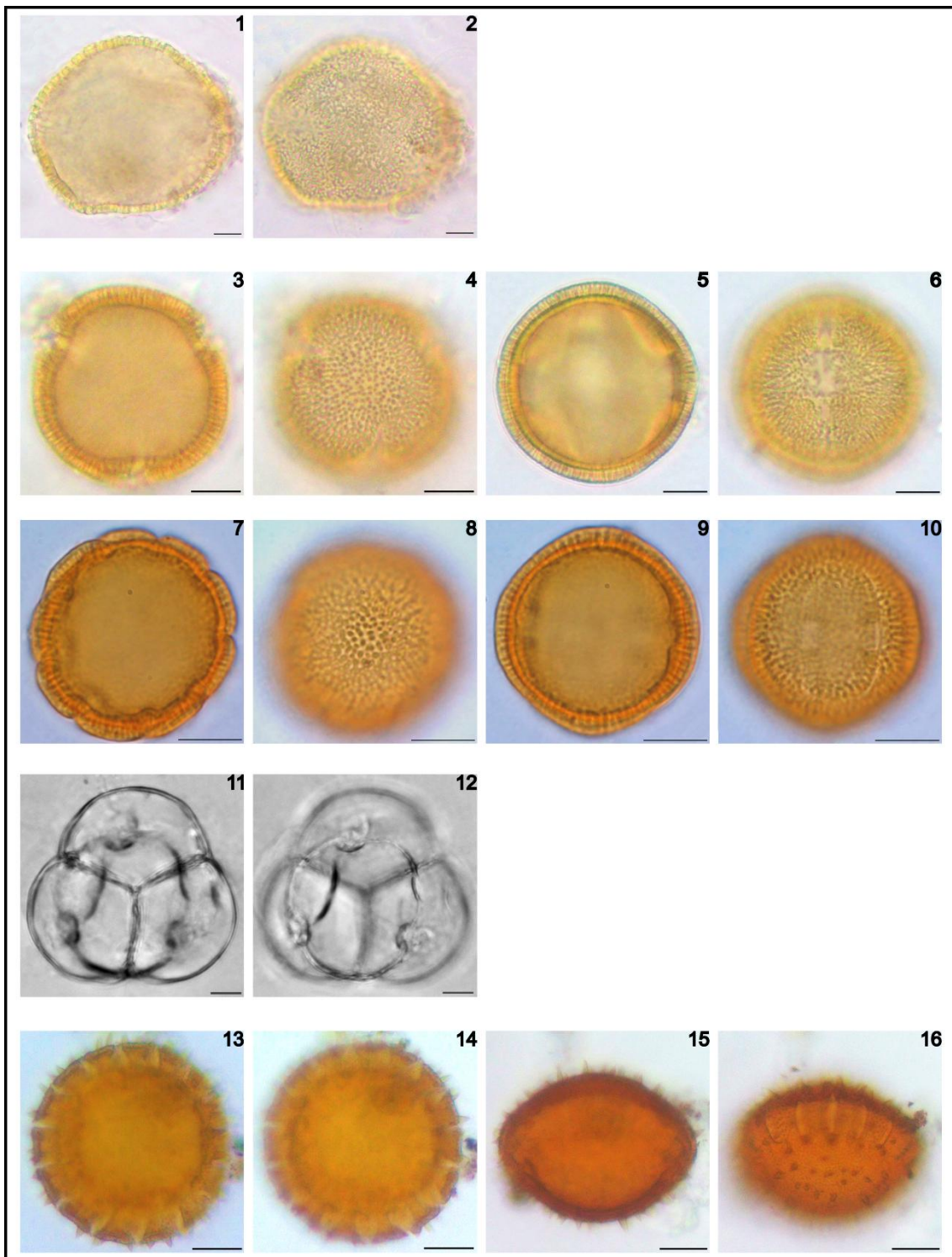


Plate LXV. Rubiaceae: *Palicourea veterinariorum* (1,2), *Perama hirsute* (3,4,5,6), *Psyllocarpus* sp. (7,8,9,10), *Randia armata* (11,12), *Richardia grandiflora* (13,14,15,16). Scale bars = 10 μ m.

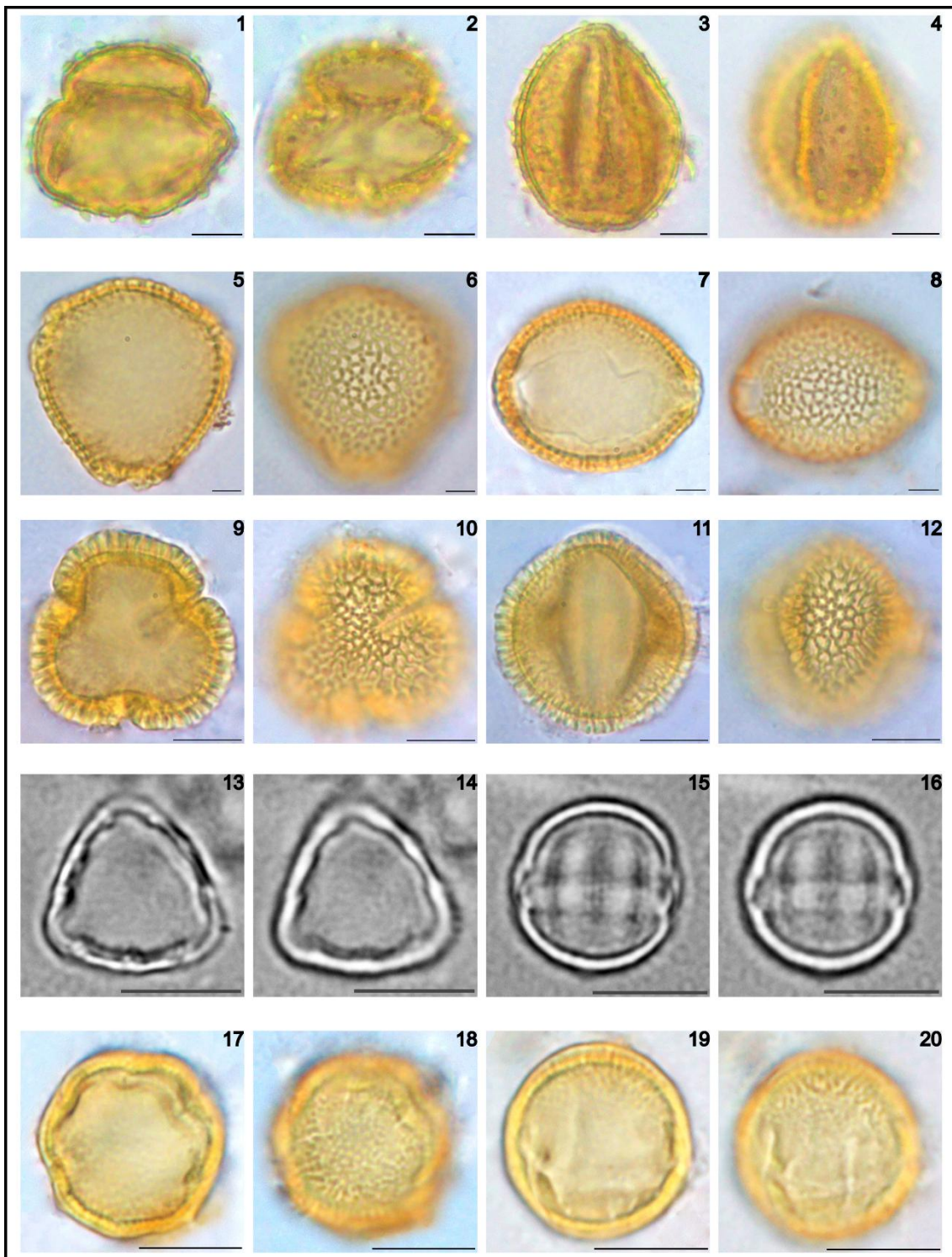


Plate LXVI. Rubiaceae: *Rudgea sp.* (1,2,3,4), *Sabicea cinerea* (5,6,7,8), *Simira gardneriana* (9,10,11,12), *Spermacoce confusa* (13,14,15,16), *Spermacoce reflexa* (17,18,19,20). Scale bars = 10 μm .

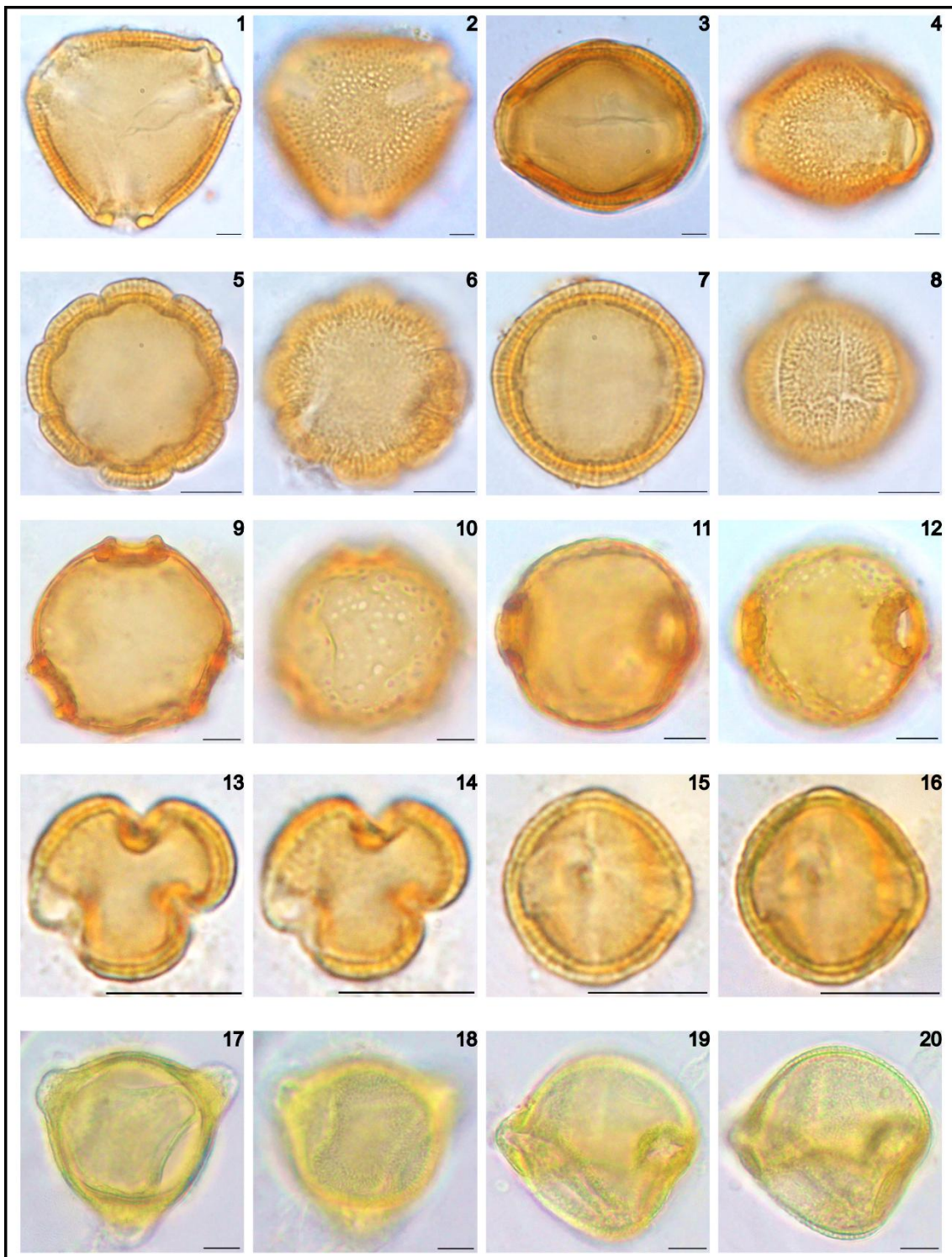


Plate LXVII. Rubiaceae: *Stachyarrhena* sp. (1,2,3,4), *Staelia virgata* (5,6,7,8), *Tocoyena hispidula* (9,10,11,12), *Warszewiczia schwackei* (13,14,15,16); Rutaceae: *Ertela trifolia* (17,18,19,20). Scale bars = 10 μ m.

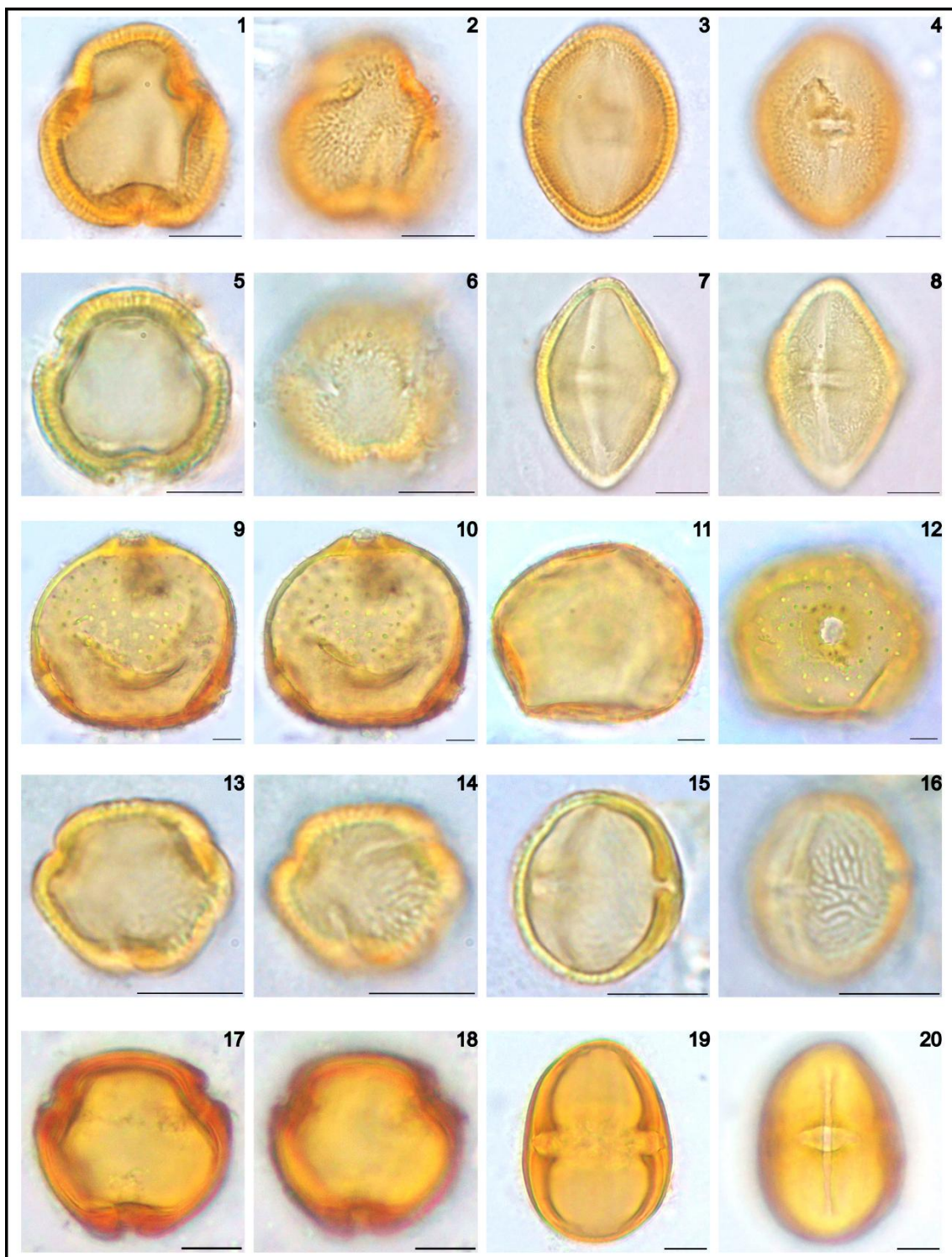


Plate LXVIII. Rutaceae: *Esenbeckia pumila* (1,2,3,4), *Pilocarpus trachylophus* (5,6,7,8), *Spiranthera odoratissima* (9,10,11,12), *Zanthoxylum stelligerum* (13,14,15,16); Salicaceae: *Casearia grandiflora* (17,18,19,20). Scale bars = 10 μ m.

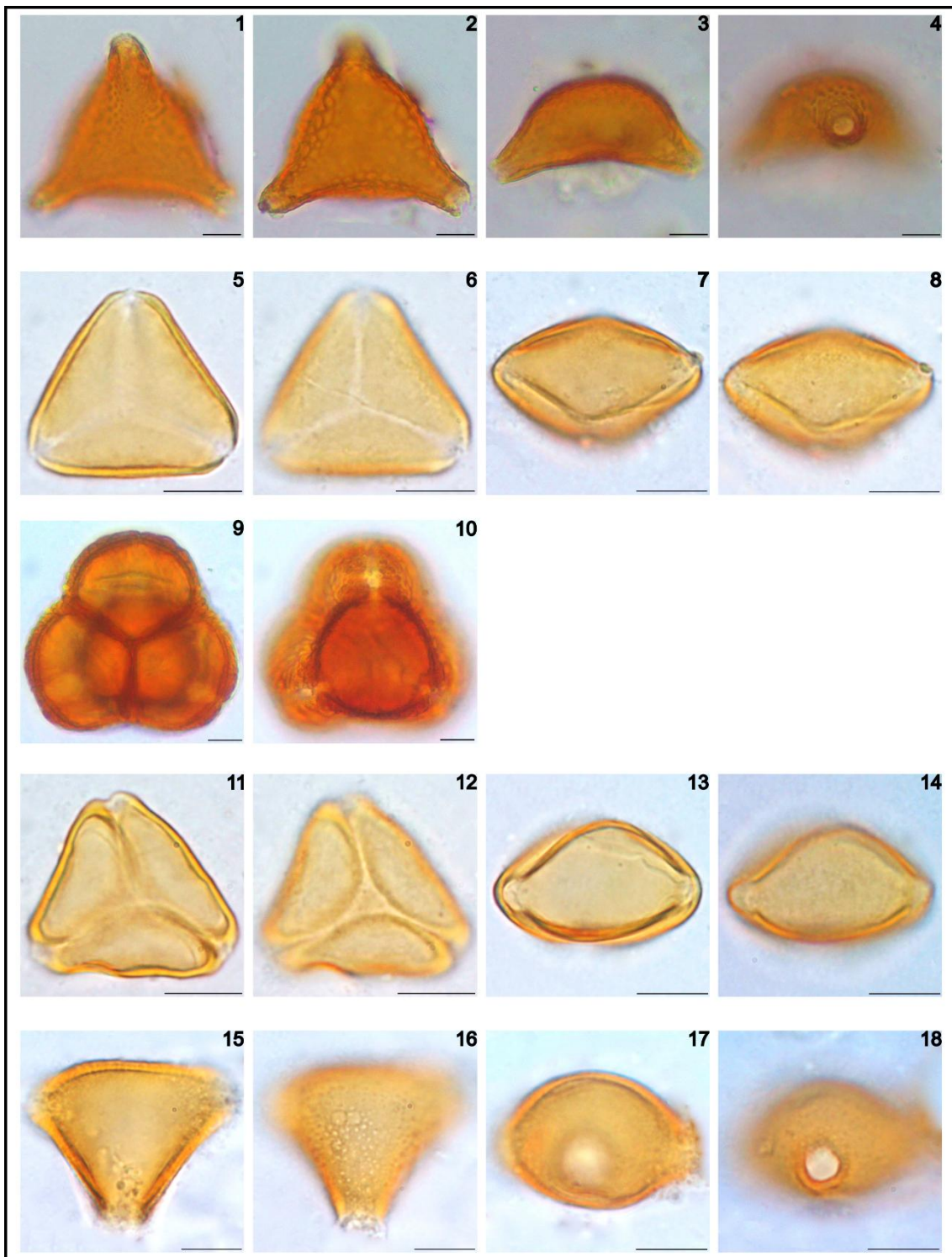


Plate LXIX. Sapindaceae: *Cardiospermum anomalum* (1,2,3,4), *Cupania sp.* (5,6,7,8), *Magonia pubescens* (9,10), *Matayba sp.* (11,12,13,14), *Paullinia sp.* (15,16,17,18). Scale bars = 10 μ m.

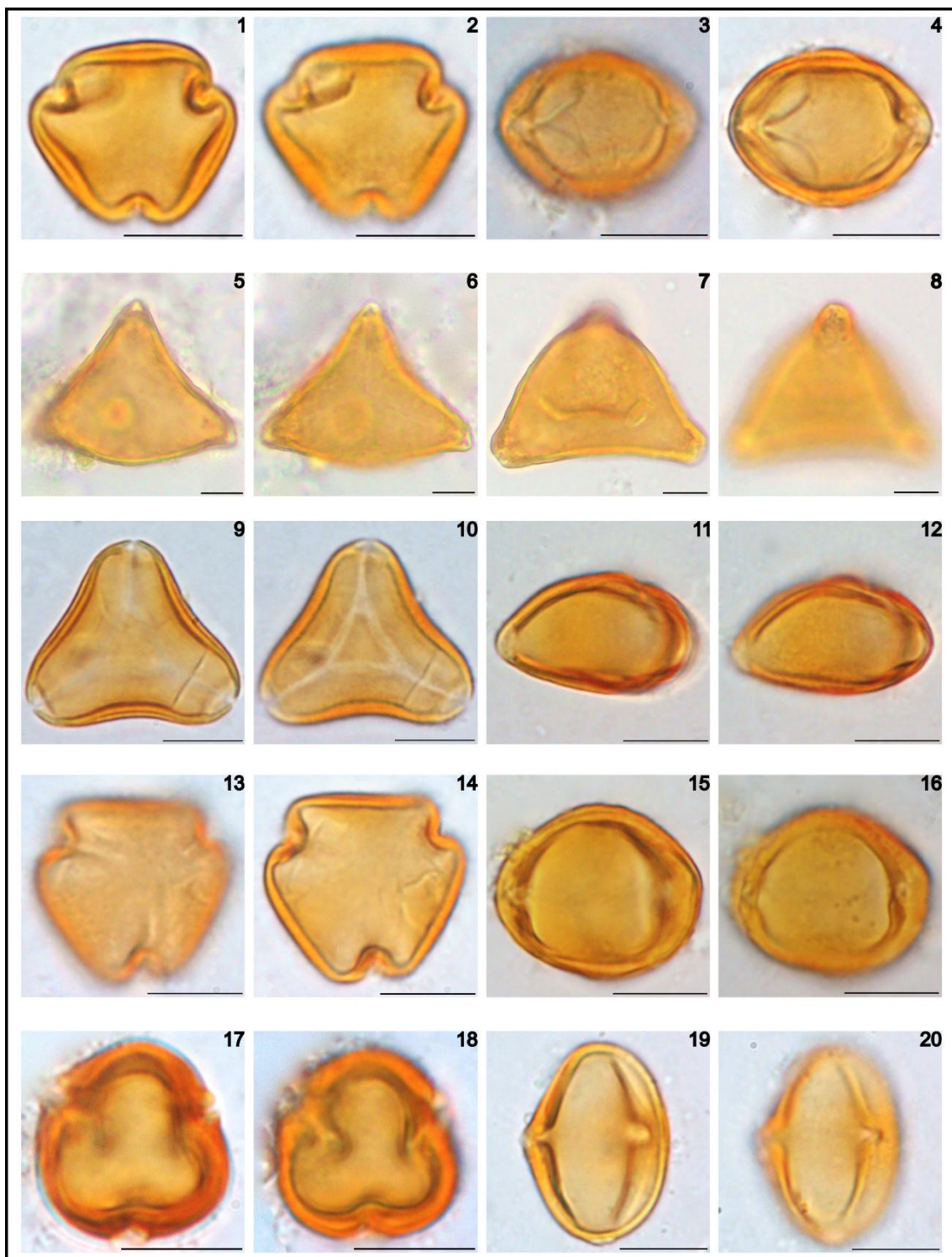


Plate LXX. Sapindaceae: *Sapindus saponaria* (1,2,3,4), *Serjania glabrata* (5,6,7,8), *Talisia* sp. (9,10,11,12), *Toulicia* sp. (13,14,15,16); Sapotaceae: *Chrysophyllum arenarium*. (17,18,19,20). Scale bars = 10 μm.

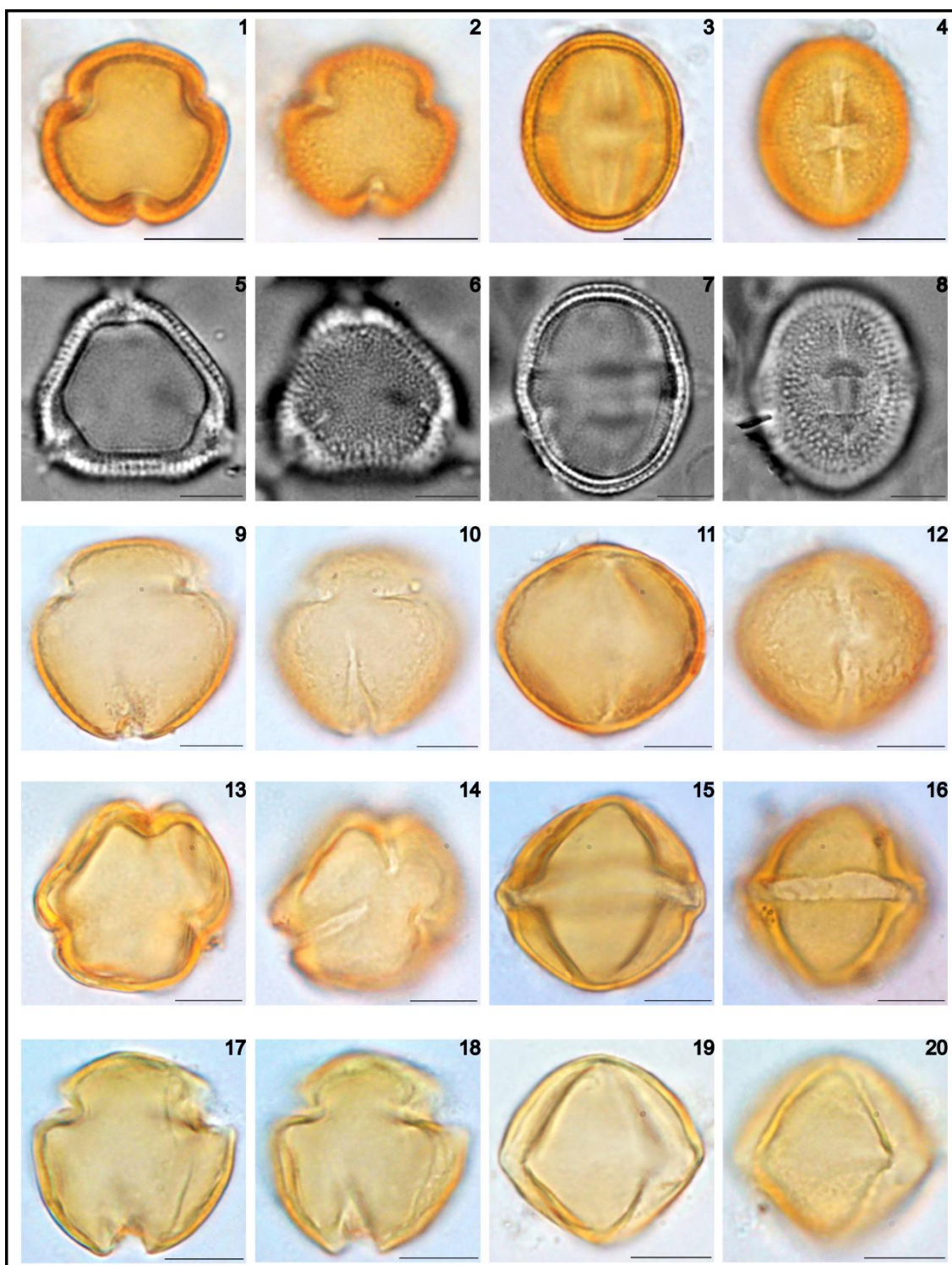


Plate LXXI. Simaroubaceae: *Homalolepis ferruginea* (1,2,3,4), *Homalolepis maiana* (5,6,7,8); Solanaceae: *Brunfelsia uniflora*. (9,10,11,12), *Cestrum* sp. (13,14,15,16), *Nicotiana glauca* (17,18,19,20). Scale bars = 10 μ m.

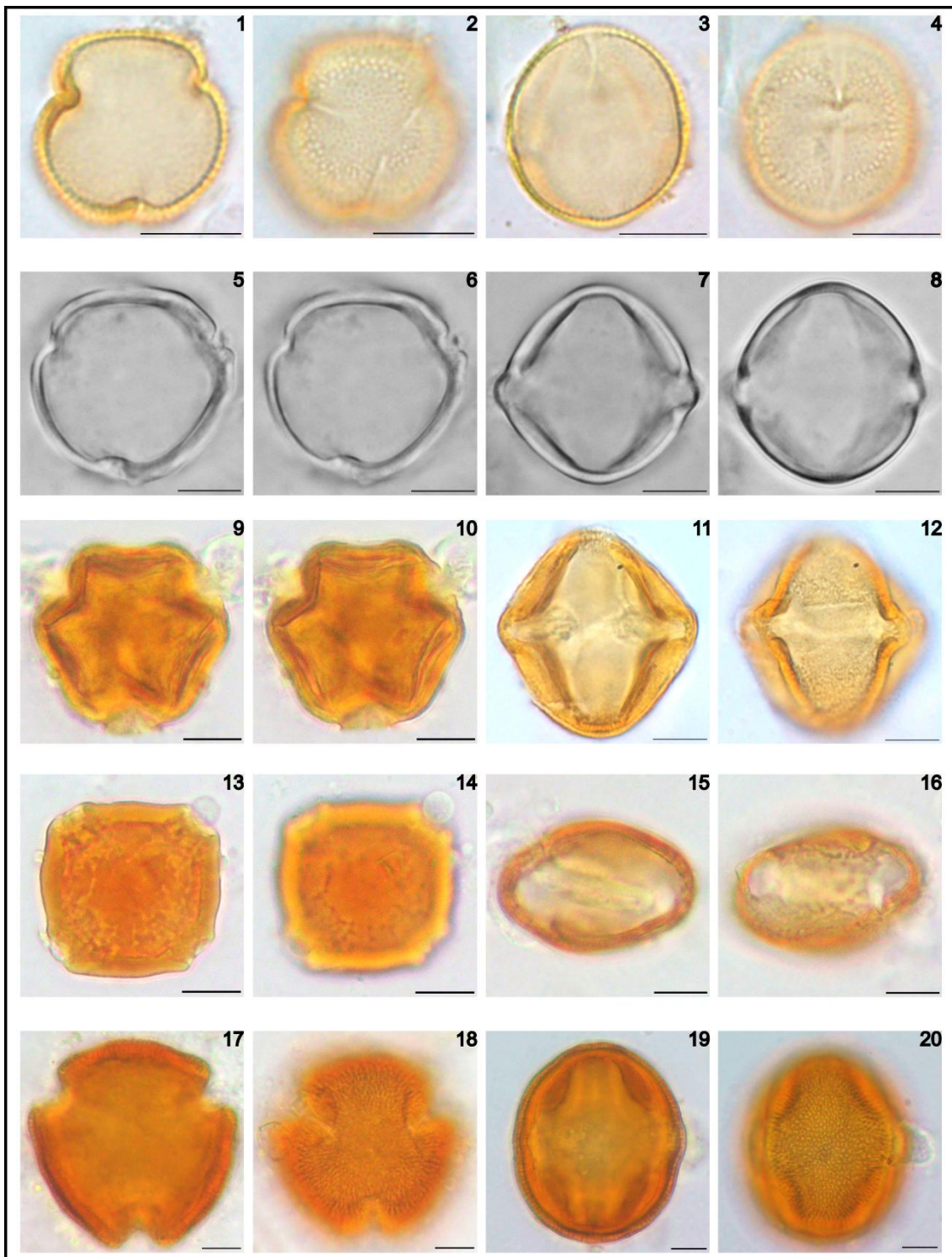


Plate LXXII. Solanaceae: *Schwenckia* sp. (1,2,3,4), *Solanum paniculatum* (5,6,7,8); Styracaceae: *Styrax* sp. (9,10,11,12); Trigonaceae: *Trigoniasp.* (13,14,15,16); Turneraceae: *Piriqueta plicata* (17,18,19,20). Scale bars = 10 μ m.

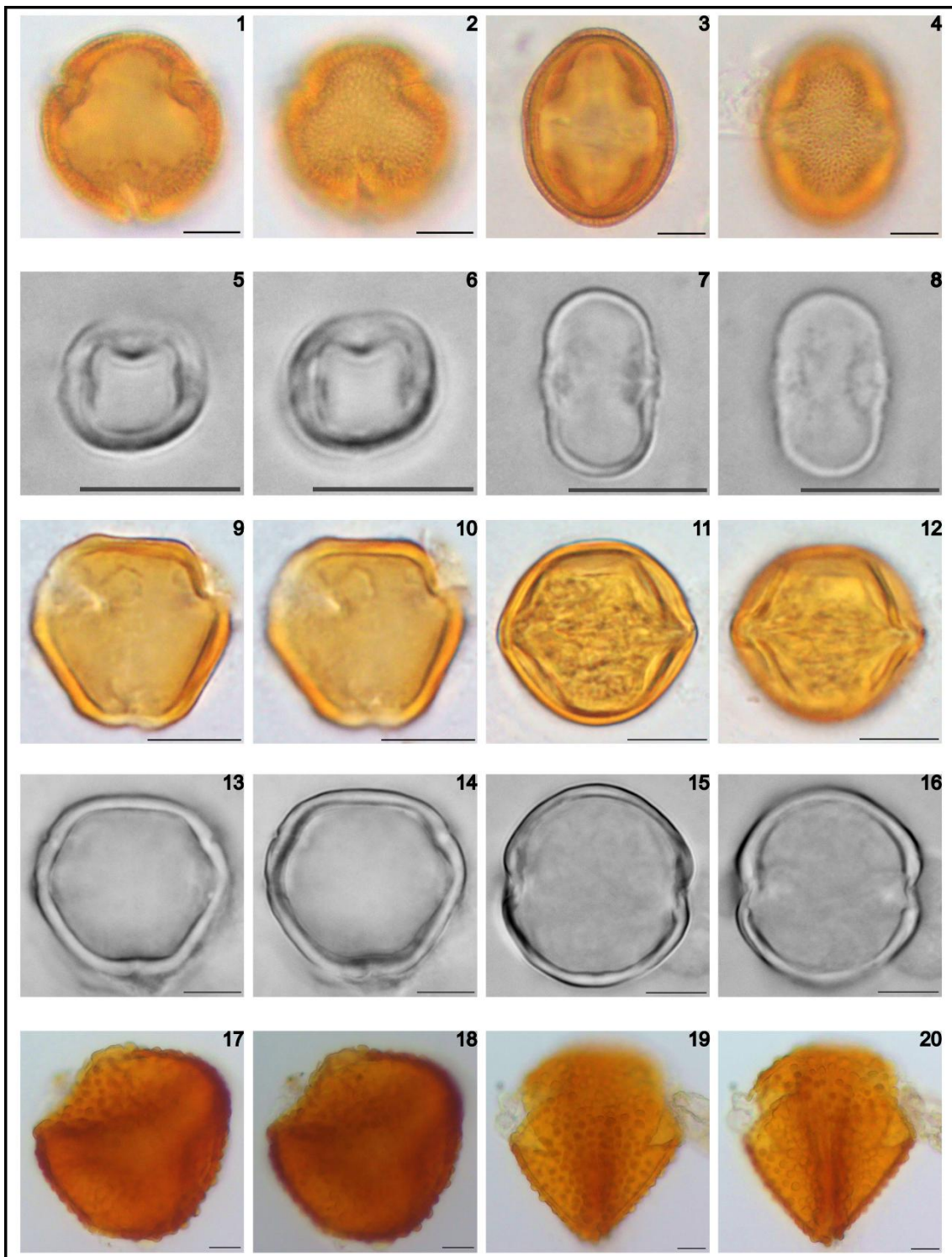


Plate LXXIII. Turneraceae: *Turnera blanchetiana* (1,2,3,4); Urticaceae: *Cecropia pachystachya* (5,6,7,8); Verbenaceae: *Aloysia gratissima* (9,10,11,12), *Lippia organoides* (13,14,15,16), *Stachytarpheta lythrophylla* (17,18,19,20). Scale bars = 10 μ m.

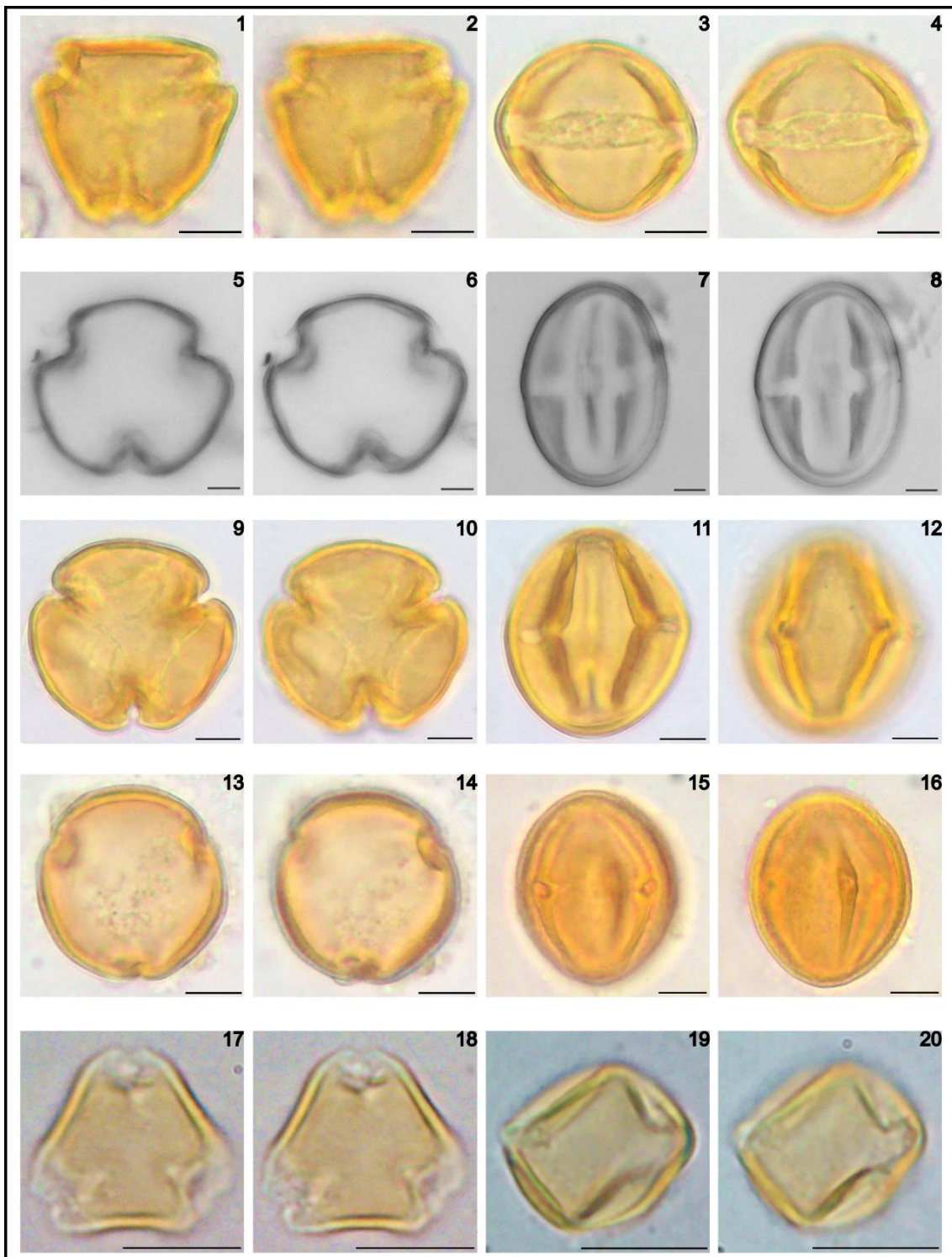


Plate LXXIV. Violaceae: *Calyptrion* sp. (1,2,3,4), *Hybanthus* sp. (5,6,7,8), *Pombalia calceolaria* (9,10,11,12); Vitaceae: *Clematicissus simsiana* (13,14,15,16); Vochysiaceae: *Callisthene microphylla* (17,18,19,20). Scale bars = 10 μ m.

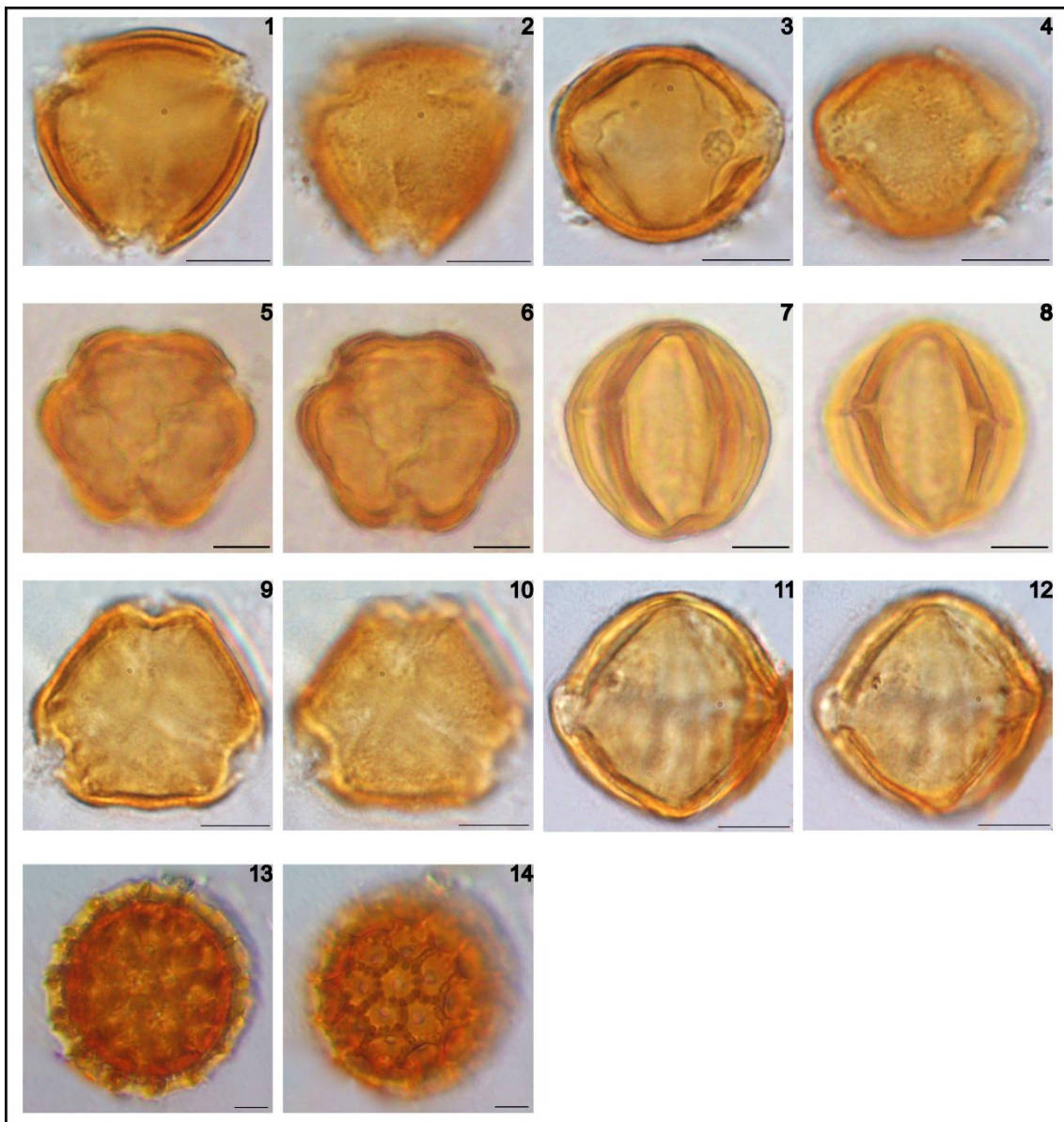


Plate LXXV. Vochysiaceae: *Qualea parviflora* (1,2,3,4), *Salvertia convallariodora*. (5,6,7,8), *Vochysia sp.* (9,10,11,12); Zygothylaceae: *Kallstroemia tribuloides* (13,14). Scale bars = 10 μm .

Appendix 2.A

Supplementary materials

Table 1. List of species present in the atlas and their confirmation reference descriptions.

Monocots		
Family	Species	Bibliography
Alismataceae	<i>Echinodorus palaefolius</i> (Ness & Mart.) J.F. Macbr.	Alves <i>et al.</i> , 2021
	<i>Limnocharis laforesti</i> Duchass. ex Griseb.	Argue, 1973
Alstroemeriaceae	<i>Alstroemeria longistaminea</i> Mart. ex Schult. & Schult.f.	Sarwar <i>et al.</i> , 2010
Araceae	<i>Spathiphyllum gardneri</i> Schott	Jiménez <i>et al.</i> , 2021
Bromeliaceae	<i>Bromelia laciniosa</i> Mart. ex Schult. & Schult.f.	DMA
	<i>Neoglaziovia variegata</i> (Arruda) Mez	DMA
	<i>Tillandsia loliacea</i> Mart. ex Schult. & Schult.f.	de Oliveira Souza <i>et al.</i> , 2021
Commelinaceae	<i>Commelina benghalensis</i> L.	Pradesh <i>et al.</i> , 2019
Cyperaceae	<i>Cyperus articulatus</i> L.	Sosam and Al-mayyahi, 2018
	<i>Cyperus metzii</i> (Hochst. ex Steud.) Mattf. & Kük	Sosam and Al-mayyahi, 2019
Iridaceae	<i>Cipura paludosa</i> Aubl.	Goldblatt and Le Thomas, 1992

	<i>Nemastylis sp.</i> Nutt.	DMA
Poaceae	<i>Andropogon fastigiatus</i> Sw.	Guimarães <i>et al.</i> , 2018
	<i>Aristida setifolia</i> Kunth	Leal <i>et al.</i> , 2011
	<i>Dactyloctenium aegyptium</i> (L.) Willd.	Nazish and Althobaiti, 2022
	<i>Eragrostis maypurensis</i> (Kunth) Steud.	Guimarães <i>et al.</i> , 2018
	<i>Lasiacis sp.</i> (Griseb.) Hitchc.	Matos <i>et al.</i> , 2014
	<i>Melinis repens</i> (Willd.) Zizka	DMA
	<i>Setaria adhaerens</i> (Forssk.) Chiov.	Morgado <i>et al.</i> , 2015
	<i>Trachypogon spicatus</i> (L.f.) Kuntze	Radaeski and Bauermann, 2018
Pontederiaceae	<i>Heteranthera rotundifolia</i> (Kunth) Griseb.	Ybert <i>et al.</i> , 2017a
	<i>Pontederia subovata</i> (Seub.) Lowden	Ybert <i>et al.</i> , 2017a
Rapateaceae	<i>Rapatea</i> Aubl.	DMA
Smilacaceae	<i>Smilax</i> L.	Chen <i>et al.</i> , 2006
Xyridaceae	<i>Xyris macrocephala</i> Vahl	da Luz <i>et al.</i> , 2015
Eudicots, Magnoliids and Nymphaeales		
Family	Species	Bibliography
Acanthaceae	<i>Dicliptera ciliaris</i> Juss.	Perveen and Kaiser, 2010
	<i>Justicia triloba</i> (Lindau) E.C.O.Chagas & Costa-Lima	Kiel <i>et al.</i> , 2017

	<i>Lepidagathis montana</i> (Nees) Kameyama	Perveen and Qaiser, 2010
	<i>Ruellia asperula</i> (Mart. ex Nees) Lindau	Perveen and Qaiser, 2011
Achariaceae	<i>Lindackeria ovata</i> (Benth.) Gilg	DMA
Amaranthaceae	<i>Alternanthera brasiliana</i> (L.) Kuntze	Saensouk and Saensouk, 2022
	<i>Amaranthus viridis</i> L.	Saensouk and Saensouk, 2023
	<i>Froelichia humboldtiana</i> (Roem. & Schult.) Seub.	Borsch, 1998
	<i>Gomphrena leucocephala</i> Mart.	Borsch, 1999
	<i>Xerosiphon angustiflorus</i> (Mart.) Pedersen	Borsch, 2000
Anacardiaceae	<i>Anacardium occidentale</i> L.	Assis <i>et al.</i> , 2021
	<i>Apterokarpos gardneri</i> (Engl.) Rizzini	Assis <i>et al.</i> , 2021
	<i>Astronium fraxinifolium</i> Schott.	Assis <i>et al.</i> , 2021
	<i>Astronium urundeuva</i> (M.Allemão) Engl.	Assis <i>et al.</i> , 2021
	<i>Schinus</i> sp. L.	Assis <i>et al.</i> , 2021
	<i>Spondias tuberosa</i> Arruda	Assis <i>et al.</i> , 2021
	<i>Tapirira guianensis</i> Aubl.	Assis <i>et al.</i> , 2021
Annonaceae	<i>Annona leptopetala</i> (R.E.Fr.) H.Rainer	Doyle and Le Thomas, 2012
Apocynaceae	<i>Aspidosperma pyrifolium</i> Mart. & Zucc.	Moreira <i>et al.</i> , 2004

	<i>Himatanthus drasticus</i> (Mart.) Plumel	DMA
	<i>Mandevilla tenuifolia</i> (J.C.Mikan) Woodson	Rodrigues <i>et al.</i> , 2017
	<i>Odontadenia hypoglauca</i> Müll.Arg.	Rodrigues <i>et al.</i> , 2018
	<i>Rhabdadenia biflora</i> (Jacq.) Müll.Arg.	Moreira <i>et al.</i> , 2004
	<i>Rhodocalyx rotundifolius</i> Müll.Arg.	DMA
	<i>Secondatia floribunda</i> A.DC.	Rodrigues <i>et al.</i> , 2017
	<i>Tabernaemontana catharinensis</i> A.DC.	Rodrigues <i>et al.</i> , 2018
Aquifoliaceae	<i>Ilex</i> sp. L.	CRUZ-BARROS <i>et al.</i> , 2006
Araliaceae	<i>Didymopanax</i> sp. Dec. & Planch	Fiaschi <i>et al.</i> , 2010
Aristolochiaceae	<i>Aristolochia gardneri</i> Duch.	Freitas <i>et al.</i> , 2023
Asteraceae	<i>Acanthospermum australe</i> (Loefl.) Kuntze	Dias <i>et al.</i> , 2022
	<i>Aspilia leucoglossa</i> Malme	Mabel <i>et al.</i> , 2014
	<i>Blainvillea acmella</i> (L.) Philipson	Dias <i>et al.</i> , 2022
	<i>Calea microphylla</i> (Gardner) Baker	Stanski <i>et al.</i> , 2013
	<i>Centratherum punctatum</i> Cass.	Nascimento <i>et al.</i> , 2021
	<i>Chresta martii</i> (DC.) H.Rob.	Siniscalchi <i>et al.</i> , 2017
	<i>Chromolaena myriocephala</i> (Gardner) R.M.King & H.Robinson	Mabel <i>et al.</i> , 2014
	<i>Clibadium armanii</i> (Balb.) Sch.Bip. ex	Salamah <i>et al.</i> , 2019

O.E.Schulz	
<i>Conocliniopsis prasiifolia</i> (DC.) R.M.King & H.Rob.	Lucas <i>et al.</i> , 2018
<i>Dasyphyllum sprengelianum</i> (Gardner) Cabrera	Urtubey and Tellería, 1998
<i>Eclipta prostrata</i> (L.) L.	Mabel <i>et al.</i> , 2014
<i>Elephantopus mollis</i> Kunth	Mabel <i>et al.</i> , 2014
<i>Emilia</i> sp. (Cass.) Cass.	Mabel <i>et al.</i> , 2014
<i>Fleischmannia remotifolia</i> (DC.) R.M.King & H.Rob.	Lorente <i>et al.</i> , 2017
<i>Lepidaploa arenaria</i> (Mart. ex DC.) H.Rob.	Mendonça <i>et al.</i> , 2007
<i>Lepidaploa remotiflora</i> (Rich.) H.Rob.	Mendonça <i>et al.</i> , 2007
<i>Lessingianthus coriaceus</i> (Less.) H.Rob.	Angulo and Dematteis, 2010
<i>Mikania officinalis</i> Mart.	Mendonça and Gonçalves-Esteves, 2000
<i>Pectis brevipedunculata</i> (Gardner) Sch.Bip.	Mendonça and Gonçalves-Esteves, 2000
<i>Pseudobrickellia brasiliensis</i> (Spreng.) R.M.King & H.Rob	DMA
<i>Rolandra fruticose</i> (L.) Kuntze	Angulo <i>et al.</i> , 2018
<i>Stilpnopappus</i> sp. Mart. ex DC.	Carrijo <i>et al.</i> , 2013
<i>Synedrella nodiflora</i> (L.) Gaertn.	Mabel <i>et al.</i> , 2014

	<i>Tagetes minuta</i> L.	Osman,2011
	<i>Tilesia baccata</i> (L.) Pruski	Mendonça and Gonçalves-Esteves, 2000
	<i>Trichogonia campestris</i> Gardner	DMA
	<i>Trichospira verticillata</i> (L.) S.F.Blake	Bolick, 1983
	<i>Vernonanthura brasiliiana</i> (L.) H.Rob.	Nascimento <i>et al.</i> , 2021
Bignoniaceae	<i>Adenocalymma divaricatum</i> Miers	Bove, 1993
	<i>Anemopaegma laeve</i> DC.	Bove, 1993
	<i>Bignonia campanulata</i> Cham.	de Souza <i>et al.</i> , 2019
	<i>Fridericia platyphylla</i> (Cham.) L.G.Lohmann	de Souza and Gasparino, 2014
	<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	de Souza <i>et al.</i> , 2019
	<i>Lundia helicocalyx</i> A.H.Gentry	de Souza <i>et al.</i> , 2019
	<i>Mansoa hirsute</i> DC.	Bove, 1993
	<i>Pleonotoma melioides</i> (S.Moore) A.H.Gentry	de Souza <i>et al.</i> , 2019
	<i>Stizophyllum perforatum</i> (Cham.) Miers	de Souza <i>et al.</i> , 2019
	<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	de Souza <i>et al.</i> , 2019
Bixaceae	<i>Cochlospermum regium</i> (Mart. ex Schrank) Pilg.	Keating, 1972
Boraginaceae	<i>Euploca lagoensis</i> (Warm.) Diane & Hilger	Dias <i>et al.</i> , 2022

	<i>Heliotropium elongatum</i> (Lehm.) I.M.Johnst.	Landi <i>et al.</i> , 2021
	<i>Myriopus salzmannii</i> (DC.) Diane & Hilger	Landi <i>et al.</i> , 2021
	<i>Varronia leucocephala</i> (Moric.) J.S.Mill.	Landi <i>et al.</i> , 2021
Burseraceae	<i>Commiphora leptophloeos</i> (Mart.) J.B.Gillett	Harley <i>et al.</i> , 2005
Cactaceae	<i>Cereus albicaulis</i> (Britton & Rose) Luetzelb.	Santos <i>et al.</i> , 1997
Cannabaceae	<i>Celtis</i> sp. L.	Zarafshar <i>et al.</i> , 2010
	<i>Trema micranta</i> (L.) Blume	Cassino and Meyer, 2011
Capparaceae	<i>Cynophalla hastata</i> (Jacq.) J.Presl	DMA
	<i>Mesocapparis lineata</i> (Dombey ex Pers.) Cornejo & Iltis	DMA
	<i>Neocalyptrocalyx longifolium</i> (Mart.) Cornejo & Iltis	DMA
Caryocaraceae	<i>Caryocar coriaceum</i> Wittm.	Lorente <i>et al.</i> , 2017
Celastraceae	<i>Fraunhoferia multiflora</i> Mart.	DMA
	<i>Monteverdia erythroxyla</i> (Reissek) Biral	Perveen and Qaiser, 2008
	<i>Prionostemma asperum</i> (Lam.) Miers	DMA
	<i>Salacia elliptica</i> (Mart.) G. Don	Gonçalves-Esteves and Melhem, 2000
	<i>Tontelea micrantha</i> (Mart.) A.C. Sm.	Gonçalves-Esteves and Melhem, 1998
Chrysobalanaceae	<i>Chrysobalanus icaco</i> L. subsp. <i>Icaco</i>	Heigl, 2021

	<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth.	Ybert <i>et al.</i> , 2017b
	<i>Exellodendron cordatum</i> (Hook.f.) Prance	DMA
	<i>Parinari campestris</i> Aubl.	Leal <i>et al.</i> , 2011
Cleomaceae	<i>Physostemon guianense</i> (Aubl.) Malme	DMA
	<i>Tarenaya microcarpa</i> (Ule) Soares Neto & Roalson	Lorente <i>et al.</i> , 2017
Clusiaceae	<i>Clusia panapanari</i> (Aubl.) Choisy	Ybert <i>et al.</i> , 2017b
Combretaceae	<i>Combretum fruticosum</i> (Loefl.) Stuntz	El Ghazali, 2016
	<i>Combretum mellifluum</i> Eichler.	El Ghazali, 2016
	<i>Terminalia corrugata</i> (Ducke) Gere & Boatwr.	El Ghazali, 2022
	<i>Terminalia fagifolia</i> Mart.	El Ghazali, 2022
Connaraceae	<i>Connarus suberosus</i> Planch.	Mondal, 1994
	<i>Rourea induta</i> Planch.	Lorente <i>et al.</i> , 2017
Convolvulaceae	<i>Evolvulus anagalloides</i> Meisn.	Vasconcelos <i>et al.</i> , 2019
	<i>Ipomoea brasiliana</i> (Choisy) Meisn.	Vasconcelos <i>et al.</i> , 2019
	<i>Jacquemontia gracillima</i> (Choisy) Hallier f.	Vasconcelos <i>et al.</i> , 2019
Dilleniaceae	<i>Curatella americana</i> L.	Sosam and Al-mayyahi, 2018
	<i>Davilla cearensis</i> Huber	Barth, 1962
Droseraceae	<i>Drosera sessilifolia</i> A.St.-Hil.	Kuprianova, 1973

Erythroxylaceae	<i>Erythroxylum squamatum</i> Sw.	Rodríguez <i>et al.</i> , 2002
Euphorbiaceae	<i>Cnidoscolus bahianus</i> (Ule) Pax & K.Hoffm.	Punt, 1961
	<i>Croton pedicellatus</i> Kunth.	de Souza <i>et al.</i> , 2020
	<i>Dalechampia fernandesii</i> G.L. Webster	Souza <i>et al.</i> , 2017
	<i>Ditaxis desertorum</i> (Müll.Arg.) Pax & K.Hoffm.	Souza <i>et al.</i> , 2017
	<i>Euphorbia hirta</i> L.	El-Ghazaly and Chaudhary, 1993
	<i>Gymnanthes boticario</i> Esser, M. F. A. Lucena & M. Alves	DMA
	<i>Jatropha mollissima</i> (Pohl) Baill.	Tiwari <i>et al.</i> , 2014
	<i>Manihot caerulescens</i> Pohl	Vieira <i>et al.</i> , 2012
	<i>Microstachys glandulosa</i> (Mart. & Zucc.) F.Dietr.	Sakugawa <i>et al.</i> , 2019
	<i>Sapium argutum</i> (Müll.Arg.) Huber	Corrêa <i>et al.</i> , 2010
<i>Tragia volubilis</i> L.	Santos <i>et al.</i> , 2019	
Fabaceae - Caesalpinioideae	<i>Cassia ferruginea</i> (Schrad.) Schrad. ex DC.	Antonio-Domingues <i>et al.</i> , 2018a
	<i>Cenostigma macrophyllum</i> Tul.	Dias <i>et al.</i> , 2022
	<i>Cenostigma pyramidale</i> (Tul.) Gagnon & G.P.Lewis	Dias <i>et al.</i> , 2022
	<i>Chamaecrista duckeana</i> (P.Bezerra & Afr.Fern.) H.S.Irwin & Barneby	Da Luz <i>et al.</i> , 2013

	<i>Dimorphandra gardneriana</i> Tul.	Leal <i>et al.</i> , 2011
	<i>Diptychandra aurantiaca</i> subsp. <i>epunctata</i> (Tul.) H.C.Lima et al.	Barata and Carreira, 2005
	<i>Libidibia ferrea</i> (Mart. ex Tul.) L.P.Queiroz	Buril <i>et al.</i> , 2011
	<i>Melanoxylon brauna</i> Schott	Lorente <i>et al.</i> , 2017
	<i>Senna cearensis</i> Afr.Fern.	Buril <i>et al.</i> , 2011
	<i>Senna obtusifolia</i> (L.) H.S.Irwin & Barneby	Buril <i>et al.</i> , 2011
	<i>Tachigali vulgaris</i> L.G.Silva & H.C.Lima	Fontes <i>et al.</i> , 2020
Fabaceae Caesalpinioideae (Mimosoid clade)	<i>Anadenanthera colubrina</i> var. <i>cebil</i> (Vell.) Brenan	Caccavari, 2002
	<i>Chloroleucon foliolosum</i> (Benth.) G.P.Lewis	DMA
	<i>Desmanthus virgatus</i> (L.) Willd.	Buril <i>et al.</i> , 2010
	<i>Entada Polystachya</i> (L.) DC.	Jumah, 1991
	<i>Enterolobium contortisiliquum</i> (Vell.) Morong	Buril <i>et al.</i> , 2010
	<i>Inga laurina</i> (Sw.) Willd.	Antonio-Domingues <i>et al.</i> , 2018a
	<i>Mimosa caesalpinifolia</i> Benth.	Lima <i>et al.</i> , 2008
	<i>Neptunia plena</i> (L.) Benth.	Buril <i>et al.</i> , 2010
	<i>Parkia platycephala</i> Benth.	Sorsa, 1969
	<i>Piptadenia retusa</i> (Jacq.) P.G.Ribeiro, Seigler & Ebinger	Lima <i>et al.</i> , 2008

	<i>Pithecellobium diversifolium</i> Benth.	Buril <i>et al.</i> , 2010
	<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson	Buril <i>et al.</i> , 2010
	<i>Plathymenia reticulata</i> Benth.	Sorsa, 1969
	<i>Samanea saman</i> (Jacq.) Merr.	Sorsa, 1969
	<i>Senegalia globosa</i> (Bocage & Miotto) L.P.Queiroz	Dias <i>et al.</i> , 2022
	<i>Stryphnodendron coriaceum</i> Benth.	da Luz <i>et al.</i> , 2013
	<i>Zygia latifolia</i> (L.) Fawc. & Rendle	DMA
Fabaceae Cercidoideae	<i>Bauhinia acuruana</i> Moric.	Taia <i>et al.</i> , 2022
	<i>Schnella glabra</i> (Jacq.) Dugand	DMA
Fabaceae Detarioideae	<i>Copaifera langsdorffii</i> Desf.	Banks, 2003
	<i>Cynometra bauhiniifolia</i> Benth.	Banks; Rico, 1999
	<i>Hymenaea courbaril</i> L.	Soares <i>et al.</i> , 2021
	<i>Peltogyne confertiflora</i> (Mart. ex Hayne) Benth.	Lorente <i>et al.</i> , 2017
Fabaceae Dialioideae	<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	Zimmerman <i>et al.</i> , 2013
	<i>Martiodendron mediterraneum</i> (Mart. ex Benth.) R.C.Koeppen	Silva <i>et al.</i> , 2005
	<i>Poeppegia procera</i> var. <i>conferta</i> Benth.	Buril <i>et al.</i> , 2011
Fabaceae Faboideae	<i>Aeschynomene evenia</i> C.Wright & Sauvalle	Antonio-Domingues <i>et al.</i> , 2018b

<i>Amburana cearensis</i> (Allemão) A.C.Sm.	Buril <i>et al.</i> , 2011
<i>Ancistrotropis firmula</i> (Mart. ex Benth.) A. Delgado	Nascimento <i>et al.</i> , 2021
<i>Andira cordata</i> Arroyo ex R.T.Penn. & H.C.Lima	da Luz <i>et al.</i> , 2013
<i>Arachis dardani</i> Krapov. & W.C.Greg.	Chaturvedi <i>et al.</i> , 1990
<i>Bionia tomentosa</i> (Benth.) L.P.Queiroz	DMA
<i>Bowdichia virgilioides</i> Kunth.	Ferguson and Stirton, 1993
<i>Cajanus cajan</i> (L.) Huth	Srivastava, 1978
<i>Camptosema</i> sp. Hook. & Arn.	Kavanagh and Ferguson, 1981
<i>Canavalia brasiliensis</i> Mart. ex Benth.	Buril <i>et al.</i> , 2011
<i>Centrosema brasilianum</i> (L.) Benth.	Buril <i>et al.</i> , 2011
<i>Clitoria guianensis</i> (Aubl.) Benth.	DMA
<i>Cranocarpus gracilis</i> Afr.Fern. & P.Bezerra	Ferguson and Skvarla, 1979
<i>Cratylia mollis</i> Mart. ex Benth.	Kavanagh and Ferguson, 1981
<i>Crotalaria incana</i> L.	Buril <i>et al.</i> , 2011
<i>Dahlstedtia araripensis</i> (Benth.) M.J. Silva & A.M.G. Azevedo	De Pádua Teixeira <i>et al.</i> , 2002
<i>Dalbergia cearensis</i> Ducke	da Luz <i>et al.</i> , 2013
<i>Deguelia nitidula</i> (Benth.) A.M.G.Azevedo &	Fontes <i>et al.</i> , 2020

R.A.Camargo	
<i>Dipteryx lacunifera</i> Ducke	Fontes <i>et al.</i> , 2020
<i>Discolobium hirtum</i> Benth.	Lattar <i>et al.</i> , 2020
<i>Eriosema crinitum</i> (Kunth) G.Don	Oliveira <i>et al.</i> , 2019
<i>Galactia jussiaeana</i> Kunth	da Luz <i>et al.</i> , 2013
<i>Harpalyce brasiliana</i> Benth.	Dos Santos <i>et al.</i> , 2022
<i>Indigofera hirsuta</i> L.	Nascimento <i>et al.</i> , 2021
<i>Leptolobium parvifolium</i> (Harms) Sch.Rodr. & A.M.G.Azevedo	DMA
<i>Lonchocarpus sericeus</i> (Poir.) Kunth ex DC.	Fontes <i>et al.</i> , 2020
<i>Luetzelburgia auriculata</i> (Allemão) Ducke	Dos Santos <i>et al.</i> , 2022
<i>Machaerium acutifolium</i> Vogel	Leal <i>et al.</i> , 2011
<i>Macroptilium lathyroides</i> (L.) Urb.	Buril <i>et al.</i> , 2011
<i>Macropsychanthus bicolor</i> (Benth.) L.P.Queiroz & Snak	Kavanagh and Ferguson, 1981
<i>Muelleria moniliformis</i> L.f.	DMA
<i>Nissolia vincentina</i> (Ker Gawl.) T.M.Moura & Fort.-Perez	Lattar <i>et al.</i> , 2020
<i>Periandra coccinea</i> (Schrad.) Benth.	da Luz <i>et al.</i> , 2013
<i>Platypodium elegans</i> Vogel	Antonio-Domingues <i>et al.</i> , 2018a

	<i>Poiretia punctata</i> (Willd.) Desv.	Lattar <i>et al.</i> , 2020
	<i>Pterocarpus villosus</i> (Mart. ex Benth.) Benth.	Fontes <i>et al.</i> , 2020
	<i>Pterodon abruptus</i> (Moric.) Benth.	DMA
	<i>Rhynchosia minima</i> (L.) DC.	Oliveira <i>et al.</i> , 2019
	<i>Sesbania exasperata</i> Kunth	Buril <i>et al.</i> , 2011
	<i>Soemmeringia semperflorens</i> Mart.	DMA
	<i>Stylosanthes viscosa</i> (L.) Sw.	Buril <i>et al.</i> , 2011
	<i>Swartzia psilonema</i> Harms	Fontes <i>et al.</i> , 2020
	<i>Tephrosia cinerea</i> (L.) Pers.	Buril <i>et al.</i> , 2011
	<i>Trischidium molle</i> (Benth.) H.E.Ireland	Buril <i>et al.</i> , 2011
	<i>Vatairea macrocarpa</i> (Benth.) Ducke	Fontes <i>et al.</i> , 2020
	<i>Zornia sericea</i> Moric.	da Luz <i>et al.</i> , 2013
Gentianaceae	<i>Schultesia pohliana</i> Progel	Ybert <i>et al.</i> , 2017b
Gesneriaceae	<i>Sinningia elatior</i> (Kunth) Chautems	Ybert <i>et al.</i> , 2017b
Hernandiaceae	<i>Sparattanthelium botocudorum</i> Mart.	Scherer <i>et al.</i> , 2011
Humiriaceae	<i>Humiria balsamifera</i> (Aubl.) A.St.-Hil.	Ybert <i>et al.</i> , 2017b
Hypericaceae	<i>Vismia guianensis</i> (Aubl.) Choisy	Ybert <i>et al.</i> , 2017b
Icacinaceae	<i>Emmotum nitens</i> (Benth.) Miers	Carvalho, 1971
Krameriaceae	<i>Krameria tomentosa</i> A.St.-Hil.	Simpson and Skvarla, 1981

Lamiaceae	<i>Amasonia sp.</i> L.f.	DMA
	<i>Eriope crassipes</i> Benth.	Silva, 2007
	<i>Hypenia salzmännii</i> (Benth.) Harley	Silva, 2007
	<i>Hyptidendron leucophyllum</i> (Pohl ex Benth.) Harley	Lorente <i>et al.</i> , 2017
	<i>Hyptis crenata</i> Pohl ex Benth.	Lorente <i>et al.</i> , 2017
	<i>Leonotis nepetifolia</i> (L.) R.Br.	Halbritter, 2016
	<i>Marsypianthes chamaedrys</i> (Vahl) Kuntze	Lorente <i>et al.</i> , 2017
	<i>Mesosphaerum suaveolens</i> (L.) Kuntze	DMA
	<i>Ocimum gratissimum</i> L.	Lorente <i>et al.</i> , 2017
	<i>Rhaphiodon echinus</i> (Nees & Mart.) Schauer	DMA
	<i>Vitex flavens</i> Kunth.	Lorente <i>et al.</i> , 2017
Lecythidaceae	<i>Eschweilera nana</i> (O.Berg) Miers	Moura <i>et al.</i> , 2004
	<i>Lecythis pisonis</i> Cambess.	Ybert <i>et al.</i> , 2017b
Loasaceae	<i>Aosa rupestris</i> (Gardner) Weigend	DMA
Loganiaceae	<i>Antonia ovata</i> Pohl.	Taylor <i>et al.</i> , 2011
	<i>Mitreola petiolata</i> (J.F.Gmel.) Torr. & A.Gray	Punt and Leenhouts, 1967
	<i>Strychnos araguaensis</i> Krukoff & Barneby	Fontes <i>et al.</i> , 2020
Loranthaceae	<i>Passovia pedunculata</i> (Jacq.) Kuijt	Grímsson <i>et al.</i> , 2018

	<i>Psittacanthus eucalyptifolius</i> (Kunth) G.Don	Grímsson <i>et al.</i> , 2018
	<i>Struthanthus polyanthus</i> (Mart.) Mart.	Grímsson <i>et al.</i> , 2018
Lythraceae	<i>Ammannia maritima</i> (Aubl.) S.A.Graham, P.W.Inglis & T.B.Cavalc.	Mahmoodi <i>et al.</i> , 2022
	<i>Cuphea campestris</i> Mart. ex Koehne	Graham and Graham, 1968
	<i>Cuphea laricoides</i> Koehne	Facco <i>et al.</i> , 2021
	<i>Diplusodon</i> sp. Pohl	Muller, 1981
	<i>Lafoensia replicata</i> Pohl	Muller, 1981
Malpighiaceae	<i>Amorimia rigida</i> (A.Juss.) W.R.Anderson	DMA
	<i>Banisteriopsis stellaris</i> (Griseb.) B.Gates	Leal <i>et al.</i> , 2011
	<i>Byrsonima crassifolia</i> (L.) Kunth	Gonçalves-Esteves <i>et al.</i> , 2007
	<i>Callaeum psilophyllum</i> (A.Juss.) D.M.Johnson	DMA
	<i>Camarea affinis</i> A.St.-Hil.	Cassino and Meyer, 2011
	<i>Dicella</i> sp. Griseb.	DMA
	<i>Diplopterys pubipetala</i> (A.Juss.) W.R.Anderson & C.C.Davis	Belonsi and Gasparino, 2015
	<i>Glicophyllum latibracteolatum</i> (Nied.) R.F.Almeida	Leal <i>et al.</i> , 2011
	<i>Heteropterys trichanthera</i> A.Juss.	Gonçalves-Esteves <i>et al.</i> , 2007

	<i>Peixotoa jussieuana</i> A.Juss.	Gonçalves-Esteves <i>et al.</i> , 2007
	<i>Stigmaphyllon paralias</i> A.Juss.	Gonçalves-Esteves <i>et al.</i> , 2007
	<i>Verrucularina</i> sp. Rauschert	DMA
Malvaceae	<i>Apeiba tibourbou</i> Aubl.	Fontes <i>et al.</i> , 2020
	<i>Ayenia erecta</i> Mart. ex K.Schum.	Saba and Santos, 2003
	<i>Byttneria divaricata</i> Benth.	Lopes <i>et al.</i> , 2022
	<i>Cienfuegosia heterophylla</i> (Vent.) Garcke	Fryxell, 1969
	<i>Helicteres muscosa</i> Mart.	Lopes <i>et al.</i> , 2022
	<i>Luehea candicans</i> Mart.	Lopes <i>et al.</i> , 2022
	<i>Malvastrum americanum</i> (L.) Torr.	Germano <i>et al.</i> , 1997
	<i>Melochia tomentosa</i> L.	Silva <i>et al.</i> , 2020
	<i>Pavonia glazioviana</i> Gürke	Nascimento <i>et al.</i> , 2021
	<i>Pseudobombax longiflorum</i> (Mart.) A.Robyns	Lopes <i>et al.</i> , 2022
	<i>Sida cordifolia</i> L.	Leal <i>et al.</i> , 2011
	<i>Sterculia foetida</i> L.	Fontes <i>et al.</i> , 2020
	<i>Urena lobata</i> L.	Cruz-Barroz <i>et al.</i> , 2006
	<i>Waltheria brachypetala</i> Turcz.	Saba and Santos, 2003
<i>Wissadula amplissima</i> (L.) R.E.Fr.	Christensen, 1986	

Marcgraviaceae	<i>Schwartzia adamantium</i> (Cambess.) Bedell ex Gir. -Cañas	Lorente <i>et al.</i> , 2017
Melastomataceae	<i>Clidemia biserrata</i> DC.	De Novais and Absy, 2013
	<i>Henriettea</i> sp. DC.	Fontes <i>et al.</i> , 2020
	<i>Macairea radula</i> (Bonpl.) DC.	DMA
	<i>Marcetia</i> sp. DC.	Lorente <i>et al.</i> , 2017
	<i>Mouriri guianensis</i> Aubl.	Lorente <i>et al.</i> , 2017
	<i>Pterolepis polygonoides</i> (DC.) Triana	Lorente <i>et al.</i> , 2017
	<i>Rhynchanthera serrulata</i> (L.C.Rich.) DC.	Lorente <i>et al.</i> , 2017
	<i>Tibouchina</i> sp. Aubl.	Lorente <i>et al.</i> , 2017
Meliaceae	<i>Melia azedarach</i> L.	Liu <i>et al.</i> , 2017
Menispermaceae	<i>Cissampelos ovalifolia</i> DC.	Teixeira <i>et al.</i> , 2013
Microteaceae	<i>Microtea</i> sp. Sw.	Neves, 2006
Molluginaceae	<i>Mollugo verticillata</i> L.	Nascimento <i>et al.</i> , 2021
Moraceae	<i>Brosimum gaudichaudii</i> Trécul	Barth, 1976
	<i>Dorstenia cayapia</i> Vell.	Barth, 1976
	<i>Maclura tinctoria</i> (L.) D.Don ex Steud.	Lorente <i>et al.</i> , 2017
Myristicaceae	<i>Virola subsessilis</i> (Benth.) Warb.	Leal <i>et al.</i> , 2011
Myrtaceae	<i>Campomanesia</i> sp. Ruiz et Pav.	Corrêa <i>et al.</i> , 2018

	<i>Eugenia gracillima</i> Kiaersk.	Corrêa <i>et al.</i> , 2018
	<i>Myrcia guianensis</i> (Aubl.) DC.	Corrêa <i>et al.</i> , 2018
	<i>Psidium myrsinites</i> DC.	Corrêa <i>et al.</i> , 2018
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	Souza <i>et al.</i> , 2010
	<i>Pisonia</i> sp. L.	DMA
Nymphaeaceae	<i>Nymphaea jamesoniana</i> Planch.	Ybert <i>et al.</i> , 2017a
Ochnaceae	<i>Ouratea castaneifolia</i> (DC.) Engl.	Lorente <i>et al.</i> , 2017
Olacaceae	<i>Dulacia</i> sp. Vell.	Lorente <i>et al.</i> , 2017
	<i>Heisteria ovata</i> Benth.	Corrêa and Barros, 2011
	<i>Ximenia coriacea</i> Engl.	Lorente <i>et al.</i> , 2017
Opiliaceae	<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook.f.	DMA
Oxalidaceae	<i>Oxalis divaricata</i> Mart. ex Zucc.	Corrêa and Fonseca, 2015
Passifloraceae	<i>Mitostemma brevifilis</i> Gontsch.	Araújo <i>et al.</i> , 2020
	<i>Passiflora cincinnata</i> Mast.	Mezzonato-Pires <i>et al.</i> , 2015
Phyllanthaceae	<i>Phyllanthus clausenii</i> Müll.Arg.	Corrêa <i>et al.</i> , 2010
Piperaceae	<i>Piper tuberculatum</i> Jacq.	Fontes <i>et al.</i> , 2020
Plantaginaceae	<i>Angelonia cornigera</i> Hook.f.	DMA
	<i>Bacopa angulata</i> (Benth.) Edwall	El-Husseini and Shamsou, 2002

	<i>Stemodia maritima</i> L.	Nascimento <i>et al.</i> , 2021
	<i>Tetraulacium veroniciforme</i> Turcz.	DMA
Polygalaceae	<i>Bredemeyera floribunda</i> Willd.	Lorente <i>et al.</i> , 2017
	<i>Monnina insignis</i> A.W.Benn.	Picanço Leite <i>et al.</i> , 2015
	<i>Polygala trichosperma</i> Jacq.	Simpson and Skvarla, 1981
	<i>Securidaca coriacea</i> Bonpl.	Cruz-Barros <i>et al.</i> , 2005
Polygonaceae	<i>Coccoloba mollis</i> Casar.	Lucas <i>et al.</i> , 2010
Rhamnaceae	<i>Colubrina cordifolia</i> Reissek	DMA
	<i>Rhamnidium molle</i> Reissek	DMA
Rhizophoraceae	<i>Rhizophora mangle</i> L.	Mohd-Arrabe' and Talip, 2013
Rosaceae	<i>Eriobotrya japonica</i> (Thunb.) Lindl.	DMA
Rubiaceae	<i>Alibertia edulis</i> (Rich.) A.Rich.	Fontes <i>et al.</i> , 2020
	<i>Borreria diacrodonta</i> L.M. Miguel & E.L. Cabral	Miguel <i>et al.</i> , 2018
	<i>Chiococca alba</i> (L.) Hitchc.	Leal <i>et al.</i> , 2011
	<i>Chomelia obtusa</i> Cham. & Schtdl.	Dutra <i>et al.</i> , 2020
	<i>Coccocypselum lanceolatum</i> (Ruiz & Pav.) Pers.	Leal <i>et al.</i> , 2011; Schroeder <i>et al.</i> , 2019
	<i>Cordia myrciifolia</i> (K.Schum.) C.H.Perss. & Delprete	Judkevich <i>et al.</i> , 2022

<i>Coussarea hydrangeifolia</i> (Benth.) Müll.Arg.	Dutra <i>et al.</i> , 2020
<i>Coutarea hexandra</i> (Jacq.) K.Schum.	Dutra <i>et al.</i> , 2020
<i>Declieuxia fruticosa</i> (Willd. ex Roem. & Schult.) Kuntze	Leal <i>et al.</i> , 2011
<i>Faramea nitida</i> Benth.	Dutra <i>et al.</i> , 2020
<i>Guettarda viburnoides</i> Cham. & Schltdl.	Dutra <i>et al.</i> , 2020
<i>Hexasepalum apiculatum</i> (Willd.) Delprete & J.H.Kirkbr.	Fader <i>et al.</i> , 2016
<i>Machaonia acuminata</i> Bonpl.	DMA
<i>Mitracarpus baturitensis</i> Sucre	Dutra <i>et al.</i> , 2020
<i>Palicourea veterinariorum</i> J.H.Kirkbr.	Leal <i>et al.</i> , 2011
<i>Perama hirsute</i> Aubl.	Rull, 2003
<i>Psyllocarpus sp.</i> Mart. ex Mart. & Zucc.	Do Carmo <i>et al.</i> , 2018
<i>Randia armata</i> (Sw.) DC.	Dutra <i>et al.</i> , 2020
<i>Richardia grandiflora</i> (Cham. & Schltdl.) Steud.	Nascimento <i>et al.</i> , 2021
<i>Rudgea sp.</i> Salisb.	Dutra <i>et al.</i> , 2020
<i>Sabicea cinerea</i> Aubl.	Lorente <i>et al.</i> , 2017
<i>Simira gardneriana</i> M.R.V.Barbosa & Peixoto	Dutra <i>et al.</i> , 2020
<i>Spermacoce confusa</i> Rendle	DMA
<i>Spermacoce reflexa</i> (J.H.Kirkbr.) Govaerts	Gonçalves-Esteves <i>et al.</i> ,

		2020
	<i>Stachyarrhena</i> sp. Hook.f.	Persson, 1993
	<i>Staelia virgata</i> (Link ex Roem. & Schult.) K.Schum.	Salas and Cabral, 2014
	<i>Tocoyena hispidula</i> Standl.	Dutra <i>et al.</i> , 2020
	<i>Warszewiczia schwackei</i> K.Schum.	DMA
Rutaceae	<i>Ertela trifolia</i> (L.) Kuntze	DMA
	<i>Esenbeckia pumila</i> Pohl	Dutra and Gasparino, 2018
	<i>Pilocarpus trachylophus</i> Holmes	Dutra and Gasparino, 2018
	<i>Spiranthera odoratissima</i> A.St.-Hil.	Morton and Kallunki, 1993
	<i>Zanthoxylum stelligerum</i> Turcz.	Dutra and Gasparino, 2018
Salicaceae	<i>Casearia grandiflora</i> Cambess.	DMA
Sapindaceae	<i>Cardiospermum anomalum</i> Cambess.	Nascimento <i>et al.</i> , 2021
	<i>Cupania</i> sp. L.	Lorente <i>et al.</i> , 2017
	<i>Magonia pubescens</i> A.St.-Hil.	González <i>et al.</i> , 2017
	<i>Matayba</i> sp. Aubl.	Lorente <i>et al.</i> , 2017
	<i>Paullinia</i> sp. L.	Silva <i>et al.</i> , 2014
	<i>Sapindus saponaria</i> L.	DMA
	<i>Serjania glabrata</i> Kunth	Nascimento <i>et al.</i> , 2021
	<i>Talisia</i> sp. Aubl.	Fontes <i>et al.</i> , 2020

	<i>Toulicia</i> sp. Aubl.	Lorente <i>et al.</i> , 2017
Sapotaceae	<i>Chrysophyllum arenarium</i> Allemão	Rull, 2003
Simaroubaceae	<i>Homalolepis ferruginea</i> (A.St.-Hil.) Devecchi & Pirani	Devecchi <i>et al.</i> , 2018
	<i>Homalolepis maiana</i> (Casar.) Devecchi & Pirani	Devecchi <i>et al.</i> , 2018
Solanaceae	<i>Brunfelsia uniflora</i> (Pohl) D.Don	Silva <i>et al.</i> , 2014
	<i>Cestrum</i> sp. L.	Fontes <i>et al.</i> , 2020
	<i>Nicotiana glauca</i> Graham	Nascimento <i>et al.</i> , 2021
	<i>Schwenckia</i> sp. L.	Lorente <i>et al.</i> , 2017
	<i>Solanum paniculatum</i> L.	Lorente <i>et al.</i> , 2017
Styracaceae	<i>Styrax</i> sp. L.	Cassino and Meyer, 2011
Trigoniaceae	<i>Trigonia</i> sp. Aubl.	Corrêa and Barros, 2011
Turneraceae	<i>Piriqueta plicata</i> Urb.	Matos <i>et al.</i> , 2014
	<i>Turnera blanchetiana</i> Urb.	Matos <i>et al.</i> , 2014
Urticaceae	<i>Cecropia pachystachya</i> Trécul.	Lorente <i>et al.</i> , 2017
Verbenaceae	<i>Aloysia gratissima</i> (Gillies & Hook.) Tronc. var. <i>gratissima</i>	Nascimento <i>et al.</i> , 2021
	<i>Lippia organoides</i> Kunth	Nascimento <i>et al.</i> , 2021
	<i>Stachytarpheta lythrophylla</i> Schauer	Nascimento <i>et al.</i> , 2021
Violaceae	<i>Calyptrium</i> sp. Ging.	Mark <i>et al.</i> , 2012

	<i>Hybanthus sp.</i> Jacq.	Mark <i>et al.</i> , 2012
	<i>Pombalia calceolaria</i> (L.) Paula-Souza	Lorente <i>et al.</i> , 2017
Vitaceae	<i>Clematicissus simsiana</i> (Schult. & Schult.f.) Lombardi	Cartaxo-Pinto <i>et al.</i> , 2017
Vochysiaceae	<i>Callisthene microphylla</i> Warm.	Barth and da Luz, 2014
	<i>Qualea parviflora</i> Mart.	Barth and da Luz, 2014
	<i>Salvertia convallariodora</i> A.St.-Hil.	DMA
	<i>Vochysia sp.</i> Aubl.	Lorente <i>et al.</i> , 2017
Zygophyllaceae	<i>Kallstroemia tribuloides</i> (Mart.) Steud.	DMA

3 CAPÍTULO III

MODERN POLLEN RAIN SIGNATURES ALONG THE PARNAÍBA RIVER BASIN IN NORTHEASTERN BRAZIL

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Modern pollen rain signatures along the Parnaíba River Basin in Northeastern Brazil

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Abstract

Recent studies of marine sediments adjacent to the Parnaíba Basin, in northeastern Brazil, have been used for continental paleoenvironmental reconstructions of the glacial epoch. As the largest basin entirely located within the Northeast region, it spans a critical transition zone between the Cerrado and Caatinga biomes. To characterize the modern pollen rain within this ecotone, we analyzed 41 surface sediment samples and compared the pollen assemblages with published botanical surveys. First, pollen assemblages were characterized using three diagrams: vegetation type, geographical location, and depositional environment. The basin presents a unique mixed signature combining Cerrado elements (e.g., *Astronium-type*, *Tapirira-type*) with Caatinga taxa (*Mimosa-type*). Spatially, the Upper and Lower sectors exhibited high heterogeneity, contrasting with arboreal consistency in the Mid-Parnaíba. Distinct hydrological markers also emerged: Cyperaceae was strictly linked to lacustrine environments, whereas *Mauritia* indicated permanently flooded soils within gallery forests and palm swamps. Landscape analysis subsequently confirmed that Arboreal Pollen (AP) frequencies accurately track woody cover, while *Borreria-type* and Poaceae serve as robust proxies for landscape openness. Multivariate analyses refined these patterns: Cluster Analysis identified six specific floristic groups (*Tapirira-Astronium*, mixed, Melastomataceae-Combretaceae, *Borreria-Aspidosperma*, mixed woody-herbaceous, and *Mimosa-type* assemblages), while Redundancy Analysis (RDA) identified Mean Annual Temperature (MAT) as a significant environmental driver within the explained variance. Critically, comparison with paleoecological records reveals a sharp floristic shift from cooler, humid glacial periods to the current warmer climate, marked by the scarcity of montane taxa. This study establishes a crucial baseline for interpreting fossil records and understanding ecosystem dynamics in this transition zone.

Keywords: Cerrado, Caatinga, Tropics, Palynology, Calibration.

Highlights

- Modern pollen rain reflects vegetation patterns along the Parnaíba river gradient;
- Cerrado, Caatinga, and transitional zones show distinct pollen assemblages;
- Analyses reveal floristic structure influenced by edaphoclimatic gradients;
- Pollen assemblages are more related to local conditions than spatial location;
- Anthropization and distinct grasslands strongly influence pollen assemblages.

3.1. Introduction

In recent years, there has been growing interest in studies of marine sediments adjacent to the Parnaíba Basin, in northeastern Brazil, due to their relevance for continental paleoenvironmental, paleoclimatic, and paleoceanographic reconstructions (Bouimetarhan et al., 2018; Piacsek et al., 2021). The Parnaíba Basin is the largest basin entirely located within the Northeast region (Fig. 1A) with a drainage area of approximately 331,000 km². It is subdivided into three main sub-basins, Upper, Mid, and Lower Parnaíba, and presents a wide range of environmental variation along its latitudinal gradient (Motta and Gonçalves, 2016; SGB, 2024).

The Parnaíba River originates in the Chapada das Mangabeiras (789 m a.s.l.) and flows northward to the Atlantic Ocean, delineating the border between Piauí and Maranhão states (MMA, 2006) (Fig. 1B). Its hydro-sedimentary dynamics are strongly modulated by the regional semi-arid climate, where intense seasonal rainfall drives the transport of terrigenous sediments and pollen from the continental interior towards the coast (Bouimetarhan et al., 2018; Piacsek et al., 2021). Thus, understanding the modern pollen signal in this basin is essential to calibrate paleoenvironmental reconstructions based on marine cores.

Despite the growing scientific output in paleoecology in Brazil, there is scarce data on the modern pollen rain composition in the northeastern region, especially in transitional zones between different phytogeographic domains (Flantua et al., 2015; Magalhães-e-Silva and Santos, 2024). Available data are mostly concentrated in the core Cerrado region (Cassino et al., 2015; Cassino and Ledru, 2021), while the Caatinga remains under-sampled (Behling et al., 2000; Ledru et al., 2022).

To address these caveats, our study aims to characterize the modern pollen rain across the Parnaíba Basin, the pollen transport and preservation within the basin and establish a reliable reference for paleoenvironmental studies. For this purpose, 41 samples have been collected along a north-south transect, crossing four main vegetation physiognomies, edaphic and climatic conditions. Sampling was also performed in lakes, riverbanks or palm swamps to collect information about the different local pollen signatures. Our pollen assemblages were then compared with the neighboring phytosociological surveys to discuss their representativeness. Specifically, we analysed how modern pollen rain composition reflects the extant vegetation in the Parnaíba Basin and the roles of climatic and edaphic gradients in driving the pollen-vegetation relationship. Our results will enhance our understanding of floristic dynamics and biogeographic connectivity in a key ecological transition zone of Northeastern Brazil.

3.2. Environmental and regional aspects of the Parnaíba river basin

3.2.1. Climatic and phytophysiological characterization of the Parnaíba basin

The Parnaíba Basin (02°21'S–11°06'S; 47°21'W–39°44'W) covers a drainage area of approximately 331,000 km² (Fig. 1A) encompassing most of the state of Piauí and parts of Maranhão, Tocantins, Ceará, and Bahia (SGB, 2024) (Fig. 1B). In Piauí, the Caatinga and Cerrado biomes predominate (Fig. 1C), distributed in an interspersed pattern that forms extensive transition zones (LIMA et al., 2020; SGB, 2024).

The Caatinga biome in Piauí (Fig. 1C) is characterized by xerophytic vegetation composed of shrubs and small trees adapted to prolonged drought (CASTRO, 2007). The most common arboreal families include Anacardiaceae (*Astronium urundeuva*); Apocynaceae (*Aspidosperma pyriformis*; *Allamanda blanchetii*); Burseraceae (*Commiphora leptophloeos*); Combretaceae (*Combretum leprosum*), Erythroxylaceae (*Erythroxylum rosuliferum*; *E. stipulosum*), Euphorbiaceae (*Croton nepetifolius*; *C. jacobinensis*), Fabaceae (*Bauhinia acuruana*; *Libidibia ferrea*), Rhamnaceae (*Colubrina cordifolia*), Rubiaceae (*Guettarda angelica*), Salicaceae (*Lindackeria ovata*) (CASTRO, 2007; CASTRO et al., 2014).

The Cerrado (Fig. 1C) presents a rich and structurally diverse savanna vegetation, composed of herbaceous, shrubby, and arboreal formations (Castro, 2007). The most frequently cited species in the arboreal component include Anacardiaceae (*Anacardium occidentale*); Annonaceae (*Annona coriacea*); Apocynaceae (*Hancornia speciosa*); Bignoniaceae (*Adenocalymma pubescens*); Caryocaraceae (*Caryocar coriaceum*); Combretaceae (*Terminalia fagifolia*); Dilleniaceae (*Curatella americana*; *Davilla cearensis*); Ebenaceae (*Diospyros brasiliensis*; *D. coccolobifolia*); Fabaceae (*Bowdichia virgilioides*; *Dimorphandra gardneriana*; *Parkia platycephala*); Malpighiaceae (*Byrsonima blanchetiana*; *B. crassifolia*); Meliaceae (*Trichilia elegans*; *T. emarginata*); Vochysiaceae (*Callisthene microphylla*; *Qualea grandiflora*; *Q. parviflora*; *Vochysia gardneri*) (CASTRO, 2007; CASTRO; MARTINS; FERNANDES, 1998).

Given the structural heterogeneity of the region, which encompasses both Cerrado and Caatinga biomes, the sampling sites in this study were classified into specific phytophysiological types following the Veloso et al., (2012) system: Arboreal Savanna, characterized by a continuous or semi-continuous canopy with a sparse herbaceous layer; Arboreal Steppe-Savanna, defined as a formation with deciduous, thorny species and lower canopy height; Parkland Steppe-Savanna, an open formation consisting of scattered trees and shrubs over a continuous herbaceous matrix; and Palm Swamps (*Veredas*), which occur on hydromorphic soils along watercourses and are

dominated by the palm *Mauritia flexuosa* (Buriti), acting as crucial humid enclaves within the savanna landscape.

The *carrasco* (dense shrubland) is a transitional vegetation type associated with the Caatinga. It is characterized by a dense, low-growing understory that gives the impression of a single, uniform layer (ARAÚJO; MARTINS, 1999). This formation is notable for its structural consistency and for hosting species adapted to flat, sandy, and shallow soils. Prominent families include Bignoniaceae (*Adenocalymma* sp.); Fabaceae (*Cenostigma macrophyllum*; *Mimosa acutistipula*; *Pityrocarpa moniliformis*; *Senegalia riparia*); Euphorbiaceae (*Croton tricolor*) (OLIVEIRA et al., 1997).

The *restinga*, a coastal vegetation formation that develops on quaternary quartz sands, is also present in the Parnaíba Basin (SANTOS-FILHO; ALMEIDA JUNIOR; ZICKEL, 2013). The most representative arboreal families include Bignoniaceae (*Fridericia* sp.); Combretaceae (*Combretum* sp.); Euphorbiaceae (*Croton* sp. ; *Manihot* sp.); Fabaceae (*Mimosa* sp.; *Senna* sp.); Malpighiaceae (*Byrsonima* sp.); Myrtaceae (*Eugenia* sp.; *Myrcia* sp.) (SANTOS-FILHO; ALMEIDA JUNIOR; ZICKEL, 2013).

In addition to restingas, Pioneer Formations occur along watercourses and in areas of natural regeneration within the basin (SILVA et al., 2020b). These formations consist of early-successional communities colonizing unstable substrates or recovering from anthropogenic disturbances (VELOSO; FILHO; LIMA, 2012). Typical pioneer and initial colonizer species in the region include *Mimosa tenuiflora* and *Croton blanchetianus*, which are highly efficient at colonizing degraded sites in the Cerrado-Caatinga transition (ANDRADE et al., 2019). In floodplains and areas with periodically waterlogged soils, *Cecropia pachystachya* is a characteristic pioneer, while *Mimosa caesalpiniiifolia* often dominates early regeneration stages due to its rapid growth and drought resistance (ANDRADE et al., 2016).

In the transition zones between the Caatinga and the Cerrado, both deciduous and semi-deciduous seasonal forests can be found (CASTRO, 2007). The key distinction lies in their response to the dry season: deciduous forests shed nearly all their foliage, whereas semi-deciduous forests lose only a portion (VELOSO; FILHO; LIMA, 2012). In general, semi-deciduous forests are more closely associated with the Cerrado, while deciduous forests are typical of the Caatinga.

Deciduous forests often include caducous (leaf-shedding) species adapted to prolonged drought, such as *Commiphora leptophloeos* and *Cenostigma pyramidale* (Castro, 2007). In

contrast, semi-deciduous forests contain species adapted to more humid conditions, including *Salvertia convallariodora* and *Curatella americana* (CASTRO, 2007).

The ecological mosaic observed in the basin reflects the region's climatic diversity, which, according to the Thornthwaite and Mather (1955) classification, ranges from semi-arid to sub-humid. The mean annual temperature is 27.5 °C and average annual precipitation is approximately 1,172 mm (Lima et al., 2020) (Fig. 1). The seasons are well defined, with a rainy period lasting 3 to 5 months, followed by a prolonged dry season (BDIA, 2022; CEPRO, 2019). The basin itself is subdivided into three main sectors (Upper, Mid, and Lower Parnaíba), each with distinct geomorphological, hydrological, and ecological characteristics (MOTTA; GONÇALVES, 2016) (Fig. 1B).

The Lower Parnaíba (2°S–5°S; 41°W–42°W), located in the northern part of the basin, includes the river's mouth at the Atlantic Ocean (Fig. 1B). This region is characterized by low altitudes, ranging from approximately 70m to sea level, and mean annual temperature (MAT) between 27.9°C and 29°C (~28,5°C) (Motta and Gonçalves, 2016). Mean annual precipitation (MAP) ranges from 1,000 to 1,600mm, with a dry season lasting up to six months (ABREU; MUTTI; LIMA, 2019). The region presents the Babaçu palm forest (Mata de Cocais), dominated by *Attalea speciosa* (syn. *Orbignya phalerata*) (CASTRO, 2007). The expansion and increasing density of these palms are linked to anthropogenic disturbance of the original vegetation, with stands occurring predominantly in lowlands and humid valleys alongside remnants of riparian vegetation (CASTRO, 2007). A complex mosaic of plant formations is present, including elements of both the Cerrado and Caatinga, which also extend into the nearby coastal zone (SANTOS-FILHO; ALMEIDA JUNIOR; ZICKEL, 2013). Proximity to the coast further influences local hydro-sedimentary and ecological processes, particularly supporting the development of Restinga ecosystems (LIMA et al., 2020).

The Mid Parnaíba (4°S–9°S; 41°W–43°W), located in the central part of the basin (Fig. 1B), is characterized by smoother relief, with elevations ranging from approximately 300m to 70m above sea level. The region features wide valleys and well-developed floodplains. MAT varies between 25.3°C and 28.2°C (~26,7°C), MAP ranges from 800 to 1,400mm, and the dry season lasts for 6 to 8 months (ABREU; MUTTI; LIMA, 2019; MOTTA; GONÇALVES, 2016). A complex vegetation mosaic is observed in the Mid-Parnaíba, shaped by the transition between the Cerrado and Caatinga (Castro, 2007). This heterogeneity reflects the presence of ecotones

(ecological tension zones) where floristic and structural elements of adjacent biomes overlap.

The Upper Parnaíba (6°S–10°S; 43°W–44°W–), located in the southern part of the basin (Fig. 1B), contains the headwaters of the Parnaíba River, primarily in the Chapada das Mangabeiras region. This sub-basin features rugged terrain, with altitudes ranging from approximately 789m near the headwaters to around 300m near the Boa Esperança Dam. MAT ranges from 26.1°C to 28°C (~27°C). MAP varies with altitude, ranging from approximately 1,600 mm in the southeastern highlands to less than 800 mm in the southwestern lowlands (Abreu et al., 2019). Watercourses in this area are younger and more incised, with a high drainage density (MOTTA; GONÇALVES, 2016).

The predominant vegetation is Cerrado, which develops on sandy soils under a sub-humid climate (Lima et al., 2020; Thornthwaite and Mather, 1955). However, Caatinga vegetation is also present in the basin and represents a significant portion of its area (Motta and Gonçalves, 2016). The dry season lasts between 4 and 5 months (IBGE, 2023).

The Intertropical Convergence Zone (ITCZ; a low-pressure belt near the equator) plays a crucial role in controlling annual rainfall patterns across the Parnaíba basin. This zone, where air masses from the Northern and Southern Hemispheres meet, is marked by rising air, cloud formation, and heavy rainfall (JOHNS; ZANTOPP; GONI, 2003). During the wet season (December to April), the ITCZ shifts southward, increasing humidity and intensifying rainfall over Northeastern Brazil (HASTENRATH, 2012). This southward shift also weakens the North Brazil Current (NBC) and the North Equatorial Countercurrent (NECC), causing the Parnaíba River plume to linger near the coast (CARNEIRO et al., 2016; MOLLERI; NOVO; KAMPEL, 2010). In contrast, during the dry season (August to December), the ITCZ migrates northward. As a result, trade winds strengthen and the NBC intensifies, carrying the river plume farther into the North Atlantic (HESP; MAIA; CLAUDINO-SALES, 2009; MAIA et al., 1999).

3.2.2. Pedological and edaphic characterization of the Parnaíba Basin

The Parnaíba Basin exhibits a wide diversity of edaphic conditions (see supplementary material, Fig. S1), reflecting its vast territorial extent and the geoenvironmental variation along its gradient (Motta and Gonçalves, 2016). According to Melo and Júnior (2025), the main soil types identified in the region — according to the Brazilian Soil Classification System (SiBCS) — include:

Latosolos, which correspond to Ferralsols in the international WRB (World Reference Base for Soil Resources) system (EMBRAPA, 2018). These soils, which account for 35.2% of the basin's total area, are highly weathered, well drained, and naturally low in fertility. They are predominant in both the Cerrado (42.4%) and Caatinga (34.9%) biomes and occur at various elevations, including those recorded at our sampling sites (e.g. 320m and 430m).

Neossolos Litólicos (Leptosols) cover 21.4% of the basin, and are typically observed in areas with rugged topography and exposed bedrock, with samples recorded at elevations around 300m. Plintossolos (Plinthosols), which cover 6.6% of the area, develop in regions influenced by seasonal water tables and are distinguished by the presence of plinthite, which can form iron-rich concretions at depth. These soil types were present at our sampling sites at 122m above sea level.

Planossolos Nátricos (Solonetz), though covering only a small portion of the basin (0.03%), are notable for their high sodium saturation, dense structure, and low permeability — all of which restrict water infiltration and root development. Our samples corresponding to this soil type were identified at 60m elevation, indicating their occurrence in lower areas, such as the Lower Parnaíba. Brunizems (Phaeozems) are typically found in regions with darker soils and moderate fertility. Neossolos Quartzarênicos (Arenosols), which make up 11.5% of the basin, are extremely sandy, with low water and nutrient retention. Our samples were recorded at elevations around 400m and are commonly associated with transitional vegetation zones.

Neossolos Flúvicos (Fluvisols), comprising 0.8% of the basin, are primarily found in alluvial plains of the Mid and Lower Parnaíba. These soils are relatively young and tend to have higher fertility. The distribution and proportion of these soil types vary across the basin's sectors, reflecting the distinct geomorphological, hydrological, and climatic characteristics of each region.

3.3. Materials and methods

3.3.1. Sampling sites

Sampling was conducted across the Parnaíba Basin, predominantly in Piauí, with an additional site in Maranhão. Samples were collected in humid environments such as lakes, palm swamps, and the riverbanks near the Parnaíba River, which serve as reliable alternatives to pollen traps (Fig. 1C; McLauchlan et al., 2007). Surface sediment samples, approximately 2 cm in depth, were collected from the margins of these areas. This sediment represents pollen accumulated over the past 5 to 20 years (MCLAUCHLAN et al., 2007). Sampling locations were pre-selected using satellite imagery via Google Earth, resulting in 41 sites distributed across the Upper, Mid, and

Lower sub-basins of the Parnaíba River, reflecting clear spatial patterns in altitude, vegetation, and climate (Table 1; Fig. 1C). To characterize specific local conditions, climatic variables (MAP and MAT) were extracted for each sampling site using the historical climate data from the Chelsa v2.1 database, based on the 1981–2010 climatological baseline (Table 1; Karger et al., 2017).

In the Lower Parnaíba, sites 25, 27–31, 34–42, and 52 are situated in lowland areas (4 to 157 m) near the river delta. This region is composed of wetlands, palm swamps, and coastal vegetation such as restinga. The vegetation mosaic includes elements of Caatinga and Cerrado. Site-specific climate data indicate high humidity levels (MAP: 972.3 to 1639.9 mm; MAT: 28–29.1 °C), with a six-month dry season (MMA, 2006).

In the Mid Parnaíba, transitional conditions dominate sites 18–24, 26, 32, and 45–47 (Table 1). These areas are characterized by mid-elevations (106–570 m) and exhibit considerable ecological heterogeneity, including Cerrado, Caatinga, and ecotonal vegetation. Local climatic conditions vary accordingly, with rainfall between 626.2 to 1412.7 mm and average temperatures from 26.1 to 28.3 °C. The Upper Parnaíba includes sites 2–17 and 51, located in southern Piauí and western Maranhão (Table 1). Samples were collected across diverse Cerrado environments such as gallery forests, temporary pools, and lake margins between 133 and 444 m elevation. For this sub-basin, the specific extracted data show more moderate rainfall (817.5–1002.1 mm) and temperatures ranging from 26.1 to 28.1 °C, associated with a shorter dry season (typically four to six months, May–September; MMA, 2006).

Land use and land cover were quantified within a 1-km radius buffer around each sampling site using the MapBiomas Land Cover dataset (10 m resolution). Spatial processing was performed in R, where we first identified five landscape categories: forest, savanna, grassland, agriculture, and wetlands. These were then aggregated into two functional groups: woody cover (comprising forest and savanna) and open cover (encompassing agriculture, grassland, and wetlands) (MAPBIOMAS, 2023).

Similarly, specific phytophysiology and soil information were extracted within these same buffers using official digital maps (shapefiles) at a scale of 1:250,000 for the states of Piauí and Maranhão, sourced from the Environmental Information Database (BDIA, 2022). This approach enabled the assignment of the dominant soil type, phytophysiology, and current land cover classification to each sampling point, as defined in the datasets (Table 1).

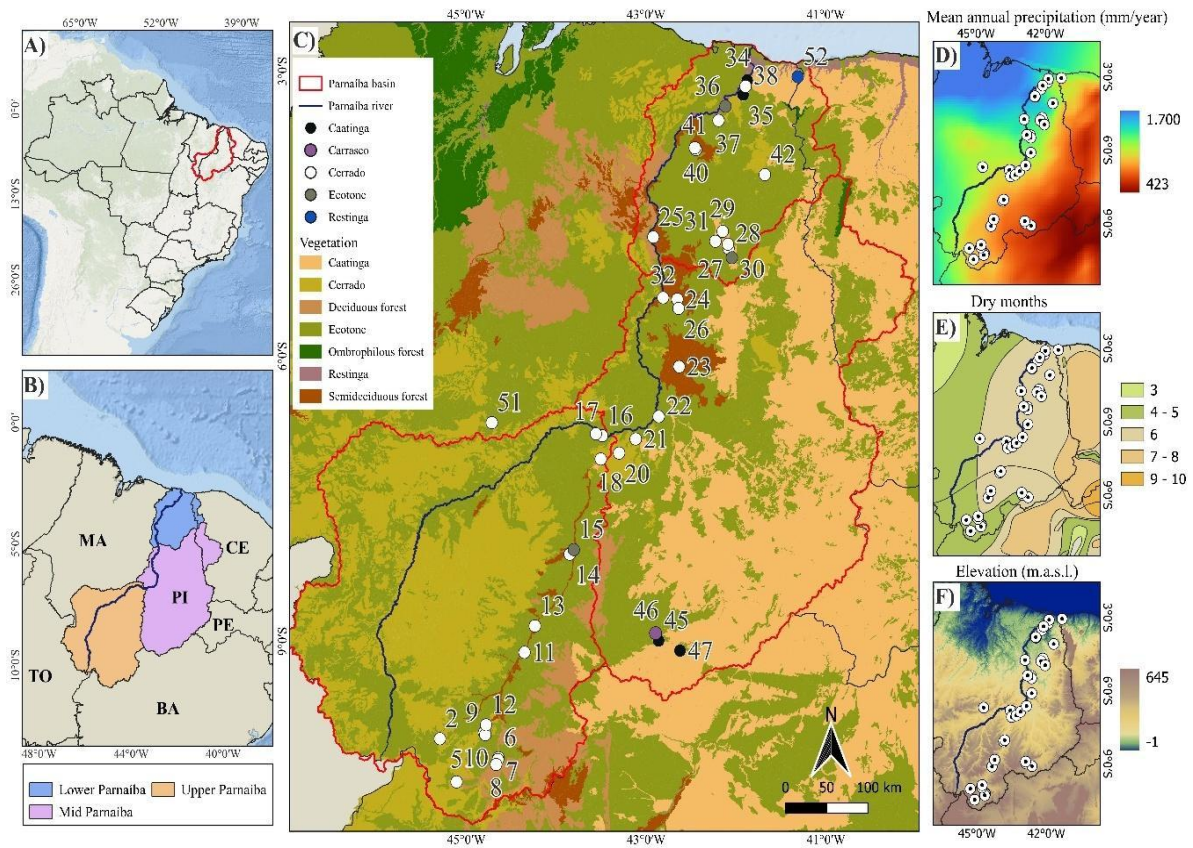


Fig. 1. Overview of the Parnaíba River Basin and its environmental gradients. A) Location of the Parnaíba river basin in South America. B) Regional division of the basin (Upper, Mid, and Lower Parnaíba), including state boundaries: Ceará (CE), Pernambuco (PE), Bahia (BA), Tocantins (TO), Maranhão (MA), and Piauí (PI). C) Detailed vegetation map of Piauí state, with the basin highlighted, showing the 41 sampling sites and their associated vegetation types. (D–F) Complementary maps displaying precipitation (D), dry season duration (E), and elevation (F) (IBGE, 2023).

Table 1. List of modern pollen rain samples collected in the Parnaíba Basin, along with their associated geographical, climatic, ecological characteristics, and references to the nearest phytosociological surveys. See Fig. 1 for sample locations. Legend: Low = Lower Parnaíba; Mid = Middle Parnaíba; Up = Upper Parnaíba; MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation).

Site n°	Geographical coordinates	Altitude (m asl)	Sub-basins	MAT (°C) MAP (mm)	Type of soil (WRB; 1km)	Dominant Phytophysionomy (1km)	Dominant Land Cover (1km)	Phytogeography domain and description (observed)	Phytosociology
2	10° 1'31.61"S 45°17'33.62"W	431	Up	26.2 944.7	Podzol	Ecotone	Woody	<i>Cerrado</i> . Gallery forest along the Gurgueia River	(CASTRO et al., 2009)
5	10°28'46.17"S 45° 6'26.14"W	417	Up	26.5 872.6	Ferralsol	Ecotone	Woody	<i>Cerrado</i> . Gallery forest along the Corrente River	Castro <i>et al.</i> , 2009
6	10°13'29.42"S 44°38'30.73"W	330	Up	27 817.5	Podzol	Ecotone	Woody	<i>Cerrado</i> . Shore of lake Parnaguá	Castro <i>et al.</i> , 2009
7	10°14'41.04"S 44°38'50.54"W	329	Up	27 825	Podzol	Ecotone	Open	<i>Cerrado</i> . Shore of lake Parnaguá	Castro <i>et al.</i> , 2009
8	10°17'47.37"S 44°40'4.50"W	329	Up	27 829.7	Podzol	Ecotone	Woody	<i>Cerrado</i> . Shore of lake Parnaguá	Castro <i>et al.</i> , 2009
9	9°57'45.44"S 44°48'8.49"W	444	Up	26.1 1002.1	Leptosol	Arboreous savanna	Woody	<i>Cerrado</i> . Temporary shallow lake	Castro <i>et al.</i> , 2009
10	9°58'57.47"S 44°47'15.70"W	436	Up	26.2 969	Podzol	Ecotone	Woody	<i>Cerrado</i> . Temporary shallow lake	Castro <i>et al.</i> , 2009
11	9° 6'58.83"S 44°21'8.91"W	253	Up	27.5 872.7	Fluvisol	Ecotone	Woody	<i>Cerrado</i> . Shore of lake Barro	Silva <i>et al.</i> , 2015; Macedo <i>et al.</i> , 2019
12	9°52'44.48"S 44°46'45.43"W	415	Up	26.2 946.9	Ferralsol	Arboreous savanna	Woody	<i>Cerrado</i> . Shore of lake Descoberta	Castro <i>et al.</i> , 2009
13	8°50'18.67"S 44°14'11.78"W	234	Up	27.7 845.3	Fluvisol	Ecotone	Woody	<i>Cerrado</i> . Temporary lake near the Gurgueia River	(ALVES et al., 2013); Souza <i>et al.</i> , 2017
14	8° 4'59.73"S 43°50'53.26"W	233	Up	27.6 884.2	Ferralsol	Ecotone	Woody	<i>Cerrado</i> . Temporary shallow lake	Castro <i>et al.</i> , 2014

15	8° 2'5.02"S 43°48'12.97"W	197	Up	27.8 875.5	Fluvisol	Ecotone	Woody	<i>Cerrado/Caatinga</i> . Temporary lake near the Gurguéia River	Castro <i>et al.</i> , 2014
16	6°50'11.30"S 43°29'15.01"W	133	Up	28 959.6	Podzol	Ecotone	Woody	<i>Cerrado</i> . Temporary shallow lake	Lima <i>et al.</i> , 2020a
17	6°49'0.80"S 43°33'27.80"W	140	Up	27.9 972.8	Podzol	Ecotone	Woody	<i>Cerrado</i> . Gallery forest along the Riacho da prata	Lima <i>et al.</i> , 2020a
18	7° 4'55.48"S 43°30'12.38"W	151	Mid	28 973	Leptosol	Ecotone	Woody	<i>Cerrado</i> . Temporary shallow lake	Lima <i>et al.</i> , 2020a
20	7° 1'5.90"S 43°17'58.91"W	182	Mid	27.8 1000.4	Ferralsols	Ecotone	Woody	<i>Cerrado</i> . Gallery forest along the Riacho da corrente	Lima <i>et al.</i> , 2020a
21	6°52'13.54"S 43° 6'53.07"W	174	Mid	27.9 1061.5	Ferralsols	Ecotone	Woody	<i>Cerrado</i> . Temporary shallow lake	Andrade <i>et al.</i> , 2016
22	6°38'4.88"S 42°51'31.91"W	154	Mid	28.1 1033.7	Leptosol	Parkland steppe-savanna	Woody	<i>Cerrado</i> . Temporary shallow lake	Andrade <i>et al.</i> , 2016
23	6° 6'33.35"S 42°37'54.49"W	194	Mid	27.9 1352.6	Phaeozem	Ecotone	Woody	<i>Cerrado</i> . Shore of lake Mulato	(LINDOSO <i>et al.</i> , 2009)
24	5°23'58.07"S 42°39'7.40"W	106	Mid	28.2 1381.8	Podzol	Ecotone	Woody	<i>Cerrado</i> . Temporary shallow lake	(ABREU; CASTRO, 2004)
25	4°44'44.26"S 42°55'8.20"W	56	Low	28.2 1464	Podzol	Semideciduous forest	Woody	<i>Cerrado</i> . Lake near the Parnaíba River	Abreu; Castro, 2004
26	5°29'45.44"S 42°38'20.67"W	141	Mid	28.1 1412.7	Podzol	Semideciduous forest	Woody	<i>Cerrado</i> . Temporary shallow lake	Abreu; Castro, 2004
27	4°51'46.17"S 42° 4'58.72"W	135	Low	28.9 1250.6	Plinthosol	Arboreous steppe-savanna	Woody	<i>Cerrado</i> . Lake near the road	(FARIAS; CASTRO, 2004)
28	4°49'12.61"S 42° 5'20.56"W	125	Low	29 1277	Plinthosol	Arboreous steppe-savanna	Open	<i>Cerrado</i> . Lake inside a farm	Farias; Castro, 2004
29	4°41'7.92"S 42° 8'52.14"W	116	Low	29 1365.9	Plinthosol	Arboreous steppe-savanna	Open	<i>Cerrado</i> . Lake near the road	Farias; Castro, 2004

30	4°57'45.58"S 42° 2'45.23"W	143	Low	28.9 1219.2	Plinthosol	Grassy-woody steppe-savanna	Open	<i>Cerrado/Caatinga</i> . Lake near the road	Farias; Castro, 2004
31	4°47'24.17"S 42°13'46.59"W	120	Low	28.9 1367.2	Plinthosol	Grassy-woody steppe-savanna	Open	<i>Cerrado</i> . Lake inside a farm with vegetation characteristic of a savanna park	Farias; Castro, 2004
32	5°23'0.61"S 42°48'37.02"W	122	Mid	28 1365.6	Ferralsols	Ecotone	Woody	<i>Cerrado</i> . Shore of lake Nazarea	Abreu; Castro, 2004
34	3° 5'46.84"S 41°52'29.82"W	6	Low	27.9 1102.8	Plinthosol	Arboreous steppe- savanna	Woody	<i>Caatinga</i> . Temporary shallow lake	(SILVA et al., 2018)
35	3°14'48.76"S 41°55'15.63"W	4	Low	28.2 1151.2	Plinthosol	Ecotone	Woody	<i>Caatinga</i> . Shore of lake Porcos	Silva et al., 2018
36	3°22'8.50"S 42° 7'0.70"W	25	Low	28.3 1192.6	Ferralsols	Pioneer formation	Open	<i>Cerrado/Caatinga</i> . Shore of lake Onça	Silva et al., 2018
37	3°31'5.63"S 42°11'37.89"W	11	Low	28.5 1220.5	Phaeozem	Ecotone	Open	<i>Cerrado</i> . Shore of lake Cajueiro	Silva et al., 2018
38	3° 9'31.65"S 41°53'36.20"W	21	Low	28 1075.6	Plinthosol	Ecotone	Woody	<i>Cerrado</i> . Palm swamp	Silva et al., 2018
40	3°48'23.26"S 42°27'26.75"W	102	Low	28 1615.4	Podzol	Semideciduous forest	Woody	<i>Cerrado</i> . Temporary shallow lake	Alves et al., 2013
41	3°49'31.09"S 42°26'44.58"W	88	Low	27.9 1639.9	Plinthosol	Semideciduous forest	Woody	<i>Cerrado</i> . Temporary shallow lake	Alves et al., 2013
42	4° 5'19.31"S 41°40'43.29"W	157	Low	28.7 1324.6	Arenosol	Arboreous savanna	Woody	<i>Cerrado</i> . Palm swamps inside Sete Cidades National Park	Alves et al., 2013
45	8°59'36"S 42°51'38"W	210	Mid	26.1 713.9	Leptosol	Arboreous steppe- savanna	Woody	<i>Caatinga</i> . Lake	(MATOS; FELFILI, 2010)
46	8°54'49"S 42°53'41"W	570	Mid	25.3 787.9	Ferralsols	Ecotone	Woody	<i>Carrasco</i> . Temporary shallow lake	(LEMONS; RODAL, 2002)
47	9°05'53"S 42°37'19"W	409	Mid	26.8 626.2	Podzol	Ecotone	Woody	<i>Caatinga</i> . Lake located in anthropized Caatinga region, with a shoreline characterized by a	Lemos; Rodal, 2002

								high abundance of Jurema Preta (<i>Mimosa tenuiflora</i>)	
51	6°41'56.97"S 44°42'54.15"W	215	Up	27.1 987.4	Podzol	Arboreous savanna	Woody	<i>Cerrado</i> . Shore of the Itapecuru river	Lemos; Rodal, 2002
52	3°03'29"S 41°18'45"W	13	Low	27.9 972.3	Podzol	Arboreous steppe-savanna	Woody	<i>Restinga</i> . Shore of the Camelo lake	Lima <i>et al.</i> , 2020a

3.3.2. Pollen extraction

Surface sediment samples were transported to the laboratory and stored at 5 °C. For chemical processing, 2 cm³ subsamples were extracted from each sample. To calculate pollen grain concentration (grains/cm³), two *Lycopodium* sp. tablets were added to each subsample (STOCKMARR, 1971). Samples 45, 46, 47, 51, and 52 used tablets from batch no. 280 521 291 (13,761 spores); all other samples used batch no. 050 220 211 (18,407 spores), as specified by the manufacturer.

Sample processing followed standard procedures (FAEGRI; IVERSEN, 1989). Silicates and silica were removed using hydrofluoric acid (HF, 70%), followed by hydrochloric acid (HCl, 50%) in a water bath at 80 °C to eliminate colloidal silica. Potassium hydroxide (KOH, 10%) was then applied at 80 °C to remove humic acids. Zinc chloride (ZnCl₂) was used for density separation to concentrate palynomorphs and reduce organic residues.

The resulting material was preserved in 95% glycerin and mounted on microscope slides. Pollen grain identification and counting were conducted under light microscopy at 600× magnification, with a minimum count of 300 terrestrial pollen grains per sample. Identifications were based on reference collections at the Federal University of Ceará and the University of Montpellier, as well as published pollen atlases (ESCOBAR-TORREZ; CASSINO; LEDRU, 2024; LORENTE et al., 2017; SALGADO-LABOURIAU, 1973; SILVA; ARAÚJO; LEDRU, 2024).

3.3.3. Statistical analysis

Three pollen diagrams were constructed using the *rioja* package in R (JUGGINS, 2023), displaying the most abundant taxa (>25% of the total assemblage). For this, arboreal pollen (AP) and non-arboreal pollen (NAP) data were converted to percentages, with aquatic taxa excluded from the total pollen count. Next, a hierarchical clustering analysis was performed using Ward's minimum variance method with the Bray-Curtis dissimilarity coefficient (LEGENDRE; LEGENDRE, 2012; WARD, 1963). The optimal number of clusters was determined using the silhouette index, which assesses clustering quality based on intra-group cohesion and inter-group separation (ROUSSEEUW, 1987). The identification of key species separating the clusters was evaluated using indicator species analysis (IndVal), which identifies the species with the highest and most significant association with each grouping.

To support the ecological interpretation of these assemblages, the Importance Value Index

(IVI) reported in regional phytosociological studies was used as a reference. The IVI quantifies the ecological weight of species based on the sum of their relative density, dominance, and frequency (CURTIS; MCINTOSH, 1951). Pollen data variation was initially explored using principal component analysis (PCA). The results of this exploratory analysis are provided in the Supplementary Material (Fig. S2).

Statistical analyses were performed to assess the relationships between pollen assemblages, vegetation cover, and environmental drivers. First, Spearman rank correlation coefficients were calculated to identify significant associations between the relative abundance of specific pollen taxa and vegetation cover classes within 1-km buffers. Subsequently, to investigate the influence of environmental variables on pollen composition, we performed a Redundancy Analysis (RDA) (LEGENDRE; LEGENDRE, 2012) using the *vegan* package in R (OKSANEN et al., 2025).

Prior to RDA, a Detrended Correspondence Analysis (DCA) yielded a gradient length < 3.0 SD, indicating a linear response, and pollen data were Hellinger-transformed to minimize the effect of double-zeros. The continuous explanatory variables included altitude, annual mean precipitation, and annual mean temperature, while categorical variables representing soil types (WRB equivalents) included Fluvisols, Arenosols, Phaeozems, Ferralsols, Leptosols, Plinthosols, and Podzols. All analyses were performed in R version 4.5.1 (R CORE TEAM, 2025).

3.4. Results

3.4.1. Landscape structure surrounding sampling sites

Regarding the percent composition of Land Use and Land Cover (Fig. 2A) and phytophysionomies (Fig. 2B) across the sampling sites, there was a predominance of classes categorized as woody cover, specifically savanna and forest. According to MapBiomass (MAPBIOMASS, 2023) and the IBGE technical standards (VELOSO; FILHO; LIMA, 2012), these physiognomies are characterized by a continuous or semi-continuous tree canopy. Conversely, open cover classes, primarily agriculture and grassland, were distributed heterogeneously, with greater prominence at sites 28, 29, 30, and 31. Wetlands occurred sporadically and showed low overall representation across the study area.

The detailed phytophysionomic analysis (Fig. 2B) showed that ecotone areas were the most widespread, appearing as the dominant class across most sites. Savanna and steppe-savanna formations (including arboreal, grassy-woody, and parkland subtypes) contributed variably to the

landscape composition. Forest formations, specifically semideciduous forest, were concentrated at sites 25, 26, 40, and 41, while deciduous forest was restricted to site 46. Pioneer formations were exclusively recorded at sites 34 and 36 (Fig. 2B).

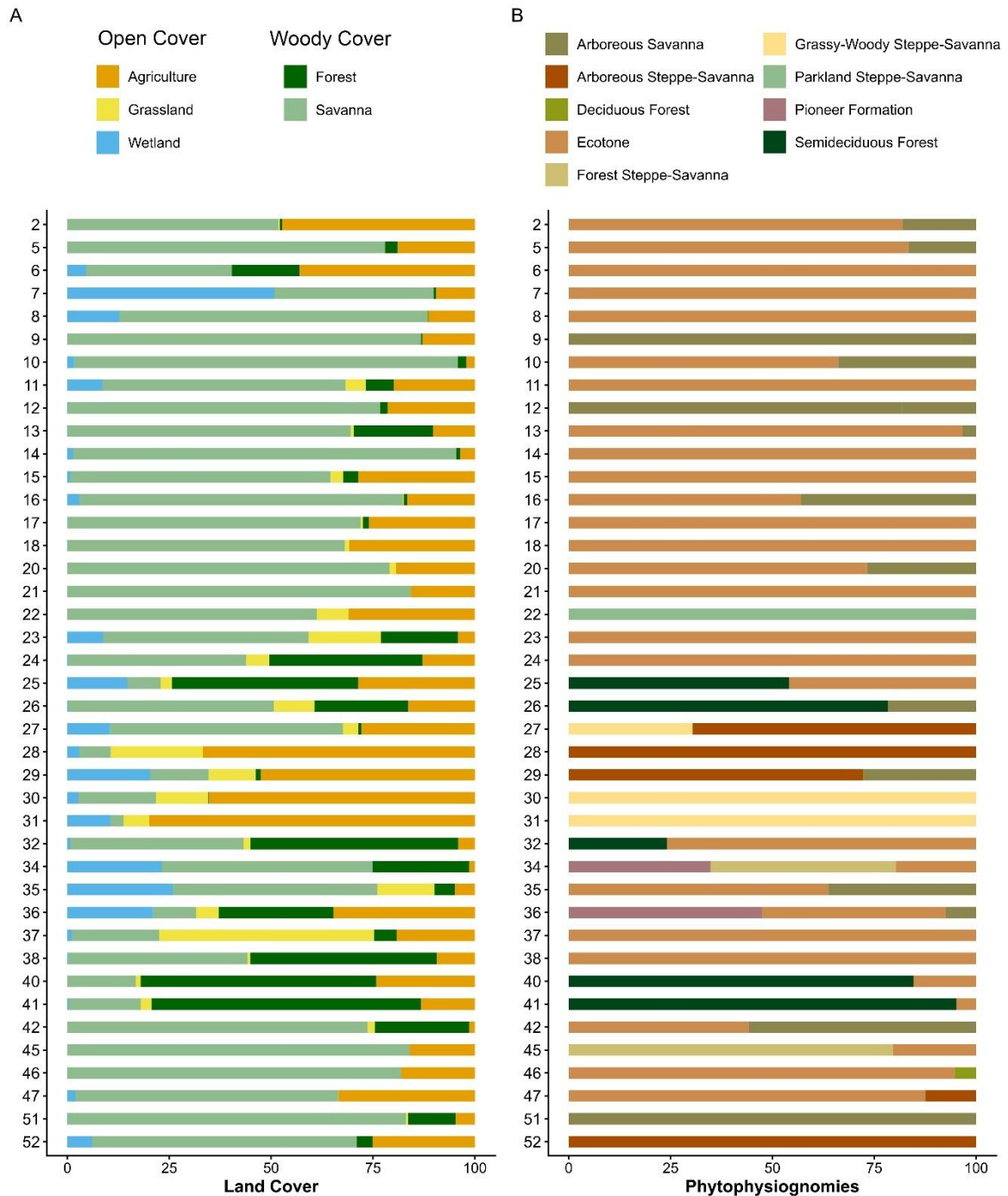


Fig. 2. Landscape characterization within a 1-km buffer of the sampling sites. (A) Proportion of vegetation cover groups, where agriculture, grassland, and wetland were classified as open cover, and forest and savanna as woody cover (MAPBIOMAS, 2023). (B) Specific vegetation physiognomies identified in the study area (IBGE, 2023)

3.4.2. Characterization of the modern pollen assemblage

Forty-one samples reached the minimum count of 300 terrestrial pollen grains and were included in the analyses. In total, 317 taxa were identified, representing 87 families. Pollen concentrations varied widely, from 1,262 to 203,070 grains/cm³. Recorded concentrations were: 2,793 grains/cm³ in the restinga sample, 12,177 grains/cm³ in the carrasco sample. For the other groups, values ranged from 4,238–12,348 grains/cm³ in Caatinga samples, 7,658–18,628 grains/cm³ in ecotone samples, and 1,262–203,070 grains/cm³ in Cerrado samples. The pollen diagram (Fig. 3) is divided into five groups, named according to the vegetation observed at the sampling sites and supported by nearby phytogeographic studies. Within each group, samples are arranged in ascending order of MAP.

Of the total identified taxa, 57% (180) correspond to non-arboreal pollen (NAP), 39% (124) to arboreal pollen (AP), and 4% (13) to aquatic species. Among NAP taxa, the most prominent families include Amaranthaceae, Araceae, Asteraceae, Malvaceae, Poaceae, Rubiaceae. Genera such as *Amaranthus*-type, *Alternanthera* and *Borreria*-type were recorded in multiple samples. *Borreria*-type and Poaceae were especially abundant and widespread across all vegetation groups.

The pollen diagram (Fig. 3), shows only taxa with pollen frequencies above 25%, and a total of 14 arboreal taxa are included. The most frequently represented families include Arecaceae, Anacardiaceae, Apocynaceae, Elaeocarpaceae, Euphorbiaceae, Fabaceae, Melastomataceae/Combretaceae, Myrtaceae, Solanaceae. Pollen types of Melastomataceae/Combretaceae and Myrtaceae were identified in 40 and 38 out of the 41 sites, with frequency ranges of 0.23–52% and 0.29–31%, respectively. *Mimosa*-type and *Piptadenia*-type pollen (both Fabaceae) were detected at 39 and 37 sites, with frequency ranges of 0.22–60% and 0.31–17%, respectively.

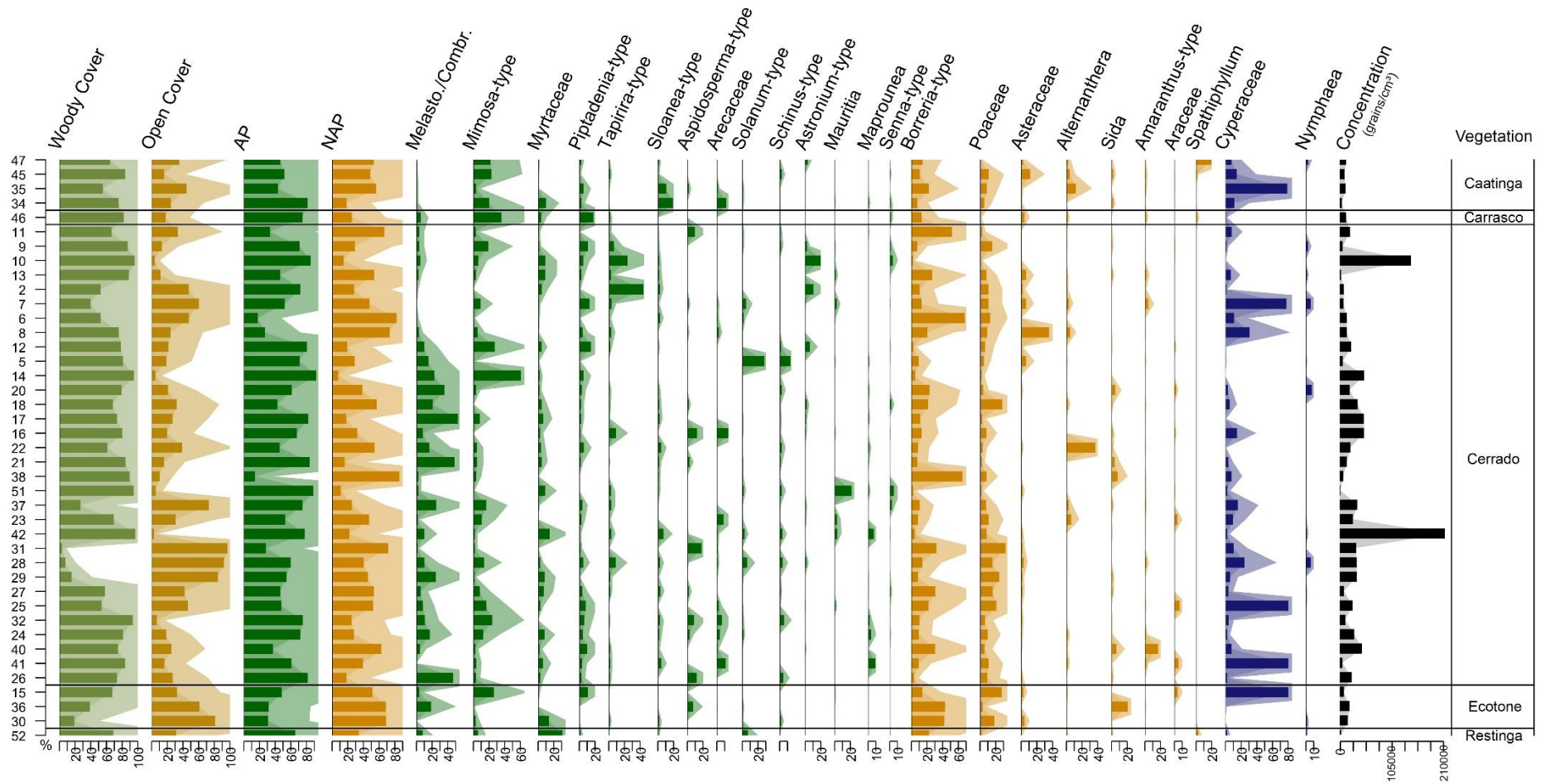


Fig. 3. Summary pollen diagram of 41 surface samples collected across the Parnaíba Basin, showing the relative frequency of pollen taxa grouped by vegetation type (see Table 1). Plant life forms are color-coded: green for arboreal pollen (AP), yellow for non-arboreal pollen (NAP), and blue for aquatic taxa, while pollen concentration is shown in black. Sample locations are shown in Fig. 1.

Pollen diversity was low in areas dominated by restinga and carrasco vegetation, with AP accounting for 56% in the restinga sample and 74% in the carrasco sample. Despite both being woody formations, their pollen compositions differed. In the restinga sample, the most abundant taxa were Myrtaceae (31%), *Borreria*-type (22.6%), Melastomataceae/Combretaceae (7.8%), and *Solanum*-type (7.4%). Fabaceae was represented by *Mimosa*-type (6%), *Piptadenia*-type (1.8%), and *Senna*-type (0.4%), while Asteraceae accounted for 0.4%.

In contrast, the carrasco sample was dominated by Fabaceae, with *Mimosa*-type (35.7%), *Piptadenia*-type (17.8%), and *Senna*-type (1.6%). Asteraceae was also more abundant (4.1%), and several taxa not observed in the restinga were present, including *Tapirira*-type (1.6%). Poaceae was rare in both environments, making up 1.8% in restinga and 0.8% in carrasco.

In Caatinga samples, NAP predominated at three of the four samples, accounting for 50–57% of the assemblage. The exception was site 34, where AP comprised 80%. Fabaceae was the most prominent family overall, with *Mimosa*-type ranging from (3–23%), *Piptadenia*-type from (0.7–5%), and *Senna*-type from (0.2–1%). Site 34 also showed a notably high frequency of Myrtaceae (9.9%), compared to just 0.4–0.8%, at the other sites. *Sloanea*-type pollen was also significant ranging from 0.7–19%. Anacardiaceae was represented by two morphotypes: *Tapirira*-type (0.4–1.5%) and *Schinus*-type (0.2–2.6%). Other prominent arboreal taxa included Arecaceae (1.4–12%). Among NAP, *Borreria*-type (7–22%) and Poaceae (1–11%) were moderately frequent, as were Asteraceae (0.5–11%), *Alternanthera* (2–12%), and *Spathiphyllum* (1–19%).

In the ecotone group (samples 15, 30 and 36), NAP were dominant ranging from 51–69%. The pollen assemblages displayed a mixed composition, consistent with the ecotonal nature of the vegetation. Common AP included Melastomataceae/Combretaceae (0.2–18%), *Mimosa*-type (3–26%), Myrtaceae (1–14%), and *Piptadenia*-type (10%). Among the NAP, the most representative were *Borreria*-type (14–43%), Poaceae (3–27%), Asteraceae (2–4%), and *Sida* (0.4–20%).

In the Cerrado group, a marked increase in pollen diversity was observed, possibly due to this vegetation type being the most extensively sampled in the study. Of the 32 Cerrado samples, 14 were dominated by NAP (52–86%), while AP was dominant in the remaining 18 (53–92%). Among AP, the most frequent were Melastomataceae/Combretaceae (0.25–52%) and Fabaceae, represented by *Mimosa*-type (0.21–60%), *Piptadenia*-type (0.31–15%) and *Senna*-type (0.24–5%). Myrtaceae also had notable frequencies (0.19–15%), as did pollen taxa of Anacardiaceae, including *Tapirira*-type (0.21–44%), *Schinus*-type (0.24–14%) and *Astronium*-type (0.22–19%).

Euphorbiaceae was represented by *Maprounea*-type (0.22–9%). Other important AP included *Sloanea*-type (0.21–7%), *Arecaceae* (0.21–15%) particularly *Mauritia* (0.24–21%), *Aspidosperma*-type (0.21–18%), and *Solanum*-type (0.2–28%).

NAP were also highly diverse. Rubiaceae was well represented by *Borreria*-type (2–68%), along with Poaceae (1–32%). Within Amaranthaceae, *Amaranthus*-type (0.2–16%), and *Alternanthera* (0.2–37%) were recorded. Asteraceae was consistently present, with values ranging from 0.2% to 35%. Aquatic pollen, particularly Cyperaceae, was also detected in several samples from Cerrado, Caatinga, and the ecotone.

Analysis of woody cover within a 1 km radius revealed distinct patterns across vegetation types. In the Caatinga, woody cover ranged from 55% to 84%, with open areas comprising 16% to 45%. The single carrasco record exhibited 82% woody cover and 18% open vegetation. Within Cerrado samples, most locations (27 samples) were dominated by woody vegetation, with cover ranging from 52% to 97%. However, five Cerrado records were characterized by predominantly open formations, exhibiting 60% to 90% open vegetation cover. The ecotone zone showed a contrasting pattern, with two samples (36 and 30) dominated by open areas (61%–81% open vegetation) and only one sample (15) displaying woody-dominated cover (68%). The single restinga sample was predominantly forested, with 69% woody cover.

In a second pollen diagram (Fig.4), samples were grouped according to their respective sub-basins (Lower, Mid, and Upper Parnaíba). In the Upper Parnaíba, 14 samples exhibited woody cover ranging from 52% to 96%, while only one sample showed a dominance of open cover (60%). In the Mid Parnaíba, woody cover was dominant across all locations, ranging from 61% to 94%. Finally, the Lower Parnaíba presented a mixed pattern: nine samples had high percentages of woody cover (54–97%), whereas six samples were dominated by open cover (61–97%).

The Lower Parnaíba presented values between 2,793 and 203,070 grains/cm³. Seven of the 15 samples were dominated by AP, with percentages ranging from 54% to 81%. The remaining eight samples were dominated by NAP, varying between 52% and 86%. Among the NAP, *Borreria*-type (4–65%) and Poaceae (1.8–32%) were the most abundant. Additional contributors included, *Amaranthus*-type (0.1–16%), Asteraceae (0.4–4%), *Alternanthera* (0.2–12%), and *Sida* (0.2–20%). The most frequent AP taxa were Melastomataceae/Combretaceae (0.2–25%), *Mimosa*-type (0.5–19%), *Myrtaceae* (0.1–31%), *Piptadenia*-type (0.4–9%), *Tapirira*-type (0.3–8%), *Sloanea*-type (0.2–19%), *Aspidosperma*-type (0.5–18%), *Arecaceae* (0.2–12%) and *Solanum*-type

(0.2-7%).

In the Mid Parnaíba, pollen concentrations varied between 8,803 and 34,205 grains/cm³. The analysis of 11 samples in the Mid Parnaíba revealed a clear division in pollen composition. Eight samples were dominated by AP, with values ranging from 51% to 83%, while the remaining five showed a more modest dominance of NAP, ranging from 53% and 57%. The AP assemblage was characterized by high frequencies of Melastomataceae/Combretaceae (0.4–48%), *Mimosa*-type (0.2–35%), Myrtaceae (0.5–8%), and *Piptadenia*-type (0.7–17%). Other significant taxa included *Sloanea*-type (0.2–4%), *Aspidosperma*-type (0.2–11%), Arecaceae (0.2–8%), *Solanum*-type (0.2-1.3%), and *Schinus*-type (0.4–5%). Among the NAP, *Borreria*-type (3–23%), Poaceae (0.8–28%), Asteraceae (0.2–11%), *Alternanthera* (1-36%), *Sida* (0.2-5%), and *Amaranthus*-type (0.2-1.6%).

Pollen concentration in the Upper Parnaíba ranged from 1,262 to 137,410 grains/cm³. The pollen signature of the Upper Parnaíba shows significant heterogeneity in its vegetation composition, evidenced by the alternating dominance of AP and NAP across the 15 samples. AP predominated in ten sites, with values ranging from 52% to 92.2%. This dominance is primarily attributed to a group of consistently represented taxa, including Melastomataceae/Combretaceae (0.2-52.8%), *Mimosa*-type (0.5–60.7%), Myrtaceae (0.5–9%), *Piptadenia*-type (0.3–14%), *Tapirira*-type (0.2–44%), *Sloanea*-type (0.6–2%), *Aspidosperma*-type (0.3–12%), Arecaceae (0.3–14%), *Solanum*-type (0.2-28%), *Schinus*-type (0.2–13%), *Astronium*-type (0.2–19%), and *Mauritia* (0.3-21%). In contrast, the NAP component was dominant in five sites, ranging from 51.5% to 82%. The prevalence of NAP in these locations is directly associated with the high abundance of *Borreria*-type (1.8–68%) and Poaceae (1.2–28%), with other contributing taxa such as Asteraceae (0.2–35%), *Alternanthera* (0.2–4%), and *Sida* (0.2–1.4%).

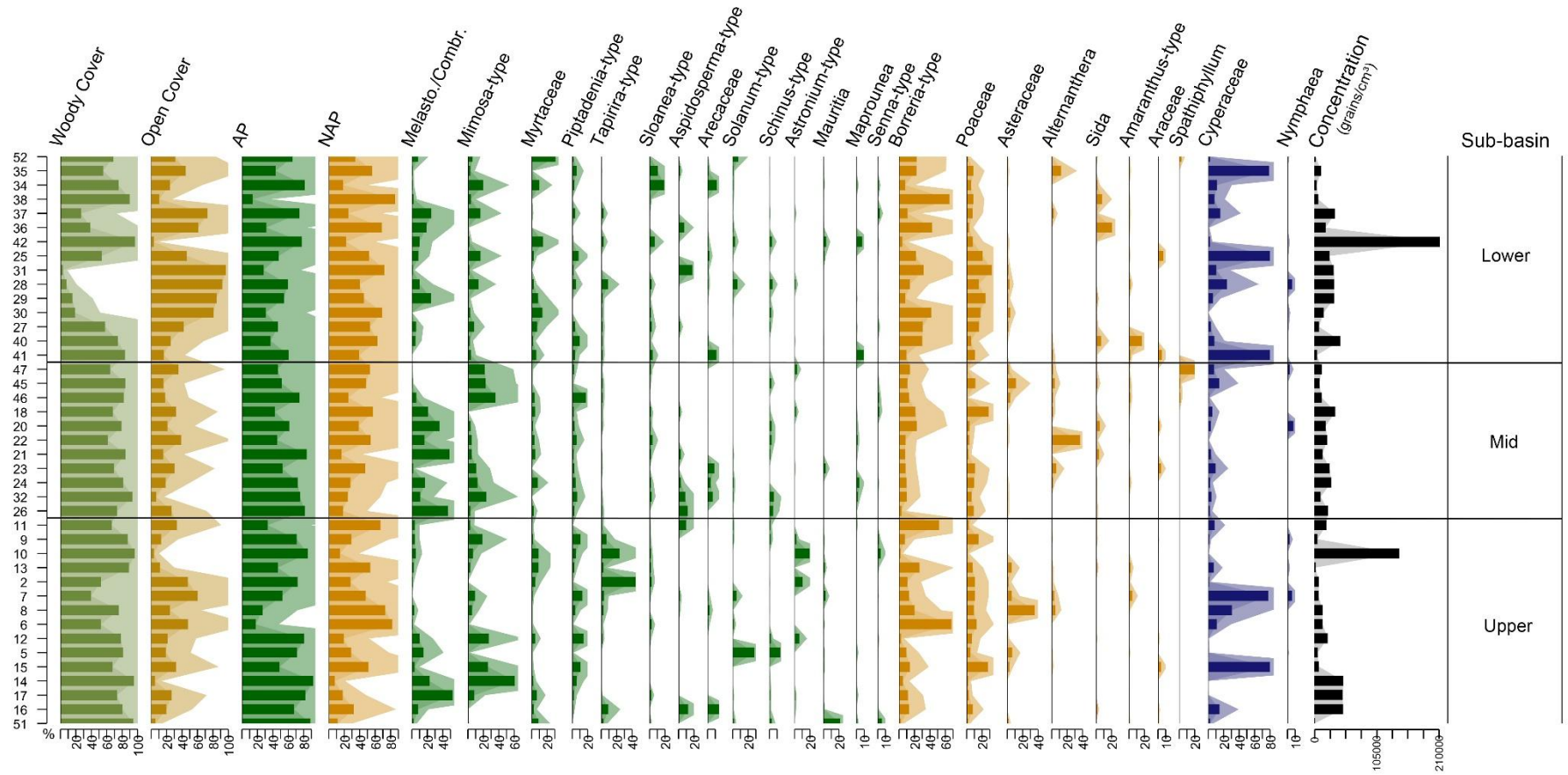


Fig. 4. Summary pollen diagram of 41 surface samples collected across the Parnaíba Basin, showing the relative frequency of pollen taxa grouped by sub-basin (Lower, Mid, and Upper Parnaíba; see Table 1). Plant life forms are color-coded: green for arboreal pollen (AP), yellow for non-arboreal pollen (NAP), and blue for aquatic taxa, while pollen concentration is shown in black. Sample locations are shown in Fig. 1.

In a third pollen diagram (Fig. 5), samples were grouped according to their depositional environments: gallery forest, lake, palm swamps (*veredas*), and temporary lake.

The five samples associated with gallery forests (Fig. 5) exhibited a predominance of woody cover (52–95%) and AP values ranging from 71% to 88%. Pollen concentrations varied from 1,262 to 46,314 grains/cm³. The AP content showed significant variation among sites; the most representative taxa included Melastomataceae/Combretaceae (1–52%), *Tapirira*-type (0.6–44%), *Solanum*-type (0.6–27%), *Schinus*-type (0.3–14%), and *Astronium*-type (0.9–10%). Other contributors were *Mimosa*-type (0.5–8%), Myrtaceae (0.6–8%), *Piptadenia*-type (0.6–3%), and *Sloanea*-type (1–2%). NAP was poorly represented overall, with *Borreria*-type (2–23%) and Poaceae (1–10%) consistently present. Cyperaceae showed minimal representation in these gallery forest systems, with values ranging only from 0.3% to 6%.

In lake environments, pollen concentrations ranged from 2,793 to 33,778 grains/cm³. Twelve sites were characterized by dominant woody cover (52–94%), while seven samples were dominated by open cover (60–97%) (Fig. 5). Regarding pollen representation, AP was dominant in nine samples (51–80%), whereas NAP predominated in ten samples (52–82%). These variations reflect the surrounding vegetation (Figs. 3 and 4), with notable differences between Cerrado and Caatinga sites. Dominant AP taxa included Melastomataceae/Combretaceae (0.2–25%), *Mimosa*-type (0.5–27%), Myrtaceae (0.1–31%), *Piptadenia*-type (0.3–8%), *Tapirira*-type (0.3–8%), and *Sloanea*-type (0.2–10%). Among the NAP, *Borreria*-type (2–68%) and Poaceae (1–32%) were present in all samples, while Asteraceae (0.2–35%), *Alternanthera* (0.2–12%), *Sida* (0.2–20%), and *Amaranthus*-type (0.1–4%) were also frequent.

In temporary lakes, pollen concentrations spanned from 2,317 to 137,410 grains/cm³, with woody cover dominating the landscape (61–96%) (Fig. 5). Ten samples showed a predominance of AP (60–92%), and five samples were dominated by NAP (51–62%). The main arboreal taxa were Melastomataceae/Combretaceae (1–48%), *Mimosa*-type (0.2–60%), *Piptadenia*-type (1–17%), Myrtaceae (0.9–10%), *Tapirira*-type (0.2–23%), *Sloanea*-type (0.2–19%), *Aspidosperma*-type (1–12%), Arecaceae (0.2–14%), and *Solanum*-type (0.2–1%). Among the NAP, *Borreria*-type (1–30%) and Poaceae (0.8–28%) occurred in all samples, whereas Asteraceae (0.2–6%), *Alternanthera* (0.2–36%), *Sida* (0.3–6%), and *Amaranthus*-type (0.2–16%) were observed only in a few samples.

Among aquatic taxa (Fig. 5), Cyperaceae showed constant representation, with

overabundance peaks (exceeding 80%) at sites 7, 15, 25, 35, and 41. These peaks occurred in lake and temporary lake environments, where Cyperaceae values often surpassed the total pollen sum (AP+NAP). In the diagram, these frequencies were capped at 80% for visual consistency.

The two palm swamp samples presented pollen concentrations of 6,834 and 203,070 grains/cm³, both associated with high woody coverage (90% and 97%) (Fig. 5). The proportions of AP and NAP varied significantly between the two: site 38 was dominated by NAP (85%), whereas site 42 was dominated by AP (77%). Dominant arboreal taxa included Myrtaceae (0.2–14%), Melastomataceae/Combretaceae (2–9%), *Sloanea*-type (1–7%), *Mimosa*-type (2–3%), and *Solanum*-type (0.5–3%). Among the NAP, *Borreria*-type (4–65%) and Poaceae (8.1–8.5%) were the most frequent, followed by *Sida* (0.5–7%) and *Amaranthus*-type (0.2–0.5%). Cyperaceae showed low representation in these sites, ranging from 2% to 7%.

In summary, the depositional environments exhibited distinct pollen signals, although a heterogeneous composition was maintained across all samples. The primary distinction among environments was the distribution of aquatic taxa, specifically the overrepresentation of Cyperaceae in lake and temporary lake sites compared to its minimal presence in gallery forests and palm swamps. Despite these local variations in aquatic proportions, a shared suite of dominant regional taxa, including Melastomataceae/Combretaceae, *Tapirira*-type, and *Borreria*-type, was recorded across all depositional contexts, reflecting the regional floristic diversity of the Parnaíba Basin.

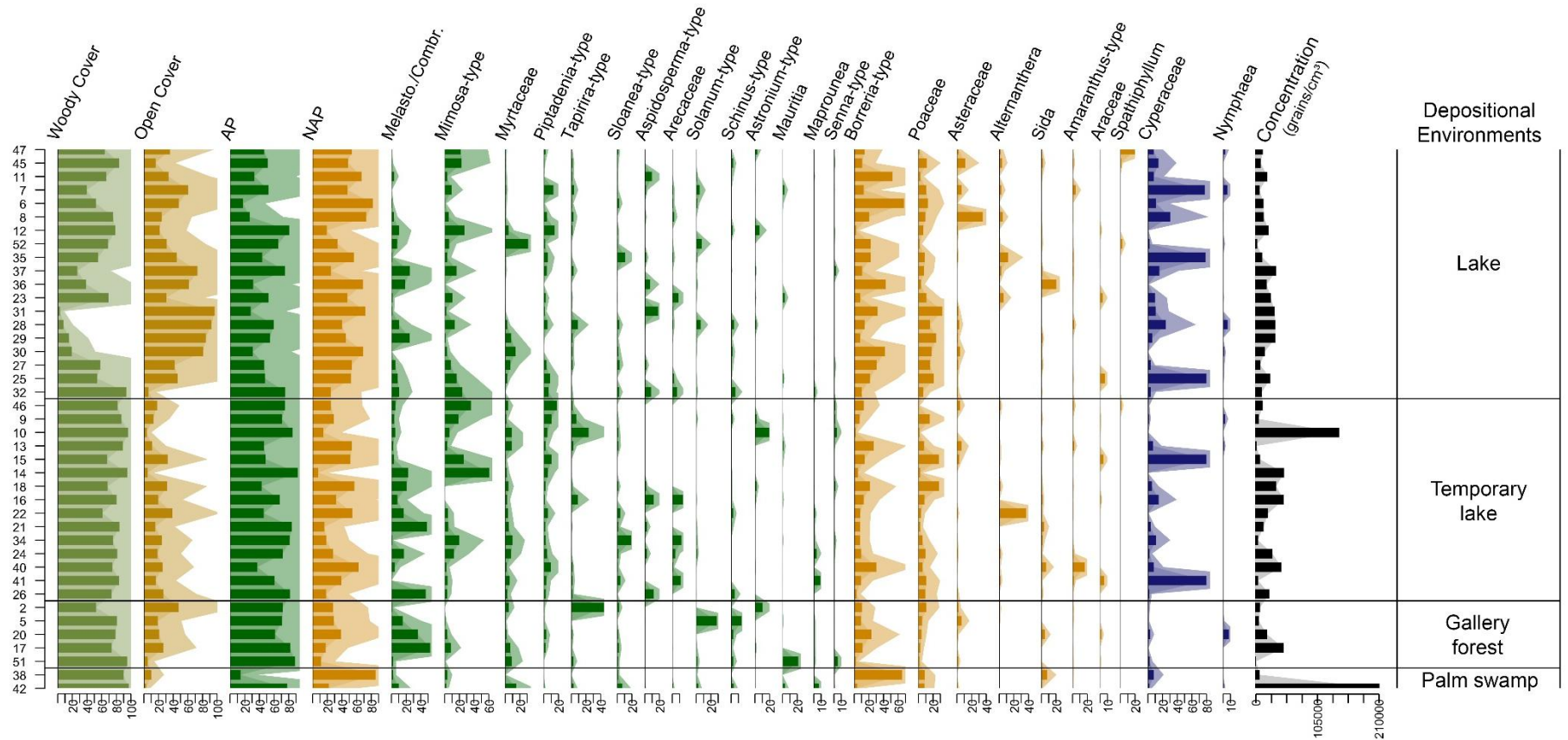


Fig. 5. Summary pollen diagram of 41 surface samples collected across the Parnaíba Basin, showing the relative frequency of pollen taxa grouped by their depositional environments (lake, temporary lake, gallery forest, and palm swamp; see Table 1), including local woody and open vegetation cover percentages. Plant life forms are color-coded: green for arboreal pollen (AP), yellow for non-arboreal pollen (NAP), and blue for aquatic taxa, while pollen concentration is shown in black. Sample locations are shown in Fig. 1.

3.4.3. Influence of landscape structure and land use on pollen signatures

Land cover analysis within a 1 km buffer around each sampling site showed that modern pollen assemblages closely reflect the surrounding vegetation structure. Sites with a higher proportion of woody vegetation (forest and savanna physiognomies) were associated with increased AP frequencies (Spearman's $\rho = 0.509$, $p = 0.001$; Fig. 6A). In contrast, landscapes dominated by open vegetation (grassland, crops and wetlands) were characterized by higher NAP frequencies ($\rho = 0.509$, $p = 0.001$; 6B).

At the taxonomic level, the pollen percentage of *Borreria*-type (Rubiaceae) varied consistently along the gradient of non-woody vegetation cover, reaching its highest values in samples dominated by open formation landscape (Fig. 6C). A similar pattern was observed for Poaceae, whose pollen percentages increased with the expansion of non-woody cover, indicating a strong association with open environments (Fig. 6D). These patterns were supported by Spearman correlation analyses, which confirmed statistically significant relationships between the pollen percentages of both taxa and the proportion of non-woody vegetation in the surrounding landscape.

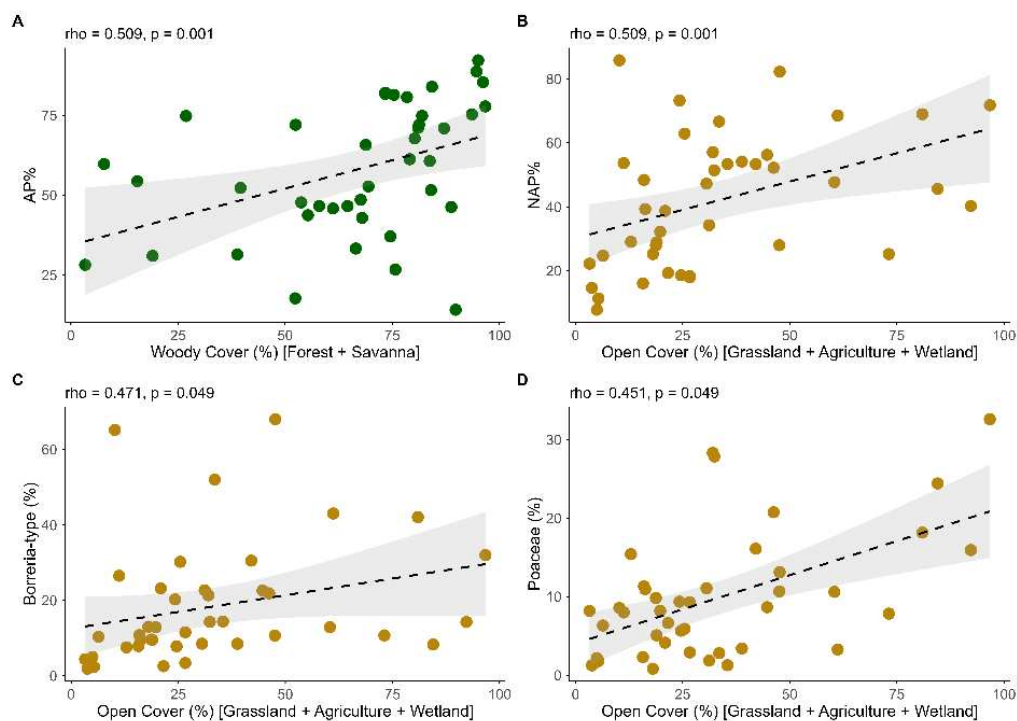


Fig. 6. Spearman correlations between modern pollen percentages and vegetation cover within a 1-km buffer around the sampling sites. (A) Arboreal Pollen (AP) (this study) versus woody cover (Fig. 2); (B) Non-Arboreal Pollen (NAP) versus open cover (Fig. 2); (C) *Borreria*-type pollen percentage versus open cover (Fig. 2); (D) Poaceae pollen percentage versus open cover (Fig. 2). Dashed lines represent linear trends, and shaded areas indicate 95% confidence intervals. Correlation coefficients and significance levels are shown in each panel.

Spearman rank correlations between pollen assemblages and more specific vegetation

types within a 1 km buffer (Fig. 7) revealed significant associations for individual taxa ($\rho \geq 0.4$; $p < 0.05$). A significant positive correlation was observed between the arboreal taxon *Copaifera* and woody savanna cover (Fig. 7A; $\rho = 0.468$; $p = 0.002$). In contrast, the herbaceous *Borreria*-type exhibited a significant negative correlation with the woody savanna physiognomy (Fig. 7B; $\rho = -0.411$; $p = 0.008$).

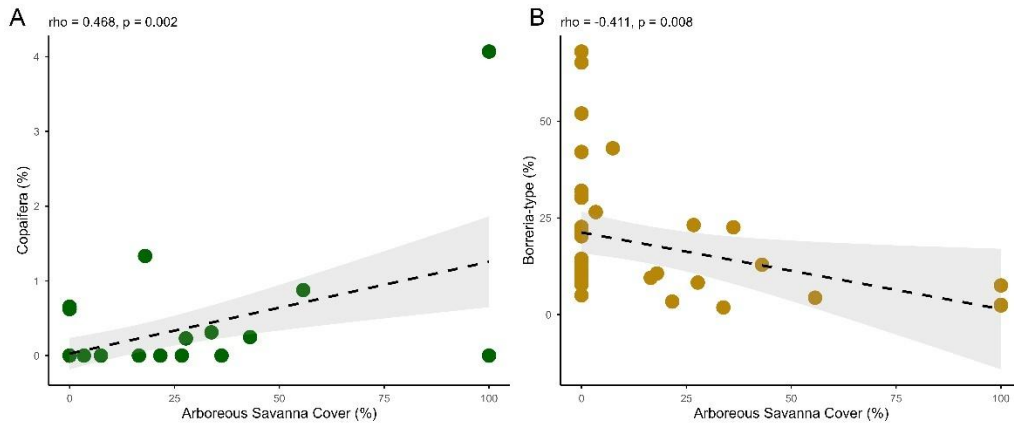


Fig. 7. Scatter plots showing the relationship between pollen percentage (%) and Arboreous Savanna cover (%) within a 1-km buffer. Dashed lines indicate linear trends with 95% confidence intervals (shaded areas). Spearman rank correlation coefficients (ρ) and p-values are provided above each panel. (A) *Copaifera* vs. Arboreous savanna cover; (B) *Borreria*-type vs. Arboreous savanna cover.

3.4.4. Cluster and Ordination

Hierarchical cluster analysis (Fig. 8), based on pollen percentages, identified six main floristic groups distributed along the south–north axis of the Parnaíba River. Cluster 1 comprised three samples characterized by the association of *Tapirira*-type and *Astronium*-type pollen, corresponding mainly to ecotone and woody savanna vegetation. Cluster 5 included seven samples dominated by Melastomataceae/Combretaceae, occurring across woody steppe-savanna, ecotone, woody savanna, and semideciduous forest physiognomies. Cluster 2 encompassed 11 samples showing no dominant taxon, reflecting a heterogeneous pollen assemblage derived from multiple physiognomies, including woody steppe-savanna, ecotone, parkland steppe-savanna, grassy-woody steppe-savanna, and semideciduous forest.

Cluster 3 consisted of six samples defined by the association of *Borreria*-type and *Aspidosperma*-type pollen, representing grassy-woody steppe-savanna, ecotone, and pioneer formations. Cluster 4, with 11 samples, was characterized by a *Mimosa*-type pollen assemblage, occurring predominantly in ecotone, woody savanna, and semideciduous forest. Cluster 6 grouped three samples from semideciduous forest, forest steppe-savanna, and ecotone physiognomies and was characterized by a mixed woody–herbaceous pollen assemblage, with

significant contributions of *Arecaceae*, *Naucleopsis*, *Ipomoea*, *Araceae*, *Qualea*-type, and *Sloanea*-type.

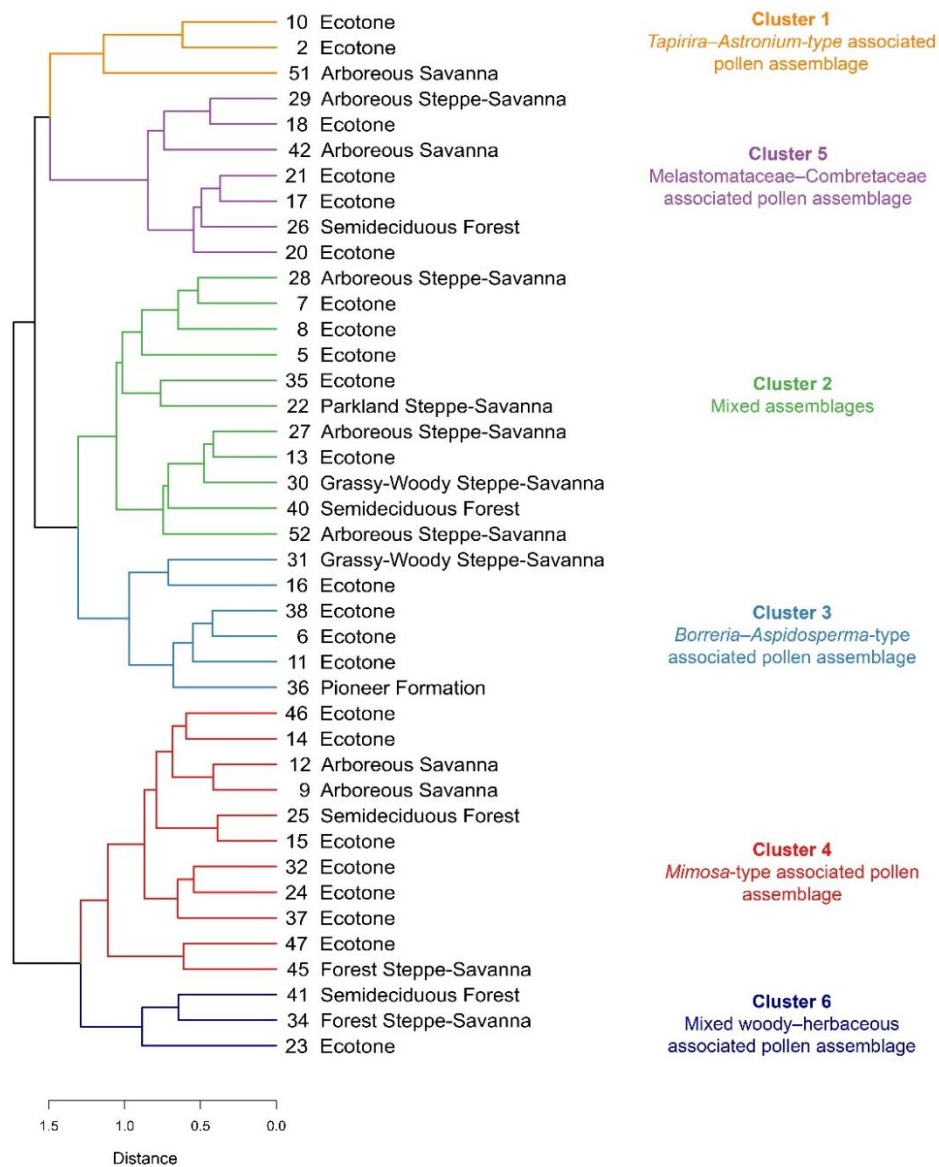


Fig. 8. Dendrogram hierarchical cluster analysis showing six floristic assemblages using Ward's method (WARD, 1963).

Redundancy Analysis (RDA) was initially performed using a set of 11 environmental variables, including climatic factors, edaphic conditions, and vegetation cover. Although the initial global model was significant ($F_{11, 29} = 1.51$; $p = 0.001$), a stepwise selection procedure was applied to identify the most parsimonious model. The final refined model retained three significant explanatory variables: MAT, woody cover, and the presence of Ferralsols (Latosolos), explaining 7.5% of the total variation in the pollen assemblage ($R^2 = 0.075$; $p = 0.001$).

Individual permutation tests indicated that MAT was the strongest environmental driver ($F = 2.85$; $p = 0.001$), followed by the influence of soil type (Ferralsols: $F = 1.96$; $p = 0.016$) and vegetation structure (woody cover: $F = 1.76$; $p = 0.026$). Variables such as MAP, altitude, and other soil types (e.g., Podzols, quartz sand) did not contribute significantly on their own ($p > 0.05$) and were excluded from the final analysis.

The RDA biplot (Fig. 9) revealed distinct ecological gradients along the first two axes (RDA1: 7.1%; RDA2: 5.2%). The second axis (RDA2) primarily captured a vegetation openness gradient. Typical tree and shrub taxa, such as *Mimosa*-type (score: 0.15), *Schinus*-type (0.12), and *Byrsonima* (0.07), showed positive correlations with woody cover and the presence of Ferralsols. In contrast, *Poaceae* (-0.19) and *Borreria*-type (-0.18) pollen grains were positioned at the opposite end of this axis, associating strongly with more open areas (open cover). The first axis (RDA1) reflected a thermal gradient, where taxa like *Melastomataceae/Combretaceae* (-0.30), *Maprounea* (-0.12), and *Sida* (-0.11) were associated with higher MAT within the studied range of 25.3 to 29.1 °C.

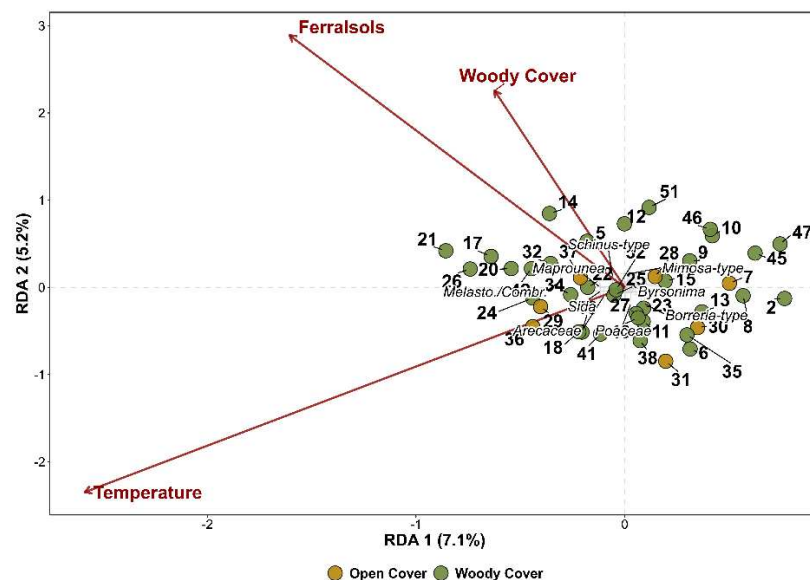


Fig. 9. Redundancy analysis (RDA) biplots illustrating the ordination of sampling sites and pollen types in relation to environmental gradients (soil types [Ferralsols], mean annual temperature [Temperature] and woody cover). The environmental variables significantly explained 7.5% of the total variation ($R^2 = 0.075$, $p = 0.001$). Axes represent RDA1 (7.1%) and RDA2 (5.2%).

In summary, our study shows that modern pollen assemblages in the Parnaíba River Basin act as sensitive recorders of the regional vegetation and landscape structure. Rather than a uniform regional signal, the pollen rain captured the nuanced transition from coastal restinga

to the complex mosaics of Caatinga and Cerrado. A key finding is the distinct biological signature of landscape openness: woody cover is strongly predicted by arboreal taxa like *Mimosa*-type and *Myrtaceae*, while open environments are consistently tracked by non-arboreal groups such as Poaceae and *Borreria*-type, particularly within the highly diverse Cerrado sites.

Multivariate analyses further reveal that these patterns are driven by specific environmental filters (primarily MAT, vegetation cover, and soil type (Ferralsols)) rather than random distribution. The strong agreement between the defined floristic clusters and the observed phytophysiognomies confirms that pollen rain accurately mirrors ecological gradients.

3.5. Discussion

3.5.1. Taxonomic richness and concentration along the transect

The 317 pollen taxa identified in this study exceeds that reported in previous research conducted in northeast Brazil. For instance, Magalhães-e-Silva and Santos (2024) identified 124 pollen types in the Caatinga. Gomes et al. (2014) recorded 149 types in bromeliad tanks, and Santos et al. (2015) found up to 372 pollen types in moss polsters, although only 140 were taxonomically determined. Other studies in the region report lower diversity: Ledru et al. (2022) identified just 90 taxa in reservoirs, and Montade et al. (2016) found 119 taxa in surface soils.

The comparatively high number of genera and families recorded here likely reflects the broader scope of this study, which encompasses the Parnaíba Basin, a transition zone between the Cerrado and Caatinga. Unlike previous investigations restricted to specific sites, such as the Caatinga of Bahia or reservoirs in Ceará (LEDRU et al., 2022; MAGALHÃES-E-SILVA; SANTOS, 2024), this wider geographic coverage accounts for the broader spectrum of taxa identified. However, it is important to note that while the regional diversity is high, specific environments such as restinga and carrasco exhibited lower taxonomic variability, consistent with the floristic composition of these specialized habitats (as seen in the dominance of Myrtaceae and Fabaceae, respectively)(SANTOS-FILHO et al., 2016).

Ecological factors significantly contribute to the complex pollen assemblages observed in this study. The high taxonomic richness recorded in the Caatinga samples reflects the biome's dynamic natural history, where long-term species exchanges and plant migrations driven by climatic fluctuations have shaped a diverse regional flora (FERNANDES; CARDOSO; QUEIROZ, 2020; LEDRU; ARAÚJO, 2023). Furthermore, the sampling of riverbanks enhances the detected diversity, not only because water bodies promote pollen preservation

(MCLAUHLAN et al., 2007), but also because fluvial transport integrates pollen from upstream catchment areas, effectively capturing a broader regional signal.

To allow for direct comparison, the discussion is limited to studies that use the same pollen concentration metric: grains/cm³. Works that use alternative units, such as grains/cm²/year or grains/g of wet sediment (MAGALHÃES-E-SILVA; SANTOS, 2024) were excluded, as these measures cannot be converted to volumetric concentration without additional data. This methodological restriction ensures analytical consistency and strengthens the reliability of the conclusions. Within this framework, the pollen concentrations observed in this study (1,262–203,070 grains/cm³), demonstrate the effectiveness of humid environments as natural pollen traps, complementing other sampling approaches in semi-arid regions (LEDRU et al., 2022; MAGALHÃES-E-SILVA; SANTOS, 2024).

In the Cerrado, pollen concentrations ranged from 1,262 to 203,070 grains/cm³. This variability mirrors findings by Cassino and Ledru (2021) in Central Brazil, where concentrations typically range from 10,000 to 60,000 grains/cm³ but reach peaks as high as 566,000 grains/cm³ in organic soils. However, the climatic context differs significantly. The Central Cerrado sites (e.g., Brasília and Grande Sertão Veredas) are located on high plateaus (700–1000 m a.s.l.) with milder conditions: MAT of 21.7–23°C, MAP of 1400–1600 mm, and a dry season of 4–5 months (CASSINO; MARTINHO; CAMINHA, 2015). In contrast, the Parnaíba Basin experiences significantly higher thermal stress (26–30.5°C) and a more severe dry season lasting up to 6 months.

While sporopollenin is generally resistant to temperature alone, these harsh conditions likely accelerate pollen oxidation driven by the combination of high temperatures and intense seasonality, promoting oxidative processes (CAMPBELL, 1999) and the alternation of wet-dry cycles (CAMPBELL, 1991), which are known to weaken pollen walls. High peaks in our dataset confirm that organic-rich environments, such as palm swamps, act as critical preservation refugia by maintaining waterlogged conditions that limit microbial activity and oxidation.

In the Caatinga, concentrations (4,238–12,348 grains/cm³) fall toward the lower range of the Cerrado studies (CASSINO; LEDRU, 2021; CASSINO; MARTINHO; CAMINHA, 2015). This pattern directly reflects the harsh climatic conditions of the Caatinga in the Parnaíba Basin. Unlike the milder Central Cerrado, this area experiences high MAT (~27–29°C) and a prolonged dry season lasting 6 to 8 months, with precipitation often falling below 1,000 mm in the driest sectors. These conditions likely limit primary productivity and accelerate pollen oxidation in the soil. Although our RDA identified MAT ($F = 2.85$; $p = 0.001$) as a significant

driver, the lower concentrations may also be influenced by differential pollen production between biomes or biological degradation by saprophytic fungi and microbial activity, which thrive in specific edaphic conditions (ELSIK, 1966; GOLDSTEIN, 1960; RÖSEL et al., 2012). Nevertheless, the literature points to significant variation within the biome: Gomes et al. (2014), for instance, observed significantly higher concentrations in bromeliad tanks, illustrating how microenvironments strongly influence pollen capture.

The low pollen concentrations observed in ecotone (7,658–18,628 grains/cm³) and restinga (2,793 grains/cm²) mirror patterns found in sandy substrates elsewhere, such as the restingas of southeastern Brazil (AMARAL et al., 2006) and sandy Cerrado soils (CASSINO; LEDRU, 2021). These findings highlight the impact of soil characteristics on preservation. As described by Magalhães-e-Silva and Santos (2024), highly porous soils allow water to drain rapidly, which can lead to the physical breakdown of grains through abrasion and accelerates oxidation (CAMPBELL, 1991). Consequently, these well-drained environments are poor pollen traps compared to organic-rich deposits.

Furthermore, when discussing riverbank samples, where concentrations varied from 1,262 to 46,314 grains/cm³, it is essential to consider sedimentological sorting. As observed in Amazonian rivers, grain size is strongly correlated with pollen concentration; silty sediments typically yield significantly higher concentrations than sandy ones (AKABANE et al., 2020). Therefore, the broad range of concentrations in our fluvial samples likely reflects a combination of local sedimentation rates, grain size variation, and the regional climatic context.

Unlike the milder Central Cerrado (CASSINO; LEDRU, 2021), the Parnaíba Basin is subject to significantly higher thermal averages (MAT 26–29 °C) and a prolonged dry season (6–8 months), which accelerate pollen oxidation even in fluvial deposits (gallery forests), limiting preservation compared to the cooler, subhumid reference sites. Given the available data, it remains challenging to definitively distinguish whether the observed variations in pollen concentration primarily reflect differential biological production, taphonomic degradation, or sedimentological sorting; therefore, all these factors must be considered as potential and likely complementary drivers.

Beyond biome-level patterns, analyzing concentrations by collection environment provides an additional perspective. Palm swamps (*veredas*) exhibited extremely high concentrations (up to 203,070 grains/cm³), consistent with findings by Cassino et al. (2015), who reported values between 35,000 and 135,000 grains/cm³ for similar environments in Central Brazil. This confirms that the palm swamp waterlogged, organic-rich soils act as exceptional pollen traps. Temporary lakes (2,317–137,410 grains/cm³) showed great

variability, supporting the view that local soil properties and organic accumulation strongly influence pollen deposition (JESKE-PIERUSCHKA et al., 2010).

Finally, beyond local depositional factors, differences in pollen productivity between biomes have significant implications for fossil interpretation. As noted by Gosling et al. (2009) distinguishing between Neotropical ecosystems requires understanding their modern representation biases. The generally lower pollen concentrations observed in the Caatinga samples compared to the Cerrado suggest lower pollen productivity in the seasonally dry forests. Consequently, the Caatinga signal may be weaker or underrepresented in downcore records compared to the more productive Cerrado or forest formations, a bias that must be considered when reconstructing past vegetation shifts in this transition zone.

3.5.2. Pollen assemblage composition and vegetation structure across biomes

The composition of modern pollen assemblages along the Parnaíba Basin closely reflects regional floristic heterogeneity and environmental variability. Distinct vegetation groups identified by pollen data (restinga, carrasco, Caatinga, ecotone, and Cerrado) demonstrate that the modern pollen rain retains a robust signal of local vegetation (Table 2). Located in a transition zone, the Parnaíba Basin serves as a critical reference for understanding regional ecological dynamics, complementing studies from other Brazilian biomes such as the Atlantic Forest, Cerrado and the Caatinga (Table S1) (CASSINO et al., 2020; MAGALHÃES-E-SILVA; SANTOS, 2024).

In the Lower Parnaíba, the pollen signal for restinga vegetation shows low taxonomic diversity, dominated by arboreal pollen (56%) with Myrtaceae (31%), *Borreria*-type (22.6%), and Melastomataceae/Combretaceae (7.8%) as prominent types. This is consistent with phytogeographical surveys of coastal sandy environments (SANTOS-FILHO et al., 2016; SANTOS-FILHO; ALMEIDA JUNIOR; ZICKEL, 2013). Similarly, the Carrasco vegetation presented a signature dominated by Fabaceae (specifically *Mimosa*-type and *Piptadenia*-type). Notably, this pollen signal overlaps significantly with the Caatinga assemblages, which are also defined by a mix of arboreal and herbaceous taxa with Fabaceae as the primary woody component.

This similarity is expected and reflects the floristic continuum observed in the region. Phytosociological assessments confirm that species such as *Pityrocarpa moniliformis* (syn. *Piptadenia moniliformis*) and *Mimosa* spp. are structural dominants in both the Carrasco-Caatinga transition (OLIVEIRA et al., 1997) and typical Caatinga formations (SILVA et al., 2020b; VASCONCELOS et al., 2019). Therefore, rather than distinct exclusive markers, the

dominance of these pollen types mirrors the high floristic connectivity and the transitional nature of these semi-arid woody formations.

Modern pollen studies in Northeastern Brazil generally link the dominance of herbs to open or human-impacted Caatinga vegetation (BEHLING et al., 2000). This relationship was recently confirmed by Ledru et al., (2022) in Ceará, where herb pollen exceeded 50% in reservoirs surrounded by human activity. Our results statistically validate this view. Poaceae and *Borreria*-type were ubiquitous across the transect, acting as robust proxies for landscape openness. This association is quantitatively confirmed by the significant negative correlation between *Borreria*-type and arboreous savanna cover ($\rho = -0.411$; $p = 0.008$), establishing both taxa as reliable indicators of reduced arboreal biomass. The significant presence of *Borreria*-type is particularly interesting: it aligns with local studies in the Caatinga (MAGALHÃES-E-SILVA; SANTOS, 2024; SANTOS et al., 2015), which highlight that eudicot herbs and subshrubs are often as important as grasses in this domain.

Regarding Cyperaceae, previous studies in Central Brazil often describe it as a broad wetland indicator found in palm swamps (*veredas*) and gallery forests, sometimes showing a random distribution across environments (CASSINO; LEDRU, 2021; CASSINO; MARTINHO; CAMINHA, 2015). In contrast, our results in the Parnaíba Basin reveal a much stricter ecological signal. Unlike the diffuse distribution observed in wetter regions, Cyperaceae here was strongly restricted to lacustrine sites. It exhibited massive overabundance peaks (>80%) specifically in lakes and temporary lakes (e.g., sites 7, 15, 25). Therefore, in this semi-arid transitional context, Cyperaceae acts not merely as a general wetland taxon, but as a specific local marker for standing water bodies, distinct from the regional terrestrial signal.

Additionally, a notable finding was the significant presence of *Sloanea*-type (0.7–19%) in samples of the Caatinga. According to the Flora e Funga do Brasil (REFLORA, 2023), the genus *Sloanea* is typically associated with humid forest formations (e.g., gallery forests, ombrophilous forests, restinga) across the Amazon, Atlantic Forest, and Cerrado domains. While its occurrence in Piauí was previously categorized only as 'possible' (REFLORA, 2023), our data confirms its presence in the state. Ecologically, its recording in the Caatinga samples likely reflects pollen input from humid enclaves embedded within the semi-arid landscape, demonstrating the sensitivity of pollen records in detecting local humid refugia.

Studies using bromeliad tanks and moss polsters reinforce key Caatinga indicators (SANTOS et al., 2015). *Acalypha* sp., *Commiphora* sp., and *Piptadenia* sp. were highly concentrated in bromeliad tanks, with *Mitracarpus* sp. being common across samples. While moss polster studies of the same area highlighted high concentrations of Fabaceae, Asteraceae,

and Rubiaceae, including taxa such as *Copaifera*, *Conocliniopsis prasiifolia*, and *Mitracarpus/Spermacoce* (GOMES et al., 2014). Overall, the Caatinga pollen assemblage reflects seasonal, open, and often human-influenced semi-arid conditions, with Fabaceae and specific herbaceous taxa as primary indicators.

Ecotone areas display mixed compositions with elements characteristic of both Cerrado and Caatinga domains. Such hybrid pollen spectra, marked by *Mimosa*-type, *Piptadenia*-type, and Combretaceae, are consistent with the high IVI of species like *Combretum glaucocarpum*, *Combretum leprosum*, *Terminalia fagifolia*, and *Mimosa caesalpiniiifolia* found in transition zones (CASTRO et al., 2014; MACEDO et al., 2019). This confirms that pollen rain accurately integrates the floristic overlap of these biomes (Fig. 3).

In the Cerrado, the high taxonomic variety and variability observed in both arboreal and non-arboreal taxa align with findings from Emas National Park and Chapada dos Veadeiros (CASSINO; LEDRU, 2021; CASSINO; MARTINHO; CAMINHA, 2015) with mainly Melastomataceae/Combretaceae, *Mimosa*-type, *Tapirira*-type, *Astronium*-type, and *Borreria*-type. This composition mirrors the floristic structure of the Parnaíba Basin Cerrado. Phytosociological studies in the region (e.g., Sampaio et al., 2018) list Combretaceae species (*Terminalia fagifolia*, *Combretum leprosum*) and Anacardiaceae (e.g., *Tapirira guianensis*, *Astronium fraxinifolium*) among the most important species, providing a direct source for the abundant Combretaceae and Anacardiaceae pollen observed.

Specific environmental conditions are well-tracked by indicator taxa. For instance, *Mauritia* is a clear marker for permanently flooded soils. Although typically considered as the indicator taxon for palm swamps, its high frequency in our riverbank samples accurately reflects the local vegetation structure. This finding is validated by phytosociological inventories in the region's riparian forests (CERQUEIRA et al., 2016; LOPES et al., 2020), which list *Mauritia flexuosa* as a dominant species alongside *Tapirira obtusa*. Thus, the pollen record successfully captures the specific swampy characteristics of the gallery forests that grow on the riverbanks. Similarly, the high frequency of *Tapirira*-type pollen is validated by Matos and Felfili (2010), who identified *Tapirira guianensis* as a species of high importance in gallery forests of Sete Cidades National Park, north of Piauí.

Regarding Poaceae, distinct interpretative models exist depending on the depositional environment. While Cassino et al. (2015) emphasize that grass pollen in palm swamps (*veredas*) primarily reflects local herbaceous growth rather than regional openness, our data aligns more closely with studies conducted in lake and soil transects where Poaceae serves as a robust indicator of landscape structure. Our landscape analysis (Section 4.2) demonstrated a

significant positive correlation between Poaceae and open vegetation cover within a 1 km radius (Fig. 6D).

This finding is consistent with McLauchlan et al. (2007), who observed similar patterns in small ponds, and is supported by Ledru (2002) for the Cerrado, who established quantitative thresholds distinguishing open fields (~50%) from dense forests (<20%). This distinction is further corroborated by Jeske-Pieruschka et al. (2010) in Southern Brazil, where Poaceae frequencies shift significantly from 29–75% in open grasslands to 14–23% in forest formations. On a regional scale, Behling et al. (2000) also linked high frequencies of herb pollen, including Poaceae, to the open Caatinga and coastal savannas of Northeastern Brazil. Therefore, in the context of the Parnaíba Basin's lacustrine sediments, Poaceae reliably tracks regional landscape openness, complementing its role as a local marker in strictly paludal environments.

Overall, the modern pollen assemblage in the Parnaíba Basin confirms that pollen rain mirrors the region's floristic heterogeneity and vegetation structure. The convergence between our dominant pollen types and the species with the highest IVI in local phytosociological survey, such as *Mimosa*, *Piptadenia*, *Terminalia* (Combretaceae), and *Mauritia*, validates the use of these taxa as robust bioindicators (ANDRADE et al., 2019; CERQUEIRA et al., 2016; MACEDO et al., 2019). Furthermore, the establishment of Poaceae as a reliable proxy for regional landscape openness, combined with the detection of humid forest elements like *Sloanea*-type within semi-arid matrices, provides a refined and powerful toolset for paleoecological reconstruction in this complex biological transition zone.

Table 2. Pollen indicators identified across the biomes and sub-basins of the Parnaíba River Basin. Abbreviations: AP = Arboreal pollen; NAP = Non-arboreal pollen.

Vegetation	Sub-basin	AP	NAP	Observations
Caatinga	Lower Parnaíba	<i>Mimosa</i> -type, <i>Piptadenia</i> -type, <i>Sloanea</i> -type.	<i>Borreria</i> -type.	The notable frequency of <i>Sloanea</i> -type suggests the presence of humid enclaves embedded within the landscape.
	Mid Parnaíba	<i>Mimosa</i> -type.	<i>Borreria</i> -type, Asteraceae.	Pollen composition reflects the open, semi-arid character of the biome, with NAP predominating in most locations.
Carrasco	Mid Parnaíba	<i>Mimosa</i> -type and <i>Piptadenia</i> -type.	Poaceae and Asteraceae.	Distinct Fabaceae dominance (<i>Mimosa</i> and <i>Piptadenia</i>), distinguishing it from restinga. Validated by high IVI of Mimosoid species in local surveys.

Cerrado	Lower Parnaíba	Myrtaceae, Melastomataceae/Combretaceae, <i>Mimosa</i> -type, <i>Piptadenia</i> -type.	<i>Borreria</i> -type, Poaceae, Asteraceae.	High taxonomic variety observed, consistent with the heterogeneous nature of the Cerrado.
	Mid Parnaíba	Melastomataceae/Combretaceae, <i>Mimosa</i> -type, <i>Piptadenia</i> -type, Myrtaceae, <i>Aspidosperma</i> -type.	Poaceae.	High heterogeneity observed, with alternating dominance between AP and NAP.
	Upper Parnaíba	Melastomataceae/Combretaceae, <i>Mimosa</i> -type, Myrtaceae, <i>Piptadenia</i> -type, <i>Tapirira</i> -type, <i>Schinus</i> -type, <i>Mauritia</i> , <i>Astronium</i> -type.	<i>Borreria</i> -type, Poaceae, Asteraceae.	<i>Astronium</i> and <i>Tapirira</i> are linked to mid-elevated plateaus and gallery forests. <i>Mauritia</i> indicates permanently flooded soils. Poaceae correlates with regional landscape openness.
Ecotone	Lower Parnaíba	Myrtaceae and Melastomataceae/Combretaceae.	Poaceae, <i>Borreria</i> -type.	Areas influenced by human activity showed a dominance of Poaceae, reflecting landscape openness.
	Mid Parnaíba	<i>Mimosa</i> -type and <i>Piptadenia</i> -type.	<i>Borreria</i> -type and Poaceae.	Hybrid pollen composition reflects the floristic overlap between biomes, consistent with transition zone vegetation.
Restinga	Lower Parnaíba	Myrtaceae and Melastomataceae/Combretaceae.	<i>Borreria</i> -type, and Asteraceae.	Low taxonomic variety but high arboreal frequency, with Myrtaceae as the defining signature, contrasting with the Fabaceae-dominated carrasco.

3.5.3. Environmental controls on pollen assemblages in the Parnaíba Basin

Multivariate analyses (RDA) confirmed that the structuring of pollen assemblages is driven by a combination of climatic, edaphic, and structural factors. The final parsimonious model explained a significant 7.5% of the total variation ($R^2 = 0.075$, $p = 0.001$). Although this percentage of explained variance is relatively low, indicating that a substantial fraction of the variance (<90%) remains unconstrained by the predictors, MAT emerged as the strongest environmental driver ($F = 2.85$; $p = 0.001$) followed by the combined influence of Ferralsols ($F = 1.96$; $p = 0.016$) and woody cover ($F = 1.76$; $p = 0.026$). These results suggest that the modern pollen rain in the Parnaíba Basin reflects a composite signal, in which vegetation structure, soil types, and climate jointly influence the pollen-vegetation relationship, although a significant portion of the variance remains driven by other local or seasonal factors.

The prominence of MAT in the model must be interpreted with caution, as temperature and precipitation exhibit positive correlation and tend to covary within the Parnaíba Basin. This covariation, combined with the narrow temperature range (~ 3.7 °C) versus the wide precipitation gradient (~ 900 mm) in the dataset (Table 1), suggests that the statistical

significance of MAT may also reflect broader hydrological and seasonal dimensions not explicitly captured by the model. Furthermore variables such as MAP and altitude did not contribute significantly on their own, likely due to statistical redundancy with the retained predictors.

The RDA biplot (Fig. 9) elucidated ecological preferences along these gradients, showing that tree and shrub taxa like *Mimosa*-type, *Schinus*-type, and *Byrsonima* correlate with woody cover supported by Ferralsols. In contrast, Poaceae and *Borreria*-type associated strongly with open cover, reinforcing their roles as markers of landscape openness or anthropized environments. Regarding the thermal gradient, thermophilous taxa such as Melastomataceae/Combretaceae, *Maprounea*, and *Sida* clustered in sites with higher MAT. While these taxa are structural elements in vegetation adapted to high temperatures (>26 °C), their distribution in the Parnaíba Basin is likely filtered by the interaction between thermal averages and moisture availability during the dry season. Ultimately, the pollen assemblages reflect a complex interaction between substrate, landscape structure, and climate, where the low explained variance highlights the importance of additional factors like local depositional settings and human impacts.

The influence of landscape structure on pollen signatures was quantitatively confirmed by the Spearman correlation analysis (Section 4.2). We observed a significant positive correlation ($\rho = 0.509$, $p = 0.001$) between AP frequencies and the proportion of woody vegetation (forest and savanna) within a 1 km radius. Conversely, landscapes dominated by open formations were strongly associated with NAP ($\rho = 0.509$, $p = 0.001$). At the taxon level, specific pollen indicators emerged: *Copaifera* showed a robust positive association with woody savanna ($\rho = 0.468$, $p = 0.002$), whereas the herbaceous *Borreria*-type exhibited a significant negative correlation with this same physiognomy ($\rho = -0.411$, $p = 0.008$). These values statistically validate the use of these taxa as robust indicators of landscape openness and woody cover in the Parnaíba Basin.

The RDA biplot (Fig. 9) further elucidated these ecological preferences along distinct gradients. The second axis (RDA2) captured a vegetation openness gradient, separating woody taxa associated with Ferralsols, such as *Mimosa*-type (score: 0.15), *Schinus*-type (0.12), and *Byrsonima* (0.07), from herbaceous markers positioned at the opposite end. Poaceae (-0.19) and *Borreria*-type (-0.18) showed a strong association with open vegetation cover, reinforcing their role as signals of open or anthropized environments. This soil-vegetation association suggests that Ferralsols support the established woody biomass contributing to the AP signal, while their absence or degradation favors herbaceous expansion (Fig. 9).

Cluster analysis complemented these ordination results by identifying recurring floristic associations (Fig. 8). Cluster 1, characterized by *Tapirira*-type and *Astronium*-type, corresponds to ecotone and woody savanna, reflecting preserved vegetation on mid-elevation. Meanwhile, Cluster 6 represents a distinct "humid" signature associated with semideciduous forest, grouping *Sloanea*-type, *Arecaceae*, and *Qualea*-type, confirming the capacity of the pollen record to detect humid refugia elements.

Finally, the thermal gradient (RDA Axis 1) was most strongly associated with Melastomataceae/Combretaceae (score: -0.30), *Maprounea* (-0.12), and *Sida* (-0.11), which clustered in sites with higher MAT. Current floristic surveys in the Parnaíba Basin document these taxa as structural elements in vegetation types where high thermal averages and intense insolation are prevalent (ANDRADE et al., 2016; MATOS; FELFILI, 2010; SANTOS-FILHO et al., 2016). Specifically, studies by Silva et al. (2015) and Souza et al. (2017) recorded dominant Combretaceae in transition areas where local MAT reaches 26.7 °C. Similarly, *Maprounea* and *Sida* have been reported in sites with mean annual temperatures ranging from 26.5 °C to 27.5 °C (Matos and Felfili, 2010; Santos-Filho et al., 2016). In our study, the MAT vector reflects these thermal associations, as thermophilous taxa reach their highest abundances in the warmest surveyed sites (MAT > 27.9 °C), such as in samples 17, 21, and 26."

Specifically, Melastomataceae/Combretaceae (e.g., *Combretum glaucocarpum*, *C. leprosum*) are frequently cited as dominant in the Cerrado-Caatinga transition, where mean temperatures reach 26.7°C, with absolute maxima exceeding 40°C during the dry season (SILVA et al., 2015; SOUZA et al., 2017). Similarly, *Maprounea* (Euphorbiaceae) is associated with gallery forests under Aw climates, thriving in areas with annual means of ~26.5°C (MATOS; FELFILI, 2010). Furthermore, the genus *Sida*, typical of open environments like restingas, is ecologically tied to areas of high surface insolation and temperatures averaging 27.5°C (SANTOS-FILHO et al., 2016).

The MAT vector in our RDA suggests a thermal influence on the distribution of the regional flora within the studied range, coinciding with areas where thermophilous taxa reach their highest abundances in the warmest surveyed sites (MAT > 27.9 °C). This is specifically observed in samples 17, 21, and 26, which are dominated by Melastomataceae/Combretaceae (>45%), and sample 36, where *Sida* peaks. While these correlations are significant in our dataset, they should be interpreted as site-specific associations rather than absolute optimum climatic ranges for these taxa, as other environmental factors and the correlation between temperature and precipitation may also play a role. Overall, the integration of significant Spearman correlations ($\rho \geq 0.4$) and multivariate metrics confirms that pollen assemblages in

the Parnaíba Basin are predictable reflections of the interaction between substrate, landscape structure, and climate, aligning with the geomorphological drivers of biogeographical diversity recently proposed by Moro et al., (2024).

3.5.4. Relationship with fossil pollen records from the Parnaíba River delta

When compared with paleoecological records from the Parnaíba Basin (Bouimetarhan et al., 2018; Piacsek et al., 2021), our research highlights a marked difference in pollen composition between glacial periods and the present day. The historical prevalence of montane and submontane forest taxa, such as *Podocarpus*, *Ilex*, *Hedyosmum*, and *Myrsine*, suggests an expansion of these formations under cooler, more humid glacial conditions. The absence of genera like *Podocarpus* and *Hedyosmum* in modern pollen rain samples from upper to lower elevations strongly suggests that current warmer and drier climatic conditions are unfavorable for their widespread occurrence and dispersal. This is particularly notable, as the present study covers altitudes up to 570m, while these pollen types are typically found in the Cerrado starting from 750m, where cooler and more humid conditions prevail (Ledru and Araújo, 2023).

Myrsine was recorded in one sample (site 11) with a frequency of 0.6%, and *Ilex* appeared in two samples (site 11: 0.3% and site 51 :1.2%). Although *Myrsine* has not been consistently reported in published phytogeographical records for Piauí, botanical surveys confirm its presence in the state (CRIA, 2023). Specifically, *Myrsine* has been documented in the Serra das Confusões National Park (506m asl) in southern Piauí (approximately 100 km from site 11), and in northern Piauí in Sete Cidades National Park (76m asl) and Fazenda Flores (137m asl).

The woody cover of sample 11 matches the known habitats for *Myrsine* species in the region, described as dry stream banks, rocky outcrops, and shrubby clumps (CRIA, 2023). Since 'woody cover' encompasses shrubby and riparian vegetation, the pollen signal likely reflects a specific microenvironment associated with the genus's occurrence. In southern Brazil, *Myrsine* is associated with humid subtropical climates, as seen in the study by Jeske-Pieruschka et al. (2010), where the local climate at that specific study site is characterized by a mean January temperature of 18.3 °C and a mean July temperature of 9.9 °C, with frequent frost and fog.

While these values reflect the specific subtropical conditions of that record, the genus is broadly recognized for its association with high humidity and mild thermal conditions. In southeastern Brazil, *Myrsine* occurs as a regional taxon in both coastal Atlantic Forest (AMARAL et al., 2006) and high-elevation Atlantic Forest, above 1,200 m a.s.l. (SCHEER; MOCOCHINSKI, 2009). In these regions, it typically thrives under high humidity and MAT

below 20 °C (with coldest months averaging ~10 °C). Similarly, in the dense rainforests of northeastern Brazil, *Myrsine* demonstrates the genus's ability to colonize and persist in more humid microenvironments (Montade et al., 2016), suggesting that its presence in our samples likely reflects its capacity to endure within specific microclimates that provide sufficient moisture interception, rather than reflecting the broader regional climate.

These populations can thrive in specific habitats, such as ridgetops at 700–950 m a.s.l., where edaphic factors and local wind patterns, influenced by orography, create favorable microclimatic conditions (such as moisture interception). Specifically, these high-elevation zones receive MAP exceeding 1600 mm and experience milder temperatures relative to the surrounding semi-arid lowlands, which are characterized by high thermal averages (~27°C) and lower rainfall (<1400 mm). These conditions allow such taxa to persist even within a broader climate that might otherwise seem unfavorable (MONTADE et al., 2016).

The presence of *Ilex* sp. in Piauí state is scarcely documented in broader phytogeographical records, with only two observations: one in Sete Cidades National Park and another in Nascentes do Rio Parnaíba National Park (CRIA, 2023). However, a phytosociological study of the Cerrado *sensu stricto* in the Parnaíba River Basin recorded *Ilex* sp., confirming that the species is a rare but existing component of the regional vegetation (Sampaio et al., 2018). Field surveys show very low phytosociological parameters for this species (absolute density of 0.3 ind. ha⁻¹ and relative frequency of 0.07%), which explains its rarity in observations.

The documented locations are over 100 km from the sampled site, suggesting that *Ilex*, like *Myrsine*, may occur closer to the collection point but remains undocumented in herbarium records. The higher frequency of *Ilex* at site 51 (1.2%) reinforces the possibility of fluvial pollen transport, as the closest documented occurrence (80 km away) was in Mirador State Park, collected in a "palm swamp, near the bank of the Itapecuru River" (CRIA, 2023), the same river where the current sample was collected.

In contrast, the consistent presence of taxa characteristic of modern Cerrado and open environments, such as Melastomataceae/Combretaceae, Myrtaceae, Fabaceae, Poaceae, *Borreria*-type, and Amaranthaceae, provides a crucial baseline for interpreting contemporary pollen dispersal. This contrast with glacial pollen records underscores a significant floristic shift in the region, driven by long-term climatic changes. It suggests that while some elements of past-floras may endure in limited niches, the overall vegetation structure has adapted to the warmer and drier conditions prevailing today.

3.6. Conclusion

This study characterized the modern pollen rain signature of the Parnaíba River Basin, confirming that pollen assemblages reflect floristic diversity and regional environmental variation. By identifying key pollen indicators that differentiate the regions, the research establishes an essential basis for future paleoecological interpretations. The Cerrado signature was marked by high taxonomic richness and arboreal taxa such as Melastomataceae/Combretaceae and Myrtaceae. Conversely, the Caatinga is defined by a predominance of non-arboreal pollen, with Fabaceae (*Mimosa*-type) serving as the dominant woody element. Additionally, the notable frequency of *Sloanea*-type in Caatinga forest areas highlights how palynology can complement botanical surveys.

Reflecting its nature as an ecotonal zone, the Parnaíba Basin exhibits a unique mixed spectrum compared to the uniform signatures of core biomes. Here, Cerrado and Caatinga elements co-occur, creating a composite signal driven by a combination of ecological filters and taphonomic processes, rather than random dispersal. Multivariate analyses demonstrate that MAT is a prominent factor in the structuring of these assemblages, strongly favoring thermophilous taxa like Melastomataceae/Combretaceae and *Sida* in the warmest sectors. Furthermore, substrate and vegetation structure proved decisive: Ferralsols and woody cover clearly separate forest indicators, such as *Copaifera*, from markers of landscape openness like *Borreria*-type. Regarding hydrological signals, the study refines local interpretations: unlike its broader regional behavior, Cyperaceae here is strictly restricted to lacustrine environments, while *Mauritia* serves as a reliable proxy for gallery forests and palm swamps across both riverbank and soil samples.

Finally, placing these modern results in a temporal context highlights a sharp floristic shift since the last glacial period. The historic prevalence of montane taxa (such as *Podocarpus*, *Ilex*, *Hedyosmum*, and *Myrsine*) under humid conditions contrasts with their current scarcity. While *Podocarpus* and *Hedyosmum* are absent from the regional signal, *Ilex* and *Myrsine* persist only as rare elements restricted to specific microclimates. Ultimately, this study offers a critical reference framework for deciphering fossil records and monitoring the resilience of these transition ecosystems. The observed variations in pollen concentration reflect a complex interplay between biological production, oxidation, and sedimentological sorting, requiring cautious interpretation in paleoenvironmental reconstructions.

Data availability statement

Data will be archived in NEOTOMA (<https://www.neotomadb.org>).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2026.113655>.

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Apendix 3.A Supplementary material

Modern pollen rain signatures along the Parnaíba River Basin in Northeastern Brazil

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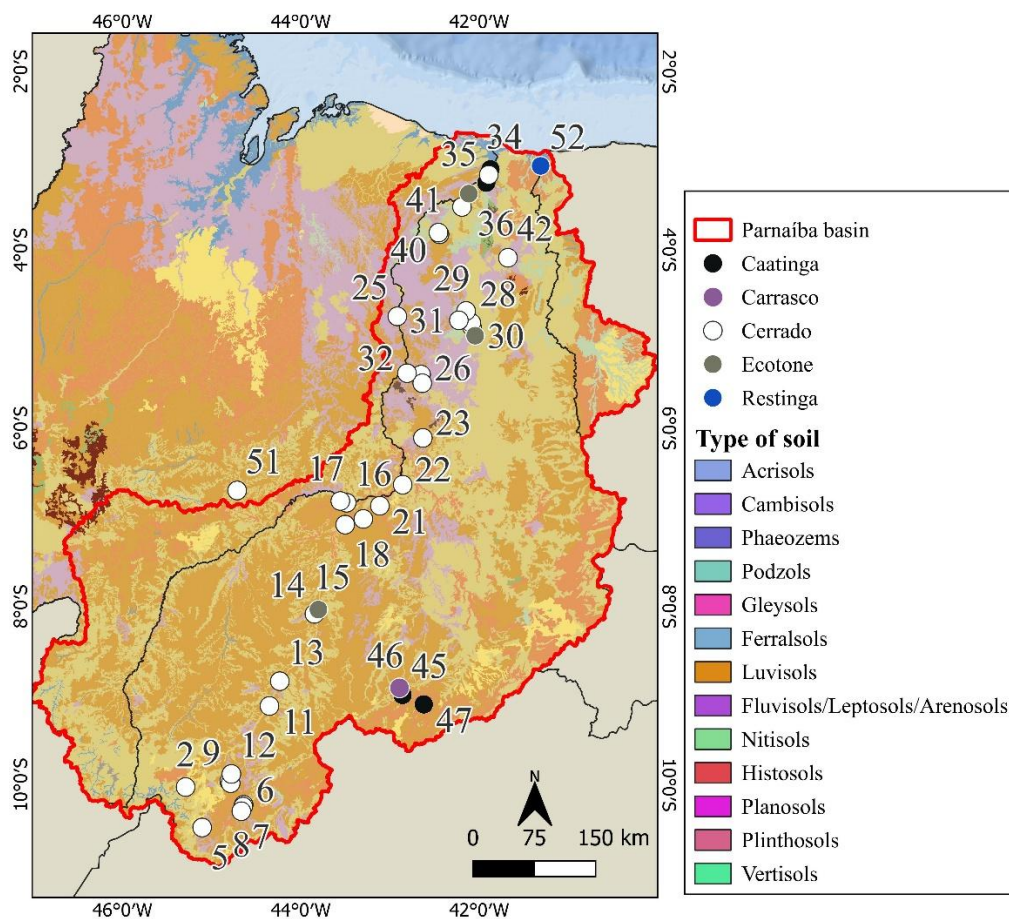


Fig. S1. Classification and Distribution of Soil Types in the Parnaíba Basin (IBGE, 2023).

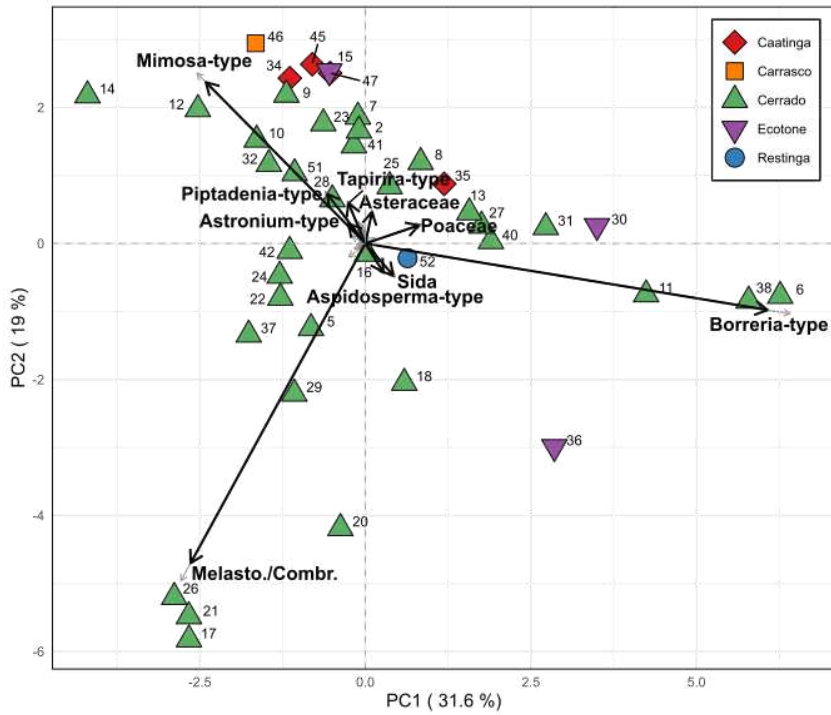


Fig. S2. Principal Component Analysis (PCA) biplot illustrating the pollen rain composition in the Parnaíba Basin. The plot displays the ordination of sampling sites (points, colored by vegetation type) and the main pollen types (vectors), revealing distinct patterns in pollen composition across different vegetation types along PC1 (31.6%) and PC2 (19%).

Table S1. Comparison of Regional Pollen Indicators from the Parnaíba River Basin with Records from Other Studies

Vegetation	This study	Behling et al. (2000)	Magalhães-e-Silva & Santos (2024)	Cassino and Ledru (2021)	Cassino et al. (2015)	Ledru et al. (2022)	Gomes et al. (2014)	Montade et al. (2016)	Santos et al. (2015)
Cerrado	Melastomataceae/Combretaceae, Myrtaceae, Bauhinia, <i>Dimorphandra</i> , <i>Astronium</i> -type, <i>Tapirira</i> -type and <i>Mauritia</i> .	-	-	<i>Astronium</i> -Type, <i>Borreria</i> -Type, <i>Byrsonima</i> , <i>Caryocar</i> , <i>Cupania</i> , <i>Forsteronia</i> -Type, <i>Matayba</i> , <i>Mimosa</i> -Type, <i>Myrtaceae</i> , <i>Plenckia</i> , <i>Rhamnus</i> -Type, <i>Richardia</i> , <i>Roupala</i> , <i>Sapium</i> , <i>Sebastiania</i> , <i>Senna</i> -Type, <i>Tabebuia</i> -Type, <i>Tapirira</i> -Type.	<i>Caryocar brasiliense</i> , <i>Curatella Americana</i> , <i>Plenckia populnea</i> e <i>Eriotheca</i> -type	-	-	-	-

Caatinga	<i>Mimosa</i> -type, <i>Piptadenia</i> - type, <i>Senna</i> - type, <i>Sloanea</i> - type.	Poaceae, Cyperaceae, <i>Borreria</i> , Asteraceae, <i>Alternanthera</i> , Amaranthaceae, <i>Gomphrena</i> , <i>Mimosa</i> .	<i>Commiphora</i> <i>leptophloeos</i> , <i>Cereus</i> <i>jamacaru</i> , <i>Pilosocereus</i> <i>tuberculatus</i> , <i>Jatropha</i> <i>mutabilis</i> , <i>Jatropha</i> <i>ribifolia</i> , <i>Spondias</i> <i>tuberosa</i> , <i>Herissantia</i> <i>tiubae</i> , <i>Caesalpinia</i> <i>microphylla</i> .	-	-	<i>Chloroleucon</i> , <i>Myracrodruo</i> <i>n urundeuva</i> , <i>Cassia</i> , <i>Poincianella</i> <i>pyramidalis</i> , <i>Mimosa</i> <i>acutistipula</i> , <i>Pithecelobiu</i> <i>m</i> , <i>Cordia</i> , <i>Amburana</i> <i>cearensis</i> , <i>Piptadenia</i> , <i>Salvinia</i> , <i>Diodella</i> , <i>Mimosa</i> <i>caesalpinifoli</i> <i>a</i> , <i>Astroemeria</i> <i>ceae</i> , <i>Ziziphus</i> <i>joazeiro</i> , Bignoniaceae , <i>Angelonia</i> - type, <i>Himatanthus</i> , <i>Copaifera</i> , Asteraceae.	<i>Barnebya</i> <i>harleyi</i> , <i>Capparis</i> <i>jacobinae</i> , <i>Commiphora</i> <i>leptophloeos</i> , <i>Cereus</i> <i>jamacaru</i> , <i>Cordia</i> <i>globosa</i> , <i>Ipomoea</i> <i>brasiliانا</i> , <i>Mimosa</i> <i>miserá</i> , <i>Pavonia</i> <i>glazioviana</i> , <i>Piriadacus</i> <i>erubescens</i> , <i>Zornia</i> <i>echinocarpa</i> .	Fabaceae- Mimosidae, Arecaceae, <i>Alternanthera</i> , Cyperaceae, <i>Mitracarpus</i> (Floresta Sazonal Decidua).	<i>Mitracarpus/Sp</i> <i>ermacoce</i> , <i>Conocliniopsis</i> <i>prasiifolia</i> , <i>Copaifera</i> , <i>Trichogonia</i> <i>campestris e</i> <i>Pityrocarpa</i> <i>moniliformis</i> , <i>Celtis</i> .
Ecotone	Mixed composition, <i>Sida</i> and Poaceae	-	-	-	-	-	-	-	-

Restinga	Myrtaceae, Melastomataceae/ Combretaceae, <i>Borreria</i> - type and <i>Solanum</i> -type	Poaceae, Cyperaceae, <i>Borreria</i> .	-	-	-	-	-	-	-
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4 CAPÍTULO IV

VEGETATION RESPONSES IN A CLIMATIC TRANSITION ZONE OF NORTHEASTERN BRAZIL OVER THE LAST 7.500 YEARS (LAGOA DE PARNAGUÁ, PIAUÍ, BRAZIL)

Capítulo preparado em formato de artigo para submissão no periódico “*The Holocene*”

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Vegetation responses in a climatic transition zone of Northeastern Brazil over the last 7.500 years (Lagoa de Parnaguá, Piauí, Brazil)

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Abstract

Vegetational paleoecology is critical for reconstructing past environmental dynamics, especially in ecotones like the Cerrado-Caatinga transition in Northeastern Brazil (NEB), where semi-arid and monsoon-related climates converge. This study reconstructs paleoenvironmental changes over the last ~7,500 years at Lagoa de Parnaguá, Piauí, using a multi-proxy approach including pollen, macro-charcoal, and geochemical XRF analyses from core PAR-21. The age model reveals a sedimentary hiatus between 7050 and 3430 cal yr BP, indicating extreme instability. Analysis of 112 pollen samples identifies five zones. Zone PAR1 (7490–7050 cal yr BP) exhibits extreme aridity, with open landscapes dominated by non-arboreal taxa (Poaceae), consistent with the vulnerability of eastern northeastern Brazil under a weakened South American Summer Monsoon (SASM). The hiatus (7050–3430 cal yr BP) suggests probable desiccation of the lake. In PAR2 (3430–3030 cal yr BP), lake reestablishment and arboreal expansion indicate climatic convergence with western NEB under a strengthened SASM. PAR3 (3020–2070 cal yr BP) features mixed vegetation and a fire peak, with fires primarily consuming herbaceous fuels during seasonal wet–dry transitions. PAR4 (2050–1520 cal yr BP) marks the peak of forest consolidation with maximum arboreal pollen dominance (*Astronium-type*), coinciding with the first anthropogenic fire evidence. PAR5 (1510 cal yr BP–Present) shows maximum instability, eutrophication, and strong fire fluctuations reflecting intense human pressure and environmental degradation. Overall, the record highlights Parnaguá’s transitional nature, its sensitivity to climatic shifts, and vulnerability to future aridity under changing monsoon dynamics.

Keywords: Anthropogenic impact; Charcoal; Fire history; Northeastern Brazil; Pollen.

4.1 Introduction

Vegetational paleoecology is an indispensable tool for reconstructing past environmental variations, providing scientific support for the management and conservation of contemporary ecosystems (Flantua et al., 2015; Traverse, 2007). Among the available proxies, palynology stands out as a robust method for inferring long-term vegetational and climatic dynamics due to the excellent preservation of pollen grains in sediments (SALGADO-LABOURIAU, 2007; TRAVERSE, 2007). Over the last millennia, pollen records have been fundamental in deciphering the complex interaction between natural climatic fluctuations and anthropogenic impacts, which are key elements for predicting the resilience of tropical regions under current global warming (BENITO-GARZÓN; LEADLEY; FERNÁNDEZ-MANJARRÉS, 2014; JAMRICOVÁ et al., 2017; WHITLOCK et al., 2018).

In Brazil, although the volume of paleoecological studies has grown significantly since the 1990s, the highest density of records remains concentrated in the southeastern and southern regions (FLANTUA et al., 2015). In Northeastern Brazil (NEB), a region comprising 1.558 million km² and hosting high levels of plant endemism, recent research indicates that vegetation boundaries have been in phase with the oscillations of the South America Summer Monsoon (SAMS) and the Intertropical Convergence Zone (ITCZ) (FERNANDES; CARDOSO; DE QUEIROZ, 2020; XAVIER et al., 2026). This east-west moisture gradient primarily modulates the distribution of the region's major biomes, from the Amazon rainforest and Cerrado in the west to the xerophilous Caatinga in the east, driving significant vegetational shifts over the last 6,000 years. (XAVIER et al., 2026).

Historical data and simulations reveal an "antiphase" pattern of precipitation between the eastern and western portions of NEB (XAVIER et al., 2026). During the Mid-Holocene (~6.0 to 4.2 ka BP), for instance, the eastern sector experienced wetter conditions than today, while the western region was subjected to oscillating or drier periods. This environmental divergence became even more pronounced after the 4.2 ka BP anomaly: intensified monsoonal rainfall drove the expansion of arboreal Cerrado and forest ecosystems in the west, whereas the eastern portion underwent severe aridification, leading to the dominance of the xerophytic Caatinga (DE OLIVEIRA; BARRETO; SUGUIO, 1999; GUERRA et al., 2024; XAVIER et al., 2024). Currently, the limit of this western monsoon moisture penetration is situated around 42° W longitude, a threshold that defines the strategic ecotone between the Cerrado and Caatinga biomes (XAVIER et al., 2026).

This bioclimatic boundary directly bisects the state of Piauí, making its interior a key area for understanding the historical shifts of the SAMS. This region is currently embedded

within the MATOPIBA agricultural frontier, where intense deforestation, illegal logging, and cattle ranching have drastically reduced the original vegetation cover (FARINASSO et al., 2006; MOTTA; GONÇALVES, 2016). Understanding how these ecosystems responded to past climate events, such as the '4.2 ka dry event' which triggered biodiversity reorganizations lasting over a century in other NEB sites, is crucial for assessing their future persistence and resilience against modern anthropogenic pressures.

To address these questions, this study aims to reconstruct the regional paleoenvironmental variations of the last ~7,500 years using a multi-proxy approach. We will analyze pollen and macro-charcoal ($>160\mu$) deposited in the sediments of Lake Parnaguá, located in southern Piauí. In this ecotonal context, charcoal peaks are essential indicators, as natural fires are rare in the Caatinga due to sparse fuel, whereas the Cerrado is a fire-prone biome; thus, these records allow us to distinguish between climatic seasonality and early anthropogenic land use (GUERRA et al., 2024; MORAES; DE OLIVEIRA; BEHLING, 2020; XAVIER et al., 2026).

We hypothesize that the Cerrado-Caatinga ecotone in southern Piauí exhibits a non-linear response to monsoon fluctuations, where severe dry events, such as the 4.2 ka BP anomaly, triggered vegetational reorganizations with recovery times exceeding a century. We expect the Lake Parnaguá record to reveal that while arboreal Cerrado expands during periods of high SAMS intensity, these ecosystems remain highly vulnerable to abrupt moisture reductions, leading to the long-lasting dominance of xerophytic Caatinga taxa. By establishing these long-term ecological baselines, this work seeks to inform more effective conservation policies that consider the dynamic nature of biodiversity in the face of the ongoing climate crisis.

4.2 Study Area

The lake of Parnaguá (Fig. 1), is a major lacustrine system in Piauí, covering 72.02 km² (12 km x 2 km) at an altitude of 334 m (IBGE, 2017; Medeiros et al., 2022). Situated within the *Chapada Extremo Sul Piauiense* (10°13'S; 44°38'W) the regional relief is dominated by a reworked tabular surface with abrupt escarpments up to 600 m high. Geologically, the area belongs to the Parnaíba Sedimentary Basin, featuring a diverse lithology (sandstones, shales, and conglomerates) that originates thick Yellow Latosols and highly erodible quartz sands (SILVA; CARVALHO, 2018).

The lake currently faces a critical state of environmental degradation and neglect (PEREIRA; SILVA; ARAGÃO, 2019). Severe siltation, resulting from the removal of riparian vegetation for agricultural and pastoral expansion, has drastically reduced the lake's depth and

storage capacity, consequently threatening local biodiversity and artisanal fishing activities (PEREIRA; SILVA; ARAGÃO, 2019; SILVA; CARVALHO, 2018). Furthermore, the water body is highly vulnerable to climatic extremes, with a strong correlation between El Niño events and recent episodes of near-total drying (SILVA; LIMA; MACHADO, 2012).

This area is relevant due to its proximity to the Serra da Capivara National Park and other archaeological sites featuring rock art, which testify to a long-term pre-historical human occupation in the region (PESSIS; GUIDON, 2007). Historical records of the municipality indicate that permanent populations were already living near the lake around 1676 EC (IBGE, 2025). The local agriculture is based on the seasonal production of rice, beans, corn, cassava (also known as manioc), and sugarcane (Medeiros et al., 2022), placing it in the agricultural frontier expansion region known as MATOPIBA (comprising Maranhão, Tocantins, Piauí, and Bahia). The current landscape, which reflects the Cerrado-Caatinga ecotone, is a mosaic that includes *Campo Cerrado* (open savanna), *Cerradão* (dense savanna), and patches of arboreal and shrubby Caatinga (CEPRO, 2010).

Climatologically, Parnaguá represents a crucial transition zone (ecotone) between the Cerrado and the Caatinga, not fitting exclusively within the characteristics of either domain (CEPRO, 2010). The predominant climate is classified as hot semi-arid tropical, which, according to the Köppen classification, corresponds to type Aw' (tropical hot and humid), characterized by a six-month dry season and rainfall concentrated in the summer months (PEEL; FINLAYSON; MCMAHON, 2007). Under interannual variability scenarios, the area may fluctuate, exhibiting predominance of arid climate (in the driest scenarios) or dry subhumid conditions (in wetter or average years) (MEDEIROS et al., 2022).

The mean annual temperature is 26°C, with high temperatures ranging from 32°C to 37°C in historical monthly averages and peaking in september (37°C) (MEDEIROS et al., 2022). Precipitation is influenced by various factors, including cold surges, the amplitude of the seasonal shift of the Intertropical Convergence Zone (ITCZ), and the southeastern trade winds (Medeiros et al., 2022), with a mean annual rainfall of 827 mm (according to the CHELSA climate model) (KARGER et al., 2017).

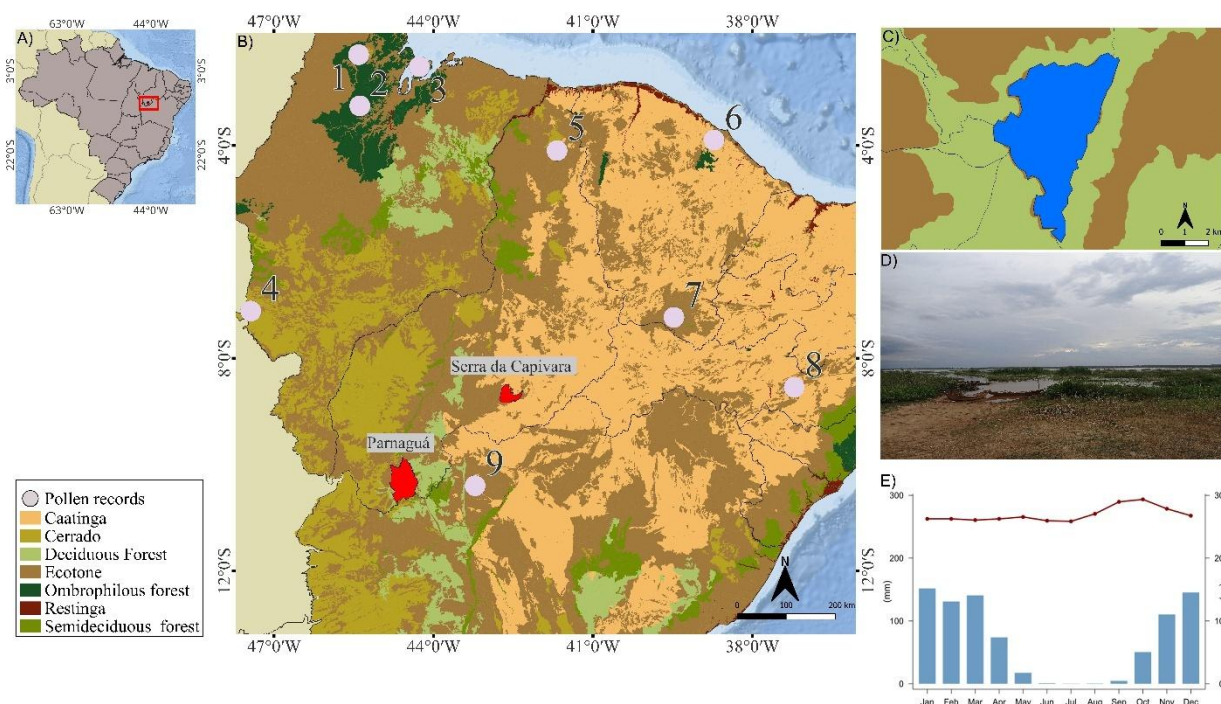


Fig. 1. (A) Map of Brazil showing the location of Parnaguá within the Northeastern Region (NEB). (B) Map displaying the distribution of the main vegetation types and the location of the municipality of Parnaguá (red), Serra da Capivara (red), and other continental records in Northeastern Brazil: 1. Cabeludo (MORAES et al., 2022); 2. Lago Formoso (MORAES et al., 2021b); 3. Lagoa do Caçó (LEDRU et al., 2006); 4. Chapada das Mesas (XAVIER et al., 2024); 5. Sete Cidades (XAVIER; ARAÚJO; LEDRU, 2022); 6. Serra de Maranguape (MONTADE et al., 2014); 7. Araripe (GUERRA et al., 2024); 8. Catimbau (MORAES; DE OLIVEIRA; BEHLING, 2020); 9. Icatu (DE OLIVEIRA; BARRETO; SUGUIO, 1999). (C) Map of Lagoa de Parnaguá (blue). (D) View of Lagoa de Parnaguá. (E) Ombrothermic diagram for the Parnaguá region, PI, Brazil, representing the variation of mean monthly temperature (red line, °C) and mean monthly precipitation (blue bars, mm) for the reference period 1981-2010. Source: CHELSA (Karger et al., 2017).

4.3 Material and methods

4.3.1 Coring and sampling

A 318 cm sediment core (PAR-21) was collected from Lagoa de Parnaguá ($10^{\circ}16'58.296''\text{S}$ - $44^{\circ}40'21.863''\text{W}$, 328 m a.s.l.) in October 2021 using a manual sediment collection device known as "Livingstone" corer. The top of the sediment was located at a water depth of 1.10 m, and the core consisted of four sections of varying sizes, classified as A, B, C, and D. The sediments were transferred to PVC tubes and sealed with a plastic covering for transportation. In the laboratory, the core was sliced at 1 cm intervals. From each slice, standardized sediment volumes were subsampled for palynological analysis, while additional material was separated for radiocarbon dating and physical-chemical characterization. All samples were then stored in a cold chamber at 4°C at the University of Montpellier, France.

4.3.2 Chronology

Ten samples were dated by Accelerator Mass Spectrometry at the Laboratoire de Mesure du Carbone 14 (LMC14), France. The radiocarbon dates were calibrated using the

SHCal20 curve (Table 1), calculated from linear interpolation (Hogg et al., 2020). The age-depth model was constructed using the Bacon package in the R software, an open-access tool for statistical analyses (R Core Team, 2018).

Table 1. Radiocarbon dates for the PAR-21 sediment core with calibrated BP ages (two standard deviations, 2σ intervals) and mean probability (95.4%, 2σ intervals) obtained from the Bacon package (Blaauw and Christen, 2011).

Lab Code	Depth (cm)	Material	^{14}C age (yr BP)	Calibrated age range (yr BP)	Median probability
SacA72257	3	Bulk	pós 1950	-	-
SacA72258	26	Bulk	1225 \pm 30	794-1141	1017
SacA72259	52	Bulk	1395 \pm 30	1143-1333	1263
SacA70279	72	Bulk	1440 \pm 40	1298-1474	1359
GifA21599	100	Bulk	1590 \pm 70	1443-1703	1544
SacA70281	217	Bulk	2465 \pm 30	2473-2712	2639
SacA74334	239	Bulk	2755 \pm 30	2772-2935	2835
SacA72261	291	Bulk	3095 \pm 30	3227-3463	3335
GifA21601	300	Bulk	4740 \pm 90	6169-7338	7048
SacA74336	314	Bulk	6560 \pm 30	7140-7540	7413

4.3.3 Pollen analysis

Subsamples of 0.5 cm³ were taken every 4 cm within the initial 50 cm of the top due to low sedimentation, and every 2-6 cm in the remainder of the sediment, resulting in 112 samples analyzed. The extraction of palynomorphs present in the sediments followed a standard protocol involving the use of acids for the elimination of silicates and silica with 70% HF, with 50% HCl in an 80% water bath for the removal of colloidal silica, and 10% KOH in an 80°C water bath subsequently used for the removal of humic acids (Faegri and Iversen, 1989). Two tablets of *Lycopodium* sp. spores were added during processing to calculate pollen concentration (Stockmarr, 1971). Additionally, the Pollen Accumulation Rate (PAR, or pollen influx), expressed as grains/cm²/yr, was calculated by multiplying the pollen concentration by the sedimentation rate (cm/yr) derived from the age-depth model.

After these treatments, the pollen residue was treated with ZnCl₂, which caused a change in the density of the palynomorphs, making it possible to extract them without the unnecessary excess of residues for analysis. Subsequently, the resulting material was stored in 95% glycerin for later slide preparation. The method for identifying, describing (qualitative analysis), and counting (quantitative analysis) the pollen grains and spores was performed under an optical microscope with a digital image capture system. Analyses were executed under magnifications

of 400x, 600x, and 1000x (oil immersion). For the identification of pollen types, reference pollen collection was used, along with consultation of specialized literature (Colinvaux et al., 1999; Lorente et al., 2017; Salgado-Labouriau, 1973; Cassino and Meyer, 2011; Silva et al., 2024, among others).

A minimum of 300 terrestrial pollen grains was counted in each sample to ensure statistical representativeness. The total pollen sum used for frequency calculations included arboreal, non-arboreal, and unidentified pollen taxa. Aquatic and water-level related taxa, such as *Typha*, *Ludwigia*, *Utricularia*, and Cyperaceae, were excluded from the main pollen sum to avoid overrepresentation of local damp-zone vegetation. The results were represented in a pollen diagram generated using the *rioja* package in the R statistical analysis program (Juggins, 2015; R Core Team, 2018).

Before ordination, the pollen count matrix was subjected to pre-processing as recommended for ecological abundance data (LEGENDRE; LEGENDRE, 2012). The data treatment, performed using the *vegan* package in R (OKSANEN et al., 2025), involved: 1) Square root transformation to reduce the influence of dominant taxa; 2) Wisconsin double standardization, which divides each element by its column maximum and then by the row total, equalizing the weight of samples and rare species; and 3) Calculation of a dissimilarity matrix using the Bray-Curtis coefficient. To visualize the distances between samples, a Non-Metric Multidimensional Scaling (NMDS) was performed. A three-dimensional solution was selected (Stress = 0.16), providing a robust representation of the original dissimilarity (KRUSKAL, 1964). Subsequently, scatter plots were generated to evaluate the grouping of samples (PAR1 to PAR5) and the influence of specific taxa on the ordination space.

4.3.4 Charcoal analysis

Subsamples of 1 cm were taken every 4 cm within the initial 50 cm of the top and every 2 cm in the remainder of the sediment. Subsequently, the subsamples were prepared for macro-charcoal analysis using bases of NaPO₃, KOH and NaOCl for bleaching and sieved through a 160 µm mesh (Stevenson and Haberle, 2005). The sieved subsamples were analyzed using a stereoscope to obtain data on the count and morphometry of the charcoal particles. Images were processed using the WinSeedle software (Regent Instruments, Quebec, Canada) and ImageJ.

Time-series analysis of charcoal was performed in R with the *tapas* package (FINSINGER; IAGO-LITO, 2022). Charcoal data were standardized and expressed as Charcoal Influx (mm²/cm²/yr) and as the mean width-to-length (W/L) ratio (ALEMAN et al., 2013). The W/L ratio acts as an indicator of the fuel type involved in burning events: values below 0.5 are

generally linked to the charring of fine herbaceous fuels under intense fires typical of open grasslands, while values above 0.5 denote the combustion of coarse woody material, commonly associated with fires in more densely vegetated, forested settings (UMBANHOWAR; MCGRATH, 1998).

4.3.4 XRF analysis

High-resolution geochemical analyses were performed using an XRF core scanner at the EDYTEM Laboratory (Université Savoie Mont-Blanc – CNRS). Measurements were acquired at a spatial resolution of 0.5 cm along the sediment core. Two analytical runs were conducted to optimize elemental detection: the first at 10 kV to measure major and minor elements (including Al, Si, K, Ca, Ti, Mn, and Fe), and the second at 30 kV to detect heavier trace elements (e.g., Zr and Sr).

Elemental data were expressed as log-ratios to minimize matrix effects inherent to XRF core scanning. The $\ln(\text{Ti}/\text{Al})$ ratio was calculated as a proxy for detrital input and hydrological energy, where Al serves as a matrix normalizer and Ti reflects the transport of heavy minerals derived from siliciclastic rocks within the drainage basin (BERTRAND et al., 2024).

4.4 Results

4.4.1 Lithology

The PAR-21 sediment core reached a total thickness of 318 cm and was predominantly composed of clay, with noticeable variations in color and compaction throughout the sequence. The upper section (0–114 cm) consisted of low-compaction clay, transitioning from orange to brown, marked by an orange-brown line at the 114 cm level. Between 114 and 173 cm, the sediment became more compacted and assumed a gray color that gradually darkened to black. From 173.5 to 238.5 cm, gray clay predominated. A distinct layer of orange clay was observed between 239 and 244 cm, which transitioned into dark gray clay from 245 cm onwards. Finally, from the 291 cm level to the base of the core (318 cm), the dark gray clay gave way to a more compacted, light gray clay.

4.4.2 Chronology

The age-depth model for the PAR-21 core indicates a sedimentation hiatus between 298 and 300 cm, with the basal age recorded at 7490 cal yr BP (318 cm). Sedimentation rates varied significantly throughout the Holocene: the basal section (314–299 cm) exhibited intermediate rates ranging from 0.03 to 0.04 mm/yr, dropping to nearly zero at the 298 cm hiatus. Above this

interval (297–290 cm), the rate increased to 0.05–0.08 mm/yr and remained high through the 289–70 cm section, reaching 0.09–0.16 mm/yr. A further slight increase was observed between 69 and 49 cm, with rates peaking between 0.12 and 0.25 mm/yr. In the upper part of the core, the sedimentation rate decreased to 0.06–0.14 mm/yr (48–25 cm), finally returning to intermediate values of 0.01–0.04 mm/yr from 24 cm to the core top (Fig. 2).

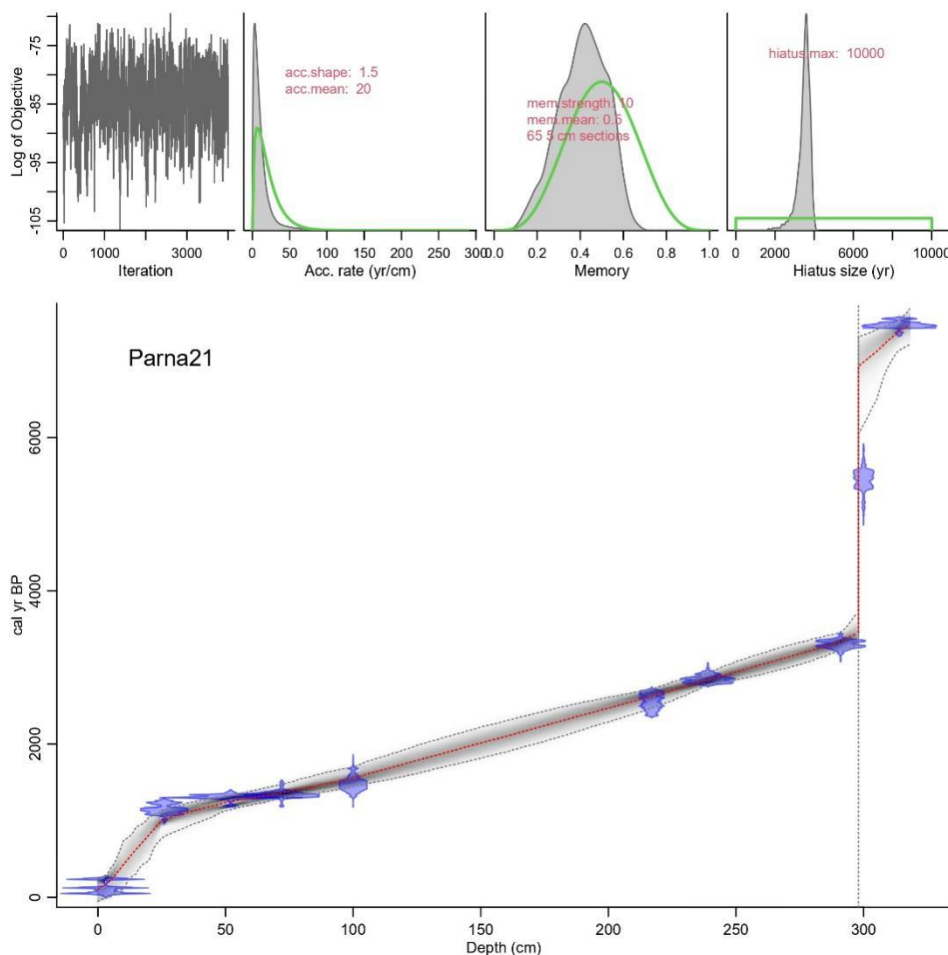


Fig. 2. Age/Depth Model (Bacon) for the PAR-21 sediment core. The dashed red line represents the model. The calibrated distributions of the individual radiocarbon dates are shown in blue (see Table 1), and the dark gray areas indicate the 95% confidence intervals of the model (BLAAUW; CHRISTEN, 2011).

4.4.3 Pollen analysis

A total of 112 samples from PAR-21 were analyzed at intervals ranging from 2 to 6 cm. The mean temporal resolution is approximately 66.5 years per sample. However, resolution varies by section: 0–80 cm: 52.2 years/sample; 82–298 cm: 26.8 years/sample (highest resolution of the record); and 300–318 cm: 48.7 years/sample. In total, 113 arboreal, 83 non-arboreal, and 12 aquatic taxa were identified, distributed across 89 botanical families. The zones were determined by the CONISS cluster analysis method, with only Zone 1 being defined by visual observation of the hiatus, where the pollen concentration showed the most evident

variation.

4.3.3.1 PAR1 Zone (318–300 cm, 7490–7050 cal yr BP, 10 samples)

The PAR1 zone is characterized by low pollen concentration (62–484 grains/cm³), pollen influx (PAR; 2.5–25.2 grains/cm²/yr) and charcoal influx (CHARa) (<0.1 mm²/cm²/yr; 0.001–0.03). The pollen assemblage is dominated by non-arboreal taxa (57–100%), mainly *Cleome* (5%), Poaceae (5–36%), *Borreria*-type (4–42%), *Mitracarpus* (2–16%), and *Solanum* (12–16%). Arboreal pollen, representing 5–42% of the assemblage, includes *Schinus* (4%), *Tapirira* (4–7%), Arecaceae (7–15%), *Euphorbia*-type (3%), *Piptadenia* (2–16%), and Myrtaceae (5%). High percentage of damaged pollen grains (27–52%). Aquatic taxa are well represented in this zone, particularly *Cabomba* (2–5%), Commelinaceae (2–23%), and Cyperaceae (4–61%), the latter likely overrepresented.

4.3.3.2 PAR2 Zone (298–260 cm, 3430–3030 cal yr BP, 20 samples)

PAR2 is characterized by an increase in pollen concentration (713–25,711 grains/cm³), and in pollen influx (50–1,732 grains/cm²/yr). Charcoal influx (CHARa) ranged from 0.02 to 0.377 mm²/cm²/yr. The pollen assemblage shows a pronounced increase in arboreal pollen (3–86%), including *Astronium* (0–8%), *Schinus* (0–6%), *Spondias* (0–2%), *Tapirira* (1–7%), Arecaceae (0–5%), Melastomataceae/Combretaceae (0–6%), *Euphorbia*-type (0–5%), *Anadenanthera* (1–15%), *Mimosa*-type (0–45%), *M. verrucosa* (0–6%), *Piptadenia*-type (2–18%), *Byrsonima* (0–4%), *Brosimum* (3–30%), *Maclura* (12–25%), *Naucleopsis* (52%), Myrtaceae (0–8%), and *Matayba* (0–1%). Among the non-arboreal taxa *Alternanthera* (2–6%), *Spathiphyllum* (2–10%), Asteraceae (0–4%), *Microtea* (0–9%), *Piper* (3–43%), *Peperomia* (0–8%), Poaceae (0–45%), *Borreria*-type (0–21%), and *Mitracarpus* (0–13%). The overrepresentation of Cyperaceae observed in the previous zone persisted, while aquatic/peripheral taxa are well represented with *Cabomba* (0–11%), Commelinaceae (0–25%). However, the percentage of damaged pollen grains decreases (0–20%).

4.3.3.3 PAR3 Zone (258–156 cm, 3020–2070 cal yr BP, 29 samples)

In PAR3 Zone pollen concentration remains high and stable (823–19,787 grains/cm³), and pollen influx reaches the highest values of the record (236–1,824 grains/cm²/yr). Charcoal influx (CHARa) also peaks in this interval (0.003–0.492 mm²/cm²/yr). The pollen assemblage is dominated by non-arboreal taxa (26–79%), including *Alternanthera* (0–30%), *Spathiphyllum* (0–21%), Asteraceae (0–3%), *Cleome* (0–3%), *Microtea* (0–8%), *Piper* (1–61%), *Peperomia* (0–28%), Poaceae (0–28%), *Borreria*-type (0–24%), and *Mitracarpus* (0–7%). Arboreal taxa

comprise *Astronium* (0–13%), *Schinus* (0–7%), *Spondias* (0–5%), *Tapirira* (0–11%), Arecaceae (0–4%), Melast./Combr. (0–9%), *Euphorbia*-type (0–6%), *Anadenanthera* (1–29%), *Mimosa*-type (0–12%), *M. verrucosa* (0–4%), *Piptadenia*-type (0–15%), *Byrsonima* (0–5%), *Brosimum* (0–1%), *Maclura* (0–17%), *Naucleopsis* (0–3%), Myrtaceae (0–3%), and *Matayba* (0–7%). Despite the persistent overrepresentation of Cyperaceae, aquatic taxa show a decline relative to previous zones, notably *Cabomba* (0–3%), Commelinaceae (0–3%). Damaged pollen grains remained at similar levels to the previous zone (0–20%).

4.3.3.4 PAR4 Zone (154–96 cm, 2050–1520 cal yr BP, 20 samples)

PAR4 Zone is characterized by a decrease in pollen concentration (222–13,649 grains/cm³) while the pollen influx remains similar to previous zone (67–988 grains/cm²/yr). Charcoal influx (CHARa) ranged from 0.003 to 0.407 mm²/cm²/yr. PAR4 is characterized by an increase in Arboreal Pollen taxa (40–82%), notably *Astronium* (0–23%), *Schinus* (0–6%), *Spondias* (0–2%), *Tapirira* (0–8%), Arecaceae (0–4%), Melast./Combr. (0–7%), *Euphorbia*-type (0–7%), *Anadenanthera* (0–11%), *Mimosa*-type (6–33%), *M. verrucosa* (0–5%), *Piptadenia*-type (0–12%), *Byrsonima* (0–6%), Myrtaceae (0–1%), and *Matayba* (0–4%). NAP (17–59%) include *Alternanthera* (0–11%), *Spathiphyllum* (0–25%), Asteraceae (0–3%), *Cleome* (0–2%), *Microtea* (0–4%), *Piper* (0–8%), *Peperomia* (0–19%), Poaceae (0–19%), *Borreria*-type (0–18%), and *Mitracarpus* (0–3%). Aquatic taxa decrease *Cabomba* (0–1%), Commelinaceae (0–3%). Damaged pollen grains varied from 1 to 23%.

4.3.3.5 PAR5 Zone (94–0 cm, 1510 cal yr BP to present, 33 samples)

PAR5 Zone shows low pollen concentration similar to PAR1 zone (46–2,890 grains/cm³), and low pollen influx accordingly (10–236 grains/cm²/yr). Charcoal influx (CHARa) varied from 0.0002 to 0.330 mm²/cm²/yr. AP remains dominant (20–100%), including *Astronium* (0–66%), *Schinus* (0–10%), *Spondias* (0–7%), *Tapirira* (0–13%), Arecaceae (0–5%), Melast./Combr. (0–16%), *Euphorbia*-type (0–16%), *Anadenanthera* (0–5%), *Mimosa*-type (0–41%), *M. verrucosa* (0–2%), *Piptadenia*-type (0–17%), *Byrsonima* (0–7%), Myrtaceae (0–3%), and *Matayba* (0–3%). NAP (0–80%) include *Alternanthera* (0–13%), *Spathiphyllum* (0–7%), Asteraceae (0–7%), *Cleome* (0–18%), *Microtea* (0–6%), Poaceae (0–27%), *Borreria*-type (0–30%), and *Mitracarpus* (0–41%). Among aquatic taxa, aside from Cyperaceae, *Typha* (0–73%) is well represented. Damaged pollen grains ranged from 0 to 33%.

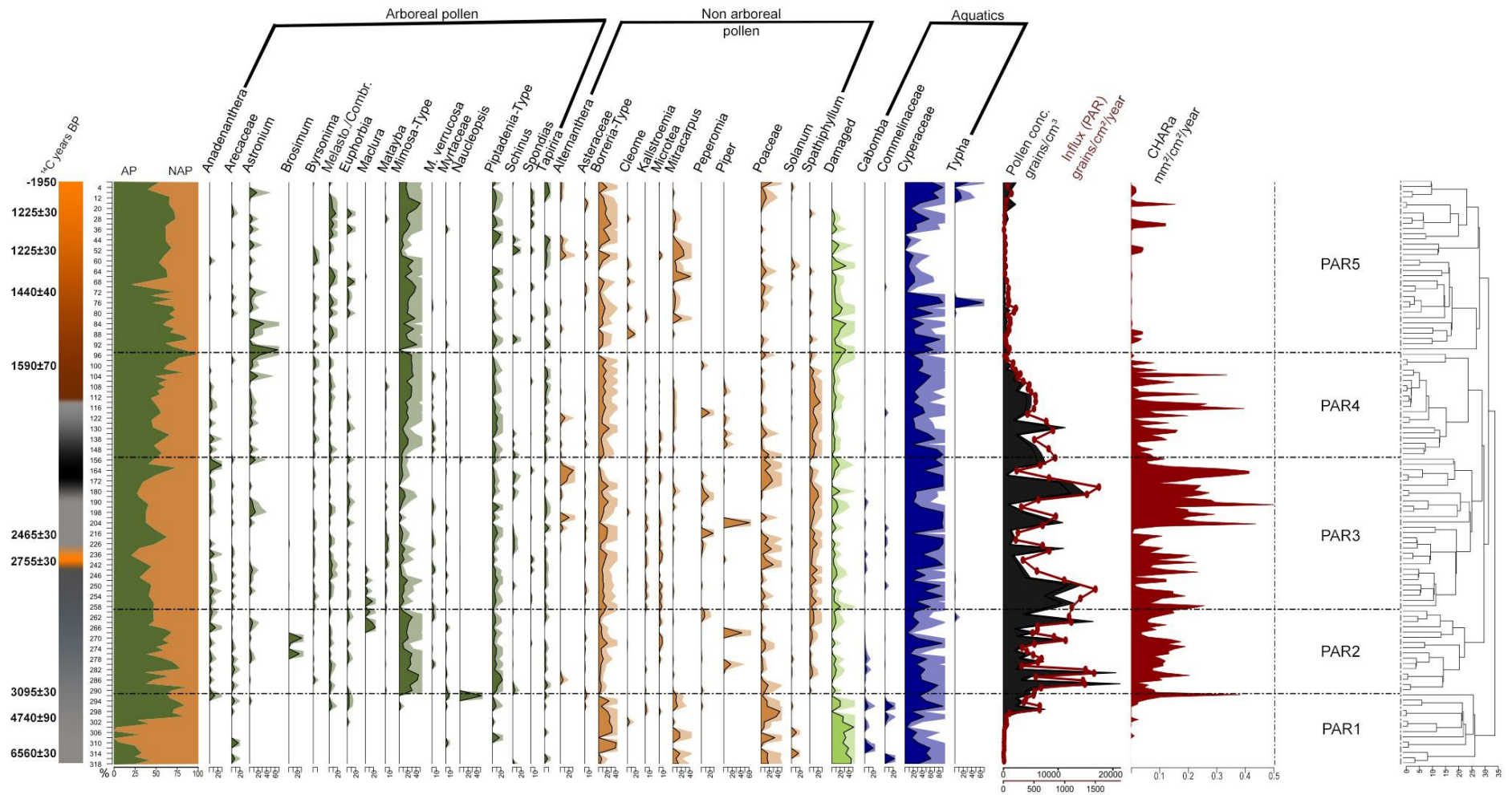


Fig. 3. Pollen diagram of the PAR-21 core. The diagram presents radiocarbon ages (^{14}C), sediment lithology, percentages of arboreal and non-arboreal pollen, and the relative frequencies of 33 selected taxa, grouped as Arboreal (dark green), non-arboreal (orange), damaged pollen (light green), and aquatic (dark blue). It also shows the total pollen concentration and pollen influx (PAR; red line), as well as the macrocharcoal concentration (CHARa).

4.4.4 Non-metric Multidimensional Scaling (NMDS) Ordination

The three-dimensional NMDS ordination (stress = 0.16) provided a good representation of the dissimilarity structure among samples, indicating that the spatial distribution of the samples reflects compositional variations along the sediment sequence. The samples grouped into the PAR zones, corresponding to different depths and ages, reveal a floristic gradient between the deeper levels (PAR1) and the upper ones (PAR2 to PAR5). Zones PAR2 to PAR5 appear closer and overlapping near the center of the axes, suggesting greater similarity among these groups and more homogeneous vegetation conditions. In contrast, the PAR1 group is more distinct from the others, indicating more pronounced vegetation changes in the older sediments.

The species plotted in red show patterns consistent with this variation. Taxa such as *Astronium*, *Brosimum*, *Naucleopsis*, *Solanum*, and Poaceae occupy peripheral positions in the ordination, indicating preferences for specific environmental conditions. Conversely, taxa located closer to the center (e.g., *Euphorbia-type*, *Mimosa-type*, *Piptadenia-type*, and Asteraceae) represent more generalist species, typically associated with transitional environments. *Naucleopsis* and *Astronium*, positioned at opposite extremes of the ordination, further reinforce the existence of environmental gradients within the record. Overall, the NMDS pattern suggests a significant shift in vegetation composition throughout the sedimentary sequence.

4.5 Interpretation and discussion

4.5.1 Vegetation changes in the Parnaguá region

The PAR-21 core recorded a significant paleoenvironmental dynamic in the Parnaguá region, characterized by a transition from open environments to woody formations. This interpretation is calibrated by the analysis of three modern surface samples (sites 6, 7, and 8) collected from lacustrine edge sediments, as detailed in Chapter 2. Although these modern samples consist of relatively uncompacted material compared to the fossil record, they serve as a primary reference for current pollen rain. These sites indicate a high overrepresentation of Cyperaceae (10–70%) and a notable rarity or absence of aquatic taxa (*Cabomba*, *Typha*) and understory elements (*Piper*, *Peperomia*) in the modern surroundings. Consequently, the occurrence of these taxa in the fossil record is assigned a high diagnostic value for reconstructing past wetter conditions or denser forest cover.

Between 7490 and 7050 cal yr BP (318–300 cm), the pollen assemblage is dominated by non-arboreal taxa (NAP) such as Poaceae, *Borreria-type*, *Mitracarpus*, and *Cleome*, indicating predominantly open vegetation, characteristic of grassland or open Savanna (Cerrado sensu lato) (Fig. 3). Although the Poaceae percentage (36%) slightly exceeds the upper limit recorded in modern Cerrado pollen rain (32%; see Chapter 2), this signal highlights the exceptionally extensive development of herbaceous savanna across the landscape. Considering the low pollen concentration and influx, the high incidence of damaged grains, and the W/L ratio below 0.5 (indicative of grass burning), the assemblage is consistent with a period of drier and more unstable conditions. This interpretation is further supported by the intermediate sedimentation rates (0.03–0.04 mm/yr) and the presence of a hiatus at the end of this interval, suggesting lower lake levels and episodic subaerial exposure of the sediment. These findings align with the wet–dry oscillation phase of the early to middle Holocene associated with SASM variability, as also recorded in central Cerrado sequences (CASSINO et al., 2020).

A long-term sedimentary hiatus (~3620 years) recorded between 300 and 298 cm (7050–3430 cal yr BP) indicates a phase of marked local instability, likely associated with the complete desiccation of the water body or intense erosional processes. This interpretation is supported by the sedimentation rate, which dropped to nearly zero during this precise interval, reflecting a lack of accommodation space and continuous deposition. This interruption during the Middle to Late Holocene aligns with widespread aridity and instability recorded in Northeast Brazil (NEB), such as the Icatu River Valley (6790–6230 yr BP) and Chapada das Mesas (4300–3900 cal yr BP), where sterile layers reflect oxidizing and dry conditions (DE OLIVEIRA; BARRETO; SUGUIO, 1999; XAVIER et al., 2024). Speleothem records, including TRA7 from

Apodi, also exhibit growth hiatuses between 4100 and 2250 yr BP, confirming reduced aquifer recharge linked to the weakening of the South American Summer Monsoon (SASM) (UTIDA et al., 2020). The resumption of sedimentation at 3430 cal yr BP (297 cm), evidenced by a significant increase in sedimentation rates (up to 0.16 mm/yr) and pollen concentration, marks a hydrological recovery and lake re-establishment, consistent with regional rehumidification events (MONTADE et al., 2014; UTIDA et al., 2020).

This phase (3430–3030 cal yr BP; 298–260 cm) marks a significant expansion of tree cover, evidenced by an abrupt increase in pollen concentration and influx, as well as improved pollen preservation. Arboreal pollen rises markedly, with the expansion of key taxa such as *Astronium*, *Tapirira*, *Piptadenia-type*, and notably *Mimosa-type*. This high proportion and diversity of AP establish a strong affinity with the woodier physiognomies of the Caatinga–Cerrado ecotone, such as Cerradão or Carrasco (see Chapter 2). The increase in CHARa indicates that the expansion of woody biomass coincided with higher fire incidence.

During the period between 3020 and 2070 cal yr BP (258–156 cm), despite high productivity (as indicated by peaks in pollen and charcoal influx), this zone is dominated proportionally by NAP (up to 79%). However, the assemblage shows a mixed composition diagnostic of ecotonal vegetation (where NAP dominates between 51–69%). The high frequency of forest-edge and disturbance taxa such as *Piper* and *Peperomia* is crucial, as their strong signal contrasts sharply with the rarity observed in modern surface samples, indicating a more shaded and humid local microclimate under intense fire disturbance.

The interval between 2050 and 1520 cal yr BP (154–96 cm) marks the peak of woody vegetation dominance, with AP values consistently ranging from 40% to 82%. This phase is characterized by high proportions of *Astronium-type* pollen (up to 23%) and the persistence of *Mimosa-type*, forming an assemblage comparable to high-AP Cerrado sites. The floristic composition indicates the maximum expansion of seasonal forest vegetation in the region, a formation in Piauí that can resemble Caatinga when deciduous or Cerrado when semi-deciduous, suggesting climatic conditions favorable for the development and maturation of this tree cover. The concurrent decline of *Cabomba*, a submerged macrophyte sensitive to light availability and water depth, supports the interpretation of a progressively shallower and less stable aquatic environment, anticipating the transition to a marsh system later dominated by *Typha*.

The most recent period, from 1510 cal yr BP to the present (94–0 cm), maintains the percentage dominance of AP, notably *Astronium-type* (up to 66%), attesting to the persistence of a mature forest structure (Cerrado/Cerradão). However, a deep alteration in the local

hydrological regime is evidenced by the remarkable appearance of *Typha* in the aquatic record, an indicator of shallow eutrophic marshes, whose absence in the modern margin confers high diagnostic value to its past occurrence. The high percentage of Poaceae (up to 27%), exceeding modern limits, together with CHARa oscillations, reflects the intensification of anthropogenic disturbance (land use) during this period, reopening the landscape to grasses.

The PAR-21 record documents five main intervals of paleoenvironmental change in the Parnaguá region, characterized by a clear transition from open landscapes to forest dominance:

- 7490–7050 cal yr BP (Base of the record):

The landscape was dominated by herbaceous savanna vegetation (Cerrado *sensu lato*), with Poaceae (~36%). The lake was present but under dry and unstable conditions, as indicated by low pollen concentration and a high proportion of damaged grains, consistent with the wet–dry oscillations of the Early to Middle Holocene.

- 7050–3430 cal yr BP (Long-term hiatus):

A prolonged depositional hiatus (~3620 years) indicates deep local instability and probable complete desiccation of the water body. This gap reflects the widespread regional aridity across Northeast Brazil (NEB) and the weakening of the SASM during the mid-to-late Holocene.

- 3430–3030 cal yr BP (Initial arboreal expansion):

Hydrological recovery and lake re-establishment triggered an abrupt expansion of woody vegetation. The landscape shifted toward a more wooded physiognomy (Caatinga–Cerrado ecotone), with an increased representation of taxa such as *Astronium* and *Mimosa-type*, coinciding with higher fire incidence (CHARa).

- 3020–2070 cal yr BP (Mature ecotone and disturbance phase):

Vegetation maintained a mixed, ecotonal composition, with NAP dominance (up to 79%). The high frequency of disturbance-related taxa (*Piper* and *Peperomia*) suggests a locally shaded and humid microclimate under intense fire disturbance.

- 2050–1520 cal yr BP (Apex of Seasonal Forest Development):

This interval marks the peak of woody dominance (AP 40–82%), indicating the maximum expansion of seasonal forest (dry or deciduous forest). The phase represents climatic conditions favorable for forest maturation, despite a local decline in hydrological stability (evidenced by the decrease of *Cabomba*).

- 1510 cal yr BP–Present (Forest persistence and anthropogenic disturbance):

A mature forest structure persisted (high AP and *Astronium-type* dominance). However,

the appearance of *Typha* indicates a hydrological shift toward a shallow, eutrophic marsh. Increased Poaceae (up to 27%) and fluctuating fire signals reflect intensified anthropogenic disturbance and land-use activity.

In summary, the lake remained present throughout the record, except during the hiatus (~7050–3430 cal yr BP). The Parnaguá landscape evolved from an open savanna to a seasonal forest within the Cerrado–Caatinga ecotone, which has persisted to the present but has been progressively shaped by local hydrological instability.

4.5.2 *The transitional nature of the region of Parnaguá*

During the mid-Holocene (~7.0 to 4.2 ka BP), the response of the eastern Northeast Brazil (NEB) to monsoonal climatic dynamics diverged markedly between its eastern and western portions, establishing an antiphase pattern (Xavier et al., 2025 *in revision*). Records from western NEB (Cerrado and Amazonian transition regions, such as Maranhão) indicate a phase of increased humidity, characterized by the expansion of rainforest and arboreal Cerrado, as observed at Lago Caçó (Ledru et al., 2006). This regional moisture increase is commonly associated with the strengthening of the South American Summer Monsoon (SASM) (Xavier et al., 2024).

In contrast, sites in the eastern NEB, where precipitation is influenced by the Intertropical Convergence Zone (ITCZ) position, already indicated aridity and vulnerability. For instance, the Icatu Valley record (Bahia) documents a period of total pollen absence (~6,790–6,230 BP), strongly suggesting severe semi-arid and oxidizing conditions (De Oliveira et al., 1999). The Lagoa de Parnaguá record during 7490–7050 cal yr BP (PAR1) aligns with this trend of open landscapes, dominated by non-arboreal taxa (Poaceae), reflecting a low-productivity, highly seasonal environment in the central-eastern region.

The sedimentary hiatus spans nearly four millennia (~7050 to 3430 cal yr BP), suggesting a prolonged period of extreme aridity that may have led to exposure and/or erosion of the lake bed. This event corresponds to the paleoenvironmental equivalent of the “Archaic Hiatus” (the absence of evidence for human occupation in Central and Eastern Brazil during the mid-Holocene) (Araujo et al., 2006) and is associated with a weakened SASM. During the mid-Holocene (~8.2–4.2 ka BP), the main monsoon pattern concentrated precipitation over central Amazonia and southeastern Brazil, while the ITCZ was displaced northward (around 10° N), this configuration resulted in negative precipitation anomalies and increased aridity across Northeastern Brazil (NEB) (CUSTÓDIO et al., 2024). The semi-arid severity observed at Parnaguá and in analogous inland NEB sites (such as the Icatu Valley)(DE OLIVEIRA;

BARRETO; SUGUIO, 1999) whose climatic intensification mechanism during the Middle Holocene is evidenced by the SASM simulation in Custodio et al. (2024), mirroring the drought conditions recorded for the same period in central Brazil and eastern Amazonia (CASSINO et al., 2020; HERMANOWSKI et al., 2012).

The vulnerability of the eastern NEB was dramatically confirmed by the Dry Event (~4.2 ka cal BP), which induced drastic vegetation changes. In the east, Serra do Maranguape (Ceará) experienced rapid reorganization, with dense rainforest being replaced by semi-deciduous forest in approximately 100 years (Montade et al., 2014). Similarly, the Icatu Valley and the Catimbau region (Pernambuco) show xerophytic species expansion and Caatinga consolidation (De Oliveira et al., 1999; Moraes et al., 2020). Meanwhile, Chapada das Mesas (Maranhão), although registering sterile samples (suggesting local drought) between ~4.3 and 3.6 ka cal BP, exhibited a general pattern indicative of higher resilience or faster recovery (Xavier et al., 2024), reaffirming the regional differences in response.

Between 3430 and 3030 cal yr BP, at Lagoa de Parnaguá, this period represented a restructuring phase, marking the onset of pollen productivity and environmental recovery following the ~4.2 ka BP global aridity event. The expansion of seasonal forest arboreal taxa, such as *Brosimum*, *Maclura*, and *Naucleopsis*, along with a slight increase in taxa indicates higher local moisture, such as Myrtaceae. This assemblage signals the establishment of wetter conditions in the Cerrado-Caatinga ecotone compared to the preceding period. This pattern aligns with the western NEB humidification scenario during the Late Holocene, driven by the strengthening of SASM. Arboreal expansion in Parnaguá coincides with transitions observed in Maranhão (Lago Caçó, Ledru et al., 2006) and Chapada das Mesas (XAVIER et al., 2024), where arboreal Cerrado and gallery forest elements expanded from ~3.6 ka BP, after local droughts.

Although climatic conditions favored tree cover expansion (PAR2), the interval between 3020–2070 cal yr BP records the greatest disturbance in the core. This phase is characterized by peak charcoal influx (CHARa), dominance of non-arboreal pollen (e.g., *Piper*, Poaceae), and a decline in aquatic taxa. This decoupling (fire peaks and open landscapes occurring during a phase of regional humidification), together with the evidence of a low W/L ratio (indicative of the combustion of fine/herbaceous material), suggests that burning was driven by anthropogenic rather than climatic factors (Fig 5). This intense landscape modulation by fire and disturbance vegetation (*Piper*) is synchronous with the period of strong Amerindian influence in the NEB, evidenced by crop pollen, such as *Phaseolus*, in Catimbau (Moraes et al., 2020) between 2,150 and 450 cal yr BP, where abundant fire was also linked to shifting

cultivation.

The subsequent interval (~2050–1520 cal yr BP) demonstrates the resilience of the region's tree cover. With an apparent reduction in fire/disturbance intensity (CHARa decreased compared to the previous period), the expansion of tree cover (*Astronium*, *Mimosa-type*) reflects continued humidification and increased water availability, which enabled the recovery of local vegetation. This recovery is further supported by the expansion of palm swamps (*Mauritia*) in areas such as the Araripe Plateau (GUERRA et al., 2024), attesting to the intensification of the SASM since approximately 2.7 ka BP.

In the most recent period (~1510 cal yr BP–Present), the drastic decline in pollen concentration and influx reflects a weakening of the biological signal, likely due to an increase in the length of the dry season and reduced local productivity, both typical of the Late Holocene in the Parnaguá region. The prevalence of herbaceous taxa (Poaceae) over arboreal species further reflects landscape opening, consolidating the installation of semi-arid climate conditions characteristic of the east.

This pattern of open-landscape consolidation and dominance of herbaceous taxa is largely attributed to anthropogenic impacts, which intensified with European colonization. The decline of hydrophilic species such as *Mauritia* (observed in nearby refugia like Araripe, Guerra et al., 2024) and the expansion of Poaceae are similar to patterns observed in Sete Cidades (XAVIER; ARAÚJO; LEDRU, 2022) after 1650 C.E., when widespread fires and deforestation occurred. The foundation of Vila de Parnaguá (1698/1751) around the lake, spurred by incursions of the Macoazes and Rodelleiros indigenous groups and establishment of sesmarias from 1676, marks the period of intensified livestock, agriculture, and conflict, making land-use impacts the dominant factor shaping the landscape during this interval (IBGE, 2025).

In summary, the Parnaguá Lake record (PAR-21) reveals a complex transitional nature in Northeastern Brazil. It highlights hydrological vulnerability and alignment with the continental aridity diagonal during the mid-Holocene (as evidenced by the extensive sedimentary hiatus), in phase with the aridity recorded in central Brazil and eastern Amazonia. In the Late Holocene, the vegetation of the region of Parnaguá shows climatic convergence responded to the strengthening of the SASM through the expansion of seasonal forest woody taxa. This pattern establishes Parnaguá as a crucial archive for documenting how ecotonal areas respond differently to the major atmospheric control systems along the east–west precipitation gradient in the region.

4.5.2 Fire dynamics and anthropogenic influence in the region of Parnaguá (PAR-21)

Fire trajectory in the Piauí ecotone provides the main evidence of increasing and human influence during the Late Holocene. Analyzing the relationship between the charcoal influx (CHARa) and the W/L ratio (a proxy for fuel type) (Fig. 5) across the five zones allows for the identification of a shift from climatically controlled fire to anthropogenic driven burning.

The earliest period, 7490–7050 cal yr BP, represents a fire-limited environment under maximum aridity. Extremely low CHARa and W/L ratios indicate a near absence of burning events. This lack of fire was not due to a shortage of ignition sources but to a severe lack of fuel, as evidenced by a landscape dominated by NAP including notable peaks of Poaceae, yet insufficient in overall biomass density due to moisture stress. This interpretation is further supported by low Ln(Ti/Al) values (Fig. 5), which confirm minimal runoff and prevailing moisture scarcity that limited continuous fuel availability.

A significant shift in the fire regime began in the intermediate zones, PAR2 and PAR3. During 3430–3030 cal yr BP, Ln(Ti/Al) remained consistently high (Fig. 5), indicating that high runoff and moisture were predominant. This aligns with the increase in AP and woody vegetation. However, the W/L Ratio remained predominantly low (< 0.5), indicating that fires primarily consumed grass fuels.

The charcoal peak (CHARa) in the 3020–2070 cal yr BP interval occurred simultaneously with the dominance of non-arboreal pollen (NAP) and disturbance taxa. The low W/L ratio (below 0.5) confirms that the intense burning was focused on herbaceous fuels (grasses) within an open landscape. This evidence supports studies indicating that in grass-dominated Cerrado landscapes, fires are driven by annual climatic variations rather than human factors (GOMES; MIRANDA; BUSTAMANTE, 2018; RAMOS-NETO; PIVELLO, 2000). Specifically, the Parnaguá scenario agrees with the pattern described by Xavier et al., (2022) who attributed the increase in burning at Sete Cidades (1350–1400 CE) to wildfires associated with dry–wet transitions.

The interval between ~2050 and 1520 cal yr BP represents a phase of significant forest recovery, driven by increased regional humidity (strengthening of the SASM) (CUSTÓDIO et al., 2024). This Late Holocene humidification trend is corroborated by the Araripe record, where the expansion of the palm *Mauritia* was observed after ~2000 cal yr BP (GUERRA et al., 2024), confirming the establishment of wetter conditions. During this recovery, the Parnaguá record shows a sharp increase in arboreal pollen (AP), while charcoal influx (CHARa) remains high.

The key evidence is the W/L ratio (Fig. 5), which reaches its highest and most stable values ($W/L > 0.5$) in the record. This pattern indicates that although fire persisted, it

predominantly consumed woody fuels. The burning of woody material within a context of forest recovery (humid phase) attests to anthropogenic activity, suggesting landscape management aimed at restraining forest expansion or clearing vegetation. The records from Guerra et al. (2024) and Xavier et al., (2024) likewise attribute peaks of woody/mixed fire occurring during humid phases to human pressure. The shift in the W/L ratio from herbaceous to woody fuels, initiated during the ~3020–2070 cal yr BP period, suggests a clear change in land-use practices and in the intensity of human impact.

The last 1500 years represent a phase of pronounced environmental instability and intensified land-use pressure. This interval is marked by a secondary decline in productivity (low pollen influx) and widespread proxy variability (Fig. 5). Strong oscillations in CHARa and in the W/L ratio (ranging from high woody values, $W/L > 0.5$, to zero) indicate a highly variable fire regime dominated by the combustion of mixed fuels. This pattern reflects extensive landscape disturbance and anthropogenic management, contrasting with the natural seasonal fire regime, and signals the intensification of land-use pressure in Northeastern Brazil. Comparable mixed-fuel fire patterns became increasingly frequent during the late Holocene at regional sites such as Araripe and Chapada das Mesas, suggesting that burning increasingly affected both woody and arboreal biomass (GUERRA et al., 2024; XAVIER et al., 2024).

The $\text{Ln}(\text{Ti}/\text{Al})$ shows high variability, indicating hydrological instability and erosive runoff within the basin. This late Holocene erosive instability is a regionally observed trend associated with increased disturbance (MORAES; DE OLIVEIRA; BEHLING, 2020; UTIDA et al., 2020; XAVIER; ARAÚJO; LEDRU, 2022). Evidence of impact is further supported by the emergence of *Typha* (an indicator of eutrophication) and strong fluctuations in disturbance taxa (Poaceae, *Borreria-type*). On the Araripe Plateau, for instance, the most recent period (last ~200 cal yr BP) showed a decline in the palm *Mauritia flexuosa* and a re-expansion of Poaceae, which has been attributed to intensified anthropogenic activities (GUERRA et al., 2024) corroborating the regression of arboreal cover observed in Parnaguá.

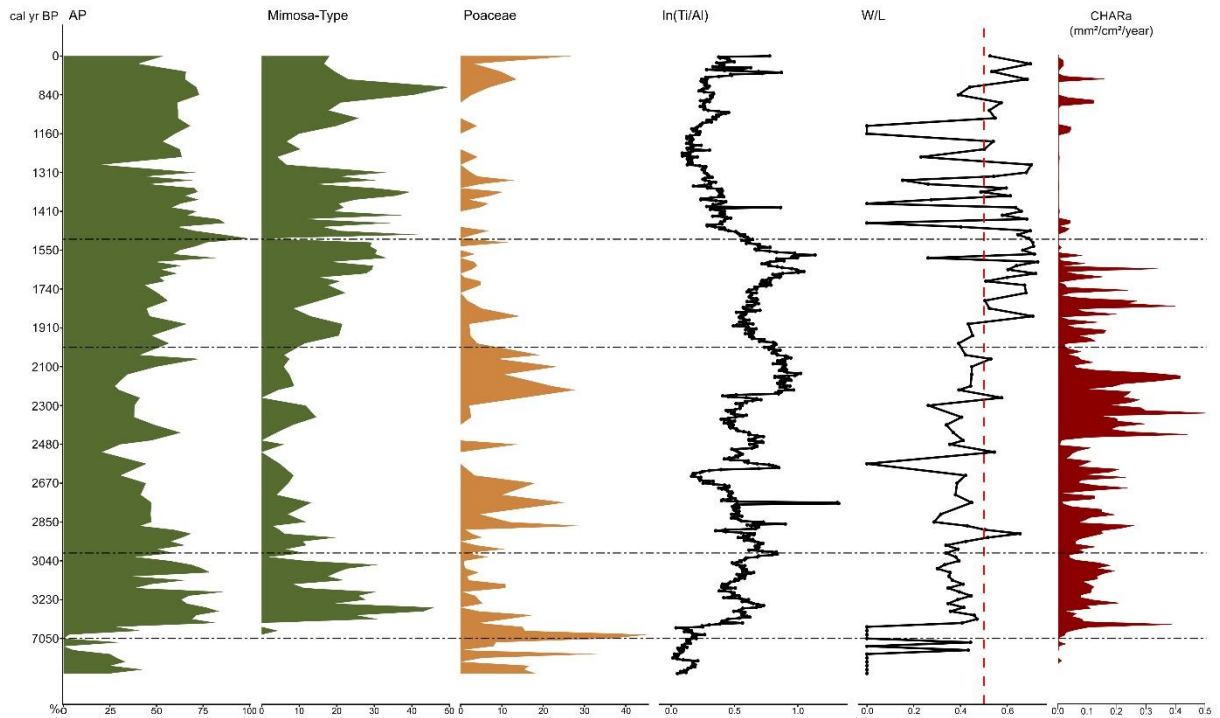


Fig. 5. Paleoenvironmental proxy diagram showing vegetation and environmental changes in the PAR-21 record over the last 7,500 cal yr BP. From left to right: arboreal pollen percentage (AP), Mimosa-type pollen percentage (both in dark green), Poaceae percentage (in orange), the geochemical proxy $\ln(\text{Ti}/\text{Al})$, and the W/L ratio of charcoal (dashed red line indicating 0.5) and charcoal microparticle concentration (CHARa; in red). Horizontal dashed lines indicate the main chronozone divisions (PARI to PAR5).

4.6 Conclusion

Our results, combined with an extensive calibration of the modern pollen rain, show that the Parnaguá region was covered by open-landscape vegetation more closely related to the Caatinga than to the Cerrado, with some expansion of ecotonal vegetation specifically during the interval 3430–1520 cal yr BP. The driest episode at Parnaguá corresponds to the sedimentary hiatus spanning 7050–3430 cal yr BP, indicating extreme instability and probable complete desiccation of the water body. The most humid phase occurred between 2050 and 1520 cal yr BP and was characterized by the maximum expansion of seasonal forest woody vegetation, indicating climatic conditions favorable to the development and maturation of the arboreal cover.

Anthropogenic activities are evident after 2050 cal yr BP (peaking between 2050 and 1520 cal yr BP), primarily through fire activity. The key evidence is the W/L ratio (>0.5), which shifts toward the combustion of woody fuels during a phase of forest recovery and increased regional humidity (strengthening of the SASM). Consequently, our findings indicate that the Parnaguá region was under the influence of the continental aridity diagonal (and indirectly of a weakened SASM) during the mid-Holocene, when no sediment accumulation occurred in the lake (7050–3430 cal yr BP), and under a strengthened SASM after 3430 cal yr BP, marked by

the expansion of ecotonal seasonal forest. The record highlights the transitional nature of Piauí, vulnerable to the mid-Holocene aridity that affected NEB, yet responsive to the late Holocene strengthening of the SASM.

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5 CONCLUSÃO

A presente tese cumpriu seu objetivo principal ao investigar a história paleoecológica do ecótono Cerrado–Caatinga, no Piauí, uma área crucial e historicamente negligenciada. O sucesso do trabalho reside na abordagem tripla e integrada que combinou o desenvolvimento de um atlas de referência, a calibração pólen-vegetação (chuva polínica moderna) e a reconstituição de longo prazo (registro sedimentar). Esta combinação se provou ser poderosa, superando a carência de uma base robusta e permitindo o entendimento do funcionamento de eventos paleoambientais em uma região-chave de transição entre dois biomas e sistemas climáticos distintos. Os resultados fornecem informações inéditas e detalhadas sobre as flutuações da vegetação, as mudanças climáticas e a crescente influência antrópica ao longo dos últimos milênios, estabelecendo, finalmente, uma base sólida para futuras pesquisas paleoecológicas no Nordeste do Brasil.

5.1 Construção de Ferramentas de Referência

A primeira etapa do trabalho cumpriu o objetivo de estabelecer as ferramentas essenciais para a palinologia regional. O Atlas Palinológico do ecótono Cerrado–Caatinga e a análise da chuva polínica moderna da bacia do rio Parnaíba representam uma contribuição inédita para o Nordeste brasileiro. O sucesso na construção desse referencial morfológico robusto deve-se, em grande parte, à colaboração institucional. A oportunidade de acesso e utilização do material depositado no Herbário Prisco Bezerra (EAC) da Universidade Federal do Ceará (UFC) foi um diferencial crucial, transformando o acervo em um pilar central da tese. Foi por meio desse material de referência, coletado do herbário, que pudemos descrever 398 gêneros e catalogar 51 táxons novos, fornecendo a base indispensável para a interpretação fidedigna dos registros polínicos modernos e fósseis da região.

A análise da chuva polínica moderna, por sua vez, estabeleceu as relações entre a vegetação atual e a assinatura polínica depositada nos sedimentos superficiais. Este estudo de calibração foi fortemente subsidiado pela riqueza dos estudos de fitossociologia disponíveis para a região, o que permitiu uma correlação precisa entre os táxons presentes no campo e o espectro polínico. Os resultados confirmaram que a composição florística do ecótono é influenciada primariamente por fatores ambientais (altitude, temperatura e solo) mais do que pela simples proximidade geográfica. A assinatura polínica única da Bacia do Parnaíba, que combina elementos do Cerrado (*Astronium-type*) e da Caatinga (*Mimosa-type*), atesta a natureza singular e mista da região de estudo, fornecendo a chave de interpretação indispensável para o registro fóssil subsequente.

5.2 Registro paleoecológico da lagoa de Parnaguá

O registro sedimentar da Lagoa de Parnaguá (PAR-21) estabeleceu um arquivo de referência inédito e fundamental para a compreensão da dinâmica paleoambiental do ecótono Cerrado–Caatinga ao longo dos últimos 7.500 anos. A aplicação da análise multi-proxy (pólen, CHARa, Ln(Ti/Al), W/L) foi indispensável, pois revelou a complexidade e a interconexão do sistema. Somente essa abordagem integrada permitiu desvendar as nuances da resposta da vegetação às flutuações climáticas, à variação do nível da água do lago e à crescente pressão antrópica que moldaram a paisagem do Piauí.

Os resultados da presente tese, validados por uma extensa calibração da chuva polínica moderna, demonstram que a região de Parnaguá foi caracterizada por uma paisagem aberta com afinidades mais próximas à Caatinga do que ao Cerrado. As flutuações climáticas foram marcadas por dois extremos regionais: o episódio mais seco ocorreu durante o hiato sedimentar (7.050–3.430 anos cal A.P.), que atesta a influência da diagonal de aridez continental e o enfraquecimento do SASM (Sistema de Monções da América do Sul) no Holoceno Médio, levando à provável dessecação completa do corpo d'água. Em contraste, a fase mais úmida (2.050–1.520 anos cal A.P.) registrou a máxima expansão da vegetação lenhosa de floresta estacional, indicando o fortalecimento do SASM. É crucial notar que o impacto antrópico se tornou evidente após 2.050 anos cal A.P., atingindo o pico na mesma fase de recuperação florestal e aumento da umidade. Consequentemente, o registro de Parnaguá realça a natureza transicional do Piauí, que se mostrou vulnerável à aridez do Holoceno médio que afetou o Nordeste do Brasil, mas, ao mesmo tempo, foi altamente responsivo ao subsequente fortalecimento do SASM no Holoceno tardio.

5.3 Desafios observados na pesquisa

A principal dificuldade metodológica residiu na carência de dados palinológicos de referência para o ecótono Cerrado–Caatinga no Piauí. Diferentemente de regiões mais estudadas (como o Sudeste e o Sul do Brasil), a ausência de coleções de pólen e de estudos modernos para a flora do Cerrado nordestino e da Caatinga impôs um obstáculo inicial. Mesmo após o desenvolvimento do Atlas, a identificação completa de táxons tanto na chuva polínica quanto no sedimento lacustre exigiu a consulta a atlas complementares para a confirmação de tipos polínicos não catalogados na presente pesquisa. Este esforço adicional evidencia a extrema diversidade de tipos morfológicos residente em áreas de transição e reforça, por conseguinte, a importância crítica do desenvolvimento e da ampliação contínua de materiais de referência palinológica nesses locais.

A natureza ecotonal da Bacia do Parnaíba introduziu uma dificuldade na interpretação, pois a assinatura polínica moderna é um mosaico. A identificação dos grãos de pólen nos sedimentos de superfície e lacustres exigiu uma cautela redobrada para diferenciar táxons de Cerrado e Caatinga que se sobrepõem e se misturam no ecótono, reforçando a necessidade da base desenvolvida.

Outra dificuldade observada foi na análise do núcleo PAR-21, O extenso hiato sedimentar (7050–3430cal anos AP) eliminou do registro um período crítico para a compreensão da resposta da vegetação ao evento de aridez global de 4.2 ka BP. Embora a presença do hiato em si seja um dado paleoambiental significativo (indicando instabilidade hídrica severa), ele impediu a obtenção de uma sequência contínua para os últimos 7.500 anos, limitando a resolução da dinâmica climática no período.

6 PERSPECTIVAS

O presente trabalho estabelece uma base robusta ao fornecer ferramentas paleoecológicas inéditas e um registro holocênico de referência para a gestão adaptativa e a conservação do ecótono Cerrado–Caatinga. No entanto, para transformar essas descobertas iniciais em um verdadeiro alicerce para a conservação, é preciso expandir e aprofundar a pesquisa em três abordagens principais.

Preencher as lacunas espaciais e temporais, a primeira abordagem consiste em ampliar a rede de arquivos paleoambientais. A obtenção de novos testemunhos de alta resolução (e.g., lagos e turfeiras) em pontos estratégicos do Piauí–Maranhão é crucial. Um foco especial deve ser direcionado ao período crítico da transição Pleistoceno-Holoceno. Com uma cobertura espacial e temporal mais ampla será possível modelar com maior confiança a vulnerabilidade do ecótono e comparar sua resiliência frente a diferentes regimes de aridez ao longo do tempo. Contudo, de nada adianta expandir os arquivos se não pudermos decifrar seus registros com precisão. Portanto, a segunda abordagem é de calibração e refinamento das proxies.

Para isso, proponho o fortalecimento das bases de referência: Criar um acervo de lâminas polínicas e macrocarvões das espécies dominantes. Este acervo é a chave para uma identificação taxonômica precisa, refinando nosso diagnóstico das mudanças na vegetação e umidade. Outro ponto importante é a necessidade de calibrar o sinal do fogo: realizar experimentos de queima controlada para calibrar o índice W/L do macrocarvão, determinando assim o limiar de resiliência da vegetação ao fogo. Implementar estudos de chuva polínica moderna em transectos do ecótono. Esta comparação direta é indispensável para qualificar a interpretação dos dados paleoecológicos e solidificar as projeções futuras.

A abordagem final e mais estratégica consiste na integração quantitativa com modelos preditivos. O registro paleoecológico de 7.500 anos produzido na presente tese possui grande importância, mas para que seu potencial seja plenamente realizado na gestão territorial, ele deve ser convertido em dados climáticos utilizáveis. O caminho que propomos é quantificar o clima passado a partir dos dados polínicos ao utilizar os próprios dados de pólen já disponibilizados, por exemplo, através de índices que relacionam a abundância de espécies da Caatinga versus Cerrado, podemos reconstruir uma série temporal semi-quantitativa das variações de umidade ao longo do Holoceno. Esta reconstrução permitirá definir, com base empírica sólida, o limiar de resiliência do ecótono à seca. E a criação de um dataset de limiares paleoclimáticos: A integração desses limiares de umidade, conjugados com os dados de regime de fogo (W/L do macrocarvão), em modelos de distribuição de espécies (SDMs), permitirá testar a sensibilidade da vegetação às mudanças climáticas passadas e futuras. O produto final será um mapeamento robusto dos refúgios climáticos potenciais e das áreas de alto risco de desertificação, oferecendo uma ferramenta concreta para o planejamento territorial frente ao avanço da fronteira agrícola do MATOPIBA.

Em síntese, essas ações conjuntas visam garantir que o conhecimento gerado sobre o passado não seja apenas um relato histórico, mas sim a base para ferramentas operacionais. Elas fornecerão os valores-limite e os insights necessários para orientar estratégias de manejo do fogo e de conservação de longo prazo em um dos ecótonos mais vulneráveis do Brasil frente às mudanças climáticas.

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