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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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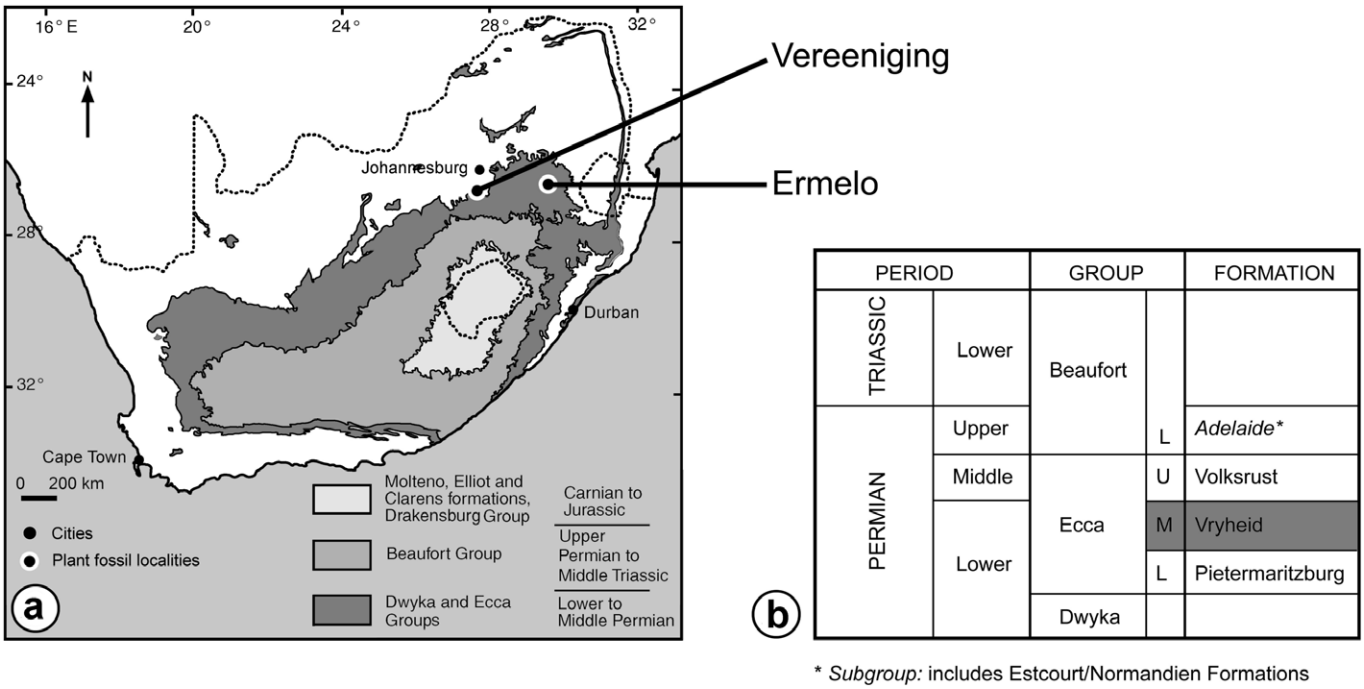


Figure 1. **a**, Locality map indicating reported occurrences of *Scutum* within deposits of the main Karoo Basin in South Africa; **b**, lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded area representing the stratigraphic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

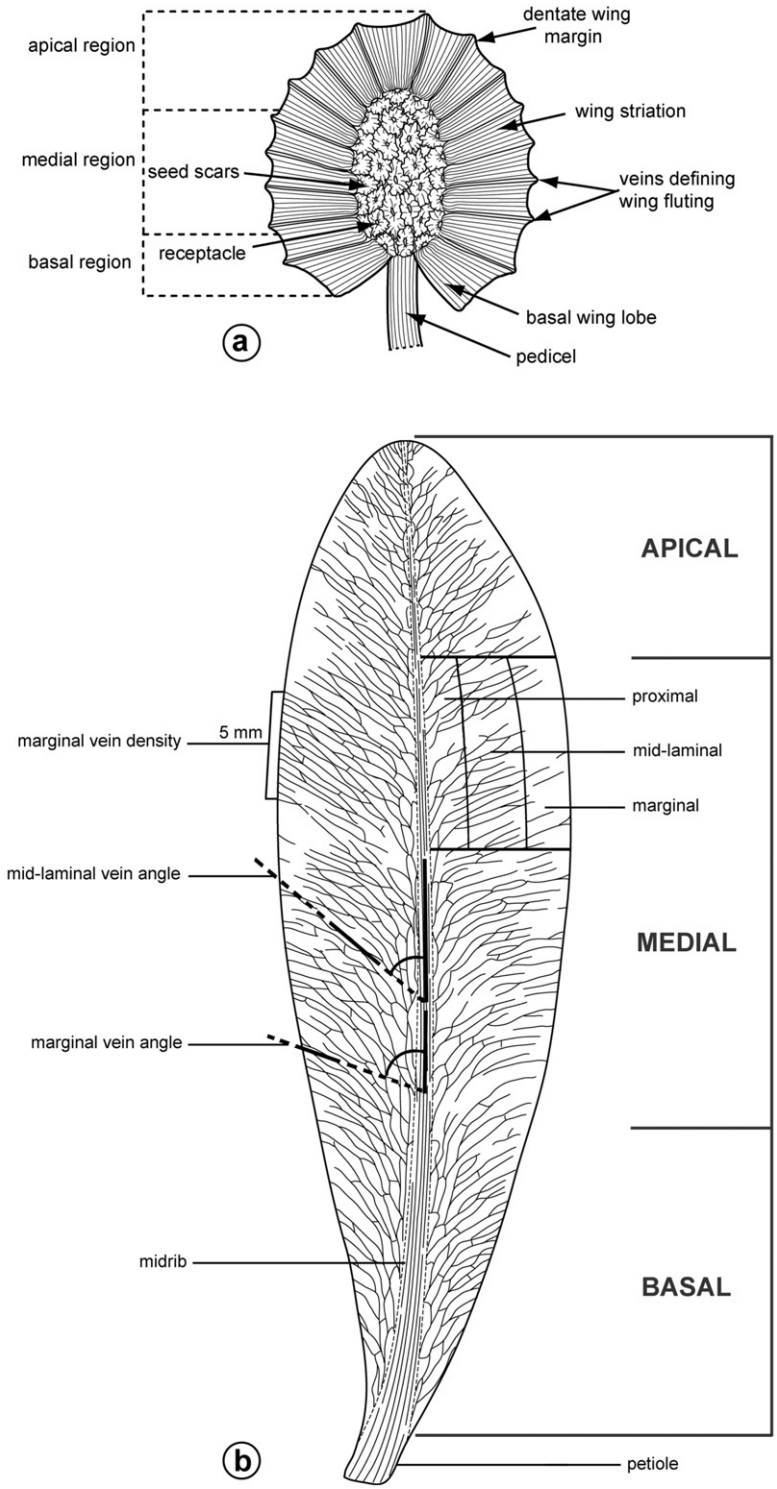


Figure 2. Diagrams indicating the basic morphological features used in the measurement and description of (**a**) *Scutum* fructifications and (**b**) attached *Glossopteris* leaves.

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 subtend-

ing *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

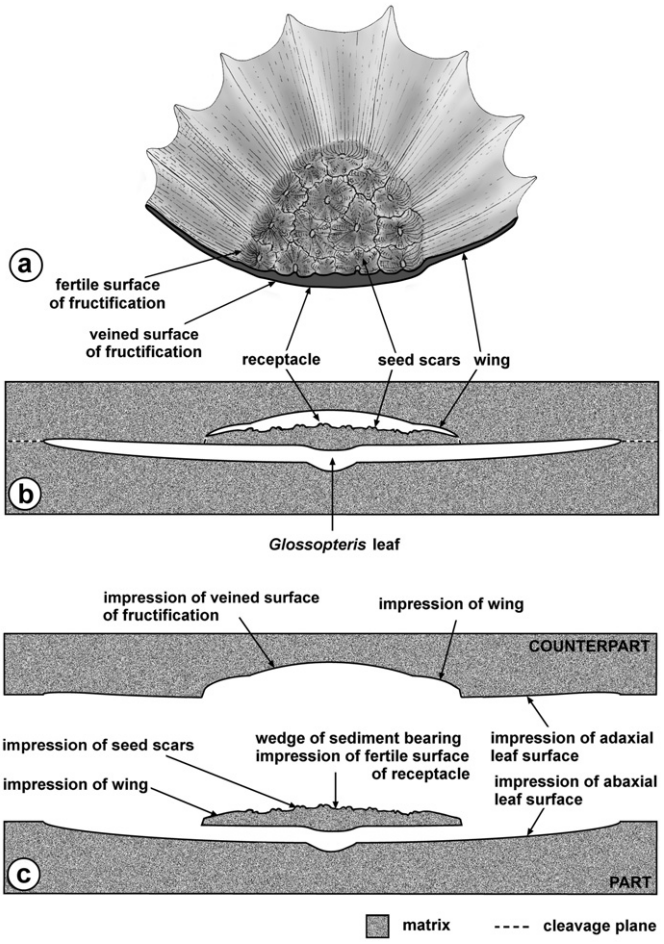


Figure 3. **a**, Reconstruction of the apical portion of a *Scutum leslii* fructification (based on BP/2/13735), showing depressed seed scars, raised cicatrices and fluted wing; transverse section illustrates smooth, veined surface and opposing fertile surface bearing depressed seed scars (raised in 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 depres-

sion 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.

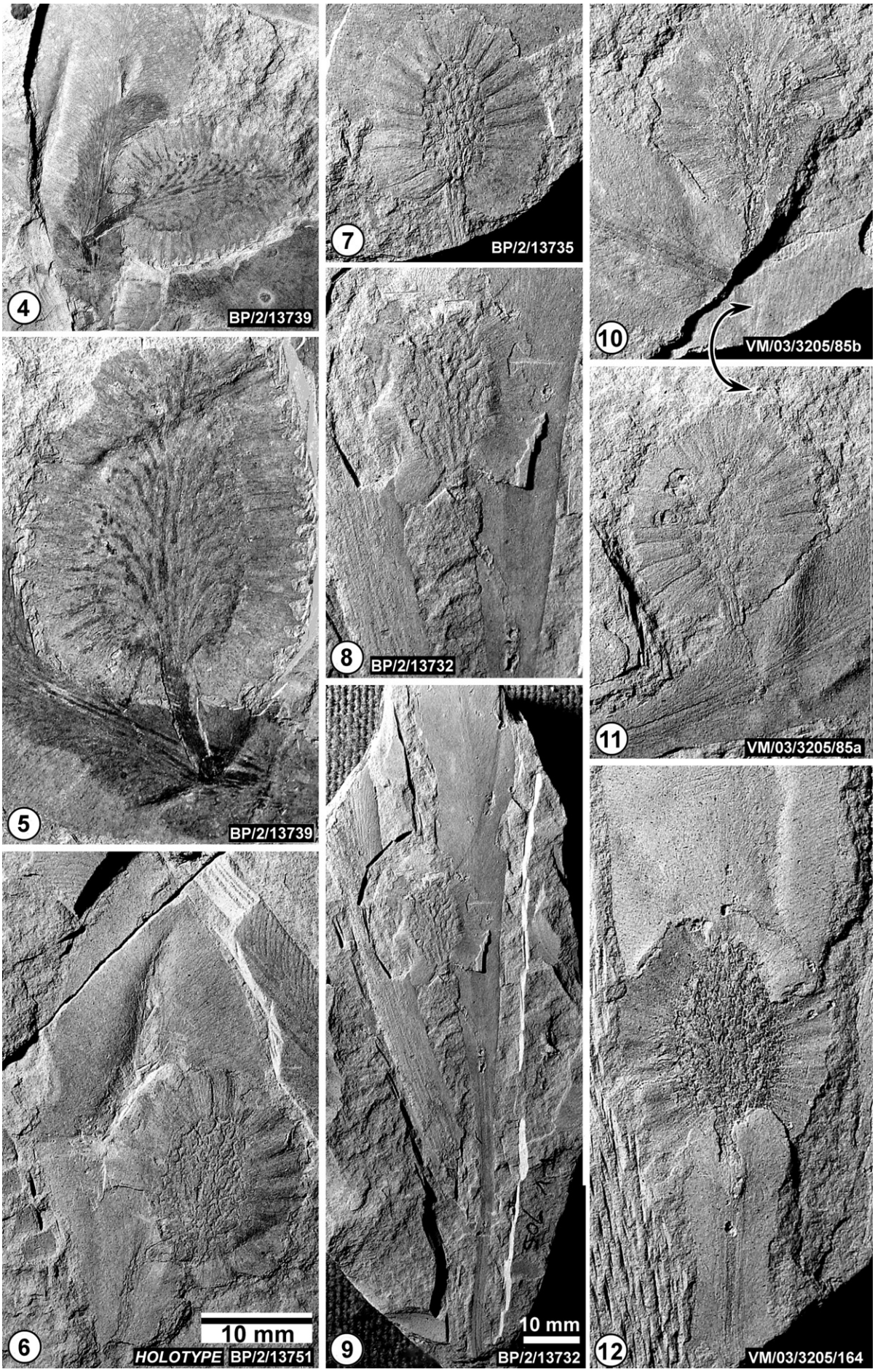
There is a large degree of variability in size and shape of the subtending leaves, of *S. leslii,* as here defined, although the venation appears to be fairly consistent. The leaf bases of the fertiligers of *S. leslii* tend to be poorly preserved, and in many cases it is not clear whether the bases 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

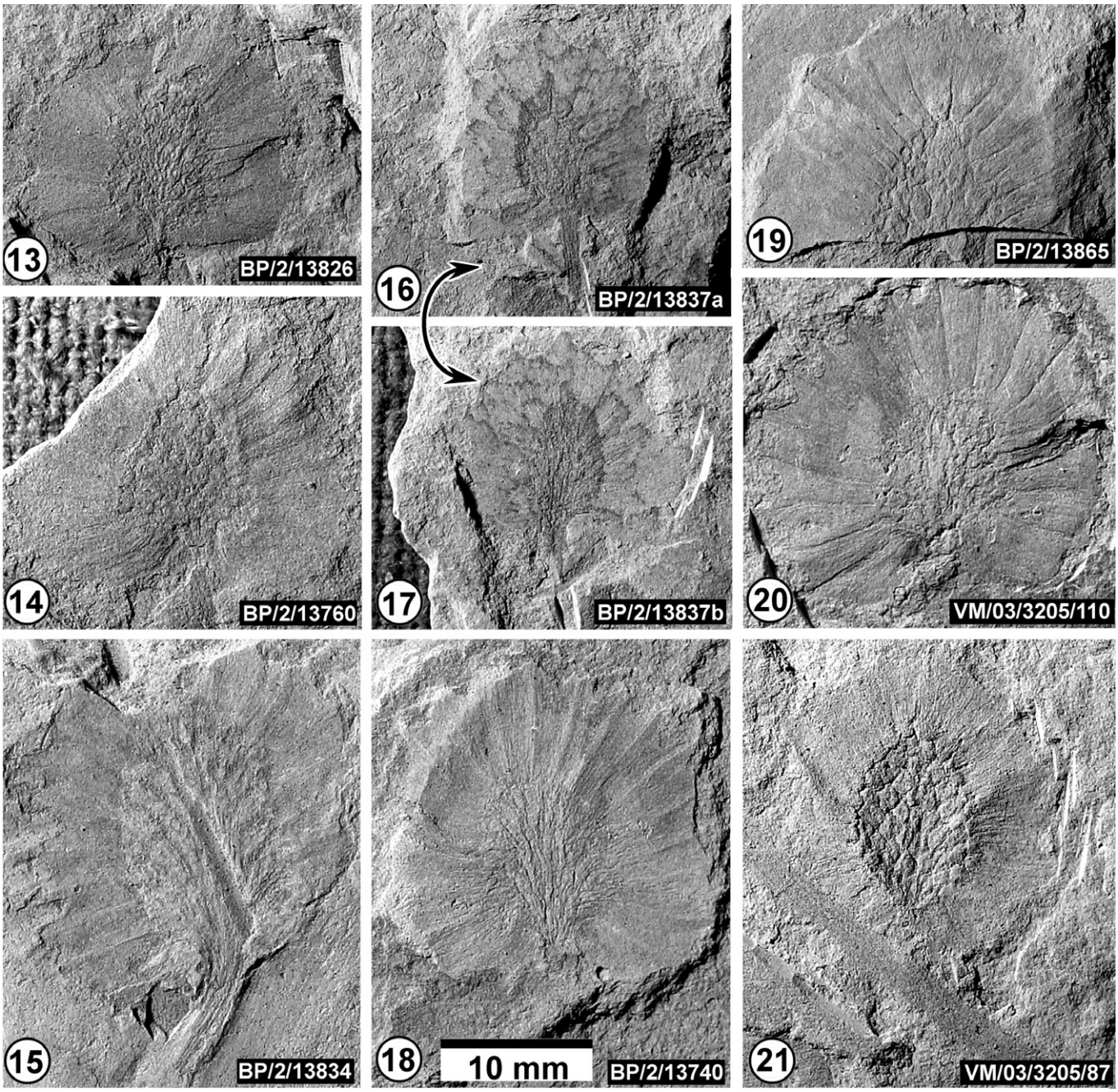
Based on the type collections from Vereeniging, the key diagnostic features of *Scutum* are the presence of a broad wing with well-defined fluting and a margin that may be dentate, pronounced seed scars and a receptacle with a low length:width ratio, i.e. the receptacle is relatively broader and squatter (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.)

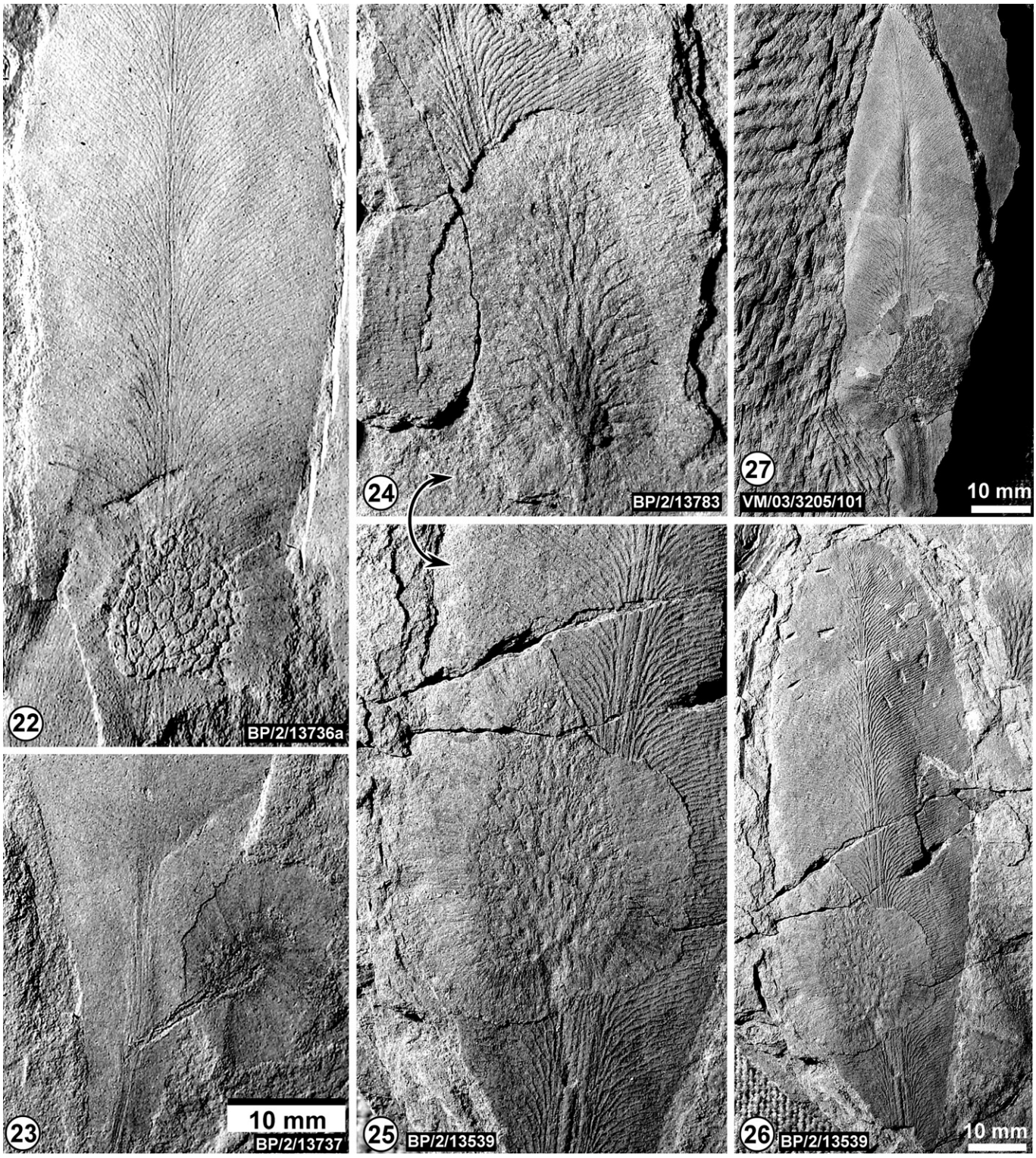


Figures 13–21. Additional examples of *Scutum leslii,* illustrating the smaller end of the spectrum of morphological variation seen in these fructifications. Note the very high wing width to receptacle width ratios in these smaller specimens, particularly in (19) and (20).

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.*

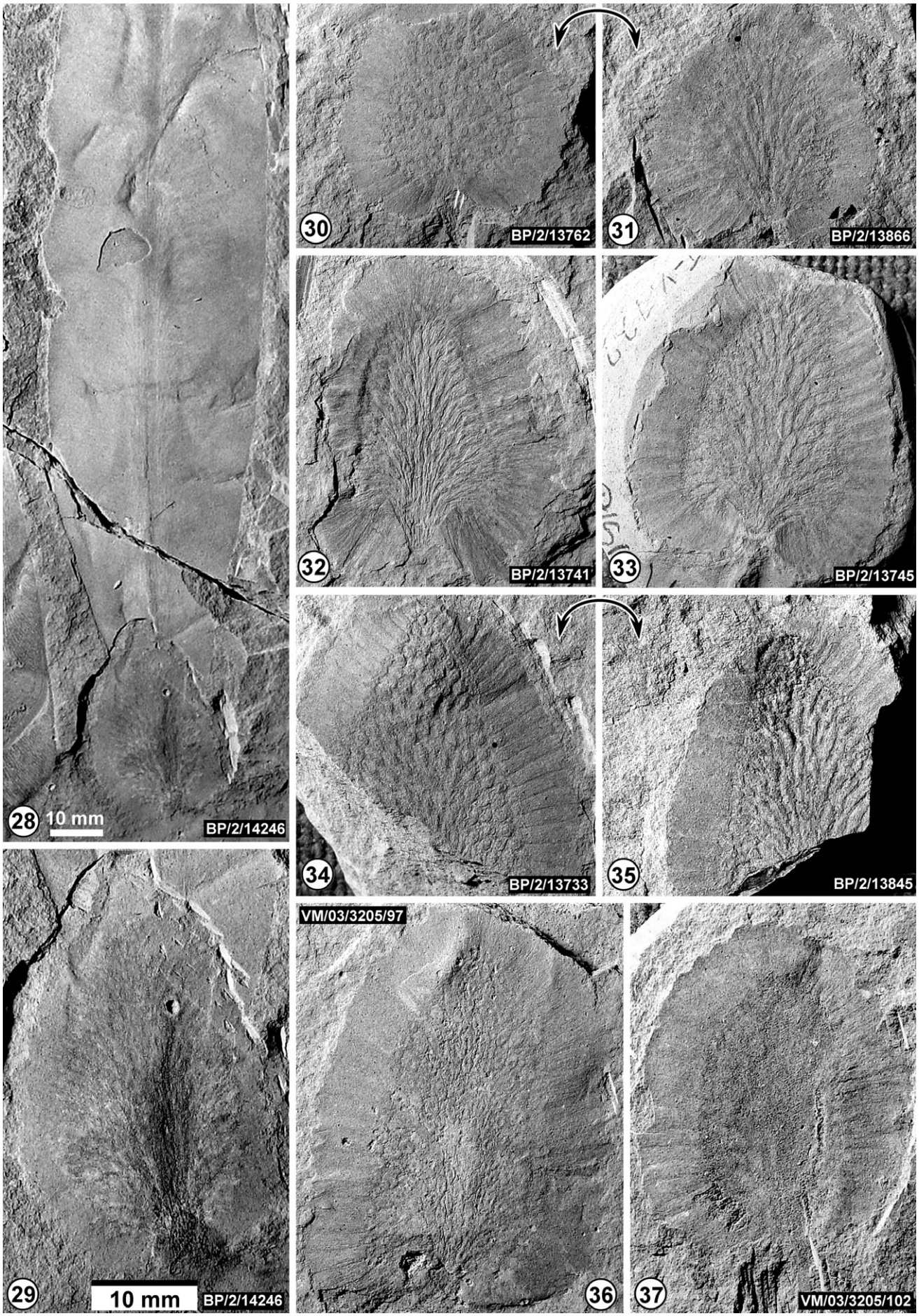
Anderson & Anderson (1985) distinguished *S. ermeloense* and *S. draperium* on the basis of differences in their subtending *Glossopteris* leaves. Unfortunately, the subtending leaf of the Ermelo specimens is unknown, hence Anderson & Anderson (1985) made this distinction on the basis of associated leaf 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



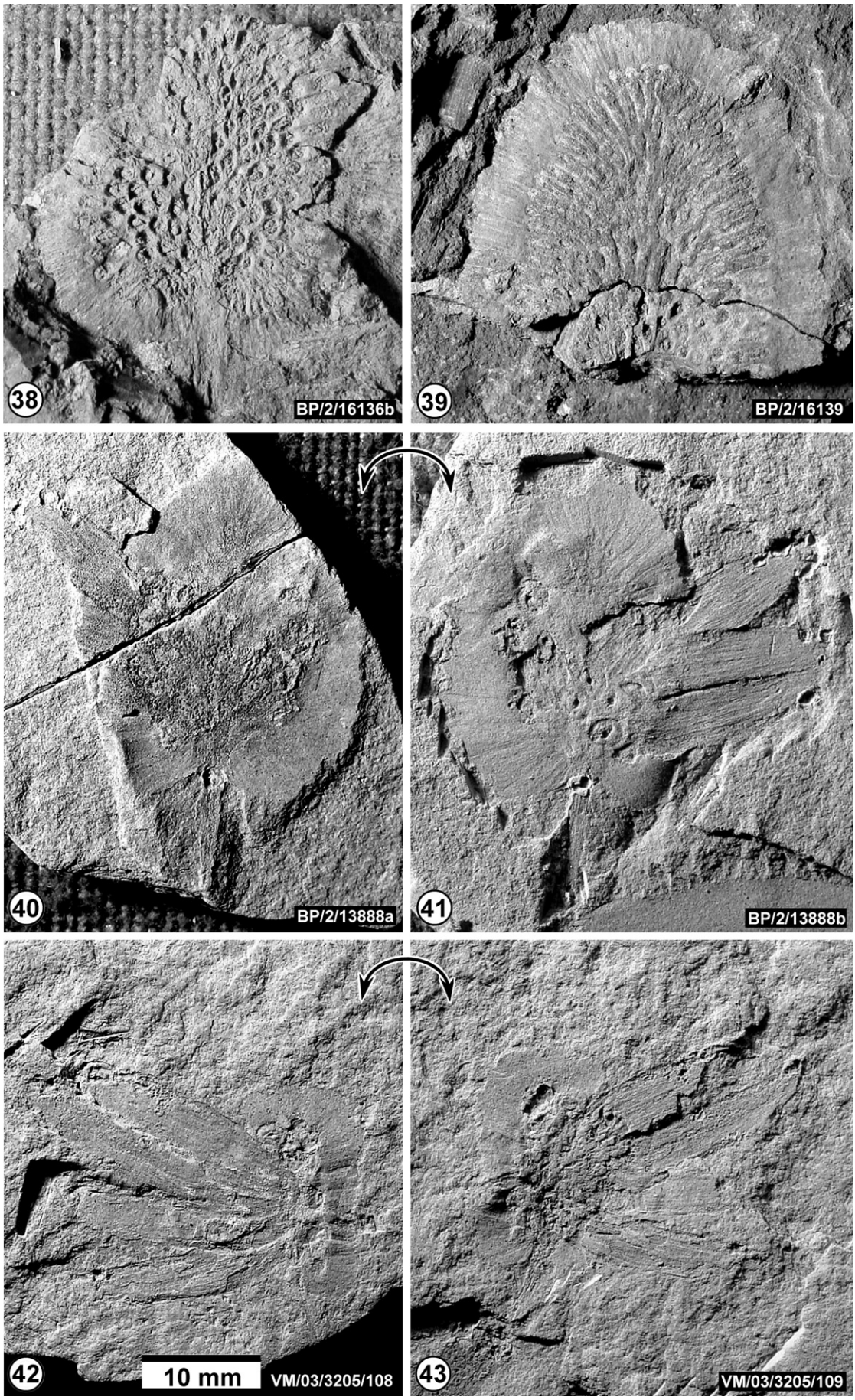
Figures 22–27. *Scutum leslii* fertiligers, illustrating a range in subtending leaf morphology. **24–26,** Plumstead's (1952) syntype for the seed-bearing surface of '*S. rubidgeum*'. Note how the impression of the seed-bearing surface lies above the leaf impression in (25), whereas the impression of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

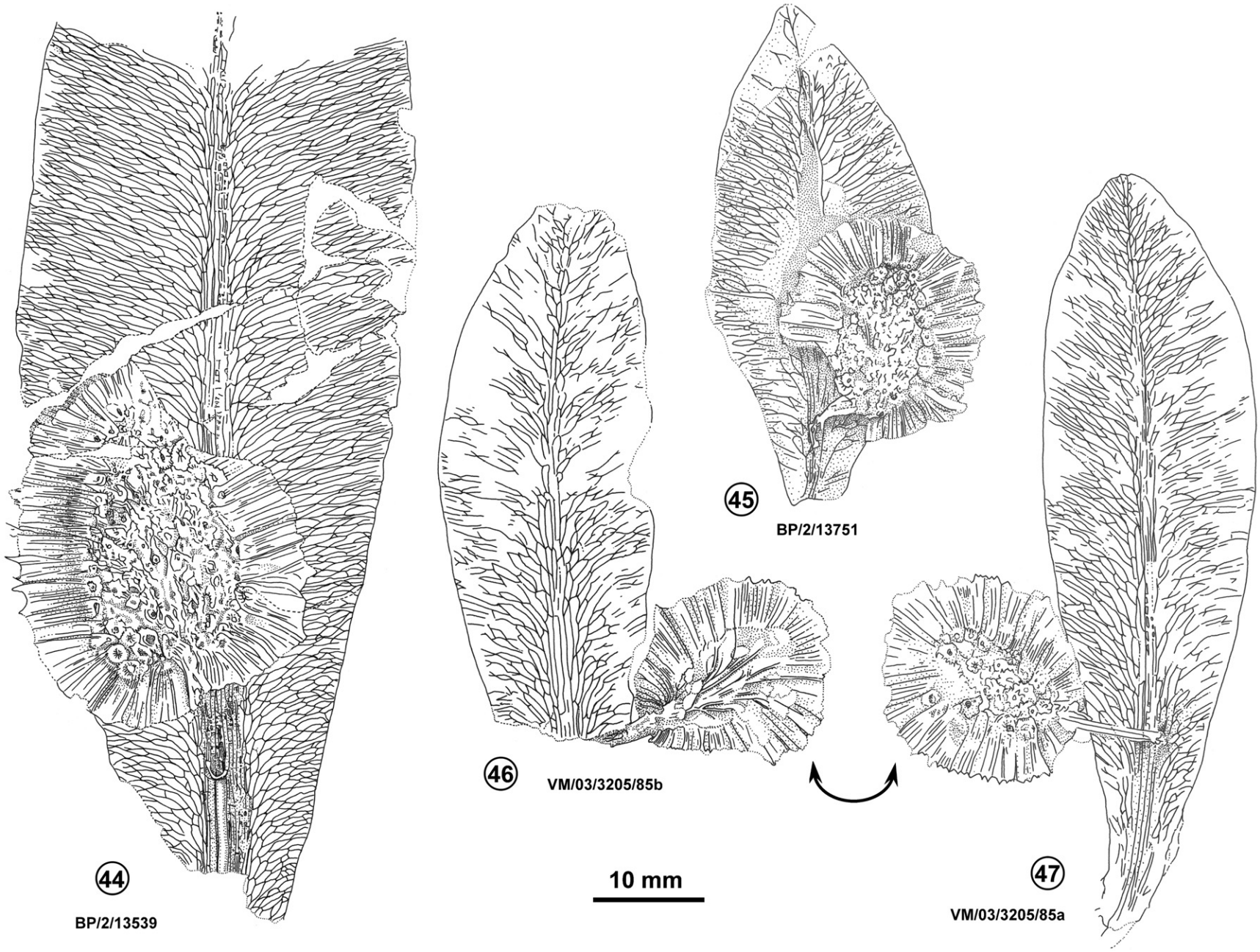
Plots of overall size and receptacle dimensions for the South African *Scutum* specimens showed a typically linear relationship between length and width (Fig. 56). The '*S. draperium*' specimens occupy the upper size ranges of *S. leslii,* although one of the specimens is well nested within the middle 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



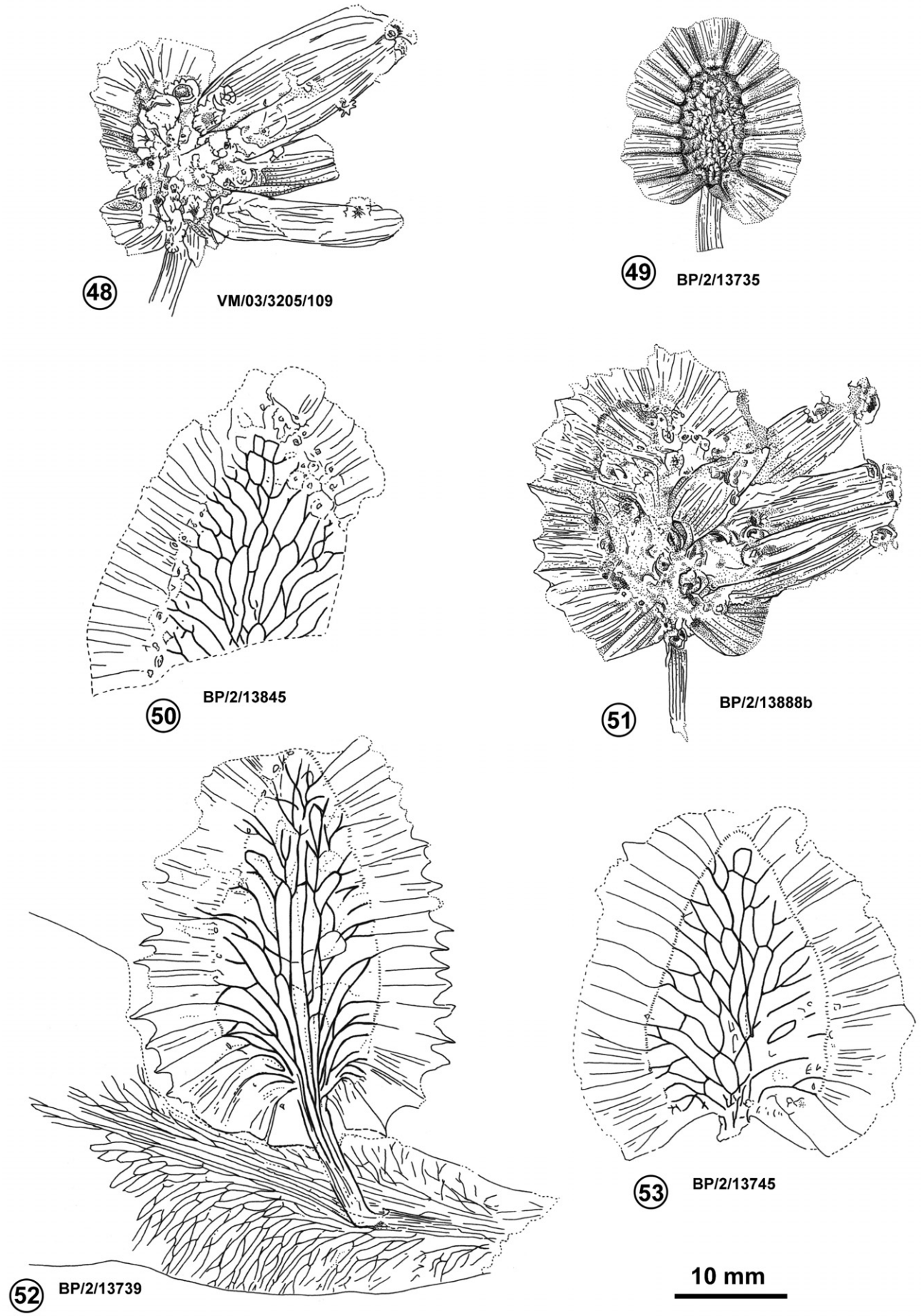
Figures 28–37. Large *Scutum leslii* fructifications. All these specimens are examples of *'S. draperium'* as per Plumstead (1952, 1956a) and/or Anderson & Anderson (1985), except for those in Figs 32, 33 and 37 that were considered to belong to *Scutum rubidgeum*.



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.



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.

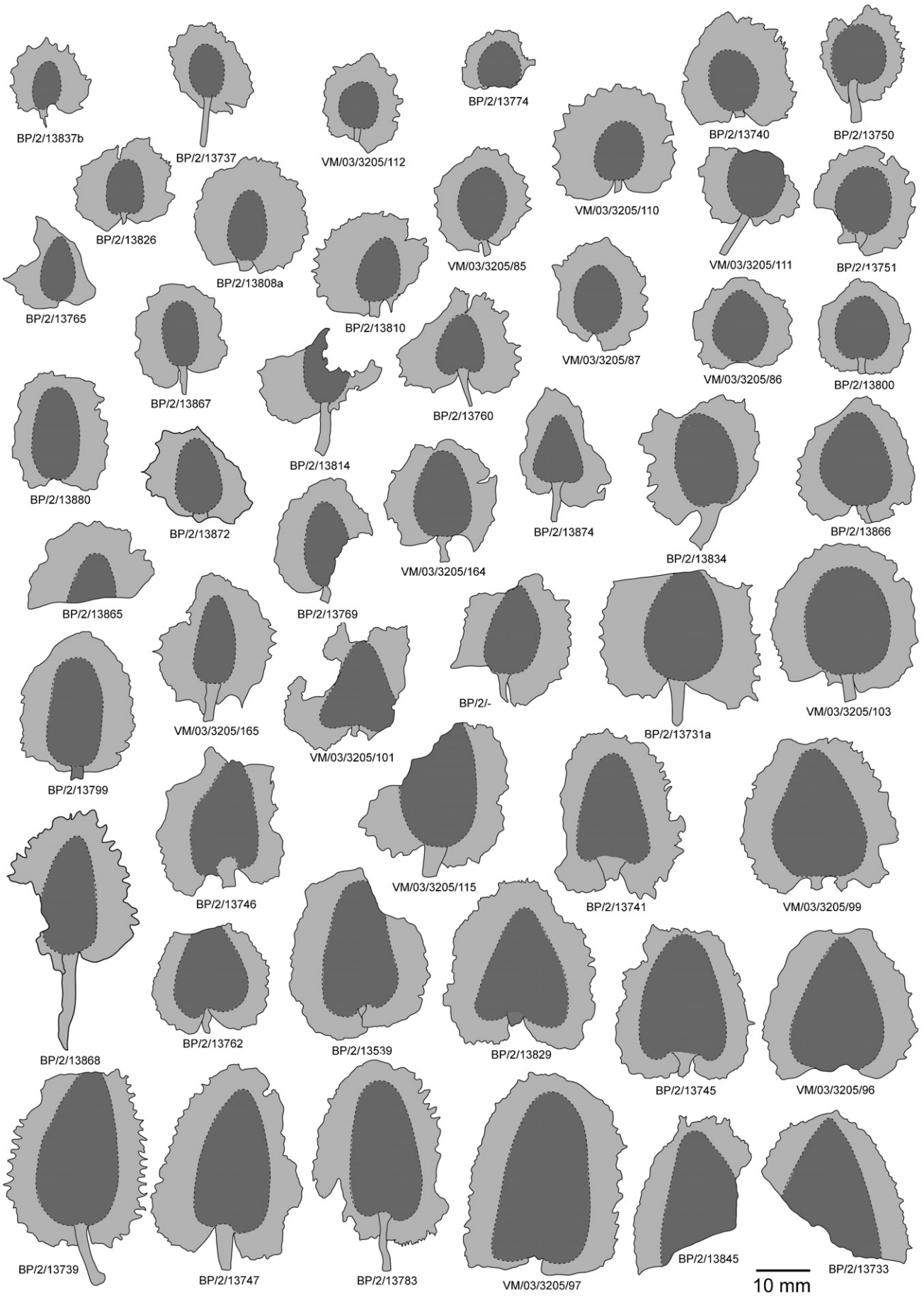


Figure 54. Silhouette drawings of *Scutum* specimens from Vereeniging, illustrating the wide range of intergrading wing and receptacle morphologies. Members of both *S. rubidgeum* and *S. draperium,* as categorized by Anderson & Anderson (1985), have been included (all drawings at approximately life-size).

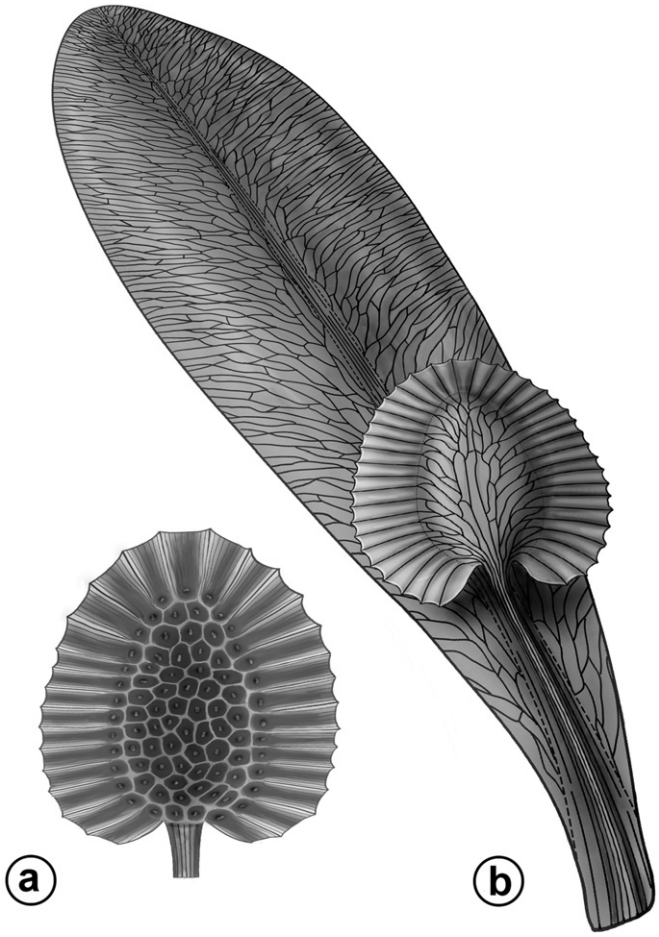


Figure 55. Reconstructions of *Scutum leslii.* **a**, A fructification illustrating the seed-bearing surface; **b**, a fertiliger with fructification attached to the midrib of a *Glossopteris* leaf, the seed-bearing surface facing the adaxial surface of the leaf.

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

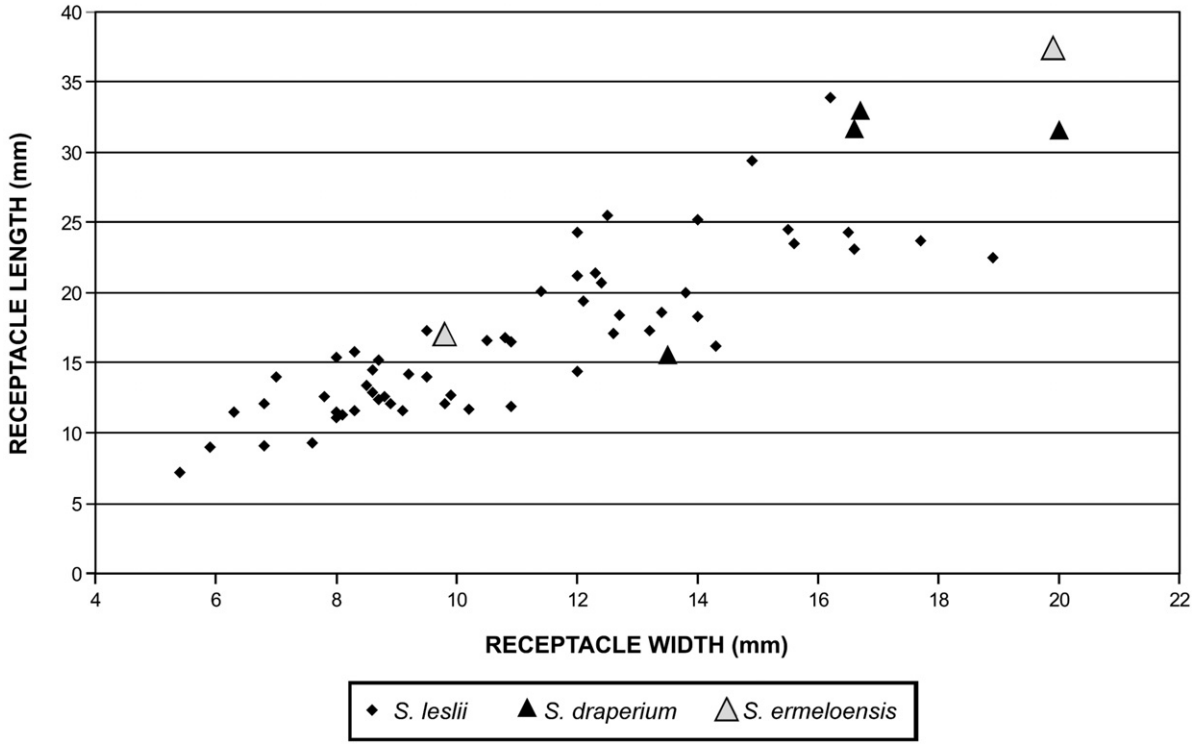


Figure 56. Scatter plot of receptacle lengths against receptacle widths of specimens here assigned to *Scutum leslii,* but including those previously assigned to *S. draperium* and *S. ermeloensis.*

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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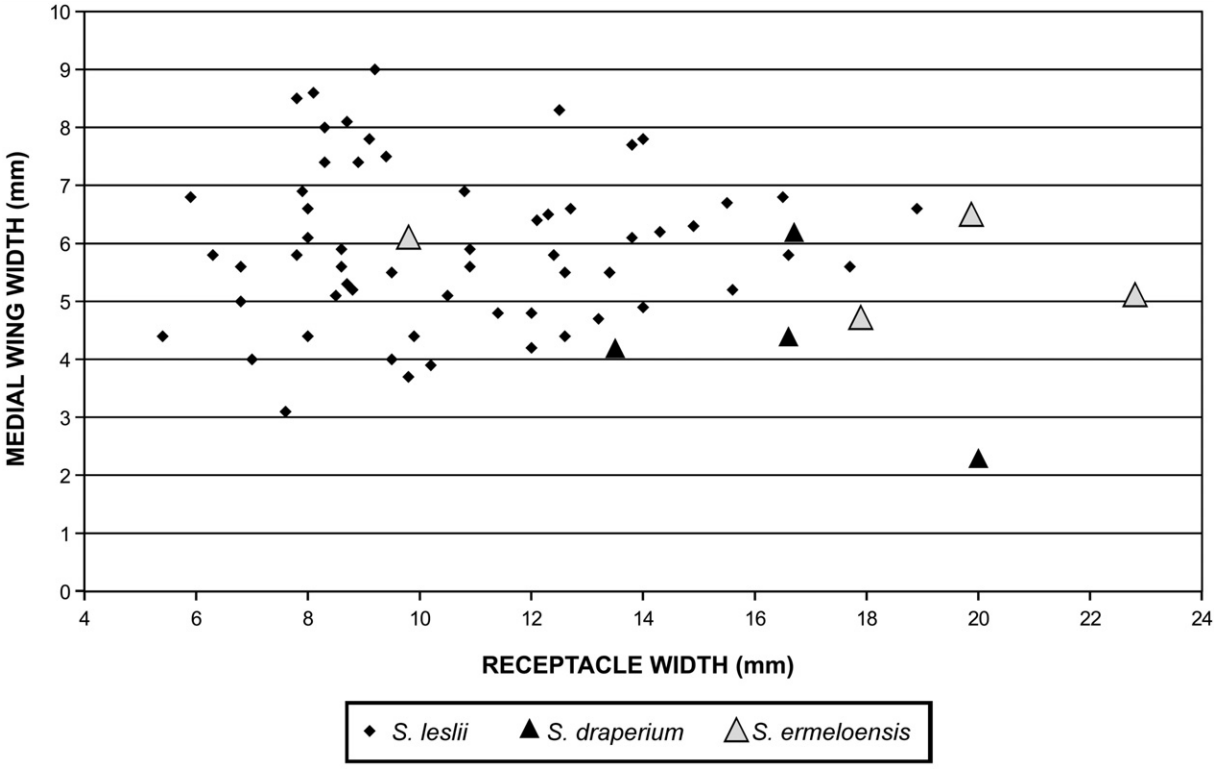

Figure 57. Scatter plot of medial wing widths versus receptacle widths of specimens here assigned to *Scutum leslii,* but including those previously assigned to *S. draperium* and *S. ermeloensis.*

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