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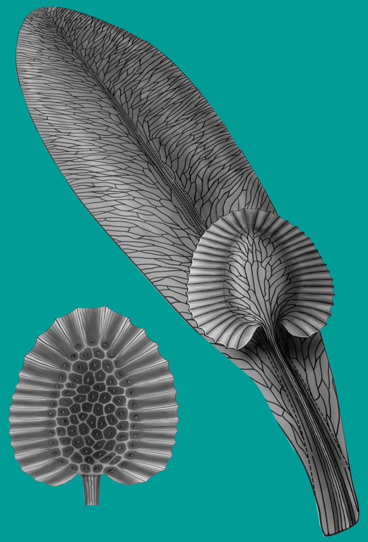

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A structural re-interpretation and revision of the type material of the glossopterid ovuliferous fructification *Scutum* from South Africa

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The Early Permian glossopterid fructification *Scutum,* described by Edna Plumstead in the 1950s from the Vereeniging locality in the Karoo Basin of South Africa, was one of the first glossopterid seed-bearing organs to be found in organic attachment to *Glossopteris* leaves. Examination of the type material necessitated a revision of this plant fossil genus and a re-evaluation of described South African species. Key characteristics of the genus are the broad and prominent wing, and a low receptacle length to width ratio (<2:1). Specimens of South African *Scutum* are currently attributed to three species, from two localities, but display intergrading morphological features that can be reasonably accommodated within a single species, *S. leslii.* Three-dimensional interpretation and reconstruction of impression fossils of *Scutum* fructifications preserved in attachment to *Glossopteris* leaves confirms that the seed-bearing surface of the receptacle faces the adaxial surface of the subtending leaf. The nature of the seed scars on the receptacle and their relationship to the peripheral wing of the fructifications is clarified.

Keywords: *Scutum, Glossopteris,* Permian, South Africa, Karoo Basin, fructification.

INTRODUCTION

Scutum was the first ovuliferous fructification to be described in organic attachment to the prolific Gondwanan taxon *Glossopteris,* over 120 years after these leaves were formally described by Brongniart (1828), albeit that Zeiller (1902) had not recognized the attachment of an *Ottokaria* fructification that he illustrated. Plumstead's (1952, 1956, 1958) series of papers describing a range of glossopterid fertile organs from the Vereeniging locality in South Africa were a significant advance in the study of this widespread group of plants, and in the 60 years since, over 30 genera of glossopterid fertile organs have come to the fore (e.g. see reviews by Anderson & Anderson 1985; McLoughlin 1990b, 1993; Pant 1977; Rigby 1978; Surange & Chandra 1975). Most of these additions to the literature have been based on compression and impression fossils, and reconstructions of these fertile structures have been heavily influenced by the ways in which the authors have interpreted the physical properties of the fossils themselves.

Plumstead's original interpretations of the Vereeniging fructifications as bivalved and bisexual organs were examined at length by Prevec *et al.* (2008), and they concluded that misinterpretation of the nature of impression fossils played a key role in the development of these hypotheses. Plumstead (1952, 1956, 1958) viewed the Vereeniging fossils as being positive representations of the original plant organs (i.e., essentially casts). She also supposed that the part and counterpart of each specimen represented distinct and separate structures that were formed by some mechanism of mineral replacement.

Keen to identify the glossopterids as angiosperm ancestors, Plumstead (1956) referred to *Scutum* as 'the first known bisexual flower of the Palaeozoic era which developed later into something resembling a modern compound fruit'. With allusions to stamens, stigmas and petals, she invoked images of a highly coloured, compound flower-like organ that enclosed the seeds within a purse-like structure. The envisioned 'purse' comprised a veined, bract-like, 'empty half' and a seed-bearing 'fertile half' that were purportedly fused together early in the development of the fructification, opening briefly to allow for pollination of the ovules in the 'female half', and dispersal of pollen from the 'male half' (Plumstead 1952, 1956, 1958). Although most of these ideas on the bisexual aspects of the glossopterids were based on *Bifariala* (*Hirsutum*) *intermittens, Scutum* also played a role. The long bract-like features attached to the receptacles of some specimens of *S. leslii* (Figs 40–43, 48, 51 this paper) were considered by Plumstead (1956, 1958) to represent pollen-bearing organs, equivalent to the purported hair-like structures she described in *Hirsutum.* As discussed by Prevec *et al.* (2008), these latter hair-like features were striations on the wing, and the bract-like features in *Scutum* are here interpreted as attached seeds with elongated wings. There is no evidence to suggest that any of the glossopterid fructifications were bisexual.

In fact, most of Plumstead's colourful ideas involving a bipartite structure have been rejected, particularly in light of evidence from permineralized fructifications that surfaced from Australia and Antarctica (e.g. Gould & Delevoryas 1977; Nishida *et al.* 2007; Pigg & Trivett 1994; Schopf 1976; Taylor & Taylor 1992). Transverse sections through these structures clearly demonstrated a simple dorsiventrally-flattened, leaf-like organ bearing seeds on one surface, and with a seed-less peripheral flange that may arch over the seed-bearing surface. These features are also apparent when viewing the Vereeniging impression fossils as compressed three-dimensional moulds, as opposed to interpreting the part and counterpart of the exposed fossil as casts or literal/positive views of the original

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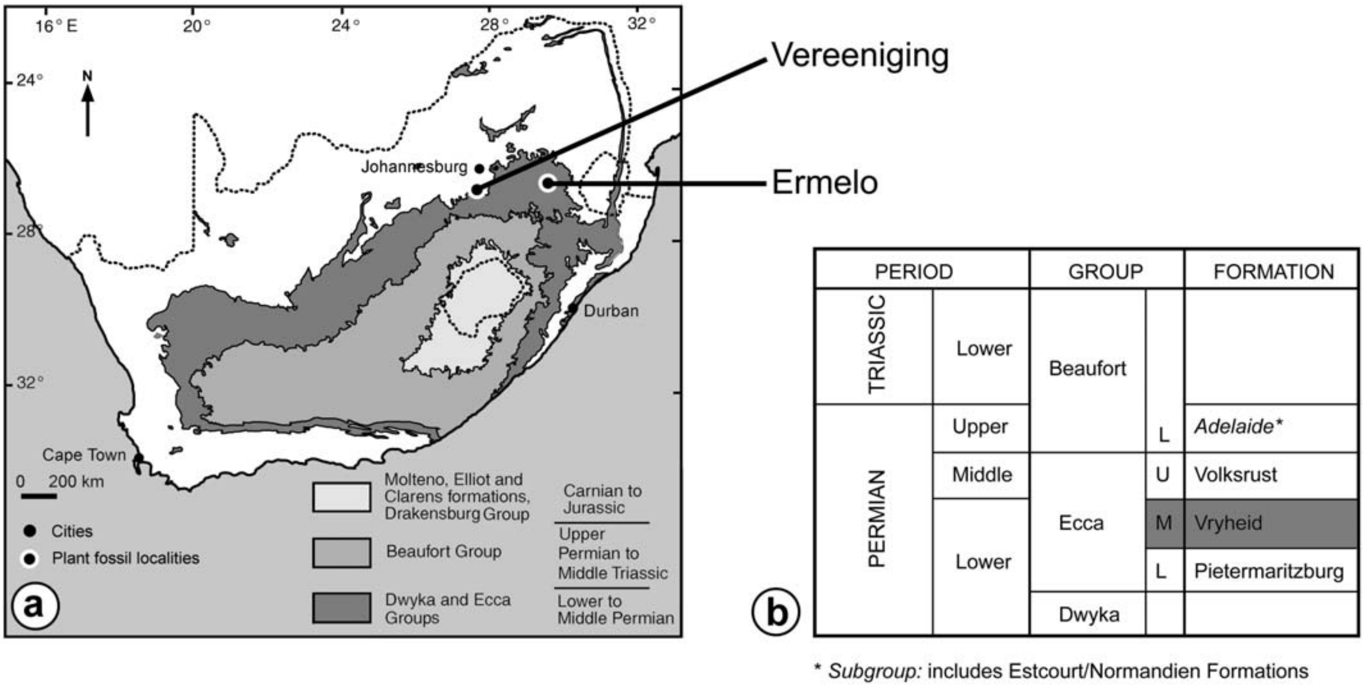


Figure 1. **a**, Locality map indicating reported occurrences of *Scutum* within deposits of the main Karoo Basin in South Africa; **b**, lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded area representing the stratigraphic distribution of *Scutum leslii* (table adapted from Keyser 1997).

plant surface. These concepts are explored further in a later section dedicated to the interpretation of the impression fossils of *Scutum* from Vereeniging that form the basis of this paper.

Plumstead (1952) initially recognized five species of *Scutum* from the Vereeniging locality, on the basis of fructification morphology and perceived differences in the attached leaves, which she assigned to various existing species of *Glossopteris* from other parts of Gondwana. Later Plumstead (1958) transferred some of these species to *Hirsutum,* eventually settling on six species of *Scutum* in the Vereeniging material, viz. *S. leslium, S. rubidgeum, S. stowanum, S. sewardii, S. thomasii* and *S. damudica.* Plumstead (1958) also proposed several varieties of *S. rubidgeum* and *S. leslium,* but these have never gained acceptance. Anderson & Anderson (1985) revised the genus, acknowledging its dorsiventral, unipartite structure, and retained two of Plumstead's (1952) species, *S. rubidgeum* and *S. draperium,* curiously excluding the type species which they synonymized with *S. rubidgeum.* Plumstead's (1956, 1958) species *S. stowanum* and *S. sewardii* were synonymized with *S. rubidgeum,* and *S. damudica* and *S. thomasii* were subsumed into *S. draperium.* Although not formally acknowledged in their synonymy lists, Anderson & Anderson (1985, pl. 74, fig. 5) figured a specimen of Plumstead's (1958) taxon *Pluma longicaulis* under '*Scutum* sp.', acknowledging that this species represents laterally compressed *Scutum* fructifications. Anderson & Anderson (1985) also created an additional species *S. ermeloense* to accommodate new specimens from the Ermelo locality.

A review of the type material has necessitated moderate revision of the diagnosis of *Scutum* proposed by Anderson & Anderson (1985), and a reassessment of the South African species.

MATERIALS AND METHODS

All 78 specimens of *Scutum* that were examined are housed in the palaeobotanical herbarium at the Bernard Price Institute (BPI), University of the Witwatersrand, Johannesburg and the Vaal Teknorama Museum (VM) in Vereeniging [Ermelo locality: 4 specimens, housed at the BPI; Vereeniging locality: 56 from the BPI, 18 from the VM]. For a complete list of all specimens examined and described see Appendix I in Adendorff (2005). Specimens from the BPI are identified by numbers with the prefix 'BP/2' and from the VM by the prefix 'VM/03/3205'.

No fossil preparation was required. Specimens were photographed under strong unilateral light with a Sony Cybershot digital camera. Measurements were made with Zeiss Axiovision 2.5 image-analysis software. Simple scatter plots were constructed in Microsoft Excel. Illustrations of *Scutum* were drawn in pen and ink on Bristol board, with the aid of a *camera lucida* microscope attachment. Other figures and plates were compiled using Adobe Illustrator and Adobe Photoshop. The reconstruction in Fig. 55 is modified and presented here with permission from the online magazine *Science in Africa* (Prevec 2006).

GEOLOGICAL SETTING

Specimens originated from the Leeukuil quarries at Vereeniging, and a fossil plant locality at Ermelo. Both localities are situated in the northern Karoo Basin (Fig. 1a) The deposits are attributed to the Vryheid Formation, middle Ecca Group and are of Early Permian (Artinskian) age (Fig. 1b).

The Vereeniging locality has yielded the most diverse array of capitate glossopterid ovuliferous fructifications in South Africa, and probably in the world, many of them preserved in attachment to subtending glossopterid leaves (Anderson & Anderson 1985; Plumstead 1952, 1956,

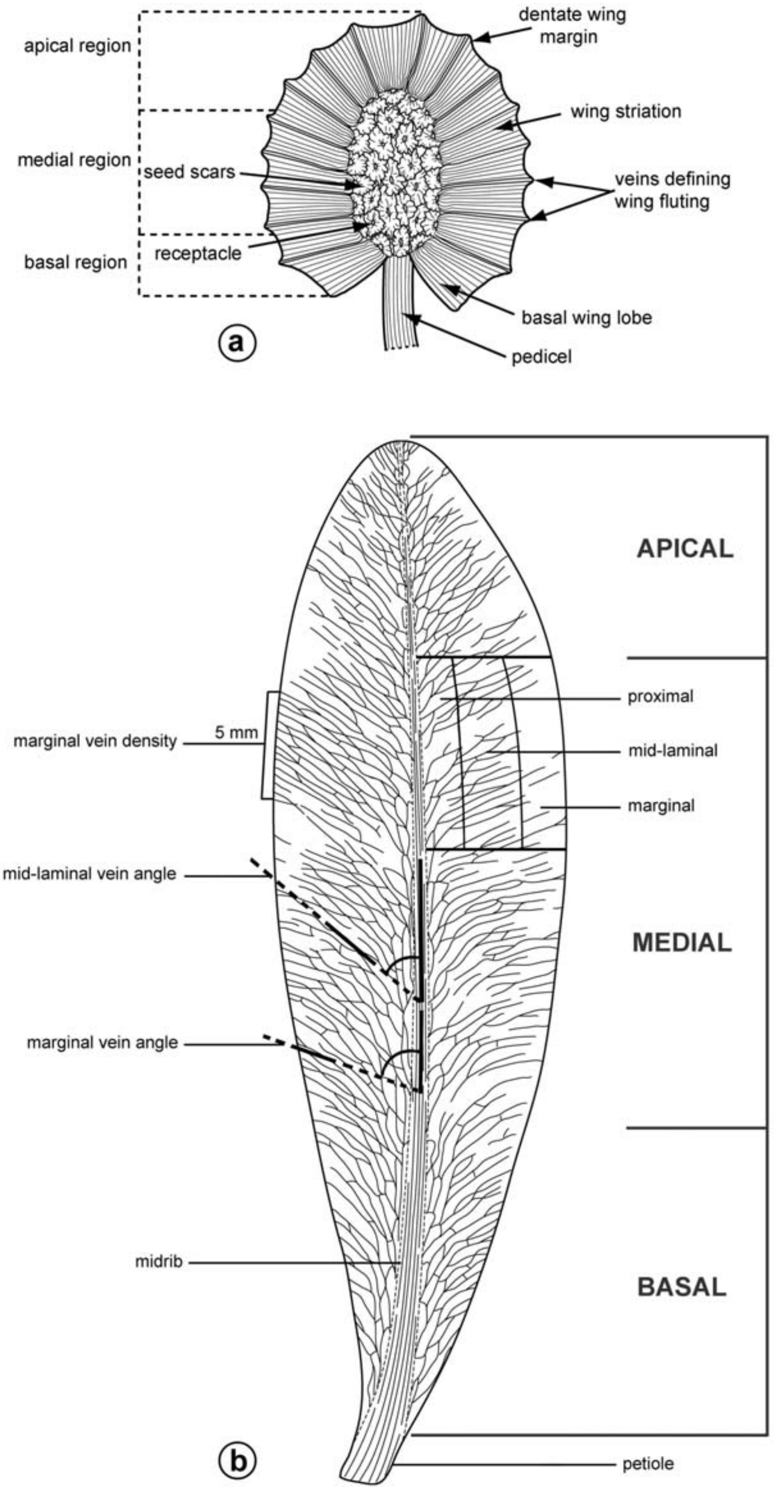


Figure 2. Diagrams indicating the basic morphological features used in the measurement and description of (**a**) *Scutum* fructifications and (**b**) attached *Glossopteris* leaves.

1958). For more detailed information on the Vereeniging locality and its fossil floras, please refer to Adendorff (2005), Adendorff *et al.* (2002, 2003), Anderson & Anderson (1985), Le Roux & Anderson (1977) and Prevec *et al.* (2008).

Anderson & Anderson (1985) made a single collection from the Ermelo locality in 1974, and did not provide the exact location of this site. The town of Ermelo is situated in the Mpumalanga Province (Fig. 1). All fossils collected were impressions in hard, buff to medium grey siltstone with orangey, light brown and pale off-white oxide staining. Bedding planes were fairly irregular and of variable thickness, and the matrix was poorly fissile. In addition to *Scutum,* the flora recovered included several species of *Glossopteris* leaf together with *Noeggerathiopsis,* the lycopod *Cyclodendron leslii,* and various seeds and scale leaves.

TERMINOLOGY AND REVISED INTERPRETATION OF *SCUTUM* BASED ON IMPRESSION FOSSILS

Terminology

Figure 2 illustrates the features used here to describe (a) *Scutum* ovuliferous fructifications and (b) their subtending *Glossopteris* leaves. The fructifications have three primary features: (1) a dorsiventrally flattened central receptacle with seed-scars on one surface and reticulate venation on the other, (2) a peripheral wing, and (3) a pedicel. In impression fossils, the seed scars on the surface of the receptacle are in most cases raised cushions, with a central depression or tubercle. The wing is divided into finely striated segments, defined by veins running from the edge of the receptacle to the wing margin. In impressions, the wing surface arches/curves slightly between consecutive veins, creating shallow flutes in the wing.

How these features are translated into a reconstruction of the original fertile organ depends heavily on how the impression fossils are interpreted.

The interpretation of impression fossils

Many of the conflicting viewpoints about the morphology of glossopterid fructifications have arisen from ambiguities regarding fossil preservation. The wide variety of preservation types encountered, in addition to the presence of artefacts such as thick mineralized crusts and distortion, can result in similar plant structures having a very different appearance in the fossil form. Confusion regarding the nature of impression fossils in particular, continues to foster disagreement regarding the three-dimensional structure of glossopterid fructifications (e.g. Ryberg 2009).

To re-iterate the principles outlined in previous works (Adendorff 2005; McLoughlin 1990b; Prevec *et al.* 2008; Rigby 1978; Schopf 1975), in its simplest form, an impression fossil can be described as one half of a complete three-dimensional mould of the original plant organ. By analogy, if a coin was pressed between two blocks of clay, the blocks separated and the coin removed, one would have a part and counterpart (the two blocks of clay), each showing a different side of the coin as a mould. It would not be a mould and cast of the same side of the coin – in this scenario there is no cast (contra Rex 1986). The same principle can be applied to plant fossils. The part and counterpart show impressions or moulds of the outside surfaces of the original plant. In the case of a dorsiventrally flattened structure preserved flush with the bedding plane, the two impressions on the part and counterpart will depict the upper and lower surface of the organ, respectively.

When the compressed, carbonized remains of the original plant are present, the situation may be more complex, with shearing of the carbon layer potentially occurring at different levels within the fossil. However, in the case of the Vereeniging material, no organic material is preserved. All that remains of the plant is the rock that surrounded it, and holds its shape. The carbonized compression weathered out, has left a cavity, representing a mould of the plant. When the matrix was cleaved to reveal the fossil, the mould was effectively split into two halves. In the case of the *Scutum* fructifications, the part held a mould of the seed-bearing surface, and the counterpart a mould of the opposing, veined surface. Only the external features of the plant are visible, the fossil preserving only those features that came into direct contact with the embedding matrix, with all details of internal structures having been lost.

This is not to say that all impression fossils are this clean, clear and simple. In any collection of specimens, even among individuals on the same slab, the quality of preservation may not be consistent. Additionally, artefacts of preservation can result in 'echos' or secondary impressions of features on the part, being present on the counterpart. This was discussed by Chaloner (1999, ch. 8, p. 37, fig. 8.1), who recognized that plant material undergoes a higher degree of compression than the surrounding matrix, leading to the differential compression of fleshy and less fleshy parts of the plant during fossilization.

Morphological interpretation of *Scutum* impressions

Although the basic structure of *Scutum* as last revised by Anderson & Anderson (1985) remains unchanged here, some refinements are required in light of the interpretation of the fossils as moulds rather than casts.

It has been well established, through the detailed examination of both permineralized glossopterid fructifications and impression fossils from across Gondwana, that dictyopteridioid fructifications are dorsiventrally flattened organs with a seed-bearing surface and a veined surface, and with a peripheral wing of variable morphology (e.g. Adendorff *et al.* 2002; Anderson & Anderson 1985; McLoughlin 1990a,b, 1995; Pant 1977; Pant & Nautiyal 1984; Prevec *et al.* 2008; Schopf 1976). There is no evidence for the presence of an additional, sterile bract such as that recognized by Plumstead (1952, 1956, 1958), Banerjee (1984), Surange & Chandra (1977) in the type material of *Scutum*, or any other glossopterid fructification from South Africa. Such a feature would be easily recognizable when observing the two superposed moulds of the fructification and subtending leaf of any impression fossil of a fertiliger.

Anderson & Anderson (1985) interpreted the raised mounds on the receptacle surface as casts of ovules, each with a small circular micropyle. This was in line with Plumstead's (1956) earlier assessment, and was an interpretation supported by several workers in the field (Surange & Maheshwari 1970; Surange & Chandra 1974; Rigby 1978). However, as some other authors have pointed out (T.M. Harris, p. 322 in Plumstead, 1952; N. Hughes, p. 224 in Plumstead 1956; McLoughlin 1990a,b; Schopf 1976), these ovoid to circular (or even square/rectangular along the margin of the receptacle) features are more accurately described as moulds of depressions in the living/dehisced plant organ where each seed base was seated, the central pit or tubercle being the point of vascular attachment of the seed prior to being shed.

Anderson & Anderson (1985) described the wing in their diagnosis as a 'fused outer ring of modified ovules'. Since the raised features on the receptacle are here seen as seed scars, rather than ovules, this derivation of the wing structure cannot apply. Here the wing is considered to be effectively a sterile thin extension of the receptacle, although it may have originated through the fusion of adjacent ovuliferous scales, such as those seen in the most basal glossopterid fructifications belonging to the genus *Arberia*

(Adendorff 2005). Each wing segment is associated with a single seed scar on the margin of the receptacle. The wing is finely striated, the striations extending from the cicatrix of the associated seed-attachment cushion to the distal margin of the wing. In all impressions of *Scutum* that were observed, the wing was either flattened in the same plane as the receptacle or, in impressions of the seed-bearing surface it arched deeper into the matrix (e.g. Figs 6, 7, 21, 22, 25, 30, 34, 36) and conversely in impressions of the sterile surface, the receptacle lay deeper in the matrix than the wing margin (e.g. Figs 12, 18, 31–33). This means that in the original plant, the wing would have been inclined or slightly arched towards the seed-bearing surface of the fructification. In other dictyopteridioid fructifications, such wings may fold over and protect the seeds during early development (Gould & Delevoryas 1977).

Anderson & Anderson (1985) were unsure about the nature of the 'scale-like appendages' attached to *S. leslii,* that were initially described by Plumstead (1956, 1958) as pollen-producing organs. They did not consider the possibility that they were winged seeds, perhaps in light of their interpretation of the wing of the fructification as being a series of modified ovules. Here, these structures are considered to be the elongated wings of platyspermic seeds. Although detached seeds of this nature have never been found at the Vereeniging locality, isolated seeds similar to these have been found in India. Surange & Maheshwari (1970) reported several 'ovule-bearing scales' that resemble the structures found attached to *Scutum leslii* fructifications. Surange & Chandra (1974) described further examples of seeds with an elongated wing at the micropylar end of an ovate sclerotesta. They assigned these seeds to *Indocarpus elongatus.*

An important aspect of the *Scutum* fertiligers that was not addressed in the diagnosis of Anderson & Anderson (1985) was whether the seed-bearing surface of the fructification faced towards or away from the subtending *Glossopteris* leaf.

In most assessments of the Vereeniging material (Plumstead 1952, 1956, 1958; Anderson *et al.* 2007), and in most reconstructions of the Dictyopteridiaceae in general (Lacey *et al.* 1975; Pant & Nautiyal 1984; Rigby 1978) the interpretation of impression fossils as casts has resulted in the assumption that the seed-bearing surface of the fructification faces away from the leaf. This misconception has been reinforced by extrapolations based on the interpretation of the anatomy of permineralized specimens from Antarctica (e.g. Taylor 1992; Taylor *et al.* 2009). To date a series of serial sections through a permineralized fertiliger has not been published, and all information on the anatomy of glossopterid fructifications has been derived from detached specimens. The only impression material cited by Taylor *et al.* (2009) in support of the arrangement whereby the fertile surface faces away from the leaf was originally published by Pant & Singh (1974). The specimens in question are impression/compression fossils of two fructifications axillary to *Glossopteris* leaves on an axis. Although this is a magnificent specimen, both fructifications are laterally compressed, and any inferences regarding the orientation of the seed-bearing surfaces remain highly speculative. Pant & Singh (1974, p. 60) made no such commitment, explaining that the fructifications had both been distorted during preservation. They were unsure whether the ovules were present or visible – they noted that the receptacles of both fructifications showed 'a number of small obscure marks of rounded or oval bodies over a shallow scale or cupule' and that the nature of the rounded marks could not be ascertained.

Schopf (1976), who was the first to examine the Antarctic permineralized material, presented a generalized reconstruction of a glossopterid capitulum with seed-bearing side facing the subtending leaf, as did Gould & Delevoryas (1977) and McLoughlin (1990b).

Through careful observation, and by recognizing that impression fossils of fertiligers are a series of superposed, flattened moulds, it is possible to demonstrate the orientation of the fructification relative to the leaf. In the model illustrated here (Fig. 3), the interpretation is made that the fertile surface faced the leaf. Exposure of the fructification and leaf along the same cleavage plane within the matrix (dotted line in Fig. 3b) resulted in the impression of the fertile surface of the fructification lying above the impression of the leaf (in the part, Fig. 3c). The impression of the sterile surface of the fructification (in the counterpart in Fig. 3c) lay at a more deeply impressed level within the sediment, than the impression of the *Glossopteris* leaf. The key to visualizing this model is to recognize that *the impression of the fructification is borne on the sediment that infiltrated between the leaf and fructification during burial.* If the seed-bearing surface of the fructification faced away from the leaf, then it would have been the impression of the opposing sterile surface that would have been imprinted on the clay that seeped between it and the leaf.

Examination of the *Scutum* fertiligers from Vereeniging (14 specimens) reveals that they all conform precisely to the interpreted pattern of impression fossil exposure. The impression of the fertile surface always lies above the impression of the subtending leaf (e.g. Figs 6, 11, 22, 25). Conversely, in the counterpart, the impression of the sterile surface lies beneath the impression of the leaf (Figs 5, 10, 12, 23, 24, 28). This pattern has also been observed consistently amongst other South African genera of the Dictyopteridiaceae found in attachment to glossopterid leaves, viz. *Dictyopteridium, Elatra* (*Hirsutum leslii*), *Plumsteadia* and *Gonophylloides* (Adendorff 2005). Where seeds are present, they lie within the wedge of sediment bearing the impression of the fertile surface that overlies the leaf impression.

Some impressions of *S. leslii* examined and figured here show hints of both veins and seed scars on the part and/or counterpart, possibly as a result of secondary impressions, or perhaps where prominent vascular traces were expressed on both surfaces of the fructification, as occurs in fructifications such as *Dictyopteridium flabellatum* (Adendorff 2005; Benecke 1976). For example, the syntype, BP/2/13732 (Figs 8 & 9) appears on first inspection to be an impression of the veined surface (as described by Plumstead, 1952). However, closer examination reveals seed

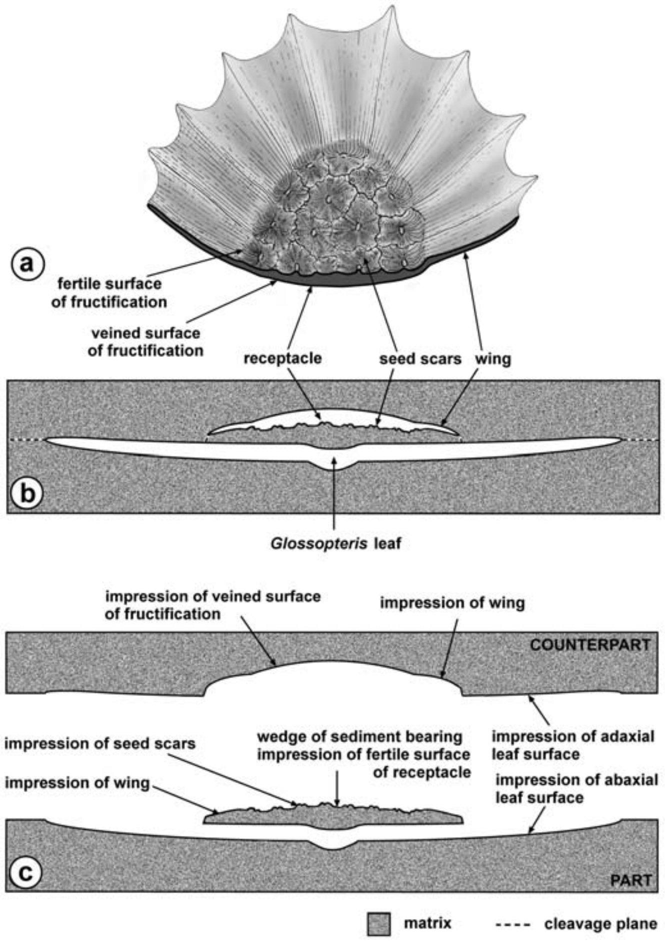


Figure 3. **a**, Reconstruction of the apical portion of a *Scutum leslii* fructification (based on BP/2/13735), showing depressed seed scars, raised cicatrices and fluted wing; transverse section illustrates smooth, veined surface and opposing fertile surface bearing depressed seed scars (raised in impressions); **b** and **c**, a hypothetical medio-lateral section through the impression fossil of a *Scutum* fructification attached to a *Glossopteris* leaf. In (b) the seed-bearing surface of the fructification is interpreted to have faced the attached *Glossopteris* leaf. Exposure of the entire fructification and part of the leaf would result from cleavage along the plane indicated by a dashed line. This would result in the part and counterpart illustrated in (c). In the part, there is a wedge of sediment bearing an impression of the fertile surface of the fructification and the peripheral wing, that overlies the impression of the leaf. The counterpart bears an impression of the sterile surface of the receptacle and continuous peripheral wing, and this impression lies at a deeper level in the matrix than the impression of the *Glossopteris* leaf.

scar impressions between the veins. The angle of the wing, dipping into the sediment supports the interpretation of this fossil as the seed-bearing surface of the fructification. It should be emphasized that within this large collection of specimens the majority showed clear features of either a seed-bearing or sterile surface.

STATISTICAL ANALYSIS

Basic scatter plots were constructed as a visual aid in assessing the relationships between specimens previously assigned to *S. draperium* and *S. leslii* (Plumstead 1952, 1956, 1958; Anderson & Anderson 1985), and those specimens from Ermelo, placed in *S. ermeloensis* by Anderson & Anderson (1985). Figures 56 and 57 demonstrate that *S. leslii* specimens form a distinct group with a high degree of continuous variation as far as the dimensions of the receptacle and wing are concerned. Specimens previously attributed to *S. draperium* and most specimens of *S. ermeloense* represent the upper size limits of the group, although one of the four *S. ermeloense* specimens falls well within the ranges occupied by *S. leslii.* Plots of wing width versus receptacle width (Fig. 57) indicate that the wing width is remarkably constant, irrespective of the overall size of the fructification.

SYSTEMATIC PALAEOBOTANY

Order Glossopteridales *sensu* Pant, 1982
Family Dictyopteridiaceae Surange & Chandra, 1975 ex Rigby, 1978 emend. Maheshwari, 1990

Genus *Scutum* Plumstead, 1952 emend.

Type species

Scutum leslii (Plumstead 1952) nom. Corr. by subsequent designation of Andrews (1970); Vryheid Formation, middle Ecca Group; Early Permian; Vereeniging, northern Karoo Basin, South Africa.

Remark

Scutum leslii was the first species of this genus to be described in Plumstead's (1952) publication. '*Scutum leslii*' is considered here to have priority over *S. rubidgeum* as type species contrary to Anderson & Anderson (1985), who considered these species to be synonyms and who retained only the latter name. The type species was originally called '*S. leslium*' by Plumstead (1952), but was later corrected to '*S. leslii*' (Andrews 1970), which according to Prof. H.J. Lam (Discussion, p. 226 in Plumstead 1956) is the appropriate genitive of the Latinized name for 'Leslie'.

Etymology

Latin: *scutum* – shield; referring to the shape of the fructification.

Generic diagnosis

Solitary, pedicellate, isobilateral, dorsiventrally flattened fructification borne proximally on midrib or petiole of otherwise unmodified glossopterid leaf. Multi-ovulate receptacle bifacial, with fertile surface bearing numerous seed scars facing subtending leaf; veined surface laminar with spreading, reticulate venation. Receptacle circular, elliptical, obovate or ovate to broadly lanceolate, with receptacle length:width <2:1. Receptacle flanked by broad, prominent wing, continuous and of regular diameter, except at point of pedicel insertion where it is sharply constricted to form a rounded or laterally truncated lobe to either side of slender, longitudinally striated pedicel. Wing with fine radial striations and fluting perpendicular to margin of receptacle and extending from receptacle to wing margin. Margin dentate, undulating, scalloped or entire. Wing fluting corresponds to venation on sterile surface of the receptacle, and to positions of marginal seed scars, which are square and form a distinctive rank along periphery of receptacle. Central seed scars tend to be oriented longitudinally to receptacle. Scars are raised cushions (in impressions), each with a central depression bearing a tubercle that represents a seed detachment scar.

Remarks

This emended diagnosis differs from that of Anderson & Anderson (1985) in that the numerous 'ovules' each with a 'small circular micropyle exposed at centre of free end' on the fertile surface of the receptacle, are re-interpreted as impressions of depressed seed scars, each with a central cicatrix, the mature seeds having been dispersed prior to preservation of the fructification. Anderson & Anderson (1985) described the wing as comprising a 'fused outer ring of modified ovules'. Here, the wing is interpreted as a peripheral extension of the edge of the receptacle, continuous with the sterile surface. Veins extend from the edge of the receptacle into the wing where they form radial ridges or grooves between the wing flutes. On the fertile surface, the fine wing striations originate at the cicatrix of each marginal seed scar.

Details of attached seed and leaf morphology have been omitted from the generic diagnosis to extend the reach of this genus. The key features of *Scutum* that distinguish it from closely affiliated genera such as *Plumsteadia* and *Dictyopteridium* are: (1) a prominent and broad wing of regular width except at pedicel insertion where it is contracted to form a rounded to truncate lobe on either side, and (2) a receptacle L:W of <2:1.

Scutum leslii Plumstead, 1952 emend. Anderson & Anderson, 1985

1952 *Scutum leslium* Plumstead, p. 286, pl. 43, figs 1, 2; pl. 44, figs 1–4; text-figs 1a,b.
1952 *Scutum rubidgeum* Plumstead, p. 295, pl. 46, figs 1–4; pl. 47, figs 1–3; text-fig. 3.
1952 *Scutum draperium* Plumstead, p. 298; pl. 48, figs 1–4; text-fig. 4.
1956 *Scutum leslium* Plumstead; Plumstead, p. 6, pl. 1, fig. 1; pl. 2, figs 1, 2; pl. 3, figs 1–5;pl. 4, fig. 1; pl. 10, figs 1, 2. [1956a].
1956 *Scutum draperium* Plumstead; Plumstead, p. 9, pl. 8, figs 1–4. [1956a].
1956 *Scutum rubidgeum* Plumstead; Plumstead, p. 7, pl. 4, fig. 1; pl. 5, figs 1–3; pl. 9, figs 3, 4 [1956a].
1958 *Scutum stowanum* Plumstead, p. 55, pl. 7. [1958a].
1958 *Scutum rubidgeum* var. *vaalense* Plumstead, p. 55, pl. 8, figs 1, 1a;pl. 9, figs 1, 2. [1958a].
1958 *Scutum leslium* var. *cornelium* Plumstead, p. 57, pl. 10, figs 1–5a. [1958a].
1958 *Scutum damudica* Plumstead, p. 57, pl. 11. [1958a].
1958 *Scutum sewardii* Plumstead, pars. p. 59, pl. 13, fig. 2; non. figs 1, 1a. [1958a].
1958 *Pluma longicaulis* Plumstead, p. 68, pl. 22; pl. 23, figs 1, 2. [1958a].
1963 *Scutum*; Plumstead, p. 150; pl. B, fig. 2.
1969 *Scutum rubidgeum* Plumstead; Plumstead, pl. 12, fig. 4.
1969 *Scutum leslium* Plumstead; Plumstead, pl. 12, fig. 4; text-fig. 3.
1973 *Scutum rubidgeum* Plumstead, pl. 3, figs 3, 9.
1985 *Scutum rubidgeum* Plumstead; Anderson & Anderson, p. 116, pl. 67, figs 1–21;pl. 68, figs 1–13; pl. 95, fig. 5; text-figs 115.1, 115.2, 115.5, 115.6, 116.1, 116.2, 116.4.
1985 *Scutum draperium* Plumstead; Anderson & Anderson, p. 117; pl. 71, figs 1–6; pl. 72, figs 1–2; pl. 95, fig. 6; text-figs. 117.1, 117.2.
1985 *Scutum* spp.; Anderson & Anderson, pl. 74, figs 1–5.
1985 *Scutum ermeloense* Anderson & Anderson; p. 117; pl. 73, figs 7–12; pl. 95, fig. 7;text-figs 115.8, 117.4
1997 *Scutum rubidgeum* Plumstead; Anderson & Anderson, p. 15, fig. 4a,b,d.
2007 *Scutum rubidgeum* Plumstead, Anderson & Anderson, p. 24, fig. 10; p. 162, figs 3, 4.

Holotype

In her original description of the species *Scutum leslii,* Plumstead (1952) assigned two type specimens, L.I.1 & L.I.4. These syntypes were subsequently re-registered as BP/2/13732 (Figs 8 & 9) and BP/2/13751 (Figs 6 & 45), and are housed at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Both are impression fossils of fertiligers. The latter specimen, BP/2/13751, is recognized here as the holotype.

Type formation and locality

Vryheid Formation (middle Ecca Group); Lower Permian (late Sakmarian to late Artinskian); Vereeniging and Ermelo, northern Karoo Basin.

Etymology

Epithet '*leslii*' – after Thomas Nicolas Leslie (1858–1942), a fossil enthusiast and avid collector of plant fossils at the Vereeniging locality.

Species diagnosis

(Adapted from Anderson & Anderson 1985)

Circular, elliptical, ovate, obovate to broadly lanceolate receptacle, with a L:W of 1.1–2.1; wing broad, most commonly dentate, with prominent and persistent striations and fluting. Seeds of the *Indocarpus* type, with a small, elliptical sclerotesta, flanked distally by an elongated, elliptical to falcate, apically pointed, striated wing. Attached in basal portion of a narrowly elliptical, oblong to narrowly oblanceolate *Glossopteris* leaf, with a long, tapering base, moderately acute to obtusely pointed apex, and a well-defined, persistent midrib; may be petiolate, or base may expand slightly into small, inconspicuous, sagittate lobes; veins diverge from midrib at steep angle and gently arch across lamina; meshes elliptical to elongate polygonal near midrib, becoming linear in mid-laminal and marginal regions.

Description (Figs 4–54)

Isobilateral, dorsiventral, multi-ovulate glossopterid fructifications comprising a central, seed-bearing receptacle and a peripheral wing. Fructifications are pedicellate, and are attached to the midrib of an apparently unmodified *Glossopteris* leaf. Overall dimensions of the fructifications (excluding the pedicel) are 12.9 (24.6) 38.4 mm long (n = 58; s.d. 6.1) and 11 (21.9) 31.5 mm wide (n = 63; s.d. 4.2).

Receptacles are highly variable in shape, ranging from circular, elliptical, ovate, obovate to broadly lanceolate (see Fig. 54), and are 7.2 (17.5) 33.9 mm long (n = 62; s.d. 6.3) and 5.4 (11.2) 20 mm wide (n = 65; s.d. 3.4), with a L:W of 1.1 (1.5) 2.1 (n = 60; s.d. 0.3), and an area of 38 (159.4)

470 mm^2 (n = 52; s.d. 101.2). Receptacle is bifacial with a sterile and a fertile surface: sterile surface bears coarsely anastomosing venation (Figs 5, 10, 15, 18, 24, 32, 33, 35, 50, 52, 53); fertile surface bears 35 (101.9) 300 (n = 26; s.d. 69.4), closely spaced seed scars at a density of 8 (16.5) 35 scars per 25 mm^2 (n = 31; s.d. 5.5). Seed scars are represented in impressions by raised, radially striated, polygonal, elliptical to circular cushions with a central depression containing a tubercle; scars 0.6 (1.1) 1.7 mm wide (n = 103; s.d. 0.2) and 1 (2) 3.2 mm long (n = 156; s.d. 0.5) (Figs 7, 22, 49). Marginal seed scars tend to be more rectangular, and are aligned into a conspicuous rank along the periphery of the receptacle.

Wing is conspicuous, with a medial width of 2.3 (5.8) 9 mm (n = 66; s.d. 1.4), and is continuous along the periphery of the receptacle except at the base, where it is sharply constricted, forming a rounded or laterally truncated lobe (1.8 (4.2) 7 mm deep (n = 47; s.d. 1)) to either side of the pedicel. The ratio of wing width to receptacle width is 0.1 (0.6) 1.2 (n = 64; s.d. 0.2). The wing bears prominent radial fluting and striations. Fluting is delimited in impressions by grooves on the fertile surface, ridges on the sterile surface (of impressions). These grooves or ridges correspond to the junctions between marginal seed scars and the exit points of veins from the receptacle into the wing on the sterile surface. Wing margin is usually poorly preserved and incomplete, but gently scalloped, entire or, most commonly, dentate (e.g. Figs 5, 20, 52). When dentate, the mid-line of each narrow, pointed ‘tooth’ corresponds to the groove/ridge that runs from the junction between two adjacent seeds scars to the wing margin (Fig. 52).

Pedicel is 3.5 (9.9) 36 mm long (n = 32; s.d. 5.7), with basal width of 1 (1.8) 3.3 mm (n = 10; s.d. 0.7), expanding slightly to 1.2 (2.3) 4.2 mm (n = 29; s.d. 0.7) at point of insertion into receptacle; long, striated, associated with an abscission scar in the midrib at point of attachment to subtending leaf (Figs 25 & 52).

Fructifications are attached to the top of the petiole or to the midrib (basal quarter) of a narrowly elliptical to oblong *Glossopteris* leaf, 45.8 (105.3) 258 mm long (n = 11; s.d. 62.8) and 14.6 (26.2) 44.3 mm wide (n = 14; s.d. 8.8), with a long, tapering base and moderately acute to obtusely pointed apex (Figs 4–6, 8–12, 22–26, 28, 44– 47). Leaf base is variable, in some cases cuneate with a well-defined, 29.7–49.5 mm long, 2.1–5.8 mm wide petiole (e.g. Fig. 9), or lamina may taper at base without delimitation of a petiole, in some cases expanding slightly into small, inconspicuous, sagittate lobes (e.g. Fig. 12). Midrib is 0.3 to 5 mm wide, well-defined and persistent to apex. Veins arise from midrib at a steep angle, and arch gently across the lamina to the margin, with a mid-laminal vein angle of 24° (48°) 75° (n = 27; s.d. 15.6), a marginal vein angle of 56° (67.5°) 79° (n = 28; s.d. 7.2), and a marginal vein density of 18 (26.4) 32 veins per 10 mm (n = 11; s.d. 5.1); in some cases veins follow a straight course across the distal two thirds of the lamina. Meshes elliptical to elongate polygonal near midrib, becoming linear in mid-laminal and marginal regions.

Seeds generally indistinct, but apparently with an elliptical sclerotesta 2(3) 4.8 mm (n = 17; s.d. 0.8) long and 1.5 (2.4) 4.5 mm (n = 17; s.d. 0.8) wide, and a distally elongated, elliptical to falcate, finely striated wing, at least 6.4 (12.1) 23.5 mm long (n = 41; s.d. 4) and 1.9 (3.6) 5.1 mm wide (n = 53; s.d. 0.8). Seed details obscured in many cases by superposed impression of the wing and receptacle, resulting in a fringe of bract-like wings protruding from the margin of the fructification (Figs 40–43, 48, 51).

Comments

As illustrated in Figs 4–53 and summarized in Fig. 54, members of this species are highly variable in both size and shape, and wing morphology. The wing margin varies from entire to scalloped to dentate, although generally the margin is dentate, and in all cases the wing fluting is persistent and pronounced. Receptacles are highly variable in size and range in shape from circular to elliptical, obovate to ovate to broadly lanceolate, with rounded, truncated to slightly cordate bases.

The elongate, bract-like structures interpreted here as seed wings, were difficult to observe, as they lie at a lower level in the sediment than the receptacle. In many cases it was only possible to measure the section of wing protruding beyond the edge of the fructification.

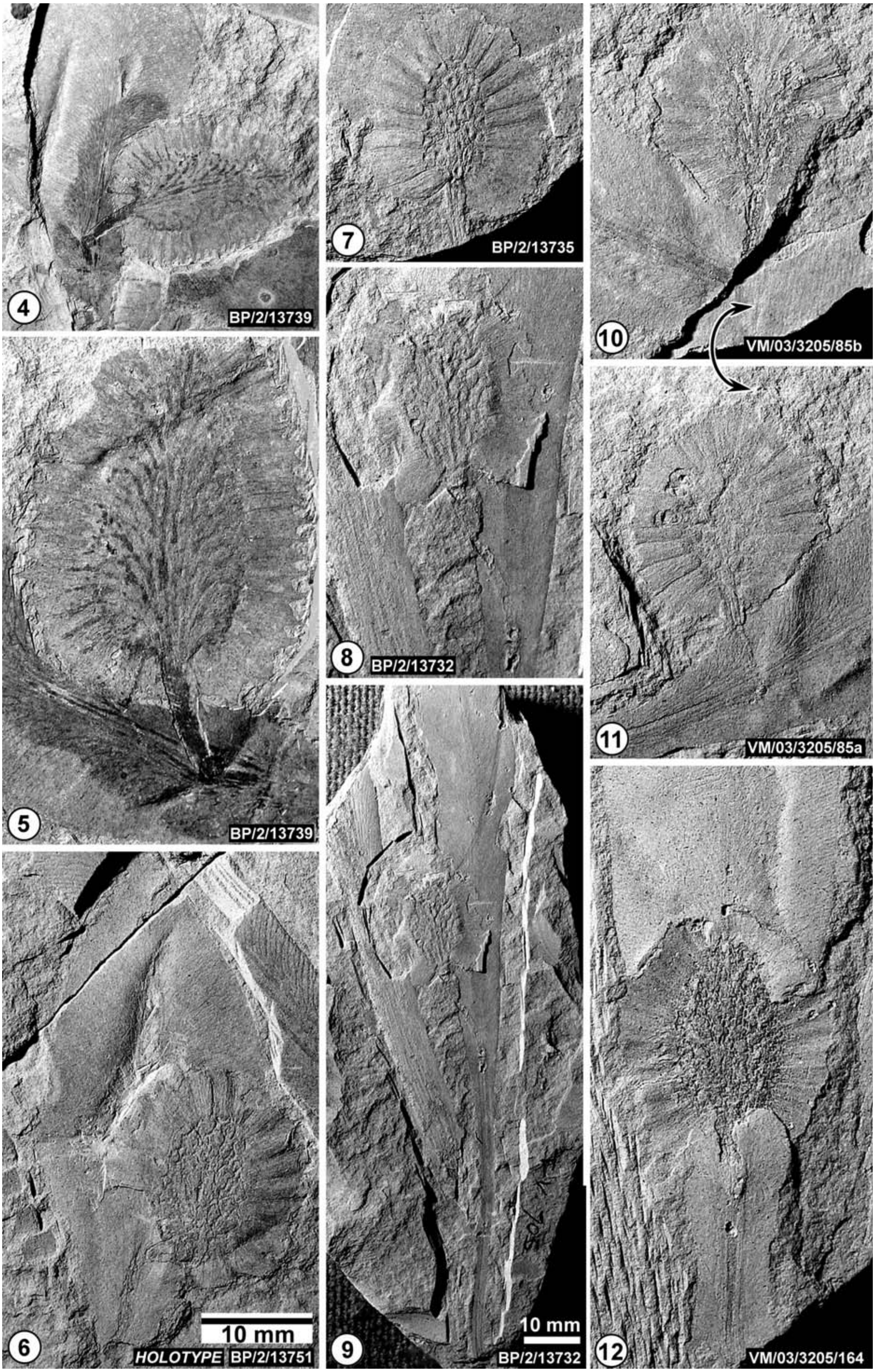
There is a large degree of variability in size and shape of the subtending leaves, of *S. leslii,* as here defined, although the venation appears to be fairly consistent. The leaf bases of the fertiligers of *S. leslii* tend to be poorly preserved, and in many cases it is not clear whether the bases are slightly expanded or whether they are differentiated into sagittate lobes. Fructifications borne on leaves with sagittate bases do not appear to differ morphologically from those borne on leaves lacking this feature.

DISCUSSION

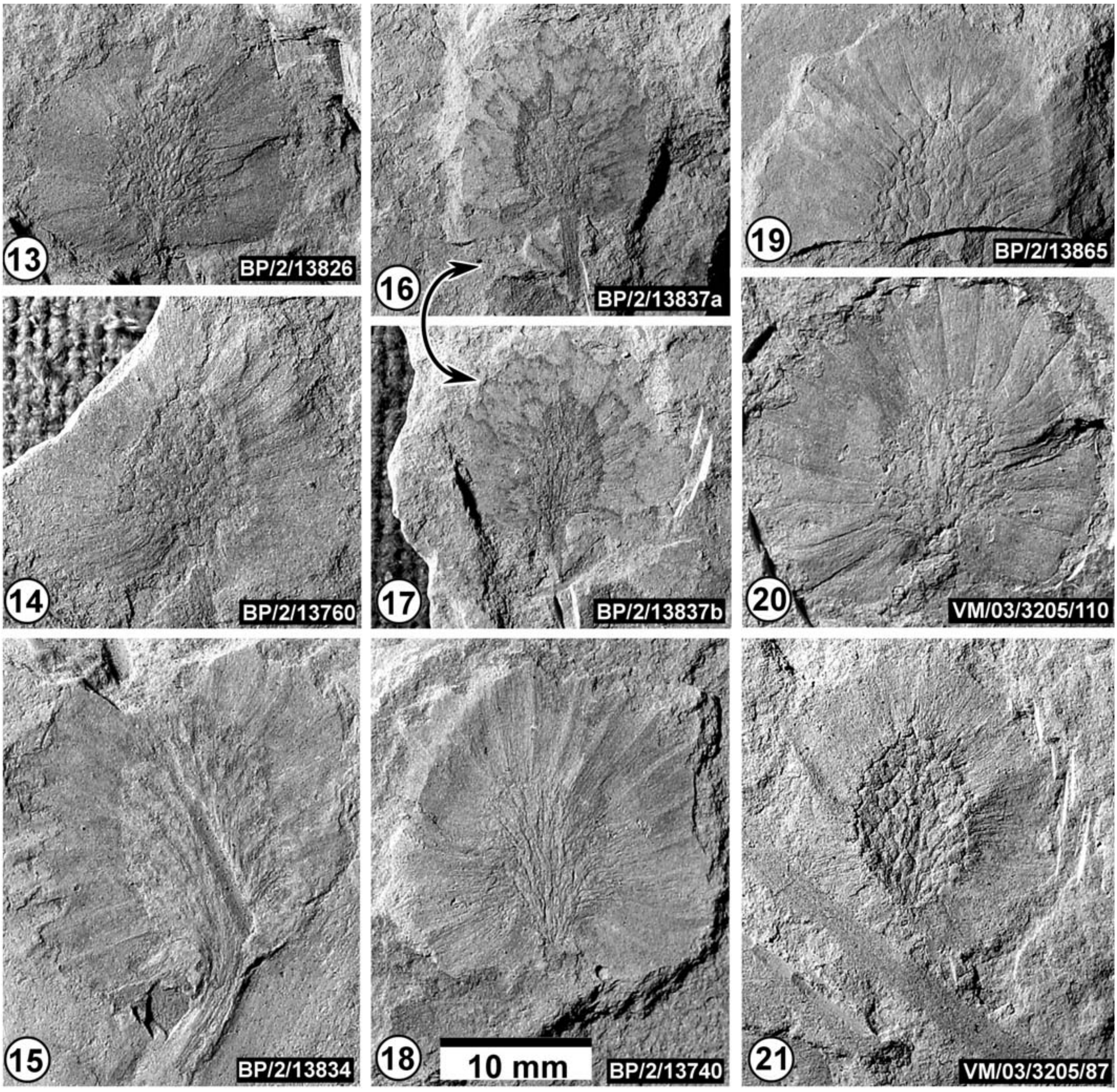
Based on the type collections from Vereeniging, the key diagnostic features of *Scutum* are the presence of a broad wing with well-defined fluting and a margin that may be dentate, pronounced seed scars and a receptacle with a low length:width ratio, i.e. the receptacle is relatively broader and squatter (circular to ovate) than in *Plumsteadia* and *Dictyopteridium.* Although peripheral wings are present in both these other genera, they tend to be much narrower, and the receptacle is more elongated. In addition to the lack of a terminal spine, *Scutum* is differentiated from *Gladiopomum* on the basis of having a generally lower length to width ratio and a wing with well-developed, persistent fluting that is uninterrupted at the apex.

Scutum as defined here has a very broad circumscription, accommodating a wide range of sizes, shapes and wing morphologies. There is potential for overlap with broad-winged members of *Plumsteadia* in particular, and differentiation of these two genera relies more on subtle quantitative distinctions than on robustly defined qualitative features.

Although Plumstead (1952, 1956, 1958) and Anderson & Anderson (1985) recognized several species of *Scutum* from Vereeniging, by their own admission, the distinctions they made were based on quantitative, rather than



Figures 4–12. *Scutum leslii* specimens from Vereeniging. One of Plumstead's (1952) syntypes for '*S. rubidgeum*' is figured in (4) and (5), and the two syntypes she assigned to *S. leslii* are figured in (6), (8) and (9). (Double-headed arrow indicates part and counterpart specimens.)

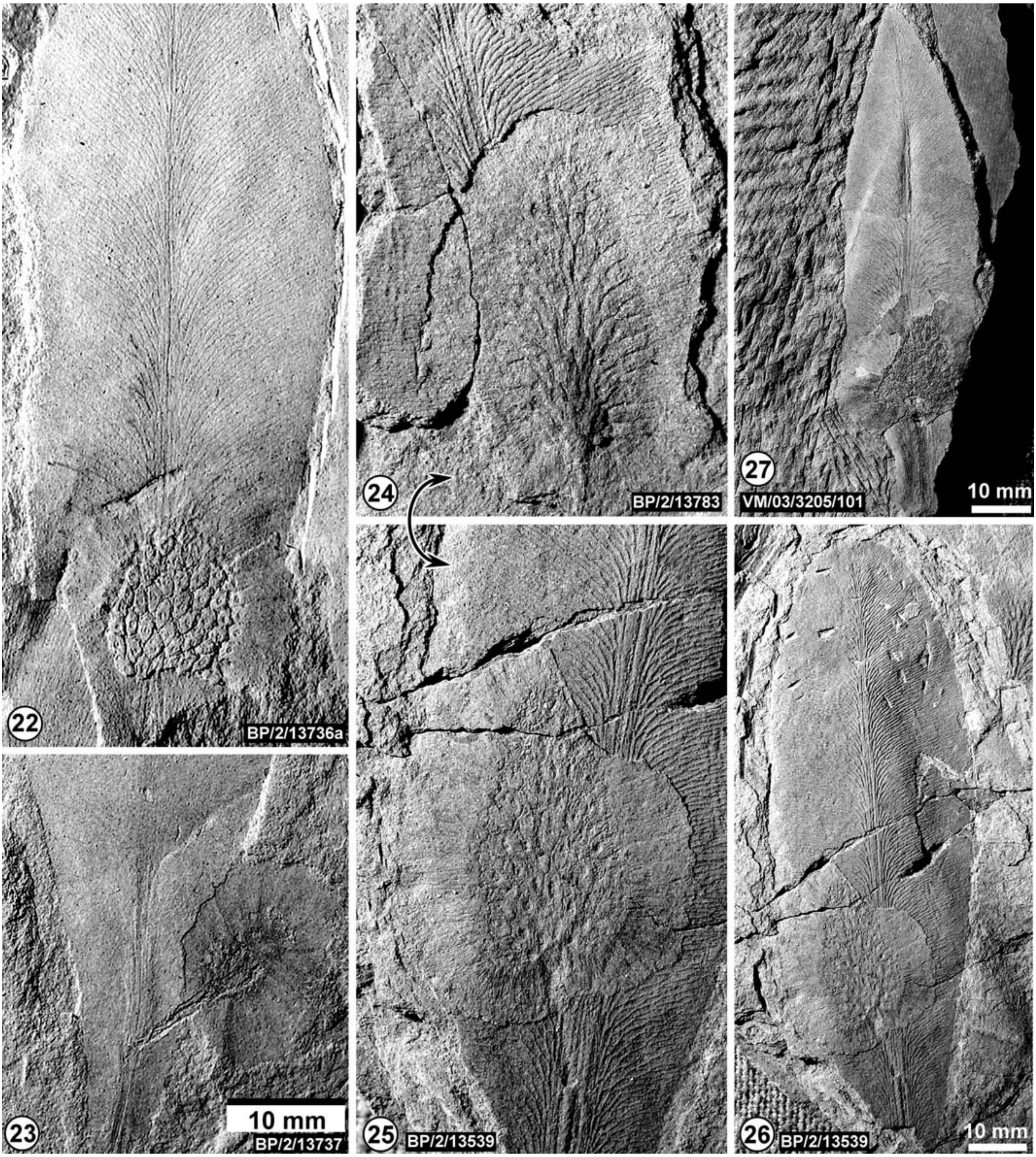


Figures 13–21. Additional examples of *Scutum leslii,* illustrating the smaller end of the spectrum of morphological variation seen in these fructifications. Note the very high wing width to receptacle width ratios in these smaller specimens, particularly in (19) and (20).

qualitative, features, and the ranges of these quantitative features overlapped. Anderson & Anderson (1985) noted that there was a morphological continuum between the polysperms of *S. rubidgeum* (= *S. leslii*) and *S. draperium,* but considered their attached leaves to be 'perfectly distinct'. However, apart from the sagittate base in some (but not all) of the leaves attached to *S. rubidgeum,* the descriptions of the leaves in these two taxa appear to be remarkably similar.

The large sizes and apparently entire wing margin of the specimens from Ermelo, may reflect regional variation within the species. On the other hand, it is not certain that the Ermelo specimens do in fact have an entire margin, as none of them has any section of wing margin that is complete and undamaged (e.g. Figs 38 & 39). In some cases, the margin appears to be gently scalloped rather than entire. A scalloped or dentate margin could not be demonstrated for most of the Vereeniging specimens, mainly because of poor preservation of the apparently delicate wing margin, and could, therefore, not be used as a diagnostic character for the species. This uncertainty contributed to the decision to synonymize *S. ermeloense* with *S. leslii.*

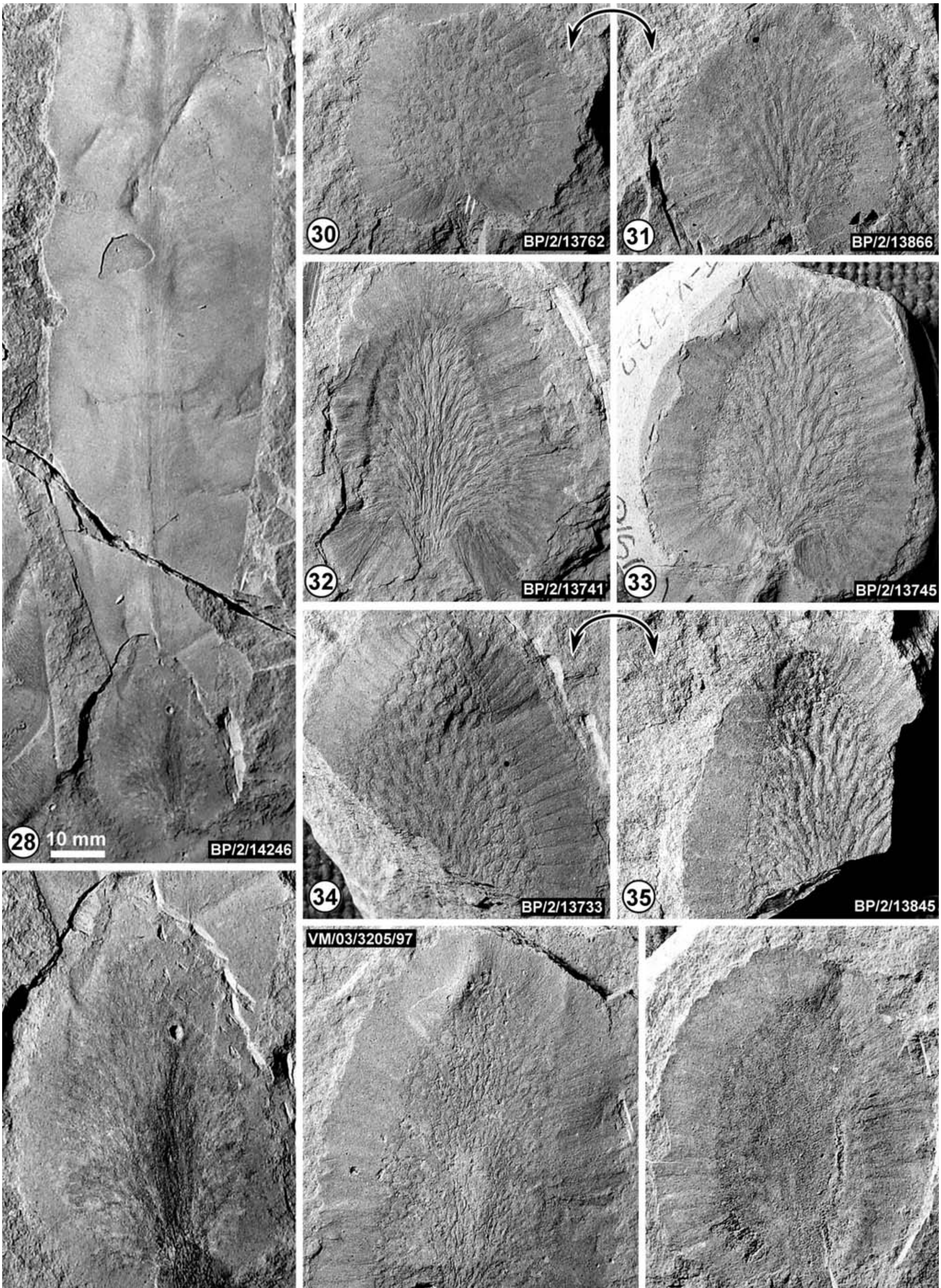
Anderson & Anderson (1985) distinguished *S. ermeloense* and *S. draperium* on the basis of differences in their subtending *Glossopteris* leaves. Unfortunately, the subtending leaf of the Ermelo specimens is unknown, hence Anderson & Anderson (1985) made this distinction on the basis of associated leaf material alone. Simple scatter plots in Figs 56 and 57 illustrate the overlapping size ranges of *S. draperium, S. ermeloense* and *S. leslii,* indicating that the first two may represent the upper size limits of a single



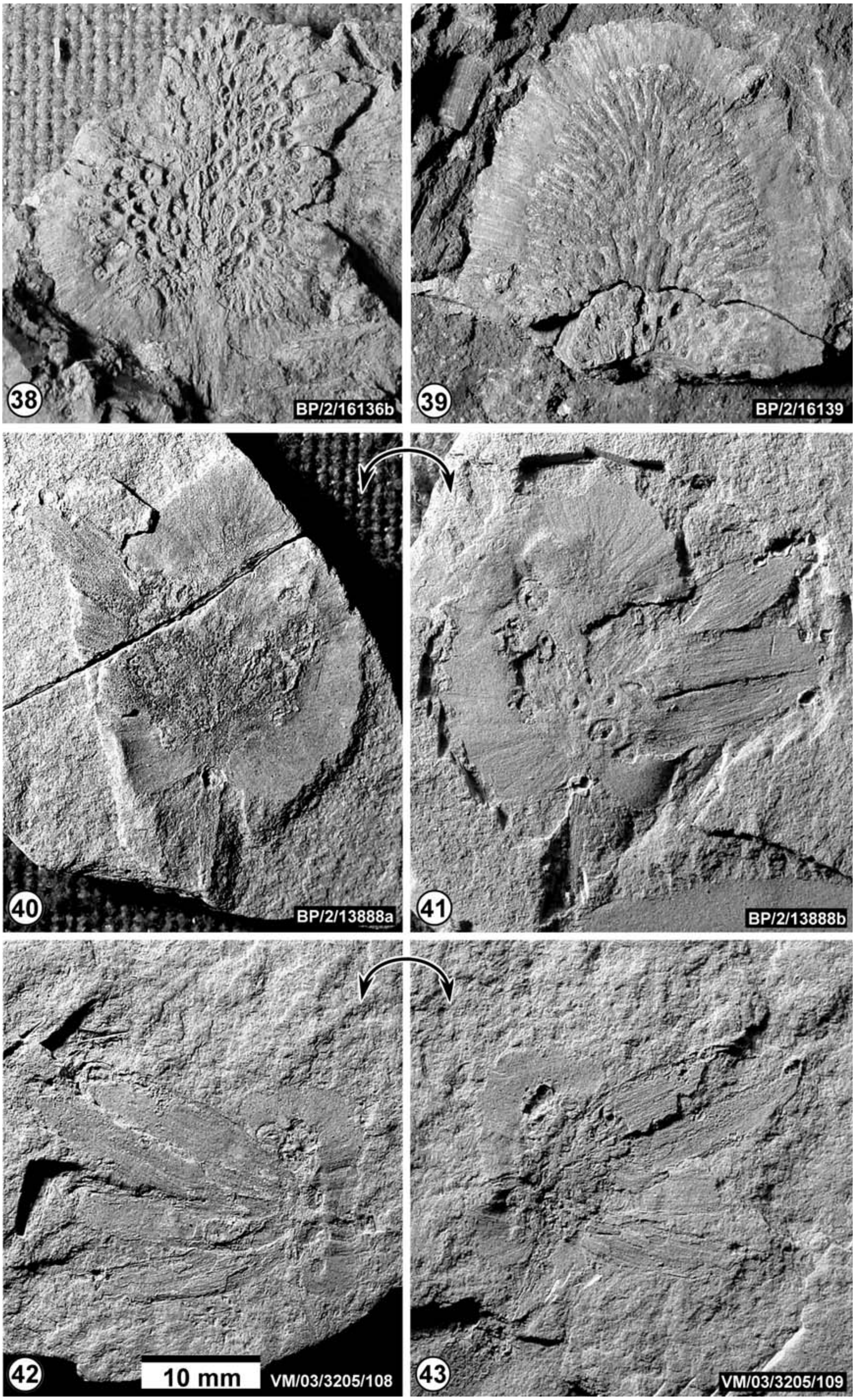
Figures 22–27. *Scutum leslii* fertiligers, illustrating a range in subtending leaf morphology. **24–26,** Plumstead's (1952) syntype for the seed-bearing surface of '*S. rubidgeum*'. Note how the impression of the seed-bearing surface lies above the leaf impression in (25), whereas the impression of the veined surface (counterpart) lies deeper within the sediment than the leaf impression in (24).

species. It should be noted that only a few, poorly preserved specimens of *Scutum* were found at the Ermelo locality.

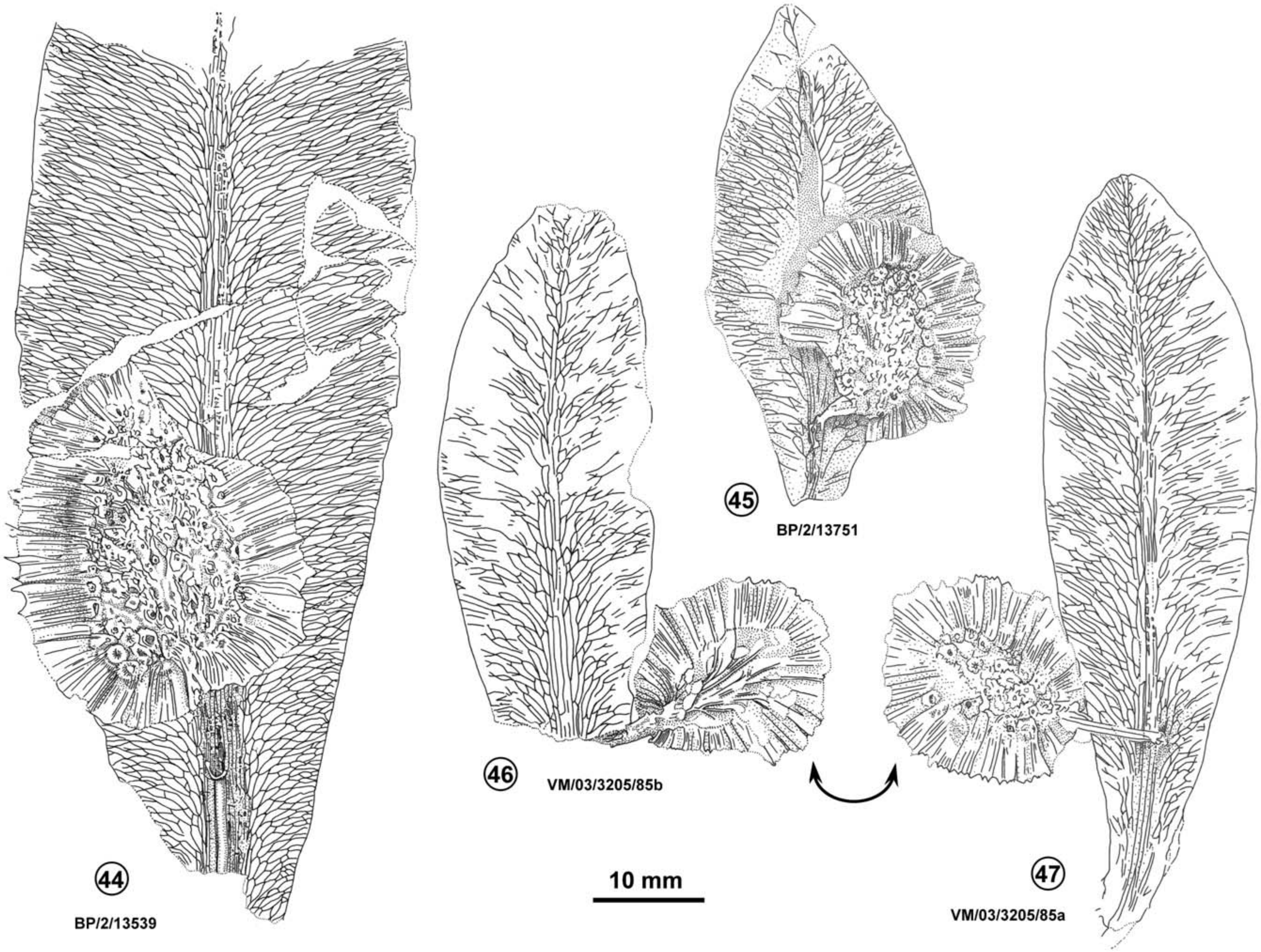
Plots of overall size and receptacle dimensions for the South African *Scutum* specimens showed a typically linear relationship between length and width (Fig. 56). The '*S. draperium*' specimens occupy the upper size ranges of *S. leslii,* although one of the specimens is well nested within the middle ranges of the latter taxon. Considering the broad and gradational nature of the variation in *S. leslii,* it is more likely that the specimens selected for inclusion in *S. draperium* by Plumstead (1952, 1956, 1958) and Anderson & Anderson (1985), were chosen because they lie at one end of the size spectrum, and when compared with moderate specimens and those at the other end of the range they appear to be dramatically different. The consistency in wing width, irrespective of receptacle size (Fig. 57), also contributes to a large but superficial



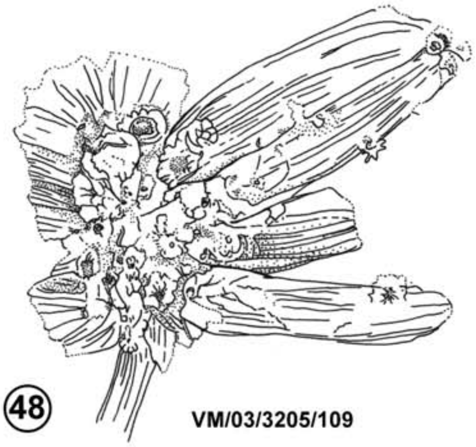
Figures 28–37. Large *Scutum leslii* fructifications. All these specimens are examples of *'S. draperium'* as per Plumstead (1952, 1956a) and/or Anderson & Anderson (1985), except for those in Figs 32, 33 and 37 that were considered to belong to *Scutum rubidgeum.*



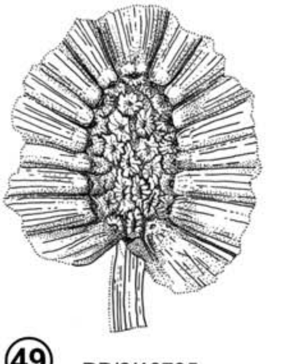
Figures 38–43. Two of the four *Scutum* specimens examined from Ermelo are represented in (38) and (39). The preservation of these fructifications was different to the simple impressions found at Vereeniging, and a mineralized crust was present in some parts of the fossils. **40–43**, part and counterpart of two of the controversial, bract-bearing *S. leslii* specimens from Vereeniging. The 'bracts', interpreted by Plumstead (1956a, 1958a) as pollenate structures, are here considered to be the elongate wings of attached seeds.



Figures 44–47. Line drawings of *S. leslii* fertiligers from Vereeniging. Note the scar on the midrib in (44), at the site of pedicel divergence, and how the midrib is more robust below this point. Specimens such as these lend support to the hypothesis that the pedicel is an axillary structure that is adnate to the leaf.

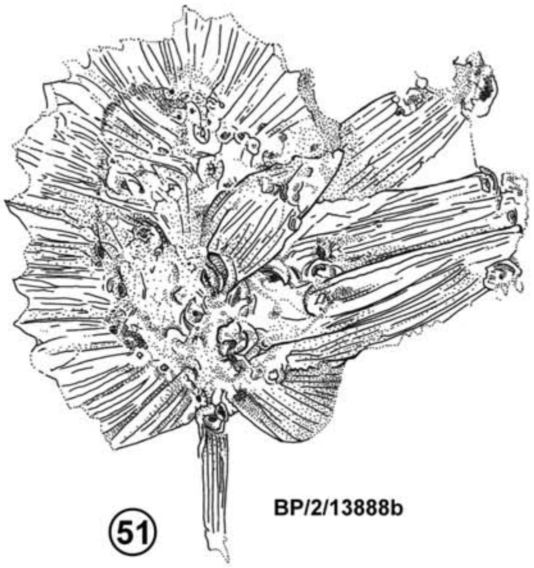


(48) VM/03/3205/109

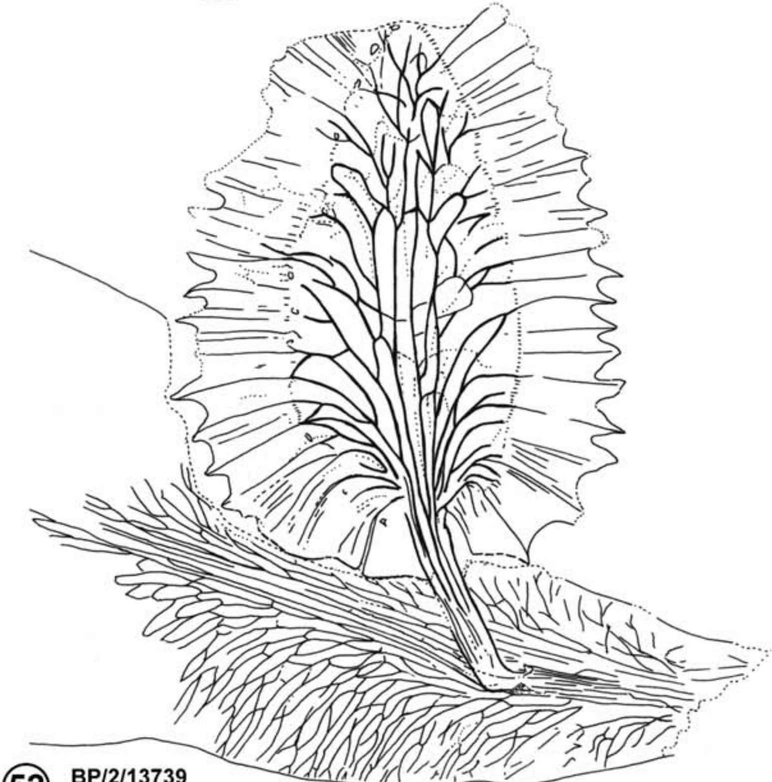


(49) BP/2/13735

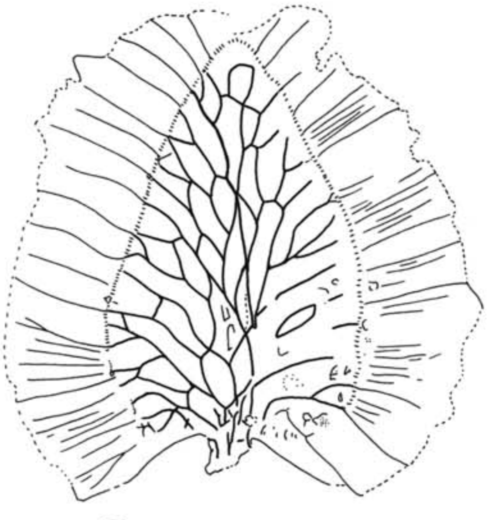
(50) BP/2/13845



(51) BP/2/13888b



(52) BP/2/13739



(53) BP/2/13745

10 mm

Figures 48–53. Line drawings of two *Scutum leslii* specimens with attached seeds in (48) and (51); **49**, drawing of a particularly beautifully preserved impression of the fertile surface of an *S. leslii* fructification; **50, 52, 53**, drawings of venation patterns observed on the sterile surfaces of *S. leslii* fructifications.

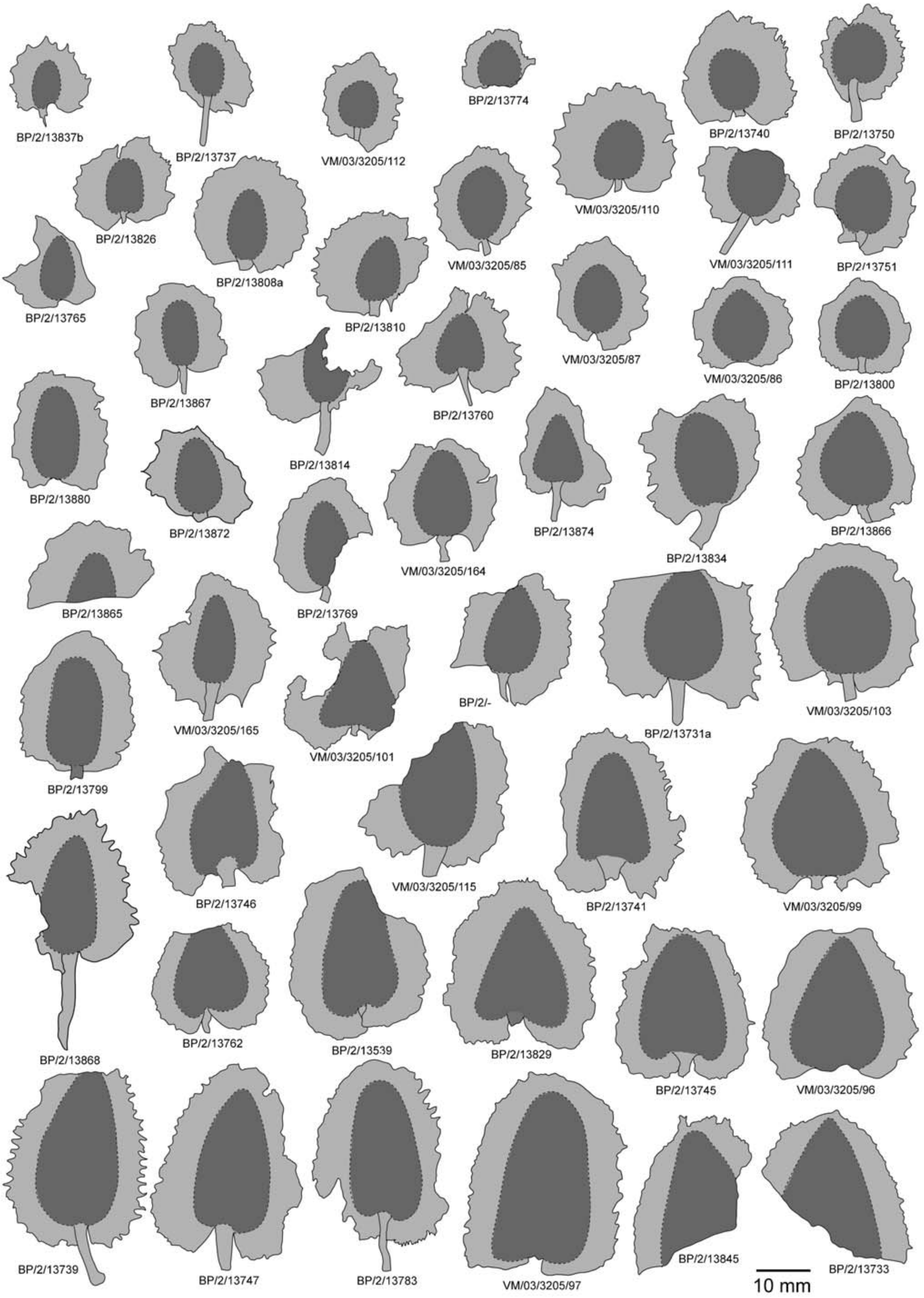


Figure 54. Silhouette drawings of *Scutum* specimens from Vereeniging, illustrating the wide range of intergrading wing and receptacle morphologies. Members of both *S. rubidgeum* and *S. draperium,* as categorized by Anderson & Anderson (1985), have been included (all drawings at approximately life-size).

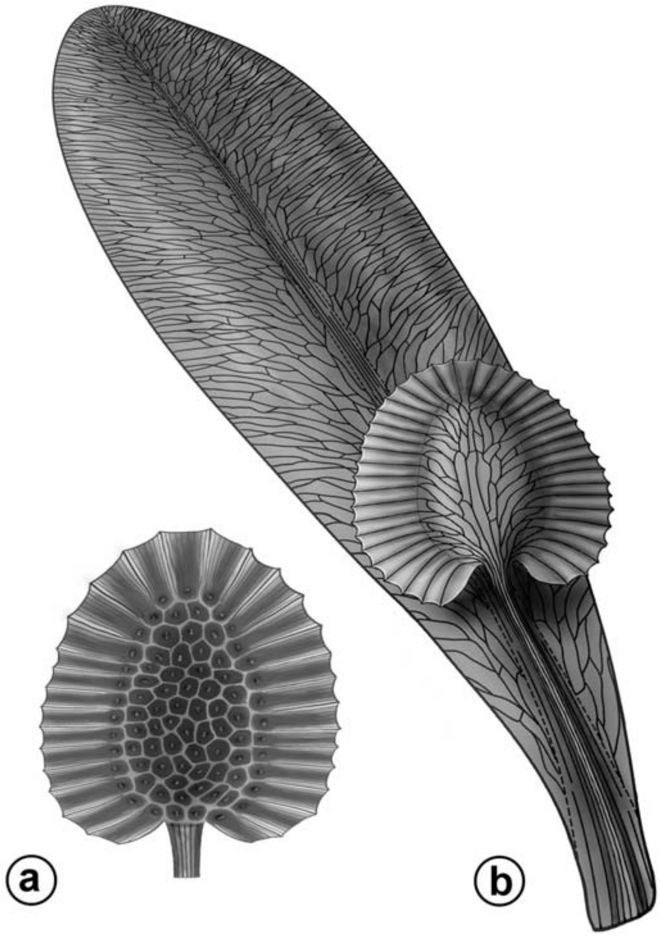


Figure 55. Reconstructions of *Scutum leslii.* **a**, A fructification illustrating the seed-bearing surface; **b**, a fertiliger with fructification attached to the midrib of a *Glossopteris* leaf, the seed-bearing surface facing the adaxial surface of the leaf.

difference in the appearance of fructifications at the two ends of the size spectrum.

Unfortunately, very few specimens of *Scutum* were recovered from the Ermelo site, so any meaningful assessment of the range of fructification morphology is not possible. What is apparent from the dimensional plots (Figs 56 & 57), is that there is at least some overlap with the *S. leslii* specimens from Vereeniging, and until additional specimens are found at Ermelo to provide more convincing proof that these specimens belong within their own species, they have been grouped within *S. leslii.*

Global distribution of *Scutum*

Scutum has a relatively broad geographical distribution, having been found in Upper Permian deposits of Australia (McLoughlin 1990b) and India (Surange & Chandra 1974). Several species of *Scutum* have been described from India, including *S. sahnii, S. elongatum, S. indicum* (Surange & Chandra 1974), which all appear to meet the diagnostic delimitations of the genus. Chandra & Surange (1977) also described *Venustostrobus,* for which the rounded receptacle (L:W 1.1–1.5) and broad, prominently fluted wing with an entire to dentate margin of the type species, *V. diademus,* are easily accommodated within *Scutum.* Other species of *Scutum* from India (Mukherjee *et al.* 1966; Banerjee 1968) that were attributed to South African species as circumscribed by Plumstead (1952, 1956, 1958), require revision.

Australian taxa *Plumsteadia ovata* Kyle, 1974, *P. semnes* Rigby, 1978 and *P. ampla* (White) Rigby, 1969 (see McLoughlin 1990b) may be better placed within *Scutum,* with their low receptacle length to width ratios and relatively broad wings, although they fall close to the boundary between the two genera. Although *P. ovata* described by Ryberg (2009) from Antarctica has a very low length to width ratio, the wing is very narrow, affiliating it more closely with *Plumsteadia* than *Scutum.*

CONCLUSIONS

This investigation has revealed that the South African *Scutum* species constitute a morphological continuum, and that the interspecific differences in attached leaf morphology as described by Plumstead (1952, 1958), are unconvincing. Consequently, the species recognized by Plumstead (1952, 1956, 1958) and Anderson & Anderson (1985) have been amalgamated into a single species, *S. leslii.*

The unusually large collections of isolated *Scutum* fructifications and fertiligers from the Vereeniging quarries in South Africa have provided a rare opportunity to examine the morphological variation within the fertile organs of a single population of glossopterids. In addition, the high quality of the impression fossils and range of cleavage patterns exhibited, allowed for a detailed examination of the morphological features and arrangement of these fertiligers, confirming the assessment of previous authors that the seed-bearing surface

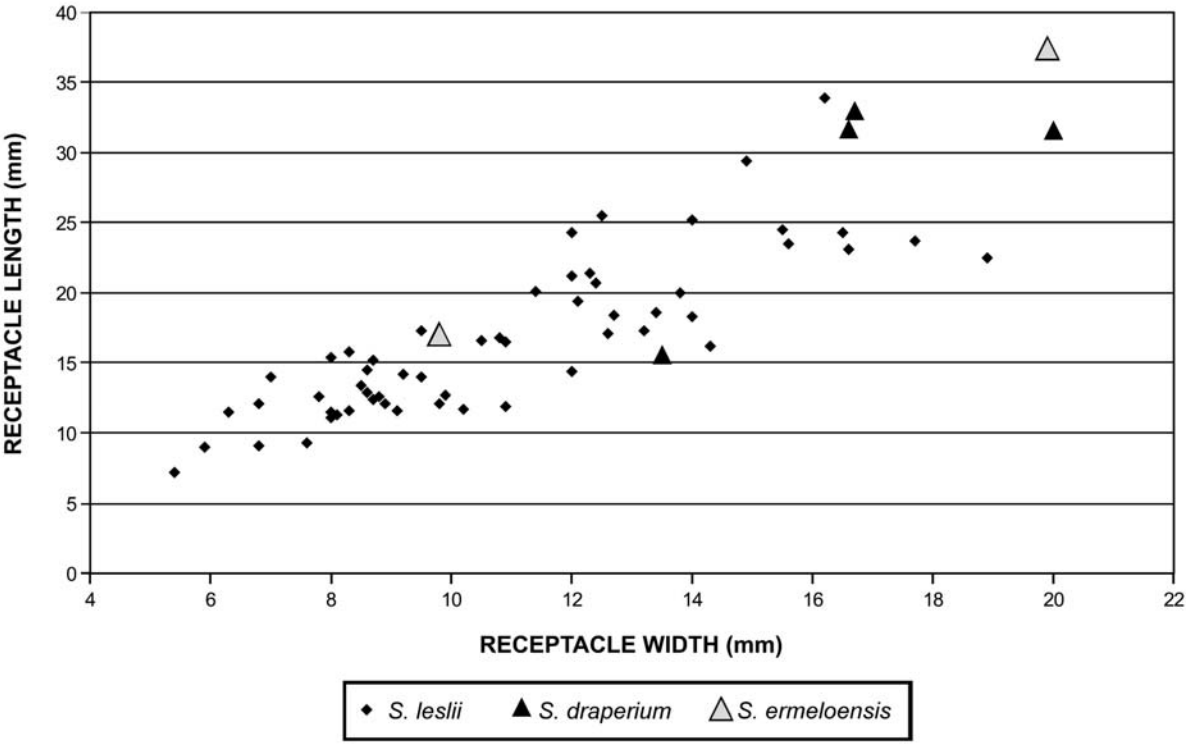


Figure 56. Scatter plot of receptacle lengths against receptacle widths of specimens here assigned to *Scutum leslii,* but including those previously assigned to *S. draperium* and *S. ermeloensis.*

of these fructifications faces the subtending leaf.

Many of the enduring controversies regarding the glossopterids hinge on disparate interpretations of the basic structure of their ovuliferous organs. Without a clear understanding of the external morphology, it becomes impossible to draw reliable and consistent conclusions about homologies and affinities, let alone to reach taxonomic agreement and make biostratigraphic and biogeographic utility of this plant group.

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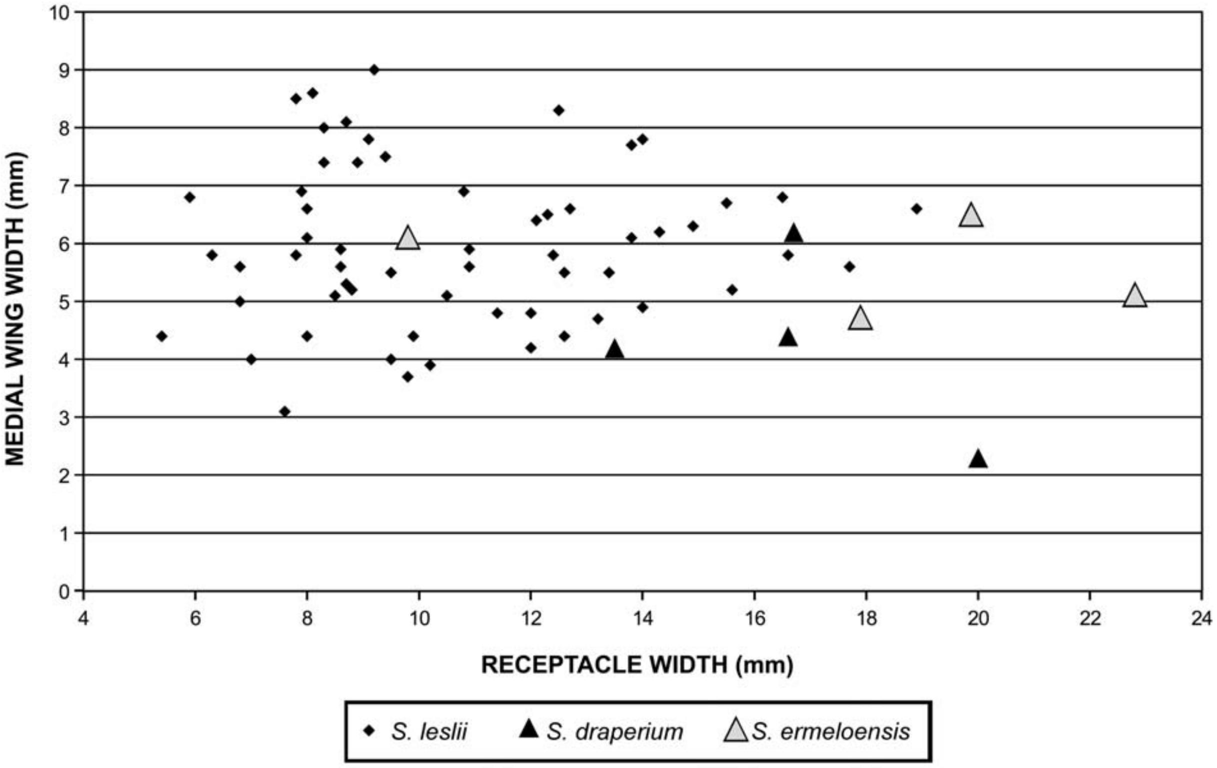

Figure 57. Scatter plot of medial wing widths versus receptacle widths of specimens here assigned to *Scutum leslii,* but including those previously assigned to *S. draperium* and *S. ermeloensis.*

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Cretaceous biozonation based on terrestrial palynomorphs from two wells in the offshore Orange Basin of South Africa

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The C-B1 and O-A1 petroleum exploration wells were drilled by SOEKOR Pty Ltd in 1988 and 1992, respectively, in the Orange Basin off the west coast of South Africa. A palynological analysis of the Cretaceous interval intersected by the two wells, for which the ages were adopted from foraminiferal studies, provides new information on the biostratigraphy and also on reconstructions of the Cretaceous palaeoflora and palaeoenvironment. The spores and pollen used in this study were extracted from over 500 samples of conventional cores, side-wall cores and ditch-cuttings. The identified terrestrial palynoflora includes 41 species of angiosperm and gymnosperm pollen, 85 species of fern and bryophyte spores, and two monolete spore taxa. Several of the pollen and spore taxa are possibly new species. Five palynological zones were established for each of the two wells, which are separated by a latitudinal distance of 300 km. Within the Early Cretaceous intervals of the two wells, there is a considerable degree of similarity in the palynological assemblages, which suggests that the terrestrial plant communities were relatively uniform. For the Late Cretaceous interval, however, there are marked differences suggesting that the plant communities had become more diverse and also that the palynomorphs were being supplied from separate geographical areas.

Keywords: South Atlantic, marine sediments, pollen, spores, Southern Hemisphere, Mesozoic.

INTRODUCTION

Onshore, Cretaceous sedimentary rocks in South Africa are preserved largely in the east within the Zululand and Algoa Basins and also within a series of smaller basins in the southern Cape between Worcester and Port Elizabeth. However, they are best represented in the thick successions of the sedimentary basins off the west, south and east coasts where they have been extensively drilled in the course of petroleum exploration since 1968. The focus of interest in the present publication is the offshore Orange Basin (Fig. 1), where 38 petroleum exploration wells have been drilled since 1976 by SOEKOR and other exploration companies. In addition, the DSDP 361 well was drilled in 1975 under the international Deep Sea Drilling Programme (Bolli *et al.* 1978).

Few palynological studies have been published on the spores and pollen of either the onshore or the offshore deposits. Publications relating to the onshore deposits include Martin (1960), Scott (1976), De Villiers & Cadman (1997, 2001), Oboh-Ikuenobe & de Villiers (2003) and Scholtz (1985), and for the offshore areas, Brown *et al.* (1995), McLachlan & Pieterse (1978), Zavada & Benson (1987) and Zavada (2004).

The fossil Cretaceous vegetation of South Africa is generally regarded as belonging to the southern Gondwanean floral province (Herngreen & Chlonova 1981). Studies of the spores and pollen led researchers (Scott 1976; McLachlan & Pieterse 1978; Sandersen 2007) to conclude that the Early Cretaceous assemblages from South Africa correspond well with forms described from elsewhere in the southern hemisphere (Dettmann 1963, 1981). However, with the breakup of East Gondwana (separation of South Africa from Antarctica, India, Australia, Madagascar about 150 million years ago) and of West Gondwana (separation of Africa from South America about 130 million years ago), South Africa became progressively distanced from the other continents (Dingle & Scrutton 1974). Correspondingly, the pollen assemblages presented by Scholtz (1985) and de Villiers & Cadman (1997, 2001) have clear southern African characteristics in the younger Cretaceous to Palaeogene palynofloras.

To further investigate these conclusions, a quantitative study was undertaken by Sandersen (2007) on samples from the Cretaceous sections of the C-B1 and O-A1 petroleum exploration wells which were drilled by the national petroleum exploration company, SOEKOR, in 1988 and 1992 respectively, in the Orange Basin, 50 to 100 km offshore from the present day coastline (Fig. 1). The ages assigned to the stratigraphic sections of the O-A1 and C-B1 wells were provided by the Petroleum Agency SA and are based on extensive and carefully calibrated foraminiferal studies carried out over several decades.

MATERIALS AND METHODS

The palynogical slides used in this study were kindly provided by the Petroleum Agency SA. They were originally prepared by SOEKOR from side-wall cores and ditch-cuttings. SOEKOR's standard palynological processing involved digestion of the sediment samples in hydrochloric and hydrofluoric acids, followed by a zinc chloride heavy liquid separation to remove mineral particles. A

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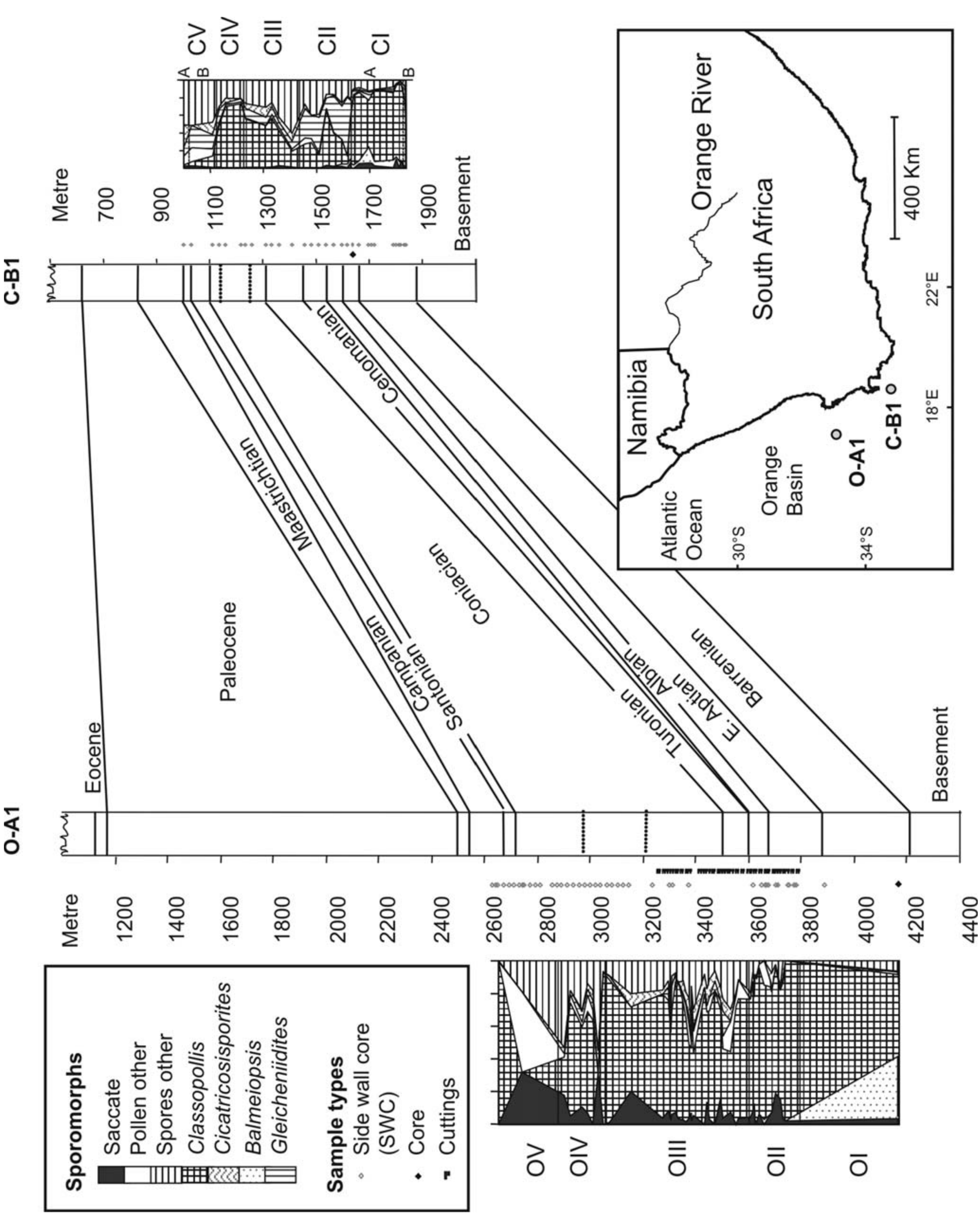

Figure 1. Locality map, idealized stratigraphic sequences and summary of pollen and spore groups for wells C-B1 and O-A1 (only the productive Cretaceous levels are indicated in the sporomorph diagram).

strew slide mounted in glycerine jelly was then prepared for petroleum source rock evaluation and a second slide for taxonomic study was made from a portion of the palynological residue, which had been subject to oxidation with dilute nitric acid, followed by staining with alizarine red.

It is important to note however, that a certain amount of down-hole contamination of palynomorphs can be expected in the slides derived from ditch-cuttings, as it is not possible to remove all traces of drilling mud and contaminating rock chips prior to palynological processing. The net effect of this is that palynomorphs from younger, stratigraphically higher formations can be expected in palynological slides prepared from older, lower formations. To counter this problem, during drilling, SOEKOR acquired a large number of side-wall cores which were carefully cleaned of contaminating drilling mud before palynological processing was started (Fig. 1). The samples prepared from the carefully cleaned conventional cores also provide control on down-hole contamination.

The palynological study was carried out under oil immersion using a ×100 objective lens on a Zeiss Axioskop Petrographic microscope at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand. The number of palynomorphs counted depended on their richness, with the ideal number of 500 only achieved in the slides containing the Late Cretaceous organic residue. Data presentation and zonation were done by means of the Tilia*Graph and CONISS programs (Grimm 1987).

The palynomorphs identified from offshore wells C-B1 and O-A1 are not formally described here. They were classified by Sandersen (2007) in a modified ‘turma’ system based on the methods of classification of form genera adopted by several authors, including van der Hammen (1956), Potonié (1956), Dettmann (1963) and Burger (1966), but here they are only listed according to their broad plant taxonomic affinities (Appendix 1).

GEOLOGICAL DETAILS

The Orange Basin constitutes the quintessential passive margin that formed during the break up of West Gondwana and the associated rifting and opening of the South Atlantic Ocean. The Late Jurassic to Early Cretaceous syn-rift portion of the basin is characterized by a series of grabens and half-grabens that trend approximately parallel to the present day coastline. The sedimentary fill comprises predominantly siliciclastic marine and lacustrine beds as well as volcanic rocks (Paton *et al.* 2007). Most of the syn-rift sequences were deposited immediately to the east of the marginal ridge, and within isolated half-grabens on the middle and inner shelf. Sediment at this time was transported into the Orange Basin by the palaeo-Orange and -Olifants Rivers which were fed by large drainage basins (Emery *et al.* 1975; Bolli *et al.* 1978a,b; Gerrard & Smith 1980; Dingle *et al.* 1983; Dingle & Hendey 1984; Broad *et al.* 2006).

The post-rift Barremian/early Aptian sequence corresponds to a transitional phase between the syn-rift and drift successions (Paton *et al.* 2007), during which time the best quality petroleum source rock was deposited. This sequence is overlain by more than 5500 m of Late Cretaceous shales and claystones. Paton *et al.* (2007) recognized eight sequence stratigraphic units within the Cretaceous Orange Basin. In this model the syn-rift successions (Berriasian, Valanganian and early Hauterivian age) are unconformably overlain by transitional systems (late Hauterivian to late Barremian age), which in turn are unconformably overlain by drift sequences (Aptian to Maastrichtian age). The contact between the Barremian and lower Aptian successions therefore constitutes the drift-onset unconformity. Several of these unconformities occur within the time spans covered in boreholes O-A1 and C-B1 (Paton *et al.* 2007).

RESULTS

A summary of the most prevalent groups found in the pollen assemblages is shown in Fig. 1. Detailed pollen diagrams are presented in Figs 2 and 3. All recorded palynomorph taxa are documented in Figs 4–14 and in Appendix 1.

The palynomorph yield of the processed samples ranged from barren to highly productive. Some major information gaps due to low sampling resolution and poor palynomorph yield occur in the Early Cretaceous part of well O-A1 (Fig. 1). Overall, the study wells O-A1 and C-B1 (Figs 2 and 3, respectively) yielded 133 distinct sporomorph types that included 41 species of pollen, 85 species of trilete spores, two species of monolete spores, four types of algal structures and one type of fungal spore. The pollen diagram for well O-A1 (Fig. 2) and C-B1 (Fig. 3) were divided into five zones each (OI, OII, OIII, OIV, OV and CI, CII, CIII, CIV, CV) with sub-zones only in C-B1 (CI-A and -B, CV-A and -B). The palynological zones and subzones described are believed to reflect the main changes in vegetation in the hinterland.

The gymnospermous cheirolepidacean pollen *Classopollis,* shows strong variation in relative abundance and is generally the most prominent pollen type in both the Early and Late Cretaceous intervals at both well sites. A variety of spores of non-vascular and vascular plants are also prominent along with a fair quantity of saccate and other gymnosperm pollen. Although appearing in the Early Cretaceous interval of both wells, tricolpate angiosperm pollen grains are more noticeable in the upper parts.

EARLY CRETACEOUS PERIOD (BARREMIAN TO ALBIAN STAGES)

Zones CI and OI

The most prolific pollen taxon of the Barremian in both these zones is *Classopollis torosus.* This cheirolepidacean conifer probably formed dense woodlands (Srivastava 1976, 1978; Sandersen 2007) along the coastline of this early rift valley (Pocock & Jansonius 1961, Ryere 1970). In the high altitude regions, gymnosperm-rich forests probably flourished which included inaperturate types such as *Zonalapollenites, Balmeiopsis* and *Excessipollenites.* In both the low-lying and high-lying regions of this early

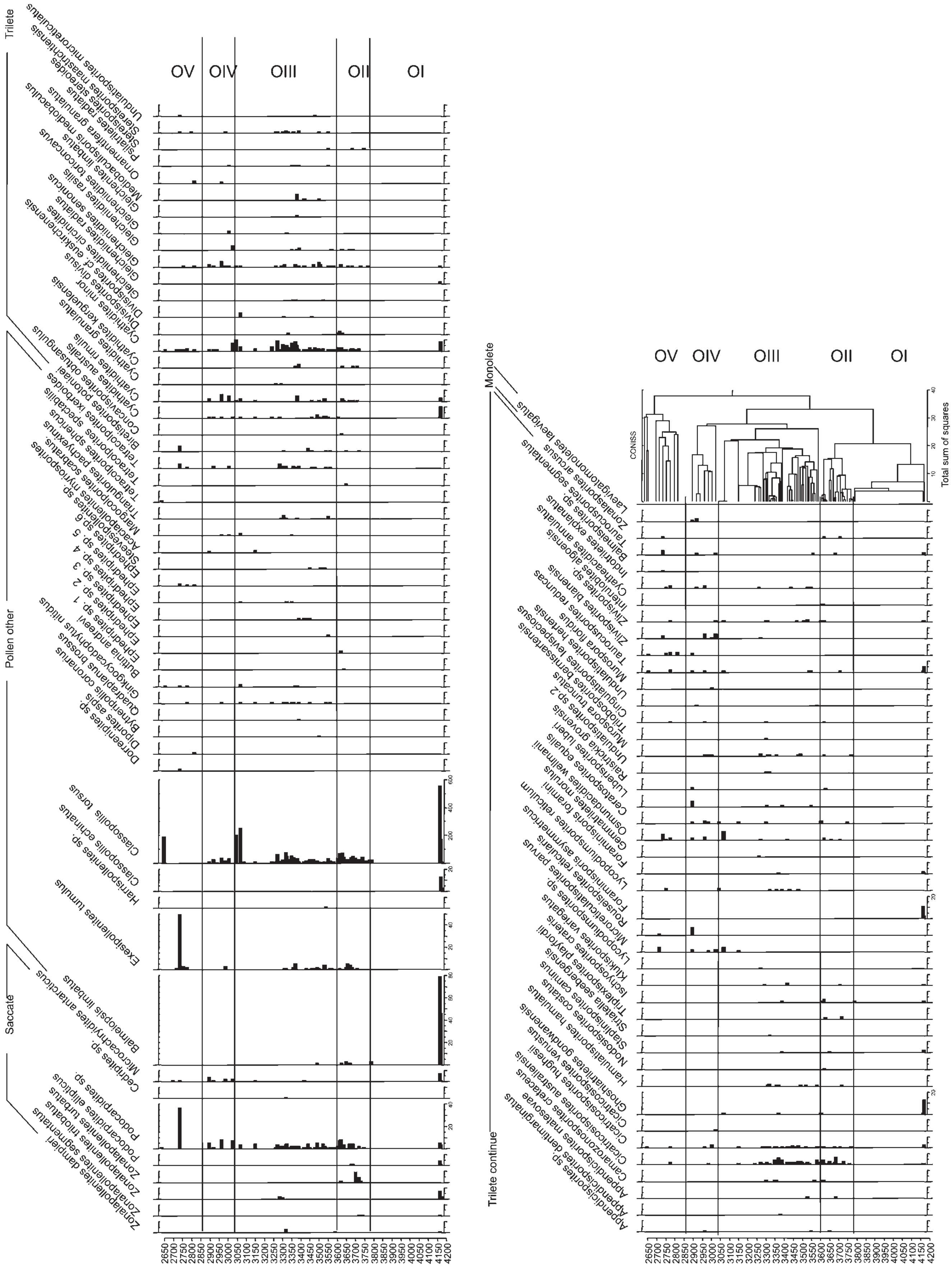

Figure 2. Pollen diagram representing pollen and spore distribution for offshore site O-A1.

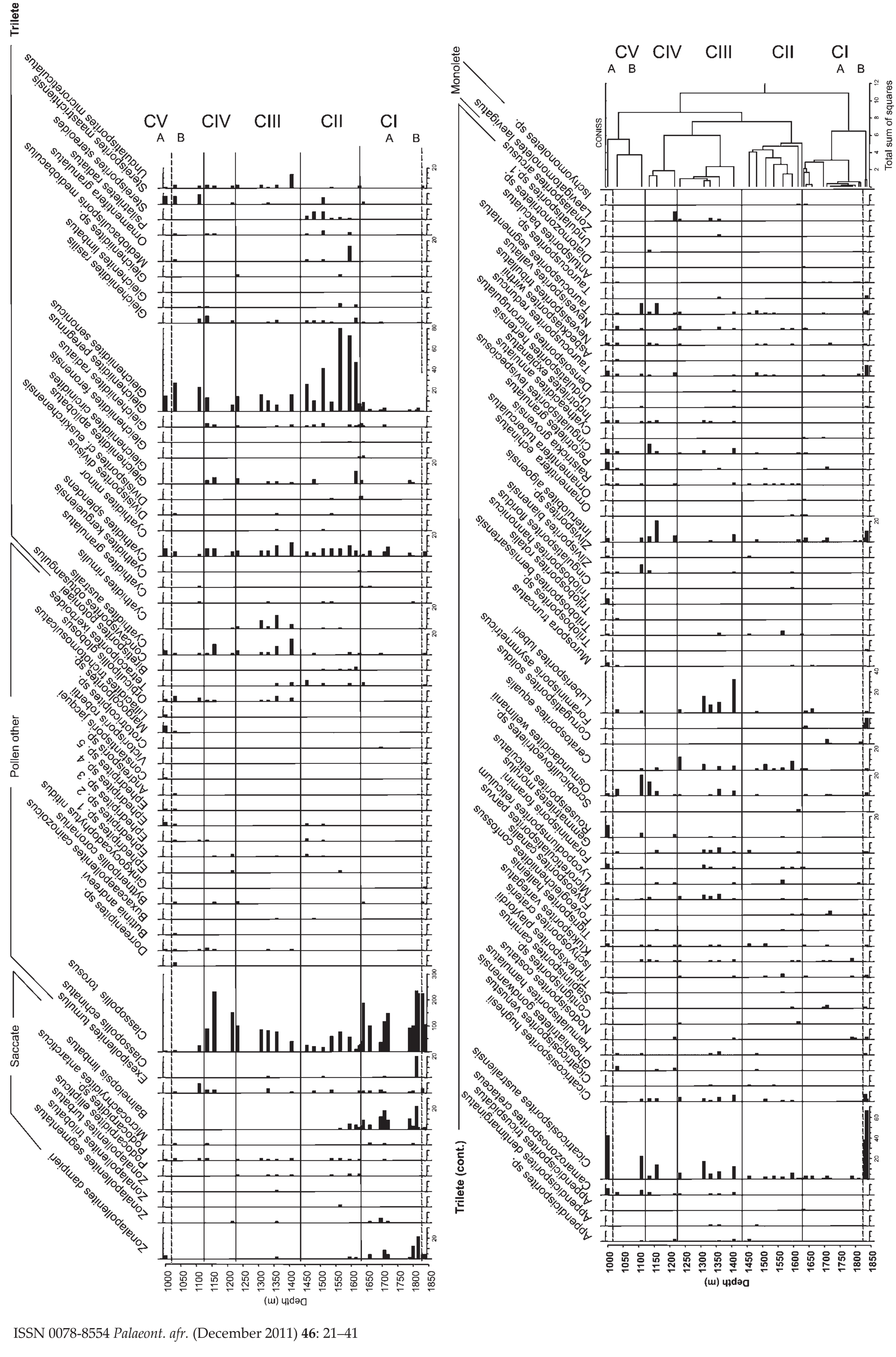

Figure 3. Pollen diagram representing pollen and spore distribution for offshore site C-B1.

rift valley, ferns (*Cicatricosisporites, Gleicheniidites* and *Cyathidities*) and mosses (*Foraminisporis*) probably dominated the ground cover especially around river systems. Both zones contain palynological elements that are typical of Herngreen & Chlonova's (1981) Southern Gondwana province.

SOEKOR assigned a Barremian to Aptian age-range to Zones CI (includes subzones CI-A and CI-B) and OI. Only one pollen grain with columellate semi-tectate sculpture (*Crototricolpites* sp.) which is recorded at the base of Zone CI (subzone CI-A), is typical of the Barremian Stage (Doyle *et al.* 1977; Hickey & Doyle 1977; Hughes *et al.* 1979; Brenner 1984). The second part of Zone CI (subzone CI-B) contains sporomorphs typical in Barremian to Aptian age ranges elsewhere. These include a single, mostly psilate tricolporate pollen grain (*Margotricolporites* sp.), two species of *Gleicheniidites* namely *G. radiatus* and *G. rasilis* that are known to make their first appearances during the Aptian Stage (Krutzsch 1959) and *Foraminisporis asymetricus,* an Early Cretaceous species that according to Krutzsch (1959) and Dettmann (1963) makes its last appearance during the Aptian Stage. None of the 25 palynomorphs identified in Zone OI can be used to support the Barremian age interpreted by SOEKOR based on foraminifera studies because only long ranging taxa were found. However, the Aptian age is supported by the presence of *Gleicheniidites radiatus* and *Foraminisporis asymetricus.* Zones CI and OI therefore represent transitional syn-rift to drift fills of a Barremian to Aptian age.

Zone CII and OII

Zones CII and OII represent deposition during the close of the early rift/late rift and early drift phases, with Africa and South America effectively separated from each other by the end of the Cenomanian Stage.

Coastal-dominated woodlands of cheirolepidacean conifers (*Classopollis*) (Pocock & Jansonius 1961) declined in abundance but still maintained a strong presence in both zones. Terrestrial ferns (*Cyathidities, Gleicheniidites* and *Cicatricosisporites* families) and mosses continued to flourish and were becoming increasingly more diverse. *Gleicheniidites senonicus* was the most dominant of the ferns in Zone CII. The vegetation was slowly becoming more depleted in species such as *Microcachryidites antarcticus* and *Balmeiopsis limbatus,* which were possibly from higher altitudes than the presumed coastal habitat characterized by *Classopollis* (Pocock & Jansonius 1961), and became richer in *Podocarpites* and *Zonalapollenites* pollen. Sedimentation under regressive marine conditions occurred at both sites during the Aptian to Cenomanian stages (Haq *et al.* 1987).

Zone CII is an Early Cretaceous/Late Cretaceous transition zone dated by SOEKOR as Aptian to Turonian in age and Zone OII is dated as Aptian to Albian. The assemblages in both zones are interpreted as Early Cretaceous based on the presence of *Gleicheniidites radiatus,* a species common only to the Aptian. Several palynomorphs also occur in a Late Cretaceous to younger age range such as *Bytneripollis coronaries, Divisisporites divisus, D. euskirchenensis* and *Stereisporites electoides* to name a few.

LATE CRETACEOUS PERIOD (CENOMANIAN TO CAMPANIAN STAGES)

Zones CIII and OIII

The sediments comprising the assemblages of Zones CIII and OIII accumulated during the middle part of the continental drift phase. In comparison to Zones CII and OII, the Cheirolepidacean woodlands gradually repopulated the coastal regions. The higher altitudes were probably covered in dense, evergreen forests of Gymnosperms that produced the pollen species *Excesipollenites* and *Podocapidites* (Srivastava 1976, 1978). Ferns (*Cyathidites, Gleicheniidites* and *Cicatricosisporites* families) and mosses formed the ground cover in the sheltered understories of the forests and woodland regions. A diversity of pteridophyte spores, particularly the presence of *Cyathidites* (Aboula Ela & Mabrouk 1978), and the more abundant *Gleichenia*-like spores and more diverse schizaeaceous derivatives would seem to indicate warmer climatic conditions (Dettmann 1981). Haq *et al.* 1987 indicate that a regression occurred during the Turonian Stage of this zone.

Several angiosperm pollen species, all of them also extending into the Palaeogene, appeared at intervals throughout Zones CIII and OIII. Especially in the case of C–B1 some of these forms have been found in side wall cores, which suggest that this is not simply a case of down-hole contamination. SOEKOR's microfaunal datings indicate a Turonian to middle Coniacian age for both Zones CIII and OIII. However, *Buttinia andreevii,* often found in the Maastrichtian, has been reported by several authors from western Africa and northern South America (Herngreen 1975; Vajda-Santivanez 1999; Vajda & McLoughlin 2005). It does appear for the first time in side-wall cores of Zones OIII and CIII generally supporting a Late Cretaceous age, therefore possibly occurring earlier here than in other records where it is usually found.

Zones CIV and OIV

The sediments representing Zones CIV and OIV accumulated during the middle of the continuing drift phase of continental separation. The presumed high and low altitude palynomorph flora of the previous zones appears to have changed character as a result of shifting vegetation belts. The sea level was high (Haq *et al.* 1987) and stable during this period.

The conifer-dominated woodlands changed noticeably during the deposition of sediments of Zones CIV and OIV. In Zone CIV *Classopollis torosus* sharply increased in relative abundance and peaks at percentages similar to those suggested for Zone CI (Barremian Stage). In comparison the same species of *Classopollis* sharply declined in abundance within Zone OIV. Ferns and mosses, however, continued to dominate the palaeoflora with the most prevalent members continuing to include the long-ranging *Gleicheniidites, Cicatricosisporites* and *Cyathidites* groups. The presence of *Cyathidities* (Aboula Ela & Mabrouk 1978), *Gleicheniidites* and the more diverse schizaeaceous spores supports warm, humid climatic conditions in the lower altitudes (Dettmann 1981). *Buttinia andreevii* and *Tetracolporites ixerboides* represent an established long-ranging angiosperm flora. Palynomorphs in Zone OIV, suggests the higher altitudes continue to be covered in dense, evergreen forests including *Podocarpidites, Microcachryidites* as well as *Exesipollenites*-producing conifers.

A middle to late Coniacian age range has been suggested for Zones CIV and OIV. As with the previous zones, the palynomorph flora gives very little indication as to the specific age of these zones.

Zones CV and OV

Zone CV (includes subzones CV-A and CV-B) and OV are Late Cretaceous in age and both reflect a shift in sporomorph composition that may in part be a result of selection due to longer transport as the distance from the shore increased. By the late drift phase, the South Atlantic had expanded considerably and deepened to more than 4 km (Thierde & van Andel 1977). Seas were transgressive, up to 200 m higher than today during this Late Cretaceous Period (Haq *et al.* 1987). Zones CV and OV are characterized by a high diversity of angiosperm as well as tropical African palm pollen which signalled a climatic shift from hot and semi-arid to a mixed warm, temperate and humid climate. This setting is reminiscent of the Palmae Province of Herngreen & Chlonova (1981).

Only remnants of the once dense cheirolepidacean woodlands of Zone CI to CIV and OI to OIV remained in both Zones CV and OV. This sudden change may be a result of very high sea levels inundating the low-lying coastal regions thereby terminating once flourishing plant communities.

In Zone CV, the continued diversity and abundance of the pteridophyte spores, particularly the presence of *Cyathidites,* more diverse schizaeaceous spores (*Cicatricosisporites*) and pollen, (*Dorreenipites* sp., *Andreisporis mariae* and *Constantisporis jacquei*) that appear for the first time at the close of this zone, indicates an adaptation to ever changing conditions. Only a few podocarp species remain of the previous diverse high altitude flora. In comparison to Zone CV, the palynomorph flora of Zone OV exhibits a sudden decrease in the diversity of ferns and mosses along with a change in the composition of forests. This change as mentioned earlier could be a result of an advancing sea. The *Gleicheniidites, Cicatricosisporites* and *Cyathidites* species are still present but low in abundance. *Dorreenipites* sp. is the only palm pollen present in this zone unlike Zone CV where numerous members of the palm families are present. The forests, however, continue to support species that include *Exesipollenites, Podocarpidites* and *Microcachryidites.*

Both Zones CV (including subzones CV-A and CV-B) and OV are late Coniacian to Campanian in age. None of the palynomorphs identified in either zone could confirm this age assignment since there are no certain indicator species present.

DISCUSSION AND CONCLUSION

Five palynological zones each, have been defined within the Cretaceous intervals of the two wells studied. Gymnosperms are represented at both well sites by the pollen genera *Classopollis, Podocarpaceae, Zonalapollenites, Balmeiopsis* and *Exesipollenites.* Spores of *Cyathidites, Gleicheniidites* and other schizeaceous types dominated the spore population.

The pollen and spore assemblages of the Early Cretaceous part of the studied well sections are both dominated by gymnosperm pollen (mainly *Classopollis* with fewer saccates) and fern spores, despite their 300 km wide geographic separation, suggesting that the vegetation of the provenance areas from which the spores and pollen derived were relatively homogeneous.

However, during the Late Cretaceous, the spore and pollen assemblages at the two well sites show significant differences but at both locations, angiosperm pollen (including characteristic marker species such as *Buttinia andreevii* and *Bytneripollis coronaries*) is more abundant and diverse. Within the Campanian interval, the angiosperm palynoflora shares many of the characteristics of the Paleogene assemblages (Scholtz 1985).

Our tentative reconstruction of the palaeoflora has been based on the known botanical affinities of the palynomorphs. Considering the current montane habitat of podocarp forests, we may speculate that the Cretaceous forests, which included *Podocarpaceae, Microcachryidites* and *Exesipollenites,* occurred at cooler higher-lying regions on the edges of the newly developing rift valley than the warmer coastal areas that were more typically associated with *Classopollis* (Pocock & Jansonius 1961). The undergrowth included varieties of ferns (*Cyathidites* and other shizeaceous plants) and mosses.

We thank the Petroleum Agency SA for providing the palynological slides from offshore wells C-B1 and O-A1 for this research and for permission to publish the results. Funding by the University of the Free State for A. Sandersen and by the National Research Foundation (NRF) for L. Scott (GUN 2053236) is gratefully acknowledged. Any opinions, findings, and conclusions are those of the authors and the NRF does not accept any liability in regard thereto. We thank Ann Cadman and Marion Bamford for initiating the project.

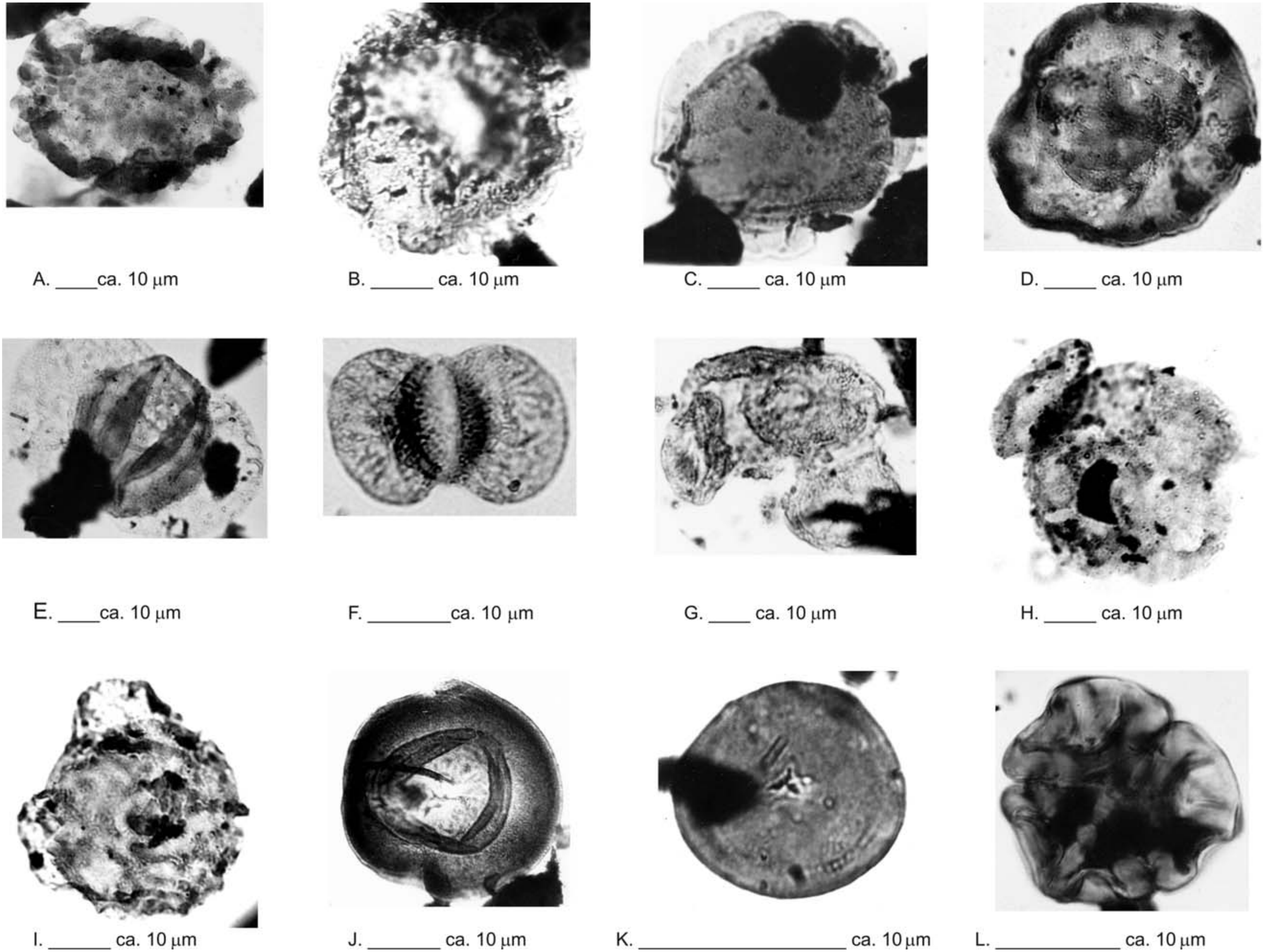

Figure 4. **A**, *Zonalapollenites dampieri* Balme, 1957. **B**, *Zonalapollenites segmentatus* Balme, 1957. **C**, *Zonalapollenites trilobatus* Balme, 1957. **D**, *Zonalapollenites turbatus* Balme, 1957. **E**, *Podocarpidites ellipticus* Cookson, 1947. **F**, *Podocarpidities* sp. **G**, *Cedriptes* sp. **H**, *Lactoripollenites* cf. *L. africanus* Zavada & Benson, 1987. **I**, *Microcachryidites antarcticus* (Cookson) Couper, 1953. **J**, *Balmeiopsis limbatus* (Balme) Archangelsky, 1977 emend. Norvick & Burger, 1976. **K**, *Exesipollenites tumulus* Balme, 1957. **L**, *Harrisipollenites* sp.

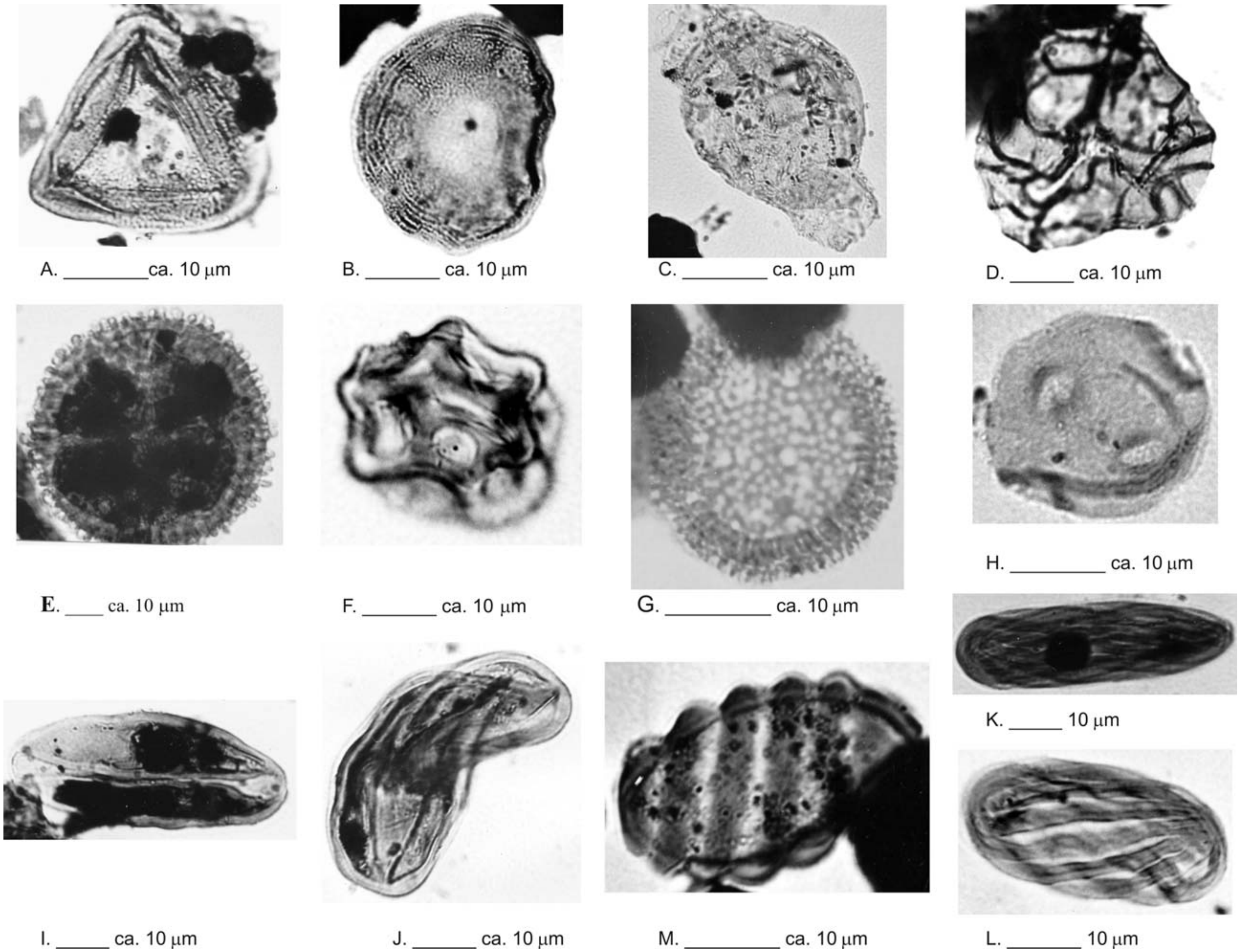

Figure 5. **A**, *Classopollis* cf. *C. echinatus* Burger, 1965. **B**, *Classopollis torosus* (Reissinger, 1950; Balme, 1957) Couper, 1958 emend. Burger, 1965. **C**, *Diporites aspis* Pocknall & Mildenhall, 1984. **D**, *Lycopodiumsporites* sp. **E**, *Quadraplanus brossus* Stover, 1973. **F**, *Buttinia andreevii* Boltenhagen, 1967. **G**, *Buxaceaepollenites cainozoicus* Sah, 1967. **H**, *Bytneripollis coronarius* Konzalová, 1976. **I**, *Ginkocycadophytus nitidus* (Balme) De Jersey, 1962. **J**, *Ephedripites* sp. 1. **K**, *Ephedripites* sp. 2. **L**, *Ephedripites* sp. 3. **M**, Ephedripites sp. 4.

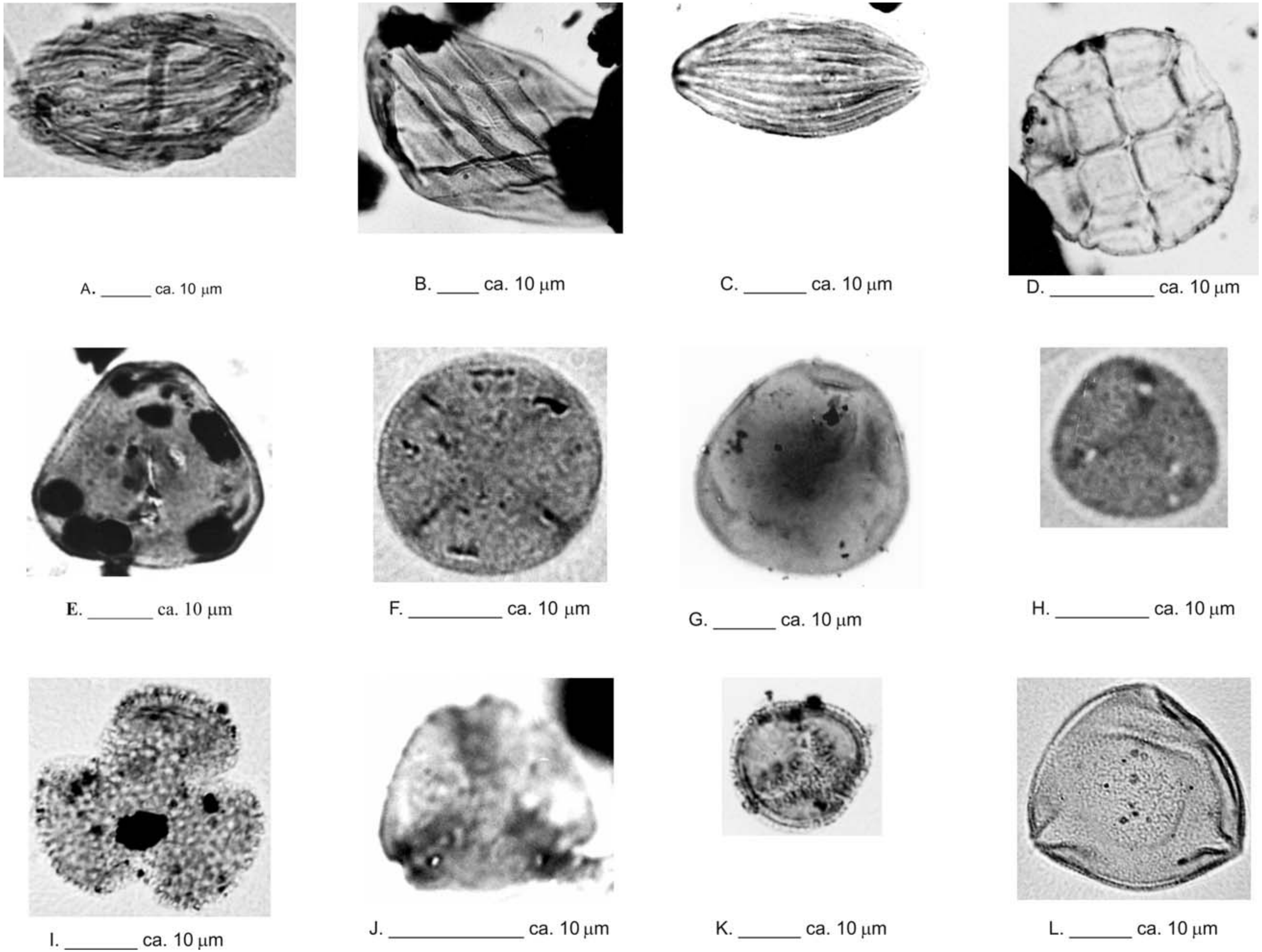

Figure 6. **A**, *Ephedripites* sp. 5. **B**, *Ephedripites* sp. 6. **C**, *Steevipollenites* sp. **D**, *Acaciapollenites myriosporites* (Cookson) Mildenhall, 1972 ex Jansonius & Hills, 1976. **E**, *Andreisporis* cf. *A. mariae* Belsky, Boltenhagen & Potonié, 1965. **F**, *Constantinisporis jacquei* Belsky, Boltenhagen & Potonié, 1965. **G**, *Dorreenipites* sp. **H**, *Victorisporis robertii* Belsky, Boltenhagen & Potonié, 1965. **I**, *Crototricolpites* sp. **J**, *Margocolporites* sp. **K**, *Liliacidites trichotomosulcatus* Singh, 1971. **L**, *Orbiculapollis globosus* Chlonova, 1961.

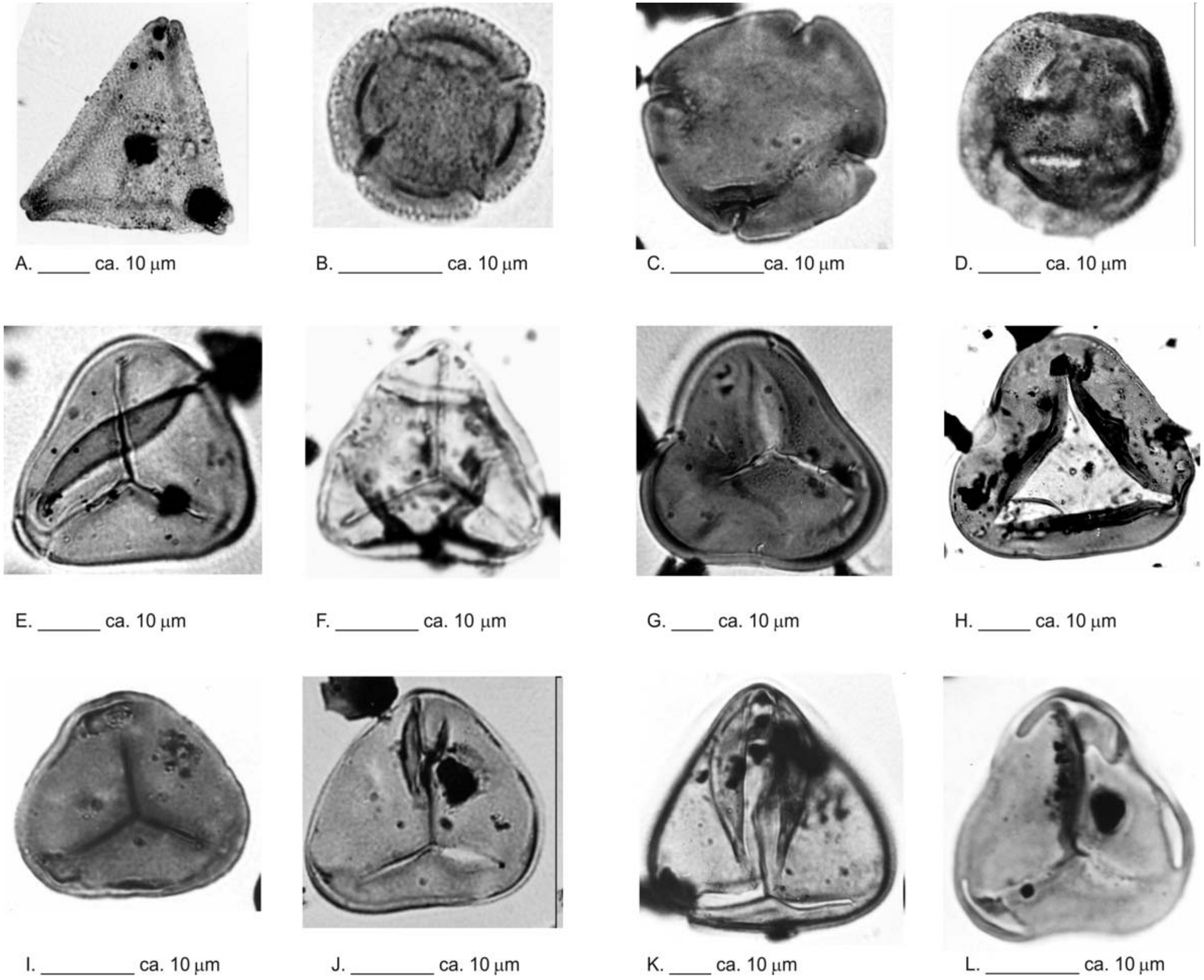

Figure 7. **A**, *Triangulorites pachyexinus* Kar & Kumar, 1986. **B**, *Tetracolporites* ixerboides Pocknall & Mildenhall, 1984. **C**, *Tetracolporites spectabilis* Pocknall & Mildenhall, 1984. **D**, *Tetracolporites sphericus* Couper, 1960 emend. Pocknall & Mildenhall, 1984. **E**, *Biretisporities potoniaei* Delcourt & Sprumont, 1955 & 1959. **F**, *Concavisporites obtusangulus* (Potonié) Krutzsch, 1959. **G**, *Cyathidites australis* Couper, 1953. **H**, *Cyathidites australis rimulis* Balme, 1957. **I**, *Cyathidites punctatus* (Delcourt & Sprumont) Delcourt, Dettmann & Hughes, 1963. **J**, *Cyathidites kerguelensis* Cookson, 1947. **K**, *Cyathidites major splendens* Harris, 1965. **L**, *Cyathidites minor* Couper, 1953.

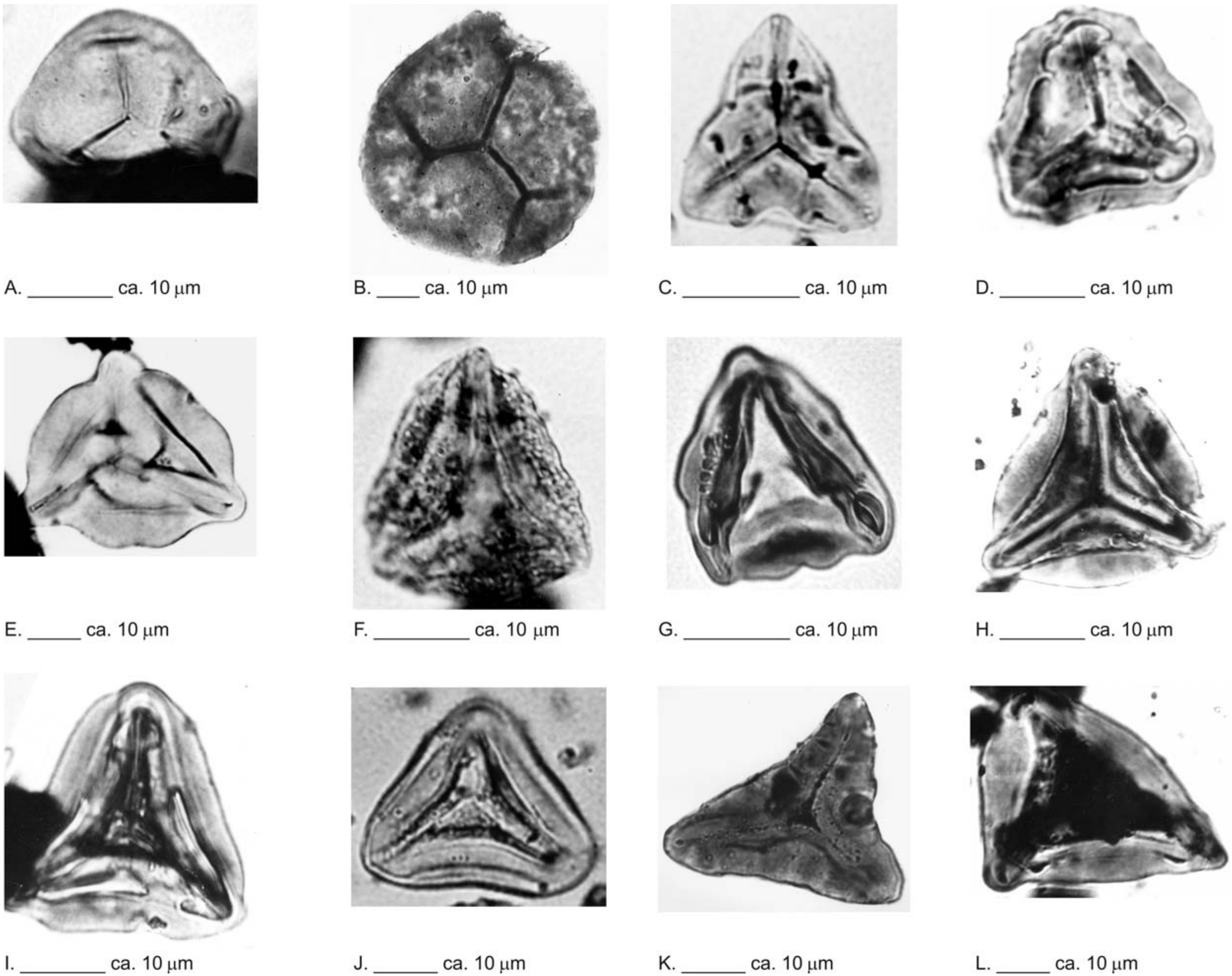

Figure 8. **A**, *Divisisporites divisus* Pflug, 1953. **B**, *Divisisporites euskirchenensis* (Thompson) Thompson & Pflug, 1953. **C**, *Gleicheniidites apilobatus* Brenner, 1963. **D**, *Gleicheniidites circindites* (Cookson) Dettmann, 1963. **E**, *Gleicheniidites feronensis* (Delcourt & Sprumont) Delcourt & Sprumont, 1959. **F**, *Gleicheniidites peregrinus* Krutzsch, 1959. **G**, *Gleicheniidites radiatus* (Bolkhovitina) Krutzsch, 1959. **H**, *Gleicheniidites rasilis* (Bolkhovitina) Krutzsch, 1959 **I**, *Gleicheniidites senonicus* Ross, 1949. **J**, *Gleicheniidites toriconcavus* Krutzsch, 1959. **K**, *Gleicheniidites* sp. **L**, *Gleichenites limbatus* Agranovskaja, 1960.

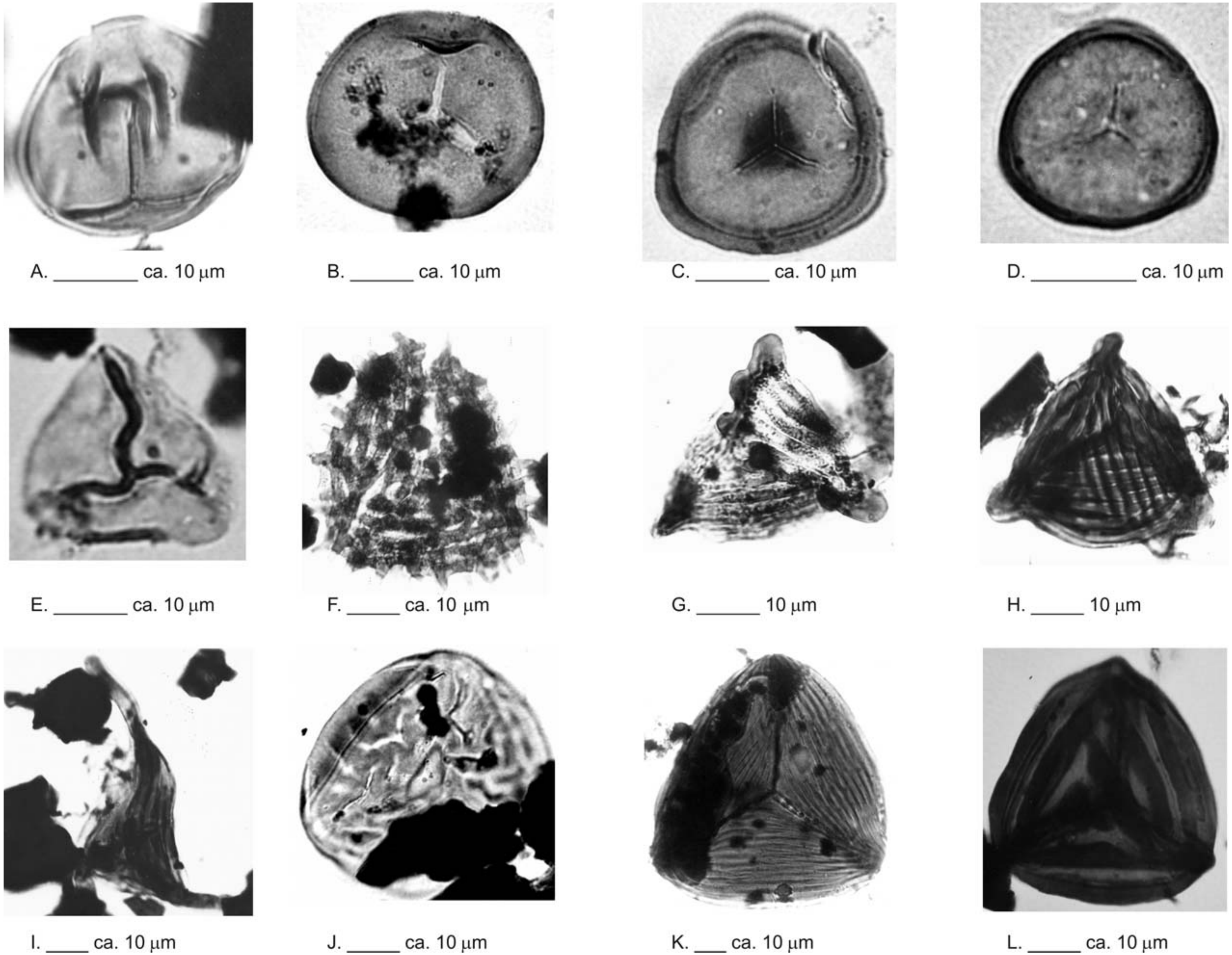

Figure 9. **A**, *Mediobaculisporis mediobaculatus* Krutzsch, 1959. **B**, *Psilatriletes radiatus* Brenner, 1963. **C**, *Stereisporites electoides* Krutzsch, 1963. **D**, *Stereisporites stereoides* (Potonié & Venitz) Pflug, 1953. **E**, *Undulatisporites microcutis* Pflug, 1953. **F**, *Appendicisporites dentimarginatus* Brenner, 1963. **G**, *Appendicisporites matesovae* (Bolkhovitina) Norris, 1967. **H**, *Appendicisporites tricorinatatus* Weyland & Greifeld, 1953. **I**, *Appendicisporites tricuspidatus* Weyland & Greifeld, 1953. **J**, *Camarozonosporites cretaceus* (Weyland & Krieger) Potonié 1956. **K**, *Cicatricosisporites australiensis* (Cookson) Potonié, 1956. **L**, *Cicatricosisporites hughesii* Dettmann, 1963.

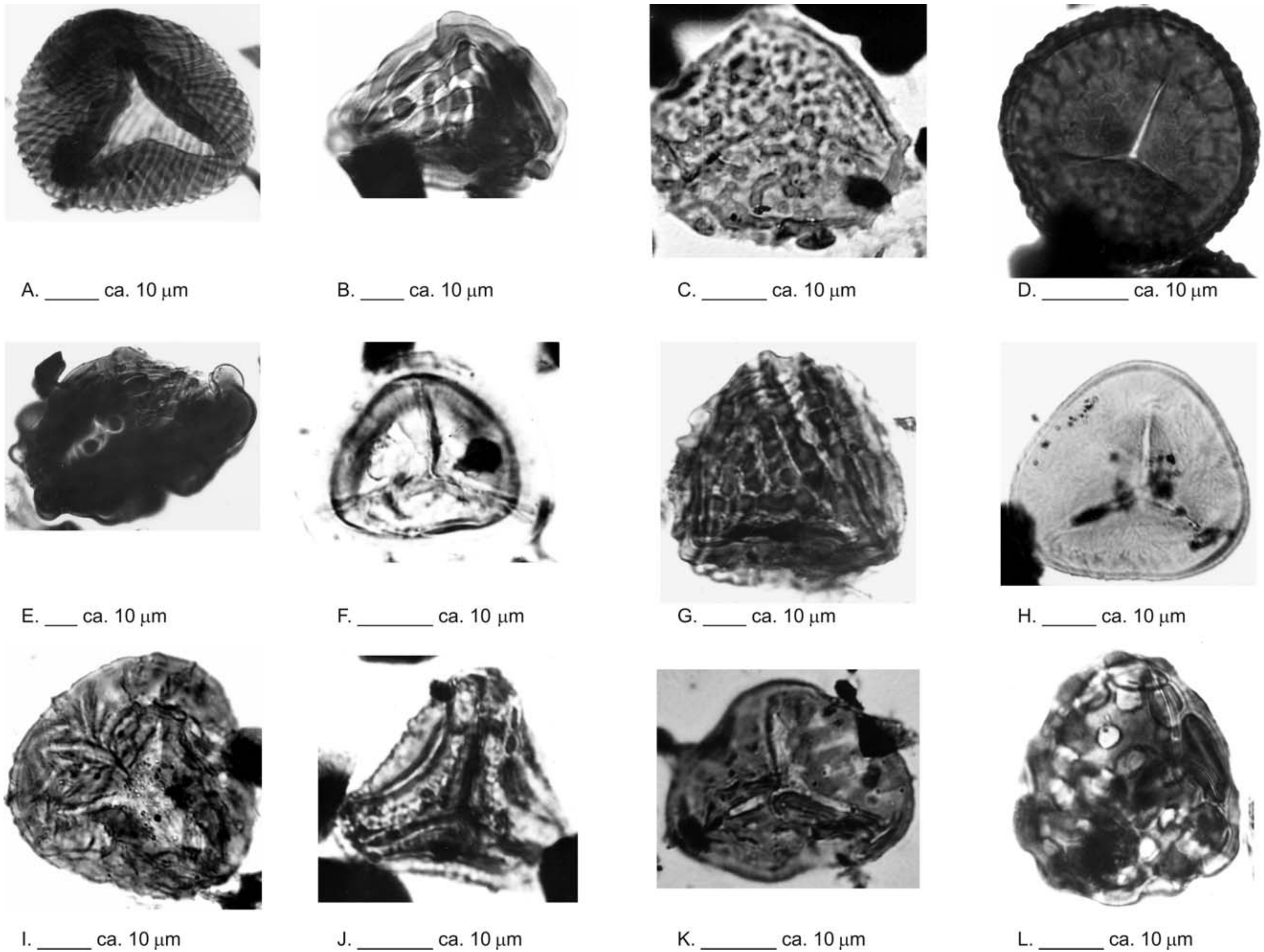

Figure 10. **A**, *Cicatricosisporites venustus* Deâk, 1963. **B**, *Contignisporites* sp. **C**, *Ghoshiatriletes gondwanensis* D'rozario & Banerjee, 1989. **D**, *Hamulatisporites hamulatus* Krutzsch, 1959. **E**, *Nodosisporites costatus* Deâk, 1964. **F**, *Staplinisporites caminus* (Balme), Pocock, 1962. **G**, *Striatella seebergensis* Mädler, 1964. **H**, *Tigrisporites halleinis* Klaus, 1960. **I**, *Triplexisporites playfordii* (de Jersey & Hamilton) Foster, 1979. **J**, *Foveogleicheniidites confossus* (Hedlund) Burger, 1976. **K**, *Foveosporites canalis* Balme, 1957. **L**, *Ischyosporites crateris* Balme, 1957.

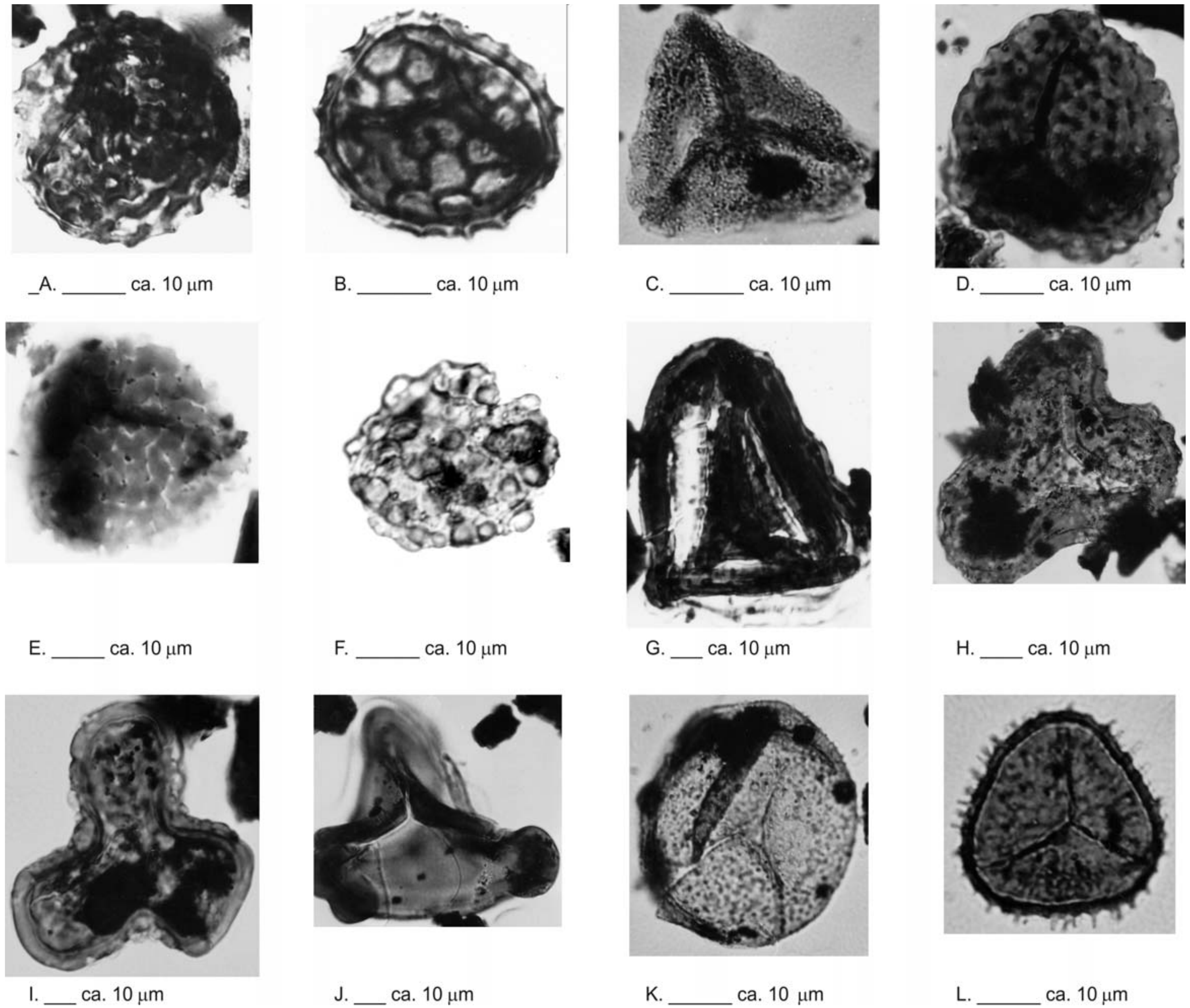

Figure 11. **A**, *Klukisporites variegatus* Couper, 1958. **B**, *Lycopodiumsporites reticulum* (Rouse) Dettman, 1963. **C**, *Microreticulatisporites parviretis* Balme, 1957. **D**, *Scrobiculifoveotriletes* sp. **E**, *Corrugatisporites* sp. **F**, *Gemmatriletes morulus* Pierce, 1961. **G**, *Trilobosporites* sp. 1, **H**, *Trilobosporites* sp. 2. **I**, *Trilobosporites* sp. 3. **J**, *Trilobosporites* sp. 4. **K**, *Osmundacidites wellmanii* Couper, 1953. **L**, *Ceratosporites equalis* Cookson & Dettmann, 1958.

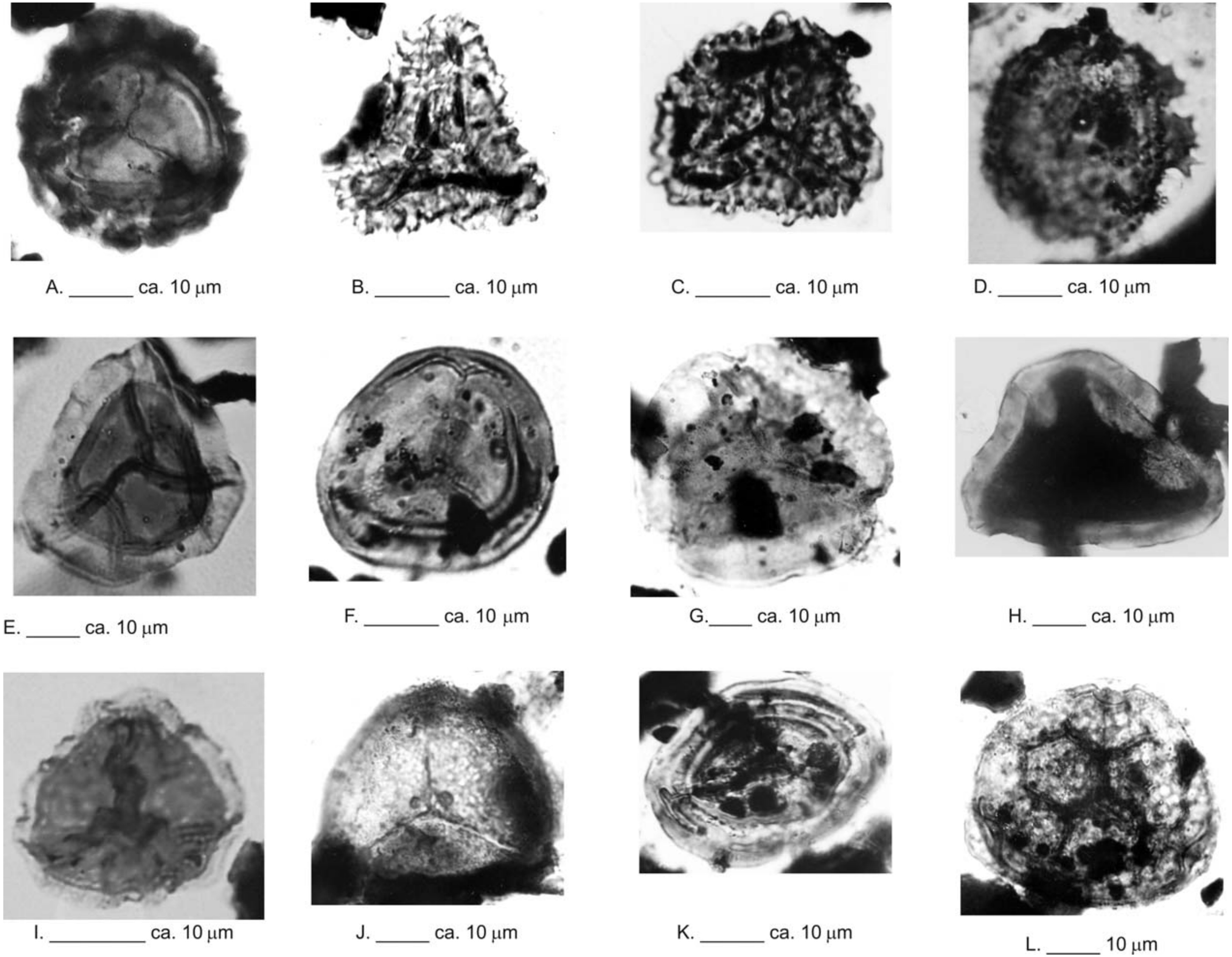

Figure 12. **A**, *Luberisporites luberi* Nakoman, 1976. **B**, *Ornamentifera echinata* (Bolkhovitina, 1953) Bolkovitina, 1966. **C**, *Ornamentifera tuberculatus* (Grigorjeva) Bolkovitina, 1966. **D**, *Raistrickia grovensis* Schopf, Wilson & Bentall, 1944. **E**, *Perotriletes granulatus* Couper, 1953. **F**, *Cingulatisporites levispeciosus* Pflug, 1953. **G**, *Murospora florida* (Balme) Pocock, 1961. **H**, *Murospora florida* (Balme) Pocock, 1961. **I**, *Undulatitriletes hertensis* Klein, 1959. **J**, *Densoisporites microrugulatus,* Brenner, 1963. **K**, *Taurocusporites reduncus* (Bolkhovitina) Stover 1962. **L**, *Rouseisporites reticulatus* Pocock, 1962.

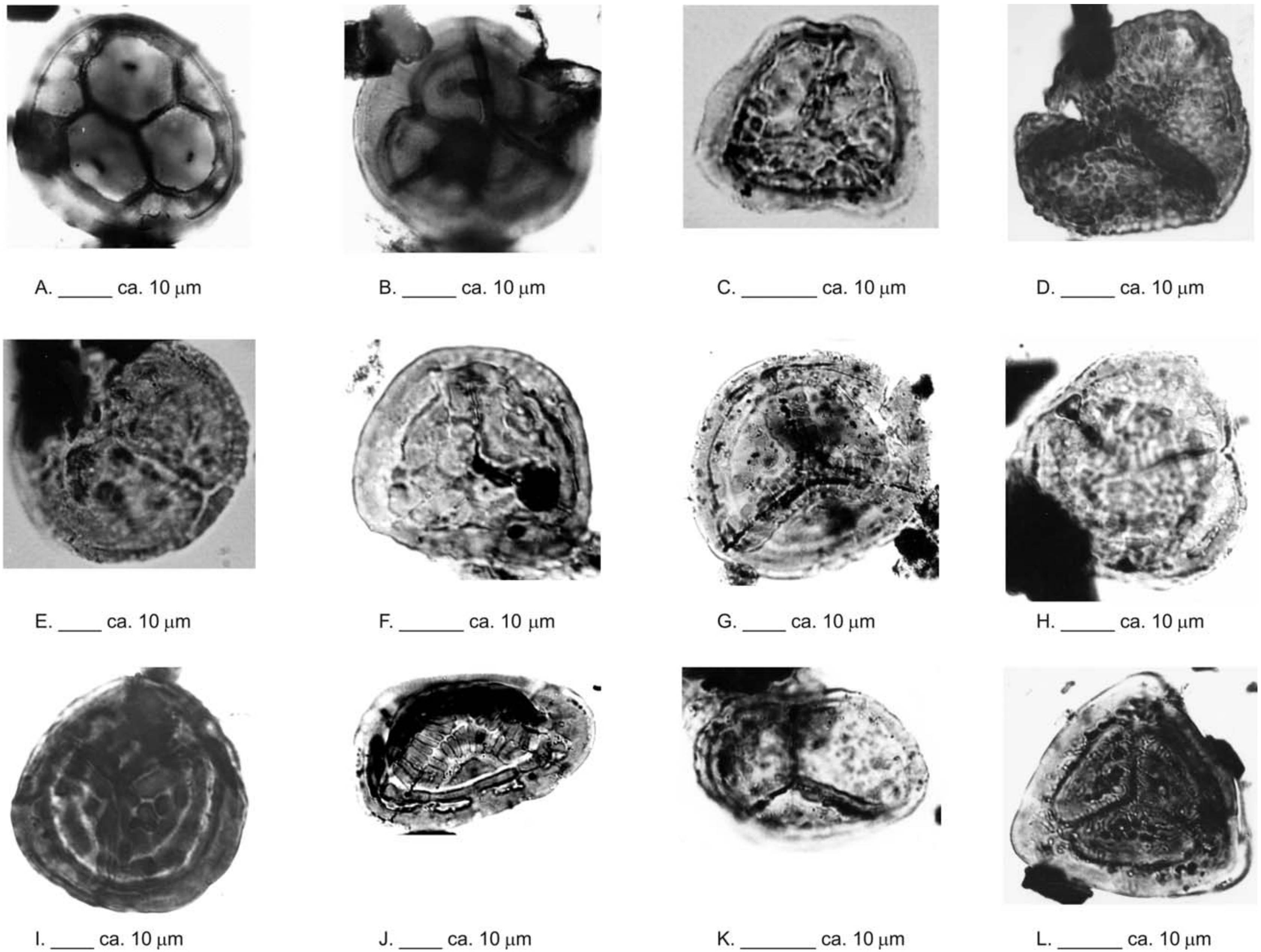

Figure 13. **A**, *Zlivisporis blanensis* Pacltová, 1961. **B**, *Zlivisporis* sp. **C**, *Asbeckiasporites wirthii* von der Brelie, 1964. **D**, *Foraminisporis asymetricus* (Cookson & Dettmann) Dettmann, 1963. **E**, *Foraminisporis foraminis* Krutzsch, 1959. **F**, *Interulobites algoensis* Scott, 1976. **G**, *Nevesisporites tribullatus* Nakoman, 1976. **H**, *Nevesisporites vallatus* De Jersey & Paten, 1964. **I**, *Taurocusporites segmentatus* Stover, 1962. **J**, *Taurocusporites* sp. **K**, *Antulsporites baculatus* (Archangelsky & Gamerro) Archangelsky & Gamerro, 1966b. **L**, *Cyatheacidites annulatus* (Cookson) Potonié, 1956.

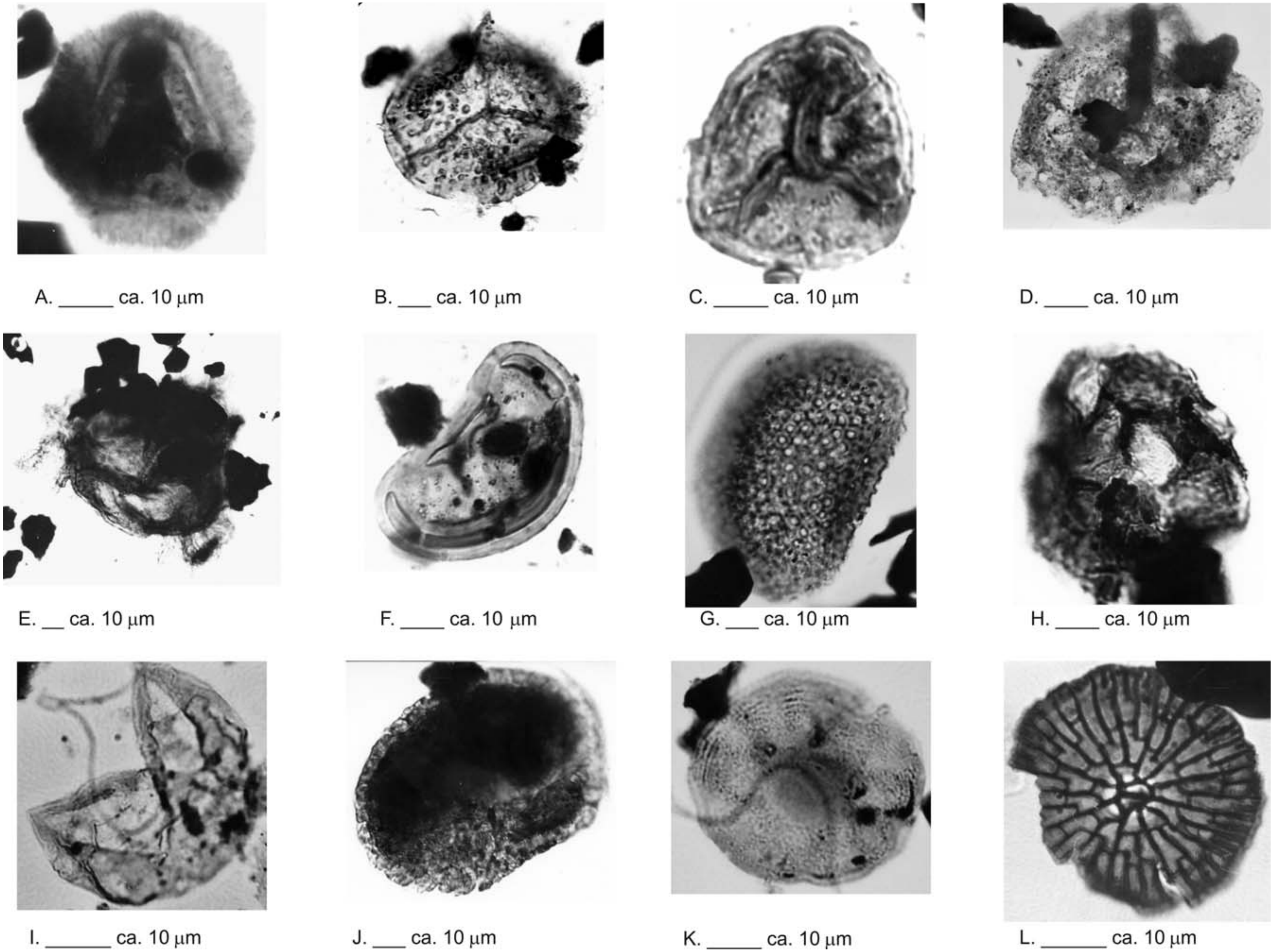

Figure 14. **A**, *Diatomozonotriletes* sp. **B**, *Indotriletes explanatus* (Luber) Playford, 1991. **C**, *Undulatitriletes* sp. **D**, *Zonalasporites arcusus* Balme 1957. **E**, *Balmeisporites* sp. **F**, *Laevigatosporites* sp. **G**, *Ischyomonoletes* sp. **H**, *Sphaeroplea* sp. **I**, *Ovoidites* sp. **J**, *Schizosporis reticulatus* Cookson & Dettmann, 1959 emend. Pierce, 1976. **K**, *Chomotriletes* sp. **L**, *Microthyriacites* sp.

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Appendix 1. Species list of palynomorphs from offshore wells C-B1 and O-A1 (Figs 4–14).

Gymnosperm pollen
Balmeiopsis limbatus (Balme) Archangelsky, 1977 emend. Norvick & Burger, 1976
Cedripites sp.
Classopollis cf. *C. echinatus* Burger, 1965
Classopollis torosus (Reissinger, 1950; Balme, 1957) Couper, 1958 emend. Burger, 1965
Diporites aspis Pocknall & Mildenhall, 1984
Ephedripites sp. 1
Ephedripites sp. 2
Ephedripites sp. 3
Ephedripites sp. 4
Ephedripites sp. 5
Ephedripites sp. 6
Exesipollenites tumulus Balme, 1957
Ginkocycadophytus nitidus (Balme) De Jersey, 1962
Lactoripollenites cf. *L. africanus* Zavada & Benson, 1987
Microcachryidites antarcticus (Cookson) Couper, 1953
Podocarpidites ellipticus Cookson, 1947
Podocarpidities sp.
Steevipollenites sp.
Zonalapollenites dampieri Balme, 1957
Zonalapollenites segmentatus Balme, 1957
Zonalapollenites trilobatus Balme, 1957
Zonalapollenites turbatus Balme, 1957

Angiosperm pollen
Acaciapollenites myriosporites (Cookson) Mildenhall, 1972 ex Jansonius & Hills, 1976
Andreisporis mariae Belsky, Boltenhagen & Potonié, 1965
Buttinia andreevii Boltenhagen, 1967
Buxaceaepollenites cainozoicus Sah, 1967
Bytneripollis coronarius Konzalová, 1976
Constantinisporis jacquei Belsky, Boltenhagen & Potonié, 1965
Crototricolpites sp.
Dorreenipites sp.
Harrisipollenites sp.
Liliacidites trichotomosulcatus Singh, 1971
Margocolporites sp.
Orbiculapollis globosus Chlonová, 1961
Quadraplanus brossus Stover, 1973
Tetracolporites ixerboides Pocknall & Mildenhall, 1984
Tetracolporites spectabilis Pocknall & Mildenhall, 1984
Tetracolporites sphericus Couper, 1960 emend. Pocknall & Mildenhall, 1984
Triangulorites pachyexinus Kar & Kumar, 1986
Victorisporis robertii Belsky, Boltenhagen & Potonié, 1965

Pteridophyte and Bryophyte spores
Antulsporites baculatus (Archangelsky & Gamerro) Archangelsky & Gamerro, 1966b
Appendicisporites dentimarginatus Brenner, 1963
Appendicisporites matesovae (Bolkhovitina) Norris, 1967
Appendicisporites tricorinatatus Weyland & Greifeld, 1953
Appendicisporites tricuspidatus Weyland & Greifeld, 1953
Asbeckiasporites wirthii von der Brelie, 1964
Balmeisporites sp.
Biretisporites potoniaei Delcourt & Sprumont, 1955
Camarozonosporites cretaceus (Weyland & Krieger) Potonié, 1956
Ceratosporites equalis Cookson & Dettmann, 1958
Cicatricosisporites australiensis (Cookson) Potonié, 1956
Cicatricosisporites hughesii Dettmann, 1963
Cicatricosisporites venustus Deâk, 1963
Cingulatisporites levispeciosus Pflug, 1953
Concavisporites obtusangulus (Potonié) Krutzsch, 1959
Contignisporites sp.
Corrugatisporites sp.
Cyatheacidities annulatus (Cookson) Potonié, 1956
Cyathidites australis Couper, 1953
Cyathidites rimulis Balme, 1957
Cyathidites kerguelensis Cookson, 1947
Cyathidites splendens Harris, 1965
Cyathidites minor Couper, 1953
Cyathidites punctatus (Delcourt & Sprumont) Delcourt, Dettmann & Hughes, 1963
Densoisporites microrugulatus, Brenner, 1963
Diatomozonotriletes sp.
Divisisporites divisus Pflug, 1953

Divisisporites euskirchenensis non Thompson; Cookson & Dettmann, 1958
Foraminisporis asymetricus Krutzsch, 1959
Foraminisporis foraminis Krutzsch, 1959
Foveogleicheniidites confossus (Hedlund) Burger, 1976
Foveosporites canalis Balme, 1957
Gemmatriletes morulus Pierce, 1961
Ghoshiatriletes gondwanensis D'rozario & Banerjee, 1989
Gleicheniidites apilobatus Brenner, 1963
Gleicheniidites circindites (Cookson) Dettmann, 1963
Gleicheniidites feronensis (Delcourt & Sprumont) Delcourt & Sprumont, 1959
Gleicheniidites radiatus (Bolkhovitina) Krutzsch, 1959
Gleicheniidites rasilis (Bolkhovitina) Krutzsch, 1959
Gleicheniidites senonicus Ross, 1949
Gleicheniidites sp.
Gleicheniidites toriconcavus Krutzsch, 1959
Gleichenites limbatus Agranovskaja, 1960
Hamulatisporites hamulatus Krutzsch, 1959
Indotriletes explanatus (Luber) Playford, 1991
Interulobites algoensis Scott, 1976
Ischyomonoletes sp.
Ischyosporites crateris Balme, 1957
Klukisporites varigatus Couper, 1958
Laevigatosporites sp.
Luberisporites luberi Nakoman, 1976
Lycopodiumsporites sp.
Lycopodiumsporites reticulumsporites (Rouse) Dettmann, 1963
Mediobaculisporis mediobaculus Krutzsch, 1959
Microreticulatisporites parviretis Balme, 1957
Murospora florida (Balme) Pocock, 1961
Murospora truncata Singh, 1971
Nevesisporites tribullatus Nakoman, 1976
Nevesisporites vallatus De Jersey & Paten, 1964
Nodosisporites costatus Deâk, 1964
Ornamentifera echinata (Bolkhovitina) Bolkhovitina, 1966
Ornamentifera tuberculatus Bolkovitina, 1966
Osmundacidites wellmanii Couper, 1953
Perotriletes granulatus Couper, 1953
Psilatriletes radiatus Brenner, 1963
Raistrickia grovensis Schopf, Wilson & Bentall, 1944
Rouseisporites reticulatus Pocock, 1962
Scrobiculifoveotriletes sp.
Staplinisporites caminus (Balme) Pocock, 1962
Stereisporites electoides Krutzsch, 1963
Stereisporites stereoides (Potonié & Venitz, 1934) Pflug, 1953
Striatella seebergensis Mädler, 1964
Taurocusporites reduncus Bolkhovitina, 1962
Taurocusporites segmentatus Stover, 1962
Taurocusporites sp.
Tigrisporites halleinis Klaus, 1960
Trilobosporites sp. 1
Trilobosporites sp. 2
Trilobosporites sp. 3
Trilobosporites sp. 4
Triplexisporites playfordii (de Jersey & Hamilton) Foster, 1979
Undulatisporites microcutis Pflug, 1953
Undulatitriletes hertensis Klein, 1959
Undulatitriletes sp.
Zlivisporis blanensis Pacltová, 1961
Zlivisporis sp.
Zonalasporites arcusus Balme, 1957

Algae
Ovoidites sp.
Schizosporis reticulatus Cookson & Dettmann, 1959
Sphaeroplea sp.

Incertae sedis
Chomotriletes sp.

Fungi
Microthyriacites sp.

Cretaceous faunas from Zululand and Natal, South Africa. The ammonite subgenus *Hauericeras* (*Gardeniceras*) Matsumoto & Obata, 1955[‡]

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Four species of the distinctive desmoceratid ammonite *Hauericeras* (*Gardeniceras*) Matsumoto & Obata, 1955, are described from KwaZulu-Natal and the Eastern Cape Province: the type species, *H.* (*G.*) *gardeni* (Baily, 1855), from the Santonian to Lower Campanian, *H.*(*G.*) *pseudoangustum* Collignon, 1961, and *H.* (*G.*) *madagascariense* Collignon, 1961, from the Lower Campanian, and *H.* (*G.*) *rembda* (Forbes, 1846) from the upper Upper Maastrichtian.

Keywords: ammonites, *Hauericeras* (*Gardeniceras*), Santonian, Campanian, Cretaceous, KwaZulu, Eastern Cape Province, South Africa.

INTRODUCTION

Hauericeras (*Gardeniceras*) *gardeni* (Baily, 1855) is one of the most distinctive and immediately recognizable ammonites from the Santonian–Campanian Mzamba Formation of the coastal outcrops in the northeast of the Eastern Cape Province. In the cliff outcrops of the St Lucia Formation on the northwestern shores of False Bay, in KwaZulu-Natal, the species is abundant, sometimes occurring as imbricate stacks of individuals lying inclined at a low angle to bedding, and overlapping like roof tiles. The distinctive keel of the genus led Matsumoto (1938) to introduce a subfamily Hauericeratinae, supported in more extensive discussions by Matsumoto & Obata (1955) and Matsumoto *et al.* (1990); the subgenus *Gardeniceras* was introduced by Matsumoto & Obata (1955, p. 134) for the 'Fairly evolute and fairly widely umbilicate subgroup of *Hauericeras*' and later (Matsumoto *in* Matsumoto *et al.* 1990, p. 456) redefined as 'a subgroup of *Hauericeras* in which ventral or ventrolateral riblets or nodes disappeared completely'. Wright (1957, p. L371; 1996, p. 85) retained the subfamily, and defined it as follows (the phrase in italics was our addition to the 1996 account): 'Rather evolute to rather involute; whorl section high, with flat sides, venter rounded (at least initially), then typically fastigiate, and later with high sharp septicarinate keel. Smooth or with weak tubercles on the shoulders. *Microconchs with lappets.* Suture with suspensive lobe retracted or not.… Origin is doubtful, either in Desmoceratinae close to point of origin of Muniericeratidae or *Parapuzosia* of Puzosiinae.' Wright defined *Hauericeras* as having 'characters as for subfamily', and noted that 'Separation of *Gardeniceras* for the less involute forms seems unnecessary.' Apart from *Hauericeras,* the genera *Mossamedites* Cooper, 2003a, and *Oiophyllites* Spath, 1953, have been referred to the Hauericeratinae. The latter is based on tiny desmoceratoidean nuclei and is best treated as a *nomen dubium.*

In introducing his new genus *Hauericeras,* de Grossouvre (1894, p. 219) stated that '…Je donne ce nom à la série de formes se rattachant à *Ammonites gardeni…*', but took *Ammonites pseudogardeni* Schlüter, 1872, p. 54, pl. 16, figs 3–6, as type species. *Hauericeras* (*Hauericeras*) *pseudogardeni* has been revised in detail by Kaplan & Kennedy (1995, p. 18, pls 1–4, pl. 5, figs 1–2; pl. 6, figs 1, 7; pls 7, 8) and Kaplan *et al.* (2006, p. 31, pl. 1, figs 4, 7, 9, 11–12). These authors redescribed the type material from Dülmen in Westphalia, and additional specimens from Braunschweig in Lower Saxony, Germany. From the material available it seems that internal moulds may be virtually smooth (but for constrictions), whereas the shell surface and composite moulds bear ribs/tubercles on the outer flanks and ventrolateral shoulders. But even some composite moulds are virtually smooth, although this might be due to postmortem effects. If this interpretation is accepted, variety *nodatum* of Schlüter (1899) and *Hauericeras buszii* Wegner, 1905 (p. 209, pl. 8, fig. 1a, b) are synonyms of *pseudogardeni.* The illustrations of the species in Müller & Wollemann (1906) of material from Braunschweig, included constricted ribbed/nodate phragmocones up to 160 mm diameter (1906, pl. 4, fig. 1; pl. 8, fig. 3) as well as smooth, delicately constricted juveniles. Matsumoto *in* Matsumoto *et al.* 1990 (p. 451) thought *Ammonites mengedensis* Schlüter, 1876 (p. 154, pl. 40, fig. 9) might be the microconch of *H.* (*H.*) *pseudogardeni,* but this is a significantly older species (Kaplan & Kennedy 1994) and does not co-occur with *H.* (*H.*) *pseudogardeni* in any of the collections studied by Kaplan & Kennnedy, who were unable to conclusively demonstrate dimorphism.

Hauericeras (*H.*) *pseudogardeni* is firmly dated as Upper Santonian to Lower Campanian in Western Europe. Matsumoto *et al.* (1990) and Kaplan & Kennedy (1995) suggested that *Hauericeras* (*H.*) *antiquum* Collignon, 1961

[‡] In current geopolitical terminology Zululand and Pondoland now form parts of the provinces of KwaZulu-Natal and the Eastern Cape, respectively. For the sake of continuity we retain the names Zululand and Natal in the title of our series of systematic descriptions of the invertebrate faunas from these regions from 1975 onwards.

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(p. 75, text-fig. 12) known from a single specimen from the Lower Coniacian of Madagascar might be the stock ancestral to *H.* (*H.*) *pseudogardeni,* having the shell shape of *Hauericeras* plus delicate ventral ribs, but no constrictions. It is transitional to the Middle Turonian *Puzosia* (*Puzosia*) *serratocarinata* Kennedy & Cobban 1988 (p. 595, text-fig. 2; text-fig. 4, figs 1–3), from northern Mexico and Angola, the type species of *Mossamedites* Cooper, 2003 (p. 115) with a fastigiate venter but no well-differentiated keel.

Gardeniceras first appears in the Middle Coniacian, with *Ammonites lagarus* Redtenbacher, 1973, from the Middle Coniacian of Austria and southeastern France (see revision in Kennedy *in* Kennedy *et al.* 1995, p. 397, pl. 4, fig. 17), and ranges to the upper Upper Maastrichtian, with *Gardeniceras rembda* (Forbes, 1846) (see revision in Kennedy & Henderson 1992, p. 408, pl. 6, figs 10–24; pl. 17, fig. 1; text-fig. 3H). *Gardeniceras* thus appears a little later than *Hauericeras sensu stricto* if *antiquum* is accepted as a *Hauericeras*: Middle versus Lower Coniacian. When compared to *Hauericeras sensu stricto*, *Gardeniceras* lacks outer flank and ventrolateral ribs/tubercles, has a keel that is present on the shell from an early ontogenetic stage, hollow when first secreted, but thereafter filled in by additional shell material so that it is solid over the phragmocone, as a result of which internal moulds of phragmocones have a rounded venter, rather than the sharply fastigiate venter with solid keel of *H.* (*H.*) *pseudogardeni.* The venter of internal moulds of *Gardeniceras* body chambers retains a rounded venter, with a keel that remains hollow. If *Hauericeras* and *Gardeniceras* are closely related, the stratigraphic evidence suggests the former gave rise to the latter during the Coniacian. Interestingly, the juvenile *Mossamedites serratocarinatus* figured by Kennedy (1988, pl. 2, figs 8–10) has the overall proportions of *Gardeniceras.*

In conclusion, we accept *Gardeniceras* as a subgenus of *Hauericeras* in the absence of evidence to the contrary, but note that a keel has appeared more than once in the Desmoceratidae; in *Damesites* Matsumoto, 1942, *Moremanoceras* Cobbban, 1972, and in an as yet undescribed form from the Lower Cenomanian of Nigeria. It may well be that *Hauericeras* and *Gardeniceras* are homoeomorphs that acquired a keel independently. The only distinctive feature to justify Hauericeratinae is the presence of a keel, and as noted, this feature has appeared more than once in the evolution of the Desmoceratidae and we regard Hauericeratinae as unnecessary, and place *Hauericeras* in Puzosiinae – contrary to the views of Matsumoto (1938, pp. 6–7)

Crick (1907, p. 242–3; pl. 15, fig. 5) referred two poorly preserved fragments of compressed ammonites from the southern branch of the Manuan Creek in northern KwaZulu-Natal to *Hauericeras.* They are illustrated here as Fig. 10 I–L, and appear to be fragments of an Albian or Cenomanian puzosiine, possibly *Bhimaites* Matsumoto, 1954.

FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); further descriptions of these localities are deposited in the Geological Collections, Oxford University Museum of Natural History, The Natural History Museum, London, and the Natural History Collections Department, Iziko South African Museum, Cape Town.

SYSTEMATIC PALAEONTOLOGY

Superfamily Desmoceratoidea Zittel 1895
Family Desmoceratidae Zittel, 1885
Subfamily Puzosiinae Spath, 1922
(= Hauericeratinae Matsumoto, 1938)

Genus *Hauericeras* de Grossouvre, 1894

Schlueteria Rollier, 1922, p. 359, *non* Fritsch in Fritsch & Kafka, 1887, p. 33; *Pseudogardenia* Tomlin, 1930, p. 23.

Type species

Ammonites pseudogardeni Schlüter, 1872, p. 54, pl. 16, figs 3–6, by original designation by de Grossouvre, 1894, p. 219.

Subgenus *Gardeniceras* Matsumoto & Obata, 1955

Type species

Ammonites gardeni Baily, 1855, p. 450, pl. 11, fig. 3, by original designation by Matsumoto & Obata, 1955, p. 134.

Hauericeras* (*Gardeniceras*) *gardeni Baily, 1855,
Figs 1A–C, 2, 3A–D, 4A–F, 5A–H, 6, 7, 10M–O

1855 *Ammonites gardeni* Baily, p. 450, pl. 11, fig. 3.
non 1865 *Ammonites gardeni* Baily; Stoliczka, p. 61, pl. 33, fig. 4. (= *H.(G.) angustum* Yabe, 1904**.**
non 1869 *Ammonites Gardeni* Baily; Favre, p. 12, pl. 4, fig. 1 (= *Hauericeras* (*Gardeniceras*) *sulcatum* (Kner, 1850)).
1871 *Ammonites rembda* Forbes; Griesbach, p. 63, pl. 3, figs 2–3.
?*non* 1879 *Ammonites Gardeni* Baily; Whiteaves, p. 102.
non 1890 *Desmoceras gardeni* (Baily); Yokoyama, p. 184, pl. 20, fig. 10 (=*Hauericeras* (*Gardeniceras*) *angustum* Yabe, 1904).
1894 *Hauericeras gardeni* (Baily); de Grossouvre, p. 219.
?*non* 1895 *Desmoceras Gardeni* (Baily); Whiteaves, p. 131.
non 1898 *Hauericeras Gardeni* (Baily); Kossmat, p. 123 (188), pl. 18 (24), fig. 7.
?*non* 1903 *Hauericeras gardeni* (Baily); Whiteaves, p. 352.
1906 *Hauericeras Gardeni* (Baily); Woods, p. 332.
?*non*1907 *Hauericeras* cf. *Gardeni* (Baily); Pervinquière, p. 166, pl. 7, fig. 1, 3–6.
?1908 *Desmoceras* (*Hauericeras)* cf. *Gardeni* (Baily); Kilian & Reboul, p. 18.
non 1913 *Hauericeras gardeni* (Baily); Nowak, p. 371, pl. 41, fig. 12; pl. 43, fig. 34; pl. 45, figs 44, 45 (= *Hauericeras* (*Gardeniceras*) *sulcatum* (Kner, 1850)
1921 *Hauericeras gardeni* (Baily); Van Hoepen, p. 27, fig. 15.
1921 *Hauericeras gardeni* (Baily); Spath, p. 238, text-fig. A-1 to A-9.
1922 *Hauericeras gardeni,* Baily sp.; Spath, p. 129.
1925 *Hauericeras gardeni* (Baily); Diener, p. 95 (*pars*).
1930 *Hauericeras gardeni* Baily; Besairie, p. 220, pl. 20, fig. 3.

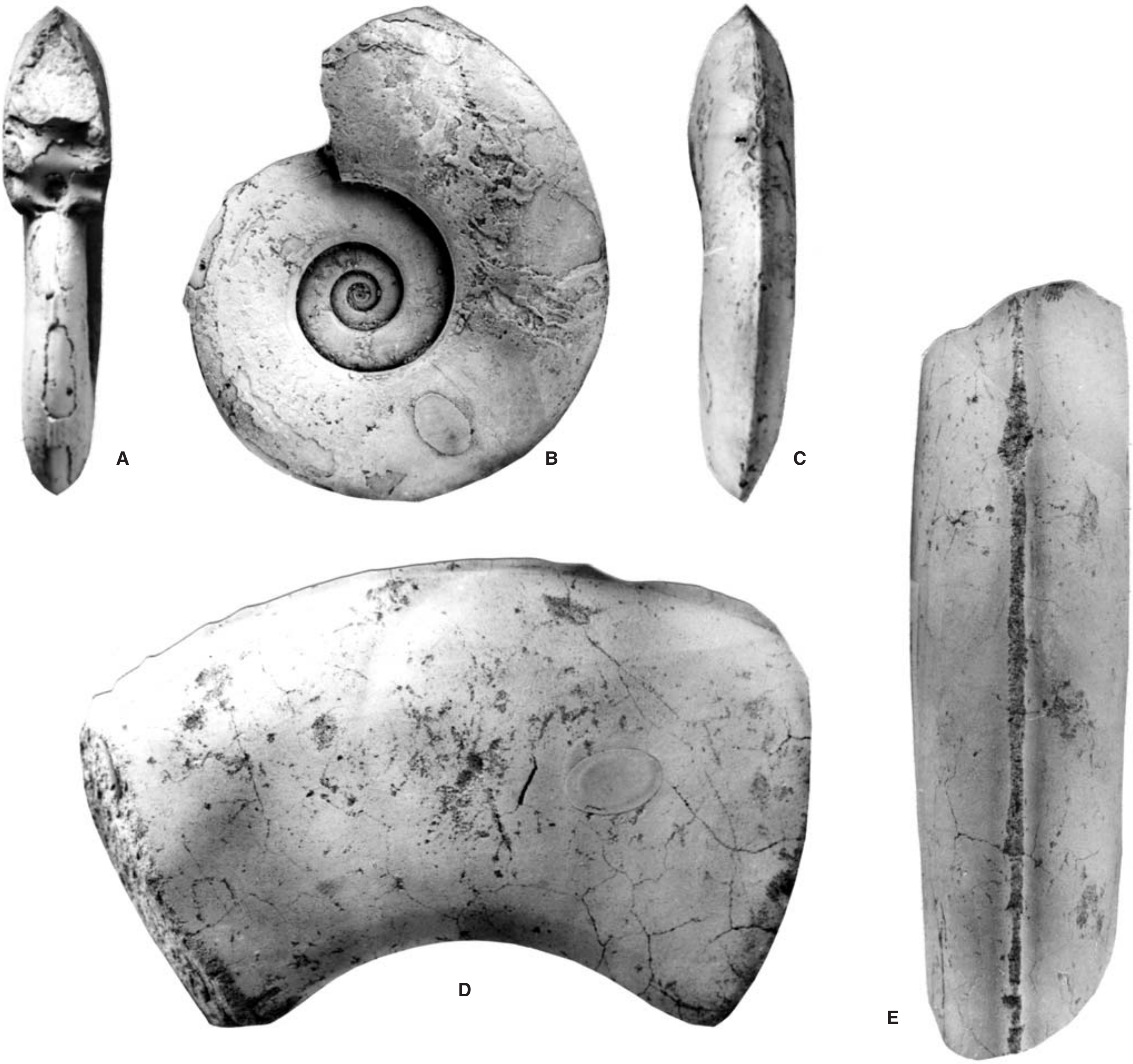

Figure 1. **A–C**, *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). The lectotype, BMNH C72219, the original of Baily 1855, p. 456. pl. 11, fig. 3a, b. **D**, **E**, *Hauericeras* (*Gardeniceras*) *pseudoangustum* Collignon, 1961, BMNH C35621, a paralectotype of *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). Both specimens are from " 'White-mens houses', coast of S. Africa near the Umzambani River", that is to say the Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

1931 *Hauericeras Gardeni* Baily; Basse, p. 23, pl. 4, figs 2–4, pl. 10, fig. 8; pl. 11, fig. 1.

1932 *Hauericeras gardeni* (Baily); Collignon, p. 17, pl. 3, fig. 3.

1938 *Hauericeras Gardeni* (Baily); Collignon, p. 74.

non 1942 *Hauericeras gardeni* (Baily); Matsumoto, p. 25 (=*Hauericeras* (*Gardeniceras*) *angustum* Yabe, 1904).

?*non* 1952 *Hauericeras gardeni* (Baily); Usher, p. 65, pl. 5, figs 1, 2; pl. 21, fig. 10.

1955 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Matsumoto & Obata, p. 140 *et seq.*; text-figs 8–10.

1961 *Hauericeras gardeni* (Baily); Collignon, p. 76, pl. 28; pl. 29; pl. 30, figs 1, 2; text-figs 13–14.

1969 *Hauericeras* (*Gardeniceras*) *gardeni* Baily; Collignon, p. 66, pl. 539, fig. 2114.

1973 *Hauericeras* cf. *H. gardeni* (Baily); Kennedy & Klinger *in* Kennedy, Kauffman & Klinger, p. 101, p. 6, fig. 2.

1975 *Hauericeras gardeni* (Baily); Kennedy & Klinger, p. 279, 280.

1977 *Hauericeras gardeni* (Baily, 1855); Klinger & Kennedy, p. 80, text-figs 7A–C, 8A.

non 1979 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Summesberger, p. 133, pl. 6, fig. 27; text-fig. 19.

1982 *Hauericeras gardeni* (Baily); Immel, Klinger & Wiedmann, p. 16 (*pars*), pl. 6, figs 2, 3, *non* pl. 5, figs 1–4; *non* pl. 6, figs 1,4; *non* text-fig. 5.

non 1982 *Hauericeras* (*Gardeniceras*) aff. *gardeni* (Baily); Renz, p. 106, pl. 35, figs 2–4.

non 1987 *Hauericeras gardeni* (Baily); Immel, p. 91.

1990 *Hauericeras gardeni* (Baily, 1855); Matsumoto, Toshimitsu & Kawashita, p. 451.

1995 *Hauericeras* (*Gardeniceras*) cf. *gardeni* (Baily, 1855); Kennedy in Kennedy, Bilotte & Melchior, p. 396.

2003b *Hauericeras* (*Gardeniceras*) *gardeni* (Baily1855); Cooper, p. 159, figs 6A–D.

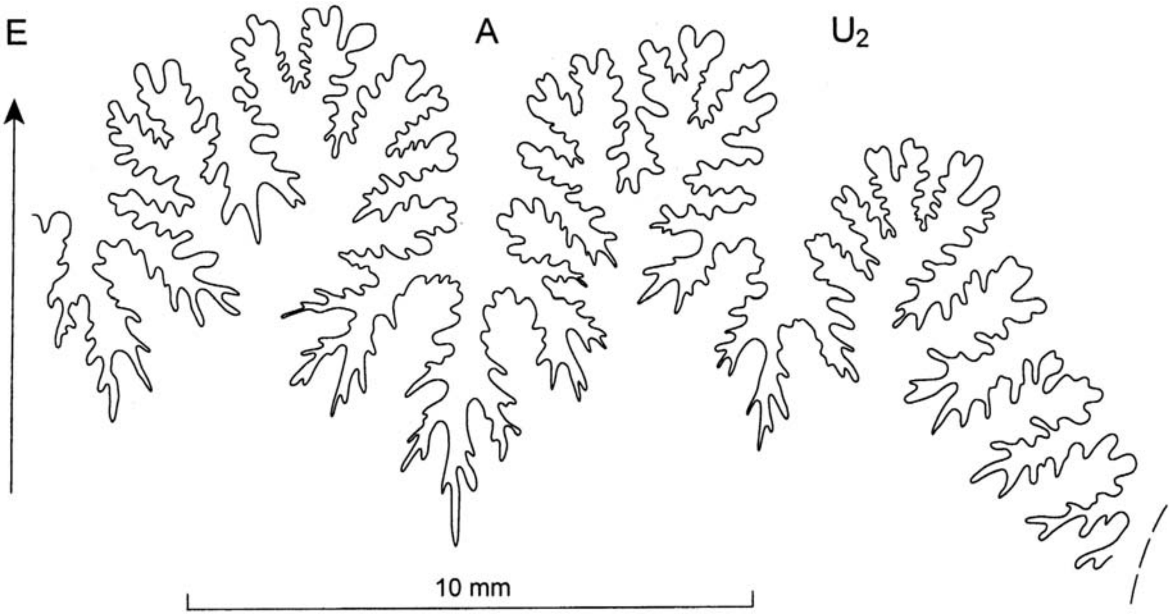

Figure 2. External suture of *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855), based on OUM KX10843.

Types

Spath (1921, p. 238) refers to 'Baily's type (BM Geol. Soc. Coll., no. 11370) and the larger of the two fragmentary cotypes (No. 11371) from which Baily's figure of the suture line was taken,' and subsequently (1922, p. 131) refers to BMNH 11371 as 'Baily's paratype'. This does not constitute a valid lectotype designation in our view. Accordingly, we designate BMNH C72219 (Geological Society Collection no. R11370) lectotype. It is the original of Baily 1855, pl. 11, figs 3a,b, and is illustrated here as Fig. 1A–C. The locality is given on an attached contemporary paper label as 'White-mens houses Umzambani River.' Paralectotype BMNH C35621 (Geological Society Collection no. R11369) is figured here as Fig. 1D,E, and is referred to *Hauericeras pseudoangustum* Collignon, 1961, below. It has an associated grey-blue paper label: '*Ammonites gardeni* nov. sp. Cretaceous Formation Amzamba River Port Natal. Presd. By Captain Garden D.B. p. 237.' Paralectotype BMNH C35622 (Geological Society Collection no. R11370) has the same associated information, and is illustrated here as Fig. 3A,B; it provided the basis for Baily's illustration of the suture line of the species (1855, pl. 11, fig. 3c).

Garden (1855, p. 453) gave the following account, 'About three miles to the southward of the river commence certain excavations in the cliffs, formed by the actions of the sea, and called by the natives 'Izinhuluzabalungu … the houses of the white men' so called probably from the caverns having once been occupied by shipwrecked sailors.' This clearly identifies the locality of the types as locality 1 of Kennnedy & Klinger (1975), illustrated as text-figs 1–3 in Klinger & Kennedy (1980), the Izinhluzabalungu Caves of Griesbach (1871, fig. 5) and the Umzamba Cliff of Plows (1921), on the north side of the Mzamba estuary.

Material

BMNH C8516 and C18517 (both mentioned by Spath 1922, p. 130), C18518 (mentioned by Spath 1922, p. 130, figured by Matsumoto & Obata 1955, p. 141, text-fig. 10), C18519, C18520 (both mentioned by Spath 1922, p. 130, the latter figured by Matsumoto & Obata 1955, p. 140, text-fig. 9), C18521 and C18522 (both mentioned by Spath 1922, p. 130), C18523–7, C18528 (the original of Spath 1921, p. 238, fig. A1–7) (Fig. 3C), C18530, C18531 (the original of Spath 1921, p. 238, text-fig. A-8 (Fig. 3D herein), C18532, C18534, C18535 (mentioned by Spath 1922, p. 131), C18536, C18537 (mentioned by Spath 1922, p. 130), C18538, C18539, C18540 (mentioned by Spath 1922, p. 130), C18541, C18544–18549, C18531. All of these specimens are from the Mzamba Formation of locality 1 of Kennedy & Klinger (1975) although the details on associated labels vary slightly. OUM KX90, SAM-PCZ* all from locality 1 of Kennedy & Klinger (1975), where the species ranges from Santonian III to Campanian I (Klinger & Kennedy 1980, fig. 4). SAM BH9/120/22, BH9/124, BH9/127, 80, from the St Lucia Formation, Santonian III, in the BH9 borehole, 14 km west of Richards Bay in northern KwaZulu-Natal. OUM KX10671–1076 and SAM-PCZ* from the St Lucia Formation, Campanian I, at locality 14 of Kennedy & Klinger (1975) south of Mtubatuba, northern KwaZulu-Natal. OUM KX5353, 5356, 10838, 10839, 10841, 10843, 10845, SAM-PCZ* from the St Lucia Formation, Santonian I, locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. OUM KX4970a–b, SAM-PCZ* from the St Lucia Formation, Campanian I at locality 105 of Kennedy & Klinger (1975; see also Klinger & Kennedy 1980a, fig. 130) on the southeastern shores of False Bay, lake St Lucia, northern KwaZulu-Natal. OUM KX12818, 12872–12876, 12880, 12881, 12891–12923, 13037, 13057–13060, 13078, SAM-PCZ* from locality 74 of Kennedy & Klinger (1975), Die Rooiwalle, northwestern False Bay, Lake St Lucia, northern KwaZulu-Natal. The species has been collected *in situ* from beds 2–22 of the section, spanning the Santonian I–Campanian I interval.

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*Unregistered.

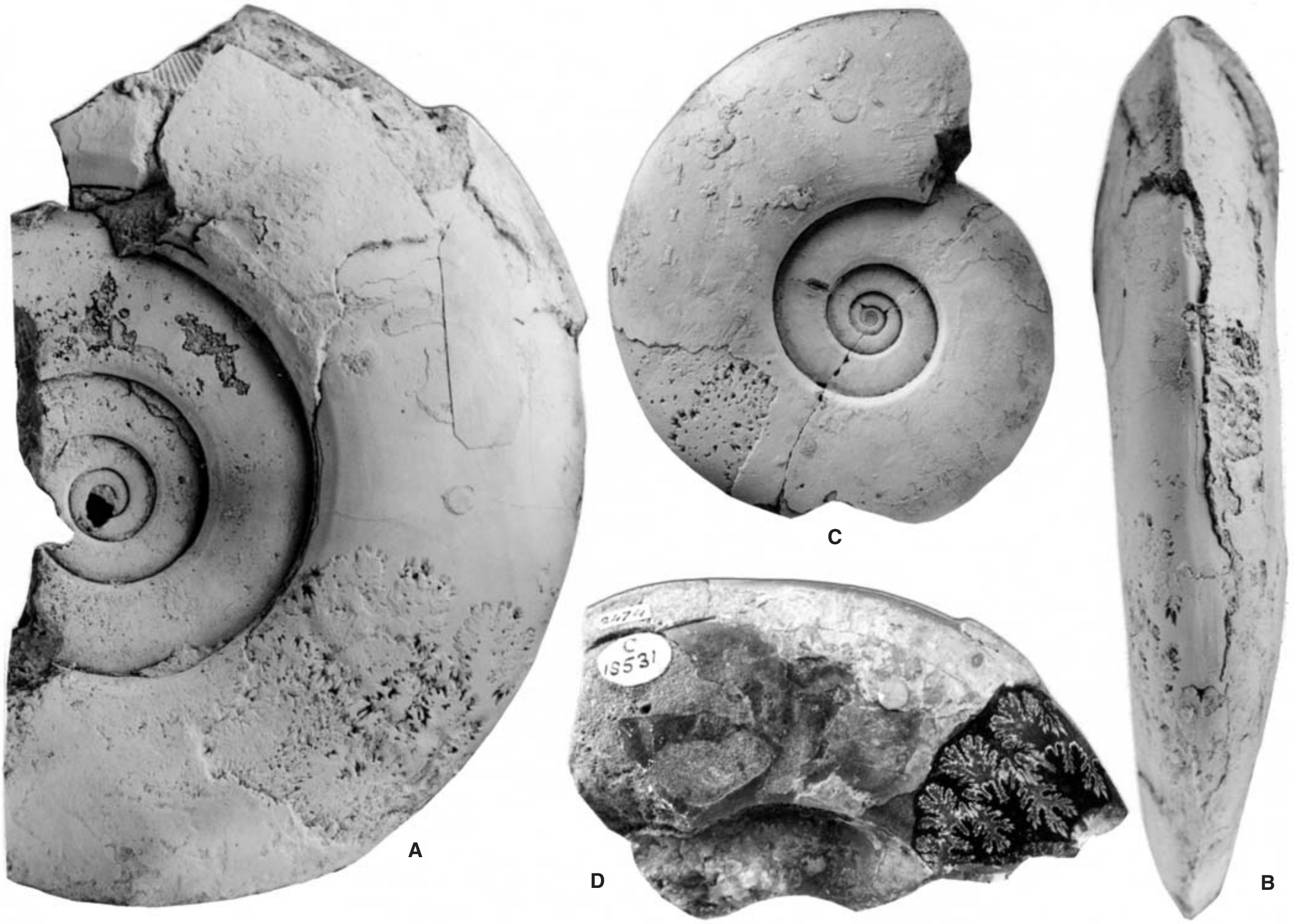

Figure 3. **A–D.** *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). **A**, **B**, paralectotype BMNH C35622, the original of Baily, 1855, pl. 11, fig. 3c (suture), from " 'White-mens houses', coast of S. Africa near the Umzambani River", that is to say the Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. **C**, BMNH C18528, the original of Spath 1921, p. 238, text-fig. A-1-7, 9. **D**, BMNH C18531, the original of Spath 1921, p. 238, text-fig. A-8, from the Upper Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

Dimensions

	D	Wb	Wh	Wb:Wh	U
KX10844	75.0 (100)	15.2(20.3)	25.5 (34.0)	0.60	31.3 (41.7)
C72219	77.9 (100)	16.4 (21.0)	29.0 (37.2)	0.57	29.5 (37.9)
C18547	81.3 (100)	16.2 (19.9)	30.4 (37.4)	0.53	28.7 (35.3)
KX5350	82.3 (100)	16.1 (19.6)	29.2 (35.5)	0.55	33.0 (40.1)
C18527	87.0 (100)	18.0 (20.7)	32.2 (37.0)	0.55	35.3 (40.6)
KX10843	89.3 (100)	16.8 (18.8)	31.7 (35.5)	0.53	37.1 (41.5)
C18526	93.1 (1000	18.0 (19.8)	33.0 (35.4)	0.55	34.6 (37.2)
C18522	93.5 (100)	19.0 (20.3)	31.6 (33.8)	0.6	38.6 (41.3)
C18538	105.8 (100)	21.4 (20.2)	37.4 (35.3)	0.57	41.0 (38.7)
KX5349	111.1 (100)	20.8 (18.7)	39.5 (35.5)	0.53	47.3 (42.6)
KX90	124.8 (100)	20.1 (16.1)	42.5 (34.1)	0.47	53.2 (42.6)
C18540	130.5 (100)	22.8 (17.5)	42.6 (32.6)	0.53	58.1 (44.5)
C18518	130.7 (100)	28.0 (21.4)	43.3 (33.1)	0.65	53.6 (41.0)
C18523	131.6 (100)	22.2 (16.8)	42.3 (32.1)	0.52	56.7 (43.1)

Description

The inner septate whorls are well represented by the lectotype, BMNH C72219 (Baily 1855, p. 456, pl. 11, fig. 3a, b; Fig. 1A–C herein) which is partially exfoliated, retaining original aragonitic shell layers. There are indications of the former presence of at least one further whorl. Coiling is very evolute, the umbilicus very broad and shallow, comprising 37.9% of the diameter, with 41% of the previous whorl covered. The low umbilical wall is flattened and outward-inclined with a shallow groove just below the umbilical shoulder. The umbilical shoulder is sharp on the penultimate whorl, becoming rounded on the outer whorl. The whorl section is compressed, with a whorl breadth to height ratio of 0.57, the greatest breadth low on the flanks, the inner flanks flattened and feebly convergent, the outer flanks convex and converging to the acutely fastigiate venter. A strong siphonal keel is present where shell is preserved, but absent on the internal mould. There is no ornament preserved on the surface of the exfoliated shell. Part of a single constriction is visible on the internal mould on one flank. The delicate growth lines shown in Baily's figure are not detectable.

Paralectotype BMNH C35622 is the basis of Baily's figure of the suture (1855, pl. 11, fig. 3c; Matsumoto & Obata

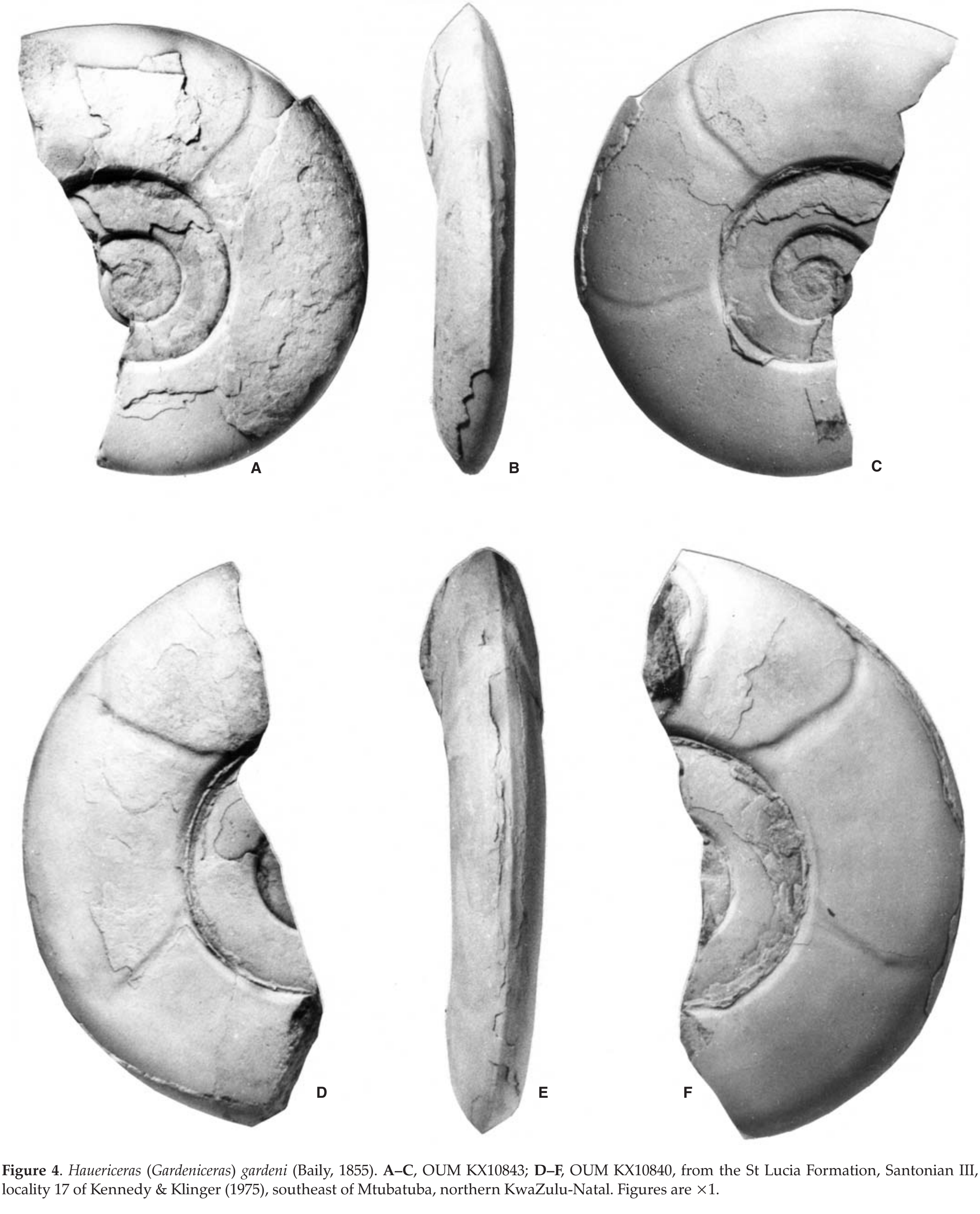

Figure 4. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). **A–C**, OUM KX10843; **D–F**, OUM KX10840, from the St Lucia Formation, Santonian III, locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. Figures are ×1.

1955, text-fig. 8; Fig. 3A,B). It comprises fragmentary inner whorls and a 180° sector of outer whorl; the estimated maximum diameter is 130 mm. The adapertural 90° sector is body chamber. The specimen retains partially exfoliated shell in places. Constrictions are not detectable on the early phragmocone whorls. A weak constriction is present at the adapertural end of the phragmocone, and there is a single constriction on the body chamber fragment. The constrictions are concave, projecting strongly forwards on the ventrolateral shoulders and venter. The constrictions are far less conspicuous than is suggested by the sketch in Matsumoto & Obata (1955, text-fig. 8a).

BMNH C18518 (Fig. 7) is the 'thickest form' mentioned by Spath (1922, p. 130), and figured by Matsumoto &

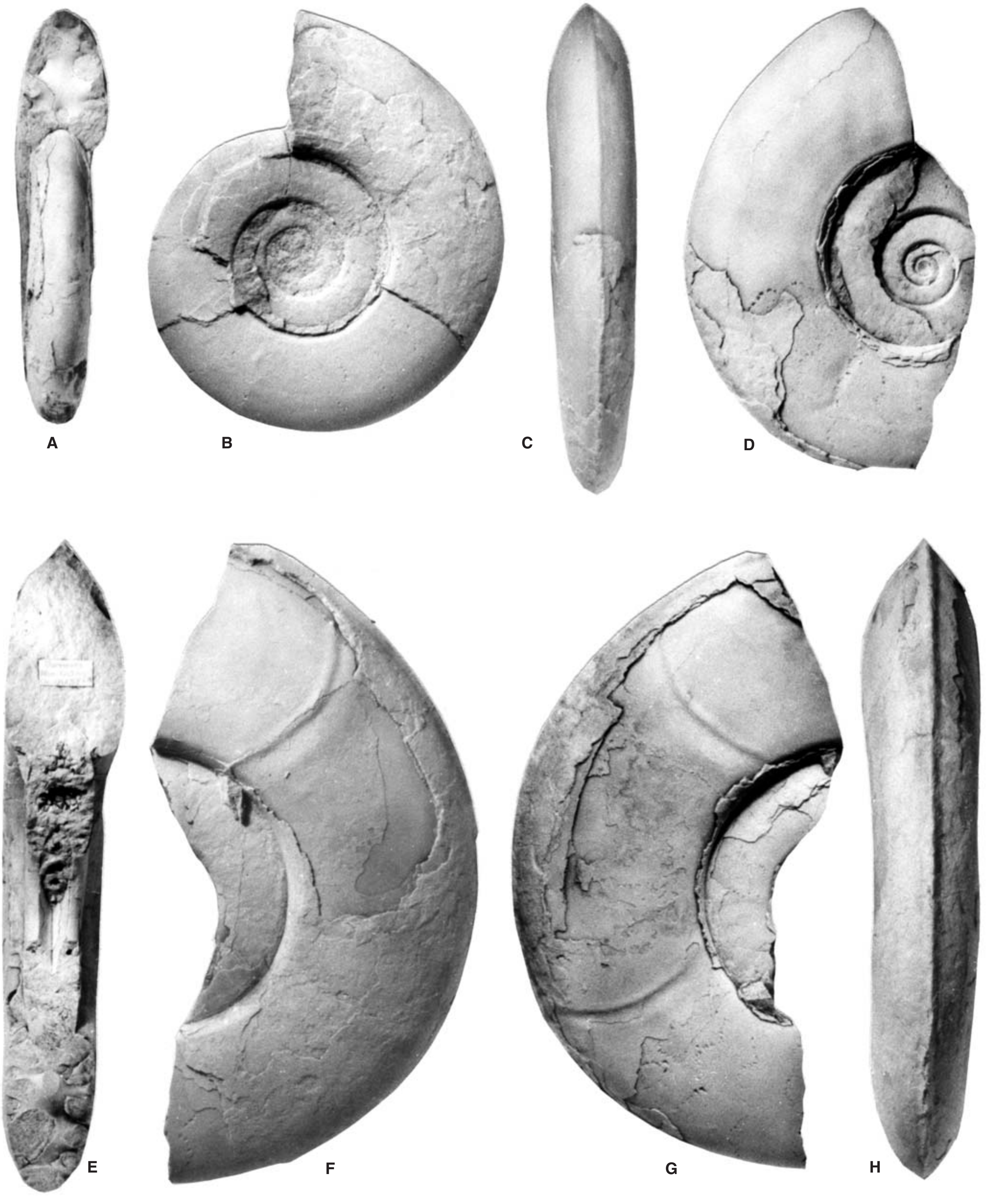

Figure 5. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). **A**, **B**, OUM KX10844; **C**, **D**, OUM KX5350; **E–H**, OUM KX5349, all from the St Lucia Formation, Santonian III, locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. Figures are ×1.

Obata (1955, text-fig. 10). The specimen has a maximum preserved diameter of 130.7 mm, and retains extensive areas of shell. Coiling is very evolute. The wide, shallow umbilicus comprises 41% of the diameter, the umbilical wall low, the umbilical shoulder very narrowly rounded. The whorl breadth to height ratio is 0.65, the flanks feebly convex, and feebly converging, the greatest breadth just outside the umbilical shoulder. The ventrolateral shoulders are broadly rounded, the venter acutely fastigiate with a strong sharp keel where shell is preserved on both phragmocone and body chamber, and on the internal mould of the body chamber. The internal mould of the phragmocone lacks a keel. The shell surface is smooth on the phragmocone, apart from delicate growth lines that

Figure 6. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). OUM KX 90, from the Mzamba Formation, Santonian III, at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

are feebly prorsiradiate on the inner flank, concave on the middle to outer flank and projected strongly forwards on the ventrolateral shoulders and venter, indicating the presence of a long ventral rostrum at the aperture. The adapertural 240° sector is body chamber, with four constrictions that become increasingly prominent as size increases. They are concave across the flanks and project strongly forwards on the ventrolateral shoulders and venter. The adapertural edge of the constrictions is marked by a feeble collar-rib. The final constriction appears to be just before a damaged apertural margin that bears a ventral rostrum.

OUM KX 90 (Fig. 6) is 120 mm in diameter, and retains extensive traces of partially exfoliated shell. Six constrictions are detectable on both the outer whorl and the penultimate whorl. Very well-preserved body chambers from locality 17 (Figs 4A–F, 5A–H) show the presence of strong constrictions, three per half whorl, with an adapical collar-rib on the internal mould. There is little or no indication of the constrictions where shell is preserved on the opposite flank of the same individual (OUM KX10843: compare Figs 4A and C; OUM KX5349: compare Figs 5F and 5G).

An unexplained feature of partially exfoliated specimens is particularly well-shown by BMNH C18520 (Fig. 10M–O, the original of Spath 1922, p. 130, and Matsumoto & Obata 1955, text-fig. 9). The translucent layers of replaced shell material show a pattern of deeply concave, narrow dark bands (much more deeply concave than the constrictions) separated by wider white bands. This feature is largely within the shell material, being scarcely indicated on the surface, as can be seen from the whitened and unwhitened picture of the specimen (Fig. 10N, uncoated; Fig. 10O, coated with ammonium chloride). These patterns presumably relate to the accretion pattern of the shell material; similar structures are shown by BMNH C18535 and C18539.

A keel is present on phragmocones and body chambers with shell preserved, and on internal moulds of body chambers. The keel was thus initially hollow and open to the interior of the shell, and thereafter infilled with shell material and solid on the phragmocone, but remained hollow on the body chamber. (See also Matsumoto & Obata 1955, text-figs 8–10; Klinger & Kennedy 1977, figs 7a,c, 8a.)

The suture (Fig. 2) is deeply incised, with asymmetrically bifid E/A and A/U2, deep asymmetrically trifid A (=L) and U2, the suspensive lobe strongly retracted.

Discussion

Hauericeras (*Gardeniceras*) *gardeni*, as interpreted from the lectotype, paralectotype BMNH C35622 and the abundant Mzamba material referred to the species, has a compressed whorl section with whorl breadth to height ratios

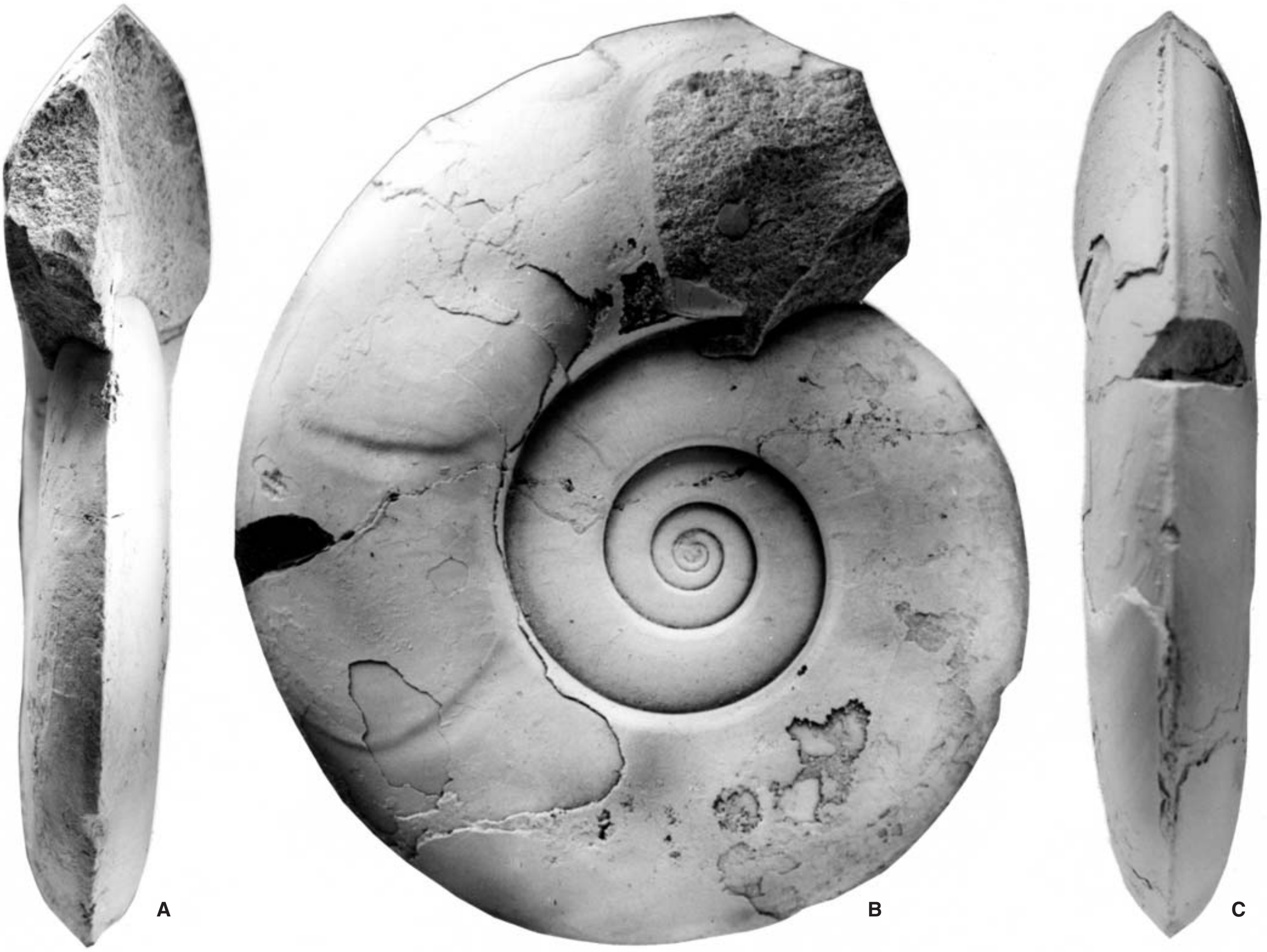

Figure 7. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). BMNH C18518, the original of Spath 1922, p. 130 and Matsumoto & Obata, 1955, text-fig. 10, from the Upper Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

of 0.47–0.6, the majority falling between 0.53 and 0.57, the umbilicus comprising between 35.3% and 47.0% of the diameter, the majority falling between 37.2% and 44.5%. Concave growth lines are only occasionally discernible, perhaps as a result of the partial exfoliation of most specimens. Concave constrictions are weak or imperceptible on the surface of the shell, but conspicuous on the internal mould, and are markedly strengthened on the body chamber, with an associated adapertural collar rib. On this basis, *H.* (*G.*) *gardeni* can be distinguished from the closely allied *H.* (*G.*) *angustum* Yabe, 1904 (p. 33, pl. 5, figs 5, 6) which was carefully revised by Matsumoto & Obata (1955, p. 137, pl. 24, fig. 6; pl. 28, figs 1, 2; pl. 29, figs 1–5; text-figs 5, 7) and Matsumoto *et al.* (1990, p. 443, text-figs 2–7). On the basis of the observations of these authors, and specimens in the Natural History Museum, London (BMNH C47749–50, mentioned by Spath, 1922 p. 131) *H.* (*G.*) *angustum* has sinuous growth lines and constrictions that are concave on the innermost flank, convex on the inner to middle flank, and concave on the outer flank. Body chambers of *gardeni* have strengthened ribs on the body chamber, with a collar rib; they are weak on body chambers of *angustum*, some specimens of which develop what appear to be coarse inner flank ribs on the body chamber (Matsumoto & Obata 1955, pl. 28, fig. 2). Dimorphism has been recognized in *H.* (*G.*) *angustum.* Matsumoto *et al.* (1990, text-fig. 2) figured what they regarded as a macroconch 225 mm in diameter with a sinuous, biconcave mouth border (1990, text-fig. 3) and microconchs, the best preserved of which (1990, text-figs 6, 7) is 113 mm in diameter, with a long lappet at mid-flank, and longer ventral rostrum. Matsumoto *et al.* (1990, p. 451) thought that BMNH C18518, figured here as Fig. 7, was the macroconch of *H.* (*G.*) *gardeni.* This specimen is 135 mm in maximum preserved diameter, with an estimated 230° sector of body chamber, what appears to be a long ventral rostrum, but no trace of a lappet. Matsumoto *et al.* (1990, p. 452) then proposed that the two large figured specimens of *H.* (*G.*) *gardeni* from Madagascar figured by Collignon (1961, pls 28, 29) were macroconchs. These appear to lack the final sector of body chamber and are preserved to diameters of 183 and 195 mm. They are far larger than any material from Mzamba or KwaZulu-Natal that we have seen, and we are unable to confirm dimorphism in the material before us.

Hauericeras (*Gardeniceras*) *pseudoangustum* Collignon, 1961 (p. 83, text-fig. 18) is smooth, with weak sinuous constrictions that are restricted to the body chamber.

Hauericeras (*Gardeniceras*) *madagascariense* Collignon,

Figure 8. *Hauericeras* (*Gardeniceras*) *madagascariense* Collignon, 1961. SAM-7043, from the uppermost beds of the Lower Campanian of the Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in the Eastern Cape Province. Figure is ×0.9.

1961 (p. 81, pl. 31, fig. 1; pl. 32, fig. 1; text-figs 15–17) differs from *H.* (*G.*) *gardeni* in its much broader whorl section, with whorl breadth to height ratios of up to 0.76, and sinuous, biconcave constrictions.

If the strength and course of the constrictions is regarded as a key feature, then material with sinuous rather than simple concave constrictions must be excluded from *H.* (*G.*) *gardeni.* These include material from Tunisia (Pervinquière 1907), Austria (Summesberger 1979; Immel *et al.* 1982; Immel 1987) and Venezuela (Renz 1982).

Occurrence

In South Africa, *H.* (*G.*) *gardeni* first appears in Santonian I and ranges into Campanian I of Kennedy & Klinger (1975), with records from the Mzamba Formation of the coastal outcrops in northeastern Eastern Cape Province, and the St Lucia Formation of northern KwaZulu-Natal. In Madagascar it ranges from Upper Santonian through all of the Lower Campanian. There are also records from the Santonian of southeastern France and Angola. Records of *H.*(*G.*) *gardeni* from the Santonian–Campanian of south India and Vancouver Island, British Columbia, Canada are best referred to *H.*(*G.*) *angustum* as pointed out by Matsumoto & Obata (1955, p. 144) and Matsumoto (1959, p. 25)

Hauericeras pseudoangustum Collignon, 1961,
Figs 1D,E; 9

1961 *Hauericeras* (*Gardeniceras*) *pseudoangustum* Collignon, p. 83, text-fig. 18

Type

The holotype, by original designation, is no. 2795 in the collections of the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris, the original of Collignon. 1961 text-fig. 18, from the Lower Campanian Zone à *Anapachydiscus arrialoorensis* (= the Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of

Figure 9. *Hauericeras* (*Gardeniceras*) *pseudoangustum* Collignon, 1961. The holotype, no. 2795 in the collections of the Laboratoire de Paléontologie of the Musém d'Histoire Naturelle, Paris, the original of Collignon. 1961, text-fig. 18, from the Lower Campanian Zone à *Anapachydiscus arrialoorensis* (= the Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Collignon, 1969) of Iampolypoly-Antsirasira-Behamotra (Belo sur Triribihina), Madagascar. Figures are ×1.

Collignon 1969) of Iampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar, illustrated here as Fig. 9.

Material

BMNH C35621 (Fig. 1D,E), a paralectotype of *Ammonites gardeni* Baily, 1855, from the Mzamba Formation at the mouth of the Mzamba River, Eastern Cape Province, corresponding to locality 1 of Kennedy & Klinger (1975).

Description

BMNH C35621 is an internal mould of a body chamber fragment with a maximum preserved whorl height of 63.2 mm and a whorl breadth to height ratio of 0.52. There are traces of a single feeble constriction that is convex on the inner flank, concave on the outer flank, and projected strongly forwards on the outermost flank and ventrolateral shoulder. The estimated total original diameter of the present specimen is 170 mm.

Discussion

Whorl section and course of the single constriction separate this specimen from *Hauericeras* (*Gardeniceras*) *gardeni*, but correspond to that of *Hauericeras* (*Gardeniceras*) *pseudoangustum,* to which it is referred. Collignon's (1961, pp. 83–84) description leaves no doubt as to the affinities of the specimen: 'Coquille très plate, discoidale, à tours élevés, se recouvrant d'un peu plus de 2/5; flancs plats, parallèles au voisinage de l' ombilic et jusque vers leur milieu, puis s'abaissent doucement vers la région externe arrondie d'abord, puis devenant ogivale avec carène. Versant ombilical relativement élevé, vertical, limité par une arrête mousse. Ombilic moyennement large dégeant les tours internes plats, en escalier. Aucune ornamentation; seule un constriction est visible très nettement au début de la chambre d'habitation, immédiatement en avant de la dernière cloison. Elle est légèrement tordue en S étiré, très allongé. Sur le plus grand exemplaire … il y a 3 constrictions visibles, toutes sur la chambre d'habitation.'

Occurrence

Uppermost Santonian or Lower Campanian, Mzamba Formation at locality 1 of Kennedy & Klinger (1975); Lower Campanian Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Madagascar.

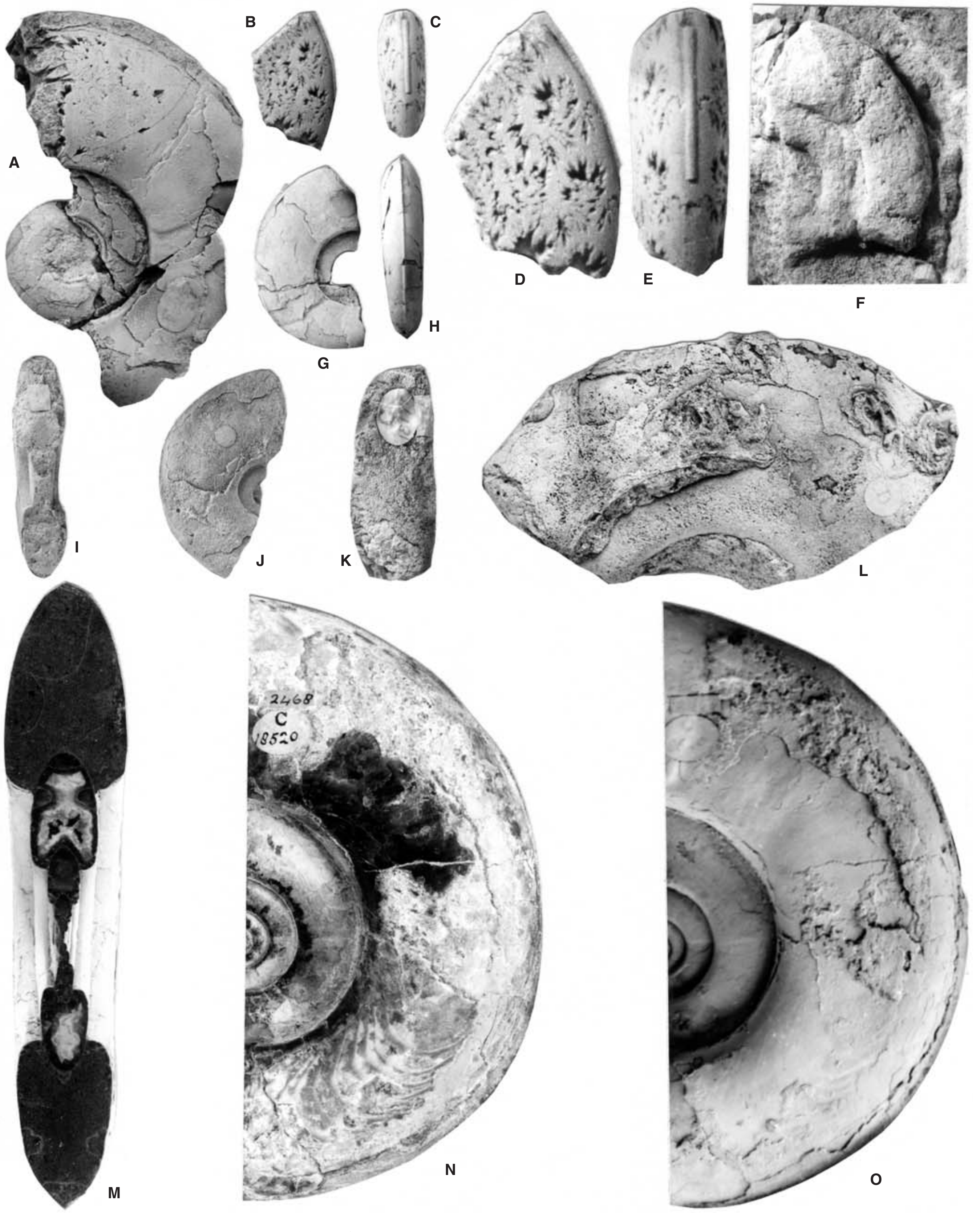

Figure 10. **A–H**. *Hauericeras* (*Gardeniceras*) *rembda* (Forbes, 1846). **A**, BMNH C51023, a paralectotype; **G**, **H**, BMNH C51024, the lectotype. Both specimens are from the Upper Maastrichtian Valudavur Formation of Pondicherry, south India. **B–E**, OUM KX6973, from the St Lucia Formation, Maastrichtian II, upper Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone of locality 20 of Kennedy & Klinger (1975), east-southeast of Mtubatuba, northern KwaZulu-Natal. **F**, OUM KX8906, from the St Lucia Formation, Maastrichtian III, upper Upper Maastrichtian of locality 128 of Kennedy & Klinger (1975), Lake St Lucia, northern KwaZulu-Natal. **I–L**, indeterminate Puzosiinae. **I**, **J**, BMNH C18275, the original of *Hauericeras* sp. of Crick, 1907, p. 242, pl. 15, fig. 5; **K**, **L**, BMNH C18276, the original of *Hauericeras* sp. of Crick, 1907, p. 243. Both specimens were described as being from the southern branch of the Manuan Creek. **M–O**, *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). BMNH C18520, the original of Spath 1922, p. 130 (table) and Matsumoto & Obata, 1955, text-fig. 9, from the Upper Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. The specimen is uncoated in Figs M and N; the latter shows the distinctive colour banding within the partially exfoliated shell material. Figures A, D, E are ×2; B, C, F–O are ×1.

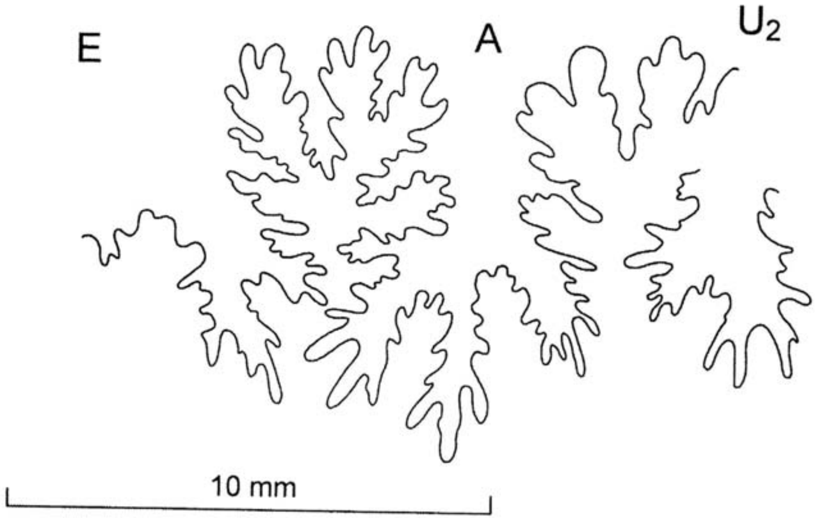

Figure 11. External suture of *Hauericeras* (*Gardeniceras*) *rembda* (Forbes, 1846), based on OUM KX6937.

Hauericeras (Gardeniceras) madagascariense Collignon, 1961, Fig. 8

- 1961 *Hauericeras* (*Gardeniceras*) *madagascariense* Collignon, p. 81, pl. 31, fig. 1; pl. 32, fig. 1; text-figs 15–17.
- 1969 *Hauericeras* (*Gardeniceras*) *madagascariense* Coll.; Collignon, p. 66, pl. 539, fig. 2115.
- 1980b *Hauericeras madagascariense* Collignon, 1961; Klinger & Kennedy, p. 219, text-fig. 5B.
- ?1996 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855); Cooper & Greyling, p. 23, fig. 7m–n.

Type

The holotype by original designation, is the orignal of Collignon, 1961, pl. 31, fig. 1, no. 2848 in the collections of the Muséum National d'Histoire Naturelle, Paris, from the Lower Campanian Zone à *Anapachydiscus arrialoorensis* (= the Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Collignon, 1969) of Iampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar.

Material

SAM-7043 from the Mzamba Formation, probably bed A15 of Klinger & Kennedy (1980, text-fig. 4) (Bed T2 of Gevers 1923; see also Gevers 1977) at locality 1 of Kennedy & Klinger (1875), Eastern Cape Province. OUM KX1781, from the St Lucia Formation, Campanian II at locality 109 of Klinger & Kennedy (1975) on the southwestern corner of the Nibela Peninsula, Lake St Lucia, northern KwaZulu-Natal.

Description

SAM-7043 (Fig. 8) is a large specimen (D = *c.*160 mm) embedded in a concretion with specimens of *Baculites sulcatus* Baily, 1855 on the reverse side (Klinger & Kennedy 1997, fig. 64a). Part of the last septum is exposed. The body chamber occupies a sector of slightly more than 180 °. Four concave constrictions are visible on the body chamber; the most prominent one near the adapical part. The umbilicus is wide, *c.* 45 % of the total diameter)

OUM KX1781 is an internal mould of a phragmocone 190 mm in diameter, the umbilicus shallow, comprising 47.5% of the diameter, with a low, feebly convex, outward-inclined umbilical wall and narrowly rounded umbilical shoulder. The whorl breadth to height ratio is 0.64, the inner and middle flanks flattened and feebly convergent, the outer flanks broadly rounded, converging to the narrowly rounded, arched venter of the internal mould. This is smooth, with no indication of constrictions. In places, traces of recrystallized shell on the venter demonstrate the presence of a sharp siphonal keel. The suture is very deeply and intricately incised, the saddles narrow-stemmed, bifid, with deep asymmetrically trifid A (=L).

Discussion

Hauericeras (*Gardeniceras*) *madagascariense* differs from *Hauericeras* (*Gardeniceras*) *gardeni* in its greater size, broader whorls, slightly larger umbilical diameter and feebly convex rather than narrowly rounded venter. The constrictions, well seen in SAM-7043, are concave, rather than sinuous as they are in *Hauericeras pseudoangustum.*

Occurrence. According to Collignon (1961, p. 82) *H.* (*G.*) *madagascariense* is restricted to the upper part of the Lower Campanian, zone of *Anapachydiscus arrialoorensis* redefined as the upper Lower Campanian Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Collignon, 1969 of Madagascar. Campanian II of KwaZulu-Natal. At Mzamba in the Eastern Cape, it has only been found in the topmost beds of the Mzamba Formation, above the level of abundant *H.* (G.) *gardeni.*

Hauericeras rembda (Forbes, 1846), Figs 10A–H, 11

- 1846 *Ammonites Rembda* Forbes, p. 111, pl. 7, fig. 3.
- 1846 *Ammonites Durga* Forbes, p. 104, pl. 7, fig. 11.
- *non* 1871 *Ammonites rembda* Forbes; Griesbach, p. 63, pl. 3, figs 2–3 (= *Hauericeras gardeni*)
- ?1978 *Hauericeras* sp. cf. *H.* (*Gardeniceras*) *rembda* (Forbes); Matsumoto, Okada & Sakurai, pp. 323–324, fig. 3.
- 1992 *Hauericeras rembda* (Forbes, 1846); Kennedy & Henderson, p. 408, pl. 6, figs 10–24; pl. 17, fig. 1; text-fig. 3H (with full synonymy).

Types

The lectotype, by the subsequent designation of Matsumoto & Obata (1955, p. 145), is BMNH C51024, the original of Forbes 1846, pl. 7, fig. 3; paralectotypes are BMNH C51023 and C51025. The figured syntype of *Ammonites Durga* Forbes, 1846, p. 104, pl. 7, fig. 11 is BMNH C51021. All of these specimens are from the Upper Maastrichtian Valudavur Formation of Pondicherry, south India.

Material

OUM KX6973, from the St Lucia Formation, Maastrichtian II, upper Upper Maastrichtian *'Inoceramus' ianjonaensis* Zone of locality 20 of Kennedy & Klinger (1975), ESE of Mtubatuba, northern KwaZulu-Natal. OUM KX8906, from the St Lucia Formation, Maastrichtian III, upper Upper Maastrichtian of locality 128 of Kennedy & Klinger (1975), Lake St Lucia, northern KwaZulu-Natal.

Description

OUM KX6937 (Fig. 10B–E) is a well-preserved phosphatized phragmocone fragment of a 60° whorl sector with a maximum preserved whorl height of 15.3 mm and a whorl breadth to height ratio of 0.64, the greatest breadth well below mid-flank. The inner and middle flanks are feebly convex, the outer flank and ventrolateral shoulders converge to the broadly rounded venter. The surface of the internal mould is smooth. A sector of a solid calcite replaced siphonal keel is present. The suture is deeply incised, with a large trifid A (= L) (Fig. 11).

OUM KX8906 (Fig. 10F) is a composite mould of a 120° sector of two successive whorls with a maximum preserved whorl height of 14.8 mm. Coiling is very evolute, the umbilicus broad and shallow, with a feebly convex outward-inclined umbilical wall and more narrowly rounded umbilical shoulder. The specimen is partially embedded in matrix, but the whorl section and proportions correspond to those of the previous specimen. A poorly preserved constriction is present toward the apertural end of the fragment. It is markedly prorsiradiate, feebly sinuous (?) and strongly projected forwards on the ventrolateral shoulders and venter.

Discussion

The type material of *Hauericeras rembda* was revised by Kennedy & Henderson (1992, p. 408, pl. 6, figs 10–24; pl. 17, fig. 1; text-fig. 3H). Given the Upper Maastrichtian horizon of the present material, the whorl section, and apparent course of the constriction on OUM KX 8906, reference to *rembda* seems appropriate; the lectotype and largest paralectotype are illustrated here as Fig. 10A, G, H for comparison. The other Maastrichtian species, *Hauericeras sulcatum* (Kner, 1848) (see revision in Kennedy & Summesberger 1987, p. 27, pl. 1, figs 1–7; pl. 13, fig. 2) has six or seven constrictions per whorl, and these are concave.

The two specimens from the type locality of the Mzamba Formation described by Griesbach (1871, p. 63, pl. 3, figs 2–3) as *Ammonites rembda* do not belong here and are probably *H. (G.) gardeni.* We have not been able to examine Griesbach's material – it is presumed to have been destroyed during aerial bombardment in World War II. (Klinger 1995).

Occurrence

Upper Maastrichtian of India and northern KwaZulu-Natal. Maastrichtian of Madagascar.

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ABBREVIATIONS

Institutional

BMNH	The Natural History Museum, London.
OUM	Oxford University Museum of Natural History.
SAM	Natural History Collections Department, Iziko South African Museum, Cape Town.

Anatomical

[Dimensions are given in millimetres]

D	diameter
Wb	whorl breadth
Wh	whorl height
U	umbilicus
c	costal dimension
ic	intercostal dimension

(Figures in brackets are dimensions as a percentage of the diameter.)

The suture terminology is that of Korn *et al.* (2003):

E	external lobe
A	adventive lobe (= lateral lobe, L, of Kullmann & Wiedmann 1970)
U	umbilical lobe
I	internal lobe.

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Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa)

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Seventy-five years after Robert Broom's discovery of the first adult *Australopithecus* in 1936, the Sterkfontein Caves (Gauteng Province, South Africa) remains one of the richest and most informative fossil hominin sites in the world. The deposits record hominin and African mammal evolution from roughly 2.6 million years (Ma) until the Upper Pleistocene. Earlier excavation efforts focused on the Member 4 australopithecine-bearing breccia and the Member 5 stone tool-bearing breccias of Oldowan and Early Acheulean age. Ronald J. Clarke's 1997 programme of understanding the cave deposits as a whole led to the discovery of the near-complete StW 573 *Australopithecus* skeleton in the Member 2 deposit of the Silberberg Grotto, and the exploration of lesser known deposits such as the Jacovec Cavern, Name Chamber and the Lincoln Cave. Our aim is to produce a cogent synthesis of the environments, palaeodietary information, fauna and stone artefacts as recorded in the Sterkfontein sequence. We begin with an overview of the site and early accounts of the interpretations of the site-formation processes, after which we discuss each Member in turn and summarize the various types of evidence published so far. Finally, we review the most pertinent debates about the site, including the ages of Sterkfontein Member 2 and 4, and the types of habitats represented at the site through time.

Keywords: Sterkfontein, *Australopithecus, Paranthropus, Homo,* mammals, hominins, stable isotopes, climatic change, cave formation.

INTRODUCTION

The Sterkfontein site lies in the Cradle of Humankind World Heritage Site (Gauteng Province, South Africa). Formed within the pre-Cambrian Malmani dolomite, the caves contain sedimentary infills that record palaeoenvironmental information relating to hominin evolution from roughly 2.6 million years until the Upper Pleistocene. Sterkfontein remains one of the most important fossil hominin and Earlier Stone Age (ESA) sites within Africa, and the world (Fig. 1). While numerous other rich fossil sites are known from this region, such as Swartkrans, Kromdraai, Drimolen and the new fossil locality Malapa (Berger *et al.* 2010), Sterkfontein inarguably contains the richest deposits of vertebrate remains spanning the Plio-Pleistocene. This site (26°00′56.44′S, 27°44′03.48′E) lies on a hill overlooking the Blaaubank (also spelled 'Bloubank') River.

Dating and climatic context for Sterkfontein Members

Climate change studies on both larger and regional scales (deMenocal 1995, 2004; Hopley *et al.* 2007) provide a vital framework for how faunal changes can be interpreted, both in terms of individual species' morphology, but also large-scale changes in faunal communities (e.g. Vrba 1974, 1975). The earlier deposits at Sterkfontein appear to sample warmer climates, while later deposits reflect the cooling drying trends associated with the Pleistocene. This fits well with broader reconstructions of climate change in Africa (e.g. deMenocal 2004: 3), which suggest step-wise drying trends resulting in 'more varied and open habitats at 2.9–2.4 Ma and after 1.8 Ma' in eastern Africa. In southern Africa, aridification in Namibia suggests that this region became drier after about 2.1 Ma (Weigelt *et al.* 2008).

However, there is a lack of clear agreement between large and regional scale signals (e.g. Hopley *et al.* 2007), and this is complicated by the cyclical nature of climate shifts and the deposition times of karst deposits (Hopley & Maslin 2010).

The year 2011 marks the 75th anniversary of Robert Broom's discovery of the first adult *Australopithecus africanus* Dart 1925 (Broom 1936). Initial excavation efforts, under the auspices of the Transvaal Museum by Robert Broom and John T. Robinson focused on the Member 4 australopithecine-bearing deposits. Later work by Robinson focused on the so-called Extension Site of Member 5 stone tool-bearing breccias (Robinson 1962; Kuman & Clarke 2000).

When Phillip V. Tobas and Alun R. Hughes began their excavation programme under the auspices of the University of the Witwatersrand in 1966, one of their aims was to establish the relationship between Member 4 and the Member 5 deposits (Clarke, in press). The ongoing research by Ronald Clarke and Kathleen Kuman concentrated on understanding the cave deposits as a whole. Specifically, the excavation and analyses of the infills of Member 5 has shown that three separate infills are present, differentiated by presence or absence of Earlier Stone Age artefacts (Kuman 1994a,b; Clarke 1994; Kuman & Clarke 2000).

The discovery of the near-complete StW 573 *Australopithecus* skeleton by Clarke in 1997 in the Member 2 deposit of the Silberberg Grotto has led to numerous studies on this deposit (Clarke 1998, 1999, 2002a,b; Berger

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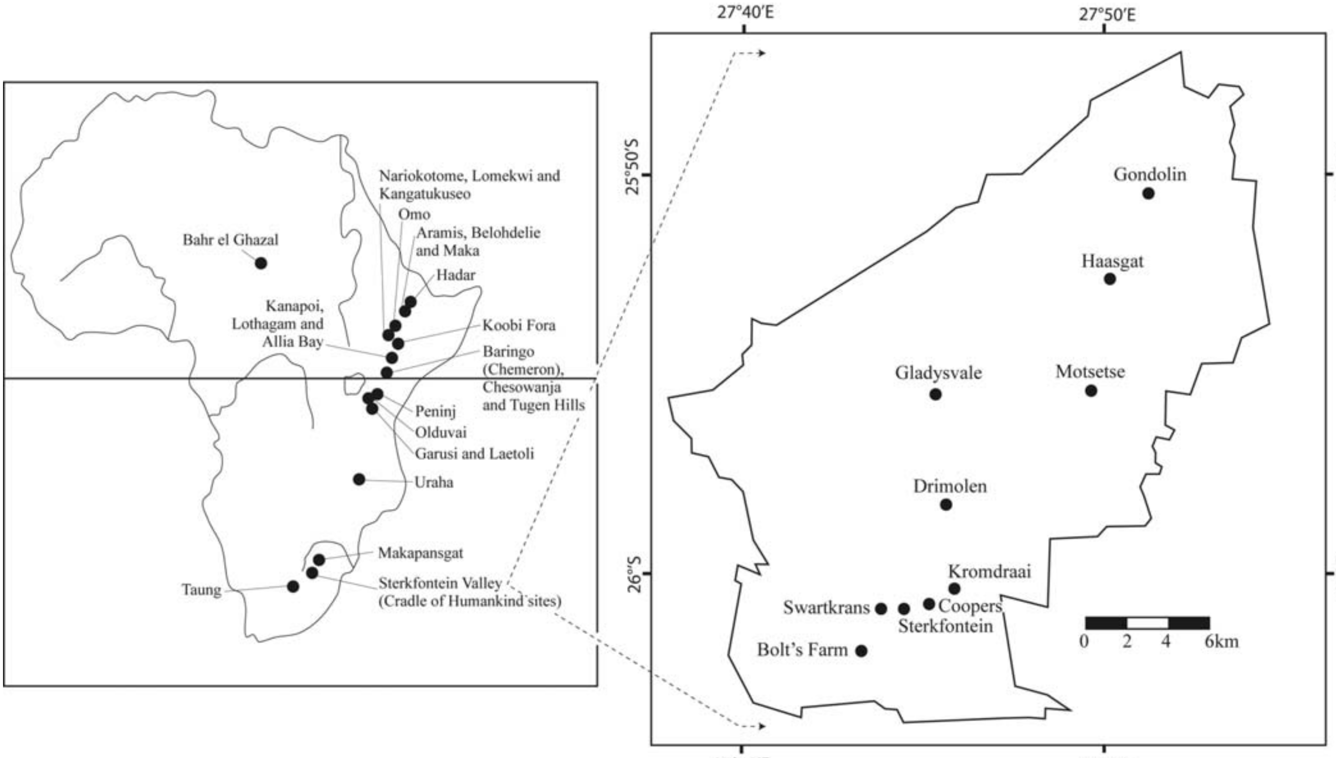

Figure 1. Major African hominin sites shown on the left (after Tobias 2000), compared with the sites of the Cradle of Humankind on the right.

et al. 2002; Partridge *et al.* 2003; Pickering *et al.* 2004a; Pickering & Kramers 2010; Herries & Shaw 2011). Several other deposits have also recently been systematically excavated and analysed, specifically the Jacovec Cavern (also spelled 'Jakovec'; Wilkinson 1973, 1983, 1985; Partridge *et al.* 2003; Kibii 2000, 2004, 2007), the Name Chamber (Partridge & Watt 1991; Clarke 2006; Stratford 2008; Avery *et al.* 2010) and the Lincoln Cave deposits (Boshoff *et al.* 1990; Reynolds *et al.* 2003, 2007). These deposits and their approximate spatial relation to each other are indicated in Fig. 2.

These studies of the Sterkfontein fauna and palaeoenvironments offer unparalleled insights into various aspects of southern African hominin morphology and habitats through time. Over 600 hominin specimens, possibly representing as many as five species, seven primates species, 52 species of macromammals, 28 micromammal species, several reptile and bird species and at least two plant species have been identified in the Sterkfontein deposits and other cave deposits within the same site region, such as the Lincoln Cave (Pickering 1999; Bamford 1999; Kuman & Clarke 2000; Avery 2001; Kibii 2004; Reynolds *et al.* 2003, 2007; Avery *et al.* 2010).

Our aim is to present and review the faunal, taphonomic and archaeological evidence from the Sterkfontein site, as pertains to hominin habitats and environments over the time periods represented. The hominin material itself has been described in detail in an extensive number of studies, (e.g. Broom 1936; Broom *et al.* 1950; Hughes & Tobias 1977; Kimbel & White 1988; Spoor *et al.* 1994; Tobias & Clarke 1996; Berger & Tobias 1996; Thackeray 1997; Spoor 1997; Lockwood 1997; Ripamonti *et al.* 1997; Schwartz *et al.* 1998; Berge & Gommery 1999; Lockwood & Tobias 1999; Tobias 2000, 2002; Häusler & Berger 2001; de Ruiter 2004; Dobson 2005; Prat 2005; Moggi-Cecchi *et al.* 2006; Curnoe & Tobias 2006; Clarke 2008; Curnoe 2010, Fornai 2010; Kibii *et al.* 2011 and many others). However, much more material awaits cleaning and reconstruction before it can be described (Clarke, pers. comm.).

We begin with a brief overview of the climate records of the African Pliocene and Pleistocene, before outlining the site stratigraphy and early accounts of the interpretations of the site-formation processes, after which we discuss each Member in turn and summarize the various types of evidence published so far.

One of the reasons why Sterkfontein is such an important site is that it samples the Pliocene to Pleistocene transition, at 2.58 Ma (Cohen & Gibbard 2011). Climatically, this transition is characterized by a series of transitions towards cooler, drier, more seasonal conditions (deMenocal 2004; Weigelt *et al.* 2008), with corresponding effects on faunal communities and morphologies (Vrba 1974; 1975; Reynolds 2007, 2010). One of the most important changes is the increase in the proportions of C_4 grasses within the vegetation present at the hominin sites. Carbon isotope data from flowstones from the Makapansgat Valley (Limpopo Province, South Africa) caves indicate that there was an increase in the proportion of C_4 grasses from the period represented by Member 1 speleothem deposits of the Collapsed Cone (4–5 Ma) to the later Buffalo Cave, for which the basal flowstone has been dated to 1.95 and 0.78 Ma, with the fossils being in the 1.07 to 0.78 Ma time range (Hopley *et al.* 2007).

Specifically the data indicate an expansion of the C_4 (grass) plants at approximately 1.7 Ma, which Hopley *et al.* (2007) have related to the onset of the Walker Circulation. Additionally, Weigelt and colleagues (2008) have identi-

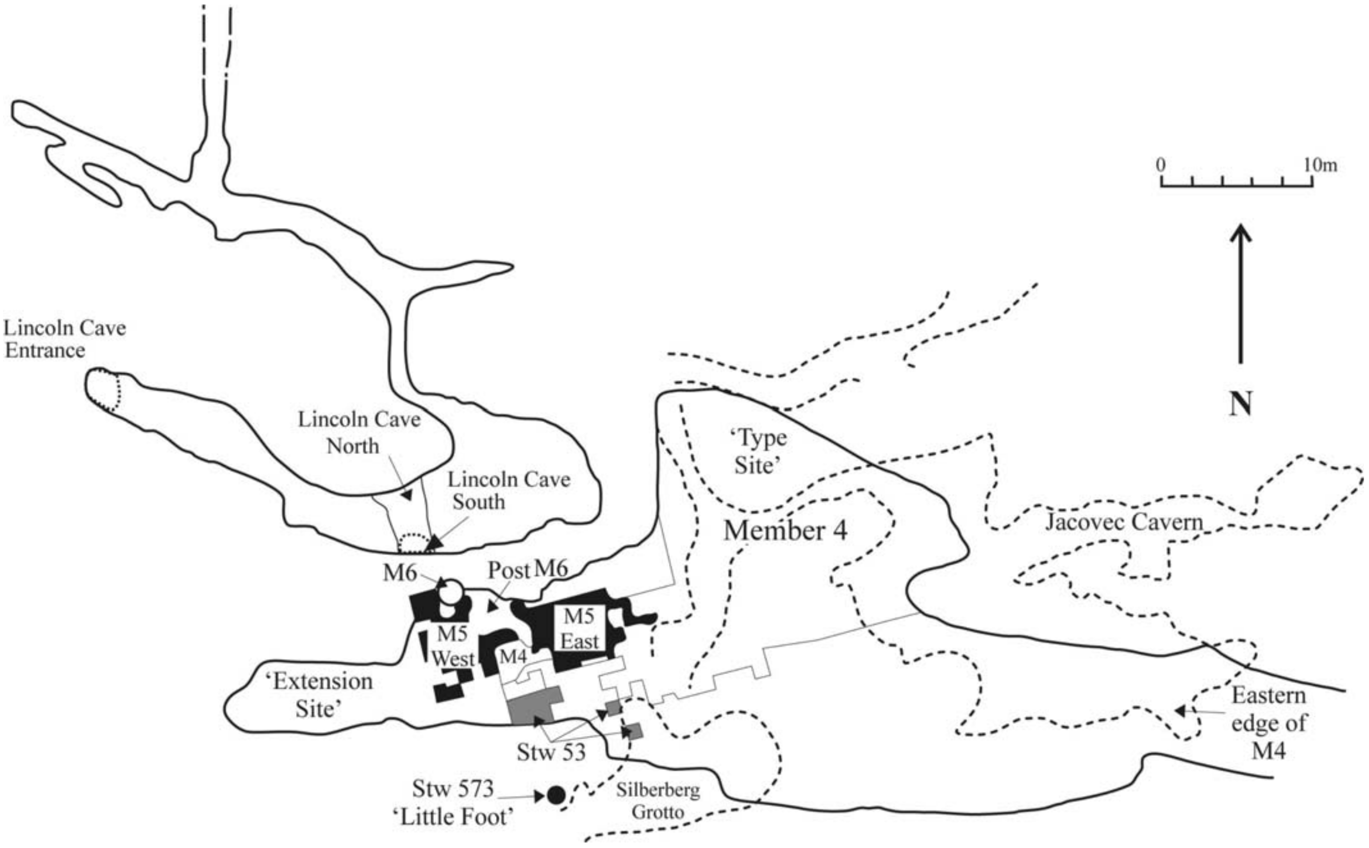

Figure 2. Composite plan view of Sterkfontein deposits, showing the exposed deposits of the Sterkfontein excavation (Member 4, and Member 5), the underground deposits (Silberberg Grotto and Jacovec Cavern) and the approximate spatial relationship of the Lincoln Cave to the main Sterkfontein Cave system. Based on Kuman & Clarke (2000), Partridge *et al.* (2003) and Reynolds *et al.* (2007). Please note: the two cave systems are not shown to exactly the same scales. The Name Chamber lies directly under Member 5 (Clarke 1994).

fied increasing aridity in southern Africa after 2.1 Ma, which would also have favoured the development of grasslands. The climate data from the Makapansgat Valley (Fig. 1) suggests that the region including Sterkfontein would have experienced similar aridification and increase in C_4 grasses over the period represented. While the Collapsed Cone predates the earliest Sterkfontein deposits, it appears likely that similar climatic trends would have been experienced by the *Australopithecus* in Member 2 through to the younger Member 4 deposits and finally to the *Paranthropus* and early *Homo*-bearing Member 5 infills (Kuman & Clarke 2000; Hopley *et al.* 2007).

Overview of the excavation of the Sterkfontein deposits

Early work on Sterkfontein sediments considered that the deposits followed a layer-cake model of deposition (Partridge's 1978 classification of Members 1–6), with the older deposits likely to be at lower levels and younger sediments at higher levels (e.g. Robinson 1952, 1962). Later excavations and analyses of Member 5 breccia have demonstrated that several different infills can exist within a single Member (Kuman & Clarke 2000) and that reworking of older artefacts and fauna into younger deposits occurs as a common process within karstic caves (e.g. for the Lincoln Cave, see Reynolds *et al.* 2007). Therefore, the site formation processes and contents of the deposits must be interpreted together as part of a larger picture of site formation (considering also cycles of collapse, erosion and reworking). The absolute dates of the deposits may differ according to which method is employed (e.g. Herries & Shaw 2011), making this interpretive framework critical in assessing the validity of dating results.

Exposed deposits

The Sterkfontein deposits were first characterized as a single conformable breccia (e.g. Brain 1958); then later as several distinct breccia bodies, specifically the 'Type Site' where the first specimens of *Australopithecus africanus* were found, and the 'Extension Site' where Robinson discovered stone tools during excavations conducted between 1957 and 1958 (Robinson & Mason 1957; Robinson 1962; Mason 1962a,b).

Robinson identified at least three disparate deposits: the pink 'Lower Breccia', which yielded the *Australopithecus* fossils and which lies within the Type Site; the red-brown 'Middle Breccia', in which the stone tools were found and which lies in the Extension Site (Fig. 2), and the youngest of the three breccias, which he termed the 'Upper Breccia': a dark brown breccia, known only from a small part of the Extension Site (Robinson 1962).

Still later, Partridge (1978, also 2000) identified six major units, and this scheme was later refined by borehole studies (Fig. 3; Partridge & Watt 1991). This study associated the deposits exposed at the surface with the underground deposits of the Silberberg Grotto, and defined the spatial relationship between these deposits and the other fossiliferous deposits in Jacovec Cavern and Name

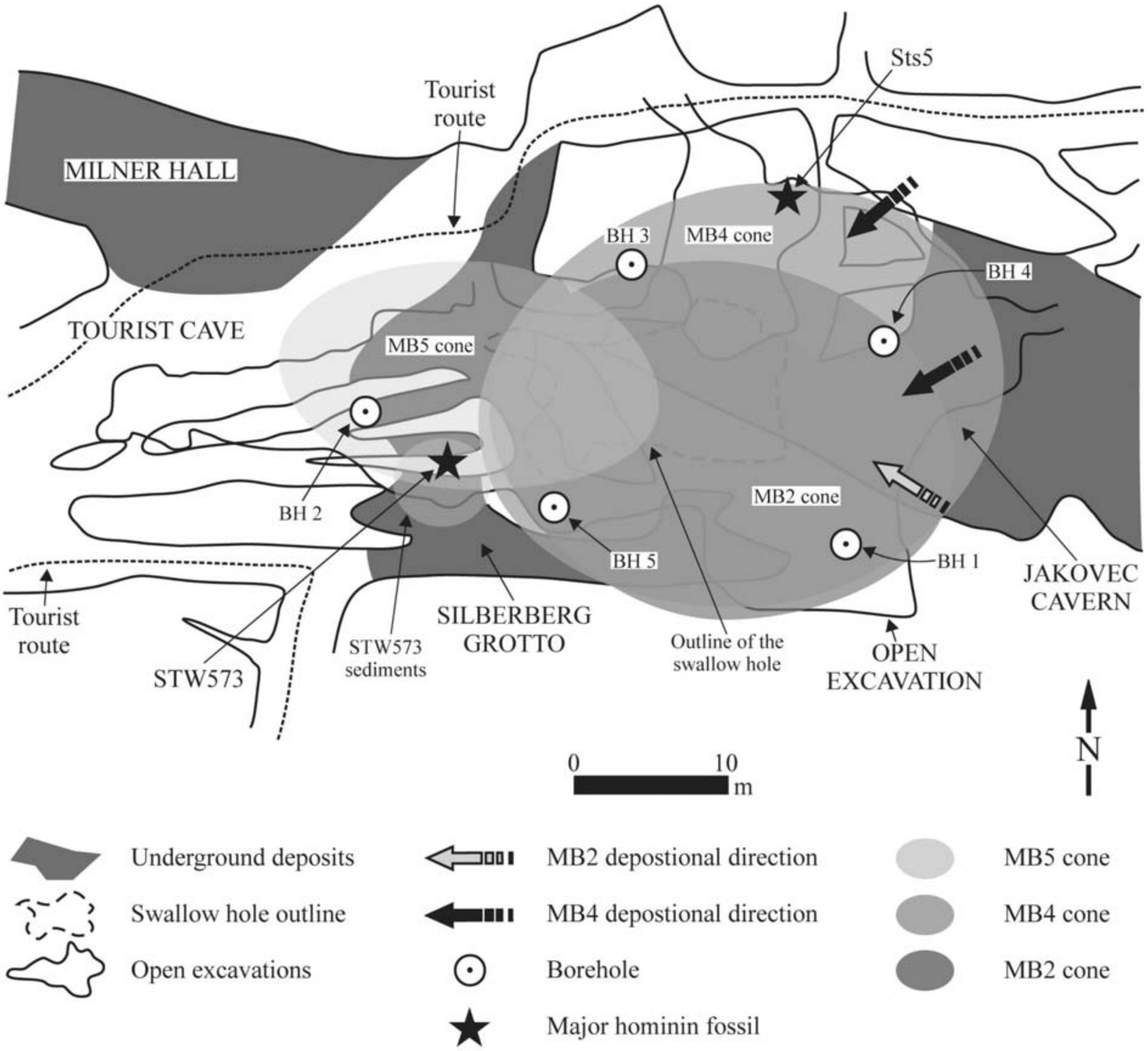

Figure 3. Recent re-examination of Sterkfontein boreholes by Pickering & Kramers (2010), based on original boreholes (labeled as BH) drilled by Partridge & Watt (1991). The conclusion of the Pickering & Kramers (2010) study was that Member 3 (exposed in the Silberberg Grotto) is likely to be part of Member 4 sediment cone. The darker arrows indicate possible entrances for the sediments during Member 4 accumulation, and the lighter grey arrow indicates the possible location of the Member 2 material (redrawn after Pickering & Kramers 2010).

Chamber. The stratigraphy was viewed as a relatively simple 'layer cake' formation, with the oldest Member 1 at the bottom of the sequence and the younger deposits exposed at the surface.

Recent studies have re-evaluated this layer-cake model, and emphasize the complexity of karst infills (e.g. Pickering *et al.* 2010). This complexity is well-illustrated by the example of Member 5, which is discussed below. A more appropriate model of successive layers of talus cone infills (Fig. 3), or even the infilling of disconnected, but contemporaneous caverns has been proposed (e.g. Partridge 2000; Herries *et al.* 2009; Pickering & Kramers 2010). The historical perspective of the changes in the understanding of the stratigraphy of Sterkfontein is reviewed by Clarke (2006).

In early studies, Member 5 appeared to be a geologically uniform deposit (Partridge 1978; Partridge & Watt 1991), but three separate infills have been identified on the basis of fauna and artefacts, namely the StW 53; the Member 5 East and Member 5 West infills (also referred to as the M5A–C by Partridge; Table 1; Kuman & Clarke 2000, Fig. 2). StW 53 is a small Member without stone tools where the StW 53 cranium was discovered (Hughes & Tobias 1977) and that is separated from the stone-tool-bearing Member 5 East and Member 5 West deposits by a thick flowstone (Clarke, pers. comm.). The Member 5 East deposit contains one of the earliest stone tool industries in South Africa, assigned to the Oldowan Industry while the Member 5 West infill contains tools of the Early Acheulean industry (Kuman & Clarke 2000) (Table 1).

The total number of Members has now been increased to seven, with the recent identification of the Sterkfontein 'Post Member 6 infill', which Kuman and Clarke (2000) suggest dates to approximately the mid- to late Pleistocene. The deposits exposed at the surface comprise the Member 4 breccia, all three Member 5 infills and Member 6 (an unexcavated small hanging remnant) (Fig. 2). The youngest deposits are the Post-Member 6 solution pocket into Member 5 West (known as the 'L/63' infill), part of which appears to be connected to the adjoining Lincoln-Fault cave system. Within this cave system, the Lincoln Cave North and South deposits have been dated to the

Table 1. Excavated Sterkfontein deposits.

Deposit	Published dates for deposits	Species	Number of artefacts and industries
Jacovec Cavern	**4.0 Ma,** Cosmogenic nuclides (Partridge *et al.* 2003) **>2.36,** fauna, in particular, *Equus* sp. (Kibii 2004)	*Australopithecus africanus*	0
Member 2	**4.0 Ma,** Cosmogenic nuclides (Partridge *et al.* 2003) **3.30–3.33 Ma,** Palaeomagnetism (Partridge *et al.* 1999) **2.2 Ma,** Uranium-Lead isotopes (Walker *et al.* 2006) **2.6–2.8 Ma,** Uranium-lead and Uranium-Thorium isotopes (Pickering & Kramers 2010) **2.6–1.8 Ma** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	*Australopithecus* sp.	0
Member 4	**2.8–2.4 Ma,** Bovid biochronology (Vrba 1976, 1980) **~ 2.5 Ma,** Primate biochronology (Delson 1984, 1988). **2.8–2.6 Ma,** Faunal seriation (McKee 1993) **~ 2.1 Ma,** Electron Spin Resonance (Schwarcz *et al.* 1994) **2.15–2.14 Ma** Palaeomagnetism (Partridge 2005). **2.65–2.01,** Uranium-lead and Uranium-Thorium isotopes (Pickering & Kramers 2010) **2.8 ~2.0 Ma,** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	*Australopithecus africanus* and a possible 'Second species' (discussed in e.g. Clarke 1988)	0
Member 5: *StW 53 Infill*	**2.6–2.0 Ma,** Fauna (Kuman & Clarke 2000) **1.8–1.4 Ma** dating seriation (Herries *et al.* 2009). **1.8–1.5 Ma** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	*Homo habilis* /or Late *Australopithecus?*	0
Member 5: East Infill	**2.0–1.7 Ma**; Biochronology and archaeology (Kuman and Clarke 2000). **1.4–1.1 Ma** dating seriation (Herries *et al.* 2009). **1.4–1.2 Ma** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011)	*Paranthropus robustus*	3245 Oldowan Industry
Member 5: West Infill	**1.7–1.4 Ma,** Biochronology and archaeology (Kuman & Clarke 2000). **1.3–0.8 Ma** dating seriation (Herries *et al.* 2009). **1.3–1.1** (Herries & Shaw 2011)	*Homo ergaster*	701 Early Acheulean industry
Post Member 6: L/63 Infill	**Mid- late Pleistocene** age, faunal correlations and archaeology; (Reynolds *et al.* 2007) **0.5–0.3 Ma** (Herries & Shaw 2011)	*Homo* sp.	50 Middle Stone Age, debitage
Lincoln Cave North	**0.253–0.115 Ma** Uranium series (Reynolds *et al.* 2003, 2007)	0	5 Early Acheulean
Lincoln Cave South	**Mid- late Pleistocene** age, archaeology, (Reynolds *et al.* 2007)	*cf. Homo ergaster*	69 Middle Stone Age, and Early Acheulean mix

mid- to late Pleistocene, a time period that was, until recently poorly represented at Sterkfontein (Boshoff *et al.* 1990; Reynolds *et al.* 2003, 2007). These two deposits are roughly equivalent to Post-Member 6 in the main excavation, and extend the hominin and human occupation of the site until less than 115 ka years ago (Reynolds *et al.* 2003, 2007). The Lincoln Cave deposits appear to be connected to the main excavation via the solution cavity in the L/63 area (Fig. 2).

Lower Cave deposits

The balance of the Sterkfontein Members lies within the extensive underground network of the Sterkfontein Cave System (Wilkinson 1973, 1983, 1985; Kuman & Clarke 2000; Clarke 2006). The underground deposits are: Member 1 (largely sterile), the Member 2 StW 573 'Little Foot' deposit, and the fossiliferous Member 3 (unexcavated), all exposed within the Silberberg Grotto. A recent re-examination of the stratigraphy and sedimentology of Sterkfontein has indicated that Member 3 should be reassigned to Member 4 (Fig. 3; Pickering & Kramers 2010).

Other underground deposits include the Jacovec Cavern and the Name Chamber. The former appears to be unconnected to the Sterkfontein Formation but contains *Australopithecus* sp. fossils and is inferred to be contemporaneous with Member 2, based on similar dating cosmogenic nuclide results (Partridge *et al.* 2003; Table 1; Fig. 4).

The Name Chamber contains a very large collapsed talus cone and lies directly beneath Member 5 (Clarke 1994). The Name Chamber contains two talus deposits, known as the Eastern and Western Talus cones (Avery *et al.* 2010). This material derived from a shaft in the vicinity of grid square R57 of the main excavation at the surface, and shows several episodes of collapse from the

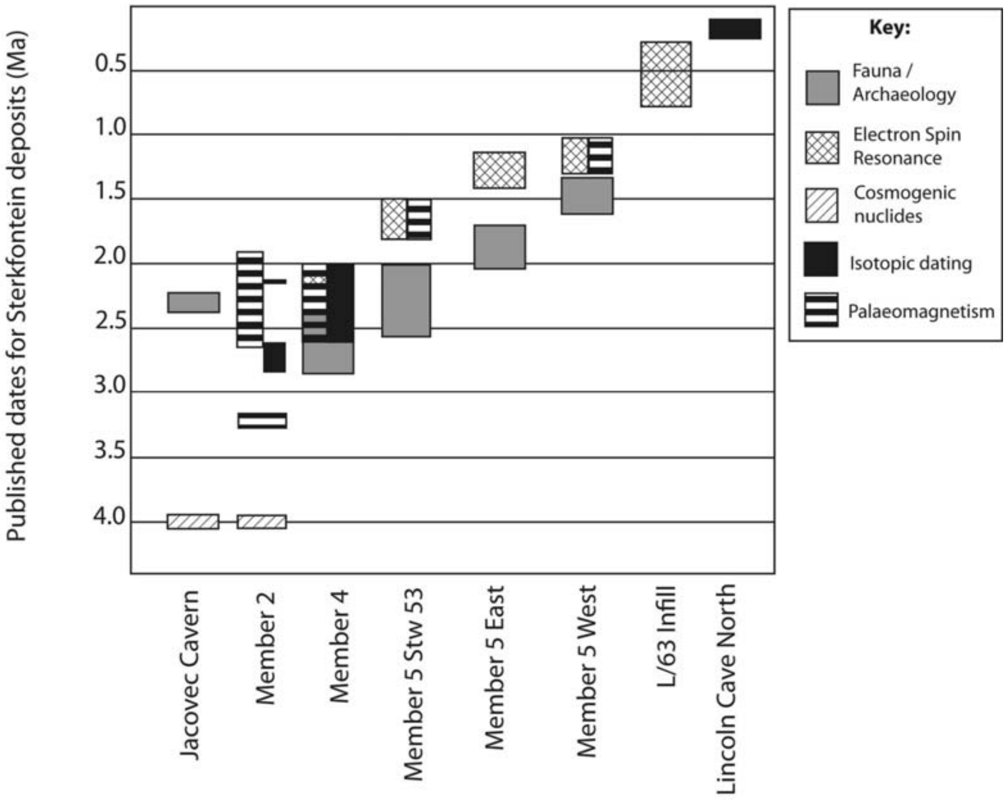

Figure 4. Dates for all Sterkfontein deposits. The dates shown here are given in Table 1, along with the references. Note: For Jacovec Cavern, the cosmogenic date comes from Partridge *et al.* (2003), while the faunal estimation is based on the presence of *Equus* sp. in this deposit, according to Kibii (2004). For Member 2, Herries & Shaw (2011) consider the previous palaeomagnetism date of Partridge *et al.* (1999; indicated) to be invalidated in favour of their date of 2.6–1.8 Ma. Uranium-lead isotope date of 2.2 Ma is from Walker *et al.* (2006), while the 2.6–2.8 Ma is from Pickering and Kramers (2010). For Member 4, there is some overlap between the faunal estimates (Kuman & Clarke 2000) and ESR and palaeomagnetism results, as well as Uranium-thorium dating (Schwarcz *et al.* 1994; Partridge 2005; Pickering & Kramers 2010, and Herries & Shaw 2011). The younger StW 53 date of 1.8–1.5 Ma is derived from the assessment of a combination of methods, in particular ESR and palaeomagnetism (Herries & Shaw 2011). Member 5 East ESR date is from Herries and Shaw (2011). Member 5 West dates are the combined palaeomagnetic and ESR dates are taken from Herries and Shaw (2011), in addition to the faunal and archaeological dates from Kuman & Clarke (2000). The Lincoln Cave North dates are from Reynolds *et al.* (2003, 2007) while the dates for the L/36 area are from Reynolds *et al.* (2007). The older dates for 'Member 6' (L/63) are ESR dates from Herries & Shaw (2011).

surface. The presence of an extinct micromammal genus, *Proodontomys*, suggests that some material in the Name Chamber derives from Members 4 and 5, while the presence of three genera found in the younger Post-Member 6 deposits suggest that younger material is also included in the Name Chamber material (Avery *et al.* 2010).

Each of these Members presents a sampling of palaeoenvironmental conditions spanning close from 2.6 Ma to less than 115 ka (Fig. 4), which can be interpreted as a series. The following presents a summary of dating and paleoenvironmental reconstructions of data for each of the Sterkfontein Members.

STERKFONTEIN MEMBERS

Member 1

Stratigraphy: Member 1 is largely sterile deposit that formed when the first cave openings were absent or too small to admit surface-derived bone (Partridge 2000). This Member, which is up to 12 m thick in places, is exposed on the floor of the Silberberg Grotto, where it lies under Member 2 and on top of a dolomite floor. This Member is also exposed as a hanging remnant in younger chambers, such as the Name Chamber (Partridge 2000).

Jacovec Cavern

Stratigraphy: The Jacovec Cavern contains the deepest fossil-bearing deposits of the Sterkfontein Cave System, approximately 30 m from the ground surface (Wilkinson 1973, 1983, 1985). The cavern comprises two breccias of different ages; the Orange and the Brown breccias (Fig. 4; Partridge *et al.* 2003). Firstly, the older Orange breccia was deposited and subsequently a portion of it collapsed onto the floor of the cavern. Part of the Orange breccia remains *in situ* as a hanging remnant in the cavern, and this is where parts of the first *Australopithecus* cranium (StW 578) were discovered in August 1995 by Ronald J. Clarke (Clarke, in Partridge *et al.* 2003). All hominin specimens recovered from Jacovec Cavern derive from this Orange breccia (Partridge *et al.* 2003; Kibii 2004). The younger Brown breccia was deposited in a talus cone into the Jacovec Cavern some time after the collapse and erosion of the older Orange breccia. Later, a partial slump or collapse of the Brown breccia resulted in some mixing of the two breccias on the floor of the cavern, but leaving a portion of the Brown breccia *in situ* (Fig. 5). The excavation of the Brown breccia has not produced any hominins.

Sedimentological analysis of breccia blocks that were excavated from the collapsed and mixed section of the cavern indicates that as many as nine different rock types

Table 2. Sediment and rock types from the Jacovec Cavern breccia (Kibii 2000).

Sample	Rock type	Description
A	Clear grey to white 5.0 mm long crystals of calcite ($CaCO_3$)	Crystallized in situ either from groundwater saturated with Ca and CO_2, or precipitation from limestone.
B	Greyish white brown calcrete ($CaCO_3$)	Formed as part of regolith (weathered rock) or soil horizon by the concentration of $CaCO_3$ and removal of other elements.
C	Reddish brown, brecciated regolith consisting of angular clasts (fragments) of 5.0–10 mm thick, finely bedded (0.5–1.0 mm) limestone, and small (0.5 mm) discrete crystals of clear grey calcite.	Slump deposits formed from collapsed limestone and other superficial material cemented together and weathered to form regolith, with calcite being formed by circulating groundwater. Angularity of clasts indicates that they have not been transported far from the origin.
D	Dark reddish brown to brown regolith with angular, 10–20 mm thick, isolated clasts of fine-grained bedded, white grey limestone, as well as discrete 0.2–0.5 mm calcite crystals.	The weathering of a breccia forms this form of brecciated regolith with some precipitation from groundwater.
E	Dark reddish brown with thin lenses (3.0–4.0 mm thick) of greyish white calcrete throughout.	This is regolith that is further weathered with calcrete resulting from the soil forming process.
F	Very dark brown regolith with small 0.5 mm dark brown rounded clasts (concretions) and angular clasts of greyish white, finely bedded, limestone (8.0–10 mm).	This is formed from the weathering of a limestone breccia, with concentrations possibly forming by the concentration of iron (Fe), or derived from another soil horizon.
G	Dark brown regolith with numerous clear grey, 2–10 mm thick, calcite veins throughout.	These form from weathered rock that was infiltrated by circulating groundwater, with precipitation out of $CaCo_3$ in joints and fractures within the host rock.
H	Dark reddish brown to red regolith with fine (2.0–3.0 mm) rounded hematite clasts throughout, with angular (10–15 mm) clasts of greyish white, finely bedded limestone, and rare fine (0.5–1.0 mm) clear grey calcite crystals.	This is formed from weathered limestone breccia where removal of other elements result in the concentration of Fe into nodules, and circulating groundwater precipitated out calcite.
I	Has two components, the first consisting of reddish brown regolith similar to Rock H, and a brown limestone regolith similar to Rock C.	This was probably formed elsewhere and cemented together in another slump deposit.

are present, some of which were formed as a result of speleothem precipitation within the cave while others were calcified sediments that were fluvially transported from the grounds above and within the cave's vicinity (Table 2; Kibii 2000). Thus far, the Jacovec Cavern appears devoid of artefacts.

Dating: The two breccias within the Jacovec cavern have been dated through cosmogenic nuclides (^{26}Al and ^{10}Be). The Orange breccia has been dated to *c.* 4.02 ± 0.27 (0.41) Ma, and the Brown breccia to *c.* 3.76 ± 0.26 (0.41) Ma (Table 1; Partridge *et al.* 2003). However, the presence of an equid in this deposit (Kibii 2000, 2004) suggests an age of less than 2.36 Ma for some of the material and that older and younger material are mixed together in this deposit (Fig. 4).

Taxonomy

Primates: Within the Jacovec Cavern, a single hominin taxon (assigned only to the genus *Australopithecus*) is identified (Table 3). Jacovec Cavern has yielded a hominin sample of 12 cranial, postcranial and dental specimens. Taken together, these specimens represent three old individuals and three juvenile individuals, all assigned to *Australopithecus* sp. (Partridge *et al.* 2003). Most complete is the partial cranium of a single old individual (StW 578). This cranial specimen also preserves portions of the occipital, parietals, the left sphenoid, right temporal, frontal, the left naso-orbital margins, nasal bones and a right maxilla containing three heavily worn molars (Partridge *et al.* 2003). Two additional elderly *Australopithecus* individuals are represented by two worn upper right premolars (StW 590), and a single heavily worn lower left fourth premolar (StW 603). Wear slope differences between these teeth confirm the presence of three elderly individuals (Partridge *et al.* 2003). Juvenile *Australopithecus* individuals are represented by a left deciduous upper canine (StW 599); a moderately worn lower first molar (StW 601), and finally, an unworn lower right second molar (StW 604; Partridge *et al.* 2003). The Jacovec femur (StW 598) has a 'small head relative to a long neck' a feature more closely resembling *Paranthropus* femora from Swartkrans, as well as the femur (StW 99) from Member 4 (Partridge *et al.* 2003: 611). Also from Jacovec Cavern, there is a well-preserved lateral portion of a left clavicle (StW 606), which preserves evidence of carnivore gnaw-marks (Partridge *et al.* 2003). It exhibits 'a unique and ape-like morphology' more similar to that of chimpanzees, relative to humans or to other *Australopithecus* clavicles (Partridge *et al.* 2003: 612).

Additionally, the species *Parapapio jonesi*, *Parapapio broomi*, colobine, *Papio izodi* and taxonomically indeterminate cercopithecoid have been identified from this breccia (Table 3; Kibii 2000, 2004, 2007; Partridge *et al.* 2003).

Carnivores: Five families of the order Carnivora are

Table 3. Hominin and non-hominin primate species from the Sterkfontein Members. Key to deposits: J C: the Jacovec Cavern; M 2: Member 2 exposed in Silberberg Grotto; M 4: Member 4, the 'Type Site' where *Australopithecus africanus* was first recovered. Stw 53: is the small infill where the StW 53 cranium was recovered; M 5 E/ W: Member 5 East / West (stone-tool-bearing breccias). L/63: named for its excavation provenance, is located within Member 5 West. L C: is Lincoln Cave, lying within a separate cave system.

Macromammalian species	Common name	J C	M 2	M 4	Stw 53	M 5 E	M 5 W	L/63	L C
Family Hominidae									
Hominidae indet.	Early *Homo* or *Australopithecus*				x				
Homo sp.	Modern human							x	
Australopithecus sp.	Extinct hominin	x	x	x					
Australopithecus africanus	Extinct hominin			x					
Homo ergaster	Extinct hominin						x		x
Paranthropus robustus	Extinct hominin					x			
Family Cercopithecidae									
Cercopithecoides indet.	Cercopithecine monkey	x		x	x	x	x		
Theropithecus oswaldi	Extinct gelada baboon				x	x			
cf. Cercopithecoides williamsi	Extinct colobine monkey		x	x	x				
cf. Colobine	Colobine	x							
Parapapio jonesi	Extinct parapapio	x	x	x					
Parapapio whitei	Extinct parapapio			x					
Parapapio broomi	Extinct parapapio	x	x	x					
Parapapio sp.	Extinct parapapio			x					
Papio izodi	Extinct baboon	x	x	x					
Papio cynocephalus	Chacma baboon							x	x

represented within the Jacovec Cavern fossil fauna (Table 4). These include: Viverridae, represented by *Genetta genetta*; Herpestidae, represented by *Cynictis penicillata* and a taxonomically indeterminate Herpestes; Canidae, represented by *Canis mesomelas, Vulpes chama,* and a taxonomically indeterminate canid; Felidae, represented by *Homotherium latidens, Felis caracal, Panthera leo, Panthera pardus* and taxonomically indeterminate felid; and Hyaenidae, represented by *Chasmaporthetes nitidula*, *Chasmaporthetes silberbergi*, *Chasmaporthetes* sp., and a taxonomically indeterminate hyaenid (Kibii 2000, 2004).

Bovids: Three subfamilies of the family Bovidae, are represented in the Jacovec Cavern fossil assemblage (Table 5). These are: Hippotraginae; Bovinae and Alcelaphinae. The tribes represented within the three subfamilies include: Hippotragini, Reduncini, Cephalophini, Tragelaphini, Bovini, and Alcelaphini (Kibii 2000, 2004). Indeterminate individuals were recovered for each of the tribes, except the Alcelaphini, which is represented by the wildebeest (*Connochaetes taurinus*) (Kibii 2000; 2004).

Other fauna: Other fauna represented in this infill include a single tortoise individual, an equid, the springhare (*Pedetes capensis*), the bushpig (*Potamochoerus porcus*), the Cape hare (*Lepus capensis*), and hyraxes (Table 6; Kibii 2000, 2004).

Taphonomy

Taphonomic assessment indicates that several processes were involved in accumulation of different taxa within the Jacovec Cavern. Carnivores and fluvial transport have been identified as having played a major role in the accumulation of the fossils (Kibii 2004). Skeletal element representation, in part, suggests that some primate individuals were victims of carnivores (Kibii 2004, 2007). The remains of primate individuals were, however, not deposited into the cave by the predators; rather the skeletal elements were accumulated within the catchment area around the cave, and subsequently water activity incorporated the remains into the cavern (Kibii 2004, 2007). Larger carnivores appear to have been responsible for accumulating the remains of smaller carnivores on the grounds above the cave (Kibii 2004, 2007). Current evidence points to natural death of the larger carnivores within the catchment area of the cave. The skeletal remains of both groups of carnivores were eventually washed into the cave through fluvial action (Kibii 2004). Paucity of biotically derived bone modification, in addition to skeletal element representation suggest that the fossil bovid assemblage from Jacovec Cavern was not accumulated by carnivores, but instead selectively washed in from the grounds above and within the vicinity of the cave (Kibii 2004).

Palaeoenvironments

The faunal composition of the Jacovec Cavern deposits suggest that a mosaic of open and closed habitats, which comprised a riverine gallery forest, with bushland and open country was present at the site (Kibii 2004). The presence of non-hominin primates, especially the colobine monkeys, suggests the presence of substantial tree cover within the vicinity of the cave. Modern colobines 'rarely leave the trees and no contemporary species occur beyond the main outliers of Africa's tropical and montane forest belt' (Kingdon 1997: 18). Thus the presence of colobine species within the Jacovec Cavern is highly indicative of the presence of a forest probably equivalent

Table 4. Carnivoran species. Key to deposits: J C: the Jacovec Cavern; M 2: Member 2; M 4: Member 4, Stw 53: is the StW 53 cranium infill; M 5 E/W: Member 5 East/West (stone-tool-bearing breccias). L/63: is an infill within Member 5 West. L C: is Lincoln Cave, lying within a separate cave system.

Macromammalian species	Common name	J C	M 2	M 4	Stw 53	M 5 E	M 5 W	L/63	L C
Family Machairodontinae									
Dinofelis barlowi	Extinct false sabretooth cat		x	x			x		
Megantereon cultridens	Extinct sabretooth cat		x	x					
Homotherium latidens	Extinct sabretooth cat	x		x					
Family Felidae									
Panthera sp.	Pantherine cat				x				
Panthera leo	Lion	x	x	x		x	x		
Panthera pardus	Leopard	x	x	x					
Acinonyx jubatus	Cheetah		x						
Felis indet.	Indeterminate felid	x		x		x		x	x
Felis caracal	Caracal	x	x						
Family Canidae									
Canis sp.	Jackal			x		x			x
Canis mesomelas	Black-backed jackal	x		x	x		x	x	x
Canis brevirostris	Short-faced jackal			x					
Canis antiquus	Extinct jackal			x					
Vulpes chama	Cape fox	x							x
Otocyon megalotis	Bat-eared fox								x
Nyctereutes terblanchei	Extinct raccoon dog						x		
Family Viverridae									
cf. Mungos sp.	Mongoose					x	x		
Suricata sp.	Suricate				x	x	x	x	x
Herpestes ichneumon	Grey mongoose							x	
Herpestes indet.	Mongoose					x			
Genetta genetta	Common genet	x							
Cynictis penicillata	Yellow mongoose	x							
Family Hyaenidae									
Hyaenidae indet.	Hyaena	x	x	x		x	x		x
Chasmaporthetes sp.	Extinct hunting hyaena	x		x	x				
Chasmaporthetes nitidula	Extinct hunting hyaena	x	x	x					
Chasmaporthetes silberbergi	Extinct hunting hyaena	x	x	x					
Pachycrocuta brevirostris	Extinct short-faced hyaena			x		x			
Crocuta crocuta	Spotted hyaena			x			x		
Parahyaena brunnea	Brown hyaena			x			x		
Proteles sp.	Aardwolf						x		

to Africa's tropical and montane forests.

Several tentative inferences can be made about the types of habitats indicated by the Jacovec fauna. Presently, leopards (*Panthera pardus*) have a wide range of habitats from dense forests to open grassland plains, while lions (*Panthera leo*) are also common in most habitats, except for very dry deserts and dense forests. The Cape fox (*Vulpes chama*) is found in open grassy countryside, while the black-backed jackal (*Canis mesomelas*) occupies most habitats ranging from bush, woodland and savannahs to coastal desert (Haltenorth & Diller 1980; Kingdon 1997). The modern habitat of the caracal (*Felis caracal*) is plains and rocky countryside, with little grass cover. Extinct species, such as the long-legged hunting hyaenas (*Chasmaporthetes silberbergi* and *C. nitidula*), and extinct sabretooth cat, the *Homotherium latidens*, are thought to have occupied open habitats (e.g. Lewis 1997). The overall scarcity of *H. latidens* in the fossil record of the Cradle of Humankind led Reynolds (2010) to propose that this species may not have been continuously resident in the but instead a transient species, perhaps to reduce competition with other large carnivore species. The morphology and inferred behaviour of the genus *Chasmaporthetes* suggests that its members 'may have preferred relatively open country and/or broken woodland, in which its cursorial adaptations could be used to best advantage' (Pickering *et al.* 2004b: 292).

The species of bovids present indicate a wide range of habitat types, from more closed deposits, (e.g. the small duikers and the tragelaphines), to those tribes indicating mixed habitats of grassland and savannah woodland (e.g. the bovines) and finally, those bovid tribes which may

Table 5. Bovid species.

Macromammalian species	Common name	J C	M 2	M 4	Stw 53	M 5 E	M 5 W	L/63	L C
Family Bovidae **Tribe Alcelaphini**									
cf. Megalotragus sp.	Extinct alcelaphine			x					x
Alcelaphini indet.	Wildebeest-sized bovid	x	x		x	x	x	x	x
Connochaetes sp.	Indet. wildebeest			x					
Connochaetes taurinus	Wildebeest	x							
Damaliscus parmularius				x					
Damaliscus sp.	Blesbok				x	x	x	x	
Tribe Hippotragini									
Hippotragus sp.	Roan /sable	x		x					x
Hippotragus equinus	Roan antelope			x					
Hippotragus cookei	Extinct Cooke's antelope			x					
Tribe Bovini									
Syncerus sp.	Buffalo	x		x					
Tribe Ovibovini									
Makapania sp.	Extinct Indet. *Makapania*			x					
Makapania broomi	Extinct musk-ox like bovid		x	x	x				
Tribe Aepycerotini									
Aepyceros sp.	Indet. impala			x			x		
Aepyceros melampus	Impala			x					
Tribe Tragelaphini									
Tragelaphini indet.	Probable eland	x					x		
cf. Taurotragus oryx	Eland					x			
Tragelaphus scriptus	Bushbuck								x
Tragelaphus strepsiceros	Kudu			x					
Tragelaphus angasi	Nyala			x					
Tribe Reduncini									
Redunca sp.	Indet. reedbuck	x						x	
Raphicerus campestris	Steenbok								
Raphicerus sp.	Steenbok					x	x		x
Redunca darti	Extinct Dart's steenbok			x					
Redunca cf. *arundinum*	Reedbuck			x					
Tribe Antelopini									
Gazella sp.	Gazelle			x					
Gazella cf. *gracilior*	Extinct small gazelle				x				
Antidorcas sp.	Springbok					x	x	x	x
Antidorcas bondi	Extinct springbok			x					
Antidorcas recki	Extinct springbok			x					
Antilopini sp.	Indet. antilopine			x					
Tribe Neotragini									
Sylvicapra grimmia	Grey duiker							x	
Cephalophini indet.	Indet. duiker	x							x
Oreotragus oreotragus	Klipspringer					x			
Tribe Peleini									
Pelea capreolus	Grey rhebok			x				x	x
Tribe Boselaphini									
Boselaphini sp.	Extinct antelope			x	x				

Table 6. Other fauna from Sterkfontein.

Macromammalian species	Common name	J C	M 2	M 4	Stw 53	M 5 E	M 5 W	L/63	L C
Family Equidae									
Hipparion lybicum	Extinct three-toed horse			x					
Equus sp.	Indet. zebra	x		x	x	x	x		
Equus burchellii/quagga	Plains zebra							x	x
Family Elephantidae									
Elephas recki	Extinct elephant			x					
Family Hippopotamidae									
Hippopotamus amphibius	Hippopotamus								x
Family Suidae									
Suidae indet	Indet. pig			x					
Phacochoerus africanus	Warthog						x		x
Potamochoerus porcus	Bushpig	x							
Metridiochoerus modestus	Extinct pig					x			
Metridiochoerus sp.	Extinct pig			x					
Family Hyracoidae									
Procavia antiqua	Small extinct hyrax			x	x	x	x		
Procavia transvaalensis	Large extinct hyrax			x	x	x			
Procavia capensis	Modern hyrax							x	x
Family Hystricidae									
Hystrix africaeastralis	Porcupine			x			x	x	x
Family Pedetidae									
Pedetes capensis	Springhare	x				x		x	x
Family Lagomorpha									
Lepus capensis	Cape hare	x						x	x
Family Aves									
Struthio camelus	Ostrich					x			
Aves indet.	Indet. bird	x							
Family Chelonia									
Chelonian indet.	Tortoise	x							

indicate more open, grassland habitats (e.g. alcelaphines, hippotragines and reduncines).

The palaeoenvironmental reconstruction is similar to that which has been suggested for Member 2, Sterkfontein (Partridge *et al.* 2003; Pickering *et al.* 2004a). However, due to the possible mix of assemblages in Jacovec due to the collapse of the Orange and Brown breccias, there is a need for further studies aimed at analysing samples from the Orange and Brown breccias separately. This might be achieved by isotope analyses of tooth elements deriving from secure horizons or that have embedded matrix that can be associated with a particular breccia.

Member 2

Stratigraphy

Member 2 is exposed in the underground cavern known as the Silberberg Grotto (formerly also known as 'Daylight Cave') and consists of 0.5–5.0 m of reddish brown sandy silt that rests unconformably on Member 1. In some places, Member 1 and 2 are separated by a flowstone layer and prior to lime-mining activities, this cavern would have contained an enormous stalagmite, which was removed during mining (Partridge 2000). The infill is calcified, devoid of artefacts and with high fossil concentration (carnivores and primate fossils are visible) in its lower levels (Partridge 1978; Brain 1981). The deposit is a talus cone, which lenses out from NE to SW (Fig. 6; Clarke 2006; Pickering & Kramers 2010).

Dating

A fossil hunting hyaena of the genus *Chasmaporthetes* provided an initial age estimate of 3.0 to 3.5 Ma, based on similar morphology noted for a fossil from the lower Pliocene site of Langebaanweg, Western Cape (Turner 1997; Clarke 1998). Subsequent palaeomagnetic dating placed Member 2 between the Mammoth-Gauss and Gilbert-Gauss magnetic polarities, as *c.* 3.22 to 3.58 Ma (Partridge *et al.* 1999). Cosmogenic nuclides (^{26}Al and ^{10}Be) burial dates pushed back the age of this Member to *c.* 4.17 Ma (Partridge *et al.* 2003).

This finding sparked debate, and some authors have pointed out that: 'the Member 2 'Little Foot' skeleton is not older than 3.04 Ma, and may be as young as 1.07–1.95 Ma

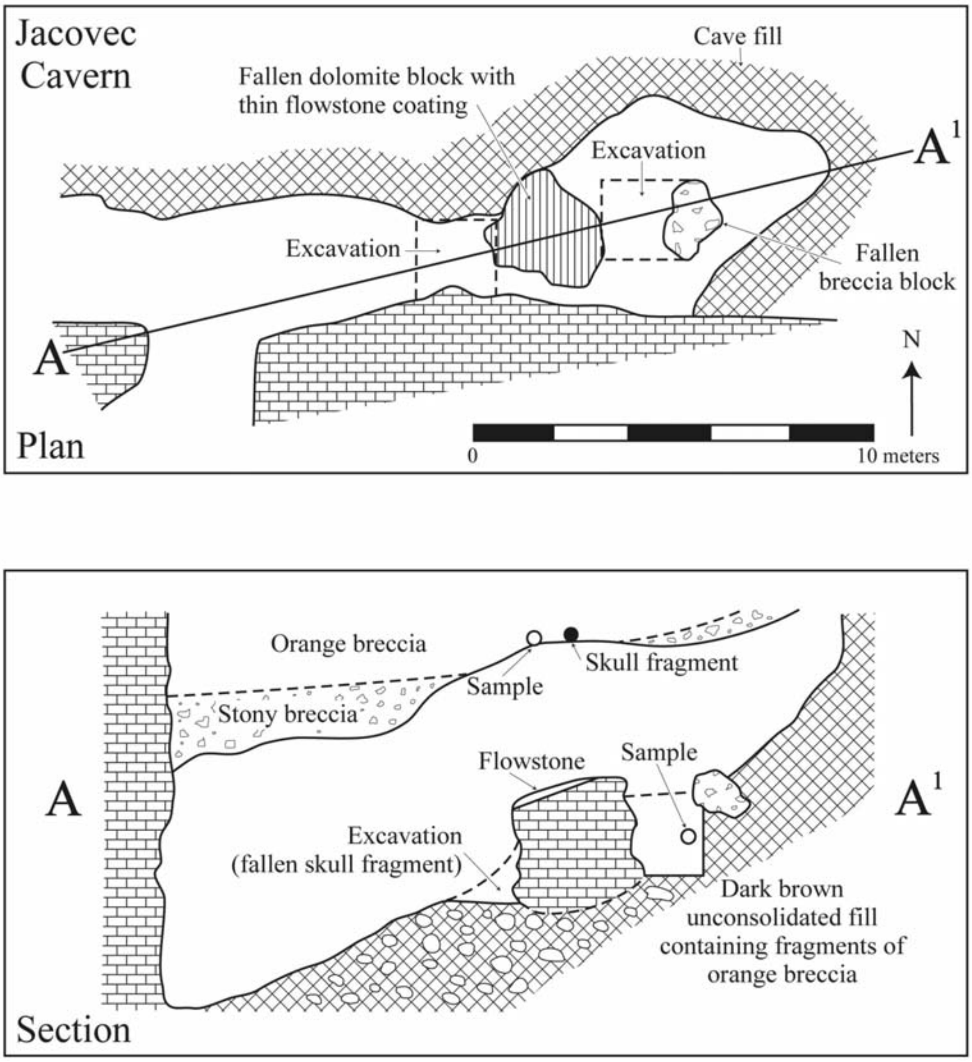

Figure 5. Jacovec Cavern profiles, showing the location of the *Australopithecus* sp. specimens, as well as the location of the collapse and mixing of the Brown and Orange breccias (redrawn from Partridge *et al.* 2003).

(Berger *et al.* 2002: 195). This claim was countered by Clarke (2002b). Recently, Walker and colleagues (2006), proposed an age of close to 2.2 Ma based on uranium–lead (U-Pb) isotopic dating while Pickering & Kramers (2010) obtained the same age within error of 2.01 ± 0.06 for the capping flowstone associated with StW 573, confirming the reproducibility of these ages. Dates ranging from 2.8 ± 0.82 to 2.6 ± 0.30 Ma using the same isotopic method (Table 1) were obtained for Member 2 (Pickering & Kramers 2010), while Herries & Shaw (2011) suggested an age range of 2.6–1.8 Ma based on palaeomagnetic analysis. The age discrepancies for Member 2 may be explained by the reworking of certain sediments (specifically, the quartz grains sampled for the cosmogenic nuclide analysis) in the cave, thus giving rise to different ages for this deposit (Pickering & Kramers 2010). A summary of these dates is presented in Fig. 4.

Taxonomy

Pickering and colleagues (2004a: 282) separate the species recovered from the *in situ* excavations from the fossil species published in several previous publications on the Silberberg Grotto by Broom (1945a,b), Broom & Schepers (1946), McKee (1996) and Turner (1997). Here we have presented the combined species lists from the Member 2 excavations and older Silberberg Grotto publications.

Primates: Member 2 has yielded one of the oldest and arguably the most complete hominin fossil recovered in southern Africa: the ‘Little Foot’ skeleton, StW 573, which has been referred to the *Australopithecus* genus (Clarke & Tobias 1995; Tobias & Clarke 1996; Clarke 1998, 1999; Partridge *et al.* 1999, 2003). In addition, four other extinct primate species; the colobus-type monkey (*Cercopithecoides williamsi*), and three species of fossil baboons (*Parapapio broomi, Parapapio jonesi* and *Papio izodi*) are also represented (Pickering *et al.* 2004a) (Table 3).

Carnivores: At least two families of the order Carnivora are presented in the Member 2 fossil fauna assemblage (Table 4). The family Hyaenidae is represented by both species of extinct long-legged hunting hyaena (*Chasmaporthetes silberbergi, C. nitidula*) as well as an indeterminate hyaena. The family Felidae is represented by extinct machairondonts (*Dinofelis barlowi, Megantereon cultridens*), as well as four extant felid species, namely the lion, leopard, cheetah and caracal (*cf. Panthera leo, Panthera pardus, Acinonyx jubatus* and *Felis caracal,* respectively; Pickering *et al.* 2004a). The cheetah is another scarce carni-

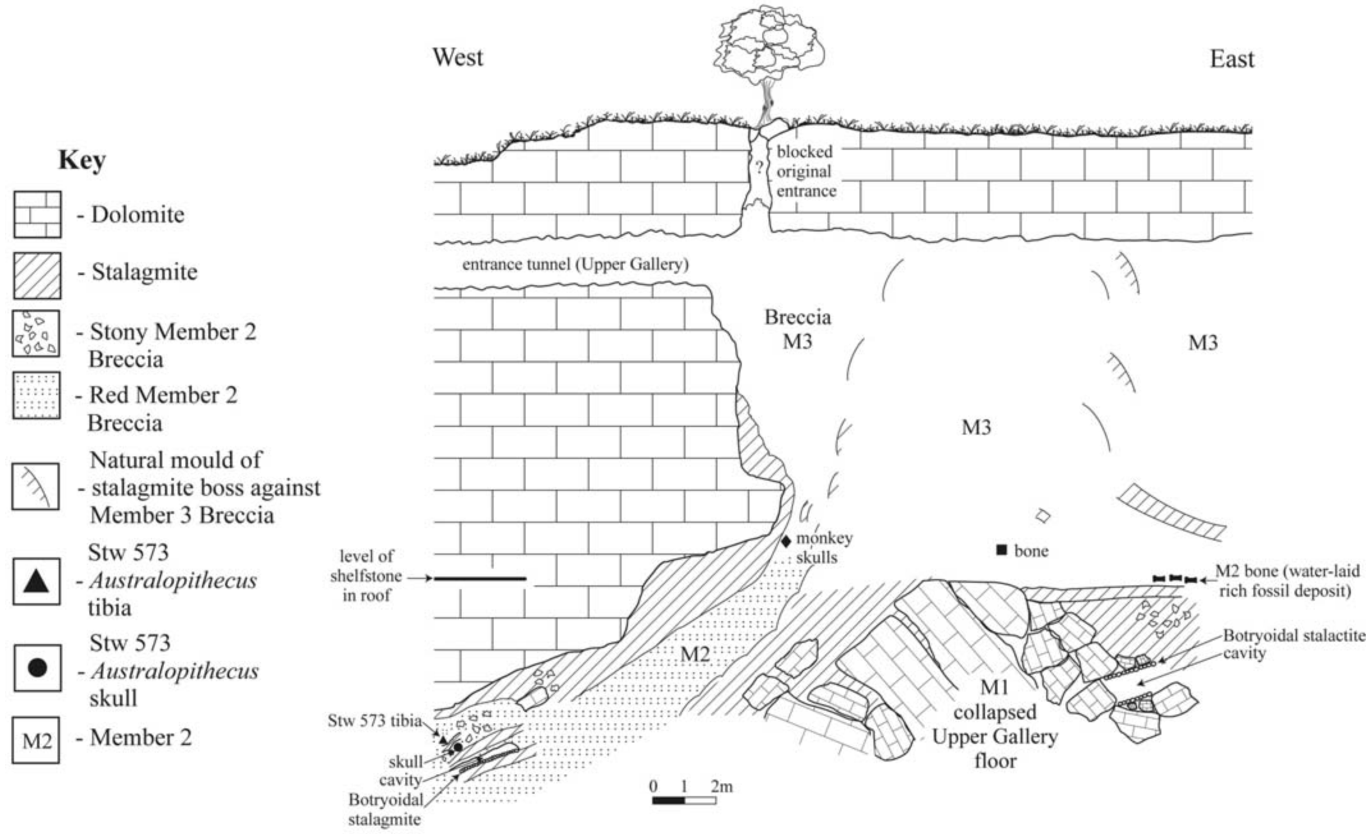

Figure 6. Profile of the Silberberg Grotto, showing the location of the *Australopithecus* sp. skeleton (StW 573). The position of exposed Members 1–3 within the cavern are also indicated (redrawn after Clarke 2006).

vore in the Cradle of Humankind, and spatial distributions show that this species is found only at the southern end of the Cradle, at Sterkfontein and Swartkrans (Reynolds 2010).

Bovids: The family Bovidae is represented by the extinct ovibovine, *Makapania broomi*, and an indeterminate Alcelaphini, and a non-Alcelaphini Size Class 2 bovid (Table 5; Pickering *et al.* 2004a).

Palaeoenvironment and taphonomy

The presence of extinct primates, specific carnivore taxa associated with open grassland, the extinct hunting hyaena (*Chasmaporthetes*) and the extinct ovibovine (*Makapania broomi*) all suggest the presence of open grassland with rocky outcrops during the deposition of Member 2. Obligate drinkers, specifically members of the Alcelaphini tribe (including hartebeests, wildebeests and blesbok), suggests a permanent water supply reasonably close to the Sterkfontein site (such as the Blaaubank river), which would in turn have supported a riverine gallery forest ideal for leopards and monkeys (Pickering *et al.* 2004a). Unpublished micromammal specimens have been provisionally identified as elephant shrew (genus *Elephantulus*), which may indicates the presence of wetter habitats (Clarke, pers. comm.). The recovery of articulating bone specimens and antimeric (i.e. both left and right elements) specimens, in addition to paucity of bone surface modification signals that a death trap within the cavern was probably responsible for the accumulation of the fauna (Pickering *et al.* 2004a).

Member 4

Stratigraphy

Partridge (1978) subdivided this Member into four stratigraphic layers, referred to as Beds A–D. Bed A is exposed in the Type Site and in the Lower Cave and consists of 2–3 m of brownish red calcified sandy silt. The bed contains occasional bone fragments and shows evidence of a series of successive major roof collapses that resulted in the enlargement of cave shaft connecting to the outside. Bed B is exposed in the Type Site, Lower Cave and lower levels of the 'Extension Site' (i.e. to the west of the Type Site) and consists of reddish brown sandy loam. Bed C rests on eroded surface of Bed B, and is exposed in the Type Site and the Lower Cave. It consists of 0.5–2.0 m of well-calcified dark reddish brown silty sand. Bed B and Bed C are the *Australopithecus*-bearing beds, including the famous 'Mrs Ples' Sts 5 specimen from Bed C (Partridge 1978). Bed D is exposed in the Type Site and lower Cave and consists of discontinuous brownish red heavily calcified silty sand. A marked erosional unconformity separates this bed from Bed C, and Bed D represents a temporal period of greater water abundance in the cave, but also episodes of roof instability and collapse (Partridge 1978).

Members 2 and 4 are important *Australopithecus*-bearing deposits, while Member 3 (exposed in the Silberberg Grotto) is as yet unexcavated. Recently, Pickering & Kramers (2010) suggested that material assigned to Member 3 may possibly be distal deposits of Member 4 (shown in Fig. 3). If this hypothesis can be confirmed through excavation and analysis, then the volume of Member 4 would be far greater than previously appreciated, which may in turn explain some of the high levels of palaeoenvironmental variation and biodiversity observed in Member 4 as being due to the temporal period covered by this deposition.

Dating

Early faunal dating relied on correlations with fossiliferous volcanic deposits in eastern Africa which could be dated absolutely (Table 1). Age estimates of *c.* 2.5 Ma based on fossil cercopithecoids (Delson 1984, 1988) and *c.* 2.8–2.4 Ma (Vrba 1975, 1976, 1980, 1985; Kuman & Clarke 2000), based on fossil Bovidae were proposed. McKee used detailed faunal seriation methods to derive a date of between 2.6 and 2.8 Ma (McKee 1993). Electron spin resonance (ESR) studies on bovid teeth yielded a date of 2.1 ± 0.5 million years old (Schwarcz *et al.* 1994). The presence of *Equus* in the deposit suggests an upper age limit of less than 2.36 Ma (Herries & Shaw 2011).

Recent reanalysis of palaeomagnetic dates has positioned Member 4 within the younger Réunion event at 2.15–2.14 Ma (Partridge 2005; Herries & Shaw 2011). Palaeomagnetic analysis suggests Member 4 formed between 2.58 and 2.05 Ma, with the Sts 5 fossil dating to between 2.16 and 2.05 Ma (Fig. 3). Pickering and Kramers (2010) propose that Member 4 is dated to between 2.65 ± 0.30 and 2.01 ± 0.06 Ma, based on isotopic (U-Pb) dating methods. Some of the Member 4 sediment may be younger than 2.36 Ma, based on the presence of fossils of *Equus.* More recently, Herries & Shaw (2011) revised the dates for the stratigraphic layers within Member 4 as: Member 4A at 2.8–2.2 Ma, Member 4B at 2.6–2.2 Ma and Member 4C at 2.2–2.0 Ma.

Taxonomy

This important Member is where the first adult cranium of australopithecine was discovered by Robert Broom in 1936. Initially assigned to a new species, *Plesianthropus transvaalensis,* some of the hominin specimens from this Member are assigned to *Australopithecus africanus* Dart, 1925, while Clarke (1988) has argued for a second species (Fornai 2010).

Primates: One hominin species, *Australopithecus africanus,* (and a proposed second *Australopithecus* species) and five primate species are identified from Member 4, including extinct primate species (*Parapapio broomi, Parapapio jonesi, Papio izodi, Parapapio whitei,* and *Cercopithecoides williamsi*). Additionally, several indeterminate hominins, parapapionins and cercopithecoid monkey specimens have been identified (Kibii 2004; Table 3). The australopithecine fossil sample from Member 4 is world-famous. Here we outline the most remarkable fossil finds, but discuss the interpretations of these fossils later in the text.

Member 4 has yielded numerous hominin specimens assigned to *Australopithecus africanus,* including the Sts 5 'Mrs Ples' cranium (Broom *et al.* 1950). Recent researches through the Transvaal Museum, Pretoria, fossil collections by de Ruiter (2004) have recovered 10 previously undescribed craniodental *Australopithecus africanus* specimens from Sterkfontein Member 4 (including a natural endocast, Sts 1960b) and a further hominin maxillary molar fragment from Sterkfontein Member 5 (de Ruiter 2004). The Member 4 hominin postcranial specimen (Sts 14) possesses a sacral specimen (Sts 14Q) appears to derive from a 'post-pubertal individual which had not finished its growth concerning the sacral breadth, and probably the pelvic breadth' (Berge & Gommery 1999: 227). Even more recently, one of us (JMK) identified a hominin scaphoid from the Member 4 faunal remains excavated by Alun Hughes and his team in 1990. This scaphoid sheds light on the wrist morphology and grip capabilities of the Sterkfontein hominins (Kibii *et al.* 2011).

The possibility of another species of *Australopithecus* being present in Member 4, the so-called 'second species' has been studied by various researchers since the original suggestion was made by Clarke (1988, 1994; Kimbel & White 1988; Kimbel & Rak 1993; Lockwood 1997; Moggi-Cecchi *et al.* 1998). Clarke (1988, 1994), in particular, has suggested that, among the better preserved crania, Sts 71, StW 252 and StW 505 can be distinguished from Sts 5, Sts 17 and Sts 52. While it does indeed appear that there are two morphological extremes (represented by specimens such as Sts 5 and Sts 71), several crania, including the male australopithecine StW 505, represent various intermediate morphologies (Lockwood & Tobias 1999, but see Clarke 2008). Another morphologically unusual specimen is Sts 19, the taxonomic attribution of which has been debated. Certain researchers maintain that this cranium 'has more affinity with *A. africanus* (especially Sts 5) than with *Homo habilis*' (Prat 2005: 221).

There are also signs of pathologies on some of the specimens from Member 4. Sts 24a is a juvenile *Australopithecus africanus* showing clear signs of pre-pubertal periodontitis (Ripamonti *et al.* 1997). A recent re-examination by D'Anastasio and colleagues (2009) of the partial skeleton, Stw 431, (representing and adult male individual of *A. africanus*) is composed of 18 bones from the axial skeleton, pelvic girdle and shoulder girdle as well as elements of the upper limb. This skeleton has pathological lesions on two of the lumbar vertebrae which are reminiscent of early brucellosis, which is an infectious disease caused by the consumption of infected animal proteins (D'Anastasio *et al.* 2009). While the authors do state that alternative cause of the lesions cannot be definitively excluded, they posit that the possible presence of this disease in a hominin from Member 4 raises the possibility that some meat was included in the diets of *Australopithecus africanus* (D'Anastasio *et al.* 2009).

StW 151 is a partial cranium of a juvenile hominin from Member 4, which is remarkable due to the preservation of a stapes (one of the three bones of the middle ear), showing similarities between the early hominins and living great apes in stapedial morphology (Moggi-Cecchi & Collard 2002).[1]

There is much scientific interest in dating and con-

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[1] Stapedial morphology suggests that *Australopithecus africanus* may have possessed more sensitivity to high frequency sounds than modern humans do (Moggi-Cecchi & Collard 2002).

texualizing the abundant and well-preserved hominin material of Member 4, and clarifying the relationship between the australopithecine-bearing Member 4 deposit exposed at the surface, with the underground australopithecine-bearing Member 2 and Jacovec Cavern deposits (e.g. Berger *et al.* 2002; O'Regan & Reynolds 2009; Hopley & Maslin 2010; Pickering & Kramers 2010). These are discussed in a later section of this paper.

Carnivores: The carnivore species total 14 taxa, including extant large carnivores, such as the lion, leopard, spotted and brown hyaenas (*Panthera leo, Panthera pardus, Crocuta crocuta, Parahyaena brunnea,* respectively), as well as the extinct machairodonts (*Megantereon cultridens, Homotherium latidens* and *Dinofelis barlowi*). Long-legged hunting hyaenas (*Chasmaporthetes silberbergi, Chasmaporthetes nitidula*) combined with the extinct giant hyaena (*Pachycrocuta brevirostris*) make for a densely populated carnivore guild, with a predominance of medium-sized carnivores (Turner & Antón 1996). Indeterminate Felidae, Canidae and Hyaenidae round out the balance of the Member 4 carnivores (Table 4). Alternative explanations for the high numbers of carnivore species include possible time averaging (O'Regan & Reynolds 2009) and also the possibility that scarce taxa were only rarely present in the Cradle of Humankind area (Reynolds 2010). In addition to these species, the common black-backed jackal (*Canis mesomelas*), and taxonomically poorly understood extinct canid species of *Canis brevirostris* and *Canis antiquus* (Ewer 1956; Brain 1981) are represented. The latter two species may instead be morphologically variable specimens of black-backed jackal (*Canis mesomelas*) or side-striped jackal (*Canis adustus*), as has been suggested elsewhere (Reynolds 2012).

Bovids: Bovids are extremely well-represented in the Member 4 assemblage. Five subfamilies of the family Bovidae have been identified: Caprinae, Alcelaphinae, Antilopinae, Hippotraginae and Bovinae (Table 5). Of the Caprinae, the tribe Ovibovini is represented by the extinct musk-ox like *Makapania broomi* and *Makapania* sp. The subfamily Alcelaphinae (tribe Alcelaphini) is represented by a mix of extinct and extant genera, including the extinct blesbok (*Damaliscus parmularis*), the wildebeest (*cf. Connochaetes* sp.) the giant hartebeest, (*cf. Megalotragus* sp.) and a wildebeest-sized indeterminate Alcelaphini individual (Table 5; Kibii 2004). The tribe Antilopini is represented by two extinct springbok species and an extinct gazelle (*Antidorcas recki, Antidorcas* cf. *bondi, Gazella* sp., respectively) as well as an indeterminate Antilopini individual. The tribe of the horse antelopes, the Hippotragini, is represented by the roan antelope (*Hippotragus equinus*), the extinct Cooke's antelope (*Hippotragus cookei*) and an indeterminate Hippotragini. The Reduncini include the extinct Dart's reedbuck (*Redunca darti*), and the extant reedbuck (*Redunca* cf. *arundinum*), with an indeterminate Reduncini also present. The impala tribe (Aepycerotini), are represented by fossils assigned to the extant impala (*Aepyceros melampus*) and by an indeterminate *Aepyceros* species. The tribe Peleini is represented by the extant grey rhebok (*Pelea capreolus*); Boselaphini by just a Boselaphini sp. specimen; the tribe Tragelaphini by the extant kudu (*Tragelaphus strepsiceros*), a possible nyala specimen (*Tragelaphus* sp. aff. *angasi*) and an indeterminate tragelaphine (*Tragelaphus* sp). Finally, the tribe Bovini is represented by an indeterminate species of African buffalo (*Syncerus* sp.) (Table 5; Kibii 2004).

Other fauna: This group includes a tortoise, a suid; an indeterminate reptile; the Cape Hare (*Lepus capensis*); an indeterminate *Equus; Hystrix africaeaustralis*; a fossil suid (*cf. Metridiochoerus* sp)., the extinct elephant (*Elephas recki*) and two extinct species of hyrax (*Procavia antiqua* and *Procavia transvaalensis*) (Table 6; Kibii 2004).

Taphonomy

The fossil bovid and carnivore remains were accumulated by several agents including: 1) carnivores, 2) death trap, and 3) slope wash (Brain 1981; Kibii 2004). These processes may have taken place at different times, or alternatively there may have existed different entrances. The majority of all modification on fossil bovid modified bones is carnivore-induced (84%); however, the recovery of low structural density skeletal elements, such as ribs and vertebrae (including juveniles) but without signs of carnivore modification indicate that some of the carcasses, and/or carcass parts were brought in naturally (by slopewash, or death-trap). Large carnivores are also implicated in the accumulation of smaller carnivores and other fossil fauna in the Member 4 assemblage (Kibii 2004). It is likely that during initial stages of cave formation, when the aven was concealed, some of the carnivore and bovid individuals fell into the cave below. Slopewash of carcasses from the catchment area into the cave cannot be ruled out, as some bovid specimens show signs of abrasion (Kibii 2004). The accumulation of numerous large carnivore cranial elements may have resulted from individuals dying within the cave, possibly while using the cave for denning or voiding (Kibii 2004).

The hominin accumulation follows a somewhat different pattern than the bovid and carnivore fossil assemblages. The *A. africanus* sample appears to show a bias toward females and small or immature males, suggesting the deliberate selection of smaller individuals by predators during the formation of this deposit (Lockwood & Tobias 2002). Skeletal element representation, in addition to bone modification, suggests that carnivores contributed significantly to the hominin assemblage (Pickering *et al.* 2004b). For the other primates, numerous cranial and postcranial elements with minimal or no biotic modification (i.e. tooth marks, evidence of digestion) indicate that some primates were naturally accumulated, perhaps while utilizing the cave as a sleeping den, or that they may have fallen to their death into the cave. Nevertheless a small number of primate elements display carnivore-related bone modification, suggesting some predator involvement (Brain 1981; Kibii 2004).

Palaeoenvironments

Member 4 palaeoenvironments were first reconstructed using fossil fauna and later, fossil wood, which is uniquely and abundantly preserved in this Member. Several earlier studies stressed the closed, forested nature of the Member 4

Table 7. Plants species identified (from Bamford 1999).

Plant species	Common name	M 4	M 5 E	M 5 W	Post M 6
Family Dichapetalaceae					
Dichapetalum mombuttense	Liana	x			
Family Scrohulariaceae					
Anastrabe integerrima	Pambati tree	x			

environments (Vrba 1975). Over time, more studies have identified indications of mosaic habitats during Member 4 accumulation. Vrba (1974, 1975, 1976, 1980) suggested a wooded environment with close proximity to open grassland based on the types of bovid species present. Specifically, the presence of ovibovines (*Makapania broomi*) and hippotragines were interpreted as suggesting wooded environments, along with open grassland indicator species such as members of the Alcelaphini and Antelopini. Vrba's conclusions were later corroborated by Reed (1997), who suggested that open woodland with bushland and thicket had been present, based on the presence of a high percentage of terrestrial animals (23.33%), a significant proportion of frugivorous mammals (16.67%) and only a few arboreal animals (3.3%). These reconstructions were corroborated by the discovery and analysis of over 300 fossil wood fragments from this infill (Bamford 1999). The presence of liana vines (most similar to the extant species *Dichapetalum mombuttense*) and the Pambati tree (*Anastrabe integerrima*) in the fossil wood sample suggested a forest fringe environment equivalent to the present day tropical forest of the Democratic Republic of Congo and Cameroon (Table 7; Bamford 1999), corroborated by the presence of the extinct colobus monkey (*Cercopithecoides williamsi*) (Kuman & Clarke 2000).

Studies of cercopithecoid postcranial morphology indicate the presence of several distinct habitat types: forest, open woodland/bushland and grassland (Elton 2001). Individuals falling into the 'open terrestrial' habitat category dominate the cercopithecoid sample, signalling a significant open component during Member 4 times. In contrast, australopithecine locomotor behaviour has been interpreted as having a strong arboreal component (Wood & Richmond 2000).

However, additional work on the micromammal species by Avery (2001) has given a different perspective to the debate regarding the Member 4 palaeoenvironments (Table 8). Member 4 contains a total of 11 identified species, and every one of those is represented in other Sterkfontein assemblages analysed by Avery (2001). This suggests that environments in Member 4 times were not dissimilar to those of subsequent Member 5 infills and Post Member 6. A single extinct species of unknown habitat preference (*Proodontomys cookei*) is represented, which also occurs in Member 5 East, Member 5 West, and at Swartkrans (Members 1–3; Avery 2001). However, the short-snouted elephant shrew (*Elephantulus fuscus*) is found only in Member 4 and Member 5 East and this species is known to prefer moist, woodland environments. Taken together, Avery's interpretation of the environmental reconstruction was that 'grass with trees along the river, bush with grass on the hillsides and grass with some trees and bushes on the plains' prevailed during Member 4 times (Avery 2001: 127).

Stable carbon isotope work by Luyt and colleagues (Luyt 2001; Luyt & Lee-Thorp 2003) has identified the full spectrum of browsers, grazers and mixed feeders within Member 4. The results revealed that the extent of woodland would have been heavier than originally proposed by Vrba (Luyt 2001). The extinct C_3 feeders (consuming trees, shrubs and herbs, or their consumers) include *Antidorcas recki*, *Hippotragus* sp. and the carnivore *Homotherium latidens.* The extinct C_4 consumers (grazers) include *Antidorcas bondi,* while the mixed feeders include *Makapania broomi,* and *Tragelaphus* sp. aff. *angasi* for bovids, and the extinct hyaena *Chasmaporthetes nitidula* (Luyt 2001).

Isotopic evidence for diets of Member 4 *Australopithecus africanus* have confirmed that these hominins were consuming significant proportions of C_4 foods, and that their diets were highly variable (van der Merwe *et al.* 2003, Sponheimer *et al.* 2005a, data reproduced in Table 9). These variable dietary signals have also been confirmed for *Australopithecus* at Makapansgat (Sponheimer & Lee-Thorp 1999). Analyses using ratios of strontium and calcium (Sr/Ca) in hominin enamel indicate that the *Australopithecus* diets from Sterkfontein Member 4 show higher Sr/Ca ratios relative to *Paranthropus robustus* from Swartkrans Member 1 (Sponheimer *et al.* 2005b; data reproduced in Table 10). The authors suggest that these results may suggest either high levels of grazing, or insectivory in the diets of *Australopithecus* from Sterkfontein (Sponheimer *et al.* 2005b). Both studies indicate that *Australopithecus* exploited grassland and woodland food sources regularly, or ate animals (termites, other fauna) that had eaten significant quantities of C_4 foods. Recent results of a study of strontium isotope analysis indicate that smaller *Australopithecus* and *Paranthropus* individuals (based on tooth size) appear to have ranged further afield than larger individuals (Copeland *et al.* 2011). The authors interpret these results as indicating that female hominins dispersed from their natal troops, while males utilized smaller home ranges on the dolomites (Copeland *et al.* 2011). Alternatively, these data may suggest a convergence of hominins to the sites of Sterkfontein and the surrounding valley from areas further afield. This may be due to the attractive combination of habitats and landscape features available at the Sterkfontein and Swartkrans (Reynolds *et al.* 2011).

Based on these data and the other palaeoenvironmental proxies discussed above, the Member 4 environments appear to have sampled a continuum of forested, open woodland, and grassland habitats, leading to debate about the possible effects of time- and climate averaging

Table 8. Micromammalian genera from Sterkfontein (species from Avery 2001, and Avery *et al.* 2010). Key to deposits: J C: the Jacovec Cavern; M 2: Member 2 M 4: Member 4, M 5 E/ W: Member 5 East / West (stone-tool-bearing breccias). N C is the Name Chamber and Post M6 is the deposit from L/ 63 and Lincoln Cave, lying within a separate cave system.

Micromammalian genera	Common name	M 4	M 5 E	M 5 W	N C	Post M 6
Family Chrysochloridae						
Cholorotalpa	Golden mole		x			
Chrysospalax	Rough-haired golden mole			x	x	x
Neamblysomus	Golden mole		x	x	x	x
Family Macroscelididae						
Elephantulus	Elephant shrew	x	x	x	x	x
Macroscelides	Elephant shrew					x
Family Soricidae						
Crocidura	Musk shrew				x	x
Mysosorex	Forest shrew	x	x	x	x	x
Suncus	Dwarf shrew	x	x	x	x	x
Family Rhinolophidae						
Rhinolophus	Horseshoe bat		x	x	x	x
Family Vespertilionidae						
Tadarida	Tomb bat				x	
Myotis	Hairy bat		x	x	x	x
Neoromicia	Serotine bat				x	
Family Gliridae						
Graphiurus	Dormouse		x	x	x	x
Family Nesomyidae						
Saccostomus	Pouched mouse				x	x
Dendromus	Climbing mouse	x	x	x	x	x
Malacothrix	Gerbil mouse		x		x	x
Steatomys	Fat mouse		x	x	x	x
Mystromys	White-tailed mouse	x	x	x	x	x
Proodontomys (extinct)	Extinct mouse species	x	x	x	x	
Family Muridae						
Acomys	Spiny mouse		x		x	
Gerbilliscus	Gerbil	x	x	x	x	x
Aethomys	Veld rat		x	x	x	x
Dasymys	Marsh rat	x	x	x	x	x
Mastomys	Multimammate mouse		x	x	x	x
Mus	Mouse		x	x	x	x
Rhabdomys	Grass mouse	x	x	x	x	x
Thallomys	Tree rat				x	x
Zelotomys	Desert mouse	x	x	x	x	x
Otomys	Vlei rat	x	x	x	x	x
Family Bathyergidae						
Cryptomys	Molerat		x	x	x	x
Georychus	Molerat		x			x

on this important deposit (O'Regan & Reynolds 2009; Hopley & Maslin 2010). Recent studies have examined the role of the landscape in creating and sustaining such mosaic habitats (Bailey *et al.* 2011; Reynolds *et al.* 2011).

Member 5 deposits

Member 5 is exposed from the Extension Site to the western end of the Type Site (Robinson 1962; Partridge 1978; Fig. 2). Study of the artefacts and fauna of the Member 5 deposit revealed that it is composed of three separate units, which together appeared geologically uniform; namely the StW 53; the Member 5 East and Member 5 West deposits. These infills contain one of the earliest records of stone tool use from a southern African site, the Oldowan industry and the later Early Acheulean artefact industry from Member 5 West. The StW 53 infill,

Table 9. Stable carbon isotope values for Member 4 *Australopithecus africanus* (data taken from van der Merwe *et al.* 2003, and Sponheimer *et al.* 2005a).

Specimen number	Species attribution	Diet	$\delta\,^{13}$C values
STS 72	*Australopithecus africanus*	Grazing	–9.7
StW 73	*Australopithecus africanus*		–8.8
StW 276 *	*Australopithecus* 'second species'		–8.0
STS 32	*Australopithecus africanus*		–7.8
StW 252 *	*Australopithecus* 'second species'	↑	–7.7
StW 211	*Australopithecus africanus*		–7.5
StW 304	*Australopithecus africanus*		–7.4
STS 31	*Australopithecus africanus*		–6.8
StW 14 *	*Australopithecus* 'second species'		–6.7
StW 315	*Australopithecus africanus*		–6.4
StW 309b *	*Australopithecus* 'second species'		–6.1
STS 2218	*Australopithecus africanus*		–5.9
StW 229	*Australopithecus africanus*		–5.8
StW 303 *	*Australopithecus* 'second species'	↓	–4.4
STS 45	*Australopithecus africanus*		–4.0
StW 236	*Australopithecus* ?		–3.7
StW 207	*Australopithecus* ?		–2.0
StW 213i	*Australopithecus* ?	Browsing	–1.8

Table 10. Strontium calcium ratios for Member 4 *Australopithecus africanus* (data taken from Sponheimer *et al.* 2005b).

Specimen number	Species attribution	Sr/Ca values
STS 72	*Australopithecus*	1.62
STS 32	*Australopithecus*	1.49
TM 1532	*Australopithecus*	1.39
STS 61	*Australopithecus*	0.98
STS 2218	*Australopithecus*	0.90
STS 31	*Australopithecus*	0.69
STS 45	*Australopithecus*	0.60
Mean ± SD		1.09 ± 0.41

however, is separated from the remaining Member 5 deposits by a thick flowstone layer, and does not contain stone tools, leading Kuman and Clarke (2000) to argue that it is a hanging remnant of Member 4, or alternatively, a temporally intermediate deposit between Member 4 and Member 5 East (Kuman & Clarke 2000). Herries and Shaw (2011) also suggest it is distinct from Member 5, but is intermediate in age between Members 4 and 5.

The StW 53 Infill

Stratigraphy

A small infill within the Member 5 area is where the StW 53 cranium was discovered in August 1976. The hominin cranium was recovered partially *in situ* in the calcified breccia and partially from a decalcified portion of the deposit, in a mokondo, or sinkhole (Hughes & Tobias 1977; Curnoe & Tobias 2006). Discovered by Alun Hughes and described initially by Hughes and Tobias as *Homo,* aff *Homo habilis* (Hughes & Tobias 1977), this specimen has continued to spark debate and controversy. The specimen was assigned to *Homo habilis,* in part due to its presumed association with stone tools (Hughes & Tobias 1977). Later stratigraphic studies done by Kuman and Clarke (2000) concluded that the StW 53 infill does not contain stone tools, thereby differentiating it from the contiguous Member 5 West infill (Clarke 1994; Kuman & Clarke 2000). Although the infill contains some fauna not present in Member 4 (e.g. *Theropithecus oswaldi,* Table 3), it does resemble Member 4 in that it contains no *in situ* stone tools. The presence of stone tools around the time of death of the StW 53 individual is confirmed by three sets of short striations on the cranium, suggesting deliberate disarticulation (Pickering *et al.* 2000). Fossil macromammalian species identified from this infill are listed in Tables 3–6.

Dating

Based on the species of fauna present, Kuman & Clarke (2000) suggested that StW 53 infill is younger than Member 4 but older that Member 5 Oldowan infill (Table 1; Fig. 4). *Theropithecus oswaldi* is present in StW 53 and Oldowan Infills, but is absent in Member 4, suggesting that Member 4 and Member 5 deposits sample slightly different environmental conditions and so are of different ages (Kuman & Clarke 2000). Closely associated with grassland environments, *T. oswaldi* is argued to have appeared within the Sterkfontein region after a shift in the environment towards drier conditions at 2.1 Ma (Weigelt *et al.* 2008). The earliest record of this genus is dated to around 3.7–3.5 Ma, is from the Kalochoro Member at Lothagam, in Kenya (Leakey *et al.* 1996). The last appearance of the species *Theropithecus oswaldi* in Africa is at Hopefield (Western Cape Province, South Africa) which dates to about 0.4 Ma (Pickford 1993).

The absence of stone tools may also indicate that the StW 53 infill predates the Oldowan infill (Kuman & Clarke 2000). From these two points, Kuman and Clarke (2000: 834) suggest that the StW 53 infill 'is likely to be less than 2.6 and more than 2 Ma'. However, Herries and colleagues (2009) have recently proposed a younger date of 1.8–1.4 Ma using palaeomagnetism and ESR. Herries & Shaw (2011) have further revised this date to 1.8–1.5 Ma for this infill (Fig. 4).

Taxonomy

Primates: At least four primate species have been identified from the StW 53 infill. These include a hominin (early

Homo or *Australopithecus*; Kuman and Clarke 2000), a species indeterminate cercopithecine monkey, *cf. Cercopithecoides williamsi* and the first recorded occurrence of *Theropithecus oswaldi* (Pickering 1999) within the site (Table 3). There are a minimum of two hominin individuals identified from the StW 53 infill; the adult cranial specimen (StW 53) and a juvenile represented by upper left maxilla with incisors, canine and third premolar present (StW75a–d). Additionally, there may be a third hominin specimen from StW53: an adult ulna (StW 571) was found a considerable distance from the StW 53 cranium and so the relationship between the adult cranium and the ulna is unclear (Pickering 1999).

The taxonomic position of the cranium StW 53 has been much debated. First assigned to *Homo* by Hughes and Tobias (1977), subsequent arguments were made that this specimen represents a late *Australopithecus* (Clarke 1985, 1998, 2008; Wolpoff 1996; Braga 1998; Thackeray *et al.* 2000; Kuman & Clarke 2000). Recent studies and reconstructions continue to highlight specific traits indicating the similarity of StW 53 to *Homo habilis* (Prat 2005; Curnoe & Tobias 2006), while other studies assert that this specimen represents a male *Australopithecus africanus* (Clarke 2008). Recently a new species has been named, *Homo gautengensis,* with StW 53 as the type specimen (Curnoe 2010). Spoor and colleagues (1994) report that the morphology of the bony labyrinth of the ear preserved in StW 53 is: 'unlike those seen in any of the hominids, or great apes' (Spoor *et al.* 1994: 645), and instead more closely resembles those of the large cercopithecoids. The authors state that this different morphology may have bearing on the locomotor repertoire of StW 53, which may have been a combination of climbing and bipedal locomotion (Spoor *et al.* 1994). Interestingly, another early *Homo* bony labyrinth specimen from Swartkrans (SK 847) shows a very modern human-like appearance (Spoor *et al.* 1994).

Carnivores: At least four families of the order Carnivora are represented, and apart from the extinct hunting hyaena, all carnivores represent extant forms (Table 4). The family Canidae is represented by *Canis* cf. *mesomelas*; Viverridae by *Suricata* sp.; Hyaenidae by the extinct *Chasmaporthetes* sp. and Felidae by a leopard-sized cat (Pickering 1999).

Bovids: Four subfamilies of the family Bovidae have been identified: the subfamily Bovinae is represented by *cf.* Boselaphini; Antilopinae by an extinct gazelle species also known from Makapansgat (*Gazella cf. gracilior*); Caprinae by the extinct musk-ox like *Makapania broomi* and Alcelaphinae by typically savannah dwelling blesbok genus (*Damaliscus* sp.) and a wildebeest-sized Alcelaphini (Table 5; Pickering 1999).

Other fauna: Although the faunal sample is small, three additional mammal species have been identified by Pickering (1999), including two extinct hyrax species (*Procavia antiqua, Procavia transvaalensis*), and an indeterminate equid (Table 6).

Taphonomy

The StW 53 infill has quite a small bone sample with relatively low numbers of biotically-modified bones. A total of 28 bone specimens show signs of mammalian feeding that is most likely carnivore in origin and just five digested bone specimens are present. While the precise identification of the carnivore species responsible is not possible, Pickering (1999) suggests that leopards (*Panthera pardus*) may have played a role in the bone damage.

The StW 53 bears cut-marks on the zygomatic arch, even though no stone tools are preserved in the StW 53 deposit (Pickering *et al.* 2000; Kuman & Clarke 2000). It appears from the type and location of these cutmarks, that the intention was to deliberately disarticulate the mandible from the StW 53 cranium. The reasons for this activity are unclear, but may be related to cannibalism, or funerary practices (Pickering 1999; Pickering *et al.* 2000).

Palaeoenvironments

The small faunal sample does not shed very much light on the palaeoenvironments, but open, drier, grassland conditions are suggested by the presence of the gelada, *Theropithecus oswaldi,* and an equid in the StW 53 infill. This is suggested by Kuman & Clarke (2000) to mark a shift from largely closed, wetter conditions present in Member 4 to drier, more grassland conditions in Member 5.

Member 5 East Oldowan

Stratigraphy

The Oldowan infill is limited to the eastern portion of Member 5 (Fig. 2). This infill contains one of the oldest artefact assemblages recovered in southern Africa (Clarke 1994; Kuman 1994a,b; Field 1999). The Sterkfontein Oldowan deposit is unique because it contains a near-complete accumulation profile, and the large number of artefacts (3245 artefacts) suggests that Oldowan toolmakers returned repeatedly to the site. In addition to these stone tools, a few *Paranthropus robustus* specimens have been recovered (Kuman & Clarke 2000).

Dating

The Oldowan infill has been biochronologically estimated to be *c.* 2.0–1.7 Ma on the basis of the presence of *Phacochoerus modestus* and a giant ostrich, *Struthio* and *Equus* (Kuman & Clarke 2000). The occurrence of *Phacochoerus modestus* is morphologically similar to the same species from Olduvai Bed I and lower Bed II. Also present is the giant ostrich (known from Olduvai Bed I) and three teeth of *Paranthropus robustus,* which are similar to teeth recovered from Kromdraai (Table 2; Clarke 1994; Kuman 1994a,b). Herries and colleagues (2009) and Herries & Shaw (2011) recently proposed a refined date of 1.4–1.2 Ma for the age of this infill based on ESR and palaeomagnetism (Fig. 4).

Taxonomy

Primates: At least three primate species have been recovered from the Oldowan infill and all are extinct: the robust hominin species *Paranthropus robustus,* the fossil gelada *Theropithecus oswaldi* and a taxonomically indeterminate cercopithecine (Table 3; Pickering 1999). In total, 10 primate individuals have been identified: two *Paranthropus* *robustus*, a *Theropithecus oswaldi* and seven indeterminate cercopithecines (Pickering 1999).

Carnivores: Four families of the order Carnivora are represented in this infill: Canidae, represented by an interminate jackal (*Canis* sp.); Viverridae, represented by a mongoose (*Mungos* sp.), individuals assigned to the meercat, or suricate (*Suricata* sp.), and the grey mongoose genus (*Herpestes* sp.); as well as the Hyaenidae represented by an indeterminate hyaena; and Felidae, represented by the lion (*Panthera leo*) and an indeterminate felid (Table 4; Pickering 1999).

Bovids: At least three subfamilies of the family Bovidae are represented in the Oldowan infill. These include: Bovinae, represented by a possible eland (*cf. Taurotragus*); the Antilopinae, represented by the small klipspringer, the steenbuck and the springbok (*Oreotragus, Raphicerus* and *Antidorcas,* respectively); and Alcelaphinae, represented by the blesbok genus (*Damaliscus*), and two indeterminate Alcelaphini species, one of which is wildebeest-sized and the other *Megalotragus*-sized (Table 5; Pickering 1999).

Other fauna: Other fauna represented in the Oldowan infill include the extinct suid, *Metridiochoerus modestus,* and indeterminate *Equus* sp., and two extinct species of hyrax (*Procavia transvaalensis, Procavia antiqua*; Table 6; Cooke 1994; Pickering 1999). A diverse micromammal assemblage has been identified from the entire Member 5 East infill, and these species are all generally recovered across the Sterkfontein deposits (Table 8; Avery 2001; Avery *et al.* 2010).

Taphonomy

The skeletal part representations observed in the Oldowan led Pickering (1999) to suggest that the fauna represents a death-trap accumulation. While one certain cut-marked bone indicates hominin butchering activities within the catchment area, the low numbers of hominin- and carnivore-modified bone (0.615% of the assemblage, Pickering 1999) indicate that the remainder of the fauna was accumulated through slope-wash action via a narrow chimney or aven in the location of rows Q and R of the main Sterkfontein excavation. This supports Kuman's (1994a,b) conclusion that the Oldowan stone tools were 'washed in from surface deposits through a small diametre, vertical opening or avens' (Pickering 1999: 132). This in turn suggests that the entrance to the cave during this time was not accessible even to the most agile of climbers such as carnivores and primates (Pickering 1999).

Palaeoenvironments

Faunal composition from the Oldowan infill, including the equids, springhare, ostrich and lion as well as the various species of antelopine and alcelaphine, have been interpreted as indicating a drier and more open environment (Pickering 1999). The tibia of the giant ostrich (*Struthio* sp.), from this infill is similar to specimens from Olduvai (Clarke 1994). Likewise, Cooke (1994) suggests a similarity between extinct giant warthog (*Metridiochoerus/ Phacochoerus modestus*) specimens with those identified from Olduvai Bed I. However, a taxon-free analysis of the bovids from this infill indicates that a significant amount of tree cover was available in the vicinity (Bishop *et al.* 1999).

Member 5 Early Acheulean

Stratigraphy

The early Acheulean deposits are more widely distributed than the Oldowan infill, and are spread across the eastern and western areas of Member 5 (Fig. 2). However, the early Acheulean infill in the best context is Member 5 West. Natural concentrations of hematite are also common in these deposits, but are absent in the preceding Oldowan infill. This may be related to drier conditions during the time of Member 5 West formation (Kuman & Clarke 2000). Robinson (1962) mentions a block of Member 4 ('Lower Breccia') found in the Member 5 excavation, suggesting that such material must be present, although it is not yet identified. The faunal sample studied by Pickering (1999) does not apparently contain any reworked material from older deposits. Clarke's schematic representation of the relationship between surface and underground Members is given in Fig. 7 (Clarke 2006).

Dating

The Acheulean infill has been estimated at *c.* 1.7–1.4 Ma based on the stone tool typology and the associated *Homo* cf. *ergaster* fossils (Table 1; Kuman & Clarke 2000). In contrast, Herries and colleagues suggest a significantly younger date of 1.3–0.8 Ma for the age of Member 5 West (Herries *et al.* 2009). Herries and Shaw (2011) suggest a more refined age of 1.3–1.1 Ma based on ESR and palaeomagnetism (Fig. 4).

Taxonomy

Primates: At least two primate species, both extinct, have been recovered from the Acheulean infill; these are the hominin species *Homo* cf. *ergaster* and an indeterminate cercopithecoid (Table 3; Pickering 1999). The hominins from Member 5 West have been studied by Pickering in collaboration with Clarke and Moggi-Cecchi (in Pickering 1999). The minimum number of individuals represented in the Member 5 West deposit is four, based on cranial specimens and teeth (Pickering 1999). Two of these individuals are juveniles in different developmental stages (represented by right maxilla SE 255 and hemimandible StW 84). The other two individuals are adults (represented by left canine SE 1937 and mandible fragment StW 80). In addition, three isolated adult specimens were recovered, namely a right upper second molar (SE 1508), a left upper second molar (SE 1579) and a right upper fourth premolar (SE 2396), which may derive from either SE 1937 or STW 80 (Pickering 1999).

Kuman & Clarke (2000) state that StW 80 mandible bears similarities to Swartkrans specimen SK 15, which has been classified as *Homo ergaster.* The second specimen, StW 84, was recovered from the post-Member 6 area (from Square M/61, whereas in this study only L/63 and M/63 are studied as the L/63 sample). While it was found in decalcified sediments, breccia adhering to the StW 84

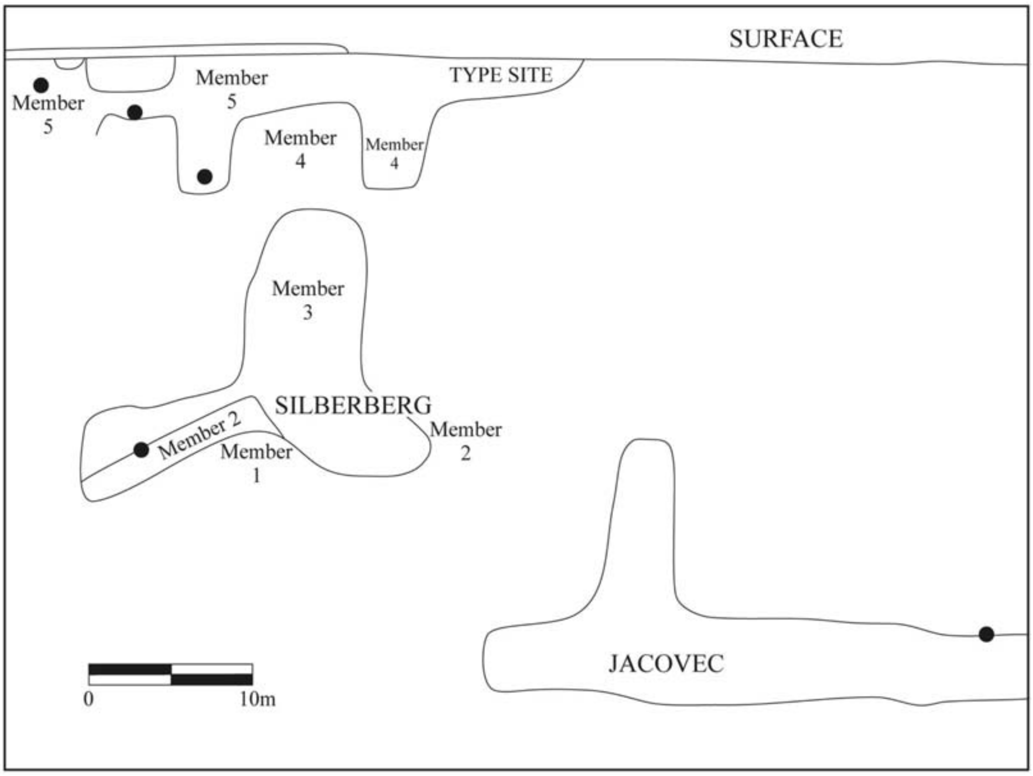

Figure 7. Schematic profile showing spatial relationships between the deposits exposed at the surface (Member 4 and 5), and the locations of the underground Silberberg Grotto and Jacovec Caverns. Black dots indicate the locations of hominin finds (redrawn after Clarke 2006).

specimen, combined with an archaic *Homo*-like morphology, led Kuman & Clarke (2000) to conclude that it derived originally from the Member 5 West deposit, but was eroded and reincorporated into the younger decalcified material. The StW 84 specimen demonstrates two points: that decalcification of the Member 5 West material occurred, and that this material was subsequently redeposited into younger deposits. Thus the process of reworking into later infills is convincing, at least within the main Sterkfontein excavation, and for the Lincoln Cave, where sediments appear to have made their way into a neighbouring cave system (Reynolds *et al.* 2003, 2007).

Carnivores: The order Carnivora is represented by at least four families, and only one extinct species. The Canidae, represented by the black-backed jackal (*Canis* cf. *mesomelas*); Viverridae, represented by mongoose and meercat species (*cf. Mungos* and *Suricata,* respectively); Hyaenidae, which include the aardwolf (*Proteles* sp.), and the brown and spotted hyaenas (*Parahyaena brunnea* and *Crocuta crocuta,* respectively); and the Felidae, represented by the extinct false sabretoothed cat species, *Dinofelis barlowi,* and the extant lion, *Panthera leo* (Table 4; Pickering 1999). Recent reassessment of the Member 5 carnivores led O'Regan (2007) to suggest that this sabretoothed species does not derive from this infill. One single maxillary specimen assigned to the extinct raccoon dog, *Nyctereutes terblanchei* (SE 125) by Ficcarelli and colleagues (1984) is likely to represent a variable specimen of either *Canis mesomelas* or *C. adustus* (Reynolds 2012).

Bovids: Four subfamilies of the family Bovidae have been recorded from this infill: Bovinae, which contains only an indeterminate Tragelaphini; Antilopinae, which are represented by a steenbok (*Raphicerus* sp). and a springbok (*Antidorcas* sp.); the Aepycerotinae, represented by an impala (*cf. Aepyceros* sp.); and finally, the Alcelaphinae, are represented by a blesbok (*Damaliscus* sp.), and an indeterminate Alcelaphini (Table 5; Pickering 1999).

Other fauna: Other fauna identified from this Acheulean infill include: the warthog (*Phacochoerus* cf. *aethiopicus*), an equid (*Equus* sp.), an extinct hyrax (*Procavia antiqua*) and specimens of the extant porcupine (*Hystrix africaeaustralis*) (Table 6; Pickering 1999). A total of 21 micromammal species are identified from the Member 5 West infill, and these are all common across the Sterkfontein deposits (Table 8; Avery 2001; Avery *et al.* 2010).

Taphonomy

The damage identified in the L/63 sample and in the contiguous Member 5 West sample highlights some salient differences between these deposits.

Member 5 West's relatively high incidences of carnivore damage (such as tooth scores, and gnaw marks) contrasts with that of the L/63 sample. It is possible that during the formation of the Member 5 West deposit, collapse within the site had created talus slopes of debris, which provided access for animals into the caves (Clarke 1994). Whatever the reason, the data suggest that the Member 5 West area was an attractive shelter for animals during the time of deposit formation (Pickering 1999). The main agent of accumulation in Member 5 West was probably hyaena activity, and more specifically, the brown hyaena, *Parahyaena brunnea.* While brown hyaenas may have made the largest contribution to the assemblage, the remains of porcupines and spotted hyaenas also suggest their involvement. Pickering (1999) proposes a scenario of 'serial denning' which has been noted in modern settings, based on the following: 1) the presence of carnivore damaged bones, 2) a large number of brown hyena-sized prey, 3) a sizeable number of hyena individuals (including juveniles), 4) the presence of hyaena coprolites, 5) digested bone and 6) complete limb bone shafts are all considered supporting evidence for Pickering's (1999) conclusion that Member 5 West was a serial denning site for carnivores. Member 5 West is the only Member 5 assemblage preserving porcupine damage in conjunction with the porcupine remains themselves, thus it may also have been used as a porcupine lair during the time of deposit formation. Slopewash probably also played an additional accumulative role (Pickering 1999).

With regard to hominin accumulation of the Member 5 West fauna: the complete absence of cut-marks, chop-marks, or hammerstone percussion damage suggests that the fauna accumulated separately from the Early Acheulean archaeological assemblage found in this deposit. The isolated chop-marked bone recovered by Brain (1981) does not point to extensive modification of the fauna in Member 5 West. Pickering concludes that the Early Acheulean tools 'are in no way causally linked to the animal remains, and thus the bones are not archaeological in derivation' (Pickering 1999: 162).

Palaeoenvironments

Fauna from the Member 5 West Early Acheulean appears to indicate open or wooded grassland or open savanna (Vrba 1975; McKee 1991; Reed 1997; Kuman & Clarke 2000). Certainly, isotope data appear to suggest Member 5 fauna being from a drier, grassland environment, compared with earlier Member 4 times (Luyt 2001; Luyt & Lee-Thorp 2003), and this is in keeping with drier conditions after 1.7 Ma and the onset of the Walker Circulation, as has been proposed by Hopley and colleagues (2007).

Member 6

Stratigraphy

Member 6 is a small hanging remnant, presumed to be mid- to late Pleistocene in age, which is exposed on the north wall of the West Pit excavation in the Member 5 West (Kuman & Clarke 2000; Fig. 2). Almost all of Member 6 has been eroded, and from what little remains, it appears that this infill does not contain artefacts, and very little fossil material (Kuman & Clarke 2000).

Post-member 6
The L/63 Infill

Stratigraphy

Within the main excavation of breccias exposed at the surface of the Sterkfontein cave system, the youngest breccia has been called the Post-Member 6 Infill by Kuman and Clarke (2000). Although this infill lacks datable materials, it is markedly different from the contiguous deposits around it (Fig. 2). Instead, it appears to be an intrusive, younger deposit that separates the older Acheulean breccias into Member 5 West and Member 5 East. Unlike the older deposits that both dip to the west, the infill area is horizontally bedded, poorly calcified and similar in appearance to the deposit in the neighbouring Lincoln Cave (Kuman & Clarke 2000).

Dating

Electron spin resonance ages on fossils from post-Member 6 give an age spread of between 684 and 251 ka (Herries & Shaw 2011). A Correspondence Analysis of fauna in Member 5 West, and the two Lincoln Cave deposits indicates that the fauna and hominin species found in the L/63 infill is more similar to the Upper Pleistocene deposits (Table 1; Reynolds *et al.* 2007). Dates are shown in Fig. 4.

Taxonomy

Primates: This group is represented by two primate species, both extant, that include an archaic *Homo sapiens* and a baboon (*Papio cynocephalus*) (Table 3; Reynolds *et al.* 2007). The isolated human specimen (StW 585) is a right upper canine (Kuman & Clarke 2000).

Carnivores: Three families of the order Carnivora are represented and none of the species identified are extinct. The family Felidae is represented by an indeterminate cat (*Felis* sp.); Canidae, specifically the black-backed jackal (*Canis mesomelas*) and Viverridae represented by the meercat (*Suricata* sp.), and the grey mongoose (*Herpestes ichneumon*) (Table 4; Reynolds *et al.* 2007). In contrast to the Member 5 West infill, no large carnivores have been recovered from this infill, suggesting that large carnivores may have been less common in the Sterkfontein area during the mid- to late Pleistocene (Reynolds *et al.* 2007).

Bovids: Five tribes of the family Bovidae are represented in the L/63 fossil assemblage, and as with the carnivore assemblage, there are no extinct species. These include: the Alcelaphini, represented by an indeterminate blesbok (*Damaliscus* sp.) and an indeterminate Alcelaphine; the Reduncini, represented by the steenbok (*Raphicerus* sp.); Antelopini, represented by the springbok (*Antidorcas* sp.); Cephalophini, represented by the grey duiker (*Sylvicapra grimmia*), and finally, the Peleini, represented by the grey rhebok (*Pelea capreolus*) (Table 5; Reynolds *et al.* 2007).

Other fauna: Other fauna represented within the L/63 infill include the Plains zebra (*Equus burchellii/quagga*), the hyrax (*Procavia capensis*), the porcupine (*Hystrix africaeaustralis*), the springhare (*Pedetes capensis*) and the Cape Hare (*Lepus capensis*) (Table 6; Reynolds *et al.* 2007).

Taphonomy

The L/63 solution cavity the main excavation has earned the nickname 'The Porcupine Lair', due to the large numbers of porcupine-gnawed bone observed there. The preliminary study indicated that, although present, the incidence of porcupine damage was not high enough to indicate a porcupine lair (O'Regan, pers. comm.). The L/63 area has the lowest incidence of non-rodent mammalian modification to the fauna, with 1.1%, contrasting markedly with the neighbouring Member 5 West totals for the same category (3.3%). A total of 1.86% of the L/63 sample was modified by porcupines and other rodents. Although this is the highest percentage of porcupine and rodent damage in all the samples compared, it does not suggest significant porcupine/rodent involvement in the damage of the sample (Reynolds *et al.* 2007).

In contrast to the Member 5 West pattern, the L/63 area has the highest incidences of porcupine/rodent gnawing, but also the lowest incidence of non-rodent mammalian (presumably carnivore) damage. In both cases the low percentages of damage, along with the fact that no large carnivore species were identified from the L/63 area, would suggest that there was probably no carnivore dens in the area during the deposition of the L/63 material, but that porcupines were probably more active in the area during the time the L/63 fauna was accumulating (Reynolds *et al.* 2007). Only one hyaena coprolite has been recovered from the sample studied for this analysis, but further excavations being conducted by Clarke have produced more hyaena coprolites (Clarke, pers. comm.). As with Member 5 West, the fauna of the L/63 sample were most probably not accumulated by humans, since no cut-marked, chop-marked bone or burnt bone have been identified in the L/63 sample.

Palaeoenvironments

The L/36 fauna differ from that of the Member 5 West deposit (Reynolds *et al.* 2007). Instead of the large carnivore species found in Member 5, this infill preserves smaller carnivores, such as the black-backed jackals and viverrids. No extinct species are represented, and the overall faunal composition is very similar to the fauna present in the area today (Reynolds *et al.* 2007).

Lincoln Cave

Stratigraphy

The Lincoln-Fault cave system lies adjacent to the Sterkfontein Cave system, approximately seven metres from the northernmost limit of the main excavation (Fig. 2). There are two fossil deposits within the Lincoln Cave: a hard and a soft, poorly calcified breccia. The South deposit contains both hard breccia and soft breccia, and these grade into each other and are difficult to separate clearly, but the bulk of the artifacts are contained in the softer breccia. The Lincoln Cave North and South deposits were systematically excavated from early 1997 until 1998 (Reynolds *et al.* 2003, 2007).

Dating

Uranium Series dating of the capping and lower flowstones in the North profile yielded age estimates of between 252 600 ± 35 600 years and 115 300 ± 7700 and (Table 1; Reynolds *et al.* 2003, 2007; indicated in Fig. 4).

Taxonomy

Primates: Hominins are represented by four specimens assigned to *Homo ergaster* (Reynolds *et al.* 2007). The three teeth from Lincoln Cave South represent a minimum of two individuals; a child of roughly three years of age (represented by StW 591 and StW 592), and an adult (StW 593). StW 594 from Lincoln Cave South is a hominin cranial fragment, which is likely to also represent the same species (Table 3).

Carnivores: Four carnivore species are represented, and all four are extant species: the Felidae, represented by an indeterminate cat (*Felis* sp.) Canidae, by a jackal (*Canis* sp.); and the Viverridae by the meerkat (*Suricata* sp.) and Hyaenidae by an indeterminate hyaena specimen (Table 4; Reynolds *et al.* 2007).

Bovids: Four bovid tribes are represented: Alcelaphini by the extinct giant hartebeest (*cf. Megalotragus* sp.); the Hippotragini by an antelope (*Hippotragus* sp.); Tragelaphini by the bushbuck (*Tragelaphus scriptus*) and Cephalophini by an indeterminate small duiker (Table 5; Reynolds *et al.* 2007).

Other fauna: Other fauna recovered from the Lincoln Cave include: the Plains zebra (*Equus burchellii/quagga*), the hippo, (*Hippopotamus amphibius*), the warthog (*Phacochoerus africanus*), the extant hyrax (*Procavia capensis*), the porcupine (*Hystrix africaeastralis*), the springhare and Cape Hare (*Pedetes capensis* and *Lepus capensis,* respectively) (Table 6; Reynolds *et al.* 2007).

Taphonomy

Relatively higher percentages of canivore damage in Lincoln Cave North and rodent gnawing in L/63 may suggest that these agents were more active in the surface catchment area during the time of deposition of the fauna. Low proportions of hyaena remains (only one piece in Lincoln Cave North) and the lack of hyaena juveniles or subadults would seem to discount a primary carnivore den accumulation for the younger deposits.

Palaeoenvironments

The majority of the fauna are extant forms which are common in the area today. In contrast with the Member 5 West assemblage, the younger deposits are dominated by small carnivore species, suggesting that larger carnivores (such as lions, leopards and hyaenas) moved out of the Sterkfontein area during the Upper Pleistocene (Reynolds *et al.* 2007, Reynolds 2010).

ARCHAEOLOGY

The presence of Earlier Stone Age (ESA) and Middle Stone Age (MSA) lithic assemblages indicate that hominins favoured the catchment area around the site of Sterkfontein for tool manufacture. Kuman (1994a,b, 2007) has proposed that the combination of available raw materials, shelter provided by the dolomite outcrops and the likely presence of shade-trees would have created an attractive locale for hominins to gather raw materials and knap tools. The abundance of artefacts, particularly for the Oldowan assemblage indicates that the accumulation occurred over a long period, as opposed to single-event sites found elsewhere.

Member 5 East Oldowan

The Oldowan tools, which derive from the lowest excavated levels of the Sterkfontein surface excavation, are one of the oldest known lithic assemblages from South Africa. Other Oldowan assemblages recently published from southern Africa include Wonderwerk Cave, in the Northern Cape Province, and these deposits date to ~0.78–1.96 Ma (Chazan *et al.* 2008). The Sterkfontein Oldowan deposit contains a near-complete accumulation profile (Kuman 1994a,b, 1996; 2003; Kuman & Clarke

2000). The assemblage comprises 3245 pieces, of which 84% are less than 20 mm in length (Kuman 2007). Since the full range of artefact sizes are represented, as well as the high levels of small pieces, this assemblage is assumed to be representative of a primary or near-primary context (Kuman 2007). The majority of the material is in a fresh condition, with only a small portion showing signs of weathering and abrasion.

The assemblage shows that hominins used simple manufacturing methods, with the emphasis on easily flaked stone types, especially quartz (Kuman 1994a,b, 2007). Quartz was the most important raw material; with 94% of all Oldowan artefacts and 68% of all cores made on quartz (Kuman 2003). Because quartz fractures so easily, the assemblage is dominated by chunks, flakes and chips which commonly result from quartz-knapping (Kuman 1994a,b). Other utilized raw materials are quartzite and, less commonly, chert. There is evidence of direct percussion, and also some use of bipolar flaking (i.e. hammer and anvil) techniques. The most commonly recovered core-types are: simple cores, chopper-like cores, discoid-like cores, at least one protobiface, casual, irregular and quartz polyhedral cores (Kuman 1994a,b, 2007).

Member 5 West Acheulean

At Sterkfontein, percentages of small flaking debris differentiate between the Acheulean and the Oldowan levels. The Early Acheulean assemblage of Member 5 West is composed of 701 pieces, but only 2.7% of the assemblage is small flaking debris ≤ 20 mm in length (Kuman 1994a,b 1998; Field 1999). Larger flakes (complete, incomplete and flaked) make up just 8.4% of that assemblage, whereas cores contribute 36.8% to the total. Manuports make up 29.7% of the assemblage (Field 1999). The relatively high percentages of small flaking debris in the Lincoln Cave South and L/63 area deposits suggest that these assemblages were not deposited during Member 5 West times, when such elements were eroded from the surface before deposition into the infill (Kuman 1994a,b; Field 1999).

Manuports and polyhedral cores are typical of the Acheulean assemblage at Sterkfontein (Kuman 1994a,b; Field 1999). Manuports are river cobbles with the cortex intact and without signs of utilization, such as battering. Hominins selected the cobbles from the gravels that lie within 300 m of Sterkfontein and brought them to the site for later use. In Member 5 West, manuports comprise 29.7% and cores 37% of the assemblage, which has lost most of its small material through erosion (Kuman 1998). However, the absolute number of manuports is also very high, a pattern which is often noted in Developed Oldowan/Early Acheulean assemblages (Schick 1987; Potts 1991).

The L/63 Infill and Lincoln Cave deposits

Prior to the Lincoln Cave excavation, the only MSA lithics derived from excavations of overburden deposits near Member 4 and material recovered from mixed or decalcified deposits (Mason 1962a,b; Kuman 1994a,b). The excavation of Lincoln Cave South deposit yielded an assemblage of 69 artefacts and manuports, of which the majority appear to have been deposited during the MSA. Specifically, the *in situ* recovery of diagnostic artefacts, including a diabase blade and flakes with facetted platforms, suggest an MSA industry was present at Sterkfontein (Reynolds *et al.* 2007). However, the recovery of a bifacial chopper core also from the Lincoln Cave South deposit is more characteristic of the Early Acheulean industry, suggesting incorporation of some older artefacts into the deposit, along with some manuports. Manuports recovered from the L/63 area deposit suggest much the same process of erosion and redeposition (Reynolds *et al.* 2007). The Lincoln Cave North assemblage does not have any small flaking debris elements, and only a small sample of non-diagnostic core tools. Raw material proportions and artifact typologies suggest that Lincoln Cave South and L/63 area are more closely related and that both these deposits are younger than the Member 5 West Early Acheulean deposit.

In contrast to the L/63 deposit, diagnostic MSA artefacts present in Lincoln Cave South indicate that this deposit was formed during the Middle Stone Age. However, the presence of a bifacial chopper core and manuports most closely resembling ESA material strongly suggest mixing between the Lincoln Cave South and material deriving from an older deposit, probably Member 5 West. When the L/63 assemblage is compared to the Lincoln Cave deposits, both the small flaking debris and raw material distributions suggest these deposits are more similar in age (Reynolds *et al.* 2007). The L/63 area assemblage contained only 50 artefacts, of which none are diagnostic of a specific industry. However, the high proportions of small flaking debris and flakes, combined with the low proportions of manuports and polyhedral cores, suggest an age younger than the contiguous Member 5 West deposit, where these elements are abundant (Field 1999; Table 1).

Now that we have reviewed the fauna and artefacts from the individual Sterkfontein deposits, we progress in the next section to a discussion of pertinent debates about the Sterkfontein material.

DISCUSSION

Complexity of karst deposits and their interpretation

One of the ongoing debates at Sterkfontein is the range of dates produced by diverse methods (see Table 1), and the lack of agreement between faunal/archaeological dates and absolute dating methods (e.g. Clarke, in press). The complexity of the karst deposits lies at the heart of this debate. These deposits result from various processes, each acting on different scales, from large-scale climatic cycles right down to the prevailing conditions at the individual site catchment area. At the very largest scale, climate conditions are linked to planetary orbital variations (Milankovitch cycles) and more local effects created by circulation patterns and variation in the Earth's surface (de Menocal 1995, 2004; Hopley *et al.* 2007). At a smaller scale, the floral communities are composed of different

Table 11. Summary of palaeoenvironmental reconstructions for Sterkfontein Members 2 to Post Member 6 deposits.

Sterkfontein Member	Palaeoenvironmental reconstruction	Data source and references
Jacovec Cavern	Mosaic habitat of open and closed habitats, with a riverine gallery forest, with bushland and open country in close proximity.	Fauna (Kibii 2004)
Member 2	Presence of open grassland with rocky outcrops, permanent water supply, and riverine gallery forest wetter habitats	Fauna (Pickering *et al.* 2004a)
Member 4	Mosaic habitats with forest fringe environment and grassland habitats close by.	Fauna (Vrba 1974, 1975, 1980) Fossil wood (Bamford 1999) Micromammals (Avery 2001) Stable carbon isotopes and Sr/Ca ratios (Sponheimer *et al.* 2005a,b)
Member 5 StW 53 infill	Open, drier, grassland conditions	Fauna (Kuman & Clarke 2000)
Member 5 East	Drier, more open environments, but with a significant amount of tree cover present	Fauna (Pickering 1999) Ecomorphology (Bishop *et al.* 1999)
Member 5 West	Open grassland and/ or wooded grassland	Fauna (Vrba 1975; McKee 1991; Reed 1997; Kuman & Clarke 2000). Stable carbon isotopes (Luyt 2001; Luyt & Lee-Thorp 2003)
Post Member 6 (L/63); Lincoln Cave deposits	Similar to modern environments	Fauna (Reynolds *et al.* 2007)

proportions of C_3 (trees) and C_4 (grass) vegetation and support fauna associated with these types of habitats (e.g. Vrba 1974, 1975; Reed 1997; Andrews & Bamford 2008). Taphonomic processes, (animals, slope wash) control how bones enter the fossil record, but the time taken by deposition means several types of processes and habitats are probably represented in a single deposit (Pickering 1999; Hopley & Maslin 2010). Finally, within breccias there is increasing evidence for cycles of deposition, erosion and redeposition (de Ruiter 2003; Reynolds *et al.* 2007; Herries *et al.* 2009). A recent study by Hopley & Maslin (2010) suggests that southern African cave deposits sample more than one processional cycle (~7000 years), and are therefore likely to be 'climate-averaged', showing a mix of species characteristic of both open, grassland-dominated periods of the climate cycle, as well as woodland-dominated extremes. Mixing may also have implications for the dating difficulties and may compounded difficulties in sampling procedures for the dating of cave sediments. Given the complexities of cave formation processes, it is not surprising that different techniques applied to the same Sterkfontein Member may provide different dates (as has been suggested by Pickering & Kramers 2010 and Herries & Shaw 2011).

In summary, the complexity of the karst formations affects all other aspects of interpretation, including evidence of climate change, understanding fossil communities, dating possibilities and identifying possible new species (e.g. O'Regan & Reynolds 2009; Hopley & Maslin 2010; Herries & Shaw 2011). As a result, the evidence for the various patterns observed in the fossil record is best viewed as having been filtered by numerous processes. Thus the consideration of all aspects (specifically the dates in the light of the stratigraphy and artefacts and faunal material contained within them) remains the most reliable means of interpretation for karst deposits (Kuman & Clarke 2000; Reynolds *et al.* 2007; Clarke, in press).

Varying environmental reconstructions for Sterkfontein Member 4

Sterkfontein Member 4 is an important deposit, due mainly to the large sample of *Australopithecus africanus* specimens that has been recovered from this Member (Lockwood & Tobias 1999, 2002; Pickering *et al.* 2004b; Moggi-Cecchi *et al.* 2006 and others). The hominins and the associated abundant faunal assemblage have the potential to reveal the preferred habitats of *Australopithecus africanus* (and possibly also of the proposed *Australopithecus* 'Second species'), as well as the environmental context prior to the appearance of early *Homo, Paranthropus* and the earliest stone tool industries in southern Africa (Oldowan and Early Acheulean Industries). One of the most important debates is exactly what type of environments are represented by the fauna, flora and sedimentological evidence, and the results of various studies indicate differing habitat types.

Sterkfontein Member 4 was previously characterized as representing closed, forested environments (e.g. Vrba 1975) but later studies have indicated that the environmental context is more complex. Some part of Member 4 fauna appears to sample grassland environments, so these are likely to have been present at least some of the time during Member 4 accumulation. Indeed, several recent studies have identified a significant grassland signal within the Member 4 fauna, based on a variety of environmental proxies, ranging from hominin diets (van der Merwe *et al.* 2003); through to micromammals (Avery 2001; Avery *et al.* 2010), primate postcranial morphology (Elton 2001) and in-depth isotopic work (Luyt 2001; Luyt & Lee-Thorp 2003), which all indicate that a significant grassland component was already present during Member 4 times. While Member 5 deposits preserve numerous species more typically associated with grasslands, including the extinct gelada baboon (*Theropithecus oswaldi*) and ostrich bones and eggshell (*Struthio*), this does not necessarily mean that Member 5 represents exclusively dry, grassland environments, nor that Member 4, in contrast, sampled only moister, more forested environments. Except for the fossil wood analysed by Bamford (1999), all other studies indicate high levels of habitat variability in Member 4, but each study suggests a slightly different mix of these habitat types. This is equally true of studies focusing on taxonomy (e.g. primates, Kibii 2004); taxon-free ecomorphological techniques (e.g. Elton 2001), and stable light isotope results of fauna and hominin tooth enamel (van der Merwe *et al.* 2003; Lee-Thorp *et al.* 2007). Likewise, high habitat variability over the same time period has been reported from Laetoli, based on vegetation evidence (Andrews & Bamford 2008).

This revised paleoenvironmental reconstruction has bearing on the occurrence of *Equus* in Sterkfontein Member 4, fossils of which have previously thought to be intrusive from a later Member 5 infill (Kuman & Clarke 2000). The first appearance of the equids in the eastern African fossil record at 2.33 ± 0.03 Ma (lower Member G of the Shungura Formation, Ethiopia) combined with the relatively younger age estimates for Member 4 suggested by combined palaeomagnetic, uranium-lead and ESR studies (Schwarcz *et al.* 1994; Pickering & Kramers 2010; Herries & Shaw 2011), show that there is no *a priori* reason why *Equus* could not occur in the later, upper beds of Sterkfontein Member 4, which date to less than 2.36 Ma. The ESR ages in particular, supported by palaeomagnetism and U-Pb suggest that Member 4 formed over a very long time period, perhaps as much as 600 ka (2.6–2.0 Ma).

Of particular relevance to this question is the in-depth isotopic study of a sample of 10 Sterkfontein Member 4 hominins, sampling specimens assigned both to *Australopithecus africanus* and to Clarke's (1988) 'second' species (van der Merwe *et al.* 2003). Not only do van der Merwe and colleagues report a significant C_4 component in the diets, but they conclude that *A. africanus* 'had the most variable dietary behaviour of all the early hominin species we have investigated' (van der Merwe *et al.* 2003: 593).

So, the question remains: does Member 4 represent a consistent mix of gallery forest that fringed the Blaaubank river, with close proximity to open grassland areas through time? Or is it perhaps a sampling of closed, wetter habitats (interglacials), interspersed with drier, open episodes (glacials)? Overall, the majority of the evidence points towards a mosaic habitat (a combination of open grassland with closed, forested areas in close proximity), which is in keeping with the speleothem signal reported from the Limeworks Member 1 Collapsed Cone and Buffalo Cave speleothem in the Makapansgat Valley (Hopley *et al.* 2007). However, this apparent combination of habitats may equally represent distinct environmental shifts between closed, forested conditions, and cooler, drier grassland conditions, which have become time-averaged in the fossil record. This process, referred to as 'climate-averaging' (Hopley & Maslin 2010) may characterize deposits which accumulate over more than one climatic cycle. Recent studies of the structure of carnivore guild community (O'Regan & Reynolds 2009) and studies of the relationship between large-scale climate changes and karst deposition (Hopley & Maslin 2010) strongly suggest that time-averaging played an important role how certain different types of habitats appear together in Member 4. An alternative hypothesis regarding the existence of Member 4 mixed environments is the Tectonic Landscape Model (TLM, Reynolds *et al.* 2011). Geomorphological evidence suggests the presence of a fault close to Sterkfontein, which would have created and sustained heterogeneous habitats consistently at Sterkfontein (Bailey *et al.* 2011; Reynolds *et al.* 2011). Modern analogies of how tectonics affects diversity are the tectonically-controlled wetlands of the Nysvley (South Africa) and Okavango (Botswana) regions; in both cases, a close proximity to faults in the presence of surface water creates high habitat diversity and promotes a wide range of plant, animal, fish and insect diversity (Ramberg *et al.* 2006; Havenga *et al.* 2007). This type of habitat creation, facilitated by tectonic motions, may have increased the biodiversity of plants and animals as has been observed in Sterkfontein Member 4

Taphonomic differences between Sterkfontein Members

Certain fossil accumulations at Sterkfontein may represent death traps, where animals have fallen into steep shafts or avens from which they could not escape (Pickering 1999). The presence of several species of carnivores within Member 2 suggests that they too fell prey to the same death trap which appears to have trapped the StW 573 hominin (Pickering *et al.* 2004a). No tooth marks have been observed on the exposed surfaces of the StW 573 bones, and this, combined with evidence of at least partial mummification of the left-hand and forearm bones of the specimen, suggest that it was not accumulated by carnivores (Pickering *et al.* 2004a). The recovery of extinct carnivores, specifically of the genera *Chasmaporthetes, Homotherium* and *Megantereon,* suggest that they were common in the area during the time of accumulation. The sabretoothed species are rare in the fossil deposits of the Cradle of Humankind, and appear spatially restricted mainly to the southern end of the Cradle of Humankind area, concentrated around the site catchment areas of Sterkfontein, Swartkrans and Kromdraai (Reynolds 2010). However, the new *Australopithecus* site of Malapa has also yielded species of extinct carnivores, such as *Dinofelis* sp., and *Megantereon whitei* at around 1.95 Ma (Dirks *et al.* 2010).

Little is known about potential bone accumulating behaviour of these extinct carnivore taxa, but the Friesenhahn site in Texas (USA) studied by Marean and Ehrhardt

(1995) has been interpreted as a *Homotherium* den. In this case, the sabretooths appear to have specialized upon juvenile proboscidean prey. In addition, this species may have damaged the bones with similar tooth-mark frequencies as has been observed in modern hyaena and leopard den assemblages (Marean & Ehrhardt 1995; Pickering *et al.* 2004b). The lack of carnivore tooth damage supports the overall interpretation that Member 2 was not accumulated by carnivores, extinct or otherwise. In the Jacovec Cavern there is only one *Australopithecus* clavicle with gnaw-marks (Partridge *et al.* 2003). There is no evidence apart from this to suggest that Jacovec was a carnivore den or a death trap accumulation. The majority of the fauna appear to have been washed into the cavern from the catchment area at the surface (Kibii 2004).

Member 4 shows a different pattern of accumulation. This Member contains the largest numbers of *Australopithecus* specimens, co-occurring with a large carnivore guild totalling 14 species (Table 4). It has been suggested that there may be a bias towards females and immature males of *Australopithecus africanus,* which may in turn reflect the prey selection of large carnivores active at the cave during the accumulation of Member 4 (Lockwood & Tobias 2002). Based on modern prey spectra, and body size estimations of fossil carnivores, the majority of the carnivores would be preying on medium-sized prey, including hominins (O'Regan & Reynolds 2009). Studies of bone surface modification suggests that the Member 4 fossils were accumulated by carnivore activity, natural death trap accumulations and slope wash (Brain 1981; Kibii 2004).

By Member 5 times (StW 53 infill, Member 5 East and West), virtually all large extinct carnivores have disappeared, and the faunal assemblage is dominated by extant medium and larger-sized carnivores such as lions (*Panthera leo*), leopards (*Panthera pardus*) and several species of hyaenas (Table 4). From the presence of coprolites, and specimens of juvenile carnivores, it appears that these species were using the cave as a denning site (Pickering 1999). The presence of cut marks on the StW 53 hominin cranium, suggests that hominins were using the site, both as an area for the manufacture of stone tools and for certain butchery activities in early Member 5 times (Pickering *et al.* 2000). This is further corroborated by an abundance of Oldowan and Acheulean stone tools in the other two Member 5 infills (Kuman & Clarke 2000). However, the dearth of chop- or cutmarked bone argues against a significant role for hominins in Member 5 faunal accumulation (Pickering 1999).

By Member 6 and Post Member 6 times (L/63 and Lincoln Cave), the only carnivores recovered in the deposits are small carnivores, such as the black-backed jackal and bat-eared fox (*Canis mesomelas* and *Otocyon megalotis,* respectively). While large carnivores become scarcer at the site through time, small canids and viverrids appear abundant in later deposits than in Member 4 or Member 5 assemblages. This pattern suggests that both canids and felids may have varied their use of areas of the Sterkfontein caverns through time, most likely for denning purposes (Reynolds *et al.* 2007). Fossils associated with the Lincoln Cave (located in a nearby miner's dump, called 'Dump 7') are dominated by small carnivores (in particular, jackals *Canis* cf. *mesomelas*), with several juveniles of more than one carnivore species, suggesting that the Lincoln Cave was commonly used as a small carnivore den at some point during the Pleistocene (Reynolds 2010). Possibly, the larger carnivore species moved out of the Sterkfontein area as humans became more technologically competent and competitive towards the Upper Pleistocene (Reynolds *et al.* 2007; Reynolds 2010).

CONCLUSIONS

The initial stages of study of many African cave sites, including Sterkfontein, suggest simple environmental differences between deposits and through time. Over time, subsequent studies revise these early, simple models by recognizing complexity of various kinds: climatic, stratigraphic, taxonomic and environmental, that was not fully appreciated before, such as the three separate infills in Sterkfontein Member 5 (e.g. Kuman & Clarke 2000).

Even after 75 years of excavation and study of the Sterkfontein deposits, the telling of the Sterkfontein story is not finished. Many researchers have all contributed to our understanding of the site and its significance (Tobias 2002). Fortunately, the use of novel techniques and new approaches continue to yield exciting insights into the cave and its remains. All we are able to present here is the Sterkfontein story as it stands so far, knowing that many chapters are yet to be written.

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Technical note

Unidentified specimens in zooarchaeology

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INTRODUCTION

A consideration of skeletal part profiles of faunal assemblages has become more or less part of conventional zooarchaeological analyses throughout the world. Studies of skeletal parts yield a wealth of information, and can inform zooarchaeologists on, for example, site function and usage (Binford 1978), carcass transportation (Marean *et al.* 1992), meat provisioning, sumptuary rules and social status (Ijzereef 1989; Schmitt & Lupo 2008), gender (Mooketsi 2001), feasting (Hayden 2001), trade or long-distance meat acquisition (Driver 1990), bone preservation (Brain 1967), as well as attributes of non-human agents such as carnivores (Marean & Spencer 1991), raptors and porcupines (Brain 1981).

The vast majority of faunal assemblages from Pleistocene and Holocene deposits in all parts of the world, regardless of the agent(s) of accumulation, consist of fragmented specimens. The fragmentary nature of these faunal assemblages is due to a complex interaction between biotic and abiotic processes, which transform complete or near-complete elements into fragments over time. These taphonomic processes include, for example, cutting, chopping, burning, cooking, trampling, weathering, rootlet etching, carnivore and rodent gnawing, digestion, diagenetic actions and retrieval damage (e.g. Lyman 1994; Reitz & Wing 1999). Complete elements are usually associated with animal burials (Muir & Driver 2004, but see Hutten 2008), which are not considered here. An aspect most often ignored in studies of animal skeletal profiles in zooarchaeology, is unidentified specimens.

UNIDENTIFIED SPECIMENS

The first step in faunal analysis is often to separate identifiable from unidentifiable specimens. In most cases, a large percentage of specimens in a faunal assemblage cannot be identified (O'Connor 2000; Table 1). The ratio of identified and unidentified specimens provides some indication of the level of fragmentation in an assemblage (Plug 1988), although this is also influenced by the method of analyses. For example, the method suggested by Driver (2005) regards all specimens that can be identified to a skeletal element as 'identifiable', whereas Brain (1974) and Voigt (1983) regard indeterminate enamel fragments, skull, vertebrae and ribs as 'unidentified' specimens.

In addition, archaeological recovery methods are also important. A lack of or poor screening and handpicking of specimens during excavations can inflate the ratio of identified to unidentified specimens. For example, the faunal assemblage from the Late Iron Age site of Simunye in Swaziland, comprised 62% identified specimens (Badenhorst & Plug 2002), which was due to a lack of screening during excavations (compare Table 1). Objects made from bone and shell are not always presented to the faunal analyst and where such objects are common, for example beads, bone points, tortoise shell containers and pendants, their absence from the faunal sample to be analysed may cause misrepresentation of taxa and skeletal elements. The proficiency of zooarchaeologists is also an important factor. In this regard, O'Connor (2000) points out that 'unidentified' specimens are not the same as those that are 'unidentifiable'. The former category indicates that the zooarchaeologist did not regard that sufficient morphological criteria were present to allow taxonomic identification. This O'Connor (2000: 42) correctly terms a positive decision, not an admission of defeat. In fact, some specimens that may be considered 'unidentified' by one zooarchaeologist is often not for another (Grayson 1984). Controversially, Binford & Bertram (1977: 125) state that, in referring to both archaeological and ethnographic faunal assemblages, they '…have always taken the position that there *is no unidentifiable bone.* All bones, even the smallest fragments, may be identified with sufficient training in osteology' (emphasis by original authors). Such statements O'Connor (2000: 42) correctly calls '…wonderfully optimistic, and utterly wrong.'

The nature of an assemblage may also determine the ratio of unidentifiable to identifiable specimens. When a collection contains a large amount of fragments that are imminently identifiable such as tortoise shell for example, and the same sample also contains a large number of fragmented mammal bones that cannot be identified, it may lead to problems of interpretation. The identifiability of certain groups is demonstrated by the assemblage from Likoaeng, a Later Stone Age site in Lesotho that was occupied between *c.* 4000 and 1200 BP. The faunal assemblage consists of *c.* 1 680 000 specimens of which *c.* 1.3 million specimens (77%) are fish remains (Plug & Mitchell 2008). Of the fish remains, over 55% could be identified to taxon or genus, while for the non-fish remains, less than 2% could be identified to taxon or genus (Plug 2006, unpubl. data).

Bone breakage tends to, initially at least increase the percentage of Number of Identified Specimens (NISP) in an assemblage. However, when an assemblage is heavily fragmented the opposite effect is produced. A greater proportion of specimens then become too small to be identified, and hence decrease the percentage of identified specimens (Marshall & Pilgram 1993). Lyman &

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Table 1. Examples of faunal assemblages from southern Africa indicating level of fragmentation (percentages rounded off).

Sites	Date and cultural association	% Identified specimens (NISP)	% Unidentified specimens	Reference
Steinaecker's Horse	AD 1899–1902 (Historical Period)	27	73	Badenhorst *et al.* 2002
Boleu	Mid AD 1800s (Terminal Late Iron Age)	17	83	Badenhorst & Plug 2004–2005
Boitsemagano	17th century (Late Iron Age)	13	87	Plug & Badenhorst 2006
Manyikeni	12th–16th/17th century (Late Iron Age)	27	73	Sigvallius 1988
Ratho	AD 1040–1240 (Middle Iron Age)	14	86	Brunton 2010
KwaGandaganda	AD 620–1030 (Early Iron Age)	23	77	Beukes 2000
Toteng 1	*c.* 2070–1480 BP (Pastoral Later Stone Age)	11	89	Robbins *et al.* 2008, Badenhorst, unpubl. data
iNkolimahashi Shelter (excluding rodents)	*c.* 360–3130 BP (Later Stone Age)	8	92	Badenhorst 2003
Olieboomspoort	<2000 BP (Later Stone Age)	33	67	Van der Ryst 2006
Maqonqo Shelter	3500–9000 BP (Later Stone Age)	2	98	Plug 1996
Sibudu Cave	Pre-38 000 BP (Middle Stone Age)	7	93	Plug 2004
Florisbad	Middle–Late Pleistocene (Middle Stone Age)	45	55	Brink 1987

O'Brien (1987: 496) pointed out that when specimens are '…reduced beyond the minimal identifiable size, then the proportion of identifiable fragments will be decreased.' It can therefore happen that, in samples with relatively high percentages of unidentified specimens, most of the absent skeleton was deposited, and in fact, recovered during excavations. However, the high percentage of unidentified specimens can preclude species or element identification (also Todd & Rapson 1988; Watson 1972). Lyman & O'Brien (1987: 496) described this effect as an 'analytic absence' of species and elements.

CASE STUDIES

We present three examples of how a consideration of unidentified specimens can lead zooarchaeologists to different interpretations. At the Middle Stone Age site of Klasies River Mouth, Klein (1976, 1989) found that the upper limb bones of larger bovids are generally absent, whereas lower limb bones and the head are common. In contrast, smaller bovids are represented by more even skeletal part representation. The 'schlepp effect' featured strongly to explain this pattern, whereby hunters discarded the bulkier limb bones of large animals at kill-sites and dragged the meat back to camp in the skin using the intact foot bones as handles (Perkins & Daly 1968). In a reply, Bartram & Marean (1999) showed that unless unidentified long bone shafts are refitted to form more complete bones, the upper limbs of large animals will be under-represented.

However, refitting is tedious and time-consuming (Klein *et al.* 1999). In addition, some faunal assemblages such as those from the Middle Stone Age are often reduced to crumbs. For example, at the Middle Stone Age site of Sibudu Cave, the vast majority of bone remains were reduced to small pieces, making it even impossible to recognize long bone flakes (*cf.* Plug 2004). Nonetheless, the research by Bartram & Marean (1999) highlighted the importance of unidentified long bones.

Reynard (2011, also J. Reynard, S. Badenhorst & C.S. Henshilwood, in prep.) studied the unidentified long bones from the Middle Stone Age layers of Blombos Cave. The identified remains (Henshilwood *et al.* 2001) indicate that small animals such as rock hyrax, Cape dune molerat and small bovids dominate the faunal sample. However, the cortical thickness of the unidentified long bones indicates that medium-sized animals were more common than smaller game. However, issues related to identification and taphonomy may also have caused this pattern.

Studies of faunal assemblages from Middle Period and early Plateau Pithouse Tradition (7000–3500 BP) sites on the Interior Plateau of British Columbia, Canada, yielded a dominance of medium (deer-sized) and large (elk-sized) artiodactyla lower limb bones. Although this pattern is consistent with results of ethnoarchaeological studies of butchering camps (Binford 1978), the very high percentage of unidentified, and very low percentage of identified specimens (Table 2), suggests that more, and missing elements of artiodactyls are probably present in assemblages, but these could not be identified. Most of the assemblage has been reduced to crumbs (Badenhorst 2009). Although it remains likely that these sites were butchering camps, the skeletal profile is more likely a taphonomic artefact rather than conforming to an ethnoarchaeological pattern (Binford 1978).

CONCLUSIONS

Skeletal part profiles form a central part understanding bone taphonomy. A factor most often overlooked when evaluating skeletal part profiles, is unidentified specimens. Faunal analysts must be aware that any profile of skeletal parts reflects a pattern within the *identified* sample, and not necessarily within the *entire* assemblage, especially in assemblages with high percentages of unidentified specimens. Conversely, in assemblages with high percentages of identified, and low percentages of unidentified specimens, any pattern of skeletal part profiles may be assumed to reflect the entire assemblage. However, it is as yet impossible to determine what constitute 'high percentages' of unidentified specimens. Ethnoarchaeological, actualistic and modelling studies may provide greater

Table 2. Middle Period and early Plateau Pithouse Tradition samples (Badenhorst 2009).

Site	% Identified specimens (NISP)	% Unidentified specimens
EdRh-31	6	94
EeRh-61	10	90
EdRh-11	1	99
EdRh-14	3	97

insights. It is useful when such studies list the number of unidentified specimens (e.g. Lupo 2001).

The role of unidentified specimens in skeletal part profiles will likely remain a problematic issue. Each assemblage has a unique taphonomic history. Nonetheless, zooarchaeologists can make a contribution by:

- providing an explicit indication about the method used to analyse an assemblage (Driver 1982);
- presenting the numbers and percentages of identified and unidentified specimens for assemblages (Grigson 1978); and
- in cases where the method of Brain (1974) and Voigt (1983) is used, presenting the numbers of unidentified fragments that could not be placed into a taxonomic category, under enamel, skull, vertebrae and rib.

In addition, it is important that archaeologists retain all excavated bone specimens, and subject all of these for analysis. Most bone specimens can be retained using a 1-mm sieve, but in some instances the use of smaller sieve sizes may be advisable (Matsui 2008). Depending on the research questions, preservation and resources, refitting may be a viable option in some cases. By being more explicit about the analytical method and ratio of identifiable *versus* unidentified specimens, zooarchaeologists will be in a better position to evaluate interpretations based on skeletal part profiles. While it is tempting to immediately associate any changes in skeletal part profiles to human behaviour, such patterns could also relate to changes in the ratio of identified *versus* unidentified specimens.

However, many studies have applied skeletal part profiles successfully. For example, Driver (1990) noted that those bison elements most likely affected by post-depositional destruction – ribs – dominate faunal samples in the Sierra Blanca region of southeastern New Mexico for sites dating to between AD 1150 and 1450. Taphonomic processes were largely excluded, as more dense elements such as distal humeri, phalanges and distal tibiae are absent or occur in very low frequencies. In addition, ethnographies from the region indicate that brisket meat cuts are highly prized (Driver 1990).

Many archaeologists and zooarchaeologists may not find a consideration of unidentified specimens, and its potential effects on interpretations appealing (but see Badenhorst 2009; Thackeray 2007; Reynard 2011). In this regard, Maltby (2002: 88–89) remarks: ‘There is a widely held belief that animal bone studies have failed to produce the answers to what other archaeologists want to know. For example, when an archaeozoologist is asked the apparent simple question of ‘What did they eat?’, there is likely to be a very convoluted answer. Of course, archaeozoologists are right to point out the complexities caused by taphonomic processes; small sample size; retrieval rates; intra- and inter-site variation; the effects of different methods of quantification, etc. However, it’s a sad fact that others are not particularly interested in such problems. They want positive answers. Counter-arguments to the effect that at least archaeozoologists are attempting to look at their data critically, although valid, are unpopular.’

It may be worth pointing out that the aims and purpose of archaeology is to understand the past, and how humans interacted with each other and the animals, environment and material culture (*cf.* Brinton 1895; Petrie 1904). At the same time, it is imperative to realize the limitations of our data, and that the archaeological record is ‘…the imperishable remnants of material culture, not the sum of artefacts in use by some particular people at some particular time’ (Summers 1958: 6).

The two reviewers offered constructive suggestions, for which we are grateful.

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Obituary
Arthur Cruickshank — 1932–2011

A native of Gondwanaland, who studied the former continent's fossil tetrapods

Dr Arthur Richard Ivor Cruickshank died on 4 December 2011, aged 79, in the Borders General Hospital, Melrose, Scotland. Arthur Cruickshank was one of a post-war generation of palaeontologists who laid the foundations on which today's researchers build. Appropriately for someone from an expatriate Scots family living in Kenya, much of his work was on the extinct reptiles of the great southern continent of Gondwanaland.

Cruickshank was born in Nairobi, Kenya, on 29 February 1932. His grandfather was traffic manager on the Uganda Railway, which went from the port of Mombasa to Nairobi in Kenya and on into the interior and Uganda proper, through fine wildlife country. A recurring problem was the need to deal with individual lions that had developed a habit of eating staff and passengers, and the family story is that the traffic manager had to shoot at least one such lion himself. This was surely one of the lion stories he told Teddy Roosevelt, the former President of the United States, when they were travelling on a special train for Roosevelt's famous African safari of 1909–10 which yielded so many zoological specimens for the Smithsonian Institution in Washington and other American museums.

Cruickshank's father was Scottish through and through, from several generations of farmers near Elgin in Moray. Cruickshank's mother was of joint Devonshire and Scottish extraction. His parents travelled widely for his father's work as an engineer in the sisal plantations, often leaving their only child in a Nairobi children's home. Cruickshank contracted chronic malaria and in 1938, aged six, he was sent back to Scotland, where he boarded at Dollar Academy in Clackmannan. Wartime restrictions considerably reduced contact with his family, but eventually he was settled for his school holidays with a family in Coldstream which gave him an experience of family life and his life-long love of the Scottish Borders.

Cruickshank entered Edinburgh University Department of Geology in 1953, at a time when the novel theory of plate tectonics, or at least its earlier variant such as set out in Arthur Holmes' *The Principles of Physical Geology,* was arousing intense debate. Cruickshank embraced the new theory, unlike some of his teachers. It is perhaps open to question who was more dissatisfied with whom, but at any rate Cruickshank found it advisable to transfer to the Department of Zoology for his Honours year. He further cemented his shift to the palaeontological side of life with his first research, a project on the teeth of the giant rhizodontid fishes from the local Carboniferous in Lothian. In 1958 Cruickshank moved to the University of Cambridge for a doctorate under Dr Rex Parrington, studying specimens which Parrington had collected in an African expedition in the 1930s; Cruickshank's allocated beast was the dicynodont *Tetragonias,* a hefty plant-eater. His external examiner was absolutely astounded by what he had achieved from the specimens to hand. The resulting 45-page monograph was published in the *Journal of Zoology* in 1967. This was a typical example of the classic vertebrate palaeontological paper of the day: a full, bone-by-bone description, and comparison with close relatives, together with consideration of the feeding and locomotor abilities of the beast.

Cruickshank continued with his interest in dicynodonts, publishing on other Triassic species, as well as writing overviews of their evolution and functional morphology. To non-experts, dicynodonts all look more or less the same – animals from 1 to 3 metres in length, with barrel-shaped bodies, a large head with somewhat beak-like jaws for chopping plant food, massive legs, and an inadequate-seeming stumpy tail. But to 'dicynodontophiles' like Cruickshank, they are objects of beauty – and of great importance to understanding the evolution of life on Earth, for dicynodonts comprise the first major group of plant-eating land vertebrates.

Cruickshank took up a lecturing post at the Edinburgh University Department of Zoology, where he met his future wife Enid, then a student, who came from Denholm near Hawick in the Scottish Borders, and they were married in 1963. In 1966 he took up a lecturing post at Napier College, Edinburgh, before moving in 1967 to the University of the Witwatersrand, Johannesburg, where he was Assistant Director of the Bernard Price Institute for Palaeontological Research. This gave him access to a wide range of unstudied dicynodont specimens, allowing him to sustain his passion for these beasts.

Cruickshank tackled the Permo-Triassic aged rocks of southern Africa, and their fossil reptiles, with alacrity. He had already been to Cape Town for three months to study specimens of the dicynodont *Lystrosaurus* in the museum, before he joined the 1963 British Museum (Natural History) (now the Natural History Museum, London) expedition through East Africa (Figure 1). The South African group drove all the way from Johannesburg through Salisbury (now Harare) and Nyasaland (now Malawi) to meet the others in the Ruhuhu Valley in southern Tanganyika (now Tanzania). This was near to where Cruickshank's mother was living in Tanga, where Enid met him after taking a ship from South Africa. He continued studying his beloved dicynodonts, but also began to explore the basal archosaurs – important as the ancestors of crocodiles, dinosaurs, and modern birds. In the 1970s, he published definitive works on the anatomy and relationships of some of the most basal archosaurs, *Proterosuchus* and *Erythrosuchus.* The archosaurs had evolved at the very end of the Permian Period, and they diversified rapidly in the Early and Middle Triassic, following the devastating end-Permian mass extinction 250 million years ago. This work sparked wider interest in the evolution of the group, which today is still a hot topic of debate and research. By chance, some of the best early archosaur fossils were in the South African museums, and Cruickshank gave detailed anatomical descriptions which today are still widely quoted as definitive sources.

This work led to wider investigations of the succession of terrestrial ecosystems through the Permian and Triassic.

Figure 1. The British Museum (Natural History) East Africa Expedition 1963 — the South African group meets up with the main team at Lindazi Castle in Zambia. From left to right, the adults are Arthur Cruickshank, Barney Hershon (an interested amateur from Cape Town), Fuzz Crompton, John Attridge, Alan Charig and Barry Cox. The child was the son of the person running the hostel. Photograph courtesy Steve Tolan via Enid Cruickshank.

Cruickshank wrote about overall patterns of evolution among the archosaurs, and focussed also on the origin of the dinosaurs. Furthermore, with the palaeobotanist John Anderson, he wrote detailed, and then state-of-the art, overviews on vertebrate faunal successions worldwide through the Permian and Triassic. All this work on Permo-Triassic reptiles provided one of the first frameworks for understanding this crucial time: not only do Triassic rocks document the recovery of life from the most devastating of Phanerozoic mass extinctions, the end-Permian event, but this was also the time of the origin of the dinosaurs, as well as key elements of modern vertebrate faunas, including the first frogs, turtles, crocodile ancestors, lizard ancestors and perhaps lizards themselves, and later the mammals.

Cruickshank found South Africa exciting but difficult, in terms of both the job and of the wider South African scene; in the U.K., he was a life-long Liberal and active in the Liberal Democratic Party, especially after the family returned to Scotland in 1978. However, the new Prime Minister, Margaret Thatcher, clamped down on university research, so Cruickshank could find no permanent teaching or research post, but took what work he could get in local universities, colleges and museums, and especially as a tutor with the Open University. He continued to collaborate with his former South African colleagues in presenting papers on Permian and Triassic faunas, and early dinosaurs from southern Africa.

The Cruickshank family moved to Hinckley in Leicestershire in 1985 when his wife obtained a post as a librarian in Rugby. Hinckley lies near the Jurassic belt that crosses England from the east to south coasts, and a contract post at Leicestershire Museums Service led Cruickshank to a change of research direction. He now began to work on the Jurassic and Cretaceous plesiosaurs, large marine reptiles with four flippers. His initial post in Leicester was a short-term contract for routine curatorial and site documentation work, but Cruickshank soon took advantage of the Museum's facilities and its fine marine reptile collections from the local Jurassic. He became for many years an honorary research associate, de facto and then de jure, of Leicestershire Museums and then its Leicester City successor, as well as an Honorary Research Fellow of the Department of Geology at the University of Leicester. Some of his research work was supported by the Leverhulme Trust (through a grant to Mike Taylor, then at Leicestershire Museums).

One highlight was the description of Leicester Museum's *Rhomaleosaurus megacephalus,* locally nicknamed 'the Barrow Kipper'. The specimen originated from earliest Jurassic deposits at nearby Barrow-upon-Soar, and has become the symbol of the town. Cruickshank and his colleagues subjected the specimen to CT-scanning to study the internal structure of its nasal passages. In 1991 this was still a fairly new and unusual technique to use on fossils, but Cruickshank seized the opportunity when he found Philip Small, a doctor at the Queen's Medical Centre in Nottingham, in the evening class which Cruickshank took over when David Martill moved to Portsmouth. More recently he was part of the team which scanned a hollow 'mouldic' fossil inside a block of sandstone from Morayshire. These data were used to recreate a 3-D computer-generated rendition of the skull of a dicynodont, and then to rapid-prototype it in plastic, an early use of this technique in palaeontology.

Another opportunistic meeting, this time at a rather lower technical level, happened when Cruickshank observed his dentist using high-fidelity dental putty; he

Figure 2. Arthur Cruickshank at Mike Raath's 'CT6' site at the Chitake River, Rhodesia (now Zimbabwe), in September 1972. This site yielded many specimens of the small theropod then called *Syntarsus* (now *Coelophysis*). Cruickshank is overdressed for the broiling heat; the dapper safari bush gear was badly needed to protect against the area's voracious tsetse flies. He is standing at one end of the exposure of a small fluvial channel in the Forest Sandstone Formation (Early Jurassic), and pointing at the bone-bed in which 30-odd individual theropods were exquisitely preserved as jumbled bones. Most of the bones are white, showing little contrast with their matrix, but manganese-blackened bones are visible in places, such as perpendicularly below the 'CT6' mark on the outcrop. Photograph courtesy Mike Raath.

promptly besought the dentist to cast the tooth marks which he had observed on a bone of a kannemeyeriid dicynodont. This helped identify the characteristic dentition of the predator, a rauisuchian archosaur. The elemental simplicity of the resulting paper evidently threw at least one *Palaeontology* referee completely off balance; one praised it as a perfect piece of work, needing no changes, and another – fortunately ignored by the editors – damned it as unworthy of the august pages of that journal.

Cruickshank also happened to meet the engineer Professor Beric Skews of the University of the Witwatersrand, simply because Skews' little boy wanted to know all about dinosaurs; the result was an elegant hydrodynamical study of the long tabular horns of the Palaeozoic nectridean amphibians *Diplocaulus* and *Diploceraspis* – which look like newts with boomerangs for heads. Cruickshank and Skews concluded that the animals lurked on the bottom of rivers, raising their heads into the flow to gain a rapid lift force to help them lunge upwards at prey. Cruickshank's evening class students were often led, through initial bafflement at the counter-intuitive use of a wind tunnel rather than a water flume tank for their model nectrideans, to an appreciation of the Reynolds number and the concepts of scaling and dynamical similarity in fluid mechanics. Professor R. McNeill Alexander, the eminent biomechanicist, chose this study to exemplify hydrodynamics in his prestigious William Smith lecture on the biomechanics of fossil vertebrates to the Geological Society of London in 1989.

Cruickshank's work on plesiosaurs included a study of the first Westbury Pliosaur, still on show at Bristol Museum and Art Gallery; today this work is highly relevant to the newly unveiled giant Dorset Pliosaur. He co-described the weird *Pachycostasaurus* in Peterborough Museum, its ribs swollen into ballast to help it swim slowly along Jurassic sea floors, perhaps to graze on shoals of Jurassic shrimps – a carnivorous reptilian analogue of modern plant-eating sea-cows. Cruickshank returned to his Morayshire roots, not just with the aforesaid dicynodont but also with a study of the plesiosaur remains from the giant Rhaetian erratic at Linksfield near Elgin, and to his Gondwanaland roots with the support of the Royal Society of London, to study Cretaceous plesiosaurs in Australia, New Zealand and South Africa. The southern continent work came about in part to examine relatives of *Leptocleidus superstes,* from the Wealden of Sussex, which was startlingly similar to the early Jurassic *Rhomaleosaurus* despite being a Lower Cretaceous form; Cruickshank suggested that these Cretaceous pliosaurians had been displaced into near-shore and estuarine environments by the rise of competitors. He also examined other southern forms, co-describing the new *Kaiwhekea* from New Zealand with Ewan Fordyce.

Cruickshank's work on plesiosaurs took place when this important group was almost completely neglected. The situation is much different today, for his work helped stimulate a younger generation of researchers with whose studies, as well as those of his nearer contemporaries, he was much involved, often working in collaboration. As with his earlier work on Permo-Triassic beasts, he was a mine of information, always on hand to provide friendly support and advice to co-workers, students, amateur collectors (so important in this area of research), and

Figure 3. Arthur Cruickshank at his 'retirement' party, at the Strode Theatre, Street, Somerset, in July 2009. The cake is an accurate model of the holotype specimen of the Triassic-Jurassic boundary plesiosaur *Thalassiodracon hawkinsi* (Owen, 1840), found at Street. Photograph by Mike Taylor.

others interested in these fascinating animals. In total, and including the Permo-Triassic work, he supervised at least 11 research students (plus two ongoing), and examined eight others. In this and in many other ways he was a deeply appreciated friend and colleague, perhaps more so than he realized, and his memory will live long in the minds of those who knew and loved him. A colleague accurately recalled that 'he was the most urbane of palaeontologists, with one of the driest and quickest senses of humour I have known'. Cruickshank's modesty shone through when he was amazed by the numbers in attendance at a special session held in his honour, at a conference on the Triassic/Jurassic boundary fossils of the West Country of England, in Street, Somerset, in 2009 – an appropriate location for its plesiosaurs of world class importance, as well as its views of the Isle of Avalon of, indeed, *Arthurian* legend (see *Palaeontology Newsletter* **73**, 40–46, www.palass.org). He has one taxon so far named after him, the dicynodont *Angonisaurus cruickshanki* Cox & Li, 1983, whose type specimen he helped to collect on the 1963 expedition, and also prepared. Also to be named after him is the Street plesiosaur *Avalonnectes arturi* Benson, Evans & Druckenmiller, in press 2012.

Cruickshank was a long-standing member of the Palaeontological Association and served on its Council as Institutional Membership Treasurer from 1990 to 1992. For many years he was a Fellow of the Geological Society, and also a member of the Institute of Geologists, taking C. Geol. status. He also served variously on the councils and committees of the Zoological Society of Southern Africa, the Geological Society of South Africa, South African Society for Quaternary Research, and the University of the Witwatersrand Faculty of Science. He was on the Museum of Man and Science Board of Governors in South Africa, was Chairman of the Dinosaur Society (U.K.), and sat on the Tutorial and Counselling Staff Committee of the Open University in Scotland.

In 2006, the Cruickshanks moved back to the Borders and lived first in Denholm and then in Hawick. Late in life he suffered, with remarkable resolve and cheerfulness, from bowel cancer, and died in the Borders General Hospital at Melrose following a fall at home. A dedicated family man, Arthur Cruickshank is survived by his wife Enid, their children Peter, Susan, and David, and three grandchildren.

We thank Enid and Peter Cruickshank and many friends and colleagues for supplying information and photos. We acknowledge permission of the respective editors to publish this obituary in both *Palaeontologia africana* and *Palaeontology Newsletter* (submitted). This publication is invalid for taxonomic/nomenclatural purposes.

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SCIENTIFIC PUBLICATIONS OF DR A.R.I. CRUICKSHANK

Arthur Cruickshank did not maintain a list of his minor publications such as book reviews and letters to the editor. We have simply included those known to us, but our listing is unavoidably incomplete in this regard.

A. Research contributions

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