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A REVISION OF THE CONIFER *SPHENOLEPIS KURRIANA* (DUNKER) SCHENK FROM THE WEALDEN OF GERMANY AND ENGLAND

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Abstract: The scale-leaved fossil conifer *Sphenolepis kurriana* (Dunker) Schenk is redescribed from the Wealden floras of Germany and England. The revised study of this fossil species encompasses specimens remaining in the nineteenth century Dunker Collection in the Museum für Naturkunde, Berlin, from which a neotype is selected; figured specimens in the Museum of Geology, Georg-August-Universität, Göttingen and the Rufford Collection in the Natural History Museum, London. Dispersed samples more recently collected from debris-beds in the English Wealden show cuticular details of particularly well-preserved leaf-bases and leaves. To date, *Sphenolepis kurriana* (Dunker) Schenk is the only non-cheirolepidiaceous conifer species confirmed as present in both the English and German Wealden floras. In situ cones, identified as female, indicate a taxodiaceous Cupressaceae affinity for *S. kurriana*.

Key words: Lower Cretaceous, Wealden, scale-leaved, fossil conifer, female cones, *Sphenolepis kurriana*, neotype, Berlin

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Introduction

The 20th Century revision of the English Wealden flora by Watson and others was long confronted by the problem of Seward (1894, 1895, 1914, 1919, 1941) having had to base his identifications of English material solely on the type descriptions of German Wealden species (Dunker 1846, Ettingshausen 1852, Schenk 1869, 1871) without access to the type specimens or, probably, any German specimens at all. Since Seward was working before the routine use of cuticle preparations this was not considered to be disadvantageous. However, many years later, when the old German collections were inaccessible, this was a serious impedence to progress. The material in question is now readily available for study and concerted efforts have been made to identify the German type specimens in order to correlate species in the English and German floras, as well as other Early Cretaceous floras. It has been established that many of the German holotypes are no longer to be found in their original collections and are probably lost forever. However, in most such cases it has been possible to select appropriate types from the various localities in the old Dunker Collection. This collection is curated in the Museum für Naturkunde, Berlin, together with the old identification catalogue still available. Other collections in the Museum of Geology, Georg-August-Universität, Göttingen include more than a dozen assorted pteridophytes and gymnosperms figured by Schenk (1871) and Lipps (1923).

The English and German Wealden floras are similar in being dominated by pteridophytes (particularly ferns) and gymnosperms, though with fewer species in common than might be expected. Two equisetalean species occur in both floras (Watson and Batten 1990), both of them known from in situ occurrences. The ferns await a similar level of detailed revision but it is already clear from earlier studies (Seward 1894, Watson 1969), and recent re-examination of the German Wealden collections, that several fern species can easily be identified as occurring in both floras. Revision of several major groups of gymnosperms, notably the Bennettitales (Watson and Sincock 1992), the Cycadales (Watson and Cusack 2005), the Czekanowskiales and Ginkgoales (Watson et al. 2001) have also been completed. The conifers however are much more enigmatic and under-represented in reliable modern literature; the exception being various cheirolepidiaceous species which proved to be easily identifiable (Watson 1977, 1988).

Accurate identification of scale-leaved Wealden fossil conifers remains problematic even in situations where the holotype or other type of a named species is known. In

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addition to problems of typification the scale-leaved conifers present particular taxonomic difficulties, especially in cases where specimens are known only from sterile shoots (often in short lengths) which are morphologically indistinguishable in the hand-specimen. Inevitably, many have been wrongly identified in the past and with such morphologically similar specimens great reliance has to be placed on cuticle characters to segregate species. This brings preservational problems to the fore as many of these conifers are in a state of poor preservation with considerable cleating, in which case the cuticles are notoriously difficult to prepare for microscopy.

All the specimens studied were preserved as compressions or impressions. Pollen grains were found in clumps on the surface of some *S. kurriana* leaves (Pl. 2, Figs 6–9) but male cones are unknown (see discussion below). The study was considerably aided by the availability of copious dispersed material from English Wealden debris-beds from which the cuticle is easily retrieved in bulk and is in a better state of preservation than the old hand specimens in museums.

Large numbers of scale-leaved fossil conifer specimens in the German collections have been sampled and have revealed that non-cheirolepidiaceous species diversity is very low; probably not more than six in total. The overwhelming majority of the specimens are those of *Sphenolepis kurriana* (Dunker) Schenk, which has also been identified in the English Wealden flora, where it is by no means common. This revision establishes *S. kurriana* as the only non-cheirolepidiaceous Wealden fossil-conifer so far known from both the English and German Wealden floras.

Methods

The illustrations presented here have been accumulated over a period of 40 years involving a wide variety of both standard and experimental palaeobotanical techniques, mechanical, chemical and photographic. The equipment used included a considerable number of cameras (film and digital), light microscopes (stereo and compound) and scanning electron microscopes.

The hand specimens were photographed when possible by immersion in paraffin (kerosene), a technique producing superior contrast. An alternative technique using crossed polars (Polaroid sheet) was also employed when necessary. Pl. 9, Fig. 9 shows a specimen in paraffin, whereas Pl. 9, Figs 10, 11 are under crossed polars. The former almost always produces better contrast. However, with material where a black fossil plant is preserved in a black matrix neither technique is viable; see the Appendix for two examples of Schenk's figured cones we were unable to photograph.

Our mechanical and chemical techniques have been described in considerable detail by Watson and Sincock (1992: 9–11) and Watson and Cusack (2005: 5–7).

Systematic palaeobotany

The conifer family Taxodiaceae Saporta becoming part of the family Cupressaceae Gray was postulated a considerable time ago (Eckenwalder 1976) followed by general acceptance based on molecular phylogenetics and other evidence. However, Page (1990) recognised the uncomfortable disappearance of the traditional family Taxodiaceae and continued with a conservative classification; see Page's key (1990: 283) quoted below. Miller and Hickey (2010) noted that most authors had accepted the Taxodiaceae as part of the Cupressaceae based on phylogenetic sequences (Kusumi et al. 2000, Gadek et al. 2000) but they retained the "Taxodiaceae against Cupressaceae sensu lato because of several morphological characters unlikely to represent reversals and because the family contains crown taxa that are radiating in their own directions". Taylor et al. (2009) adopted the use of subfamilies in discussing fossil Cupressaceae, including the Taxodioideae, which seems an acceptable compromise for use here. Farjon (2005, 2008), has pointed out how slow some palaeobotanists have been to accept the disappearance of the Taxodiaceae; not surprising given the nature of the fossil record. Palaeobotanists are often microscopists whose stock-in-trade is grappling to extract the meanest information from minute scraps of cuticle extracted from short lengths of sterile shoots. The end result for the diagnosis and description of a Mesozoic gymnosperm is often a so-called morphotaxon without relevance to the niceties of phylogenetics. This opportunity to confirm *Sphenolepis kurriana* in the 'Taxodiaceae' is a rarity helped by the simplicity and familiarity of Page's (1990) key as follows:

Leaves evergreen or deciduous, mostly spirally arranged, spreading or if reduced, usually awl-like and rarely highly scale-like or appressed; shoot frequently with annual growth increments; female cones of a few to many oppositely or (usually) spirally arranged scales with or without distinct bracts or cone scales and bracts fused when mature.

Retaining the species within the genus *Sphenolepis* Schenk is clearly indicated but the two most recent generic diagnoses (Harris 1953, Miller and Hickey 2010) are very different and neither is a precise fit for the two named Wealden species of *Sphenolepis*.

The Harris diagnosis is based on prolific Belgian Wealden material preserved as uncompressed charcoal, showing exquisite anatomical details of branching twigs and leafy shoots together with many intact female cones and numerous seeds. The epidermis is ill-preserved however and the leaf cuticle is sketchily illustrated, though he includes stomatal distribution as a generic character. Unusually for Harris his diagnosis is excessively restrictive, particularly for attribution of compression material lacking any anatomical information, such as is described here. Curiously, whilst extending the generic diagnosis to include leafy shoots with attached female cones he is quite dismissive of the two German Wealden species on which he bases his generic emendment (the type species *Sphenolepis kurriana* (Dunker) Schenk and *Sphenolepis sternbergiana* (Dunker) Schenk). He appears neither to have considered how his diagnosis could be used in revising them, nor whether the Belgian Wealden material is actually *S. kurriana.*

The more recently emended diagnosis of Miller and Hickey (2010) is based on early Cretaceous specimens in the Winthrop Flora from Washington State, USA in which the cuticle has been totally destroyed by tectonic heating and the entire study relies on macromorphology alone. However, the resulting restricted diagnosis renders it similar to Page's key above and this approach is much less problematic in affording a comfortable fit for *S. kurriana*, and similar species. Apart

from gross morphology, our evidence draws heavily on cuticle features with no anatomical evidence at all. We thus present an emended diagnosis embracing the morphological features common to the three sources above (Harris 1953, Page 1990, Miller and Hickey 2010) omitting anatomical and epidermal features as characters for specific diagnosis. This will definitely accommodate *Sphenolepis sternbergiana* (Dunker) Schenk (Pott et al. 2014, Fisher and Watson, in prep.) and probably many of the specimens which have been tentatively attributed to *S. kurriana* in floras worldwide.

Order Pinales Dumort., 1829 ('Coniferales') Family Cupressaceae Gray, 1822 nom. cons. Subfamily Taxodioideae Endl. ex K.Koch, 1873

Genus *Sphenolepis* Schenk, 1871

1871 *Sphenolepis* Schenk, p. 243.
1881 *Sphenolepidium* Heer, p. 196.
1895 *Sphenolepidium* Heer; Seward, p. 199.
1953 *Sphenolepis* Schenk; Harris, p. 1.
2010 *Sphenolepis* Schenk; Miller and Hickey, p. 51.
2014 *Sphenolepis* Schenk; Pott et al., p. 96. [discussion of Harris's diagnosis]

Type species. *Thuites kurrianus* Dunker, 1846, p. 20.

Emended diagnosis. Branched shoots bearing spirally arranged leaves; each free leaf arising from a well-developed leaf-base cushion, contracting gradually from the basal cushion to an acute apex. Leaves wth median keel, more or less spreading; awl-like if reduced; more rarely short, scale-like, flattened and adpressed. Female cones arranged in a cluster, each cone borne terminally on short peduncle; cones small, globose; cone scales numerous, spirally arranged, deltoid with blunt, obtuse apex, persistent when mature.

Discussion. The name *Sphenolepis* Schenk was changed to *Sphenolepidium* by Heer (1881) because of an earlier use of *Sphenolepis* by Agassiz for a fish genus. The present rule of Botanical Nomenclature upholds the name *Sphenolepis*, ignoring its use in the animal kingdom (Turland et al. 2018).

The genus *Sphenolepis* originally referred essentially to a type of female cone but Harris (1953) extended the usage to include the whole plant where attribution is clear. Cuticular details of the type species of this genus are presented here for the first time by light, and scanning electron, microscopy. Harris (1953) noted that the female cones of *Sphenolepis* preclude it belonging to any other existing conifer family than the Taxodiaceae and there are no other possible affinities. The cones, in a cluster on short peduncles, are similar to those seen in *Sequoia sempervirens* though the fossil ones are the smallest known.

Sphenolepis kurriana (Dunker) Schenk, 1871
Pls 1–5

?1839 *Muscites imbricatus* A.Roem., p. 9, pl. 17, fig. 1c, d.
1846 *Thuites* (*Cupressites*) *kurrianus* Dunker, p. 20, pl. 7, fig. 8.
?1846 *Thuites germari* Dunker, p. 19, pl. 9, fig. 10.
1871 *Sphenolepis kurriana* (Dunker) Schenk, p. 243, pl. 37, figs 5–8, pl. 38, fig. 1.
1881 *Sphenolepidium kurrianum* (Dunker) Heer, p. 19, pl. 12, fig. 11, pl. 13, figs lb, 8b, pl. 18, figs 1–8.
?1936 *Sphenolepidium kurrianum* f. *typicum* R.Michael (nom. inval.), p. 56. [cuticle unknown; identity not confirmed]
?1953 *Sphenolepis kurriana* (Dunker) Schenk; Harris, p. 6, figs 1–3, pls 1–3.
1976 32 TAXOD Sp A.; Oldham, p. 464, pl. 78, figs 1–3. [code number used in place of Linnaean name for English material]

Neotype. Specimen 1980/329 figured by Schenk (1871: pl. 38, fig. 1) is from Deister and is here designated as the neotype (Pl. 1, Figs 1–4). The slab bearing this shoot with female cones is housed in the Museum für Naturkunde, Berlin.

Plant Fossil Names Registry Number. PFN003379 for neotype.

Locality of neotype. Deister, Lower Saxony, Germany.

Stratigraphic Time Range. Berriasian – Valanginian.

Emended diagnosis. [Main stem unknown]. Twigs sparsely branched, branches borne irregularly at 50°–70°, branches 1.5–3 mm wide. Leaves in a simple helix, parasitichies 2 + 3 on larger branches, reduced to 1 + 2 on smallest twigs. Leaves scale-like, adpressed or slightly spreading, arising as a continuation of the rhomboidal leaf-base cushion; leaf and basal cushion combined 1 mm × 1 mm on smallest shoots, longer and wider on larger shoots; free part of leaf up to one-third of total length. Leaf margins entire, converging towards bluntly-pointed or awl-shaped apex, leaf biconvex in section with median keel on abaxial surface of cushion and leaf.

Cuticle thin on all surfaces. Stomata occurring on both surfaces. Abaxial stomata confined to two patches just below free leaf, each midway between keel and margins, stomata within a patch crowded. Stomata on adaxial surface forming a single band on each side of the leaf, converging towards apex. Stomatal apparatus circular, guard cells deeply sunken below ring of 5–8 subsidiary cells with inner anticlinal walls forming an oval stomatal pit. Stomatal apparatus monocyclic; subsidiary cells of adjacent abaxial stomata frequently shared; stomatal orientation irregular. Ordinary epidermal cells within stomatal areas irregular in shape and arrangement; anticlinal walls straight and deeply cutinised. Ordinary epidermal cells of non-stomatal areas on both surfaces varying from isodiametric to rectangular and elongate, with slightly sinuous walls mostly arranged in longitudinal files converging towards leaf apex.

Female cone ovoid to spherical, up to 12.5 mm wide, terminal, borne singly on short lateral branches occurring in a cluster. Cone scales deltoid, arranged in a spiral with blunt, obtusely pointed distal end.

Material. Dunker based *Sphenolepis kurriana* on specimens collected from three Wealden localities; Duingen, Osterwald and Deister. Details of the original locations in the relevant literature, as well as the museum labels with the specimens, are not very specific. The Deister and the Osterwald localities are in adjacent hill ranges in the Hannover region of Lower Saxony, where the specimens were collected from an area composed of

stratified sandstones, siltstones and clays which form part of the stratigraphic sequence known as the German Wealden. These facies are now named the Bückeberg Formation (Elstner and Mutterlose 1996). More recently, Pott et al. (2014) described fossil plants newly collected from German Wealden localities, presented updated stratigraphical terminology and also more precisely indicated the localities of Dunker and Schenk.

The English hand-specimens, now in various museums, were collected by Rufford, a Victorian professional collector (Watson and Sincock 1992: 8) at Ecclesbourne Glen near Hastings, from the Fairlight Clay facies. As the earliest member of the Hastings Beds (late Berriasian) these strata are thought to be contemporaneous with the Osterwald Member of the Bückeburg Formation (P. Allen, D. J. Batten pers. comm.; see Watson and Sincock 1992: 4). The dispersed English material of *S. kurriana* was found in coaly lenses which occur throughout the Wealden succession in Sussex, Dorset and the Isle of Wight.

The chosen neotype is a fertile specimen from Deister with a little cuticle remaining which is identifiable but not suitable for illustration purposes. This is also the case for a single English hand-specimen (Pl. 3, Fig.1). The diagnosis and descripton are more or less based on hand specimens from Germany in conjunction with dispersed material from Hastings and the Isle of Wight (Oldham 1976, Fisher 1981). Although many specimens yielded cuticle sufficient to verify the identity of the species it was not of a quality fit to publish. The most exquisite microscopic details are seen in the short lengths of shoot isolated on both sides of a small block from Osterwald (Pl. 4, Fig. 1; Spec. No. 1984/573). These shoots are unique, amongst all those available to us, in being 3-dimensionally embedded in the rock. For this reason, in most cases, the plates represent the cuticle of the best specimens rather than the more important figured specimens.

In view of Dunker's figured specimens being lost, it seems worth pointing out that many of the Dunker and Schenk lithographs, not unusually, have the specimens figured within a fictitious representation of a neat square or rectangle of rock matrix. This can be seen in Pl. 1, Fig. 3 reproduced from Schenk (1871: pl. 38, fig. 1) compared to the actual considerably larger block in Pl. 1, Fig. 1. It is not impossible that some of the original types remain unrecognised in the various collections because of this misleading feature, although the collection has been reassessed many times by curators.

Specimen details. Details of localities, museum collections, registration numbers and figures are listed in the Appendix below.

Description. *Sphenolepis kurriana* (Dunker) Schenk is well-known from Germany where it is one of the most common named species found as hand specimens in the museum collections. They vary enormously in quality of preservation. In England there are hand specimens collected by Rufford in various museum collections (e.g., London, Manchester, Hastings, Cambridge, Brighton, Sheffield) but almost all of them have failed to yield satisfactory, identifiable cuticle. Specimen V.2303a (Pl. 3, Figs 1, 2) is the only English hand-specimen confirmed as *S. kurriana* from scraps of cuticle.

Dispersed material from the English Wealden found by Oldham (1973, 1976) was assigned to the genus *Sphenolepis* under a code number. Its cuticle agrees in all respects with the cuticle from German hand specimens. The dispersed leaves with intact leaf-bases, in the coaly plant-debris lenses (collectable throughout the succession in Sussex, Dorset and the Isle of Wight) give a perfect overview of stomatal distribution and structure with clear details of the various cells in non-stomatal areas (Pl. 3, Figs 3–5). However, even these specimens have problematic outer surfaces unsuitable for illustration.

Leafy shoot specimens attributed to *S. kurriana* are somewhat variable in size and appearance. The largest combined leaves and leaf-cushions encountered so far are only 3–4 mm long and about 2 mm wide on specimen P18-4 (Pl. 2, Figs 1, 2) which also has some of the smallest leaves on side shoots. Some shoots display slightly spreading falcate leaves with a long, acute leaf tip, as originally figured by Dunker (1846: pl. 7, fig. 8) and later by Schenk (1871: pl. 38, fig. 1). The original Schenk figure is reproduced here (Pl. 1, Figs 3, 4) and refigured in Pl. 1, Figs 1, 2. The leaves are certainly no longer seen all over the shoot, as depicted in Schenk's figure, the specimen surface now being quite blurred and fragile. There might, of course, have been a degree of enhancement of leaf coverage involved in preparing the lithograph, much as the cone-scales can clearly be seen to have imaginary rounded edges. However, some spreading leaves are still visible on the cone shoots in Pl. 1, Fig. 2. This type of shoot is most clearly displayed on the borehole core shown in Pl. 1, Fig. 9. Others have more adpressed leaves with less obvious free tips (Pl. 1, Figs 10, 11), some of them short and blunt. The English specimen V.2303a (Pl. 3, Figs 1, 2) is this intermediate type. Additionally, other shoots have very closely adpressed leaves including the shoot P18-4 figured by Lipps (Pl. 2, Figs 1, 2.; cuticle not confirmed but almost certainly *S. kurriana*). We suspect that this third type of shoot was figured by Dunker as a different species. Certain specimens which Dunker named as a separate species, *Thuites germari*, have closely adpressed leaves giving a straight smooth appearance to the shoots (Dunker 1846: pl. 9, fig. 10). All specimens sampled with this appearance required extended periods of maceration, in excess of three weeks in some instances, but when obtained the cuticle preparation clearly showed them to belong to *S. kurriana.* It seems likely that preservational differences are involved. It should be noted that Schenk (1871: 245) considered *T. germari* merely to be examples of younger twigs of *S. kurriana*.

The unusual distribution of stomata in dense patches at the base of the abaxial surface, as well as the deep pit above the guard cells make this species quite distinctive (Pl. 4, Fig. 4). In some specimens the patches are quite extensive, separated from each other by about fourteen epidermal cell rows (Pl. 3, Fig. 6) whereas in other specimens the abaxial surface is almost devoid of stomata. The stomatal apparatus on both surfaces varies considerably in diameter having been measured within the range 40 μm to 70 μm. The cuticle on both surfaces appears to be uniformly about 2.5 μm thick. When the outside surface of the cuticle is viewed in the SEM it can be seen that the inner anticlinal walls of the subsidiary cells bulge into the stomatal pit, a feature more pronounced in the German than in the English material (Pl. 5, Figs 1, 3). They somewhat resemble the large papillae seen in several

species of the Cheirolepidaceae (first demonstrated by Reymanówna and Watson 1976, Alvin 1977, Watson 1977, 1988). The cuticle of the German specimen in Pl. 4, Fig. 3 shows extensive pitting of the outer surface and the pits can be detected on the inner surface inside the non-stomatal cells in Pl. 5, Figs 2, 5. These pits could be crystal cavities. Such pitting has not been seen in the English dispersed material. The non-stomatal epidermal cells show a lot of variation in shape and size, with measurements varying between 15–50 µm long and 12–30 µm wide.

Schenk (1871) figured several fertile specimens in which female cones are borne in clusters on the ends of short side shoots (Schenk 1871: pl. 37, figs 6, 7, pl. 38, fig. 1). A typical cone scale has a slightly convex lower surface which ends in an obtusely pointed distal end. The upper surface of the scale has a thickened edge which is exposed on the surface of the cone. Presumably, the thickened edge pressed against the under surface of the scales above and sealed the cone. The poorly preserved cuticle is the same thickness as that of the leaves and appears to have identical stomata (not illustrated here). Schenk (1871) also figured single female cones named as *Sphenolepis sternbergiana* (Schenk 1871: pl. 38, figs 10–13) but Michael (1936) thought these were mature, opened female cones of *S. kurriana*. These missing specimens certainly appear very similar to the shoot and cone figured here in Pl. 1, Fig. 5.

Pollen grains are seen on the surface of various samples. In particular, the isolated leafy shoot in Pl. 2, Figs 3–5 has copious pollen grains compressed onto the surface in several places (Pl. 2, Figs 6–9). It seems likely that this is the pollen of *S. kurriana* but, unfortunately, male cones remain unknown and this cannot be confirmed. It has not been possible to isolate grains for study by light microscopy so only views in the SEM are available. The grains are around 15 µm in length and 10 µm wide, ovoid in shape with bluntly rounded polar ends; the exine surface seemingly smooth and lacking any signs of pores or sulci. We have been unable to find anything similar in literature searches and are ill-equipped to offer a well-founded description. Most of the grains are concave, presumably collapsed, with the appearance of an equatorial thickening. However, on the closest inspection we can muster (Pl. 2, Fig. 9) this feature shows a double wall thickness across the middle and we wonder if each 'grain' is actually a desiccated dryad. However, if this is the case the individual grains would then be exceedingly small. Page (1990: 154) gives 19 µm as the smallest taxodiaceous pollen diameter in *Metasequoia*.

Discussion and comparison

Sphenolepis kurriana might have been first described by Römer (1839) as *Muscites imbricatus*. Schenk (1871) noted the resemblance but expressed no decided opinion as he had not seen the type specimen. Furthermore, Dunker also figured and named a similar shoot as *Thuites germari* (Dunker 1846: 19, pl. 9, fig. 10). Both of these look suspiciously like the very small smooth twigs from which we obtained *S. kurriana* cuticle. However, since the specimens in question are unidentified the attribution is unverifiable in both cases and the rule of priority has never been enforced.

None of the four specimens of *S. kurriana* in the old Dunker collection (see Appendix) were figured by him and none are accompanied by written information from which we can deduce their being syntypes or lectotypes. Given the very small size of these shoots and lack of both the diagnostic female cones and stomata led us to conclude that selection of a neotype from amongst the later figured material of Schenk (1871) was the best way forward. The specimen selected and designated above displays all the diagnostic characters of the genus *Sphenolepis* as well as typifying the type species *S. kurriana*.

Lipps (1923) described and illustrated a flora from Hildesheim in which specimens identified as *S. kurriana* were present (Pl. 2, Fig. 1). We have been unable to positively identify this specimen from cuticle characters but its close resemblance to specimens yielding cuticle suggests that it can be assigned to *S. kurriana* with a degree of confidence. We can confirm that it is not assignable to the other named conifers in the German Wealden. This specimen is the largest shoot we have encountered and thus has the largest leaf bases at the base of the central stem, figured here in Pl. 2, Fig. 2. The leaves of all sizes have more or less the same diamond shape with some variability in details of the free leaf and there is no evidence that heterophylly might have been a feature of this conifer.

Michael (1936) studied the Berlin collection and divided specimens into two forms which she named as "*Sphenolepidium kurrianum* forma *typica*" and "*S. kurrianum* forma *sternbergiana*", depending on the openness of the leaves*. The actual specimens studied by Michael are not indentifiable in the Berlin collection. No cuticle was obtained from her specimens designated "*S. kurrianum* f. *typica*". However, cuticle prepared from her "*S. kurrianum* f. *sternbergiana*" proved to have cells which each bear a prominent papilla and we now know that this cuticle is not from *S. kurrianum*.

Sphenolepis sternbergiana (Dunker) Schenk, is one of three other similar conifer species described in the 19th Century from the German Wealden which are also now under reinvestigation (Fisher and Watson, in prep.).

Over many years the species *S. kurriana* has tentatively been identified, by various workers, as present in early Lower Cretaceous floras elsewhere in the world. These include France (Carpentier 1927, 1939), Portugal (Heer 1881), Belgium (Harris 1953), Spain (Dépape and Doubinger 1960), Hungary (Barale et al. 2002), Ukraine (Stanislavsky and Kiselevich 1986), America (Fontaine 1889), Canada (Bell 1956), and China (Dai et al. 2013).

Carpentier (1927, 1939) figured French material which proved to have very different cuticle from *S. kurriana* and the sterile shoot material was described as a new species, *Brachyphyllum carpentieri* H.L.Fisher et J.Watson (Fisher and Watson 1983).

Cuticle described by Harris (1953) from the Belgian Wealden has poorly preserved cuticle from which Harris was able to illustrate only the haziest of cuticular features. It

* Editorial note: The name *Sphenolepidium kurrianum* f. *typicum* R.Michael is not validly published because it contains the type of the species *S. kurrianum*, and superfluously replaces an automatically generated autonym S. *kurrianum* f. *kurrianum*; see Art. 24.3 of the Shenzhen Code (Turland et al. 2018).

shows some agreement with *S. kurriana* but clearly differs in the distribution, form and orientation of the stomata. Although the female cone cuticle which Harris described agrees to some extent with that of *S. kurriana* the bulk of his description is devoted to anatomical characters. No such details are available for the cones of German or English *S. kurriana* which are all in compression or impression form. We consider that the Belgian material is almost certainly not *S. kurriana*.

There is no evidence from cuticle for any of the other material assigned to *S. kurriana* by the authors listed above and it thus seems pointless for us to speculate further on the accuracy or otherwise of these accounts. In effect none of these authors were in a different situation from that facing Seward in 1895. It remains to be seen how many of these identifications can be verified if newly-prepared cuticle preparations could be obtained. It seems likely that many of them will be found to require worldwide re-identification.

Of the many English specimens which Seward (1895) identified in the Rufford Collection (held in the Natural History Museum, London) as *S. kurriana* all but one (Pl. 3, Figs 1, 2) proved to have quite distinct cuticle or did not yield cuticle at all. Several new species were recognised and described by Fisher (1981); none of which have been identified in the German Wealden (Fisher and Watson, in prep.). In total there are about a dozen non-cheirolepidiaceous Wealden conifer species awaiting revision or formal desciption; four from the German flora and the others from the English flora. Most of these will be designated incertae sedis and assigned to the familiar series of artificial conifer genera which are themselves in need of revision.

Conclusion

This revision of *Sphenolepis kurriana* (Dunker) Schenk is the first publication of detailed cuticle characters based on sampling a wide variety of conifer specimens from some of the same German Wealden localities as the material described and figured by Dunker in 1846 and Schenk in 1871, including some of their figured specimens. Clearly, this is just the first example of success in clarifying the the very longstanding inability to identify individual Wealden conifers based on evidence of their distinctive cuticles. We can confirm that *S. kurriana* has proved to be the easiest of the species to typify and *Sphenolepis sternbergiana* (Dunker) Schenk the most difficult. Despite considerable confusion and loss of type material associated with the German collections we can confirm that the holotypes of the species originally described as *Lycopodites curvifolius* Dunker (1846: 20) and *Pachyphyllum crassifolium* Schenk (1871: 240) have been recognised and have yielded distinctive, well-preserved cuticles. Thus all four species can now readily be distingushed and further revisions await publication (Fisher and Watson, in prep.).

Acknowledgements

This contribution is dedicated to the late Cedric Shute, an ever-present, delightful helpmeet during our visits to the BM(NH) in the early days of us studying the exceedingly intractable conifer material under his care.

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Explanations of the plates

PLATE 1

Sphenolepis kurriana (Dunker) Schenk, neotype (Spec. No. 1980/329)

1. Whole specimen showing branched shoot with terminal female cones borne in clusters. ×1.
2. Enlargement of cone cluster, showing some poorly-preserved falcate leaves on twigs and curving cone scales with pointed tips. ×2.5.
3. Lithograph of neotype reproduced from Schenk (1871: pl. 38, fig. 1). Note imaginary shape of rock matrix. ×1.
4. Reproduced lithograph of cone cluster enlarged from Schenk (1871: pl. 38, fig. 1) to match Fig. 2. Female cones with rounded scales loosely illustrated. Note also abundance of leaves compared to actual specimen in Fig. 2. ×2.5.

Sphenolepis kurriana (Dunker) Schenk, additional specimens

5. Female cone on leafy shoot which yielded cuticle for identification. Spec. No. 1981/22; ×5.
6. Female cone figured by Schenk (1871: pl. 38, fig. 12). Spec. No. 1984/328; ×1.
7. Female cone figured by Schenk (1871: pl. 38, fig. 13). Spec. No. 1984/329; ×1.
8. Same female cone as Fig. 6 enlarged to show wide spirally arranged, upward curving scales narrowing to a bluntly pointed apex. Spec. No. 1984/328; ×5.
9. Well-preserved shoots on surface of borehole core showing long free leaves with acutely pointed curving tips. Spec. No. 1984/349a; ×5.
10. Shoots figured by Schenk (1871: pl. 37, fig. 5). Spec. No. P4-20; ×1.
11. Enlargement of shoot at centre of specimen in Fig. 10, showing well preserved, convex, keeled leaves with variable tips. Spec. No. P4-20; ×10.

PLATE 2

Sphenolepis kurriana (Dunker) Schenk

1. Branched leafy shoot figured by Lipps (1923: fig. 33). Largest specimen so far identified as *S. kurriana*. Spec. No. P18-14; ×1.
2. Lowest part of central stem and branches in Fig. 1 enlarged to show largest leaf-base cushions and curving free leaves. Spec. No. P18-14; ×2.5.

3., 4. SEM of both sides of loose shoot with well preserved leaves. Spec. No. 1984/340; ×4.

5. Same shoot, SEM. Top right leaf of this shoot is seen in Pl. 4, Fig. 2; several leaves have patches of pollen grains compressed on the surface. Spec. No. 1984/340; ×15.

Sphenolepis kurriana (Dunker) Schenk, SEM views of pollen grains from clusters on leaves of shoot in Figs 3–5

6., 7. Spec. No. 1984/340; ×1,000.

8. Spec. No. 1984/340; ×1,250.
9. Spec. No. 1984/340; ×2,000.

PLATE 3

Sphenolepis kurriana (Dunker) Schenk

1. Branched shoot from English Wealden. Spec. No. V.2303a; ×1.
2. Part of shoot V.2303a, enlarged to show details of leaf-bases with curving awl-shaped free leaves. Spec. No. V.2303a; ×2.5.
3. Adaxial surface of isolated leaf showing stomatal bands near the leaf margins. English dispersed material. Spec. No. TCBO, 44Ha; LM, ×100.
4. More complete isolated leaf-base and leaf, opened up to show abaxial surface centrally with dark stomatal patch lower right; adaxial surface seen laterally with stomatal bands. Spec. No. TCBO, P55/7; LM, ×50.
5. Montage of almost whole isolated leaf-base and leaf showing adaxial stomatal bands on right and a dark abaxial stomatal patch left. Spec. No. TCBO, P55/5; LM, ×150.
6. Abaxial stomatal patches with rows of elongate epidermal cells between. Spec. No. 1984/573; LM, ×100.
7. Adaxial cuticle with stomatal band from Schenk figured specimen. Spec. No. P4-20; LM, ×200.
8. Non-stomatal abaxial cuticle; orientation probably with leaf apex to right. Part of the Dunker Collection. Spec. No. 1981/24; LM, ×100.

PLATE 4

Sphenolepis kurriana (Dunker) Schenk

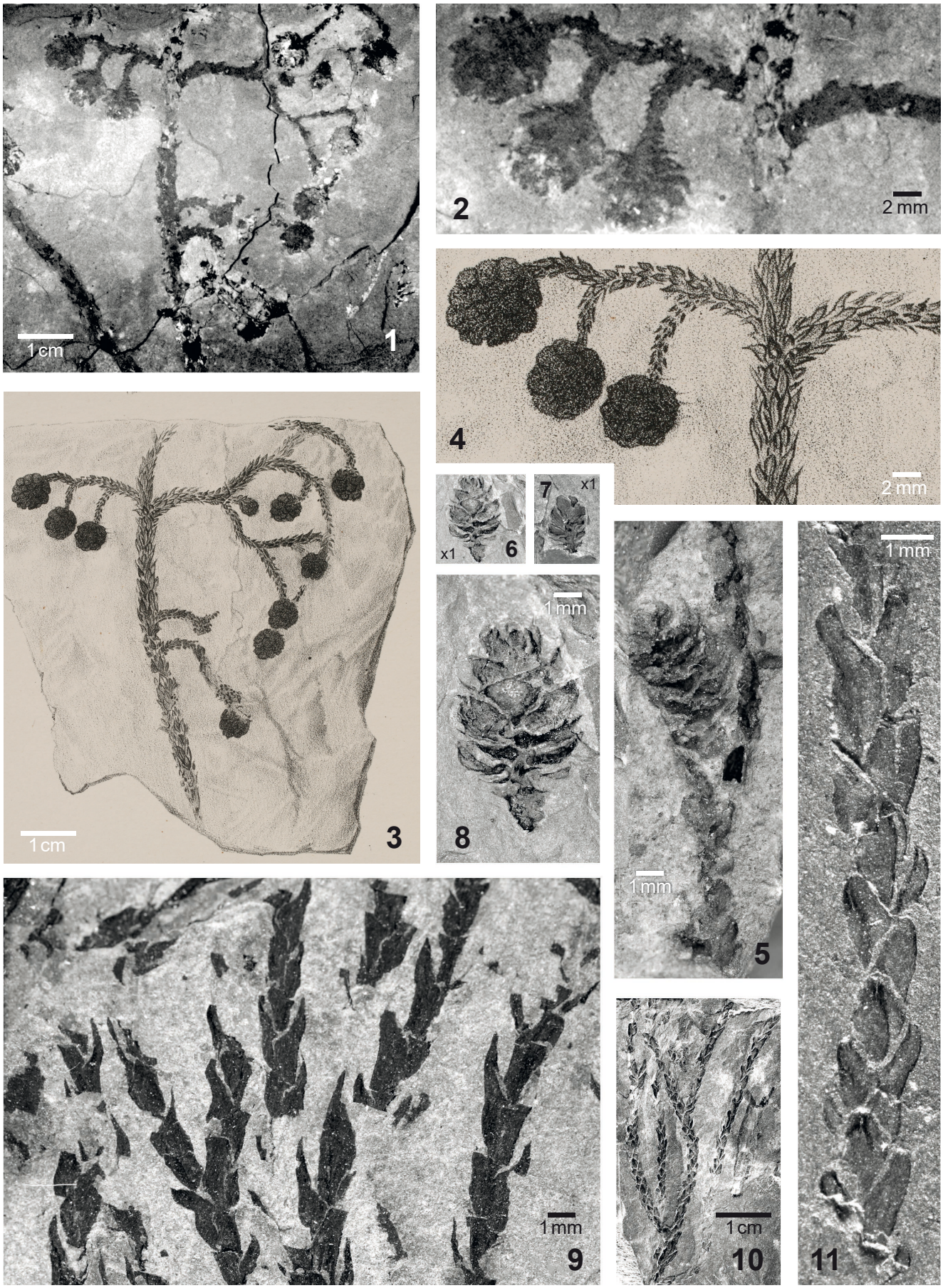
1. Shoots preserved 3-dimensionally which retain best cuticlar details. Spec. No. 1984/573; ×4.
2. Top right leaf in Pl. 2, Fig. 5, showing point at leaf apex, striated surface of ordinary epidermal cells; abaxial stomatal patch indicated by arrow. Spec. No. 1984/340; SEM, ×100.
3. External surface of abaxial stomata fluted rim with bulging subsidiary cell wall below; non-stomatal surface extensively pitted. Spec. No. 1984/573; SEM, ×400.
4. Abaxial internal surface with closely packed, sunken stomata; guard cells missing. Spec. No. 1984/573; SEM, ×400.
5. Internal surface adaxial stomatal band showing intact guard cells. Spec. No. 1984/349a; SEM, ×250.
6. Internal surface adaxial stomatal band showing intact guard cells. Spec. No. TCBO, 44Hb; SEM, ×200.
7. Edge of abaxial stomatal patch with stomata less crowded. Spec. No. 1981/22; LM, ×400.
8. Striated effect of cuticular thickening on surface of abaxial non-stomata cells. Spec. No. 1984/349a; LM, ×400.

PLATE 5

Sphenolepis kurriana (Dunker) Schenk

1. Abaxial external surface with stomatal pit rim showing bulging subsidiary cells below; guard cells missing. Spec. No. 1984/573; SEM, ×1,000.
2. Internal view of abaxial cuticle showing 3 adjacent stomata with deeply cutinised subsidiary cells. Spec. No. 1984/573; SEM, ×1,000.
3. Abaxial stomatal patch showing crowded stomata with subsidiary cells bulging into stomatal pit. Spec. No. 1984/573; LM, ×1,000.
4. Single adaxial stoma with 6 subsidiary cells much less heavily cutinised than abaxial stomata. Spec. No. 1981/324; LM, ×1,000.
5. Ordinary epidermal cells next to abaxial stoma showing variation in shape of cells with slightly sinuous anticlinal walls. Spec. No. 1984/573; SEM, ×600.
6. Left half of bottom edge of a leaf-base cushion marking junction with top of leaf cushion below. Spec. No. P4-20; LM, ×200.

PLATE 1



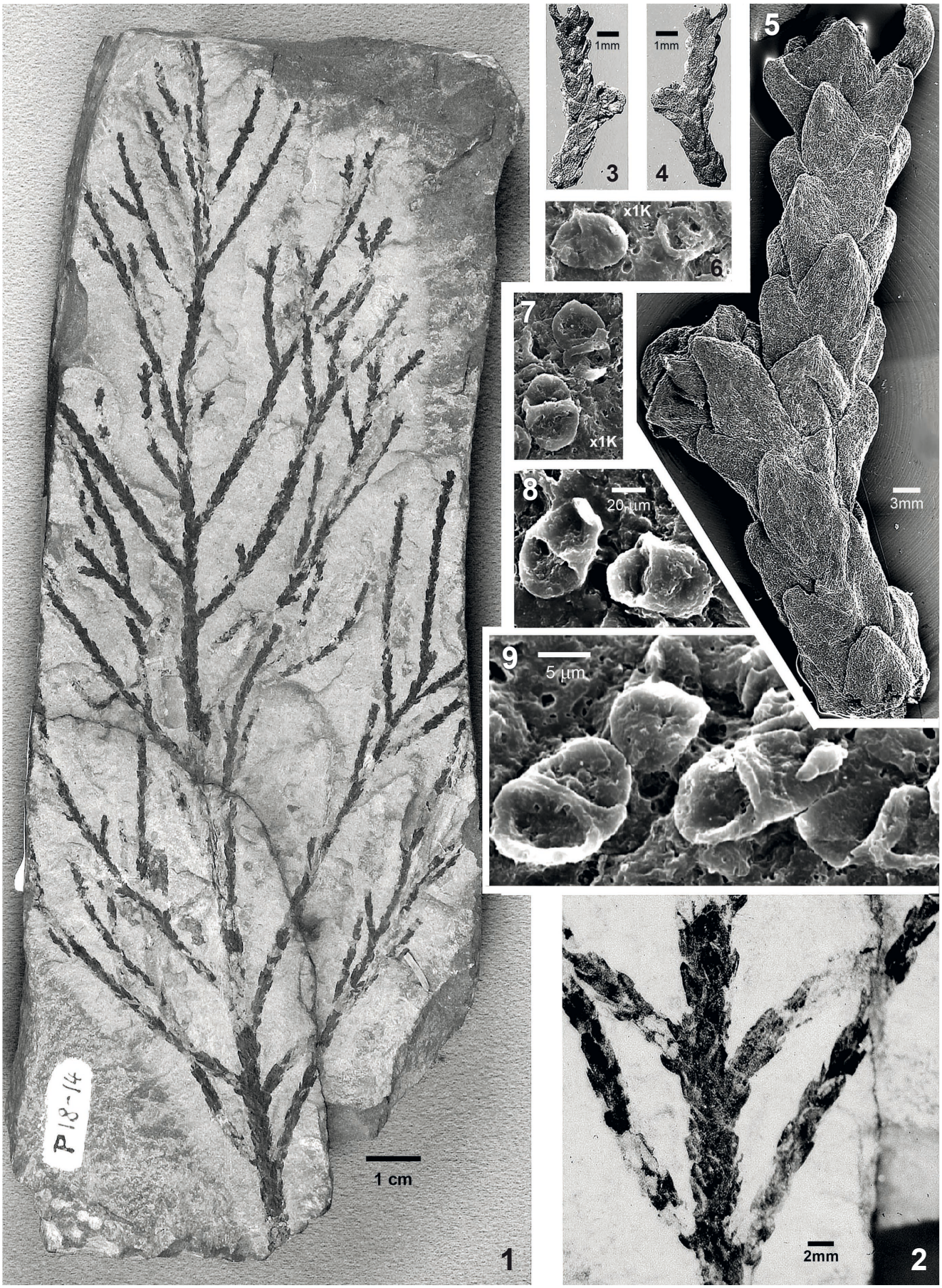

1
P18-14
1 cm
2
2mm
3
1mm
4
1mm
5
3mm
6
x1K
7
x1K
8
20 µm
9
5 µm

PLATE 3

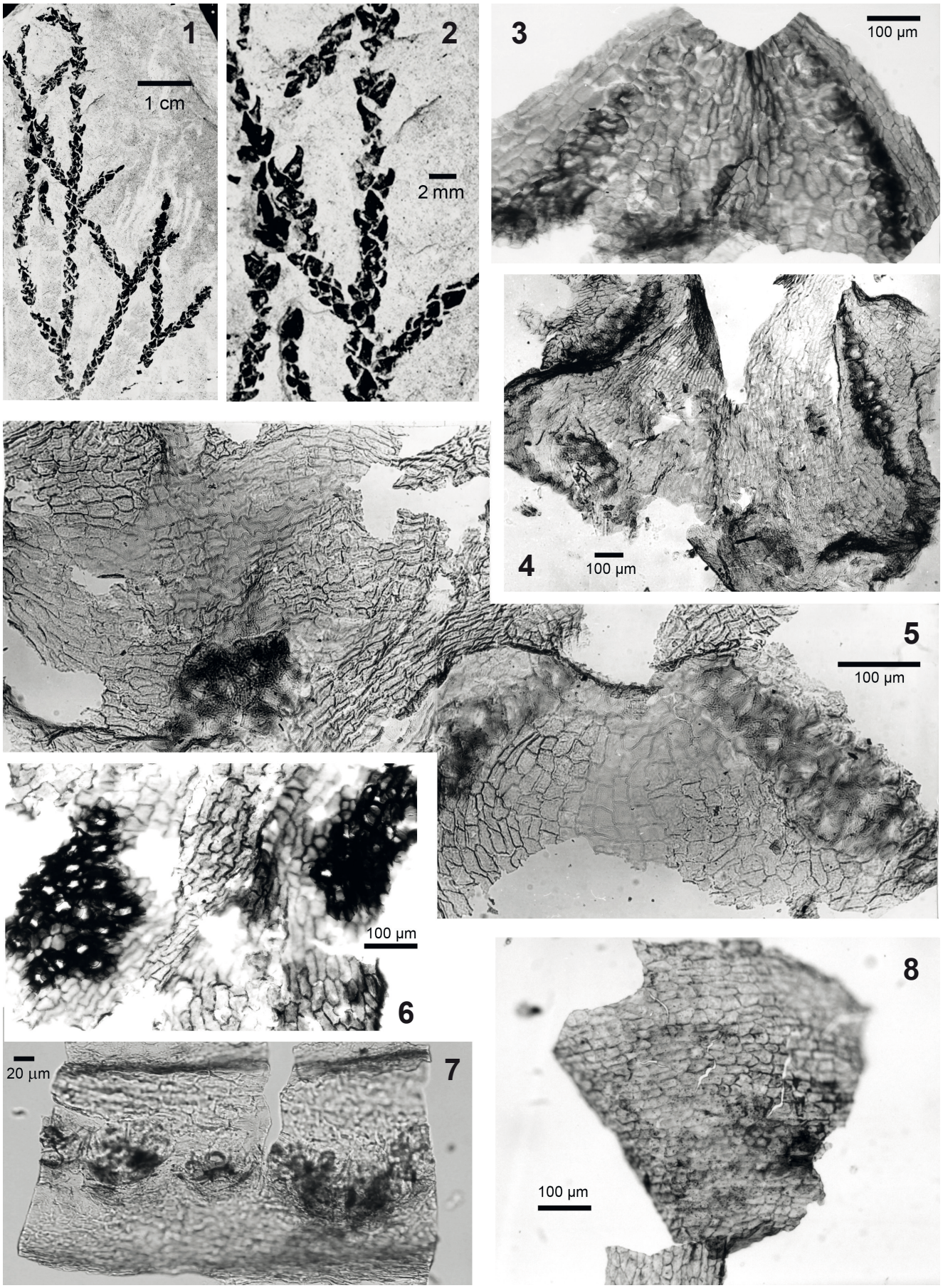


PLATE 4

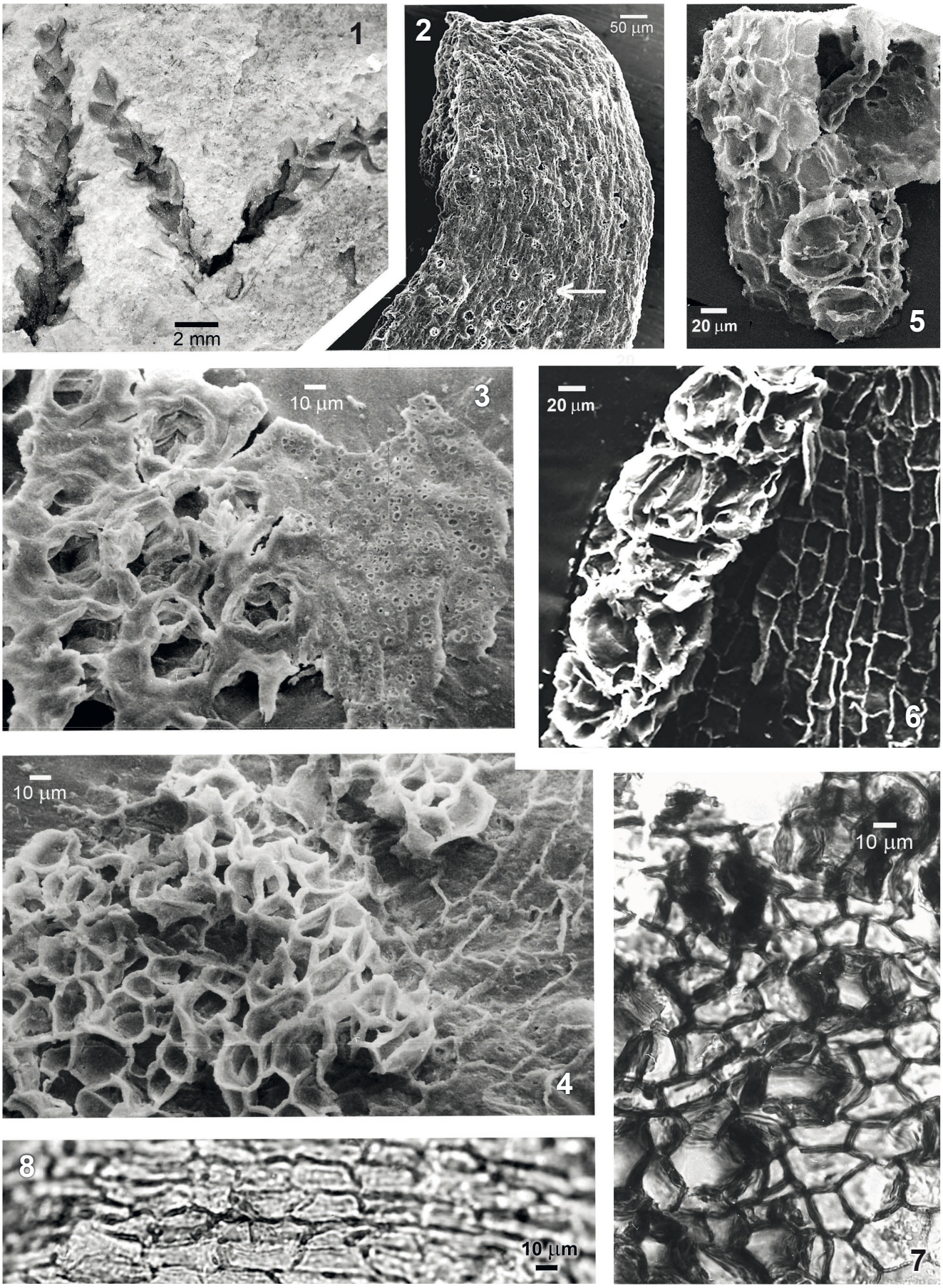
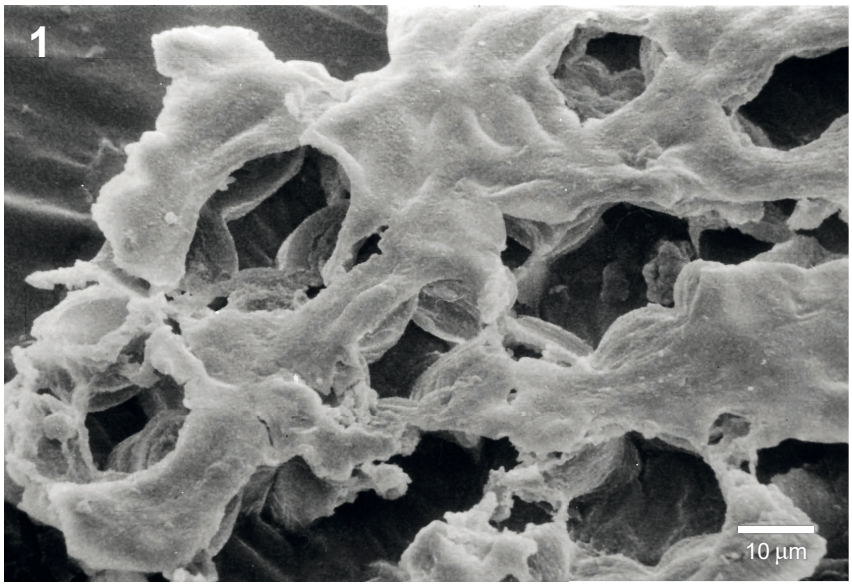
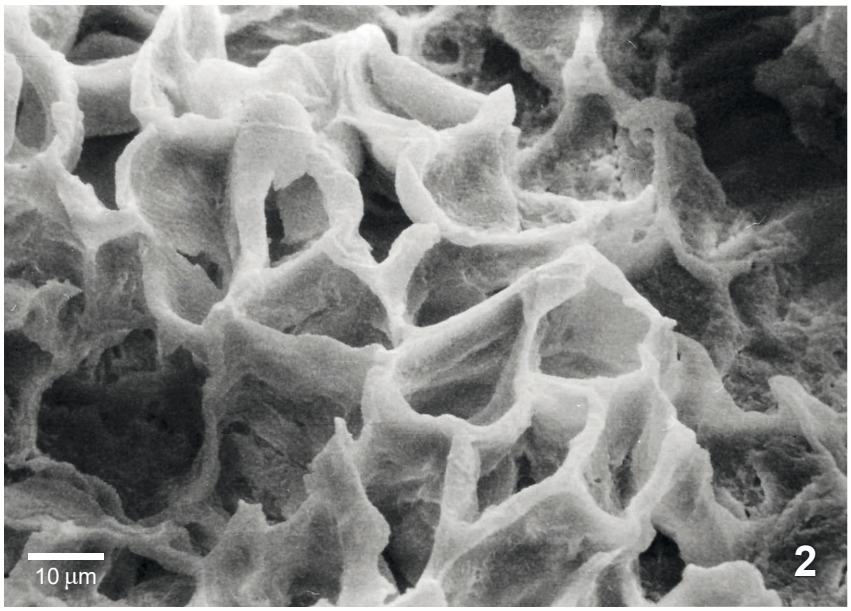
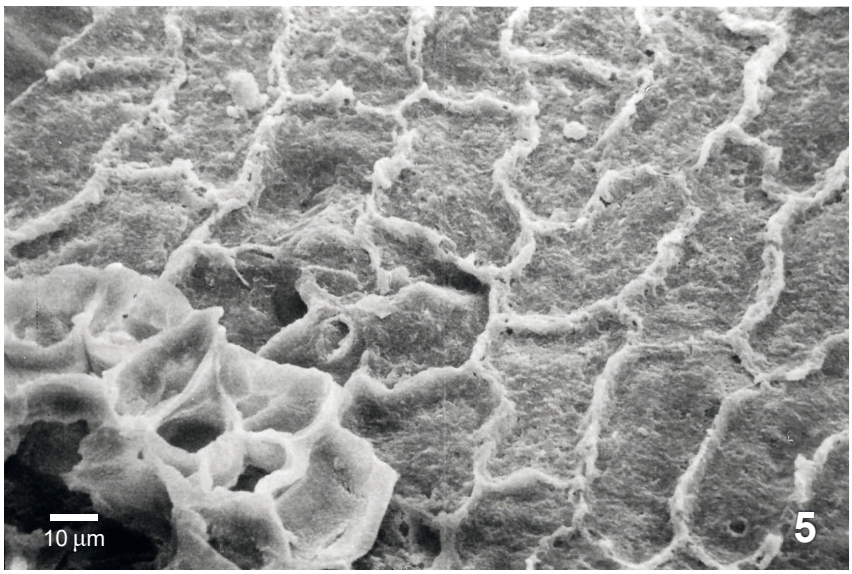
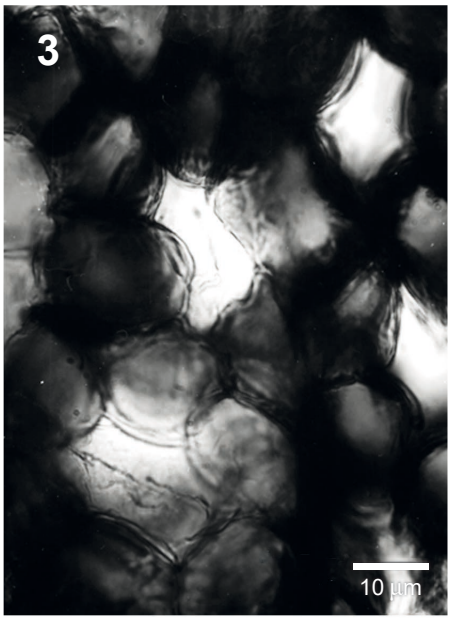


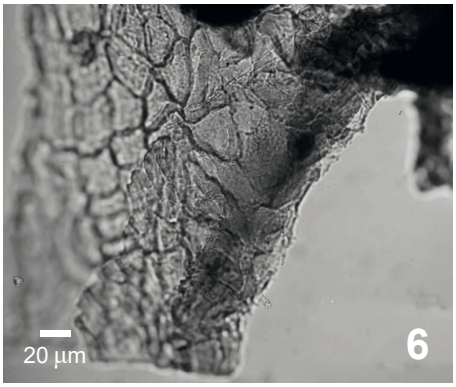
PLATE 5











Appendix

Specimens identified as *Sphenolepis kurriana* with details of localities, registration numbers in museum collections, figures in works of previous authors and in this revision.

Specimen numbers	Museum collections	Previously noted and/or figured	Figured here	Locality	Cuticle	Comments
1980/329	Museum für Naturkunde, Berlin	Schenk 1871: pl. 38, fig. 1	Pl. 1, Figs 1–4	Deister	yes	Selected as neotype.
1981/24	“		Pl. 3, Fig. 8	Deister	yes	Dunker Collection No. 73. 2.5 cm branched sterile shoots, stomata unknown.
1981/324	“		Pl. 5, Fig. 4	Deister	yes	
1984/350	“			Deister	no	
1984/340	“		Pl. 2, Figs 3–9, Pl. 4, Fig. 2	Gröser Süntel	yes	Shoot with pollen on leaves.
1984/385	“			Gröser Süntel	yes	
1981/21	“			Osterwald	yes	
1981/22	“		Pl. 1, Fig. 5, Pl. 4, Fig. 7	Osterwald	yes	
1984/326	“			Osterwald	yes	Gothan & Knopp Collection dated 1933.
1984/328	“	Schenk 1871: pl. 38, fig. 12	Pl. 1, Figs 6, 8	Osterwald	no	Isolated female cone.
1984/329	“	Schenk 1871: pl. 38, fig. 13	Pl. 1, Fig. 7	Osterwald	no	Isolated female cone.
1984/341	“	Schenk 1871: pl. 37, fig. 6		Osterwald	no	Cluster of female cones; too dark to figure.
1984/446	“			Osterwald	yes	Dunker Collection No. 31. 1.5 cm long leafy shoot.
1984/356a	“			Osterwald	no	Dunker Collection No. 72. 2 cm long branched shoot.
1984/356b	“			Osterwald	yes	Dunker Collection No. 71. 1.5 cm long shoots, isolated.
1984/372	“			Osterwald	yes	Gothan & Knopp Collection dated 1933.
1984/374	“			Osterwald	yes	
2003/1113	“	Schenk 1871: pl. 37, fig. 7		Osterwald	no	Two female cones on ends of shoots; too dark to figure.
1984/336	“			Obernkirchen	yes	
1984/349a	“		Pl. 1, Fig. 9, Pl. 4, Figs 5, 8	Isenbüttel	yes	Shoots on borehole core.
1984/379	“			Locality illegible	yes	Naumann Collection dated 1923.
1984/573	“		Pl. 3, Fig. 6, Pl. 4, Figs 1, 3, 4, Pl. 5, Figs 1, 2, 3, 5	Osterwald	yes	3-dimensional shoots; best preserved cuticle.
P4-20	Museum of Geology, Georg-August-Universität, Göttingen	Schenk 1871: pl. 37, fig. 5	Pl. 1, Figs 10, 11, Pl. 3, Fig. 7, Pl. 5, Fig. 6	Osterwald	yes	
P18-14	“	Lipps 1923: text-fig. 33	Pl. 2, Figs 1, 2	Hildesheim	no	Largest leaves/ leaf-cushions seen.

Specimen numbers	Museum collections	Previously noted and/or figured	Figured here	Locality	Cuticle	Comments
V.2303a	Natural History Museum, London		Pl. 3, Figs 1, 2	Ecclesbourne	yes	Rufford Collection. Only English hand spec. identified.
392	Manchester Museum			Ecclesbourne	no	Collected by Rufford.
GP12	Hastings Museum			Ecclesbourne	no	Collected by Rufford.
TCBO, P55/7	Unknown	Oldham 1976: pl. 78, fig. 1	Pl. 3, Fig. 4	Ecclesbourne	yes	Debris material; figured negative donated by Oldham.
TCBO, P55/5	Unknown	Oldham 1976: pl. 78, fig. 2	Pl. 3, Fig. 5	Ecclesbourne	yes	Debris material; figured negatives donated by Oldham.
TCBO, 44Ha	Unknown		Pl. 3, Fig. 3	Ecclesbourne	yes	Debris material; figured negative donated by Oldham.
TCBO, 44Hb	Unknown		Pl. 4, Fig. 6	Ecclesbourne	yes	Debris material; figured negative donated by Oldham.