



A gymnosperm pollen not a dinoflagellate: a new combination for *Mendicodinium? quadratum* and description of a new pollen species from the Jurassic of Tanzania

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Abstract

A palynological investigation of outcrop samples from the Upper Jurassic part of the dinosaur-bearing Tendaguru Beds, southeast Tanzania, yielded well-preserved material of the alleged dinoflagellate *Mendicodinium? quadratum*. Combined scanning electron microscopy (SEM) and light microscopy showed that this species does not possess an epicystal archeopyle encircling the grain as would be expected in the dinoflagellate genus *Mendicodinium*. Rather, its opening is a sulcus confined to one side of the grain, commonly expanded at one or both ends. Therefore, *M.? quadratum* is interpreted here as a monosulcate gymnosperm pollen, and transferred to the genus *Shanbeipollenites*, which was originally described from the Jurassic of China.

In the Tendaguru Beds *Shanbeipollenites quadratus* is associated with the new species *Shanbeipollenites proxireticulatus*. Both species occur in marine and possibly nonmarine parts of the section. This distribution pattern and some morphological peculiarities of the latter species (proximal reticulum, rare dyads) support the interpretation of both species as gymnosperm pollen. © 2004 Elsevier B.V. All rights reserved.

Keywords: palynology; dinoflagellates; gymnosperm pollen; Jurassic; Tanzania

1. Introduction

A restudy of the alleged dinoflagellate *Mendicodinium? quadratum* Kumar (1987), was carried out in the framework of a more comprehensive palynological investigation of the famous dinosaur deposits at Tendaguru in southeast Tanzania (Fig. 1). Major dinosaur excavations were carried out there by the German Tendaguru Expedition (1909–1913). The complex history of this research was recently summarized by Heinrich et al. (2001) and Maier (2003).

Initial palynological studies of the Tendaguru site were based on the sediment material collected by the early Expedition (1909–1913), which is still housed in the Museum für Naturkunde, Berlin. Preliminary palynological results (Schrank, 1999) indicated the presence of *Classopollis*-dominated palynofloras in the Middle Saurian Bed and in the overlying marine *Trigonia smeei* Bed (Fig. 1). The latter unit yielded in addition marine dinoflagellates, and in both units few specimens of the problematic palynomorph *Mendicodinium? quadratum* were found. Previously, this species had been listed as a dinoflagellate (e.g., Jiang et al., 1992; Bucefalo Palliani et al., 1997; Williams et al., 1998), but the morphology of the Tendaguru

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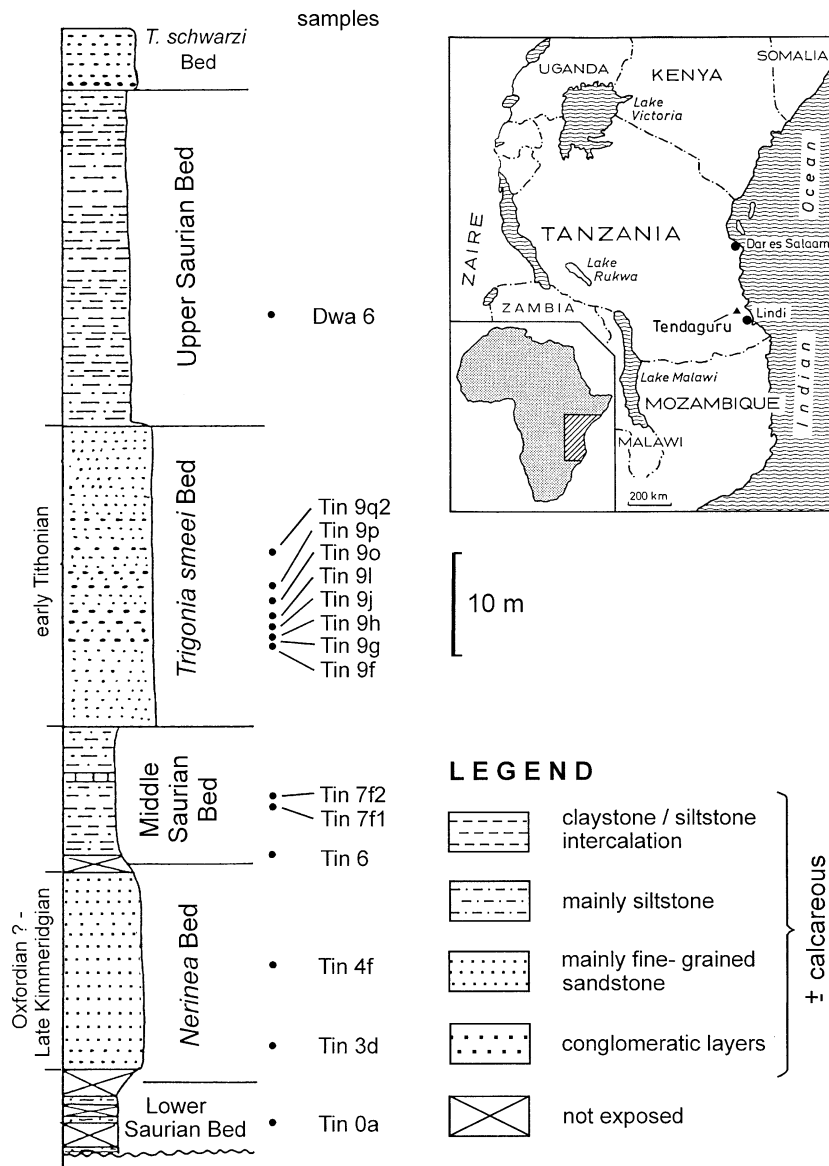


Fig. 1. Sketch map and simplified section (modified from Bussert in Aberhan et al., 2002) of the Tendaguru site. Tentative ages on the left side are from Aberhan et al. (2002).

specimens (presence of a sulcus rather than an archaeopyle) and their occurrence in possibly nonmarine parts of the Middle Saurian Bed raised doubts about the dinoflagellate nature of this palynomorph, which was recorded as a questionable dinoflagellate and a potential Kimmeridgian–Tithonian marker in Schrank (1999).

2. Material and stratigraphic framework

The present paper is based mainly on samples that I collected in September 2000 in the course of the German–Tanzanian Tendaguru Expedition (Heinrich et al., 2001). Samples which yielded *Mendicodinium? quadratum* or related forms are shown in Fig. 1 and

listed in Table 1. They are derived, in ascending order, from the Lower Saurian Bed, the *Nerinea* Bed, the Middle Saurian Bed, the *Trigonia smeei* Bed and the Upper Saurian Bed. A Late Jurassic age for this part of the Tendaguru Beds has been widely accepted, and preliminary biostratigraphic results suggest an Oxfordian? to Late Kimmeridgian age for the *Nerinea* Bed (based on ostracods and ammonites) and an early Tithonian age (based on ammonites and charophytes) for the *T. smeei* Bed (sources cited in Aberhan et al., 2002, p. 24). This is consistent with the Kimmeridgian–Tithonian age postulated for the Middle Saurian Bed and the *T. smeei* Bed as a result of the preliminary palynological study by Schrank (1999).

The samples collected in September 2000 have yielded new material of *Mendicodinium? quadratum* and of a closely related second species. The aim of this paper is to describe these two species, based on combined light microscopy and scanning electron microscopy (SEM). Thus, *M.? quadratum* is no lon-

ger regarded as a dinoflagellate but as a gymnosperm pollen, and is transferred to the genus *Shanbeipollenites* previously known from the Jurassic of China.

All specimens illustrated in this paper are from nonoxidized HCl/HF-resistant residues and are housed in the Technische Universität Berlin (catalogue numbers Pn66–Pn77).

3. Systematic palynology

Monosulcate gymnosperm pollen.

Genus *Shanbeipollenites* Qian Lijun and Wu Jingyun in Qian et al. (1987), emend.

Type species: *Shanbeipollenites quadrangulatus* Qian Lijun and Wu Jingyun in Qian et al. (1987)

Emended diagnosis: Monosulcate pollen; equatorial outline ranging from broadly ellipsoidal to subcircu-

Table 1

Distribution of *Shanbeipollenites quadratus*, *Shanbeipollenites proxireticulatus* and some associated palynomorphs in the Tendaguru Beds

	Sample no.	Slide no.	<i>S. quadratus</i>	<i>S. proxireticulatus</i>	Dinoflagellates, marine	Pollen and spores	
Upper Saurian Bed	Dwa 6/0	AVB	+	+		+	
<i>Trigonia smeei</i> Bed	Tin9q2	AZK		+	+	+	
	Tin9p/1 m	AZG	+	+	+	+	
	Tin9p/0	AZF	+		+	+	
	Tin9o/1 m	AZE	+		+	+	
	Tin9o/50 cm	AZD	+		+	+	
	Tin9o/30 cm	AZC		+	+	+	
	Tin9o/0	AZB	+		+	+	
	Tin9l/45 cm	AZA	+	+	+	+	
	Tin9l/0	AYY		+	+	+	
	Tin9j/0	AYX	+	+	+	+	
	Tin9h/0	AYU	+	+	+	+	
	Tin9g	AYT		+	+	+	
	Tin9f/0	AYR		+	+	+	
	Middle Saurian Bed	Tin7f2/0	ATN		+		+
		Tin7f1/44 cm	AYP		+		+
Tin7f1/35 cm		AYO	+	+		+	
Tin7f1/11 cm		AYL		+		+	
Tin7f1/0		AXB	+			+	
Tin6/16 cm		ATI	+			+	
<i>Nerinea</i> Bed	Tin6/0	ATH	+		+	+	
	Tin4f	AYD		+	+	+	
	Tin3d/73 cm	AXZ	+		+	+	
	Tin3d/0	AXY	+		+	+	
Lower Saurian Bed	Tin0A/0	ATD	+			+	

lar, rhombic or quadrangular. Sulcus extending diagonally over the full length of the distal side. Exine surface largely smooth on the distal side and smooth or variously sculptured (e.g., foveolate to irregularly reticulate) on the proximal side.

Remarks: An English translation of the original diagnosis was published by Jansonius et al. (2002, card 5494). The emendation includes a wider range of variation in the equatorial outline and the sculptural features of the proximal side of the new species *Shanbeipollenites proxireticulatus*. Alternatively, the latter species could be placed in a new genus. For the time being, this has not been done because the closely related genus *Cycadopites* in the sense of Cornet and Traverse (1975) and Fowell and Traverse (1995) also contains species (e.g., *C. andrewsii*) with a psilate distal surface and a variously sculptured proximal side.

Shanbeipollenites quadratus (Kumar (1987) Schrank, comb. nov. and emend. (Plate I, 1–5).

Basionym: *Mendicodinium quadratum* Kumar (1987, Revista Española de Micropaleontología 19, p. 242, plate 2, fig. 8 (holotype), 9).

1992 *Mendicodinium quadratum*, Jiang et al., p. 80, plate 5, fig. 6.

1996 *Mendicodinium quadratum*, Dina, plate 8, fig. 11; plate 14, fig. 1.

1997 *Mendicodinium quadratum*, Bucefalo Palliani et al., p. 101 (listed).

1998 *Mendicodinium quadratum*, Williams et al., p. 398 (listed).

1999 *Mendicodinium quadratum*, Schrank, p. 176, plate 2, fig. 1.

Emended diagnosis: Monosulcate pollen, outline quadrangular with more or less rounded corners. Sulcus extending (diagonally) over full length of the distal

side, narrow or closed (overlapping) in the middle, and open at the ends. The margins of the sulcus may appear dark due to infolding of the exine. Exine is thin and largely psilate.

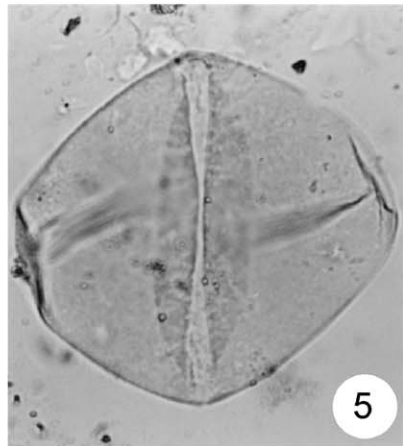
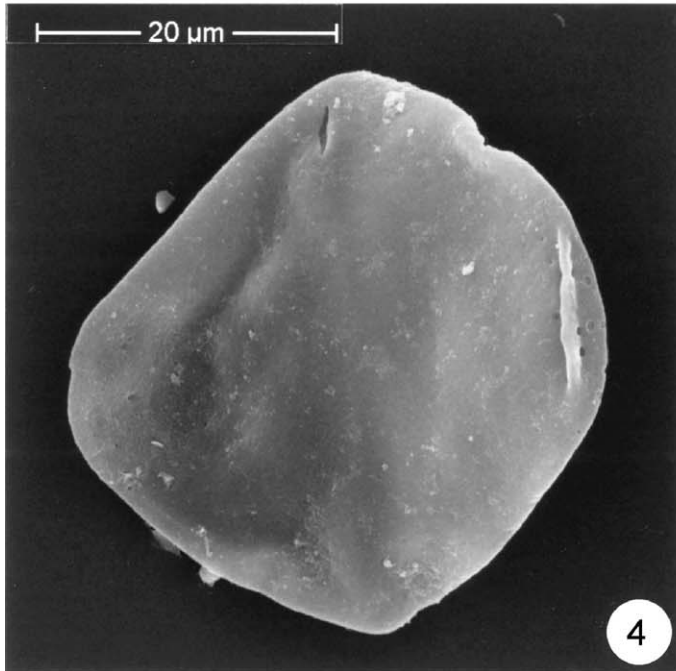
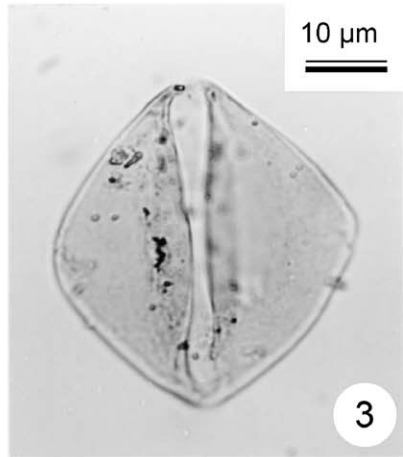
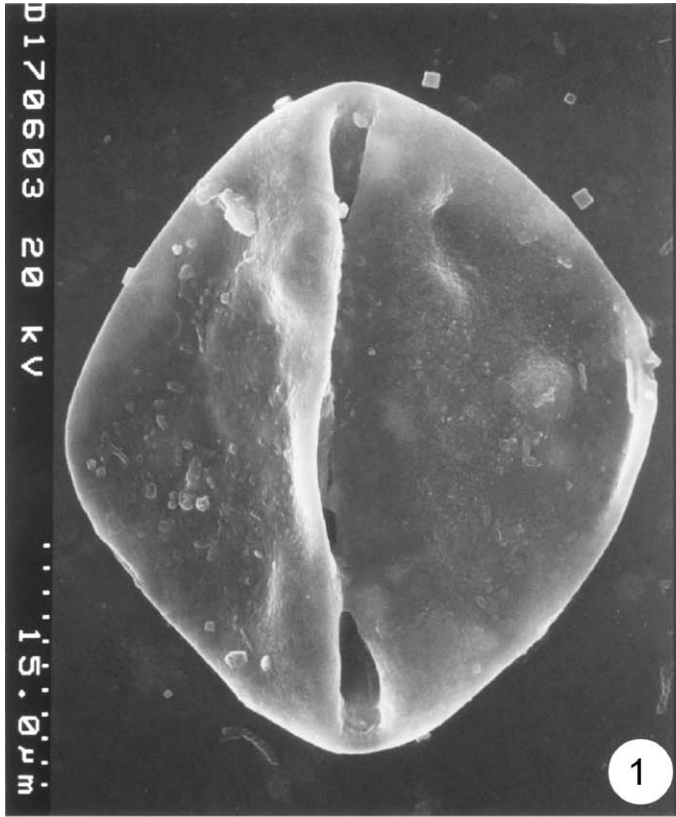
Description: Pollen grains typically quadrangular, but are often deformed or folded resulting in rounded, elongate or broadened outlines. Ratio of length to width about 0.8–1.4, in most specimens around 1.1. Length along the sulcus: 32 (41.9) 50 μm (26 specimens). Maximum exine thickness about 1 μm .

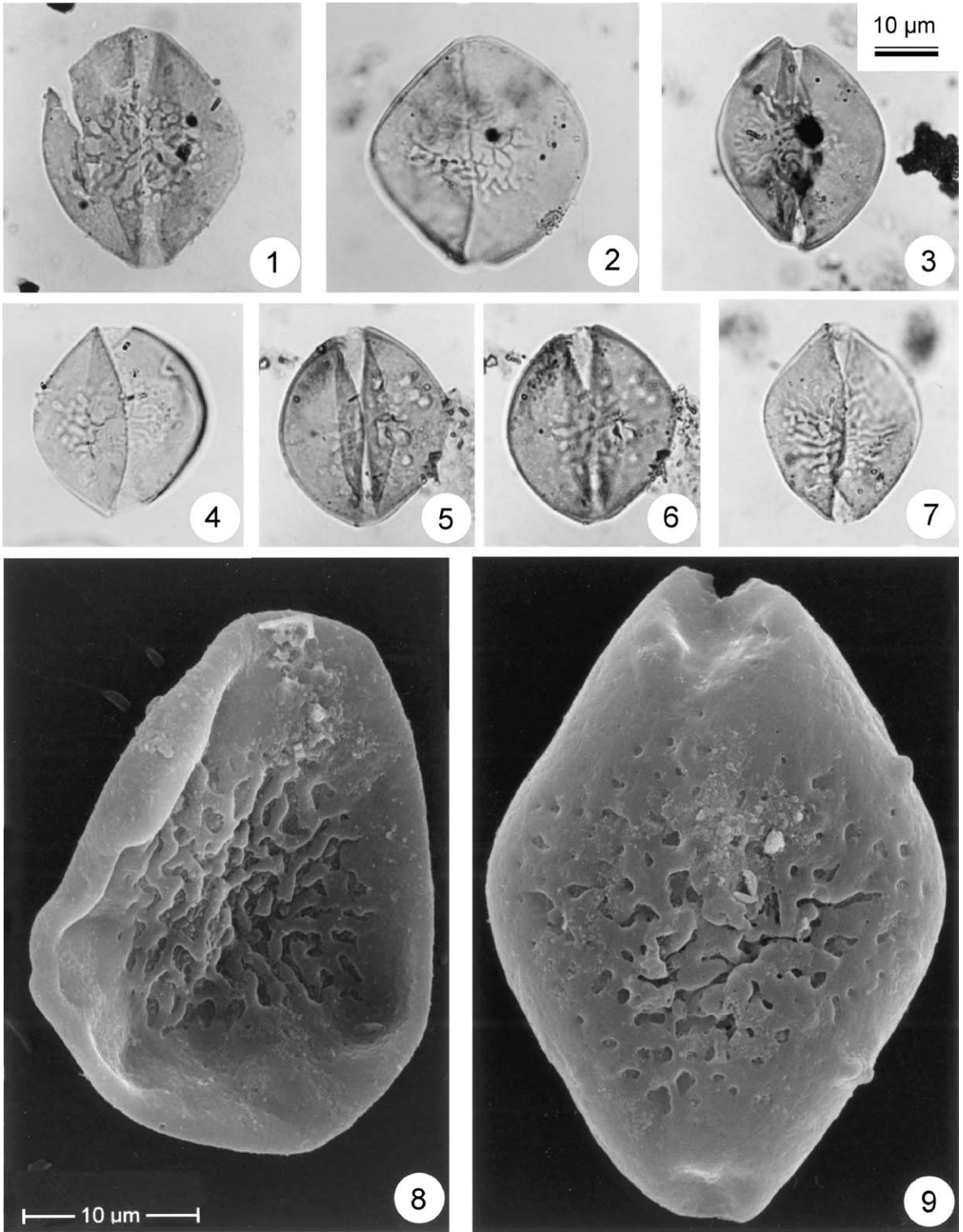
Remarks: This species is transferred from the dinoflagellate genus *Mendicodinium* to the gymnosperm pollen genus *Shanbeipollenites*, according to its emended diagnosis. *Mendicodinium* is characterized by an epicystal archeopyle and a ventrally adnate operculum (Bucefalo Palliani et al., 1997). Therefore, typical specimens of *Mendicodinium* often appear to be split into two more or less equal halves which may be connected by a narrow strip of the autophragm on the ventral side. In contrast to this, typical specimens of the species *quadratum* have the “archaeopyle opening on only one side of the cyst” as already noted by Kumar (1987, p. 242). An analysis of the present material and illustrations in the literature (see above) demonstrate that this opening represents a sulcus of the “double key hole type” occurring in gymnosperm pollen such as *Cycadopites* (e.g., Jansonius et al., 1998, card 5072). This sulcus can be narrow, nearly parallel-sided or gaping at one or both ends. In general the habitus of the species *quadratum* corresponds closely to that of *Cycadopites* apart from the outline which is typically quadrangular in the former and ellipsoidal, about twice as long as wide in the latter.

The type species of *Shanbeipollenites*, *Shanbeipollenites quadrangulatus* (see Song et al., 2000, p. 529, plate 90, figs. 21–22; Jansonius et al., 2002, card 5494) from the Jurassic of China, resembles the species *quadratus*

Plate I

- 1–5. *Shanbeipollenites quadratus* (Kumar) Schrank, comb. nov. and emend. from the Middle Saurian Bed (3 and 5) and from the *Trigonia smeei* Bed (1, 2, 4).
- 1, 2. SEM (1, CC3) and LM (2, LC10) of same specimen, AZG5/Tin9p/1 m; 42 μm .
3. IT18/ALB, 40 μm .
4. CD61, AYX8/Tin9j/0; 38 μm .
5. JM34, ATH1/Tin6; 47.5 μm . Photo, slide and sample numbers are indicated in addition to the maximum grain diameter. Magnification (scale bar in panel 3) is identical for the light micrographs (2, 3 and 5).





with respect to its outline and the shape of the sulcus, but differs in its intragranulate structure.

Shanbeipollenites quadratus has superficial similarity to some zygospores or cysts of freshwater algae; e.g., *Zygodites major* (Rshanikova) Krutzsch and Pacltová (1990, plate 10, figs. 180 and 181) and Sp. indet. 6 (indeterminant algal cyst of Zippi (1998, plate 23, figs. 1–2, 4–5). It is distinguished from these forms by its well-defined *Cycadopites*-like sulcus and its typically quadrangular and less variable shape. In addition, the occurrence in the present material of very rare dyads, in one case (*Shanbeipollenites proxireticulatus*) united at the (foveolate to reticulate) proximal sides, suggests a gymnosperm rather than an algal affinity.

Previous records: Lower Kimmeridgian–Tithonian of Kachchh, India (Kumar, 1987); topmost Kimmeridgian (*sensu gallico*) of Kenya (Jiang et al., 1992); middle Oxfordian to Tithonian, Madagascar (Dina, 1996); Middle Saurian Bed and *Trigonia smeei* Bed of the Tendaguru section (probably Kimmeridgian–Tithonian, Schrank, 1999).

Occurrences in the studied sections: Lower to Upper Saurian Bed (see Table 1).

Shanbeipollenites proxireticulatus Schrank, sp. nov. (Plate II, 1–9).

Etymology: Proximal and Latin *reticulatus* (net-like) in reference to the reticulate sculpture on part of the proximal side.

Holotype: TUB catalogue number Pn70/LD10 (Plate II, 1).

Repository: Institut für Angewandte Geowissenschaften, Technische Universität Berlin (TUB), Germany.

Type locality: Tingutinguti stream section southwest of Tendaguru.

Type stratum: Middle Saurian Bed, sample Tin7f1/11 cm (Kimmeridgian to Tithonian).

Diagnosis: Monosulcate pollen, outline primarily subcircular, oval to quadrangular. Sulcus extending over full length of the distal side, parallel-sided or widened at one or both ends and/or overlapping at distal pole. Exine is largely psilate on the distal side and reticulate to rugulate and foveolate on the proximal side.

Description: Thin-walled pollen grains that are commonly deformed resulting in strong variability of outline and sulcus shape. Ratio of length to width about 1–1.4. Sulcus always long, otherwise highly variable, lips of up to 6 µm width may surround the sulcus. Distal and equatorial surfaces are largely psilate. Ornamentation restricted to a subcircular (or rarely elongate) area of the proximal side, consisting of an irregular reticulum (maximum diameter of lumina about 4 µm) or of rugulate elements (especially in small grains) in the center. This pattern tends to become finer towards the margin of the ornamented area where the larger elements may grade into foveolae of less than 1-µm diameter. Granules of less than 0.5-µm diameter may be visible under SEM in the lumina of the reticulum.

Dimensions: Holotype—37 × 32 µm. Range and mean value of maximum diameter (27 specimens)—23 (30.4) 42 µm.

Remarks: *Shanbeipollenites proxireticulatus* is distinguished from the type species *Shanbeipollenites quadrangulatus* and from *S. quadratus* by the distinct ornamentation of its proximal side. The presence in the genus *Cycadopites* of species (like *C. andrewsii*,

Plate II

1–9. *Shanbeipollenites proxireticulatus* Schrank, sp. nov. from the Middle Saurian Bed (1, 3 and 4) and from the *Trigonia smeei* Bed (2, 5–9).

1. Holotype, LD10, AYL1/Tin7f1/11 cm; 37 µm.
2. KX30, AYY1/Tin9l/0; 37 µm.
3. LD8, AYP1/Tin7f1/44 cm; 33 µm.
4. IL30, AKA; 30 µm.
- 5, 6. LD6, 7 AYT1/Tin9g; 31 µm. Note that angular openings on the right side are artefacts.
7. KO3, AYY1/Tin9j/0; 30 µm.
8. CD65, AYY8/Tin9j/0; 31 µm.
9. CD71, AYY8/Tin9j/0; 38 µm. Magnifications (scale bars in panels 3 and 8) are identical for the light micrographs panels 1–7 and for the scanning electron micrographs panels 8–9, respectively.

see above) having a sculptured proximal side and a psilate distal side like *S. proxireticulatus* is remarkable, and may suggest that both forms are related to each other.

Occurrences in the studied sections: *Nerinea* Bed to Upper Saurian Bed (see Table 1).

4. Conclusions

New material of the presumed dinoflagellate *Mendicodinium? quadratum* Kumar (1987), was recovered from the Upper Jurassic part (probably mainly Kimmeridgian–Tithonian) of the dinosaur-bearing Tendaguru Beds in southeast Tanzania. Combined light and scanning electron microscopy confirmed the presence of an opening, on one side of the grain only, that is clearly different from the epicystal archeopyle of the dinoflagellate genus *Mendicodinium*, and not distinguishable from the sulcus of monosulcate gymnosperm pollen such as *Cycadopites*. Therefore, *M.? quadratum* is interpreted as a gymnosperm pollen, and is transferred to the monosulcate pollen genus *Shanbeipollenites* Qian Lijun and Wu Jingyun (in Qian et al., 1987). *Shanbeipollenites* is similar to *Cycadopites* but can be distinguished because of its typically rhombic/quadrangular outline.

In the Tendaguru Beds, *Shanbeipollenites quadratus* and a related new species, *Shanbeipollenites proxireticulatus*, occur as rare forms from the Lower to the Upper Saurian Bed and from the *Nerinea* Bed to the Upper Saurian Bed, respectively. This includes possibly nonmarine parts of the section where marine dinoflagellates are missing (Table 1). This distribution pattern supports a gymnosperm affinity of these palynomorphs as does the presence of rare specimens (of *S. proxireticulatus*) united in dyads at their sculptured proximal side. Dyads are not known in dinoflagellates, but occasionally occur in gymnosperm pollen.

Shanbeipollenites quadratus has the potential to become a Kimmeridgian–Tithonian key form, at least in parts of Gondwana (India, East Africa, Madagascar).

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