

Palynology of the Dinosaur Beds of Tendaguru (Tanzania) – Preliminary Results

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With 2 figures, 3 plates and 2 tables

Abstract

The Tendaguru Beds, southeastern Tanzania, have yielded two palynological assemblages of Kimmeridgian to Tithonian age: (1) the *Anapiculatisporites-Densoisporites-Trisaccites* assemblage from the Middle Saurian Beds and (2) the *Barbatocysta-Pareodinia* assemblage from the overlying *Smeei* Beds. A third assemblage with *Rhizophagites* and rare angiosperm pollen from the Upper Saurian Beds is contaminated by recent and subrecent material.

The *Anapiculatisporites-Densoisporites-Trisaccites* assemblage is characterized by the presence of freshwater algae (*Ovoidites*), pteridophytic-bryophytic spores and gymnosperm (conifer) pollen, with *Classopollis* as the most abundant element. Among the rare elements of this assemblage is the questionable dinoflagellate *Mendicodinium ? quadratum*, possibly a Kimmeridgian-Tithonian marker. The miospores show palaeobiogeographic links to Southern Gondwana, especially Madagascar, Australia, Argentina and India. Deposition of this assemblage took place in an aquatic environment with strong palynological influx from a terrestrial source and questionable marine influence.

The *Barbatocysta-Pareodinia* assemblage contains a considerable number of dinoflagellates suggesting deposition in a marine environment. The terrestrially-derived miospores are impoverished and dominated by conifer pollen, while pteridophytic-bryophytic spores form a very subordinate element or are absent.

Key words: Dinoflagellates, pollen, spores, Late Jurassic, Tanzania.

Zusammenfassung

Die Tendaguru-Schichten, Südost-Tansania, haben zwei palynologische Assoziationen, deren Alter als Kimmeridge bis Tithon interpretiert wird, geliefert. Die *Anapiculatisporites-Densoisporites-Trisaccites*-Assoziation stammt aus den Mittleren Saurierschichten, und die *Barbatocysta-Pareodinia*-Assoziation charakterisiert die darüberlagernden *Smeei*-Schichten. Eine dritte Vergesellschaftung mit *Rhizophagites* und seltenen Angiospermen-Pollen aus den Oberen Saurierschichten ist durch rezentes bis subrezent Material kontaminiert.

Die *Anapiculatisporites-Densoisporites-Trisaccites*-Assoziation ist durch die Anwesenheit von Süßwasser-Algen (*Ovoidites*), Pteridophyten-Bryophyten-Sporen und Gymnospermen-Pollen (Koniferen) gekennzeichnet mit *Classopollis* als dem häufigsten Element. Zu den seltenen Elementen dieser Assoziation gehört der fragliche Dinoflagellat *Mendicodinium ? quadratum*, der möglicherweise als leitend für das Kimmeridge-Tithon angesehen werden kann. Die Miosporen zeigen paläobiogeographische Verbindungen nach Südgondwana, besonders nach Madagaskar, Australien, Argentinien und Indien. Das Ablagerungsmilieu dieser Assoziation war aquatisch mit starker Zufuhr von terrigenem Material, während mariner Einfluß fraglich ist.

Die Dinoflagellaten-führende *Barbatocysta-Pareodinia*-Assoziation wurde in einem marinen Milieu gebildet, in dem die Zufuhr terrigener Palynomorphe reduziert und im wesentlichen auf Koniferen-Pollen beschränkt war, während Pteridophyten-Bryophyten-Sporen nur sehr untergeordnet vorkommen oder ganz fehlen.

Schlüsselwörter: Dinoflagellaten, Pollen, Sporen, Oberjura, Tansania.

Introduction

The area around Tendaguru, a hill in southeastern Tanzania (Fig. 1), is known to harbour one of the most important dinosaur deposits of Africa. Descriptions of the regional geology and stratigraphy of this area have been given by Aitken (1961), Kent et al. (1971) and Zils et al. (1995).

These sources also provide information on the extensive history of research including the German Tendaguru Expedition (1909–1913) which Russell et al. (1980) praise as “one of the greatest multidisciplinary paleontological expeditions of all time”.

Despite the fact that the Tendaguru Beds have also yielded rich marine invertebrate faunas

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Received January 1999, accepted April 1999

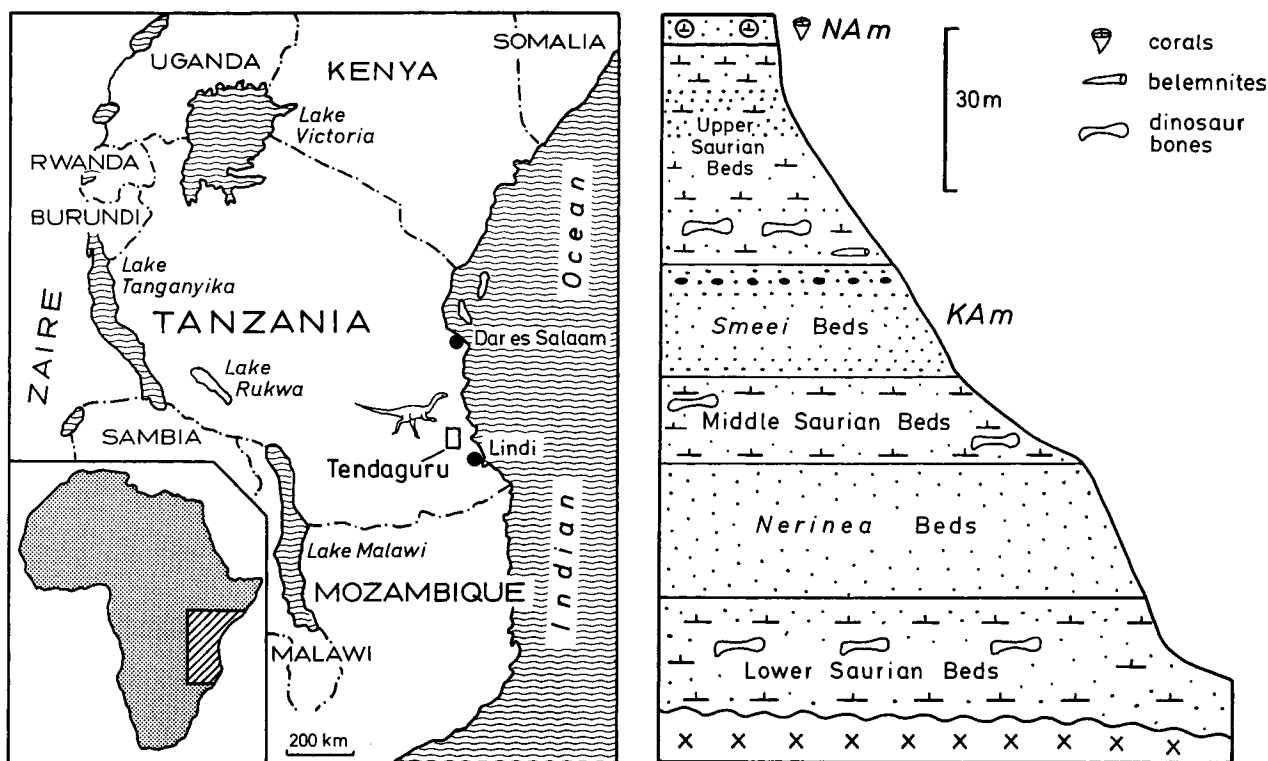


Fig. 1. Sketch map of Eastern Africa showing the approximate position of the Tendaguru dinosaur locality

(e.g. Janensch 1914, Zwierzycki 1914, see also Fig. 2), there are still problems related to the biostratigraphy and depositional history of the dinosaur beds. In the classical reports of the German Tendaguru Expedition, the various micropalaeontological disciplines are for obvious reasons absent. Among these palynology is nowadays a standard tool used in the interpretation of intercalating marine and nonmarine sedimentary successions as present in the Tendaguru Beds. Earlier attempts of a few palynologists to study Tendaguru sediments on the basis of a low number of samples remained largely inconclusive (Herngreen, personal communication) or re-

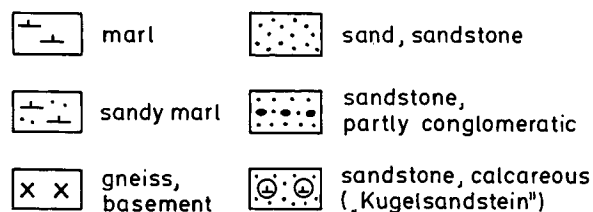


Fig. 2. Generalized section of the Tendaguru dinosaur beds compiled from the descriptions of Janensch (1914). Abbreviations: **NA m**, Neocomian ammonites; **KA m**, late Kimmeridgian to Tithonian ammonites according to Zwierzycki (1914)

sulted in the recovery of few palynomorph types from a single sample (Jarzen 1981).

For the present study more than 100 samples from the Tendaguru collections of the Museum für Naturkunde (Berlin) were investigated. Among them about 9 samples (Table 1) are pro-

Table 1

Palynologically productive samples from the Tendaguru Beds used in the present study.

TU Berlin slide numbers	Stratigraphic level	Text from original label
AKA	Middle Saurian Beds	Grünliche <i>Cyrena-Mytilus</i> -Sandmergel der mittleren Saurierschicht, Tingutiguti-Bach unterhalb der Quelle
ALB		Cyrenen-Mergel der mittleren Saurierschicht
AMB		<i>Cyrena</i> -Mergel der mittleren Saurierschicht, Kitukituki-Bach
AMC		Cyrenenmergel der mittleren Saurierschicht, Kitukituki-Bach, Schlammrückstand, <0,2 mm >0,1 mm
APL	<i>Smeei</i> Beds	<i>Smeei</i> -Schicht, Doanika-Bach
AKS		Grünlicher Schiefer über <i>Smeei</i> -Bank, Tingutiguti-Bach
AKT		Grünlicher Schiefer über <i>Smeei</i> -Bank, Tingutiguti-Bach
APH		<i>Pseudomonotis</i> -Schiefer über <i>Trigonia smeei</i> -Schicht, Tingutiguti-Bach südlich von Tendaguru
AKR		<i>Smeei</i> -Konglomerat, Tingutiguti-Bach

ductive enough to be interpreted from a palynological point of view. As usual in tropical areas, weathering is probably the main factor preventing preservation of palynomorphs in a larger number of samples.

A considerable number of additional samples, most of them from the Upper Saurian Beds, yielded hyphae, *Rhizophagites* and other fungal remains which certainly represent contamination from recent and subrecent sources.

Palynological results

A comprehensive systematic treatment of the palynomorphs so far recovered from the Tendaguru Beds is beyond the scope of this preliminary report. In the following systematic paragraph selected dinoflagellates are listed alphabetically while some terrestrially-derived miospores are arranged roughly according to morphological criteria, starting with smooth trilete spores and proceeding via several sculptured types to the more complex gymnosperm pollen. Reference to previous records is selective with some emphasis placed on African or southern Gondwanan occurrences to back up the palynostratigraphic discussion below. An alphabetical list of all palynomorphs encountered so far in the Tendaguru beds is given in Appendix A, and their distribution in the Tendaguru section is depicted in Table 2.

Systematic palynology

Dinoflagellate cysts in alphabetic order

Barbatacysta creberbarbata (Erkmen & Sarjeant, 1980) Courtinat, 1989

Plate 1/10, 11

Previous records: Callovian-Kimmeridgian, Madagascar (Chen 1978 as Dinoflagellate Form I); topmost Kimmeridgian to earliest Tithonian, Kenya (Jiang et al. 1992); Kimmeridgian, Mada-

gascar (Dina 1996); Callovian-Oxfordian, France (Rauscher & Schmitt 1990); Kimmeridgian to Portlandian, France (Dürr 1988); Oxfordian, Germany (Kunz 1990); Oxfordian to lower Tithonian, Germany (Dürr 1988); Malm alpha, Germany (Brenner 1988).

Dingodinium tuberosum (Gitmez, 1970) Fisher & Riley, 1980

Plate 1/8, 9

Remarks: The present species is closely related to *Dingodinium scabratum* (Kumar) Lentin & Williams, 1989 which was originally described from the Kimmeridgian-Tithonian of India (Kumar 1986). *D. scabratum* is interpreted by Poulsen (1996) as synonym of *D. minutum* Dodekova, 1975

Previous records: Basal Pindirol Shales in the Kizimbani well, southeastern Tanzania, which Balduzzi et al. (1992) interpret as ?Callovian-Oxfordian. Lower Kimmeridgian, Spain (Van Erve et al. 1988); topmost Kimmeridgian to earliest Tithonian, Kenya (Jiang et al. 1992); Kimmeridgian, Madagascar (Dina 1996); latest Oxfordian to Portlandian, Great Britain (Riding & Thomas 1992).

Lithodinia sp. cf. *L. jurassica* Eisenack sensu Helby et al., 1988

Plate 1/1, 2

Previous records (of *L. jurassica*): Tithonian, New Zealand (Helby et al. 1988).

Lithodinia sp. cf. *L. sp. 1* Davey, 1988

Plate 1/3, 4

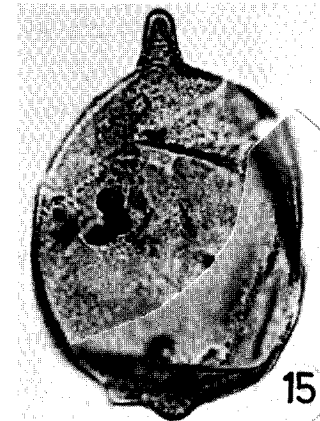
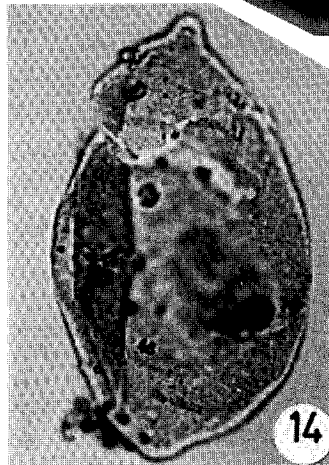
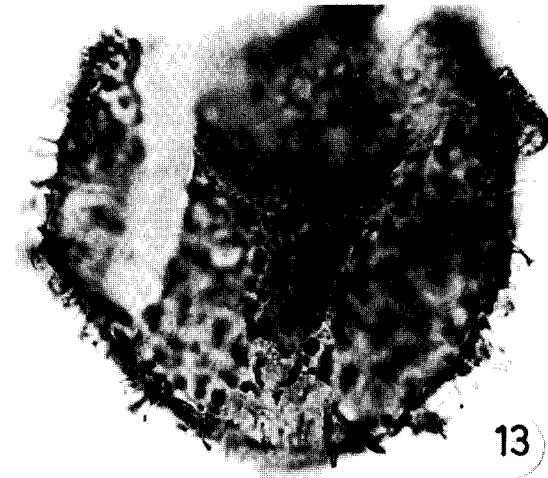
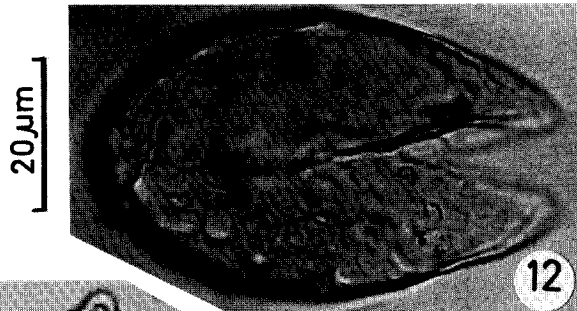
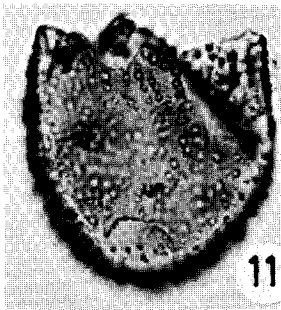
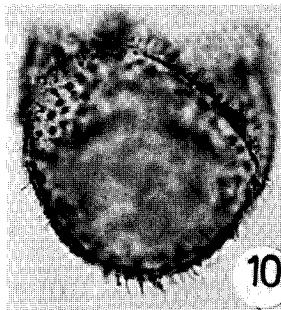
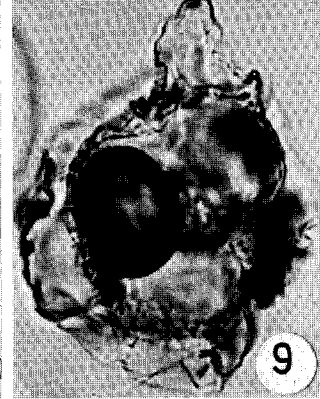
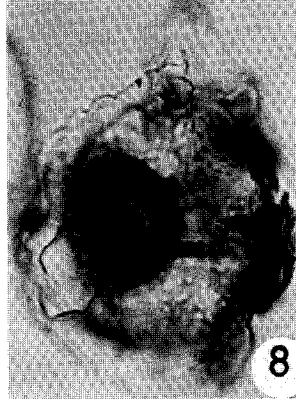
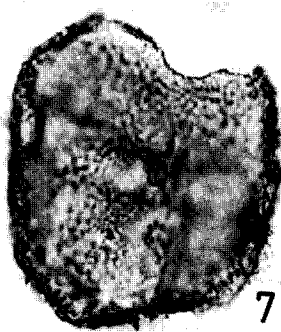
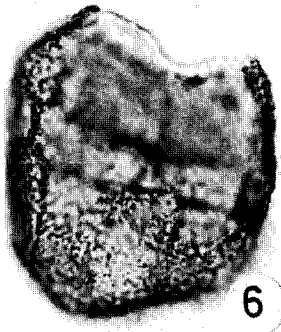
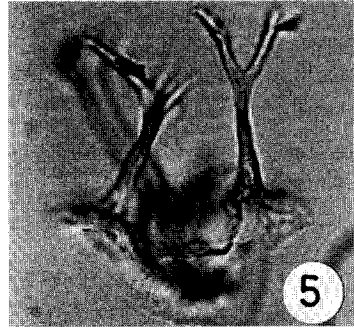
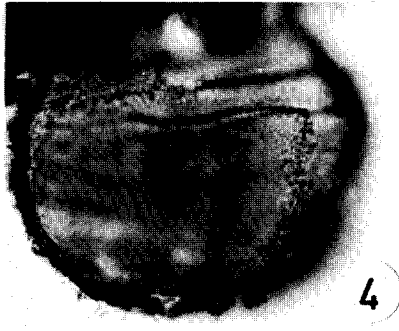
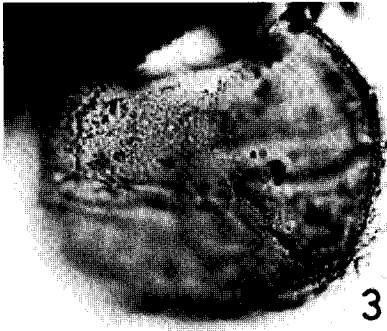
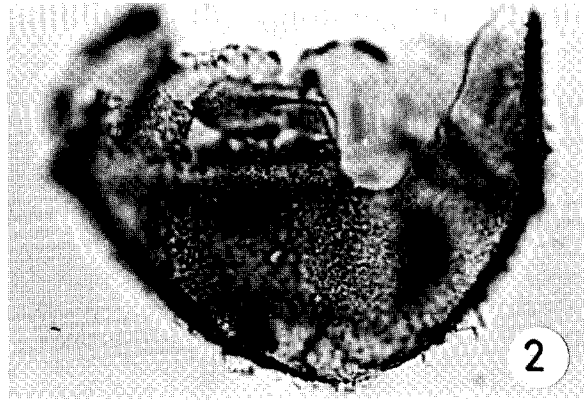
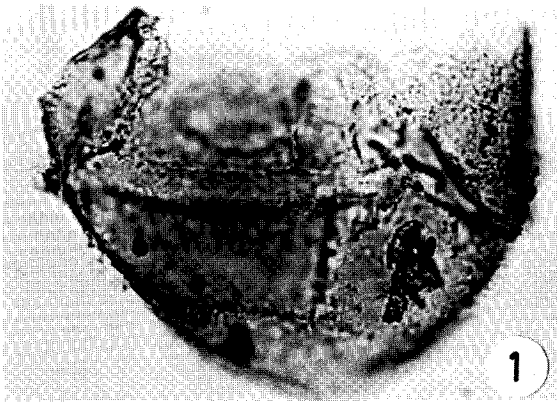
Previous records (of *L. sp. 1*): "Early" Tithonian, Papua New Guinea (Davey 1988).

Meiourogonyaux sp. C Helby et al., 1988

Plate 1/6, 7

Previous records: Puti Siltstone of New Zealand (Tithonian, Helby et al. 1988).

Plate 1. Marine dinoflagellates from the *Smei* Beds (1–11, 13–15) and a freshwater alga (12) from the Middle Saurian Beds. All magnifications $\times 1000$. After the sample number the TU Berlin negative number (e.g. IR14 etc.) is always given. **1, 2:** *Lithodinia* sp. cf. *L. jurassica* Eisenack (sample AKS; IR14, 15). **3, 4:** *Lithodinia* sp. cf. *L. sp. 1* Davey (sample AKS; IQ38, 39). **5:** *Surculosphaeridium* sp., operculum (sample AKR; IN30). **6, 7:** *Meiourogonyaux* sp. C Helby et al. (sample AKT; IS20, 21). **8, 9:** *Dingodinium tuberosum* (Gitmez) Fisher & Riley (sample AKR; IN8, 9). **10, 11:** *Barbatacysta creberbarbata* (Erkmen & Sarjeant) Courtinat (sample AKS; IQ15, 16). **12:** *Ovoidites* sp. cf. *O. microligneolus* Krutzsch, Middle Saurian Beds (sample AKA; IL10). **13:** *Circulodinium distinctum* (Deflandre & Cookson) Jansonius, *Smei* Beds (sample AKS; IQ31). **14:** *Pareodinia angulata* Kumar, *Smei* Beds (sample AKT; IS4). **15:** *Pareodinia* sp. cf. *P. brevicornuta* Kunz sensu Dina, *Smei* Beds (sample AKS; IR12, 13)



Mendicodinium ? *quadratum* Kumar, 1987

Plate 2/1

Remarks: The species *M. ? quadratum* is easily recognizable and so far restricted to a relatively short stratigraphic interval (see below), but its assignment to the genus *Mendicodinium* and even to the dinoflagellates is questionable. Alternatively it might belong to a different palynomorph group, e.g. Zygnemataceae (freshwater green algae) or to pollen of the *Cycadopites* type.

Previous records: Lower Kimmeridgian to Tithonian, India (Kumar 1987); middle Oxfordian to Tithonian, Madagascar (Dina 1996); top-most Kimmeridgian to earliest Tithonian, Kenya (Jiang et al. 1992).

Oligosphaeridium ? sp. cf. *O. dividuum* Williams, 1978

Previous records: (of *O. dividuum*): Valanginian to Barremian, offshore West Africa (Williams 1978).

Pareodinia angulata Kumar, 1987

Plate 1/14

Remarks: Although many authors regard the presence of an intercalary archaeopyle as diagnostic for the genus *Pareodinia*, illustrations of *Parodinia* specimens exhibiting a different, possibly apical archaeopyle are not uncommon in the literature (e.g. *Pareodinia* sp. Davey 1982, Aptian, Germany; *Pareodinia* sp. I sensu Leereveld 1995, Lower Cretaceous, Spain; *P. ceratophora* sensu Conway 1990, Bathonian, Israel). Courtinat (1989) emphasises the variability in the number of paraplates in *Pareodinia* and tentatively interprets the archaeopyle of the type species, *P. ceratophora*, as apical. Lentin & Vozzhennikova (1990) note that the holotype of the type species does not exhibit an archaeopyle at all and thus prefer to use the genus *Pareodinia* for forms without archaeopyle. Under consideration of this situation, forms with apical archaeopyle (Plate 1/14: *P. angulata*) and with unclear archaeopyle type (Plate 1/15: *Pareodinia* sp. cf. *P. brevicornuta*) are

included in *Pareodinia* in the present paper. Kumar (1987) described the archaeopyle of *P. angulata* as intercalary, which is, however, not supported by his photographic illustrations.

Previous records: Lower Kimmeridgian to Tithonian, India (Kumar 1987).

Pareodinia sp. cf. *P. brevicornuta* Kunz, 1990 sensu Dina, 1996

Plate 1/15

Remarks: This species is closely related to shorthorned varieties of *Pareodinia ceratophora* Deflandre, 1947 as illustrated e.g. by Dürr (1988, plate 6, fig. 7, Oxfordian to lower Tithonian of Germany; Kimmeridgian to Portlandian, France) and Conway (1990, plate 17, fig. 1, Bathonian, Israel). A special feature in some Tenda-guru cysts is the presence of a short, round, antapical knob, probably a rudimentary antapical horn. This feature also occurs in the *P. ceratophora* specimen from Israel mentioned above.

Another closely related species is *Kalyptea* sp. cf. *K. monoceras* Cookson & Eisenack, 1960 (Norvick & Burger, 1975, plate 12, fig. 2) from the Cenomanian of Australia.

Previous records of *P. brevicornuta*: Callovian, Madagascar (Dina 1996); Tithonian, Germany (Kunz 1990).

Zygnemataceae (freshwater algae)

Ovoidites parvus (Cookson & Dettmann, 1959) Nakoman, 1966

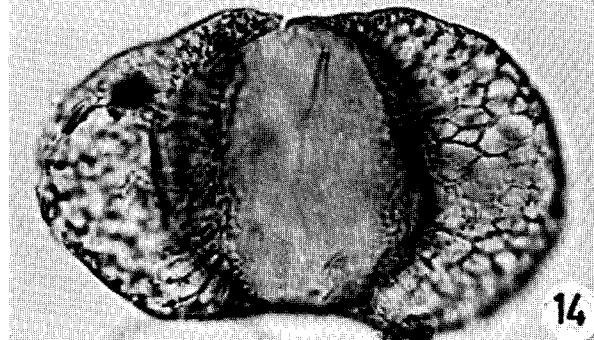
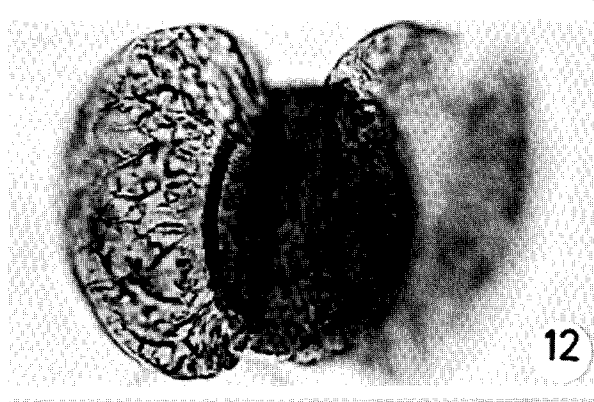
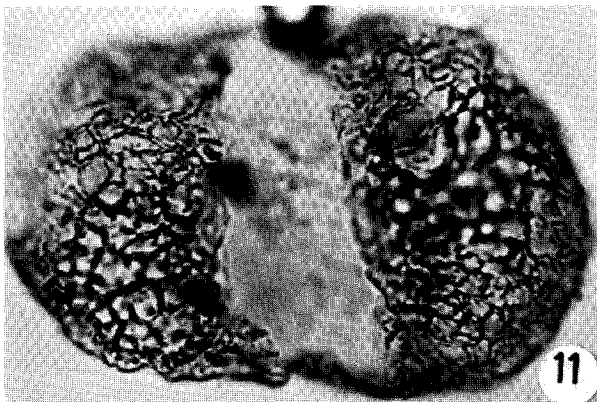
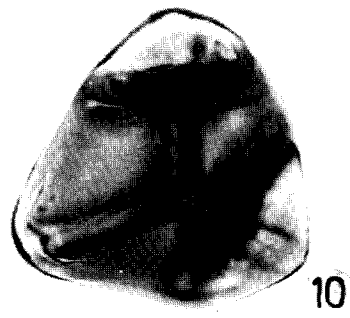
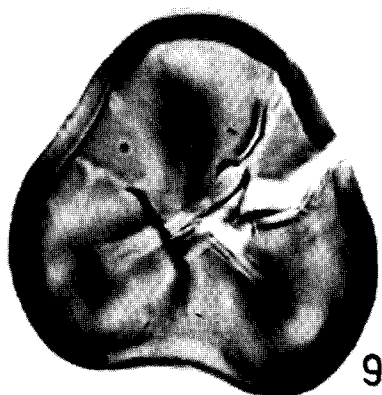
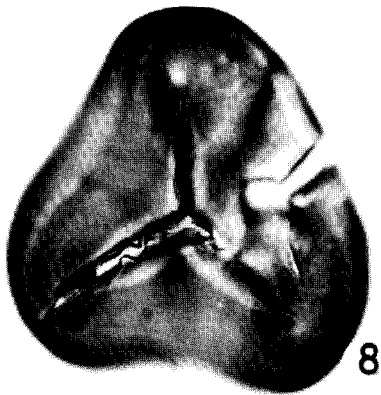
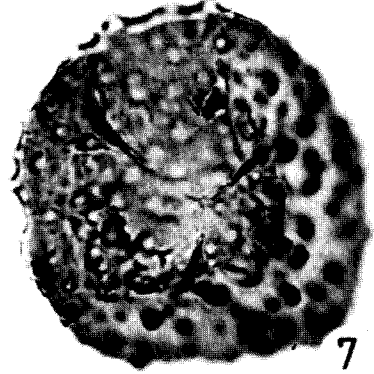
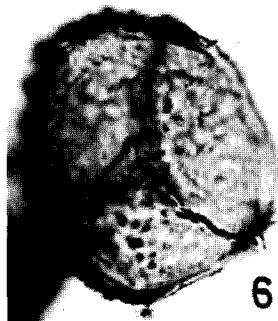
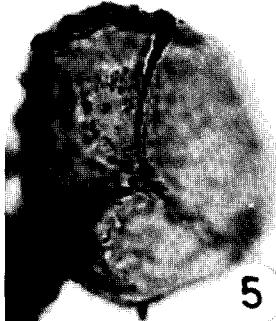
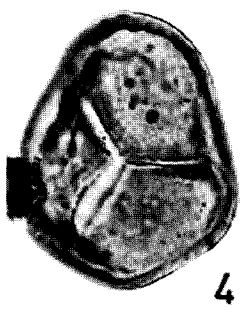
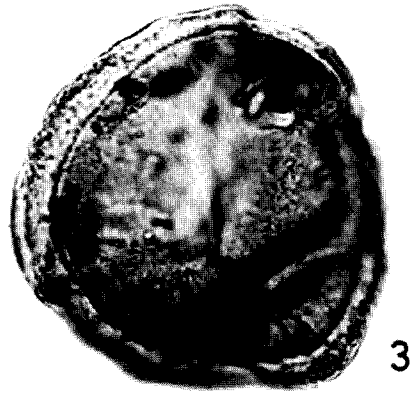
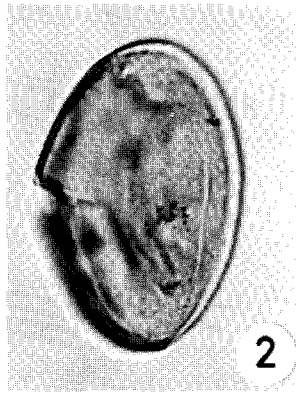
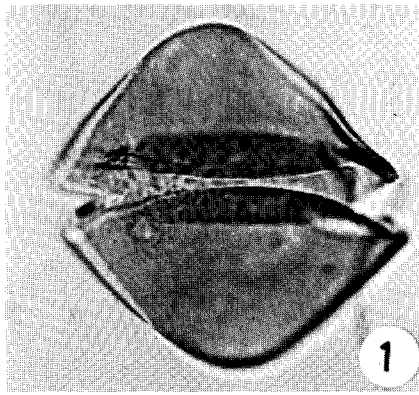
Plate 2/2

Previous records: Upper Tithonian to lower Aptian, Australia (Backhouse 1988, p. 111); Stanleyville Group, Zaire, near the Jurassic-Cretaceous border (Maheshwari et al. 1977, p. 56); Lower Cretaceous, Egypt (Schrank & Mahmoud 1998); Albion, Canada (Zippi 1998); Eocene, California (Frederiksen et al. 1983).

Botanical affinity: Zygosporangia of *Spirogyra* and *Zygonium*, Zygnemataceae, freshwater algae (Zippi 1998).



Plate 2. Palynomorphs from the Middle Saurian Beds (1–10, 12–14) and from the *Smei* Beds (11). All magnifications $\times 1000$. **1:** *Mendicodinium* ? *quadratum* Kumar (sample AKA; IM29). **2:** *Ovoidites parvus* (Cookson & Dettmann) Nakoman (sample ALB; IU17). **3:** *Densoisporites velatus* Weyland & Krieger (sample ALB; IT25). **4:** *Foraminisporis dailyi* (Cookson & Dettmann) Dettmann (sample AKA; IM31). **5–7:** *Anapiculatisporites dawsonensis* Reiser & Williams (sample AKA; IJ6). **8, 9:** *Matonisporites equixinus* Couper (sample AKA; IM8, 9). **10:** *Concavisporites jurienensis* Balme (sample AKA; IL21). **11:** *Alisporites thomasi* (Couper) Nilsson, (sample AKR; IN37). **12:** *Podocarpidites* cf. *P. multesimus* (Bolshovitina) sensu Dettmann (sample AKA; IM33). **13:** *Phrixipollenites* sp. Volkheimer et al. (sample ALB; IT29). **14:** *Alisporites* sp. cf. *A. grandis* (Cookson) Dettmann (sample AKA; IM22)



Pteridophytic and bryophytic spores

Note: Throughout this paper the term bryophytic spores is meant to include the spores of hornworts and liverworts, that is bryophytes in the sense of e.g. Taylor & Taylor (1993).

Foraminisporis dailyi (Cookson & Dettmann, 1958) Dettmann, 1963

Plate 2/4

Previous records: Tithonian-Aptian, Australia (Backhouse 1988); Berriasian to Albian, Australia; Barremian to Aptian, Argentina; Barremian to Albian, U.S.A. (Archangelsky & Gamarro 1967).

Botanical affinity: Similar to spores of the hepatics *Phaeoceras bulbiculosus* and *Nothylas breutelii* (Dettmann 1963).

Anapiculatisporites dawsonensis Reiser & Williams, 1969

Plate 2/5–7

Previous records: Mkuju Formation (Rhaetian), Luwegu Basin, Tanzania (Hankel 1987); Lower Jurassic to lower Kimmeridgian, Kizimbani well, southeastern Tanzania (Balduzzi et al. 1992); upper Bathonian to Callovian, Madagascar (Dina 1996); Early Cretaceous, Congo (Dejax 1987).

Densoisporites velatus Weyland & Krieger, 1953

Plate 2/3

Previous records: Rhaetian to Senonian, widespread (Srivastava 1987).

Botanical affinities: *Selaginellites polaris* Lundblad (Dettmann 1963).

Gymnosperm pollen

Alisporites similis (Balme, 1957) Dettmann, 1963

Plate 3/4

Previous records: Kimmeridgian, Madagascar (Dina 1996); late Toarcian to early Bajocian, Australia (McKellar 1974); upper Kimmeridgian to Aptian, Australia (Backhouse 1988).

Phrixipollenites sp. Volkheimer et al., 1977

Plate 2/13

Previous records: Hauterivian to Barremian, Argentina (Volkheimer et al. 1977).

Podocarpidites ellipticus Cookson, 1947

Plate 3/2, 3

Previous records: Middle Oxfordian, Madagascar (Dina 1996); Upper Cretaceous, offshore South Africa (McLachlan & Pieterse 1978); Tertiary, Kerguelen Archipelago (Cookson 1947).

Trisaccites microsaccatus (Couper, 1953) Couper, 1960

Plate 3/10–12

Remarks: A closely related or identical form is *Trisaccites variabilis* (Sukh Dev) Haskell, 1968, from the Jurassic of Australia (McKellar 1974, pl. 10, fig. 12).

Previous records: Upper Jurassic, Lower Cretaceous, Lower Tertiary, Australia (Burger 1980); upper Bathonian to Callovian of Madagascar (Dina 1996, plate 2, fig. 22 as *Microcahyridites antarcticus*).

Trisaccites microsaccatus (Couper, 1953) Couper, 1960, sensu Volkheimer et al. (1977), triangular variety

Plate 3/14–16

Previous records: Hauterivian to Barremian, Argentina (Volkheimer et al. 1977); Callovian to Albian, Argentina (Volkheimer & Quattrocchio 1981).

Botanical affinities: Podocarpaceae (Gamarro 1965).

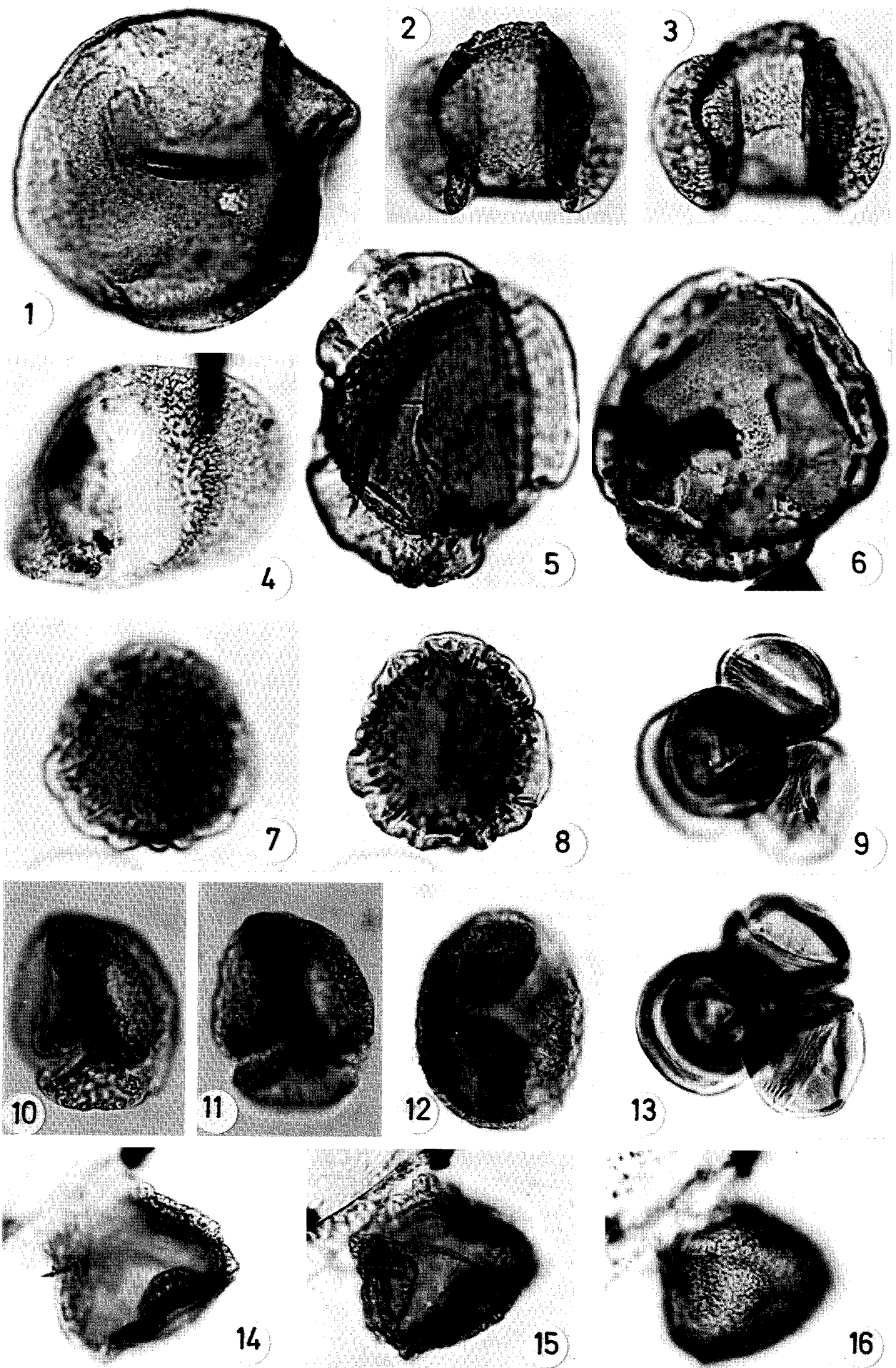
Callialasporites dampieri (Balme, 1957) Sukh Dev, 1961

Plate 3/7, 8

Previous records: Lias to Kimmeridgian, Sahara (Reyre 1973); worldwide Bajocian to Lower Cretaceous (Srivastava 1987).

Botanical affinity: As for *C. trilobatus*.

Plate 3. Pollen from the Middle Saurian Beds (2–5, 7–13) and from the *Smeei* Beds (1, 6, 14–16). All magnifications $\times 1000$. **1:** *Araucariacites australis* Cookson (sample AKS; IR27). **2, 3:** *Podocarpidites ellipticus* Cookson (sample ALB; IT36, 37). **4:** *Alisporites similis* (Balme) Dettmann (sample ALB; IT16). **5:** *Callialasporites trilobatus* (Balme) Sukh Dev (sample AMC; IV31). **6:** *Callialasporites trilobatus* (Balme) Sukh Dev (sample AKS; IQ2). **7, 8:** *Callialasporites dampieri* (Balme) Sukh Dev (sample AKA; IK23, 24). **9, 13:** *Classopollis* spp., tetrad (sample AKA; IJ2, 4). **10, 11:** *Trisaccites microsaccatus* (Couper) Couper (sample AKA; IM10, 11). **12:** *Trisaccites microsaccatus* (Couper) Couper (sample ALB; IU12). **14–16:** *Trisaccites microsaccatus* (Couper) Couper sensu Volkheimer et al., triangular variety (sample AKT; IS 9, 10, 11)



Callialasporites trilobatus (Balme, 1957) Sukh Dev, 1961

Plate 3/5, 6

Previous records: "Infralias" to Upper Jurassic (?), Sahara (Reyre 1973); worldwide Middle Jurassic to Lower Cretaceous (Srivastava 1987).

Botanical affinity: More likely Araucariaceae than Podocarpaceae (Batten & Dutta 1997).

Distribution of palynomorphs in the Tendaguru Beds

The distribution of selected palynomorph species in the Tendaguru Beds is shown in Table 2. From this overview it is evident that the Middle Saurian Beds and the *Smeei* Beds yielded two rather different palynofloras which are here informally designated as (1) *Anapiculatisporites-Densoisporites-Trisaccites* assemblage and (2) *Barbatacysta-Pareodinia* assemblage, respectively.

The *Anapiculatisporites-Densoisporites-Trisaccites* assemblage from the Middle Saurian Beds is dominated by terrestrially-derived miospores with pteridophytic and bryophytic elements attaining a similar degree of diversity as the gymnosperm pollen. Among the aquatic palynomorphs, marine dinoflagellates are rare or questionable, and freshwater algae (*Ovoidites*, Zygnemataceae) are present.

In contrast to this, the *Barbatacysta-Pareodinia* assemblage from the *Smeei* Beds contains common marine dinoflagellates, while freshwater algae, pteridophytic and bryophytic spores are rare or absent. Among the terrestrially-derived miospores, gymnosperm pollen are represented by bisaccates, *Araucariacites*, *Callialasporites*, and particularly *Classopollis*. *Classopollis* tends to be abundant or dominant in most productive samples from the Tendaguru Beds.

A third palynoflora, the *Rhizophagites* assemblage mainly from the Upper Saurian Beds, is characterized by the presence of hyphae and other fungal remains, which may be associated with rare conifer (bisaccates) and angiosperm pollen (tricolpates, tricolporates, triporates). *Rhizophagites* is known to be a major contaminant of palynological surface samples from carbonates and limy soils (Wood et al. 1996). Therefore the *Rhizophagites* assemblage is regarded as contaminated from recent and subrecent sources, and no further interpretation is attempted. The presence of rare angiosperm pollen makes the *Rhizophagites* assemblage comparable with the

palynoflora that Jarzen (1981) reported from his only productive sample, likewise from the Upper Saurian Beds.

Palynostratigraphic results

The combined ranges of *Barbatacysta creberbarbata*, *Dingodinium tuberosum*, *Mendicodinium ? quadratum* and *Pareodinia angulata* suggest a Kimmeridgian to Tithonian age for the *Barbatacysta-Pareodinia* assemblage and therefore for the *Smeei* Beds. Among the palynomorphs mentioned, only *Mendicodinium ? quadratum* was also encountered in the Middle Saurian Beds. Its records from India (ammonite-dated Lower Kimmeridgian to Tithonian, Kumar 1987) and Kenya (topmost Kimmeridgian to earliest Tithonian, Jiang et al. 1992) suggest that this species may be a potential Kimmeridgian-Tithonian marker although it is reported to range down to the middle Oxfordian in Madagascar (Dina 1996).

The pollen and spores of the *Anapiculatisporites-Densoisporites-Trisaccites* assemblage are generally stratigraphically long-ranging (Jurassic to Lower Cretaceous or even Tertiary) and offer little additional biostratigraphic information on the age of the Middle Saurian Beds.

The composition of this assemblage suggests broad correlation with the upper part of the *Callialasporites dampieri* Superzone (*Murospora florida* Zone, Oxfordian-Kimmeridgian) and the lower part of the *Microcachryidites* Superzone (*Retitriletes watheroensis* Zone, Tithonian) of Australia (Helby et al. 1987). The *Anapiculatisporites-Densoisporites-Trisaccites* assemblage also shows some similarity with terrestrial palynomorph assemblages from the Tithonian of Argentina (Volkheimer & Quattrocchio 1975) which Quattrocchio et al. (1996) place in the *Microcachryidites antarcticus* Zone.

The dinoflagellate age of the *Smeei* Beds given above is in good agreement with their late Kimmeridgian to Tithonian ammonite age postulated by Zwierzycki (1914). However, Zils et al. (1995) adopt a slightly older age for the *Smeei* Beds after indentifying the ammonite *Aspidoceras richthofeni* which they consider to be Middle Kimmeridgian in age because Gröschke & Kapilima (1995) reported this species from beds of the same age near Nchia, southern Tanzania. If correct then the latter age determination would imply an age not younger than Middle Kimmeridgian for the *Anapiculatisporites-Densoisporites-Trisaccites* assemblage and for the *Barbatacysta-Pareodinia* assemblage. From a palynostratigraphic point of view this can be neither confirmed nor rejected.

Palaeoecological conclusions

The abundance of dinoflagellates in the *Smeei* Beds indicates deposition in a marine environment. Scarcity or absence of dinoflagellates in the Middle Saurian Beds together with the presence there of freshwater algae and dominance of terrestrially-derived miospores suggest an aquatic environment with strong influx from a terrestrial source and questionable marine influence. Influx of terrestrially-derived palynomorphs into the *Smeei* Beds was relatively low and mainly confined to a few conifer pollen types. Pteridophytic and bryophytic spores, which mainly represent the vegetation growing close to the aquatic depositional sites, are absent or very subordinate in the *Smeei* Beds. This may be related to transport sorting or to other local factors such as drowning by the sea of the fluvio-coastal plain environments where the pteridophytic-bryophytic communities existed during the time of deposition of the Middle Saurian Beds.

A conifer vegetation, mainly Cheirolepidaceae, Podocarpaceae and Araucariaceae was predominant on the topographically higher and relatively dry environments, which would be less affected by an advancing sea.

If the Tendaguru palynofloras are compared on a larger scale with Late Jurassic miospore assemblages elsewhere in the world, the following points may be emphasised. Closest palaeobiogeographical links exist with Southern Gondwanan regions such as Madagascar, Australia, Argentina and India. The relatively low diversity of the pteridophytic-bryophytic element and the abundance of *Classopollis* even in the palynofloras from the Middle Saurian Beds is remarkable. *Classopollis* producers (Cheirolepidaceae, see Traverse 1988) are commonly regarded as xerophytic. Under consideration of the palaeocontinental position of Tendaguru on the huge Gondwana Continent in the southern dry zone, this may be taken as evidence for prevailing semiarid conditions with pronounced dry seasons during the time of deposition of the Tendaguru Beds.

Acknowledgements

I am grateful to Dr. W.-D. Heinrich for making available samples from the Tendaguru collections of the Museum für Naturkunde (Berlin) and for relevant informations. Technical help from M. Baudisch, D. Machander (HF laboratory), H. Glowa, B. Kleeberg (photographic laboratory) and B. Dunker (drawings) is gratefully acknowledged. Thanks are also due to the German Research Foundation (DFG) for financi-

al support and, last not least, to Dr. G. F. W. Herngreen, Haarlem, for discussions (in 1992) of problems related to Tendaguru palynology.

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Appendix A.

Alphabetical index of palynomorph species with reference to plate figures and to position in the range chart (number in Table 2).

	Plate	No.
Phytoplankton species		
<i>Acanthaulax</i> spp.		2
<i>Barbatacysta creberbarbata</i> (Erkmen & Sarjeant, 1980) Courtinat, 1989	1/10, 11	3
<i>Circulodinium distinctum</i> (Deflandre & Cookson, 1955) Jansonius, 1986	1/13	4
<i>Cleistosphaeridium</i> ? spp.		5
<i>Cometodinium</i> sp. Chen, 1978		6
<i>Cymatiosphaera</i> sp.		1
<i>Dingodinium tuberosum</i> (Gitmez, 1970) Fisher & Riley, 1980	1/8, 9	7
<i>Exochosphaeridium</i> sp.		8
<i>Kleithriasphaeridium</i> sp. cf. <i>K. corrugatum</i> Davey, 1974		9
<i>Lithodinia</i> sp. cf. <i>L. jurassica</i> Eisenack sensu Helby et al., 1988	1/1, 2	10
<i>Lithodinia</i> sp. cf. <i>L.</i> sp. 1 Davey, 1988	1/3, 4	11
<i>Meiourogonyaulax</i> sp. C Helby et al., 1988	1/6, 7	12
<i>Mendicodinium</i> ? <i>quadratum</i> Kumar, 1987	2/1	13
<i>Oligosphaeridium</i> ? sp. cf. <i>O. dividuum</i> Williams, 1978		14
<i>Ovoidites parvus</i> (Cookson & Dettmann, 1959) Nakoman, 1966	2/2	19
<i>Ovoidites</i> sp. cf. <i>O. microligneolus</i> Krutzsch, 1959	1/12	20
<i>Pareodinia angulata</i> Kumar, 1987	1/14	15
<i>Pareodinia</i> sp. cf. <i>P. brevicornuta</i> Kunz, 1990 sensu Dina, 1996	1/15	16
<i>Saepodinium</i> ? sp.		17
<i>Surculosphaeridium</i> sp.	1/5	18
Miospore species		
<i>Alisporites similis</i> (Balme, 1957) Dettmann, 1963	3/4	33
<i>Alisporites thomasii</i> (Couper, 1958) Nilsson, 1958	2/11	34
<i>Alisporites</i> sp. cf. <i>A. grandis</i> (Cookson, 1953) Dettmann, 1963	2/14	35
<i>Alisporites</i> spp.		36
<i>Anapiculatisporites dawsoneensis</i> Reiser & Williams, 1969	2/5–7	30
<i>Araucariacites australis</i> Cookson, 1947	3/1	44
<i>Bisaccates</i> indet.		41
<i>Callialasporites dampieri</i> (Balme, 1957) Sukh Dev, 1961	3/7, 8	45
<i>Callialasporites trilobatus</i> (Balme, 1957) Sukh Dev, 1961	3/5, 6	46
<i>Classopollis</i> spp.	3/9, 13	47
<i>Concavisorites juriensis</i> Balme, 1957	2/10	24
<i>Concavissimisporites</i> sp.		26
<i>Deltoidospora</i> spp.		21
<i>Densoisporites velatus</i> Weyland & Krieger, 1953	2/3	31
<i>Foraminisporis dailyi</i> (Cookson & Dettmann, 1958) Dettmann, 1963	2/4	29
<i>Klukisporites</i> sp.		32
<i>Leptolepidites</i> spp.		27
<i>Matonisporites equixinus</i> Couper, 1958	2/8, 9	22
<i>Osmundacidites</i> sp.		25
<i>Phrixipollenites</i> sp. Volkheimer et al., 1977	2/13	37
<i>Podocarpidites ellipticus</i> Cookson, 1947	3/2, 3	38
<i>Podoc.</i> cf. <i>P. multesimus</i> (Bolikh.) Pocock, sensu Dettmann (1963)	2/12	39
<i>Podocarpidites</i> spp.		40
<i>Polycingulatisporites</i> spp.		28
<i>Todisporites minor</i> Couper, 1958		23
<i>Trisaccites microsaccatus</i> (Couper, 1953) Couper, 1960	3/10–12	42
<i>Trisaccites microsaccatus</i> sensu Volkheimer et al. (1977), triangular variety	3/14–16	43