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The ultrastructure of Upper Palaeozoic and Mesozoic pollen from southern Africa and Asia

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The dispersed pollen taxa *Cycadopites, Monosulcites, Bennetitteaepollenites, Pityosporites,* and *Inaperturopollenites* recovered from Permian to Jurassic sediments in southern Africa and Asia were examined ultrastructurally. *Cycadopites, Monosulcites, Bennetitteaepollenites* and *Inaperturopollenites* wall structure is characterized by homogeneous outer layer that is variously lacunate, and is underlain by a lamellated basal layer. Only one species of *Monosulcites* recovered from Jurassic sediments of Afghanistan showed a well-developed tectum, an infrastructural layer composed of columellae, or irregularly shaped columellae underlain by a basal layer. The saccate pollen of *Pityosporites* has an infrastructural layer of irregularly shaped anastomosing rods, the sacci are formed by an expansion of infrastructural layer in the region of the saccus (i.e. protosaccate *sensu* Scheuring). A majority of Permian, Triassic and Jurassic saccate and non-saccate monosulcate pollen is characterized by limited morphological diversity with regard to sculpturing and wall structure type compared to the diversity in angiosperm monosulcate pollen; however, there are pre-Cretaceous monosulcate pollen types that exhibit angiospermous pollen characteristics.

Keywords: ultrastructure, monosulcate pollen, Palaeozoic, Mesozoic, Africa, Afghanistan, China.

INTRODUCTION

Monosulcate pollen is one of the most ubiquitous pollen types found in the Mesozoic and has been recovered from sediments distributed throughout the world. The first appearance of this pollen type is in the Upper Palaeozoic. The common occurrence of monosulcate pollen and its wide distribution suggest that a number of vascular seed plant groups have derived this pollen aperture type (Walker 1974; Walker & Doyle 1975; Doyle 1978; Crane 1985; Doyle & Donoghue 1993; Brenner 1996; Dilcher 2001a,b). Monosulcate pollen occurs in every major extant vascular seed plant group, including the angiosperms. The common occurrence of this pollen type in the basal dicots and the monocots suggests that this aperture type is also shared by the angiosperm sister group, which at present has not been unequivocally identified based on anatomical, morphological, fossil or molecular evidence (APG 1998; Judd *et al.* 2002).

This paper is part of an ongoing investigation to assess and document pollen variation of monosulcate pollen from Upper Palaeozoic and Mesozoic localities throughout the world using characters obtained by light, scanning electron and transmission electron microscopy. This paper describes selected saccate and non-saccate dispersed monosulcate pollen of unknown affinity from localities in southern Africa and Asia. Understanding the morphological diversity of non-angiospermous Upper Palaeozoic and Mesozoic monosulcate pollen can more clearly define the morphological transformation that may have taken place in the gymnosperm–angiosperm transition, clarify distributional patterns of pre-angiospermous monosulcate pollen, and permit the elucidation of pollen features restricted to and characteristic of angiosperm monosulcate pollen. The latter is especially useful for tracking the first appearance and geographical distribution of early angiosperms or their stem relatives.

MATERIALS AND METHODS

Three localities were sampled in South Africa (Table 1). Palynological samples from Lower and Middle Permian age sediments of the Ecca were recovered from Hammanskraal located in the northern Karoo Basin. The collection locality was previously described by Anderson (1977) and Anderson & Anderson (1985). Palynological samples from the Triassic Molteno Formation were collected from Little Switzerland near Bergville, KwaZulu-Natal. This locality was previously described by Anderson & Anderson (1983, 1985, 1989). Palynological samples from the Lower Cretaceous Kirkwood Formation were collected from Dunbrodie, a locality previously described by Anderson & Anderson (1985) (also see Scott 1976) along the Wit River in the Eastern Cape Province.

A single sample of a cannel coal was received from D.L. Dilcher of the Florida State Natural History Museum, Gainesville, FL, U.S.A. The sample was recovered from the undifferentiated Jurassic of Afghanistan (Table 1).

Six palynological samples of Triassic age (Norian) were recovered from the Xiaotangzi Member of the Xujiahe Formation, Sichuan Province, China (Shang & Li 1992). The samples were provided by Yuke Shang of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China (Table 1).

All palynological samples were processed following a modified version of the method of Barss & Williams (1973). The palynological residues were processed and prepared for SEM and TEM after Zavada (2003).

SYSTEMATIC PALYNOLOGY

***Cycadopites* type**, Figs 1–4, 13–14

Cycadopites is characterized by the osteoid shape of the sulcus (Figs 1, 3), i.e. the sulcus margins are narrow in the central region and flare at the distal ends of the sulcus (Figs 1, 3). Dispersed pollen grains range from ellipsoidal

Table 1. List of individual pollen types examined in this study, their country of origin, age of the formation they are extracted from, and figures. Each entry represents a pollen type examined with light, scanning electron and/or transmission electron microscopy.

Pollen type	Locality	Age	Figures
Cycadopites	Hammanskraal, South Africa	Permian	1, 2
Cycadopites	Hammanskraal, South Africa	Permian	3, 4, 13, 14
Monosulcites	Little Switzerland, South Africa	Triassic	24
Monosulcites	Little Switzerland, South Africa	Triassic	25
Monosulcites	Little Switzerland, South Africa	Triassic	26, 36
Monosulcites	Little Switzerland, South Africa	Triassic	27
Monosulcites	Little Switzerland, South Africa	Triassic	28
Monosulcites	Dunbrodie, South Africa	Early Cretaceous	41
Monosulcites	Dunbrodie, South Africa	Early Cretaceous	42, 46, 47
Monosulcites	Dunbrodie, South Africa	Early Cretaceous	43
Monosulcites	Sichuan, China	Triassic	48
Monosulcites	Sichuan, China	Triassic	49
Monosulcites	Sichuan, China	Triassic	50
Monosulcites	Afghanistan	Jurassic	51, 56
Monosulcites	Afghanistan	Jurassic	52
Monosulcites	Afghanistan	Jurassic	53
Monosulcites	Afghanistan	Jurassic	54, 57, 58
Bennettiteaepollenites	Little Switzerland, South Africa	Triassic	30, 31, 32, 35
Pityosporites	Hammanskraal, South Africa	Permian	5, 6, 15, 16
Pityosporites	Hammanskraal, South Africa	Permian	7, 8, 17
Pityosporites	Hammanskraal, South Africa	Permian	9, 10, 19, 22, 23
Pityosporites	Hammanskraal, South Africa	Permian	11, 12, 18, 20, 21
Pityosporites	Little Switzerland, South Africa	Triassic	29, 38, 39, 40
Pityosporites	Dunbrodie, South Africa	Early Cretaceous	44, 45
Inaperturopollenites	Little Switzerland, South Africa	Triassic	33, 34, 37
Inaperturopollenites	Sichuan, China	Triassic	55, 59, 60

to sub-circular in shape (Figs 1–4). Pollen size varies, ranging from 18 to 40 μm. Pollen sculpturing ranges from psilate to scabrate-granulate (Figs 1–4). Pollen wall structure is homogeneous to slightly lacunate (Figs 13–14), and in many taxa a lamellated basal layer is present (not shown).

This taxon is distinguished from other monosulcate taxa by lacking folds or sacci flanking the conspicuous sulcus. In *Monosulcites* the sulcus is ellipsoidal and lacks the conspicuous osteoid appearance of the sulcus in *Cycadopites.* This pollen type ranges from the Upper Palaeozoic to the Late Cretaceous and has a cosmopolitan distribution (Zavada 1984, 1990).

***Monosulcites* type**, Figs 24–28, 36, 41–43, 46–47, 48–54, 56–58

The sulcus in *Monosulcites* is straight and narrow to somewhat wide and ellipsoidal (Figs 24–28, 41–43, 48–54). Dispersed pollen grains are generally ellipsoidal (Figs 24–28, 41–43, 48–50, 53) but may occasionally be subcircular (Figs 51, 52) to circular in shape (Fig. 54). Pollen size varies, most frequently ranging between 18 and 40 μm. Pollen sculpturing is psilate (Figs 24–27, 41, 42, 48–53) to scabrate-granulate to psilate (Figs 28, 43, 54).

Pollen wall structure is primarily homogeneous (Figs 36, 46–47) to slightly lacunate (Fig. 56); however, a number of taxa have numerous lacunae (Zavada 1984, 1990). In one dispersed taxon recovered from Afghanistan (Fig. 54) the wall structure is composed of a well-developed tectum (Fig. 57), an infrastructural layer composed of columellae, irregularly shaped rods and occasional granules (Fig. 57). The infrastructural layer is underlain by a thin, homogeneous basal layer (Fig. 57).

Although *Monosulcites* exhibits a number of similarities to other non-saccate monosulcate dispersed pollen, this Mesozoic morphotype has the greatest wall structure diversity. This taxon ranges from the Upper Palaeozoic to the Late Cretaceous, and has a cosmopolitan distribution.

***Bennettiteaepollenites* type**, Figs 30–32, 35

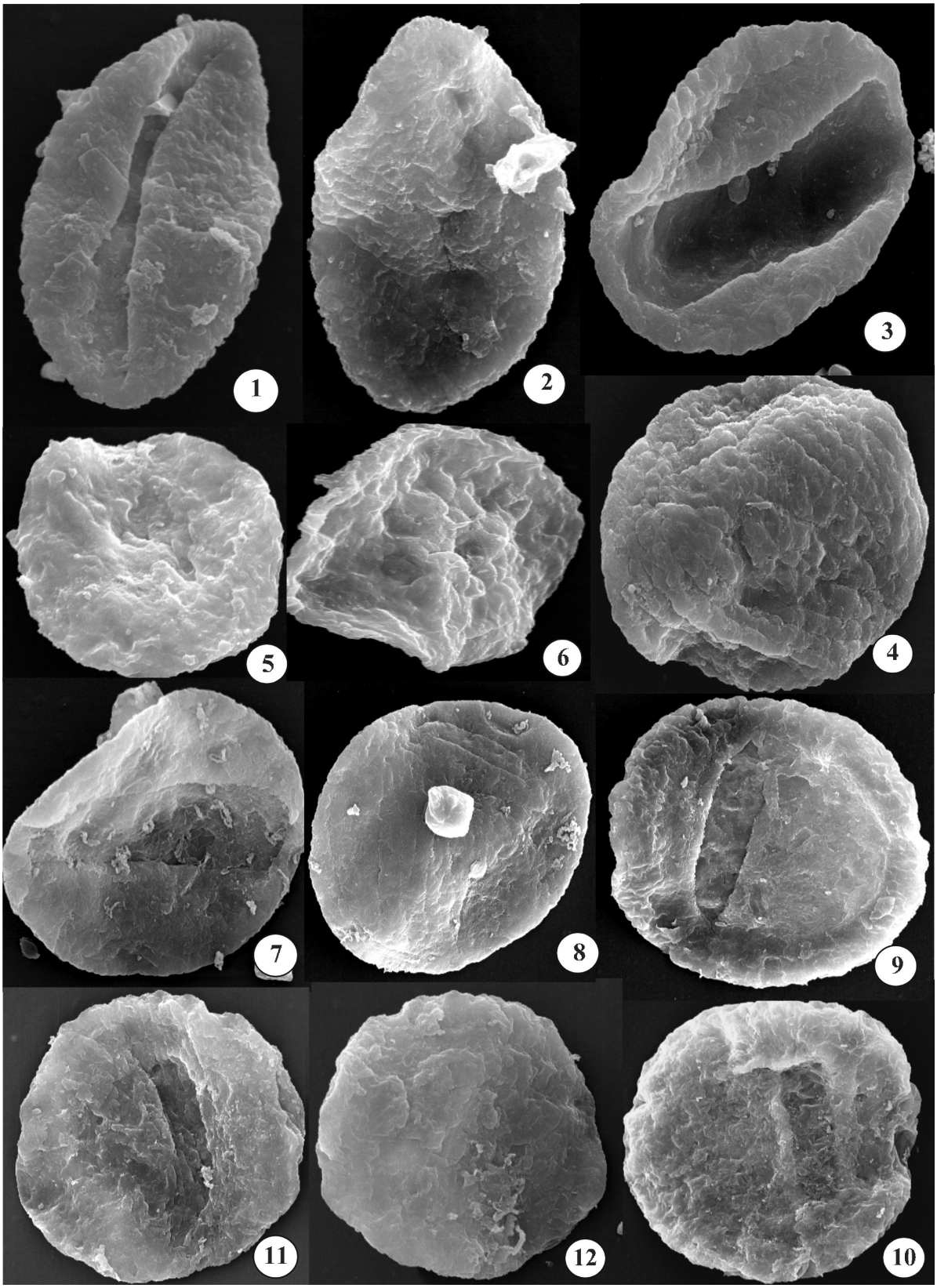
The sulcus is straight and ellipsoidal (Figs 30, 31). Dispersed pollen grains are ellipsoidal to sub-circular in shape (Figs 30–32). Pollen varies in size but most frequently ranges between 18 and 40 μm. Pollen sculpturing is psilate (Figs 30–32) to granulate-scabrate (Zavada 1984). Often long conspicuous folds flank both sides of the sulcus.

Pollen wall structure is homogenous to slightly lacunate (Figs 35). The outer homogenous layer is underlain by a differentially staining basal layer that occasionally exhibits lamellations (Figs 35). This taxon ranges from the Lower Mesozoic to the lower Upper Cretaceous, and has a cosmopolitan distribution. This taxon differs from *Cycadopites* and *Monosulcites* by the regular occurrence of exinal folds on both sides of the sulcus (Figs 30, 31).

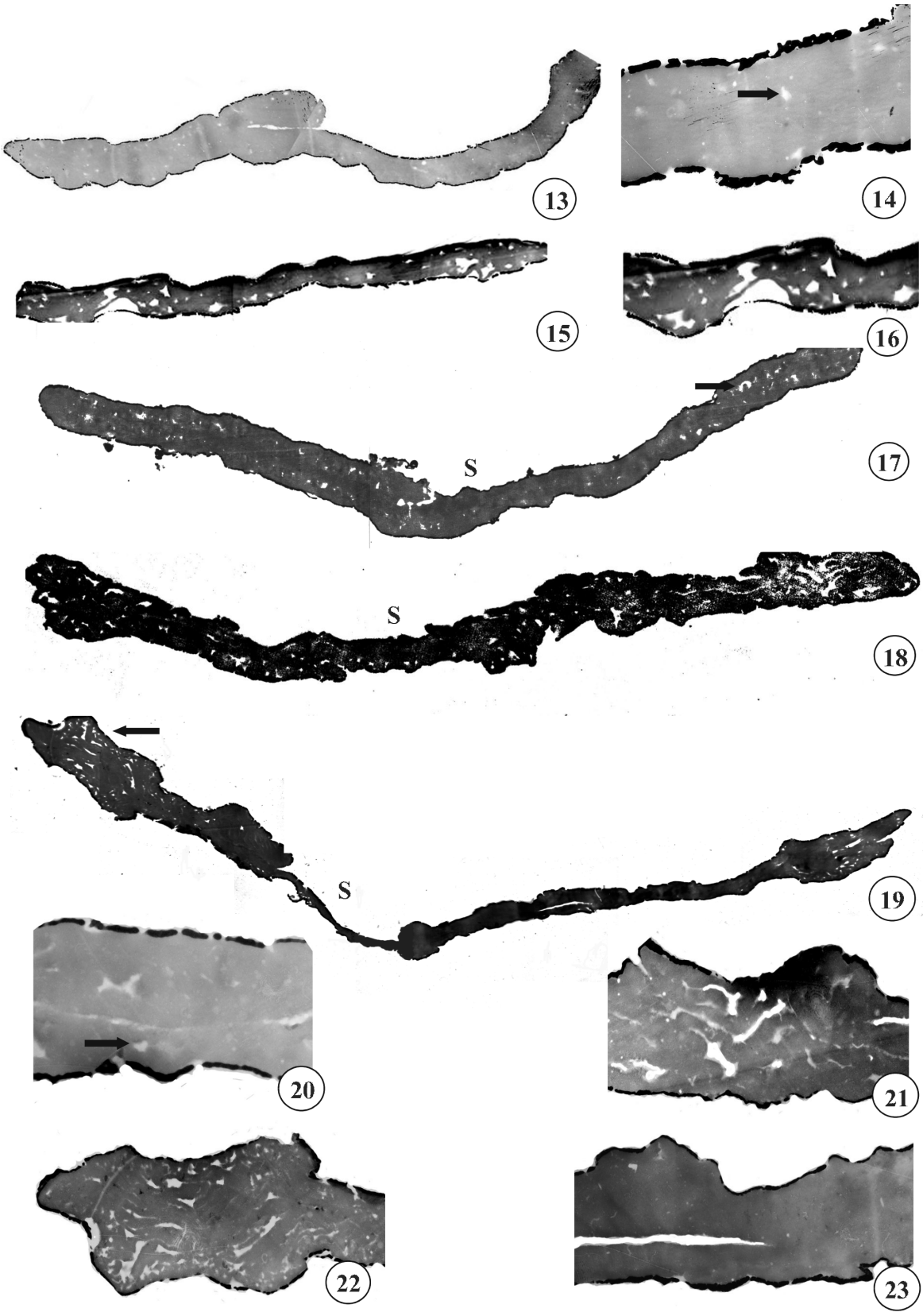
***Pitysporites* type**, Figs 5–12, 15–23, 29, 38–40, 44–45

This taxon encompasses a large and diverse group of dispersed pollen types. Pollen is monosulcate, circular to slightly elongate (Figs 5–12, 29, 44–45). Exine sculpturing is psilate (Figs 5–6, 9–12, 29, 44–45); however, a few species are reported to be striate (Figs 7–8) (Anderson 1977). Pollen is generally interpreted to be saccate, the sacci forming a marginal fringe (Figs 9–12, 29, 44–45). Pollen ranges in size from 24 to 136 μm.

Pollen wall structure is composed of an outer tectum that varies in thickness and that is underlain by a struc-



Figures 1–12. SEM of pollen from the Permian Northern Karoo locality Hammanskraal, South Africa. **1–4**: *Cycadopites* type 1, distal view, ×2000; **2**, proximal view of the same grain in Fig. 1, ×2000; **3**, distal view, ×2100; **4**, proximal view of the same grain in Fig. 3, note the slightly rugulate sculpturing, ×2100. **5–12**: *Pityosporites* type; **5**, distal view, ×1800; **6**, proximal view of the same grain in Fig. 5, ×1800; **7**, distal view, ×1200; **8**, proximal view of the same grain in Fig. 7, note the regularly spaced exinal grooves at the top of the pollen grain, ×1200; **9**, distal view, note what appears to be an equatorial saccus, ×600; **10**, proximal view of the same grain in Fig. 9, ×600; **11**, distal view, ×1400; **12**, proximal view of the same grain in Fig. 11, note the slightly rugulate exine sculpturing, ×1400.



Figures 13–23. TEM of pollen from the Permian Northern Karoo locality Hammanskraal, South Africa. **13–14**: *Cycadopites* type; **13**, TEM of the whole pollen grain in Figs 3 and 4 showing the homogeneous wall structure that is occasionally interrupted by small lacunae; in similar grains a thin, differentially staining, lamellated basal layer is present, ×4100; **14**, high-magnification TEM of the same grain in Figs 3, 4 and 13 showing the small occasional lacunae (arrow); the black outer layer on the wall is the gold coating applied for SEM, ×20 000. **15–23**: *Pityosporites* type; **15**, TEM of the whole grain in Figs 5 and 6 showing structured wall; although the pollen grain is compressed the wall appears to be composed of irregularly shaped, robust elements, ×2700; **16**, high-magnification TEM of the same grain in Figs 5, 6 and 15 showing the structured wall, ×4100; **17**, TEM of the whole grain in Figs 7 and 8 showing the sulcus region (S) (also see Fig. 7) and the homogeneous wall structure with what appear to areas of regularly placed lacunae (arrow); note that the wall structure becomes more homogeneous in the sulcus region, ×4000; **18**, TEM of the whole grain illustrated in Figs 11 and 12 showing the wall structure composed of cylindrical, branching elements; this pollen grain is similar to the one illustrated in Figs 5, 6, 15 and 16;

Continued on p. 63

tured layer (Figs 15–23, 38–40). Adjacent to the apertures this structured layer is composed of a thick, homogeneous layer that is variously lacunate (Figs 15–20, 23). In the region of the sacci the infrastructural layer is composed of anastomosing irregular shaped interconnecting elements (Figs 15–19, 21–22). The sacci are not formed by a separation of the nexine and sexine. The infrastructural layer is underlain by a homogeneous to lamellated basal layer that varies in thickness (Figs 20, 23)

***Inaperturopollenites* type**, Figs 33–34, 37, 55, 59–60

Pollen of this type is inaperturate (Figs 33–34), large, ranging in size from 26 to 80 μm. Exine sculpturing can be psilate, scabrate, or verrucate (Figs 33–34, 55).

Pollen wall structure is homogeneous (Fig. 37) to slightly lacunate (Figs 59–60). A homogeneous to lamellate basal layer is often distinguishable (Fig. 60).

DISCUSSION

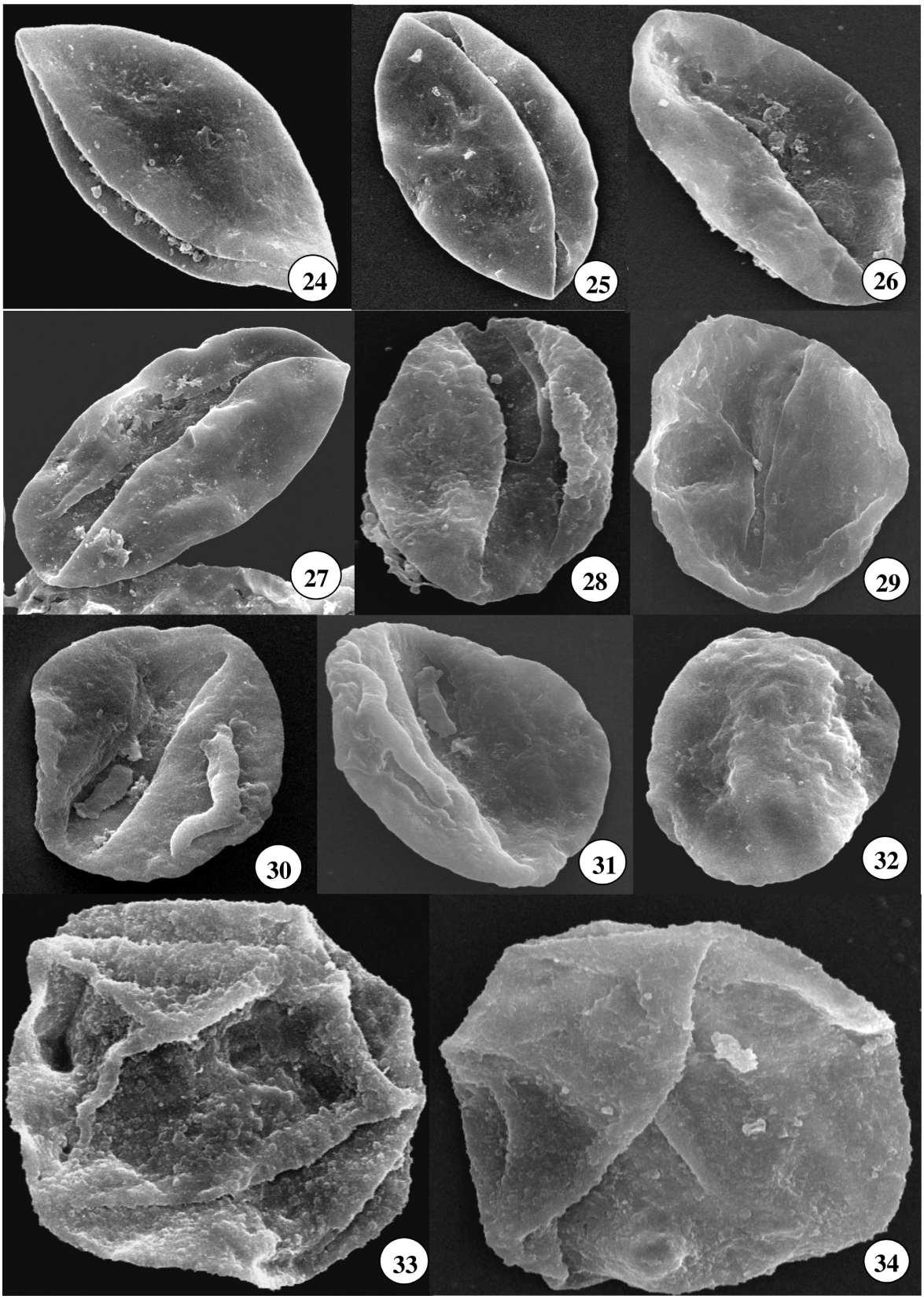
The monosulcate aperture type occurs in a wide variety of fossil and extant groups. This pollen aperture type makes its first appearance in the Late Palaeozoic, and is distributed among the Palaeozoic and Mesozoic pteridosperms, gymnosperms and the dicots and monocots. The occurrence of this aperture type in a particular group, in and of itself, offers little insight into determining the taxonomic position, or evolutionary relationships of these groups. The association of this aperture type with other distinctive pollen features, however, may permit palynologists to estimate the time of origin, and to track the geographical distribution of various plant groups through time and space.

In this study three types of dispersed pollen from various localities and ages were investigated, a) monosulcate non-saccate pollen types, b) monosulcate saccate pollen types, and c) pollen with an indistinct monosulcate aperture, or inaperturate pollen. The monosulcate non-saccate pollen has been assigned to *Cycadopites* (Figs 1–4, 13–14), *Monosulcites* (Figs 24–28, 41–43, 46–47, 48–54, 56–58) and *Bennettiteaepollenites* (Figs 30–32, 35). Except for the configuration of the sulcus and/or the presence of exinal folds, all three taxa have a similar shape, range in size, sculpturing and wall structure, despite the fact that they are derived from localities widely separated in time and space. Previous studies on similar forms from the Triassic Chinle Formation, western United States (Zavada 1990), Cretaceous sediments of the United States (Zavada 1984), and the Upper Cretaceous Dakota Formation, central United States (Zavada & Dilcher 1988) exhibit the same narrow range in characteristics, i.e. pollen is oval to circular in shape, ranges in size from 18 to 45 μm and is monosulcate, the sculpturing is psilate to slightly scabrate to verrucate; the pollen wall is homogeneous to homogeneous lacunate; and the outer sexine is generally underlain by a homogeneous or lamellated basal layer (nexine). The outstanding feature of these pollen types is the lack of morphological diversity over a wide geographical area and long geological time compared to superficially similar forms in the angiosperms. This morphological monotony, however, is occasionally punctuated by Triassic and/or Jurassic monosulcate pollen that, although in size, shape and, in some cases, sculpturing, is superficially similar to the above taxa, has a pollen wall structure that is more similar to the pollen wall structure observed in the monosulcate pollen of the angiosperms (e.g. Figs 54, 55, 57, 58, 59, 60; Cornet 1989; Cornet & Habib 1992).

Saccate monosulcate pollen, much like the non-saccate monosulcate pollen, exhibits limited variation in shape, size and sculpturing. Sacci are generally described as bladder-like extensions of the exine that result from the separation of the sexine from the nexine. Ultrastructural studies of fossil and extant saccate pollen have shown that saccus formation is a result of a number of exinal modifications (Osborn & Taylor 1994, and references therein; Kurmann & Zavada 1994). The sacci in *Pityosporites* (Figs 5–12, 15–23, 29, 38–40, 44–45) are of the protosaccate type (*sensu* Scheuring 1974). Scheuring (1974) has considered protosacci to be fundamentally different from the formation of sacci in the conifers, i.e. coniferalean sacci are formed by a separation of the sexine and the nexine (eusaccate condition, *sensu* Scheuring 1974). Meyen (1987) suggested that the term protosaccate might imply a plesiomorphic condition, and suggested that the term quasi-saccate would be more accurate, because the evolutionary relationship of the protosaccate condition and the eusaccate condition (*sensu* Scheuring 1974) has not been established. Among the fossil saccate pollen investigated in this study, the sacci are formed by an elaboration of the infrastructural elements, i.e. anastomosing, irregularly shaped rods (Figs 18–22). In none of the taxa investigated in this study is there a clear separation of the sexine and the nexine. The variation in saccus number, morphology, and the mode of formation suggest that this pollen feature was derived independently in a number of taxonomic groups through time.

Two species of *Inaperturopollenites* were investigated (Figs 33–34, 37, 55, 59–60). These pollen types have exines that are more conspicuously sculptured than the exines observed in a number of monosulcate taxa (Figs 33–34, 55). The pollen wall of both types, however, are comparable to

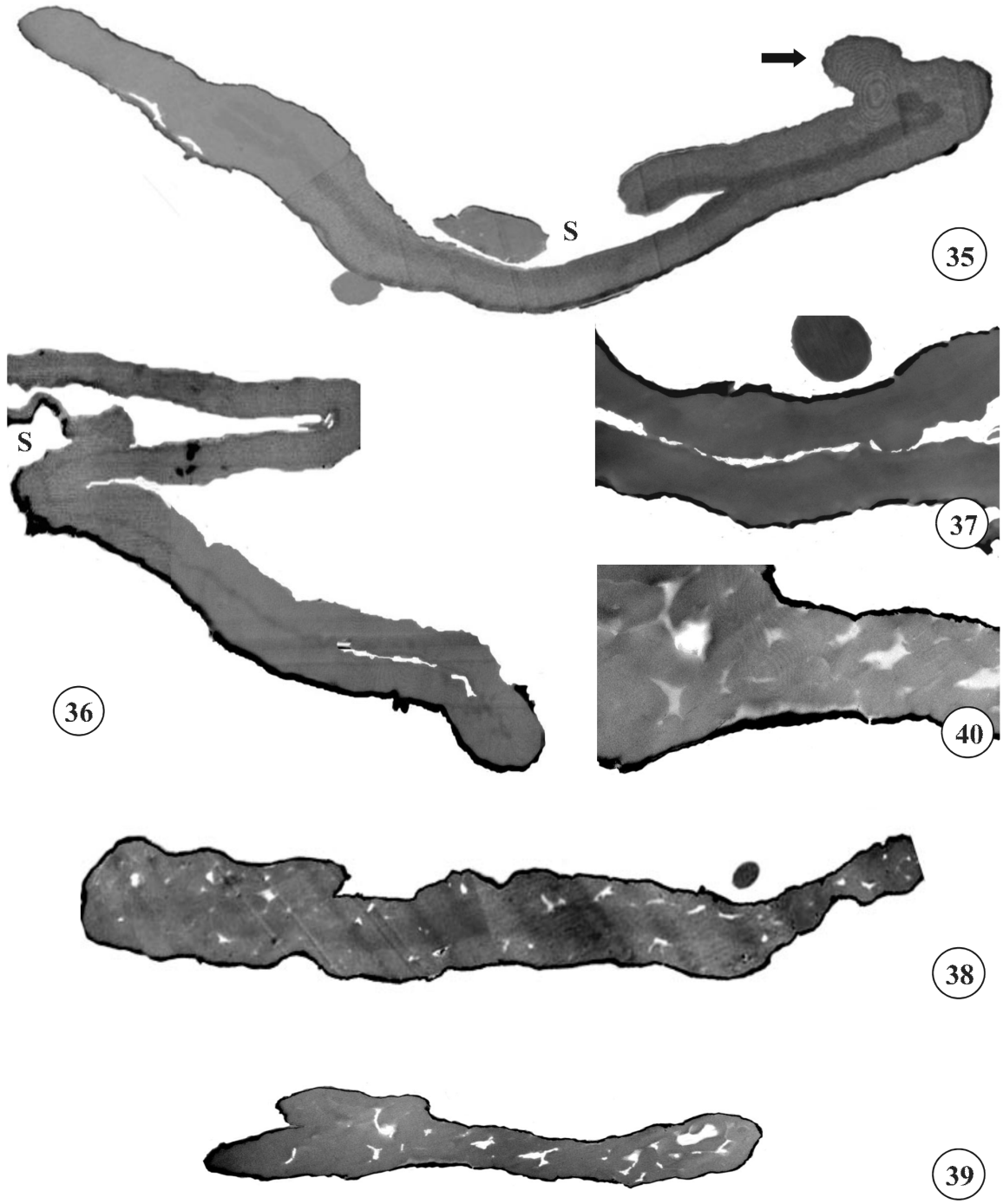
however, the pollen grain and the wall appear to less compressed, and more representative of the wall structure, the (S) indicates the sulcus region seen in the SEM of the same grain illustrated in Fig. 11, ×3400; **19**, TEM of the whole grain illustrated in Figs 9 and 10 showing the thin, homogenous wall structure adjacent to the aperture (S) that is occasionally interrupted by small lacunae; the portion of the pollen wall adjacent to the aperture grades into a marginal portion that is characterized by irregular, cylindrical elements that comprise a wall that is thicker and more elaborated than the wall adjacent to the aperture (*cf.* protosaccate), ×2800; **20**, high-magnification TEM of the same grain in Figs 11, 12 and 18 showing the lacunate (arrow) wall structure adjacent to the apertural region, ×15000; **21**, high-magnification TEM of the same grain in Figs 11, 12, 18 and 20 showing the irregularly shaped cylindrical infrastructural elements that comprise wall structure of the periphery of the pollen grain, ×11000; **22**, high-magnification of the peripheral pollen wall of the same grain in Figs 9, 10 and 19 showing the irregularly shaped cylindrical elements; this structure is similar to a protosaccus, ×4300. **23**, high magnification of the pollen wall in the vicinity of the apertural region of the same grain in Figs 9, 10, 19 and 22 showing the homogeneous wall structure, ×11200.



Figures 24–34. SEM of pollen from the Triassic locality Little Switzerland, Molteno Formation, South Africa. **24–28**: *Monosulcites* type; **24**, ×2700; **25**, ×2300; **26**, ×2000; **27**, ×1200; **28**, ×2700. **29**: *Pityosporites* type, ×1600. **30–32**: *Bennettiteaepollenites* type; **30**, distal view, ×1500; **31**, side view of the same grain in Fig. 30, ×1500; **32**, proximal view of the same grain in Figs 30 and 31, ×1500. **33–34**: *Inaperturopollenites* type; **33**, ×1,500; **34**, flip side of the same grain in Fig. 33, ×1500.

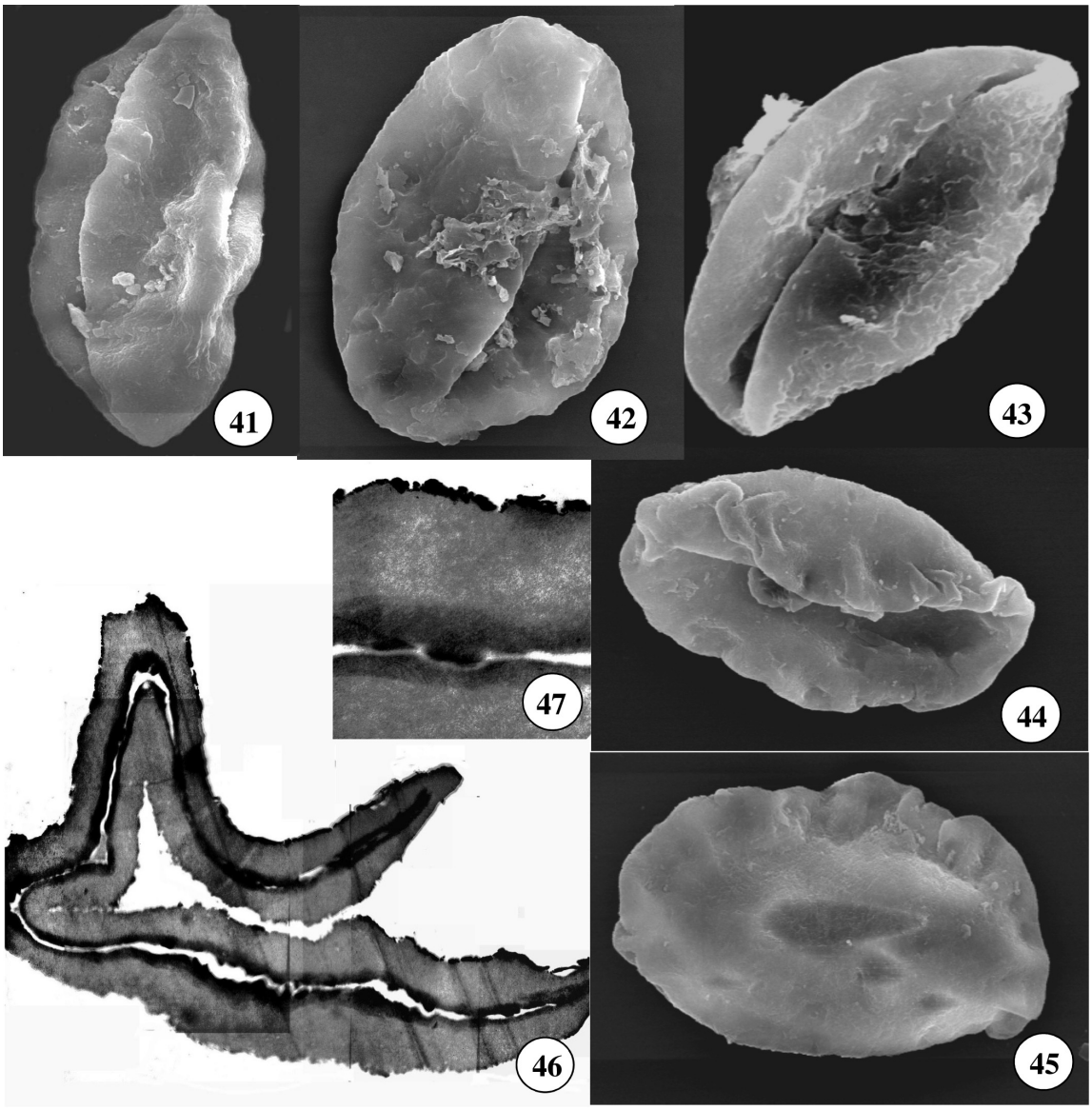
the pollen wall structure in monosulcate, non-saccate pollen types, i.e. the outer exine is homogeneous (Fig. 37) to lacunate (Figs 59–60) and is underlain by a homogeneous to lamellated basal layer. The type of sculpturing and wall structure fall within the range observed in the monosulcate non-saccate pollen types.

A majority of the monosulcate (and inaperturate) pollen types of the Upper Palaeozoic and the Triassic and Jurassic,



Figures 35–40. TEM of pollen from the Triassic locality Little Switzerland, Molteno Formation, South Africa. **35–36**: *Bennettiteaepollenites* type; **35**, TEM of the whole grain illustrated in Figs 30, 31 and 32 showing homogeneous wall structure and thin basal layer; note that the fold adjacent to the aperture in Fig. 30 which appears to be a vestigial saccus is actually a random fold of the exine due to post-depositional compression (arrow); the (S) indicates the apertural region, ×3300; **36**, TEM of the same grain in Fig. 26 showing homogeneous wall structure and thin basal layer, the (S) indicates the apertural region, ×12 800. **37**: *Inaperturopollenites* type; TEM of the pollen wall of the same grain in Figs 33 and 34 showing the homogeneous wall structure, and thin basal layer, ×12 500. **38–40**: *Pityosporites* type; **38**, TEM of the whole grain in equatorial region of the same grain in Fig. 29 showing the scattered lacunae in the wall, × 4000; **39**, TEM of the same grain in Figs 29 and 38 near the periphery of the grain showing the more open lacunate infrastructure; compare with pollen from the Permian in Figs 7, 8 and 17, and 11, 12 and 18, ×4000; **40**, high-magnification TEM of the pollen wall in the same grain in Figs 29, 38 and 39 showing the irregular, robust cylindrical elements which comprise the infrastructure, ×12 500.

although possessing an aperture type similar to primitive angiosperms, exhibits a narrow range in morphological diversity with regard to sculpturing and pollen wall structure, features that provide little insight into the relationships of pre-Cretaceous plant groups to the angiosperms. Among the morphological monotony of the Triassic and Jurassic monosulcate pollen are monosulcate pollen types that have a wall structure that is more similar to the pollen wall structure observed in angiosperm pollen, i.e. the pollen wall has a well-developed tectum, and an infrastructural layer composed of columella-like structures that are fused to a distinctive basal layer (e.g. Fig. 57). In addition, Cornet (1989), and Cornet & Habib (1992) have reported dispersed pollen from the Triassic of North America, and the Jurassic of France with reticulate exine sculpturing, a feature found only in angiosperms. These



Figures 41–47. SEM and TEM of pollen from the Lower Cretaceous locality Dunbrodie, Kirkwood Formation. **41–43**: *Monosulcites* type; **41**, SEM , ×1000; **42**, SEM, ×1500; **43**, SEM, ×2500. **44–45**: *Pityosporites* type; **44**, SEM, ×1500; **45**, SEM of the same grain in Fig. 44, note the marginal fringe that appears to be a vestigial saccus, ×1500. **46–47**: *Monosulcites* type; **46**, TEM of the whole grain in Fig. 42 showing thick homogeneous wall and thin basal layer; note the similarity of this wall structure type to that of the pollen in Figs 3, 4, 13, 14, and 30, 31, 32, 35, and 26, 36, ×3300; **47**, high-magnification TEM of the same grain in Figs 46 and 47 showing the homogeneous wall structure and differentially staining basal layer, ×13 300.

pollen types occur in low frequency, but may represent the occurrence of pre-Cretaceous angiosperms or an angiosperm stem group (also see Doyle & Hotton 1991; Doyle & Donoghue 1993; Dilcher 2001a,b).

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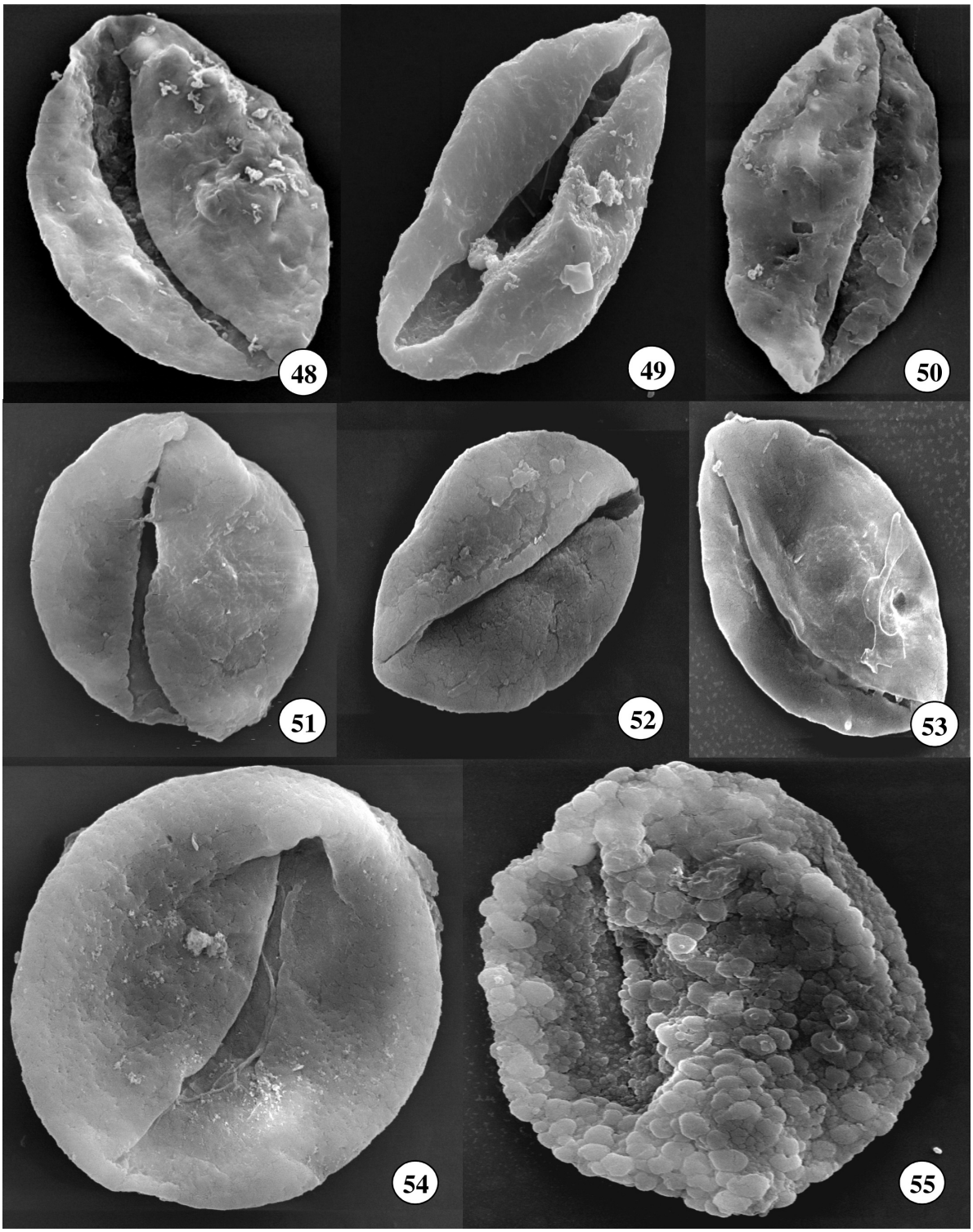
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Figures 48–55. SEM of pollen from the Triassic (Norian) of Sichuan, China, Xujiahe Formation. **48–50**: *Monosulcites* type, **48**, ×2000; **49,** ×2000; **50**, ×1800. **51–55**: SEM of pollen from the undifferentiated Jurassic of Afghanistan; **51–54**: *Monosulcites* type; **51**, ×2500; **52**, ×2200; **53**, ×2600; **54**, ×3500. **55**: *Inaperturopollenites* type, SEM of pollen from the Triassic (Norian) of Sichuan, China, Xujiahe Formation, ×2100.

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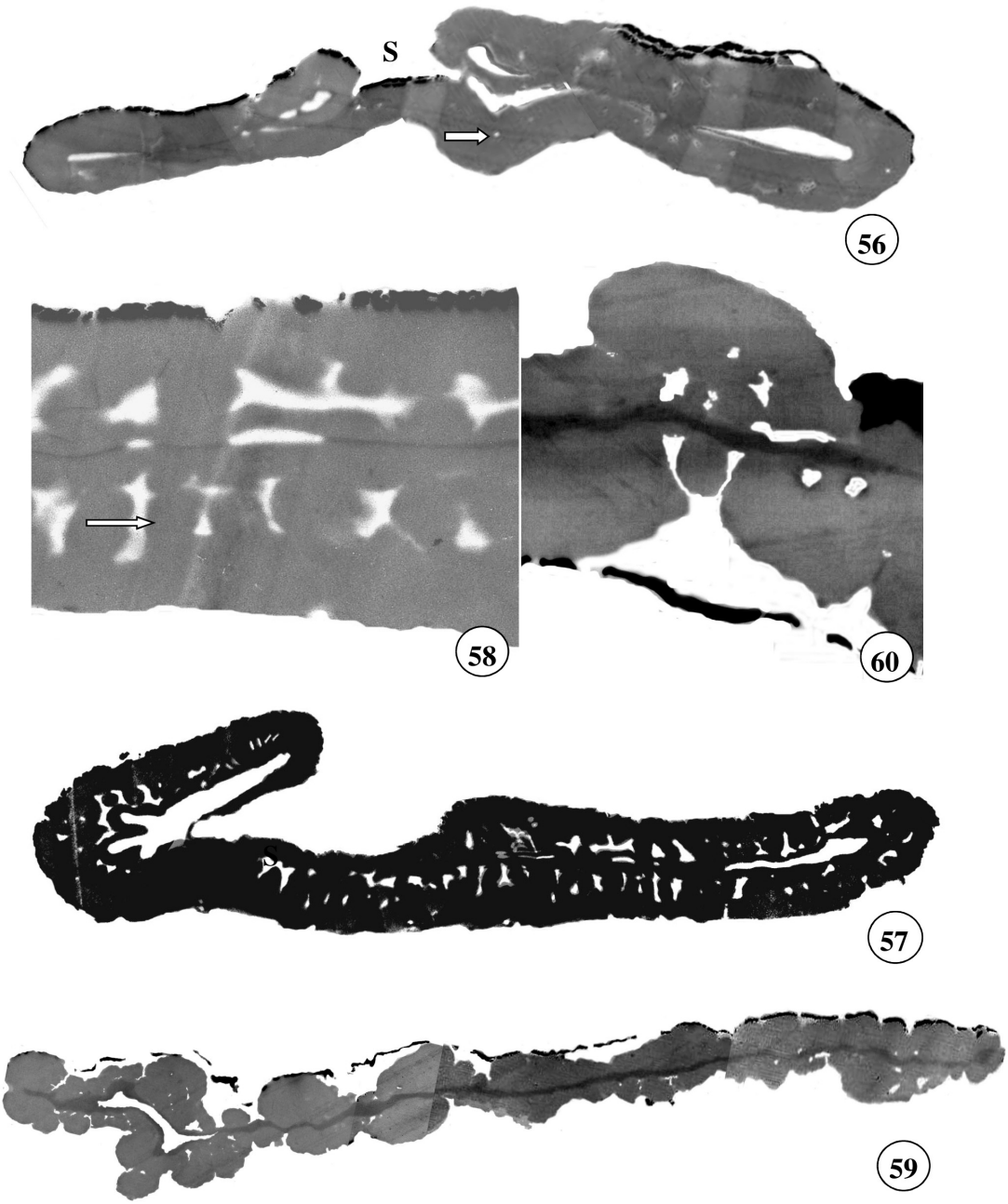
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Figures 56–60. TEM of pollen from the undifferentiated Jurassic of Afghanistan. **56–58**: *Monosulcites* type; **56**, TEM of the whole grain illustrated in Fig. 51 showing the homogeneous wall structure with the occasional lacuna (arrow), and the thin basal layer, (S) indicates the apertural area; compare the wall structure of this taxon with the wall structure of pollen recovered from Africa in Figs 3, 4, 13, 14, and 30, 31, 32, 35, and 26, 36, ×5000; **57**, TEM of the whole grain illustrated in Fig. 54 showing the columellate-like elements of the infrastructure, the imperforate tectum and the thin basal layer; the (S) indicates the apertural area, ×6800; **58**, high-magnification TEM of the pollen wall of the same grain in Figs 54 and 57 showing the columellate-like structures (arrow) that are not fused to the thin basal layer; note that the tectum is imperforate, ×16 000. **59–60**: TEM of pollen from the Triassic (Norian) of Sichuan, China, Xujiahe Formation; **59**, TEM of the whole grain illustrated in Fig. 55 showing rugulate sculpturing, occasionally lacunate wall and thin basal layer, ×4500; **60**, high-magnification TEM of the non-apertural wall of the same grain in Figs 55 and 59 showing the rugulate sculpturing, the thin basal layer and the infrastructural lacunae, ×17 500.

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