POLLEN AND SPORE ATLAS

For The Cenozoic of The Malay Basin, Malaysia

Robert J. Morley and Jaizan Hardi Mohamed Jais

Pollen and Spore Atlas For The Cenozoic of The Malay Basin, Malaysia

Based on a full analysis of the Malay Basin Malong 5G-17.2 and Delah
5H-14.1 wells, providing a detailed record from the early Oligocene to Pliocene

Published by
The Geological Society of Malaysia

PETRONAS
In collaboration with
PETRONAS

Authors:

Robert J. Morley and Jaizan Hardi Mohamed Jais

Contributors:

Sanatul Salwa Hassan, Harsanti P. Morley,
A. Hadi A. Rahman, Amiruddin Mansor,
M. Raziken Aripin,
M. Hafiz Nordin,
M. Helmi Rohaizar,
Zulhaimi A. Rahman and
Nur Syazwani Mohamad Sabry

Reviewed by:
Dr Keith Richards, Honorary Senior Research Fellow, University of Liverpool, United Kingdom
Associate Professor Dr Huasheng Huang, Sun Yat-sen University, Guangzhou, Guangdong, China

Cover photo *by Harsanti P. Morley*

Published by
Geological Society of Malaysia
Department of Geology
University of Malaya
50603 Kuala Lumpur
Malaysia

First published in 2024
This edition published with the permission of PETRONAS 2024

ISBN 978-629-99024-1-6

9 786299 902416

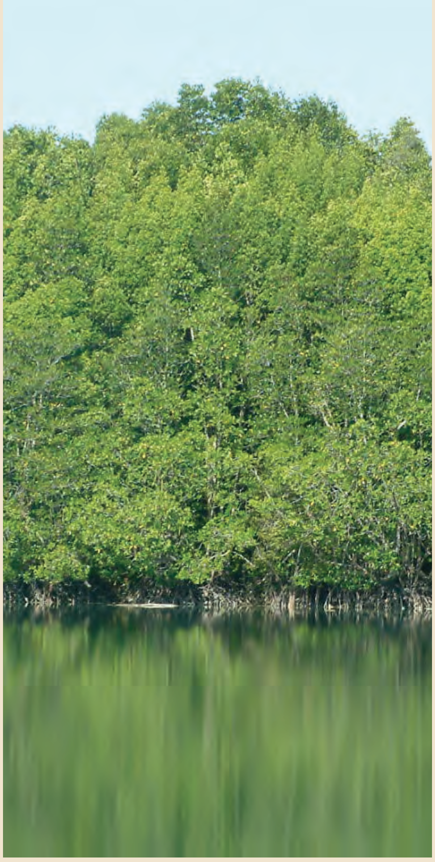
DOI: https://doi.org/10.7186/gsm_atlas112024

Designed by **Nova Fusion Sdn Bhd**
Printed in Malaysia by **Welcome2print Sdn Bhd**

Dedication

This Atlas is dedicated to our reviewer
Dr Keith Richards, who sadly passed away
just before the volume was to be published

Foreword


Bakau mangroves, Sedili


Freshwater intertidal zone, Sedili


Forest canopy, Temburong


Cyperus swamp, Pahang River

This Atlas is a very welcome resource for anyone working in palynology from Malaysia and the wider Asia-Pacific region. It is the first compilation of pollen and spores from Malaysia, and I'm not aware of another comparable work from anywhere in the world where the pollen/spore floras are documented clearly (i.e. with photo plates) but also critically examined taxonomically and re-assigned where necessary. There is also a wealth of information on the regional vegetation, autecology of individual species/taxa, details on botanical lineages and stratigraphic ranges of the studied taxa. Those extra details add significantly to the overall 'usefulness' of the book.

I am certain that it will become the 'go to' reference book for pollen and related studies from the region, providing for students and academics, but also to many working in applied palynology. Especially useful are the re-appraisals of several pollen lineages. For example, the present-day mangrove genus Sonneratia and its ancestral form taxon Florschuetzia. It is extremely useful to have suggestions of the preferred names to use depending on the type of study, e.g. 'form taxa' (usually for stratigraphic studies) and 'modern' names (for Quaternary studies). The 'vegetation' details in their own right will be useful for anyone involved in vegetation or plant ecological studies from around the region.

Dr Keith Richards (April 12th, 2024)
Honorary Senior Research Fellow, University of Liverpool.

Preface

The publication of this Pollen Atlas is the result of a project initiated by Resource Exploration, Malaysia Petroleum Management of PETRONAS. The goal is to develop and enhance data and knowledge based on the offshore petroleum industry in Malaysia. PETRONAS strongly believes that success in exploration is the outcome of blending insight and knowledge derived through the integration of in-depth geological understanding with advanced seismic and subsurface technology, and application of innovative methods to analyse large data volumes. For PETRONAS, successful exploration is crucial for future production and value creation.

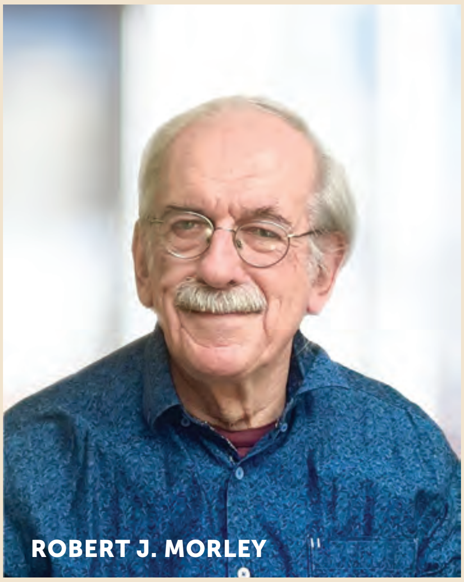
The importance of palynological applications in Oil and Gas (O&G) exploration has been well established as early as the 1960s. In recent decades, the application of high-resolution palynology has proven its benefits in many aspects of O&G exploration and production. In exploration activities, it is a primary tool in chronostratigraphic correlations, paleoenvironmental reconstructions and evaluation of source rocks. In geological modelling and petroleum system studies, palynology is required to be integrated with sedimentology, geophysics, geochemistry and petrophysics to improve and optimise reservoir exploitation.

Petroleum exploration companies in Malaysia widely use palynology as a tool for the stratigraphic correlation and dating of the Cenozoic sediments. A common issue faced by these companies is the lack of a comprehensive taxonomic and nomenclatural system for palynomorphs from the region. The taxonomic and the nomenclatural perspective of Malaysian basin palynomorphs are delicate and complex because almost none of the species from these basins and surrounding areas, except those described in Germeraad et al. (1968), have been described and illustrated following the International Code of Botanical Nomenclature (ICBN) rules. The nearest pollen floras with which Malaysian pollen types could be referred to are from the Australian, Indian and Chinese regions, and other tropical areas such as the South American and African continents.

The systematics for the Malay Basin palynomorphs established in this study is the first standard and comprehensive reference available, not only for Malaysia but also for the Southeast Asia region. Hopefully, this work will facilitate future evaluation of palynomorphs for this region and for comparison to those occurring elsewhere.

Over many years, PETRONAS laboratories have worked together with Palynova Ltd. with respect to palynology. Collaboration in the form of a training program in the 1990s with PRSS (PETRONAS Research and Scientific Services) resulted in a publication on methodology (Morley, 1991) followed by a regional palynological zonation scheme, the 'PR' palynological zonation (Azmi Yakzan et al., 1994, 1996), and also the supervision of a PhD study by Jaizan Hardi Mohamed Jais at the University of Sheffield in the UK on pollen taxonomy (Jaizan Jais, 1999). With these early studies there were problems in accurately dating the palynological zones. Also, it was clear that although some palynological events appeared to have application over a wide area, others were more local in nature, and related to successive phases of sea level and climate change. It was thought that such events could be better evaluated when viewed within the perspective of sequence stratigraphy (van Gorsel, Lunt and Morley, 2014; Morley et al., 2021).


JAIZAN HARDI MOHAMED JAIS


ROBERT J. MORLEY

The initial training program was therefore followed up with a sequence biostratigraphic study during 2004 to 2006, undertaken alongside a regional sequence stratigraphic evaluation of the Malay Basin by ISIS, an Australian company specialising in sequence stratigraphy. The results of this study were presented at several conferences (Morley and Shamsudin Jirin, 2006; Shamsudin Jirin and Morley, 2006) and it became clear that the scheme could be applied elsewhere in the region (Morley et al., 2011). At the same time, the ages applied to the PR zones were updated, by reference to work undertaken in the nearby West Natuna Basin (Morley et al., 2003).

The application of the methods of sequence biostratigraphy opened up many new ideas as to how biostratigraphy should be used in Malaysia, and this led to the fruition of the 'Biofacies' program, which was aimed at looking in detail at cored intervals and modern depositional analogues from the Malaysian region, looking especially at modern sedimentation on three contrasting delta systems, the Klang-Langat Delta, close to Kuala Lumpur, the Pahang Delta on the east coast, and the Sedili River system in Johor. This study resulted in many clarifications as to how pollen and foraminifera are preserved in deltaic and coastal settings in the region, and papers contrasting microfossil deposition in different delta systems (Azmi Yakzan et al., 2010), on improved environment interpretation (Shamsudin Jirin et al., 2010) and on the formation of Miocene peats in Malaysia (Shamsudin Jirin et al., 2011) followed.

Meanwhile, the sequence biostratigraphic method was proving its value in resolving major stratigraphic issues across the Sunda region (Morley et al., 2015) and this prompted two further research projects as part of the YTF (Yet to Find) program. The first of these, termed the Chrono-Sequence project, had the aim to evaluate PETRONAS entire biostratigraphic database and to build a rigorous sequence biostratigraphic framework that would have application across all the major sedimentary basins of Malaysia, from Sabah, Sarawak and the Malay and Penyu Basins. This program resulted in a major paper (Morley et al., 2021), which divided the Malaysian stratigraphic succession into 46 transgressive-regressive packages, termed 'SEA' (Southeast Asia) depositional cycles, and the scheme is now being incorporated into TimescaleCreator (timescalecreator.org), developed by the International Commission on Stratigraphy. A major conclusion of this study was that despite the influence of tectonics across the Malaysian region for much of the Cenozoic, the actual timing of sand deposition was largely controlled by allocyclic processes, and that it was the pattern of global sea level change, especially relating to phases of Antarctic glaciation, that drove the sea level changes that determined precisely when major sands were likely to have been deposited.

The second project was to build on the PhD study by Jaizan Hardi Mohamed Jais to provide a fully illustrated, up-to-date taxonomic treatment of the Malaysian Cenozoic pollen flora, brought together as a single comprehensive Atlas, available in hard copy, and also in digital form. An Atlas of the pollen and spore types found in the Cenozoic deposits of Malaysia is the subject of this volume. The aim is to provide an easily accessible source of information on the Malaysian Cenozoic pollen flora which would guide current and future palynologists working in the region, and hopefully ensure consistency in terms of identifications, nomenclature and interpretation for future industry reports and academic studies.

The current Atlas describes nearly 200 pollen and spore types, as form-taxa following the International Code of Botanical Nomenclature, together with a discussion of sediment sampling, processing and logging methods, and a revised zonation scheme for the Oligocene to Pliocene for Malaysia. Also included is a discussion of palynomorph transportation processes and pollen deposition, and an outline of the vegetation types from which the fossil pollen is likely to be derived, and their environmental and climatic significance. It is hoped that this volume will act as a training manual for future biostratigraphers for many years to come.

The authors are grateful to Malaysia Petroleum Management (MPM) of PETRONAS for releasing the data, enriching discussions and permitting the publication of this work. We also appreciate the Malaysia Basin and Petroleum System of Exploration, PETRONAS, for engaging in fruitful technical discussions. The progress and accomplishment of these studies has required invaluable support of many individuals within and outside PETRONAS. Individuals who have made significant contributions to the succession of projects that have allowed this volume to come to fruition include: Azmi Yakzan, Shamsudin Jirin, Awalludin Harun, Bahari Md. Nasib, Fauzi A. Kadir, Khalid Ngah, Jalil Mohamad, Mahani Mohammed, Maizatul and Awang Sapawi A. Jamil, PETRONAS, and Peter Barber and Rob Kirk from ISIS. We also acknowledge The Geological Society of Malaysia for publishing this atlas.

Robert J. Morley
Palynova Ltd.
Littleport, United Kingdom

and

Jaizan Hardi Mohamed Jais
DrJ Advisors PLT.
Kuala Lumpur, Malaysia
March 2024

Contents

SECTION 1

Scan here for the
online version of
Pollen and Spore Atlas

Preamble

This Pollen and Spore Atlas for the Cenozoic of Malaysia presents for the first time detailed descriptions with full nomenclatural details of 186 pollen, spore and algal form-taxa that are important in the evaluation of the palynostratigraphy and environment interpretation in the Oligocene to Pliocene succession of the Malay Basin. The Atlas will also be useful in the neighbouring areas of Sarawak and Sabah, and in Indonesia, Brunei, Vietnam, Thailand and Myanmar, where the Cenozoic sediments yield a similar pollen flora. The Atlas also discusses palynological sampling methods, processing, and interpretation of palynological data and presents a palynological zonation for the region building on earlier studies from the Malay Basin. It also discusses the mode of dispersal and deposition of pollen and spores into sediments and outlines the main vegetation types from which the pollen and spores are likely to have been derived.

The Atlas will be of use for stratigraphic palynologists working across the broad region, but also for workers on Quaternary palynology and archaeology, for whom a suggested name is given for each taxon in addition to the form-taxon name.

The 186 form-taxa represent all the main groups of pollen and spores, and are distributed as follows: alete, 1; monolete, 18; trilete, 21; polyplicate, 1; monosaccate, 2; bisaccate, 6; inaperturate, 3; monocolpate, 7; dicolpate, 3; tricolpate, 16; stephanocolpate, 1; monoporate, 3; diporate, 1; triporate, 32; stephanoporate, 7; periporate, 6; tricolporate, 26; stephanoporate and periporate, 8; heterocolpate, 2; syncolpate, 8; tetrads, 5; polyads, 1 and algae, 8.

The Atlas describes 7 new genera, 55 new form-species, 4 new forms and 10 new combinations as follows:

New genera:
Claritricolporites Morley and Jaizan Jais gen. nov.
Manggispollenites Jaizan Jais and Morley gen. nov.
Merantipollis Jaizan Jais and Morley. gen. nov.
Minutitriaperturites Morley and Jaizan Jais gen. nov.
Pandanpollenites Jaizan Jais and Morley gen. nov.
Pelahpollis Jaizan Jais and Morley gen. nov.
Psilaheterocolpites Jaizan Jais and Morley gen. nov.

New form-species:
Arengapollenites diminutus Jaizan Jais and Morley sp. nov.
Arengapollenites gracilis Jaizan Jais and Morley sp. nov.
Camarozonosporites minor Jaizan Jais and Morley sp. nov.
Celtispollenites rotundatus Morley and Jaizan Jais sp. nov.
Clavatisporites fungi Morley and Jaizan Jais sp. nov.
Cricotriporites microreticulatus Jaizan Jais and Morley sp. nov.
Echinatisporis lepidus Morley and Jaizan Jais sp. nov.
Echinatisporis minor Jaizan Jais and Morley sp. nov.
Echinatisporis undulosus Morley and Jaizan Jais sp. nov.
Echinosporis conspicuus Jaizan Jais and Morley sp. nov.
Echinosporis obscurus Jaizan Jais and Morley sp. nov.
Echistephanoporites camptostemonoides Jaizan Jais and Morley sp. nov.
Echistephanoporites malaysianus Jaizan Jais and Morley sp. nov.
Euphorbiacites virgatus Jaizan Jais and Morley sp. nov.
Florschuetzia ovata Jaizan Jais and Morley sp. nov.
Florschuetzia ovalis Jaizan Jais and Morley sp. nov.
Florschuetzia retiovata Jaizan Jais and Morley sp. nov.
Florschuetzia retiovalis Jaizan Jais and Morley sp. nov.
Foveogleicheniidites marginatus Jaizan Jais and Morley sp. nov.
Gemmamonocolpites borassoides Jaizan Jais and Morley sp. nov.
Gemmatosporis microgemmatus Jaizan Jais and Morley sp. nov.
Graminidites rotandinii Morley and Jaizan Jais sp. nov.
Iugopollis interruptus Jaizan Jais and Morley sp. nov.
Lakiapollis pachydermus Jaizan Jais and Morley sp. nov.
Laevigatosporites elongatus Morley and Jaizan Jais sp. nov.
Lanagiopollis tenuiexinus Jaizan Jais and Morley sp. nov.
Lanagiopollis diminutus Jaizan Jais and Morley sp. nov.
Malvacipollis austrobuxoides Jaizan Jais and Morley sp. nov.
Manggispollenites psilatriporata Jaizan Jais and Morley sp. nov.
Manggispollenites retitriporata Jaizan Jais and Morley sp. nov.
Merantipollis cuneatus Morley and Jaizan Jais sp. nov.
Merantipollis gracilis Jaizan Jais and Morley sp. nov.
Merantipollis quadricolpatus Jaizan Jais and Morley sp. nov.
Minutitriaperturites minutus Morley and Jaizan Jais sp. nov.
Minutitricolporites duplibaculatus Jaizan Jais and Morley sp. nov.
Minutitricolporites microechinatus Jaizan Jais and Morley sp. nov.
Nepenthidites neogenicus Morley and Jaizan Jais sp. nov.
Pandanpollenites malaysianus Jaizan Jais and Morley sp. nov.
Pelahpollis variabilis Jaizan Jais and Morley sp. nov.
Podocarpidites minuticorpus Morley and Jaizan Jais sp. nov.
Psilodiporites jejawii Morley and Jaizan Jais sp. nov.
Psilastephanocolporites validus Jaizan Jais and Morley sp. nov.
Retibrevitricolpites simpohi Morley and Jaizan Jais sp. nov.
Retitetrabrevicolporites elongatus Jaizan Jais and Morley sp. nov.
Rhoipites apiensis Jaizan Jais and Morley sp. nov.
Rhoipites transversalis Jaizan Jais and Morley sp. nov.
Stenochlaenidites cristatus Jaizan Jais and Morley sp. nov.
Striatopollis malaysianus Jaizan Jais and Morley sp. nov.
Striacolporites anacardiensis Jaizan Jais and Morley sp. nov.
Tricolpites malongii Jaizan Jais and Morley sp. nov.
Tricolpites terengganuensis Jaizan Jais and Morley sp. nov.
Triporopollenites stemonuroides Jaizan Jais and Morley sp. nov.
Triporotetradites microreticulatus Morley and Jaizan Jais sp. nov.
Undulatosporites bracteatus Morley and Jaizan Jais sp. nov.
Verrutricolporites oblatus Morley and Jaizan Jais sp. nov.

New forms:
Florschuetzia trilobata forma A. Jaizan Jais and Morley forma nov.
Florschuetzia trilobata forma B Jaizan Jais and Morley forma nov.
Florschuetzia trilobata forma C Jaizan Jais and Morley forma nov.
Florschuetzia trilobata forma D Jaizan Jais and Morley forma nov

New combinations:
Celtispollenites minutipori (Muller 1968) Jaizan Jais and Morley comb. nov.
Celtispollenites festatus (Muller 1968) Jaizan Jais and Morley comb. nov.
Claritricolporites annulatus (Salard-Cheboldaeff 1978) Morley and Jaizan Jais comb. nov.
Fenestripollenites longispinosus (Lorente 1986) Jaizan Jais and Morley comb. nov.
Incrotonipollis reticulatus (Da Silva Caminha et al. 2009) Jaizan Jais and Morley comb. nov.
Propylipollis subscabratus (Couper 1960) Jaizan Jais and Morley comb. nov.
Psilaheterocolpites laevigatus (Salard-Cheboldaeff 1978) Jaizan Jais and Morley comb. nov.
Rugutricolporites undulatus (Salard-Cheboldaeff 1978) Jaizan Jais and Morley comb. nov.
Tubifloridites spinosus (Van der Hammen 1956) emend Morley and Jaizan Jais comb. nov.
Psilaheterocolpites combretoides (Rao and Ramanujam 1982) Jaizan and Morley comb. nov.

Section 1

1.1 INTRODUCTION

Nypa swamp along the Sedili River in the state of Johor, Malaysia (photo by RJM).

This Atlas presents detailed descriptions and a comprehensive taxonomic assessment of nearly 200 palynomorph species from the Oligocene, Miocene and Pliocene of the Malay Basin, a major hydrocarbon-producing sedimentary basin to the east of the Peninsular Malaysia. The descriptions are accompanied by 29 plates, and a detailed assessment of the likely parent taxa of the palynomorphs described. This is the first comprehensive assessment of Cenozoic palynomorphs from the Southeast Asian region, and places Southeast Asian palynology on a similar footing to that achieved by monographs from Africa (e.g. Salard-Chebaldaeff, 1978) and the Neotropics (e.g. Jaramillo and Dilcher, 2003).

The Atlas is based on the PhD thesis work by Jaizan Hardi Mohamed Jais (Jaizan Jais, 1999) and a full re-evaluation of the taxonomy, nomenclature, botanical affinities, and stratigraphic interpretation by Robert J Morley, with assistance from the other contributors.

All taxa are described as form-taxa following the International Code of Botanical Nomenclature (Stafleu et al., 1978; McNeill et al., 2012). In addition to each form taxon name, the botanical affinity is discussed. The ecology of the parent plants which produced the pollen is discussed mainly in relation to the present day vegetation of the Malay Peninsula, by reference to Wyatt-Smith (1964) and Whitmore (1975), and to Ashton (2014) for Sarawak and Sabah. It is hoped that this Atlas will bring uniformity to palynomorph identification by palynologists working on the Cenozoic across Southeast Asia.

The Atlas is organised as follows:

After the introduction, Section 1 provides general information on the source of the pollen and spores described, and interpretation, whereas Section 2 presents the pollen and spore flora proper. Section 1.1 presents introductory notes, whereas Section 1.2 gives information on the location of the studied wells and 1.3 the geological setting. Sections 1.4 and 1.5 present methodology which discusses the approach to logging techniques, whereas the method of data presentation is given in Section 1.6. Section 1.7 discusses the results, with a summary of the Malong 5G-17.2 well being presented in section 1.8 and the Delah 5H-14.1 in Section 1.9. Updated zonal definitions for the PR zones 1 to 15 are the subject of Section 1.10. Section 1.11 presents a discussion of pollen dispersal and transportation into marine environments, and Section 1.12 provides a summary of the vegetation types that have yielded the pollen and spores described in this Atlas and includes a discussion of their climate requirements and environmental significance. Section 2 presents the Atlas proper, and each form-taxon is described and illustrated, and listed according to morphology. The Atlas includes a list of synonymies, showing other publications where each palynomorph is described and illustrated, followed by a full description, and an indication of size variation, and remarks on how the palynomorph might differ from closely related taxa. This is followed by an indication of its stratigraphic distribution, and the likely botanical source.

The final part presents a discussion of the probable ecology of the parent plant, a suggested name that may be applied by Quaternary palynologists, who may prefer to compare pollen and spores with extant plant taxa rather than form-taxa, and a suggested ecological group, into which sporomorph types could be placed when grouping pollen and spores to help with climate and environment interpretation.

1.2 LOCATION OF STUDIED WELLS

The Malong 5G-17.2 is situated in the eastern flank of the Tenggol Arch at 4° 36′ 57.956″ N, 104 48′ 02.672″ E. It was drilled in 1984 to a total depth of 1618 m and penetrated sediments of Miocene to Recent age. Pre-Cenozoic igneous basement was encountered at 1615 m (Fig. 1.1).

The Delah 5H-14.1 was drilled in 1991, approximately 44 km east of Malong 5G-17.2. It is situated in the southern part of the Malay Basin at 4° 36′ 41.936″ N, 105° 10′ 49.860″ E. The well penetrated 2958 m of Oligocene to Recent sediments and reached a total depth at 2988 m in pre-Cenozoic basement (Fig. 1.1).

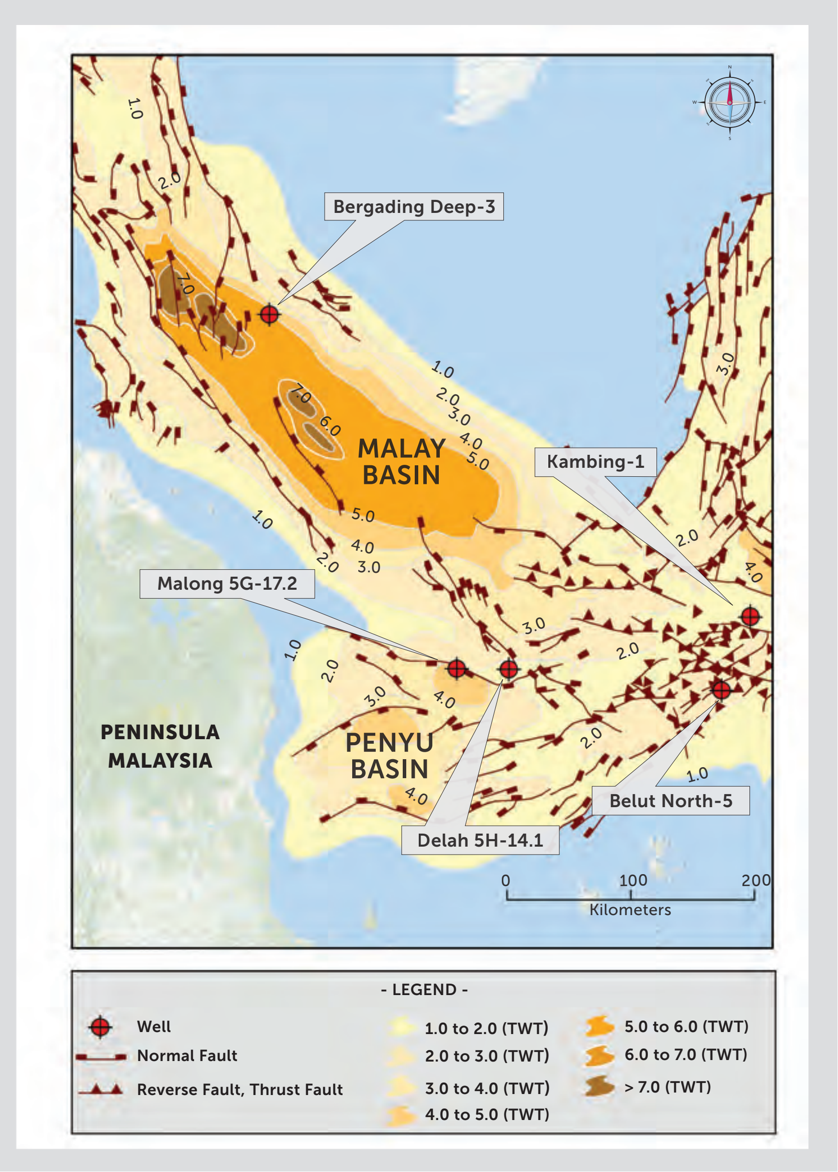


Fig 1.1. The location map of Malay Basin, offshore Malay Peninsula, with the locations of the Malong 5G-17.2 and Delah 5H-14.1 wells indicated together with critical wells from the Malay and West Natuna Basins (from Morley et al., 2003, 2007, 2021).

1.3 GEOLOGICAL FRAMEWORK

1.3.1 Introduction

The Cenozoic Malay Basin is an extensional strike-slip basin located offshore the east coast of Peninsular Malaysia that extends from the Gulf of Thailand to the Natuna Sea in Indonesia. This elongated and asymmetrical sedimentary basin trends northwest-southeast and is approximately 500 km long and 200 km wide. The basin is an intracratonic basin or interior fracture trough situated entirely within the Sunda Shelf.

The regional tectonics of Southeast Asia was initially described by Pupilli (1973), Carey (1975), White and Wing (1978), Tapponnier et al. (1982), and Daines (1985). Early brief geological descriptions of the basin were published by Hamilton (1979), Armitage (1980) and ASCOPE (1981). In the 1990s, several detailed accounts of the structural geology and tectonic evolution of the Malay Basin were published by Khalid Ngah et al. (1996), Tjia (1994a, 1994b), Mazlan Madon (1997), Mazlan Madon and Watts (1998) and Tjia and Liew (1996). Good summaries of the geology and petroleum geology can be found in Mazlan Madon et al. (1999), Bishop (2002) and recently Mazlan Madon (2021).

Azmi Yakzan et al. (1996) and Mohd Tahir Ismail et al. (1994) discussed biostratigraphic and paleogeographic development of the basin and highlighted its early Miocene marine inundation. The schematic paleogeographic reconstruction of the basin in Mazlan Madon et al. (1999) was based on the EPIC (1994) regional study, Nik Ramli (1986) and Mazlan Madon (1994). These publications highlighted the transition from a mainly synrift-related nonmarine depositional phase (alluvial- to coastal plain) to marine influenced depositional setting from the latest Oligocene to the Pliocene.

Recent evaluations of the stratigraphy, biostratigraphy and paleoenvironmental evolution can be found in Shoup et al. (2012), Morley et al. (2021) and Lunt (2021). The recent study of Morley et al. (2021) was based on the evaluation of extensive quantitative biostratigraphic data from 101 petroleum exploration wells from the Malay, Sarawak and Sabah basins. They proposed a new chronostratigraphic framework which allows correlation of unconformities across Malaysia and facilitated the evaluation of the effect of fluctuating sea levels and tectonics on the stratigraphy of the region. In this Atlas we have attempted to update the stratigraphic scheme of Mazlan Madon (2021) using the time and event framework of Morley et al. (2021). This is discussed further below.

1.3.2 Geological Setting

The Malay Basin, located at the centre of the Mesozoic continental core of Southeast Asia, developed along the south-eastern extension of the left-lateral strike-slip fault zone of the Three Pagodas Fault. This late Eocene fault movement is related to the southeast expulsion of Indochina that resulted from the collision of India with Asia.

The basin is flanked to the north-east by the Mesozoic Khorat Swell, to the north-west by the Narathiwat High, to the southwest by the Western Hinge Fault zone and to the south-east by the shallowing of the West Natuna Basin. It is separated from the Penyu Basin to the south-west by the Tenggol Arch. The basin is asymmetrical along its width; the southwestern flank, marked by the Western Hinge Fault (WHF), is generally steeper than its north-eastern flank, which is adjacent to the Khorat Swell in Vietnam waters.

The continental basement rocks of pre-Cenozoic age occur at depths from more than 12,000 m to less than 3000 m; in places where these have been penetrated by exploration wells, igneous, metamorphic, and sedimentary rocks have been reported (Daines, 1985; Khalid Ngah et al., 1996; Mazlan Madon et al., 1999; Tjia, 2000; Bishop, 2002; Mohd Yazid Mansor et al., 2014). Liew (1994) reported basement rocks from the southwestern margin of the basin as Permo-Carboniferous metasediments and volcanics, Cretaceous granites, and possible Cretaceous rift-fill. Mesozoic-to-Carboniferous carbonates and Mesozoic granites form the basement in the northwest was reported by Leo (1997). These rocks are generally thought to be the offshore extension of the onshore geology of the eastern parts of the Malay Peninsula (Fig. 1.2).

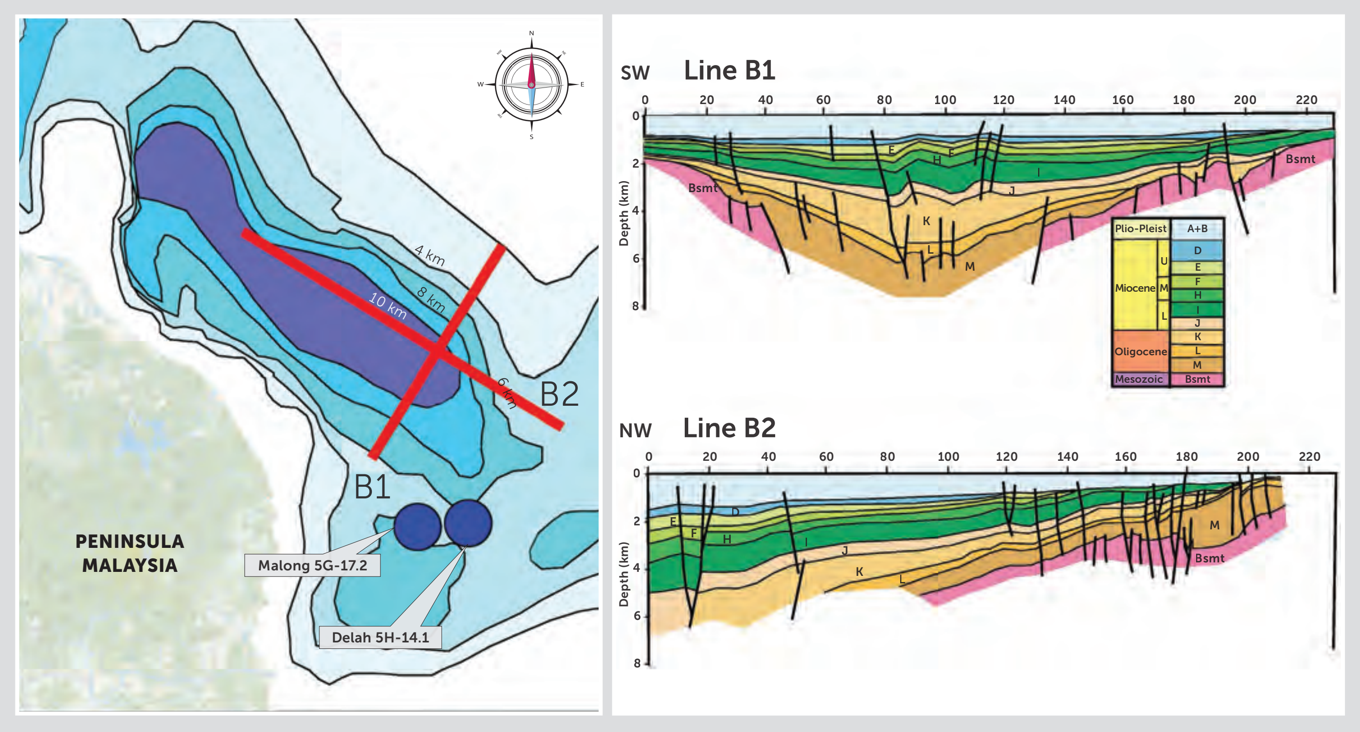


Fig.1.2. *Bathymetry (left) and seismic profiles (right) across the width (B1) and length (B2) of the Malay Basin. Line B1 shows a transverse profile and Line B2 a longitudinal profile. The two blue circles show the positions of the Malong 5G-17.2 and Delah 5H-14.1 wells. (From Mazlan Madon, 1999; Mazlan Madon et al., 1999; Mohd Yazid Mansor et al., 2014).*

This Cenozoic oil and gas sedimentary basin has been filled by an estimated 14 km of Oligocene to Recent sediments. The Oligocene sediments are generally terrestrial and lacustrine deposits with minor marine influence. The Miocene to Quaternary sediments comprise mostly coastal plain to shallow marine deposits (Mazlan Madon et al., 1999).

1.3.3 Structural Geology and Tectonic Evolution

Structural Geology

The Malay Basin developed through multiple episodes of rifting which produced a complex network of extensional grabens. Most of these grabens have not been penetrated due to their great depths of burial. The grabens have been interpreted using magnetic, gravity and seismic data. The structural geological framework of the Malay Basin has been well described in Khalid Ngah et al. (1996), Tjia and Liew (1996) and Mazlan Madon et al. (1999). Tjia and Liew (1996) identified five major fault and fracture trends in the basin; these are N-S, NW, NNW, E-W and NNE (Fig. 1.3).

N-S trending fractures are dominant in the northern sector, which continues north into the Northern Malay and Thao Chu basins and the multiple basins of the Gulf of Thailand. Two prominent north-trending zones here are the Kuda-Ular fault, and the Kapal-Bergading fault zone. Three N-S trends were identified towards the centre of the basin – the Dulang fault, Bundi fault and Mesah fault. However, the exact nature and extent of these faults are less certain (Khalid Ngah et al., 1996; Tjia and Liew, 1996).

The NW trending Western Hinge Fault (WHF) defines the southwestern margin of the basin. This is a zone of *en echelon* normal faults and associated fault-bounded, pull-apart basins. Numerous anticlinal features have been seismically imaged along the WHF. These folds, parallel or near parallel to the fault zone, form fold trends resembling left-lateral wrenching drag-folds. Two NNW-striking fault zones are closely linked to the WHF; these are the Dungun and Tenggol fault zones. The Dungun Fault is a southern splay of the WHF, cutting across the Terengganu Platform. Several small pull-apart grabens developed along the Dungun fault. These have been interpreted to have developed during the right-lateral movement of the fault (Liew, 1994; Mazlan Madon et al., 1999). The Tenggol fault zone, which was active during the late Oligocene, marks the north-eastern edge of the Tenggol Arch. Mazlan Madon (1992) interpreted this as the shelf edge of the early Miocene transgression. The Selambau fault is the only NW-striking trend identified in the axial zone Central Malay fault system (Liew, 1997).

East-West basement faults and fractures are the dominant trends in the southeastern and central parts of the basin. These faults have influenced the development of E-W trending compressional anticlines in the Neogene successions; these anticlines are the result of dextral motion along the Axial Malay Fault Zone, which is thought to be the southeastern extension of the Three Pagodas Fault (Tjia, 1996).

Tjia and Liew (1996) highlighted the NNE trends in the southeastern corner of the basin. Mazlan Madon et al. (2020) imaged the presence of these NNE basement faults from gravity data. The area is characterised by fractured basement features.

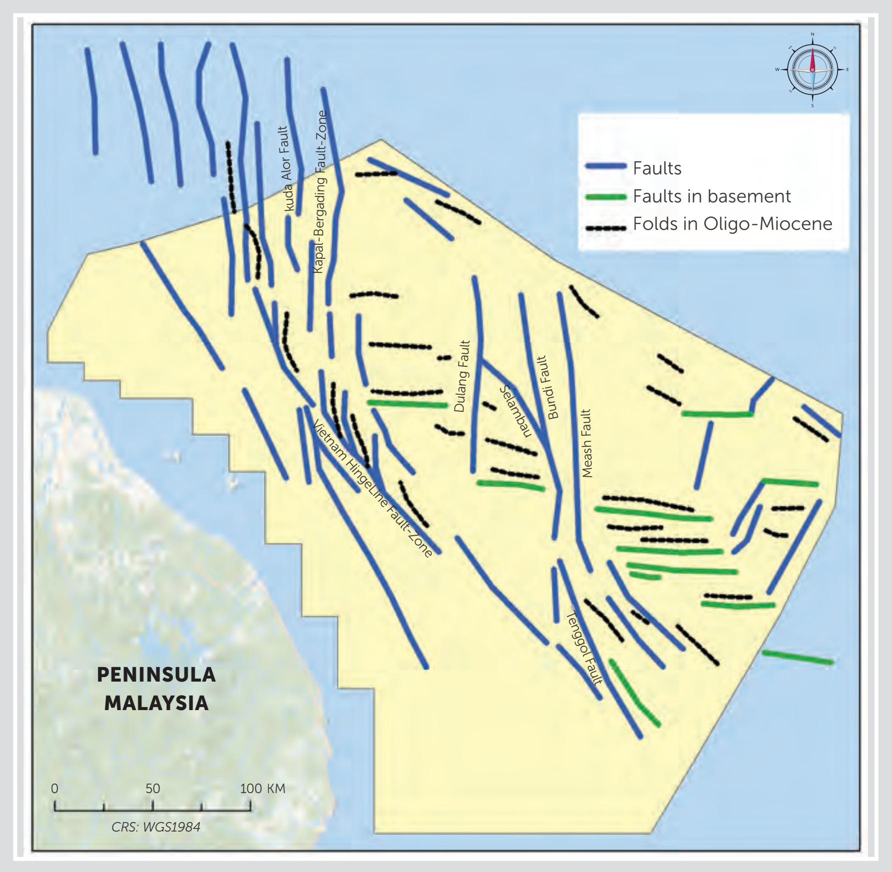


Fig. 1.3. Major fault zones identified within the Malay Basin (modified from Khalid Ngah et al., 1996; Tjia, 1996 and Mazlan Madon et al., 1999).

Tectonic Evolution

The Malay Basin evolved during the course of expulsion of Southeast Asia subsequent to the northward indentation of India into Eurasia. Initial transtensional sinistral shear and crustal extension along the southeastern arm of the Three Pagodas fault zone during the late Eocene and Oligocene created pull-apart basins and half-grabens. These were filled with thick syn-rift successions of fluvio-lacustrine sandstones and mudstones. During the late Oligocene to early Miocene onwards, extensional faulting ceased, and an extended period of subsidence prevailed. This post-rift period witnessed rapid subsidence due to intensive sediment loading and lithospheric cooling. This period is characterised by the deposition of coal-bearing coastal-to-shallow marine strata. Biostratigraphic evidence indicates that the cyclical successions of fluvial, coastal-plain, tidal estuarine and near shallow marine sediments were deposited near sea level. This post-rift thermal subsidence caused the regional sagging of the basin (Azmi Yakzan et al., 1996; Mohd Tahir Ismail et al., 1994; Mazlan Madon et al., 1999).

During the early to middle Miocene, the continuing combined effects of northward and westward convergence on Indian, Australian and Pacific plates resulted in the reversal motion of the Axial Malay fault (the southeastern part of the Three Pagodas Fault). This right-lateral wrenching led to a phase of compression, and inversion of half-graben successions, subsequently forming anticlinal folds. This episodic basin inversion started during the later early Miocene and most likely continued into the Pliocene. Most of these inverted half-grabens formed anticlinal folds trending East-to-West; however, along the SW margin, the anticlines trend NW-SE and in the NW sector, the anticlines trend N-S. This NW-trending dextral shear, and transpressive tectonic compression resulted in a period of erosion, with an estimated 1200 m of the Miocene section being removed (Tapponnier et al., 1982; Khalid Ngah et al., 1996; Tjia and Liew, 1996; Mazlan Madon et al., 1999; Mazlan Madon et al., 2006). The resulting regional unconformity formed has been dated at about 7 Myr. The overlying depositional successions were deposited in a fully marine setting. During the late Miocene to Quaternary, moderate subsidence with minimal tectonic activity resulted in the establishment of fully open marine conditions throughout the basin (Mazlan Madon et al., 1999; Bishop, 2002; Mazlan Madon et al., 2006).

1.3.4 Stratigraphy and Paleogeographic Evolution

The Cenozoic stratigraphy of the Malay Basin, introduced by Esso in the 1960s, was based on seismic-stratigraphic units, referred to as Seismic Groups (EPIC 1994). Division into stratigraphic units based on seismic has proven to be much more useful than attempting to apply formational names (Mazlan Madon et al., 1999). The subdivision into eleven alphabetically named stratigraphic packages, from A (the youngest) to M (the oldest), was initially based solely on seismic stratigraphy, but later refined by biostratigraphy. Several of the seismic reflectors have been identified to be major regional unconformities on the basin flanks (Mazlan Madon et al., 1999; Mazlan Madon et al., 2006).

The basin fill history and stratigraphic development of the Malay Basin is directly related to the structural development and has been grouped into four tectonostratigraphic episodes (Fig. 1.4). These are:

a) *Late Eocene and Oligocene extensional or syn-rift episode*: The syn-rift Group M, the oldest stratigraphic unit penetrated by drilling, was deposited during the mid-Oligocene. The available data suggest that older, undrilled syn-rift deposits representing Seismic Groups P, O and N of late Eocene to early Oligocene age are present below this (Mazlan Madon et al., 2020 and Mazlan Madon, 2021). The nearby Cuu Long Basin, to the south of the Mekong Delta, shows many similarities to the Malay Basin in its early development. Morley et al. (2019) applied a high resolution sequence biostratigraphic approach and identified multiple flood-fill depositional packages that could be correlated to the 'heartbeat of the Oligocene' 406 kyr climatic oscillations of Pälike et al. (2006). The study showed that deposition began at about 37 Myr during the late Eocene, and a similar scenario may apply in the Malay Basin. The initial fault-related subsidence resulted in the deposition of thick, non-marine fluvio-lacustrine sedimentary facies in isolated half-grabens. Deposits of braided streams, coastal plains, lacustrine deltas and lakes have been identified within this interval (Mazlan Madon et al., 1999).

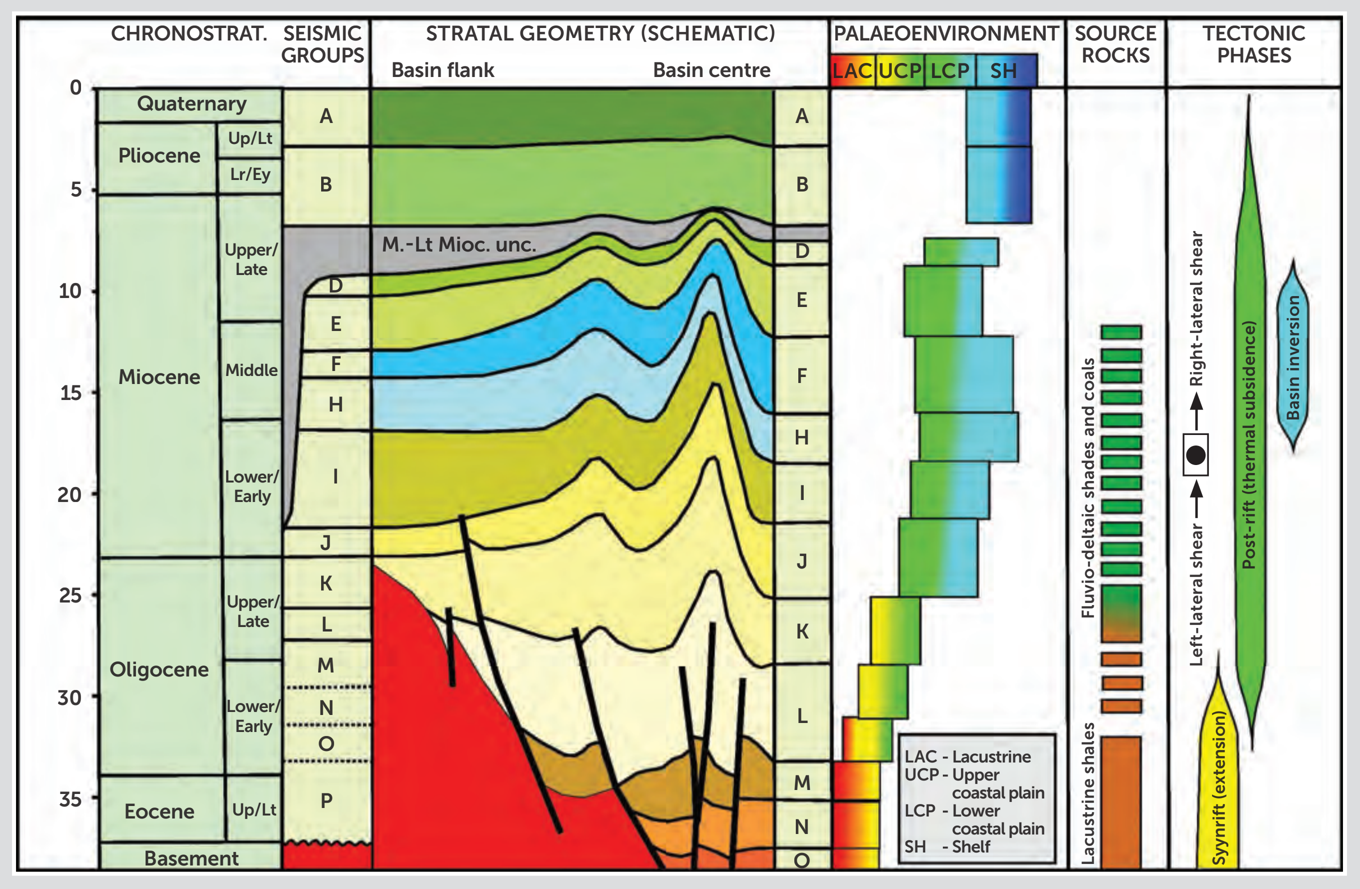


Fig 1.4. Stratigraphic chart summarizing the main characteristics of the different stratigraphic groups of the Malay Basin. Note the gradual transition of the depositional paleoenvironment from non-marine (terrestrial-lacustrine) through coastal plain and eventually developing into a fully open shelf marine setting (modified from Mazlan Madon (2021). The chronostratigraphy has been updated by reference to Morley et al. (2021).

b) *Late Oligocene to middle Miocene, post-rift thermal subsidence phase*: Seismic and biostratigraphic evidence acquired since 1980's indicates that marine influence in the Malay Basin began during late Oligocene times (Mazlan Madon et al., 2006; Mazlan Madon, 2021). Group L successions, that include lacustrine shales, were probably brackish. A good analogue of Group L shales is seen in the West Natuna Basin, in the North Belut Field, where the presence of successive maxima of the brackish water foraminifer *Miliammina fusca* within the time-equivalent Udang Formation suggested that the shales within the Udang Formation formed in a brackish rather than freshwater lake (Morley et al., 2007). This brackish incursion resulted in a dramatic reduction in the occurrence of the freshwater alga *Bosedinia* and is reflected in the palynological record at the zone PR2/PR3 boundary and its lateral equivalent, an event which can be followed across the West Natuna and Malay Basins (Morley et al., 2003; Morley et al., 2021). With respect to Seismic Group K, the laterally extensive 'K shale' signifies the transition from an essentially landlocked lacustrine basin into a more open and marine-connected basin (Mazlan Madon, 2021). However, the water body remained essentially brackish, as evidenced by the continued overwhelming representation of the agglutinated foraminifer *Miliammina fusca* through time equivalent intervals of the Barat Formation in nearby West Natuna wells such as North Belut-5 (Morley et al., 2007), and the Kambing-1, which in addition to abundant *M. fusca* also yielded scattered specimens of the brackish calcareous benthonic *Ammonia* sp. (Morley et al., 2003).

Stratigraphic units of Seismic Groups J, I, H, F, E, and D were deposited in settings close to, or just below sea level (Mazlan Madon et al., 1999). Groups J and I comprise fluvial to tide-dominated estuarine sandstones and associated mudstones. There is a trend to increased salinities within these packages compared to the underlying succession, as evidenced to the greatly increased representation of mangrove pollen of the family Rhizophoraceae at the base of Seismic Group J. This can be seen in the Malong 5G-17.2 well, presented here, and also in nearby wells, such as the well shown in Fig. 4.8 in Morley (2012), located close to the North Belut-5 well. This event could be envisaged as a 'marine' transgression, as opposed to the 'brackish' transgression at the beginning of Seismic Group L discussed above.

Seismic Groups H and F were deposited during a period of sea level rise, coinciding with the Middle Miocene Climate Optimum (MMCO) (Morley et al., 2021) and are characterised by marine and deltaic sedimentary facies, in places dissected by fluvial/estuarine channel sandstones. These two seismic groups are characterised by very short-lived maxima of the NN5 marker nannofossil *Sphenolithus heteromorphus* (Azmi Yakzan et al., 1996; Morley et al., 2021), which are useful for local correlation, and these are thought to reflect sudden phases of higher sea level and global warmth during the MMCO, as recorded by Holbourn et al. (2013) (see below).

Seismic Groups E and D on the other hand display progradational successions of coal-bearing coastal and fluvial/estuarine channel deposits, terminated by localised erosional unconformities. These were deposited following the 13.8 Myr global sea level fall and are well-developed in the Central and Northern Malay Basins (Morley et al., 2021). The coals characteristic of Group E are of interest as they were formed from peats that accumulated in mainly brackish, rather than freshwater settings, and are thought to reflect condensed deposition on coastal plains following the 13.8 Myr global sea level fall (Morley et al., 2021).

c) *Later middle to late Miocene compression and uplift.*The later middle Miocene and late Miocene was a period marked by compressional deformation in the Malay Basin. Local inversion of half-grabens and major uplift in the southern part of the basin has been documented. Interpretation of seismic data shows the presence of a major unconformity (middle-late Miocene regional unconformity) formed as a result of folding and uplift and erosion of sedimentary units as old as Group H. This unconformity has been dated using biostratigraphy to be 7 Myr (Mazlan Madon et al., 2006). It should not be confused with the 'Middle Miocene unconformity' or 'MMU' seen in Sarawak, which is composed of two unconformities, one relating to the 17 Myr South China Sea breakup, and the other to the 13.8 Myr global sea level fall (Morley et al., 2021).

d) *Late Miocene to Quaternary, gentle subsidence.* Open marine conditions were established from the later late Miocene onward, resulting in the deposition of transgressive deposits above the regional unconformity followed by marine deposition. These are Groups B and A, which comprise predominantly marine clays and silts (Mazlan Madon, 1999; Bishop, 2002).

Paleogeography

Paleogeographic reconstruction illustrating the changing configuration of highland, lowland, shallow and deeper seas across the Malay Basin during the last 35 million years has been proposed by Md Nazri Ramli (1988), EPIC (1994) in Mazlan Madon et al. (1999), Shoup et al. (2012) and Shoup (2019). Fig. 1.5 a-f, modified from Shoup et al. (2012), shows paleogeographic reconstructions of the Malay and adjacent basins based on a large regional seismic dataset and integrated with biostratigraphic data from Gulf of Thailand basins, Tho Chu, West Natuna, Nam Con Son and Cuu Long basins as well as the Malay Basin.

The paleogeography of the syn-rift, extensional phase of the basin (late Eocene to 'mid' Oligocene), representing the environmental setting for the Seismic Group M in the Malay Basin (and presumably older formations that have not been penetrated), the Gabus, Belut, Lama and Benua formations in West Natuna, the Tra Tan and Tra Cu formations in the Cuu Long Basin and the Tien Cau and Cau formations in the Nam Con Son Basin is shown in Fig. 1.5a. In all basins, the presence of extensive freshwater lakes is indicated by floods of the freshwater probable dinocysts *Bosedinia* spp., and acritarchs, such as *Granodiscus staplini* and complete absence of foraminifera. These formations are also characterised by extensive fluvial deposition. The content of pollen from these formations indicate that the climate was tropical but distinctly seasonal, and that in all instances the lakes would have borne similarities with the largest freshwater lake seen in Southeast Asia, the Tonle Sap in Cambodia. These freshwater lakes would have been bordered with seasonally inundated freshwater swamp, just as in Tonle Sap today, which are dominated by trees and shrubs such as *Barringtonia acutangula* (producing the pollen *Marginipollis concinnus*) and *Brownlowia paludosa* (producing the pollen *Discoidites novaguineensis*), as discussed in section 1.2.8 below. The tropical seasonal climate was most strongly developed in northern basins, such as the Cuu Long Basin (Morley et al., 2019), and least developed is Sarawak (Morley et al., 2021). This suggests that the palaeoequator and the locus of the intertropical convergence zone, was positioned much further to the south than at present (Morley and Morley, 2018).

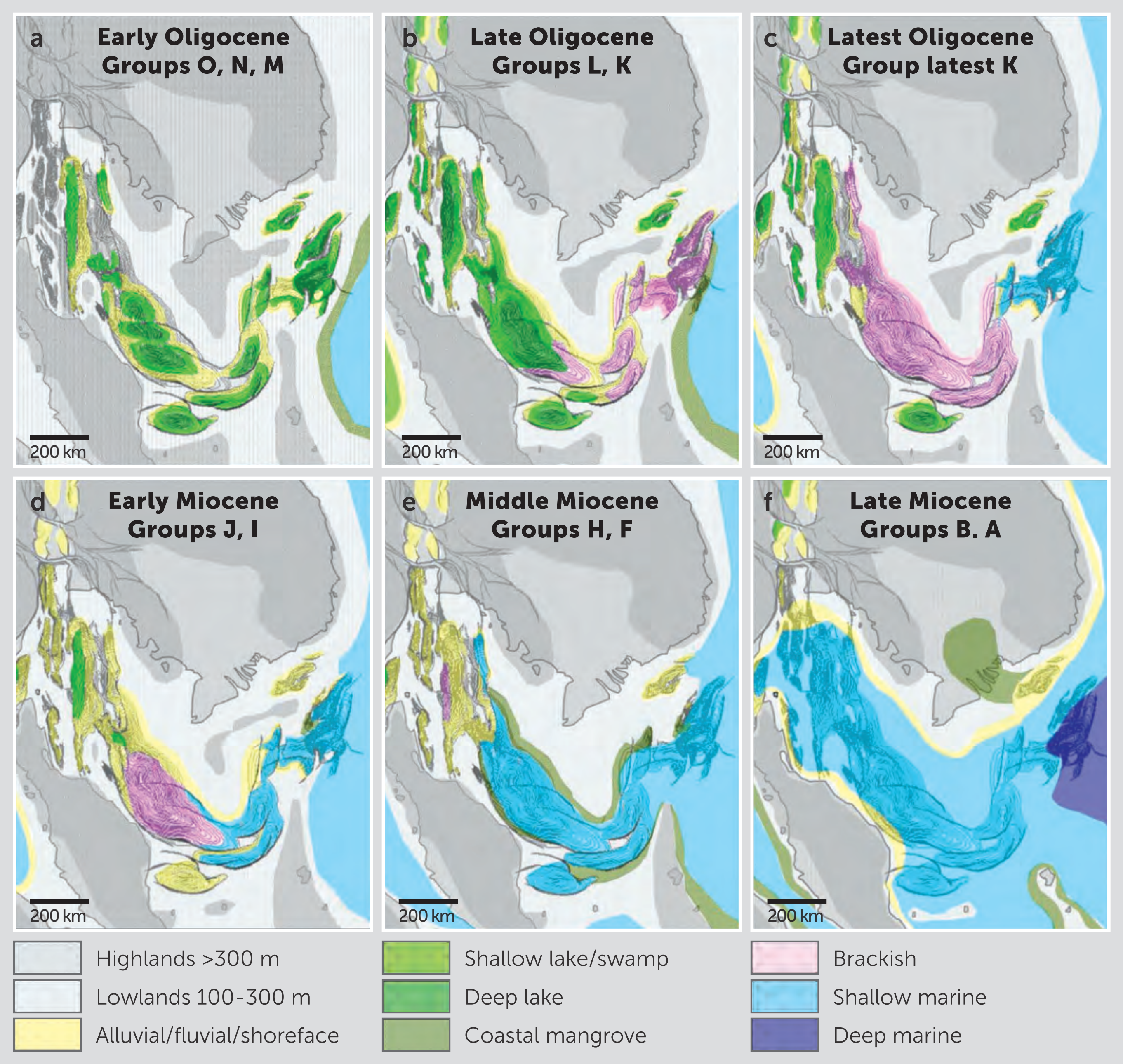


Fig. 1.5. Palaeogeographic setting of the Malay Basin from the Oligocene to Pliocene. a) palaeogeography during the early and mid-Oligocene, with deposition of extensive freshwater lakes and/or swamps with widespread alluvial, fluvial and lacustrine successions alongside rift basin margins; b) during the late Oligocene, repeated Miliammina fusca maxima in the Group L-equivalent successions indicate the presence of brackish water transgressions and it is likely that these reached the southern Malay Basin; c) widespread latest Oligocene flooding, due to the sea level rise of the late Oligocene thermal maximum, resulted in deposition of a thick marine-influenced shale in the Malay Basin (Seismic Group K and Trengganu Shale); d) the early Miocene period is marked by slow intermittent transgression, with fully marine influence reaching the southernmost Malay Basin (Groups J and I) and brackish conditions extending widely across the basin; e) the middle Miocene is marked by widespread open marine conditions in the Malay Basin relating to the MMCO, open marine and deltaic facies of groups H and F were deposited within this setting; during late Miocene to early Pliocene times, after the regressive phase of seismic groups E and D, more open marine conditions prevailed across most of the Malay Basin and Gulf of Thailand, with water depths being similar to present-day, with depths of 50 to 70 meters. Groups B & A stratigraphic units were deposited during this phase (Fig. 1.5f). Modified from Shoup et al. (2012).

The termination of extensional faulting during the late Oligocene resulted in rapid thermal subsidence leading to marine incursion. Sediments of Group L formed within a brackish lake-embayment setting. There are no good biostratigraphic datasets from the Malay Basin to show this incursion, but it is clearly reflected in the nearby North Belut-5 well, in the West Natuna Basin. The Udang Formation, equivalent to Seismic Group L, studied by Morley et al. (2007) is characterised by maxima of *Miliammina fusca* as noted above, reflecting the successive expansion of brackish water lakes. The North Belut study involved the detailed evaluation of a 200m core for palynology and foraminifera, and clearly demonstrated an inverse correlation between the abundance of *Miliammina fusca* and the probable dinocyst genus *Bosedinia*. This suggests that *Bosedinia* is entirely confined to freshwater settings, contrary to statements in many unpublished petroleum industry reports from the region. The overall reduction in abundance of *Bosedinia* spp. at the beginning of palynological zone PR2 of Azmi Yakzan et al. (1996), coinciding with the increased representation of pollen of the Rhizophoraceae (*Zonocostites ramonae*) is most easily explained by a change from an entirely freshwater lake during Seismic Group M to a brackish lake during Group L. Environments for Seismic Group L and equivalent sediments are shown in Fig. 1.5b. A similar setting continued into Seismic Group K, although there are suggestions that the extent of the brackish incursion increases during the latter part of Group K deposition (Fig. 1.5c).

Fully marine transgression within the Malay Basin became established within seismic Group J and lower Group I. In the wells that clearly show this event, foraminiferal taxa not seen in older seismic groups include small rotaliids such as *Ammonia* spp., the miliolid *Quinqueloculina*, shelf taxa such as *Heterolepa* and the agglutinated taxa *Eggerella* and *Textularia*, all suggesting deposition under near normal salinities. Group J and lower Group I are also characterised by the increased representation of mangrove pollen compared to the Oligocene. The mangroves include common *Zonocostites ramonae*, derived mainly from the stilt-rooted *Rhizophora*, and also common *Florschuetzia trilobata*, derived from an extinct Sonneratioid mangrove, the abundance maximum of this taxon reflecting palynological zone PR9A (see below). The increased representation of marine foraminifera and mangrove pollen reflects the marine transgression alluded to above. Similar assemblages are seen across West Natuna and the Nam Con Son Basin (Fig. 1.5d), but in the Cuu Long Basin, the base Miocene marine transgression is reflected just in the presence of regular *Ammonia* spp., often termed the '*Rotalia*' event (Morley et al., 2019). The beginning of the Miocene is also characterised by a change of climate, from distinctly seasonal within the Oligocene, to a more perhumid climate in the early Miocene, reflected by a distinct increase in several taxa widely distributed in rain forests, but particularly common in peat swamps, such as pollen of *Calophyllum,* Sapotaceae and *Cephalomappa*.

During the later part of Group I, the representation of foraminifera is generally reduced, with taxa more indicative of brackish conditions becoming prominent rather than the more open marine elements mentioned above. These include small rotaliids, and agglutinated foraminifera. This would be consistent with sedimentological data that suggests the widespread deposition of fluvial to tide-dominated estuarine sandstones and associated mudstones.

During the MMCO, marine transgression occurred across the whole of Malay Basin. and resulted in distinctly marine-influenced deposition, often with deltaic facies, forming Seismic Groups H and F (Fig. 1.5e). Within this succession, benthonic foraminifera such as *Ammonia umbonata* and *Asterorotalia* are often common, together with diverse *Quinqueloculina*, open shelf benthonics, especially *Cibicides, Heterolepa, Lagenia* and *Nonion*, and the agglutinated *Textularia* and *Eggerella*. Also, scattered larger foraminifera, including *Operculina* and *Amphistegina* are often regularly present. The marine incursions at times of sea level high are recorded widely across the broad region and form the flooding surfaces of the SEA depositional cycles of Morley et al. (2021), often indicated by nannofossil floods with *Sphenolithus heteromorphus*, and planktonic foraminifera such as *Cassigerinella chipolensis*. The zone N8-restricted planktonic foraminifer *Globorotalia binageae* was recorded in the northern part of the Gulf of Thailand during one of these floods (Restrepo-Pace et al., 2015), reflecting the very wide extent of this flood during sequence SEA52 of Morley et al. (2021). The amplitude of successive sea level changes during the MMCO is often considerable (Holbourn et al., 2013), with the result that within a single depositional cycle, lacustrine deposition may occur during phases of low sea level, but with short-lived acmes of calcareous nannofossils, especially of *Sphenolithus heteromorphus*, during times of sea level maxima, as seen in the North Malay Basin in Bergading Deep-3 within Sequence SEA 53 (Morley et al., 2021). During the time of deposition of Seismic Groups H and F, the climate became successively more perhumid, with the result that pollen of peat swamp taxa become a major component of pollen assemblages (see Bergading Deep-3, Morley et al., 2021).

Seismic Groups E and D were deposited following the 13.8 Myr sea level fall, which one might expect to have been associated with a major period of non-deposition or erosion, as is the case across Sarawak (Morley et al., 2021). This succession is well represented in the Central and North Malay Basin. Seismic Group E is characterised by repeated, thick coals, that show up as strong reflectors on seismic. Palynological analysis of the coals indicates deposition in a brackish, rather than freshwater setting, and cyclical patterns shown by their pollen content, suggests repeated marine transgressions, and the likelihood that the coals are very condensed (Shamsudin Jirin et al., 2011; Morley et al., 2021). A major part of the time represented immediately after the 13.8 Myr sea level fall is thought to have been characterised by the slow accumulation of brackish peats in a sediment-starved setting (Morley et al., 2021). For Seismic Group D, most sedimentation across the Malay Basin was within a coastal plain or shallow marine depositional setting.

Following the phase of compression and uplift resulting in the middle to late Miocene unconformity, gentle subsidence, coupled with reduced sediment input resulted in open marine deposition across the Malay Basin, and the whole of the Sunda Shelf (Fig. 1.5f) resulting in the deposition of shallow marine shelf deposits of Seismic Groups B and A. Foraminiferal assemblages within this succession are often characterised by moderate numbers of planktonics, and open shelf foraminifera, such as *Anomalina, Cibicides, Eponides* and *Heterolepa* with deeper water taxa such as *Bolivina, Bulimina* and *Uvigerina*, indicative of poorly oxygenated muddy substrates below storm wave base.

1.4 METHODOLOGY

The palynological analysis of Malong 5G-17.2 was done using mostly sidewall and conventional cores. Samples from Delah 5H-14.1 consisted mostly of ditch cuttings. The samples selected are shown in Fig. 1.6.

All analyses were undertaken quantitatively. The quantitative method has long been used in Quaternary palynology, and many of the basic principles used today were established as far back as 1916 when von Post (1916) initiated the method of pollen analysis of Quaternary bogs in Sweden. Morley (1991) laid out the concept of quantitative analysis for the Malaysian region and described how it can be applied to the Cenozoic sediments in Southeast Asia. Palynological zonations have been developed based on the quantitative method, for Malaysian Borneo by Shell (Ho, 1978; Chow, 1996), Elf-Aquitaine (Poumot, 1989), but without publishing the zone definitions. Detailed zonation schemes are available for the West Natuna Basin (Morley et al., 2003) and for the Malay Basin by Azmi Yakzan et al. (1996), who developed the 'PR' zonation which is applied here.

Approximately 20 to 30 g of each sample was taken for processing. The amount taken depended on sample lithology, with sandy samples requiring greater amounts than shaley samples. After crushing, the samples were soaked in concentrated hydrochloric acid for 12 hours or overnight to remove carbonates. Following this the samples were treated with 40% hydrofluoric acid to digest siliceous minerals and then washed with hot 10% hydrochloric acid to remove silica gels formed during the reaction with hydrofluoric acid. After centrifuging off the hydrochloric acid, the remaining mineral components and heavy particles were separated in a zinc bromide solution of a specific gravity 2.2. The organically enriched residues were then oxidised in cold 50% nitric acid before treating with one percent of potassium hydroxide solution to dissolve humic acids. Finally, a small amount of one or two drops of the organic residue was mounted onto slides using canada balsam. The size of coverslip used was 40 x 22 mm. The remaining residues are stored with a drop of phenol as an anti-bacterial agent, in small, labelled phials.

All slides examined in this study are lodged in the Centre for Palynological Studies, University of Sheffield, United Kingdom for future reference. The slides were labelled according to the well name, sample depth and type, and slide number. Sidewall cores, conventional cores and ditch cuttings are abbreviated as SWC, CC and DC respectively.

For this study, mainly core and sidewall core samples were used to ensure that all the palynomorphs described and illustrated are in situ and have not been subjected to contamination due caving. For that reason, the sample spacing is less than would be ideal.

For selecting samples from well sections where drill cuttings may be the only source of samples, sampling should be systematically spaced. Also, the sample spacing should be designed to ensure that all the stratigraphic intervals present are sufficiently sampled. For many years samples for palynology from petroleum exploration wells from Malaysia were sampled at 20 m intervals, but work undertaken during the last 20 years shows that to adequately sample in order to show depositional cycles during a sequence biostratigraphic study, 10 m sampling is the preferred spacing. A good example is the Bergading Deep-3 well from the North Malay Basin presented in Morley et al. (2021). For many years well sections in this area were sampled for palynology at 20 m or 30 m intervals, and studies were generally unsuccessful in establishing the stratigraphic succession. With Bergading Deep-3 and subsequent wells in this area, sampling at 10 m spacing beautifully revealed the details of multiple high frequency transgressive-regressive cycles, and the stratigraphic succession in this area became clear for the first time.

For field sections, geologists often collect a single sample for biostratigraphic evaluation, but this is mostly inadequate. Palynology works well when a succession of closely spaced samples is analysed through each lithological package within a sedimentary succession, and the significance of changes in assemblage through the sample succession is evaluated, as well as the presence of age-restricted palynomorphs.

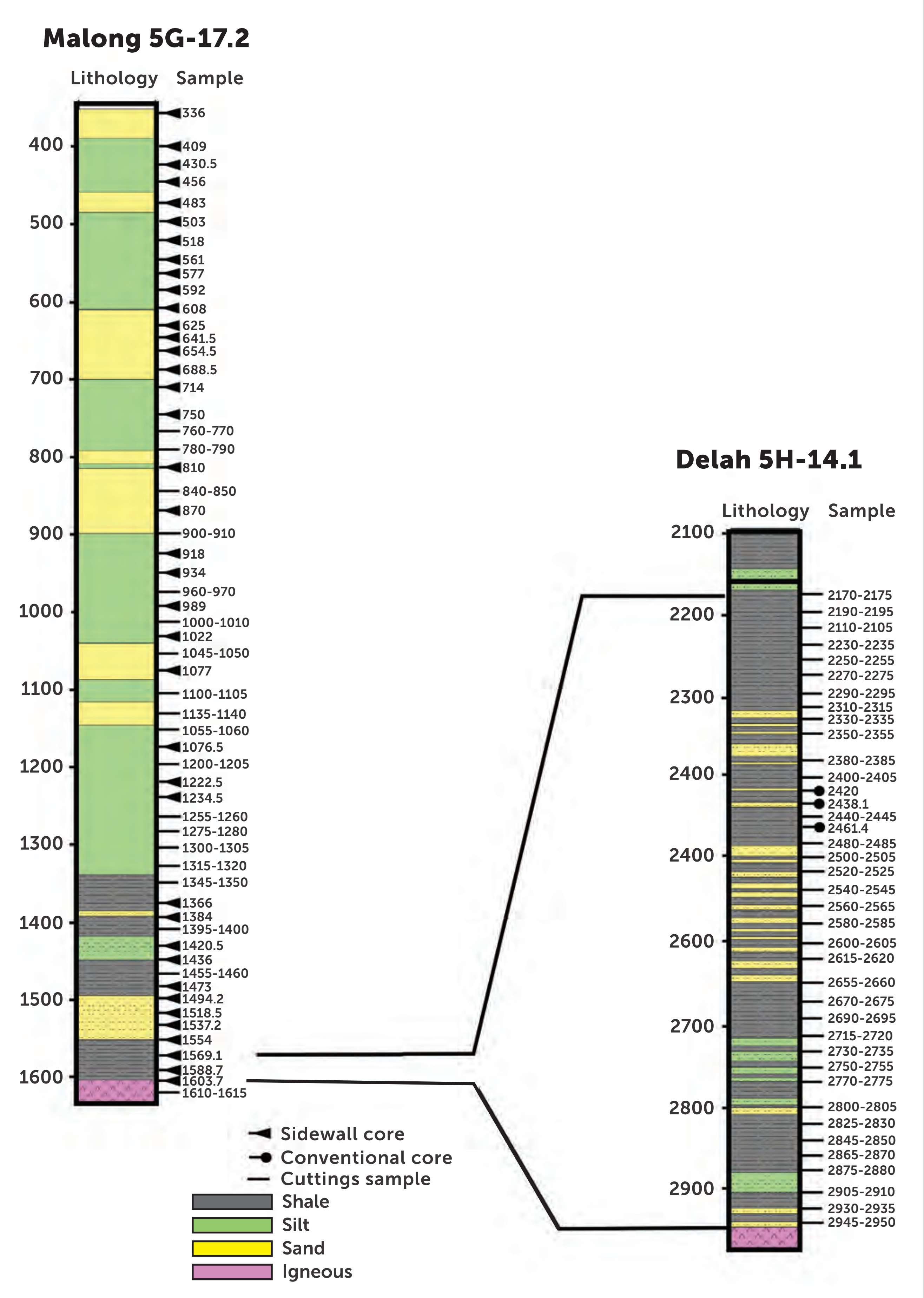


Fig. 1.6. Columns representing the sampled intervals of wells Malong 5G-17.2 and Delah 5H-14.1. The numbers along the columns represent the depths/position in meters of the samples analysed and documented in this volume.

1.5 SAMPLE LOGGING

To obtain a statistically viable count of palynomorphs, 200 specimens of pollen and spores were counted in each sample. Other palynomorph groups such as dinocysts, algae and fungal spores were also counted until the end of pollen and spore counts in each sample but were excluded from the 200 pollen/ spore count.

The aim in palynomorph counting is to obtain at least 100 specimens of freshwater sporomorphs in each sample for it to be feasible for detecting regional climate signals that may be useful for regional correlation. For samples which were relatively poor in palynomorph content, a maximum of three slides was examined. Six samples yield less than 50 pollen and spore specimens and three contain more than 50 but less than 100. These samples are considered valid for quantitative determination of floral assemblages since they contain mostly freshwater sporomorphs and were not over-represented by local facies-related taxa. The remaining samples each contain at least 100 freshwater taxa. In the middle Miocene and younger section which was very rich in palynomorphs, additional taxa were also recorded beyond the basic pollen count.

All samples were examined using an Olympus BH-2 transmitted light microscope. Slides were systematically logged using a X20 objective by traversing from left to right. To avoid overlapping, an England Finder was used to locate the traverses made during slide logging. Prior to the examination, slides were rapidly scanned to give an idea of their richness in palynomorph content. In rich slides, the traverses were evenly spread across to get an equal representation of palynomorphs and to avoid bias resulting from the uneven distribution of palynomorphs on the slides.

Except for plant cuticles, all palynomorphs encountered during the slide logging were identified. These include pollen, spores, dinocysts, fungal palynomorphs, colonial algae and acritarchs. Identifications of most species were made using a X100 objective and oil immersion. The location on the slide of representative specimens of each palynomorph type were recorded using an England Finder which was positioned so that its reading was upright, and the label of the slide examined was on the left hand side of the examiner. At the same time, the size of the specimen was also measured. The abundance of all species identified in the samples was recorded in a counting sheet designed for this study.

All species identified were photographed using Kodak Gold II-200 ASA film. These photographs have been used to illustrate the palynomorphs identified in this study and are presented as Plates, which form the main part of this Atlas.

1.6 DATA PRESENTATION

The data was evaluated by means of percentage plots using a ‘main’ pollen sum of ‘total hinterland pollen’. The choice of correct pollen sums is a very important stage in planning the study. It helps to separate ‘local’ and ‘regional’ palynomorph signals by reducing the effects of local swamping and permits the differentiation of local and regional vegetation change. Regional signals from hinterland pollen are more likely to reflect changes of climate, that can be used for regional correlation, whereas the local changes are useful for environment interpretation. The main palynomorph groupings are as follows:

Guidelines for 'pollen sum' calculation

- Mangrove and backmangrove sporomorphs are plotted outside the main sum.
- Other pollen groups (coastal, rain forest, peat swamp, freshwater swamp, kerapah, riparian, seasonal and montane) are included in the main pollen sum, whereas spores are plotted ‘outside’ main sum.
- Other palynomorph groups (freshwater dinocysts and acritarchs, other freshwater algae, marine dinocysts) are also presented outside the main sum.

1.7 SUMMARY OF RESULTS

Results are summarised in two analysis charts (Malong 5G-17.2, Fig. 1.7 and Delah 5H-14.1, Fig. 1.8). These charts present summary results for the ecological groupings, details of *Florschuetzia* spp., and other critical taxa used to zone the section, and the PR zone interpretation against the gamma log.

The palynological groupings are listed as follows:

1.7.1 Pollen Groupings

Tropical vegetation is very diverse, and many taxa have adapted to many different habitats, often within the same genus, and since most pollen variation is at the genus level, many of the taxa listed here may have been derived from several different vegetation types. Here taxa are listed as to the most likely source of pollen in sediments based on their ecology in Malaysia. For example, the genus *Calophyllum* has representatives in most non-brackish habitats, but it is very abundant in peat swamps, and so is included in the 'peat swamp' group. However, if it occurs without other peat swamp taxa, it may be from a different source. Details of the ecology of the parent plants for each taxon is given in the systematic part of this Atlas.

The groupings for each taxon which can be referred to a nearest living relative (NLR) is indicated here:

Rhizophoraceae group: *Rhoipites apiensis, Zonocostites ramonae, Florschuetzia meridionalis;*
Backmangrove: *Discoidites novaguineensis, D. pilosus, D. angulosus, Echistephanoporites campylostemonoides, E. malaysianus, Florschuetzia levipoli, F. trilobata* + vars., *F. ovalis, F. ovata, F. retiovalis, F. retiovata, F. semilobata, Racemonocolpites hians;*
Nypa: *Spinizonocolpites echinatus, Proxapertites minutus*
Coastal: *Marginipollis concinnus, Psilaheterocolpites psilatus, Podocarpidites minuticorpus, Echiperiporites estelae, Striatopollis catatumbus, Trivestibulopollenites betuloides, Manggispollenites retitriporata, Psilaheterocolpites laevigatus, P. combretoides;*
Rain forest: *Merantipollis gracilis, M. cuneatus, M. quadricolpatus, Incrotonipollis reticulatus, Retipollenites confusus, Cheilanthoidspora enigmata, Verrutriporites vermiculatus, Cricotriporites microreticulatus, Guettardidites ivirensis, Praedapollis* spp., *Thymelipollis* sp., *Proteacidites* cf. *tenuiexinus, Propylipollis subscabratus, Cupuliferoipollenites* sp. A., *Claritricolporites annulatus, Psilastephanocolporites validus, Iugopollis interruptus, Retitetrabrevicolporites elongatus, Cupanieidites* spp., *Gothanipollis gothani, Tricolpites simatus, Triporotetradites microreticulatus, Inaperturotetradites reticulatus;*
Kerapah swamp: *Casuarinidites cainozoicus, Dacrydiumites florinii, Graminidites rotandinii, Nepenthidites neogenicus;*
Peat swamp: *Lanagiopollis emarginatus, L. diminutus, Tricolpites malongii, T. terengganuensis, Malvacipollis austrobuxoides, Cryptopolyporites cryptus, Minutitricolporites duplibaculatus, M. microechinatus, Pelahpollis variabilis, Retistephanocolpites williamsi, Anacolosidites luteoides, Manggispollenites psilatriporata, Verrutricolporites oblatus, Rugutricolporites undulatus, Lakiapollis ovatus, L. pachydermus, Triporopollenites stemonuroides, Striacolporites anacardiensis, Rhoipites transversalis, Euphorbiacites virgatus, Meyeripollis naharkotensis, Ornatetradites droseroides, Triporotetradites campylostemonoides;*
Freshwater swamp: *Dicolpopollis kalewensis, D. reticulatus, D. verrucatus, Arengapollenites diminutus, Tricolporopollenites endobalteus, Persicarioipollis meuseli, Polygalacidites clarus, P. speciosus, Ctenolophonidites costatus. Ranunculacidites operculatus;*
Riparian: *Arengapollenites gracilis, Canthiumidites reticulatus, Striatopollis catatumbus, Retibrevitricolpites* sp. 1, *Psilodiporites jejawii, Pandanpollenites malaysianus, Myrtaceidites* spp., *Paravuripollis mulleri, Brevicolporites guinetii, Ilexpollenites clifdenensis, Ilexpollenites anguloclavatus, Drasipollenites cryptus, Marginipollis quilonensis, Myrtaceidites* spp;
Seasonal: *Polyadopollenites* spp., *Graminidites annulatus, Malvacipollis subtilis, Minutitriaperturites minutus, Tubifloridites spinosus, Tricollareporites echinatus, Pinuspollenites* spp., *Ephedripites* spp., *Gemmamonocolpites borassoides, Celtispollenites minutipori, C. rotundatus, Chenopodipollis chenopodiaceoides, Proteacidites franktonensis, Lanagiopollis tenuiexinus;*
Montane gymnosperms: *Abiespollenites* spp., *Piceapollis* spp., *Podocarpidites* cf. *ellipticus, Zonalapollenites igniculus, Z. spinulosus;*
Montane angiosperms: *Cupuliferoidaepollenites* cf. *liblarensis, C. oviformis. Quercoidites* spp., *Alnipollenites verus, Fenestrites longispinosus, Intratriporopollenites instructus;*
Pteridophyte spore groupings
Taxa with clear nearest living relatives
Acrostichum: *Leiotriletes adriennis*
Climbing: *Crassoretitriletes vanraadshooveni, Foveotriletes lacunosus, Verrucatosporites usmensis, Stenochlaenidites papuanus, S. cristatus;*
Terrestrial dry (terra firma): *Camarazonosporites minor, C. heskermensis, Cingulatisporites psilatus, Peridacidites variabilis, Polypodiisporites megabalticus, Verrucatosporites pseudoregulatius, Matonisporites mulleri, Foveogleicheniidites marginatus, Cicatricosisporites chattensis, C. dorogensis;*
Terrestrial wet (swamp): *Magnastriatites grandiosus, Echinatisporis minor, E. lepidus, E. undulosus, Gemmatosporis gemmatoides, Scolocyamus magnus, Echinosporis conspicuus, E. obscurus, Clavatisporites fungi;*

Pteridophyte taxa without a clear nearest living relative
Monolete psilate: *Laevigatosporites discordatus, L. haardti, L. elongatus;*
Monolete ornamented: *Microfoveolatosporites* spp., *Punctatosporites* spp., *Verrucatosporites favus, Undulatosporites bracteatus, Gemmatosporis microgemmatus;*
Trilete psilate: *Deltoidospora* spp., *Cyathidites minor, Matonisporites* spp;
Trilete ornamented: *Converrucosisporites sundaicus.*

1.8 PALYNOLOGY OF MALONG 5G-17.2 WELL

A summary of the Malong 5G-17.2 results is shown in Fig. 1.7. Palynological zones within Malong 5G-17.2 well are defined as follows:

Zone PR6/7 (late Oligocene) is defined based on an abundance maximum of *Merantipollis gracilis*.

Zone PR8 (early Miocene) is based on the presence of common *Florschuetzia trilobata* s.l., and the absence of *F. levipoli.*

Zone PR9A (early Miocene) is characterised by abundant *Florschuetzia trilobata* s.l. together with the presence of *F. levipoli.*

Zone PR9B(Lower) (early Miocene) contains the much-reduced representation of *Florschuetzia trilobata* s.l. The presence of *F. levipoli*, and common *Casuarinidites cainozoicus*. The zone contains extremely rare *F. meridionalis*.

Zone PR9B(Upper) (early Miocene) is characterised by the very low representation of *Casuarinidites cainozoicus*, and a corresponding increase in abundance of *Myrtaceidites* spp. It yielded extremely rare specimens of *Florschuetzia meridionalis*, and consistent numbers of *F. trilobata* s.l. and F. *levipoli.*

Zone PR10 (early -middle Miocene) is defined on the presence of the consistent and regular occurrence of *Florschuetzia meridionalis*, and highest stratigraphic occurrence of *F. semilobata*.

Zone PR11 (middle Miocene) is characterised by the highest continuous stratigraphic occurrence of *Florschuetzia trilobata* s.l. with regular *F. levipoli* and *F. meridionalis*.

Zone PR12A (middle Miocene) lacks *Florschuetzia trilobata*, and contains the highest consistent occurrence of *Pinuspollenites* spp.

Zone PR12B (middle Miocene) contains consistent *Echistephanoporites campylostemonoides* and *E. malaysianus*.

Zone PR13 (middle to late Miocene) the base of the zone is characterised by the first consistent presence of *Camarozonosporites minor* and *C. heskermensis*.

Zone PR14 (late Miocene) is distinguished by the consistent presence of *Stenochlaenidites papuanus*.

Zone PR15 (Pliocene) is characterised by the consistent occurrence of *Stenochlaenidites cristatus*.

The main palynomorph assemblage changes within the Malong 5G-17.2 succession

There are some clear assemblage changes through the well section that reflect major changes in the landscape and palaeoclimate evolution of the South Malay Basin region. Within zones PR6/7 mangroves are of low representation, and the abundance of *Merantipollis gracilis* (derived from *Shorea* or *Hopea*) suggests a distinctly seasonal climate as currently occurs in Indochina in areas with semi-evergreen or deciduous forest. At the beginning of the early Miocene, in zone PR8, mangrove swamps become widespread, at the time of the basal Miocene marine transgression, and the climate became much wetter, but was not perhumid, as a result of which swamps were dominated by *Pandanus (Pandanpollenites malaysianus), Oncosperma (Racemonocolpites hians)* and *Brownlowia (Discoidites borneensis)* rather than peat swamp elements. Within zone PR9A and PR9B (Lower), peat swamp elements increase in representation, indicated by increased *Calophyllum (Rhoipites transversalis)* and *Cephalomappa (Pelahpollis variabilis)*, suggesting a change to a perhumid climate and *Casuarinaceae (Casuarinidites cainozoicus)* are common, probably representing the widespread occurrence of kerangas vegetation and kerapah peats. Within zone PR9B(Upper), the kerangas elements become reduced and peat swamp and riparian elements increase, probably reflecting a change in regional soil conditions.

Zone PR10 is characterised by a major increase in mangroves, probably reflecting rising global sea levels associated with the Middle Miocene Climate Optimum, and such high sea levels continue through zones PR11 and PR12A. During this period, rattans (*Dicolpopollis kalewensis*) show a general and long-term reduction in representation, and this is thought to reflect a reduction in seasonality of climate regionally.

There is a major reduction of mangrove pollen within zone PR12B following the end of the Middle Miocene Climate Optimum, and a distinct increase in the presence of peat swamp elements, suggesting a wetter climate. However, within zones PR14 and PR15, grasses (*Graminidites annulatus*) increase in representation, probably reflecting increased late Miocene climate seasonality associated with the strengthening of the South Asian monsoon.

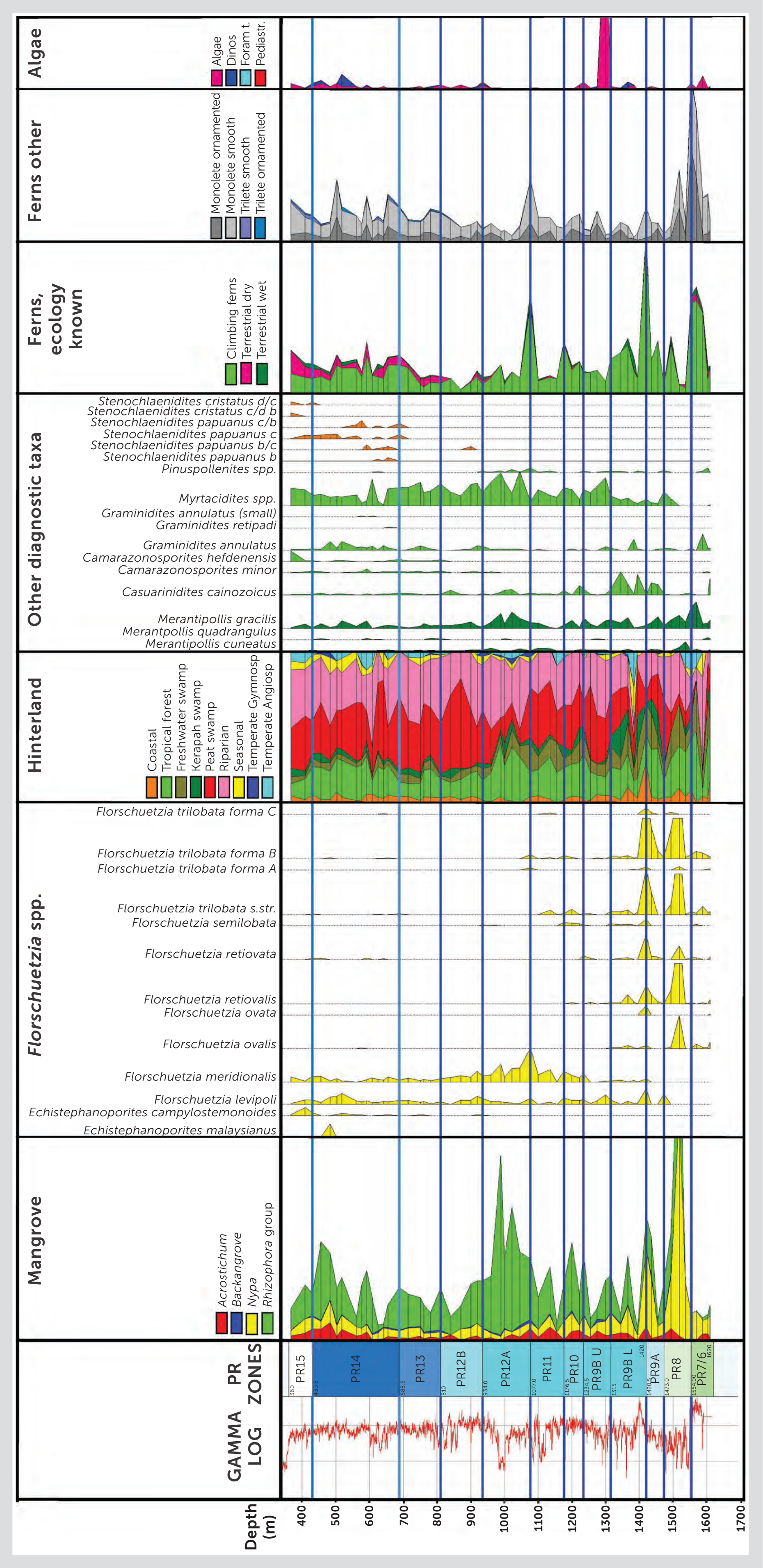


Fig. 1.7. Biostratigraphic summary chart for Well Malong 5G-17.2 using palynological groupings presented in Section 1.7. Spectra for Florschuetzia spp. and other diagnostic taxa are shown individually. The pollen sum used is 'total hinterland pollen'. The definitions of the 'PR' palynological zones, indicated to the right of the Gamma Ray log, are explained in the accompanying text.

1.9 PALYNOLOGY OF DELAH 5H-14.1 WELL

A summary of the Delah 5H-14.1 results is shown in Fig. 1.8. Palynological zones within the Delah 5H-14.12 well are defined as follows:

Zone PR1 (early to late Oligocene) is defined based on the common occurrence of the freshwater dinocysts *Bosedinia infragranulata* with regular *Granodiscus staplinii*, but in reduced values compared to the overlying zone.

Zone PR2 (late Oligocene) is characterised by very abundant *Bosedinia infragranulata* with regular *Granodiscus staplinii*, comprising up to 90% of the palynomorphs present.

Zone PR3 (late Oligocene) contains an abundance maximum of *Magnastriatites grandiosus*, the regular presence of *Zonocostites ramonae*, and a major reduction in abundance of *Bosedinia* spp. and *Granodiscus staplinii*.

Zone PR4 (late Oligocene) is characterised by increased *Bosedinia* spp. but without *Granodiscus staplinii*, and a major increase in abundance of *Graminidites annulatus*.

Zone PR5 (late Oligocene) continues to include common *Graminidites annulatus*, but *Bosedinia* spp. are essentially missing. There is a slight increase in abundance of *Magnastriatites grandiosus*, and marine dinocysts are represented in increased numbers.

Zones PR6/7 (late Oligocene) is distinguished by the common occurrence of *Merantipollis gracilis*.

The main palynomorph assemblage changes within the Delah 5H-14.1 succession

During zone PR1, the Delah 5H-14.1 location was characterised by extensive freshwater lakes, containing large numbers of freshwater algae. The presence of common *Pinus* pollen (*Pinuspollenites* spp.) and grasses (*Graminidites annulatus*) indicates a distinctly seasonal climate, and the presence of common *Barringtonia* (*Marginipollis concinnus*) reflects the development of extensive seasonal swamps around the lake, in the manner of the Tonle Sap in Cambodia. The system of freshwater lakes expanded dramatically within zone PR2, but the climate remained distinctly seasonal, and seasonal swamps with *Barringtonia* continued to surround the lakes.

During zone PR3, the representation of freshwater swamps reduced dramatically, but the climate remained distinctly seasonal and seasonal swamps with *Barringtonia* continued to be widespread. The presence through this zone of regular *Rhizophora* pollen (*Zonocostites ramonae*) suggests that a distinct brackish influence was present. Zone PR4, on the other hand saw an increase in representation of freshwater lakes, based on a maximum of *Bosedinia* spp., but seasonal swamps are much reduced. The climate was probably more strongly seasonal based on a strong abundance maximum of grass pollen.

Evidence for lacustrine conditions is much reduced within zone PR5, and the local environment was probably characterised by a seasonal swamp with *Oncosperma (Racemonocolpites hians)*, *Brownlowia (Discoidites novaguineensis)* and *Pandanus (Pandanpollenites malaysianus)*. The climate remained distinctly seasonal, indicated by the presence of abundant grass pollen. Within zone PR5, these conditions continued, but the regional vegetation was probably characterised by deciduous Dipterocarp forest, indicated by a maximum of *Shorea* type pollen *(Merantipollis gracilis)*.

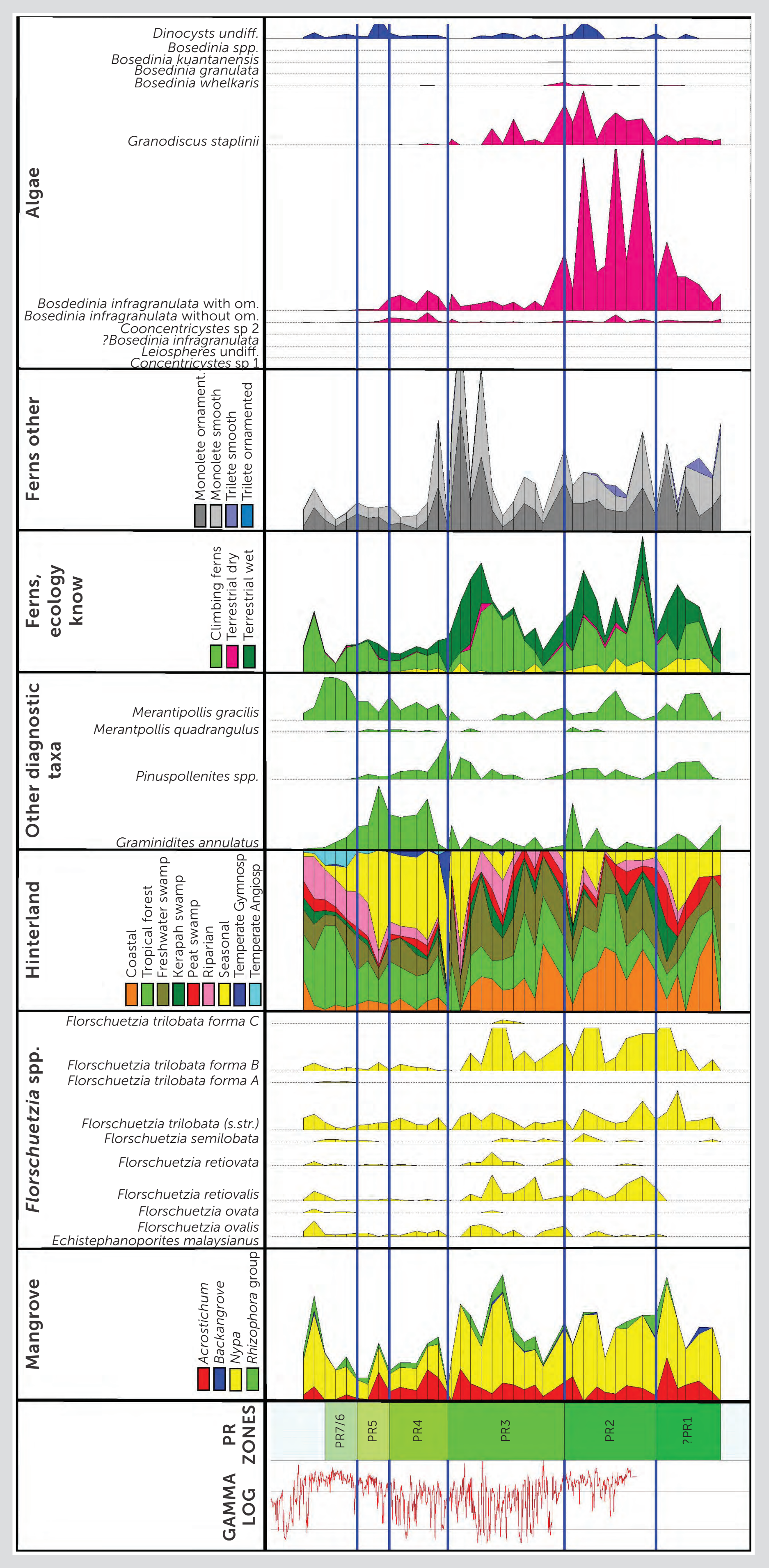


Fig. 1.8. Biostratigraphic summary chart for Well Delah 5H-14.1 using palynological groupings presented in Section 1.7. Spectra for Florschuetzia spp. and other diagnostic taxa are shown individually. The pollen sum used is 'total hinterland pollen'. The definitions of the 'PR' palynological zones, indicated to the right of the Gamma Ray log, are explained in the accompanying text.

1.10 DEFINITION OF MALAY BASIN PALYNOLOGICAL ZONES

The 'PR' zonation scheme is used which was originally proposed by Azmi Yakzan et al. (1996). The scheme is essentially the same, but several zonal definitions are updated, and some zones further subdivided (Fig. 1.9). This zonal scheme has now been successfully applied in the Cuu Long and Song Hong Basins in Vietnam (Morley et al., 2019; Chung et al., 2021), and across Sarawak (Morley et al., 2021). In this evaluation, a number of zones have been updated, especially zone PR9, which is divided into three subzones. The age of palynological zone boundaries follows Morley et al. (2021), where zonal boundaries have been calibrated against nannofossil and planktonic foraminiferal zones by reference to datasets from northern Luconia, where each of the diagnostic palynomorphs occur together with age-restricted nannofossils and planktonics.

It is important to bear in mind that to make a zonal 'attribution', a succession of at least 5 continuous samples is needed from the same lithological succession. Obtaining a single rock sample from a field section and expecting a 'date' will not result in a reliable zonal attribution.

Zone PR1

Definition: The zone is characterised by common freshwater algae with *Bosedinia infragranulata* dominant, but also common *Granodiscus staplinii* and rare *Bosedinia whelkaris*. The overall abundance of algal palynomorphs is less than for zone PR2.

Additional characters: Among shoreline elements *Marginipollis concinnus*, *Florschuetzia trilobata* vars. and *F. semilobata* are prominent, and *Gemmatosporis* spp. are present in low numbers. *Pinuspollenites* spp. and *Graminidites annulatus* occur regularly and are derived from *terra firma* vegetation.
Comparison: Equivalent to zone PIVC of Morley et al. (2003), for the West Natuna Basin, and approximately with CLO7 for Cuu Long Basin (Morley et al., 2019).

Zone PR2

Definition: This zone is characterised by an abundance maximum of *Bosedinia infragranulata* and *Granodiscus staplinii*. *Bosedinia whelkaris* is also present.

Additional characters: The additional characters of this zone are similar to zone PR1, with the shoreline elements *Marginipollis concinnus, Florschuetzia trilobata* vars, and *F. semilobata* being prominent. In addition to *Florschuetzia trilobata* vars,, *Florschuetzia ovalis, F. ovata* and *F. retiovata* are present in this zone. Among other taxa, *Gemmatosporis* spp. is present in low numbers. *Pinuspollenites* spp. and *Graminidites annulatus* occur regularly and are derived from *terra firma* vegetation.
Comparison: Equivalent to zone PIVD of Morley et al. (2003), for the West Natuna Basin, and with CLO8 for Cuu Long Basin (Morley et al., 2019).

Zone PR3

Definition: Characterised by an abundance maximum of *Magnastriatites grandiosus*, the low representation of *Bosedinia infragranulata* with the highest consistent occurrence of *Granodiscus staplinii*.

Additional characters: The additional characters of this zone are broadly similar to zone PR2, with the shoreline elements *Marginipollis concinnus* and *Florschuetzia trilobata* vars and *F. ovalis* being prominent, but also with regular *Zonocostites ramonae*. *Gemmatosporis* spp. are present in low numbers. *Graminidites annulatus* occurs regularly whereas *Pinuspollenites* spp. are of reduced occurrence. This zone shows a further increase in diversity of *Florschuetzia* spp., with the incoming of *F. retiovata* and *F. retiovalis*.
Comparison: Equivalent to zone PVA of Morley et al. (2003) for the West Natuna Basin, and approximately with CLO9A for the Cuu Long Basin (Morley et al., 2019).

Zone PR4

Definition: Zone PR4 is characterised by a second abundance maximum of *Bosedinia infragranulata*, but without *Granodiscus staplinii*, coinciding with a strong abundance maximum of *Graminidites annulatus*.

Additional characters: This zone has much reduced *Marginipollis concinnus* compared to the zones below. The diversity of *Florschuetzia* spp. is similar to zone PR3 but their abundance is much less. The fern spores *Converrucosisporites sundaicus*, *Echinosporis obscurus* and *Gemmatosporis* spp. show their highest consistent occurrence in this zone, and *Pinuspollenites* spp. shows increased abundance compared to the underlying zone.
Comparison: Equivalent to zone PVB of Morley et al. (2003), for the West Natuna Basin, and approximately with part of CLO9B for Cuu Long Basin (Morley et al., 2019).

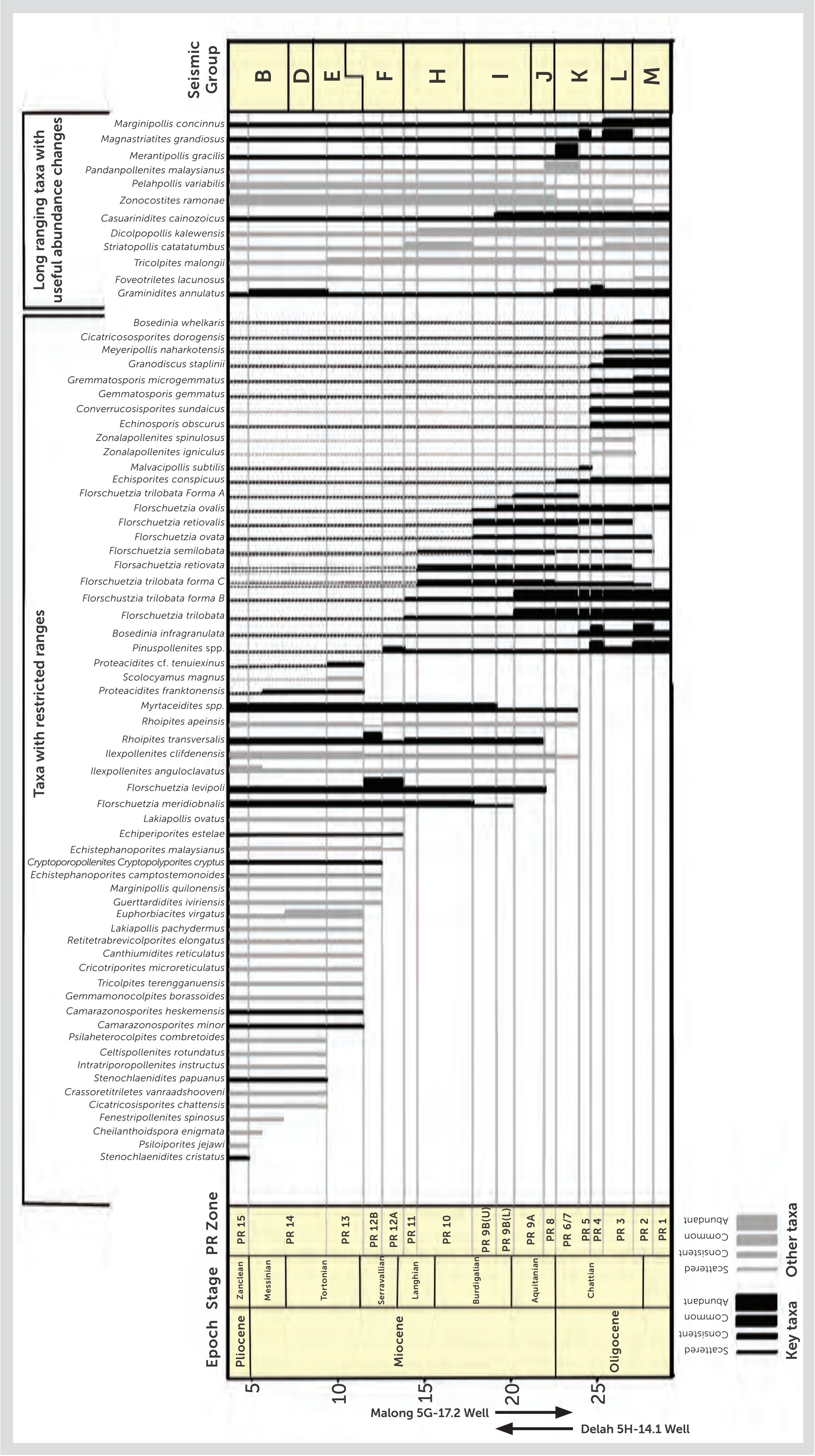


Fig. 1.9. Definition of palynological zones updating the 'PR' scheme of Yakzan et al. (1996). The ranges of taxa used to define the 'PR' palynological zones are shown in black, with the line width indicating taxon abundance. Supporting taxa are shown in grey. This range chart is constructed only using data from the Malong 5G-17.1 and Delah 4H-14.1 wells.

Zone PR5

Definition: The zone is characterised by an abundance maximum of *Magnastriatites grandiosus* and low numbers of *Bosedinia infragranulata*, but consistent values for *Graminidites annulatus*.

Additional characters: There is a consistent representation of *Malvacipollis subtilis* in this zone. Values for *Florschuetzia* spp. are similar to the underlying zone.
Comparison: Equivalent to zone PVC of Morley et al. (2003), for the West Natuna Basin, and approximately with part of CLO9B for Cuu Long Basin (Morley et al., 2019).

Zone PR6/7

Definition: Zone PR6/7 is characterised by an abundance maximum of *Merantipollis gracilis*.

Additional characters: This zone is also characterised by common *Pandanpollenites malaysianus*, and moderate numbers of *Graminidites annulatus* which show a distinct increase compared to the overlying zone. Values of *Florschuetzia* spp. remain reduced, but diversity increases, with the first appearance of *F. retiovalis* and *F. trilobata* forma A. *Echinosporis conspicuus* has its highest occurrence in this zone.
Comparison: Equivalent to zone PVI of Morley et al. (2003), for the West Natuna Basin, and approximately with part of CLO9C for Cuu Long Basin (Morley et al., 2019).

Zone PR8

Definition: The zone is characterised by increased values of *Florschuetzia* spp., with the same diversity as for the underlying zone, but without *F. levipoli*.

Additional characters: The zone is also characterised by moderate values for *Pandanpollenites malaysianus*. Values for *Graminidites annulatus* are low. Values for *Zonocostites ramonae* show a major increase in this zone.
Comparison: The zone is equivalent to zone PVIIA in the West Natuna Basin (Morley et al., 2003), and with zone CLM1 in the Cuu Long Basin (Morley et al., 2019).

Zone PR9

Definition: Zone PR9 is defined on the occurrence of *Florschuetzia levipoli* without, or with extremely rare *F. meridionalis*. It is divided into three subzones as follows:

Zone PR9A

Definition: Subzone PR9A is defined on the basis of a down-section increase of *Florschuetzia trilobata*, vars., *F ovata* and *F. retiovata*, coupled with the occurrence of *F. levipoli*.

Additional characters: There is an up section increase in abundance of *Rhoipites transversalis* and *Pelahpollis variabilis* at the base of the zone.
Comparison: This subzone is equivalent to zone PVIIB in the West Natuna Basin (Morley et al, 2003) and zone CLM2 in the Cuu Long Basin (Morley et al., 2019).

Zone PR9B (Lower)

Definition: The top of this subzone is marked by a sudden down-section increase of *Casuarinidites cainozoicus*, coinciding with increased *Myrtaceidites* spp. within the overlying zone, whereas the base coincides with the down-section increase of *Florschuetzia trilobata* which defines the top of subzone PR9A. *Florschuetzia meridionalis* occurs very rarely through the zone..

Comparison: This subzone corresponds approximately to the West Natuna Basin zone PVIII of Morley et al. (2003).

Zone PR9B (Upper)

Definition: The subzone consists of the interval between the down-section increase of *Casuarinidites cainozoicus*, which defines the top of the underlying subzone, and the regular occurrence of *Florschuetzia meridionalis*, that defines the base of the overlying zone. The base of the subzone is also characterised by an up-section increase of *Myrtaceidites* spp. Note that *Florschuetzia meridionalis* occurs very rarely through the subzone.

Additional characters: *Florschuetzia ovata* and *F. retiovalis* show a further down-section reduction in abundance at the top of the zone.
Comparison: This zone is equivalent to the West Natuna Basin zone PIX of Morley et al. (2003).

Zone PR10

Definition: The base of the zone is marked by the regular occurrence of *Florschuetzia meridionalis*, whereas the top of the zone is marked by the highest consistent occurrence of *Florschuetzia semilobata*.

Zone PR11

Definition: The zone is defined as the interval between the highest occurrence of *Florschuetzia semilobata*, and the highest occurrence of consistent *Florschuetzia trilobata*.

Subzone PR12A

Definition: Zone PR12 is defined as the interval between the deepest consistent occurrence of *Echistephanoporites camptostemonoides* and *E. malaysianus*, and the incoming of *Camarozonosporites* spp., that characterise the overlying zone. Subzone PR12A is characterised by low values of *Rhoipites transversalis* compared to zone PR11 and subzone PR12B, increased *Pinuspollenites* spp. a reduction of *Striatopollis malaysianus* at the top of the subzone.

Additional characters: *Florschuetzia levipoli* tends to be very common within this subzone.

Subzone PR12B

Definition: Subzone 12B is defined on an abundance maximum of *Rhoipites transversalis*, with reduced *Pinuspollenites* spp. compared to the underlying subzone. The top of the subzone corresponds to the base of *Camarazonosporites* spp., as noted below. *Cryptopolyporites cryptus* and *Echiperiporites estelae* have their deepest consistent occurrence in this subzone.

Additional characters: *Florschuetzia levipoli* tends to be very common within this subzone.

Zone PR13

Definition: The base of this zone is based on a distinctive up-section increase in abundance of *Camarazonosporites minor* and *C. heskermensis*.

Additional characters: The base of the zone is also characterised by an up-section increase of *Foveotriletes lacunosus*. The base of the zone is also characterised by the deepest stratigraphic occurrence of *Proteacidites franktonensis*, and coincides with the short-lived appearance of *Proteacidites* cf. *tenuiexinus*. *Scolocyamus magnus* is also confined to this zone. The zone also coincides with the deepest consistent occurrences of *Tricolpites terengganuensis*, *Cricotriporites microreticulatus*, *Canthiumidites reticulatus*, and *Euphorbiacites virgatus*.

Zone PR14

Definition: The base of this zone is defined based on the deepest stratigraphic occurrence of *Stenochlaenidites papuanus*, and with an increase in abundance of *Graminidites annulatus*.

Zone PR15

Definition: The zone is defined on the range of *Stenochlaenidites cristatus*.

1.11 WHERE DOES THE POLLEN COME FROM? THE MAIN VEGETATION TYPES SOURCING THE POLLEN FOUND IN MALONG AND DELAH WELLS

1.11.1 Pollen and Spore Dispersal

Pollen and spores are produced by plants growing on exposed dry land and coastal swamps from land areas around a site of deposition. A large amount of the pollen from a particular sample will have been produced by the vegetation closest to the depositional site, but pollen can be transported great distances by wind and water, and so some of the pollen may have been sourced by vegetation growing far from the area of deposition. The process of pollen dispersal and transportation has been extensively studied in both temperate and tropical regions (e.g., Tauber, 1967; Janssen, 1966; Kershaw and Sluiter, 1982), and the concept of 'pollen rain' has been introduced. In a small site, such as a pond or bog, most pollen will be carried to the site by air, and the 'pollen rain' will reflect the character of the *terra firma* vegetation growing around the depositional site. Locally produced pollen is likely to reflect vegetation growing on the bog, or around the pond, but on a larger scale, most pollen will eventually be washed into rivers, and most of the pollen on a landscape scale will be water carried. Since pollen grains are the same size as small silt particles, transportation will follow processes established by sedimentologists, and pollen grains will eventually settle out when energy levels reduce in the lower reaches of flood plains, and in marine environments. In the marine realm, most pollen will be deposited within proximity to the shoreline, and pollen concentrations will reduce with increasing distance from the shore, as shown in a classic study on the Orinoco Delta by Muller (1959). This pattern applies unless sediment is carried into the marine realm by gravity flow processes, in which case pollen may be carried in large numbers into deep marine environments in turbidites (Morley et al., 2004). As the depositional setting moves well away from the coastline, the airborne component will gradually increase, so that in settings distant from the source, the airborne component may begin to dominate assemblages, although pollen concentrations will be low. This effect is the 'Neves effect' first recognised in the Carboniferous (Chaloner and Muir, 1968).

When moving from *terra firma* settings, through alluvial swamps on the upper coastal plain, and mangrove swamps on the lower coastal plain, and then into the marine environment, the pattern of pollen transportation is likely to follow the trend shown in Fig. 1.10, based on work by Poumot (1989) and Morley (1991). A pollen sample collected from beneath *terra firma* vegetation in the hinterland will be dominated by pollen from the hinterland. A sample collected from beneath alluvial swamps on the upper coastal plain is likely to be dominated by locally produced pollen from the upper coastal plain, but a proportion of the pollen is likely have been carried by water from the hinterland. Similarly, a sample from beneath mangrove swamps on the lower coastal plain will most likely be dominated by pollen from mangroves, but there would most likely be some transportation from both the upper coastal plain and from the hinterland vegetation. Then, as samples are collected from successively more marine settings, away from the coastal swamps, the Neves effect will result in the increased representation of hinterland pollen.

Based on this concept, provided detailed fully quantitative counts of palynomorph assemblages are made allowing the hinterland component to be recorded, it is possible to make a judgment as to the environment deposition. In marine settings, the presence of marine dinocysts and acritarchs and other fossils of marine origin may provide additional information, but across the Southeast Asian region, the presence of marine derived fossils is not guaranteed (Morley, 1978), so the absence of marine fossils should not be used as evidence for the absence of marine influence.

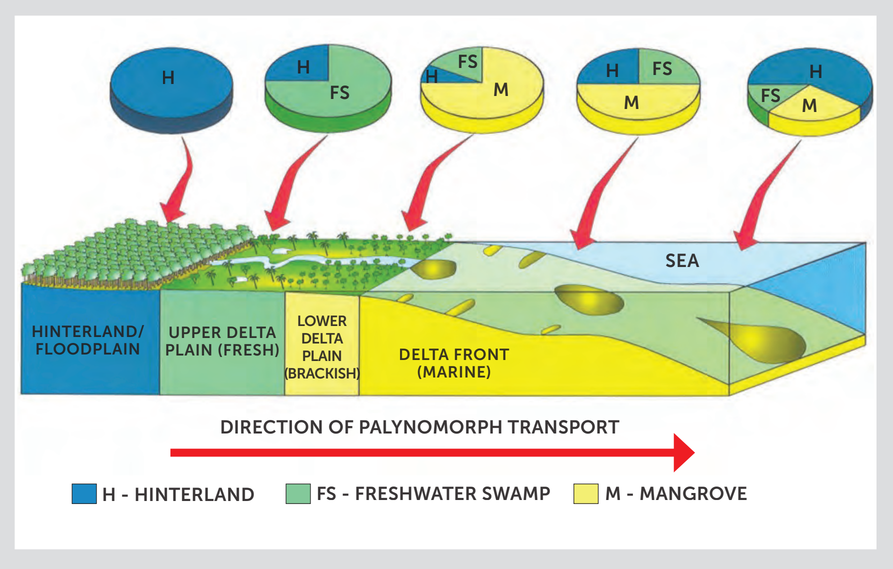


Fig. 1.10. Pattern of pollen transportation and deposition along a tropical coastline from Jaizan Jais (1999).

However, because marine environments may contain pollen and spores that have been carried from each of the vegetation types occurring within a river catchment, with careful evaluation, the marine record can yield information on each of the main vegetation types that might occur within the catchment.

1.12 MAIN VEGETATION TYPES IN MALAYSIA AND INDOCHINA

The following section summarises the main vegetation types (following Wyatt-Smith, 1964; Whitmore, 1975; Morley, 2000 and Ashton, 2014) that have produced the pollen that may be found in Malaysian late Cenozoic sediments. These vegetation types not only include communities that occur in Malaysia today where the climate is currently perhumid, but during the Oligocene, when climates were more strongly seasonal, also include vegetation types currently restricted to areas of more seasonal tropical climate, as found across Indochina.

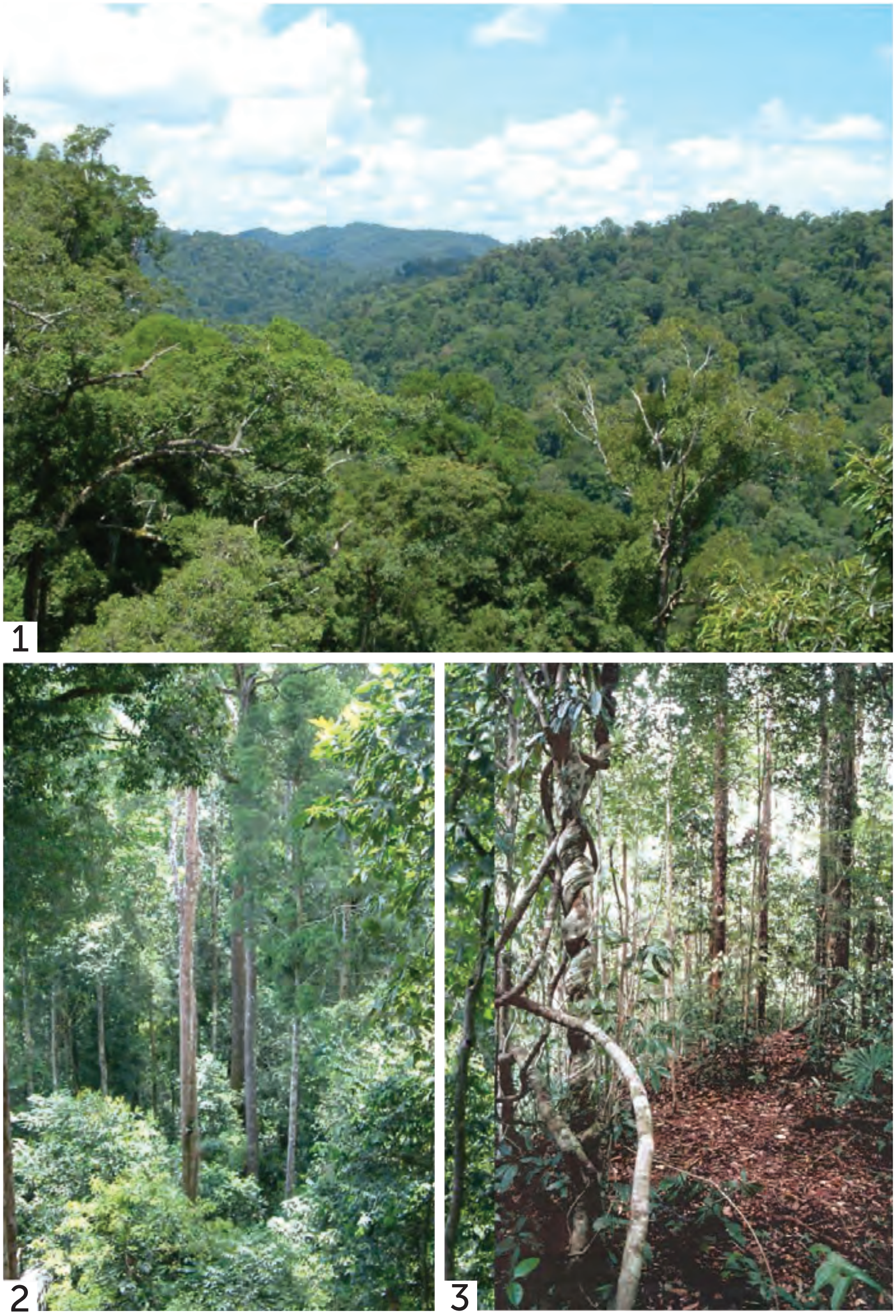


Fig. 1.11. Tropical lowland evergreen rain forests. 1, Lowland evergreen rain forest, Temburong Forest Reserve, Brunei, showing the variety of crown shapes that reflect the highly diverse nature of these forests, which is higher than any other ecosystem. 2, Inside the forest canopy, showing the cathedral-like atmosphere created by the trunks of the canopy and emergent trees. 3, The ground flora is often limited in these forests due to the limited light availability. Note the presence of common lianes (photos 1-2 by RJM, photo 3 from Morley, 2000).

1.12.1 Tropical Lowland Evergreen Rain Forests

Tropical lowland evergreen rain forests are the richest and most luxuriant of all plant communities, and occur in areas that experience a wet tropical climate without pronounced dry seasons. It is typically dense, and evergreen, with trees reaching 50 to 70 m (Fig. 1.11.1-2) and is often void of ground flora (Fig. 1.11.3). The tree component is generally very diverse, but with the family Dipterocarpaceae (Meranti) dominant. Boles are usually straight (Fig. 1.11.2) and buttresses are common. Cauliflory and ramiflory are frequent. Leaves and leaflets are mostly of mesophyll size, with pinnate leaves being common, and with entire leaf margins with drip tips. After Dipterocarpaceae, some of the most common tree families seen in tropical lowland rain forest are Burseraceae (kedongdong family), Fabaceae (bean family), Sterculiaceae (cacao family), Euphorbiaceae (rubber tree family), Myrtaceae (myrtles), Apocynaceae (Jelutong family), Moraceae (fig family), Sapotaceae (gutta percha family) and Annonaceae (kenanga family).

Many of the pollen types described here could have been sourced from this vegetation, especially *Merantipollis* spp., *Inaperturopollenites* spp., *Psilodiporites* spp., *Psilastephanocolporites* spp., *Margocolporites* spp., *Minutitrocolporites* spp., *Myrtaceidites* spp., *Striatopollis* spp. and many others. These forests would have been major producers through palynological zones PR8 to PR15, during the Miocene and Pliocene, when the climate of the Malay Basin would have been mostly perhumid.

1.12.2 Tropical Seasonal Forests

Tropical seasonal forests occur in areas with a significant dry season, and in Malaysia today occur as semi-evergreen forests only in the northernmost part of Perlis. They are, however, widespread across Indochina, and would have occurred in the area surrounding the Malay Basin during the Oligocene when climates were more strongly seasonal (Morley, 2000, 2012). Tropical seasonal forests include semi-evergreen, and deciduous forests, and also pine forests, dominated by *Pinus merkusii*. Here we consider deciduous and pine forests (Figs. 1.12.1-3).

Deciduous forests in Indochina are often of much lesser stature than evergreen rain forests with lower species diversity and may be more open, allowing for the development of a rich herbaceous ground flora which may include common grasses. These forests are often dominated by deciduous species of Dipterocarpaceae, within the genera *Dipterocarpus* and *Shorea*, but may also include common *Lagerstroemia*, Combretaceae and Fabaceae.

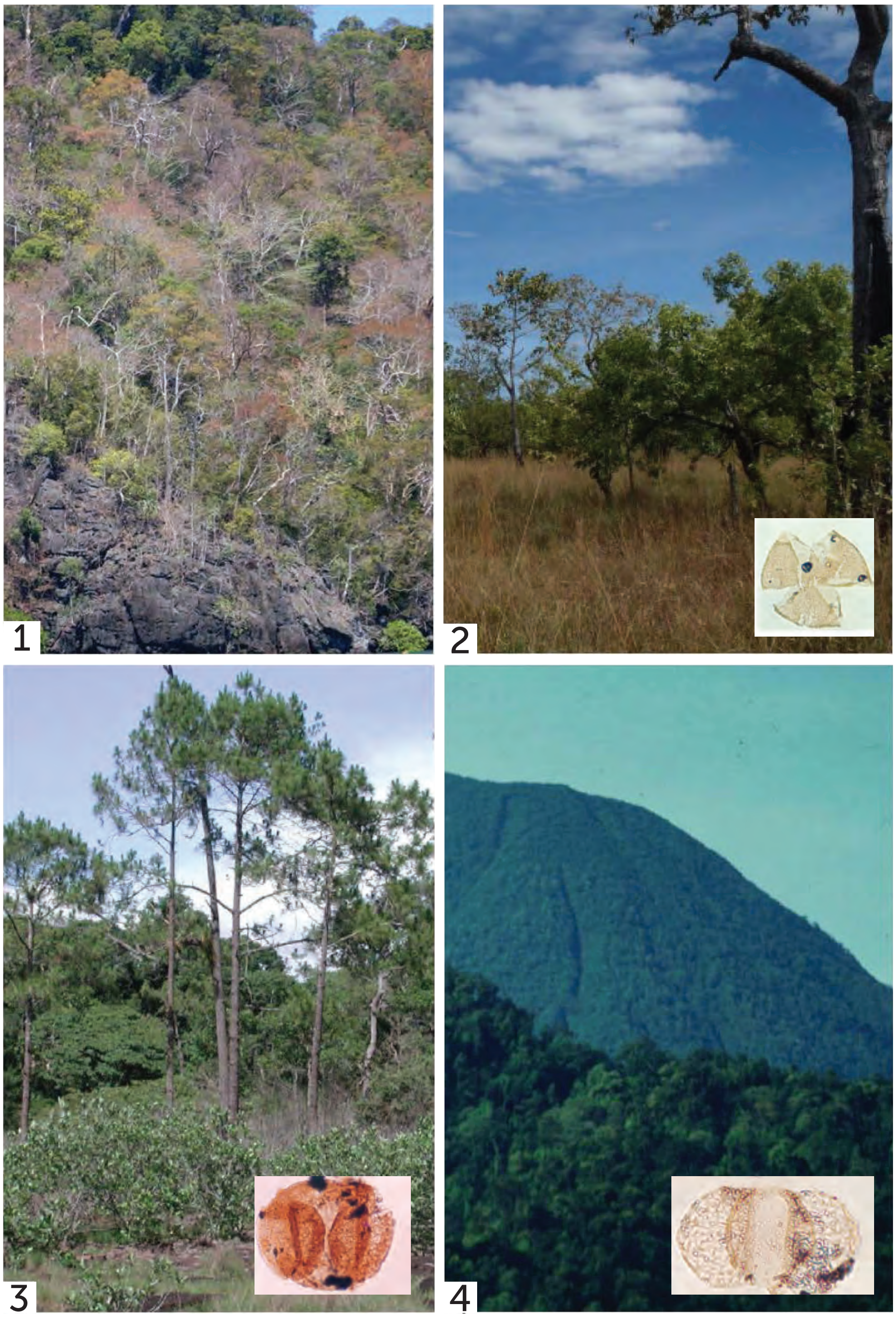


Fig. 1.12. Seasonal and montane forests. 1, Tropical deciduous forests, from north-western Thailand; 2, Dipterocarpus intricatus *forest from north-eastern Thailand, inset,* Merantipollis cuneatus*; 3,* Pinus merkusii *forest, North Vietnam, inset,* Pinuspollenites *sp.; 4, lower and upper montane forest, Gunung Pangrango, Java, inset* Podocarpidites *cf.* ellipticus *(photos 1-3 from GBIF and photo 4 by RJM).*

Much of the pollen recorded in the Oligocene section of the Delah 5H-14.1 well is likely to have been produced by seasonal deciduous forests. The abundance maximum of *Merantipollis gracilis*, derived from *Shorea* spp., within zone PR6/7 is thought to be derived from deciduous or semi-evergreen dipterocarp forests. *Shorea* spp. are low pollen producers in perhumid settings (Morley, 1982a), since flowering is driven by the El Nino climatic oscillation (Ashton et al., 2021) and so takes place only every 5 years or so, with the result that the production of Dipterocarpaceae pollen by perhumid rain forests is disproportionally low (Morley, 1982a), but in seasonal climates, dipterocarps flower annually (Ashton et al., 2021), and deciduous *Shorea* spp. such as *S. robusta* in India are significant pollen producers (Bera, 1990). For this reason it is thought that the maximum of *M. gracilis* in zone PR6/7 suggests an origin from deciduous or semi-evergreen forests (Fig. 1.12.1-2). This is supported also from the presence of common Poaceae pollen in this zone (indicated by regular *Graminidites annulatus*), which may reflect an open forest canopy with Poaceae as a ground flora element. Another indicator of seasonal forests is a small maximum of *Malvacipollis subtilis* within zone PR4, derived from the seasonal climate species of the genera *Austrobuxus* or *Dissiliaria*.

Maxima of *Pinuspollenites* spp., most probably derived from *Pinus merkusii*, are thought to reflect periods when fire-climax pine forests were widespread, as was the case across the northern Sunda Shelf during the last glacial maximum (Morley and Morley, 2021). *Pinus merkusii* forests were probably previously more widespread across Indochina than is the case today (Ratnam, 2016). They are particularly characteristic of well-drained soils under a seasonal climate across Indochina (Morley and Morley, 2021). Maxima of *Pinuspollenites* spp. occur in zones PR4 and PR1 to 2, and are present together with common *Graminidites annulatus* (Poaceae), suggesting that they may be derived from the same vegetation type, and that Pine savanna characterised the *terra firma* vegetation (Fig. 1.12.3) during zones PR4, and PR1 to PR2, as was the case during an early Pleistocene period in the area of Kuala Lumpur (Morley, 1998; Morley and Morley, 2021).

1.12.3 Kerangas Forests

Kerangas, or heath forests occur in areas of perhumid climate on oligotrophic coarse-grained, free-draining siliceous soils and are especially widespread across Sarawak (Brunig, 1974). The canopy in Kerangas is low compared to tropical evergreen rain forests (Fig. 1.13.1-3), uniform and generally dense, with brown and red colours prevailing in the upper canopy, and a prevalence of sclerophylly and small leaf sizes. Buttressing tends to be of limited occurrence, and bryophytes, epiphytes, myrmecophytes and insectivorous plants are common. The most well-represented tree families are Myrtaceae, Dipterocarpaceae, Sapotaceae, and Euphorbiaceae, with Casuarinaceae (*Gymnostoma*) and Podocarpaceae (especially *Dacrydium*) particularly well represented (Fig. 1.13.1-3).

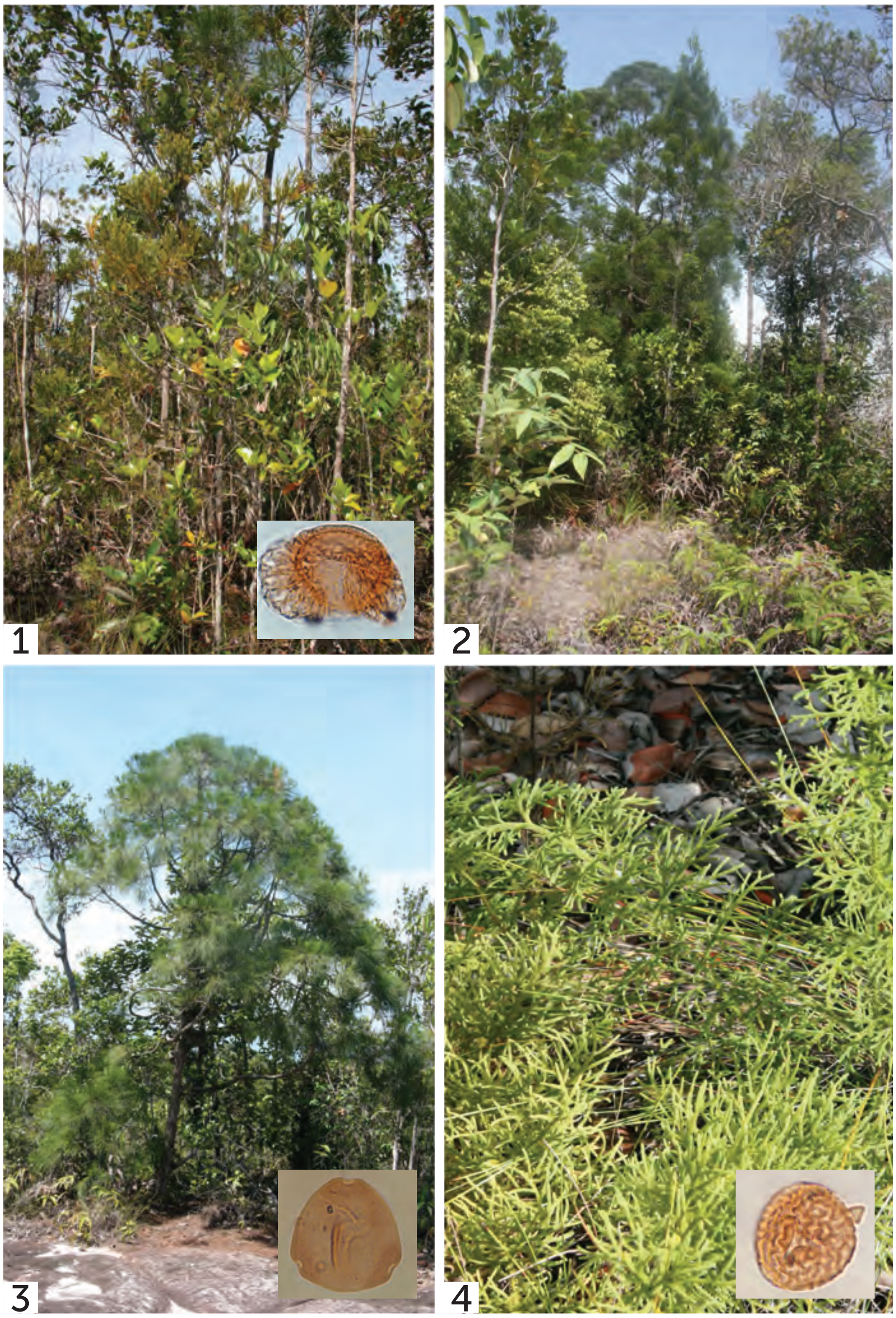


Fig. 1.13. Kerangas forests. 1, Dacrydium elatum*, inset,* Dacrydiumites florinii*; 3,* Gymnostoma nobilis*, inset* Casuarinidites cainozoicus*; 4,* Lycopodiella cernuua*, inset* Camarozonosporites minor *(photos by RJM).*

This vegetation type is reflected in the fossil pollen record from the occurrence of *Dacrydiumites florinii* derived from *Dacrydium*, and *Casuarinidites cainozoicus*, much of which is thought to be derived from *Gymnostoma*. *C. cainozoicus* may also be derived from *Casuarina* (see below) but when abundance maxima of *C. cainozoicus* are associated with *D. florinii* maxima, a Kerangas origin is considered most likely. Sometimes, *C. cainozoicus* occurs commonly in coals (Morley, 2000, 2013; Sia et al., 2014), and in such instances, the coals are thought to have originated from kerapah peats, which form in areas of kerangas where drainage has been impeded by a humic pan (Brunig, 1974; Morley, 2000, 2013). Such coals are widespread across the Sunda region, occurring in the early Miocene in the West Natuna Basin (Morley, 2013), in early Miocene coals from Mukah in Sarawak (Sia et al., 2014) and in the late Oligocene Talang Akar Formation in the West Java Sea (Morley, 2013). *Casuarinidites cainozoicus* and *Dacrydiumites florinii* are particularly well represented in the fossil pollen record in zone PR9B(Lower) and the underlying succession and suggest that kerangas forests and kerapah swamps may have been of widespread occurrence in the early Miocene. *Camarozonosporites minor*, derived from *Lycopodiella cernuua*, is regularly present from zones PR13 to PR15, and today *L. cernuua* (Fig. 1.13.4) is also particularly characteristic of kerangas. Its regular occurrence during the late Miocene and Pliocene may also indicate the more widespread occurrence of Kerangas vegetation in the area surrounding the Malay Basin during this period (Muller, 1972).

1.12.4 Montane Forests

Montane forests occur in areas of perhumid and seasonal climate above about 1000 m and are an important pollen source. In areas of perhumid climate, montane forests are largely characterised by Fagaceae, especially *Quercus, Lithocarpus* and *Castanopsis*, with *Engelhardia*, Lauraceae, and at higher altitudes, Podocarpaceae and Ericaceae (Fig. 1.12.4). In areas of seasonally cool climate, Fagaceae again dominate at lower altitudes (Ashton, 2014), whereas at higher altitudes, deciduous temperate taxa, such as *Alnus*, *Carya*, and *Juglans* may be present, with Laurasian conifers, such as *Tsuga*, *Picea* and *Abies* at higher altitudes (Morley and Morley, 2018). There are few good modern analogues today for upper montane seasonal forests, but they occurred extensively during the mid-Cenozoic.

1.12.5 Coastal Vegetation

Coastal vegetation is a major source of pollen found in marine-influenced sediments (Muller, 1972a) and includes mangroves and beach vegetation. Mangroves are adapted to living in tidal land through their ability to live in poorly oxygenated muds and to tolerate inundation by salt water through physiological mechanisms. They are characteristic of depositional, especially muddy, coastlines in the vicinity of muddy outflows across the tropics and may form a belt that may reach many kilometres in width. Mangroves can occur in both brackish and completely freshwater depositional systems, provided that they are affected by occasional tidal inundation. Here mangrove vegetation is discussed under headings of mangrove forests (characterised by obligate halophytes) as well as backmangrove and other vegetation occurring along tidally influenced rivers in Malaysia.

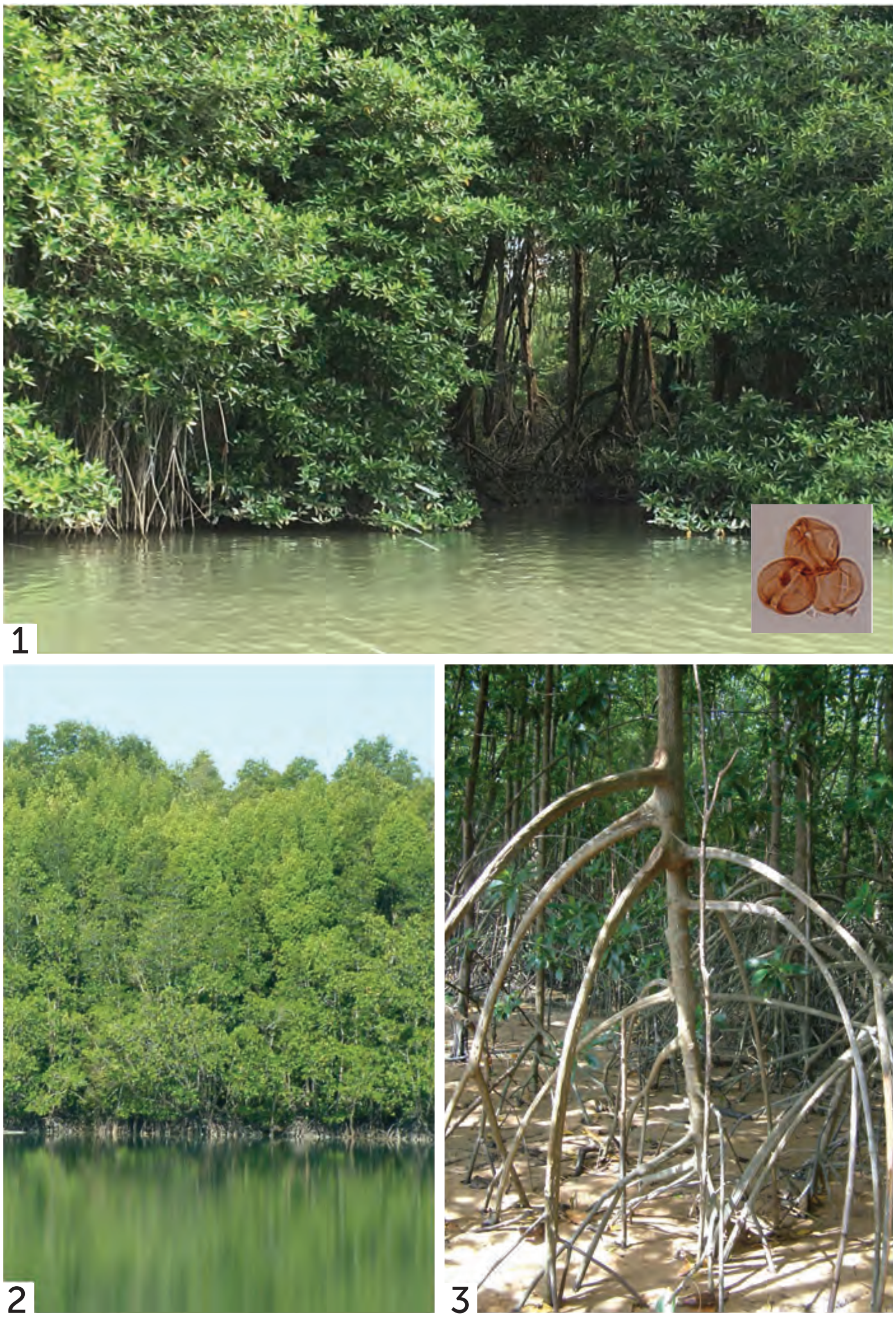


Fig. 1.14. Mangrove forests. 1, Rhizophora mucronata*, Brunei River, inset* Zonocostites ramonae*; 2,* Bruguiera *spp., Sedili River, Johor, Malaysia; 3, old growth* Rhizophora mucronata *root, showing pneumatophores (photos by RJM).*

Mangrove forests

Compared to other forest types in Malaysia, mangrove forests are of very low diversity, and consist of members of several unrelated families, with Rhizophoraceae dominant. They are mostly characterised by the joint tendencies of xerophily, sclerophylly, and vivipary and their constituent taxa form together a remarkable example of convergent evolution.

Obligate mangroves are most exposed to tidal inundation and are dominated by the families Rhizophoraceae (the genera *Rhizophora*, *Bruguiera*, *Ceriops* and *Kandelia*), Sonneratiaceae (*Sonneratia* alba) Acanthaceae (*Avicennia* spp.) and Combretaceae (*Lumnitzera* spp.). In Malaysia the genera *Rhizophora* and *Bruguiera* are dominant (Figs. 1.14.1-3) together with *Sonneratia alba* on the seaward edge and with *Avicennia* spp. occurring frequently on freshly accumulating muds along tidal rivers.

Mangrove forests are reflected in the pollen record by the presence of *Zonocostites ramonae*, which is produced by the genera *Rhizophora* and *Bruguiera*. Although modem pollen from these genera shows a size difference, with *Rhizophora* being slightly larger than *Bruguiera*, this size difference cannot be used for fossil pollen, since the process of fossilisation and compression may result in fossil pollen being smaller than their modern counterparts. *Rhizophora* is thought to be pollinated by wind (Tomlinson, 2016), and as a result, *Rhizophora* pollen is produced in very large quantities. Large-flowered species of *Bruguiera* are pollinated by birds, and the smaller flowered species by butterflies (Tomlinson, 2016) and so it is likely that *Bruguiera* is a much smaller pollen producer than *Rhizophora*. Samples collected from beneath mangrove swamps may contain up to 95% *Rhizophora* type pollen. *Zonocostites ramonae* is represented in moderate quantities in zone PR3 in the Oligocene, but otherwise occurs in low frequencies in the Oligocene. There is a major increase in representation at the beginning of the early Miocene, within zone PR8, especially during times of transgression, but then during the Middle Miocene Climatic Optimum, from zones PR10 to PR12A, it becomes particularly abundant. It then remains in reduced frequencies through zones PR12B to PR15.

Florschuetzia meridionalis, produced by *Sonneratia alba*, is extremely rare in zone PR9B, and occurs regularly within zone PR10, remaining common through to the end of the Middle Miocene Climatic Optimum, after which time it occurs consistently but in quite low frequencies. *Sonneratia* species are all pollinated by bats, and bat-pollinated taxa generally produce lots of pollen. The bat clumsily grabs the flower, making many of the anthers fall to the ground, and this probably helps to ensure a large amount of *Sonneratia* pollen is incorporated into sediments.

The pollen type *Rhoipites apiensis* is produced by *Avicennia* spp. It occurs in consistently low numbers from zone PR6/7 to PR15. *Avicennia* is pollinated by insects and is a very low pollen producer. The abundance of *Rhoipites apiensis* in sediments is therefore difficult to use as a proxy for the abundance of *Avicennia* in former vegetation.

Fig. 1.15. Mangrove palms, Nypa *and* Oncosperma. *1,* Nypa fruticans *lining brackish creeks in the vicinity of the Pahang Tua River, Pahang, inset* Spinizonocolpites echinatus*; 2,* Oncosperma tigillarium*, Langat River, near Banting, inset* Racemonocolpites hians*; 3, dense* Nypa fruticans *stand, Sedili River, Johor (photos by RJM).*

Back mangroves

Back mangroves occur behind the *Rhizophora* belt, where brackish influence is reduced, or absent, but still within the tidal limit. Back mangroves include *Nypa* (Fig. 1.15.1, 3) *Sonneratia caseolaris* (Fig. 1.16.1, 3) *Oncosperma* swamps (Fig. 1.15.2) and *Acrostichum* swamps (Fig. 1.17.1-3).

Nypa, Sonneratia caseolaris and Oncosperma swamps

The mangrove palm *Nypa fruticans* (Fig. 1.15.1, 3) forms an extensive belt along tidal river systems directly behind the mangrove belt, and sometimes occurs as a consocies in widespread swathes between distributaries as seen on the Mahakam Delta in East Kalimantan and the Rajang Delta in Sarawak. Going up-river, *Nypa fruticans* first appears as salinities are still brackish, about 10 ppt, and usually continues well beyond the limit of brackish influence where the surface and channel base are characterised by entirely freshwater conditions, but still within the range of significant tidal activity. This is best shown on the Langat River south of Port Klang, where after a short stretch of brackish water, *Nypa* occurs in a pure belt with entirely freshwater over many kilometres, but gradually reducing in density up-river.

The past record of *Nypa fruticans* is revealed from the occurrence of the dispersed pollen type *Spinizonocolpites echinatus*, which occurs in low frequencies in most samples from the zone PR1 (mid-Oligocene) to zone PR15 (Pliocene). The low representation of *S. echinatus* is probably due to the very low pollen production of *Nypa fruticans*, although sometimes it occurs commonly, as in the early Pleistocene Perning Delta (in Java), where it reaches up to 90% in some samples (Morley et al., 2020).

As *Nypa* reduces in representation up-river, it occurs together with *Sonneratia caseolaris* (Fig. 1.16.1.3) and in some places *S. caseolaris* may then dominate. This is seen in both the Sedili (Fig. 1.16.3) and Langat rivers. Along the Sungai Langat *S. caseolaris* continues virtually to the tidal limit of the river where it also sometimes occurs as a consocies.

As *Nypa fruticans* reduces in abundance up-river, the nibong palm *Oncosperma tigillarium* often forms a belt, sometimes occurring just behind the *Nypa* belt. This is seen in the Mahakam Delta as well as along the Langat River (Fig. 1.15.2). The history of *Oncosperma* is revealed in the fossil record from the presence of *Racemonocolpites hians*, which occurs in low numbers in many samples, but is particularly common within pollen zones PR6/7 and PR8, where it occurs together with common *Pandanpollenites malaysianus* (from *Pandanus*) and *Discoidites* spp. (from *Brownlowia* spp.), and the vegetation in the Delah/Malong area during the latest Oligocene and earliest Miocene would have consisted of a unique alluvial swamp with *Pandanus*, *Brownlowia* and *Oncosperma* dominant, which has no modern analogue.

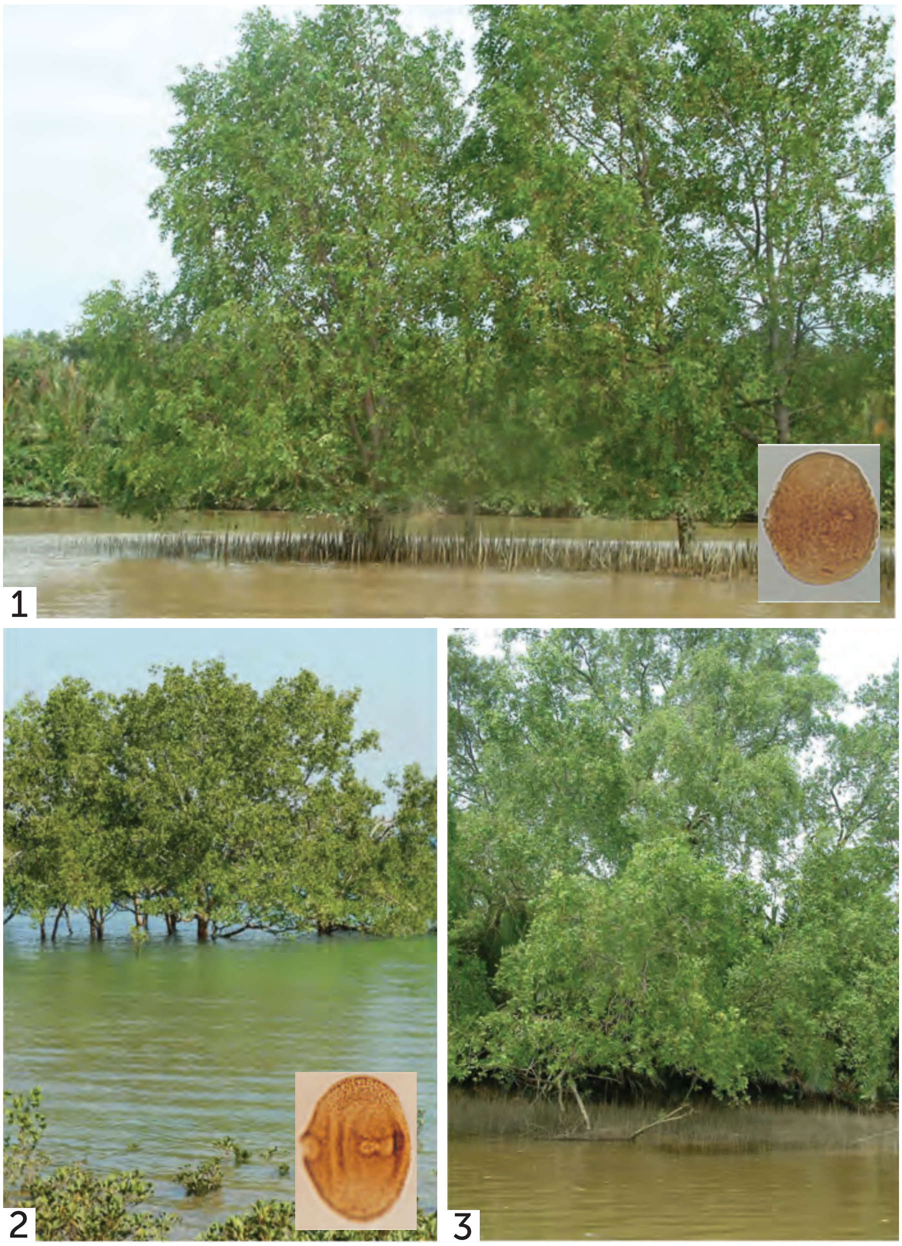


Fig. 1.16. Sonneratia. *1,* Sonneratia caseolaris *at the mouth of the Pahang River, showing the extent of the pencil-like pneumatophores characteristic of this genus, inset,* Florschuetzia levipoli*; 2,* Sonneratia alba*, at the seaward margin of mangrove swamps on Pulau Ketam, at the mouth of the Klang River delta, inset,* Florschuetzia meridionalis*; 3,* Sonneratia caseolaris *within the range of tidal influence, but beyond the brackish limit, Sedili River, Johor (photos by RJM).*

Acrostichum *swamps*

Acrostichum is a fern of the family Pteridaceae that is characteristic of mangroves across Southeast Asia today but should be envisaged as a facultative mangrove taxon since it can sometimes occur far inland in completely freshwater settings, such as at Lake Kerinci (900m asl) in Sumatra, Indonesia (van Steenis and Schippers-Lamertse, 1965). In the mid Cenozoic of Europe it exhibited a similar pattern. On the one hand it was a pioneer of floodplain areas in completely freshwater settings (Collinson, 2002; Moreno-Dominguez et al., 2016), and on the other it was a component of mangrove swamps at the time of thermal maxima during the Eocene and middle Miocene (Popescu et al., 2021). *Acrostichum* macrofossils and accompanying spores have also been reported from fluvio-lacustrine sediments with associated volcanics from the Oligocene of the Ethiopian Plateau (Massini et al., 2006)

In the Cuu Long Basin to the south of the Mekong delta, *Acrostichum* spore maxima correlate closely with maxima of *Ceratopteris* spores, algal palynomorph maxima and more sandy lithologies within a freshwater lacustrine setting (Morley et al., 2019, Well C, Fig. 3 and Well E, Fig. 11), whereas in areas such as the North Malay Basin, *Acrostichum* spore maxima are clearly associated with maxima of pollen of Rhizophoraceae (Morley et al., 2021, Fig. 11, Bergading Deep-3 Well). In both the Cenozoic of Southeast Asia or during times of thermal maxima in the European Palaeogene, *Acrostichum* spores cannot be used alone as an indicator of mangrove swamps, or of tidal influence, but their occurrences should be evaluated by examination of assemblages with which the spores are associated.

In Malaysia *Acrostichum aureum* is a member of backmangrove vegetation, and typically forms an element of vegetation along riverbanks within the reach of tides (Fig. 1.17). It is often noted to occur on lobster mounds, above the action of tides, but within the tidal limit (Watson, 1928). It has a strong weedy tendency, and can be very aggressive in disturbed sites, often forming dense thickets in areas where mangroves had previously been clear felled or killed as a result of changes in hydrology (e.g., Fig. 1.15.1, 3). It is also believed to suppress the regeneration of other mangrove species (Tomlinson, 2016). *Acrostichum speciosum*, on the other hand, is much less vigorous, and typically occurs as an understorey element beneath the canopy.

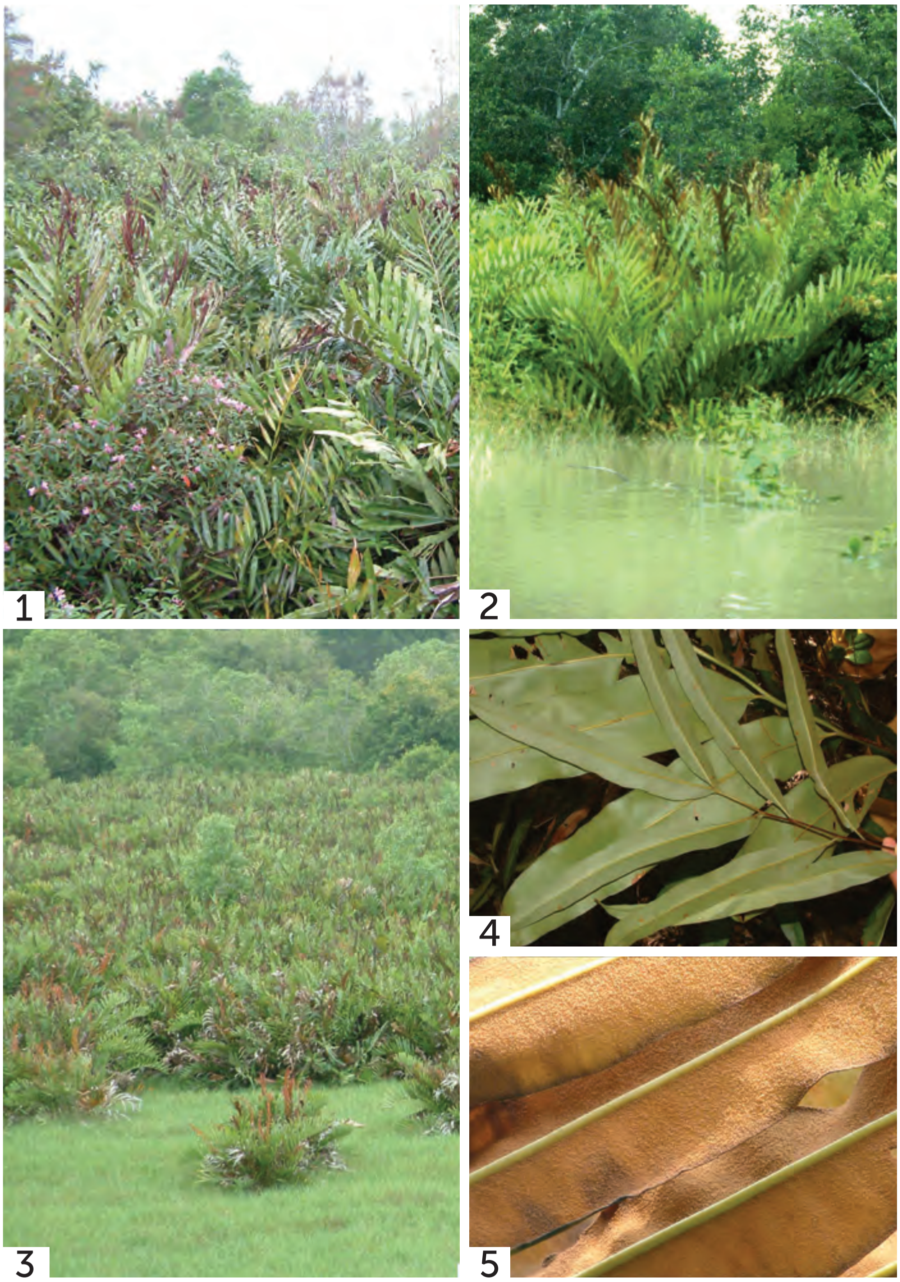


Fig. 1.17. Acrostichum. *1,* Acrostichum aureum *thicket on area of clear-felled* Rhizophora *swamp, Tanjung Ages, Pahang River Delta; 2,* Acrostichum aureum *beside* Bruguiera *stand, Sedili River, Johor; 3,* Acostichum aureum *replacing grass swamp which formed after* Rhizophora/Bruguiera *mangroves had been killed following disturbance of salinity regime, Kuala Selangor; 4,* Acrostichum aureum *(large pinnae) and* A. speciosum *(small pinnae) Langkat River, near Port Klang; 5, close up of* Acrostichium aureum *frond, showing 'acrostichoid' character in which sori are so closely packed over lamina, explaining high spore productivity of this taxon (photos by RJM).*

1.12.6 Riverine Vegetation at the Tidal Limit

There is a clear pattern of vegetation zonation along tidally influenced rivers, best seen in the Sungai Sedili in Johor, and described in detail by Corner (1978) who studied this river system in the 1930's and is summarised in Morley (2000). This classic zonation is also seen in nearby rivers such as the Kuantan River to the north, and the Kapuas River in East Kalimantan. Beyond the mangrove zone, and a belt with *Sonneratia caseolaris* and *Hibiscus tiliaceus*, and the *Nypa* zone where brackish influence is present, the longitudinal zonation is characterised by belts with common *Ficus macrocarpa* (Fig. 1.18.2, 3). Beyond the limits of brackish water but still within the reach of tides, *Pandanus helicopus* then forms a broad belt (Fig. 1.18.4), with the pioneering shrub *Barringtonia conoidea* along the water's edge, and *Tristaniopsis sumatrana* behind on a belt of levees. *Pandanus helicopus* continues beyond the tidal limit, where it is joined by *Nauclea subtida*, and landward, the riverine vegetation gives way to alluvial swamp forest (Fig. 1.18.1).

Several elements of this vegetation zonation can be seen in the upper part of the Malong 5G-17.2, and occur especially during the late Miocene and Pliocene, within zones PR14 and PR15, suggesting that this vegetation zonation may well have been in place over a similar time period. These include the regular occurrence of *Marginipollis quilonensis*, derived from *Barringtonia conoidea*, *Psilodiporites jejawii*, derived from *Ficus*, and *Pandanpollenites malaysianus (Pandanus)*, together with regular swamp forest elements, such as *Minutitricolporites duplibaculatus*, derived from *Blumeodendron*, and *M. microechinatus*, from *Austrobuxus nitidus*.

1.12.7 Beach Vegetation

On accreting sandy coastlines, beach forest forms a distinctive zone, perhaps a few 10's of metres in width, but which contributes significantly to the pollen record in shallow marine sediments. Beach forest is well developed along the Malay Peninsula east coast (Fig. 1.19.1-,3) and is characterised by *Barringtonia asiatica*, *Calophyllum inophyllum*, *Syzygium grandis*, *Terminalia catappa*, *Thespesia populnea* and *Hibiscus tiliaceus* (Fig. 1.19.3), often with *Podocarpus polystachyus* (Fig. 1.19.2), and their pollen may contribute to the fossil pollen record with taxa with dispersed pollen such as *Marginipollis concinnus*, *Rhoipites transversalis*, *Myrtaceidites* spp, *Psilaheterocolpites laevigatus*, *Echiperiporites estelae* and *Podocarpidites minuticorpus*.

One widespread species that can form a continuous belt on accreting sandy coastlines is *Casuarina equisetifolia* which can reach single species dominance (Fig. 1.18.1). For beach vegetation elements, most can also be derived from other vegetation types, so care is needed in its interpretation based on the fossil pollen record.

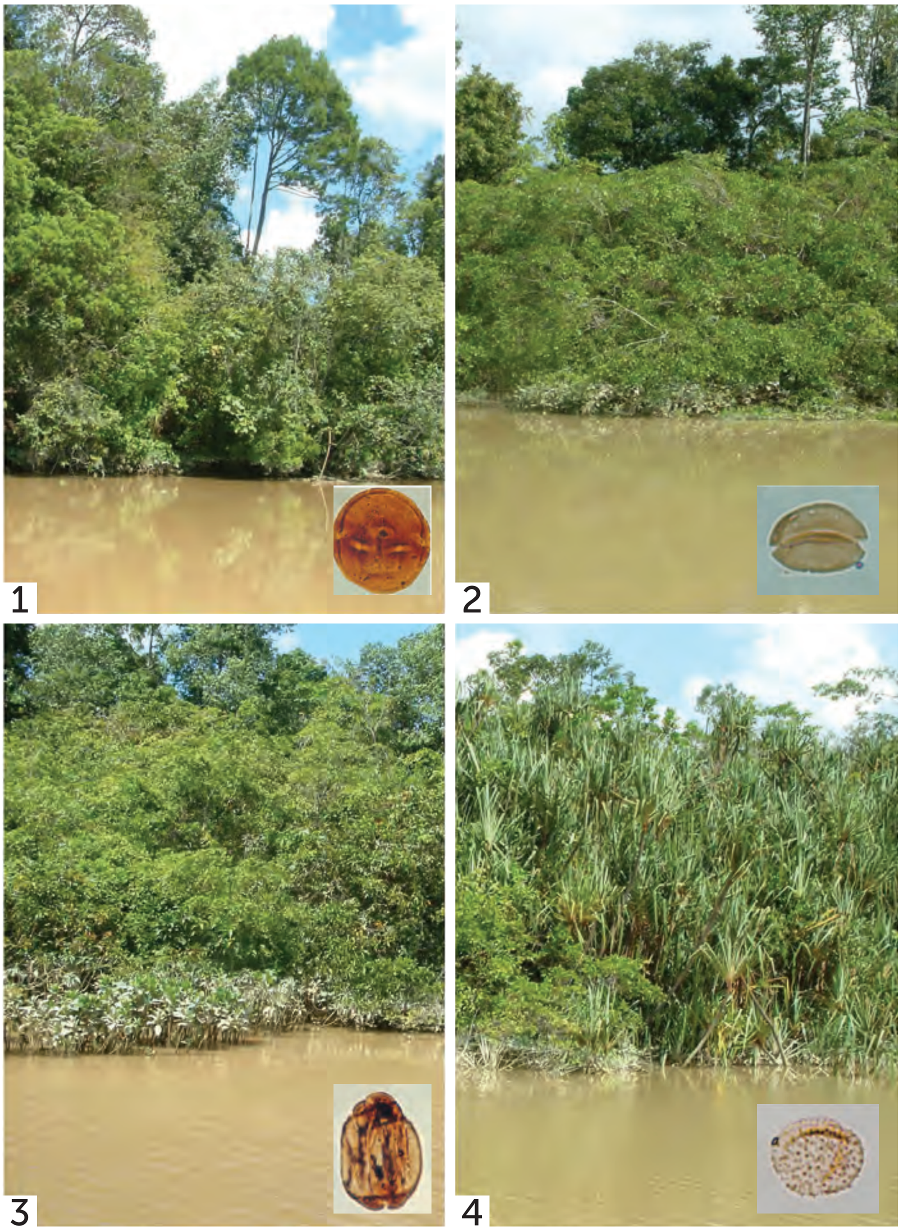


Fig. 1.18. Riverine vegetation at Sungei Sedili and Sungei Pahang. 1, Freshwater alluvial swamp away from the river margin, within the freshwater zone with Palaquium *spp. dominant, inset,* Psilastephanocolporites validus*; 2,* Ficus macrocarpa *lining the Sungei Sedili just beyond the limit of brackish influence, but within range of tidal influence, inset,* Psilodiporites jejawii*; 3,* F. macrocarpa *with* Barringtonia conoidea*, inset,* Marginipollis quilonensis*; 4,* Pandanus helicopus*, just beyond tidal limit, inset,* Pandanpollenites malaysianus *(photos by RJM).*

Other sources of *Casuarina* type pollen are kerapah type peat swamps, which are often dominated by *Gymnostoma nobilis*, which produces the same pollen type, so in interpreting records of *Casuarinidites cainozoicus*, it is useful to look at associated pollen, and lithologies. Association with *Dacrydiumites florinii* and coaly or shale-dominated lithologies would suggest a kerapah source, whereas association with sands and other beach flora elements, such as *Echiperiporites estelae* or *Marginipollis concinnus* and sandier lithologies might suggest an origin from beach vegetation.

1.12.8 Freshwater Swamp Vegetation

Landward of mangroves, and surrounding freshwater lakes, freshwater swamp vegetation are a major source of pollen and spores. There are five main swamp types that may have contributed pollen to the Malong 5G-17.2 and Delah 5H-14.1: successions: 1) ombrotrophic peat swamp forests, 2) rheotrophic alluvial swamp forests, 3) seasonal swamp forests, 4) herbaceous swamp or marsh and 5) floating vegetation mats, or schwingmoor. Ombrotrophic swamps are fed solely by rainfall, whereas rheotrophic swamps are fed by water flow. Peat swamp forests can further be divided into basinal peats, such as occur at the present day behind mangrove swamps along the west and east coasts of the Malay Peninsula and along the coasts of Sarawak, and kerapah swamps, that occur inland where drainage is impeded by a humic pan, and occur inland in Sarawak, and in Kalimantan (Brunig, 1974; Morley, 2013).

Basinal peat swamps

The classic examples of ombrotrophic basinal peat swamps are the giant peat domes inland of mangrove swamps along the coast of Sarawak and Brunei, and studied in detail by Anderson (1963, 1964, 1983). Basinal peat swamp forests principally develop along relatively stable or subsiding, prograding coastlines in areas previously occupied by mangrove swamps or extend along lowland river valleys in areas such as South Kalimantan and Central and South Sumatra. These peat swamps developed following stabilisation of sea levels around 6000 years ago (Dommain et al., 2011), and are thus closely tied to the cycle of eustatic sea level change. Although the character of both basinal peat swamp forests in Sarawak and Brunei has been known for some time through the work of Anderson, the extent to which these are representative of peat-forming swamps on a more regional basis, and the timing of peat formation, is only just becoming clear (Morley, 2013).

Anderson (1964) differentiated the basinal peat swamps in Sarawak/Brunei into six phasic communities, along a gradient, or catena, of decreasing soil fertility and increasing waterlogging, from the periphery to the centre of mires (Figs. 1.20, 1.21,1-4). The structure of Sarawak swamps and the representation of phasic communities (Ph) is strongly influenced by the presence of one dominant species, *Shorea albida*, which is absent from swamps outside Sarawak, western Brunei and northwest Kalimantan.

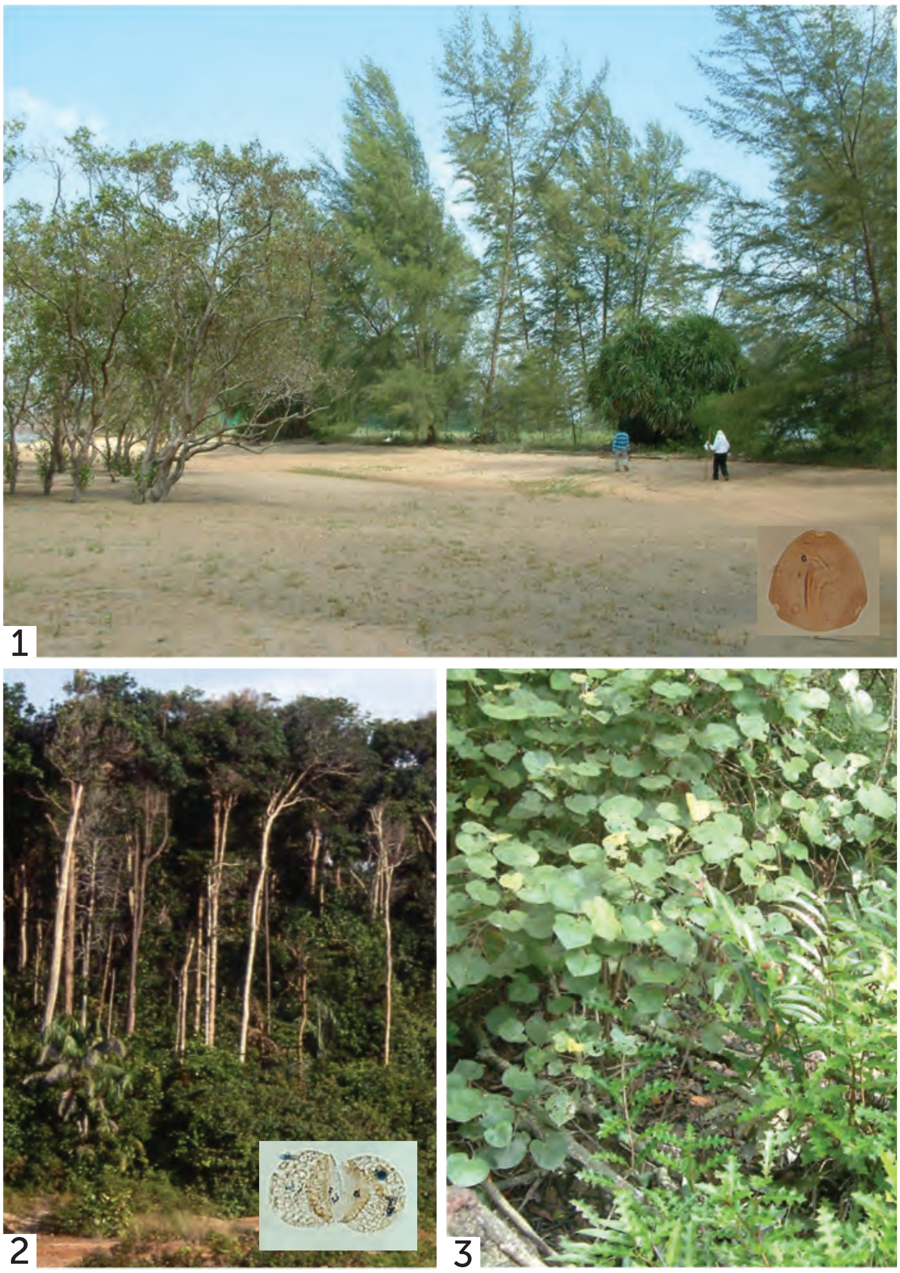


Fig. 1.19. Beach vegetation. 1, Casuarina equisetifolia*, Pahang River mouth, with the grass* Spinifex littoreus *in the foreground, inset,* Casuarinidites cainozoicus*; 2, coastal forest in Johor with* Podocarpus polystachyus *and* Cerbera odollam *in the foreground, inset* Podocarpidites corpusculus*; 3,* Hibiscus tiliaceus *with* Acanthus ilicifolius *(photos by RJM).*

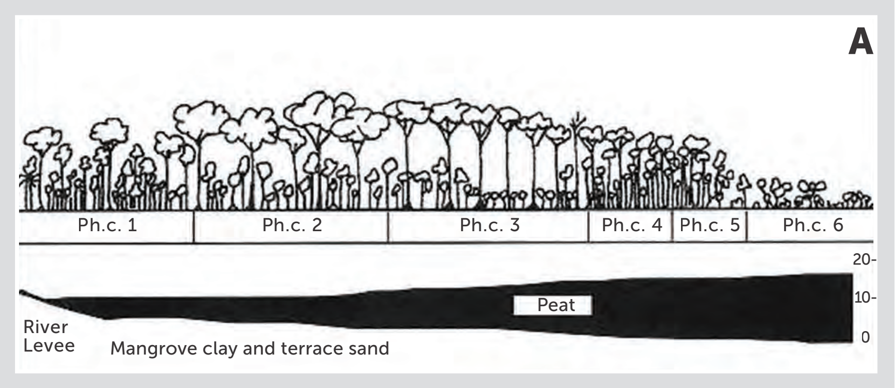


Fig. 1.20. Basinal peat swamp catena, from Morley (2000), based on Anderson (1964).

Phasic community 1 (Ph.1) occurs around the periphery of a swamp dome and shows many similarities with lowland evergreen rain forest but includes typical peat swamp elements such as *Gonystylus bancanus* and *Dactylocladus stenostachys*. Ph.2 shows reduced diversity, but with *Shorea albida* being well represented. Ph.3 on the other hand is composed almost exclusively of large trees of *S. albida*. Ph.4 and Ph.5 are characterised by very dense notophyll leaved pole forests, whereas Ph.6 consists of notophyll to microphyll open woodland or savanna, with *Combretocarpus rotundifolius* as the dominant tree (Anderson, 1964; Morley, 2013). This succession was shown to be a true temporal succession by Anderson and Muller (1975) based on a palynological study. Outside Sarawak and Brunei, beyond the range of *Shorea albida*, the catena is simpler, with Ph. 2-4 being absent, although substantial interstand variation may occur within the same phasic community (Morley, 2013), and in these areas, just two, or possibly three phasic communities may be present. These consist of mesophyllous mixed swamp forest (Ph.1) around the margins of mires; notophyllous pole forest (Ph.5), which is often termed *Padang*, in central areas; and open microphyllous/notophyllous woodland comparable to Ph.6 may occur in very mature swamps.

Kerapah peats

Kerapah peats are also ombrotrophic peats which develop in areas of podsolic soils where drainage is impeded through the development of an iron or humic pan (Brunig, 1974, 1990), and the term *watershed peats* applies to such swamps occurring on low lying interfluves (Morley, 2000). Thus, they are particularly widespread as drapes on low-lying, lowland watersheds in areas of podsolic soils but also occur adjacent to freshwater lakes.

Fig. 1.21. Peat swamp forest. 1, view along logging road in mixed peat swamp forest, Pekan, Pahang; 2, Shorea albida*, Phasic community Ph.2, Belait River, Brunei, inset,* Merantipollis gracilis*; 3,* Gonystylus bancanus*, dominant in mixed swamp forest, Pekan, Pahang, inset,* Cryptopolyporites cryptus*; and 4, pneumatophores, mixed swamp forest Pekan, Pahang (photos by RJM).*

Kerapah peats develop over quite different timescales to basinal peats, their formation depending primarily on climate and secondarily on drainage factors, and unlike basinal peats need not be directly connected to the cycle of sea level change. Their ecology has been studied in Sarawak and Brunei by Bruning (1974) but are best developed, and their development most intensively studied, in the Sebangau region of South Kalimantan, where their succession has been evaluated by Morley (1981a, 2013), Page et al. (1999, 2006) and others. A key floristic difference between kerapah and basinal peats is that kerapah is often characterised by abundant *Gymnostoma nobilis* and *Dacrydium elatum* (Morley, 2013), which prior to felling were dominant in a peat swamp at Lawas in Brunei (Muller, 1963; Morley, 2013). The association of the pollen types *Casuarinidites cainozoicus* and *Dacrydiumites florinii* can be used to trace the geological history of this forest type, which appears to be much older than basinal peats (Morley, 2013).

Rheotrophic alluvial swamps

Rheotrophic swamps occur widely throughout Southeast Asia, although few have been studied in detail. They vary from large swamps within tectonically controlled depressions to infilled volcanic craters, infilled oxbow lakes, and many others. The extensive Berbak swamp in Jambi province, South Sumatra is likely to be mainly rheotrophic, as it shows a planar, rather than domed succession (Esterle and Ferm, 1994). Some rheotrophic swamps are peat-forming, whereas others may form on fluvial muds. Rheotrophic swamps are often characterised by pandans and palms although peat swamp tree species may also be present. The Tasek Bera in Pahang is a good example of a rheotrophic alluvial swamp (Fig. 1.22.1) and is dominated by extensive swathes of *Pandanus helicopus*, which have built up during the course of the late Holocene (Morley, 1981b). Formerly this swamp also included *Elaeocarpus* as a significant swamp element. The Berbak swamp in Jambi, Sumatra is noteworthy in being characterised not only by *Pandanus*, but also by diverse palms, including *Calamus* and *Korthalsia*, together with *Pinanga*, *Licuala* and *Pholidocarpus* (Dransfield, 1974). The palm *Livistona kingiana* is also a common element in alluvial swamp along the Sedili River in Johor (Fig. 1.22.3).

It is thought that maxima of *Pandanpollenites malaysianus* may reflect former developments of alluvial swamps, as seen in the Malong 5G-17.2 and Delah 5H-14.1 wells within zone PR6/7 and PR8, at the time of the Oligo-Miocene boundary. In the Oligocene of the Cuu Long Basin, to the south of the Mekong Delta, maxima of *Livistona* pollen are thought to reflect the former development of alluvial swamp on prograding lacustrine deltas (Morley et al., 2019). Maxima of *Dicolpopollis kalewensis*, as seen in the late Eocene Yaw Formation in Myanmar (Huang et al., 2021), are thought to reflect the former development of alluvial swamp dominated by rattans. Today, *Calamus* spp. dominate swamps exhibiting some degree of seasonality of climate in Sulawesi, Java, Myanmar (Morley and Morley, 2013) and Cambodia (Campbell et al., 2006).

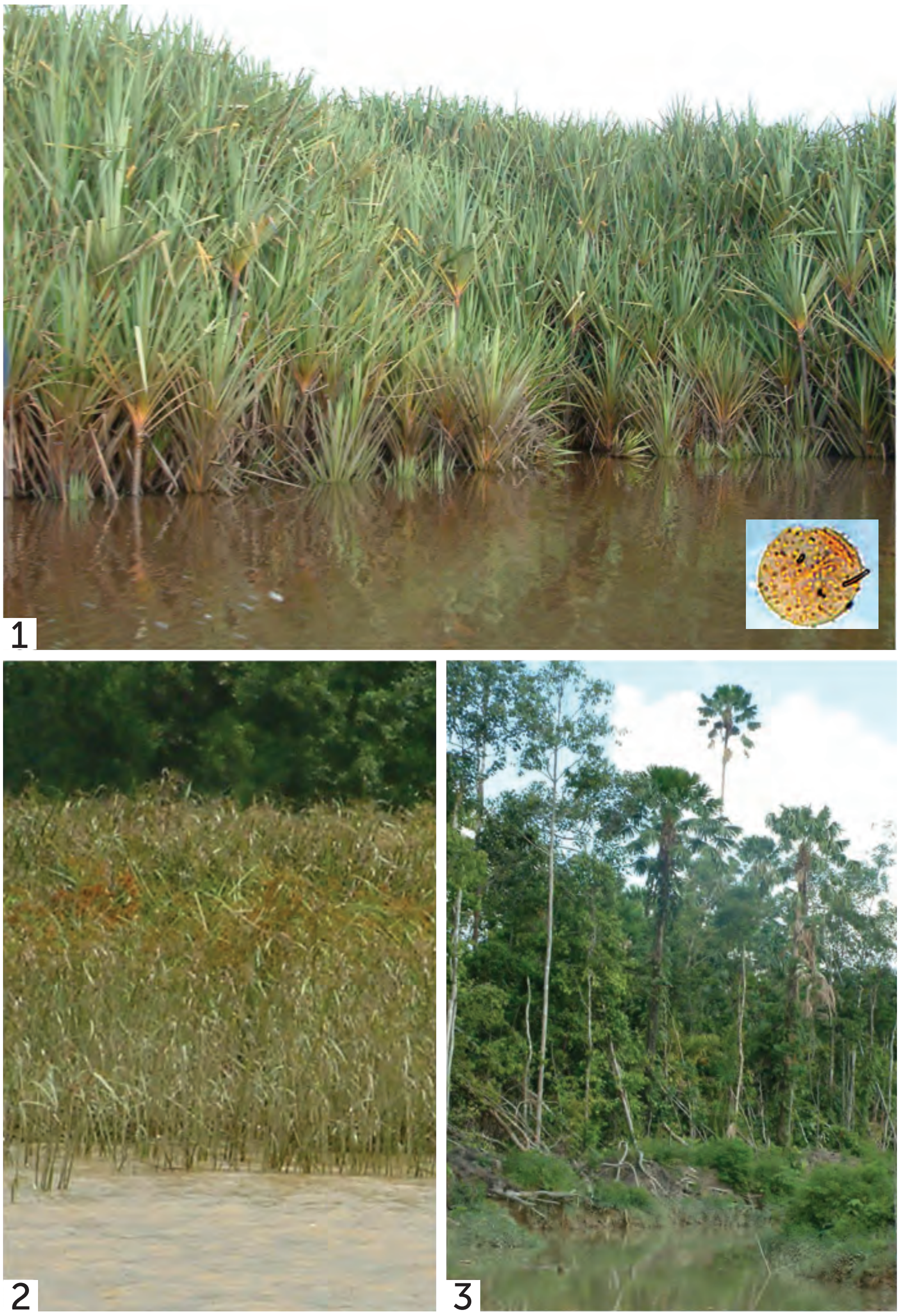


Fig. 1.22. Alluvial swamps. 1, Pandanus helicopus *at Tasek Bera, Pahang, an example of a rheotrophic swamp, inset,* Pandanpollenites malaysianus*; 2,* Cyperaceae *growing on emergent banks in the lower reaches of the Pahang River; and 3,* Livistona *growing on alluvial swamp in Johor (photos by RJM).*

Seasonal swamps

Seasonal swamps occur widely around lakes in areas of seasonal climate in Indochina. The best area to observe seasonal swamp vegetation is the Tonle Sap, in Cambodia which also acts as an excellent analogue for the lake-filled tectonic depressions that characterised the Malay Basin during the Oligocene. The Tonle Sap is a huge inland sea, that has an outflow into the Mekong River. During the dry season, it is a shallow lake, perhaps 20 km in width and 100 km long, and just 1 to 2 m in depth whereas during the wet season, monsoon rains cause it to expand dramatically, and typically attains a depth of 15 m (Fig. 1.23). The area flooded during the wet season is characterised by swamp forests, swamp scrublands and herbaceous and aquatic vegetation (Dy Phon, 1981; Campbell et al., 2006).

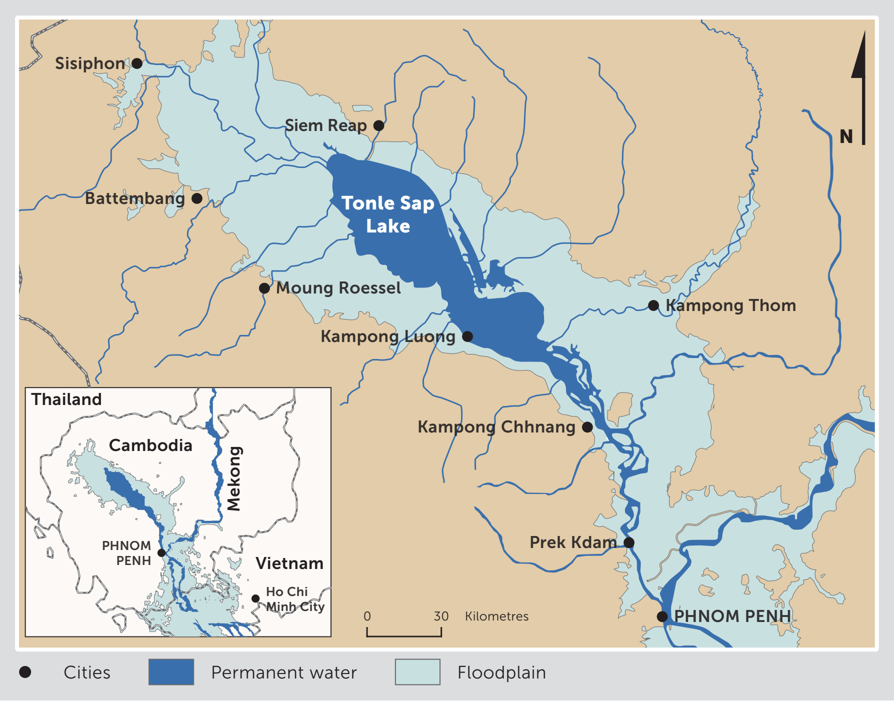


Fig. 1.23. The Tonle Sap, Cambodia, showing the extent of the permanent lake, and the extent of the floodplain, which is flooded during the wet season.

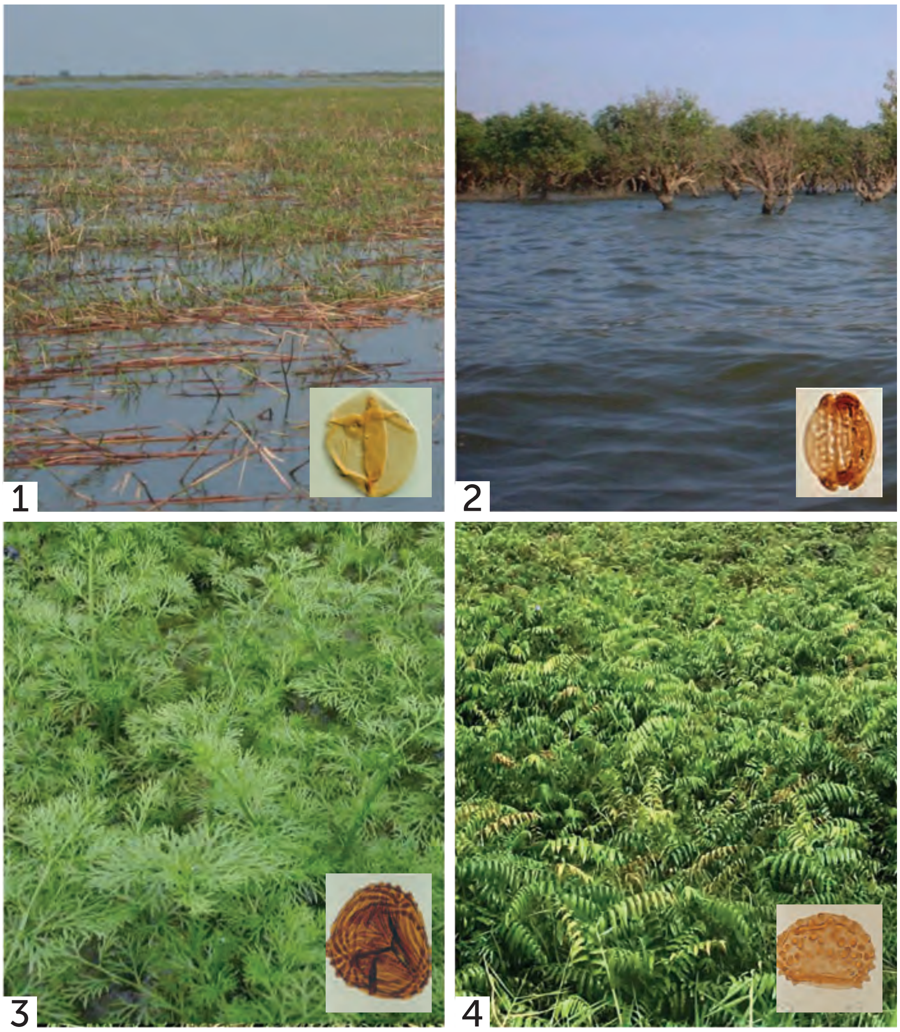


Fig. 1.24. Seasonal and fern swamps. 1, Grass-dominated swamp at Tonle Sap, inset, Monoporites annulatus*; 2,* Barringtonia acutangula *swamp during the flood at Tonle Sap , inset,* Marginipollis concinnus*; 3,* Ceratopteris thalictroides *forming a floating vegetation mat , inset,* Magnastriatites grandiosus*; 4,* Stenochlaena palustris *swamp in Brunei , inset,* Verrucatosporites usmensis *(photo 2 by D. Penny, photos 1, 3, 4 by RJM).*

Swamp forests, which currently occupy about 10% of the floodplain, but formerly would have been more extensive (Campbell et al., 2006), are of low diversity and are dominated by *Barringtonia acutangula* and *Diospyros cambodiana*, forming the 'Forét Inondée' of Rollet (1972), and Legris and Blasco (1972). Additional woody genera include *Acacia*, *Brownlowia*, *Combretum*, *Elaeocarpus*, *Ficus*, *Xanthophyllum* and others. During the flood, trees are submerged up to their lower crowns (Fig. 1.24.2). Swamp scrublands form the dominant vegetation over 80% of the floodplain and are characterised by similar species such as *Barringtonia acutangula* and *Brownlowia paludosa*, but also with other shrubby elements (Campbell et al., 2006).

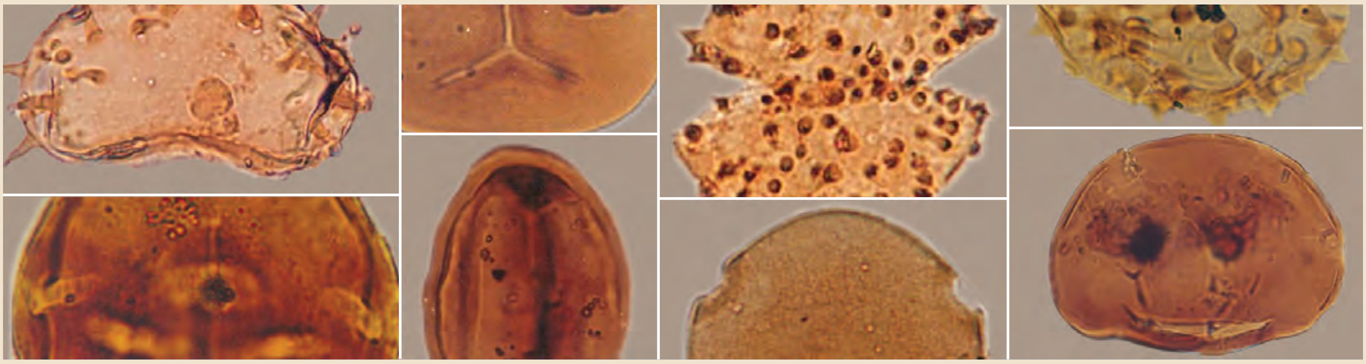
The presence of former seasonal swamps, especially in the Oligocene of the Malay Basin, may be reflected by the presence of common *Marginipollis concinnus* with *Discoidites novaguineensis*, reflecting the presence of *Barringtonia* and *Brownlowia* swamps.

Floating vegetation mats

The shallow shoreline of Tonle Sap supports dense mats of 1 to 3 m-tall herbaceous vegetation that may be emergent from shallow water, but typically becomes dislodged and forms floating mats that float freely over the lake (Fig. 1.24.1), which are dominated by a wide variety of grasses and sedges, together with *Alocasia*, *Ipomoea*, *Ludwigia*, *Merremia* and *Polygonum* (Campbell et al., 2006). These floating mats are also characterised by floating ferns, especially of the introduced *Salvinia* and *Pistia*, and it is possible that these replaced *Ceratopteris* (Fig. 1.24.4), which is a floating fern that is very common in Cenozoic palaeolakes in the Oligocene of the Malay, West Natuna and Cuu Long Basins (Morley et al., 2003; Morley et al., 2019) and is also thought to have formed floating mats (Morley and Morley, 2013).

Floating vegetation mats in the Oligocene and Miocene of the Malay Basin are thought to be reflected by maxima of *Magnastriatites grandiosus*, indicating the presence of *Ceratopteris*, which as noted above, is very common in many Malay Basin and other successions.

Section 2



DESCRIPTION OF POLLEN AND SPORES

Taxa are presented under headings of increasing morphological complexity, beginning with Pteridophyte spores, and followed by Gymnosperms and Angiosperms, with a final section on freshwater algae. Taxa are illustrated on Plates 1-29 and a representative image from each relevant Plate is included with the taxon description to aid characterisation. After discussion of the likely botanical affinity and ecology in instances where botanical attribution is clear, a photograph is included of the plant that is likely to have produced each pollen or spore type.

For each taxon, after the taxon name, a list of synonymies is presented, showing other publications where each palynomorph is described and illustrated. This may not be complete, but sufficient for the reader to understand the nomenclatural history of each taxon. This is followed by a full description, and an indication of size variation, and remarks on how the palynomorph might differ from closely related taxa. This in turn is followed by an indication of its stratigraphic distribution, and its likely botanical source. The final part presents a discussion of the probable ecology of the parent plant, a suggested name to be applied by Quaternary workers, who may prefer to compare pollen and spores with extant plant taxa rather than form-taxa, and a suggested ecological group, into which pollen types could be placed when grouping pollen to help with climate and environment interpretation.

Naming fossil pollen in the Quaternary (From Morley, 2020)

Palynologists working on the Quaternary identify pollen by comparing fossil pollen with modern reference material taken from named herbarium specimens. All palynological laboratories should have a reference collection of modern pollen, classified by plant family. Identification just by comparing with the literature will never be as accurate as if actual named pollen is examined, because referenced pollen can be examined in different perspectives, and the exine structure can be evaluated using LO analysis.

In looking at Recent pollen, identifications can be made at different levels of certainty in different taxa, as plant groups can be either eurypalynous (many pollen types) or stenopalynous (very few types).

Some examples:

In the mangrove genus *Sonneratia*, all species can be identified on pollen characters (Muller, 1969), e.g.,

'*Sonneratia caseolaris* pollen',
'*Sonneratia alba* pollen',
'*Sonneratia ovata* pollen',
Nypa has only one species (Nypa fruticans), so we can confidently name *Nypa* pollen as '*Nypa fruticans* pollen', etc.

In *Alangium* most species can be identified on pollen characters (Morley, 1982b), but some species pairs have the same pollen type.

We can deal with these by adding 'type' after a species name, so because the two Indonesian species *Alangium rotundifolium* and *A. kurzii* have the same pollen type, one species could be nominated, followed by 'type' e.g., '*Alangium kurzii* type pollen'.

There are only a few genera in which pollen varies at the species level in this manner, as a 'rule of thumb' pollen types compare to plant genera. Some good examples are: *Acanthus, Durio, Ilex, Gonystylus, Oncosperma, Neoscortechenia, Pometia, Pandanus* pollen

However, some closely related genera have the same pollen type, for instance the two oak genera *Lithocarpus* and *Castanopsis* have the same pollen type, so rather than to say '*Lithocarpus/Castanopsis* pollen' we can simply use: - '*Lithocarpus* type pollen'.

Similarly, the genera *Casuarina* and *Gymnostoma* have the same type, and so we name it: - '*Casuarina* type pollen'.

Some stenopalynous families have a single pollen type, all grasses produce basically similar pollen, so we could say: - 'Poaceae pollen'.

But Chenopodiaceae and Amaranthaceae pollen is very similar, so these should be named: - 'Chenopodiaceae type pollen'. These are now incorporated into the same family, Amaranthaceae.

The above approach, suggested by Anderson and Muller (1975), is very simple and unambiguous.

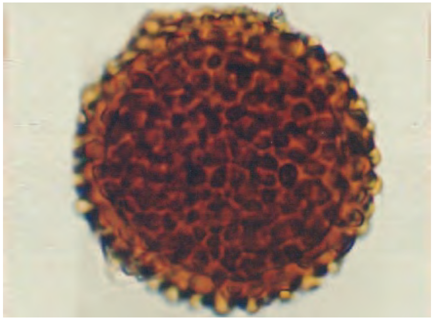
For pollen, it is not appropriate to add 'spp.' as we are dealing with pollen types that essentially relate to clades, and not species. Such notation can be used for foraminifera, which is OK, but not for pollen. The only exception is for those genera in which all species can be identified using pollen, such as *Sonneratia* and *Alangium*.

2.1 ALETE SPORES

Genus *Corrusporis*
Krutzsch 1967

Type species:
Corrusporis tuberculatus Krutzsch 1967.

Corrusporis tuberculatus
Krutzsch 1967. Plate 1, Fig. 1



Selected synonymy:
1967 *Corrusporis tuberculatus* Krutzsch, p. 226, Pl. 89, Figs. 1-4.

Description:
Spores alete, radially symmetrical, spherical, amb circular; exine sculptured with baculae to verrucae of 3 to 5 μm in diameter, two-layered and approximately 1 μm thick.

Dimensions:
Diameter 33 (54) 71 μm (3 specimens measured from various horizons).

Distribution:
Very rare.

Stratigraphic distribution:
First recorded from the middle Oligocene of Germany (Krutzsch, 1967) and subsequently from the middle Miocene of Poland by Worobiec (2009).

Botanical affinity:
Characteristic in the genus *Pohlia* (Bryaceae), discussed by Krutzsch (1967).

Ecological group:
Alete spores.

2.2 MONOLETE SPORES

Schizaea dichotoma*, kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).*

Genus *Laevigatosporites*
Ibrahim 1933

Type species:
Laevigatosporites vulgaris (Ibrahim 1932) Ibrahim 1933.

Generic remarks:
Smooth monolete spores which may either be a true reflection of the spore morphology or may be derived from species which bear perine, but from which the perine is lost through fossilisation. Because of this the form-genus *Laevigatosporites* Ibrahim 1933 which accommodates laevigate monolete spores is really a ‘junk basket’ of many unrelated spore types. Occasionally, however, a morphotype of *Laevigatosporites* may occur which is stratigraphically useful. A review of spore morphology of over 500 species of Malaysian ferns by Morley (1976), by reference to the fern flora according to Holttum (1954) indicated that just a few Malaysian genera exhibit this morphology in a fresh state, including *Aglaomorpha, Dipteris, Gleichenia* (in part), *Leptochilus, Lindsaya, Microsorium* (in part) and *Polypodium* (in part). The following list, however, which is not exhaustive, includes genera which may lose their perine during fossilisation or palynological processing and subsequently appear either psilate or weakly scabrate: *Asplenium, Athyrium, Blechnum, Bolbitis, Crypsinus, Cyclosorus, Diplazium, Drynaria, Drymoglossum, Dryopteris, Elaphoglossum, Hypolepis, Lepisorus, Leptochilus, Lindsaya, Microsorium, Phymatodes, Polystichum, Pyrrosia, Selliguea, Sphenomeris, Tectaria, Tapeindium* and *Woodwardia*. Anderson and Muller (1975) referred all smooth laevigate spores to *Asplenium* type, because they were studying a Holocene peat swamp, where *Asplenium nidus* was the dominant fern. Outside the Marudi locality, many additional taxa are likely, and to follow Anderson and Muller (1975) in this instance is misleading, for instance, at Danau Padang in Sumatra, most smooth monolete spores were thought to be derived from either *Cyclosorus* or *Blechnum* based on their association with scattered well-preserved spores that retained their perine (Morley, 1976).

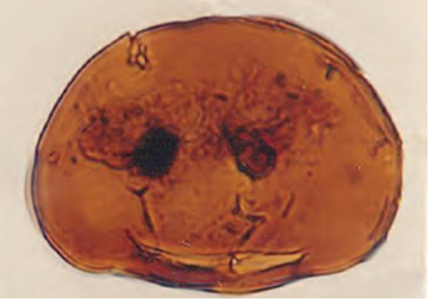
Laevigatosporites has a very long stratigraphic distribution, first appearing during the Late Carboniferous and Permian (e.g., Balme and Hennelly,

1956) and then returning during the Late Cretaceous, where its appearance may relate to the diversification of modern ferns in the shadow of the rain forest canopy (Schneider et al., 2004; Morley, 2011).

Here, smooth laevigate spores are divided somewhat arbitrarily into three taxa, based broadly on size and shape as given below. No attempt has been made to make comparisons with taxa described from other tropical regions, since the spore type shows such variability, for instance, there are 12 species of *Laevigatosporites* described from the Indian Cenozoic (Saxena and Trivedi, 2006). Also, two species are described from the Batu Arang coalfield near Kuala Lumpur, by Trivedi et al. (1982). The Batu Arang species, *L. mulleri* and *L. kualalumpurensis* are excluded from this discussion due to their low-quality illustrations and inadequate circumscription.

Laevigatosporites discordatus

Pflug in Thomson and Pflug 1953.
Plate 1, Figs. 3, 4



Selected synonymy:

1953 *Laevigatosporites discordatus* Pflug in Thomson and Pflug, p. 59, Pl. 3, Figs. 39-44.
1957 *Laevigatosporites discordatus* Pflug in Thomson and Pflug; Pflug, p. 173, Fl. 8, Fig. 3.
1959 *Laevigatosporites discordatus* Pflug in Thomson and Pflug; Krutzsch, p. 195, Pl. 39, Figs. 429-430.

Description:

Spores bilaterally symmetrical, heteropolar, with convex distal outline and straight to slightly concave proximal outline in equatorial view, amb oval; monolete; laesura simple, more or less straight, extending half to two-thirds of the spore length; exine laevigate, 1 to 2 µm thick.

Dimensions:

Length 40 (48) 60 µm, width 25 (32) 45 µm (10 specimens measured from various horizons).

Stratigraphic distribution:

The oldest records are from the European early Maastrichtian and subsequently it is commonly recorded in the European Cenozoic (Thomson and Pflug, 1953; Kedves, 1973; Roche, 1973; Ashraf and Erben, 1986; Thiele-Pfeiffer, 1988; Russo-Ermolli, 1991; Jolley, 1992). In Malaysia, this spore type occurs commonly in Cenozoic sediments and was regularly present at most levels in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:

Laevigatosporites discordatus Pflug in Thomson and Pflug 1953 differs from *Laevigatosporites haardti* (Potoniè and Venitz) Thomson and Pflug 1953 in its thicker exine and larger size, and from *Laevigatosporites elongatus* sp. nov. in its thicker exine and less elongate shape.

Botanical affinity:

Derived from any of many fern genera, which have lost their perine, as discussed above.

Suggested name for Quaternary records:

Smooth monolete spores.

Ecological/Morphological group:

Undifferentiated monolete spores.

Plate 1

Fig. 1 *Corrusporis tuberculatus* Krutzsch 1967 (x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder F28/1.

Fig. 2 *Laevigatosporites haardti* (Potonié and Venitz) Thomson and Pflug 1953 (x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder F28/1.

Figs. 3, 4 *Laevigatosporites discordatus* Pflug in Thomson and Pflug 1953.
Fig. 3 (x 400), 4 (x 1000): Slide Malong-2, 1554 m, CC (S1); England Finder H39.

Figs. 5-7 *Laevigatosporites elongatus* Morley and Jaizan Jais sp. nov.
Figs. 5, 6 (x 400): Slide Malong-2, 1554 m, CC (S1); England Finder P33/1. Fig. 7 (x 400): Slide Malong-2, 1603.7 m, CC (S1); England Finder V25/3.

Figs. 8-10 *Microfoveolatosporis* spp.
Figs. 8, 9 (x 400):Slide Malong-2, 641.5 m, SWC (S2); England Finder V44/3. Fig. 10 (x 400): Slide Malong-2, 518 m, SWC (S1); England Finder T33.

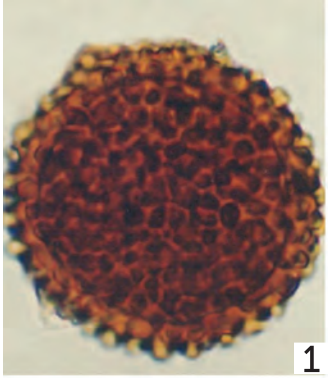
Fig. 11 *Punctatosporites* spp. (x 1000): Slide Malong-2, 1135-1140 m, DC (S1); England Finder N44.

Fig. 12 *Verrucatosporites usmensis* (van der Hammen 1956b) Potonié 1960a (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L40/4.

Fig. 13 *Verrucatosporites pseudoregulatius* Krutzsch 1967 (x 1000), 6 (x 400): Slide Malong-2, 1569.1 m, CC (S1); England Finder L8/1.

Figs. 14, 15 *Polypodiisporites favus* (Potonié in Potonié and Gelletich 1933) ex Potonié.
Fig. 14 (x 400), 15 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder G8.

Figs. 16, 17 *Polypodiisporites megabalticus* (Krutzsch 1967) Nagy 1973.
Fig. 16 (x 1000): Slide Malong-2, 1554 m, CC (S1); England Finder K20. Fig. 17 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder Q52/4.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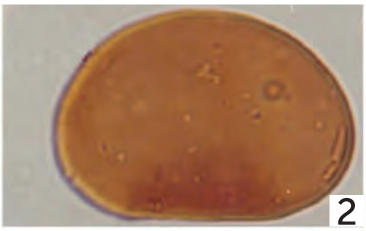
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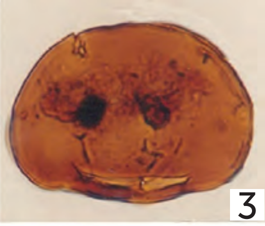
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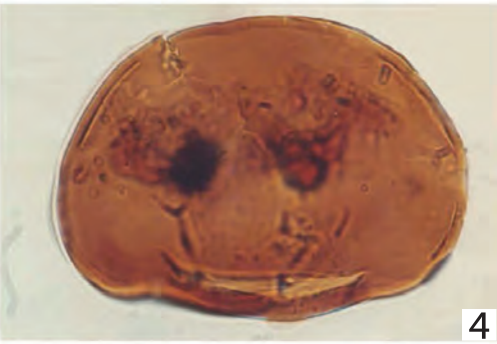
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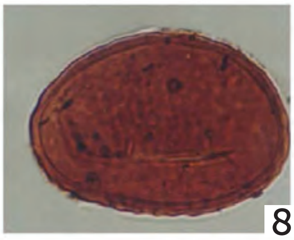
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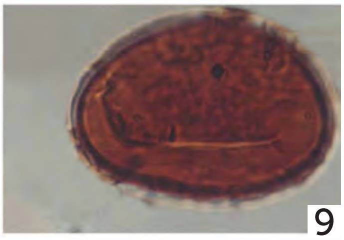
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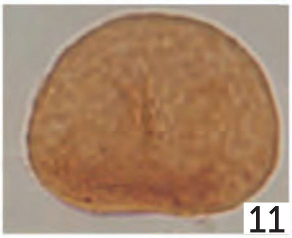
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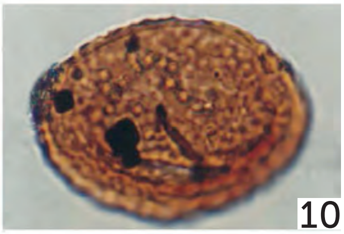
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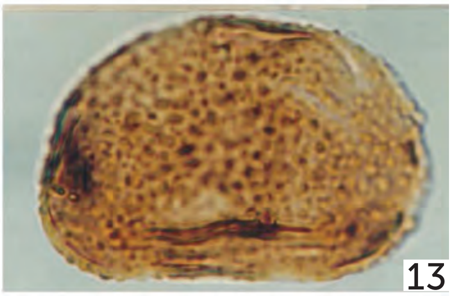
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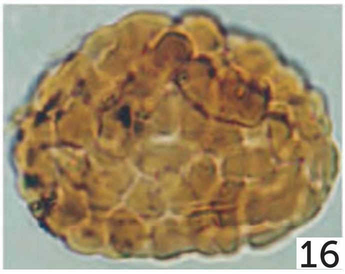
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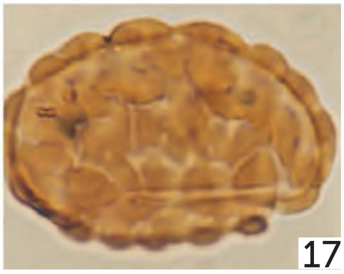
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Laevigatosporites haardti

(Potonié and Venitz) Thomson and Pflug 1953. Plate 1, Fig. 2

Selected synonymy:

1934 *Sporites haardti* Potonié and Venitz, p. 13, Pl. 1, Fig. 13.
1938 *Polypodiaceaesporites haardti* (Potonié and Venitz) Thiergart, p. 297, Pl. 22, Fig. 17.
1946 *Laevigatosporites ovatus* Wilson and Webster, p. 273, Fig. 5.
1947 *Monolites minor* Cookson, p. 135, Pl. 15, Figs. 27-38.
1953 *Laevigatosporites haardti* (Potonié and Venitz) Thompson. and Pflug., p. 59, Pl. 3, Figs. 27-38.

Description:

Spores bilaterally symmetrical, heteropolar, with convex distal outline and straight to slightly concave proximal outline in equatorial view, amb oval; monolete; laesura simple, more or less straight, extending half to two-thirds of the spore length; exine laevigate and 0.5 to 1 µm thick.

Dimensions:

Length 26 (35) 40 µm, width 14 (24) 31 µm (11 specimens measured from various horizons).

Stratigraphic distribution:

The oldest records are from the late Campanian of Sakhalin (Takahashi 1997), and it has subsequently been recorded globally in Cenozoic strata. This spore type is common in most Cenozoic sediments in Malaysia and is common through both Malong 5G-17.2 and Delah 5H-14.2 wells.

Remarks and comparison:

This species differs from *Laevigatosporites discordatus* in its smaller size and thinner exine; from *Laevigatosporites elongatus* sp. nov. by its smaller size and less elongate shape.

Botanical affinity:

Derived from any of many fern genera, which have lost their perine, as discussed above.

Suggested name for Quaternary records:

Smooth monolete spores.

Ecological/Morphological group:

Undifferentiated monolete spores.

Laevigatosporites elongatus

Morley and Jaizan Jais sp. nov. Plate 1, Figs. 5-7

Derivation of name:

Name derived from the elongated nature of the spore.

Holotype:

Plate 1, Figs. 5, 6. Slide Malong-2, 1554 m, CC (S1), England Finder P33/1.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1554 m depth, (S1); England Finder P33/1. Age latest Oligocene zone PR6/7.

Description:

Spores bilaterally symmetrical, heteropolar, elongate bean-shaped in equatorial view with slightly convex distal outline and straight to slightly concave proximal outline, polar view not observed; monolete; laesura indistinct; exine laevigate, 0.5 to 1 µm thick.

Dimensions:

Length 44 (55) 64 µm, width 23 (30) 41 µm (4 specimens measured from various horizons).

Stratigraphic distribution:

Common throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:

This species differs from *Laevigatosporites discordatus* in its thinner exine and more elongate or slender shape; and from *Laevigatosporites haardti* due to its more slender shape.

Botanical affinity:

The distinctive shape of this species suggests that it could be derived from a single fern taxon, but to identify it with an extant genus would require a detailed study of Malaysian fern spores.

Suggested name for Quaternary records:

Smooth monolete spores.

Ecological/Morphological group:

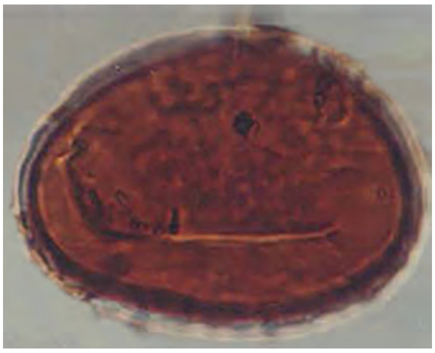
Undifferentiated monolete spores.

Microfoveolatosporis Krutzsch 1959

Type species:
Microfoveolatosporis pseudodentatus Krutzsch 1959 (by original designation).

Generic remarks:
According to Jansonius and Hills (1976), *Microfoveolatosporites* Nakoman 1966 is an obligate junior synonym of *Microfoveolatosporis*.

***Microfoveolatosporis* spp.** Plate 1, Figs. 8-10



Description:
Spores bilaterally symmetrical, heteropolar, elongate, bean-shaped in equatorial view, monolete; with plano- to slightly concavo-convex shape, simple laesura, exine 2 to 3 µm thick, microfoveolate to foveolate (foveolae 0.5 to 1.5 µm in diameter).

Dimensions:
Length 41 (53) 64 µm, width 29 (36) 46 µm (9 specimens measured from various horizons).

Stratigraphic distribution:
Regularly present in most sediments of Cenozoic age from Malaysia. Present in low frequencies throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
Some specimens resemble *Microfoveolatosporis pseudodentatus* and part of *Microfoveolatosporis* spp. from the Neogene of Papua New Guinea as photographed by Playford (1982).

Botanical affinity:
Most likely from Oleandroideae/ Oleandraceae, and other 'higher' ferns, many of which have lost their perine as for *Laevigatosporites* but leaving a foveolate exine structure.

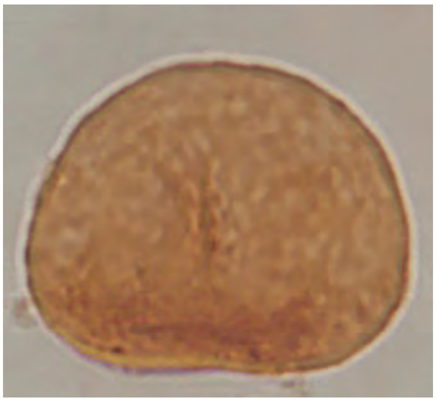
Suggested name for Quaternary records:
Ornamented monolete spores.

Ecological/Morphological group:
Undifferentiated monolete spores.

Genus *Punctatosporites* Ibrahim 1933

Type species:
Punctatosporites minutus Ibrahim 1933.

***Punctatosporites* spp.** Plate 1, Fig. 11



Description:
Spores bilaterally symmetrical, heteropolar, plano-convex in equatorial view, amb oval; monolete; laesura straight, simple, extending half to two-thirds of the spore length; exine punctate with scabrate to granulate sculpture, thin (0.5 µm thick).

Dimensions:
Length 25 (28) 34 µm, width 16 (20) 24 µm (10 specimens measured from various horizons).

Stratigraphic distribution:
Common throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Comparison:
This spore type shows some resemblance to *Punctatosporites* sp. of Kemp and Harris (1977), but the latter is differently sculptured in detail and is generally smaller.

Botanical affinity:
Probably derived from a variety of taxa that have lost their perine, as discussed above.

Suggested name for Quaternary records:
Ornamented monolete spores.

Ecological/Morphological group:
Most likely from 'higher' ferns, which have lost their perine as for *Laevigatosporites* but leaving a scabrate to granulate exine structure.

Many Verrucatosporites *spp. are probably sourced from* Nephrolepis *spp., here growing in alluvial swamp behind mangroves at Kuala Selangor, Selangor, Malaysia (photo by RJM).*

Genus *Verrucatosporites*
(Pflug ex Thomson and Pflug 1953)
emend. Potonié 1956

Type species:
Verrucatosporites alienus (Potonié 1931) Thomson and Pflug 1953 (by original designation).

Generic remarks:
This genus is strictly used here for monolete spores which bear discrete and widely spaced verrucae without giving appearance of a negative reticulum. Khan and Martin (1971) emended the genus *Polypodiisporites* to include the genera *Verrucatosporites* and *Polypodiidites*. In doing so, they have included monolete spores of closely spaced verrucae which gives a negative reticulum appearance with spores of more widely spaced verrucae without negative reticulum appearance.

Verrucatosporites usmensis

(van der Hammen 1956b) Potonié 1960.
Plate 1, Fig. 12

Selected synonymy:

1954 *Verrumonoletes usmensoides* van der Hammen.
1956 *Verrumonoletes usmensis* van der Hammen, p. 116, Pl. 2, Fig. 7.
1960a *Verrucatosporites usmensis* (van der Hammen) Potonié, p. 69.
1968 *Verrucatosporites usmensis* (van der Hammen) Germeraad, Hopping and Muller, p. 290, Pl. II, Fig. 3.
1971 *Polypodiisporites usmensis* (van der Hammen) Khan and Martin, p. 478.
1972 *Polypodiidites usmensis* (van der Hammen) Hekel, p. 6, Pl. 1, Figs. 8-9.
1975 *Verrucatosporites usmensis* (van der Hammen) Germeraad, Hopping and Muller; Salard, p.107, Pl. 3, Figs. 3-4.
1982 *Polypodiidites usmensis* (van der Hammen) Hekel; Playford, p. 42, Pl. 5, Figs. 4, 7.

Description:
Spores, bilaterally symmetrical, heteropolar, with convex distal outline and straight or slightly concave proximal outline; in polar view ellipsoidal; laesura monolete; exine with verrucae or gemmae up to 3 μm high and 3 μm wide, rather widely and variably spaced, exine thickness about 1 μm, exine often pale coloured compared to other spores.

Dimensions:
Length 30 (37) 49 μm, width 21 (24) 33 μm (8 specimens measured from various horizons).

Remarks:
According to Jansonius and Hills (1976), Potonié (1960a) considers *Verrumonoletes* van der Hammen 1956 to be a synonym of *Verrucatosporites* and assigns the type species to *Verrucatosporites* (van der Hammen) Potonié 1960a. This was later echoed by Germeraad et al, (1968) who also transferred the genus *Verrumonoletes* to *Verrucatosporites*.

Stratigraphic distribution:
Verrucatosporites usmensis has been recorded from the middle Eocene to Holocene of northern South America and Nigeria and the Oligocene onward from Borneo (Germeraad et al., 1968), and also from the middle Eocene Nanggulan Formation in Java (Lelono, 2000), the late Eocene of Myanmar (Huang et al., 2021), the Neogene of Queensland (Hekel, 1972), and Oligo-Miocene of India (Kumar, 1994; Misra and Kapoor, 1994; Ramanujam et al., 1991) and Pliocene of Papua New Guinea (Cookson, 1957; Playford, 1982). Widely represented from the late Eocene onwards across Malaysia, and abundant throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:
Stenochlaena palustris (Blechnaceae).

Source ecology:
Climbing fern characteristic of relatively open settings, especially in freshwater swamps, sometimes floating, mostly in the lowlands, but it can occur at higher altitudes. In well sections from the North Malay Basin and offshore Vietnam, *V. usmensis* is sometimes extremely abundant, and is thought to reflect widespread fern-dominated swamps (Morley and Morley, 2013).

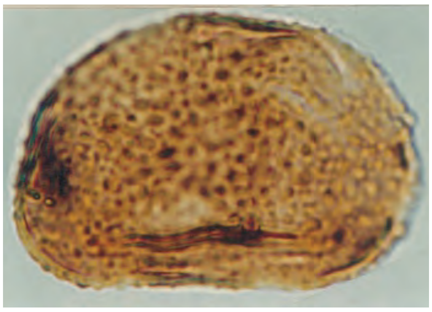
Stenochlaena palustris *growing on peat after forest was felled, Seria, Brunei (photo by RJM).*

Fertile frond of Stenochlaena palustris*, Singapore Botanical Gardens (photo by RJM).*

Suggested name for Quaternary records: *Stenochlaena palustris.*

Ecological/Morphological group: Climbing ferns.

Verrucatosporites pseudoregulatius
Krutzsch 1967. Plate 1, Fig. 13



Selected synonymy:
1967 *Verrucatosporites pseudoregulatius* Krutzsch, p. 192, Tab. 3, Pl. 72, Figs. 1-4.
1973 *Polypodiisporites pseudoregulatius* (Krutzsch) Nagy, p. 458.

Description:
Spores, bilaterally symmetrical, heteropolar, plano-convex in equatorial view, amb elliptical; monolete; laesura straight, simple, extending half to two-thirds of the spore length; exine sculptured with a mixture of fine and coarse polygonal verrucae (ranging from 0.5 to 2 µm in diameter and 0.5 to 1 µm in height); exine thickness 1 µm.

Dimensions:
Length, minimum 45 µm, maximum 47 µm; width, minimum 31 µm, maximum 34 µm (2 specimens measured).

Stratigraphic distribution:
Regularly present in the Oligocene to Pliocene of Malaysian sediments, present in low percentages in Malong 5G-17.2 and Delah 5H-14.1 wells and more frequently distributed in the lower part of the succession. Also found in the Miocene of Germany (Krutzsch, 1967) and Japan (Takahashi, 1981).

Comparison:
This species shows some resemblance to *Verrucatosporites tenellis* (Krutzsch, 1959) Krutzsch 1967 photographed by Salard (1975), but the latter differs in having more or less uniform sized verrucae. *V. microverrucatus* Krutzsch 1967 is generally smaller, and its verrucae are more angular in shape and more uniform in size. *V. pseudoregulatius* differs from *V. usmensis* by having finer, lower, and denser sculptural elements.

Botanical affinity:
Possibly *Polypodium* or *Microsorium* (Polypodiaceae).

Suggested name for Quaternary records:
Ornamented monolete spores.

Ecological/Morphological group:
Undifferentiated monolete spores.

Stenochlaena palustris *festooning trunks of swamp forest trees, along the forest margin, freshwater swamp forest, Sedili River Johor, Malaysia (photo by RJM).*

Genus *Polypodiisporites*

Potonié in Potonié and Gelletich 1933 ex Potonie 1956

Type species:

Polypodiisporites favus (Potonié in Potonie and Gelletich 1933) ex Potonie 1956.

Generic remarks:

This genus is used here for monolete spores with flat verrucae or areolae that are closely distributed giving appearance of a negative reticulum as per Potonié's original diagnosis and not as emended by Khan and Martin (1971). *Polypodiidites* Ross 1949 bears higher verrucae and, as indicated by Jansonius and Hills (1976), have markedly reduced proximal sculpture.

Polypodiisporites favus

(Potonié in Potonié and Gelletich 1933) ex Potonié 1956. Plate 1, Fig. 14

Selected synonymy:

1931 *Polypodii* (?) *-sporonites favus* Potonié, p. 556, Fig. 3.

1933 *Polypodiisporites favus* (Potonié) in Potonié and Gelletich, p. 524, Pl. 2, Fig. 16.

1934 *Polypodiisporites favus* (Potonié) Potonié, p. 38, Pl. 1, Figs. 19, 20.

1953 *Verrucatosporites favus* (Potonié 1931) Thomson and Pflug, p. 60. Pl. 3, Figs. 52-55, Pl. 4, Figs. 1-4.

1956 *Polypodiisporites favus* (Potonié 1931) ex Potonié, Synopsis I, p. 78, Pl. 10, Fig. 105.

1967 *Verrucatosporites favus* (Potonié 1931) Thomson and Pflug 1953 subsp. *favus* Krutzsch, p. 184, Tab. 3, Pl. 68, Figs. 1-8.

1979 *Polypodiidites pohangensis* Takahashi in Takahashi and Kim, p. 25, Pl. 1, Fig. 22, Pl. 2, Fig. 1.

Description:

Spores bilaterally symmetrical, heteropolar, with convex distal outline and more or less straight proximal outline, amb oval; monolete; laesura simple, straight, extending half to two-thirds of the spore length and open in some specimens; sculpture consists of low (1 to 3 μm high), close-spaced, smooth verrucae often separated by a fine negative reticulum; verrucae irregularly rounded in basal outline, 3 to 6 μm in diameter and 1 to 3 μm high; exine 1 to 3 μm thick; low and flat verrucae giving the undulating appearance of spore outline.

Dimensions:

Length 39 (48) 63 μm, width 29 (33) 45 μm (14 specimens measured from various horizons).

Stratigraphic distribution:

Initially described from the Eocene of Germany (Potonié, 1931), with the oldest records from the Late Cretaceous of North America (e.g., Brideaux, 1971) and Siberia (Levina et al., 1978). Widely represented throughout the Oligocene to Pliocene of Malaysian sediments, Present throughout the Malong 5G-17.2 and Delah 5H-14.1 wells, but more common in the lower part of the section.

Comparison:

Verrucatosporites rugufavus Krutzsch 1967 from the Miocene of Germany and *Polypodiisporites* sp. cf. *P. rugufavus* Kemp and Harris 1977 from the Eocene to Oligocene of the Ninetyeast Ridge differ in having verrucae in distinct radial alignment of their long axes. *Polypodiidites inangahuensis* Couper 1953 is generally larger in size.

Botanical affinity:

Based on the work of Nayar and Devi (1964, 1965) similar verrucate spores occur in many Malaysian fern genera, including *Belvisia*, *Ctenopteris*, *Drynaria*, *Histiopteris*, *Lemmaphyllum*, *Lepisorus*, *Microsorium*, *Nephrolepis*, *Oleandra* and *Polypodium*. The closest comparison is with *Polypodium* and other Polypodiaceae.

Source ecology:

The most likely source of this spore type in Malaysia is either the epiphytic Polypodiaceae or the terrestrial, largely swamp fern *Nephrolepis* (Morley, 1976).

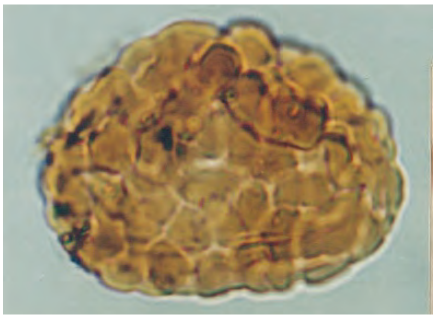
Suggested name for Quaternary records:

Polypodium type.

Ecological/Morphological group:

Ornamented monolete spores.

Polypodiisporites megabalticus (Krutzsch 1967) Nagy 1973. Plate 1, Figs. 16, 17



Selected synonymy:

1967 *Verrucatosporites megabalticus* Krutzsch, p. 180, Tab. 3, Pl. 66, Figs. 1-13.
1973 *Polypodiisporites megabalticus* (Krutzsch) Nagy, p. 458.
1974 *Verrucatosporites megabalticus* Krutzsch; Ziembinska-Tworzydlo, p. 341, Pl. 7, Figs. 5a-5b.

Description:

Spores bilaterally symmetrical, heteropolar, plano-convex in equatorial view, amb elliptic; monolete; laesura straight, simple, slightly open, extending to two-thirds of the spore length; exine coarsely verrucate; verrucae irregularly rounded, closely spaced giving the appearance of negative reticulum, 3 to 5 µm in diameter and 1.5 to 2 µm high, and coalesce to form broad and elongate discrete ridges of about 5 µm in breadth and 10 µm in length; exine thickness 1 µm.

Dimensions:

Length 36 (39) 45 µm, width 26 (28) 30 µm (4 specimens measured from various horizons).

Stratigraphic distribution:

First described from the Oligocene of Germany (Krutzsch, 1967), and subsequently often reported from the European Oligo-Miocene, and occasionally from China (Song et al., 1985). The oldest references are, however, from the Late Cretaceous of North America (Kidson, 1971). Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:

This species was first described as *Verrucatosporites megabalticus* by Krutzsch (1967). Because of its verrucae that are low, closely spaced and giving the appearance of negative reticulum, in the authors' opinion, it should be classified under *Polypodiisporites*. It differs from *Polypodiisporites favus* by its elongate and coalescing verrucae forming broad discrete ridges. *Polypodiidites* sp. photographed by Playford (1982, Pl. 4, Figs. 1-3) shows some resemblance to this species.

Botanical affinity:

As for *Polypodiisporites favus* above, probably derived from ferns within the family Polypodiaceae, or the mainly swamp fern *Nephrolepis*.

Source ecology:

Species producing this spore type commonly occur as epiphytes and in terrestrial settings.

Suggested name for Quaternary records:

Polypodium type.

Ecological/Morphological group:

Ornamented monolete spores.

Genus *Undulatopsorites*
Leschik 1959

Type species:
Undulatosporites lucens Leschik 1959 (by original designation).

Undulatosporites bracteatus

Morley and Jaizan Jais sp. nov. Plate 2, Figs. 1-2

Derivation of name:

From '*bracteae*', Latin for 'ridged'.

Holotype:

Plate 2, Fig. 1, 2. Slide Malong-2, 641.5 m, SWC (S2); England Finder Q21/3.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene, zone PR14.

Description:

Spores bilaterally symmetrical, heteropolar, plano-convex in equatorial view; amb elliptic; monolete, laesura straight, simple, extending to two-thirds of the spore length; exine bearing sculptural elements arranged into undulating ridges, that are not forming a reticulum.

Dimensions:

Length 30 (33) 37 µm, width 17 (22) 24 µm (3 specimens measured from various horizons.

Stratigraphic distribution:

Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:

This spore type closely resembles the fern *Nephrolepis cordifolia* (Oleandraceae), but not all *Nephrolepis* spp.

Source ecology:

Various terrestrial ecological niches.

Suggested name for Quaternary records:

Nephrolepis type.

Ecological/Morphological group:

Ornamented monolete spores.

Plate 2

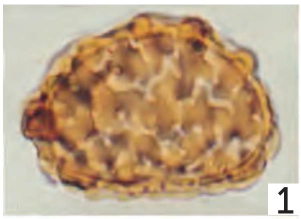
Figs. 1, 2 *Undulatisporites bracteatus* Morley and Jaizan Jais sp. nov. Figs. 1, 2 (x 1000 holotype): Slide Malong-2, 641.5 m, SWC (S2); England Finder Q21/3.

Figs. 3-6 *Stenochlaenidites papuanus* (Cookson 1957) Khan 1976a.
Figs. 3, 4 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder N19. Figs. 5, 6 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder K28.

Figs. 7-11 *Stenochlaenidites cristatus* Jaizan Jais and Morley sp. nov. Figs. 7, 8 (Holotype, x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder V5. Figs. 9, 10 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder Q31.

Figs. 11 *Stenochlaenidites papuanus* (Cookson 1957) Khan *1976a,* SEM image by Playford (1982), from Papua New Guinea (x 1000) Plate 4 Fig. 8.

Figs. 12, 13 *Scolocyamus magnus* Playford 1982.
Fig. 12 (x 800): Slide Malong-2, 900-910 m, DC (S1); England Finder M39.
Fig. 13 Holotype (x1000) SEM image by Playford (1982) Plate 8 Fig. 9.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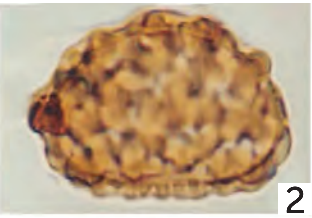
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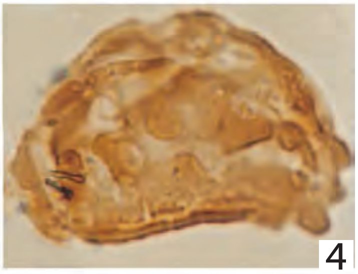
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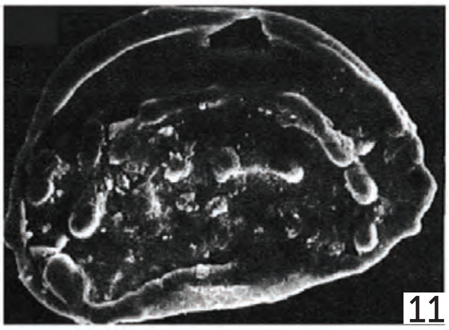
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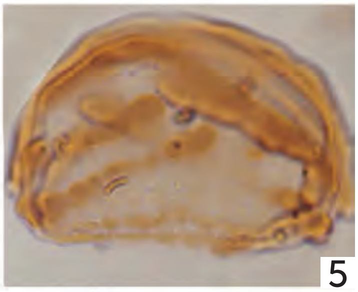
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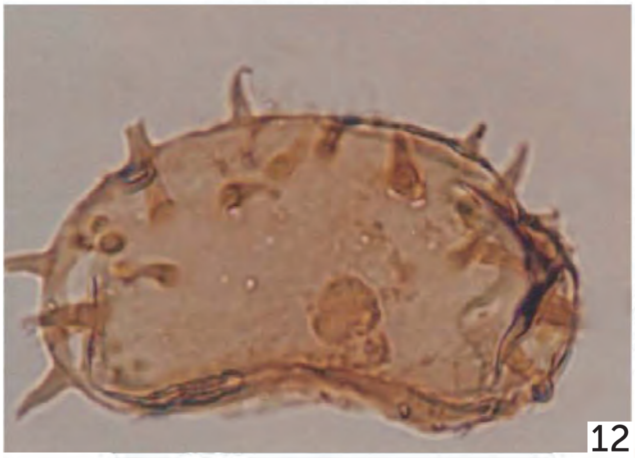
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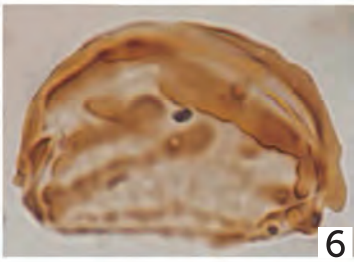
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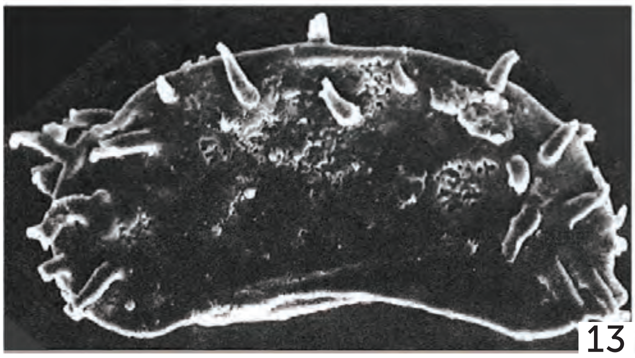
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Genus *Stenochlaenidites*

Khan 1976a

Type species:
Stenochlaenidites papuanus (Cookson 1957) Khan 1976a (by original designation).

The genus *Stenochlaenidites* is applied to spores of species of *Stenochlaena* that bear tuberculate ridges rather than verrucae, as in the widespread species *S. palustris*. The value of spore morphology in species differentiation in *Stenochlaena* was brought to attention by Holttum (1932) who noted that spores were either verrucate, as in *S. palustris* (form-taxon *Verrucatosporites usmensis*), with tuberculate ridges, as in *S. laurifolia*, and *S. milnei*, and also the African species *S. tenuifolia* (Tardieu-Blot, 1964) and *S. mildbraedii*, or echinate, as in the *S. areolaris*. Muller (1972) noted that the form with tuberculate ridges, which he termed the *S. laurifolia* type, had a restricted, late Miocene to Pliocene stratigraphic range in Brunei and Sarawak. The stratigraphic range of this morphotype which has subsequently been shown to be a useful index fossil, was evaluated across tropical Asia by Morley (1978, 1991) who showed that it formerly extended to northern India and China during the Pliocene but may occur earlier in the middle Miocene in New Guinea and the Philippines. At the time of Holttum's taxonomic review (Holttum, 1932, 1937), he was unable to access the type specimen of *S. laurifolia* in Prague due to political reasons. Later, Holttum (1968) examined the type specimen and found that it was in the range of variation of *S. palustris*, and therefore not conspecific with duplicate herbarium specimens at Kew and British Museum, bearing the same number. Holttum (1969) subsequently published a new name for this species, *S. cumingii.* based on the Kew specimen (Cuming 226).

The name *S. laurifolia* is therefore a junior synonym of *S. palustris* and it was suggested that the term '*S. laurifolia* type' should be replaced with '*Stenochlaena milnei* type' by Morley (1991).

Fossil spores of this type show additional variation, dependent on the number of tubercles, versus the number of verrucae. Some specimens simply show an alignment of verrucae, termed 'type a' (Fig. 2.1), others show weak tubercles interspersed with verrucae (type b), well developed tubercles with a few verrucae (type c) and strong tubercles without verrucae (type d). *S. milnei* is more like type b, whereas *S. cumingii* resembles c or d. Types a and b have a longer stratigraphic range, whereas types c and d are restricted to the Pliocene and latest Miocene.

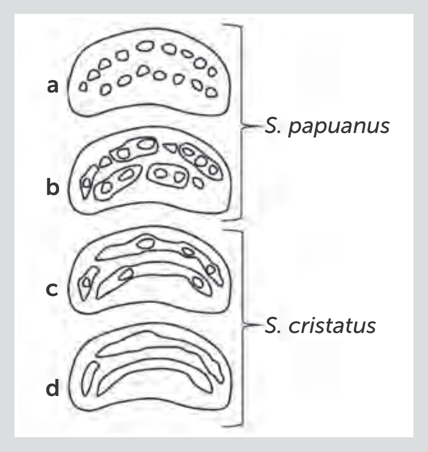
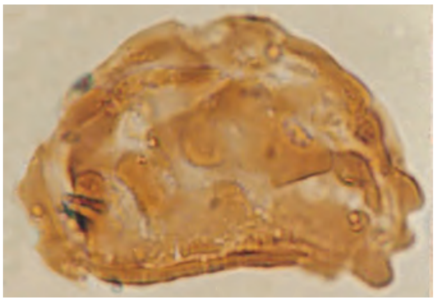


Fig. 2.1 Stenochlaenidites *morphotypes*

Stenochlaena spores have been illustrated in SEM by Tyron and Lugardon (1991) and Chambers (2013). Unfortunately, Chambers mis-labelled the tuberculate specimen as *S. palustris,* adding additional confusion to naming spores attributable to *Stenochlaena*.

Stenochlaenidites papuanus

(Cookson 1957) Khan 1976a. Plate 2, Figs. 3-6



Selected synonymy:

1957 *Schizaea papuana* Cookson (partim), p. 44, Pl. 8, Figs. 8, 9, 11 (non Pl. 8, Figs. 10, 12)
1960a *Schizaeoisporites papuana* (Cookson) Potonié, p. 70, Pl. 5, Fig. 74.
1976a *Stenochlaenidites papuanus* (Cookson) Khan, p. 759, Fig. 11.
1982 *Stenochlaenidites papuanus* (Cookson) Khan; Playford, p. 40, Pl. 4, Fig. 8; Pl. 5, Figs. 1-3.
1988 *Stenochlaena laurifolia* Caratini and Tissot, Pl. 1, Figs.1-2.
2020 *Stenochlaena milnei* type spores Morley et al. Supplement Fig. 1.13.

Description:
Spores bilaterally symmetrical, heteropolar, with convex distal outline and straight to concave proximal outline in equatorial view (polar view not observed); monolete; laesura indistinct; exine verrucate outside the contact area; verrucae mostly uniserially arranged to form crenate and discontinuous ridges; the overall curvature of the ridges more or less follow the distal outline of the spore; exine 2 to 4 µm thick.

Dimensions:
Length 35 (44) 60 µm, width 25 (28) 33 µm (10 specimens measured from various horizons).

Remarks:
This spore type most closely resembles *S. milnei* type b, discussed above.

Stratigraphic distribution:
Stenochlaenidites papuanus has been recorded from the middle Miocene to Recent of Papua New Guinea (Cookson, 1957; Khan, 1976a; Playford, 1982; Morley, 1991) and from the late Miocene to Pliocene of Borneo (Muller, 1972; Morley, 1991). The extinction of *S. papuanus* in northwest Borneo has been dated at 1.5 Myr, at the time of extinction of the nannofossil *Calcidiscus macintyrei*, and the same date is thought to apply in Java (Morley et al., 2020). It is present in low percentages from the late Miocene and Pliocene in Malong-5G-17.2 well within zones PR14 and 15.

Comparison:
This species differs from *S. cristatus* by its shape and distinct verrucate and crenate ridges. The distal outline and the curvature of the ridges of *S. papuanus* are strongly convex as compared to *S. cristatus*.

Botanical affinity:
Stenochlaena milnei and *S. cumingii*, ferns of the family Blechnaceae. The name *S. laurifolia* has been previously applied, but his name is a junior synonym of *S. palustris*, as discussed above.

Source ecology:
Climbing ferns which in New Guinea occur in the same habitat as *S. palustris*, and commonly occur in swamps. (Holttum, 1968).

Suggested name for Quaternary records:
Stenochlaena milnei type b.

Ecological/Morphological group:
Climbing ferns.

Stenochlaenidites cristatus
Jaizan Jais and Morley sp. nov. Plate 2, Figs. 7-10

Derivation of name:
Name derived from the cristate or ridge-like sculpture.

Holotype:
Plate 2, Fig. 7-8. Slide Malong-2, 430.5 m, SWC (S2), England Finder V5. Grain compressed in equatorial aspect; grain length 39 μm, width 24 μm; exine 3 μm thick; verrucae 4 μm in diameter and 3 μm in height.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 430.5 m depth; age Pliocene, zone PR15.

Description:
Spores bilaterally symmetrical, heteropolar, with convex distal outline and straight to slightly concave proximal outline in equatorial view, polar view not observed; monolete; laesura indistinct; exine sculptured with well developed, slightly verrucate ridges which are more or less parallel to each other and follow the curvature of the spore distal outline; verrucae 4-5 μm in diameter and 3-4 μm in height; exine thickness 2-3 μm.

Dimensions:
Length 30 (41) 49 μm, width 21 (26) 34 μm (21 specimens measured from various horizons).

Remarks:
This spore is most similar to *S. cumingii* type c or d, as discussed above. There are transitional forms between *S. papuanus* and *S. cristatus*.

Stratigraphic distribution:
Present in low percentages from the upper part of the Malong 5G-17.2 succession within zone PR15.

Comparison:
This species is distinguished from *S. papuanus* by its slender shape and much reduced verrucae and more developed ridges. The distal outline and the curvature of the ridges of *S. cristatus* are less convex as compared to *S. papuanus*.

Botanical affinity:
Stenochlaena cumingii, ferns of the family Blechnaceae.

Source ecology:
Climbing and swamp ferns, as for *Stenochlaena palustris*.

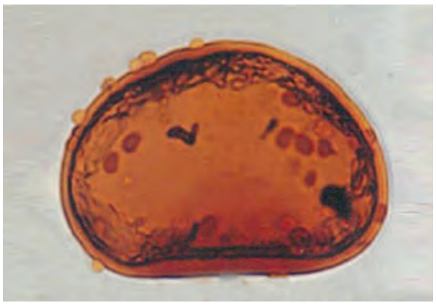
Suggested name for Quaternary records:
Stenochlaena milnei type c.

Ecological/Morphological group:
Climbing ferns.

Genus _Gemmatosporis_
Krutzsch 1959

Type species:
Gemmatosporis gemmatoides Krutzsch 1959 (by original designation).

Gemmatosporis gemmatoides
Krutzsch 1959. Plate 3, Fig. 1



Selected synonymy:
1955 Monolete, gemmate in Kuyl Muller and Waterbolk. p. 69, Pl. 4, Fig. 7.
1959 *Gemmatosporis gemmatoides* Krutzsch, p. 203.
1975 *Gemmatosporis gemmatoides* Krutzsch; Salard, p. 106, Pl. 2, Fig. 18.
1979 *Gemmatosporis gemmatoides* Krutzsch; Takahashi and Kim, p. 25, Pl. 2, Figs. 3-4.

Description:
Spores bilaterally symmetrical, heteropolar; plano-convex in equatorial view, polar view not observed; monolete; laesura simple, long, extending two-thirds to the total of the spore length; exine 1-2 μm thick, laevigate with loosely or widely spaced sculptural elements consist of gemmae and verrucae of 2-4 μm in diameter and 1-2 μm in height.

Dimensions:
Length 53 (57) 63 μm, width 26 (37) 48 μm (4 specimens measured from various horizons).

Stratigraphic distribution:
Gemmatosporis gemmatoides was originally described from middle Eocene brown coals in Germany by Krutzsch (1959) and has subsequently been reported from the Cenozoic of Cameroon (Salard, 1975), the Neogene of Borneo (Kuyl et al., 1955) and Miocene of Korea (Takahashi and Kim, 1979). Nik Ramli (1988a) uses this species to define a palynological zone in the late Oligocene of the Malay Basin, but it is difficult to use it to define a zone, since it also occurs in the Neogene of the same area, but when common it does help to establish an Oligocene age. Common in the Delah 5H-14-1 section within zone PR2, and present in lower numbers through zones PR3-4.

Comparison:
This species is distinguished from *G. microgemmatus* by its coarse exine sculpture.

Botanical affinity:
Huang et al. (2021) suggest that this spore type may be tentatively attributed to *Cyclophorus* (a synonym of *Pyrrosia*) based on the presence of large gemmae, but the match is not clear-cut, and it may be from an extinct fern). Salard (1975) also suggested affinity to species of *Pyrrosia*, but Uffelen (1991) thought that this is unlikely.

Source ecology:
Presumably ferns of terrestrial wet environments (Huang et al., 2021).

Suggested name for Quaternary records:
Not applicable.

Ecological/Morphological group:
Monolete ornamented spores.

Gemmatosporis microgemmatus
Jaizan Jais and Morley sp. nov. Plate 3, Figs. 2-4

Derivation of name:
Name derived from the fine gemmae of less than 1 µm in diameter.

Holotype:
Plate 3, Figs. 1, 2, 3. Slide Delah-5H-14-2, 2290-2295 m, DC (S1), England Finder T30/2. Grain in equatorial compression, length 52 µm, width 36 µm; gemmae 0.5-1 µm in diameter; exine thin, less than 1 µm thick.

Type locality:
Well Delah 5H-14.1, Malay Basin, offshore Peninsular Malaysia; ditch-cuttings sample at 2290-2295 m depth; age late Oligocene, zone PR5.

Description:
Spores bilaterally symmetrical, heteropolar, plano-convex in equatorial view, amb elliptic; monolete; laesura straight, simple, sometimes open, extending half to two-thirds of the spore length; exine thin (less than 1 µm thick), bearing discrete, scattered microgemmate (diameter less than 1 µm) sculpture with few conae or echinae of less than 1 µm long; exine otherwise laevigate to scabrate.

Dimensions:
Length 40 (51) 60 µm, width 30 (36) 42 µm (11 specimens measured from various horizons).

Variability:
In the density of exine sculpture.

Stratigraphic distribution:
Present in moderate percentages in the Oligocene of Delah 5H-14-1, where it is common through zones PR1-3, but does occur very rarely above.

Comparison:
This species differs from _G. gemmatus_ by its finer gemmate sculpture.

Botanical affinity:
Unknown.

Suggested name for Quaternary records:
Not applicable.

Ecological/Morphological group:
Ornamented monolete spores.

Genus *Scolocyamus*
Playford 1982

Type species*:*
Scolocyamus magnus Playford 1982 (by original designation).

Scolocyamus magnus
Playford 1982. Plate 2, Figs. 12-13

Selected synonymy:
1975 Dispersed spores attributed to *Stenochlaena areolaris* in Anderson and Muller, p. 295, Pl. I, Fig. 1.
1976 Dispersed spores attributed to *Stenochlaena areolaris* in Morley, Vol. II, Pl. 8.23, Fig. 15.
1982 *Scolocyamus magnus* Playford, p. 39, Pl. 4, Figs. 4-7, Text-fig. 2.

Description:
Spores bilaterally symmetrical, monolete; amb roundly elliptical to oval; distal and proximo-equatorial regions of exine sculptured with prominent, discrete, elongate projections of spine-like form having simple or, more typically, branched apices.

Dimensions:
Length 54 (61) 70 μm, width 25 (35) 40 μm, length of projections 8 to 10 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
This species was described from the Neogene of Papua New Guinea by Playford (1982). According to Muller (1972), Anderson and Muller (1975) and Morley (1978), this species was common in Northwest Borneo in the Miocene and gradually disappeared in the Pliocene. They also mentioned that today *Stenochlaena areolaris*, the supposed parent plant is only present in the Philippines and New Guinea and absent in Borneo. Muller (1972) suggested that this species is relict and was formerly of wider distribution. Bearing in mind the present and fossil distribution, it has been recorded as a common element within the Holocene of a coastal peat deposit from Southwest Sulawesi (Yulianto et al., (2004) and a single specimen has been recorded from the Holocene sediments of Peninsular Malaysia (Morley, 1976). This species occurs regularly but in low numbers from the middle Miocene zone PR13 of the Malong 5G-17.2 well.

Remarks:
This rather large and slender monolete spore bears unique spine-like sculptural projections. The size of the Malay Basin species is smaller than the species from Papua New Guinea described by Playford (1982). The latter range from 78 to 126 μm in length and from 45 to 73 μm in width.

Botanical affinity:
Stenochlaena areolaris (Blechnaceae).

Source ecology:
S. areolaris is an epiphyte on *Pandanus* spp. in the Philippines and New Guinea, occurring only at altitudinal range of 150 to 1200 m (Anderson and Muller, 1975). It is likely that its ecology may have differed from this in the past in view of its common occurrence in marine sediments. The large size of specimens described by Playford (1982) led Chambers (2013) to doubt their identification with *Stenochlaena;* however, the specimens reported here are within the same size range as those described by Chambers (2013).

Suggested name for Quaternary records:
Stenochlaena areolaris spores.

Ecological/Morphological group:
Based on its association with *Pandanus*, it is likely to be a fern of freshwater swamps (terrestrial wet group).

Plate 3

Fig. 1 *Gemmatosporis gemmatoides* Krutzsch 1959 (x 500): Slide Malong-2, 625 m, SWC (S3); England Finder U9.

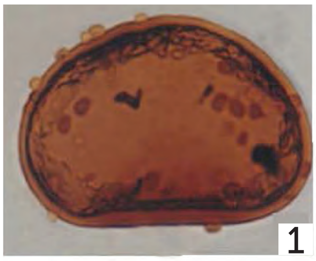
Figs. 2-5 *Gemmatosporis microgemmatus* Jaizan Jais and Morley sp. nov. Figs. 2, 3 (Holotype, 1; x 400, 2; x 1000): Slide Delah-1, 2290-2295 m, DC (S1); England Finder T30/2. Fig. 4 (x 1000), 5 (x 400): Slide Delah-1, 2580-2585 m, DC (S3); England Finder J18/1.

Fig. 6 *Echinosporis conspicuus* Jaizan Jais and Morley sp. nov. Fig. 6 (Holotype; x 400): Slide Malong-2, 1603.7 m, CC (S2); England Finder O42/3. Fig. 3 (x 1000), 5 (x 400): Slide Malong-2, 1588.7 m, CC (S1); England Finder G27/4.

Figs. 7-9 *Echinosporis obscurus* Jaizan Jais and Morley sp. nov. Figs. 7, 8, (Holotype, x 1000): Slide Delah-1, 2770-2775 m, DC (S1); England Finder K41/1. Fig. 9, (x 1000): Slide Delah-1, 2670-2675 m, DC (S1); England Finder H9.

Figs. 10, 11, 14 *Foveogleicheniidites marginatus* Jaizan Jais and Morley sp. nov. Figs. 10-12 (Holotype, x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder V38.

Figs. 12, 13 *Foveotriletes lacunosus* Partridge in Stover and Partridge 1973.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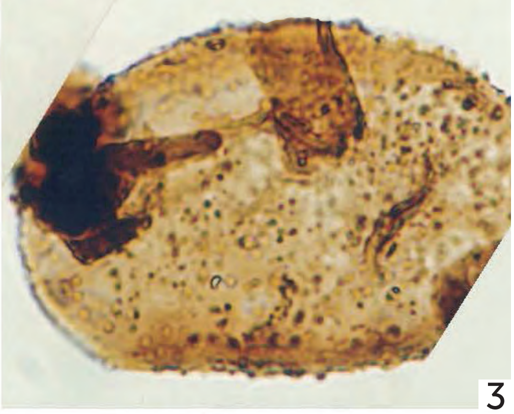
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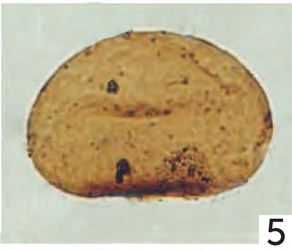
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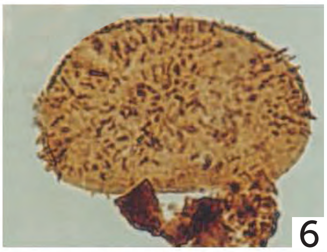
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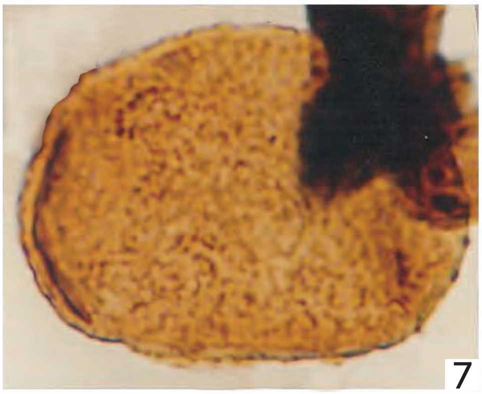
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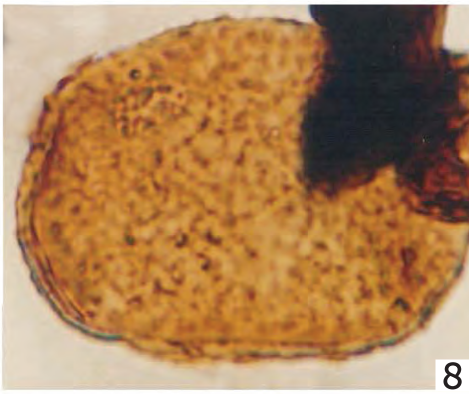
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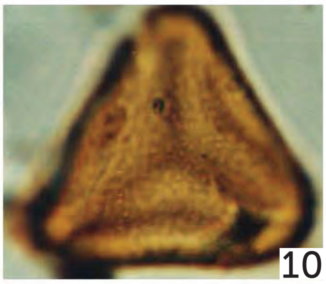
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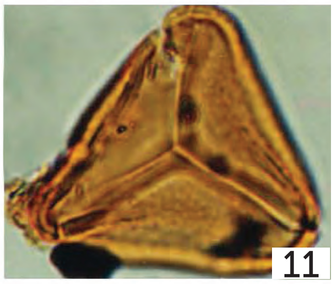
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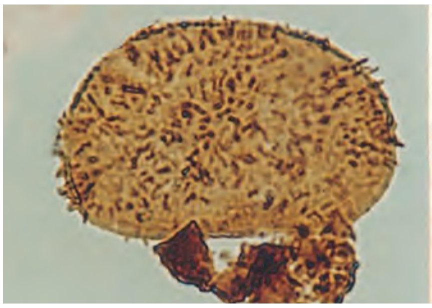
Genus *Echinosporis*
Krutzsch 1967

Type species:
Echinosporis echinatus Krutzsch 1967.

Echinosporis conspicuus

Jaizan Jais and Morley sp. nov. Plate 3, Fig. 6



Derivation of name:

Name derived from the conspicuous sculptural projections. Latin *conspicuus* meaning clearly visible.

Holotype:

Plate 3, Fig. 6. Slide Malong-2, 1603.7 m, CC (S2), England Finder O42/3. Grain equatorially compressed, length 65 µm, width 42 µm; exine 1 µm thick; sculptural projections 1.5 to 3 µm long.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1603.7 m depth; age late Oligocene, zone PR6/7.

Description:

Spores bilaterally symmetrical, heteropolar, with convex distal outline and straight to concave proximal outline in equatorial view, amb elliptical; monolete; laesura simple, straight, short, extending one-third to half of the spore length; exine thin (0.5-1 µm thick), laevigate to scabrate with discrete spinose projections; spines fine to coarse, 1.5-4 µm long, variable, irregularly distributed, with both tapered and non-tapered or sharp and blunt tipped.

Dimensions:

Length 37 (49) 65 µm, width 23 (32) 42 µm (12 specimens measured from various horizons).

Stratigraphic distribution:

Present in moderate numbers throughout the Delah 5H-14-1 section (late Oligocene), occurring in low numbers in zones PR6/7 to PR5, but more commonly in zones PR4-2.

Comparison:

This species differs from *E. obscurus* sp. nov. by having longer and coarser spines. *E. echinatus* Krutzsch is different in the shape of its echinae and is smaller in size.

Botanical affinity:

Identical spores occur within the closely related genera *Crypsinus* (Morley, 1976) and *Leptochilus* (Chen et al., 2021) of the family Polypodiaceae.

Source ecology:

Crypsinus and *Leptochilus* are epiphytes commonly occur throughout Malesia.

Suggested name for Quaternary records:

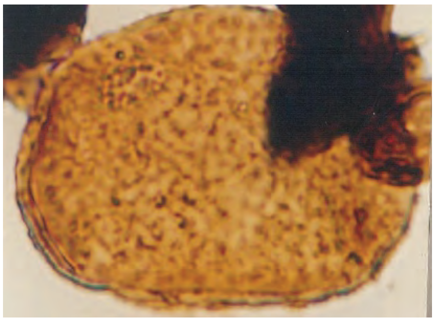
Crypsinus type.

Ecological/Morphological group:

Terrestrial wet ferns.

Echinosporis obscurus

Jaizan Jais and Morley sp. nov. Plate 3, Figs. 7-9



Derivation of name:

Name derived from the obscure and difficult to see sculptural projections. Latin *obscurus* meaning dark.

Holotype:

Plate 3, Figs. 7, 8. Slide Delah 5H-14-1, 2770-2775 m, DC (S1), England Finder K41/1. Grain equatorially compressed, length 36 µm, width 27 µm; exine 1 µm thick; sculptural projections 0.5-1 µm long.

Type locality:

Well Delah 5H-14.1, Malay Basin, offshore Peninsular Malaysia; ditch cuttings sample at 2770-2775 m depth; age late Oligocene, zone PR2.

Description:

Spores bilaterally symmetrical, heteropolar, plano-convex in equatorial view, amb elliptic; monolete; laesura simple, straight, extending one-third to two-thirds of the spore length; exine 0.5-1 µm thick, laevigate to scabrate with scattered sculptural elements consisting of primarily obscure, tiny and variable echinae and conae of 0.5-1.5 µm in height, and in part, fine gemmae and verrucae.

Dimensions:

Length 31 (46) 60 µm, width 22 (31) 42 µm (14 specimens measured from various horizons).

Stratigraphic distribution:

Present in moderate frequencies from the Oligocene succession in Delah 5H-14-1 well within zones PR2-4, but less commonly than *E. conspicuus*. This spore type was also observed at Danau Padang, a Late Quaternary site in the Kerinci region of Sumatra (Morley, 1976, 1982a).

Comparison:

This species is distinguished from *E. conspicuus* by having obscure and shorter sculptural projections. *E. microechinatus* Krutzsch is smaller in size.

Suggested name for Quaternary records:

Cyclosorus sect. *Sphaerostephanos* type.

Ecological/Morphological group:

Terrestrial wet ferns.

2.3 TRILETE SPORES

Genus *Leiotriletes*
(Naumova 1937) Potonié and Kremp 1954

Type species:
Leiotriletes sphaerotriangulus (Loose 1932) Potonié and Kremp 1954 (by designation of Potonié and Kremp, 1954).

Generic remarks:
Smooth trilete spores having a subtriangular amb are here attributed to the genera *Leiotriletes* (Naumova) Potonié and Kremp, *Deltoidospora* Miner (1935) or *Cyathidites* Couper (1953) according to their convex, straight, or concave sides respectively.

Cyathea *sp., montane forest, Kawah Putih, West Java. Most* Cyathea *spp. produce smooth trilete spores (photo by RJM).*

Leiotriletes adriennis
(Potonié and Gelletich 1933) Krutzsch 1959. Plate 4, Figs. 1-3

Selected synonymy:
1933 *Punctatisporites adriennis* Potonié and Gelletich, p. 521, Pl. 2, Fig. 14.
1956 *Lygodiumsporites adriennis* (Potonié and Gelletich) Potonié 1956, p. 19.
1959 *Leiotriletes adriennis* (Potonié and Gelletich) Krutzsch, p. 57.
1964 *Acrostichum* type Muller Fig. 1
1975 *Leiotriletes adriennis* (Potonie and Gelletich) Krutzsch; Salard, p. 98, Pl. 1, Fig.1.
1983 *Deltoidospora adriennis* (Potonie and Gelletich) Frederiksen et al., p. 18, Pl. 1, Fig. 11.
1982 *Biretisporites huonenis* Playford, Pl. 1, Figs. 9-15.

Description:
Spores radially symmetrical, heteropolar; amb subtriangular, with rounded apices and convex to almost straight sides; trilete; laesurae distinct, straight, simple, often open, and relatively short extending about half to three-fourths of spore radius; exine laevigate to slightly scabrate, two-layered, 1-2 μm thick.

Dimensions:
Equatorial diameter 41 (51) 65 μm (20 specimens measured from various horizons).

Stratigraphic record:
This morphotype was first described from the middle Eocene brown coals of West Germany by Potonie (1933) as *Punctatisporites adriennis* and transferred to *Leiotriletes* by (Krutzsch, 1959). It is widely recorded, especially from the Palaeogene of Europe and Asia. However, older records have been suggested, extending back to the mid Cretaceous, such as Li et al. (1978) from the Aptian of China, and these require confirmation. In the Americas and Africa, it is often placed in the genus *Deltoidospora* (e.g., Rull, 2001) where it displays a similar range (Jaramillo et al., 2010). In Southeast Asia, it is a common element from the middle Eocene onward, occurring commonly in the Nanggulan Formation of Java (Morley, 2000, Fig. 9.10) and in low numbers in the early Eocene of Papua (Morley, 2000, Fig. 9.6). In the wells, Malong 5G-17.2 and Delah 5H-14.1 wells it is abundant throughout both sections.

Remarks:
There are many issues in understanding the significance of this spore type, with respect to its nomenclature, its botanical affinity, and its value for environmental interpretation. Working in Quaternary and Neogene deposits in the Southeast Asian region, the spore type seemingly presents few problems, as it is closely comparable to spores of extant *Acrostichum* (see below), but in trying to establish the oldest occurrences, to identify it in areas outside the palaeotropics, and to understand the ecology of its parent plant, major problems present themselves on all fronts, discussed below.

With respect to nomenclature, the subrounded to subtriangular trilete laevigate spores with short laesurae have been placed on the form genera *Deltoidospora*, *Leiotriletes*, *Punctatisporites* and others by different authors. However, placement in *Leiotriletes*, based on the convex sides is followed here (see above). The genus *Acrostichumsporites meghalayaensis* Kar (1991), described from India is proximally granulose and probably not from *Acrostichum*.

Botanical affinity:
This spore type has been variously compared to *Lygodium*, *Antrophyum* and *Acrostichum* (e.g., Smith et al., 2011). A possible affinity to *Lygodium* has been suggested based on the similarity of spores from fossil sporangia, such as charcoalified sorophores of *Lygodium bierhorstiana* from the Turonian of eastern North America (Gandolfo et al., 2000). In extant *Lygodium*, which includes about 40 mainly tropical species but with a few temperate representatives in eastern Asia and eastern North America, most exhibit distinctly ornamented exines, such as in *L. scandens*, that produces coarsely reticulate spores referable to the form-taxon *Crassoretitriletes vanraadshooveni*, or *L. flexuosum*, with clearly gemmate exine. The North American *L. palmatum*, however, has psilate exine which may explain why North American palynologists frequently make this comparison. SEM images of *L. palmatum* (Wang et al., 2022) and Gandolfo et al. (2000) show longer and more robust laesurae and a more pronounced differentiation of the distal and proximal faces (Plate 4, Fig. 7), and these features need to be considered in evaluating *L. adriennis*, perhaps using a biometric approach. SEM evaluations of *Acrostichum* spores (Vaganov et al., 2017) emphasise their rounded amb, short laesurae, and the weak differentiation of the proximal and distal faces (Plate 4, Figs. 4-6). SEM images of *Antrophyum* spp. (Plate 4, Fig. 8) emphasise their more concave sides, and longer and more robust laesurae (Chen et al., 2015, 2020).

A molecular evaluation of *Acrostichum*, which is calibrated using the fossil *A. intertrappeum* Bonde and Kumaran (2002) from the intertrappean beds of India suggests a stem age of 93 Myr and a late Eocene crown age of 34 Myr for *Acrostichum*, and that *A. aureum* or *A. speciosum*, which have the same spore type (Vaganov et al., 2017), diverged at 2.2 Myr.

Acrostichum aureum*, disturbed mangrove swamp, Tarakan, Kalimantan (photo by HPM).*

Acrostichum aureum *showing densely packed sori on fertile frond (photo by RJM).*

Source ecology:
In Southeast Asia *Acrostichum aureum* and *A. speciosum* are ferns of disturbed mangrove habitats, but the American *A. danaeifolium*, found for instance in the Everglades, is entirely freshwater (Tomlinson, 2016), as is the case for fossil *Acrostichum* from the Paleocene of England (Collinson, 1990). Morono-Dominguez et al. (2016) demonstrates that in the Oligocene of Spain, *Acrostichum* ferns were pioneers of freshwater floodplains, and abundance maxima of *Acrostichum* spores in the Oligocene of the Cuu Long Basin in Vietnam (Morley et al., 2019) are thought to reflect the widespread occurrence of *Acrostichum* in ephemeral settings around large freshwater rift valley lakes rather than in a coastal setting. To understand the ecology of the vegetation that produced *Leiotriletes adriennis*, the ecology of associated taxa thus needs to be considered.

Suggested name for Quaternary records:
Acrostichum aureum type.

Ecological group:
Backmangrove.

Plate 4

Figs. 1,2 *Leiotriletes adriennis* (Potonié and Gelletich 1933) Krutzsch 1959. Fig. 1 (x 500): Slide Malong-2, 625 m, SWC (S3); England Finder P55. Fig. 2 (x 400): Slide Malong-2, 1234.5 m, SWC (S1); England Finder Q38/1.

Figs. 3 *Leiotriletes adriennis* SEM image (x 500), from Huon Peninsula (named as *Biretisporites huonensis* by Playford 1982 Plate 1 Fig. 13).

Figs. 4-6 *Acrostichum aureum* spores SEM image (x 500) from Vagarov et al. (2017) 4 = Fig. 3a of Vagarov et al. (2017). 5 = Fig. 4a, 6 = Fig. 4b).

Fig. 7 SEM image (x500) of *Lygodium palmatum* spore from Fig. 3E of Gandolfo et al. (2000). This species is often compared to *L. adriennis* but differences are clear in SEM.

Fig. 8 *Antrophyum solomonense* SEM image (x 500) from Chen et al. (2015, Fig. 6c) This genus is often compared to *L. adriennis* but differences are clear in SEM.

Fig. 9 *Deltoidospora* spp. (x 1000): Slide Malong-2, 780-790 m, DC (S1); England Finder T26/2.

Fig. 10 *Cyathidites minor* Couper 1953 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder P11/1.

Fig. 11 *Matonisporites mulleri* Playford 1982 (x 1000): Slide Malong-2, 1554 m, CC (S1); England Finder H31/1.

Fig. 12 *Matonisporites* sp. A. (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder L13/2.

Figs. 13, 14 *Matonisporites* sp B. Figs. 13 (x 400), 14 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder R9/4.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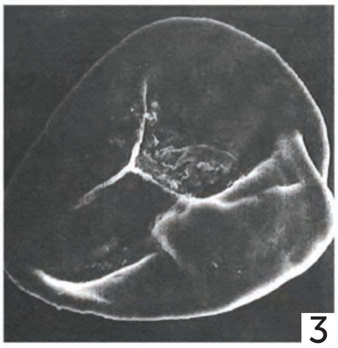
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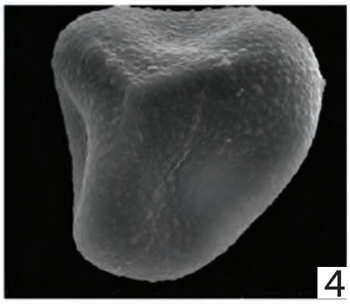
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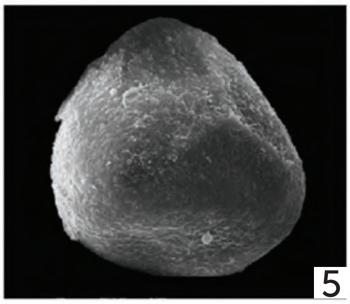
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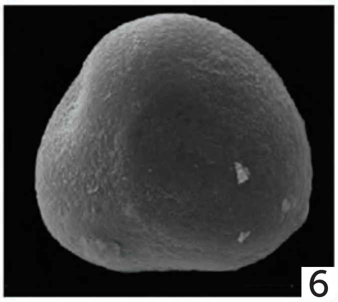
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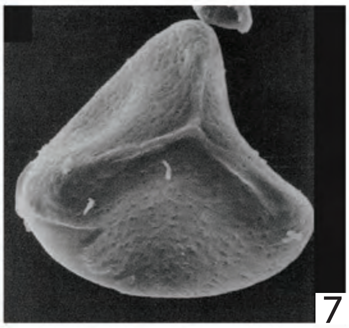
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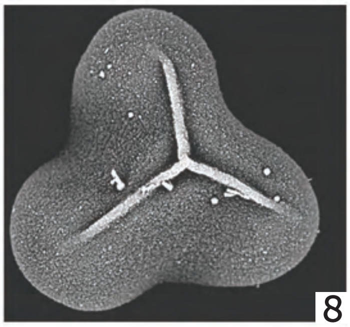
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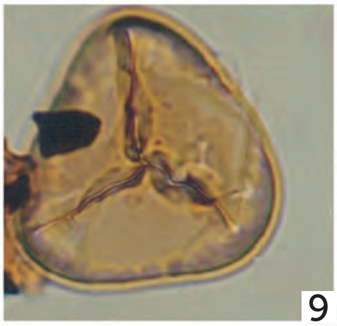
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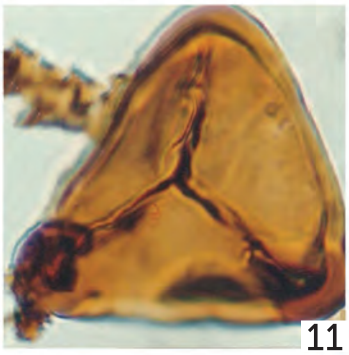
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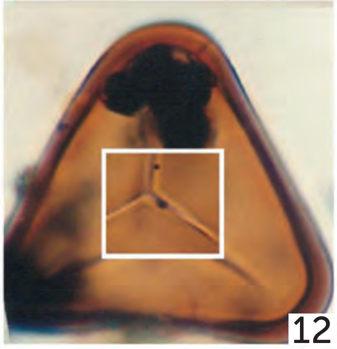
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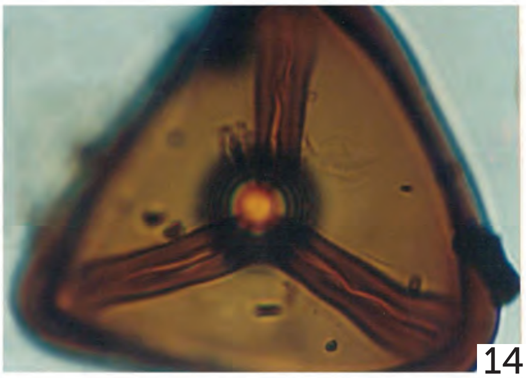
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Genus *Deltoidospora*
Miner 1935 emend. Potonié 1956

Type species:
Deltoidospora halii Miner 1935 (by original designation).

***Deltoidospora* spp.** Plate 4, Fig. 9

Description:
Spores radially symmetrical, heteropolar; amb subtriangular, with pointed apices and straight sides; trilete; laesurae mostly distinct, straight, simple, open or closed often long; exine psilate.

Stratigraphic distribution:
Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14-1 wells.

Remarks:
Included here are various laevigate trilete spores with a subtriangular amb and straight sides.

Suggested name for Quaternary records:
Trilete spores undiff.

Ecological/Morphological group:
Smooth trilete spores.

Genus *Cyathidites*
Couper 1953

Type species:
Cyathidites australis Couper 1953 (by original designation).

Cyathidites minor
Couper 1953. Plate 4, Fig. 10

Selected synonymy:
1953 *Cyathidites minor* Couper, p. 28, Pl. 2, Fig. 13.

Description:
Spores radially symmetrical, heteropolar; amb subtriangular, with concave sides; trilete, laesurae mostly distinct, straight, simple, open or closed often long; exine psilate.

Dimensions:
Equatorial diameter 21 (23) 25 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
This species has been recorded from the Triassic to the Cenozoic of various regions. Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14.2 wells.

Remarks:
This species is distinguished by its concave-sided amb and thin exine. Note that the forms identified here are slightly smaller than those originally described from New Zealand by Couper (1953).

Suggested name for Quaternary records:
Trilete spores undiff.

Ecological/Morphological group:
Smooth trilete spores.

Genus *Matonisporites*

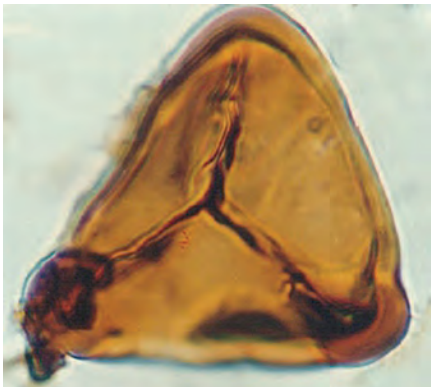
Couper 1958 emend. Dettmann 1963

Type species:

Matonisporites crassiangulatus (Balme) Dettmann 1963 (senior synonym of *M. phlebopteroides* Couper 1958, originally designated as type species).

Matonisporites mulleri

Playford 1982. Plate 4, Fig. 11



Selected synonymy:

1982 *Matonisporites mulleri* Playford, p. 38, Pl. 2, Figs. 8-10.

Description:

Spores radially symmetrical, trilete; amb nearly triangular with rounded apices and almost straight sides; laesurae distinct, sinuous, long, reaching equatorial margin; accompanied by narrow, elevated lips, about 1 µm in overall width; exine psilate, thicker at amb apices (3-4 µm) than along amb interradii (1.5-2.5 µm).

Dimensions:

Equatorial diameter, minimum 36 µm, maximum 48 µm (2 specimens measured).

Stratigraphic distribution:

This species has been recorded from the Miocene to Pliocene sediments of Papua New Guinea (Playford, 1982). This species was rarely recorded in Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:

This laevigate trilete spore bears distinct sinuous laesurae and thicker exine at its rounded apices as described by Playford (1982). The laesurae of *Matonisporites* sp. A are straight and *Matonisporites* sp. B has wider thickened margines bordering its laesurae.

Botanical affinity:

According to Playford (1982) possibly with either the fern *Matonia* (Matoniaceae) or *Dicksonia* (Dicksoniaceae) as per Couper (1958) and Dettmann (1963).

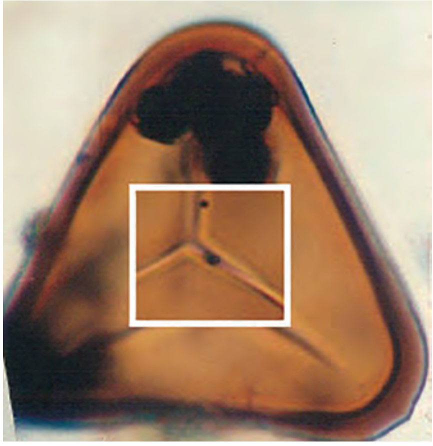
Suggested name for Quaternary records:

Matonia type.

Ecological/Morphological group:

Terrestrial spores.

Matonisporites sp. A. Plate 4, Fig. 12



Dimensions:

Equatorial diameter 32 (43) 60 µm (5 specimens measured from various horizons).

Stratigraphic distribution:

Sparsely present in low percentages.

Comparison:

This species differs from *M. mulleri* by having straight laesurae, and from *Matonisporites* sp. B by its straight and non-marginate laesurae.

Botanical affinity:

Possibly with Matoniaceae or Dicksoniaceae as noted above.

Suggested name for Quaternary records:

Matonia type.

Ecological/Morphological group:

Smooth trilete spores.

Matonisporites sp. B. Plate 4, Figs. 13, 14

Dimensions:

Equatorial diameter 53 µm (1 specimen measured).

Stratigraphic distribution:

Only one specimen found in the Malong 5G-17.2 well at 561 m (SWC) depth.

Comparison:

This species is differentiated from *M. equiexinus* Couper (1958) by its thicker exine at the apices and the presence of sinuous laesurae. It differs from *M. mulleri* by its wider thickened margines bordering the laesurae and from *Matonisporites* sp. A by its sinuous and wide marginate laesurae.

Botanical affinity:

Possibly with Matoniaceae or Dicksoniaceae as noted above.

Suggested name for Quaternary records:

Matonia type.

Ecological/Morphological group:

Smooth trilete spores.

Genus *Foveotriletes*

van der Hammen 1954 ex Potonié 1956

Type species:

Foveotriletes scrobiculatus (Ross ex Weyland and Krieger) Potonié 1956 (by original designation).

Foveotriletes lacunosus

Partridge in Stover and Partridge 1973.
Plate 3, Figs. 12, 13

Selected synonymy:

1973 *Foveotriletes lacunosus* Partridge in Stover and Partridge, p. 248, pl. 14, fig. 6.
1976 *Lycopodium phlegmaria* Morley Pl. 8.25, Figs. 11, 12.

Description:

Spores radially symmetrical, heteropolar; amb subtriangular with moderately to narrowly rounded apices and straight to slightly convex sides; trilete; laesurae distinct, long, extending almost to the apices, sometimes displaying terminal 'y' mark, straight to sinuous, narrowly marginate; exine 1 μm thick, psilate proximal surface and foveolate distal surface; foveolae 1-1.5 μm in diameter, widely spaced.

Dimensions:

Equatorial diameter 28 (29) 30 μm (5 specimens measured from various horizons).

Stratigraphic distribution:

Originally described from the late Oligocene to Pliocene of Australia (Stover and Partridge, 1973) and subsequently widely reported from the Eocene onward in Australia (Harris, 1984) and Oligocene onward in New Zealand (Pocknall and Mildenhall, 1984). Regularly present in most Neogene successions across Southeast Asia, with fewer records from the Oligocene. Present in low percentages and sparsely distributed in zones PR13-15 in Malong 5G-17.2 and in zone PR2 in Delah 5H-14.1.

Remarks and comparison:

This species is generally smaller than the specimens identified by Partridge (in Stover and Partridge, 1973) that range from 30 to 41 μm in equatorial diameter. It also shows some resemblance to *Foveotriletes* sp. A photographed by Playford (1982) but as noted by him the latter is bigger and differently sculptured, being characterised by coalescing foveolae. *F. ornatus* Regali et al. (1974) is recorded extensively from the Neotropics and Africa but does not show the characteristic 'y' mark seen in fossil specimens recorded here and in fresh *Huperzia phlegmaria* spores.

Botanical affinity:

Huperzia phlegmaria (Lycopodiaceae) and related species (sometimes placed in *Phlegmariurus*).

Huperzia phlegmaria*, Bogor, Java (photo by RJM).*

Source ecology:

Common epiphyte growing on forest trees.

Suggested name for Quaternary records:

Huperzia phlegmaria type.

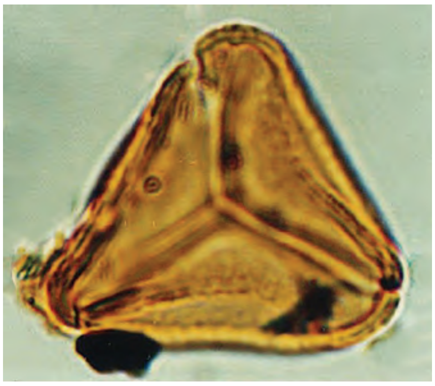
Ecological/Morphological group:

Epiphytic spores.

Genus *Foveogleicheniidites*
Burger in Norvick and Burger 1976

Type species:
Foveogleicheniidites confossus (Hedlund) Burger in Norvick and Burger 1976 (by original designation).

Foveogleicheniidites marginatus Jaizan Jais and Morley sp. nov. Plate 3, Figs. 10, 11, 14



Derivation of name:
From its marginate laesurae.

Holotype:
Plate 3, Figs. 10-12. Slide Malong-2, 430.5 m, SWC (S2), England Finder V38. Grain equatorially compressed, 30 μm in equatorial diameter; foveolae 1 μm in diameter; wall 1 μm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 430.5 m depth; age Pliocene, zone PR15.

Description:
Spores radially symmetrical, heteropolar; amb subtriangular with straight to slightly convex sides and rounded apices; trilete; laesurae distinct, straight, long, extending to apices, bordered by narrow margins; proximal surface with concave kyrtomes in interradial areas; exine foveolate or pitted on both surfaces; foveolae up to 1.5 μm in diameter, regularly distributed; exine thickness distinct, 1-1.5 μm.

Dimensions:
Equatorial diameter 29 (32) 40 mm (6 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Comparison:
This species differs from the Late Cretaceous *Foveogleicheniidites confosus* (Hedlund) Burger in Norvick and Burger (1976) in having narrow margines bordering its laesurae and from *Foveotriletes balteus* Partridge in Stover and Partridge (1973) by its shape.

Botanical affinity:
Trilete spores with well-developed kyrtomes and foveolate exine occur in *Dicranopteris* (Gleicheniaceae), according to Morley (1976).

Source ecology:
Dicranopteris linearis is one of the commonest indicators of disturbance in Malaysia.

Dicranopteris linearis *(Resam), kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).*

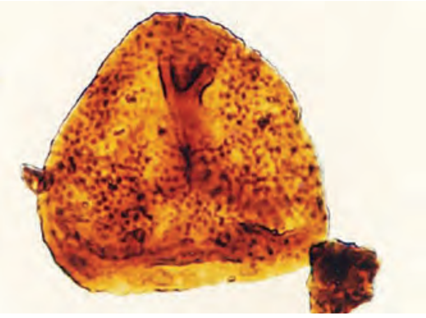
Suggested name for Quaternary records:
Dicranopteris type.

Ecological/Morphological group:
Ferns of regrowth vegetation.

Genus *Converrucosisporites* Potonié and Kremp 1954

Type species:
Converrucosisporites triquetrus (Ibrahim 1933) Potonié and Kremp 1954 (by original designation).

Converrucosisporites sundaicus Morley and Jaizan Jais sp. nov. Plate 5, Figs. 1-2



Derivation of name:
The name refers to the Sunda region.

Holotype:
Plate 5, Fig. 2. Slide Delah 5H-14-1, 2330-2335 m, DC (S2); England Finder D15/4.

Type locality:
Well Delah 5H-14-1, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 2330-2335 m depth; age late Oligocene, zone PR5.

Description:
Spores radially symmetrical, heteropolar; amb convexly subtriangular to subrounded; trilete; laesura distinct, straight, widely marginate, extending to, protruding, and thickening toward apices; exine variable thickness, sculptured with fine to coarse verrucae.

Dimensions:
Equatorial diameter 40 (62) 80 µm (12 specimens measured from various horizons).

Remarks:
There are just over 100 species referred to the genus *Converrucosisporites* according to Palynodata (Palynodata Inc.., 2008). Most are from the Palaeozoic and Mesozoic. To check all these against the Malaysian specimens is a mammoth task, but if undertaken, *C. sundaicus* may prove to be a synonym of another species. Included here are various convexly subtriangular, verrucate trilete spores. The specimens described here are recovered from ditch cuttings and are mostly dark in colour.

Stratigraphic distribution:
Restricted to the lower part of the Delah 5H-14.1 well, within the Oligocene zones PR2-4 and has potential as an index taxon.

Suggested name for Quaternary records:
Not applicable.

Ecological/Morphological group:
Ornamented trilete spores.

Genus *Echinatisporis*
Krutzsch 1959

Type species:
Echinatisporis longechinus Krutzsch 1959 (by original designation).

Echinatisporis minor

Jaizan Jais and Morley sp. nov. Plate 5, Fig. 3

Derivation of name:
The name *'minor'* refers to the small size of the spore.

Holotype:
Plate 5, Fig. 3. Slide Malong-5G-17.2, 430.5 m, SWC (S2); England Finder T21.

Type locality:
Well Malong 5G-17.1 well, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 430.5 m depth; age Pliocene, zone PR15.

Description:
Spores radially symmetrical, heteropolar; amb convexly subtriangular to subrounded; trilete; laesura distinct, straight to sinuous, narrowly marginate, extending to four-fifths of spore radius; exine thin, sculptured with echinae; a few echinae appear quite long, up to 3 μm, whereas most are short (1 μm), and the likelihood is that most spines are broken off; spines regularly distributed on distal face. Sometimes found as tetrads.

Dimensions:
Equatorial diameter 15 μm (17) 18 μm (5 specimens measured from various horizons).

Stratigraphic distribution:
Present in low percentages throughout both sections.

Comparison:
The small size, subtriangular to subrounded amb, thin exine differentiates this species from other trilete echinate taxa.

Botanical affinity:
The small spore with scattered, short echinae compares to the *Selaginella latifrons* group (Selaginellaceae) of Knox (1950).

Selaginella *spp., common in damp places in perhumid forests and along streams (photo by RJM).*

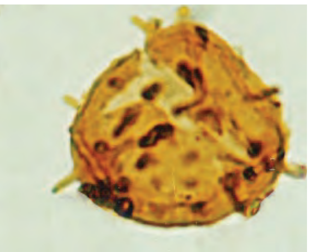
Source ecology:
Terrestrial fern. Present in both lowland and highland areas.

Suggested name for Quaternary records:
Selaginella latifrons type.

Ecological/Morphological group:
Terrestrial wet spores.

Echinatisporis lepidus

Morley and Jaizan Jais sp. nov. Plate 5, Fig. 4



Derivation of name:

from '*lepida*' Greek for blade.

Holotype:

Plate 5, Fig. 4. Slide Delah 5H-14-1, cuttings sample at 2580-2585 m, DC (S3), England Finder N18.

Type locality:

Well Delah 5H-14-1 well, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 2580-2585 m depth; age late Oligocene, zone PR3.

Description:

Spores radially symmetrical, heteropolar; amb convexly subtriangular to subrounded; trilete; laesura distinct, straight, without margines, extending to apices with clear 'y' mark; exine thin, sculptured with blade-like echinae, a few echinae appear quite long, up to 3 µm, whereas most are short (1 µm).

Dimension:

Equatorial diameter 20 (22) 24 µm (4 specimens measured from various horizons).

Stratigraphic distribution:

Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is distinguished by its convex subtriangular to subrounded amb, long sinuous laesurae and sculptured with widely spaced blade-like spinae (blunt and sharp ends).

Botanical affinity:

Selaginella uncinata group of Knox (1950).

Suggested name for Quaternary records:

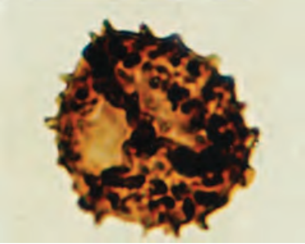
Selaginella uncinata type.

Ecological/Morphological group:

Terrestrial wet spores.

Echinatisporis undulosus

Morley and Jaizan Jais sp. nov. Plate 5, Fig. 5



Derivation of name:

From the undulating nature of the laesura.

Holotype:

Plate 5, Fig. 5. Slide Delah-1, 2845-2850 m, DC (S2), England Finder E21.

Type locality:

Well Delah 5H-14.1 well, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 2845-2850 m depth; age late Oligocene, zone PR3.

Description:

Spores radially symmetrical, heteropolar; amb convexly subtriangular to subrounded; trilete; laesura distinct, strongly undulating, strongly marginate, extending to apices; exine thicker than in other species, proximal face psilate, distal face sculptured with blunt cone-shaped, often truncated projections or verrucae, up to 2 µm in height.

Dimensions:

Equatorial diameter 20 (22) 24 µm (4 specimens measured from various horizons).

Stratigraphic distribution:

Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is distinguished by its convex subtriangular to subrounded amb, long sinuous laesurae and sculptured with a mixture of cone-shaped projections and verrucae.

Botanical affinity:

Compares to the *Selaginella radiata* group of Knox (1950).

Suggested name for Quaternary records:

Selaginella radiata type.

Ecological/Morphological group:

Terrestrial wet spores.

Genus *Clavatisporites*

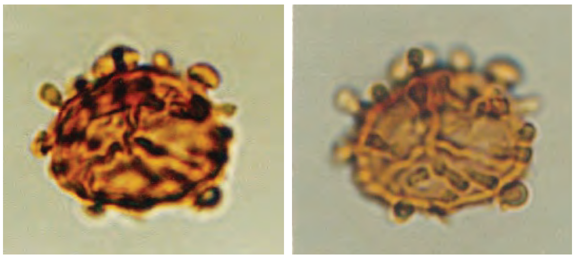
Kedves and Simoncsics 1964

Type species:

Clavatisporites clarus Kedves and Simoncsics 1964 (by original designation).

Clavatisporites fungi

Morley and Jaizan Jais sp. nov. Plate 5, Figs. 6-9



Derivation of name:

From the clavae, that resemble mushrooms.

Holotype:

Plate 5, Figs. 8-9. Slide Malong-2, 934 m, SWC (S1); England Finder H38.

Type locality:

Well Malong 5G-17.2 well, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 934 m depth; age middle Miocene, zone PR12A.

Description:

Spores, radially symmetrical, heteropolar; amb subrounded to circular; trilete; laesura distinct, sinuous, marginate with margines narrowing toward and nearly reaching apices; exine sculptured with mushroom-shaped clavae, 2-3 μm in height, up to 3 μm across, irregularly distributed over exine surface.

Dimension:

Equatorial diameter 13 (17) 20 μm (4 specimens measured from various horizons).

Stratigraphic distribution:

Rare and sparsely distributed throughout the Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is differentiated by its rounded triangular to subrounded amb, long, sinuous, and narrowly marginate laesurae and clavate sculpture on proximal and distal surfaces. Clavae 1-3 μm long and 2-4 μm apart.

Botanical affinity:

compares closely *Selaginella biformis* (Selaginellaceae) group of Knox (1950).

Source ecology:

Terrestrial fern. Widespread in both lowland and highland swamps and forest.

Suggested name for Quaternary records:

Selaginella biformis type.

Ecological/Morphological group:

Terrestrial wet spores.

Plate 5

Figs. 1, 2 *Converrucosisporites sundaicus* Morley and Jaizan Jais sp. nov. Fig. 1 (x 400): Slide Delah 5H-14--1, 2210-2215 m, DC (S1); England Finder K32/1. Fig. 2 (x 400 holotype): Slide Delah 5H-14--1, 2330-2335 m, DC (S2); England Finder D15/4.

Fig. 3 *Echinatisporis minor* Jaizan Jais and Morley sp. nov. (x 1000 holotype): Slide Malong 5G-17.2, 430.5 m, SWC (S2); England Finder T21.

Fig. 4 *Echinatisporis lepidus* Morley and Jaizan Jais sp. nov. (x 1000 holotype): Slide Delah 5H-14-1, 2580-2585 m, DC (S3); England Finder N18.

Fig. 5 *Echinatisporis undulosus* Morley and Jaizan Jais sp. nov. (x 1000 holotype): Slide Delah 5H-14-1, 2845-2850 m, DC (S2); England Finder E21.

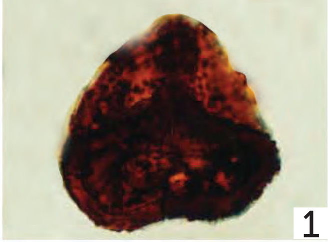
Figs. 6-9 *Clavatisporites fungi* Morley and Jaizan Jais sp. nov. Fig. 6 (x 1000): Slide Malong-2, 1200-1205 m, DC (S1); England Finder W15. Fig. 7 (x 1000): Slide Malong-2, 1200-1205 m, DC (S1); England Finder W15. Figs. 8, 9 (x 1000 holotype): Slide Malong-2, 934 m, SWC (S1); England Finder H38.

Figs. 10, 11 *Magnastriatites grandiosus* (Kedv. and Solé de Porta 1963) Dueñas 1980. Figs. 10,11 (x 400): Slide Malong-2, 1420-1425 m, DC (S1); England Finder U13.

Fig. 12 *Cicatricosisporites chattensis* Krutzsch 1967 (x 400): Slide Malong-2, 592 m, SWC (S1); England Finder T39.

Fig. 13 *Cicatricosisporites dorogensis* Potonie and Gelletich 1933. (x 1000): Slide Delah-1, 2370-2375 m, DC (S2); England Finder Y17.

Figs. 14, 15 *Crassoretitriletes vanraadshooveni* Germeraad et al. 1968. Figs.14, 15 (x 500): Slide Malong-2, 561 m, SWC (S1); England Finder O17/3.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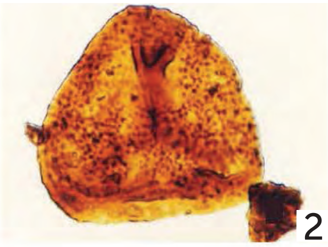
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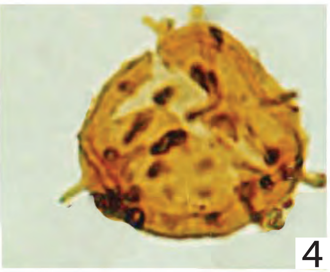
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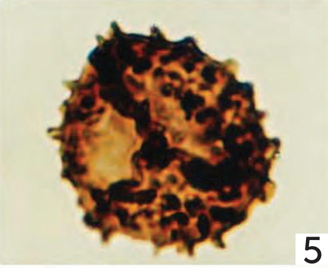
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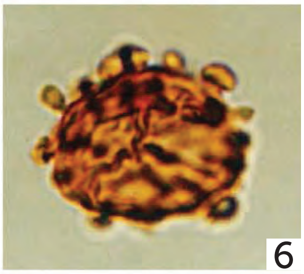
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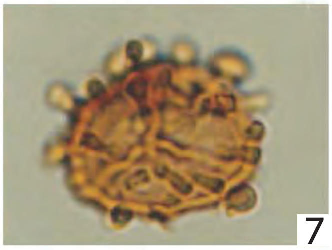
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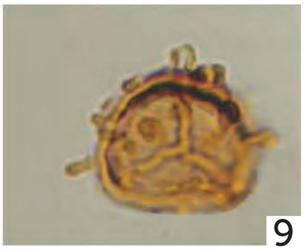
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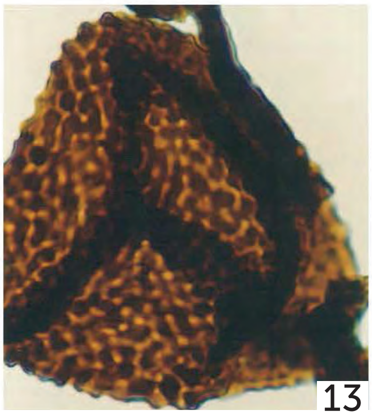
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15

Genus *Magnastriatites*

Germeraad Hopping and Muller 1968

Type species:

Magnastriatites grandiosus (Kedves and Solé de Porta 1963) Dueñas 1980 (senior synonym of *M. howardi* Germeraad Hopping and Muller 1968, originally designated as type species).

Selected synonymy:

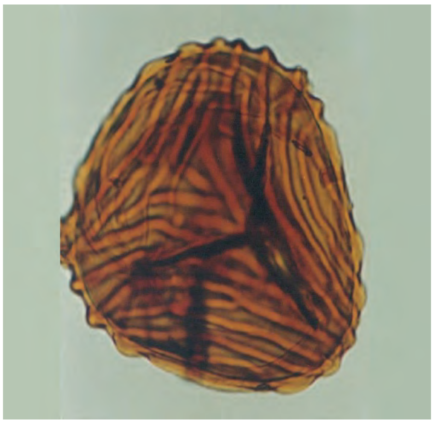
1954 Triletes subgen. *Striatriletes* van der Hammen – nomen nudum.
1956 (Dec.) *Striatriletes susannae* van der Hammen, Junior homonym of *Striatriletes* Potonié (1956, Sept.).

Remarks:

Van der Hammen (1954) proposed '*Striatriletes*' as a name for 'trilete striate' spores, then realised that it needed to be designated a holotype and published the name '*Striatriletes susannae*' (Van der Hammen, 1956, Dec.) for a trilete, striate spore that was 'similar to some spores of the genus *Anaemia*, but also in some respects to types found in Parkeriaceae', implying affinity in part to *Ceratopteris*. However, Potonie (1956, Sept.) also published a spore genus from Germany, also with the name *Striatriletes*, and so despite attempting to validate *Striatriletes*, Van der Hammen's genus became a junior homonym of *Striatriletes* Potonie (1956). Hence *Magnastriatites* Germeraad, Hopping and Muller 1968 remains the senior homonym.

Magnastriatites grandiosus

(Kedves and Solé de Porta 1963) Dueñas 1980. Plate 5, Figs. 10, 11



Selected synonymy:

1956 *Striatriletes susannae* Van der Hammen
1963 *Cicatricosisporites grandiosus* Kedves and Solé de Porta, p. 59, Pl. 7, Figs. 1,2.
1968 *Magnastriatites howardi* Germeraad Hopping and Muller., p. 288, Pl. 3, Fig. 1.
1980b *Magnastriatites grandiosus* (Kedves and Solé de Porta) Dueñas, p. 331, Pl.1, Figs. 1-3.

Description:

Spores radially symmetrical heteropolar, with rounded distal pole and more pointed proximal pole, in polar view nearly circular, laesura trilete, costate; costae 2 µm wide, exine of uniform thickness, contact areas of proximal face psilate, surrounded by a circular ridge, distal face coarsely striate, with striae converging at the ends of the laesura, striae mostly parallel, typically 3 µm wide and 2 µm high, separated by grooves, typically 3 µm in width, striae psilate under SEM (Vaganov et al., 2017).

Dimensions:

Equatorial diameter 45 (78) 105 µm (19 specimens measured from various horizons).

Variability:

Most horizons with *M. grandiosus* also yield specimens with very narrow striae, which may be considered as an additional species, possibly '*Magnastriatites microstriatus*' but as it occurs only in samples with *M. grandiosus* it is assumed to be a variant of the latter species. *Malayaeaspora costata* may also be a variant of this species (see below).

Remarks:

Dueñas (1980) showed that *Magnastriatites grandiosus*, originally described as *Cicatricosisporites grandiosus*, is the senior synonym of *M. grandiosus*, but the type of the generic name remains as the specimen illustrated by of Germeraad, Hopping and Muller (1968). However, with respect to the species, Jansonius and Hills (1976, card 4084) thought it remained unclear if *M. grandiosus* (Kedves and Sole de Porta) Duenas 1980 is, or is not, the senior synonym of *Striatriletes susannae*. In India, Kar (1979) emended *S. susannae*, and considered *M. grandiosus* a junior synonym, but did not take into account that *Striatriletes* van der Hammen is a junior homonym of *Striatriletes* Potonie (1956), nor did he consider the status of *Cicatricosisporites grandiosus* Sole de Porta. On the other hand, Germeraad et al. (1968) considered *Striatriletes susannae* to be a junior synonym of *Cicatricosisporites dorogensis*, presumably on Van der Hammen's suggested affinity to the shizaeaceous genus *Anaemia*.

Stratigraphic distribution:

It has been suggested that this species has a longer range in India than elsewhere (Kar, 1983), based on Indian specimens referred to *Striatriletes susannae*, but Morley (2000) demonstrated that *M. grandiosus* appeared at about the same time across the whole tropics, being reported from the late Eocene of South America (Graham, 1985) and Africa (Kedves, 1971), and in India reported in the late Eocene by Handique (1992, analyses by R.J. Morley) whereas in Southeast Kalimantan, its evolutionary appearance has been independently dated to about 35 Myr in the Tanjung Formation (Witts et al., 2012), and also in Vietnam (Morley et al., 2019). Morley (2018a) has emphasised that the first appearance is about the same age in both Southeast Asia and India, which is not surprising since there was a land connection between India and Southeast Asia from about 41 Myr onward (Klaus et al., 2014; Morley, 2018a). This species has also been reported from the Miocene of the East China Sea (Song et al., 1985) and the southern United states (Wrenn et al., 2003) but not from Australia. In Malaysia, commonly recorded from the Oligocene onward (late Eocene not studied). Present throughout both sections, abundant in the Oligocene of Delah 5H-14-1 well with maxima in zones PR3 and PR5.

Ceratopteris thalictroides*, in pond, Jakarta, Java (photo by RJM).*

Botanical affinity:
The parent plant is the freshwater fern *Ceratopteris* especially *C. thalictroides* (Germeraad et al., 1968). This species exhibits the same geographical range as *M. grandiosus*, except that it is common in tropical Australia.

Source ecology:
Tropical-subtropical aquatic, rooted or floating freshwater fern. The spore type is sometimes hyperabundant when associated with lacustrine facies in the late Eocene to Oligocene rift basins of Southeast Asia (Morley and Morley, 2013; Morley et al., 2019, 2021), where it is thought to have formed extensive floating mats.

Suggested name for Quaternary records:
Ceratopteris thalictroides type spores.

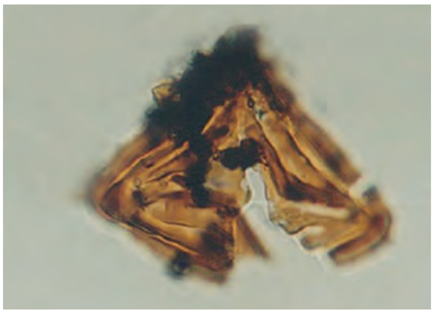
Ecological group:
Freshwater swamp spores.

Genus *Cicatricosisporites*
Potonié and Gelletich 1933 emend. Potonié 1966

Type species:
Cicatricosisporites dorogensis Potonié and Gelletich 1933.

Cicatricosisporites chattensis

Krutzsch 1967. Plate 5, Fig. 12



Description:
Spores radially symmetrical, heteropolar; amb triangular to subtriangular with narrowly rounded apices and straight to slightly concave sides; trilete; laesurae simple, straight, extending to four-fifths of the spore radius, often open or broken; exine thick (4-5 µm), sculptured with 1-2 µm thick striae (5-6 µm wide) more or less parallel to the spore amb, a narrow, equi-thickness psilate cingulum.

Dimensions:
Equatorial diameter 60 (63) 68 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
This distinct species is recorded extensively from the Eocene and Oligocene of Europe (Krutzsch, 1967), with some records as young as the Pliocene (Ashraf et al., 1995). There are also older records, from the early Cretaceous of the USSR and Japan (Miki, 1973; Voronova, 1977) but these need confirmation. This record is the first from Southeast Asia. Very rare. Restricted to the topmost part of Malong 5G-17.2 well in zones PR14 and PR15, within the late Miocene and Pliocene.

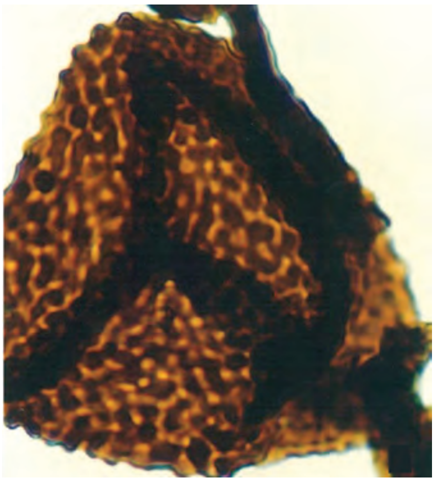
Remarks:
The specimens found here can easily be distinguished by their wide striae and psilate cingulum despite of their broken state.

Botanical affinity:
Spores with a ridged or striate distal face and a cingulum are found in the Pteridoid genus *Onychium* (Jing et al., 2001; Chao and Huang, 2018), a genus centred in subtropical East Asia.

Suggested name for Quaternary records:
Onychium type spores.

Ecological/Morphological group:
Terrestrial spores.

Cicatricosisporites dorogensis Potonie and Gelletich 1933. Plate 5, Fig. 13



Selected Synonymy:

1968 *Cicatricosisporites dorogensis* Potonie and Gelletich 1933 in Germeraad Hopping and Muller 1968.

Description:

Spore, radially symmetrical, heteropolar, with rounded distal pole and pointed proximal pole, in polar view semi-angular to almost circular; laesura trilete, short; proximal face close to laesura unsculptured, distal face striate or striate-rugulate; striae 1-2 µm high, up to 1 µm wide; grooves between striae up to 1 µm wide. Exine up to 2 µm thick.

Dimensions:

Equatorial diameter 55 to 70 µm.

Remarks:

Trivedi (1981) and Trivedi et al. (1982) described a striate spore from the Batu Arang coalfield, near Kuala Lumpur, which they attributed to a new genus, *Malayaeaspora*, based on the species *M. costata*, to which they considered *Cicatricosisporites dorogensis* should be transferred. They suggest that the new genus is justified as *M costata* has a psilate proximal face. The circumscription of *Cicatricosisporites* as emended by Pocock (1965), *Potonie* (1966), or Dettmann and Clifford (1992) does not consider the presence or absence of psilate contact areas as part of the diagnosis. Dettmann and Clifford (1991) made a careful evaluation of the exines of extant striate Schizaeaceae and many species of *Cicatricosisporites* and determined that *Cicatricosisporites* compares to the *Anaemia mexicana* and *Anaemia dregeana* type spores. *A. mexicana* includes forms with partially psilate contact areas as in *Cicatricosisporites dorogensis*, *Malayaeaspora*, on the other hand, from the poor illustrations, appears to resemble the outline of *Magnastriatites grandiosus*, and is thought to be a slightly verrucate variant of *M. grandiosus*, and hence of no nomenclatural significance.

Stratigraphic distribution:

This species occurs rarely in zones PR2 to PR3 in Delah 5H-14.1 well. Across Southeast Asia this is an important index taxon, ranging from the late Eocene, about 36 Myr, to the end of the late Oligocene at 23.1 Myr. Its evolutionary appearance is dated at about 36 Myr in the Tanjung Formation in Kalimantan as it appears between the base of the late Eocene and the evolutionary appearance of *Magnastriatites grandiosus*, at about 35 Myr (Witts et al., 2012). The value of *C. dorogensis* as a stratigraphic marker in the Palaeogene rift basins of the Sunda shelf increases toward the east and south. In the Cuu Long Basin, it first appears at the beginning of the Oligocene, and remains relatively common up to the top of the Cuu Long palynological zone CLO9B, within Cuu Long depositional cycle 26b, just before 25 Myr, at about the same time as its first appearance in Delah 5H-14.1 Well. It then occurs in low numbers to the end of the Oligocene (Morley et al., 2021). It shows a similar distribution in the Song Hong Basin (Chung, 2021).

Botanical affinity:

Clearly from a member of Schizaeaceae, with closest affinity to *Anaemia* or *Mohria* (Germeraad et al., 1968).

Suggested name for Quaternary records:

Anaemia type.

Ecological/Morphological group:

Terrestrial spores.

Genus *Crassoretitriletes*

Germeraad et al. 1968

Type species:

Crassoretitriletes vanraadshooveni Germeraad Hopping and Muller 1968 (by original designation).

Crassoretitriletes vanraadshooveni

Germeraad, Hopping and Muller 1968. Plate 5, Figs. 14, 15

Selected synonymy:

1968 *Crassoretitriletes vanraadshooveni* Germeraad et al., p. 287, Pl. 1, Fig. 3.
1972 *Crassoretitriletes vanraadshooveni* Germeraad et al.; Hekel, p. 4, Pl. 2, Figs. 9, 12.
1980 *Crassoretitriletes vanraadshooveni* Germeraad et al.; Huang, Pl. 119, Fig. 8.
1985 *Crassoretitriletes vanraadshooveni* Germeraad et al.; Song et al., p. 63, Pl. 16, Fig. 1.
1986 *Crassoretitriletes vanraadshooveni* Germeraad et al.; Lorente, p. 146, Pl. 3, Fig. 3.

Description:

Spores radially symmetrical, heteropolar; amb triangular to subtriangular with narrowly rounded apices and straight to slightly concave sides; rounded distal pole slightly pointed proximal pole, trilete; laesurae simple, without margines, straight, extending to four-fifths of the spore radius, often open or broken, often obscured by sculpture; exine thick (4-5 μm); exine including reticulum 4-5 μm thick, reticulate over entire surface, muri undulating, 3-4 μm wide, 2 μm high, lumina 2-4 μm wide, 6-12 μm long.

Dimensions:

Equatorial diameter 40 (55) 70 μm (4 specimens measured from various horizons).

Stratigraphic distribution:

This is an important index taxon in West Africa and the Neotropics (Germeraad et al., 1968; Jaramillo et al., 2011) ranging from early Miocene (Burdigalian) to middle Miocene. In Southeast Asia it has a very different distribution, and so the 'pantropical' *Crassoretitriletes vanraadshooveni* zone of Germeraad et al. (1968) does not apply. The taxon becomes quite common in the Oligocene, but in the Cuu long Basin, the only Southeast Asian Palaeogene basin which is accurately dated (Morley et al., 2019), it appears abruptly at the beginning of the early Oligocene. The same spore type has been recorded from the late Eocene of Queensland, Australia (Foster, 1982). In South India, it is regularly recorded from the late Oligocene onward (e.g., Mandaokar, 1996, 2000; Mandal and Vijaya, 2004), and there are possible records from the late Eocene. The range in India is thus similar to that in Southeast Asia. In Malaysia, it occurs in low numbers from the Oligocene onward, and is present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

The species identified here fully agree with the original description by Germeraad et al. (1968).

Botanical affinity:

Lygodium microphyllum or *L. scandens* (Schizaeaceae).

Source ecology:

Climbing fern, common in open vegetation and on open freshwater swamps.

Suggested name for Quaternary records:

Lygodium scandens type spores.

Ecological group:

Freshwater swamp spores.

Genus *Camarazonosporites*
Pant 1954 ex Potonié 1956 emend. Klaus 1960

Type species:
Camarozonosporites cretaceus (Weyland and Krieger 1953) Potonié 1956 (by designation of Potonié 1956).

Generic remarks:
Krutzsch (1963) subdivided *Camarozonosporites* into three subgenera; *C.* subgen. *Camarozonosporites* is diagnosed as having hamulate sculpture that is restricted to the distal surface, and at the most only suggested proximally, more or less psilate contact area and is morphologically similar to *Lycopodiella cernuua; C.* subgen. *Inundatisporis* is characterised by its hamulate sculpture more or less restricted to the distal face, with verrucate contact areas and is similar to *Lycopodium inundatum; C.* subgen. *Hamulatisporis* is distinguished by its hamulate sculpture which overlaps onto the proximal surface and is probably similar to *Lycopodium carolinianum*. These subgenera have not been used here as the system of conventional binomial names are followed.

Camarozonosporites minor
Jaizan Jais and Morley sp. nov. Plate 6, Figs. 1, 2.

Derivation of name:
From its relatively small size.

Holotype:
Plate 6, Figs. 1, 2. Slide Malong-2, 518 m, SWC (S1), England Finder G46/2. Grain equatorially compressed, 21 µm in equatorial diameter; cingulum 2 µm wide at equatorial interradii and 1 µm wide at amb apices.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 518 m depth; age late Miocene, zone PR14.

Description:
Spores radially symmetrical, heteropolar; amb subtriangular to subrounded with a narrow cingulum developed around the spore body; trilete; laesura simple, straight, often open, extending to three-fourths of the spore radius; exine thin, rugulate distally; rugulae more or less reduced proximally; cingulum psilate, more distinct and wider at equatorial interradii (1-2 µm wide), less distinct and narrower (0.5-1 µm wide) at amb apices.

Dimensions:
Equatorial diameter 18 (20) 22 µm (5 specimens measured from various horizons).

Variability:
In the thickness of cingulum.

Stratigraphic distribution:
Present in low percentages and restricted to the PR13-15 zone.

Comparison:
This species is smaller than *Camarozonosporites* sp. Harris 1974 (Kemp and Harris 1977) and *Camarozonosporites* subgen. *Camarozonosporites heskemensis* (Pflanzl 1955) Krutzsch 1959. *Camarozonosporites* subgen. *Inundatisporis minoris* Krutzsch 1963 is punctate or verrucate proximally in contact areas and is generally bigger in size.

Botanical affinity:
C. minor conforms in all ways with spores of extant *Lycopodiella cernuua* (Lycopodiaceae).

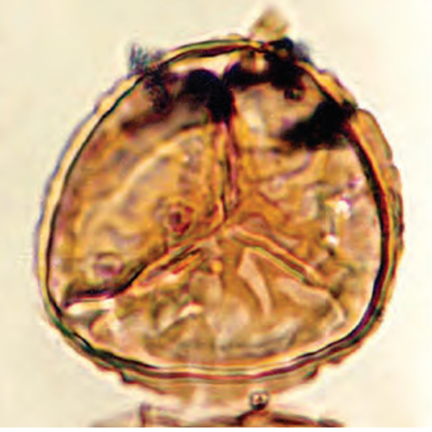
Source ecology:
Scrambling herb of open areas, also occurring in swampy areas and in Kerangas (Anderson and Muller, 1975).

Suggested name for Quaternary records:
Lycopodiella cernnua type spores.

Ecological group:
Freshwater swamp.

Lycopodiella cernuua, *kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).*

Camarozonosporites heskermensis (Pflanzl 1955) Krutzsch 1959. Plate 6, Figs. 3, 4



Description:

Spores radially symmetrical, heteropolar; amb subtriangular to subrounded with a distinct cingulum developed around the spore body, appearing as a well-defined rim, trilete; laesura simple, slightly sinuous, often open, extending to three-fourths of the spore radius with clear raised margines; exine thin, with wrinkled rugulae distally; rugulae reduced proximally; cingulum sculptured, wider at equatorial interradii (2-3 μm wide), and narrower (1-2 μm wide) at amb apices.

Dimensions:

Equatorial diameter 25 (29) 33 μm (7 specimens measured from various horizons).

Stratigraphic distribution:

Present in low percentages especially within zones PR13 to PR15 in Malong 5G-17.2 well.

Remarks and comparison:

Relative to *Camarazonosporites minor* sp. nov. above, included here are the larger forms of narrowly cingulate and distally rugulate trilete spores with convex subtriangular to subrounded amb. A few specimens observed have rugulate sculpture that extends proximally which may fall into *Camarozonosporites* subgen. *Hamulatisporis* (Krutzsch 1959) Krutzsch 1963. Otherwise, specimens resemble the generally bigger *Camarozonosporites* subgen. *Camarozonosporites heskemensis* (Pflanzl 1955) Krutzsch 1959 and the Cretaceous *C. ambigens* (Fradkina) Playford 1971. Apart from their bigger size, these species have more distinct rugulae as compared to *C. minor* sp. nov.

Botanical affinity:

Lycopodium carolinianum type (Lycopodiaceae) according to Wilce (1972).

Source ecology:

Fern allies growing in presumably open areas.

Suggested name for Quaternary records:

Lycopodium carolinianum type spores.

Ecological/Morphological group:

Terrestrial fern spores.

PTERIS-LIKE SPORES

Relatively low numbers of *Pteris*-type spores were recovered through the Malong 5G-17.2 and Delah 5H-14.1 wells. However, in many Malaysian sections *Pteris* spores can be quite common and show considerable diversity. *Pteris* spores are of interest in that most *Pteris* species can be identified on spore characters (Chao and Huang, 2018) although their morphological characters are only partly of use in taxonomy because many spore morphologies have evolved multiple times (Chao and Huang, 2018). Seven characters are of value in classifying *Pteris* spores as follows:

1) Presence of an equatorial flange (or cingulum);
2) laesural ridges;
3) peripheral ridges on the proximal face;
4) distal ridges;
5) tubercula on distal faces;
6) coarse reticula on distal faces, and
7) a row of verrucae or gemmae between the distal face and equatorial flange (Chao and Huang 2018).

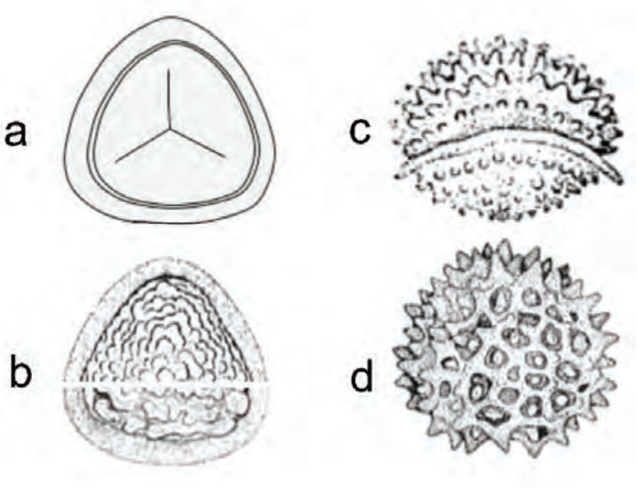


Fig. 2.2 Line drawings of Pteris *spores, in part from Devi (1979).*

Here we use these characters to differentiate species. Typically, *Pteris* spores described from Southeast Asia are placed either in *Cingulatisporites* Thomson and Pflug (1953) or *Polypodiaceoisporites* Potonie 1956 (e.g., Muller, 1968; Stover and Partridge, 1973). *Cingulatisporites* as emended by Pocock (1961) has a smooth to scabrate central body. No fresh *Pteris* spp. possess psilate exine, the spore wall consists of a thin exine layer covered with ornamented perine. However, during fossilisation or processing, the perine may become dislodged, leaving a psilate exine, as in the case of *Laevigatosporites* (see above). *Polypodiaceoisporites*, on the other hand is defined as having a central body which is distally reticulate (Potonie, 1956), a character which applies to just a few complex *Pteris* species. Here *Pteris*-like spores are placed in *Pteridacidites* Sah (1967), the diagnosis of which encompasses most variation within extant *Pteris* spores. Shatilova, Kvavadze and Kokolashvili (2016) provide a very good perspective from Georgia of the morphological diversity of South Asian Miocene *Pteris* spores and how to differentiate them.

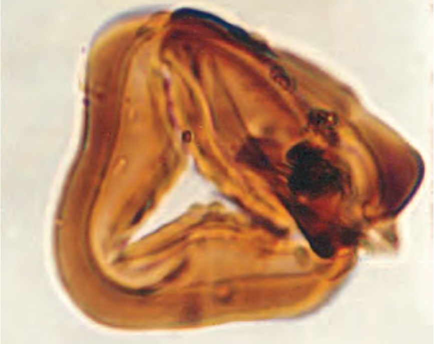
Pteris *spp., showing typical branched basal pinnae (photo from Wen Ling Tsai, Creative Commons).*

Genus *Cingulatisporites* Thomson in Thomson and Pflug 1953 emend. Hiltman 1967

Type species:
Cingulatisporites levispeciosus Pflug in Thomson and Pflug 1953.

Generic remarks:
Cingulate trilete spores with psilate exine, both on the proximal and distal surfaces, are here classified under this genus. Verrucate and rugulate forms are classified under the genus *Polypodiaceoisporites*.

Cingulatisporites psilatus
Khan 1976a. Plate 6, Fig. 5



Selected synonymy:
cf. 1976a *Cingulatisporites psilatus* Khan, p. 758, Figs. 9A, 9B.

Description:
Spores radially symmetrical, heteropolar; amb subtriangular with cingulum developed around the spore body of rounded apices and slightly concave to almost straight sides; trilete; laesura straight, often open, extending to three-fourths or more of the spore radius, not reaching spore margin (inner margin of cingulum), bordered by thickened ridges 2 to 3 µm wide; exine psilate proximally and distally.

Dimensions:
Equatorial diameter, minimum 26 µm, maximum 27 µm (2 specimens measured).

Distribution:
Very rare.

Stratigraphic distribution:
Khan (1976a) recorded *C. psilatus* from the Pliocene to Pleistocene of Papua New Guinea. Present in low percentages throughout both Malong 5G-17.2 and 5H-14.1 wells.

Remarks and comparison:
This species resembles *C. psilatus* Khan in all aspects except for its smaller size.

Botanical affinity:
Pteris (Pteridaceae).

Source ecology:
Terrestrial ferns of open areas.

Suggested name for Quaternary records:
Undifferentiated *Pteris* type spores.

Ecological/Morphological group:
Terrestrial pores.

Genus *Pteridacidites*
Sah 1967

Type species:
Pteridacidites africanus Sah 1967.

Pteridacidites variabilis
Stuchlik and Shatilova 1987. Plate 6, Figs. 6, 7

Selected synonymy:
1963 *Pteris* aff. *cretica* L. Mchedlishvili, p. 74, Pl. II, Fig. 8.
1987 *Pteris cretica* L.; Stuchlik & Shatilova, Pl. 6, Figs. 3, 4.
1996 *Pteridacidites variabilis* Stuchlik & Shatilova Shatilova, Stuchlik, p. 18, Pl. 10, Figs. 4a-c, 5.

Description:
Spores radially symmetrical, heteropolar; amb subtriangular with cingulum developed around the spore body of rounded apices and slightly concave to almost straight sides; trilete; laesura straight, often open, extending to three-fourths or more of the spore radius, not reaching spore margin (inner margin of cingulum), bordered by thickened ridges 2 to 3 µm wide; exine psilate proximally and verrucate distally; verrucae 1 to 3 µm in diameter, finer in the marginal area, coarser and some with irregular rugulae in the distal polar area; cingulum psilate, 3 to 5 µm wide, of constant width or slightly narrower around apices.

Dimensions:
Equatorial diameter 29 (33) 42 µm (15 specimens measured from various horizons).

Stratigraphic distribution:
Present in low percentages throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Comparison:
Polypodiaeoisporites retirugatus Muller is much larger, while *Cingulatisporites ivirensis* Khan and *C. papuanus* Khan has a wider cingulum. Among other species with thickened ridges paralleling the laesura, *Pteridacidites contortus* and *P. georgensis* Stuchlick and Shatilova 1987 have wider or more robust laesural ridges, *P. guriensis* Stuchlick and Shatilova 1987 has a convoluted cingulum and *P. remotifoloides* Stuchlick and Shatilova 1987 has a cingulum that narrows at the apices.

Botanical affinity:
Pteris (Pteridaceae), probably the widespread *Pteris cretica*.

Source ecology:
Terrestrial ferns of open areas.

Ecological/Morphological group:
Terrestrial spores.

Plate 6

Figs. 1, 2 *Camarozonosporites minor* Jaizan Jais and Morley sp. nov. Figs. 1, 2 (x 1000 holotype): Slide Malong-2, 592 m, SWC (S1); England Finder S40.

Figs. 3, 4 *Camarozonosporites heskermensis* (Pflanzl 1955) Krutzsch. Figs. 3, 4 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder Q9.

Fig. 5 *Cingulatisporites psilatus* Khan 1976a (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder R21.

Figs. 6, 7 *Pteridacidites variabilis* Stuchlik and Shatilova 1987 (x 1000): Slide Malong-2, 918 m, SWC (S1); England Finder Y12/2.

Fig. 8 *Ephedripites* sp. (x 1000): Slide Malong-2, 366 m, SWC (S1); England Finder S5/3.

Figs. 9, 11, 12 *Zonalapollenites igniculus (Potonié 1931)* Pocock 1968. Fig. 9 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder Q23. Figs. 11, 12 (x 1000): Slide Malong-2, 456 m, SWC (S2); England Finder T17.

Figs. 10, 13 *Zonalapollenites spinulosus* Krutzsch 1971. Fig. 10 (x 400): Slide Delah-1, 2540-2545 m, DC (S1); England Finder H36/2. Fig. 13 (x 400): Slide Malong-2, 1494.2 m, CC (S1); England Finder U5/4.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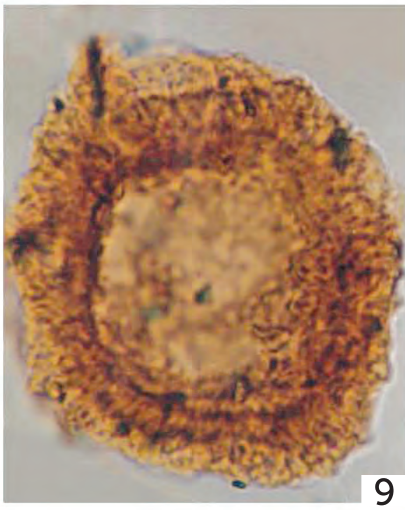
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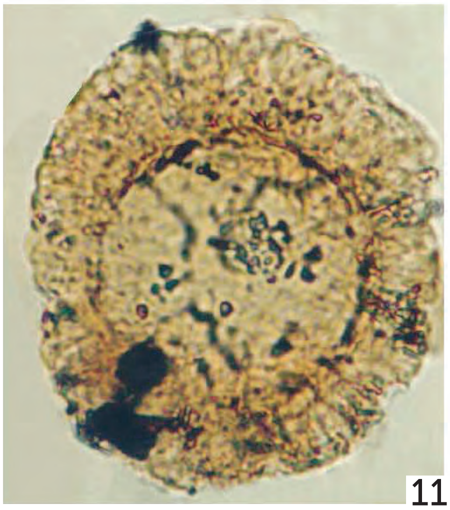
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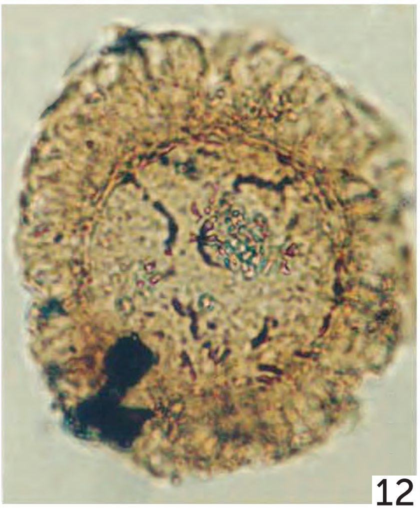
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2.4 POLYPLICATE POLLEN

Genus *Ephedripites*
Bolkhovitina 1953 ex Potonié 1958
emend. Krutzsch 1961

Type species:
Ephedripites mediolobatus
Bolkhovitina 1953.

Ephedroid pollen is polyplicate and oval in outline and bears numerous ridges that extend longitudinally along the grain separating pseudosulci that often display branching, and that the shortest axis is polar, and the longest, equatorial (Huyhn 1975; El-Ghazaly et al., 1998).

The earliest ephedroid pollen is probably found in the Permian, and rapidly increases in abundance, diversity of morphotypes and distribution within the low latitudes until the mid-Cretaceous (Bolinder et al., 2016), and then rapidly reduces in abundance in the low latitudes during the Late Cretaceous (Crane and Lidgard, 1989) while angiosperms increase in dominance. After the K-Pg boundary, diversity is reduced, with morphological variation being consistent with that seen in extant *Ephedra*. Low latitude records are scattered, and the locus shifts to the seasonally dry Hadley Cells to the north and south of the equatorial region (Garcia et al., 2015; Han et al., 2015).

Bolinder et al. (2016) shows that *Ephedra* pollen occurs in two distinct forms (Fig. 2.3), an ancestral type, with unbranched pseudocolpi (A), which are recorded as fossils in the Late Cretaceous Pedawan Formation in Sarawak, studied by Muller (1968), and the late Eocene Yaw Formation in Myanmar (Huang et al., 2021) and a derived type, with branched pseudocolpi (B), which has only been reported from the Cenozoic, and occurs infrequently in Southeast Asia, such as in the Nanggulan Formation in Java (Lelono, 2000).

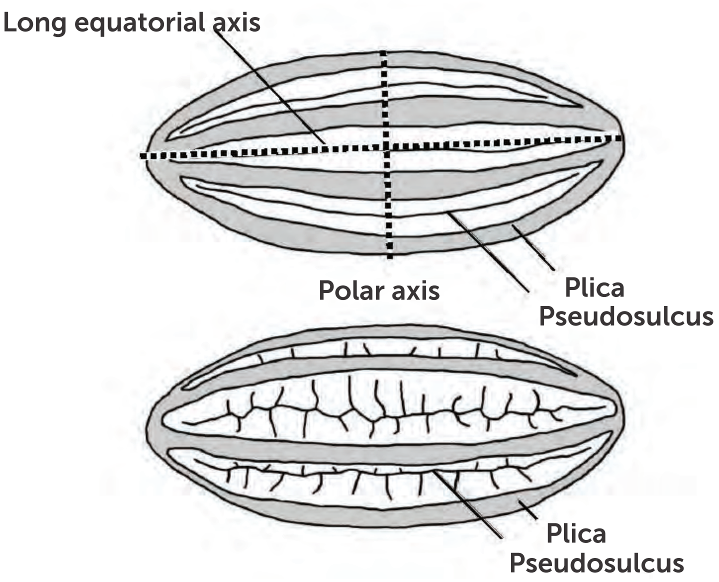


Fig. 2. 3. Main types of Ephedra *pollen.*

***Ephedripites* sp.** Plate 6, Fig. 8

Description:
Pollen polyplicate, outline oval, exine thin, generally 10 to 14 ridges, broadly elliptical pollen, radially symmetrical; a smaller or larger number of parallel ribs (plicae) run from one pole to the other, the valleys between the ribs are psilate, reflecting thinning of the exine.

Dimensions:
Length 25 μm, width 12 μm (1 specimen measured).

Stratigraphic distribution:
Only one specimen was found in the uppermost sample at 366 m (SWC) depth in the Malong 5G-17.2 well. *Ephedripites* spp. occur in low numbers in many Oligocene successions across the Sunda Shelf.

Botanical affinity:
Ephedra (Ephedraceae).

Source ecology:
Shrub of arid to semi-arid areas, carried by wind and water from the north.

Suggested name for Quaternary records:
Ephedra.

Ecological group:
Seasonal.

2.5 MONOSACCATE POLLEN

In Asia Tsuga *spp. are restricted to the Himalayas and southern China and occur in wet foggy forest at high altitude.* Tsuga dumosa *from Bhutan (photo by wonderlane on Flickr, CC BY 2.0, via Wikimedia Commons).*

Genus *Zonalapollenites*
Pflug in Thomson and Pflug 1953

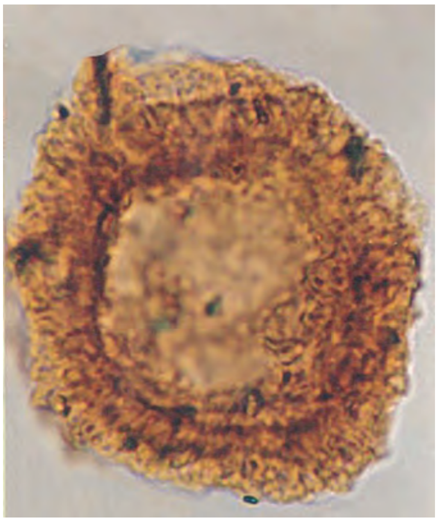
Type species:
Zonalapollenites igniculus
Potonié 1931 (Pocock 1968) (by designation of Pocock 1968).

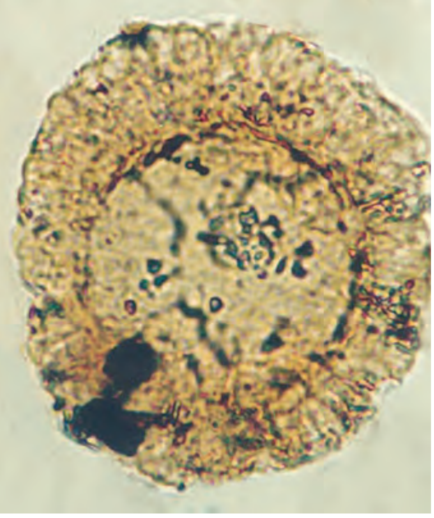
Generic remarks:
The genus *Zonalapollenites* Pflug is intended for monosaccate pollen with morphology like that of *Tsuga*, which has a single saccus encompassing a central body. This arrangement is also seen in the New Caledonian podocarp *Dacrydium guillauminii*, which is sometimes found as fossil in the Oligocene of Java (Morley 2000). *Callialasporites* is similar but differs in the character of the saccus (Sukh Dev, 1961), and is essentially a genus applicable to Mesozoic monosaccate grains, whereas *Tsuga* is a Cenozoic genus, with a crown age of about 42 Myr (Havill et al. 2008). Pocock (1968), who designated the type species, discusses the confusion over the validity of the genera *Zonalapollenites* and *Tsugaepollenites* Potonié and Venitz 1934 ex Potonié 1958 and concluded that the former has priority over the latter. Jansonius and Hills (1976) have also stated that *Tsugaepollenites*, which was not validated until 1958 and having the same type species as of *Zonalapollenites*, is an obligate junior synonym of *Zonalapollenites*.

Krutzsch (1971) has described 17 species of *Zonalapollenites* from the mid Cenozoic of Germany, and at least 4 of these can be found in the Oligocene of the Sunda Shelf, with two occurring in the Delah 5H-14.1 well.

Zonalapollenites igniculus

(Potonié 1931) Pocock 1968. Plate 6, Figs. 9, 11, 12





Selected synonymy:

1931 *Sporonites igniculus* Potonié, p. 556, Fig. 2.

1934 *Tsugae-pollenites igniculus* (Pot. 1931) Potonié and Venitz, p. 17, Pl. 1, Fig. 8.

1953 *Zonalapollenites igniculus* (Pot. 1931) Thomson and Pflug, p. 66-67, Pl. 4, Figs. 75-79.

1968 *Zonalapollenites igniculus* (Pot. 1931) Pocock, p. 640.

1971 *Zonalapollenites igniculus* (Pot. 1931) Thomson and Pflug 1953; Krutzsch, p. 138, Pl. 37, Figs. 1-23.

Description:

Pollen almost radially symmetrical, monosaccate; approximately circular in polar view, peroblate in equatorial view, inner body punctate to verrucate and enclosed in a single approximately circular saccus, larger than the body, manifest with a distinct undulate equatorial fringe.

Dimensions:

Equatorial diameter including saccus 40 (44) 56 μm; corpus diameter 24 (29) 42 μm; saccus width 5 (8) 10 μm (6 specimens measured from various horizons).

Stratigraphic distribution:

This morphotype has been recorded widely in Europe (summarised in Krutzsch, 1971), and from some localities in North America (e.g., Frederiksen, 1984). Also, from the Neogene of Southwest China (Chen and Zhong, 1983) and Korea (Takahashi and Kim, 1979), and the Oligocene of the Cuu Long and Song Hong basins offshore Vietnam and elsewhere on the Sunda Shelf (Morley and Morley, 2018; Chung et al., 2021; Morley et al., 2021). Rare and sparsely distributed in zones PR3 to PR4 in Delah 5H-14.1 well.

Remarks and comparison:

Zonalapollenites igniculus differs from *Z. spinulosus* by the absence of minute echinae superimposed on the saccus.

Botanical affinity:

Derived from *Tsuga* spp. producing *T. canadensis* type (Pinaceae) pollen.

Source ecology:

Trees of foggy, wet, upper montane forests, presently occurring in the mountains of the Himalayan region and southern China to Taiwan (Havill, 2008).

Suggested name for Quaternary records:

Tsuga canadensis type.

Ecological group:

Upper montane forests.

Zonalapollenites spinulosus

Krutzsch 1971. Plate 6, Figs. 9, 13

Selected synonymy:

1960 *Tsuga* f. *spinosa* Doctorowicz-Hrebnicka, p. 38, Pl. 9, Fig. 39.
1971 *Zonalapollenites spinulosus* (*Tsuga spinulosus*) Krutzsch, p. 148, Pl. 41, Figs.1-10.
1974 *Zonalapollenites spinosus* (Doctorowicz-Hrebnicka) Ziembinska-Tworzydlo, p. 353, Pl. 11, Figs. 1a, 1b.
1978 *Tsugaepollenites spinulosus* (Krutzsch) Ke and Shi, p. 92, Pl. 19, Figs. 15, 16.
1979 *Zonalapollenites koreanus* Takahashi in Takahashi and Kim (1979)

Description:

Pollen almost radially symmetrical, monosaccate; approximately circular in polar view, peroblate in equatorial view, inner body punctate to verrucate and enclosed in a single approximately circular saccus, larger than the body, manifest with a distinct undulate equatorial fringe with minute superimposed echinae.

Dimensions:

Equatorial diameter including saccus 67 (73) 80 µm; corpus diameter 50 (55) 65 µm; saccus width 5 (11) 15 µm; echinae length 1 (1.5) 2 µm (4 specimens measured from various horizons).

Stratigraphic distribution:

In Europe, this species is widely distributed and ranges from the late Oligocene to Pliocene (Krutzsch, 1971). It is also recorded from the Hubei Province of China where it is first recorded in the middle Eocene (Sun et al., 1979), with additional Chinese records from the late Eocene to early Pliocene of Qinghai Province, China (Zhu et al., 1985) and the Pliocene of East China Sea (Song et al., 1985). In Vietnam, it is widely recorded from the Oligocene (Morley et al., 2019). Rare and sparsely distributed in zones PR3 to PR4 in Delah 5H-14.1.

Remarks and comparison:

This species is characterised by the presence of minute echinae sparsely distributed at the margin of the encompassing saccus.

Botanical affinity:

Pollen is identical to that of *Tsuga diversifolia* (Pinaceae).

Source ecology:

Trees of montane forests, presently occurring in the mountains of Japan (Havill et al., 2008).

Suggested name for Quaternary records:

Tsuga diversifolia type.

Ecological group:

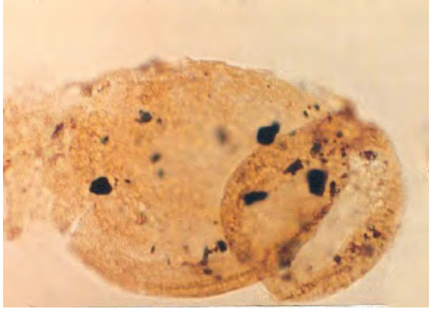
Wet, foggy, upper montane forests.

2.6 BISACCATE POLLEN

Genus *Abiespollenites*
Thiergart in Raatz (1937) 1938 emend. Potonié 1958

Type species:
Abiespollenites absolutus Thiergart 1937.

***Abiespollenites* spp.** Plate 7, Figs. 10, 13



Description:
Pollen grains bilaterally symmetrical, bisaccate, very large, corpus reticulate on distal face, psilate proximally, with distinct demarcation between cappa and cappula, without marginal ridge, sacci reticulate, smaller than corpus, with clear demarcation between sacci and corpus.

Dimensions:
Overall length 80 (96) 110 µm (3 specimens), height, minimum 54 µm, maximum 76 µm (2 specimens), width 75 µm (1 specimen); corpus length, minimum 70 µm, maximum 79 µm (2 specimens), height, minimum 54 µm, maximum 58 µm (2 specimens), width 65 µm (1 specimen); saccus length 53 µm (1 specimen), height 40 (45) 49 µm (3 specimens), width 75 µm (1 specimen).

Stratigraphic distribution:
Abiespollenites is widely recorded across the Cenozoic in the mid-latitudes of the northern hemisphere, with records occurring further south in the Sunda shelf region than anywhere else (Muller, 1966, 1972; Morley and Morley, 2018). There are many records from the Mesozoic, but these do not relate to the extant Pinaceae as the *Abies*-*Keteleeria* clade has a molecular age of 60 Myr (Ran et al., 2018). Distributed in low percentages throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
Specimens assigned to this group consisting of large bisaccate pollen with separated, proximally attached sacci. Sacci reticulate and smaller than corpus. *Pinuspollenites* spp. are smaller in size and sacci of *Piceapollis* spp. are more finely reticulate and merge with corpus.

Botanical affinity:
This pollen type is characteristic for the montane conifer *Abies* (Pinaceae) but is also found in the Indochinese montane to lower montane tree *Keteleeria* within the same family (van Campo, 1950; Erdtman, 1965).

Source ecology:
Abies are trees of high mountains, typically above 2000 m, occurring along the Himalaya, in Central China and in Taiwan (Farjon and Filer, 2013). *Keteleeria*, on the other hand, is a genus restricted to East Asia, and includes three species, which in addition to being found in the mountains of Central China and Taiwan, extend into the montane forests of Laos and Vietnam, with the southernmost records occurring to 12°S in the Annamite range. *Keteleeria evelyniana* ranges in altitude from 700 m up to about 2000 m and is the only Laurasian conifer other than *Pinus* (see below) and *Taxus* that extends into Southeast Asian rain forests, where it often acts as a pioneer tree in the manner of *Pinus* (Farjon, 1989). Most of the '*Abies*' type pollen found in Sunda Shelf sediments are probably derived from *Keteleeria* (Morley and Morley, 2018).

Suggested name for Quaternary records:
Abies type.

Ecological group:
Montane forest trees.

Genus *Dacrydiumites*
Cookson and Pike 1953 ex Harris 1965

Type species:
Dacrydiumites florinii Cookson and Pike 1953 ex Harris 1965.

Generic remarks:
According to Jansonius and Hills (1976) Cookson and Pike originally proposed *Dacrydiumites* in 1953 to replace the genus *Phyllocladidites* which she proposed in 1947 because the species she earlier assigned to the latter were found to show more close similarity to pollen of *Dacrydium franklinii*. Both Cookson's genera *Phyllocladidites* and *Dacrydiumites* were not validly published in 1947 and 1953 respectively because the former were proposed without naming a type species and the latter without a diagnosis nor type species. In 1953 Couper validated *Phyllocladidites* and designated *P. mawsonii* Cookson 1947 as type species. Later in 1965 Harris rejects Cookson's reasoning for replacing *Phyllocladidites* with *Dacrydiumites* but he uses again and validly proposes the generic name *Dacrydiumites* for a morphologically different type of pollen and designated *D. florinii* Cookson and Pike as a type species. This procedure is valid according to the ICBN but as Jansonius and Hills (1976) further commented, it is unfortunate because it may cause confusion which is illustrated by the fact that *Dacrydiumites* in the original sense of Cookson was later validated by Nagy in 1969. Consequently, having the same type species, *Dacrydiumites* Cookson ex Nagy 1969 is an obligate junior synonym of *Phyllocladidites* Cookson ex Couper 1953 as well as a junior homonym of *Dacrydiumites* Cookson ex Harris 1965. More confusion arose when in 1973, Stover and Evans proposed a new genus *Lygistepollenites* to replace *Dacrydiumites* Cookson ex Harris. According to Jansonius and Hills (1976) because *Dacrydiumites* had never been validly proposed by Cookson, Stover and Evans (1973) incorrectly consider *Dacrydiumites* Cookson ex Harris as a junior homonym of *Dacrydiumites* Cookson, which in turn is a junior synonym of *Phyllocladidites* Cookson ex Couper. Jansonius and Hills (1976) considered *Lygistepollenites* Stover and Evans to be a junior synonym of *Dacrydiumites* Cookson ex Harris, hence the latter is used here. However, *Lygistepollenites* is continued to be used especially in the Australian region.

Dacrydiumites florinii
Cookson and Pike ex Harris 1965. Plate 7, Figs. 3, 4

Selected synonymy:
1953b *Dacrydiumites florinii* Cookson and Pike, p. 479, pl. 3, Figs. 20-35.
1965 *Dacrydiumites florinii* Cookson and Pike ex Harris, p. 87, Pl. 26, Fig. 18.
1965 *Dacrydiumiites mawsonii* (Cookson and Pike) Sah and Jain, p. 279, Pl. 6, Fig. 123.
1973 *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans, p. 64.
1973 *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans; Stover and Partridge, p. 252.
1974 *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans; Harris, p. 513, Pl. 2, Figs. 3, 4.
1976b *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans; Khan, p. 786, Fig. 4.
1977 *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans; Kemp and Harris, p. 25.
1982 *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans; Playford, p. 43, Pl. 5, Fig. 8.

Description:
Pollen grains bilaterally symmetrical, bisaccate, corpus reticulate to rugulate, sacci attached proximally and with a distinct rugulate-reticulate pattern.

Dimensions:
Overall length 37 (47) 62 µm (9 specimens), height 28 (34) 42 µm (7 specimens), width 32 µm (1 specimen); corpus diameter (long axis) 27 (32) 37 µm (8 specimens); saccus length 19 (26) 37 µm (7 specimens), height 13 (18) 27 µm (8 specimens), width 32 µm (1 specimen).

Stratigraphic distribution:
Dacrydium pollen is widespread throughout the Australian Cenozoic, with the oldest records in the Santonian (86.3-83.6 Myr) of the Late Cretaceous (Dettmann, 1994). It is also reported from the late Oligocene/early Miocene of Patagonia (South America) by Palazzesi and Barreda (2007) and the Paleocene and Oligocene of the Ninetyeast Ridge (Kemp and Harris 1975). In Southeast Asia its oldest records are from the late Eocene of Java (Lelono and Morley, 2011). *Dacrydium* pollen is distinctly absent from middle Eocene and older sediments of Southeast Asia and is thought to have dispersed to Southeast Asia via the Indian Plate (Morley, 2010). There are also records from the middle Miocene climatic optimum of China, Japan and Korea (Morley, 2010). Present throughout both Malong 5G-17-2 and Delah 5H-14-1 in moderate percentages.

Remarks:
The bisaccate pollen assigned to this species appear in all respect identical with *Dacrydiumites florinii* originally described by Cookson and Pike (1953).

Dacrydium elatum, *kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).*

Botanical affinity:
Dacrydium (Podocarpaceae).

Source ecology:
Trees of montane forests and also characteristic of heath forest or Kerangas in Sarawak (Brunig, 1974), and Kerapah peats, such as the Lawas peat from Brunei (Muller, 1963; Morley, 2010), and it is thought that most pollen found in the Malaysian sediments is from kerangas and kerapah vegetation, with just a small proportion coming from montane forests.

Suggested name for Quaternary records:
Dacrydium.

Ecological group:
Trees of kerangas, kerapah and montane forests.

Plate 7

Figs. 1, 2 *Abiespollenites* spp. Figs. 1, 2 (x 400): Slide Malong-2, 483 m, SWC (S2); England Finder W8/4.

Figs. 3, 4 *Dacrydiumites florinii* Cookson and Pike ex Harris 1965. Figs. 3, 4 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder H28/3.

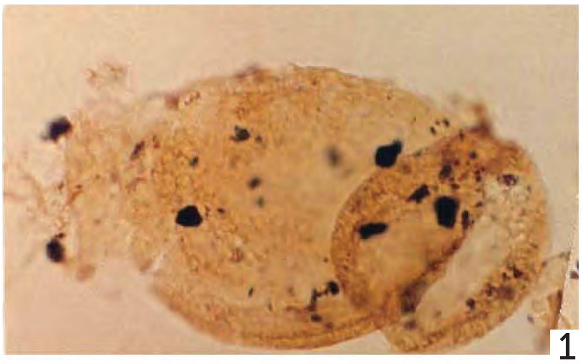
Figs. 5, 6 *Pinuspollenites* spp. Figs. 5, 6 (x 400): Slide Malong-2, 934 m, SWC (S1); England Finder G33.

Fig. 8 *Podocarpidites* sp. cf. *P. ellipticus* Cookson 1947. Fig. 8 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder N22/4.

Figs. 7, 10 *Podocarpidites minuticorpus* Jaizan Jais and Morley sp. nov. Fig. 7 (x400), Fig 10 (x 1000 Holotype): Slide Malong-2, 592 m, SWC (S1); England Finder P16.

Fig. 9 *Piceapollis* sp. (x 400): Slide Malong-2, 483 m, SWC (S2); England Finder J6.

Figs. 11, 12 *Incrotonipollis reticulatus* (Da Silva Caminha et al., 2009) Jaizan Jais and Morley comb. nov. Figs. 11, 12 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder W38/2.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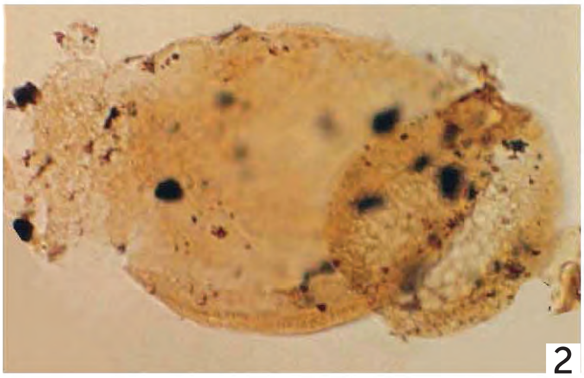
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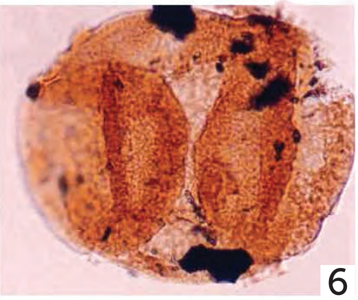
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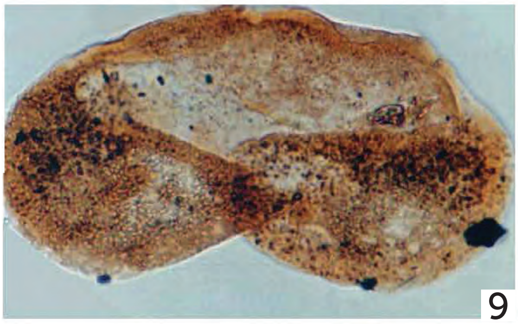
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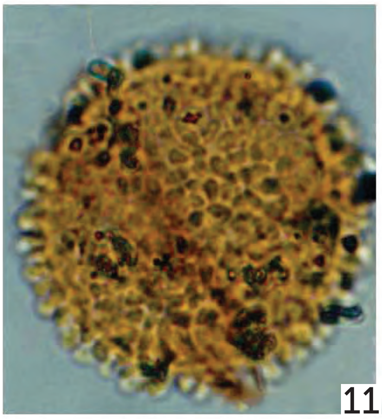
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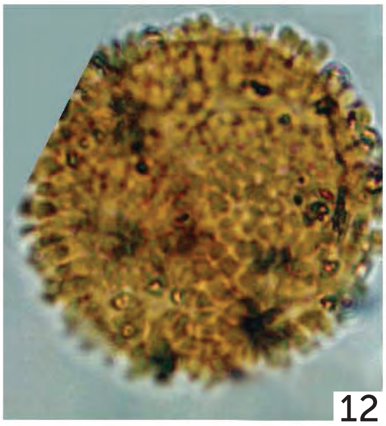

12


10

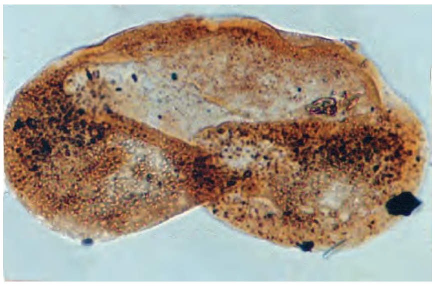
Genus *Piceapollis*

Krutzsch 1971

Type species:

Piceapollis praemarianus Krutzsch 1971.

***Piceapollis* sp.** Plate 7, Fig. 9



Description:

Pollen grains bilaterally symmetrical, bisaccate, corpus reticulate on distal face, with gradational change to psilate proximally, without marginal ridge, sacci reticulate, smaller than corpus, with indistinct demarcation between sacci and corpus.

Dimensions:

Overall length 48 (85) 120 µm (17 specimens), height 45 (59) 73 µm (6 specimens), width 32 (57) 77 µm (11 specimens); corpus length 55 (80) 90 µm (6 specimens), height 26 (41) 50 µm (6 specimens), width 26 (45) 60 µm (11 specimens); saccus length 40 (49) 67 µm (6 specimens), height 18 (35) 51 µm, width 30 (56) 95 µm (11 specimens).

Stratigraphic distribution:

Many records from the Cenozoic of Eurasia, but also frequently recorded from the Cretaceous of Japan and China, which may be possible since the molecular age of stem *Picea* is 186 Myr within the Jurassic (Ran et al., 2018). Sparsely distributed in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:

Included in this group are specimens characterised by finely reticulate (piceoid) sacci merging into the corpus. *Pinuspollenites* spp. and *Abiespollenites* spp. have more coarsely reticulate sacci.

Botanical affinity:

Picea (Pinaceae).

Source ecology:

Trees of wet and foggy upper montane forests in the Himalaya, Central China and Taiwan (Morley, 2018b).

Suggested name for Quaternary records:

Picea.

Ecological group:

Upper montane forest trees.

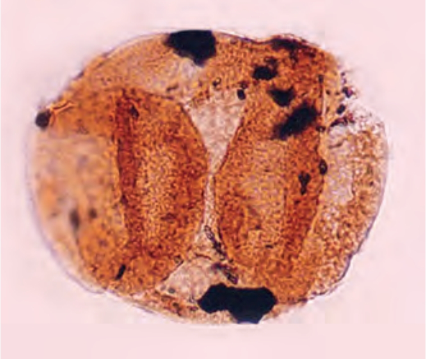
Genus *Pinuspollenites*

Raatz 1937 ex Potonié 1958

Type species:

Pinuspollenites labdacus (Potonié 1931) Raatz 1937 ex Potonié 1958 (by designation of Potonié 1958).

***Pinuspollenites* spp.** Plate 7, Figs. 5, 6



Description:

Pollen grains bilaterally symmetrical, bisaccate, corpus reticulate on distal face, with gradational change to psilate proximally, with distinct marginal ridge or frill, sacci reticulate, smaller than corpus, with clear demarcation between sacci and corpus.

Dimensions:

Overall length 49 (77) 95 (10 specimens), height 36 (56) 75 µm, width 43 (54) 69 µm (4 specimens); corpus length 36 (62) 95 µm, height 30 (44) 60 µm, width 35 (41) 48 µm (4 specimens); saccus length 23 (43) 70 µm, height 21 (34) 45 µm, width 43 (49) 53 µm (4 specimens).

Stratigraphic distribution:

Pinuspollenites spp. are widely represented across the northern hemisphere, with the oldest macrofossil record of *Pinus* from the Triassic of Nova Scotia (Falcon-Lang, 2016). *Pinuspollenites* spp. are widely recorded through Cenozoic of China, such as in the early Eocene Hengyang Basin (Xie et al., 2020) and the late Eocene Xining Basin, China (Hoorn et al., 2012). The oldest record in the Southeast Asian region is of *Pinuspollenites* cf. *spherisaccus* from the Paleocene of Borneo (Muller, 1968). It is common across the broad Sunda shelf region, especially in the Oligocene, and also through the Neogene in more northern localities. *Pinuspollenites* spp. are abundant through the Oligocene of the Cuu Long Basin (Morley et al., 2019) and Song Hong Basin (Chung et al., 2021), and also through the Oligocene and early Miocene of the Bukoh-1 well in northern Luconia (Morley et al., 2021). *Pinus* pollen may also be common in the Malaysian Pleistocene (see below). It has never been recorded as fossil south of the equator, except in some Quaternary sections where it has been transported in low numbers by air or water (e.g. Van der Kaars et al., 2010), Present in both Malong 5G-17.2 and Delah 5H-15-4.1 with relatively higher percentages in the Delah section, where it occurs regularly in zones PR1 to PR4.

Remarks and comparison:

The bisaccate pollen included here is distinguished by its irregularly reticulate or pseudo-reticulate sacci which are smaller than the corpus, the distinct marginal ridge and finely but distinctly reticulate corpus. The reticulum of the sacci is finer than in *Podocarpidites* spp. *Pinuspollenites* divides into two sections, widely seen at higher palaeotitudes, 'Haploxylon', and 'Diploxylon' (Singh et al., 2021). The former mostly preserves on polar orientation, whereas section Diploxylon mostly preserves in equatorial view. Malaysian specimens are mostly the Diploxylon type.

Botanical affinity:
Pinus (Pinaceae).

Pinus merkusii *Cemara, Bogor Java (photo by RJM).*

Source ecology:
Pinus is a genus of coniferous trees of seasonal mountains and in Southeast Asia, seasonally dry lowlands, where the genus occurs further south than anywhere else, reaching 2° S in Sumatra (Cooling, 1968). Species occur either in the mountains of the Himalaya and Indochina, such as *P. roxburghii* and *P. wallichii*, or are widespread in the lowlands of Indochina, the Philippines, and parts of Sumatra, with the species *P. kesiya* and *P. merkusii*. The ecology of *Pinus* in lowland tropical Asia is generally poorly understood. *Pinus* savanna is widespread In Indochina and occurred as far south as the Sunda Shelf when sea levels were lower during the last glacial maximum (Morley, 1988; Morley and Morley, 2021), with the present populations being relict (Werner, 1997). Examination of pollen assemblages with abundant *Pinus* from the Cuu Long Basin, south of the Mekong Delta, suggested that most fossil *Pinus* pollen originated from lowland habitats (Morley et al., 2019). In seasonally dry vegetation across Indochina its common occurrence suggests well-drained habitats (Ashton, 2014).

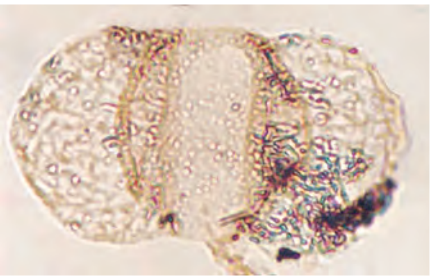
Suggested name for Quaternary records:
Pinus.

Ecological group:
Seasonally dry fire climax forest and savanna.

Genus *Podocarpidites*
Cookson 1947 ex Couper 1953

Type species:
Podocarpidites ellipticus Cookson 1947 (by designation of Couper 1953).

Podocarpidites* sp. cf. *P. ellipticus
Cookson 1947. Plate 7, Fig. 8



Selected synonymy:
cf. 1947 *Podocarpidites ellipticus* Cookson, p. 131, Pl. 13, Figs. 5-7.
cf. 1957 *Pityosporites ellipticus* (Cookson) Balme, p. 35, Pl. 9, Fig. 104; Pl. 10, Figs. 105-107.
cf. 1973a *Podocarpus elliptica* (Cookson) Martin, p. 15, Figs. 59, 60.

Description:
pollen grains bilaterally symmetrical, bisaccate, corpus circular to elliptical in polar view; weakly reticulate, exine thin, finely granulate to pitted, sacci with thin wall and coarsely reticulate, same size as, or slightly larger than the corpus, saccus thin, grain hemispherical in polar view.

Dimensions:
Overall length 40 (51) 70 µm (6 specimens), height 26 µm (1 specimen), width 25 (31) 43 µm (6 specimens); corpus length 22 µm (1 specimen), height 17 µm (1 specimen), width 22 (27) 37 µm (5 specimens); saccus length 26 µm (1 specimen), height 18 (23) 30 µm (6 specimens), width 25 (32) 43 (5 specimens).

Stratigraphic distribution:
Bisaccate pollen attributable to *Podocarpidites ellipticus* has been widely recorded from the Late Triassic (De Jersey, 1975) onwards, with many records from

the Cretaceous and Cenozoic of Australia, New Zealand, South America and Africa. There are also several records from the Mesozoic of India (e.g., Venkatachala, 1974; Kumar, 1992). There are also numerous records from the Mesozoic of the Northern Hemisphere which may support suggestions that Podocarpaceae had a more global distribution in the Mesozoic. Sparsely distributed in low percentages in the Malong 5G-17.2 well with increased percentages and more regularly distributed from Zone PR13 upward.

Remarks and comparison:
These specimens are comparable to *Podocarpidites ellipticus* Cookson 1947 in having coarsely reticulate sacci which are the same size as, or slightly larger in relation to the corpus. The sacci in *Podocarpidites corpusculus* are much larger than the corpus.

Botanical affinity:
Similar to pollen of *Podocarpus amarus*, *P. neriifolius* and *P. wallichianus* (Podocarpaceae).

Source ecology:
Podocarpus amarus and *P. neriifolius* are montane forest trees.

Suggested name for Quaternary records:
Podocarpus amarus type.

Ecological group:
Montane forest trees.

Podocarpus *sp. Bogor, Java (photo by RJM).*

Podocarpidites minuticorpus
Morley and Jaizan Jais sp. nov.
Plate 7, Figs. 7, 10

Derivation of name:
From the small size of the corpus.

Holotype:
Plate 7, Fig. 7 (x 400) Fig. 10 (x 1000): Slide Malong-2, 592 m, SWC (S1); England Finder P16.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 592 m depth; age late Miocene, zone PR14.

Description:
Pollen bilaterally symmetrical, heteropolar; bisaccate; corpus circular in polar view, exine thin, finely granulate to pitted, sacci much larger than the corpus; saccus wall thin, coarsely reticulate.

Dimensions:
Overall length 46 (48) 50 µm (5 specimens), height 29 µm (1 specimen), width 26 (31) 36 µm (4 specimens); corpus length 29 µm (1 specimen), height 18 µm (1 specimen), width 25 (30) 36 µm (4 specimens); saccus length 25 µm (1 specimen), height 17 (20) 25 µm (5 specimens), width 26 (30) 36 µm (4 specimens).

Stratigraphic distribution:
Sparsely distributed in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
This species is distinguished by its much larger sacci in comparison to the corpus. *Podocarpidites multesimus* (Bolkhovitina 1956) Pocock 1962 has a similar shape but a the sacci bear a much finer reticulum.

Botanical affinity:
Podocarpus polystachyus (Podocarpaceae).

Source ecology:
Podocarpus polystachyus is a common tree of coastal forests, sometimes occurring in mangroves along the coasts of Malaysia.

Suggested name for Quaternary records:
Podocarpus polystachyus type.

Ecological group:
Coastal forest trees.

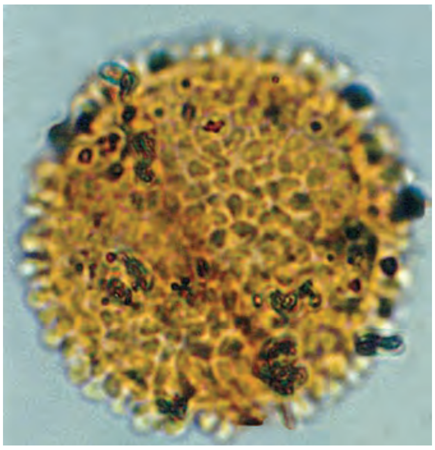
2.7 INAPERTURATE POLLEN

Genus *Incrotonipollis*
Baksi et al. in Jansonius and Hills 1981

Type species:
Crotonipollis araripensis De Lima 1976.

Generic remarks:
Incrotonipollis (Baksi Deb and Siddhanta) Jansonius and Hills 1981 is intectate, whereas *Crotonoideaepollenites* Rao and Ramanujam 1982 is tectate. Since *Crotonoidaepollenites reticulatus* (Da Silva Caminha et al. 2009) is described as intectate, it should be moved to the intectate genus *Incrotonipollis* (Baksi Deb and Siddhanta) Jansonius and Hills 1981.

Incrotonipollis reticulatus
(Da Silva Caminha et al. 2009) Jaizan Jais and Morley comb. nov. Plate 7, Figs. 11, 12



Selected Synonymy:
Crotonoidaepollenites reticulatus da Silva-Caminha, Jaramillo and Absy 2009, Plate 4, Figs. 6-10.

Description:
Pollen grains, inaperturate, oblate to spheroidal, intectate. ektexine consists of subspherical to rounded, smooth clavae, arranged roughly in groups of 6–7 units, forming a croton pattern.

Dimensions:
Equatorial diameter, minimum 36 µm, maximum 39 µm (2 specimens measured).

Stratigraphic distribution:
Rare and sparsely distributed in the Malong 5G-17.2 from zones PR14 and PR15.

Remarks:
Included here are inaperturate pollen characterised by its spheroidal shape and tectate exine with distinct clavate sculpture arranged in croton-pattern.

Botanical affinity:
The crotonoid pattern, with rounded clavae, suggests the genus *Croton* of the family Euphorbiaceae (Bansal et al., 2021).

Source ecology:
Small trees or shrubs commonly occur in both forest and non-forest areas.

Suggested name for Quaternary records:
Croton type.

Ecological group:
Lowland forest.

Genus *Retipollenites*

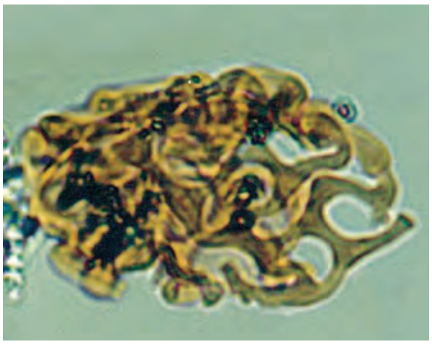
González-Guzmán 1967

Type species:
Retipollenites confusus González-Guzmán 1967.

Generic remarks:
Venkatachala et al. (1989) compared this form-genus with superficially similar but aperturate *Spirosyncolpites* González-Guzmán 1967, *Praedapollis* Boltenhagen and Salard-Cheboldaeff 1973 emend. Legoux 1978 and *Periretitricolpites* Jan du Chêne et al 1978. Following Venkatachala et al (1989), forms that are enmeshed in a broad reticulum with no apparent apertures are treated under the genus *Retipollenites* even though apertures in *Praedapollis* are often indistinct or not discernible (Boltenhagen and Salard-Cheboldaeff, 1973; Legoux, 1978).

Retipollenites confusus

González-Guzmán 1967. Plate 8, Figs. 1, 2



Selected synonymy:
1967 *Retipollenites confusus* González Guzmán 1967, p. 61, Pl. 30, Figs. 1a-c.
1989 *Retipollenites confusus* González Guzmán 1967; Venkatachala et al., p. 4, Pl. 1, Figs. 1-6; Pl. 2, Figs. 1-6.

Description:
Pollen, inaperturate, irregularly subspherical, with coarse reticulum, formed of tectum composed of narrow muri with wide lumina, supported on widely spaced columellae on thin, poorly characterised inner body composed of nexine.

Dimensions:
Equatorial diameter 35 (41) 45 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
This species has been recorded from the Eocene of Colombia (González - Guzmán, 1967) and India (e.g., Rawat et al., 1977; Kar, 1995). Rare in Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:
This pollen type compares closely with that of *Myristica*, with its coarse reticulum (Sauquet and Le Thomas, 2003) that easily becomes detached from the body, and very thin nexine. *Myristica* pollen is sulcoid, and in fresh specimens appears boat-shaped, but in fossil specimens it is difficult to see the sulcus, and so the grain is classified as inaperturate.

Source ecology:
Myristica cinnamomea, *M. iners* and *M. maingayi* are common lowland rain forest trees, whereas *M. elliptica* and *M. lowiana* are trees of peat swamp and riversides (Whitmore, 1972).

Suggested name for Quaternary records:
Myristica type.

Ecological group:
Lowland dipterocarp forest and peat swamp.

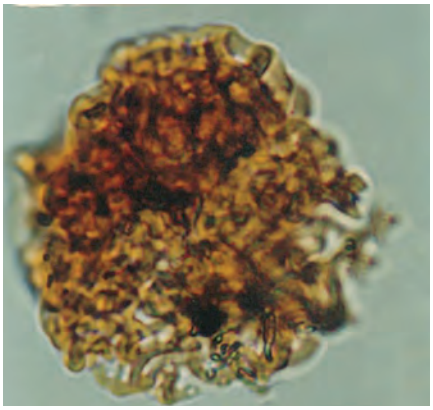
Myristica fragrans *(photo by Delmer Jonathan, Creative Commons)*

Genus *Cheilanthoidspora*
Sah and Kar 1974

Type species:
Cheilanthoidspora enigmata Sah and Kar 1974.

Generic remarks:
This genus is differentiated by the presence of a trilete mark and is usually classified with spores (e.g., Kar, 1985). It is easily confused with similar morphology angiosperm genera such as *Spirosyncolpites* González-Guzmán 1967, *Retipollenites* González-Guzmán 1967 and *Praedapollis* Boltenhagen and Salard-Cheboldaeff emend. Legoux 1978. It is more likely to be from an angiosperm source as it possesses a tectum, with the apparent trilete mark comprising a sulcus.

Cheilanthoidspora enigmata
Sah and Kar 1974. Plate 8, Fig. 3



Selected synonymy:
1974 *Cheilanthoidspora enigmata* Sah and Kar, p. 166, Pl. 1, Figs. 7-10.

Description:
Pollen, inaperturate, irregularly subspherical, with coarse reticulum, formed of tectum composed of narrow muri with wide lumina, supported on widely spaced columellae of varying height encompassing an inner body composed of nexine which appears to be scabrate, and which displays an apparent trilete mark, which may possibly be a trichotomosulcate or ulcerate aperture.

Dimensions:
Equatorial diameter 34 (35) 36 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
This species is widely recorded from the Eocene of India (Venkatachala et al., 1988), with some records from the Oligocene, and Miocene (Kar et al., 1994). Rare and sparsely distributed in zone PR15 of the Malong 5G-17-2 well. This is the first record of *C. enigmata* outside India.

Remarks:
Sah and Kar (1974) describe *C. enigmata* with an apparent trilete mark and *C. monoleta* for specimens which are apparently monolete, and these may reflect the same taxon with a variable monosulcate to trichotomosulcate sulcus. These specimens agree with the description of the type specimen described by Sah and Kar (1974). Venkatachala et al. (1989) commented that the specimen illustrated by Kar (1985; Pl. 22, Fig. 2) does not show a trilete mark or any other apertures so the former attributed it to *Retipollenites* sp.

Botanical affinity:
There are several similarities between *Cheilanthoidspora* and the pollen of *Myristica*, as described by Sauquet and Le Thomas (2003), this includes the coarse reticulum, supported by widely spaced columellae and encompassing an inner body, which in modern *Myristica* bears scattered gemmae in SEM. The similarity of *Cheilanthoidspora* with *Retipollenites*, also thought to be from *Myristica*, is noted above.

Suggested name for Quaternary records:
Myristica type.

Ecological group:
Lowland forest.

2.8 MONOCOLPATE POLLEN

Genus *Proxapertites*
van der Hammen 1956

Type species:
Proxapertites operculatus van der Hammen 1956.

Proxapertites minutus
Dueñas 1980. Plate 8, Fig. 7

Selected synonymy:
1980 *Proxapertites minutus* Dueñas, p. 317, Pl. 1, Figs. 2, 3, 4.

Description:
Pollen grains radially symmetrical, slightly heteropolar, approximately circular in polar view, oblate., with encircling sulcus, exine tectate, psilate to scabrate. Thickness of exine 1 to 1.5 μm; sexine thicker than nexine.

Dimensions:
Diameter 30 μm (1 specimen measured).

Stratigraphic distribution:
Oligocene to Miocene of Colombia (Dueñas, 1980); Oligocene to Pleistocene of Venezuela (Lorente, 1986). Only one specimen found in Malong 5G-17.2 well at 1200-1205 m (DC) depth (Zone PR10).

Remarks:
This specimen corresponds with the Colombian species described by Dueñas (1980).

Botanical affinity:
Ultrastructural studies of *Proxapertites operculatus* by Zetter et al. (2001) suggest a derivation from the genus *Gonatopus* (Araceae), and a similar source within the family Araceae may be appropriate for *P. minutus*. A full discussion of the affinity of *Proxapertites* is given by Huang et al. (2020).

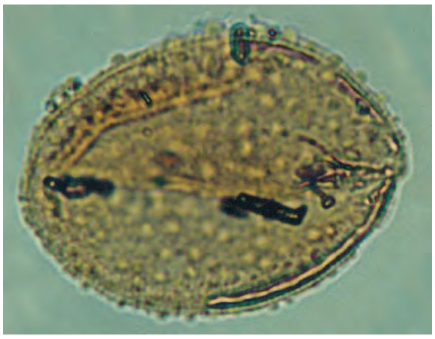
Suggested name for Quaternary records:
Araceae.

Ecological group:
Herbs.

Genus *Gemmamonocolpites*
van der Hammen and Garcia de Mutis 1965

Type species:
Gemmamonocolpites gemmatus (van der Hammen 1954) van der Hammen and Garcia de Mutis 1965 (by original designation).

Gemmamonocolpites borassoides
Jaizan Jais and Morley sp. nov. Plate 8, Figs. 8-10



Derivation of name:
After its modern affinity, *Borassus*.

Holotype:
Plate 8, Figs. 8, 10. Slide Malong-2, 641.5 m, SWC (S2), England Finder Q30/3. Grain compressed in polar aspect; amb elliptical with tapering ends; grain length 43 μm, width 31 μm; exine 1 μm thick; gemmae 1-2 μm high.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene zone PR14.

Description:
Pollen grains bilaterally symmetrical, heteropolar, amb elliptical with tapering ends; monosulcate; sulci indistinct; exine 1 μm thick, tectate-columellate; tectum microreticulate and distinctly sculptured with sparsely distributed gemmae of 0.5 to 2 μm high; columellae distinct, fused into microreticulate pattern; muri < 1 μm thick; lumina rounded to polygonal, even in size, < 1 μm across.

Dimensions:
Length 32 (40) 48 *μm*, width 20 (27) 34 *μm* (6 specimens measured from various horizons).

Variability:
In shape and size.

Stratigraphic distribution:
Rare and sparsely distributed in Malong 5G-17.2 well within zone PR13 to PR15.

Comparison:
This species differs from *G. amicus* González-Guzmán 1967 in its general form and in the distribution and size (smaller) of gemmae. It also resembles the Magnoliaceous *Liriodendroipollis verrucatus* Krutzsch 1970, but the latter is verrucate in sculpture. *Racemonocolpites hians* has closely packed verrucae.

Botanical affinity:
This pollen closely matches that of *Borassus* (Palmae) (Dransfield et al., 2008). Based on a molecular analysis, the crown group age for *Borassus* is about 34 Myr (Bellot et al., 2020), evolving from Asian ancestors close to the beginning of the Oligocene, as seasonal climates expanded across the Southeast Asian region (Morley, 2012, 2018). *Borassus* dispersed from the Indian Plate, following the collision of India with Asia in the Eocene. Related pollen is recorded from the Paleocene of India (Parmar et al., 2023).

Source ecology:
Common palms of coastal and inland areas of Indochina and Indonesia which experience a marked dry season, especially in East Java and Nusa Tenggara, Thailand, Cambodia and Myanmar.

Suggested name for Quaternary records:
Borassus.

Ecological group:
Seasonal lowland.

Borassus flabellifer *(Siwalan), cultivated in rice paddy area, area naturally with deciduous forest, Siem Reap, Cambodia (photo by RJM).*

Genus *Arengapollenites*
Kar 1985

Type species:
Arengapollenites achinatus Kar 1985 (by original designation).

Arengapollenites gracilis
Jaizan Jais and Morley sp. nov. Plate 8, Figs. 13, 14

Derivation of name:
Latin *gracilis*, slender; from its slender spines.

Holotype:
Plate 8, Figs. 13, 14. Slide Malong-2, 625 m, SWC (S3), England Finder T21/4. Grain compressed in polar aspect, length 34 µm, width 23 µm; spines 3 to 4 µm long, 1 µm wide at base; exine 0.5 µm thick.

Type locality:
Malong 5G-17.2 Well, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains, bilaterally symmetrical, heteropolar, amb elliptical; monosulcate; colpi distinct, extending to whole length of grain, more or less uniform in width; exine up to 0.5 µm thick, sculptured with slender spines, otherwise psilate; spines sharply pointed, narrow, 2 to 4 µm long, 1 µm wide at base, sparsely distributed, but with a row of inwardly pointing and often interlocking spines along the sulcus margins.

Dimensions:
Length 27 (30) 34 µm, width 21 (22) 23 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Comparison:
This species differs from *Arengapollenites achinatus* Kar 1985 in having more slender spines and in its smaller size; and from *A. diminutus* sp. nov. in having coarser spines and in its larger size.

Botanical affinity:
Very similar to *Arenga pinnata*, *A. obtusifolia* and *A. caudata* (Arecaceae).

Arenga pinnata *(Aren), secondary forest, West Java (photo by RJM).*

Source ecology:
Palms of lowland forest, riversides and swamps.

Suggested name for Quaternary records:
Arenga.

Ecological group:
Lowland forest, riparian.

Arengapollenites diminutus

Jaizan Jais and Morley sp. nov. Plate 8, Figs. 4-6

Derivation of name:

Diminutus, Latin for diminished, with reference to its tiny spines.

Holotype:

Plate 8, Figs. 4, 5. Slide Malong-2, 503 m, SWC (S2), England Finder G11. Grain compressed in polar aspect, length 20 μm, width 13 μm; spines 1 to 2 μm long; exine thin, less than 5 μm thick.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 503 m depth; age latest Miocene, zone PR14.

Description:

Pollen grains, bilaterally symmetrical, heteropolar, amb elliptical to subcircular; monosulcate, colpi distinct, extending to whole length of grain; exine thin, less than 0.5 μm thick, sculptured with tiny spines, otherwise psilate; spines minute, 1 to 2 μm long, usually sharply pointed, base in some specimens slightly swollen.

Dimensions:

Length 14 (20) 26 μm, width 10 (16) 20 μm (8 specimens measured from various horizons).

Variability:

In its shape and the form of its spines.

Stratigraphic distribution:

Present in low percentages throughout both sections.

Comparison:

This species is smaller in size and has finer spines than *A. gracilis* sp. nov. and *A. achinatus* Kar 1985.

Botanical affinity:

The grains compare closely with *Alocasia* (Araceae) as shown by Wang and Zhao (2002). The specimen of Araceae undiff. by Cheng et al. (2020), Plate 3, Fig. k, is very similar.

Source ecology:

Herbs of lowland forest, swamps and riversides.

Suggested name for Quaternary records:

Alocasia type.

Ecological group:

Herbaceous swamp.

Alocasia *sp. (Keladi), freshwater zone, Pahang River, Malaysia (photo by RJM).*

Plate 8

Figs. 1, 2 *Retipollenites confusus* González-Guzmán 1967.
Fig. 1 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder X39/3. Fig. 2 (x 1000): Slide Malong-2, 577 m, SWC (S2); England Finder X39/2.

Fig. 3 *Cheilanthoidspora enigmata* Sah and Kar 1974 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder V15.

Figs. 4, 5, 6 *Arengapollenites diminutus* Jaizan Jais and Morley sp. nov.
Figs. 4, 5 (Holotype, x 1000): Slide Malong-2, 503 m, SWC (S2); England Finder G11. Fig. 6 (x 1000): Slide Malong-2, 1300-1305 m, DC (S1); England Finder H14.

Fig. 7 *Proxapertites minutus* Dueñas 1980 (x 1000): Slide Malong-2, 1200-1205 m, DC (S1); England Finder D20/4.

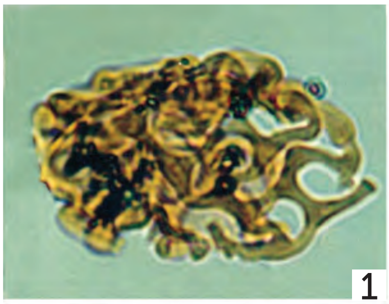
Figs. 8, 9, 10 *Gemmamonocolpites borassoides* Jaizan Jais and Morley sp. nov.
Figs. 8, 9 (Holotype, x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder Q30/3. Fig. 10 (x 1000): Slide Malong-2, 900-910 m, DC (S1); England Finder R14.

Figs. 11, 12 *Paravuripollis mulleri* Rao and Ramanujam 1978.
Figs. 11, 12 (x 1000): Slide Malong-2, 1135-1140 m, DC (S2); England Finder O50/4.

Figs. 13, 14 *Arengapollenites gracilis* Jaizan Jais and Morley sp. nov.
Figs. 13, 14 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder T21/4.

Fig. 15 *Spinizonocolpites echinatus* Muller 1968 (x 400): Slide Malong-2, 1436 m, SWC (S1); England Finder Q30/4/4.

Figs. 16, 17 *Racemonocolpites hians* Legoux 1978.
Figs. 16. 17 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder T9/2.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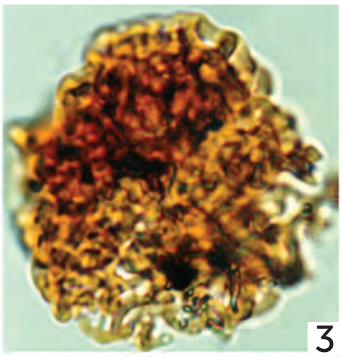
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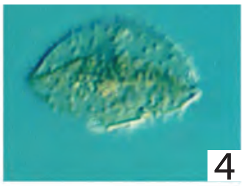
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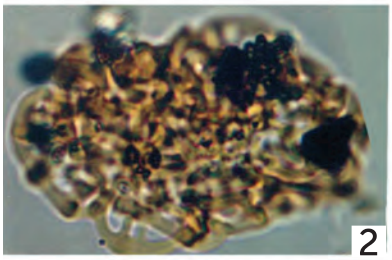
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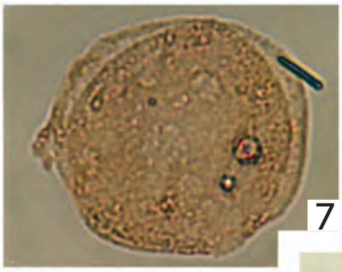
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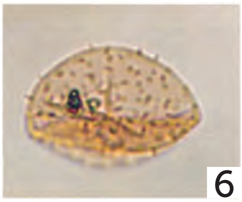
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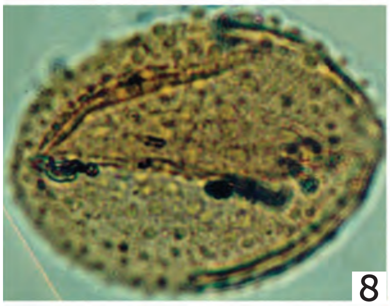
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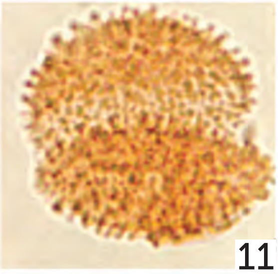
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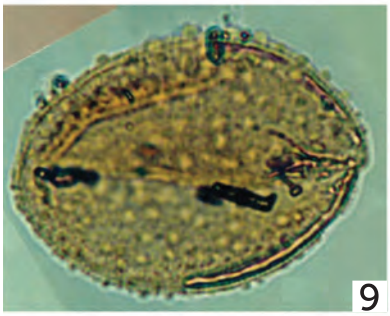
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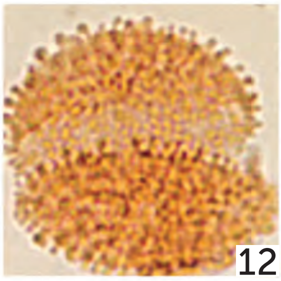
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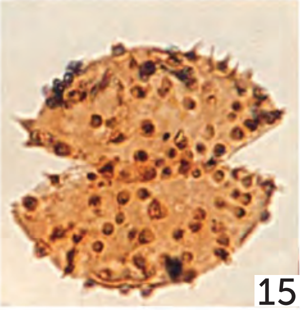
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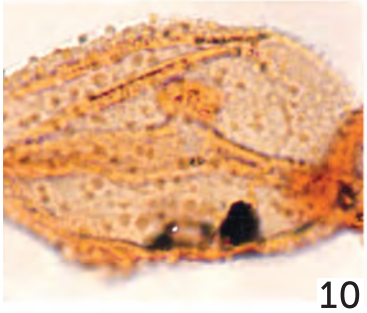
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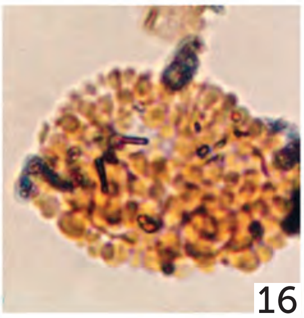
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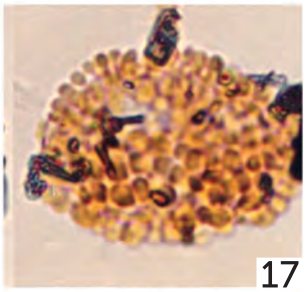

17

Genus *Spinizonocolpites*

Muller 1968

Type species:
Spinizonocolpites echinatus Muller 1968.

Spinizonocolpites echinatus

Muller 1968. Plate 8, Fig. 15

Selected synonymy:
1964 Dispersed pollen attributed to *Nypa* pollen in Muller 1964, p. 35, Pl. 1, Fig. 1.
1968 *Spinizonocolpites echinatus* Muller, p. 11, Pl. 3, Fig. 3.
1968 *Spinizonocolpites echinatus* Muller; Germeraad, Hopping and Muller (partim), p. 295, Pl. 4, Fig. 3, (non Fig. 2).
1972 *Spininocolpites echinatus* Muller; Hekel, p. 7, Pl. 3, Figs. 20, 21.

Description:
Pollen, monad, heteropolar, oblate, outline oval to circular in equatorial and polar view; zonasulcate; exine tectate, columellae indistinct; sculpture echinate; echini variable, conical, bulbous above the base, irregularly distributed.

Dimensions:
Length 30 (42) 52 μm, width 20 (29) 46 μm (7 specimens measured from various horizons).

Stratigraphic distribution:
This pollen type is recorded from the Paleocene to Quaternary of the Southeast Asian region (Muller, 1964, 1968; Morley, 1978, 1991), Late Cretaceous to Eocene of West Africa (Germeraad et al., 1968; Salard-Cheboldaeff, 1979) and the Caribbean (Germeraad et al., 1968); Eocene to early Miocene of Australia (Hekel, 1972; Stover and Partridge, 1973); Paleocene to Eocene Europe (Lenz et al., 2020); and the Paleocene to early Miocene of India (e.g., Khanolkar and Sharma, 2019). Its disappearance from equatorial Africa and the Caribbean at the end of the Oligocene was most likely due to the terminal Eocene sea level fall, which resulted in destruction of its habitat (Lim et al., 2021). Present throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
Stover and Evans (1973) consider *S. echinatus* a junior synonym of *S. prominatus* (McIntyre) Stover and Evans. However, Australasian specimens generally have slightly fewer spines than Southeast Asian ones and a more circular outline, and here *S. echinatus* is retained for the typical *Nypa* type pollen from the Southeast Asian Cenozoic. According to Schrank (1994), *S. prominatus* Mcintyre (1965) is transitional between *S. echinatus* and *S. baculatus* Muller 1968 and should therefore be maintained as a separate species.

Botanical affinity:
This taxon is comparable to pollen of the *Nypa* palm (Muller, 1968; Frederiksen, 1980). *Nypa* is also represented by fruits, recorded from Brunei but also widely recorded from the Eocene of Europe. Statistical analysis of fossil *Nypa* fruits from Belgium (Collinson, 1993) showed that their variation (in size and shape) is very similar to that observed in modern *Nypa*. Therefore, it is likely that the species producing the pollen in the Oligocene and also older sediments may have been closely related to modern *Nypa*.

Nypa fruticans *(Nipah), intertidal zone, Tarakan, Kalimantan (photo by HPM).*

Nypa fruticans *flower, intertidal zone, Mahakam River, Kalimantan (photo by HPM).*

Source ecology:
Palm which is common in the upper tidal reaches of rivers in brackish to fresh water.

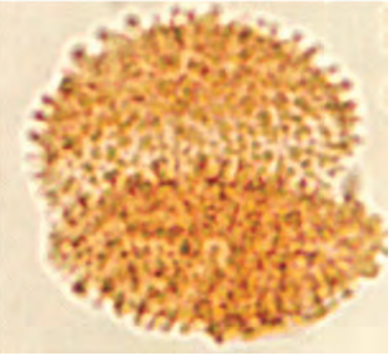
Suggested name for Quaternary records:
Nypa fruticans.

Ecological group:
Backmangrove.

Genus *Paravuripollis*
Rao and Ramanujam 1978

Type species:
Paravuripollis mulleri Rao and Ramanujam 1978 (by original designation).

Paravuripollis mulleri
Rao and Ramanujam 1978. Plate 8, Figs. 11, 12



Selected synonymy:
1978 *Paravuripollis mulleri* Rao and Ramanujam, p. 415, Pl. 4, Figs. 53, 54.
1984 *Paravuripollis mulleri* Rao and Ramanujam; Thanikaimoni et al., p. 63, Pl. 44, Figs. 606-616.

Description:
Pollen grains bilaterally symmetrical, heteropolar, amb elliptical with rounded ends; meridionosulcate or monosulcate with very long sulcus; sulci generally gaping, extending almost around grain, exine 1 µm thick, sexine and nexine not distinguished, distinctly sculptured with evenly distributed clavae on the tectum.

Dimensions:
Length 25 (29) 38 µm, width 19 (23) 28 µm (9 specimens measured from various horizons).

Stratigraphic distribution:
Miocene to Pliocene of India (Rao and Ramanujam, 1978; Nandi, 1981; Srisailam and Ramanujam, 1982). Present in low percentages throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
These specimens are in accordance with the species from Miocene of India as described by Rao and Ramanujam (1978) in having meridionosulcate aperture, clavate sculpture and elliptical amb. *Racemonocolpites hians* Legoux 1978 is monosulcate instead of meridionosulcate and is ornamented with clavae and gemmae.

Botanical affinity:
Korthalsia (Arecaceae) according to Rao and Ramanujam (1978) and Harley (2006).

Korthalsia zippelii, *Birds Head, Irian (photo courtesy of William Baker).*

Source ecology:
Climbing palms of lowland rain forests and disturbed vegetation.

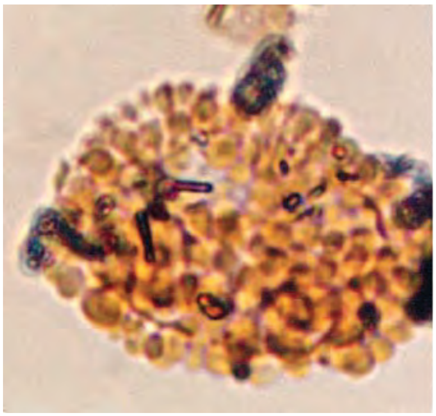
Suggested name for Quaternary records:
Korthalsia.

Ecological group:
Rain forest.

Genus *Racemonocolpites*
González-Guzmán 1967

Type species:
Racemonocolpites racematus (van der Hammen) ex González-Guzmán 1967 (by original designation).

Racemonocolpites hians
Legoux 1978. Plate 8, Figs. 16, 17



Selected synonymy:
1975 Dispersed pollen attributed to *Oncosperma* in Anderson and Muller, p. 311, Pl. 2, Fig. 13.
1975 Dispersed pollen attributed to Arecaceae in Medus (partim), p. 572, Pl. 2, Fig. 3 (non Figs. 4-14); Pl. 3, Figs. 4, 14 (non Figs. 1-3, 5-13, 15).
1978 *Racemonocolpites hians* Legoux, p. 269, Pl. 1, Figs. 1-7.

Description:
Pollen grains bilaterally symmetrical, heteropolar, amb elliptical with rounded ends; monosulcate; sulci narrow; as long as the longest axis of the grain, exine 1 µm thick, sexine and nexine not distinguished, distinctly sculptured with densely packed evenly distributed baculae or clavae on the tectum.

Dimensions:
Length 24 (31) 39 µm, width 18 (24) 30 µm (5 specimens measured from various horizons).

Stratigraphic distribution:
Present in moderate percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Selected stratigraphic record:
This pollen type is widely reported from the Neogene sediments in Southeast Asia (Muller, 1972), being illustrated from a Miocene coal in Brunei by Anderson and Muller (1975). Originally described from the Miocene of West Africa by Legoux (1978) where it ranges from the late Eocene to the late Miocene (Morley, 2000).

Oncosperma tigillarium *(Nibong), freshwater intertidal zone, Mahakam, Kalimantan (photo by RJM).*

Remarks and comparison:
This species which is characterised by its densely packed clavate and gemmate sculpture, monocolpate aperture and elliptical amb is similar to *Racemonocolpites hians* originally described from the Neogene of Nigeria by Legoux (1978). She also noted that the colpus of this species, which is as long as the grain length and cutting through its distal surface, often extends to its proximal surface probably because of the accidental movement of the two-halves of the grain. It differs from *Paravuripollis mulleri* in having a monocolpate instead of meridionosulcate aperture and from *Clavapalmaedites hammeni* Rao and Ramanujam 1978 in its sculptural detail.

Botanical affinity:
Oncosperma (Arecaceae). This taxon resembles pollen of *Oncosperma,* as suggested by Morley (2000). With its oldest occurrence in India during the Eocene, *Oncosperma* is thus an 'out-of-India' taxon (Huang et al., 2021).

Source ecology:
Mainly trees growing in the back-mangrove belt, in brackish settings, such as *Oncosperma tigillarium*. Some pollen may have come from inland settings, from *O. horridum* which occurs on low undulating hillsides across Southeast Asia.

Suggested name for Quaternary records:
Oncosperma.

Ecological group:
Backmangrove.

2.9 DICOLPATE POLLEN

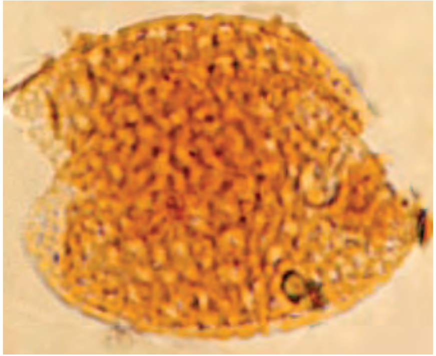
Genus *Dicolpopollis*
Pflanzl 1956 ex Potonié 1966

Type species:
Dicolpopollis kockelii Pflanzl 1956 ex Potonié 1966.

The genus *Dicolpopollis* was initially proposed by Pflanzl (1956) based on material from Germany and has subsequently been widely recorded across the low and mid latitudes (Huang et al., 2020). The pollen type occurs in the Calamoid palms (Dransfield et al., 2008), particularly in the genus *Calamus*. Here we find three pollen types that comply with this genus, one is reticulate to retirugulate, the second is coarsely reticulate and the third verrucate. Huang et al. (2020) showed that the reticulate *Dicolpopollis malesianus* is synonymous with *D. kalewensis*. The reticulate form is therefore placed in *D. kalewensis*, the finely retirugulate form in *D. reticulatus* Salujha, Kindra and Rehmann (1974), whereas the third, verrucate type is described as a new species, *D. verrucatus* sp. nov.


Calamus sp. (rattan), freshwater zone, Pahang River, Malaysia (photo by HPM).

Dicolpopollis kalewensis
(Potonié 1960) Potonié 1966. Plate 9, Figs. 3, 4



Selected synonymy:
1960b *Disulcites kalewensis* Potonié, p. 464, Pl. 2, Fig. 39.
1966 *Dicolpopollis kalewensis* (Potonié) Potonié, p. 160.
1966 *Disulcipollenites kalewensis* (Potonié) Nakoman, p. 78.
1968 *Dicolpopollis malesianus* Muller, p. 13, Pl. 3, Fig. 5.
1982 *Dicolpopollis malesianus* Muller; Takahashi, p. 310, Pl. 50, Figs. 4-10.
1990 *Dicolpopollis kalewensis* (Pot.) Pot.; Ediger, Bali and Alisan et al., p. 99, Pl. 1, Figs. 1-4; Pl. 2, Figs. 1-29.
1995 *Dicolpopollis malesianus* Muller; Harley and Morley Pl VII, Figs. 1-12.
2021 *Dicolpopollis kalewensis* Huang et al. (2020).

Description:
Pollen, heteropolar, oblate, outline trapezoidal in equatorial view, oval in polar view (proximal side longer than distal side, parallel and both slightly arched); disulcate, sulci long and gaping; exine 0.7 to 1.3 μm thick, nexine around 0.5 μm thick, nexine thinner than sexine pollen wall tectate; tectum is supported by robust columellae, sculpture foveolate to perforate, foveolate in interapertual areas, becoming perforate towards apertures.

Remarks:
Dicolpopollis malesianus was proposed as a new species because of its pronounced sculpture as compared to *D. kalewensis* by Muller (1968). A comparison of the material from Kalewa with the holotype and specimens of *D. malesianus* from Java by Harley & Morley (1995), suggests that the pollen grains are identical (Huang et al., 2021). Muller was probably misled due to the low quality of the LM (light microscopy) micrographs of *D. kalewensis* by Potonié (1960), emphasizing the importance of displaying clear LM-SEM micrographs in publications. Based on scanning electron microscopy, Huang et al. (2021) consider *D. malesianus* as a junior synonym of *D. kalewensis*.

Dimensions:
Longest axis 17 (23) 35 μm (16 specimens measured from various horizons).

Stratigraphic distribution:
The oldest reliable Asian record of *Dicolpopollis kalewensis* is from the Paleocene of Sarawak (Muller, 1968; Morley, 1998). *Dicolpopollis* is also

a frequent component in middle Eocene samples from the southern Sunda margin, from central Java (Takahashi, 1982; Harley & Morley, 1995; Lelono, 2000; Morley, 2000), from southern Sulawesi (Morley, 1998) and from the late Eocene of Myanmar (Potonié, 1960b; Huang et al., 2020). In India, *D. kalewensis* has been recorded the Paleocene (e.g., Mathur & Jain, 1980), commonly in the Eocene (e.g., Rawat et al., 1977), and as young as the Pliocene (Mehrota et al., 2002). It has also been commonly recorded in Turkey (Ediger et al., 1990) and the Eocene of North America (e.g., Tschudy, 1973). Present in moderate percentages throughout both sections; decreases in relative abundance in the upper part of Malong 5G-17.2 well, above zone PR10.

Remarks and comparison:
This dicolpate pollen is characterised by more or less oval amb with V-shaped colpi on both ends and rounded triangular to trapezoidal or axed-shaped in equatorial view, and finely reticulate to microreticulate wall. It differs from *D. elegans* Muller 1968 by having finely reticulate sculpture on both proximal and distal faces. *D. proprius* Salujha et al. 1972, *D. luteticus* Gruas-Cavagnetto 1976, *D. microreticulatus* Rao and Ramanujam 1978 and *D. bungonensis* Truswell and Owen 1988 are also similar in having very finely reticulate (microreticulate) sculpture. A detailed study of these species is recommended to find out if they are identical.

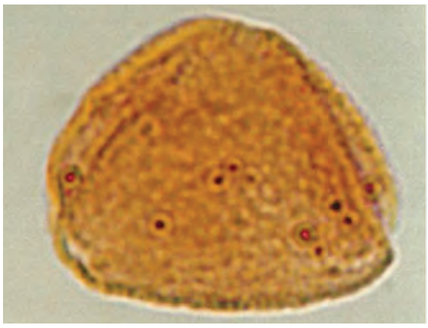
Botanical affinity:
From the genus *Calamus* (Arecaceae), which, as currently defined (Baker, 2015) includes the genera *Daemonorops* and *Ceratolobus*, which are the rattan palms. There is considerable pollen morphological diversity in *Calamus*, and *D. kalewensis* is most similar to *Calamus longisetus, C. platyspathus, C. paspalanthus, C. myrianthus* and *C. tetradactylus* (Muller, 1968).

Source ecology:
Mostly climbers, common from coasts to mountain tops across the Southeast Asian region, but may become common in swamps, particularly in areas of slightly seasonal climate where peat swamps will not form, such as the rattan breaks of Myanmar (Dudley-Stamp, 1925), the Tonle Sap in Cambodia (Campbell et al., 2006) or the Citarum Delta in West Java (Morley, 2014).

Suggested name for Quaternary records:
Calamus, or *Calamus longisetus* type.

Ecological group:
Mostly from freshwater swamp.

Dicolpopollis reticulatus
Salujha, Kindra and Rehmann 1974.
Plate 9, Figs. 1, 2



Selected synonymy:
1974 *Dicolpopollis reticulatus* Salujha, Kindra and Rehmann, p. 673, Pl. 2, Figs. 38-39.

Description:
Pollen, heteropolar, oblate, outline trapezoidal in equatorial view, oval in polar view (proximal side longer than distal side, parallel and both slightly arched); disulcate, sulci long and gaping; exine 1 to 1.5 µm thick, nexine around 0.5 µm thick, nexine thinner than sexine pollen wall tectate; tectum is supported by robust columellae, sculpture perforate to reticulate.

Stratigraphic distribution:
Recorded from the Neogene of Assam by Salujha et al. (1974), sparsely distributed in the Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
These specimens are distinguished from *D. kalewensis* (Potonié) Potonié by having a more pronounced reticulum, and from *D. elegans* in having reticulate sculpture on both distal and proximal faces.

Botanical affinity:
As for *D. kalewensis*, from the genus *Calamus* (Arecaceae), which, as currently defined by Baker (2015) includes the genera *Daemonorops* and *Ceratolobus,* which are the rattan palms.

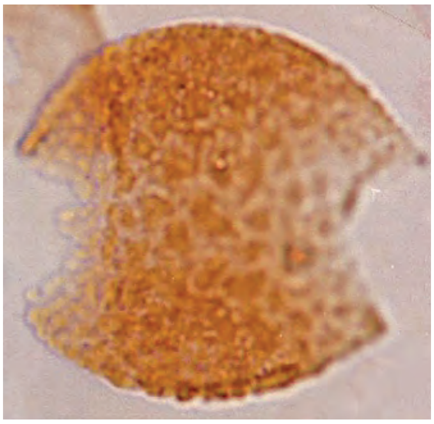
Source ecology:
Mostly climbers, common from coasts to mountain tops across the Southeast Asian region, but may become common in swamps, particularly in areas of slightly seasonal climate where peat swamps will not form, such as the rattan breaks of Myanmar (Dudley-Stamp, 1925) or the Citarum Delta in West Java (Morley, 2014).

Suggested name for Quaternary records:
Calamus type.

Ecological group:
Mostly from freshwater swamp.

Dicolpopollis verrucatus

Morley and Jaizan Jais. sp. nov. Plate 9, Figs. 5, 6



Derivation of name:
From its verrucate sculpture.

Holotype:
Plate 9, Figs. 5, 6. Slide Malong-2, 625 m, SWC (S3), England Finder W18/4.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age latest Miocene, zone PR14.

Dimensions:
Length 30 μm, width 28 μm (1 specimen measured).

Description:
Pollen, heteropolar, oblate, outline, oval in polar view (proximal side longer than distal side, disulcate, sulci long and gaping; exine about 1.5 μm thick, nexine around 0.5 μm thick, thinning toward apertures nexine thinner than sexine pollen wall tectate; tectum appears finely reticulate and bears regular verrucae or areolae.

Stratigraphic distribution:
Rare and sparsely distributed in both sections; three specimens found, one at the top part of Malong 5G-17.2 well and two in the Delah 5H-14.1 well.

Remarks and comparison:
This dicolpate form is characterised by its reticulate tectum that is also ornamented with verrucae which distinguishes it from other *Dicolpopollis* species described above.

Botanical affinity:
Calamus (Arecaceae), notably *Calamus microcarpa* (Sowunmi, 1972) and *Calamus gracilis* (Muller, 1981a).

Source ecology:
Rattan palms, occur from coasts to mountains of tropical areas. Can be common in swampy areas.

Suggested name for Quaternary records:
Calamus gracilis type.

Ecological group:
Lowland forest.

Calamus scipionum *flowering in forest at Kepong, Malaysia, emphasising that rattans may be prolific pollen producers (photo from Whitmore, 1973).*

2.10 TRICOLPATE POLLEN

Genus *Cupuliferoidaepollenites* Potonié, Thomson and Thiergart, 1950 ex Potonié 1960

Type species:
Cupuliferoidaepollenites liblarensis (Thomson in Potonié et al.) Potonié 1960.

Generic remarks:
This form-genus is used here to accommodate smooth, slender, prolate tricolpate pollen grains. The form-genus *Psilatricolpites* van der Hammen 1956 is invalid, being typified by a recent pollen species, even though it has been widely used in the Cenozoic palynological studies of tropical areas. The form-genus *Tricolpopollenites* Pflug and Thomson in Thomson and Pflug 1953, erected to accommodate many varieties of tricolpate forms, is too broad for this highly diverse pollen type.

Cupuliferoidaepollenites* sp. cf. *C. liblarensis
(Thomson in Potonié, Thomson and Thiergart 1950) Potonié 1960a. Plate 9, Fig. 7

Selected synonymy:
cf. 1950 *Pollenites liblarensis* Thomson in Potonié, Thomson and Thiergart, p. 55, Pl. B, Figs. 26, 27.
cf. 1953 *Tricolpopollenites liblarensis* subsp. *liblarensis* Thomson in Thomson and Pflug, p. 96, Pl. 11, Figs. 111-132.
cf. 1960 *Cupuliferoidaepollenites liblarensis* (Thomson in Potonié, Thomson and Thiergart 1950) Potonié, p. 92, Pl. 9, Fig. 94.
cf. 1968 *Cupuliferoidaepollenites liblarensis* Thomson in Potonié, Thomson and Thiergart 1950; Sah and Dutta, p. 188, Pl. 2, Figs. 3, 8.
cf. 1968 *Tricolpopollenites liblarensis* subsp. *liblarensis* Thomson in Thomson and Pflug; Nakoman, p. 541, Pl. 5, Figs. 23-25.
cf. 1974 *Cupuliferoidaepollenites liblarensis* Thomson in Potonié, Thomson and Thiergart1950; Ziembinska-Tworzydlo, p. 392, Pl. 22, Figs. 1-4c.

Description:
Pollen radially symmetrical, tricolpate, prolate in equatorial view, lobate in polar view, slightly tapering toward poles, which are rounded, colpi long, almost reaching poles, exine thin, difficult to differentiate sexine from nexine, psilate with faint infratexture.

Dimensions:
Length 12 (16) 19 μm, width 8 (12) 18 μm (11 specimens measured from various horizons).

Stratigraphic distribution:
Cupuliferoidaepollenites liblarensis has been recorded from the Paleocene to Pleistocene across Eurasia by many authors (Thomson and Pflug, 1953; Ziembinska-Tworzydlo, 1974 and others); and North America, and from the Paleocene to Oligocene of India (Sah and Dutta, 1968). This pollen type is present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
Compared to the specimens illustrated by the authors cited above the Malay Basin specimens seem to have a thinner wall and are slightly smaller. European specimens are invariably attributed to Fagaceae, discussed below.

Botanical affinity:
Many papers attribute *C. liblarensis* to Fagaceae (e.g., Lenz et al., 2020), but without further clarification. The tricolpate prolate configuration is characteristic of very few Fagaceae, modern or fossil, since tricolpate pollen occurs only in *Quercus*. Grimsson et al. (2015) illustrate small tricolp(or)ate pollen from the early Cenozoic of Greenland as Castanoideae (e.g., Fig. 8d, which has a very weak endoaperture) and Denk et al. (2012) show similar small pollen from the European Oligocene as *Trigonobalanopsis*. It is tentatively possible that the Malaysian pollen is from one of these genera but that the endoapertures are obscured.

Source ecology:
Possibly montane forest trees.

Suggested name for Quaternary records:
cf. *Fagaceae*.

Ecological group:
Forest undifferentiated.

Genus *Quercoidites*

Potonié, Thomson and Thiergart 1950 ex Potonié 1960

Type species:

Quercoidites henrici (Potonié 1931) Potonié 1960.

Generic remarks:

This form-genus is diagnosed as having more or less tapered ends, geniculate colpi which almost reaches the poles and an infrabaculate, granulate wall. In this study specimens with clear geniculae were not seen, but their presence could not be fully excluded due to preservation issues. Tricolpate forms with scabrate or granulate exine are informally treated under this genus. *Tricolpopollenites* Pflug in Thomson and Pflug 1953, and *Quercopollenites* Nagy 1969 are possible alternative genera. *Scabratricolpites* van der Hammen 1956a is illegitimate (Jansonius and Hills, 1976).

***Quercoidites* sp. A.** Plate 9, Figs. 8, 9

Description:

Pollen radially symmetrical, tricolpate, prolate in equatorial view, more or less circular in polar view, poles rounded, colpi long, slightly open, almost reaching poles, exine thin, appears to be two layered possibly reflecting sexine and nexine, exine scabrate or granulate with feint infratexture.

Dimensions:

Length 14 (16) 17 µm, width 11 (13) 15 µm (3 specimens measured from various horizons).

Stratigraphic distribution:

Sparsely distributed in low percentages in both sections.

Remarks:

This species is characterised by its small size, subprolate-prolate shape with rounded poles, slightly open colpi and finely granulate or scabrate wall.

Botanical affinity:

The tricolpate configuration and granulate-scabrate wall is reminiscent of *Quercus* (Fagaceae), but this identification is not certain.

Source ecology:

Possibly trees of montane forests, but some species may be found in peat swamps.

Suggested name for Quaternary records:

cf. *Quercus* type.

Ecological group:

Possibly montane forest trees.

***Quercoidites* sp. B.** Plate 9, Fig. 10

Description:

Pollen radially symmetrical, tricolpate, prolate in equatorial view, more or less lobate in polar view, tapering toward rounded poles, colpi long, closed, almost reaching poles, slightly sinuous, possibly reflecting geniculus, exine clearly two layered reflecting tectate, columellate, sexine and an inner nexine layer, exine punctate.

Dimensions:

Length, minimum 16 µm, maximum 19 µm; width, minimum 12 µm, maximum 15 µm (2 specimens measured).

Stratigraphic distribution:

Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is characterised by having a tectate, faintly columellate and punctate wall, long colpi. The infolded lobate exine may give the suggestion of margins.

Botanical affinity:

The general character of the grain is similar to some types of *Quercus*, except for the presence of columellae, which suggest otherwise. Therefore undifferentiated.

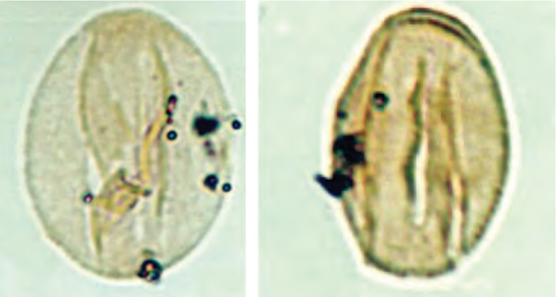
Suggested name for Quaternary records:

Not applicable.

Ecological group:

Undifferentiated.

***Quercoidites* sp.** C. Plate 9, Figs. 11, 12



Description:

Pollen radially symmetrical, tricolpate, prolate to perprolate in equatorial view, more or less lobate in polar view, outline tapering toward rounded poles; colpi long, closed, almost reaching poles, appear to have margines, deflected in equatorial area possibly geniculus or endoapertures; exine clearly two layered reflecting sexine and nexine, sexine thicker at poles, where columellae are more clearly discernible.

Dimensions:

Length 20 µm-22 µm; width, 10-12 µm (2 specimens measured).

Stratigraphic distribution:

Sparsely distributed in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is characterised by its elongated ovoid shape, long colpi with thickened margines and tectate, faintly punctate wall.

Botanical affinity:

The grain shows some similarities with *Koompassia* (Fabaceae) except that the endoapertures appear indistinct.

Source ecology:

Koompassia spp. are common trees of lowland forest.

Suggested name for Quaternary records:

cf. *Koompassia* type.

Ecological group:

Rainforest.

Note added in proof:

For an up to date perspective on the identification of Fagaceae pollen using combined LM and SEM, please see Malaikanok et al. (2023) who show the differences between pollen of the taxa *Eotrigonobalanus*, *Castanoideae* and *Quercus* section *Cyclobalanopsis*, *Ilex* and *Quercus*. The pollen of these taxa are described from the early Miocene of the Ban Pa Kha Subbasin in northern Thailand, and provide a record of montane dry tropical oak-pine forests.

The importance of using SEM for identification of Fagaceae pollen is emphasised here by bringing to attention some of the main morphological features of oak pollen as seen using the SEM microscope discussed in this paper as follows:

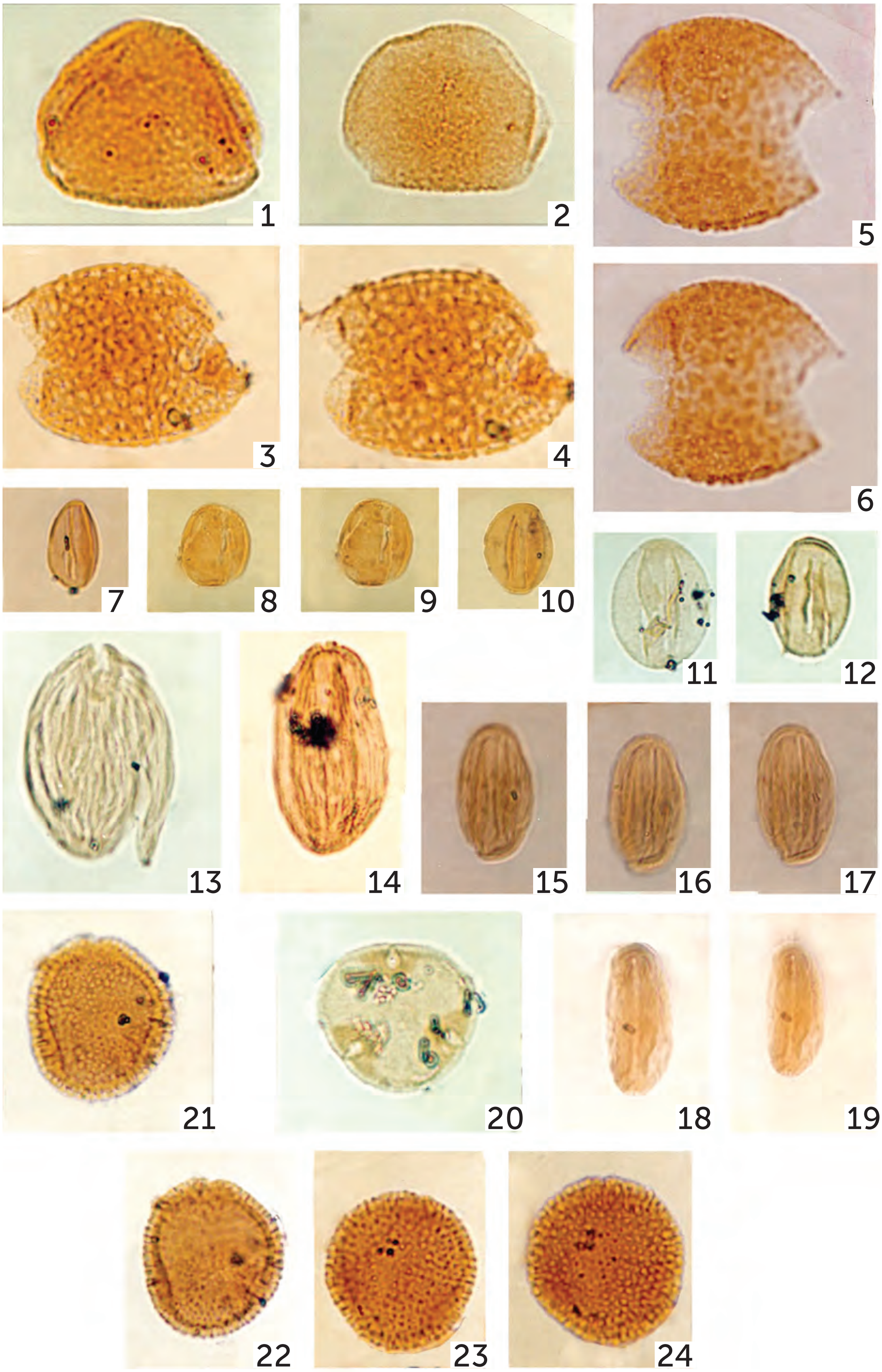
Castanoideae (*Lithocarpus* and *Castanopsis*), grains small, 11 to 16 µm clearly tricolporate, prolate lobate, exine psilate to scabrate in LM, fossulate in SEM.

Quercus sect. *Cyclobalanopsis*, grains intermediate, 18 to 27 µm, tricolporoidate, pori small and indistinct, prolate, lobate, scabrate in LM, areolate to rugulate, fossulate and perforate in SEM, areolae/rugulae with nanorugulate (rod-shaped) to nanoechinate suprasculpture. Most species of *Quercus* section *Cyclobalanopsis* produce pollen showing this diagnostic areolate/rugulate basal sculpture with numerous minute suprasculptural elements.

Quercus sect. *Ilex* grains larger, 21 to 29 µm, tricolporoidate, pori small and indistinct, prolate, lobate, scabrate in LM, nanorugulate to nanogemmate (rod-shaped) and perforate in SEM.

Quercus section *Quercus* 27 to 28 µm tricolporoidate, pori small and indistinct, prolate, lobate, sculpture scabrate in LM, granulate to areolate, fossulate and perforate in SEM. The presence of areolate sculptural elements is a typical feature for this section (Malaikanok et al., 2023).

Plate 9



Figs. 1, 2 *Dicolpopollis reticulatus* Salujha, Kindra and Rehmann (1974).
Fig. 1, (x 1000): Slide Malong-2, 1395-1400 m, DC (S1); England Finder K31/4. Fig. 2 (x 1000): Slide Malong-2, 1395-1400 m, DC (S1); England Finder P27.

Figs. 3, 4 *Dicolpopollis kalewensis* (Potonié 1960) Potonié 1966.
Figs. 3, 4 (x 1000): Slide Malong-2, 714 m, SWC (S2); England Finder U33/4.

Figs. 5, 6 *Dicolpopollis verrucatus* Morley and Jaizan Jais sp. nov.
Figs. 5, 6 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder W18/4.

Fig. 7 *Cupuliferoidaepollenites* sp. cf. *C. liblarensis* (Th. in Pot. et al., 1950) Pot. 1960. (x 1000): Slide Malong-2, 688.5 m, SWC (S2); England Finder L16.

Figs. 8, 9 *Quercoidites* sp. A.
Figs. 8, 9 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder P34/1.

Fig. 10 *Quercoidites* sp. B (x 1000): Slide Malong-2, 608 m, SWC (S2); England Finder T34.

Figs. 11, 12 *Quercoidites* sp. C.
Fig.11 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder K25/1. Fig. 12 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder X38/4.

Figs. 13, 14 *Striatopollis catatumbus* (González-Guzmán 1967) Ward 1986.
Fig. 13 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder H8/3. Fig. 14 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder D40/2.

Figs. 15-19 *Striatopollis malaysianus* Jaizan Jais and Morley sp. nov.
Figs. 15, 16, 17 (Holotype, x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder P24. Figs. 18, 19 (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder U29/2.

Fig. 20 *Intratriporopollenites instructus* (Potonie) Thomson and Pflug 1953 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder X8/4.

Figs. 21-24 *Retibrevitricolpites simpohi* Morley and Jaizan Jais sp. nov.
Figs. 21, 22 (x 1000 holotype): Slide Malong-2, 625 m, SWC (S3); England Finder R52/1. Figs. 23, 24 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder W25/1.

Genus *Striatopollis*
Krutzsch 1959

Type species:
Striatopollis sarstedtensis Krutzsch 1959.

Striatopollis catatumbus
(González Guzmán 1967) Ward 1986.
Plate 9, Figs. 13, 14

Selected synonymy:
1967 *Striatricolpites catatumbus* González-Guzmán, p. 30, Pl. 8, Figs. 7-7d.
1968 *Striatricolpites catatumbus* González-Guzmán; Germeraad, Hopping and Muller., p. 319, Pl. 7, Fig. 4.
1975 Dispersed pollen attributed to *Crudia* in Anderson and Muller, p. 303, Pl. 2, Fig.5.
1986 *Striatopollis catatumbus* (González-Guzmán) Ward, p. 50.
1987 *Striatopollis catatumbus* (González-Guzmán) Mathur and Chopra, p. 114, Pl. 2, Fig. 22.
1989 *Striatopollis catatumbus* (González-Guzmán) Takahashi and Jux, p. 225, Pl. 24, Figs. 4-6, Pl. 35, Figs. 4, 5.

Description:
Pollen radially symmetrical, tricolpate, prolate, outline in polar view trilobate to spherical, colpi, long, intruding with straight, simple borders and pointed ends. Pores absent or indistinct. Exine layered, basal nexine overlain by tectate sexine with striate sculpture, sexine columellate, columellae closely spaced, resulting in microreticulate pattern below the thin, sometimes perforate tectum; striae approximately 1 µm high and 1 to 1.5 µm wide, subparallel or slightly anastomosing.

Dimensions:
Length 23 (30) 38 µm, width 14 (20) 30 µm (9 specimens measured from various horizons).

Stratigraphic distribution:
The oldest records are from the Maastrichtian of Nigeria (Jan du Chene, 1978), after which time it has been recorded from the Paleocene of Africa (Agedoke et al., 1978) and South America (Rull, 2000), continuing in both areas to the present day. In India it has been reported from the early Eocene (Mehrota et al., 2002) to Pliocene (Mathur et al., 1987). In Southeast Asia, it is first recorded in the Nanggulan Formation in Java (Lelono, 2000) and continues to the present day. This species is common in zones PR3 and PR4 from the Delah 5H-14.1 well and occurs scattered in low numbers through the Malong 5G-17.2 well with an acme in zones PR10 to PR11.

Remarks:
Except that they are generally smaller in size, the Malay basin specimens agree in all aspects with the type specimen that ranges from 49 to 56 µm in length. The former, however, overlapped in size with the specimens given in Germeraad et al. (1968) that range in length from 33 to 50 µm in length.

Botanical affinity:
This pollen type compares most closely to that of the pantropical genus *Crudia* (Fabaceae) but is also found in the African genera *Anthonotha* and *Isoberlinia* and South American *Macrolobium*. The latter species have larger pollen than *Crudia* and this may explain why outside Southeast Asia, this pollen type may display a larger size range.

Source ecology:
Coastal and forest trees; *Crudia wrayi* is locally common on riverbanks and swampy places in Malaysia.

Suggested name for Quaternary records*:*
Crudia type.

Ecological group:
Coastal and riverbank forests.

Striatopollis malaysianus

Jaizan Jais and Morley sp. nov. Plate 9, Figs. 15-18

Derivation of name:
Named after Malaysia where this species was discovered.

Holotype:
Plate 9, Figs. 15-17. Slide Malong-2, 641.5 m, SWC (S2), England Finder P24. Grain in equatorial aspect, length 19 μm, width 12 μm; exine 1 μm thick, finely striate.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, prolate with oval-rhombic outline in equatorial view, amb subcircular; tricolpate; colpi long, sometimes with the suggestion of a geniculus, sometimes intruding with simple borders; exine tectate, ±1 μm thick; tectum finely and densely striate; striae <0.5 μm in thickness and width, up to 1 μm apart, subparallel; between striae exine very thin and sometimes vaguely perforate.

Dimensions:
Length 18 (20) 25 μm, width 10 (13) 15 μm (10 specimens measured from various horizons).

Stratigraphic distribution:
Present in both sections from the PR3 zone upward, relatively more consistently distributed and higher in percentages from the PR8 zone upward and sparsely distributed and lower in percentages downward.

Comparison:
This species differs from *Striatopollis catatumbus* by being smaller. *S. sarstedtensis* Krutzsch 1959 differs from the present species in having extrapunctate striae and *S. striatellus* (Takahashi 1961) Takahashi 1979 is larger in size.

Botanical affinity:
Striate tricolporate grains are known from several families, notably the Fabaceae, Anacardiaceae, Burseraceae and Rosaceae, but striate tricolpate grains are less common. It is thought that a member of Anacardiaceae may be the most likely source, as seen in *Gluta* (Baksi, 1976).

Source ecology:
Gluta spp. are common in lowland rain forest, but are particularly well represented in peat swamp forest. *Gluta velutina* occurs in swamps and along rivers.

Suggested name for Quaternary records:
Anacardiaceae, possibly *Gluta*.

Ecological group:
Rainforest.

Gluta velutina*, (renghas), freshwater swamp, Sedili River, Johor, Malaysia (photo by RJM).*

Genus *Merantipollis*

Jaizan Jais and Morley gen. nov.

Derivation of name:
From Meranti, the Malay name for *Shorea* spp.

Diagnosis:
Pollen, radially symmetrical, isopolar, typically in oblate compression, tricolpate or tetracolpate, colpi gaping, long, without margines, sometimes torn, exine two layered, with a thin basal layer and a thicker outer layer composed of columellae and tectum tectate or exhibiting a tilioid structure, variable in size but smaller than 35 μm.

Generic remarks:
Tricolpites Cookson ex Couper 1953 has been used as a broad category to accommodate tricolpate forms with reticulate surface, but the circumscription is extremely broad, making the genus the ultimate dustbin taxon. A criterion that can be assessed in most tricolpate pollen is the differential thickness of sexine and nexine. The extremely thin nexine in Dipterocarpaceae is shown to be of major taxonomic importance (Maury et al., 1975; Bansal et al., 2021) and so is here used to characterise the new genus *Merantipollis*. The genus *Tricolpites* is modelled on pollen of *Gunnera* (Wanntrop et al., 2004) which is characterised by pollen with a thick nexine, which thickens dramatically toward the pollen (Praglowski, 1970), very different from that seen in Dipterocarpaceae.


Emergent dipterocarps *in primary forest canopy, Lambir, Sarawak, Malaysia (photo by RJM).*

Merantipollis gracilis

Jaizan Jais and Morley sp. nov. Plate 10, Figs. 1, 2

Selected synonymy:
2021 *Shorea* type Huang et al. 2021, Pl. 1, Fig. 7.

Derivation of name:
From the graceful outline of the exine.

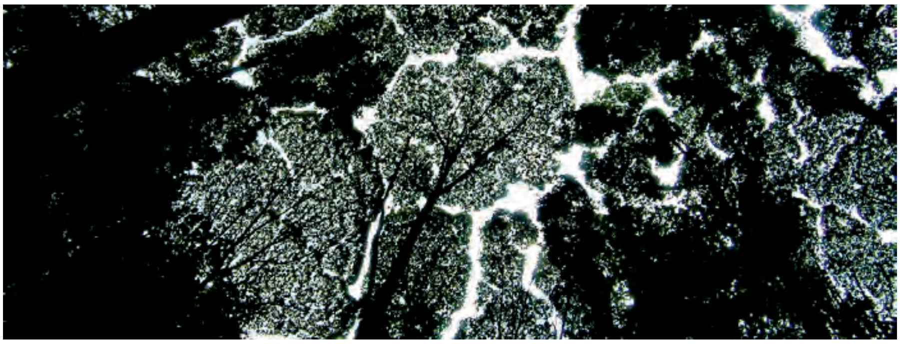
Holotype:
Plate 10, Figs. 1, 2. Slide Malong-2, 1610-1615 m, DC (S1), England Finder S8. Grain in polar aspect. Equatorial diameter 22 μm, exine 0.5 μm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 1610-1615 m depth; age late Oligocene, zone PR6/7.

Description:
Pollen grains radially symmetrical, isopolar, suboblate to prolate in equatorial view, circular in equatorial outline; tricolpate; colpi meridionally aligned, extends to one-half to three-quarter distance to pole, non-marginate, often gaping at equator margins, sometimes torn; exine thin, up to 1 μm thick, uniform in thickness, columellate with indiscernible nexine, appearing microreticulate with a more or less continuous tectum; reticulum regular, with largely isodiametric lumina of less than 1 μm in diameter.

Dimensions:
Equatorial diameter 16 (19) 23 μm (8 specimens measured from various horizons).

Stratigraphic distribution:
Present in moderate percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells. It is particularly common within zone PR6/7. This event is identified in the West Natuna Basin as zone PVI based on a maximum of *Shorea* type pollen (Morley et al., 2003). The event has a wide stratigraphic utility to mark the end of the Oligocene, being noted also by Morley (2000, Fig. 9.16), as a maximum of Dipterocarpaceae pollen, dated then as early Miocene, prior to the correct placement of the Oligo-Miocene boundary by Wong et al. (2006).


Dryobalanops aromatica *(Kapur), plantation at FRIM, near Kuala Lumpur, Malaysia (photo by HPM).*

Comparison:
This species differs from other *Tricolpites* spp. by the very thin inner exine layer.

Botanical affinity:
Small tricolpate oblate pollen with gaping colpi and finely reticulate exine and very thin nexine is characteristic of the genera *Shorea, Hopea* and *Anisoptera* of the family Dipterocarpaceae (Hamilton et al., 2019).

Source ecology:
Dipterocarpaceae form the dominant arboreal family in lowland perhumid forest in Malaysia and seasonally dry forest in Indochina; *Shorea* are trees are especially dominant in the lowlands but also in hill forests.

Suggested name for Quaternary records:
Shorea type.

Ecological group:
Rainforest and seasonal forest.

Shorea stenoptera *(meranti) Bogor, Java (photo by RJM).*

Merantipollis cuneatus
Morley and Jaizan Jais sp. nov. Plate 10, Figs. 3-5

Derivation of name:
Named after the Latin word for wedge shaped, referring to the thinning of the exine toward the apertures.

Holotype:
Plate 10, Figs. 3-5. Slide Malong-2, 641.5 m, SWC (S2), England Finder S29/3. Grain in polar aspect, 33 μm in diameter; exine 1 μm thick; lumina 1 μm in diameter.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, with circular equatorial outline; tricolpate; colpi meridionally aligned, long, extends at least to three-quarter distance to pole, gaping at equator; exine thin, less than 1 μm thick, mainly visible as columellae, due to very thin nexine, sexine tectate to semi-tectate, thinning slightly toward the apertures, appearing reticulate; reticulum regular with largely isodiametric lumina of approximately 1 μm in diameter but brochi larger in meridional area.

Dimensions:
Equatorial diameter 29 (31) 33 μm (4 specimens measured from various horizons).

Stratigraphic distribution:
Regularly present in both sections in low to moderate percentages.

Comparison:
Merantipollis gracilis sp. nov. is smaller in size. Most other tricolpate pollen differ in their possession of better developed nexine.

Botanical affinity:
This pollen type falls within the size range of *Shorea* and *Hopea* pollen as determined by Hamilton et al. (2019). However, with an equatorial diameter of 33 μm, this falls within the lager end of the size spectrum, allowing additional morphological characters to be resolved. The gentle thinning of the exine toward the apertures, characteristic of many Dipterocarpoid pollen is very clear, and compares very closely to the image of *Shorea assamica* pollen (Plate II, Fig. 3) of Hamilton et al. (2019).

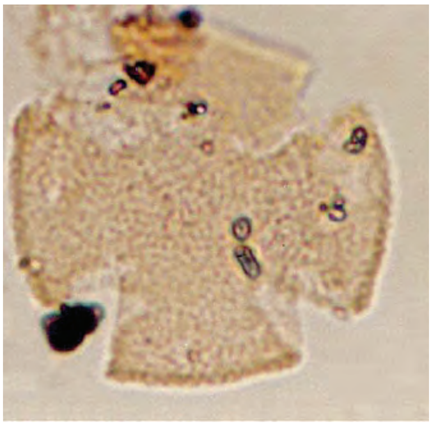
Source ecology:
Trees in the perhumid lowlands and hill forests in Malaysia and seasonal forests in Indochina.

Suggested name for Quaternary records:
Shorea assamica type since this morphology may occur also in other *Shorea* spp.

Ecological group:
Rain forest and seasonal forest.

Merantipollis quadricolpatus

Jaizan Jais and Morley sp. nov. Plate 10, Figs. 6, 7



Derivation of name:
From the presence of four colpi.

Holotype:
Plate 10, Figs. 6, 7. Slide Malong-2, 592 m, SWC (S1), England Finder U26. Grain in polar aspect, 25 µm in diameter; exine 1 µm thick; lumina <1 µm in diameter.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 592 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, subcircular to rounded tetragonal in polar view; tetracolpate, colpi meridionally aligned, extend to approximately one-half distance to poles, gaping at equator, v-shaped, without margines, sometimes with apertural membrane; exine thin, up to 1 µm thick, uniform in thickness, presented as a layer of columellae with a very thin nexine, and a thin tectum, appearing microreticulate; reticulum regular, with isodiametric to elongated lumina of less than 1 µm in diameter.

Dimensions:
Equatorial diameter 16 (19) 25 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Present in low percentages in both sections; relatively sparse in Malong 5G-17.2 well and more regularly distributed in the Delah 5H-14.1 section.

Comparison:
This species differs from all other tetracolpate pollen in the extremely thin nexine.

Botanical affinity:
This species resembles tetracolpate specimens of *Shorea* and *Hopea*. Tetracolpate dipterocarpoid pollen has been noted to occur in *Shorea negrosensis* by Morley (1976) and *S. teysmanniana* and *Hopea gregaria* by Hamilton et al. (2019). The most thorough evaluation is by Talip (2008) who notes tetracolpate grains in *Neobalanocarpus heimii, Shorea maxima, S. pauciflora, S. ovalis, Hopea beccariana, H. ferruginea, H. odorata* and *H. subalata* and suggests that the tetracolpate condition may relate to polyploidy.

Source ecology:
Dipterocarpaceae is a dominant arboreal family in West Malesia; Shorea are trees in the lowlands and hill forests but also characterise seasonal forests in Indochina.

Suggested name for Quaternary records*:*
Shorea negrosensis type.

Ecological group:
Rain forest and seasonal forest.

Shorea robusta *in India. Under seasonal climates Dipterocarps flower annually and can produce significant amounts of pollen (Bera, 1990). (Image licensed under the Creative Commons Attribution-Share Alike 4.0 International license).*

Genus *Tricolpites*

Cookson ex Couper 1953 emend. Jarzen and Dettmann 1989

Type species:

Tricolpites reticulatus Cookson 1947 ex Couper 1953 (by designation of Couper 1953).

Generic remarks:

Tricolpites has been used as a broad category to accommodate tricolpate forms with reticulate surface. In this study the genus is used in a restricted manner following Jarzen and Dettmann's (1989) emendation [see Jarzen and Dettmann (1989, p. 99)] for the emended diagnosis.

Tricolpites malongii

Jaizan Jais and Morley sp. nov. Plate 11, Figs. 1-5

Derivation of name:

Named after the Malong 5G-17.2 well in which this species was discovered.

Holotype:

Plate 11, Figs. 1, 5. Slide Malong-2, 625 m, SWC (S3), England Finder T14. Grain in equatorial aspect, length 19 µm, width 9 µm; exine 0.5 µm thick, microreticulate.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:

Pollen grains radially symmetrical, isopolar, prolate to slightly perprolate with slightly convex sides and broadly rounded poles, oval in equatorial view; tricolpate; colpi long, extending almost to poles, slightly marginate sometimes or suggestion of a geniculus; exine about 0.5 µm thick, stratified; sexine thicker than nexine, pilate, semitectate with microreticulate surface; reticulum composed of smooth-crested and simplicolumellate muri, and regular lumina that are of uniform size and up to 0.5 µm in maximum dimension.

Dimensions:

Length 15 (18) 21 µm, width 8 (10) 13 µm (15 specimens measured from various horizons).

Stratigraphic distribution:

Present in both sections from the PR4 zone upward, but most common in zones PR9 to PR13.

Comparison:

This species compares in most characters with pollen of *Melanorrhoea* (Anacardiaceae) as described by Baksi (1976), in terms of its overall shape, and exine structure. It differs from *T. terengganuensis* sp. nov. by its smaller size.

Botanical affinity:

The prolate to perprolate shape, long colpi and uniform thickness reticulate exine is very reminiscent of some Anacardiaceae, especially *Melanorrhoea*, although this generally shows the presence of an endoaperture. For this reason, the identification to *Melanorrhoea* is questioned.

Source ecology:

Melanorrhoea spp. are trees of lowland forests and peat swamps.

Suggested name for Quaternary records:

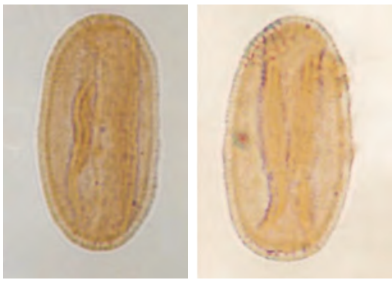
? *Melanorrhoea* type.

Ecological group:

Peat swamp forest.

Tricolpites terengganuensis

Jaizan Jais and Morley sp. nov.
Plate 11, Figs. 6-9



Derivation of name:
Named after Terengganu, an oil producing state on the east coast of Peninsular Malaysia, near the Malay Basin where this species was discovered.

Holotype:
Plate 11, Figs. 6, 7. Slide Malong-2, 625 m, SWC (S3), England Finder T55/1. Grain in equatorial aspect, oval in outline, length 27 µm, width 15 µm; exine 1 µm thick, microreticulate.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, prolate to perprolate with broadly rounded poles, slightly convex to almost straight sides, slender ovoid in equatorial view; tricolpate; colpi long, with thickened margines, extending almost to poles, with a weak endoaperture most probably present; exine three layered, ±1 µm thick; sexine thicker than nexine, sexine with distinct columellae, semitectate, microreticulate in surface view; columellae up to 1 µm high.

Dimensions:
Length 25 (26) 27, width 11 (14) 15 µm (7 specimens measured from various horizons).

Stratigraphic distribution:
Present in low percentages in Malong 5G-17.2 well from the PR13 to PR15 zones.

Comparison:
This very consistent species compares in most characters with pollen of *Melanorrhoea* (Anacardiaceae) as described by Baksi (1976), in terms of its overall shape, and exine structure. The main difference is that *Melanorrhoea* is invariably tricolporate, but in the specimens observed here the endoapertures are weak and represented by a possible geniculus or weakly formed pore. The species differs from *T. malongii* by its larger size.

Botanical affinity:
This pollen is thought to be derived from *Melanorrhoea*, based on its prolate shape, rounded pole, uniform thickness exine with long, parallel evenly spaced columellae. *Melanorrhoea* displays some variation in shape and size, with the specimen illustrated by Anderson and Muller (1975) tapering toward the poles, whereas many species illustrated by Baksi (1976) are more parallel sided, as in the specimens recorded here. This species differs from *T. malongii* sp. nov. by its larger size.

Source ecology:
Melanorrhoea spp. are trees of lowland forests and peat swamps.

Suggested name for Quaternary records:
Melanorrhoea type.

Ecological group:
Peat swamp forest.

Plate 10

Figs. 1, 2 *Merantipollis gracilis* Jaizan Jais and Morley sp. nov.
Figs. 1, 2 (Holotype, x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder S8.

Figs. 3, 4, 5 *Merantipollis cuneatus* Morley and Jaizan Jais sp. nov.
Fig. 3 (Holotype, x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder S29/3. Fig. 4 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder H29/3. Fig. 5 (x 1000): Slide Malong-2, 654.5 m, SWC (S2); England Finder J35/1.

Figs. 6, 7 *Merantipollis quadricolpatus* Jaizan Jais and Morley sp. nov.
Figs. 6, 7 (Holotype, x 1000): Slide Malong-2, 592 m, SWC (S1); England Finder U26.

Figs. 8, 9 *Discoidites novaguineensis* Khan 1976a.
Figs. 8, 9 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder X7.

Figs. 10, 11 *Discoidites pilosus* (Venkatachala and Rawat 1973) Morley et al. 2000.
Figs. 10, 11 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder F16.

Figs. 12 -15 *Discoidites angulosus* Huang, Morley and Hoorn (2021).
Figs. 12, 13 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder S33.
Figs. 14, 15 (x 1000): Slide Malong-2, 1234.5 m, SWC (S1); England Finder O29/2.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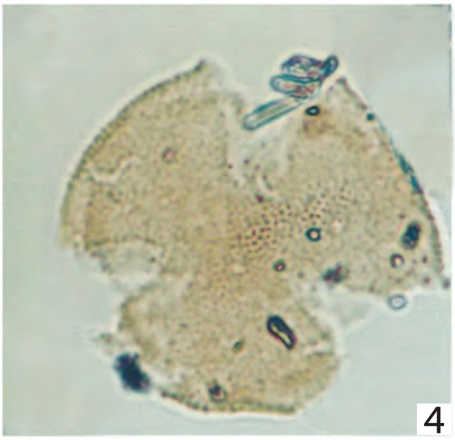
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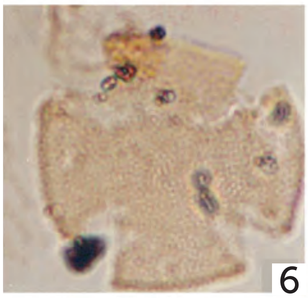
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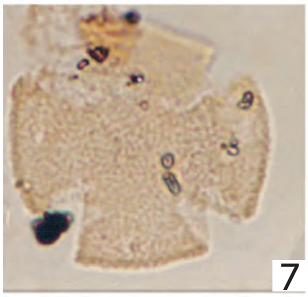
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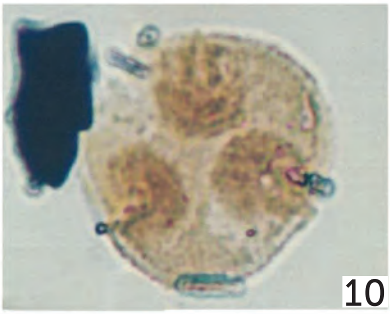
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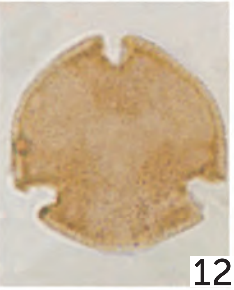
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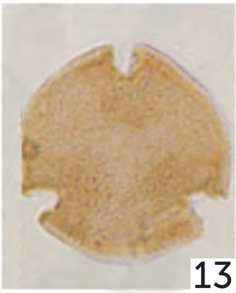
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Genus *Discoidites*
Muller 1968

Type species:
Discoidites borneensis Muller 1968.

Generic remarks:
The form-genus *Lacrimapollis* Venkatachala and Rawat 1973 with *L. pilosus* as the type species, is a junior synonym.

Discoidites novaguineensis

Khan 1976a. Plate 10, Figs. 8, 9

Selected synonymy:

1976a *Discoidites novaguineensis* Khan, p. 766-767, Fig. 33.
2021 *Discoidites* cf. *novaguineensis* Huang et al., Pl. 1, Fig. 9.

Description:

Pollen, radial, isopolar, prolate; tricolpate (actually tricolporate but apertures difficult to observe in dispersed specimens reflected by circular fold around apertures), rounded amb, colpi short, narrow, 'U' shaped, reaching less than halfway to the pole, exine thickness 1 to 2 µm, with well-developed columellae, which in very well preserved specimens can be seen as digitate. In polar view exine structure appears to be finely reticulate, tectum psilate.

Dimensions:

Equatorial diameter 19 (23) 29 µm (9 specimens measured from various horizons).

Stratigraphic distribution:

Khan (1976a) has recorded this species from the Pliocene to Pleistocene sediments of Papua New Guinea. *Discoidites*, recorded by Muller (1968) from the Sarawak first appears in the stratigraphic record in the Paleocene (Morley, 1998; van Gorsel et al., 2014) and is subsequently well represented throughout the Southeast Asian Cenozoic. Present in high percentages throughout both sections; relatively more abundant in the Delah 5H-14.1 well.

Remarks and comparison:

The Malay Basin specimens agree in all aspects with the type material described and illustrated by Khan (1976a). This species differs from *D. borneensis* in the presence of columellae, and *D. pilosus* comb. nov. by not having thickenings around the apertures.

Botanical affinity:

Compares closely with pollen of *Brownlowia* (Tiliaceae) as described by Muller (1964). However, the related genera *Berrya, Diplodiscus, Jarasandersonia* and *Pentace* have similar pollen.

Source ecology:

Brownlowia is typically seen as a backmangrove species (Muller, 1963), but it is actually rare in mangroves in Malaysia. It is more typically represented in the lower reaches of rivers, within the floodplain (Morley et al., 2000). Sometimes it may be seen in mangrove swamps, there is a single specimen in the Sungai Buloh mangrove reserve in Singapore. *Brownlowia paludosa* occurs commonly in seasonally inundated swamp forest in Tonle Sap, Cambodia (Campbell et al., 2006). *Jarandersonia* is a peat swamp tree (Anderson, 1964) and *Pentace* a tree of primary forests (Kochummen, 1973).

Suggested name for Quaternary records:

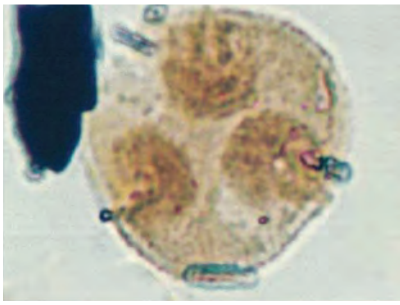
Brownlowia type.

Ecological group:

Riparian to backmangrove.

Discoidites pilosus

(Venkatachala and Rawat 1973) Morley et al., 2000. Plate 10, Figs. 10. 11



Selected synonymy:

1973 *Lacrimapollis pilosus* Venkatachala and Rawat, p. 245, Pl. 4, Figs. 16-20.

Description:

Pollen, radially symmetrical, isopolar, oblate; amb near circular; tricolpate, angulaperturate, colpi fairly short and narrow, reaching less than halfway to the pole; exine thin, 1.0 μm thick, thicker in the apertural areas resulting in the characteristic thickened costae; exine three-layered, with a clear endexine and well-developed columellae and a psilate or granulate tectum.

Dimensions:

Equatorial diameter 19 (22) 25 μm (4 specimens measured from various horizons).

Stratigraphic distribution:

The earliest record is from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000). Subsequent records include the late Eocene Yaw Formation in Myanmar (Huang et al., 2021) and the Oligocene–Miocene Cauvery Basin in Tamil Nadu, India (Venkatachala and Rawat, 1973). It is common in the early and middle Miocene in Indonesia (Morley et al., 2000). Present in low to moderate percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells; generally decreasing upward.

Remarks and comparison:

The Malay Basin specimens conform to the description and illustration of the type material by Venkatachala and Rawat (1973).

Botanical affinity:

Brownlowoideae, the broad morphotype occurs in *Brownlowia, Pentace, Diplodiscus* and *Berrya* (Morley et al., 2001) but the thickened costae seen in this morphotype cannot be attributed to any extant taxon.

Source ecology:

Possibly trees from lowland riverbanks or possibly freshwater intertidal settings.

Suggested name for Quaternary records:

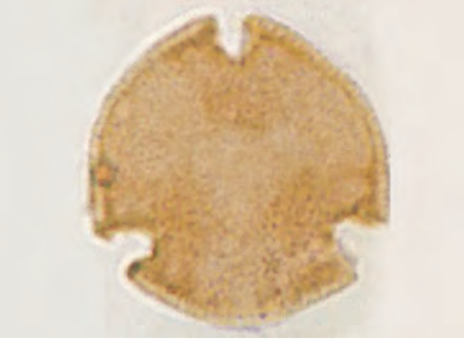
Not applicable.

Ecological group:

Riparian to backmangrove.

Discoidites angulosus

Huang, Morley et Hoorn 2021. Plate 10, Figs. 12-15



Description:

Pollen, radial, isopolar, oblate; amb triangular with convex sides; tricolpate, angulaperturate, colpi short and gradually wider to the apices, reaching ca. 2/3 to the pole; exine less than 1.0 to 1.5 μm thick, thicker at colpate areas; sculpture finely microreticulate, and psilate in the polar area; columellae indiscernible.

Dimensions:

Equatorial diameter 21 (25) 27 μm (6 specimens measured from various horizons).

Stratigraphic distribution:

Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is distinguished by its acute end or V-shaped, non-costate colpi of intermediate length (PAI 0.7) and microreticulate wall. Better preserved specimens need to be analysed before it can be proposed as a new species.

Botanical affinity:

Brownlowoideae, the broad morphotype occurs in *Brownlowia, Pentace, Diplodiscus* and *Berrya* (Morley et al., 2000) but the thickened costae seen in this morphotype cannot be attributed to any extant taxon.

Source ecology:

Possibly trees from lowland riverbanks or possibly freshwater intertidal settings.

Suggested name for Quaternary records:

Not applicable.

Ecological group:

Riparian to backmangrove.

Genus *Intratriporopollenites*

Pflug and Thomson in Thomson and Pflug 1953

Intratriporopollenites instructus (Potonié) Thomson and Pflug 1953. Plate 9, Fig. 20

Description:

Pollen radially symmetrical, isopolar, oblate; amb interangular with convex sides; tricolpate, colpi short, exine less than 1.0 and 1.5 µm thick, thicker at colpate areas; sculpture finely microreticulate, and psilate in the polar area; columellae indiscernible.

Dimensions:

Equatorial diameter 18 (22) 30 µm (10 specimens measured from various horizons).

Remarks:

According to Krutzsch (1961), the type specimen of *Tiliaepollenites* Potonie 1931 is a recent contamination. *Tiliaepollenites* is therefore an obligate junior synonym of *Tilia* L.

Stratigraphic distribution:

Widely distributed across the northern Hemisphere from the Paleocene onward. In the Sunda region, commonly represented in the Oligocene, becoming rare in the Miocene. Rare and restricted to the top part of Malong 5G-17.2 well, from the PR14 zone upward.

Botanical affinity*:*

Intratriporopollenites instructus is derived from the genus *Tilia* (Tiliaceae).

Source ecology:

Tilia is a genus of temperate deciduous trees, which is widespread across most of the northern hemisphere, but never present in the tropics. Most species are found in East Asia, and in southern China it is a tree of montane forest. During the mid-Cenozoic, there were extensive upland areas across Indochina (Morley, 2018b) and the pollen recorded here is thought to have been transported from these upland areas to the depositional site by wind or water.

Suggested name for Quaternary records:

Tilia pollen.

Ecological group:

Montane (seasonal).

Genus *Retibrevitricolpites*

van Hoeken-Klinkenberg 1966

Type species:

Retibrevitricolpites triangulatus van Hoeken-Klinkenberg 1966.

Retibrevitricolpites simpohi

Morley and Jaizan Jais sp. nov. Plate 9, Figs. 21-24

Derivation of name:

Named after 'simpoh', the Malay name for *Dillenia suffraticosa*.

Holotype:

Plate 9, Figs. 21, 22. Slide Malong-2, 625 m, SWC (S3), England Finder R52/1. Grain in polar aspect, circular in outline, diameter 20 µm.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:

Pollen grains radially symmetrical, isopolar, oblate, amb circular, tricolpate; colpi very short, with diffused edges and without margines; exine 2-3 µm in thickness, sexine thicker than nexine, tectum finely reticulate, simplibaculate, supported by columellae up to 2 µm in length.

Dillenia suffraticosa *(Simpoh) Bogor, Java (photo by RJM).*

Dimensions:

Equatorial diameter 18 (20) 21 µm (6 specimens measured from various horizons).

Stratigraphic distribution:

Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:

This oblate reticulate species is characterised by its very short colpi with diffused edges and large PAI. It is different from *Brevitricolpites circularis* Takahashi 1982 by having reticulate instead of punctate surface.

Botanical affinity:

Dillenia (Dilleniaceae).

Source ecology:

Trees and shrubs commonly growing on swampy ground, riverbanks and forests.

Ecological group:

Freshwater swamp and riparian.

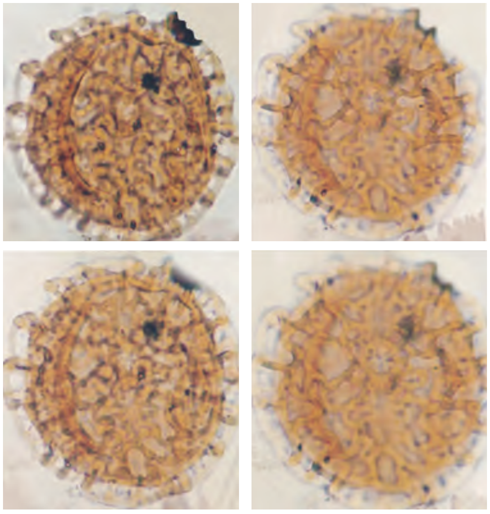
Genus *Spirosyncolpites*

González Guzmán 1967 emend. Legoux 1978

Type species:
Spirosyncolpites spiralis González Guzmán 1967.

Spirosyncolpites bruni

Legoux 1978. Plate 11, Figs. 10-13



Selected synonymy:
1970 *Spirosyncolpites spiralis auct.* non González-Guzmán 1967 Schuler and Doubinger, p. 440, Pl. 15, Figs. 1, 2.
1975 cf. *Spirosyncolpites* González-Guzmán 1967 in Médus, Pl. 15, Figs. 15, 19, 20.
1978 *Spirosyncolpites bruni* Legoux, p. 281, Pl. 13, Figs. 5, 6; Pl. 14, Figs. 2, 3; Pl. 15, Figs. 1, 2.

Description:
Pollen radially symmetrical, isopolar, subprolate, amb circular, tricolpate; colpi reduced and indistinct; exine coarsely reticulate, lumina polygonal in shape, muri narrow, simplibaculate, baculi appear as widely separated columellae which support the tectum.

Dimensions:
Equatorial diameter 41 (46) 48 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Cenozoic of Senegal (Médus, 1975); middle Eocene to basal middle Miocene of Nigeria and Cameroon (Legoux, 1978). Rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:
Unknown. Possibly with Leguminosae.

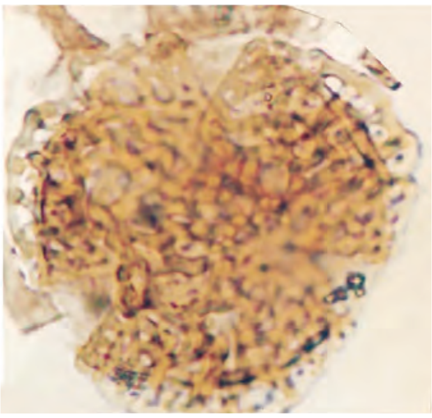
Ecological group:
Undifferentiated.

Genus *Periretitricolpites*

Jan du Chêne et al. 1978

Type species:
Periretitricolpites anambraensis Jan du Chêne et al. 1978.

Periretitricolpites sp. Plate 15, Figs. 1, 2



Description:
Pollen radially symmetrical, isopolar, oblate, amb circular; tricolpate, colpi gaping, with weak margines; exine thick, sexine much thicker than nexine, nexine coarsely reticulate, semitectate, with long columellae, simplibaculate; nexine much thinner, of uniform thickness.

Dimensions:
Equatorial diameter, minimum 33 µm, maximum 42 µm (2 specimens measured).

Stratigraphic distribution:
Rare and sparsely distributed in Malong 5G-17.2 well.

Remarks:
This distinctively reticulate, tricolpate form is characterised by its course, free reticulum without apparent connection with the central body and V-shaped colpi that are not covered by the reticulum.

Botanical affinity:
Unknown.

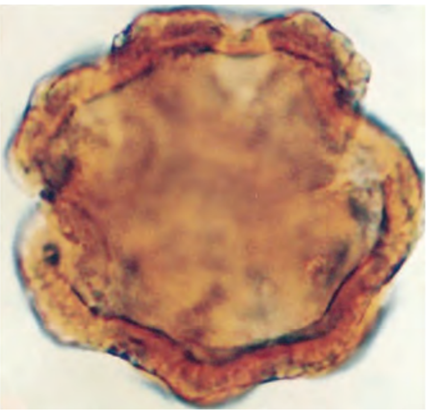
Ecological group:
Undifferentiated.

2.11 STEPHANOCOLPATE POLLEN

Genus *Retistephanocolpites*
Leidelmeyer 1966 emend. Saxena 1982

Type species:
Retistephanocolpites angelii Leidelmeyer 1966 (by original designation).

Retistephanocolpites williamsi
Germeraad et al. 1968. Plate 15, Figs. 3, 4



Selected synonymy:
1968 *Retistephanocolpites williamsi* Germeraad et al., p. 325, Pl. 14, Figs. 1, 2.
1978 *Retistephanocolpites williamsi* Germeraad et al.; Naskar and Baksi, p. 320, Pl. 3, Fig. 35.
1985 *Retistephanocolpites williamsi* Germeraad et al.; Salami, p. 12, Pl. 1, Fig. 11; Pl. 2, Fig. 5.

Description:
Single grain, radially symmetrical, isopolar, oblate; 6 to 7 colpate, colpi ectexinous, 14 µm long. Wall 2 to 4 µm thick; endexine 1 to 3 µm thick, columellae less than 1 µm long and thick, irregularly arranged and forming a spongy structure; tectum less than 1 µm thick, reticulate-foveolate; lumina oval to circular 1 to 2 µm in diameter, muri 1 µm wide (Germeraad et al., 1968).

Dimensions:
Equatorial diameter 30 (37) 42 µm (5 specimens measured from various horizons).

Stratigraphic distribution:
Retistephanocolpites williamsi is first recorded in the Paleocene of Africa (Germeraad et al., 1968) and India, and then diversified in the early Eocene in India (Morley, 2000). Possible variants within this morphotype are illustrated schematically by Krutzsch (1989). In the Sunda region *R. williamsi* variants first occur in the middle Eocene (Morley, 1998), and subsequently occur in the late Eocene Yaw Formation in Myanmar (Huang et al., 2021). It has also been recorded in the latest early Oligocene Lanzhou Basin in China (Miao et al., 2013). In Myanmar, it was also found in the early Miocene Letkat Formation (Lwin et al., 2017). This is an 'out-of-India' taxon (Morley, 2000, 2018).

Present in low numbers in both Malong 5G-17.2 and Delah 5H-14.1 wells, more regularly distributed in the top part of Malong well, sparsely distributed elsewhere.

Remarks:
This 6 to 7 colpate pollen resembles in all aspects with *Retistephanocolpites williamsi* originally described by Germeraad et al. (1968) except that the Malay Basin specimens are generally smaller. The former ranges from 41 to 47 µm in diameter. Thanikaimoni et al. (1984) noted that this species is polycolporate in which endoapertures are visible only in meridional view, but they are not seen in the present specimens.

Botanical affinity:
Ctenolophon parvifolius (Ctenolophonaceae).

Source ecology:
Swamp forest trees.

Suggested name for Quaternary records:
Ctenolophon parvifolius type.

Ecological group:
Peat swamp.

Plate 11

Figs. 1-5 *Tricolpites malongi* Jaizan Jais and Morley sp. nov. Fig. 1 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder T14. Fig. 2 (x 1000): Slide Malong-2, 780-790 m, DC (S1); England Finder O22/3. Fig. 3 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder O40/4. Fig. 4 (x 1000): Slide Malong-2, 760-770 m, DC (S1); England Finder Z19/3. Fig. 5 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder T14.

Figs. 6-9 *Tricolpites terengganuensis* Jaizan Jais and Morley sp. nov. Figs. 6, 7 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder T55/1. Figs. 8, 9 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder E42/2.

Figs. 10-13 *Spirosyncolpites bruni* Legoux 1978. Figs. 10-13 (x 1000): Slide Malong-2, 780-790 m, DC (S1); England Finder V36/3.

Figs. 14, 15 *Graminidites annulatus* (van der Hammen 1954) Potonié 1960. Figs. 14, 15 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder Y26/4.

Figs. 16, 17 *Graminidites rotandinii* Morley and Jaizan Jais sp. nov. Figs. 16, 17 (x 1000 holotype): Slide Malong-2, 1135-1140 m, DC (S1); England Finder H33/4.

Figs. 18-20 *Pandanpollenites malaysianus* Jaizan Jais and Morley sp. nov. Fig. 18 (x 1000): Slide Malong-2, 1384 m, SWC (S2); England Finder N41/4. Figs. 19, 20 (Holotype, x 1000): Slide Malong-2, 918 m, SWC (S1); England Finder K9/1.

Fig. 21 *Psilodiporites jejawii* Jaizan Jais and Morley sp. nov. (x 1000 holotype): Slide Malong-2, 430.5 m, SWC (S2); England Finder F7.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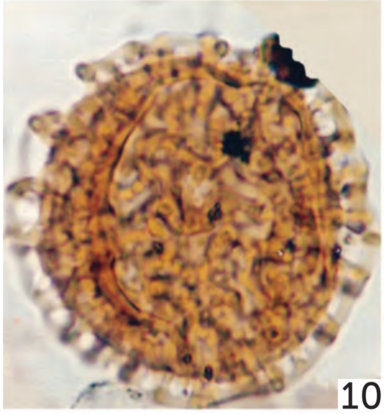
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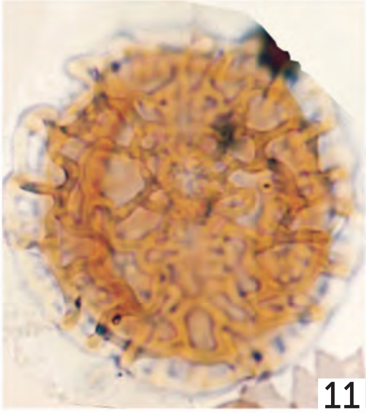
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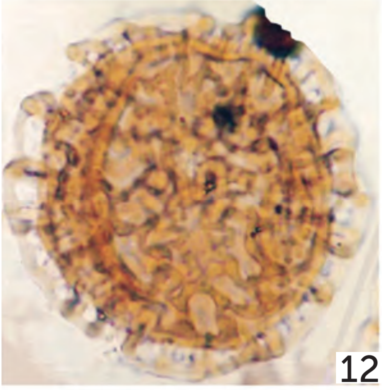
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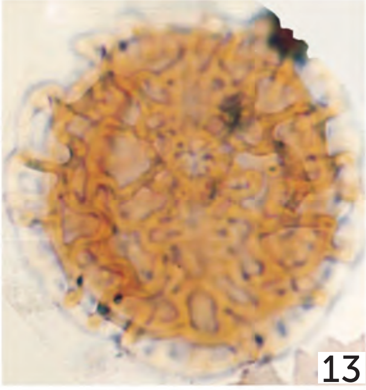
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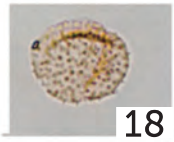
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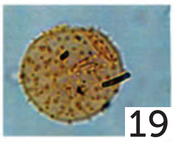
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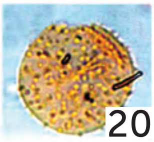
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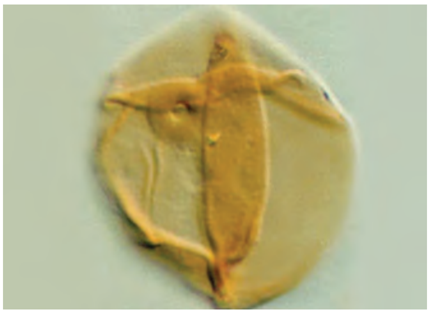
2.12 MONOPORATE POLLEN

Poaceae growing along bank of Pahang River in freshwater zone, Tebu Gajah, Pahang, Malaysia (photo by RJM).

Genus *Graminidites*
Cookson 1947 ex Potonié 1960 emend. Krutzsch 1970

Type species:
Graminidites medius (Cookson 1947) ex Potonié 1960.

Graminidites annulatus
(van der Hammen 1954) Potonié 1960b. Plate 11, Figs. 14, 15



Selected synonymy:
1954 *Monoporites annulatus* van der Hammen, p. 90, Pl. 6, Fig. 4.
1956 *Monoporites unipertusus* van der Hammen, p. 82, Pl. 5, Fig. 10.
1960b *Graminidites annulatus* (van der Hammen) Potonié, p. 111.
1968 *Monoporites annulatus* van der Hammen; Germeraad et al., p. 294, Pl. 3, Fig. 3.
1974 *Monoporites annulatus* van der Hammen, Regali et al., p. 273, Pl. 16, Fig. 7.
1977 *Graminidites annulatus* (van der Hammen) Potonié; Salard-Cheboldaeff, p. 241, Pl. 1, Fig. 10.
2001 *Monoporopollenites annulatus* Meyer; Jaramillo and Dilcher p. 136, Pl. 13, Figs. 17-19.

Description:
Pollen grains, radially symmetrical, heteropolar, almost spherical; single aperture, small, circular, penetrating entire wall, with annulus; annulus up to 4 μm wide, slightly protruding, endexine thin, typically less than ½ μm thick; columellae indistinct, ektexine typically >1 μm thick, psilate-very finely perforate or scabrate.

Dimensions:
Diameter 17 (28) 45 μm (13 specimens measured from various horizons).

Stratigraphic distribution:
Muller (1981) visualised the oldest records of *Graminidites* as Paleocene, with records from Brazil by Regali et al. (1974) and West Africa by Salard-Chebaldaeff (1978). There are also possible Cretaceous records, considered pending by Muller (1981) but the presence of Poaceae cuticle material in dinosaur coprolites from the Maastrichtian of India (Prasad et al., 2005; Sonkusare et al., 2017) and from teeth of dinosaurs from the Albian of China (Wu et al. 2018) suggests that Cretaceous records are expected. Across the low latitude tropics *Graminidites annulatus* is well represented from the middle Eocene onward, and

often shows a cyclic distribution, with maxima coinciding with periods of drier climate (e.g., Morley and Richards, 1993), often reflecting transgressive-regressive depositional cycles. In this study it occurs throughout the succession. In Delah 5H-14.1 it is common in the Oligocene zones PR1 to PR6/7, where it is particularly abundant in zone PR4 reflecting a long period of drier climate, and then is present in low numbers in Malong 5G-17.2, within zones PR14 and PR15A, again reflecting a period of more seasonal climate.

Remarks and comparison:
This pollen is placed in *Graminidites* Cookson 1947 ex Potonié 1960a following Krutzsch 1970, Atlas VII, p. 12, who considered *Monoporites* van der Hammen 1954, and *Monoporopollenites* Meyer (1956) to be junior synonyms of *Graminidites*. *Graminidites annulatus* differ from *Restioniidites punctulosus*, which has much wider annuli and more distinctly punctate exine (Huang et al., 2021).

Botanical affinity:
Poaceae (formerly called Gramineae).

Imperata cylindrica *(Lalang), disturbed ground, Singapore (photo by RJM).*

Source ecology:
Grasses are herbs, common in terra firma vegetation of seasonal climate; dominant in savanna, and abundant in the understorey of deciduous forests. Will also be present in semi-evergreen forests but rare in perhumid forests. Also dominant at high altitudes above the treeline. Grasses are also common in herbaceous swamps, where they can become dominant (Morley, 1982a).

Suggested name for Quaternary records:
Poaceae.

Ecological group:
Seasonal vegetation and herbaceous swamp.

Graminidites rotandinii

Morley and Jaizan Jais sp. nov. Plate 11, Figs. 16, 17

Derivation of name:

Named after 'rotan dini', the Malay name for *Flagellaria indica*.

Holotype:

Plate 11, Figs. 16, 17. Slide Malong-2, 1135-1140 m, DC (S1), England Finder H33/4.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 1135-114 m depth; age middle Miocene, zone PR11.

Description:

Pollen grains small, radially symmetrical, heteropolar, amb spherical to subspherical; monoporate; pore circular with annulus which is often faintly visible; exine thin, indistinctly perforated.

Derivation of name:

From rotan dini, the Malay name for *Flagellaria indica*.

Dimensions:

Diameter 16 (16.5) 17 µm (3 specimens measured from various horizons).

Stratigraphic distribution:

Rare and sparsely distributed throughout the Miocene section in Malong 5G-17.2 well.

Comparison:

This species is smaller than most *Graminidites annulatus*, with thinner exine and less pronounced annulus. Also it has a thinner indistinctly perforated wall. It is also much smaller than restionaceous pollen, such as *Milfordia homeopunctata* (McIntyre) Partridge in Stover and Partridge, 1973.

Botanical affinity:

Derived from the rotan-like *Flagellaria* (Flagellariaceae).

Flagellaria indica *(Rotan dini), Kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).*

Source ecology:

Climbing herbs commonly occur in herbaceous and woody vegetation.

Suggested name for Quaternary records:

Flagellaria indica type.

Ecological group:

Freshwater swamp or kerangas.

Genus *Pandanpollenites*

Jaizan Jais and Morley gen. nov.

Type species:

Pandanpollenites malaysianus sp. nov.

Derivation of name:

From extant pollen *Pandanus* (Pandanaceae).

Diagnosis:

Pollen grains small, spherical to oblate, echinate, monoporate; pore non- or very weakly annulate, pore often indistinct; exine stratification obscure but appears to be two layered, thin, structureless and with minutely echinae uniformly distributed over the tectum.

Remarks and comparison:

This genus is distinguished from *Pandaniidites* Elsik 1968 by having a non-to weakly annulate pore as seen in extant *Pandanus*. Elsik (1968) suggested a similarity in morphology of *Pandaniidites* from the North American Paleocene to modern pollen *Pandanus*, and Jarzen (1983) found specimens with more weakly developed pores which misled Muller (1981) into extending the range of Pandanaceae to the Maastrichtian. The North American specimens were later shown by Stockey et al. (1997) to be derived from Lemnaceae, as they found identical pollen in inflorescences of the fossil species *Limnobiophyllum scutatum*, and it is likely that most northern hemisphere Palaeogene records of *Pandaniidites* (reviewed in Jarzen, 1983) are also from Lemnaceae. *Spinamonoporites* Sah 1967 differs from *Pandanpollenites* in having densely distributed spinules with weakly reticulate ornamentation and also closely comparable to the modern family of Lemnaceae. *Spinamonoporites* Norton and Hall 1969 is a junior homonym of *Spinamonoporites* Sah and therefore illegitimate (Jansonius and Hills, 1976). *Pandanpollenites* is related to the modern genus *Pandanus*.

Pandanus helicopus *(pandan) alluvial freshwater swamp, Tasek Bera, Pahang, Malaysia (photo by RJM).*

Pandanpollenites malaysianus
Jaizan Jais and Morley sp. nov.
Plate 11, Figs. 18-20

Selected synonymy:
1975 Dispersed pollen attributed to *Pandanus* in Anderson and Muller, p. 311, Pl. 2, Fig. 12.
2021 *Pandaniidites* sp. Huang et al., Pl. 1, Fig. 2.

Derivation of name:
Named after the country of Malaysia where the species is discovered.

Holotype:
Plate 11, Figs. 19, 20. Slide Malong-2, 918 m, SWC (S1), England Finder K9/1. Grain circular in outline, diameter 16 µm; exine thin (less than 0.5 µm thick); echinae 1 µm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 918 m depth; age late Miocene, zone PR12B.

Description:
Pollen grains small, radially symmetrical, heteropolar, spherical to sub-spherical; monoporate; pore indistinct; exine thin (less than 0.5 µm thick), appears to be two layered, covered with more or less evenly distributed echinae, otherwise psilate; echinae minute, sharply pointed, up to 1 µm long.

Dimensions:
Diameter 12 (15) 17 µm (27 specimens measured from various horizons).

Stratigraphic distribution:
The oldest records of *Pandanpollenites malaysianus* are by Lelono (2000) from the middle Eocene Nanggulan Formation of Java, followed by a late Eocene record from the Yaw Formation in Myanmar (Huang et al., 2021) and the Oligocene of the East Java Sea by Lelono and Morley (2011). It has also been reported as *Pandanus* pollen from the Miocene coal of Brunei (Anderson and Muller, 1975). According to Gallagher et al. (2015), the molecular stem age for *Pandanus* plus the related genus *Benstonea* is about 39 Myr, and the crown age for *Pandanus* just 12 Myr, which is likely to be an underestimate based on the fossil pollen record from Malaysia. Present in moderate to high percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells and is especially common within zones PR6 to PR8 (late Oligocene) in the Delah 5H-14.1.

Comparison:
This species differs from *Pandaniidites texus* Elsik 1968 by the absence of an annulus around its pore and having thinner wall as noted above. *P. radicus* Leffingwell 1970 also differs in the presence of a distinct annulus.

Botanical affinity:
Pandanus (Pandanaceae).

Source ecology:
Pandanus are trees and shrubs, commonly from swamp or coastal environments found throughout the palaeotropics and tropical Pacific. The genus can be particularly common in rheotrophic riverine swamps, such as at Tasek Bera in the Malay Peninsula (Morley, 1981), and the Berbak swamp in south Sumatra (Morley and Morley 2013) but can also be a common element in peat swamps (Morley, 2013).

Pandanus *sp. (Pandan), coastal forest, West Java (photo by RJM).*

Suggested name for Quaternary records:
Pandanus.

Ecological group:
Riparian swamp.

2.13 DIPORATE POLLEN

Genus *Psilodiporites*
Varma and Rawat emend. Venkatachala and Rawat 1972

Type species:
Psilodiporites hammenii Varma and Rawat 1963.

Generic remarks:
The spelling of this generic name is as originally proposed by Varma and Rawat (1963). Subsequent authors (van der Hammen and Wijmstra, 1964; González-Guzmán, 1967) have used the spelling *'Psiladiporites'*.

Ficus *sp. (Aru). Alluvial swamp forest, Kuala Selangor, Malaysia (photo by RJM).*

Psilodiporites jejawii

Morley and Jaizan Jais sp. nov. Plate 11, Fig. 21

Derivation of name:

From *Jejawi*, the Malay name for *Ficus macrocarpa* which lines the tidal reaches of the Sedili River in Johor, Malay Peninsula (Corner, 1978).

Holotype:

Plate 11, Fig. 21. Slide Malong-2, 1135-1140 m, DC (S1), England Finder H33/4.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 1135-1140 m depth; age middle Miocene, zone PR11.

Description:

Pollen of small size and bilaterally symmetrical to slightly asymmetrical, diporate; peroblate, pores round, without annuli; exine thin, possibly two layered, psilate.

Dimensions:

Length 12 (14) 16 µm, width 8 (9) 11 µm (3 specimens measured from various horizons).

Stratigraphic distribution:

According to Muller (1981) the oldest record of *Ficus* pollen is 'Diporate sp. A', recorded from the middle Eocene of North America by Potter (1976). It has also been reported from the middle Miocene of Brunei by Anderson and Muller (1975) and from the late Miocene of Spain by Van Campo (1976). In the Malong 5G-17.2 well it is very rare and restricted in the PR15 zone.

Remarks and comparison:

This smooth diporate pollen is characterised by its thin wall, small size and oblate or peroblate shape compares closely to *Ficus* pollen. The type species of *Paleoficus* Biswas 1962, even though being described as similar to modern pollen of *Ficus*, has some sort of thickening around the pores and is unlikely to be *Ficus*. Compared to *P. minimus* van der Hammen and Wijmstra 1964, *Psilodiporites* sp. is distinctly flattened.

Botanical affinity:

Derived from *Ficus* (Moraceae). It is always surprising that this pollen type should occur regularly is sediments since the *Ficus* flower is entirely contained within the enclosed inflorescence, and dispersal of airborne pollen seems most unlikely. Many *Ficus* spp. occur in abundance along rivers and in swamps, and the probability is that the whole inflorescence dropped and disintegrated into the swamp surface or into the river, from where it is subsequently dispersed in the manner of other pollen. With a record of *Ficus* pollen from the middle Eocene of North America, a molecular age of 43 Mya has been suggested for the crown group of *Ficus* by Pederneiras et al. (2018), whereas Zhang et al. (2019) date the crown group a little older, at 48 Myr, approximately in line with ages suggested by fossil pollen.

Source ecology:

Trees, shrubs or herbs in forests or non-forest areas or on swamps. As noted above some species are particulary common along rivers, such as *Ficus macrocarpa*, which lines the tidal reaches of the Sedili River in Johor, Malay Peninsula, as noted by Corner (1978).

Suggested name for Quaternary records:

Ficus type.

Ecological group:

Riparian.

Ficus macrocarpa *(Aru), supratidal freshwater zone, Sedili River, Johor, Malaysia (photo by RJM).*

2.14 TRIPORATE POLLEN

Genus *Florschuetzia*
Germeraad et al. 1968 emend. Yamanoi 1984.

Type species:
Florschuetzia trilobata Germeraad et al. 1968 (by original designation).

Generic remarks: Even though *Florschuetzia* is the most important genus for stratigraphic correlation in the Southeast Asian Cenozoic, it is probably the most poorly understood which causes considerable confusion. This is partly due to the inconsistency between different palynologists with respect to identification. The identification of species within this genus is even more confusing since many more morphotypes occur outside its type locality. To solve this problem, the taxonomic treatment of the genus has been revised and tested in this study. This involves emendation and division of *Florschuetzia trilobata* Germeraad et al. (1968) and the proposal of several new species within the genus. The emended diagnosis of Yamanoi (1984) is used here to allow the inclusion of new species that have pores with colpoid grooves or colpi (colporate). Germeraad et al. (1968) erected the genus *Florschuetzia* to include the fossil sonneratioid pollen types, including *F. trilobata*, the presumed ancestral type which have the combination of Lythraceous and Sonneratiaceous characters (Muller, 1978, 1981b). They compared this genus to the similar genus *Verrutricolporites* van der Hammen and Wijmstra 1964 which they considered to be derived from the genus *Crenea* (Lythraceae). However, an affinity with sonneratioid Lythraceae is considered more likely (Morley, 2000). Subsequent emendation of *Verrutricolporites* by Legoux (1978) has since been made to include several new species within that genus. Consequently, the similarity of these two genera has become even closer and several African specimens photographed by Legoux (1978) look strikingly similar to some of the *Florschuetzia* morphotypes observed in this study. Although these two genera clearly overlap morphologically, we do not think it would be of benefit to combine them. Since structural details cannot be observed on photomicrographs alone, it may be worthwhile to examine these specimens in detail and reconsider their taxonomic status as was similarly done by Muller (1978) to differentiate *F. levipoli* Germeraad et al. 1968 to superficially morphologically similar species of *Santalumidites cainozoicus* Cookson and Pike 1954. Here we follow an approach similar to that of Morley (2000, Fig. 9.37), who informally divided morphotypes within the broad *F. trilobata* group based on the presence or absence of colpi and nature of exine structure and formally propose those pollen types as new species, or in the case of *Florschuetzia trilobata*, new forms.

Sonneratia *spp., berembang/perapat, mangroves, Bali (photo by RJM).*

Sonneratia *flowers are pollinated by bats. After clumsily feeding, most of the anthers fall to the ground, or onto the water surface, ensuring that the pollen is abundantly represented in coastal sediments (photo by RJM).*

Florschuetzia trilobata

Germeraad et al. 1968 emend. Jaizan Jais and Morley. Plate 12, Figs.3-5

Selected synonymy:

1968 *Florschuetzia trilobata* Germeraad et al. (partim), p. 306, Pl. 7, Figs. 2, 3 (non Pl. Fig. 4).

1987 *Florschuetzia trilobata* Germeraad et al.; Mathur and Chopra, p. 127, Pl. 4, Fig. 88.

Emended description:

Pollen grains radially symmetrical, isopolar, prolate in equatorial view, often bluntly pointed at poles and with meridional ridges, amb strongly lobate; triporate; pores circular, 2 to 4 µm in diameter, intersubangular, ectexinous and endexinous; exine tectate, 2 to 3 µm thick on poles and meridional ridges, ±1 µm thick on porate fields, with no visible structure; endexine ±0.5 µm thick; columellae generally indistinct, 0.5 to 1 µm long; tectum psilate, not clearly differentiated from underlying columellae, 1 to 2 µm thick on poles and meridional ridges, probably <1 µm thick on porate fields; dimensions 20 to 35 µm.

Remarks:

Germeraad et al. (1968) in their original description of the Bornean type species included rare specimens which have pores combined with ± colpoid grooves (in this study they are considered interchangeable with the term colpi even though they are weakly developed, and their functions are uncertain, hence the combined apertures are categorised as colporate). The newly emended diagnosis of this species is made to exclude these tricolporate forms and restrict the *F. trilobata* Germeraad et al. emend. to triporate forms with smooth wall (i.e., with no visible exine structure observed under x100 objective of light microscope). The size range of this species is also widened to include smaller forms identified in this study. This emendation allows separation of several morphotypes within the species *F. trilobata* which in turn give a better insight into the evolution of this group. Four other morphotypes of *F. trilobata* are identified in this study, based on the aperture type, exine structure and wall thickness. They are informally designated as forma A to forma D.

Holotype and type locality:

As designated by Germeraad et al., 1968, p. 306, Plate 7, Fig. 2, slide TC-156, surface sample Dz-4493, north-western Borneo.

Dimensions:

Length 23 (26) 29 µm, width 14 (18) 25 µm (14 specimens measured from various horizons).

Stratigraphic distribution:

The oldest record of *Florschuetzia trilobata* (sensu lato) is from the basal middle Eocene in Southwest Sulawesi (Morley, 2018). Subsequently it has been recorded from the middle Eocene of the Nanggulan Formation in Java (Morley, 2000, 2018; Lelono, 2000), the late Eocene of Myanmar (Huang et al., 2021) and subsequently many records from across Southeast Asia from the early Oligocene through to the middle Miocene (Germeraad et al., 1968; Muller, 1978; Morley, 1978, 1991; Watanasak, 1990). Outside Southeast Asia, there are records from the late Eocene through to the Miocene of Assam (Handique, 1992), and Pliocene of offshore Bengal, (Mathur and Chopra, 1987), the Eocene to Miocene of China (Lei, 1998; Liu et al., 1999; Mao et al., 2012, 2013) and also the mid Cenozoic of the Red Sea (Morley, 2000). In this study, *Florschuetzia trilobata* (sensu strictu) is common in the Malong 5G-17.2 well, from zone PR6/7 to PR9A, and then occur consistently but in lower numbers from zone PR9B to PR11, whereas in the Delah 5H-14.1 well, it occurs commonly through zones PR1 to PR6/7.

Comparison:

This species differs from *F. trilobata* forma A by its triporate aperture; from *F. trilobata* forma B in its exine structure; from *F. trilobata* forma C in its triporate aperture and exine structure; from *F. trilobata* forma D by its wall which is relatively less robust and thinner on porate fields; and from *F. ovalis* sp. nov. in its trilobate form.

Botanical affinity:

Florschuetzia trilobata is visualised as being derived from the ancestor of *Sonneratia caseolaris* (Morley, 2000) within the families Lythraceae/ Sonneratiaceae (Muller, 1981b). Mao et al. (2013) have evaluated the ancestral biogeography of *Sonneratia* based on the fossil record of *Florschuetzia.*

Source ecology:

There is very good evidence to suggest that the source taxon of *Florschuetzia trilobata* was a species which could grow in both freshwater and brackish swamp settings (Morley, 1991). This species is well represented throughout the thick late Eocene to Oligocene freshwater lacustrine successions seen in the Cuu Long Basin (Morley et al., 2019) and in intermontane basins, such as the Na Plong intermontane basin in Kra Isthmus where maxima of *F. trilobata* alternate with maxima of *Alnus* pollen (Azmi Yakzan, 1999). On the other hand, it would also have been present as a backmangrove element in mangrove swamps on brackish deltas, where *F. trilobata* pollen is associated with pollen of *Nypa* and other mangroves.

Suggested name for Quaternary records:

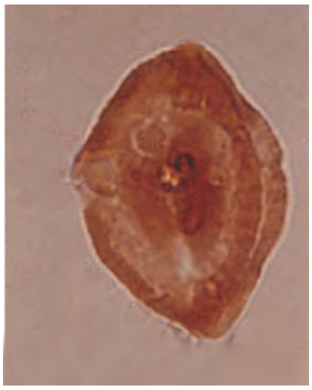
Not applicable.

Ecological group:

Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia trilobata

forma A Jaizan Jais and Morley forma nov. Plate 12, Figs. 1, 2



Selected synonymy:

1968 *Florschuetzia trilobata* Germeraad, Hopping and Muller (*partim*), p. 306, Pl. 7, Fig. 4 (non Pl. 7, Figs. 2, 3).

Holotype:

Germeraad et al. 1968, Pl. VII, Fig. 4. Grain equatorially compressed, prolate with bluntly pointed poles.

Type locality:

Borneo.

Description:

Pollen grains radially symmetrical, isopolar, prolate in equatorial view, often bluntly pointed at poles and with meridional ridges, amb strongly lobate; tricolporate; pores circular, 2 to 4 μm in diameter, intersubangular, ectexinous and endexinous, combined with colpoid grooves or colpi; colpi weakly developed, not reaching the poles, extending half to three-fourths of grain length, ±1 μm wide, may be flanked by relatively short secondary meridional thickenings; exine tectate, 1 to 3 μm thick on poles and meridional ridges, ±1 μm thick on equatorial belts, with no visible structure; endexine ±0.5 μm thick; columellae generally indistinct, 0.5 to 1 μm long; tectum psilate, not clearly differentiated from underlying columellae, 1 to 2 μm thick on poles and meridional ridges, probably <1 μm thick on equatorial belts.

Dimensions:

Length 20 (24) 29 μm, width 15 (16) 20 μm (6 specimens measured from various horizons).

Stratigraphic distribution:

Sparsely distributed in low percentages in Malong 5G-17.2 well from zones PR6/7 to PR9A.

Remarks and comparison:

This form was originally included in *F. trilobata* Germeraad et al. (1968) as one of its variations. The species is closely similar and probably closely related to *Verrutricolporites laevigatus* Legoux (1978) that was incorporated into *V. rotundiporus* van der Hammen and Wijmstra (1964). The holotype or lectotype of *V. laevigatus* has not been examined to determine with certainty its similarity and its relationship to *F. trilobata* forma A. Germeraad et al. (1968) also noted the superficial similarity of *F. trilobata* (as per original diagnosis) with the psilate variations of *V. rotundiporus* van der Hammen and Wijmstra and distinguished the former by its larger size, trilobate condition, thickened meridional ridges, variable wall thickness and generally indistinct columellae. Until detailed comparison studies are made, the taxonomic standings and the relationship of these closely similar Southeast Asian and African/South American species will remain uncertain. The findings of such studies could improve the understanding of the ancestors of genus *Florschuetzia* and the present day Sonneratiaceae. *Florschuetzia. trilobata* forma A differs from *F. trilobata* Germeraad et al. emend. in having colporate apertures; from *F. trilobata* forma B by its colporate aperture and exine structure; from *F. trilobata* forma C by its exine structure; from *F. trilobata* forma D by its colporate aperture and in having the wall which is less robust and thinner on equatorial belts; from *F. ovata* sp. nov. by its trilobate form.

Botanical affinity:

Lythraceae/Sonneratiaceae.

Source ecology:

As for *Florschuetzia trilobata* sstr (see above).

Suggested name for Quaternary records:

Not applicable.

Ecological group:

Backmangrove and freshwater swamp (Morley, 1991).

Plate 12

Figs. 1, 2 *Florschuetzia trilobata* forma A Jaizan Jais and Morley forma nov.
Fig. 1 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder V29.
Fig. 2 (Holotype, x 1000): From Plate VII, fig. 4 of Germeraad et al. (1968).

Figs. 3-5 *Florschuetzia trilobata* Germeraad et al. 1968 emend. Jaizan Jais and Morley.
Fig. 3 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder F39. Fig. 4 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder V31. Fig. 5 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder V31.

Figs. 6-8 *Florschuetzia trilobata* forma B Jaizan Jais and Morley forma nov.
Fig. 6 (Holotype, x 1000): Slide Malong-2, 1554 m, CC (S1); England Finder V30. Fig. 7 (x 1000): Slide Delah-1, 2540-2545 m, DC (S1); England Finder J4/4. Fig. 8 (x 1000): Slide Malong-2, 1345-1350 m, DC (S1); England Finder H29/3.

Figs. 9-14 *Florschuetzia trilobata* forma C Jaizan Jais and Morley forma nov.
Figs. 9, 10 (Holotype x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder X19/1. Figs. 11, 12 (x 1000): Slide Malong-2, 1200-1205 m, DC (S1); England Finder M10/2. Figs. 13, 14 (x 1000): Slide Malong-2, 1384 m, SWC (S2); England Finder N24.

Figs. 15-17 *Florschuetzia trilobata* forma D Jaizan Jais and Morley forma nov.
Fig. 15 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder J33/4. Fig. 16 (x 1000): Slide Delah-1, 2540-2545 m, DC (S1); England Finder P9.
Fig. 17 (Holotype, x 1000): Slide Malong-2, 1603.7 m, CC (S1); England Finder J30/1.

Figs. 18-19 *Florschuetzia* sp. (columellate).
Figs. 18, 19 (x 1000): Slide Malong-2, 1155-1160 m, DC (S1); England Finder V27.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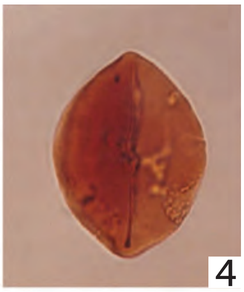
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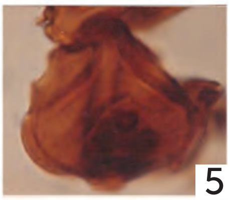
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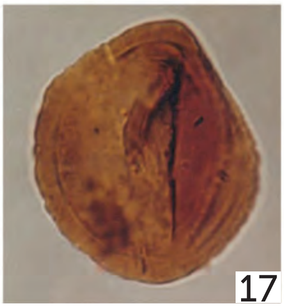
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Florschuetzia trilobata
forma B Jaizan Jais and Morley forma nov. Plate 12, Figs. 6-8

Holotype:
Plate 12, Fig. 6. Slide Malong-2, 1554 m, CC (S1), England Finder V30. Grain in equatorial aspect, length 25 µm, width 21 µm; pores 2 to 3 µm in diameter; exine 2 µm thick on poles and meridional ridges, 1 µm on porate fields; endexine ±0.5 µm thick; columellae 0.5 to 1 µm long; tectum 1 µm thick on poles, probably <1 µm thick on porate fields.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1554 m depth; age late Oligocene, zone PR6/7.

Description:
Pollen grains radially symmetrical, isopolar, prolate in equatorial view, often bluntly pointed at poles and with meridional ridges, amb strongly lobate; triporate; pores circular, 2 to 4 µm in diameter, intersubangular, ectexinous and endexinous; exine tectate, 2 to 3 µm thick on poles and meridional ridges, ±1 µm thick on porate fields, microreticulate in structure (visible under high magnification); endexine ±0.5 µm thick; columellae generally indistinct, 0.5 µm long; tectum smooth, generally not clearly differentiated from underlying columellae (some are relatively clearer than others), 1 to 2 µm thick on poles and meridional ridges, probably <1 µm thick on porate fields.

Dimensions:
Length 23 (27) 30 µm, width 14 (19) 22 µm (19 specimens measured from various horizons).

Stratigraphic distribution:
Present throughout the Delah 5H-14.1 well (through zones PR1 to PR6/7), but more commonly represented in zones PR1 to PR3. In Malong 5G-17.2, common up to zone PR9A, then consistently present from zone PR9B to PR11.

Comparison:
This species differs from *F. trilobata* Germeraad et al. emend. by its microreticulate exine structure; from *F. trilobata* forma A in having triporate apertures and microreticulate exine structure; from *F. trilobata* forma C by its triporate aperture; from *F. trilobata* forma D in having microreticulate exine structure and by its wall which is relatively less robust and thinner on porate fields; and from *F. retiovalis* sp. nov. by its trilobate form.

Botanical affinity:
Lythraceae/Sonneratiaceae.

Source ecology:
As for *Florschuetzia trilobata* sstr. (see above).

Suggested name for Quaternary records:
Not applicable.

Ecological group:
Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia trilobata
forma C Jaizan Jais and Morley forma nov. Plate 12, Figs. 9-14

Holotype:
Plate 12, Figs. 9, 10. Slide Malong-2, 1518.5 m, CC (S1), England Finder X19/1. Grain in equatorial aspect, length 26 µm, width 18 µm; pores 2 to 3 µm in diameter; colpi 15 µm long, 1µm wide; exine 1 to 2 µm on poles and meridional ridges, ±1 µm thick on equatorial belts; endexine ±0.5 µm thick; columellae <1 µm long; tectum 0.5 µm thick on poles, probably < 0.5 µm thick on equatorial belts.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1518.5 m depth; age Early Miocene, zone PR8.

Description:
Pollen grains radially symmetrical, isopolar, prolate in equatorial view, often bluntly pointed at poles and with meridional ridges, amb strongly lobate; tricolporate; pores circular, 2 to 4 µm in diameter, intersubangular, ectexinous and endexinous, combined with colpoid grooves or colpi; colpi weakly developed, not reaching the poles, extending half to three-fourths of grain length, <1 µm wide, may be flanked by relatively short secondary meridional thickenings; exine tectate, 1 to 3 µm thick on poles and meridional ridges, ±1 µm thick on equatorial belts, microreticulate in structure (visible under high magnification); endexine ±0.5 µm thick, columellae generally indistinct, 0.5 µm long; tectum smooth, generally not clearly differentiated from underlying columellae (some are relatively clearer than others), 1 to 2 µm thick on poles and meridional ridges, probably <1 µm thick on equatorial belts.

Dimensions:
Length 25 (26) 27 µm, width 17 (18) 19 µm (4 specimens measured from various horizons).

Stratigraphic distribution:
Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells from zone PR8 to PR10.

Comparison:
This form differs from *F. trilobata* Germeraad et al. emend. in having colporate apertures and microreticulate exine structure; from *F. trilobata* forma A by its microreticulate exine structure; from *F. trilobata* forma B in having colporate apertures; from *F. trilobata* forma D by its colporate apertures and in having a wall which is less robust and thinner on equatorial belts; and from *F. retiovata* sp. nov. by its trilobate form.

Botanical affinity:
Lythraceae/Sonneratiaceae.

Source ecology:
As for *Florschuetzia trilobata* sstr. see above.

Suggested name for Quaternary records:
Not applicable.

Ecological group:
Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia trilobata forma D Jaizan Jais and Morley forma nov. Plate 12, Figs. 15-17

Holotype:
Plate 12, Fig. 17. Slide Malong-2, 1603.7 m, CC (S1), England Finder J30/1. Grain in equatorial aspect, length 30 µm, width 27 µm; pores 3 µm in diameter; exine 3 µm thick on poles and meridional ridges, 2 to3 µm thick on porate fields; endexine ±0.5 µm thick; columellae 1 µm long; tectum 1 to 2 µm thick on poles, 1 µm thick on porate fields.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1603.7 m depth; age early Miocene, zone PR8.

Description:
Pollen grains radially symmetrical, isopolar, prolate in equatorial view, often bluntly pointed at poles and with meridional ridges, amb lobate; triporate; pores circular, 2 to 4 µm in diameter, intersubangular, ectexinous + endexinous; exine tectate, 2 to 4 µm thick on poles and meridional ridges, 2 to 3 µm thick on porate fields; endexine ±0.5 µm thick; columellae indistinct, 1 µm long; tectum psilate to scabrate, not clearly differentiated from underlying columellae, 1 to 2 µm thick on poles and meridional ridges, 1 µm thick on porate fields.

Dimensions:
Length 26 (28) 31 µm, width 17 (21) 27 µm (11 specimens measured from various horizons).

Stratigraphic record:
Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells from zone PR3 to PR9B.

Comparison:
This form differs from *F. trilobata* Germeraad et al. emend. by its wall which is relatively more robust and thicker on porate fields; from F. trilobata forma A in having triporate aperture and relatively more robust and thicker wall; from *F. trilobata* forma B by its exine structure and relatively robust and thicker wall; from *F. trilobata* forma C in having triporate apertures and by its exine structure and a more robust and thicker wall; and from *F. ovalis* sp. nov. by its trilobate form.

Botanical affinity:
Lythraceae/Sonneratiaceae.

Source ecology:
As for *Florschuetzia trilobata* sstr. (above).

Suggested name for Quaternary records:
Not applicable.

***Ecological* group:**
Backmangrove and freshwater swamp (Morley, 1991).

***Florschuetzia* sp. (Columellate).** Plate 12, Figs. 18, 19

Dimensions:
Length 22 µm, width 14 µm (1 specimen measured).

Distribution:
Only one specimen found in Malong 5G-17.2 well at 1160 m (DC) depth.

Remarks and comparison:
This specimen differs from other *Florschuetzia* spp. in having distinct columellae on the poles. This pollen type is common in areas of more distinctly seasonal climate, especially in areas such as the Nam Con Son Basin south of Vietnam. The polar columellae are reminiscent of *Lagerstroemia*.

Botanical affinity:
Probably Lythraceae/Sonneratiaceae.

Source ecology:
Perhaps Backmangroves under a seasonal climate.

***Suggested name for Quaternary* records:**
Not applicable.

Ecological group:
Backmangrove.

Ecological group:
Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia ovalis

Jaizan Jais and Morley sp. nov. Plate 13, Figs. 1, 2

Derivation of name:

From its oval shape.

Holotype:

Plate 13, Fig. 2. Slide Malong-2, 1518.5 m, CC (S1), England Finder O18/2. Grain in equatorial aspect; length 29 µm, width 20 µm; pores 3 µm in diameter; exine 2 µm thick.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1518.5 m depth; age early Miocene, zone PR8.

Description:

Pollen grains radially symmetrical, isopolar, non-lobate, prolate to prolate spheroidal, often oval in equatorial view, with meridional ridges, amb not observed; triporate; pores circular, 2 to 4 µm in diameter, ectexinous and endexinous, may be flanked by relatively short secondary meridional thickenings; exine tectate, 1 to 2 µm thick, with no visible structure; tectum smooth; columellae indistinct.

Dimensions:

Length 19 (25) 29 µm, width 17 (20) 25 µm (13 specimens measured from various horizons).

Variability:

In shape and size with some transitional forms to *F. trilobata* included.

Stratigraphic distribution:

Present in moderate percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells from zone PR2 to PR9B (Lower).

Comparison:

This form differs from *F. trilobata* in its non-lobate shape; from *F. ovata* sp. nov. in having triporate apertures; from *F. retiovalis* sp. nov. in its exine structure; from *F. retiovata* sp. nov. by its triporate aperture and exine structure.

Botanical affinity:

Lythraceae/Sonneratiaceae.

***Source* ecology:**

Probably as *F. trilobata* group, backmangrove and freshwater swamp (Morley, 1991).

Suggested name for Quaternary records:

Not applicable.

Ecological group:

Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia ovata

Jaizan Jais and Morley sp. nov. Plate 13, Figs. 3, 4

Derivation of name:
From its oval shape.

Holotype:
Plate 13, Figs. 3, 4. Slide Malong-2, 1420.5 m, SWC (S2), England Finder S8/4. Grain in equatorial aspect, length 20 µm, width 15 µm; pores 3 µm in diameter; colpi 11 µm long, ±1 µm wide; exine 1.5 µm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 1420.5 m depth; age Early Miocene, zone PR9A.

Description:
Pollen grains radially symmetrical, isopolar, nonlobate, prolate to prolate spheroidal, often oval in equatorial view, with meridional ridges, amb not observed; tricolporate; pores circular, 2 to 4 µm in diameter, ectexinous + endexinous, combined with colpoid grooves or colpi; colpi weakly developed, not reaching the poles, extending half to three-fourths of grain length, ±1 µm wide, may be flanked by relatively short secondary meridional thickenings; exine tectate, 1 to 2 µm thick, with no visible structure; tectum smooth; columellae indistinct.

Dimensions:
Length 20 (24) 26 µm, width 15 (17) 19 µm (5 specimens measured from various horizons).

Variability:
In shape and size with some transitional forms to *F. trilobata* forma A included.

Stratigraphic distribution:
Sparsely distributed in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells from zone PR6/7 to zone PR9B.

Comparison:
This form differs from *F. trilobata* forma A in its non-lobate shape; from F. ovalis sp. nov. in having colporate aperture; from *F. retiovalis* sp. nov. by its exine structure and colporate aperture; from *F. retiovata* sp. nov. in its exine structure.

Botanical affinity:
Lythraceae/Sonneratiaceae.

Source ecology:
Probably as *F. trilobata* group, backmangrove and freshwater swamp (Morley, 1991).

Suggested name for Quaternary records:
Not applicable.

Ecological group:
Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia retiovalis

Jaizan Jais and Morley sp. nov. Plate 13, Figs. 5-8

Derivation of name:
From its microreticulate exine structure and oval shape.

Holotype:
Plate 13, Fig. 8. Slide Malong-2, 1518.5 m, CC (S1), England Finder O28. Grain in equatorial aspect, length 27µm, width 22µm; pores 3 to4µm in diameter; exine 1µm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1518.5 m depth; age early Miocene, zone PR8.

Description:
Pollen grains radially symmetrical, isopolar, nonlobate, prolate to prolate spheroidal, often oval in equatorial view, with meridional ridges, amb not observed; triporate; pores circular, 2 to 4 µm in diameter, extexinous and endexinous, may be flanked by relatively short secondary meridional thickenings; exine tectate, 1 to 2 µm thick, microreticulate in structure (visible under high magnification); tectum smooth; columellae generally indistinct (some are relatively clearer than others).

Dimensions:
Length 22 (25) 30µm, width 14 (18) 22µm (17 specimens measured from various horizons).

Variability:
In shape and size with transitional forms to *F. trilobata* forma B included.

Stratigraphic distribution:
Present in moderate and high percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells from zone PR2 to PR9B.

Comparison:
This species differs from *F. trilobata* forma B by its nonlobate shape; from *F. ovalis* sp. nov. in having microreticulate wall structure; from *F. ovata* sp. nov. in its triporate apertures and microreticulate exine structure and from *F. retiovata* sp. nov. in having triporate apertures.

Botanical affinity:
Lythraceae/Sonneratiaceae.

Source ecology:
Probably as *F. trilobata* group, backmangrove and freshwater swamp (Morley, 1991).

Suggested name for Quaternary records:
Not applicable.

Ecological group:
Backmangrove and freshwater swamp (Morley, 1991).

KEY TO *Florschuetzia* spp.

1	Exine sculpture and/or structure in meridional region different to that at poles	2
2	Exine with elongated columellae in polar region	*Florschuetzia* sp. (columellate)
2	Exine with verrucate sculpture in region of pores and psilate at poles	3
3	Exine at poles smooth, with columellae clearly visible	*Florschuetzia meridionalis*
3	Exine at poles smooth, but without polar columellae	*Florschuetzia levipoli*
3	Exine showing a weak transition to a psilate polar cap	*Florschuetzia semilobata*
1	Exine sculpture in meridional area approximately the same as at the poles	4
4	Exine verrucate over entire grain but less pronounced at poles	*Florschuetzia semilobata*
4	Exine psilate	5
5	Grains strongly lobate	6
6	Grains triporate	7
7	Exine without structure	*Florschuetzia trilobata*
7	Exine with structure, microreticulate	*F. trilobata var* A
6	Grains tricolporate	8
8	Exine without structure	*F. trilobata var* B
8	Exine with structure, exine up to 3 µm thick	*F. trilobata var* C
8	Exine with structure, exine thick, typically 4 µm	*F. trilobata var* D
5	Grains non-lobate, with meridional thickenings or ridges adjacent to apertures	9
9	Grains triporate	10
10	Exine without structure	*Florschuetzia ovalis*
10	Exine with structure, microreticulate	*Florschuetzia retiovalis*
9	Grains tricolporate	11
11	Grains without structure	*Florschuetzia ovata*
11	Grains with structure, microreticulate	*Florschuetzia retiovata*

Plate 13

Figs. 1, 2 *Florschuetzia ovalis* Jaizan Jais and Morley sp. nov. Fig. 1 (x 1000): Slide Delah-1, 2520-2525 m, DC (S1); England Finder Z19/4. Fig. 2 (Holotype, x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder O18/2.

Figs. 3, 4 *Florschuetzia ovata* Jaizan Jais and Morley sp. nov. (Holotype x1000) Slide Malong-2. 1420.5 m SWC (S2); England Finder S8/4.

Figs. 5-8 *Florschuetzia retiovalis* Jaizan Jais and Morley sp. nov.
Figs. 5, 6 (x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder S33/3. Fig. 7 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder V20/3.
Fig. 8 (Holotype x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder O28.

Figs. 9-12 *Florschuetzia retiovata* Jaizan Jais and Morley sp. nov.
Figs. 9, 10 (Holotype, x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder O18/1. Figs. 11, 12 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder H14.

Figs. 13-16 *Florschuetzia semilobata* Germeraad et al. 1968.
Figs. 13, 14 (x 1000): Slide Malong-2, 1234.5 m, SWC (S1); England Finder W8.
Figs. 15, 16 (x 1000): Slide Malong-2, 1366 m, SWC (S2); England Finder V35.

Figs. 17-19 *Florschuetzia levipoli* Germeraad et al. 1968.
Figs. 17, 18 (x 1000): Slide Malong-2, 760-770 m, DC (S1); England Finder Y33/4.
Fig. 19 (x 1000): Slide Malong-2, 1135-1140 m, DC (S1); England Finder X45.


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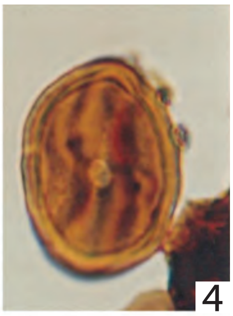
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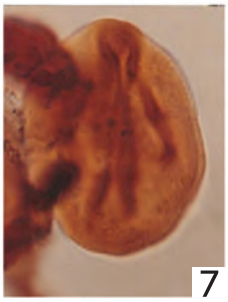
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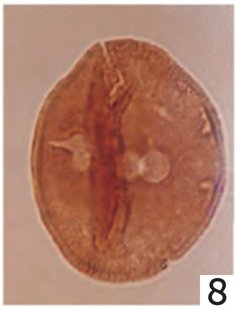
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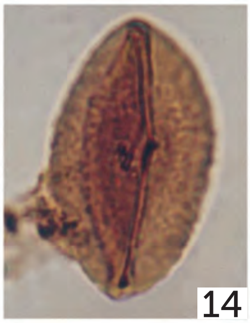
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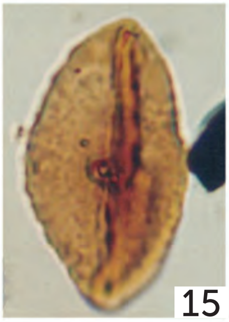
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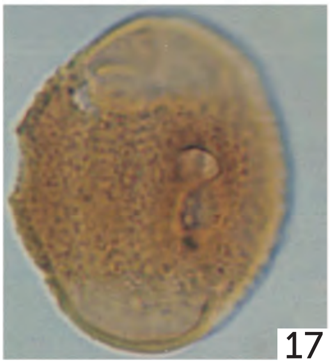
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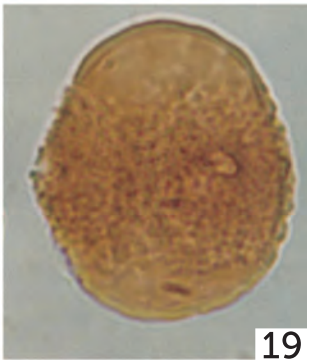
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Florschuetzia retiovata

Jaizan Jais and Morley sp. nov. Plate 13, Figs. 5-8

Derivation of name:
From its microreticulate exine structure and oval shape.

Holotype:
Plate 13, Figs. 9, 10. Slide Malong-2, 1518.5 m, CC (S1), England Finder O18/1. Grain in equatorial aspect, length 27 μm, width 20 μm; pores 2 to 3 μm in diameter; colpi 14 μm long, ±1 μm wide; exine 1 to 1.5 μm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; conventional core sample at 1518.5 m depth; age early Miocene, zone PR8.

Description:
Pollen grains radially symmetrical, isopolar, nonlobate, prolate to prolate spheroidal, often oval in equatorial view, with meridional ridges, amb not observed; tricolporate; pores circular, 2 to 3 μm in diameter, ectexinous and endexinous, combined with colpoid grooves or colpi; colpi weakly developed, not reaching the poles, extending half to three-fourths of grain length, ±1 μm wide, may be flanked by relatively short secondary meridional thickenings. Exine tectate, 1 to 2 μm thick, microreticulate in structure (visible under high magnification); tectum smooth; columellae generally indistinct (some are relatively clearer than others).

Dimensions:
Length 20 (25) 28 μm, width 13 (17) 22 μm (7 specimens measured from various horizons).

Variability:
In shape and size with transitional forms to *F. trilobata* forma C included.

Stratigraphic distribution:
Present in moderate percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells from zone PR3 to PR10.

Comparison:
This species differs from *F. trilobata* forma C by its non-lobate shape; from *F. ovalis* sp. nov. in having microreticulate exine structure and colporate apertures; from *F. ovata* sp. nov. in its microreticulate exine structure; from *F. retiovalis* sp. nov. by its colporate apertures.

Botanical affinity:
Lythraceae/Sonneratiaceae.

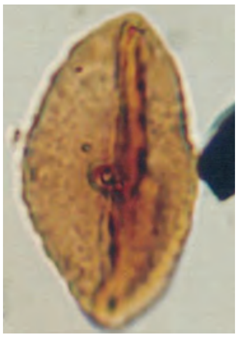
Source ecology:
Probably as *F. trilobata* group, backmangrove and freshwater swamp (Morley, 1991).

Suggested name for Quaternary records:
Not applicable.

Ecological group:
Backmangrove and freshwater swamp (Morley, 1991).

Florschuetzia semilobata

Germeraad, Hopping and Muller 1968. Plate 13, Figs. 13-16



Selected synonymy:

1968 *Florschuetzia semilobata* Germeraad et al., p. 307, Pl. 7, Figs. 7, 8.

1987 *Florschuetzia semilobata* Germeraad et al.; Mathur and Chopra, p. 126, Pl. 4, Fig. 84.

Description:

Pollen radially symmetrical, isopolar; prolate; in polar view lobate, triporate, pores circular, 1 to 2 μm in diameter, interlobate, endexinous (in less well preserved grains appearing as endexine and ektexine), total wall thickness 1 to 2 μm at poles and meridional ridges, probably <1 μm on porate fields; endexine <½ μm in thickness, columellae generally indistinct; tectum ±1 μm thick, areolate to verrucate, coarser on meridional ridges, finer on porate fields, on poles often showing a transition to a psilate polar cap (Germeraad et al., 1968).

Dimensions:

Length 24 (27) 31 μm, width 15 (18) 27 μm (11 specimens measured from various horizons).

Stratigraphic distribution:

This species ranges from the late Oligocene through to the middle Miocene (Morley, 1991). It has been recorded from the early to middle Miocene of Northwest Borneo by Germeraad et al. (1968). In Thailand, where the Oligocene has little brackish influence, it tends to be restricted to the early and middle Miocene (Watanasak, 1990) There are some anomalous records such as from the Pleistocene of Bengal Basin, India (Mathur and Chopra, 1987). In the Cuu Long Basin, it is restricted to the early Miocene; its absence from the Oligocene, is probably due to environments being entirely freshwater (Chung et al., 2021). In the Malong 5G-17.2 and Delah 5H-14.1 wells, it is oldest occurrences are in zone PR2 with the youngest consistent records in zone PR10.

Remarks:

The Malay Basin specimens are slightly larger than the Bornean specimens originally described by Germeraad et al. (1968) that range from 23 to 24 μm in length.

Botanical affinity:

Lythraceae/Sonneratiaceae.

Source ecology:

This species shows a different distribution to *Florschuetzia trilobata* ssl, in that it is absent from Oligocene successions that are clearly freshwater, as in the Cuu Long Basin but present in late Oligocene sections with brackish influence. It is therefore likely to be derive from a *Sonneratia* precursor that was restricted to brackish or tidally influenced coastal settings.

Suggested name for Quaternary records:

Not applicable.

Ecological group:

Backmangrove.

Florschuetzia levipoli

Germeraad et al. 1968. Plate 13, Figs. 17-19

Selected synonymy:

1968 *Florschuetzia levipoli* Germeraad Hopping and Muller, 1968, p. 307, Pl. 7, Fig. 9; Pl. 8, Fig. 2.

1987 *Florschuetzia levipoli* Germeraad Hopping and Muller, 1968, Mathur and Chopra, p. 126, Pl. 4, Fig. 86.

Description:

Pollen radially symmetrical, isopolar; prolate; in polar view circular to rounded triangular, sometimes bulging at equator. Triporate, pores circular, endexinous, in well preserved grains covered by thin ectexinous membrane, 2 to 8 µm in diameter (depending on size grain). Total wall thickness 1 to 2 µm, generally thicker on poles than on equatorial area; endexine 5 µm thick; columellae mostly indistinct, slightly enlarged (intra-areolate) on polar caps: tectum about 1 µm thick, psilate on poles, broken up into a verrucate-areolate pattern on equatorial belt. Verrucae rounded-polygonal, of varying sizes, uniform height, regularly distributed (Germeraad et al., 1968).

Dimensions:

Length 22 (29) 38 µm, width 17 (22) 27 µm (31 specimens measured from various horizons.

Stratigraphic distribution:

Near-base of the Miocene to Recent of Northwest Borneo and Natuna Sea (Germeraad et al., 1968; Muller, 1978; Morley, 1991, 2000; Morley et al., 2021); Pliocene of offshore Bengal, India (Mathur and Chopra, 1987). Present in moderate to high percentages from the base of zone PR9 (21.9 Myr) upward (Morley et al., 2021).

Remarks:

The Malay Basin specimens are generally smaller than the Bornean forms originally described by Germeraad et al. (1968). The latter averages from 30 to 50 µm in length and increases from older to younger strata.

Botanical affinity:

This pollen type compares closely with *Sonneratia caseolaris* (Sonneratiaceae) (Germeraad et al., 1968; Muller, 1969, 1978, 1981b).

Source ecology:

Sonneratia caseolaris is a backmangrove species and will occur in both brackish and freshwater settings when there is tidal influence (Morley and Morley, 2013). It is especially well represented in the *Nypa* belt of the Sedili River in Johor, Malay Peninsula (Corner, 1978), and the Mahakam Delta in Kalimantan.

Suggested name for Quaternary records:

Sonneratia caseolaris.

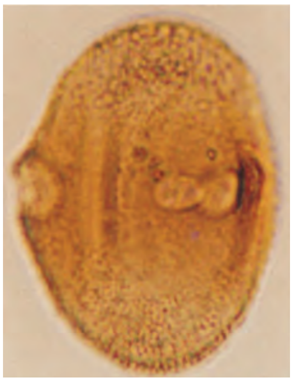
Ecological group:

Backmangrove.

Sonneratia caseolaris, *freshwater intertidal zone, Pahang River, Pahang, Malaysia (photo by RJM).*

Florschuetzia meridionalis

Germeraad, Hopping and Muller 1968. Plate 14, Figs. 1, 2



Selected synonymy:

1968 *Florschuetzia meridionalis* Germeraad et al., p. 308, Pl. 8, Figs. 4, 5.

1987 *Florschuetzia meridionalis* Germeraad et al.; Mathur and Chopra, p. 126, Pl. 4, Fig. 87.

Description:

Pollen radially symmetrical, isopolar; prolate; in polar view circular to rounded triangular; triporate; pores circular; endexinous, in well preserved grains covered by thin ectexinous membrane, 5 to 12 μm, in diameter. Total wall thickness approximately 3 μm, generally thinner on porate fields; endexine less than 1 μm thick; columellae distinct on meridional ridge where they are thin, uniform and rather dense, on polar caps probably fused to form a typical intra-areolate pattern, not visible on porate fields. Tectum 1 to 1½ μm thick, psilate on polar caps, broken up into an areolate-fossulate pattern on meridional ridges and into a verrucate pattern on porate fields. The meridional ridges are quite sharply outlined against the porate fields, but merge gradually with the tectate-psilate polar caps (Germeraad et al., 1968).

Dimensions:

Length 24 (31) 38 μm, width 12 (21) 25 μm (22 specimens measured from various horizons).

Stratigraphic distribution:

Middle Miocene to Recent (Germeraad et al., 1968; Muller, 1978; Morley, 1991); Pleistocene to Holocene of offshore Bengal, India (Mathur and Chopra, 1987). In Malong 5G-17.2 well, very rare in zone PR9B, but regularly present from zone PR10 to PR15. The oldest scattered records are thus at about 21 Myr, and the increase in abundance within zone PR10 occurs at 18.4 Myr.

Remarks:

The Malay Basin specimens are generally smaller than the Bornean forms originally described by Germeraad et al. (1968). The latter averages from 35 to 60 μm in length and increases from older to younger strata.

Botanical affinity:

Sonneratia alba of the family Sonneratiaceae (Germeraad et al., 1968; Muller, 1969, 1978, 1981b).

Source ecology:

Sonneratia alba characterises the seaward margin of mangroves swamps, together with or seaward of *Rhizophora* spp. subject to frequent tidal inundation and where salinities may be high.

Suggested name for Quaternary records:

Sonneratia alba.

Ecological group:

Mangrove.

Plate 14

Figs. 1, 2 *Florschuetzia meridionalis* Germeraad et al. 1968.
Figs. 1, 2 (x 1000): Slide Malong-2, 1045-1050 m, DC (S1); England Finder P37.

Figs. 3-4 *Verrutriporites vermiculatus* Rao and Ramanujam 1982.
Fig. 3 (x 1000): Slide Malong-2, 456 m, SWC (S2); England Finder O29/4. Fig. 4 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder U15.

Figs. 5, 6 *Tricollareporites echinatus* Venkatachala and Rawat 1973.
Figs. 5, 6 (x 1000): Slide Malong-2, 1315-1320 m, DC (S1); England Finder E26/4.

Figs. 7-9 *Cricotriporites microreticulatus* Jaizan Jais and Morley sp. nov.
Figs. 7-9 (Holotype, x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder P9.

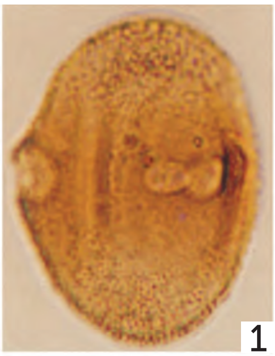
Figs. 10, 11 *Cricotriporites* spp.
Fig. 10 (x 1000): Slide Malong-2, 456 m, SWC (S2); England Finder U39. Fig. 11 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder F27.

Figs. 12, 13 *Canthiumidites reticulatus* Khan 1976a
Figs. 12, 13 (x 1000): Slide Malong-2, 760-770 m, DC (S1); England Finder V34/2.

Fig. 14 *Subtriporopollis* sp. cf. *S. rotundis* Sah 1967 (x 1000): Slide Malong-2, 577 m, SWC (S2); England Finder P20/3.

Fig. 15 *Subtriporopollis* sp. (x 1000): Slide Malong-2, 1603.7 m, CC (S1); England Finder V41/1.

Figs. 16-18 *Guettardidites ivirensis* Khan 1976a.
Fig. 16 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder L15/2. Figs. 17, 18 (x 1000): Slide Malong-2, 366 m, SWC (S1); England Finder Q38/3.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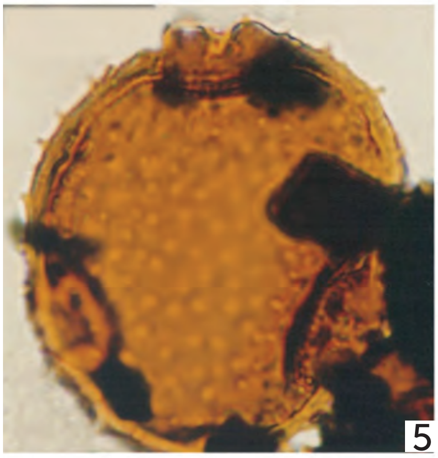
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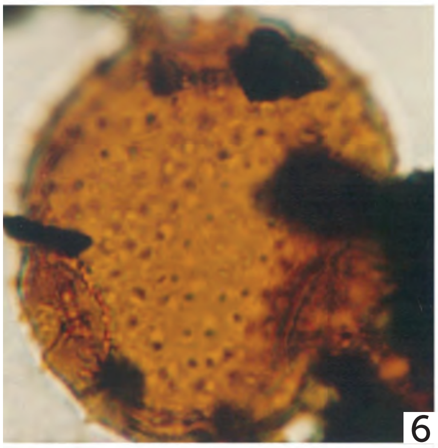
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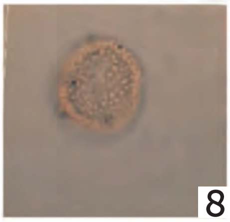
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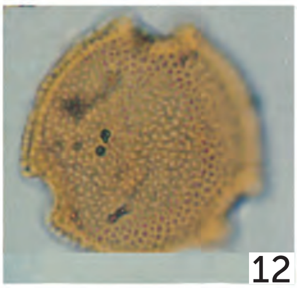
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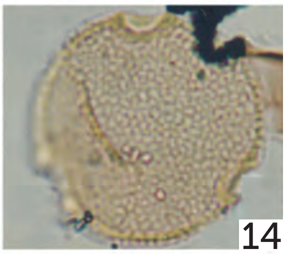
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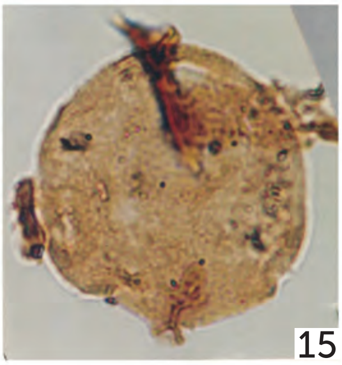
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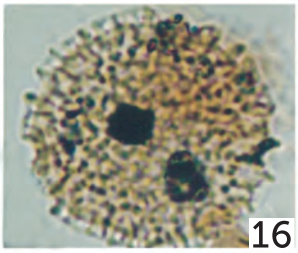
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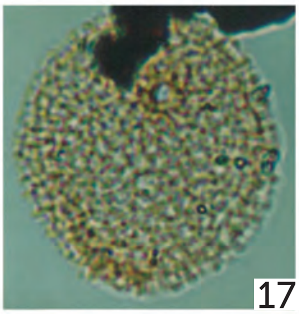
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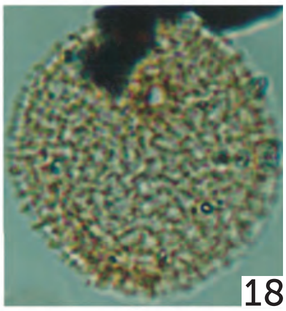
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Genus *Triporopollenites*

Pflug and Thomson in Thomson and Pflug 1953

Type species:

Triporopollenites coryloides Pflug in Thomson and Pflug 1953 (by original designation).

Triporopollenites stemonuroides

Jaizan Jais and Morley sp. nov. Plate 15, Figs. 9-11

Selected synonymy:

1975 Dispersed pollen attributed to *Stemonurus* in Anderson and Muller, p. 303, Pl. 2, Fig. 6.

Derivation of name:

Abbreviated from *Stemonurus* pollen, its modern affinity.

Holotype:

Plate 15, Figs. 10, 11. Slide Malong-2, 561 m, SWC (S1), England Finder P22. Grain in polar aspect, diameter 10 µm; exine 0.5 µm thick; pores 2 µm in diameter.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 561 m depth; age late Miocene, zone PR14.

Description:

Pollen grains small, simple, radially symmetrical, isopolar, amb subtriangular to rounded triangular with convex sides; triporate; pores circular, open, 2 to 3 µm in diameter, equatorial, pore rim appears slightly thickened; exine psilate to very faintly microreticulate, thin (±0.5 µm thick), slightly thickened around pores; sexine about as thick as nexine.

Dimensions:

Equatorial diameter 10 (11) 14 µm (12 specimens measured from various horizons).

Stratigraphic distribution:

Present in both Malong 5G-17.2 and Delah 5H-14.1 wells; scattered specimens are present within zones PR1 to PR6/7, but then regularly present in moderate numbers through zones PR8 to PR15. Otherwise reported from the middle Miocene of Brunei as *Stemonurus* pollen by Anderson and Muller (1975), from the late Miocene of Southeast Kalimantan by Demchuk and Moore (1993), and the Pleistocene of the Mahakam Delta by Caratini and Tissot (1985, 1988).

Comparison:

Triporopollenites minutus Rao and Ramanujam 1978 has a thicker wall and narrower pores.

Botanical affinity:

Stemonurus (Stemonuraceae, formerly Icacinaceae).

Source ecology:

Trees, most species occur in lowland and lower montane forests but *Stemonurus secundiflorus* is a peat swamp tree and can become a dominant element in the *Shorea albida-Gonystylus-Stemonurus* association (Phasic Community II) of Anderson (1964).

Suggested name for Quaternary records:

Stemonurus type.

Ecological group:

Peat swamp forests.

Stemonurus secundiflorus, *peat swamp forest, near Pekan, Pahang, Malaysia (photo by RJM).*

Genus *Celtispollenites*

Ke and Shi 1978

Type species:

Celtispollenites dongyingensis Ke and Shi 1978.

Celtispollenites minutipori

(Muller 1968) Jaizan Jais and Morley comb. nov. Plate 15, Figs. 5-7

Selected synonymy:

1968 *Triorites minutipori* Muller, p. 14, Pl. 3, Fig. 9.

Description:

Triporate, occasionally with four pores; spherical; equatorial contour round; pores circular, small, 1 to 2 µm in diameter; wall very thin, <1 µm thick, slightly thickened endexinally into annuli around pores, structureless or finely granulate; grains often folded.

Dimensions:

Equatorial diameter 13 (16) 17 µm (5 specimens measured from various horizons).

Stratigraphic distribution:

Muller (1968) first described this pollen type from the Late Cretaceous of western Sarawak, with the oldest records dated as Santonian by Morley (2000). This pollen has since been reported from the Late Cretaceous of Africa (e.g., Shrank, 1994), and South America (Doubinger and Chotin, 1975). The occurrence of this genus in the Late Cretaceous is possible since the crown group of Celtidaceae has a molecular age of 66 Myr and a stem age of 70 Myr. This species is sparsely distributed in the Malong 5G-17.2 and Delah 5H-14.1 wells, but shows an abundance peak within zone PR9B (Lower), where it occurs together with maxima of *Graminidites annulatus* and *Chenopodipollis chenopodiaceoides.*

Remarks:

This species is characterised by its small size, circular amb, circular and slightly annulate pores and very thin psilate or finely granulate wall. Muller (1968) commented that due to its annulate pores this species cannot be assigned to *Momipites* Wodehouse 1933 on the grounds of its pore shape. Consequently, pending further revision, he included this species within the genus *Triorites* Cookson 1950 ex Couper 1953 which was taken in the broad sense to include psilate triporate forms which do not belong to any other genera. The new combination is proposed here since the genus *Celtispollenites* Ke and Shi 1978 can now better accommodate this species.

***Bot*anical affinity:**

Muller (1968) was uncertain of the affinity of this species, but later suggested that affinity with *Celtis* (Celtidaceae) is most likely (Muller, 1981).

Source ecology:

Some species occur in perhumid forest, but *Celtis philippinensis* is a widespread tree of seasonal climates across Southeast Asia (Soepadmo, 1973) and bearing in mind that the maximum of *C. minutipori* coincides with a maximum of seasonal climate indicators, maxima of this species may be an indicator former seasonal climate.

Suggested name for Quaternary records:

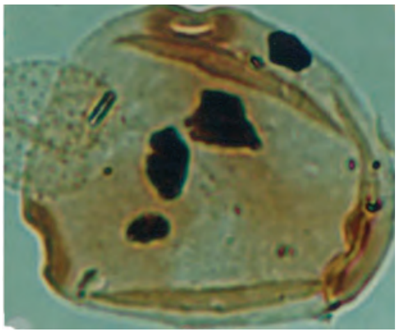
Celtis type.

Ecological group:

Seasonal and lowland forest.

Celtispollenites festatus

(Muller 1968) Jaizan Jais and Morley comb. nov. Plate 15, Fig. 8



Selected synonymy:

1961 *Triporopollenites festatus* Takahashi, p. 301, Pl. 19, Figs. 29-37.

1968 *Triorites festatus* (Takahashi 1961) Muller, p. 15, Pl. 3, Fig. 10.

Description:

Pollen triporate, spherical, equatorial contour circular or rounded triangular; pores circular, up to 3 μm in diameter; wall about 1 μm thick, slightly thickened endexinally around the pores, forming a 2 μm wide annulus; wall structure indistinct or more or less finely granulate (Muller, 1968).

Dimensions:

Equatorial diameter, minimum 27 μm, maximum 32 μm (2 specimens measured).

Stratigraphic distribution:

Originally described from the Santonian to Eocene of West Sarawak by (Muller, 1968). Also reported from the Campanian of Japan (Takahashi, 1964); Miocene of Korea and Japan (Takahashi and Kim, 1979; Takahashi, 1981); Paleocene to Eocene of West Africa (Salard Chebaldaeff, 1981) and Eocene of Chile (Takahashi, 1977). Rare and sparsely distributed in the Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species which is larger in size and has relatively larger and more pronounced annulus than *C. minutipori* (Muller) comb. nov. was also included within the broad genus of *Triorites* Cookson 1950 ex Couper 1953 by Muller 1968. It is now proposed that the species to be included within the more specific genus *Celtispollenites* Ke and Shi 1978.

Botanical affinity:

Unknown.

Suggested name for Quaternary records:

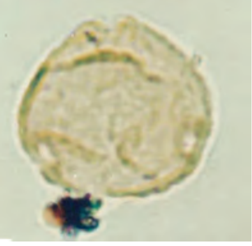
Not applicable.

Ecological group:

Undifferentiated.

Celtispollenites rotundatus

Morley and Jaizan Jais sp. nov. Plate 15, Figs. 12, 13



Derivation of name:

From the rounded shape of the grain.

Holotype:

Plate 15, Fig. 12. Slide Malong-2, 561 m, SWC (S1), England Finder P22.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 430.5 m depth; age Pliocene, zone PR15.

Description:

Pollen grains radially symmetrical, isopolar, spherical, amb circular to subcircular; triporate; pores circular, up to 4 μm in diameter, equatorial, clearly annulate; annuli ±2 μm wide; exine 1 to 1.5 μm thick, thickened around pores, exine finely granulate.

Dimensions:

Equatorial diameter 16 (18) 21 μm (7 specimens measured from various horizons).

Stratigraphic distribution:

Present in low percentages in Malong 5G-17.2 well from zone PR14 to PR15.

Comparison:

This species differs from *Celtispollenites minutipori* (Muller) comb. nov. mainly by its thicker wall and more pronounced annuli and from *C. festatus* (Muller) comb. nov. by its smaller size.

Botanical affinity:

Probably *Celtis* (Ulmaceae).

Source ecology:

Lowland evergreen and seasonal forests.

Suggested name for Quaternary records:

?*Celtis*.

Ecological group:

Seasonal and lowland forest.

Genus *Casuarinidites* Cookson and Pike 1954

Naming fossil pollen comparable to *Casuarina* presents a major problem due to issues of nomenclature and priority. In 1953 Couper proposed the genus *Haloragacidites* for triporate pollen that showed similarities to *Haloragis* using *H. trioratus* as type species, but also suggested a possible affinity to *Casuarina*. Couper (1953) also introduced *Triorites harrisii*, which clearly showed affinity to *Casuarina*, and later (Couper, 1960) synonymised these species which clearly reflect two separate pollen types. Mildenhall and Harris (1971) made a thorough evaluation of Couper's original slides and showed that *Haloragacidites harrisii* is the correct combination for Couper's *'Casuarina*-like' pollen.

On the other hand Cookson and Pike (1954) independently proposed the name *Casuarinidites cainozoicus* for pollen resembling *Casuarina*, but as pointed out by Mildenhall and Harris (1971) this becomes a junior synonym of *H. harrisii* based on Couper's rather broad diagnosis of *Haloragacidites*. The issue can be resolved by emending the definitions of *Haloragacidites* and *Casuarinidites* based on the clear differences in aperture configurations seen in the extant genera *Haloragis*, in which the endexine remains equithickness, or thickens, in the apertural area (Praglowski, 1970), and *Casuarina*, in which the endexine thins toward the apertures (Kershaw, 1970; Coetzee and Praglowski, 1974). This avoids attributing *Casuarina*-like pollen to a misleading and poorly configured form genus.

Genus *Haloragacidites*
(Couper 1953) emend. Morley and Jaizan Jais

Type species:
Haloragacidites trioratus Couper 1953 (by original designation).

Emended diagnosis:
Based on specimen on slide L4928/2, single grain mount SM478 as illustrated by Mildenhall and Harris (1971, Fig. 5), showing exine structure. Pollen isopolar. three or more pores, clearly aspidate, pouting, circular up to 5 µm in diameter, projecting up to 6 µm; grain small, subspherical to subtriangular in polar view; exine 1.5 to 2 µm thick, faintly scabrate to psilate, endexine continuous or showing thickening below the apertures.

Selected synonymy:
1953 *Triorites trioratus* Couper, p. 41, Pl. 5, Fig. 50.
1960 *Triorites trioratus* Couper, p. 67.
1971 *Haloragacidites trioratus* (Couper) Harris in Mildenhall and Harris, p. 304, Figs. emend. 1-5.

Genus *Casuarinidites*
(Cookson and Pike 1954) emend. Morley and Jaizan Jais

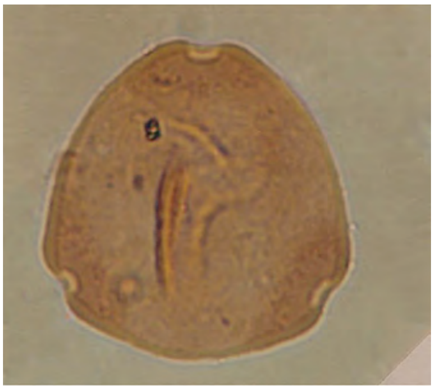
Type species:
Casuarinidites cainozoicus Cookson and Pike 1954.

Emended diagnosis:
Pollen triporate, suboblate to lenticular shape, amb more or less triangular, sides convex; pores equatorial, more or less circular to lolongate, situated on exinal protrusions; exine somewhat thickened around pores, outline smooth, exine in part with infratexture, sexine thicker than nexine, nexine absent in area of vestibula.

Selected synonymy:
1954 *Casuarinidites cainozoicus* Cookson and Pike, p. 200, Pl. 1, Figs. 1-3.
1984 Fossil pollen pertaining to a *Casuarina* sp. in Coetzee and Muller, Fig. 6A-I.
1994 *Haloragacidites harrisii* Couper 1953 in MacPhail et al., Fig. 10.10e.
2006 *Haloragacidites harrisii* (Couper) Harris in Zamaloa et al., Fig. 5C-D.

Casuarinidites cainozoicus

Cookson and Pike 1954. Plate 15, Fig. 14



Description:

Pollen grains radially symmetrical, isopolar, amb subtriangular with convex sides and slightly bulging pore rims; triporate; pores angulaperturate, equatorial, circular, 2 to 3 µm in diameter, aspidate; pore canal 2.5 µm, pore margin up to 3 µm wide; exine 1 to 1.5 µm thick in the interradial region, thickening around pore up to 2.5 µm thick, psilate to scabrate, tectate; sexine approximately as thick as nexine.

Dimensions:

Equatorial diameter 21 (25) 35 µm (7 specimens measured from various horizons).

Stratigraphic distribution:

This pollen type is widely reported from the Paleocene onwards in Australia and New Zealand (see Martin, 1994)., originally being described from New Zealand by Couper (1953) and Australia by Cookson and Pike (1954). There are also records from the Ninetyeast Ridge (Kemp and Harris, 1977) and numerous records from Argentina and Chile (e.g., Archangelsky, 1973; Doubinger and Chotin, 1975). It occurs in the late Eocene of Myanmar (Huang et al., 2021) but there are very few convincing records from India (e.g., Rao and Ramanujam, 1982). Across the broad Southeast Asian area, the oldest records are from the early Eocene or Paleocene of Irian (Morley, 2000, Fig. 9.6) relating to the time when Irian was part of the Australian Plate. Subsequently, this pollen type is recorded from the late Eocene onward from the Java Sea (Lelono and Morley, 2011), and from the Oligocene onward is well represented across the region. The pollen type is common throughout the Malong 5G-17.2 and Delah 5H-14.1 wells and is particularly well represented in the Oligocene and early Miocene sections. It is common through zones PR1 to PR9B (Lower) and then occurs in consistently low numbers through zones PR9B (Upper) to PR15.

Remarks and comparison:

The pores of this species are relatively less protruding and aspidate as compared to specimens illustrated by Cookson and Pike (1954). Several form-species which had been previously described from North America and Europe and referred by Srivastava (1972) to *Casuarinidites* were excluded by Muller (1981).

Botanical affinity:

Casuarina and *Gymnostoma* (Casuarinaceae).

Gymnostoma nobilis *(Rhu), kerangas, Bako National Park, Sarawak Malaysia (photo by RJM).*

Source ecology:

There are three species of Casuarinaceae in Southeast Asia that are sources of this pollen. *Casuarina equisetifolia* occurs commonly along coastlines on beach ridges and was probably the source of this pollen when found in sand-rich successions. *Gymnostoma nobilis* is a tree of peat swamps and Kerangas (Brunig, 1974, 1990), and pollen found in coals and muddy lithologies are probably from this genus (e.g., Morley, 2000), whereas in seasonally dry areas of Java and Nusa Tenggara, *Casuarina* type pollen is most likely derived from *C. junghuhniana*, a montane forest tree, when the pollen is associated with other montane elements such as *Podocarpus* (Morley et al., 2020).

Suggested name for Quaternary records:

Casuarina type.

Ecological group:

For Malaysia, peat swamp, kerangas and coastal.

Plate 15

Figs. 1, 2 *Periretitricolpites* sp.
Figs. 1, 2 (x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder U15/1.

Figs. 3, 4 *Retisephanocolpites williamsi* Germeraad et al. 1968.
Figs. 3, 4 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder S25/1.

Figs. 5, 6, 7 *Celtispollenites minutipori* (Muller 1968) comb. nov. Jaizan Jais and Morley.
Fig. 5 (x 1000): Slide Malong-2, 1384 m, SWC (S2); England Finder H34. Fig. 6 (x 1000): Slide Malong-2, 1384 m, SWC (S2); England Finder H32/4. Fig. 7 (x 1000): Slide Malong-2, 1384 m, SWC (S2); England Finder H30/4.

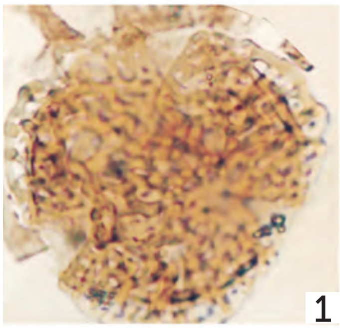
Fig. 8 *Celtispollenites festatus* (Muller 1968) Jaizan Jais and Morley comb. nov. (x 1000): Slide Malong-2, 366 m, SWC (S1); England Finder Q28/3.

Figs. 9, 10, 11 *Triporopollenites stemonuroides* Jaizan Jais and Morley sp. nov.
Fig. 9 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder Q20. Figs. 10, 11 (Holotype, x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder P22.

Figs. 12, 13 *Celtispollenites rotundatus* Jaizan Jais and Morley sp. nov.
Fig. 12 (x 1000 holotype): Slide Malong-2, 430.5 m, SWC (S2); England Finder N18. Fig. 13 (x 1000): Slide Malong-2, 592 m, SWC (S1); England Finder N12.

Fig. 14 *Casuarinidites cainozoicus* Cookson and Pike 1953 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder Q24.

Figs. 15 - 17 *Manggispollenites psilatriporata* Jaizan Jais and Morley sp. nov.
Figs. 15, 16 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder O10/2. Fig. 17 (x 1000): Slide Malong-2, 1366 m, SWC (S2); England Finder V37/1.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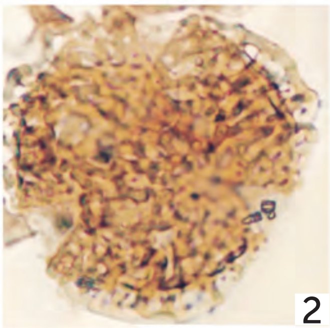
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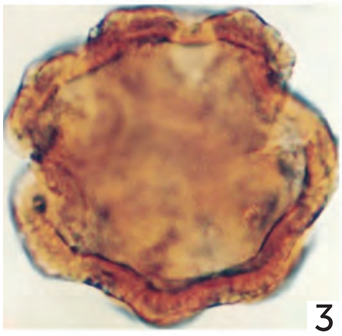
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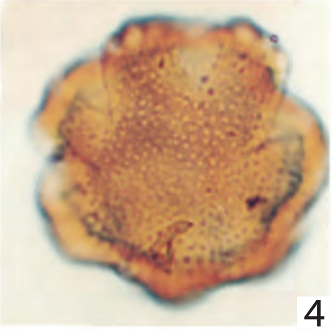
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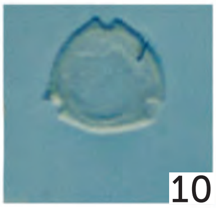
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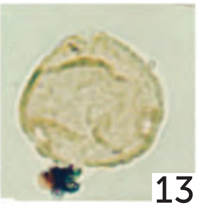
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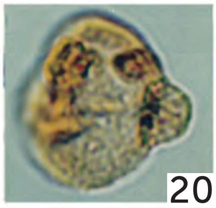
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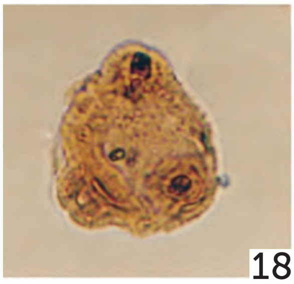
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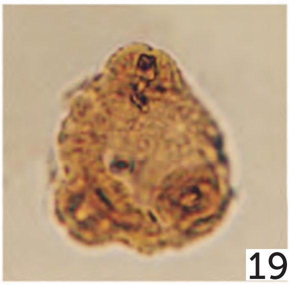
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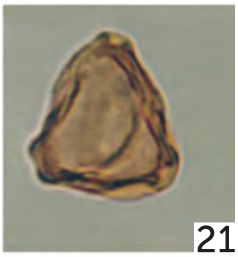

21

Figs. 18-20 *Manggispollenites retitriporata* Jaizan Jais and Morley sp. nov.
Figs. 18, 19 (Holotype, x 1000): Slide Malong-2, 714 m, SWC (S2); England Finder X19/2. Fig. 20 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder V29.

Fig. 21 *Trivestibulopollenites betuloides* Pflug in Thomson and Pflug 1953 (x 1000): Slide Malong-2, 1155-1160 m, DC (S1); England Finder M33.

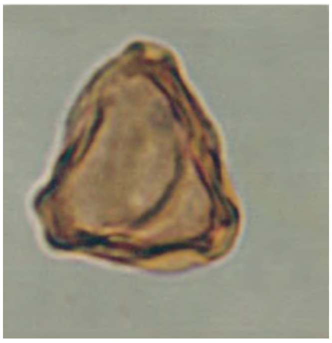
Genus *Trivestibulopollenites*

Pflug in Thomson and Pflug 1953

Type species:
Trivestibulopollenites betuloides Pflug in Thomson and Pflug 1953.

Trivestibulopollenites betuloides

Pflug in Thomson and Pflug 1953. Plate 15, Fig. 21



Selected synonymy:
1953 *Trivestibulopollenites betuloides* Pflug in Thomson and Pflug, p. 85, Pl. 9, Figs. 25-34.

Description:
Pollen grains radially symmetrical, isopolar, amb subtriangular with convex sides; triporate; pores angulaperturate, with distinct vestibulum; exine 1 μm thick in the interradial region, thickening round pores; exine psilate, sexine approximately as thick as nexine.

Dimensions:
Equatorial diameter 12 (16) 20 μm (4 specimens measured from various horizons).

Remarks:
Trivestibulopollenites Pflug and *Myricipites* Wodehouse are very similar, and the names suggest a source from *Betula* and *Myrica*.

Stratigraphic distribution:
Widely reported from the Paleocene onward in temperate areas across the northern hemisphere. Rare and sparsely distributed in Malong 5G-17.2.

Botanical affinity:
In Southeast Asia, *Betula* is a montane tree occurring in seasonally cool montane forests in parts of Indochina, whereas *Myrica* occurs either on volcanoes *(Myrica javanica)* or along sandy coastlines and in kerangas, as *M. esculenta. M. esculenta* is the most likely source for this pollen. However, in Oligocene freshwater and lacustrine successions, *Betula* may be the main source.

Suggested name for Quaternary records:
Betula or *Myrica*.

Source ecology:
Probably mainly from the coastal *Myrica esculenta*.

Ecological group:
Coastal.

Genus *Manggispollenites*

Jaizan Jais and Morley gen. nov.

Type species:
Manggispollenites psilatriporata Jaizan Jais and Morley sp. nov.

Derivation of name:
After manggis, the Malay word for mangosteen, the fruit of *Garcinia mangostana*, a tree from the genus that is thought to have produced this pollen.

Diagnosis:
Pollen grains small to medium, oblate spherical to slightly prolate in equatorial view, amb subtriangular with concave sides and protruding apertures; triporate to stephanoporate; pores markedly protruding, vestibulate, aspidate, circular to oval. Wall tectate, clearly differentiated, thickened around pores, psilate, scabrate or microreticulate; sexine thicker than nexine; columellae indistinct to distinct.

Remarks and comparison:
This genus is morphologically similar to some types of pollen in the genus *Garcinia* (Clusiaceae). It differs from *Trivestibulopollenites* Pflug and *Casuarinidites* Cookson and Pike in its shape, the number of pores, exine sculpture and relative thickness of nexine and sexine. *Rugulitriporites* Muller 1968 is rugulate and restricted to triporate pollen. *Pelahpollis* gen. nov. is different in the sculpture of its exine and pore structure. The pores of *Myriophyllumpollenites* are relatively less aspidate.

The genus *Garcinia* produces a remarkable diversity of pollen types (Seetharam, 1989) including tricolpate, triporate, stephanoporate, tricolporate and stephanocolporate morphologies with great variation in exine sculpture. The forms included in *Manggispollenites* fall within the triporate group, with protruding pores, and variable exine ornamentation, as seen in the *G. afzelii* type of Seetham (1989), also seen in *G. rostrata* and *G. cuspidata* and *G. eugeniifolia* (Morley, 1976).

Manggispollenites psilatriporata Jaizan Jais and Morley sp. nov. Plate 15, Figs. 15-17

Derivation of name:
From its psilate exine and triporate apertural configuration.

Holotype:
Plate 15, Figs. 15, 16. Slide Malong-2, 625 m, SWC (S3), England Finder O10/2. Grain in equatorial aspect, length 17 µm, width 16 µm; exine 1 µm thick; pores 2 to 3 µm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains small to medium, radially symmetrical, isopolar, oblate spherical to slightly prolate in equatorial view, amb subtriangular with concave sides; triporate; pores markedly protruding, vestibulate, aspidate, circular to oval, 2 to 4 µm in length and diameter; annuli 2 to 4 µm wide; wall psilate to scabrate, 1 to 2 µm thick, thicker around pores, tectate; sexine thicker than nexine; columellae indistinct.

Dimensions:
Longest axis 15 (18) 21 µm (10 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in the Malong 5G-17.2 well, more consistently represented in zones PR14 to PR15.

Comparison:
This form differs from *Trivestibulopollenites betuloides* by its thicker sexine than nexine; from *Manggispollenites retitriporata* sp. nov. by its psilate exine.

Botanical affinity:
This pollen type is seen in *Garcinia rostrata, G. cuspidate, G. eugeniifolia* (Clusiaceae) and falls within the triporate group of Seetharam (1989).

Source ecology:
Garcinia spp. are rain forests trees and in Malaysia are very diverse, occurring in a wide range of habitats. Many species occur in lowland rain forests, but they are also very well represented in lower montane forests. There are several species that occur in riverine settings and along coasts, and it is these that are most likely to be the source of fossil pollen. Species characteristic of stream sides are *G. bancana*, and *G. cataractalis*, whereas *G. celebica* occurs along coasts (Whitmore, 1973). The triporate species with psilate exine include *G. caudata, G. eugeniifolia, G. cuspidata* and *G. rostrata*. The latter species is a peat swamp tree and probably the source of most of this pollen.

Suggested name for Quaternary records:
Garcinia rostrata type.

Ecological group:
Mostly peat swamp forests.

Manggispollenites retitriporata

Jaizan Jais and Morley sp. nov. Plate 15, Figs. 18-20

Derivation of name:

From its microreticulate wall and triporate aperture.

Holotype:

Plate 15, Figs. 18, 19. Slide Malong-2, 714 m, SWC (S2), England Finder X19/2. Grain in polar aspect; equatorial diameter 20 μm; exine 1 μm thick; pores 3 μm long.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 714 m depth; age late Miocene, zone PR13.

Description:

Pollen grains small to medium, radially symmetrical, isopolar, oblate spherical to slightly prolate in equatorial view, amb subtriangular with concave sides; triporate; pores markedly protruding, vestibulate, aspidate, circular to oval, 2 to 4 μm in length and diameter; annuli 2 to 4 μm wide; wall microreticulate, 1 to 2 μm thick, thicker around pores, tectate; sexine thicker than nexine; columellae ± dense, ±1 μm long.

Dimensions:

Longest axis 14 (17) 20 μm (5 specimens measured from various horizons).

Stratigraphic distribution:

Rare and sparsely distributed in Malong 5G-17.2 well, mainly in zones PR12 to PR15, with only one specimen found in the Delah 5H-14.1 section at 2485 m (DC) depth.

Comparison:

This form differs from *Rugulitriporites vestibulipori* Muller 1968 in its shape and exine sculpture; from *M. psilatriporata* sp. nov. by having microreticulate wall.

Botanical affinity:

This pollen type is found in *Garcinia celebica* type (Clusiaceae).

Garcinia celebica *(Beruas), seashore mangosteen, Bogor, Java (photo by RJM).*

Source ecology:

Garcinia celebica is a tree of coastal vegetation throughout Malaysia (Whitmore, 1973).

Suggested name for Quaternary records:

Garcinia celebica type.

Ecological group:

Coastal forests.

Genus *Verrutriporites*
Muller 1968

Type species:
Verrutriporites lunduensis Muller 1968 (by original designation).

Verrutriporites vermiculatus

Rao and Ramanujam 1982. Plate 14, Figs. 3, 4

Selected synonymy:
1982 *Verrutriporites vermiculatus* Rao and Ramanujam, p. 84, Pl. 4, Figs. 69, 70.

Description:
Pollen grains radially symmetrical, isopolar, amb subtriangular to circular; triporate; pores circular, 2 to 3 μm in diameter; pore margins thickened and bearing verrucae; exine 1 to 2 μm thick, verrucate; verrucae low, closely spaced, subrounded to vermiculate and may coalesce locally.

Dimensions:
Equatorial diameter 16 (20) 28 μm (7 specimens measured from various horizons).

Stratigraphic distribution:
Early to middle Miocene of South India (Rao and Ramanujam, 1982). Sparsely distributed in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Comparison:
V. lunduensis Muller 1968 differs in having non-thickened pores and rounded verrucae.

Botanical affinity:
According to Zavada (1983) triporate verrucate pollen is characteristic of the genus *Gironniera* (Celtidaceae).

Source ecology:
In Malaysian *Gironniera* spp. occur mainly in perhumid lowland rain forests.

Suggested name for Quaternary records:
Gironniera type.

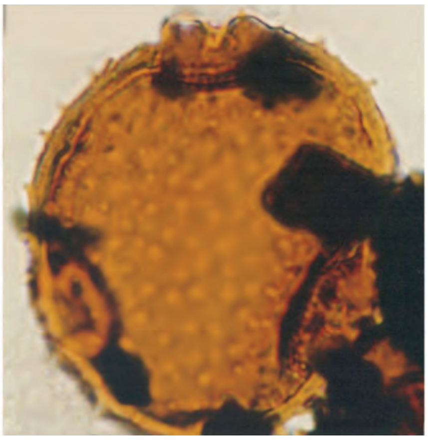
Ecological group:
Rainforest.

Genus *Tricollareporites*
Venkatachala and Rawat 1973

Type species:
Tricollareporites echinatus Venkatachala and Rawat 1973 (by original designation).

Tricollareporites echinatus

Venkatachala and Rawat 1973. Plate 14, Figs. 5, 6



Selected synonymy:
1973 *Tricollareporites echinatus* Venkatachala. and Rawat., p. 254, Pl. 5, Figs. 29, 30; Pl. 6, Fig. 5.

Description:
Pollen spheroidal, amb circular in polar view; triporate; pores surrounded by a thick annulus (collar); exine thick, sexine surface psilate with superimposed baculi and echinae (Venkatachala and Rawat, 1973).

Dimensions:
Equatorial diameter 42 μm (1 specimen measured).

Stratigraphic distribution:
Oligocene to Miocene of India (Venkatachala and Rawat, 1973). Only one specimen found at 1320 m (DC) depth in Malong 5G-17.2 well.

Remarks:
This specimen is characterised by having thick collared pores, echinate sculpture and thick wall and resembles *T. echinatus* Venkatachala and Rawat (1973) described from India.

Botanical affinity:
Pterospermum (Sterculiaceae).

Source ecology:
Widespread in seasonal tropical forests across Southeast Asia, but with some species occurring in perhumid forests.

Suggested name for Quaternary records:
Pterospermum type pollen.

Ecological group:
Seasonal forest.

Genus *Cricotriporites*

Leidelmeyer 1966 emend. Jaizan Jais and Morley

Type species:
Cricotriporites guianensis Leidelmeyer 1966 (by original designation).

Emended diagnosis:
Pollen grains, isopolar, with circular amb, triporate; pores distinct, circular to oval, annulate and/or costate, subequatorial; wall psilate to microreticulate.

Generic remarks:
The diagnosis is emended to include within this genus forms which agree with the original diagnosis (Liedelmeyer, 1966) but with microreticulate wall. *Canthiumidites* Khan emend. Mildenhall and Pocknall 1989 is triporate to pentaporate and more coarsely reticulate.

Cricotriporites microreticulatus

Jaizan Jais and Morley sp. nov. Plate 14, Figs. 7-9

Derivation of name:
From its microreticulate sculpture.

Holotype:
Plate 14, Figs. 7-9. Slide Malong-2, 456 m, SWC (S1), England Finder P9. Grain in polar aspect; equatorial diameter 11 µm; exine <1 µm thick; pores 2 µm in diameter; annuli 1 µm wide.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 456 m depth; age Pliocene, zone PR15.

Description:
Pollen grains small, radially symmetrical, isopolar, amb circular; triporate; pores circular, ±2 µm in diameter, annulate; annuli psilate, ±1 µm wide; wall microreticulate, ±1 µm thick, pilate; pila up to 1 µm long.

Dimensions:
Equatorial diameter 10 (11) 12 µm (6 specimens measured from various horizons).

Stratigraphic distribution:
Regularly present in zones PR13 to PR15 in Malong 5G-17.2, but with scattered occurrences in the underlying section, and with a single record in zone PR4 in the Delah 5H-14.1 well.

Comparison:
Triporopollenites bellus Partridge in Stover and Partridge 1973 is larger and reticulate in sculpture.

Botanical affinity:
Cricotriporites spp. have variously been attributed to Apocynaceae, Euphorbiaceae and Rubiaceae. Some Rubiaceae, especially *Randia*, shows similarities with *C. microreticulatus*.

Source ecology:
Trees or shrubs common in the lowlands.

Suggested name for Quaternary records:
?*Randia* type pollen.

Ecological group:
Rainforest.

***Cricotriporites* spp.** Plate 14, Figs. 10, 11

Remarks:
Included here are small annulate triporate Rubiaceous pollen with psilate to scabrate sculpture.

Dimensions:
Equatorial diameter 11 (15) 18 µm (5 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in both sections.

Botanical affinity:
?Rubiaceae.

Source ecology:
Lowland.

Ecological group:
Rainforest.

Genus *Guettardidites*

Khan 1976 emend. Jaizan Jais and Morley

Type species:

Guettardidites ivirensis Khan 1976a (by original designation).

Emended diagnosis:

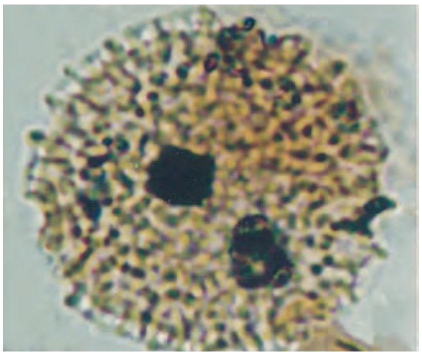
Pollen grains, isopolar, amb spherical, triporate; pores indistinct, circular, simple; exine intectate, reticulate; reticulum coarse, dense, simplicolumellate.

Comparison:

This genus differs from *Canthiumidites* Khan emend. Mildenhall and Pocknall 1989 by its spherical shape, simple pores and in having a distinct simplicollumellate exine.

Guettardidites ivirensis

Khan 1976a. Plate 14, Figs. 16-18



Selected synonymy:

1976a *Guettardidites ivirensis* Khan, p. 763, Fig. 24.

Description:

Pollen grains radially symmetrical, isopolar, amb spherical; triporate; pores indistinct, simple, circular, ±3 to 5 µm in diameter; exine intectate, 1.5 to 3 µm thick including columellae, reticulate; lumina 2 to 5 µm in diameter, angular, polygonal; muri simplicolumellate, supported by few, but distinct columellae in single rows; columellae 1 to 3 µm long, ±0.5 µm wide.

Dimensions:

Equatorial diameter 19 (25) 34 µm (21 specimens measured from various horizons).

Stratigraphic distribution:

Pliocene of Papua New Guinea (Khan, 1976a). Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells; very rare in the Oligocene, scattered within zones PR8 to PR14, regularly present in zone PR15.

Remarks:

Included in this species are also specimens of smaller size and finer reticulum than the Papuan materials originally described by Khan (1976a) that range from 25 to 47 µm in diameter. In his description of the *G. ivirensis* type species, Khan (1976a) does not mention this species being simplicollumellate, the obvious feature observed here. However, through the examination of his photograph, the type specimen does show some simplicolumellate features.

Botanical affinity:

This pollen compares to *Timonius* (Rubiaceae).

Source ecology:

Lowlands.

Suggested name for Quaternary records:

Timonius type pollen.

Ecological group:

Rainforest.

Genus *Canthiumidites*

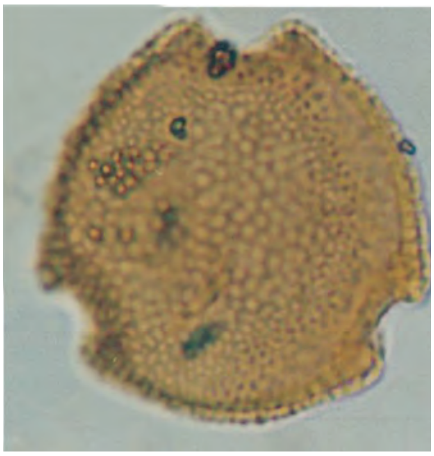
Khan 1976 emend. Mildenhall and Pocknall 1989

Type species:

Canthiumidites reticulatus Khan 1976a (by original designation).

Canthiumidites reticulatus

Khan 1976a. Plate 14, Figs. 12, 13



Selected synonymy:

1976a *Canthiumidites reticulatus* Khan, p. 766, Fig. 29.

Description:

Pollen grains spheroidal to triangular in polar view; triporate; pores distinct, rounded, about 3 µm in diameter; exine about 2 µm, sexine as thick as nexine, uniformly reticulate.

Dimensions:

Equatorial diameter 22 (25) 28 µm (16 specimens measured from various horizons).

Stratigraphic distribution:

Pliocene of Papua New Guinea (Khan, 1976a). Regularly present in low percentages in the upper part of Malong 5G-17.2 well; one specimen found in the top part of Delah 5H-14.1 section.

Remarks:

Mildenhall and Pocknall (1989) found that the holotype of *C. reticulatus* is triporate not tricolporate as originally described by Khan (1976a). The Malay Basin specimens are also triporate and generally smaller than the New Guinea forms that range from 32 to 36 µm in equatorial diameter.

Botanical affinity:

This pollen shows close similarity to *Canthium* (Rubiaceae), especially C. *dicoccum* (Morley, 1976).

Source ecology:

Canthium is a common genus of stream sides and occurs widely throughout the region.

Suggested name for Quaternary records:

Canthium pollen.

Ecological group:

Riparian forests.

Genus *Subtriporopollis*

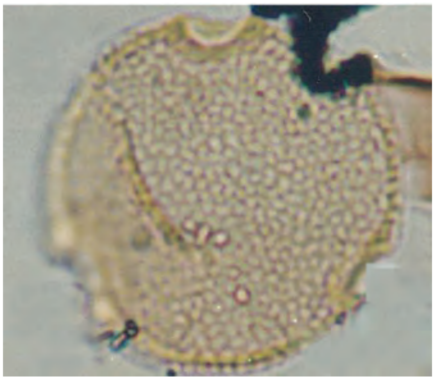
Sah 1967

Type species:

Subtriporopollis tenuis Sah 1967 (by original designation).

Subtriporopollis spp cf. S. *rotundis*

Sah 1967. Plate 14, Fig. 14



Selected synonymy:

cf. 1967 *Subtriporopollis rotundis* Sah, p. 120, Pl. 10, Figs. 17-19.

Description:

Pollen grains circular in polar view, triporate; pores distinct, rounded, about 3 µm in diameter with psilate annulus; exine about 2 µm, sexine thicker than nexine, sexine uniformly reticulate.

Dimensions:

Equatorial diameter 24 (25) 26 µm (3 specimens measured from various horizons).

Stratigraphic distribution:

S. rotundis has been recorded from the Neogene sediments of Burundi (Sah, 1967). Rare and sparsely distributed; only one specimen found in the Delah 5H-14.1, and the others concentrated in the upper part of the Malong 5G-17.2 well.

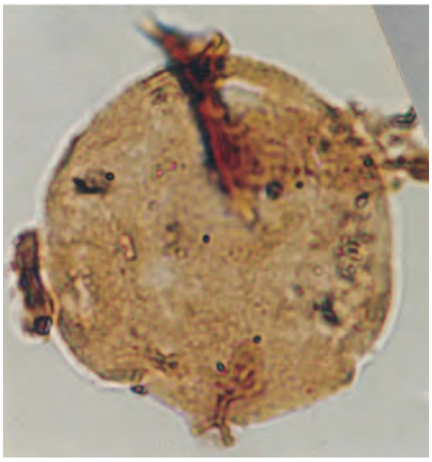
Remarks and comparison:

These specimens are comparable to the original description of *S. rotundis* Sah from Burundi with the exception that the Malay Basin materials are much smaller in size.

Botanical affinity:

Unknown.

***Subtriporopollis* sp.** Plate 14, Fig. 15



Description:

Pollen grains circular in polar view, triporate, pores approximately circular, distinct, about 3 µm in diameter with structured annulus, exine about 3 µm, sexine thicker than nexine, sexine structure indistinct.

Remarks and comparison:

These specimens differ from *Subtriporopollis cf rotundis* Sah by the thicker and indistinctly structured sexine. They occur very rarely in the sections.

Botanical affinity:

Unknown.

Ecological group:

Undifferentiated.

Genus *Pelahpollis*

Jaizan Jais and Morley gen. nov.

Type species:

Pelahpollis variabilis sp. nov.

Derivation of name:

From Batu Pelah, the Sarawak name for *Cephalomappa paludicola*.

Diagnosis:

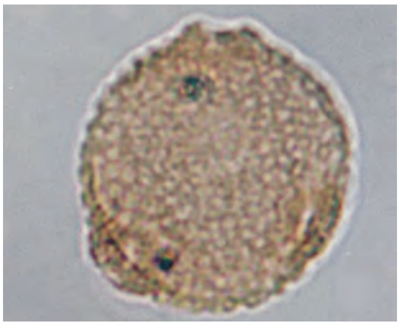
Pollen grains, isopolar, oblate to oblate spheroidal, sides convex, triporate to tetraporate; pores circular, annulate, slightly protruding, aspidate. Exine intectate, reticulate, homobrochate to heterobrochate.

Remarks and comparison:

This genus is morphologically similar to modern pollen of *Cephalomappa* (Euphorbiaceae). It differs from *Manggispollenites* gen. nov., *Cricotriporites* Leidelmeyer 1966 emend. and *Canthiumidites* Khan 1976a emend. Mildenhall and Pocknall 1989 in the exine sculpture and pore structure.

Pelahpollis variabilis

Jaizan Jais and Morley sp. nov. Plate 16, Figs. 1-9



Selected synonymy:

1975 Dispersed pollen attributed to *Cephalomappa* in Anderson and Muller, p. 302, Pl. 2, Fig. 1.

Derivation of name:

From its variable number of pores.

Holotype:

Plate 16, Figs. 1, 2, 3. Slide Malong-2, 561 m (S1) SWC, England Finder P14. Grain in polar aspect; equatorial diameter 22 µm; exine <1 µm thick; pores 3 µm in diameter.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 561 m depth; age late Miocene, zone PR14.

Description:

Pollen grains radially symmetrical, isopolar, oblate to oblate spheroidal; triporate to tetraporate; pores slightly protruding, aspidate, circular, 3 to 5 µm in diameter; exine ±1 µm thick, intectate, reticulate, homobrochate; reticulum 1 to 2 µm wide, muri broad.

Dimensions:

Equatorial diameter 20 (24) 31 µm (19 specimens measured from various horizons).

Stratigraphic distribution:

Cephalomappa pollen has been recorded as a dominant element by Anderson and Muller (1975) from the middle Miocene coal of Brunei. In the Malong 5G-17.2 well, this species occurs commonly through zones PR9A to PR15, but in low numbers in zones PR6/7 to PR8. Very sparsely distributed in the Delah 5H-14.1 section.

Botanical affinity:

Derived from *Cephalomappa* (Euphorbiaceae).

Source ecology:

Cephalomappa paludicola is a common peat swamp tree in phasic communities Ph. 2 and Ph. 3 in central Sarawak (Anderson, 1963) and is probably the main source of this pollen.

Suggested name for Quaternary records:

Cephalomappa pollen.

Ecological group:

Peat swamp forests.

Plate 16

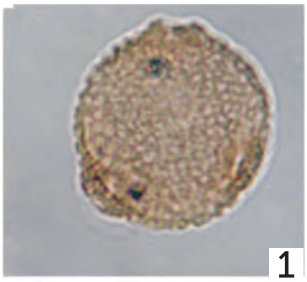
Figs. 1-9 *Pelahpollis variabilis* Jaizan Jais and Morley sp. nov.
Figs. 1, 2, 3 (Holotype, x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder P14. Figs. 4, 5, 6 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder Y32/4. Fig. 7 (x 1000): Slide Malong-2, 577 m, SWC (S2); England Finder W18/1. Figs. 8, 9 (x 1000): Slide Malong-2, 1135-1140 m, DC (S1); England Finder U42/3.

Fig. 10 *Praedapollis* sp. (x 1000): Slide Delah-1, 2250-2255 m, DC (S1); England Finder U8.

Figs. 11, 12 *Proteacidites franktonensis* Couper 1960. Figs. 11, 12 (x 1000): Slide Malong-2, 750 m, SWC (S2); England Finder X10/4.

Fig. 13 *Proteacidites* sp. cf. *P. tenuiexinus* Stover in Stover and Partridge 1973 (x 1000): Slide Malong-2, 780-790 m, DC (S1); England Finder H30/1.

Figs. 14-16 *Propylipollis subscabratus* (Couper 1960) Jaizan Jais and Morley comb. nov.
Figs. 14, 15 (x 1000): Slide Malong-2, 1100-1105 m, DC (S1); England Finder E29. Fig. 16 (x 1000): Slide Malong-2, 577 m, SWC (S2); England Finder L18/3.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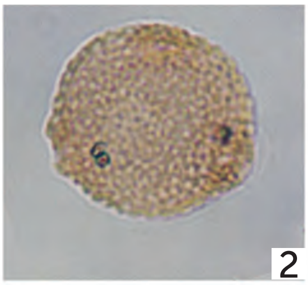
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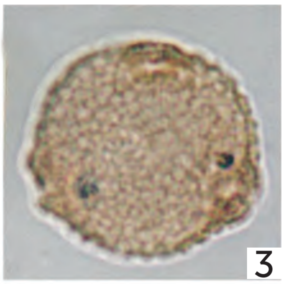
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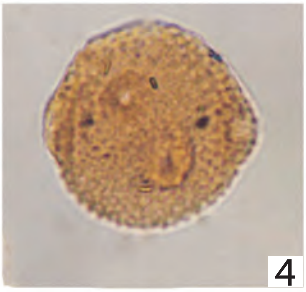
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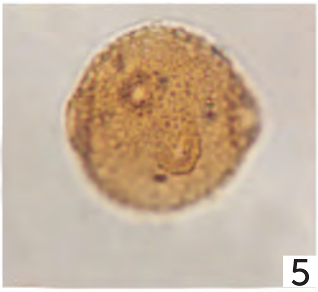
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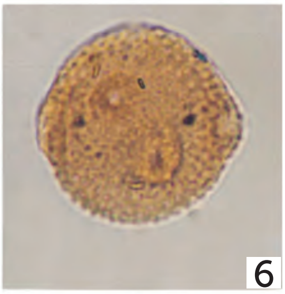
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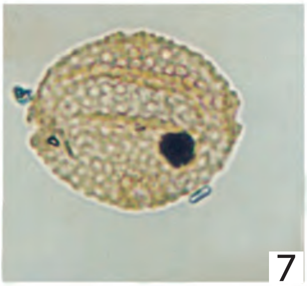
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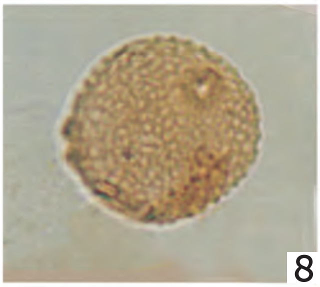
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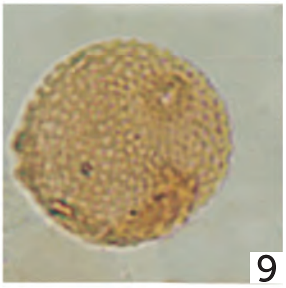
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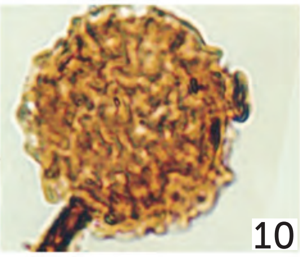
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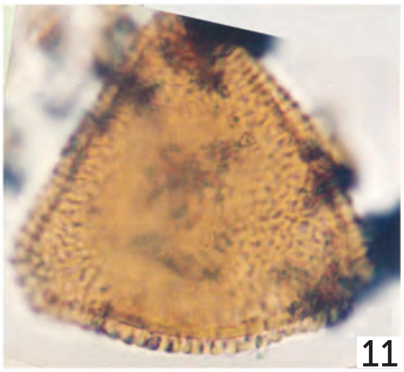
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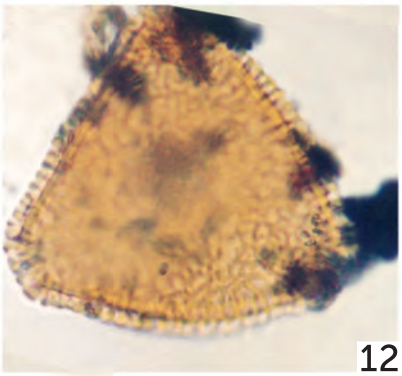
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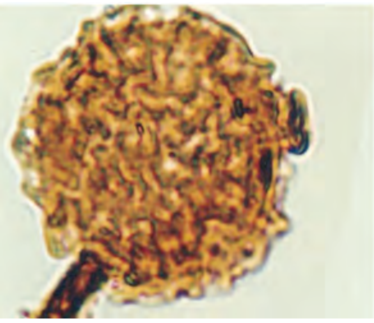
Genus *Praedapollis*
Boltenhagen and Salard-Cheboldaeff emend. Legoux 1978

Type species:
Praedapollis africanus Boltenhagen and Salard-Cheboldaeff 1973.

***Praedapollis* sp.** Plate 16, Fig. 10

Plate 16, Fig. 10



Description:
Pollen grains generally spherical, to subspherical, surrounded by a free reticulum; triporate, but pores can only be clearly seen in specimens that have lost their reticulum; reticulum not attached to the inner exine layer, but forms a coarse and irregularly meshed net.

Dimensions:
Equatorial diameter 26 (31) 36 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Regularly present in Malong 5G-17.2 well in zone PR15, but otherwise very scattered in zones PR6/7 to PR14. In the Delah 5H-14.1 well, very rarely recorded.

Remarks and comparison:
The smaller size of these specimens distinguished them from other *Praedapollis* species.

Botanical affinity:
Probably with Leguminosae (Morley, 2000).

Source ecology:
Possibly from rain forest trees.

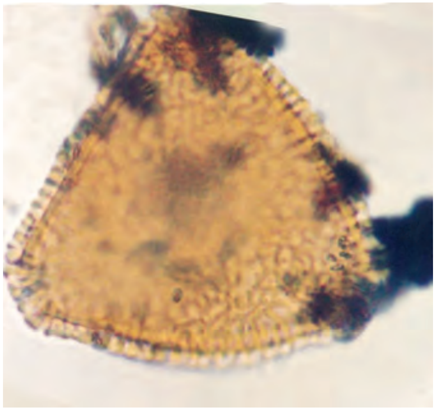
Suggested name for Quaternary records:
Not applicable.

Ecological group:
?Rainforest.

Genus *Proteacidites*
Cookson ex Couper 1953 emend. Martin and Harris 1975

Type species:
Proteacidites adenanthoides Cookson 1950.

Proteacidites franktonensis
Couper 1960. Plate 16, Figs. 11, 12



Selected synonymy:
1960 *Proteacidites franktonensis* Couper, p. 51, Pl. 6, Figs. 4, 5.

Description:
Pollen grains radially symmetrical, isopolar, amb subtriangular with straight to slightly convex sides; triporate, angulaperturate; pores simple, circular, 8 to 9 µm in diameter, sometimes facing obliquely into proximal hemisphere; exine clearly differentiated; nexine 1 to 1.5 µm thick, sexine 1 µm thick, reticulate; reticulum irregular, 1 to 2 µm in diameter, simplicolumellate; columellae or pila 1 to 2 µm long, tightly spaced; thickness of exine and coarseness of sculpture reduced around apertural regions.

Dimensions:
Equatorial diameter 41 (43) 44 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Previously recorded from the middle Miocene to upper Pliocene of New Zealand (Couper, 1960). In Malong 5G-17.2 well, rare and restricted to zones PR13 to PR14.

Comparison:
The Malay Basin specimens are generally smaller than the New Zealand materials originally described by Couper (1960) that range from 55 to 85 µm in equatorial diameter.

Botanical affinity:
Comparable with some species of the tribe Proteoideae.

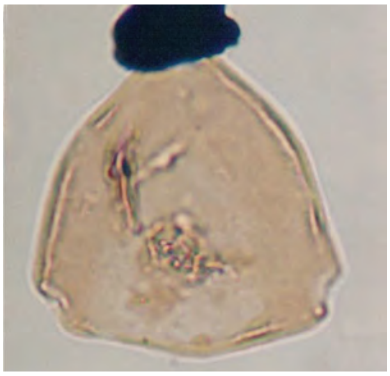
Source ecology:
Probably from tropical seasonally dry forests.

Suggested name for Quaternary records:
Proteoideae pollen.

Ecological group:
Seasonal forests.

Proteacidites* sp. cf. *P. tenuiexinus

Stover in Stover and Partridge 1973. Plate 16, Fig. 13



Selected synonymy:

cf. 1973 *Proteacidites tenuiexinus* Stover in Stover and Partridge, p. 268, Pl. 25, Figs. 6-7.

Description:

Pollen symmetrical to slightly asymmetrical, amb convexly triangular; triporate; pore margins gently concave in polar view; exine stratification faint, but nexine very thin, with thicker sexine, tending to be thicker around the apertures; exine granulate to unevenly scabrate.

Dimensions:

Equatorial diameter, minimum 24 µm, maximum 30 µm (2 specimens measured).

Stratigraphic distribution:

P. tenuiexinus has been found in sediments of late Paleocene to middle Eocene age in Australia (Stover and Partridge, 1973; Alley and Broadbridge, 1992). Rare and restricted to the PR13 zone in the Malong 5G-17.2 well.

Remarks and comparison:

The Malay Basin specimens are comparable to the original description of *P. tenuiexinus* Stover in Stover and Partridge except that the exine of the former is smoother. Since only two specimens are found, they are tentatively compared to *P. tenuiexinus* until more specimens are found for further study. Even though they are rare, their brief occurrence in the upper part of Malong 5G-17.2 well might be stratigraphically useful.

Botanical affinity:

Proteaceae.

Source ecology:

Unknown.

Suggested name for Quaternary records:

Proteaceae undiff.

Ecological group:

Undifferentiated.

Genus *Propylipollis*

Martin and Harris 1975

Type species:

Propylipollis reticuloscabratus (Harris 1965) Martin and Harris 1975 (by original designation).

Generic remarks:

Martin and Harris (1975) proposed this genus to exclude forms with post atrium and annulate pores from *Proteacidites* Cookson ex Couper.

Propylipollis subscabratus

(Couper 1960) Jaizan Jais and Morley comb. nov. Plate 16, Figs. 14-16

Selected synonymy:

1960 *Proteacidites subscabratus* Couper, p. 52, Pl. 6, Figs. 8-10.

1965 *Proteacidites subscabratus* Couper; Harris, p. 92, Pl. 29, Figs. 8-10.

Description:

Pollen grain, radially symmetrical; triporate; pores circular 2 to 3 µm in diameter, outline sides straight to slightly convex in polar view; plano-convex in equatorial view, nexine less than 1 µm, thickening toward pores; sexine less than 0.5 µm thick, finely scabrate to more or less psilate.

Dimensions:

Equatorial diameter 13 (17) 18 µm (5 specimens measured from various horizons).

Stratigraphic distribution:

This species is widely reported from Australia and New Zealand, from the Paleocene to Pliocene (e.g., Couper, 1960; Harris, 1971) the Late Cretaceous to Palaeogene of Antarctica (Dettmann and Thomson, 1987; Kemp, 1975), the Late Cretaceous to Palaeogene of India (Jain et al., 1973; Venkatachala, 1974), and from the Maastrichtian to Palaeogene of South America (Fasola, 1969), with a few records from Europe and temperate Asia. This species is rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

This species is characterised by having slightly thickened pores, straight to slightly convex sides and finely scabrate to more or less psilate wall as originally described by Couper (1960).

Botanical affinity:

Proteaceae.

Suggested name for Quaternary records:

Proteaceae undiff.

Ecological group:

Rainforest forests.

2.15 STEPHANOPORATE POLLEN

Genus *Anacolosidites*
Cookson and Pike 1954 emend. Potonié 1960

Type species:
Anacolosidites luteoides Cookson and Pike 1954 (by selection of Krutzsch 1959 and designation of Potonié 1960).

Anacolosidites luteoides
Cookson and Pike 1954. Plate 17, Figs.1, 2

Selected synonymy:
1954 *Anacolosidites luteoides* Cookson and Pike, p. 207, Pl. 1, Figs. 47-50.
1955 Dispersed pollen attributed to *Anacolosa* tp. in Kuyl, Muller and Waterbolk, p. 64, Pl. 2, Fig. 28.
1959 *Anacolosidites luteoides* Cookson and Pike; Krutzsch, p. 244.
1960 *Anacolosidites luteoides* Cookson and Pike; Potonié, p. 124.
1965 *Anacolosidites luteoides* Cookson and Pike; Harris, p. 94, Pl. 27, Fig. 29.
cf. 1968 *Anacolosidites luteoides* Cookson and Pike; Germeraad, Hopping and Muller., p. 313, Pl. 9, Figs. 9,10.
1968 *Anacolosidites luteoides* Cookson and Pike; McIntyre, p. 195, Figs. 55, 56.
1973 *Anacolosidites luteoides* Cookson and Pike; Stover and Partridge, p. 270, Pl. 27, Fig. 6.
1982 *Anacolosidites luteoides* Cookson and Pike; Rao and Ramanujam, p. 86, Pl. 5, Figs. 82, 83.
2021 *Anacolosidites luteoides* Cookson and Pike; Huang et al., Pl. 2, Fig. 20.

Description:
Pollen, radially symmetrical, isopolar; amb triangular, with straight or slightly concave sides, apices obtuse; hexaporate, three pores towards the angles of each hemisphere, forming six nonequatorial pores, pores circular and 2.1 to 3.7 µm in diameter, located ca. 1/3 of the equatorial diameter from the equator; exine 0.5 µm thick; exine layers indiscernible; sculpture psilate (Huang et al., 2021).

Dimensions:
Equatorial diameter 17 (19) 20 µm (6 specimens measured from various horizons).

Stratigraphic distribution:
There are several records of *Anacolosidites* from the Late Cretaceous, and some from the Paleocene (Malécot and Lobreau-Callen, 2005). The genus reached its maximum distribution and diversity in the Eocene, occurring in all continents (Malécot and Lobreau-Callen, 2005). The morphotype then reduced its range dramatically in the Oligocene, with only a few records from Africa, South America, India and Australia in the Oligo–Miocene. *Anacolosidites luteoides* is recorded from the late Paleocene to Eocene of Australia (Cookson and Pike, 1954; Harris, 1965; Stover and Partridge, 1973); early to later Eocene (McIntyre, 1968) and middle Miocene of New Zealand (Mildenhall and Pocknall, 1989); Eocene to Miocene of India (Sah and Dutta, 1968; Baksi, 1972; Salujha et al., 1972; Venkatachala and Rawat, 1972; Rawat et al., 1977; Ramanujam and Rao, 1977; Rao and Ramanujam, 1982) and Africa (Salard-Cheboldaeff, 1977; Partridge, 1978); middle Eocene of Germany (Krutzsch, 1959). Germeraad et al. (1968) recorded *Anacolosidites* cf. *A. luteoides* from Paleocene to Recent of Borneo, Paleocene to Oligocene of Nigeria and from Paleocene to Eocene of the Caribbean. In Malong 5G-17.2 and Delah 5H-14.1 wells, *A. luteoides* is present in low percentages in both sections, but consistently present through zone PR11.

Botanical affinity:
Anacolosa (Olacaceae).

Source ecology:
Trees of perhumid forests and swamps. This genus is used as a stratigraphic and environmental marker for tropical and megathermal climate conditions (Malécot and Lobreau-Callen, 2005).

Suggested name for Quaternary records:
Anacolosa pollen.

Ecological group:
Peat swamp.

Genus *Alnipollenites*

Potonié 1931

Type species:
Alnipollenites verus (Potonié 1931) ex Potonié 1931.

Alnipollenites verus

(Potonié 1931) ex Potonié 1931. Plate 17, Fig. 5

Selected synonymy:

1931 *Pollenites verus* Potonié, p. 332, Pl. 2, Fig. 40.
1931 *Alni-pollenites verus* (Potonié) ex Potonié, p. 4.
1934 *Alni-pollenites verus* (Potonié) ex Potonié; Potonié, p. 58, Pl. 2, Figs. 13, 17, 18; Pl. 6, Fig. 28.
1953 *Polyvestibulopollenites (Alnipollenites) verus* (Potonié) Thomson and Pflug, p. 90, Pl. 10, Figs. 62-76.
1968 *Alnipollenites verus* (Potonié) ex Potonié; Germeraad et al., p. 314, Pl. 9, Fig. 13.
1974 *Alnipollenites verus* Potonié; Ziembinska-Tworzydlo, p. 379, Pl. 18, Figs. 1, 2.

Description:
Pollen, radially symmetrical, isopolar, oblate; amb near circular; pentaporate, angulaperturate, five or six pores connected by distinct arci, 1.0 µm wide, pores vestibulate; exine 1.5 µm in thick, thicker (2.5 µm) near the pores; exine layers and columellae indiscernible; sculpture psilate (Huang et al., 2021).

Dimensions:
Equatorial diameter 22 µm (1 specimen measured).

Stratigraphic distribution:
The oldest records are from the Santonian of Japan (Miki, 1977) and similar age deposits from China (Song et al., 2004). It is widely reported from the Maastrichtian of North America, but not until the Paleocene of Europe (Muller, 1981a). This Laurasian taxon dispersed to South America following the closure of the Panama Isthmus (Hooghiemstra, 1984). In Southeast Asia, the oldest record is from the late Eocene Yaw Formation in Kalewa (Huang et al., 2021) after which time it recorded from the Oligocene and Miocene of the Sunda Shelf (Muller, 1966; Morley, 2018), Tibet (Wei et al., 2011), Thailand (Watanasak, 1990; Songtham et al., 2003). Its common occurrence in the Oligocene to middle Miocene sediments of the Sunda Shelf reflects former uplands along the Natuna Arch and Con Son Swell (Morley, 2014, 2018) and Song Hong Basin (Chung et al., 2021) Rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:
Alnus (Betulaceae).

Source ecology:
Lower montane deciduous trees, growing in northern seasonal wet evergreen montane forests from Vietnam to the Himalayan foothills (Ashton, 2014).

Suggested name for Quaternary records:
Alnus pollen.

Ecological group:
Montane seasonal forests.

Genus *Malvacipollis*

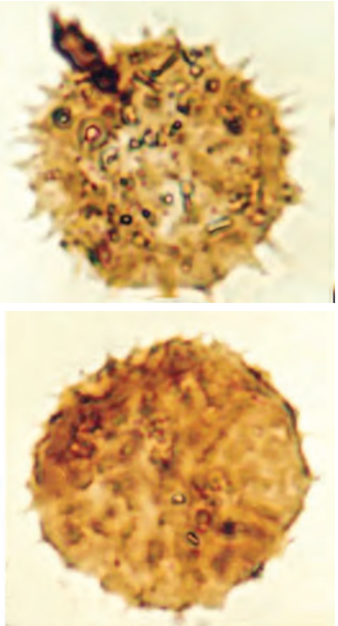
Harris 1965

Type species:

Malvacipollis diversus Harris 1965 (by original designation).

Malvacipollis subtilis

Stover and Partridge 1973. Plate 17, Figs. 3, 4



Selected synonymy:

1953 Dispersed pollen attributed to *Plagianthus* sp. in Couper, Pl. 5, Fig. 65.
1960 Dispersed pollen attributed to *Plagianthus* sp. in Couper, p. 53, Pl. 7, Fig. 16.
1965 *Malvacipollis diversus* Harris (*partim*), pl. 29, Fig. 19 (non Fig. 18).
1973 *Malvacipollis subtilis* Stover in Stover and Partridge, p. 272, Pl. 26, Figs. 7-9.

Description:

Pollen, oblate, stephanoporate, amb circular, exine stratified, sexine much thicker than nexine, columellae small, evenly distributed, dense, sexine psilate, with superimposed spines, with bases equal to or slightly wider than their height; apertures porate, equatorial, 5 to 8 in number (usually 6), circular to elliptical.

Dimensions:

Equatorial diameter 19 (22) 23 µm (4 specimens measured from various horizons).

Stratigraphic distribution:

Early Eocene to Recent of New Zealand (Couper, 1953; Pocknall, 1982); Paleocene to Pleistocene of Australia (Martin, 1994; Stover and Partridge, 1973). Rare; present in the Delah 5H-14.1 well within zone PR4, characterised by the driest climates of the succession; absent in Malong 5G-17.2 well.

Remarks and comparison:

These specimens resemble *Malvacipollis subtilis* as described by Stover in Stover and Partridge (1973) from Gippsland Basin, Australia. They are distinguished from *M. diversus* by having spines or spinules instead of conate sculpture and from *M. austrobuxoides* sp. nov. by having finer spines and a thinner wall.

Botanical affinity:

Picodendraceae (Grimsson et al., 2019), but a possible affinity with Malvaceae cannot be ruled out (Martin, 1974); specimens from this area are most probably derived from species of *Austrobuxus,* such as *A. swainii* or *Dissiliaria,* currently occurring in Australia and New Caledonia.

Source ecology:

Trees of seasonal evergreen rain forests in Australia and New Caledonia (Harris, 1965).

Suggested name for Quaternary records:

Austrobuxus swainii type pollen.

Ecological group:

Seasonal forest.

Malvacipollis austrobuxoides

Jaizan Jais and Morley sp. nov. Plate 17, Figs. 9-12

Derivation of name:

Named after its botanical affinity, *Austrobuxus* pollen.

Holotype:

Plate 17, Figs. 9, 10. Slide Malong-2, 625 m, SWC (S3), England Finder D42/2. Grain in polar aspect, circular in outline, 27 µm in diameter; exine 2 µm thick; spines 5 µm long, 2 µm wide at base; pores 4 µm in diameter. Type locality: Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:

Pollen grains radially symmetrical, isopolar, spherical; stephanoporate; pores 4 to 6 (usually 6), circular to elliptical, up to ±4 µm in diameter, with thickened annuli of ±1 µm width, equatorially to subequatorially arranged, not always clearly visible; wall thick (± 2 µm thick), stratification distinct, tectate-columellate, spinose, microreticulate in between spines; sexine thicker than nexine; tectum thin; columellae dense, evenly distributed; spines coarse, robust, 3 to 5 µm long, ±2 µm wide at base; straight to slightly curved, tapered, sharply pointed, sparsely distributed.

Dimensions:

Equatorial diameter 21 (24) 27 µm (9 specimens measured from various horizons).

Stratigraphic distribution:

Present in low percentages in zones PR2 to PR3 in Delah 5H-14.1 and from PR9B to PR15 in Malong 5G-17.2 well.

Comparison:

This species differs from *Malvacipollis diversus* Harris emend. Stover and Partridge 1973 and *M. subtilis* Stover and Partridge 1973 by having coarser and robust spines, microreticulate surface and thickened annuli.

Botanical affinity:

Malvacipollis austrobuxoides conforms in all aspects with extant pollen *Austrobuxus nitidus* (Picodendraceae).

Source ecology:

Common in the Phasic community 1 of peat swamps in Sarawak and Brunei (as *Longetia malayana*) according to Anderson (1963).

Suggested name for Quaternary records:

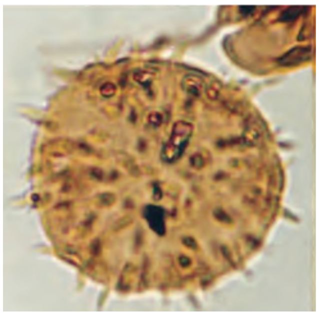
Austrobuxus nitidus pollen.

Ecological group:

Peat swamp forests.

Malvacipollis* sp. cf. *M. subtilis

Stover in Stover and Partridge 1973. Plate 17, Figs. 7, 8



Selected synonymy:

cf. 1965 *Malvacipollis diversus* Harris (partim), Pl. 29, Fig. 19 (non Fig. 18).
cf. 1973 *Malvacipollis subtilis* Stover in Stover and Partridge, p. 272, Pl. 26, Figs. 7-9.

Dimensions:

Equatorial diameter 22 (25) 29 µm (5 specimens measured from various horizons).

Stratigraphic distribution:

Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

These specimens fit the description of *Malvacipollis subtilis* Stover in Stover and Partridge 1973, but the former have microreticulate surface visible between the spines, the character which is not mentioned in the description of the *M. subtilis* type specimen by the above authors. Until this type specimen is examined, the present specimens are provisionally compared to *M. subtilis*.

Botanical affinity:

Picodendraceae, particularly with *Austrobuxus*, possibly *Austrobuxus nitidus*.

Source ecology:

Austrobuxus nitidus commonly occur in peat swamps within Phasic community 1 (Anderson, 1963).

Suggested name for Quaternary records:

Austrobuxus cf. *nitidus* pollen.

Ecological group:

Peat swamp forests.

Austrobuxus nitidus *flowers, from S.S. Larsen, Flora of Thailand (photo by Muhamad Ibqal, 2010).*

Plate 17

Figs. 1, 2 *Anacolosidites luteoides* Cookson and Pike 1954. Figs. 1, 2 (x 1000): Slide Malong-2, 608 m, SWC (S2); England Finder N11/3.

Figs. 3, 4 *Malvacipollis subtilis* Stover and Partridge 1973. Fig. 3 (x 1000): Slide Delah-1, 2350-2355 m, DC (S2); England Finder Q40/2. Fig. 4 (x 1000): Slide Delah-1, 2330-2335 m, DC (S2); England Finder P12/2.

Fig. 5 *Alnipollenites verus* (Potonié 1931) ex Potonié 1931 (x 1000): Slide Malong-2, 989 m, SWC (S1); England Finder G36/4.

Figs. 7, 8 *Malvacipollis* sp. cf. *M. subtilis* Stover in Stover and Partridge 1973. Figs. 7, 8 (x 1000): Slide Malong-2, 1436 m, SWC (S1); England Finder W4/1.

Figs. 9-12 *Malvacipollis austrobuxoides* Jaizan Jais and Morley sp. nov. Figs. 9, 10 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder D42/2. Figs. 11, 12 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder E50/3.

Figs. 6, 13, 14 *Echistephanoporites camptostemonoides* Jaizan Jais and Morley sp. nov. Fig.6 (x 400): Slide Malong-2, 518 m, SWC (S1); England Finder N28/2. Figs. 13, 14 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder H22.

Figs. 15, 16 *Chenopodipollis chenopodiaceoides* (Martin 1973b) Truswell in Truswell et al. 1985. Figs. 15, 16 (x 1000): Slide Malong-2, 654.5 m, SWC (S2); England Finder X8/4.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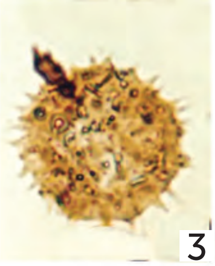
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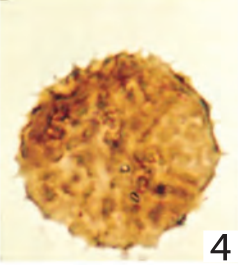
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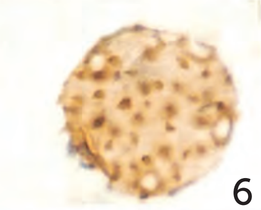
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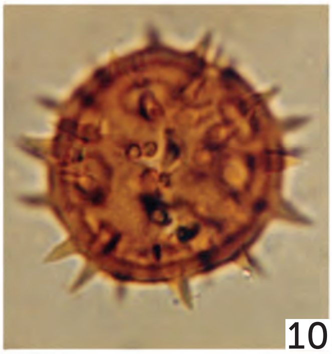
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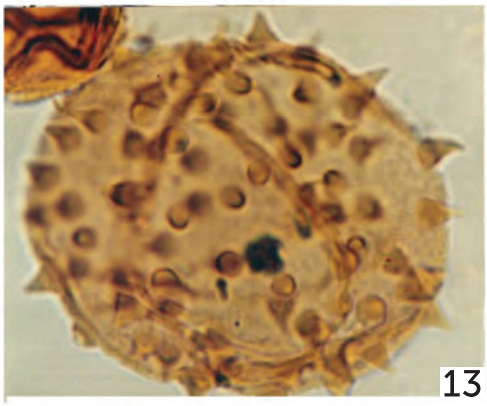
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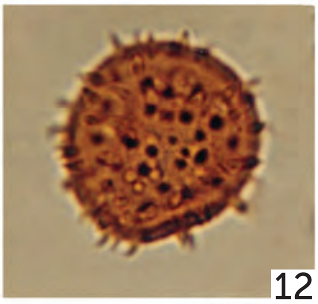
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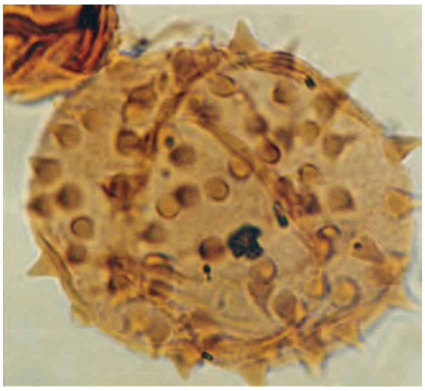
Genus *Echistephanoporites* Leidelmeyer 1966

Type species:
Echistephanoporites alfonsi Leidelmeyer 1966 (by original designation).

Echistephanoporites camptostemonoides

Jaizan Jais and Morley sp. nov. Plate 17, Figs. 6, 13, 14



Derivation of name:
Named after *Camptostemon* pollen, which with the pollen closely compares.

Holotype:
Plate 17, Figs. 13, 14. Slide Malong-2, 625 m, SWC (S3), England Finder H22. Grain in polar aspect, circular in outline, 46 μm in diameter; exine 1 μm thick; pores ±4 μm in diameter; spines 4 μm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, spherical; stephanoporate, pentaporate; pores 4 to 6 μm in diameter, circular to elliptic, equatorial to subequatorial, annulate, distinct or indistinct (on some specimens, pores appear to be diffused and difficult to locate); annuli variable in thickness, ±1 to 2.5 μm wide; exine thin (<1 μm thick), slightly thicker at the base of spines, tectate, columellate, spinose, microreticulate in between spines; sexine thicker than nexine; tectum <0.5 μm thick, slightly thickened at the root of spines; columellae <1 μm long, slightly longer at the base of spines; spines bulging at the base, tapered, sharply pointed, widely spaced, 2 to 4 μm long, 2 to 3 μm wide at the base.

Dimensions:
Equatorial diameter 30 (40) 53 μm (18 specimens measured from various horizons).

Variability:
In the visibility of pores and in the thickness of annuli.

Stratigraphic distribution:
Camptostemon pollen has been recorded from the early Miocene to Pleistocene of Borneo (Muller, 1970, 1972, 1981; Morley, 1978, 1991). This species has a single record in zone PR6/7 in the Delah 5H-14.1 well. In Malong 5G-17.2, however, it shows a very interesting distribution, being restricted to zones PR12B to PR15, occurring consistently from zone PR14, and commonly, often with abundance maxima, in zone PR15.

Remarks and comparison:
This species differs from *Echistephanoporites malaysianus* sp. nov. in having a thinner wall and shorter spines, and from *Malvacearumpollis papuaensis* Khan 1976 in being pentaporate and having shorter spines. It may also be confused with superficially similar Malvaceous type pollen, but the present specimens have equatorial apertures even though some are slightly subequatorial.

Botanical affinity:
This species closely resembles the pollen of the mangrove genus *Camptostemon* (Bombacaceae).

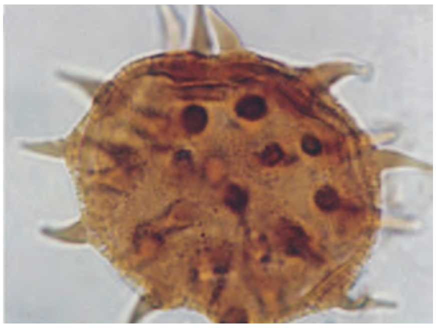
Source ecology:
Today, *Camptostemon* is restricted to Eastern Indonesia and northern Australia with a couple of records from southeast Borneo (Tomlinson, 2016). The occurrence of *Camptostemon* might be due to the presence of hypersaline estuaries, where it is commonly present today in northern Australia (Wells, 1981; Morley et al., 2020). *Camptostemon* particularly occurs in the transitional areas between brackish and freshwater environments (Muller, 1972) and in areas exhibiting marked seasonality of climate (Morley, 1978). Echistephanoporites *camptostemonoides* thus provides a very useful climatic and environmental indicator.

Camptostemon schultzii, *observed in northern Australia by Atlas of Living Australia by M. Fagg (ALA; http://www.ala.org.au).*

Suggested name for Quaternary records:
Camptostemon pollen.

Ecological group:
Backmangrove.

Echistephanoporites malaysianus Jaizan Jais and Morley sp. nov. Plate 18, Figs. 1-6



Derivation of name:
Named after the country of Malaysia, where the species was discovered.

Holotype:
Plate 18, Figs. 1-3. Slide Malong-2, 561 m, SWC (S1), England Finder O20. Grain in polar aspect, circular in outline, 45 μm in diameter; exine 2 μm thick; pores 7 μm in diameter; spines 5 to 7 μm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 561 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, spherical; stephanoporate, pentaporate; pores circular to elliptic, 4 to 6 μm in diameter, equatorial to subequatorial, annulate, distinct or indistinct (on some specimens, pores appear to be diffused and difficult to locate); annuli variable in thickness, ±1-5 μm wide; exine thick (±2 μm thick), slightly thicker at the base of spines, tectate, columellate, echinate, microreticulate in between spines; sexine thicker than nexine; tectum <0.5 μm thick, slightly thickened at the root of spines; columellae distinct, dense, 1 to 2 μm long, slightly longer at the root of spines; spines robust, bulging at the base, tapered, sharply pointed, widely spaced, 4 to 9 μm long, 2 to 5 μm wide at base.

Dimensions:
Equatorial diameter 30 (38) 47 μm (23 specimens measured from various horizons).

Variability:
In the visibility of pores and in the thickness of annuli.

Stratigraphic distribution:
As for *Echistephanoporites camptostemonoides*, recorded from the early Miocene to Pleistocene of Borneo (Muller, 1970, 1972, 1981; Morley, 1978, 1991; Morley et al., 2020). This species occurs only in the Malong 5G-17.2 well, where it is confined to zones PR12B to PR15 and may be common to abundant in zone PR15.

Remarks and comparison:
This species is distinguished from *Echistephanoporites camptostemonoides* sp. nov. by its thicker wall, and longer and more robust spines, and from *Malvacearumpollis papuaensis* Khan 1976a by being pentaporate. As with the previous species described above, it may be confused with superficially similar malvaceous pollen. There are two species of *Camptostemon*, which have different distributions, *C. schultzii* is essentially restricted to northern Australia, with some records in New Guinea, whereas *C. philippinensis* occurs in the Philippines and Sulawesi with a record from southeast Borneo and several records from New Guinea. The pollen of *C. philippinensis* has been described by Fuchs (1967) but *C. schultzii* has never been described. It is possible that the two forms of *Echistephanoporites* described here may reflect the former range of two *Camptostemon* species.

Botanical affinity:
This species is similar to extant pollen *Camptostemon* (Bombacaceae).

Source ecology:
Today, *Camptostemon* is restricted to eastern Indonesia and northern Australia with a couple of records from southeast Borneo (Tomlinson, 2016). The occurrence of *Camptostemon* might be due to the presence of hypersaline estuaries, where it is commonly present today in northern Australia (Wells, 1981; Morley et al., 2020). *Camptostemon* particularly occurs in the transitional areas between brackish and freshwater environments (Muller, 1972) and in areas exhibiting marked seasonality of climate (Morley, 1978). *Echistephanoporites camptostemonoides* thus provides a very useful climatic and environmental indicator. Commonly occurs in mangrove swamps, particularly in the transitional zones between brackish and freshwater environments in the south-east coast of Borneo, the Philippines and Papua New Guinea (Muller, 1972) and in the area exhibiting marked seasonality (Morley, 1978).

Suggested name for Quaternary records:
Camptostemon pollen.

Ecological group:
Backmangrove.

2.16 PERIPORATE POLLEN

Genus *Chenopodipollis*
Krutzsch 1966

Type species:
Chenopodipollis multiplex (Weyland and Pflug 1957) Krutzsch 1966.

Chenopodipollis chenopodiaceoides (Martin 1973b) Truswell in Truswell et al. 1985. Plate 17, Figs. 15, 16

Selected synonymy:
1973 *Polyporina chenopodiaceoides* Martin, p. 28, Figs. 118-120.
1985 *Chenopodipollis chenopodiaceoides* (Martin) Truswell in Truswell et al., p. 283, Figs. 7a-d.

Description:
Pollen grains small, centro-symmetrical, spherical; periporate; pores approximately 60 in number, circular to slightly elliptical, ±2 µm in diameter, ±2 µm apart, regularly distributed; exine <1 µm thick, scabrate.

Dimensions:
Equatorial diameter 15 (17) 20 µm (4 specimens measured from various horizons).

Distribution:
Rare in Malong 5G-17.2 well, absent in the Delah 5H-14.1 section.

Stratigraphic distribution:
Chenopodipollis spp. are very widely recorded, with most records from the Neogene, but with scattered records from the Oligocene and Eocene. The age of the family Amaranthaceae is poorly restrained (Kadereit et al., 2012) but probably originated during the Palaeogene. There are some records from the Cretaceous, especially from China, but these may be from other taxa, such as *Cretacaeiporites*. *Chenopodipollis chenopodiaceoides* is widely reported from Australia and New Zealand and Argentina (e.g., Martin, 1994; Mildenhall et al., 1989; Barreda, 1997). Occurs in low numbers within the Malong 5G-17.2 well.

Remarks and comparison:
The present specimens resemble *Chenopodipollis chenopodiaceoides* (Martin 1973) Truswell in Truswell et al. 1985 described from South Australia. It differs from many other *Chenopodipollis* species by being smaller. *Chenopodipollis* sp. described by Hekel (1972) and *Chenopodipollis minor* Song in Song et al. (1985) are also similar in size with the Malay Basin specimens.

Botanical affinity:
Probably with Amaranthaceae (Chenopodioideae is not known to be present in the tropics).

Source ecology:
Herbs, mainly annuals of open places but with several species occurring on tidal flats such as *Acryanthes*.

Suggested name for Quaternary records:
Amaranthaceae type pollen.

Ecological group:
Backmangrove.

Genus *Cryptopolyporites*
Venkatachala and Kar 1969

Type species:
Cryptopolyporites cryptus Venkatachala and Kar 1969 (by original designation).

Cryptopolyporites cryptus
Venkatachala and Kar 1969. Plate 18, Fig. 10

Selected synonymy:
1969 *Cryptopolyporites cryptus* Venkatachala and Kar, p. 175, Pl. 2, Fig. 28.
1975 Dispersed pollen attributed to *Gonystylus* in Anderson and Muller, p. 309, Pl. 2, Fig. 11.

Description:
Pollen spherical, periporate, pores indistinctly outlined, exine with scattered minute supratectate echinae and foveolate-columellate wall.

Dimensions:
Equatorial diameter 34 (43) 51 µm (7 specimens measured from various horizons).

Stratigraphic distribution:
Early Eocene of India (Venkatachala and Kar, 1969; Kar, 1985) and middle Eocene of Sulawesi (Morley, 1998) with a range of Oligocene to Recent in Borneo (Muller, 1972; Anderson and Muller, 1975). Present in low percentages in Malong 5G-17.2 well from zone PR12B to PR15, with one record from zone PR9B (Upper). Absent in the Delah 5H-14.1 well.

Remarks:
This periporate form is characterised by its indistinctly outlined pores and scattered minute supratectate echinae and foveolate-columellate wall which agrees with the original description by Venkatachala and Kar (1969).

Botanical affinity:
This pollen is derived from the genus *Gonystylus*. (Thymelaeaceae). *Gonystylus* is a good example of an 'out of India' taxon, that originated on the Indian Plate, then dispersed to Southeast Asia following the collision of the Indian Plate with Asia in the Eocene, and subsequently diversified on Borneo (Morley, 1998, 2018).

Gonystylus bancanus*, ramin. Peat swamp forest near Pekan, Pahang, Malaysia (photo by RJM).*

Source ecology:
The species *Gonystylus bancanus* is the most important dominant in Phasic community P.C. 1 of Sarawak peat swamps, and the most important peat swamp timber tree (Anderson, 1963). It does also occur in smaller numbers in phasic community P.C. 2-4.

Suggested name for Quaternary records:
Gonystylus pollen.

Ecological group:
Peat swamp forests.

Plate 18

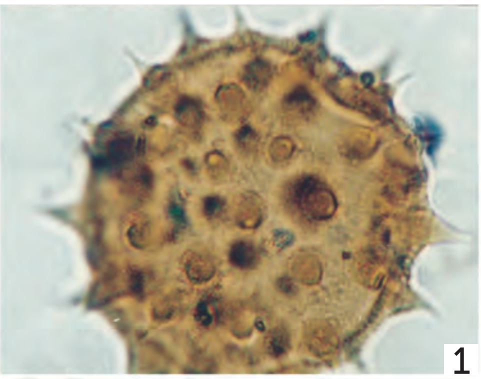
Figs. 1-6 *Echistephanoporites malaysianus* Jaizan Jais and Morley sp. nov. Figs. 1-3 (Holotype, x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder O20. Fig. 4 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder X11/4. Figs. 5, 6 (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder R13/3.

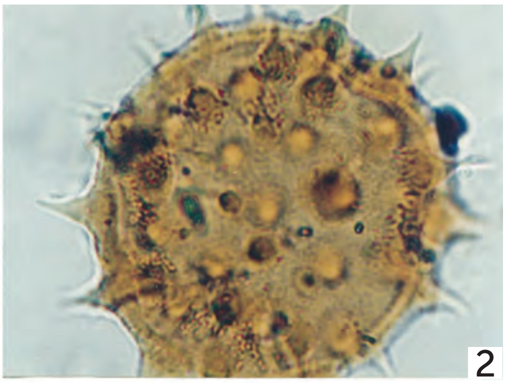
Figs. 7. 8 *Thymelipollis* sp. Fig. 7, 8 (x 1000): Slide Malong-2, 1000-1010 m, DC (S1); England Finder G26.

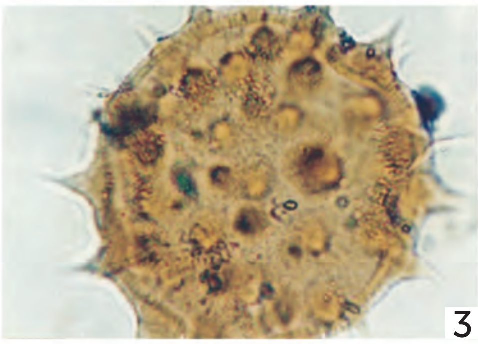
Fig. 9. *Persicarioipollis meuseli* Krutzsch 1962 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder J36/3.

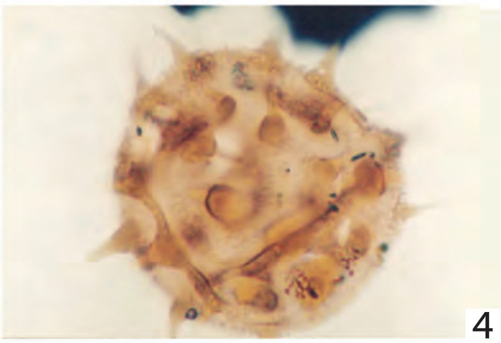
Fig. 10 *Cryptopolyporites cryptus* Venkatachala and Kar 1969 (x 400): Slide Malong-2, 561 m, SWC (S1); England Finder W18/3.

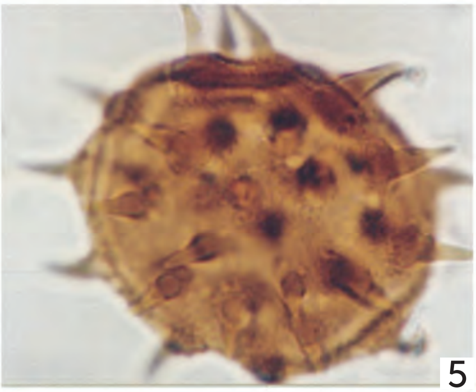
Fig. 11 *Echiperiporites estelae* Germeraad et al. 1968 (x 200), 2 (x 400): Slide Malong-2, 430.5 m, SWC (S2); England Finder U35.

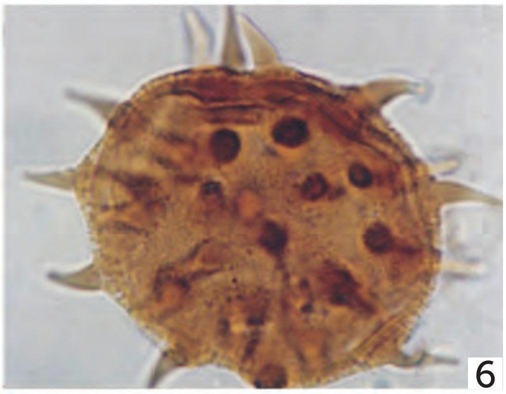


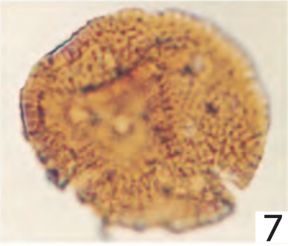


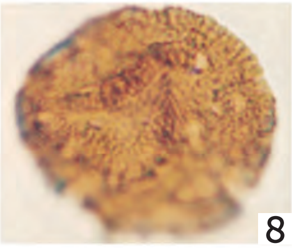


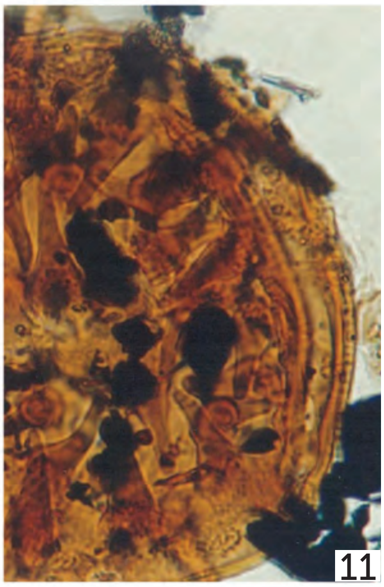


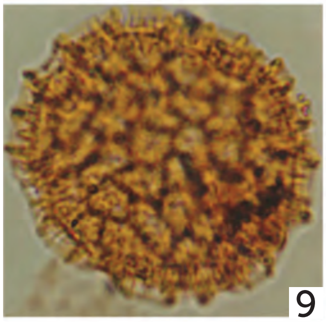


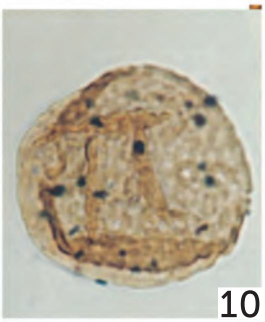








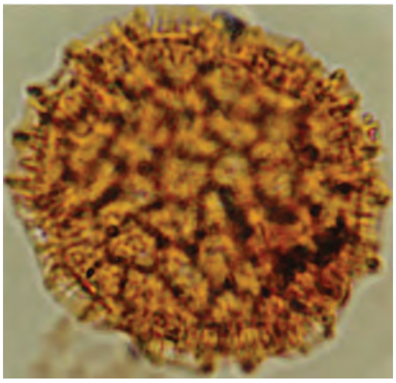




Genus *Persicarioipollis*
Krutzsch 1962

Type species:
Persicarioipollis meuseli Krutzsch 1962 (by original designation).

Persicarioipollis meuseli
Krutzsch 1962. Plate 18, Fig. 9



Selected synonymy:
1962 *Persicarioipollis meuseli* Krutzsch, p. 282, Pl. 8, Figs. 9-16.
1974 *Persicarioipollis meuseli* Krutzsch; Ziembinska-Tworzydlo, p. 407, Pl. 26, Figs. 6a-c.
1978 Dispersed pollen attributed to *Polygonum* cf. *persicaria* in Koreneva and Kartashova, Pl. 10, Fig. 10.

Description:
Pollen spherical, polyporate, pores circular, small, obscured by sexine; exine coarsely reticulate, sexine much thicker than nexine, sexine with sinuous, duplicolumellate, palisade muri and irregularly polygonal meshes with pores positioned in their centres.

Dimensions:
Equatorial diameter, minimum 40 µm, maximum 43 µm (2 specimens measured).

Stratigraphic distribution:
Miocene and Pliocene of Germany (Krutzsch, 1962); Upper Miocene of Gierlachowo, Western Poland (Ziembinska-Tworzydlo, 1974); Pliocene of the Black Sea (Koreneva and Kartashova, 1978). Rare and restricted to the upper part of Malong 5G-17.2 well, absent in the Delah 5H-14.1 section.

Remarks and comparison:
This polyporate form resembles *Persicarioipollis meuseli* Krutzsch 1962 in having coarsely reticulate sculpture with sinuous, duplicolumellate, palisade muri and irregularly polygonal meshes with small, obscured, and circular pores in the centres. It is also superficially similar to the Polygonaceous *Glencopollis ornatus* Pocknall and Mildenhall (1984), but the latter is polycolpate instead of polyporate.

Botanical affinity:
Polygonum (Polygonaceae).

Source ecology:
Common in freshwater swamp environments.

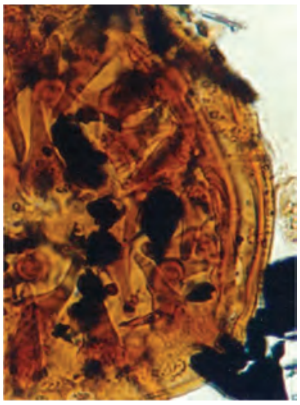
Suggested name for Quaternary records:
Polygonum type pollen.

Ecological group:
Freshwater swamp.

Genus *Echiperiporites*
van der Hammen and Wymstra 1964

Type species:
Echiperiporites estelae Germeraad et al. 1968.

Echiperiporites estelae
Germeraad, Hopping and Muller 1968. Plate 18, Fig. 11



Selected synonymy:
1968 *Echiperiporites estelae* Germeraad et al., p. 318, Pl. 10, Fig. 1.
1972 *Malvacearumpollis estelae* (Germeraad et al.) Hekel, p. 18, Pl. 6, Fig. 27.
1975 *Echiperiporites estelae* Germeraad et al.; Salard-Cheboldaeff, p. 183, Pl. 2, Figs. 8-10.

Description:
Pollen grain, centro-symmetrical, isopolar, spherical; periporate, pores 20 to 24, ectexinous and endexinous, slightly annulate, annuli 1½ to 2 µm wide, pores 4 to 6 µm wide, 10 to 12 µm apart. Nexine 1 µm thick; columellae about ½ µm thick, ~ 1 µm long; tectum smooth, < 1 µm thick, thickened at roots of spines; spines 6-9 µm high, 2 to 4 µm thick at base, conical, blunt, 6 to 10 µm apart (Germeraad et al., 1968).

Dimensions:
Equatorial diameter 50 (72) 110 µm (6 specimens measured from various horizons). Divides into two size ranges, one smaller, one very large.

Stratigraphic distribution:
Echiperiporites estelae ranges in age from the middle Eocene to Pleistocene in the Neotropics (Germeraad et al., 1968). In Nigeria, Germeraad et al. found this species to be rare, but subsequently it has been widely recorded from the late Eocene onward (Jan du Chene, 1978; Salard Chebaldaeff, 1975). This species has also been recorded from the late Eocene onward in Australia (as *Malvacearumpollis estelae*) by Hekel (1972) and the Miocene of India (Kumaran et al., 1995). In Borneo, Germeraad et al. (1968) record *E. estelae* from the middle

Miocene onward, a range which can be understood from the record in Malong 5G-17.2 well (see below) although it is also recorded in the Delah 5H-14.1 well in the Oligocene. In Thailand, Watanasak (1990) record this species in the early and middle Miocene. The pollen is sparsely distributed in low numbers in both Malong 5G-17.2 and Delah 5H-14.1 wells. The larger forms (80 to 110 µm) which according to Germeraad et al. (1968) are probably derived from *Hibiscus tiliaceus* (Malvaceae) are observed to be restricted to the topmost part of Malong well, within zone PR15. The smaller forms that occur in zones PR12B to PR14, and in zones PR3 to PR4 are more likely derived from *Thespesia populnea* (Germeraad et al., 1968).

Botanical affinity:
Malvaceae; smaller forms are probably derived from *Thespesia populnea,* whereas the larger ones are probably from *Hibiscus tiliaceus* (Germeraad et al., 1968).

Source ecology:
Hibiscus tiliaceus is common on sandy and rocky shores extending up rivers in their brackish reaches. *Thespesia populnea* grows widely along coasts and in mangrove swamps.

Suggested name for Quaternary records:
Thespesia and Hibiscus pollen (depending on size).

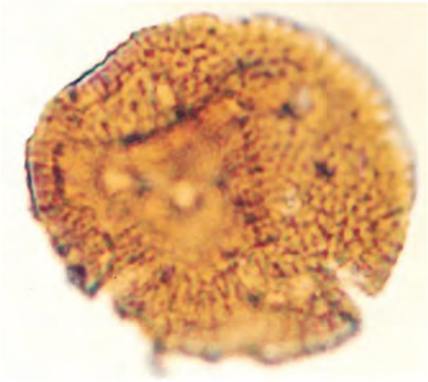
Ecological group:
Backmangrove.

Thespesia populnea*, Waru, Tanjung Ages, Pahang, Malaysia (photo by RJM).*

Genus *Thymelipollis*
Krutzsch 1966

Type species:
Thymelipollis retisculpturius Krutzsch 1966 (by original designation).

***Thymelipollis* sp.** Plate 18, Figs. 7, 8



Description:
Pollen grains amb circular to oval, with a thick wall up to 5 µm, with several layers, and a reticulate structure with several (13 to 25) small open pores that are more or less regularly distributed over the surface (modified from Krutzsch, 1966).

Dimensions:
Equatorial diameter 33 µm (1 specimen measured).

Stratigraphic distribution:
Only one specimen found in Malong 5G-17.2 well at 1010 m (DC) depth.

Botanical affinity:
Probably from *Daphne* (Thymelaeaceae).

Source ecology:
Common in perhumid forests, especially in lower montane forest.

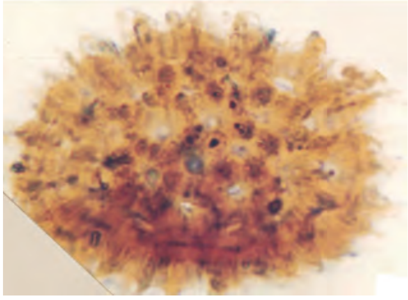
Suggested name for Quaternary records:
Daphne type pollen.

Ecological group:
Rainforest.

Genus *Polygonacidites*
Sah and Dutta 1968

Type species:
Polygonacidites frequens Sah and Dutta 1968.

***Polygonacidites* sp.** Plate 19, Fig. 1



Dimensions:
Equatorial diameter 57 μm (1 specimen measured).

Stratigraphic distribution:
Only one specimen found in Malong 5G-17.2 well at 625m (SWC) depth.

Botanical affinity:
Polygonum.

Suggested name for Quaternary records:
Polygonum.

Ecological group:
Freshwater swamp.

2.17 TRICOLPORATE POLLEN

Remarks:
The genera erected by van der Hammen (1954, 1956) to accommodate tricolporate pollen have been widely used even though they are contrary to the ICBN due to their typification using recent pollen. This has also added to the difficulty of applying names to these forms since van der Hammen invalidated a large number of especially useful names based on morphology. Thomson and Pflug's (1953) form-genera such as *Tricolporopollenites*, which is widely used to treat various tricolporate forms, is too widely circumscribed to have any a useful application. The form-genus *Tricolporites* proposed by Cookson in 1947 has also been widely used in a broader sense, especially in the Australian region, to accommodate a variety of tricolporate pollen types (e.g., Stover and Partridge, 1973). Potonié (1960) validated some of the more useful generic names previously published without reference to the requirements of the botanical code and other authors (e.g., Krutzsch, 1961, 1970; Kedves, 1978) have further developed a generic nomenclature based on the rules of the ICBN, and consequently, many species, which were previously classified under the generalised genera, of Thomson and Pflug (1953) have been transferred to these more appropriately defined genera.

In this study, the proposal of new genera and species of tricolpate and tricolporate forms have been kept to a minimum so as not to add more confusion to these taxonomically problematic groups. As far as possible, these species are attributed to tightly defined taxa.

Genus *Minutitriaperturites*
Morley and Jaizan Jais gen. nov.

Type species:
Minutitriaperturites minutus sp. nov.

Derivation of name:
From the very small size and triaperturate configuration.

Diagnosis:
Pollen grains, isopolar, prolate to subprolate, tricolporoidate or tricolporate, very small (less than 15 μm), essentially psilate.

Generic remarks:
This form-genus is used here to accommodate small sized (15 μm and less), tricolporoidate and tricolporate essentially psilate pollen with subprolate to prolate shape, which occur widely in tropical plant families today, such as Actinidiaceae, Achariaceae, Clethraceae, Cunoniaceae Datiscaceae, Elaeocarpaceae, and some Rhizophoraceae. Hamilton and Stephenson (2020) provide a recent attempt to differentiate modern pollen in this group and bring to attention many of the problems in identifying such pollen as fossils. A good example within this group is pollen of the *Elaeocarpus* configuration, which without doubt is a common element of Australian Cenozoic floras (has a range of Oligocene to Pleistocene in Australia according to Martin, 1994), but an appropriate form-taxon has yet to be proposed to accommodate it.

Minutitriaperturites minutus

Morley and Jaizan Jais sp. nov. Plate 19, Figs. 2, 3

Derivation of name:
From the very small size of the grain.

Holotype:
Plate 19, Figs. 2, 3. Slide Malong-2, 934 m, SWC (S1), England Finder P34/4.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 934 m depth; age late Miocene, zone PR12A.

Description:
Pollen spherical to prolate with rounded poles, tricolporate, very small, with a size range from 5 to 15 μm; long and equatorially constricted colpi, with small polar area index; exine psilate, difficult to discern any layers.

Dimensions:
Length 13 (14) 15 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
Martin (1994) suggested that in Australia Elaeocarpaceae pollen ranges from the Oligocene to recent, but the range and identity of this pollen type is rarely considered prior to the Quaternary. Present in low percentages in the Malong 5G-17.2 well.

Remarks:
This small tricolporate subspheroidal pollen resembles some species of *Cyrillaceaepollenites* in having broadly rounded poles, with more or less rounded pores and psilate exine, but differ in being smaller.

Botanical affinity :
The Malay Basin specimens are probably derived from Elaeocarpaceae based on their small size tricolporate configuration and psilate exine. Hamilton and Stephenson (2020) provide a useful comparison of small tricolporate pollen.

Source ecology:
Elaeocarpaceae are small trees occurring from coasts to mountains. They occur in swamp forest, for instance as at Tasek Bera in Pahang (Morley, 1981), in primary and secondary forest and are particularly common in montane forests.

Suggested name for Quaternary records:
Elaeocarpus type.

Ecological group:
Freshwater swamp forests.

Genus ***Cupuliferoipollenites***

Potonié 1951 ex Potonié 1960

Type species:
Cupuliferoipollenites pusillus
(Potonié) Potonié 1960.

Generic remarks:
The form-genus *Cupuliferoipollenites* Potonié 1951 ex Potonié 1960 is used here to accommodate small to medium sized tricolporate pollen with prolate to perprolate shape and psilate to scabrate wall of the *'Lithocarpus'* configuration.

Oaks in montane forest, Quercus ngochoaensis *(det. Dr Huong Son) Ba Vi National Park, Vietnam (photo by RJM).*

Cupuliferoipollenites oviformis (Potonié) Potonié 1960. Plate 19, Figs. 4, 5

Selected synonymy:
1931 *Pollenites oviformis* Potonié, p. 328, Pl. 1, Fig. 20.
1934 *Pollenites oviformis* Potonié; Potonié, p. 95, Pl. 5, Figs. 23-27.
1953 *Tricolporopollenites cingulum* subsp. *oviformis* (Potonié) Thomson and Pflug, p. 100, Pl. 12, Figs. 42-49.
1960a *Cupuliferoipollenites oviformis* (Potonié) Potonié, p. 98.

Description:
Pollen, radially symmetrical, isopolar, prolate; in equatorial view near circular or oval; tricolporate, colpi long, pores small, oval; exine thin, 0.5 μm thick, without indiscernible layers; sculpture psilate to faintly scabrate especially at poles; columellae indiscernible, or weakly discernible at the poles.

Dimensions:
Length 11 (14) 19 μm, width 6 (8) 10 μm (18 specimens measured from various horizons).

Stratigraphic distribution:
Pollen comparable to Fagaceae and placed into the genus *Cupuliferoipollenites* are widely reported from the Northern Hemisphere (Muller, 1981), with many records from the Cenozoic of Europe, e.g., by Potonié (1931, 1934); Thomson and Pflug (1953); Kedves (1978); Kedves and Herngreen (1980); Wilkinson and Boulter (1980) and others. Also recorded from the Paleocene to Pliocene of China (Li, 1989; Tong et al., 2001; Yuan et al., 2020; Tang et al., 2020) and Myanmar (Huang et al., 2021). Present in moderate to high percentages in the Malong 5G-17.2 within zones PR8 to PR15. More rarely represented in the Delah 5H-14.1 well, being absent from zones PR1 to PR2 and present in low numbers in zones PR3 to PR6/7.

Remarks and comparison:
These specimens are similar to those described and illustrated by Potonié (1931, 1934).

Botanical affinity:
This pollen type compares especially to the genera *Lithocarpus* and *Castanopsis* (Fagaceae).

Source ecology:
Lithocarpus and *Castanopsis* are trees, especially common in lower montane forests (e.g., Ashton, 2014; Cockburn, 1972) but with some lowland species, especially within peat swamps (Morley, 1982).

Suggested name for Quaternary records:
Lithocarpus type.

Ecological group:
Montane forest.

***Cupuliferoipollenites* sp. A.** Plate 19, Figs. 11, 12

Description:
Pollen radially symmetrical, isopolar, perprolate in equatorial view, exine psilate or scabrate, colpi transversales long, extending beyond colpus margins, colpi transversal with thickened margines.

Dimensions:
Length 19 μm, width 9 μm (1 specimen measured).

Stratigraphic distribution:
Very rare, only one specimen found in each well.

Remarks and comparison:
This tricolporate form is distinguished by its perprolate shape, psilate to scabrate wall with long colpi and narrow costate colpi transversales that extend beyond colpus margins and length being twice the width. It differs from *C. oviformis* in being larger in size and more elongated in shape.

Botanical affinity:
Antidesma (Euphorbiaceae).

Source ecology:
Common in forests of Peninsular Malaysia.

Suggested name for Quaternary records:
Antidesma type.

Ecological group:
Lowland forests.

Plate 19

Fig. 1 *Polygonacidites* sp. (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder F14.

Figs. 2, 3 *Minutitriaperturites minutus* Morley and Jaizan Jais sp. *nov*. Figs. 2, 3 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder P34/4.

Figs. 4, 5 *Cupuliferoipollenites oviformis* (Potonié) Potonié 1960. Figs. 4, 5 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder P43.

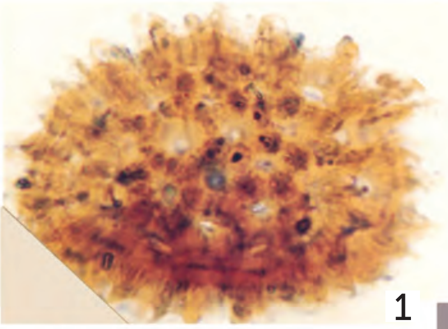
Figs. 6-10 *Zonocostites ramonae* Germeraad et al. 1968. Fig. 6 (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder M23. Fig. 7 (x 1000): Slide Malong-2, 1045-1050 m, DC (S1); England Finder P25/2. Fig. 8 (x 1000, clustered): Slide Malong-2, 934 m, SWC (S1); England Finder P24. Figs. 9, 10 (x 1000): Slide Malong-2, 518 m, SWC (S1); England Finder L31/1.

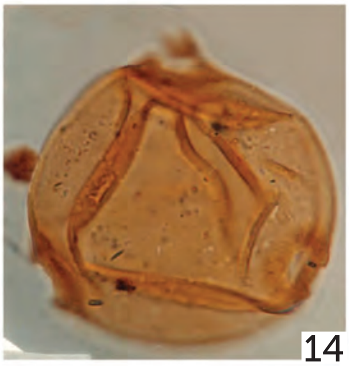
Figs. 11, 12 *Cupuliferoipollenites* sp. A. Figs. 11, 12 (x 1000): Slide Malong-2, 760-770 m, DC (S1); England Finder L21/1.

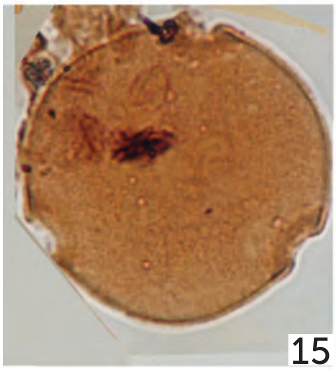
Figs. 13, 14 *Lakiapollis ovatus* Venkatachala and Kar 1969. Figs. 13, 14 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder P19/3.

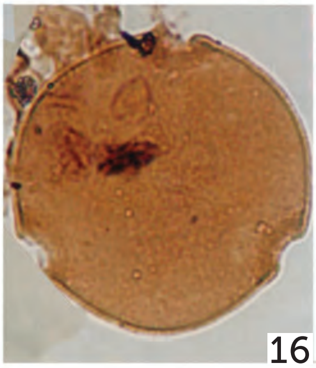
Figs. 15, 16 *Brevicolporites guinetii* Salard-Cheboldaeff 1978. Figs. 15, 16 (x 1000): Slide Malong-2, 1345-1350 m, DC (S1); England Finder U17/2.

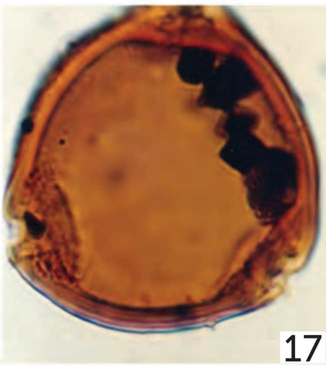
Figs. 17-20 *Lakiapollis pachydermus* Jaizan Jais and Morley sp. nov. Fig. 17 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder P21/4. Figs. 18, 19, 20 (Holotype, x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder H34/2.

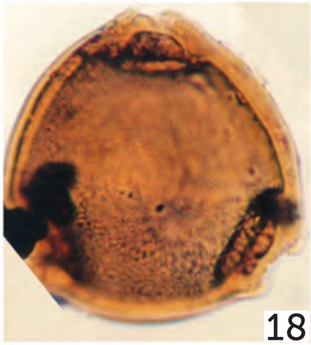


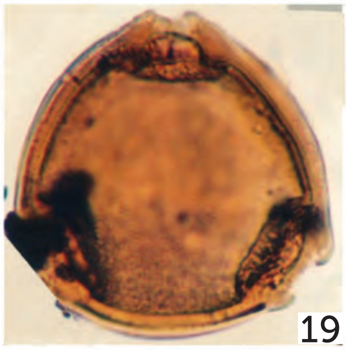


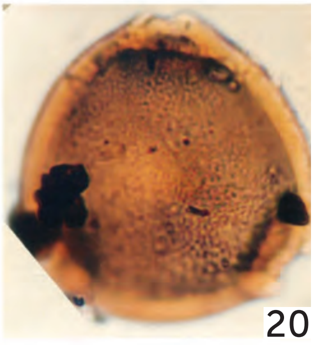












Rhizophora *spp. (Bakau), mangrove belt, Brunei River, Brunei (photo by RJM).*

Genus *Zonocostites*
Germeraad, Hopping and Muller 1968

Type species:
Zonocostites ramonae Germeraad, Hopping and Muller 1968.

Zonocostites ramonae
Germeraad, Hopping and Muller 1968. Plate 19, Figs. 6-10

Selected synonymy:

1955 Dispersed pollen attributed to Rhizophoraceae in Kuyl, Muller and Waterbolk, p. 64, Pl. 2, Figs. 4-7.

1964 Dispersed pollen attributed to *Rhizophora* type in Muller, p. 37, Pl. 1, Fig. 3.

1968 *Zonocostites ramonae* Germeraad, Hopping and Muller; p. 333, Pl. 15, Figs. 6, 7.

1972 *Zonocostites ramonae* Germeraad, Hopping and Muller; Hekel, p. 13, Pl. 3, Figs. 9, 10, 15.

1986 *Zonocostites ramonae* Germeraad, Hopping and Muller; Lorente, p. 204, Pl. 23, Figs. 12, 13.

Description:

Pollen grain, radially symmetrical, isopolar, spherical, tricolporate, colpi medium long, straight with pointed ends, slightly marginate, endoapertures equatorially elongated to almost fused, distinctly costate, in polar view slightly vestibulate, endexine about ½ μm thick; columellae < ½ μm thick and high; tectum < ½ μm thick, densely perforate, coarser on poles and finer to almost psilate at the equatorial belt, perforations < ½ μm wide (Germeraad et al.,1968).

Dimensions:

Length 12 (15) 19 μm, width 10 (12) 17 μm (21) specimens measured from various horizons).

Stratigraphic distribution:

Recorded from the later Eocene to Recent of Southeast Asia (Muller, 1964; Germeraad et al., 1968; Anderson and Muller, 1975; Morley, 2000; Morley et al., 2003) and South America (Germeraad et al., 1968; Regali et al., 1974; Dueñas, 1980; Fosola et al., 1985; Lorente, 1986; Muller et al., 1987); early Miocene to Pleistocene of Nigeria (Germeraad et al., 1968; Rao and Kumaran, 1988; Oboh

Rhizophora mucronata *in fruit, Kuala Selangor Malaysia (photo by RJM).*

et al., 1992); Oligocene to Pliocene of Queensland, Australia (Hekel, 1972); Oligocene to Pliocene of South China Sea; Oligocene to Recent of India (Venkatachala and Rawat, 1973; Mathur and Chopra, 1987). Present in moderate percentages through the Oligocene succession (zones PR1 to PR6/7) seen in Delah 5H-14.1 well, but in high frequencies throughout the Malong 5G-17.2 well from zone PR8 to PR15.

Remarks:
The Malay Basin specimens are similar to those described and illustrated by Germeraad et al. (1968) that range from 16 to 19 μm in length. Smaller specimens are also included here.

Botanical affinity:
This pollen is derived from *Rhizophora* and *Bruguiera* (Rhizophoraceae). *Rhizophora* pollen tends to be larger than *Bruguiera*, (Muller and Caratini, 1977; Thanikaimoni, 1987). Since fossil pollen tends to be smaller than its modern counterparts due to compression, it is not advised to use size to differentiate these genera in fossil pollen.

Source ecology:
Mangrove trees, especially those occurring on the outer edge of mangrove swamps where tidal inundation is most frequent. *Zonocostites ramonae* is one of the most important pollen types that are used in sequence biostratigraphy (Morley, 1996; Morley et al., 2021) since maxima may coincide with the transgressive systems tract.

Suggested name for Quaternary records:
Rhizophora type.

Ecological group:
Mangrove.

Rhizophora mucronata*, Bali (photo by RJM).*

Genus *Lakiapollis*

Venkatachala and Kar 1969

Type species:

Lakiapollis ovatus Venkatachala and Kar 1969.

Lakiapollis ovatus

Venkatachala and Kar 1969. Plate 19, Figs. 13, 14

Selected synonymy:

1969 *Lakiapollis ovatus* Venkatachala and Kar, p. 168, Pl. 3, Figs. 77, 78.

1975 Dispersed pollen attributed to *Durio* in Anderson and Muller, p. 299, Pl. 1, Fig. 4.

1984 *Lakiapollis ovatus* Venkatachala and Kar; Thanikaimoni et al., p. 39, Pl. 20, Figs. 301-305; Pl. 21, Figs. 306-309.

1989 *Lakiapollis ovatus* Venkatachala and Kar; Venkatachala et al., p. 19, Pl. 9, Figs. 1-6.

1998 *Lakiapollis ovatus* Venkatachala and Kar; Morley, p. 233 Fig. 3.

Description:

Pollen grains radially symmetrical, isopolar, subspherical to spherical, tricolporate, brevicolpate, ectoapertures elliptic, short, without margins, endoapertures elliptic, also short, with wide costae, sexine thicker than nexine, except in area of costae, tectum psilate.

Dimensions:

Equatorial diameter 34 (43) 53 µm (11 specimens measured from various horizons).

Stratigraphic distribution:

Paleocene to Eocene of India (Venkatachala and Kar, 1969; Kar, 1978; Kar and Saxena, 1981; Thanikaimoni et al., 1984; Kar, 1985; Kar and Kumar, 1986; Raha et al., 1987); middle Eocene of Sulawesi and Java (Morley, 1998, 2000), Oligocene to Miocene of Borneo (Muller, 1972; Anderson and Muller, 1975; Barré de Cruz, 1982). In Malong 5G-17.2 well, regularly present in the upper part, from zone PR12 to PR15, but rare from zone PR8 to PR11. Very rare in Delah 5H-14.1 well.

Remarks and comparison:

The Malay Basin specimens agree in all aspects with the type specimen described and illustrated by Venkatachala and Kar (1969). It differs from *L. pachydermus* sp. nov. in having a thinner wall. Very rare in Delah 5H-14.1 well (zones PR1 to PR6/7, in Malong 5G-17.2, present in low numbers in zones PR9 to PR12A, consistently present in zones PR12B to PR14, and moderately common in zone PR15.

Botanical affinity:

This pollen type compares closely with that of *Durio* and also *Cullenia* (Bombacaceae). *Durio* is the classic example of an ‘out of India’ taxon, that evolved on the Indian Plate, and dispersed to Southeast Asia after India collided with Asia (Morley, 1998, 2000, 2018), and then went extinct in India following the expansion of monsoonal climates in younger Cenozoic (Morley and Morley, 2020).

Source ecology:

Durio carinatus are medium to large trees common in phasic community P.C.1 in peat swamps in Sarawak (Anderson, 1963), Other *Durio* spp. are found in the lowland and primary forests.

Suggested name for Quaternary records:

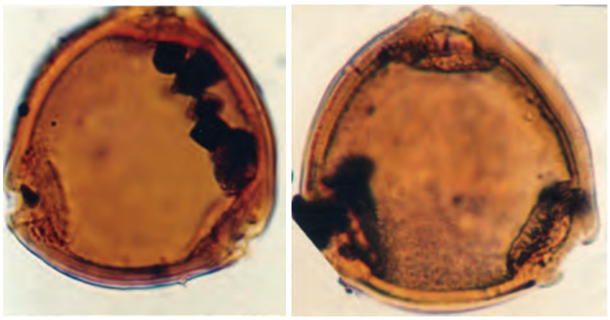
Durio type.

Ecological group:

Peat swamp forests.

Durio zibethinus *(Durian), Singapore (photo by Ng Yu Fei, Creative Commons).*

Lakiapollis pachydermus
Jaizan Jais and Morley sp. nov. Plate 19, Figs. 17-20



Derivation of name:
Latin *pachydermus*, thick walled.

Holotype:
Plate 19, Figs. 18-20. Slide Malong-2, 483 m, SWC (S2), England Finder H34/2. Grain in polar aspect, subcircular in outline, diameter 41 μm; exine 3 μm thick, pores 7 μm in diameter, colpi 8 μm long.

Type locality:
Well, Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 483 m depth; age Pliocene, zone PR15.

Description:
Pollen grains radially symmetrical, isopolar, subspheroidal; tricolporate; colpi short, about 10 μm long; pores elliptic, up to 10 μm in diameter with up to 5 μm wide costae; exine psilate to faintly per-reticulate, more than 2.5 μm thick, thicker at the costae; sexine thicker than nexine except at the costae, 1.5 to 2 μm thick; tectum perforate, infratectum columellate, 1 to 1.5 μm in height; nexine around 2 μm thick, thicker at the costae (up to 8 μm).

Dimensions:
Equatorial diameter 35 (43) 54 μm (4 specimens measured from various horizons).

Stratigraphic distribution:
Present in low percentages and restricted to the upper part of Malong 5G-17.2 well, from zone PR13 to PR15.

Remarks and comparison:
This species differs from *L. ovatus* by its thicker wall and from *L. matanamadhensis* Venkatachala and Kar 1969 in its wall structure.

Botanical affinity:
Most likely derived from *Durio* (Bombacaceae).

Source ecology:
As noted above, *Durio carinatus* are medium to large trees common in phasic community P.C.1 in peat swamps in Sarawak (Anderson, 1963). Other *Durio* spp. are also found in the lowland forests.

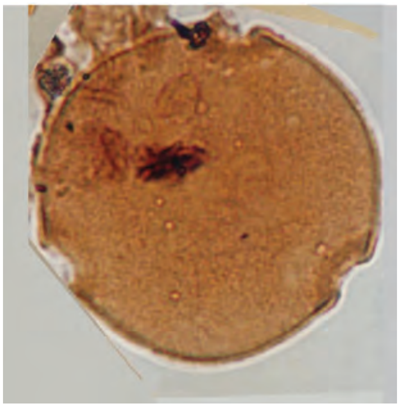
Suggested name for Quaternary records:
Durio type.

Ecological group:
Peat swamp forests.

Genus _Brevicolporites_
Anderson 1960

Type species:
Brevicolporites colpella Anderson 1960.

Brevicolporites guinetii
Salard-Cheboldaeff 1978. Plate 19, Figs. 15, 16



Selected synonymy:
1978 *Brevicolporites guinetii* Salard-Cheboldaeff, p. 226, Pl. 2, Fig. 6.

Description:
Pollen, radially symmetrical, isopolar, oblate, outline circular in polar view, not seen in equatorial view, tricolporate, with indistinct, short colpi and large, annulate endospores, exine consists of a thin nexine which thickens around the endoapertures, and much thicker sexine, which is psilate, without discernible structure.

Dimensions:
Equatorial diameter 29 (34) 38 μm (15 specimens measured from various horizons).

Stratigraphic distribution:
Eocene to early Miocene of Cameroon (Salard-Cheboldaeff, 1978). Mainly present in low percentages in the bottom part of Delah 5H-14.1 well within zones PR1 to PR3.

Remarks:
The Malay Basin specimens are similar to those described and illustrated by Salard-Cheboldaeff (1978) except that the former are generally slightly smaller in size.

Botanical affinity:
Pentaclethra (Fabaceae), probably *P. macrophylla* (Salard-Cheboldaeff, 1978).

Source ecology:
Pentaclethra is a genus of trees occurring widely in swamp forests in the Neotropics and equatorial Africa (Marchant et al., 2002). *P. macrophylla* is restricted to equatorial Africa. It does not occur in Southeast Asia, so may reflect a different genus of Fabaceae, or the genus may now be extinct in the region.

Suggested name for Quaternary records:
Pentaclethra macrophylla type.

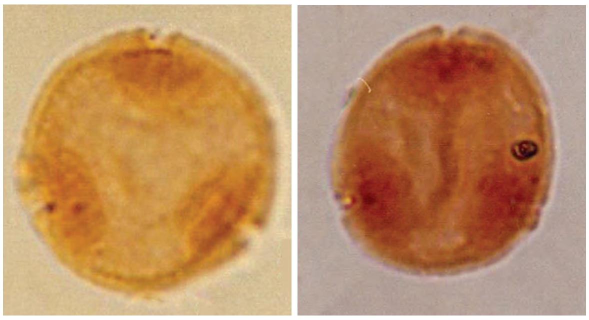
Ecological group:
Swamp forest.

Genus *Tricolporopollenites*
Pflug and Thomson in Thomson and Pflug 1953

Type species:
Tricolporopollenites delium (Potonié 1931) ex. Thomson and Pflug 1953.

The broadly defined form genus *Tricolporopollenites* is used for small tricolporate oblate pollen of the *Macaranga* configuration following McIntyre (1965), attribution to *Nyssapollenites* as per Kemp and Harris (1977) seems inappropriate.

Tricolporopollenites endobalteus
(McIntyre 1965) Kemp and Harris 1977 emend. Mildenhall and Pocknall 1989. Plate 20, Figs. 1-3



Selected synonymy:
1965 *Tricolporopollenites endobalteus* McIntyre, p. 211, Figs. 27-29.
cf. 1977 *Nyssapollenites endobalteus* (McIntyre) Kemp and Harris, p. 42, Pl. 6, Figs. 14, 15.
1989 *Nyssapollenites endobalteus* (McIntyre) Kemp and Harris emend. Mildenhall and Pocknall, p. 47, Pl. 11, Figs. 5, 6.

Description:
Pollen radially symmetrical, isopolar, oblate, outline circular in polar view, tricolporate, with distinct, short colpi lacking margines and large, lalongate endoapertures clearly discernible in equatorial view; endoapertures with thickened costae; nexine thicker than sexine except in endoapertural region, sexine finely microreticulate.

Dimensions:
Equatorial diameter 14 (17) 21 µm (23 specimens measured from various horizons).

Stratigraphic distribution:
In Australia, *T. endobalteus* ranges from the late Eocene to the Pleistocene (Martin, 1994). In New Zealand, the range is Oligocene to Miocene (McIntyre, 1965; Pocknall and Mildenhall, 1989). Present in low to moderate percentages through both the Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:
The Malay Basin specimens fit the description of *Tricolporopollenites endobalteus* McIntyre (1965). No attempt is made to transfer this species to a more appropriate genus.

Botanical affinity:
This small tricolporate oblate pollen with a distinct endoaperture is found in the genus *Macaranga* and also occurs in *Mallotus* (Euphorbiaceae).

Source ecology:
Macaranga spp. are trees of secondary vegetation, but also occur is swamps, especially seasonal swamps such as the Rawa Danau in West Java (van der Kaars et al., 2001). *Mallotus* spp. are characteristic of lowland forest.

Suggested name for Quaternary records:
Macaranga type.

Ecological group:
Disturbed vegetation and swamp.

Macaranga grandifolia, *Bogor, Java (photo by RJM).*

Genus *Ranunculacidites*

Sah 1967

Type species:
Ranunculacidites communis Sah 1967.

Ranunculacidites operculatus

(van der Hammen and Wijmstra 1964) Jaramillo and Dilcher 2001. Plate 20, Fig. 4

Selected synonymy:

1964 *Psilatricolporites operculatus* van der Hammen and Wijmstra, p. 236, Pl. 1, Fig. 13.

1968 *Psilatricolporites operculatus* van der Hammen and Wijmstra; in Germeraad et al., p. 238, Pl. 15, Fig. 3.

1972 *Psilatricolporites operculatus* van der Hammen and Wijmstra; in Hekel, p. 13, Pl. 4, Fig. 5.

1986 *Psilatricolporites operculatus* van der Hammen and Wijmstra; in Lorente, p. 196, Pl. 21, Fig. 3.

2001 *Ranunculacidites operculatus* van der Hammen and Wymstra, Jaramillo and Dilcher, Pl. 15, Fig. 23.

2021 *Ranunculacidites operculatus* van der Hammen and Wymstra, Jaramillo and Dilcher in Huang et al., Pl. III, Figs. 13-15.

Description:
Pollen, radially symmetrical, isopolar, oblate; amb triangular-convex to circular; tricolporate, colpi marginate with distinct opercula covering pores, opercula 2.8 to 4.9 μm long, 1.0 to 2.0 μm wide at the equator; exine quite thin, 0.3 to 0.5 μm thick, slightly thicker at margins of the colpi; sculpture psilate to scabrate (Huang et al., 2021).

Dimensions:
Equatorial diameter 16 (17) 18 μm (3 specimens measured from various horizons).

Distribution:
Present in low percentages in both sections.

Stratigraphic distribution:
The oldest record is from the Paleocene in Venezuela and Colombia (Jaramillo et al., 2010, 2011), with subsequent records from the middle Eocene of Caribbean area and Nigeria (Germeraad et al., 1968), and the late Eocene of the Yaw Formation in Myanmar (Huang et al., 2021) but not until the Oligocene in Australia (Martin, 1994) and the early Miocene in India (Ramanujam et al., 1991). Scattered in low numbers through the Malong 5G-17.2 and Delah 5H-14.1 wells.

Alchornea rugosa, *Bogor, Java (photo by RJM).*

Remarks:

The Malay Basin specimens agree in all aspects with the description of *Psilatricolporites operculatus* by van der Hammen and Wijmstra (1964). The form-genus *Psilatricolporites* van der Hammen 1956 ex van der Hammen and Wijmstra 1964, however, is contrary to the ICBN despite an attempt to assign a lectogenotype to the genus. Hence the above species was referred to the form-genus *Ranunculacidites* Sah 1967 by Jaramillo and Dilcher, 2001.

Botanical affinity:

This pollen type is found in the genus *Alchornea* (Euphorbiaceae).

Source ecology:

Trees of seasonal swamp forests in tropical and subtropical areas.

Suggested name for Quaternary records:

Alchornea pollen.

Ecological group:

Swamp forest.

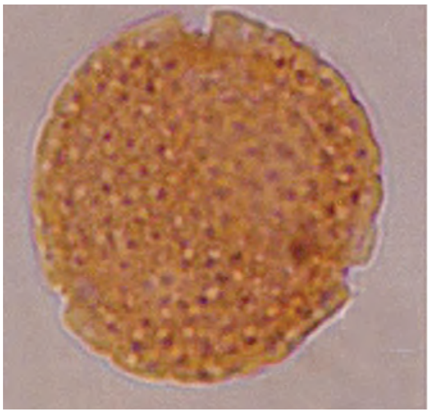
Genus *Minutitricolporites*
Kar 1985 emend. Jaizan Jais and Morley

Type species:
Minutitricolporites minutus Kar 1985.

Emended diagnosis:
Small oblate pollen grains with subcircular to circular amb; tricolporate to tricolporoidate, brevicolpate; colpi short, tapering at ends; pores 1 to 2 μm across, often indistinct, exine ±1 μm thick, sculptures more or less uniform in size, either finely reticulate, foveolate or minutely echinate.

Remarks:
This genus is emended to include small brevicolporate oblate forms with foveolate and a minutely echinate wall. It differs from other brevicolporate genera by its exine ornamentation.

Minutitricolporites duplibaculatus
Jaizan Jais and Morley sp. nov. Plate 20, Figs. 5-8



Synonymy:
1975 Dispersed pollen attributed to *Blumeodendron* in Anderson and Muller, p. 299, Pl. 1, Fig. 4.

Derivation of name:
From its duplibaculate or duplicolumellate muri.

Holotype:
Plate 20, Figs. 5, 6. Slide Malong-2, 934 m, SWC (S1), England Finder K42/3. Grain in polar aspect, circular in outline, diameter 21 μm; exine 1.5 μm thick, pores 1.5 μm wide, colpi 3 μm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 934 m depth; age middle Miocene, zone PR12A.

Description:
Pollen grains radially symmetrical, isopolar, oblate spheroidal; tricolporate; pores small, up to 1.5 μm wide, slightly costate; colpi very short and narrow, up to 3 μm long, slightly costate; exine tectate, duplicolumellate, up to 1.5 μm thick; tectum perforatum with broad muri and small lumina of up to 1 μm in diameter.

Dimensions:
Equatorial diameter 13 (17) 21 μm (10 specimens measured from various horizons).

Distribution:
Present in low to moderate percentages in Malong 5G-17.2 well.

Stratigraphic distribution:
Blumeodendron has been recorded from the Oligocene to Miocene of Borneo (Anderson and Muller, 1975). It is regularly present in the Malong 5G-17.2 well from zone PR12A to PR15, with a few additional specimens within zone PR9. It is absent from the Delah 5H-14.1 well.

Comparison:
This form differs from *Tricolporopollenites. endobalteus* and *Minutitricolporites. microechinatus* sp. nov. in having a perforate wall.

Botanical affinity:
Blumeodendron (Euphorbiaceae).

Source ecology:
Herbs, shrubs, or trees in swamp forests.

Ecological group:
Peat swamp forests.

Genus *Verrutricolporites*

van der Hammen and Wijmstra 1964

Type species:
Verrutricolporites rotundiporus van der Hammen and Wijmstra 1964.

Verrutricolporites oblatus

Morley and Jaizan Jais sp. nov. Plate 20, Figs. 20, 21

Derivation of name:
From its oblate shape.

Holotype:
Plate 20, Fig. 20. Slide Delah-1, 2400-2405 m, DC (S1), England Finder R25.

Type locality:
Well Delah 5H-14.1, Malay Basin, offshore Peninsular Malaysia; cuttings sample at 2400-2405 m depth; age late Oligocene, zone PR4.

Description:
The pollen grains of this genus are spherical-suboblate, 35 µm in size, tricolporate with long, equatorially bridged, ektoapertures and a fairly thick tectate exine, covered with a characteristic irregularly rugulate sculpture and with a dense layer of minute columellae.

Dimensions:
Equatorial diameter 21 (24) 27 µm (5 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:
Included here are oblate, brevicolpate forms with fine to medium verrucate wall.

Parastemon urophyllum, *a large tree, common in peat swamp forests but also along river banks, the seashore and secondary forests with poor soil (photo from www.nparks.gov.sg/FloraFaunaWeb/Flora/4/5/4515).*

Botanical affinity:
Parastemon.

Source ecology:
Peat swamp, river banks and lowland forest trees.

Ecological group:
Peat swamp forests.

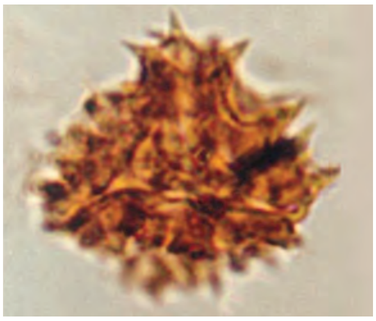
Genus *Tubifloridites*
Cookson ex Potonié 1960

Type species:
Tubifloridites antipodica Cookson 1947.

Generic remarks:
Hekel (1972), Kemp and Harris (1977) and Truswell and Owen (1988), among others, have discussed the inadequacies of the diagnoses of spinose tricolporate form genera. This is partly due to the invalidity of *Echitricolporites* van der Hammen 1956 despite the attempt to validate the genus by Germeraad et al. (1968) by selecting a lectogenotype in place of the extant species designated by the former author. Cookson's *Tubulifloridites* (Cookson, 1947) was initially published following the 'coenotype' scheme of Erdtman (1947) and was not validly published following the ICBN rules until validated by Potonié (1960) and is used here, with *Echitricolporites spinosus* of Germeraad et al. being a junior synonym. The relationship to the genus *Compositoipollenites* Potonié 1951 remains vague.

Tubifloridites spinosus

van der Hammen emend. Morley and Jaizan Jais comb. nov. Plate 21, Figs. 1, 2



Selected synonymy:
1956 *Echitricolporites spinosus* van der Hammen, p. 92, Pl. 10, Fig. 30.
1968 *Echitricolporites spinosus* van der Hammen ex Germeraad, Hopping and Muller, p. 335, Pl. 16, Figs. 11, 12.

Description:
Single grain, radially symmetrical, isopolar, spherical, tricolporate. Colpi ectexinous, straight with pointed ends, fairly long; pores indistinct, endexine < ½ µm thick; columellae ½ µm long (½ to 1 µm long underneath spines), < ½ µm thick; tectate-echinate, tectum < ½ µm thick, spines 3 to 6 µm long, 2 to 4 µm thick at base, sharply pointed, rather densely spaced (Germeraad et al., 1968).

Dimensions:
Equatorial diameter, minimum 20 µm, maximum 23 µm (excluding spines; 2 specimens measured).

Stratigraphic distribution:
Pollen of the 'Tubiflorae' (see below). is widely recorded from the early Miocene onward (Muller, 1981). However, older records are also noted, from the Oligocene of Europe (e.g., *Tricolporopollenites microechinatus* Hochuli 1978) and the Ninetyeast Ridge (*Tubifloridites antipodica* Kemp and Harris 1975, 1977). The oldest pollen of this type is *Mutisiapollis telleriae* from the middle Eocene of Patagonia, from an inflorescence attributable to the subfamily Mutisoideae (Barreda et al., 2010) and comparable to records from Angola (Morley unpublished). Very rare and sparsely distributed through the early, middle and late Miocene in the Malong 5G-17.2 well.

Remarks:
The Malay Basin specimens are similar to the type material described by Germeraad et al. (1968) and are smaller than those placed in *Tubifloridites antipodica* by Cookson (1947).

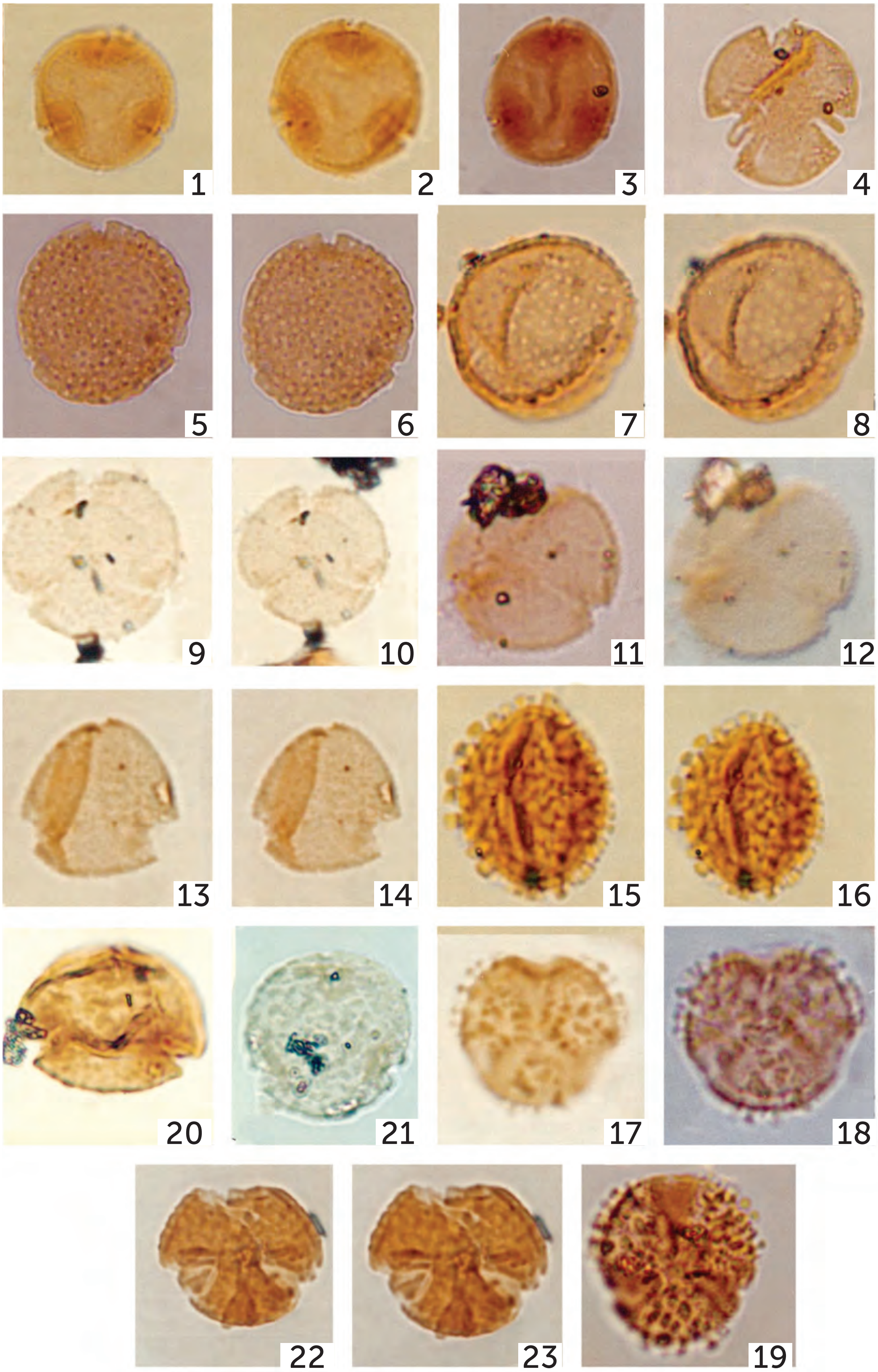
Botanical affinity:
Tubiflorae of the Asteraceae (formerly Compositae).

Source ecology:
Most Asteraceae in the Malay Peninsula are herbs and shrubs in open areas, except for *Vernonia,* which is a large montane forest tree but has lophate pollen. Asteraceae are also characteristic of more open seasonal, deciduous and semi evergreen forest, disturbed areas, such as *Eupatorium*, pictured below, and also from swamps (Morley et al., 2020), which are thought to be the main source of pollen recorded here.

Eupatorium *sp., shrub of secondary vegetation, West Java (photo by RJM).*

Ecological group:
Seasonal and disturbed vegetation and swamp.

Plate 20



Figs. 1-3 *Triporopollenites endobalteus* (McIntyre 1965) Kemp and Harris 1977 emend. Mildenhall and Pocknall 1989. Fig. 1 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L34/1. Fig. 2 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L34/1. Fig. 3 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder V37.

Fig. 4 *Ranunculacidites operculatus* (van der Hammen and Wijmstra 1964) Jaramillo and Dilcher (2001), p. 146, Pl. 15. Fig. 23. Fig. (4) (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder F41.

Figs. 5-8 *Minutitricolporites duplibaculatus* Jaizan Jais and Morley sp. nov. Figs. 5, 6 (Holotype, x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder K42/3. Figs. 7, 8 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder J21/3.

Figs. 9-14 *Minutitricolporites microechinatus* Jaizan Jais and Morley sp. nov. Figs. 9, 10 (Holotype, x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder T30/3. Figs. 11, 12 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder T27/3. Figs. 13, 14 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder L8/4.

Figs. 15, 16 *Ilexpollenites clifdenensis* McIntyre 1968. Figs. 15, 16 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder H20/4.

Figs. 17-19 *Ilexpollenites anguloclavatus* McIntyre 1968. Figs. 17, 18 (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder M33/1. Fig. 19 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder Q37/3.

Figs. 20, 21 *Verrutricolporites oblatus* Morley and Jaizan Jais sp. nov. Fig. 20 (x 1000): Slide Delah-1, 2400-2405 m, DC (S1); England Finder R25. Fig. 21 (x 1000 Holotype): Slide Malong-2, 503 m, SWC (S2); England Finder J25/1.

Figs. 22, 23 *Rugutricolporites undulatus* (Salard-Cheboldaeff 1978) Jaizan Jais and Morley comb. nov. Figs. 22, 23 (x 1000): Slide Malong-2, 900-910 m, DC (S1); England Finder L23/2.

Genus *Ilexpollenites*

Thiergart 1937 ex Potonié 1960

Type species:

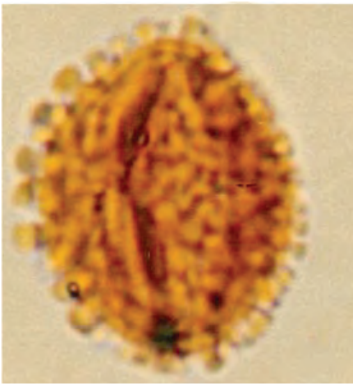
Ilexpollenites iliacus (Potonié) Thiergart ex Potonié 1960.

The fossil and evolutionary history of *Ilex*, based on the record of *Ilexpollenites* has been reviewed by Loizeau et al. (2005) and summarised in Huang et al. (2021). *Ilexpollenites* has been recorded from the Turonian of Australia by Martin (1977) and the Coniacian of equatorial Africa by Boltenhagen (1976) suggesting a Gondwanan origin. There is subsequently a gap in its distribution, until the Maastrichtian, where it has been reported from California (Chmura, 1973). From the Paleocene and Eocene, it is widely reported from the Americas, Eurasia and Australia but not from Africa or India (Loizeau et al., 2005).

In Southeast Asia, the oldest record is *Gemmatricolpites gemmatus* from the Paleocene of Sarawak (Muller, 1968; Morley, 2000), with subsequent records from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and the late Eocene Yaw Formation in Myanmar (Huang et al., 2021) and subsequently from the Oligocene onward (Muller, 1972). The oldest records from India are all from Assam, and restricted to the Neogene (e.g., Mandaokar, 2004) suggesting that *Ilex* dispersed into India during the Neogene (Huang et al., 2021). There are two common morphotypes recorded in the Malaysian Neogene, prolate and oblate-spheroidal, differentiated below as two separate species.

Ilexpollenites clifdenensis

McIntyre 1968. Plate 20, Figs. 15, 16



Selected synonymy:

1968 *Ilexpollenites clifdenensis* McIntyre, p. 182, Figs. 9-11.

Description:

Pollen tricolporate, equatorial view prolate; generally, in polar view colpi often gaping, long, endoapertures circular; often obscured, exine about 1 µm thick and layers indiscernible; columellae indiscernible; sculpture densely clavate with clavae 1 to 1.5 µm high, 0.1 to 2 µm wide.

Dimensions:

Length 13 (19) 28 µm, width 11 (14) 20 µm (7 specimens measured from various horizons).

Stratigraphic distribution:

The global distribution of *Ilexpollenites* is discussed above. *Ilexpollenites* spp. are very rare in the Oligocene of Delah 5H-14.1 well, but common in the Miocene and Pliocene in Malong 5G-17.2. *Ilexpollenites clifdenensis* is very common in zones PR6/7 and PR8, where they occur in maxima immediately preceding maxima of mangrove pollen, suggesting a sequence biostratigraphic control on abundance. It is consistently present in moderate numbers within zones PR9 to PR12 and is then abundant in zones PR13 to PR15.

Remarks and comparison:

The Malay Basin specimens are smaller than those from the New Zealand as described and illustrated by McIntyre (1968).

Botanical affinity:

Derived from the genus *Ilex* (Aquifoliaceae).

Source ecology:

Trees or shrubs common montane forests, but also occurring in lowland forests and in in swamps, especially along lowland rivers. *Ilex maingayi* is often found in swamp areas behind mangroves.

Suggested name for Quaternary records:

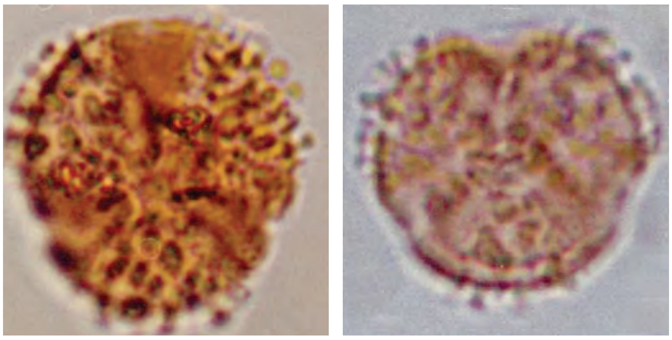
Ilex pollen.

Ecological group:

Riparian forests.

Ilexpollenites anguloclavatus

McIntyre 1968. Plate 20, Figs. 17-19



Selected synonymy:

1968 *Ilexpollenites anguloclavatus* McIntyre, p. 183, Figs. 12, 13.

Description:

Equatorial view rounded; generally preserved in polar view, tricolporate, colpi gaping, long, endoapertures circular; often obscured, exine about 1 µm thick and layers indiscernible; columellae indiscernible; sculpture densely clavate with clavae 1 to 1.5 µm high and 1 to 1.5 µm wide.

Dimensions:

Length 13 (15) 18 µm, width 10 (14) 17 µm (7 specimens measured from various horizons).

Stratigraphic distribution:

The global distribution of *Ilexpollenites* is discussed above. *Ilexpollenites* spp. are very rare in the Oligocene Delah 5H-14.1 well, but common in the Miocene and Pliocene in Malong 5G-17.2. *Ilexpollenites anguloclavatus* is scattered in zones PR6/7 to PR11, occurs in moderate numbers through zones PR12 to PR14, and then occurs abundantly in zone PR15.

Remarks and comparison:

The Malay Basin specimens are slightly smaller than those from New Zealand as described and illustrated by McIntyre (1968).

Botanical affinity:

Ilex cymosa (Aquifoliaceae).

Source ecology:

Trees or shrubs common in lowland forests, especially in swamps, peat forests, coastal and secondary forests and along rivers.

Suggested name for Quaternary records:

Ilex cymosa type pollen.

Ecological group:

Riparian forests.

Genus ***Rugutricolporites***

González-Guzmán 1967

Type species:

Rugutricolporites felix González-Guzmán 1967.

Rugutricolporites undulatus

(Salard-Cheboldaeff 1978) Jaizan Jais and Morley comb. nov. Plate 20, Figs. 22, 23

1975 Dispersed pollen attributed to *Parastemon* in Anderson and Muller, p. 307, Pl. 2, Fig. 9.
1978 *Psilatricolporites undulatus* Salard-Cheboldaeff, p. 235, Pl. 2, Figs. 2, 3.

Description:

Pollen, radially symmetrical, isopolar, spherical-suboblate, 35 µm in diameter, tricolporate with long, equatorially bridged, ektoapertures and a fairly thick tectate exine, covered with a characteristic irregularly rugulate sculpture and with a dense layer of minute columellae (Anderson and Muller, 1975).

Dimensions:

Equatorial diameter 20 (22) 24 µm (3 specimens measured from various horizons).

Stratigraphic distribution:

Oligocene to early Miocene of Cameroon (Salard-Cheboldaeff, 1978); late Miocene of Borneo (Anderson and Muller, 1975). Rare and sparsely distributed in Malong 5G-17.2 well.

Remarks:

This species is transferred to the form-genus *Rugutricolporites* that accommodates rugulate tricolporate forms since *Psilatricolporites* van der Hammen ex Pierce 1961 is illegitimate for the reasons discussed earlier.

Botanical affinity:

Parastemon (Rosaceae); Salard-Cheboldaeff (1978) compares this species with *Parinari* and *Hirtella* that have similar pollen grains as *Parastemon*.

Source ecology:

Parastemon commonly occurs in peat swamps in Borneo (Anderson, 1963) but also occur along river banks and in lowland forest.

Suggested name for Quaternary records:

Parastemon type pollen.

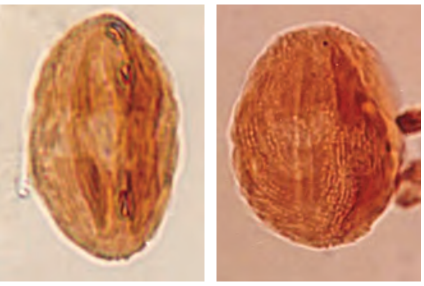
Ecological group:

Peat swamp forests.

Genus *Striacolporites*
Sah and Kar 1970

Type species:
Striacolporites striatus Sah and Kar 1970.

Striacolporites anacardiensis
Jaizan Jais and Morley sp. nov. Plate 21, Figs. 3-7



Selected synonymy:
1975 Dispersed pollen attributed to *Campnosperma* in Anderson and Muller, p. 297, Pl. 1, Fig. 2.

Derivation of name:
After its modern affinity, Anacardiaceae.

Holotype:
Plate 21, Figs. 3, 4. Slide Malong-2, 561 m (S1) SWC, England Finder V37/3. Grain in equatorial view. Length 21 µm, width 15 µm, exine 1.5 µm thick, pore 5 µm long and 2 µm wide.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 561 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, prolate to subprolate; tricolporate; colpi long, extending almost to the poles, marginate; pores conspicuous, lalongate, around 4 to 6 µm long and 2 to 3 µm wide; exine ±1.5 µm thick, finely and densely striato-reticulate; striae, meridionally parallel; reticulum <1 µm in diameter, lumina regular.

Dimensions:
Length 18 (20) 26 µm, width 12 (15) 18 µm (13 specimens measured from various horizons).

Stratigraphic distribution:
Dispersed pollen attributed to *Campnosperma* has been recorded from the middle Eocene of Java (Morley, 2000; Lelono, 2000), the late Eocene of East Kalimantan (Morley, 2000) the late Eocene of Myanmar (Huang et al. 2021), and the Oligocene and early Miocene of the West Natuna Basin (Morley, 2000). Also recorded from the Oligocene to Miocene of northwest Borneo (Anderson and Muller, 1975; Muller, 1970, 1972) and from the Miocene of Palau in the east Pacific (Leopold, 1969). Present in moderate to high percentages throughout both Malong 5G-17.2 and Delah 5H-14.1 wells.

Comparison:
This species differs *Simpsonipollis mulleri* Kemp and Harris 1977 from Ninetyeast Ridge in its general form and shape of pores; from *Striatricolporites striatus* in being smaller and having lalongate instead of lolongate pores; and from *S. striolatus* Takahashi 1982 by its conspicuous endoapertures and striato-reticulate wall.

Botanical affinity:
Campnosperma (Anacardiaceae).

Source ecology:
Trees widely distributed in the lowlands including swamp forest and often gregarious in peat swamps.

Suggested name for Quaternary records:
Campnosperma type pollen.

Ecological group:
Peat swamp forests.

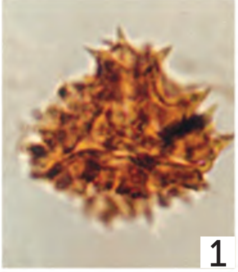
Plate 21

Figs. 1, 2 *Tubifloridites spinosus* van der Hammen ex Germeraad et al. 1968. Figs. 1, 2 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder R34.

Figs. 3-7 *Striacolporites anacardiensis* Jaizan Jais and Morley sp. nov. Figs. 3, 4 (Holotype, x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder V37/3. Fig. 5 (x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder F45. Figs. 6, 7 (x 1000): Slide Malong-2, 1518.5 m, SWC (S1); England Finder F29.

Figs. 8-11 *Lanagiopollis emarginatus* Morley 1982. Figs. 8-10 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L22/2. Fig. 11 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder Z20/2.

Figs. 12-16 *Rhoipites apiensis* Jaizan Jais and Morley sp. nov. Figs. 12, 13 (x 1000 holotype): Slide Malong-2, 625 m, SWC (S3); England Finder F17/3.
Figs. 14 (x 1000): Slide Malong-2, 518 m, SWC (S1); England Finder Q20/1.
Figs. 15, 16 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder O12/1.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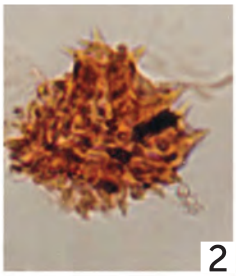
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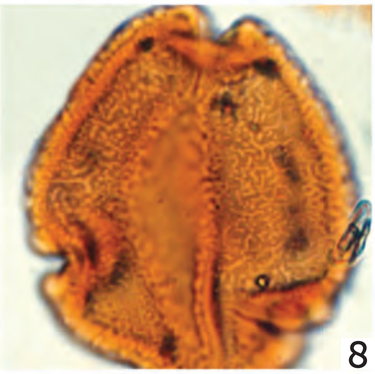
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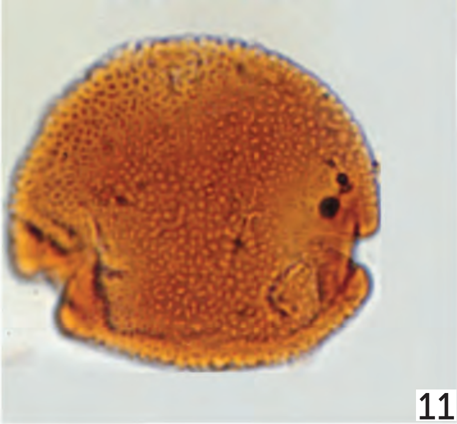
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Genus *Lanagiopollis*

Morley 1982

Type species:

Lanagiopollis regularis Morley 1982.

Lanagiopollis emarginatus

Morley 1982. Plate 21, Figs. 8-11

Selected synonymy:

1982b *Lanagiopollis emarginatus* Morley, p. 75, Pl. 3, Figs. 2, 5, 6.

Description:

Grains radially symmetrical, tricolporate (?occasionally di- or tetracolporate) oblate, circular or semi-angular in polar view, equatorial view not observed; ectoapertures variable in length, up to 10 μm in width at equator, colpi margins being composed of sexinous muri of the reticulum; endoapertures generally lalongate, ca. 14 μm in length with broad costae up to 10 μm wide and 6 μm thick; exine up to 5 μm thick, nexine thicker than sexine, often, though not always, showing thinning toward apertures; sexine eureticulate or eurugulate, sometimes bearing irregular warty elements; sexinal elements show considerable size variation, muri simpli-, dupli- or pluricolumellate (Morley, 1982b).

Dimensions:

Equatorial diameter 37 (46) 53 μm (14 specimens measured from various horizons).

Stratigraphic distribution:

The oldest records are from the middle Eocene Nanggulan Formation in Central Java (Lelono, 2000), and Yaw Formation of Myanmar (Huang et al. 2021), otherwise recorded from the Miocene to Pliocene of Northwest Borneo, East Kalimantan, Java Sea and South China Sea (Anderson and Muller, 1975; Morley, 1978, 1982b). Present in low percentages in both Delah 5H-14.1 and Malong 5G-17.2 wells, from zone PR3 to PR15.

Remarks:

This form agrees in all features with the description and illustration of the type specimen by Morley (1982b).

Botanical affinity:

Alangium havilandii of the family Alangiaceae (Morley, 1982b). The pollen types seen in extant *Alangium* have been illustrated by Reitsma (1969).

Source ecology:

Constituent of peat swamp flora, common within Phasic Community P.C.1 of Anderson (1963).

Suggested name for Quaternary records:

Alangium havilandii type pollen.

Ecological group:

Peat swamp forests.

Alangium chinense, *produces the pollen* Lanagiopollis tenuinexinus *(photo by Wikipedia Commons).*

Lanagiopollis tenuiexinus

Jaizan Jais and Morley sp. nov. Plate 22, Figs. 5-8

Derivation of name:
From its thin wall; Latin, *tenuiexinus*.

Holotype:
Plate 22, Figs. 5, 6. Slide Malong-2, 714 m SWC (S2), England Finder G38. Grain in oblique polar view; distorted by transverse fold. Diameter 54 µm, exine 1 µm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; Sidewall core sample at 714 m depth; age late Miocene, zone PR13.

Description:
Pollen grains radially symmetrical, isopolar, oblate with circular amb; tricolporate; colpi short to moderate in length, indistinct, narrow with tapered ends; pores lalongate, length ±15 µm, width ±6 µm, surrounded by heavy costae 18 µm in width and 6 µm thick; exine thin, 1 to 1.5 µm thick, with nexine thinner than sexine, microreticulate, tectate; columellae short; muri simplibaculate, lumina regular.

Dimensions:
Equatorial diameter 38 (45) 54 µm (7 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in Malong 5G-17.2 well.

Remarks and comparison:
It differs from *Lanagiopollis diminutus* sp. nov. in being larger and having a surface area with uniform thickness and from other *Lanagiopollis* species in having a thinner wall.

Botanical affinity:
Alangiaceae; the thin exine with nexine being thinner than sexine and microreticulate tectum suggests *Alangium* section *Marlea* and *A. chinense* type. A of Reitsma (1969), discussed in Morley (1982b).

Source ecology:
Alangium chinense producing the 'type A' pollen of Reitsma (1969) occurs in seasonal forests in northern Indochina and Taiwan.

Suggested name for Quaternary records:
Alangium chinense type pollen.

Ecological group:
Seasonal forest.

Lanagiopollis diminutus

Jaizan Jais and Morley sp. nov. Plate 22, Figs. 1-4

Derivation of name:
From its relatively small size.

Holotype:
Plate 22, Figs. 3, 4. Slide Malong-2, 430.5 m SWC (S2), England Finder F3/2. Grain in polar aspects. Equatorial diameter 31 µm, exine 1.5 µm thick.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 430.5 m depth; age Pliocene, zone PR15.

Description:
Pollen grains radially symmetrical, isopolar, oblate (equatorial view not observed) with circular to semi-angular amb; tricolporate; colpi long, extending approximately three-fourth to poles, widening to 8 to 10 µm at equator, ends acute, bordered by thickened margines; pores 8 µm in diameter, slightly costate; exine with thickened mesocolpia, 1 µm in thickness outside mesocolpium and 1.5 to 2 µm thick in mesocolpium, microreticulate, tectate; sexine thicker than nexine in mesocolpium, thinning towards apertures; columellae shortens towards apertures; muri simplibaculate, lumina regular.

Dimensions:
Equatorial diameter 30 (32) 34 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in Malong 5G-17.2 well.

Remarks and comparison:
Lanagiopollis diminutus differs from *L. tenuiexinus* sp. nov. by its smaller size and in having thickened mesocolpia and from other *Lanagiopollis* species by its smaller size and thinner wall.

Botanical affinity:
This form closely resembles *Mastixia* pollen.

Source ecology:
Mastixia occurs commonly throughout montane forests in Southeast Asia (Morley, 1976).

Suggested name for Quaternary records:
Mastixia type pollen.

Ecological group:
Montane forests.

Plate 22

Figs. 1-4 *Lanagiopollis diminutus* Jaizan Jais and Morley sp. nov. Figs. 1, 2 (x 1000): Slide Malong-2, 780-790 m, DC (S1); England Finder G36. Figs. 3, 4 (Holotype, x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder F3/2.

Figs. 5-8 *Lanagiopollis tenuiexinus* Jaizan Jais and Morley sp. nov. Figs. 5, 6 (Holotype, 1; x 1000, 2; x 400): Slide Malong-2, 714 m, SWC (S2); England Finder G38. Figs. 7, 8 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder F14/2.

Figs. 9. 10 *Rhoipites isoreticulatus* Kemp in Kemp and Harris 1977. Figs. 9, 10 (x 1000): Slide Malong-2, 366 m, SWC (S1); England Finder J30.

Figs. 11-14 *Euphorbiacites virgatus* Jaizan Jais and Morley sp. nov. Figs. 11, 12 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder H48/4. Figs. 13, 14 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder G12.


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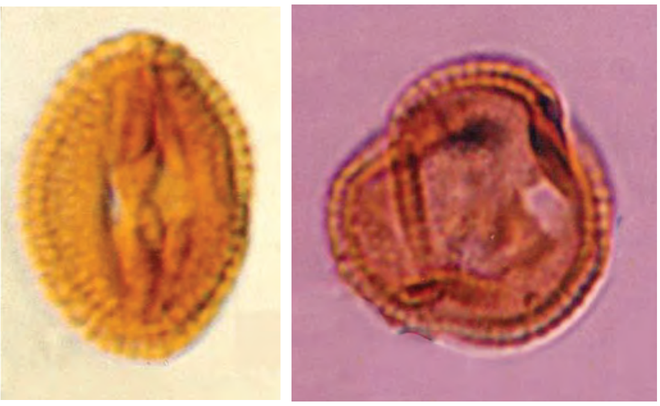
Genus *Rhoipites*
Wodehouse 1933

Type species:
Rhoipites bradleyi Wodehouse 1933 (by monotypy).

Generic remarks:
In this study the form-genus *Rhoipites* is used based on the definition given by Wodehouse (1933) which accommodates ellipsoidal tricolporate pollen with finely reticulate sculpture. The usage of this genus is also discussed by Kemp and Harris (1977), Pocknall and Crosbie (1982) and Truswell and Owen (1988).

Rhoipites apiensis
Jaizan Jais and Morley sp. nov. Plate 21, Figs. 12-16



Synonymy:
1964 Dispersed pollen attributed to *Avicennia* type in Muller, p. 39, Pl. 1, Fig. 2.

Derivation of name:
Named after *api-api*, a local name in Malaysia for *Avicennia*.

Holotype:
Plate 21, Figs. 12, 13. Slide Malong-2, 625 m, SWC (S3), England Finder U38/4. Grain in equatorial aspect, oval in outline, length 23 µm, width 15 µm; exine 1.5 µm thick, finely reticulate.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, subprolate to prolate, ovoid in equatorial view, amb lobate; tricolporate; colpi long, broad in middle, tapering from top of the pores towards the poles, bordered by straight smooth margins suggestive of colpus membrane; pores oval, relatively large, up to 8 µm in diameter, often inconspicuous; exine finely reticulate, semitectate, columellate, ±2 µm thick, occasionally thicker over poles; sexine thicker than nexine, thinner near apertures; columellae thick, ±1.5 µm long, with partly fused tips forming the muri of the reticulum; muri fairly thick; lumina small, irregular; reticulum finer along colpi.

Dimensions:
Length 19 (21) 24 µm, width 13 (15) 17 µm (6 specimens measured from various horizons).

Stratigraphic distribution:
The oldest records are from the early Eocene of the eastern Alps in Krappfeld, Austria (Hofmann et al., 2012), and the middle Eocene of Helmstedt in northern Germany (Riegel et al., 2015). In Southeast Asia, the oldest records from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000) and the late Eocene Yaw Formation in Myanmar (Huang et al., 2021). Across the Sunda Shelf, where there were many non-marine basins during the mid-Cenozoic and as a result in many areas, *Avicennia* pollen does not appear until the early Miocene (e.g., Watanasak, 1989; Morley, 2000). This is the case with the Malay Basin, where it first appears in zone PR6/7 in both Malong 5G-17.2 and Delah 5H-14.1 wells. Records are scattered in zones PR6/7 to PR12, and then it occurs in low numbers through zones PR13 to PR15. Its earliest occurrence in South America and Africa is in the late Miocene (Morley, 2000).

Comparison:
This species differs from *R. isoreticulatus* Kemp in Kemp and Harris 1977 in having finer reticulum near the colpi and from *R. cryptoporus* Srivastava 1972 in its colpus features.

Botanical affinity:
Avicennia (Acanthaceae).

Avicennia marina *(api-api), mangroves, Kuala Selangor, Malaysia (photo by RJM).*

Avicennia officinalis*, mangroves, Kuala Selangor, Malaysia (photo by RJM).*

Source ecology:

A common mangrove pioneer across the tropics. *Avicennia* is a low pollen producer, accounting for the low numbers of its pollen.

Suggested name for Quaternary records:

Avicennia type pollen.

Ecological group:

Mangrove.

Rhoipites isoreticulatus

Kemp in Kemp and Harris 1977. Plate 22, Figs. 9-10

Selected synonymy:

1974 *Tricolpites* sp. Kemp, p. 816, Pl. 1, Figs. 6-8.

1977 *Rhoipites isoreticulatus* Kemp and Harris, p. 38, Pl. 6, Figs. 7-9, 17.

Description:

Pollen, radially symmetrical, isopolar, prolate to perprolate, amb lobate in polar view, colpi long, extending to poles, without margins, endoapertures weakly developed, without costae, sexine thicker than nexine, uniform thickness, ektexine evenly and finely reticulate.

Dimensions:

Length 29 (30) 31 μm, width 15 (16) 17 μm (3 specimens measured from various horizons).

Stratigraphic distribution:

This species has been recorded from the late Eocene to Oligocene of the Indian Ocean (Kemp and Harris, 1977).

Remarks:

The Malay Basin specimens resemble the type material described and illustrated by Kemp and Harris (1977). Rare and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:

Unknown.

Suggested name for Quaternary records:

Not applicable.

Ecological group:

Undifferentiated.

Rhoipites transversalis

Jaizan Jais and Morley sp. nov. Plate 23, Figs. 1-9

Synonymy:

1975 Dispersed pollen attributed to *Calophyllum* in Anderson and Muller, p. 302, Pl. 2, Fig. 2.

Derivation of name:

After its long transverse aperture.

Holotype:

Plate 23, Figs. 2, 3, 5. Slide Malong-2, 641.5 m, SWC (S2), England Finder T16/4. Grain in equatorial aspect, subcircular in outline, equatorial diameter 28 μm; exine 2 μm thick.

Type locality:

Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene, zone PR14.

Description:

Pollen grains radially symmetrical, isopolar, prolate to spheroidal, amb subtriangular to circular; tricolporate; colpi long, extending almost to the poles, narrow, marginate; endoapertures equatorially elongated, long, ±8 μm long, ±3 μm wide, always present but some inconspicuous; exine ±2 μm thick, uniform in thickness, slightly thickened near endoaperture edges, tectate-perforate with rather uniform finely reticulate or retirugulate sculpture; tectum supported by closely spaced baculae; sexine thicker than nexine.

Dimensions:

Length 21 (25) 28 μm, width 19 (22) 25 μm (9 specimens measured from various horizons).

Stratigraphic distribution:

Dispersed pollen attributed to *Calophyllum* type pollen (see below) has been recorded from the Miocene and Holocene of northwest Borneo (Anderson and Muller, 1975), and from the Miocene of the Malay Basin (Azmi Yakzan et al., 1996) and West Natuna Basin (Morley et al., 2003). Very common through most of the Malong 5G-17.2 well. Low representation in zone PR6/7 to PR8, then common in zones PR9 to PR11 followed by low representation in zone PR12A. It is then abundant in zone PR12B, with moderate representation in zones PR13 to PR15. Low representation in zones PR1 to PR6/7 in Delah 5H-14.1 well. According to Azmi Yakzan et al. (1996), *Calophyllum* type pollen occurs commonly in zones PR9 to PR12, and also in the stratigraphically equivalent zones PVIIIA to PIX in the West Natuna Basin (Morley et al., 2003). Abundance changes in *Calophyllum* type pollen have been critical in defining previous palynological zonations from the region.

Calophyllum inophyllum, *(Penaga laut or Bintangor) coastal vegetation, Bako National Park, Sarawak, Malaysia (photo by RJM).*

Comparison:

This species differs from *Rhoipites rhomboidaliformis* (McIntyre) Mildenhall and Pocknall 1989 in having a uniform wall thickness. *Tricolporopollenites donatus* Pflug is larger in size.

Botanical affinity:

This pollen type occurs in the genus *Calophyllum* (Clusiaceae). More detailed study would allow this pollen type to be divided into additional form-taxa. The related genus *Cratoxylon*, produces similar but smaller pollen.

Source ecology:

Calophyllum is a very widespread forest tree in Malaysia with many species, several of which are ecologically important, and ranges from montane to lowland forest. There are many species in peat swamp forest (Anderson, 1963), and these can become dominant. In peat swamps from south

Kalimantan, *Calophyllum* pollen proved to be dominant in the early stage of the succession, and also in Kerapah swamps (Morley, 1982, 2013). *Calophyllum inophyllum* is a prominent tree of coastal vegetation. Peat swamps and coastal forests are thought to be the main producers of fossil pollen, and of these, peat swamps are thought to be the most important source.

Suggested name for Quaternary records:
Calophyllum type pollen.

Ecological group:
Mainly peat swamp but also coastal.

Genus Euphorbiacites

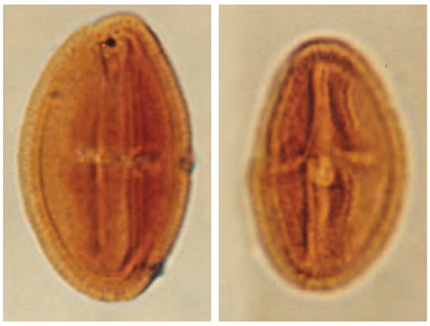
Zaklinskaja, Sung & Li, 1978 emend. Li et al 1978

Type species:
Euphorbiacites wallensenensis (Pflug) Jansonius and Hills 1978.

Remarks:
Euphorbiacites is used here, as emended by Li et al. (1978) to accommodate elliptical reticulate tricolporate pollen with slightly pointed poles and large, distinct pores. Despite the misleading name, it exactly complies with pollen attributable to the extant genus *Melanorrhoea* (Anacardiaceae), a very common pollen type in Malaysian Neogene sediments.

Euphorbiacites virgatus

Jaizan Jais and Morley sp. nov. Plate 22, Figs, 11-14



Synonymy:
1975 Dispersed pollen attributed to *Melanorrhoea* in Anderson and Muller, p. 297, Pl. 1, Fig. 2.

Derivation of name:
From its rather long rodlike (Latin, *virgatus*) columellae.

Holotype:
Plate 22, Figs. 11, 12. Slide Malong-2, 625 m, SWC (S3), England Finder H48/4. Grain in equatorial aspect, oval in outline, length 27 µm, width 16 µm; exine 2 µm thick, columellae 1.5 µm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, prolate with tapering and often slightly pointed poles, ovoid in equatorial view; tricolporate; colpi long, almost reaching the poles, wide at the equator, tapering towards the poles, bordered by straight margins; pores lalongate, subrectangular, generally 7 µm long and 3 µm wide, often conspicuous; exine tectate, columellate with faintly microreticulate tectum, ±2 µm thick; tectum thin, simplicolumellate, microreticulate; columellae prominent, long (±2 µm long), dense, rod-like, tips mostly fused to form muri of ±0.5 µm wide.

Dimensions:
Length 23 (25) 30 µm, width 13 (16) 23 µm (9 specimens measured from various horizons).

Stratigraphic distribution:
Dispersed pollen attributed to *Melanorrhoea* has been recorded from the Miocene of Borneo (Anderson and Muller, 1975). Present in moderate to high percentages in the upper part of Malong 5G-17.2 well, with a maximum in zones PR13 and PR14, and sparsely distributed in very low percentages below.

Comparison:
This species differs from *R. apiensis* by its thin, long and dense columellae.

Botanical affinity:
Melanorrhoea (Anacardiaceae). *Melanorrhoea* is now considered a junior synonym of *Gluta*, but since their pollen is different, the old generic usage is retained.

Source ecology:
Trees common in peat swamp in Southeast Asia.

Suggested name for Quaternary records:
Melanorrhoea type pollen.

Ecological group:
Peat swamp forests.

Plate 23

Figs. 1-9 *Rhoipites transversalis* Jaizan Jais and Morley sp. nov. Figs. 1, 4 (x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder D44/1. Figs. 2, 3, 5 (Holotype, x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder T16/4. Figs. 6, 9 (x 1000): Slide Malong-2, 1473 m, SWC (S1); England Finder E10. Figs. 7, 8 (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder H20/1.

Figs. 10, 11 *Claritricolporites annulatus* (Salard-Cheboldaeff) Morley and Jaizan Jais comb. nov. Figs. 10, 11 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder G18.

Figs. 12, 13 *Drasipollenites cryptus* Mathur and Jain 1980. Figs. 12, 13 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder D49.

Fig. 14 *Polygalacidites clarus* Sah and Dutta 1966 (x 1000): Slide Delah-1, 2580-2585 m, DC (S3); England Finder E24/4.

Figs. 15, 16 *Polygalacidites speciosus* Takahashi 1982. Figs. 15, 16, (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder T14.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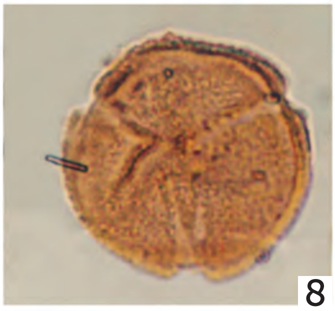
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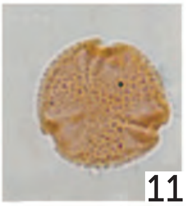
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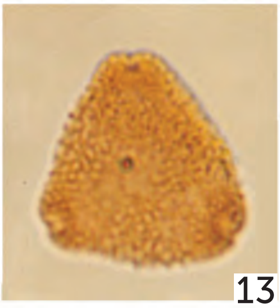
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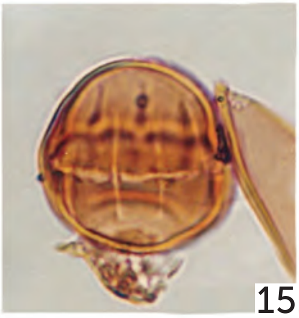
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Genus *Claritricolporites*

Morley and Jaizan Jais gen. nov.

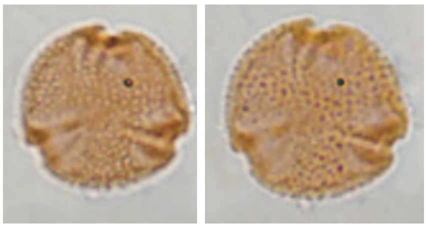
Derivation of name:
From the clear circular pore as seen in LM, reflecting the presence of an oncus.

Diagnosis:
Pollen, prolate to subprolate, tricolporate, with long colpi, with or without margines, pores circular to lolongate, and bear a clear annulus when seen in equatorial view; sexine may be reticulate to microreticulate or psilate as seen in LM.

Generic remarks:
This genus is proposed to incorporate the small, tricolporate pollen with a distinct annulus, reflecting the presence of a protruding oncus (sensu Tilney and van Wyke, 1997), as found within the subtribe Naucleeae of the family Rubiaceae (Kuang et al., 2008). Grains with reticulate exine are found in the genera *Adina*, *Mitragyna* and *Neonauclea,* whereas *Nauclea* has psilate exine.

Claritricolporites annulatus

(Salard-Cheboldaeff) Morley and Jaizan Jais comb. nov. Plate 23, Figs. 10, 11



Selected synonymy:
1978 *Retitricolporites annulatus* Salard-Cheboldaeff, p. 236-237, Pl. 4, Figs. 7-9.

Description:
Pollen, radially symmetrical, isopolar, small, spherical, circular outline in polar view, tricolporate, colpi moderately long, with intermediate polar area index, weak margines, endoapertures circular, with clear annulus, sexine thicker than nexine, distinctly reticulate, reticulum slightly coarser toward mesocolpium.

Dimensions:
Equatorial diameter 13 (16) 20 μm (8 specimens measured from various horizons).

Stratigraphic distribution:
This species has been recorded from the Oligocene to lower Miocene of Cameroon (Salard-Cheboldaeff, 1978). Present in low percentages in the Malong 5G-17.2 well.

Remarks:
The Malay Basin specimens agree in all aspects with the description and illustration of the type material by Salard-Cheboldaeff (1978).

Botanical affinity:
Mitragyna (Rubiaceae).

Source ecology:
Rain forest trees.

Suggested name for Quaternary records:
Mitragyna type pollen.

Ecological group:
Rainforest.

Genus *Drasipollenites*

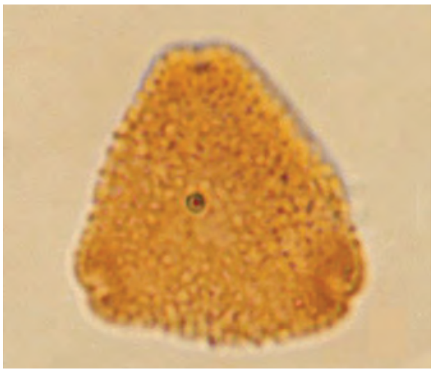
Mathur and Jain 1980

Type species:

Drasipollenites indicus (Ramanujam 1966) Mathur and Jain 1980.

Drasipollenites cryptus

Mathur and Jain 1980. Plate 23, Figs. 12-13



Selected synonymy:

1980 *Drasipollenites cryptus* Mathur and Jain, p. 69, Pl. 1, Fig. 40.

Description:

Pollen grain, radially symmetrical, isopolar, oblate, plano-convex outline in polar view, tricolporate, colpi very short, endoapertures circular, characterised by thickening of the endexine, sexine thicker than nexine, endexine distinctly reticulate.

Dimensions:

Equatorial diameter 18 (20) 23 µm (10 specimens measured from various horizons).

Stratigraphic distribution:

This species has previously been recorded from the Paleocene of India (Mathur and Jain, 1980). Present in low to moderate percentages in the Malong 5G-17.2 and very low numbers in Delah 5H-14.1 wells.

Remarks:

The Malay Basin specimens resemble the type material described and illustrated by Mathur and Jain (1980).

Botanical affinity:

Pometia (Sapindaceae), illustrated by Muller and Leenhouts (1976). Based on its stratigraphic range in India and Southeast Asia, *Pometia* is likely to be an 'out of India' taxon.

Pometia pinnata*, Bogor, Java (photo by RJM).*

Source ecology:

Common in lowland forests, particularly along streams and freshwater swamps.

Suggested name for Quaternary records:

Pometia pollen.

Ecological group:

Riparian vegetation.

2.18 STEPHANOCOLPORATE POLLEN

Genus *Polygalacidites*
Sah and Dutta 1966

Type species:
Polygalacidites clarus Sah and Dutta 1966 (by original designation).

Polygalacidites clarus
Sah and Dutta 1966. Plate 23, Fig. 14

Selected synonymy:
1966 *Polygalacidites clarus* Sah and Dutta, p. 81, Pl. 2, Figs. 24, 25.
1970 *Polygalacidites clarus* Sah and Dutta; Dutta and Sah p. 43, Pl. 9, Figs. 23, 24.

Description:
Pollen radially symmetrical, prolate, pericolporate with about 9 colpi, colpi long, narrow, without margines, endoapertures obscure but shown as thickened costae which encircle the grain, sexine thicker than nexine, nexine thickens toward equator, appears psilate or granulate.

Dimensions:
Length 24 (25) 26 μm, width 19 (20) 21 μm (4 specimens measured from various horizons).

Stratigraphic distribution:
Paleocene to Miocene of India (e.g., Sah and Dutta, 1966; Dutta and Sah, 1970; Rawat et al., 1977; Nandi, 1980; Rao and Ramanujam, 1982). Rare and sparsely distributed in the Delah 5H-14.1 well.

Remarks:
This polycolporate form resembles *Polygalacidites clarus* Sah and Dutta 1966 in having long colpi, faint ora and psilate wall but rare specimens with more than 6-colporate aperture are also included here.

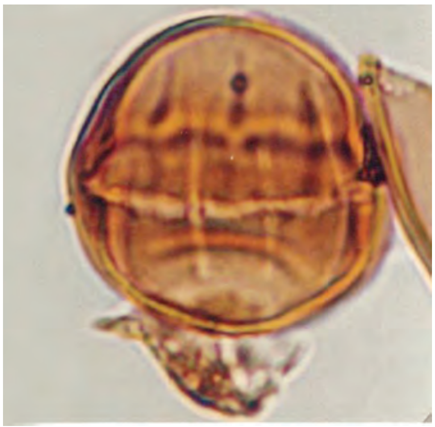
Botanical affinity:
Polygalaceae, *Polygala* and *Xanthophyllum*. Species of the mainly Southeast Asian genus *Xanthophyllum* are thought to be the main source of this pollen.

Source ecology:
Xanthophyllum spp. are trees and shrubs and occur scattered or rarely gregariously in primary, often riverine, lowland rain forest, and rarely in lower montane forest. They are also found in freshwater swamp forest, monsoon forest and kerangas. Riparian and freshwater swamps are thought to be the main source of this pollen.

Suggested name for Quaternary records:
Polygala type pollen.

Ecological group:
Freshwater and riparian swamps.

Polygalacidites speciosus
Takahashi 1982. Plate 23, Figs. 15, 16



Selected synonymy:
1982 *Polygalacidites speciosus* Takahashi, p. 318, Pl. 52, Figs. 4-14.

Description:
Pollen grains, radially symmetrical, isopolar small, amb prolate to spheroidal, pericolporate (about 9 colpi), colpi long, narrow, without margines, endoapertures long, creating colpus transversalis, with thickened costae, sexine thicker than nexine at poles but thickens toward equator.

Dimensions:
Longest axis 21 (23) 25 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
Recorded from the middle Eocene of Java (Takahashi, 1982; Lelono, 2000). Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
The Malay Basin specimens closely resemble *Polygalacidites speciosus* originally described by Takahashi (1982) from the Eocene of Java in having 6 to 8 colporate apertures and distinctly synorate which distinguishes it from *Polygalacidites clarus* Sah and Dutta 1966.

Botanical affinity:
Polygala and *Xanthophyllum* (Polygalaceae).

Source ecology:
Xanthophyllum spp. are trees and shrubs and occur scattered or rarely gregariously in primary, often riverine, lowland rain forest, and rarely in lower montane forest. They are also found in freshwater swamp forest, monsoon forest and kerangas. Riparian and freshwater swamps are thought to be the main source of this pollen.

Suggested name for Quaternary records:
Polygala type pollen.

Ecological group:
Freshwater and riparian swamps.

SAPOTACEAE POLLEN

Sapotaceae is an ecologically important family in Malaysia that yields abundant pollen (Morley, 1982) but has proved difficult to subdivide palynologically (Morley, 1976). Since the publication of the monograph on Sapotaceae pollen by Harley (1991), pollen of this family has been much easier to classify. Harley (1991) shows that Sapotaceae pollen can be divided into 12 main types, termed types I to XII. Some of the pollen types tie closely to the taxonomic groups of Pennington (1991), but in others, the types are spread widely among the different subfamilies (Harley, 1991, Table 1). A recent attempt to use the key of Harley (1991) was made by Huang et al. (2021) for pollen from the late Eocene of Myanmar. Harley's key is reproduced here, together with a list indicating the pollen types that occur in genera of Sapotaceae that occur in Malaysia.

KEY TO SAPOTACEAE POLLEN TYPES (from Harley, 1991)

1.	Average polar length not exceeding 35 µm:	
2.	Supratectal spines, spinules or coarse granules present:	
3.	Tectum protrudent, spinules or coarse granules present:	type XI *Sarcaulus* type.
3.	Tectum not protrudent, spines present:	type XII *Diploon* type.
2.	Supratectal spines, spinules or coarse, granules absent:	
4.	Pollen grains 3 to 4-colporate, perforate or coarsely perorate and rugulate, or coarsely rugulate, perforations often coarser in apocolpium, up to 35 µm average polar length:	type X *Elaeoluma* type.
4.	3 to 5-colporate, tectum striate, up to 25 µm average polar length:	type IX *Oxethece* type.
1.	Average polar length usually exceeding 35 µm:	
5.	Endexine thickened in mesocolpia forming a continuous band in equatorial region:	type VII *Pouteria caimoto* type.
6.	Apocolpium and mesocolpium differentiated, tectum protrudent:	
6.	Apocolpium and mesocolpium not differentiated, tectum not, or semi-protrudent:	type VIII *Pouteria alnifolia* type.
5.	Endexine thin or absent in mesocolpia, not forming a continuous band in equatorial region:	
7.	Poles always hemispherical:	
8.	Occasionally subspheroidal or spheroidal, up to 65 µm average polar length:	
9.	Mesocolpial wall thickness up to 3 to 6 µm, rarely 6 µm. Costae not present, average polar length 24-57 µm:	type IV *Sarcosperma* type.
9.	Mesocolpial walls usually 3 to 6 µm. Costae frequently present, average polar length 33 to 65 µm:	type V *Pichonia* type.
8.	Usually prolate-spheroidal or subprolate, up to 85 µm average polar length:	
10.	Entire surface of tectum usually finely or distinctly granular:	type I *Mimusops* type.
10.	Entire surface of tectum usually finely striate-rugulate:	type II *Palaquium* type.
7.	Poles always hemispherical, colpi frequently up to 0.85 of polar length:	
11.	Equatorial faces slightly convex, tectum usually psilate, subpsilate or scabrate, poles frequently pointed:	type III *Manilkara* type.
11.	Equatorial faces usually parallel, tectum frequently striate, poles frequently hemispherical:	type VI *Sideroxylon* type.

Sapotaceae Genera in Malaysia

Genus	Ecology	Pollen type
Chrysophyllum	Lowlands common throughout	**Mainly type VII**
Isonandra	Limestone hills	**Type II**
Madhuca	Many spp. some in freshwater swamps	**Mainly types I and II**
Manilkara	Uncommon on islands	**Mainly types I and III**
Mimusops	Seasonal forests mainly planted	**Mainly type I**
Palaquium	Many spp. lowlands along rivers, swamps	**Types I and II**
Payena	Several spp. lowland forest	**Type I**
Planchonella	Mountains lowlands coasts swamps	**Type VII**
Pouteria	Lowlands	**Mainly type VII**

Genus *Psilastephanocolporites* Leidelmeyer 1966

Type species:
Psilastephanocolporites fissilis Leidelmeyer 1966 (by original designation).

Generic remarks:
The above genus is used here for Sapotaceous/Meliaceous type pollen since *Sapotaceoidaepollenites Potonié* et al. 1950 ex Potonié 1960 may be a junior synonym of *Tetracolporopollenites* Pflug and Thomson in Thomson and Pflug 1953 (Jansonius and Hills 1976, card no. 2500). Furthermore, these form-genera are restricted to 4-colporate forms, and the specimens found in this study have 4 to 6 colporate apertures.

Psilastephanocolporites validus
Jaizan Jais and Morley sp. nov. Plate 24, Figs. 1-3

Derivation of name:
From Latin, *validus*, strong.

Holotype:
Plate 24, Fig. 1. Slide Malong-2, 641.5 m, SWC (S2), England Finder Y8/3. Grain in equatorial aspect, length 46 μm, width 44 μm; endoapertures 3 μm long, 10 μm wide; ectoapertures 15 μm long; exine 2 μm thick on poles, 4 μm thick near endoapertures and at equatorial areas.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene, zone PR14.

Description:
Pollen grains radially symmetrical, isopolar, oblate to subprolate; stephanocolporate, tetracolporate to pentacolporate; colpi (ectoapertures) slit-like, extending up to three-fourths of the polar diameter; endoapertures distinct, costate, elliptical, equatorially elongated (lalongate), up to ±5 μm long and ±15 μm wide; exine psilate to finely granulate, tectate, robust, 2 to 5 μm thick, slightly thicker near endoapertures, faintly columellate; sexine thicker than nexine.

Dimensions:
Length 35 (44) 49 μm (10 specimens measured from various horizons).
Variability: In size and wall thickness.

Stratigraphic distribution:
Harley (1991) reviewed the stratigraphic distribution of Sapotaceae pollen, showing that there are numerous records. The oldest records are from the Paleocene of Europe, followed by the early Eocene in the Americas and India, whereas the oldest records from Africa are early Miocene. Sapotaceae pollen has also been recorded from the middle Eocene of Java (Lelono, 2000) and late Eocene of Myanmar (Huang et al., 2021). In the Malong 5G-17.2 and Delah 5H-14.1 wells, they occur throughout in low percentages, but are most common in zones PR9A to PR12A.

Comparison:
Sapotaceoidaepollenites robustus Muller 1968 is tricolporate to tetracolporate; *Psilastephanocolporites grandis* Salard-Cheboldaeff 1978 is tetracolporate and larger; *Psilastephanocolporites laevigatus* Salard-Cheboldaeff 1978 is also tetracolporate and has thinner wall.

Botanical affinity:
The large size, spheroidal to subprolate shape, medium length colpi, and uniformly structured more or less smooth exine suggests type II of Harley (1991), which includes *Palaquium* and *Manilkara*.

Source ecology:
Trees, treelets, rarely shrubs, very common in the understorey of lowland primary forests and especially in peat swamps.

***Suggested* name for Quaternary records:**
Palaquium type pollen.

Ecological group:
Rain forest and peat swamp.

Plate 24

Figs. 1-3 *Psilastephanocolporites validus* Jaizan Jais and Morley sp. nov. Fig. 1 (Holotype, x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder Y8/3. Figs. 2, 3 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder N41/4.

Figs. 4-9 *Psilastephanolcoporites* spp. Figs. 4, 5 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder N41/3. Figs. 6, 7 (x 1000): Slide Malong-2, 840-850 m, DC (S1); England Finder X6/1. Figs. 8, 9 (x 1000): Slide Malong-2, 1135-1140 m, DC (S1); England Finder J33.

Figs. 10, 11 *Iugopollis tetraporites* Venkatachala and Rawat emend Venkatachala and Rawat in Thanikaimoni et al. 1984. Fig. 10 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder P38/3. Fig. 11 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L53.

Figs. 12-15 *Iugopollis interruptus* Jaizan Jais and Morley sp. nov. Figs. 12, 13 (Holotype, x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L32. Figs. 14, 15 (x 1000): Slide Malong-2, 1000-1010 m, DC (S1); England Finder G4/2.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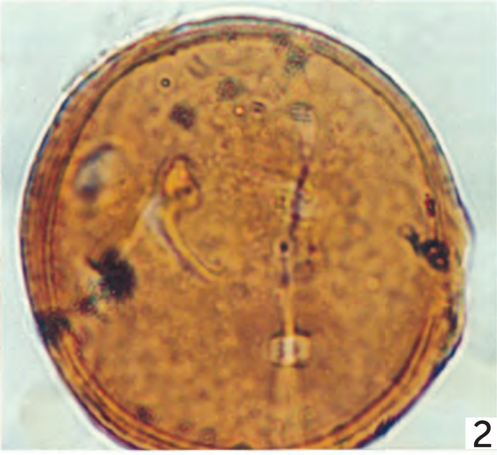
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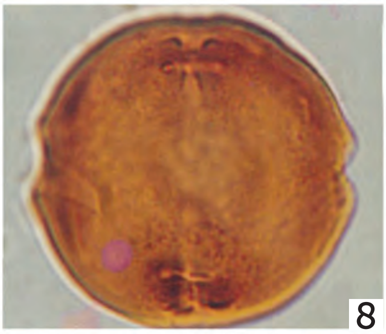
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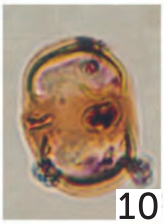
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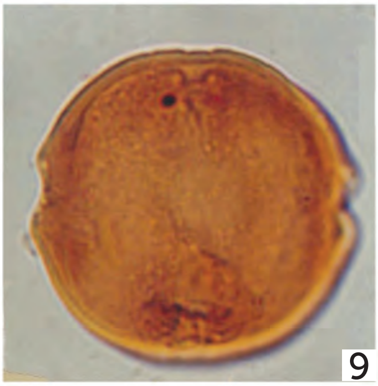
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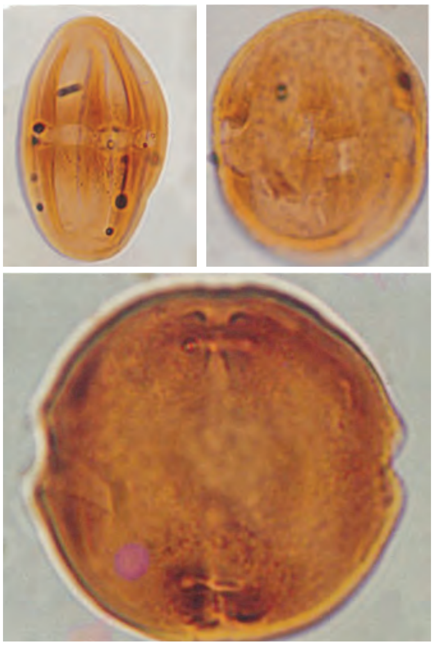
***Psilastephanocolporites* spp.** Plate 24, Figs. 4-9



Dimensions:
Length 27 (33) 44 µm, width 15 (25) 40 µm (17 specimens measured from various horizons).

Stratigraphic distribution:
Common throughout both sections; more regularly distributed in Malong 5G-17.2 well than in the Delah 5H-14.1 section.

Remarks and comparison:
Included in this group are various stephanocolporate specimens with 4 to 6 colporate apertures, subprolate to prolate shape and a psilate to finely granulate wall. An attempt has been made to separate this form into two morphological species, but it appears that more detailed subdivision is needed to assess their stratigraphic value. Hence, they are provisionally grouped together pending further studies. They differ from *Psilastephanocolporites validus* sp. nov. in having a thinner wall.

Botanical affinity:
Most specimens of this group resemble Sapotaceae. Plate 24, Figs. 4, 5, compare to type III of Harley (1991) and may be derived from *Manilkara*. Plate 24, Figs. 6-9, are granulate and may compare to type I of Harley (1991) and to *Mimusops*.

Source ecology:
Sapotaceae are generally trees in the lowlands and hill forests, some are restricted to the swamp forests.

Ecological group:
Rain forest and swamp.

Palaquium obovatum, *gutta percha tree, or Nyatoh Putih, a source of latex. Singapore Botanical Gardens* *http://bit.ly/sbgheritagetrees*.

Genus *Iugopollis*
Venkatachala and Rawat 1972 emend. Jaizan Jais and Morley

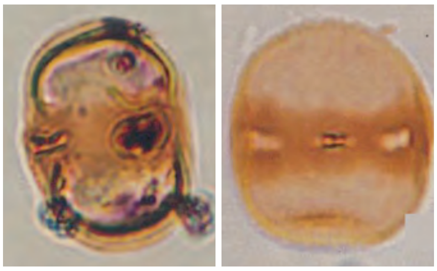
Type species:
Iugopollis tetraporites
Venkatachala and Rawat 1972.

Emended diagnosis:
Pollen grains elliptic in equatorial view, tricolporate to tetracolporate; endoapertures very narrow and short, perpendicular to the ectoapertures; sexine psilate to reticulate except at the equatorial region where the underlying nexine is thickened as a dark, continuous, or discontinuous band bordering endoapertures.

Generic remarks:
This genus was originally proposed in 1972 by Venkatachala and Rawat (1972) as being tetraporate. In 1984, the same authors in Thanikaimoni et al. (1984) emended the genus from being tetraporate to tetracolporate. As a result, *Kindopollis* Mathur and Jain 1980 may be a junior synonym of *Iugopollis* (Jansonius and Hills, 1985). In this study, the latter is emended to include forms with tricolporate apertures found in the Malay Basin.

Iugopollis tetraporites

Venkatachala and Rawat emend. Venkatachala and Rawat in Thanikaimoni et al. 1984. Plate 24, Figs. 10, 11



Selected synonymy:
1972 *Iugopollis tetraporites* Venkatachala and Rawat, p. 322, Pl. 4, Figs. 26, 27.

Description:
Monad pollen, radial, isopolar, prolate; in equatorial view oval; tricolporate, lalongate, pores small and costate, colpi long; exine thin, 0.9 µm thick, sexine thicker than nexine; sculpture psilate; columellae indiscernible (modified from Huang et al., 2021).

Dimensions:
Length 16 (17) 18 µm (3 specimens measured from various horizons).

Stratigraphic distribution:
Middle to late Eocene of India (Venkatachala and Rawat, 1972; Venkatachala,1974; Rawat et al., 1977), late Eocene of Myanmar (Huang et al., 2021). Present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks and comparison:
The Malay Basin specimens agree with the description of *Iugopollis tetraporites* Venkatachala and Rawat as given in Thanikaimoni et al. (1984) but the latter are slightly larger measuring 21 to 30 µm in length. The tricolporate forms, which could be a variant of this species, are also included here. This species differs from *Iugopollis interruptus* sp. nov. in having a continuous equatorial band and longer colpi.

Botanical affinity:
This pollen compares to *Pouteria* (Type VIIA of Harley, 1991) in the family Sapotaceae.

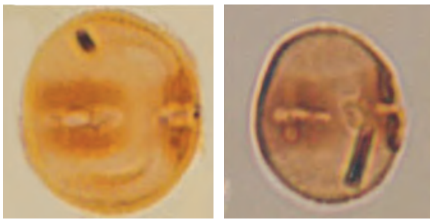
Source ecology:
Trees in the lowlands and hill forest.

Suggested name for Quaternary records:
Pouteria type pollen.

Ecological group:
Rainforest.

Iugopollis interruptus

Jaizan Jais and Morley sp. nov. Plate 24, Figs. 12-15



Derivation of name:
From its interrupted or discontinuous equatorial band bordering the endoapertures.

Holotype:
Plate 24, Figs. 12, 13. Slide Malong-2, 625 m, SWC (S3), England Finder L32. Grain in equatorial aspect, 15 µm long, 13 µm wide; exine 1 µm thick on poles; endoapertures 1.5 µm long, 4 µm wide; ectoapertures 3 µm long.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore Peninsular Malaysia; sidewall core sample at 625 m depth; age late Miocene, zone PR14.

Description:
Pollen grains small, radially symmetrical, isopolar, elliptic or subprolate to prolate in equatorial view; tricolporate; ectoapertures short, narrow, occasionally indistinct, 3 to 4 µm long; endoapertures costate, elliptic, equatorially elongated, 2 to 3 µm long, 3 to 5 µm wide, costae pori broad, discontinuous forming an interrupted equatorial band which is darker around endoapertures and lighter in between; exine psilate to faintly microreticulate except at the equatorial region, tectate, faintly columellate; nexine thicker around endoapertures.

Dimensions:
Length 13 (15) 16 µm, width 10 (13) 15 µm (4 specimens measured from various horizons).

Stratigraphic distribution:
Regularly present in low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells. It occurs more commonly as short-lived maxima within zones PR9 to PR12A where abundance maxima probably relate to sequence biostratigraphic events and is also more common in zone PR3.

Comparison:
This species differs from *Iugopollis tetraporites* in being exclusively tricolporate and in having discontinuous costae pori and an interrupted equatorial band.

Botanical affinity:
Iugopollis interruptus sp. nov. closely resembles *Aglaia* and *Amoora*, e.g., *Amoora cucullata* (Meliaceae) as illustrated in Thanikaimoni et al. (1984).

Source ecology:
Aglaia are trees or shrubs common in the lowlands and hill forests.

Suggested name for Quaternary records:
Aglaia type pollen.

Ecological group:
Rainforest.

Genus *Ctenolophonidites*

van Hoeken-Klinkenberg 1966 emend. Salard-Cheboldaeff 1977

Type species:

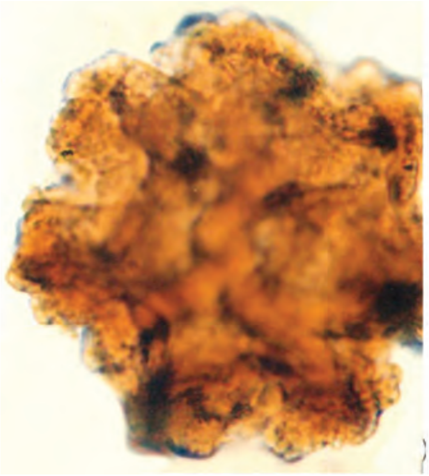
Ctenolophonidites costatus (van Hoeken Klinkenberg 1964) van Hoeken-Klinkenberg 1966.

Generic remarks:

This genus was originally diagnosed as stephanocolpate by van Hoeken-Klinkenberg in 1964 but later emended as being stephanocolporate by Salard-Cheboldaeff in 1977.

Ctenolophonidites costatus

(van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966. Plate 25, Figs. 7, 8



Selected synonymy:

1955 Dispersed pollen attributed to Ctenolophonaceae in Kuyl, Muller and Waterbolk, Pl. 2, Fig. 10.

1964 *Stephanocolpites costatus* van Hoeken-Klinkenberg, p. 221, Pl. 4, Figs. 10a-d.

1966 *Ctenolophonidites costatus* (van Hoeken-Klinkenberg) van Hoeken-Klinkenberg, p. 42.

1968 *Ctenolophonidites costatus* (van Hoeken-Klinkenberg) van Hoeken Klinkenberg; Germeraad, Hopping and Muller, p. 326, Pl. 14, Figs. 5, 6.

1982 *Ctenolophonidites costatus* (van Hoeken-Klinkenberg) van Hoeken-Klinkenberg; Rao and Ramanujam, p. 74, Pl. 2, Figs. 25, 26.

1985 *Ctenolophonidites costatus* (van Hoeken-Klinkenberg) van Hoeken-Klinkenberg; Salami, p. 11, Pl. 1, Figs. 8, 9; Pl. 3, Fig. 13.

Description:

Pollen, radially symmetrical, isopolar, oblate; amb spheroidal and eight-lobed; polycolpate with eight short colpi, 5.7 to 6.2 μm deep, reaching 1/3 to the poles; exine up to 2.1 μm thick; sculpture scabrate to microreticulate (Huang et al., 2021).

Dimensions:

Equatorial diameter 46 μm (1 specimen measured).

Stratigraphic distribution:

The oldest records of *Ctenolophonidites costatus* are from the Maastrichtian of Africa and Yemen (Germeraad et al., 1968; Alaug, 2019), with the related form *C. lisamae* recorded from the Paleocene of the Neotropics (as *Scabrastephanocolpites lisamae*) by van der Hammen and Garcia de Mutis (1965), suggesting a Gondwanan origin for Ctenolophonaceae. It is subsequently widely recorded from equatorial Africa where it can be found today in *Ctenolophon englerianus*, *Ctenolophonidites costatus* is also extensively reported from the early Eocene to Miocene of India (summarised in Morley, 2000 and Thanikaimoni et al., 1984). Only one specimen found in Malong 5G-17.2 well at 688.5 m (SWC) depth. The record in the Malong 5G-17.2 well is the first record for Southeast Asia.

Remarks:

This specimen agrees with the description of the type specimen by van Hoeken-Klinkenberg (1964, 1966) except that the former is stephanocolporate instead of stephanocolpate. Thanikaimoni et al. (1984) suggested a critical study of the type specimen is needed to confirm the presence of endoapertures which can be faintly seen in the photographs published by van Hoeken-Klinkenberg (1964) and also observed in their studied specimens. The presence of endoapertures is also seen in the Malay Basin specimen.

Botanical affinity:

This pollen type is identical to that seen in *Ctenolophon englerianus* from equatorial Africa (van der Ham, 1989) but also occurs in *Ctenolophon philippinensis* recorded from the Philippines. The fossil record shows that the *C. englerianus* clade is an ‘out of India’ taxon.

Source ecology:

Occurs in Gabon in swamp forests.

Suggested name for Quaternary records:

Ctenolophon philippinensis type pollen.

Ecological group:

Seasonal swamp forests.

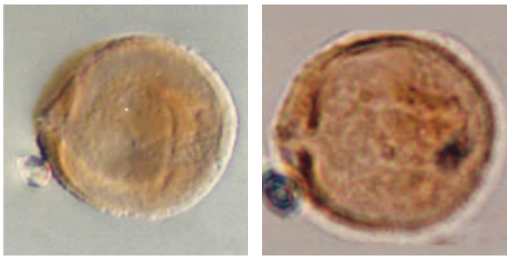
Genus *Retitetrabrevicolporites*

Kar 1985

Type species:
Retitetrabrevicolporites delicatus Kar 1985 (by original designation).

Retitetrabrevicolporites elongatus

Jaizan Jais and Morley sp. nov. Plate 25, Figs. 1-6



Derivation of name:
From its elongated colpi transversales endoapertures.

Holotype:
Plate 25, Figs. 1, 2. Slide Malong-2, 456 m, SWC (S1), England Finder V43/3. Grain in equatorial aspect, 18 μm long, 16 μm wide; colpi 6 μm long; colpi transversales 1 μm long, 8 μm wide; exine 1 μm thick on poles; reticulum up to 1 μm in diameter.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore peninsular Malaysia; sidewall core sample at 456 m depth; age Pliocene, zone PR15.

Description:
Pollen grains radially symmetrical, isopolar, amb circular to subcircular, oblate spheroidal to spherical in equatorial view with circular amb; tetracolporate; colpi short (5 to 15 μm long depending on grain size, slit-like, distinct; endoapertures (colpi transversales or poroid slits) elongated (±2 μm long, ±10 μm wide), slightly costate; exine microreticulate to finely reticulate (reticulum 0.5 to 1.5 μm in diameter), tectate, 1 μm thick, slightly thicker near apertures.

Dimensions:
Longest axis 14 (17) 22 μm (11 specimens measured from various horizons).

Stratigraphic distribution:
Present in low numbers and restricted to the upper part of the Malong 5G-17.2 well from zones PR13 to PR15.

Comparison:
This species differs from *Retitetrabrevicolporites delicatus* Kar 1985 in having transversales endoapertures.

Botanical affinity:
This species closely resembles *Claoxylon* pollen (Euphorbiaceae).

Source ecology:
Claoxylon is common in lowland forests (Whitmore, 1973).

Suggested name for Quaternary records:
Claoxylon type pollen.

Ecological group:
Rainforest.

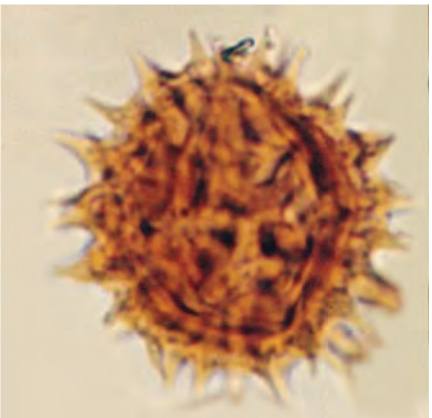
2.19 FENESTRATE POLLEN

Genus *Fenestripollenites*
Nakoman 1966

Type species:
Fenestripollenites lacunosus Nakoman 1966 (by original designation).

Generic remarks:
The form-genus *Fenestrites* was proposed by van der Hammen (1956) and admirably suited this pollen morpohotype, but unfortunately van der Hammen used modern pollen of the genus *Crepis* (Asteraceae) as the holotype, making *Fenestrites* a junior synonym of *Crepis*, and hence this name is invalid. Proposals to validate the genus by designating a new holotype by Germeraad et al. (1968) and Lorente (1986) are contrary to the rules of the ICBN. Nakoman (1966) has proposed the form-genus *Fenestripollenites*, which accommodates lophate forms to replace *Fenestrites* van der Hammen 1954. Despite a rather brief description of its type species, *Fenestripollenites* has been formally and validly proposed (Jansonius and Hills, 1976).

Fenestripollenites longispinosus
(Lorente 1986) Jaizan Jais and Morley comb. nov. Plate 26, Figs. 5, 6



Selected synonymy:
1986 *Fenestrites longispinosus* Lorente, p. 180, Pl. 15, Figs. 2, 3.

Description:
Single grain, tricolporate, typically spherical to subprolate, weakly sublophate, tectate with distinct columellae, difficult to see sublophate exine structure in poorly preserved specimens, echinate, sometimes echinae slightly angled due to lophate exine configuration.

Dimensions:
Polar axis 23 (27) 32 μm, equatorial axis 18 (21) 26 μm (excluding spines; 7 specimens measured from various horizons).

Remarks:
The weakly fenestrate (sublophate) Malay Basin specimens agree in all aspects with the description and illustration of *Fenestrites longispinosus* by Lorente (1986). This species is newly combined under the form-genus *Fenestripollenites* Nakoman (1966) as the former genus is invalid under the ICBN rules. The exine structure compares closely to that of *Vernonia arborea* pollen illustrated by Skvarla et al. (2005) and Bunwong and Chantarnothai (2008).

Stratigraphic distribution:
Rare; only present in the topmost part of Malong 5G-17.2 well from the late Miocene and Pliocene within zones PR14 and PR15, and similarly distributed across the Southeast Asian region.

Botanical affinity:
This pollen is mostly derived from *Vernonia arborea*. The pollen morphology of *Vernonia* is varied, with six morphotypes among about 1000 species that vary from tall trees to herbs (Keeley and Jones, 1979), varying from sublophate to strongly lophate. The sublophate echinate pollen seen in *Vernonia arborea* (Type A of Keeley and Jones, 1979) is the most primitive type seen in the genus, and hence the most widely distributed geographically across the tropics (Kingham, 1976). The image of *V. arborea* pollen shown by Jones and Pearce (2014) does not show any sublophate structure (Plate 4, Fig. 6) and its identity is questioned.

Source ecology:
Vernonia arborea is a prominent tree of hill and lower montane forest but ranges in altitude from near sea level to 3000 m altitude (Bakker and Backhuizen van den Brink, 1968). In the lowlands it occurs in secondary forest across Southeast Asia.

Suggested name for Quaternary records:
Vernonia arborea type pollen.

Ecological group:
Montane forests.

Plate 25

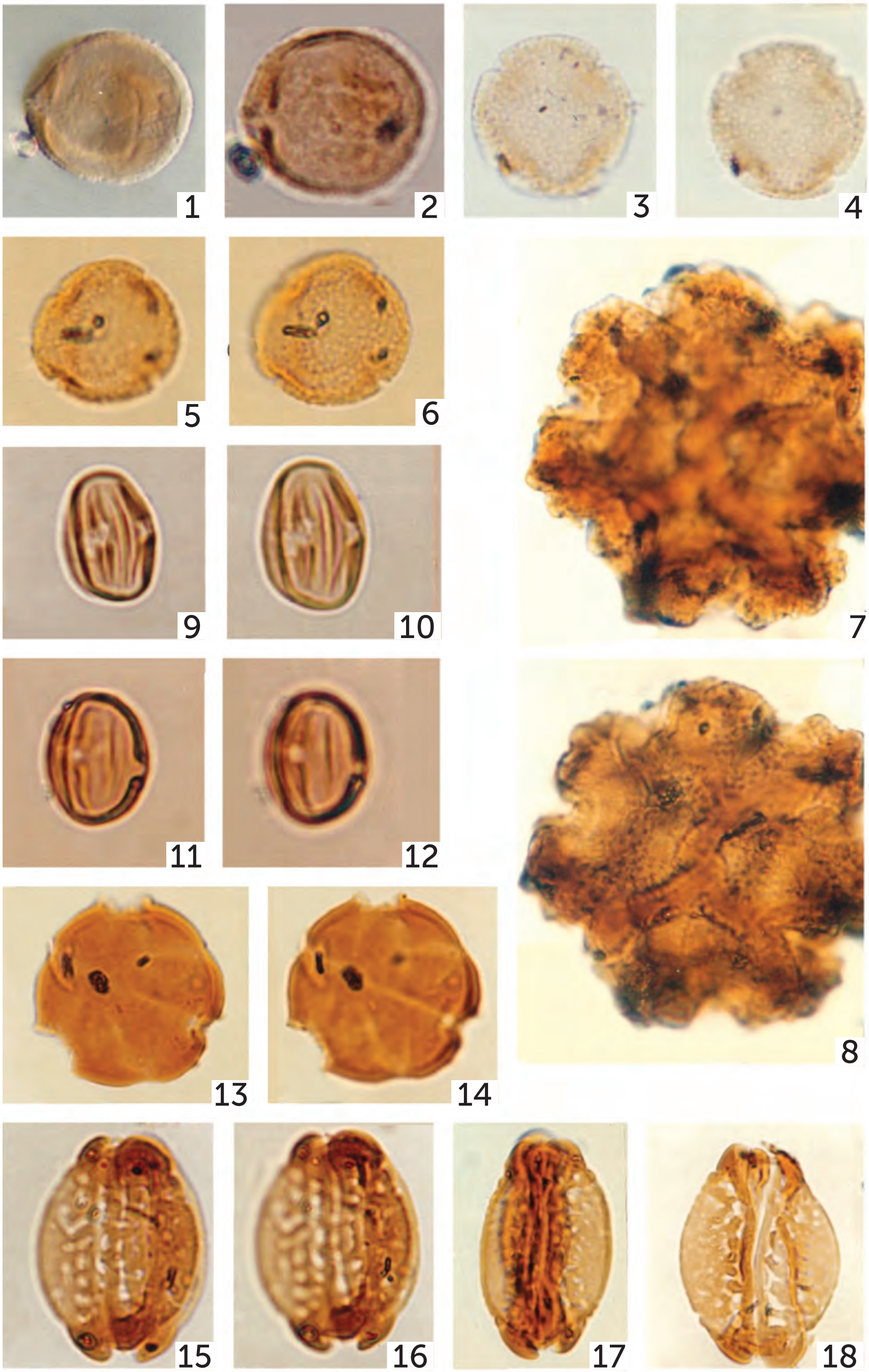
Figs. 1-6 *Retitetrabrevicolporites elongatus* Jaizan Jais and Morley sp. nov. Figs. 1, 2 (Holotype, x 1000): Slide Malong-2, 456 m, SWC (S1); England Finder V43/3. Figs. 3, 4 (x 1000): Slide Malong-2, 688.5 m, SWC (S2); England Finder Q6/1. Figs. 5, 6 (x 1000): Slide Malong-2, 810 m, SWC (S1); England Finder T11.

Figs. 7, 8 *Ctenolophonidites costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966. Figs. 7. 8 (x 1000): Slide Malong-2, 688.5 m, SWC (S2); England Finder R17/4.

Figs. 9-12 *Psilaheterocolpites laevigatus* (Salard-Cheboldaeff 1978) Jaizan Jais and Morley comb. nov. Figs. 9, 10 (x 1000): Slide Malong-2, 654.5 m, SWC (S2); England Finder R18/3. Figs. 11, 12 (x 1000): Slide Malong-2, 561 m, SWC (S1); England Finder H8.

Figs. 13, 14 *Psilaheterocolpites combretoides* (Rao and Ramanujam 1982) Jaizan Jais and Morley comb. nov. Figs. 13, 14 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder J14/1.

Figs. 15-18 *Marginipollis concinnus* Clarke and Frederiksen 1968. Figs. 15, 16 (x 1000): Slide Malong-2, 503 m, SWC (S2); England Finder S20. Fig. 17 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder O26/1. Fig. 18 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder W25.



2.20 HETEROCOLPATE POLLEN

Genus *Psilaheterocolpites*
Jaizan Jais and Morley gen. nov.

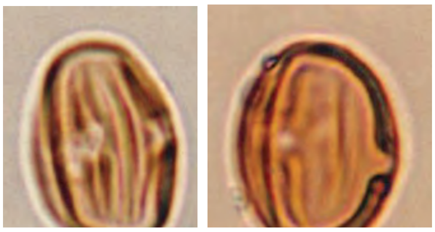
Type species:
Psilaheterocolpites laevigatus (Salard-Cheboldaeff 1978) comb. nov.

Derivation of name:
From its psilate exine and heterocolpate apertures.

Diagnosis:
Pollen grains prolate to subprolate, lobate with six lobes in polar view; heterocolpate with three colporate apertures alternating with three colpi/pseudocolpi, zono-aperturate; wall psilate to scabrate.

Remarks and comparison:
The form-genus *Heterocolpites* proposed by van der Hammen (1954) is a nomen nudum and was subsequently made illegitimate by van der Hammen (1956) by designating recent pollen of *Bucquetia glutinosa* (Melastomataceae) as the holotype. The proposed change of the type species to *Heterocolpites palaeocenica* by van der Hammen and Garcia de Mutis (1965) is contrary to the ICBN (Jansonius and Hills, 1976, card 1242). *Retiheterocolpites* González-Guzmán 1967 is different in having a reticulate wall.

Psilaheterocolpites laevigatus
(Salard-Cheboldaeff 1978) Jaizan Jais and Morley comb. nov. Plate 25, Figs. 9-12



Selected synonymy:
1978 *Heterocolpites laevigatus* Salard-Cheboldaeff, p. 229, Pl. 3, Figs. 6-8.

Description:
Single grain, lobate with six lobes in polar view, heterocolpate with three colporate apertures alternating with three colpi/pseudocolpi, grains prolate to subprolate, zono-aperturate, endoapertures more or less circular, endexine thickens slightly around endoapertures, nexine and sexine clearly visible in well-preserved specimens, exine sculpture psilate to scabrate.

Dimensions:
Longest axis 11 (13) 20 µm (16 specimens measured from various horizons).

Remarks:
This pollen type agrees in all aspects with *Heterocolpites laevigatus* Salard-Cheboldaeff who illustrated the holotype (Plate III, Fig. 6), with a detailed description. This species differs from *Psilaheterocolpites combretoides* (Rao and Ramanujam 1982) comb. nov. which is larger in size (see below).

Stratigraphic distribution:
Common in both studied wells, and thus ranges from the Oligocene to Pliocene. In West Africa, recorded from the late Eocene to early Miocene in Cameroon by Salard-Cheboldaeff (1978, 1979).

Botanical affinity:
This species was compared to *Terminalia* (Combretaceae) by Salard-Cheboldaeff (1978). In Southeast Asia, *Melastoma*, *Medinilla* (Melastomataceae) and *Dactylocladus* (Crypteroniaceae) are common genera that also produce this pollen type (Anderson and Muller, 1975; Muller, 1975). *Medinilla* pollen is smaller than the other genera with a polar axis of 14 µm, and more strongly prolate or perprolate (Morley, 1976).

Source ecology:
With similar pollen occurring in widely separated genera, the source ecology requires detailed explanation. *Terminalia* are medium to large deciduous or semi-deciduous trees with *Terminalia catappa* occurring commonly near coasts and T. *calamansanai* and *T. triptera* common on coastal limestones. *Terminalia phellocarpa* is a widespread tree that sometimes occurs commonly on seasonal and permanent swamps including peat swamps and also on river levees. Other species are scattered in lowland forest (Kochummen, 1972). The coastal tree *T. catappa* is thought to be the main source of fossil pollen, but *T. phellocarpa* may also contribute to this, especially if found in peats or coals. *Melastoma* and other Melastomataceae are mainly shrubs and herbs and commonly occur in disturbed lowland settings and on herbaceous swamps; *Medinilla* are common especially in forests and along forest edges and sometimes on swamps (Morley, 1976).

Dactylocladus, within the family Crypteroniaceae, is a common peat swamp tree, and occurs in all peat swamp phasic communities in East Malaysia, becoming dominant in Padang forests in Phasic communities V or VI (Anderson and Muller, 1975).

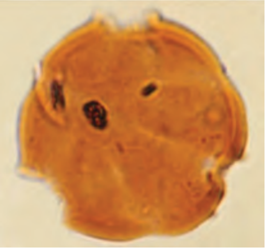
Suggested name for Quaternary records:
As this pollen type is found in more than one genus, the suffix 'type' should be added for Quaternary records. In marine and coastal sediments, the pollen is most likely to be from *Terminalia*, and the term '*Terminalia* type' is suggested. In early Pleistocene sediments from Java, this pollen was found in sediments also yielding *Terminalia* leaf impressions (Morley et al., 2020). In peats and coals, '*Dactylocladus* type' was used by Anderson and Muller (1975), whereas in Holocene lake deposits, subject to human disturbance, '*Melastoma* type' would be appropriate (Morley, 1982a).

Ecological group:
In marine and coastal deposits, placement in the 'coastal' group is suggested, whereas for peat and coal studies, this taxon should be placed in the 'Padang' group. For inland Holocene sites, placement in a 'secondary' or 'disturbance' group is appropriate.

Melastoma malabathricum (Senduduk), kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).

Psilaheterocolpites combretoides

(Rao and Ramanujam 1982) Jaizan Jais and Morley comb. nov. Plate 25, Figs. 13, 14



Selected synonymy:
1982 *Heterocolpites combretoides* Rao and Ramanujam, p. 75, Pl. 2, Figs. 30, 31.

Description:
Single grain, lobate with six lobes in polar view, heterocolpate with three colporate apertures alternating with three colpi/pseudocolpi, grains prolate to subprolate, zonoaperturate, endoapertures more or less circular, nexine and sexine clearly visible, sexine thickens away from pseudoapertures, exine psilate, columellae not visible.

Dimensions:
Longest axis 23 (25) 26 μm (9 specimens measured from various horizons).

Stratigraphic distribution:
Early to middle Miocene of South India (Rao and Ramanujam, 1982; Ramanujam and Reddy, 1984), in this study rare and restricted to the top part of Malong 5G-17.2 well, from the late Miocene and Pliocene within zones PR14 to PR15.

Remarks and comparison:
The Malay Basin specimens resemble *Heterocolpites combretoides* Rao and Ramanujam 1982 in all aspects except that they do not show distinct columellae. Rao and Ramanujam (1982) in the description of the type species, noted the presence of a distinct columellae in their specimens, but they are not clearly seen in their photographs. This species differs from *Psilaheterocolpites laevigatus* (Salard-Cheboldaeff 1978) comb. nov. in its larger size.

Botanical affinity:
The heterocolpate configuration and large size compared to *P. laevigatus* suggests the family Combretaceae, which are mainly characteristic of semi-evergreen and deciduous forests in Southeast Asia (Ashton, 2014). In perhumid forests of the Malay Peninsula, Combretaceae are present mainly as climbers in lowland rain forest (Kochummen, 1972) except for *Terminalia* (see above) and *Lumnitzera*. *Lumnitzera* is a genus of backmangrove vegetation and has characteristic looped pneumataphores. It prefers settings with sandy substrates, and commonly occurs along the east coast of the Malay Peninsula. There are two species, *L. littorea* and *L. racemosa*. *Lumnitzera littorea* pollen shows minimal exine structure and would appear psilate in LM although is weakly punctate in SEM (Mao et al., 2012). *L. racemosa* pollen, however, is finely reticulate in SEM (Mao et al., 2012), and in LM would appear to be columellate. The Indian specimens might then be from *L. racemosa*, and the Malaysian specimens from *L. littorea*.

In areas of seasonally dry climate, Combretaceae pollen similar to *P. combretoides* may be derived from a variety of genera, especially *Combretum* and *Quisqualis*. Combretaceae pollen from Thailand has been described in detail by Krachai and Krachai (2015).

Source ecology:
In settings characterised by perhumid climates, *Lumnitzera* is a backmangrove taxon preferring sandy substrates. In areas of semi-evergreen and deciduous forests, *Combretum* and *Quisqualis*, and also *Terminalia* are common elements of terra firma forests and could produce this pollen type and *P. laevigatus.*

Suggested name for Quaternary records:
Lumnitzera type pollen, in settings where derivation from mangroves is suspected; Combretaceae pollen for settings with seasonally dry climates.

Ecological group:
Areas of perhumid climate, backmangrove; areas of seasonal climate, hinterland, seasonal.

2.21 SYNCOLPATE POLLEN

Genus *Marginipollis*
Clarke and Frederiksen 1968

Type species:
Marginipollis concinnus Clarke and Frederiksen 1968 (by original designation).

Generic remarks:
According to Jansonius and Hills (1976), the form-genus *Rostriapollenites* Venkatachala and Kar 1968 maybe a junior synonym of *Marginipollis* which was later confirmed by Kar (1986) who noted that the latter has been published earlier and therefore has priority over the former. *Planchoniidites* Khan 1976a, even though described as being 'tricolporoidate or tricolporate', is obviously very closely allied to *Marginipollis* (Playford, 1982). These pollen types compare closely with pollen of the Lecythidaceae subfamily Planchonoideae (Muller, 1972). *Marginipollis* has marginal ridges and polar 'cushions' and compares to Lecythidaceae aperture Type IV of Muller (1972b), whereas *Planchoniidites* Khan (1976a) lacks polar cushions, and compares to Type III of Muller (1972b), complying with the genera *Planchonia* and *Careya*.

Marginipollis concinnus
Clarke and Frederiksen 1968. Plate 25, Figs. 15-18

Selected synonymy:
1968 *Rostriapollenites kutchensis* Vankatachala and Kar 1968.

Description:
Single grain, tricolpate, syncolpate, prolate; colpi with marginal ridges bordered by marginal grooves; polar 'cushions' are present, the colpial surface is usually smooth or has sparsely or densely scattered verrucate-gemmate elements, mesocolpial sculpturing is psilate to scabrate with areolae becoming coarsely developed toward the colpi. Dimensions: Length 29 (35) 44 µm, width 18 (23) 30 µm (7 specimens measured from various horizons).

Remarks and comparison:
This syncolpate pollen is characterised by its crassimarginate colpi with polar 'cushions', marginal ridges and grooves. The average size of the Malay Basin specimens is generally smaller than the Nigerian specimens described by Clarke and Frederiksen (1968) that average 40 µm in length and 27 µm in width. This species differs from *Marginipollis quilonensis* Rao and Ramanujam 1982 by having coarse areolae at the colpi margins.

Stratigraphic distribution:
In Africa, recorded from Eocene to Miocene (Clarke and Frederiksen, 1968; Salard-Cheboldaeff, 1977, 1979). In India, this pollen type is present in the early Eocene (Venkatachala and Rawat, 1972, 1973; Venkatachala, 1974), with macrofossils recorded from the Deccan Traps (Wheeler et al., 2017), whereas in Southeast Asia *Marginipollis* occurs from the middle Eocene, about 46 Myr, onward (Morley, 2018). Scattered in low numbers in the Malong 5G-17.2 well, and in the upper part of the Delah 5H-14.1 well, but common within Delah through zones PR1 to PR3.

Botanical affinity:
Barringtonia, especially *B. asiatica* but most likely also other species. The pollen of Southeast Asian Planchonoideae are described in detail by Thammarong et al. (2019). *Barringtonia* extends from East Africa and Madagascar to tropical Asia and the Pacific and thus became extinct in West Africa during the Plio-Pleistocene based on records by Clarke and Fredriksen (1968) and Salard-Cheboldaeff (1977, 1979). The occurrence of *Barringtonia* pollen in the early Eocene of India, but not occurring until the middle Eocene (about 46 Myr) in the Sunda region, suggests that this genus dispersed to Southeast Asia as the Indian Plate collided with Asia during the Eocene (Morley, 2018) and is thus an 'Out of India' taxon.

Barringtonia asiatica *(Putat), Bogor, Java (photo by RJM).*

Source ecology:

The ecology of *Barringtonia* is varied, but many species are typical of swamp environments, riversides and coasts, and their pollen record provides important information on palaeoenvironment, provided that the climatic setting in known (Morley and Morley, 2013). Barringtonia spp are pollinated by bats. In perhumid settings, *Barringtonia* occurs commonly in swamps, and along rivers and coasts, but it also occurs in primary forest up to 1200 m (Whitmore, 1973). *Barringtonia asiatica* is widespread along sandy coasts from Madagascar to the Pacific. *Barringtonia conoidea* and *B. racemosa* occur along brackish rivers whereas *B. filirachis*, *B. macrocarpa* and *B. reticulata* are characteristic of swamp forests and along rivers beyond brackish influence (Corner, 1978). Some coals from the Malay and Barito Basins have yielded abundant *Barringtonia* pollen, suggesting that under certain conditions *Barringtonia* swamps may sometimes be peat-forming (Morley and Morley, 2013). In areas of seasonally dry climate with seasonal evergreen and semi-evergreen forests, *Barringtonia* may become very common in seasonal swamp settings. The classic locality for seasonal *Barringtonia* swamps is the Tonle Sap in Cambodia, where *B. acutangula* occurs today as a dominant in seasonally inundated swamp forest together with *Diospyros cambodiana* (Ebenaceae). Other tree genera in these swamps are *Elaeocarpus*, *Garcinia*, *Homalium*, *Lophopetalum* and *Xanthophyllum*, together with common climbers (Campbell et al., 2006). Seasonally inundated swamps are likely to be a major source of *Barringtonia* pollen in Malaysian sediments, especially in the Oligocene, when the climate was distinctly seasonal (Morley, 2012), and the area was characterised by numerous lakes (Morley and Morley, 2013).

Suggested name for Quaternary records:

Barringtonia asiatica type pollen.

Ecological group:

Perhumid climates; coastal forests and backmangrove. Wet seasonal climates; seasonally inundated swamp forests.

Marginipollis quilonensis

Rao and Ramanujam 1982. Plate 26, Figs. 1-4

Selected synonymy:

1982 *Marginipollis quilonensis* Rao and Ramanujam, p. 73, Pl. 2, Figs. 20, 21.

Description:

Single grain, tricolpate, syncolpate, prolate, colpi with marginal ridges bordered by marginal grooves, polar 'cushions' are present, colpial surface is usually smooth or has sparsely or densely scattered verrucate-gemmate elements, mesocolpial sculpturing is much less pronounced, with punctae or foveolae instead of being coarsely areolate as in *M. concinnus*.

Remarks and comparison:

These specimens agree in all aspects with the type material from India, originally described by Rao and Ramanujam (1982).

Dimensions:

Length 37 (38) 40 μm, width 22 (24) 28 μm (3 specimens measured from various horizons).

Stratigraphic distribution:

Early to middle Miocene of South India (Rao and Ramanujam, 1982; Ramanujam and Reddy, 1984). Present in low percentages within zones PR12B to PR15 in the Malong 5G-17.2, with scattered occurrences below.

Botanical affinity:

Barringtonia (Lecythidaceae). Based on the less pronounced exine sculpture, is likely that these specimens are from *B. conoidea,* whereas *M. concinnus* with pronounced areolae is from *B. acutangula* or *B. asiatica.*

Source ecology:

Barringtonia conoidea occurs along brackish rivers.

Suggested name for Quaternary records:

Barringtonia conoidea type pollen.

Ecological group:

Perhumid climates; tidal rivers and backmangrove.

Barringtonia conoidea, *freshwater intertidal zone, Sedili River, Johor, Malaysia (photo by RJM).*

Genus *Meyeripollis*

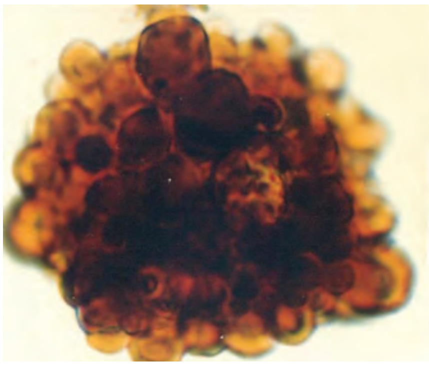
Baksi and Venkatachala 1970 emend. Baksi and Venkatachala in Thanikaimoni et al., 1984

Type species:

Meyeripollis naharkotensis Baksi and Venkatachala 1970 (by original designation, holotype in Meyer, 1958).

Meyeripollis naharkotensis

Baksi and Venkatachala 1970. Plate 26, Figs 7, 8



Selected synonymy:

1962 Gemmate syncolpate pollen in Biswas, Pl. 3, Figs. 37, 38.

Description:

Tricolporate, triangular in polar view, ectoapertures united at poles resulting in syncolpate configuration, exine covered with verrucae and gemmae which often obscure apertural configuration, two much larger gemmae occurring adjacent to each of the endoapertures, gemmae striate, clearly seen in SEM images and sometimes using LM if specimens well preserved.

Dimensions:

Longest axis 32 (43) 55 µm (6 specimens measured from various horizons).

Remarks:

This distinctive tricolporate-syncolpate form is characterised by having a pair of large gemmae situated adjacent to the apertures at the poles and at the equatorial regions. Its exine is sculptured with vaguely striate gemmae, tubercles and verrucae of different sizes that often obscure the apertures. The Malay Basin materials agree in all aspects with the description of the type specimen from India as described by Baksi and Venkatachala in Thanikaimoni et al. (1984).

Stratigraphic distribution:

Late Eocene to early Miocene of India (Meyer, 1958; Baksi, 1962; Baksi and Venkatachala, 1970; Baksi, 1972; Mathur and Mathur, 1980; Nandi, 1981); late Oligocene of the northwest Borneo (Kemp, 1974; Morley, 1991). In southern Kalimantan and Sumatra, this species also ranges from the late Eocene to early Miocene (Lelono, 2001) and can be very common in some settings, such as late Eocene coals from Mangklihat (Morley, 2000). It also occurs commonly in the Oligocene of Sarawak and the Nam Con Son Basin (Morley et al., 2011) but is absent from the Cuu Long Basin (Morley et al., 2019). The pollen type becomes less common in West Natuna and the Malay Basin, which is thought to relate to drier climates to the west, probably due to a rain shadow effect caused by uplands in the area of the Natuna Arch and the Con Son Swell. In Sarawak, it shows an increase in abundance within the mid Oligocene, and this has been used as the basis for subdivision of the Eocene in the local unpublished palynological zonation by Shell (Ho, 1978). It is common in the Eocene of the Yaw Formation in Myanmar (Huang, 2021) which has been dated at latest middle Eocene, 38 Myr (Westerweel et al., 2020).

Its earliest appearance is used to position the base of the late Eocene palynological zone E8 (Witts et al., 2012; van Gorsel et al., 2014). This species appears around the same time in India and Southeast Asia (Morley, 2018), and this is thought to be due to a land connection between the Indian and Asian Plates from about 41 Myr onward (Klaus et al., 2015).

Rare in Malay Basin, six specimens found, concentrated in the lower part of Delah 5H-14.1 section within zones PR1 to PR3.

Botanical affinity:

The identity of *Meyeripollis* has long been an enigma. Thanikaimoni et al. (1984) suggested an affinity with Sapindaceae, based on the syncolpate gemmate configuration seen in *Mischocarpus grandissimus*. However, some Australian *Eucalyptus* spp. display a much closer similarity, especially *Eucalyptus spathulata* and *E. leuhmannia*, illustrated by Thornhill and MacPhail (2012, Fig. 2). There is also a close similarity with the fossil taxon *Myrtaceidites lipsis* (MacPhail and Truswell, 1993) from the late Neogene of southern Australia. The likelihood therefore is that *Meyeripollis* pollen is derived from an extinct section of *Eucalyptus*.

Source ecology:

Since this taxon is common in late Eocene coals from Mangkalihat Peninsula, Kalimantan, it is thought to be derived from a peat swamp taxon (Morley, 1991), but it also occurs in paralic stratigraphic successions lacking coals, and thus it most likely that the parent plant also grew in other settings.

Suggested name for Quaternary records:

Not applicable.

Ecological group:

Peat swamp forests (Morley, 1991).

Genus *Myrtaceidites*

Cookson and Pike 1954 ex Potonié 1960

Type species:
Myrtaceidites mesonesus Cookson and Pike 1954 ex Potonié 1960.

Generic remarks:
Fossil pollen assignable to this form-genus are very common in both sections studied and they are easily identifiable at the generic level. However, due to the large number of specimens recovered, most species described by Cookson and Pike (1954) are difficult to determine consistently and reliably. This difficulty is mainly due to their small size and the considerable variability of the few morphological features present in this simple morphotype, but also to the the enormous taxonomic diversity of the family Myrtaceae that produces this pollen type. The relevant species of Cookson and Pike (1954) are outlined below in anticipation that further studies could clarify the group. The form-genus *Syncolporites* van der Hammen (1954) proposed for forms of similar morphology is invalid under the ICBN since van der Hammen used modern pollen of *Cupania cineria* as the holotype, and thus *Syncolporites* is a junior synonym of *Cupania*.

Thornhill and MacPhail (2012) have summarised fossil pollen attributable to *Myrtaceidites* based mainly on Australian material and divide the genus into five ‘complexes’ that allow Malaysian specimens to be placed in perspective. Their ‘complexes’ are as follows:

1. *Myrtaceidites parvus-mesonesus* complex accommodates parasyncolporate grains with unthickened exine around the endopores, ±psilate ornamentation, and the presence or absence of apocolpial islands. This group is well represented in Malaysian sediments and can be referred to *M. mesonesus, M. parvus* and *M. eugeniioides.*

2. *Myrtaceidites verrucosus* complex accommodates predominantly brevicolporate grains with granulate to verrucate ornamentation, absent from Malaysia.

3. *Myrtaceidites eucalyptoides* complex accommodates parasyncolporate grains with thickened nexine around the endospores and ±psilate exine, absent from Malaysia.

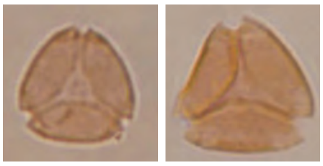
4. *Myrtaceidites tenuis* complex accommodates parasyncolporate to syndemicolporate grains with thickened exine around the endospores and psilate ornamentation, absent from Malaysia.

5. *Myrtaceidites leptospermoides* complex accommodates syncolporate grains with more or less psilate to scabrate/granulate ornamentation. *Myrtaceidites leptospermoides* specimens are commonly found in Malaysian Neogene sediments.

The Malaysian taxa can be keyed out as follows:		
1.	Grains parasyncolorate.	
2.	Grains with rounded apices, amb with straight or slightly convex sides.	
3.	Arci well developed, enclosing distinct polar islands.	*M. mesonesus*
3	Arci weakly developed and may or may not enclose polar islands.	*M. parvus*
2.	Grains with truncated apices, straight or concave sides.	*M. eugeniioides*
1.	Grains syncolpate, exine generally scabrate.	*M. leptospermoides*

Myrtaceidites parvus

Cookson and Pike 1954. Plate 26, Figs. 9-11



Description:

Grains small, amb subtriangular with convex sides; arci present which may or may not enclose polar islands, exine psilate, indistinctly patterned or granular.

Myrtaceidites mesonesus

Cookson and Pike 1954, not illustrated.

Description:

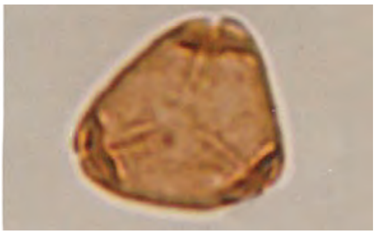
Grains parasyncolporate, small, amb with straight or slightly convex sides; arci prominent enclosing distinct polar islands, exine ca 1 μm, of uniform thickness, psilate.

Myrtaceidites eugeniioides

Cookson and Pike 1954, not illustrated.

Description:

Parasyncolporate, grains very small, amb with straight or slightly concave sides and truncate apices. Arci distinct, enclosing small polar islands, exine psilate or faintly mottled.



Myrtaceidites leptospermoides

Cookson and Pike 1954. Plate 26, Fig. 12

Description:

Syncolporate, colpi long, straight, narrow, meeting at the poles, amb straight sided to weakly concave with pointed to subround apices; exine about 1 μm thick, ±psilate to granulate or scabrate.

Myrtaceidites sp. (tetrasyncolpate)

Plate 26, Figs. 13, 14

Description:

Grains tetrasyncolpate.

Dimensions:

Equatorial diameter 10 (11) 13 μm (9 specimens measured from various horizons).

Remarks:

Most specimens recorded closely resemble *Myrtaceidites parvus* Cookson and Pike (1954), some are assignable to *Myrtaceidites eugeniioides* Cookson and Pike (1954) and a few to *Myrtaceidites mesonesus* Cookson and Pike (1954). Sometimes 4-syncolporate forms may be present (Plate 26, Figs. 13, 14).

A major issue in using the record of *Myrtaceidites* spp. as a stratigraphic indicator in Malaysia is that due to its small size, it is often lost during palynological processing by sieving to remove fine debris and in doing so concentrate the representation of larger index taxa on microscope slides. The process of sieving with a 10 μm will effectively remove all specimens of this genus, whereas a major part of the group will be removed with a 5 μm sieve.

Stratigraphic distribution:

Various *Myrtaceidites* species have been recorded from Paleocene to Pliocene of Australia (summarised in Thornhill and MacPhail, 2012). The oldest records are of *M. lisamae* the Santonian of West Africa, on which basis it is thought that the family Myrtaceae originated from West Africa (Morley, 2018). Their earliest occurrence in South America is from the Maastrichtian (van der Hammen, 1954). They were also recorded from the Paleocene of New Zealand (Mildenhall, 1980) and Eocene to Oligocene of Ninetyeast Ridge, Indian Ocean (Kemp and Harris, 1977).

Muller (1968) recorded *Myrtaceidites* spp. from the Kayan Formation of Western Sarawak. He thought that these could occur in the Late Cretaceous, but Morley (1998, 2000) demonstrated that the oldest records are Paleocene. Muller (1972) also noted an increase in abundance of *Myrtaceidites* spp. in the early Miocene of Sarawak, that he attributed to dispersal from the Australian Plate, further discussed by Morley (2000). This event is recorded in the Malong 5G-17.2 with an increase in abundance at the base of zone PR9B (Upper) and provides a useful datum for the Malay Basin. Present in high and moderate percentages throughout the upper part of the Malong 5G-17.2 well. In Delah 5H-14.1 well Myrtaceidites spp. are rare.

Botanical affinity:
Myrtaceae, most recorded specimens are probably derived from *Syzygium*, one of the commonest and most widespread tree genera in Malaysia with over 100 species (Kochummen, 1978). The many species of Malaysian *Syzygium* were formerly placed in the genus *Eugenia*, shown by Schmidt (1972) to be mainly restricted to South America. Anderson and Muller (1975) continued to term this pollen '*Eugenia* type', and this has been followed by palynologists such as Murtaza et al. (2018). Such practice is misleading should be abandoned. Other common taxa that produce this pollen type are *Melaleuca* and *Tristaniopsis*.

Source ecology:
The many species of *Syzygium* spp. are trees and shrubs from various habitats from high tide level to mountains and are particularly common in swamp vegetation. *Tristaniopsis* characterises the lower reaches of rivers, forming the '*Tristania*' belt of Corner (1978). *Melaleuca* is also common along riversides, especially in areas of disturbance (Wyatt-Smith, 1964). From the perspective of pollen recovered in Neogene sediments in Malaysia, Myrtaceae are thought to be more important as an indicator of riverside settings but may also be derived from swamps.

Syzygium *sp. Mekong Delta, Vietnam (photo by RJM).*

Suggested name for Quaternary records:
Syzygium type pollen for *Myrtaceidites parvus*, *M. mesonesus* and M. *eugeniioides; Leptosperma* pollen for *M. leptospermoides*.

Ecological group:
Riparian forests.

Plate 26

Figs. 1-4 *Marginipollis quilonensis* Rao and Ramanujam 1982. Figs. 1, 2 (x 1000): Slide Malong-2, 503 m, SWC (S2); England Finder S20. Figs. 3, 4 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder O26/1.

Figs. 5, 6 *Fenestripollenites longispinosus* (Lorente 1986) Jaizan Jais and Morley comb. nov. Figs. 5, 6 (x 1000): Slide Malong-2, 625 m, SWC (S3); England Finder L43/3.

Figs. 7, 8 *Meyeripollis naharkotensis* Baksi and Venkatachala 1970. Figs. 7, 8 (x 1000): Slide Delah-1, 2730-2735 m, DC (S3); England Finder E29.

Figs. 9-11 *Myrtaceidites parvus* Cookson and Pike 1954. Fig. 9 (x 1000): Slide Malong-2, 760-770 m, DC (S1); England Finder E21. Figs 10, 11 (x 1000): Slide Malong-2, 366 m, SWC (S1); England Finder R8.

Fig. 12 *Myrtaceidites leptospermoides* Cookson and Pike 1954, (x 1000): Slide Malong-2, 1315-1320 m, DC (S1); England Finder N15/1.

Figs. 13, 14 *Myrtaceidites* sp. (tetrasyncolpate). Figs. 13, 14 (x 1000): Slide Malong-2, 1000-1010 m, DC (S1); England Finder G18.

Fig. 15 *Cupanieidites* sp. (x 1000): Slide Malong-2, 1395-1400 m, DC (S1); England Finder K31.

Figs. 16, 18 *Tricolpites simatus* Stover and Partridge 1973. Fig. 16 (x 1000): Slide Malong-2, 780-790 m, DC (S1); England Finder T18. Fig. 18 (x 1000): Slide Malong-2, 934 m, SWC (S1); England Finder J29/4.

Figs. 17, 19 *Gothanipollis gothani* group Krutzsch 1959. Fig. 17 (x 1000): Slide Malong-2, 1518.5 m, CC (S1); England Finder W17/3. Fig. 19 (x 1000): Slide Malong-2, 1603.7 m, CC (S1); England Finder S29/1. Fig. 20 (x 1000): Slide Malong-2, 483 m, SWC (S2); England Finder U21/3.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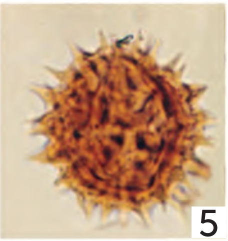
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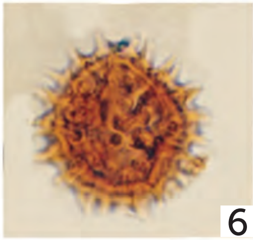
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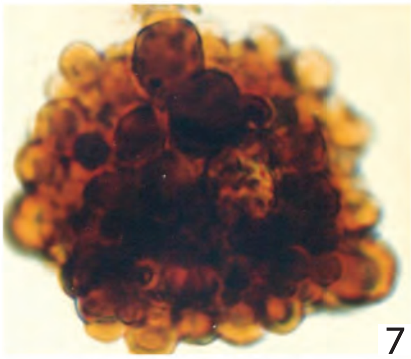
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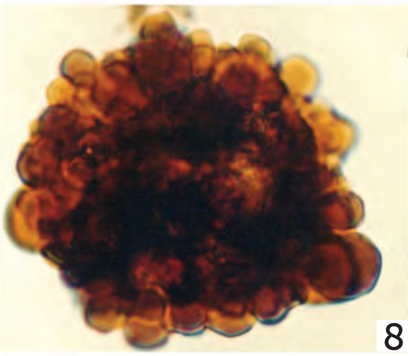
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14

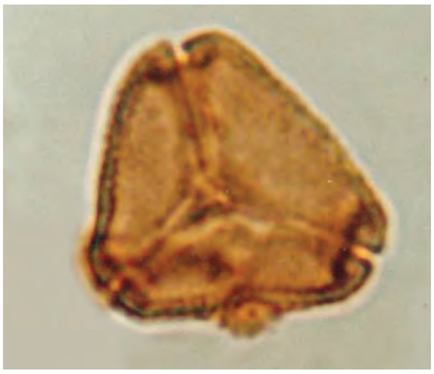
Genus *Cupanieidites*

Cookson and Pike 1954 ex Krutzsch 1959

Type species:
Cupanieidites major Cookson and Pike 1954 (by designation of Krutzsch, 1959).

Generic remarks:
Comments on the usage of the form-genera *Cupanieidites* and *Duplopollis* Krutzsch 1959 can be found in Stover and Partridge (1973). Kemp and Harris (1977) also noted that forms with comparable morphology continue to be assigned to *Syncolporites* van der Hammen 1954 which is invalid under the ICBN (see above).

***Cupanieidites* spp.** Plate 26, Fig. 15



Description:
Syntricolporate, oblate, amb triangular, with truncated or broadly rounded apices, with polar islands in both hemispheres, endoapertures well formed, with thickened endexine, exine faintly microreticulate, uniform thickness.

Dimensions:
Equatorial diameter 16 (20) 26 µm (10 specimens measured from various horizons).

Remarks:
Included here are tricolporate-syncolpate specimens with triangular amb, which conforms to the form-genus *Cupanieidites*. They lack polar cushions, which characterise the family Loranthaceae. No attempt to speciate this group has been made due to their low numbers of occurrence.

Stratigraphic distribution:
Pollen comparable to *Cupaniopsis* has been recorded from the Santonian and Coniacian as *Cupanieidites reticularis* and *C. acuminatus* (Belsky et al., 1965; Boltenhagen, 1976). *Cupanieidites* species have also been widely recorded from Paleocene to Pliocene of Australia (Cookson and Pike, 1954; Harris, 1965; Hekel, 1972; Martin, 1973; Stover and Partridge, 1973); and New Zealand (Couper, 1960). Sparsely distributed in low numbers in Malong 5G-17.2 and Delah 5H-14.1 wells.

Botanical affinity:
Sapindaceae. The diverse pollen types of this family are described by Muller and Leenhouts (1976). Syntricolporate pollen is confined mainly to the tribe Cupanieae that in Malaysia includes several lowland forest tree genera such as *Arytera*, *Guoia*, *Mischocarpus* and *Paranephelium*.

Source ecology:
Climbing herbs, shrubs to large trees common in lowland forests.

Suggested name for Quaternary records:
Cupaniopsis type pollen.

Ecological group:
Lowland forest.

Genus *Gothanipollis*

Krutzsch 1959

Type species:
Gothanipollis gothanii Krutzsch 1959 (by original designation).

The genus *Gothanipollis* accommodates lobate pollen derived from the mistletoe family Loranthaceae, which is characterised mostly by syncolpate, oblate pollen with endexinal thickenings, termed 'polar cushions'. Pollen attributable to mistletoes occurs in low numbers through most Neogene successions in Malaysia but is of little stratigraphic significance. Toward Vietnam and China however, the regular presence of *Gothanipollis basensis* Stover and Partridge (1973) is important in identifying the Oligocene (Chung et al., 2015).

Loranthaceae pollen is represented by four distinctive pollen types: type A , which is 3 to 5 colpate and echinate, is considered primitive in the family, and occurs in species from Australia and South America; type B is trisyncolpate, with lobate forms attributed to *Gothanipollis*, and triangular forms placed in *Tricolpites simatus* (see below) and is found in most Southeast Asian genera such as *Elytranthe* and *Dendropthoe*; type C, which occurs in the Southeast Asian genus *Amylotheca*, is syndemicolpate, whereas type D is lophate, considered advanced, and occurs in the South American genus *Oryctanthus* (Grimsson et al., 2018). Molecular data indicates that the family originated in Australia (Liu et al., 2018).

Gothanipollis gothani

Krutzsch 1959. Plate 26, Figs. 17-19

Description:

Trisyncolpate or trisyncolporate, strongly trilobate, with concave triangular shape and typically truncated apices, ectoapertures long, extending to poles, endoapertures difficult to characterise, but are suggested from thickened endexine in apical area, sexine psilate to faintly microreticulate sculpture and with polar 'cushions' (thickening of the endexine in the polar region).

Dimensions:

Equatorial diameter 20 (25) 28 μm (3 specimens measured from various horizons).

Stratigraphic distribution:

Present in low numbers and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

Included here are syncolp(or)ate pollen with a trilobate amb. There is a lot of variation in this taxon but as it occurs in low numbers. No attempt has been made to suggest additional species.

Botanical affinity:

Loranthaceae, such as *Dendropthoe* and *Elytranthe*.

Source ecology:

Parasitic shrubs on forest and non-forest trees.

Suggested name for Quaternary records:

Elytranthe type pollen.

Ecological group:

Lowland forest.

Genus *Tricolpites*

Cookson ex Couper 1953

Type species:

Tricolpites reticulatus Cookson 1957.

Remarks:

The following species is placed in *Tricolpites* Cookson ex Couper following Stover and Partridge (1973) p. 255. Pending availability of better material, this taxon requires a new genus, to accommodate tricolpate pollen with affinity to Loranthaceae.

Tricolpites simatus

Stover and Partridge 1973. Plate 26, Figs. 16, 18

Description:

Trisyncolpate, with triangular amb, typically rounded apices, endoapertures long, extending to poles, sexine psilate to faintly microreticulate sculpture and with polar 'cushions' (thickening of the endexine in the polar region).

Stratigraphic distribution:

Present in low numbers and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:

Included here are syncolpate pollen with a triangular amb. Differentiated from *Cupanieidites* by the presence of polar cushions.

Botanical affinity:

Loranthaceae, the triangular amb is suggestive of *Loranthus*.

Source ecology:

Parasitic shrubs on forest and non-forest trees.

Suggested name for Quaternary records:

Loranthus type pollen.

Ecological group:

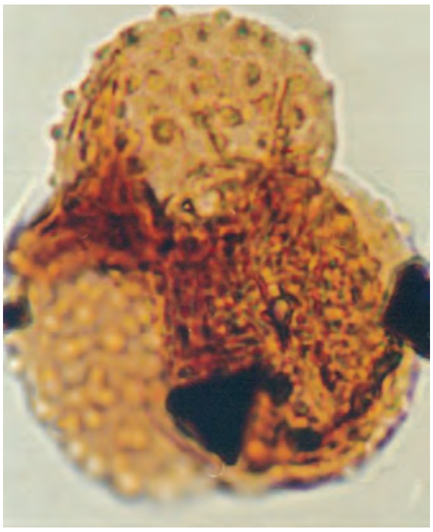
Lowland forest.

2.22 TETRAD POLLEN

Genus *Ornatetradites*
Rao and Ramanujam 1982

Type species:
Ornatetradites droseroides Rao and Ramanujam 1982.

Ornatetradites droseroides
Rao and Ramanujam 1982. Plate 26, Figs. 16, 18



Selected synonymy:
1982 *Ornatetradites droseroides* Rao and Ramanujam, p. 87, Pl. 5, Figs. 85, 86.

Description:
Grains in tetrahedral tetrads, individual grains spherical, porate, pores partially obscured by ornamentation, sexine thicker than nexine, tectate, columellae distinct, tectum appearing to be punctate, supratectal ornamentation consisting of slightly irregular warty verrucae or gemmae.

Dimensions:
Tetrad length 37 µm, width 33 µm (1 specimen measured).

Stratigraphic distribution:
Early to middle Miocene of South India (Rao and Ramanujam, 1982). Only one specimen found in Malong 5G-17.2 well at 1022 m (SWC) depth.

Remarks:
This gemmate tetrad form agrees in all aspects with the description of the type specimen from India given by Rao and Ramanujam (1982) and Thanikaimoni et al. (1984).

Botanical affinity:
Tetrahedral porate verrucate tetrads occur in just a few genera of Rubiaceae, such as *Casasia* and *Olicogodon* (Erdtman, 1953; Morley, 2000), and also *Lophopetalum* in Celastraceae. This pollen type exactly matches *Lophopetalum pachyphyllum* and *L. wightianum*, illustrated by Hou (1969). *Lophopetalum pachyphyllum* is a large tree of lowlands and hill forests of the Malay peninsula and Sumatra and *L. wightianum* is common on coastal hills (Kochummen and Whitmore, 1972). The Malong 5G-17.2 record indicates that the *Lophopetalum pachyphyllum* clade has been present in India and Malaysia from the early Miocene.
Rao and Ramanujam (1982) suggested affinity of *Ornatetradites droseroides* with *Drosera* (Droseraceae), but this suggestion was rejected by Thanikaimoni et al. (1984) since *Droseridites* has pores associated with a system of proximal channels (Thaikaimoni, 1978).

Source ecology*:*
Tree of lowland and hill forests.

Suggested name for Quaternary records:
Lophopetalum pachyphyllum type pollen.

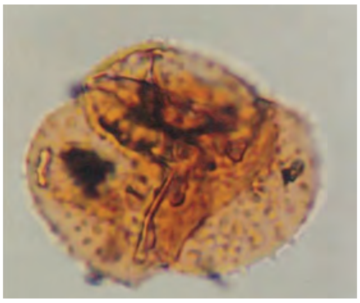
Ecological group:
Lowland trees/shrubs.

Breathing roots of Lophopetalum tanahgambut, *a new species from Sumatra, with* Augusti Rambut, *National University of Singapore (photo by Lahiru Wijedasa).*

Genus *Nepenthidites*
Kumar 1995

Type species:
Nepenthidites laitryngewensis Kumar 1995.

Nepenthidites neogenicus
Morley and Jaizan Jais sp. nov. Plate 27, Figs. 5, 6



Derivation of name:
Being derived from the Neogene.

Holotype:
Plate 27, Figs. 5, 6. Slide Malong-2, 641.5 m, SWC (S2), England Finder O35.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore peninsular Malaysia; sidewall core sample at 641.5 m depth; age late Miocene, zone PR14.

Description:
Tetrahedral tetrads, small in size, individual grains subtriangular, inaperturate, closely adhering, exine thin, structure not discernible in LM but finely granulate in SEM (Adam and Wilcock, 1999), spinulate, spinules short, bluntly pointed.

Dimensions:
Tetrad length 26 µm, width 21 µm; diameter of monads 17 µm (1 specimen measured).

Remarks:
This tetrad specimen is characterised by its echinate sculpture and inaperturate monads. *Nepenthidites* differs from *Droseridites* in that individual grains are more closely packed and lack proximal channels.

Stratigraphic distribution:
Only one specimen found in the Malong 5G-17.2 well at 918 m (SWC) depth.

Nepenthes *sp. Kerangas, Bako National Park, Sarawak, Malaysia (photo by RJM).*

Botanical affinity:
Nepenthes (Nepenthaceae).

Source ecology:
Nepenthes spp. are plants of very nutrient-poor settings, especially kerangas and swamps.

Suggested name for Quaternary records:
Nepenthes pollen.

Ecological group:
Herb common in kerangas.

Plate 27

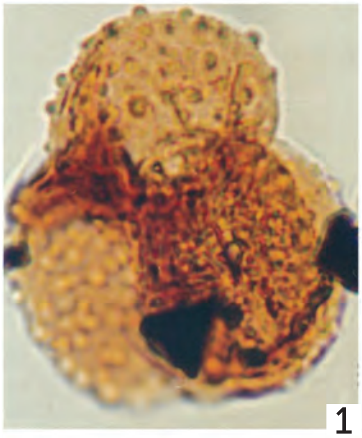
Figs. 1, 2 *Ornatetradites droseroides* Rao and Ramanujam 1982. Figs. 1, 2 (x 1000): Slide Malong-2, 1022 m, SWC (S1); England Finder K11/4.

Figs. 3, 4 *Triporotetradites campylostemonoides* Salard-Cheboldaeff 1974. Figs. 3, 4 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder O35.

Figs. 5, 6 *Nepenthidites neogenicus* Morley and Jaizan Jais sp. nov. Figs. 5, 6 (x 1000 holotype): Slide Malong-2, 918 m, SWC (S1); England Finder E23/1.

Figs. 7-9 *Triporotetradites microreticulatus* Morley and Jaizan Jais sp. nov. Figs. 7, 8, 9 (x 1000 holotype): Slide Malong-2, 561 m, SWC (S1); England Finder V9.

Figs. 10, 11 *Inaperturotetradites reticulatus* Salard-Cheboldaeff 1978. Fig. 10 (x 400), Fig. 11 (x 1000): Slide Malong-2, 1200-1205 m, DC (S1); England Finder E21/4.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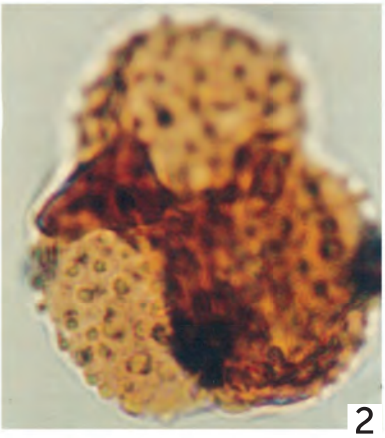
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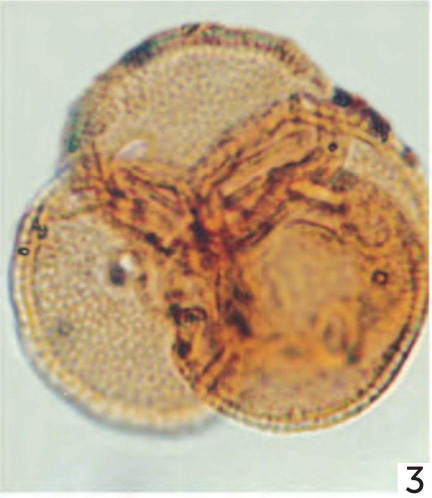
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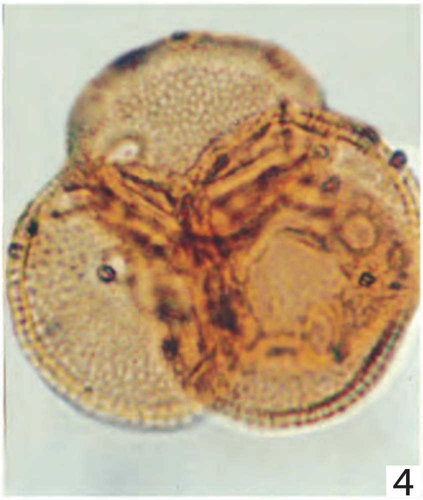
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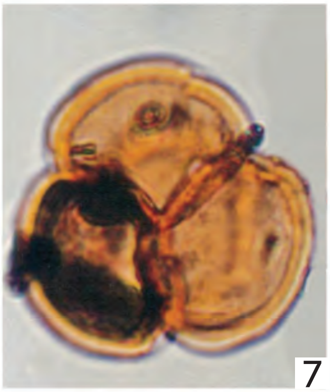
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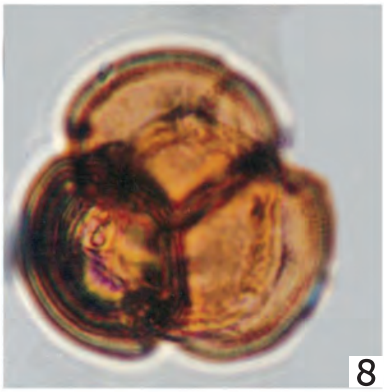
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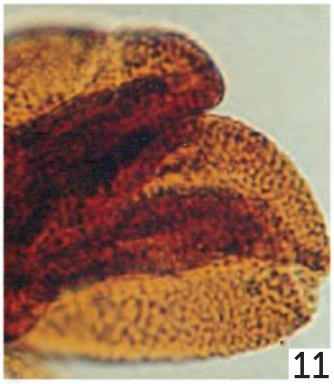
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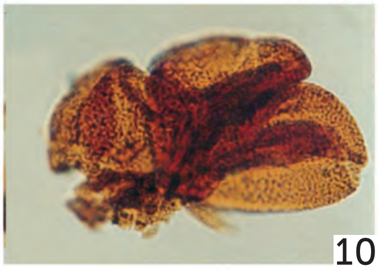
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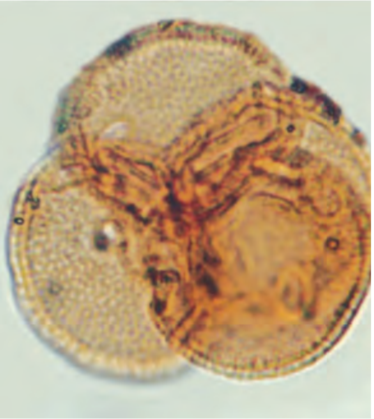
Genus *Triporotetradites*

van Hoeken-Klinkenberg 1964

Type species:
Triporotetradites scabratus van Hoeken-Klinkenberg 1964 (by original designation).

Triporotetradites campylostemonoides

Salard-Cheboldaeff 1974. Plate 27, Figs. 3, 4



Selected synonymy:
1974 *Triporotetradites campylostemonoides* Salard-Cheboldaeff, p. 502, Pl. 1, Figs. 9, 10.

Description:
Tetrahedral tetrads, individual grains spherical, triporate, pores circular with narrow annulus, sexine thicker than nexine, clearly reticulate, columellae distinct, lumina uniform in size and shape.

Dimensions:
Tetrad diameter 30 (36) 40 μm (4 specimens measured from various horizons).

Stratigraphic distribution:
Oligocene to Miocene of Cameroon (Salard-Cheboldaeff, 1974, 1978). Present in low numbers and sparsely distributed in both Malong 5G-17.2 and Delah 5H-14.1 wells, and thus ranging from the late Oligocene to Pliocene. Late Miocene to Recent of Borneo (Muller, 1972, recorded as *Lophopetalum*; Morley (1976) recorded this type as *L. multinervium*).

Remarks and comparison:
This tetrad form is characterised by its reticulate and annulate triporate monads which resembles the type specimen originally described by Salard-Cheboldaeff (1974) from Cameroon. It differs from *Triporotetradites microreticulatus* sp. nov. in having a more pronounced and coarser reticulum.

Botanical affinity:
Lophopetalum multinervium, *L. floribundum*, *L. javanicum* and *L. pallidum* (Celastraceae) in Southeast Asia (Hou, 1969); *Campylostemon laurentii* (Celastraceae) in Africa (Salard-Cheboldaeff, 1974).

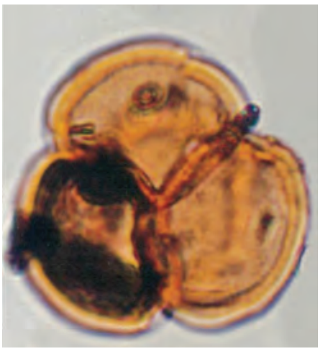
Source ecology:
The Malaysian species are mainly medium to large peat swamp trees, except for *L. pallidum*, which is a tree of hillsides and ridgetops in the Malay Peninsula.

Suggested name for Quaternary records:
Lophopetalum multinervium type pollen.

Ecological group:
Peat swamp forests.

Triporotetradites microreticulatus

Morley and Jaizan Jais sp. nov. Plate 27, Figs. 7-9



Derivation of name:
From the finely reticulate exine.

Holotype:
Plate 27, Figs. 7-9. Slide Malong-2, 561 m, SWC (S1), England Finder V9.

Type locality:
Well Malong 5G-17.2, Malay Basin, offshore peninsular Malaysia; sidewall core sample at 561 m depth; age late Miocene, zone PR14.

Description:
Tetrahedral tetrads, individual grains spherical, triporate, pores circular with narrow annulus, sexine thicker than nexine, finely reticulate, columellae obscure.

Dimensions:
Tetrad diameter 24 (26) 28 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in Malong-1 well; absent in the Delah 5H-14.1 section.

Remarks and comparison:
This tetrad specimen is distinguished by its spherical, triporate and microreticulate-columellate monads. This form represents a new species. It differs from *Triporotetradites campylostemonoides* Salard-Cheboldaeff 1974 in having faint and much finer reticulum.

Botanical affinity:
This species compares closely with the finely reticulate species of *Lophopetalum* (Celastraceae). as discussed by Hou (1969). However, Hou does not illustrate or discuss the species with very finely reticulate pollen, and so the specific attribution cannot be made.

Source ecology:
Probably lowland forest.

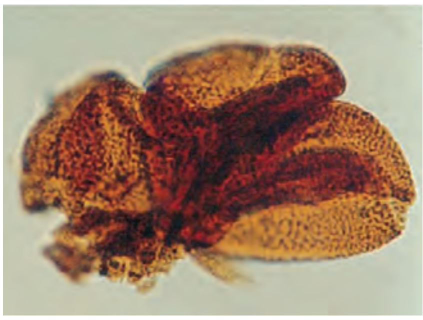
Suggested name for Quaternary records:
Lophopetalum type pollen.

Ecological group:
Lowland forest.

Genus *Inaperturotetradites*
van Hoeken-Klinkenberg 1964

Type species:
Inaperturotetradites lacunosus van Hoeken-Klinkenberg 1964 (by original designation).

Inaperturotetradites reticulatus Salard-Cheboldaeff 1978. Plate 27, Figs. 10, 11



Selected synonymy:
1978 *Inaperturotetradites reticulatus* Salard-Cheboldaeff, p. 249, Pl. 7, Figs. 1, 2.

Description:
Large tetragonal tetrads, individual grains inaperturate, exine finely and uniformly reticulate, sexine thicker than nexine.

Dimensions:
Tetrad length 90 μm, width 50 μm (1 specimen measured).

Stratigraphic distribution:
Oligocene of Cameroon (Salard-Cheboldaeff, 1978).

Remarks:
This large tetrad form resembles the type specimen described by Salard-Cheboldaeff (1978) in having inaperturate and finely reticulate monads. Only one specimen found in Malong G-17-2 well at 1205 m (DC) depth.

Botanical affinity:
Annonaceae, this pollen compares to the African species *Annona senegalensis* (Salard-Cheboldaeff, 1978). In Malaysia, tetrad pollen occurs in the genera *Disepalum, Goniothalmus Pseudouvaria* and *Xylopia*.

Source ecology:
Trees of lowland forests and swamps.

Suggested name for Quaternary records:
Annona type pollen.

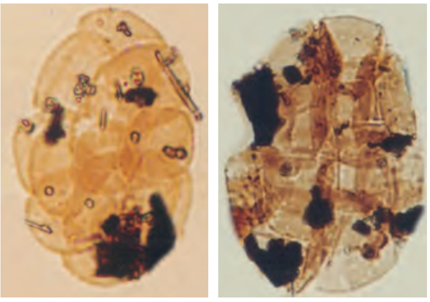
Ecological group:
Lowland forest.

2.23 POLYAD POLLEN

Genus *Polyadopollenites*
Pflug and Thomson in Thomson and Pflug 1953

Type species:
Polyadopollenites multipartitus Pflug in Thomson and Pflug 1953 (by original designation).

***Polyadopollenites* spp.** Plate 28, Figs. 1-4



Description:
Polyads consisting of three or four tetrahedral tetrads, individual grains inaperturate, psilate, exine thin, exine structure not discernible.

Dimensions:
Polyad length 32 (47) 75 μm, width 22 (33) 53 μm (3 specimens measured from various horizons).

Stratigraphic distribution:
Rare and sparsely distributed in Malong 5G-17.2 and Delah 5H-14.1 wells.

Remarks:
Included here are polyad forms of various sizes, consisting of 12 to 16 psilate grains. These specimens are comparable to *Polyadopollenites myriosporites* (Cookson 1954) Partridge in Stover and Partridge 1973, *P. varpalotaensis* Nagy 1962 and *P. vancampoi* Salard-Cheboldaeff 1978.

Botanical affinity:
Most probably derived from *Pithecellobium* (Mimosaceae).

Source ecology:
Common trees of lowland forests.

Suggested name for Quaternary records:
Pithecellobium type pollen.

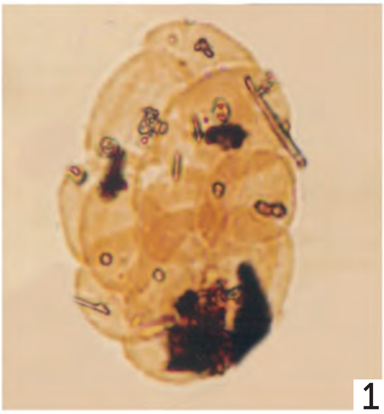
Ecological group:
Lowland forest.

Plate 28

Figs. 1-4 *Polyadopollenites* spp. Figs. 1, 3 (x 1000): Slide Malong-2, 409 m, SWC (S2); England Finder K8. Fig. 2 (x 1000): Slide Malong-2, 430.5 m, SWC (S2); England Finder R30/2. Fig. 4 (x 1000): Slide Malong-2, 641.5 m, SWC (S2); England Finder M39/1.

Figs. 5-8 *Bosedinia infragranulata* He 1984. Fig. 5 (x 1000): Slide Delah-1, 2270-2275 m, DC (S1); England Finder L32/4. Fig. 6 (x 1000): Slide Malong-2, 1588.7 m, CC (S1); England Finder P15. Fig. 7 (x 400): Slide Malong-2, 592 m, SWC (S1); England Finder N23/4. Fig. 8 (x 1000): Slide Malong-2, 1588.7 m, CC (S1); England Finder X23/3.

Figs. 9, 10 *Bosedinia whelkaris* Cole 1992. Fig. 9 (x 400): Slide Delah-1, 2400-2405 m, DC (S1); England Finder V44/4. Fig. 10 (x 400): Slide Delah-1, 2655-2660 m, DC (S2); England Finder H24/1.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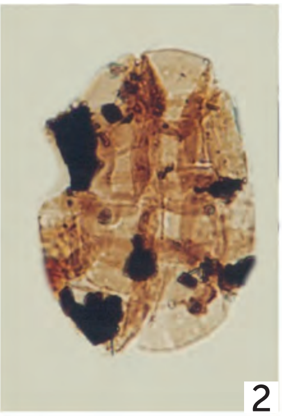
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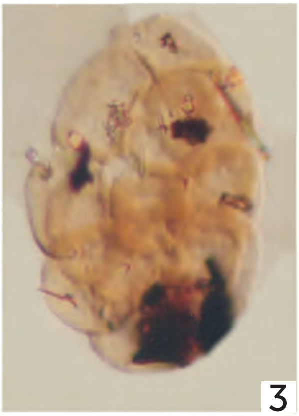
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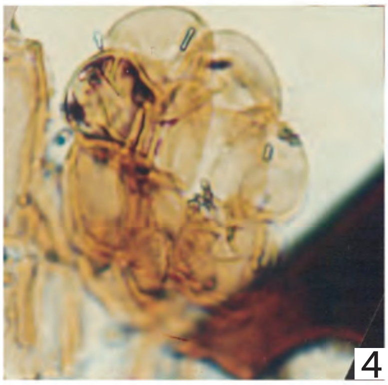
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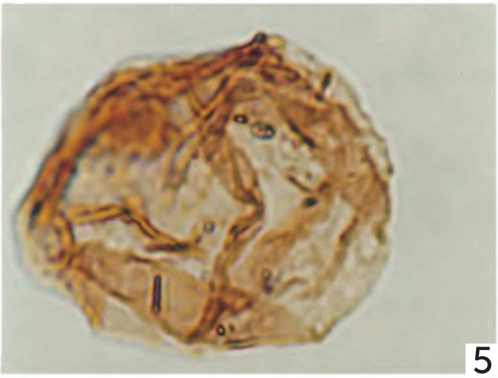
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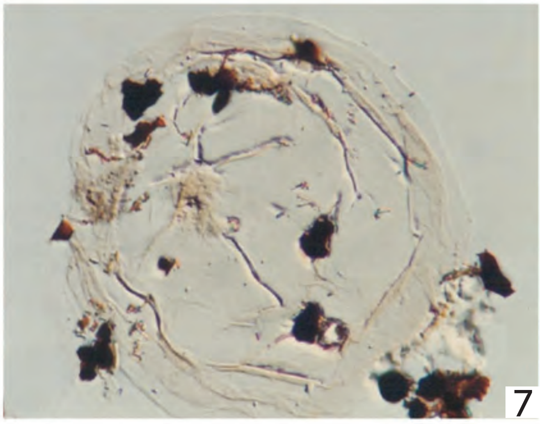
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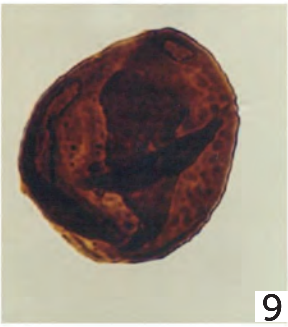
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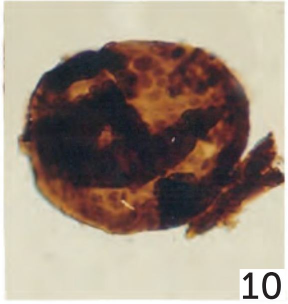
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2.24 FRESHWATER DINOCYSTS AND ACRITARCHS

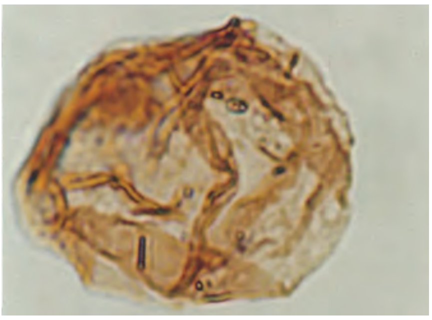
Genus *Bosedinia*

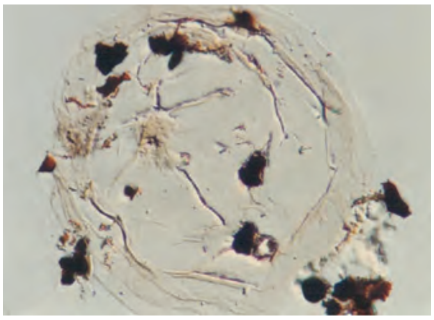
He 1984

Type species:
Bosedinia granulata (He and Qian 1979) He 1984 (by designation of He and Qian 1979.

Bosedinia infragranulata

He 1984. Plate 28, Figs. 5-8





Selected synonymy:
1984 *Bosedinia infragranulata* He, p. 174, Pl. 6, Figs. 17-23.
1992 *Bosedinia infragranulata* He; Cole, p. 185, Pl. 1, Figs. 1-8; Text-Fig. 3A-E.

Description:
Cysts subspherical with single layered, thin (less than 0.5 μm) wall often strongly folded and with a smooth surface. Omphalos not always present, excystment aperture evident as a narrow slit or small notch on either side of the cyst (Cole, 1992).

Dimensions:
Diameter 25 (37) 52 μm (9 specimens measured from various horizons).

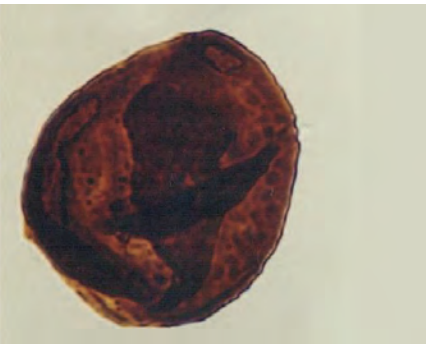
Stratigraphic distribution:
This species has been recorded from the ?Eocene to early Miocene of East China (He, 1984) and from the late Oligocene (age corrected by Azmi Yakzan et al., 1996 and by Morley et al., 2003) of the South China Sea (Cole, 1992), and is abundant from the late Eocene to late Oligocene of the Cuu Long Basin, offshore southern Vietnam (Morley et al., 2019). Present in very high percentages in the Delah 5H-14.1 well and generally decreases upward. Present in low percentages in the lower part of Malong 5G-17.2 well.

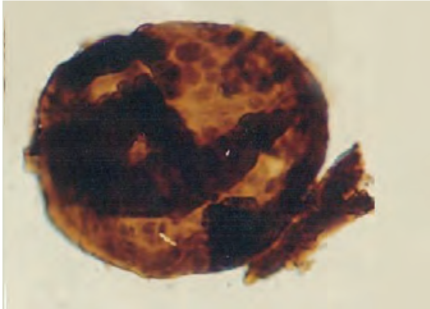
Remarks:
The Malay basin specimens agree in all aspects with those described and illustrated by Cole (1992).

Ecological/Morphological group:
Freshwater dinocysts.

Bosedinia whelkaris

Cole 1992. Plate 28, Figs. 9, 10





Selected synonymy:
1992 *Bosedinia whelkaris* Cole, p. 188, Pl. 3, Figs. 3-5; Text-fig. 4.

Description:
Verrucate, subspherical cyst with a single layered wall 1 μm in thickness with rare folds, verrucae up to 3 μm in diameter, tend to be concentrated in patches leaving some areas unornamented, excystment aperture usually visible as a slightly gaping split, omphalos large and prominent, oblong in shape (Cole, 1992).

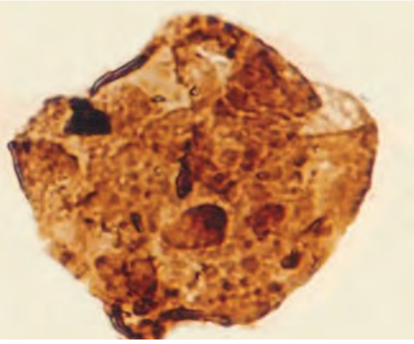
Dimensions:
Diameter, minimum 45 μm, maximum 55 μm (2 specimens measured).

Stratigraphic distribution:
Cole (1992) and Azmi Yakzan et al. (1996) have reported this species from the mid Cenozoic of the South China Sea, later dated to the Oligocene by Morley (2003). Present in low percentages in the lower part of the Delah 5H-14.1 well.

Remarks:
The Malay Basin specimens agree in all aspects with the type material described and illustrated by Cole (1992).

Ecological/Morphological group:
Freshwater dinocysts.

Bosedinia granulata
(He and Qian) He 1984 emend. Chen et al. 1988. Plate 29, Figs. 1, 2



Selected synonymy:
1979 *Bosea granulata* He and Qian, p. 178, Pl. 1, Figs. 1-5.
1984 *Bosedinia granulata* (He and Qian) He, p. 173, Pl. 7.
1992 *Bosedinia granulata* (He and Qian) He; Cole, p. 185, Pl. 2, Fig. 3, Text-fig. 3H.

Description:
Thin walled (0.5 μm) oval shaped, microgranulate cyst with a prominent epicystal archaeopyle and attached operculum, distinct omphalos present in antapical area of cyst, has well developed 'V' shaped notches along the edge of the archaeopyle that may mark paraplate boundaries (Cole, 1992).

Dimensions:
Diameter, minimum 48 μm, maximum 55 μm (2 specimens measured).

Stratigraphic distribution:
This species has been reported from the Eocene to early Miocene of China (He and Qian, 1979; He, 1984) and from the mid Cenozoic of the South China Sea by Cole (1992) and Azmi Yakzan et al. (1996), later dated to the late Oligocene by Morley et al. (2003). Only two specimens were found, and these were in the 2660 m (DC) of the Delah 5H-14.1 well.

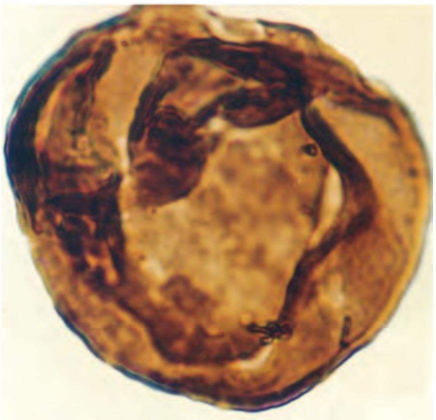
Remarks:
The Malay basin specimens resemble *B. granulata* described and illustrated by Cole (1992), but the former are generally smaller in size as compared to the latter that measured 70 μm in diameter.

Ecological/Morphological group:
Freshwater dinocysts and acritarchs.

Genus *Granodiscus*
Mädler 1963

Type species:
Granodiscus granulatus Mädler 1963.

Granodiscus staplinii
(Pocock 1972) Jiabo 1978. Plate 29, Figs. 3-6



Selected synonymy:
1972 *Leiosphaeridia staplinii* Pocock, p. 104, Pl. 25, Fig. 11.
1978 *Granodiscus staplinii* (Pocock) Jiabo, p. 103, Pl. 38, Figs. 1-6.
1992 *Granodiscus staplinii* (Pocock) Jiabo; Cole, p. 190, Pl. 2, Figs. 1, 2; Text-figs. 3F, G.

Description:
Finely granulate, spherical to subspherical with a single layered wall of 'medium' thickness (0.5 to 1.0 μm) as reflected by a few long, heavy folds that are subparallel to the edge of the cyst; omphalos appears as a darker rounded, oblong or dumb-bell shaped mass; excystment suture visible as a slit, although occasionally an operculum of epicystal type is formed, remaining attached along one edge (Cole, 1992).

Dimensions:
Diameter 38 (43) 48 (5 specimens measured from various horizons).

Stratigraphic distribution:
This species has been recorded in China from the early Cenozoic (Jiabo, 1978) and the early to middle Miocene (Zhu et al., 1985). It has also been reported from the mid Cenozoic of the South Shina Sea (Cole, 1992; Azmi Yakzan et al., 1996), later dated to the late Oligocene by Morley et al. (2003). Present in high percentages in the lower part of the Delah 5H-14.1 well.

Remarks:
The Malay basin specimens resemble, in all aspects, those described and illustrated by Cole (1992).

Ecological/Morphological group:
Freshwater acritarchs.

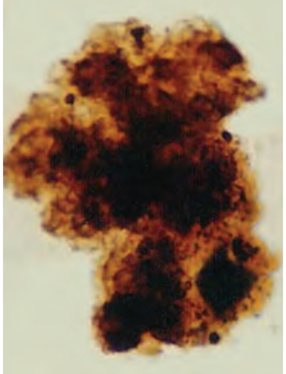
2.25 COLONIAL ALGAE

Two genera of colonial algae were identified in this study, *Botryococcus* Kützing 1849 and *Pediastrum* Meyen 1829. They are briefly described below following the basic format used in the systematic description of pollen and spores.

Genus *Botryococcus*
Kützing 1849

Type species:
Botryococcus braunii Kützing 1849.

Botryococcus braunii Kützing 1849. Plate 29, Fig. 7



Selected synonymy:
1973 *Botryococcus braunii* Kützing; Martin, p. 46, Fig. 201.
1993 *Botryococcus braunii* Kützing; Fernández, p. 196, Pl. 3, Figs. 3-5.

Stratigraphic distribution:
Distributed in high percentages in the Delah 5H-14.1 well and in moderate percentages at the basal part of the Malong 5G-17.2 well.

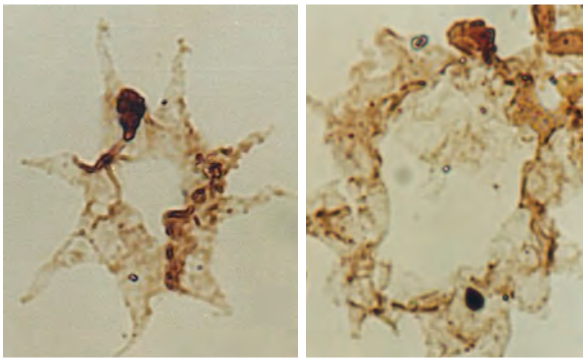
Remarks:
Included here are globose colonial algae with the appearance of small cauliflower, of irregular shape and variable in size depending on the number of cells remaining attached to one another. The cells are generally ellipsoidal and spherical in shape and arranged radially or in rows to form a colony.

Source ecology:
Fresh to brackish water algae.

Ecological/Morphological group:
Algae.

Genus *Pediastrum Meyen 1829*

***Pediastrum* spp.** Plate 29, Figs. 8-10



Distribution:
Present in low and high percentages in the Delah 5H-14.1 well; only one specimen found in the Malong 5G-17.2 well.

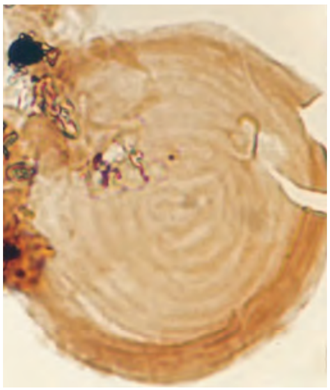
Remarks:
Included here are various *Pediastrum* spp. of compact and perforate types of various sizes and shapes. For this evaluation, no attempt is made to consistently speciate the genus.

Source ecology:
Cosmopolitan green algae in freshwater, lakes and ponds.

Ecological/Morphological group:
Algae.

2.26 OTHER FRESHWATER ALGAE

Genus *Concentricystes*
Concentricystes circulus Rossingol 1962. Plate 29, Fig. 11



Distribution:
Present in very low percentages in both Malong 5G-17.2 and Delah 5H-14.1 wells.

Plate 29

Figs. 1, 2 *Bosedinia granulata* (He and Qian) He 1984 emend. Chen et al. 1988. Fig. 1 (x 400): Slide Delah-1, 2655-2660 m, DC (S2); England Finder P40. Fig. 2 (x 400): Slide Delah-1, 2655-2660 m, DC (S3); England Finder E37.

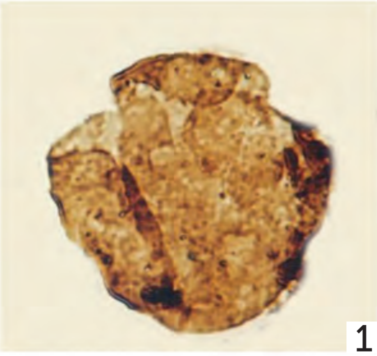
Figs. 3-6 *Granodiscus staplinii* (Pocock 1972) Jiabo 1978. Figs. 3, 4 (x 1000): Slide Delah-1, 2400-2405 m, DC (S1); England Finder N15. Fig. 5 (x 1000): Slide Delah-1, 2400-2405 m, DC (S3); England Finder P33/1. Fig. 6 (x400): Slide Delah-1, 2400-2405 m, DC (S1); England Finder X12/4.

Figs. 8, *Pediastrum delicatites* Wilson and Hoffmeister 1953. (x 400): Slide Delah-1, 2250-2255 m, DC (S1); England Finder P29.

Fig. 9 *Pediastrum* sp. (x 1000): Slide Delah-1, 2520-2525 m, DC (S1); England Finder E17/3.

Fig. 10 *Pediastrum kajaites* Slide Delah-1, 2730-2735 m, DC (S1); England Finder M40/4.

Fig. 11 *Concentricystes circulus* Rossingol 1962 (x 1000): Slide Malong-2, 1610-1615 m, DC (S1); England Finder F14/1.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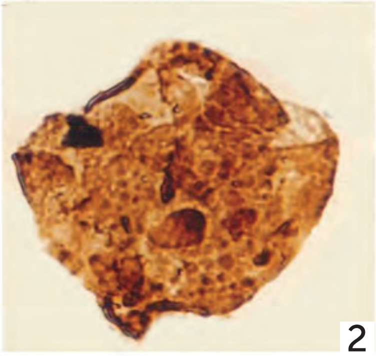
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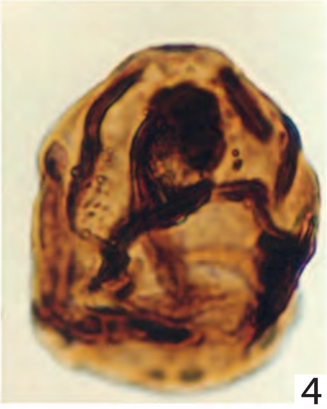
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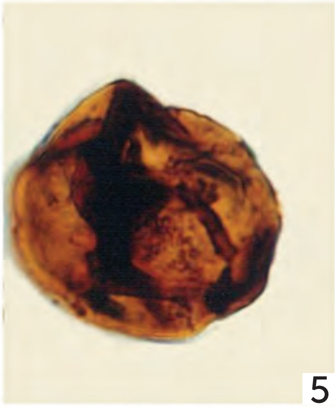
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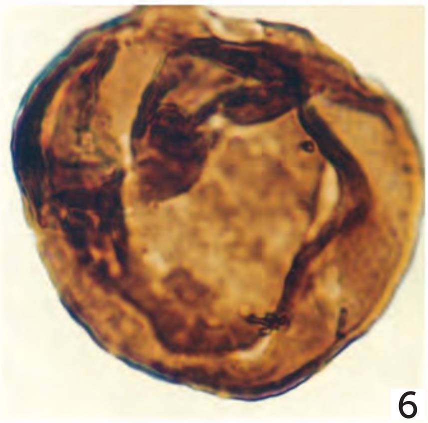
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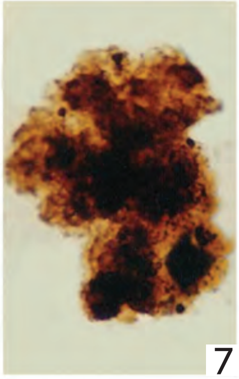
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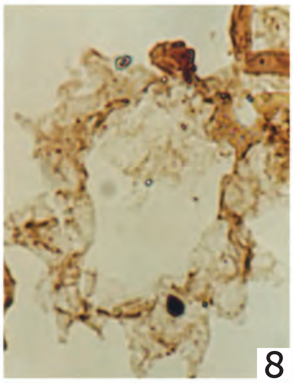
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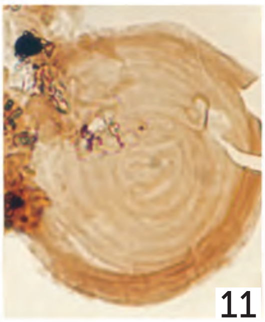
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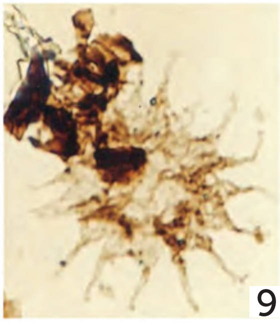
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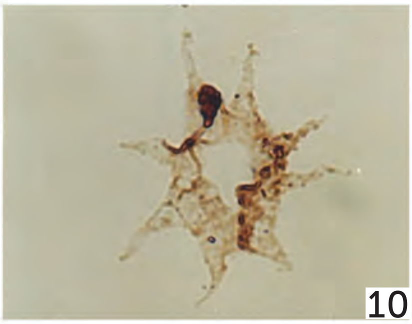
10

GLOSSARY

Glossary of palynological terms, based mainly on Punt et al. (2007) with numerous additions.

Terms in *italics* are defined elsewhere in the glossary.

A

Alete – A spore without a *laesura*.
Amb – The outline of a pollen grain or spore as seen in polar view.
Angulaperturate – Describing a pollen grain with *apertures* positioned at the angles of the outline in polar view.
Annulus – An area of *exine* surrounding a pore that is sharply differentiated from the remainder of the *exine* either in thickness or ornamentation.
Aperture – an area of the exine that is thinner than the remaining exine and in living pollen forms the site of germination.
Apex, apices – In spores, applied to the corner of *trilete* spores.
Apocolpial island – Region at the poles of *parasyncolpate* pollen delimited by the margins of anastomosing *colpi*.
Arcus, arci – A thickened band of *sexine* that extends in a curve from one aperture to another.
Areolae, areolate – *Sexine* ornamentation composed of circular to polygonal areas separated by grooves forming a negative *reticulum*.
Archaeopyle – An *excystment* aperture in the wall of a dinoflagellate cyst.
Aspidate – Having a space between the *ectopore* and *endopore* in *porate* pollen.

B

Baculum, baculate – A free-standing *sexine* sculptural element with height greater than width and more than 1µ high.
Bisaccate – Describing pollen with two *sacci*.
Brevicolpate – Prefix for short; with short *colpi*.
Brochus, brochi – A brochus consists of one *lumen* and half the width of the adjacent *muri* with respect to a *reticulum*.

C

Cappa – The thick-walled *proximal* side of the corpus of a *saccate* pollen grain.
Cappula – The thin-walled *distal* side of the corpus of a saccate pollen grain.
Cingulum, cingulate – A thin or thick outer rim of a spore that projects at the equator but does not extend over the distal or proximal face.
Clava, clavate – A club-shaped element of the *sexine* with height greater than width, thicker at the apex than the base, and more than 1µ high.
Colpoid grooves – Thinned areas of exine similar to *colpi* but not functioning as germinating apertures.
Colpus, colpi, colpate – An elongated *aperture* with a length/breadth ratio of more than 2, occurring in the *ektexine*, and thus an *ectoaperture*.
Colpus transversalis – A term used for endoapertures that fuse into a single encircling aperture.
Columella, columellae, columellate – A rod-like element of the *sexine* supporting a *tectum*.
Compound aperture – An aperture which is composed of an *endoaperture*, occurring within the *endexine* combined with an *ectoaperture,* occurring within the *ektexine.*
Conus, conae – Cone-shaped element on the surface of spores in which the height is less than the basal diameter.
Corpus – The body of a *saccate* pollen grain.
Costa, costae, costate – A thickening of the *endexine* bordering an *endoaperture.*
Contact area – Area on the *proximal* face of a spore considered to have formed in contact with other spores in the *tetrad.*
Crenate – Having a round-toothed or scalloped edge.
Croton pattern – A characteristic type of ornamentation comprising rings of five or six (sometimes more) raised, essentially triangular, *sexine* elements arranged in a circle giving a pentagonal or hexagonal appearance.

D

Dicolpate, disulcate – Pollen grains with two *colpi* or *sulci.*
Dicolporate – Pollen grains with two compound *apertures*.
Digitate – With *columellae* or *baculae* which are branched distally into two or more parts.
Diporate – Pollen grains with two *pores.*
Distal face – The part of a palynomorph that faces outward relative to the centre of the tetrad.
Duplibaculate – With *columellae* in two rows beneath *muri*.
Dyad - A general term for a group of two united pollen grains or spores.

E

Echinate – Describing pollen and spores with sculpture consisting of spines longer than 1 µm.

Ectexine – The outer part of the exine that stains positively with basic fusain in optical microscopy and has high electron density in transmission electron microscopy. This may consist of a *foot layer*, *columellate* layer and *tectum* and is perforated by *ectoapertures*. This is in contrast with *endexine*, which stains negatively with basic fusain, has low electron density, and is perforated by endoapertures. In light microscopy, it is not possible to differentiate the *foot layer* of the *ectexine* from the *endexine*, and so the combined *ectexine* plus the *foot layer* is termed the *nexine*, and the *ectexine* minus the *foot layer* is termed *sexine*.

Ectoaperture – An *aperture* which perforates the *ectexine.*

Endexine – The inner part of the *exine* which remains poorly stained by basic fusain and has low electron density. See *Ectexine.*

Endoaperture – An *aperture* that perforates the inner layer of the *exine*, the *endexine*.

Eureticulate – Reference to *reticulate* structure defined by the *columellae,* rather than a *reticulum* that occurs above the *tectum*, which would be termed *supraretuculate*.

Eurugulate – Reference to *rugulate* structure defined by the *columellae,* rather than *rugulae* that occur above the *tectum*, which would be termed *suprareticulate*.

Equatorial axis – The line dividing the *distal* and *proximal* parts of a pollen grain or spore.

Equatorial fringe – In *monosaccate* pollen, an area of thickening of the *saccus* wall, often with more pronounced ornamentation, around the equatorial region of the grain.

Excystment aperture – The opening in the wall of a dinocyst formed by the release of a single plate or group of plates.

Exine – The outer layer of the wall of a palynomorph which is composed of *sporopollenin*, a polymer which is highly resistant to oxidation and is readily preserved in sediments, and also to the effect of strong acids and bases. It contrasts with intine, the inner layer of the palynomorph wall, which readily decays following deposition and is removed by strong acids and bases.

F

Fenestrate – Describing a group of pollen in which the *exine* is characterised by large window-like lacunae. See also *lophate.*

Fossula, fossulate – A feature of ornamentation consisting of an elongated, irregular groove in the surface.

Foveolae, foveolate – A feature of ornamentation consisting of more or less rounded depressions or *lumina* more than 1 µm in diameter, with the distance between foveolae being greater than their breadth.

Furrow – A term for an elongate *aperture*.

G

Gemma, gemmate – A spherical *sexine* element which has the same width as height and is constricted at the base.

Geniculus, geniculate – A bulge in the equatorial *exine* of the *colpus*, often associated with a separation of the *sexine* from the *nexine* and the rupturing of the latter.

Granule, granulate – A general word for small, rounded elements, smaller than *gemmae.*

H

Hamulate – Describing a form of *rugulate* ornamentation consisting of irregularly arranged, winding, or angular rounded *muri* of varying thickness, which do not form a distinct *reticulum*, but rather a maze-like pattern.

Heterobrochate – Describing a *reticulum* with *brochi* of different sizes.

Heterocolpate – Describing pollen grains with both simple *colpi* or *pseudocolpi*, and compound *colpi* present.

Heteropolar – Describing pollen or spores in which the *distal* and *proximal* faces of the *exine* are different, either in shape, ornamentation or apertural system.

Hexaporate – Having six non-equatorial pores, with three on the proximal and three distal side of a grain.

Homobrochate – Describing a *reticulum* with *brochi* of the same size.

I

Inaperturate – Describing a pollen grain or spore without *apertures* or a-lete mark.

Intersubangular – With respect to *aperture* position, for a grain that is weakly angular in polar view, with the *apertures* between the angles of the grain outline.

Intectate – Describing pollen grains without a *tectum*, but with *sculpturing*.

Interangular – With respect to *aperture* position, for a grain that is distinctly angular in *polar* view, with the *apertures* between the angles of the grain outline.

Isopolar – Describing a pollen grain or spore in which the *proximal* and *distal* faces of the *exine* are alike.

K

Kyrtome – A more or less arcuate fold or band in the *contact areas* outside the *laesurae* of *trilete* spores.

L

Laesura – the arm of a *proximal* scar of a spore that reflects the line of contact in the *tetrad.* Spores derived from a *tetrahedral tetrad* will bear a *trilete laesura,* whereas in the case of a *tetragonal tetrad* the laesura will be *monolete*.

Laevigate – A general term for smooth, as if polished, a synonym of *psilate.*

Lalongate – Describing the shape of a transversely elongated *endoaperture.*

LO analysis – A method for analysing patterns of *sexine* organization by means of light microscopy. The method is valuable for elucidating *exine* patterns. When focused at high level (H), raised *sexine* elements appear bright (Lux), whereas holes in the *tectum* are relatively dark *(Obscuritas)*. At lower focus (L) holes become lighter and the *sexine* elements become darker.

Lobate – Describing an equatorially *aperturate* pollen grain with a lobed shape in polar view.

Lolongate – Describing the shape of a longitudinally elongated *endoaperture*.

Lophate – Describing a pollen grain in which the outer exine is raised in a pattern of ridges (lophae) surrounding depressions (lacunae).

Lumen, lumina – The space enclosed by the *muri* with respect to a *reticulum.*

M

Margo, margines, marginate – An area of *exine* around an *ectoaperture* that is differentiated from the remainder of the *sexine,* either in ornamentation or by difference in thickness.

Meridional ridge – Describing longitudinal raised or thickened areas on the surface of a pollen grain which run along lines perpendicular to the *equator.*

Mesocolpium – The area of a pollen grain surface delimited by lines between the apices of adjacent *colpi* or the margins of adjacent *pores.*

Microfoveolate – A *foveolate* ornamentation consisting of *muri* and *lumina* smaller than 1 μm.

Microreticulate – A *reticulate* ornamentation consisting of *muri* and *lumina* smaller than 1 μm.

Marginal ridge – A thickened frill along the margins of the *cappa* where in contact with the *sacci* in *bisaccate* pollen, especially in *Pinus*.

Monad – A pollen grain or spore dispersed as an individual unit, rather than in association with others, such as in a *dyad, tetrad* or *polyad*.

Monocolpate – Describing a pollen grain with a single *colpate aperture*.

Monolete – Describing a spore with a linear *laesura*.

Monoporate – Describing a pollen grain with a single *porate aperture.*

Monosaccate – Describing a pollen grain with a single encircling *saccus*.

Monosulcate – A *monocolpate aperture* has the same shape as a *colpus* but is essentially positioned longitudinally.

Murus, muri – A ridge that is part of the ornamentation of the sexine and separates the lumina in a reticulate pollen grain.

N

Nexine – The inner, non-sculptured part of the *exine* which lies below the *sexine*.

O

Oblate – Describing the shape of a pollen grain in which the *polar axis* is shorter than the equatorial diameter.

Omphalos – A thickened area in the wall of an algal cyst.

Oncus – A lens-shaped structure that is not resistant to acetolysis and occurs beneath the apertures of many kinds of pollen grains.

Operculum – A distinctly delimited *ectexine* structure which covers part of an *ectoaperture* and which is isolated from the rest of the *ectexine.*

P

Parasyncolpate – Describing *syncolp(or)ate* pollen grains in which the apices of the *colpi* divide into two branches and anastomose towards the poles, delimiting an isolated area known as the *apocolpial island*.

Pentaporate – With five equatorially located *pores*.

Pentacolporate – With five equatorially located *compound apertures*.

Perforate – A general adjective indicating the presence of holes, applied in palynology to holes less than 1 μm in diameter and generally situated in the *tectum*.

Pericolporate – A pollen grain with more than *six compound apertures.*

Perine – A loosely attached thin outer *exine* layer found in many spores that is highly ornamented and allows many spores to be identified to specific pteridophyte species. However, perine is not always acetolysis resistant and if lost, the remaining spore body may be a simple *laevigate* or weakly ornamented spore which may be impossible to identify with individual genera.

Periporate – A pollen grain with many pores spread over the surface sometimes forming a regular pattern. A synonym for this apertural organisation is **pantoporate**.

Peroblate – Describing the shape of a pollen grain or spore in which the ratio between the polar axis and the equatorial diameter is less than 0.50 and the grain appears flattened.

Perprolate – Describing the shape of a pollen grain or spore in which the ratio between the polar axis and the equatorial diameter is more than 2, and the grain appears extremely elongated.

Pila, pilate – A *sexine* element, usually standing directly on the *nexine*, consisting of a rod-like part *(columella)* and a swollen apical part.

Pluricolumellate – With the *columellae* arranged in several rows beneath each *murus*.

Polar axis – The straight line between the *distal* and *proximal* poles of a pollen grain or spore.

Polyad – A dispersal unit comprising more than four pollen grains, such as two, four or more cojoined *tetrads.*

Polycolpate – A pollen grain with many (more than six) *colpi.*

Polycolporate – A pollen grain with many (more than six) *compound apertures.*

Polyplicate – Describing a pollen grain with more than three meridional ridges (plicae) separated by deep grooves.

Pore – A general term, applied to a circular or elliptic *aperture* with a length/breadth ratio less than 2.

Porate fields – the broad region of the exine surrounding the pores, as in the genus *Florschuetzia.*

Prolate – Describing the shape of a pollen grain or spore in which the polar axis is larger than the equatorial diameter. Prolate is defined as a ratio between the polar axis and the equatorial diameter of 1.33 to 2.00.

Prolate spheroidal – Describing the shape of a pollen grain or spore in which the ratio between the *polar axis* and the *equatorial diameter* is 1.00 to 1.14.

Proximal face – That part of a palynomorph which faces towards the centre of the *tetrad*, between *equator* and *proximal pole*.

Pseudocolpus, pseudosulcus – A thinning of the *exine* which, although superficially resembling a *colpus*, is presumed not to function as a germinal *aperture*.

Psilate – Describing a pollen or spore with a smooth surface.

Puncta, punctate – A rounded or elongate tectal perforation, less than 1 µm in length or diameter.

R

Reticulum, reticulate – A network-like pattern seen within the *sexine*, consisting of *lumina* wider than 1 µm, bordered by muri that are narrower than the *lumina.*

Rugulate – Describing a type of ornamentation consisting of elongated and sinuous *sexine* elements more than 1 µm long, arranged in an irregular pattern that is intermediate between *striate* and *reticulate.*

S

Saccus, sacci, saccate – In conifer pollen, sacci are balloon-shaped extensions of the *corpus*, consisting of *exine* with the *saccus* wall exhibiting an internal *reticulate* structure.

Scabrate – Describing granular elements of ornamentation, smaller than 1 µm.

Sculpture – The surface relief, or topography, of a pollen grain or spore.

Semitectate – A discontinuous tectum characterised by tectal perforations which are equal to or wider than the muri and usually larger than 1 µm in diameter.

Sexine – The outer, sculptured layer of the *exine*, which lies above the *nexine.* – See entry under *'ectexine'* for further clarification.

Simplicolumellate – With a single row of *columellae* under each *murus*.

Spheroidal – Describing the shape of a pollen grain or spore in which the *polar axis* and the *equatorial diameter* are approximately equal. Based on measurements of the *polar axis (P)* and *equatorial diameter (E)*, spheroidal is defined as a P/E ratio of 0.88 to 1.14.

Spine – A general word, applied to long and tapering pointed elements, exceeding 1 µm in length.

Stephanocolpate – Pollen grains with four to approximately seven *colpi*, arranged along the *equatorial axis.*

Stephanocolporate – Pollen grains with four to approximately seven *compound apertures*, arranged along the *equatorial axis.*

Stephanoporate – Pollen grains with four to approximately seven pores, arranged along the *equatorial axis.*

Striate – A general descriptive term applied in palynology to elongated, generally parallel elements of the *sexine* or spore wall separated by grooves.

Structure – The internal construction of the pollen or spore wall. Compare with *sculpture.*

Subequatorial – Pertaining to the position of *apertures* when they are slightly offset from the *equatorial axis.*

Suboblate – Describing the shape of a pollen grain in which the ratio between the polar axis and the *equatorial diameter* is 0.75 to 0.88.

Subprolate – Describing the shape of a pollen grain in which the ratio between the polar axis and the *equatorial diameter* is 1.14 to 1.33.

Subspheroidal – Describing the shape of a pollen grain in which the ratio between the *polar axis* and the *equatorial diameter* is 0.75 to 1.33.

Sulcus, sulci – An elongated latitudinal *aperture* situated at the *distal* or *proximal* pole of a pollen grain. A sulcus has the same shape as a *colpus*, but differs in orientation, being essentially latitudinally positioned. Sulci may be *distal* (anasulcate), *proximal* (catasulcate) or extend right around the grain *(zonasulcate)*.

Syncolpate – Describing pollen with three or more *colpi* the ends of which anastomose at the *pole.*

Syncolporate – Describing colporate pollen with three or more *colpi* the ends of which anastomose at the *pole*.

Syndemicolpate – Describing pollen grain with three *colpi,* the ends of which anastomose at the pole, each with two *endoapertures* positioned *subequatorially* on each *colpus.*

Syntricolporate – Describing *tricolporate* pollen with three *colpi* the ends of which anastomose at the *pole.*

T

Tectum, tectate – The layer of *sexine,* which forms a roof over the columellae, and other *infratectal* elements. See also *semitectum.*

Tetracolpate – Pollen with four *colpi.*

Tetracolporate – Pollen with four compound *apertures.*

Tetrad – A general term for a group of four united pollen grains or spores, either as a dispersal unit or as a developmental stage.

Tetragonal tetrad – A uniplanar *tetrad* in which all four members are in contact at the centre of the *tetrad* so that, in the correct orientation, the adjacent walls form a cross.

Tetrahedral tetrad – A multiplanar *tetrad* in which each member is in contact with three others, so that the centres of the grains define a tetrahedron.

Tetraporate – Pollen with four *pores.*

Tilioid structure – *Sexine* structure describing a *tectum* provided with funnel-like concavities of which the bottoms coalesce with a single underlying *columella,* to form one unit.

Triaperturate – Describing pollen which has three *apertures.*

Trichotomosulcate – Describing a pollen grain with a three-armed *sulcus* reflecting origin in a *tetrahedral tetrad.*

Tricolpate – Describing pollen which has three *colpi.*

Tricolporate – Describing pollen grains with three *compound apertures.*

Tricolporoidate – Describing pollen grains with three *colpi,* but with the suggestion of a feature at the equator possibly indicating the presence of an *endoaperture,* but which cannot be seen clearly.

Trilete mark – A trilete expression present on the d*istal face* of the *corpus* in some gymnosperm pollen.

Triporate – Describing pollen which has three *pores.*

Trilete – Describing a spore with a triradiate *laesura.*

Tuberculate – A general term for the presence of knobby projections or excrescences.

U

Ulcus, ulcerate – A rounded *ectoaperture* situated at the *distal or proximal pole* of a pollen grain. An ulcus has the same shape as a *pore.* Ulci may be *distal* (ana-ulcerate) or *proximal* (cata-ulcerate).

V

Vermiculate – A general descriptive term used to describe winding features.

Verrucae, verrucate – A wart-like *sexine* element, more than 1 µm wide, that is broader than it is high and is not constricted at the base.

Vestibulum, vestibulate – A separation between layers of the exine forming a cavity between the inner and outer part of a pore.

Y

Y mark – In some trilete spores, especially in hornworts, the *laesurae* may divide into two at the extremity of the contact areas.

Z

Zonosulcus, zonosulcate – A ring-like *sulcus* that extends around the equator and may cause a grain to divide into two halves on fossilisation.

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