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The type specimen of *Nilssoniopteris solitaria* (Phillips 1829) Cleal et P.M.Rees 2003 (Bennettitales)

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ABSTRACT. We identified and located the type specimen of *Scolopendrium solitarium*, which is the basionym to what for decades was commonly referred to as "*Nilssoniopteris vittata*" and is now known as *Nilssoniopteris solitaria* (Phillips) Cleal et P.M.Rees. As Cleal and Rees (2003) never located and studied the type specimen of *Scolopendrium solitarium* and simply trusted Harris (1969), who included *Scolopendrium solitarium* in the synonymy of *Nilssoniopteris vittata*, it remained to be shown that this specimen indeed has bennettitalean affinities. Here we provide results of a cuticular analysis of the material and confirm the bennettitalean nature of *Scolopendrium solitarium*, and consequently that its placement in *Nilssoniopteris solitaria* is valid. *Nilssoniopteris solitaria* is, as a senior synonym of *Nilssoniopteris tenuinervis*, the type species of *Nilssoniopteris*. The name "*Nilssoniopteris vittata*" should no longer be used because it was based on *Taeniopteris vittata*, which is the conserved type of *Taeniopteris*, a genus in which taeniopterid fossils are placed if epidermal anatomy is unknown. Specimens identified as this species but yielding a bennettitalean cuticle should be referred to as *Nilssoniopteris solitaria*.

KEYWORDS: *Taeniopteris*, *Nilssoniopteris*, *Scolopendrium*, type species, holotype, typification, Bennettitales

INTRODUCTION

TAENIOPTERID LEAVES

Fossil strap-shaped sterile leaves with an entire margin, a prominent midvein and secondary veins that may or may not bifurcate are generally aggregated in a larger, artificial group commonly called taeniopterids. This group comprises leaves that belonged either to certain marattialean ferns or to cycadophytes (Cycadales, Nilssoniales, Bennettitales), or other gymnosperms. Definite assignment to any group is difficult and in many cases only possible if either epidermal details in the form of preserved cuticle are available or if reproductive structures such as sporangia are preserved. Placement in Cycadales, Nilssoniales or Bennettitales is warranted if the respective epidermal characteristics such as stomata and cell walls are known, with the exception of *Nilssonia*, where the mode of lamina insertion allows placement based on macroscopic morphology as well (see later), while assignment to marattialean ferns can be done if sporangia are preserved. If none of these features is available, such fossils are commonly placed in the fossil genus *Taeniopteris* (see Van Konijnenburg-van Cittert et al. 2017).

Depending on the natural affinities, several genera are in use for such leaves (e.g., *Danaeopsis*, *Taeniopteris*, *Macrotaeniopteris*, *Taeniozamites*, *Nilssoniopteris*, *Nilssonia*, *Yabeiella*, *Jacutiella*, *Nipaniophyllum*, *Rhabdotaenia*, *Doratophyllum*, *Bjuvia*) and the nomenclatorial issues surrounding these generic names are still causing confusion among palaeobotanists. In a recent study, Van Konijnenburg-van Cittert et al. (2017) made an attempt to help palaeobotanists easily differentiate between several genera comprising such taeniopterid leaves; the authors also provided an elaborate taxonomic key to help determine the generic affiliation of such fossils.

Macromorphologically, taeniopterid leaves can easily be assigned to the cycad-like foliage fossil genus *Nilssonia* based on the adaxial insertion of the lamina, in contrast to the lateral insertion in the other genera in question. Further discrimination of the more abundant genera is achieved only by epidermal features (except for *Danaeopsis*, which is a marattialean fern). If no cuticle is preserved or the cuticle is unknown, leaves are assigned to *Taeniopteris*. Preserved cuticle with cycadalean (haplocheilic) stomata identifies the leaves as belonging to either *Bjuvia*, *Rhabdotaenia* or *Doratophyllum*, while a bennettitalean cuticle with syndetocheilic stomata warrants assignment to either *Nilssoniopteris* or *Nipaniophyllum* (see Van Konijnenburg-van Cittert et al. 2017; but regarding *Nipaniophyllum*, see Pott et al. 2017).

During that study of Van Konijnenburg-van Cittert et al. (2017), the nomenclatural history of *Taeniopteris*, *Taeniozamites* and *Nilssoniopteris* was re-evaluated also. For all three genera, species carrying the epithet "*vittata*" had occasionally been considered types in the past, based on different or even the same specimens, complicating this issue even further. During the mentioned study, additional information was obtained on the different "*vittata*" species and on the specimens on which they were based; the results of the analysis were, however, outside the scope of that paper. Here we briefly evaluate these different "*vittata*" species, giving their correct names and type specimens.

NOMENCLATORIAL HISTORY OF *TAENIOPTERIS* AND *NILSSONIOPTERIS*

Taeniopteris was erected by Brongniart (1828) with *Taeniopteris vittata* as its type species. Brongniart (1828) made reference to a specimen that had been figured by Sternberg (1823, p. 42, pl. 37, fig. 2) under the name *Phyllites scitamineaeformis* (or "*Scitaminearum folium*" according to some authors [e.g., Harris 1969]). This specimen (OUMNH J.23456 from Stonesfield, Oxfordshire, UK, Middle Jurassic [Bajocian]), thus has to be considered the type for *Taeniopteris vittata*, which was first proposed by Cleal and Rees (2003), even though Cleal and Rees (2003) considered the species name to have been validly published only by Brongniart (1831). In order to allow the name to continue to be used for leaves unattributable to one of the major plant groups, Zijlstra et al. (2016) proposed to conserve the generic name *Taeniopteris* Brongniart, 1828 (Brongniart 1828, p. 61) and its type species *Taeniopteris vittata* Brongniart 1828 (Brongniart 1828, p. 194) with a conserved type (the Stonesfield specimen).

Taeniopteris vittata was earlier regarded as the type species of *Nilssoniopteris* by many authors (as *Nilssoniopteris vittata*; e.g., Florin 1934, Harris 1969), but as shown above, it is the type species of *Taeniopteris* and not of *Nilssoniopteris*. Leaves identified as this species but having a bennettitalean cuticle should be referred to *Nilssoniopteris*, but under a name different from *Nilssoniopteris vittata*.

The general confusion around the "*vittata*" species arose because Brongniart (1831) figured four specimens that he included in *Taeniopteris vittata* in addition to the Stonesfield specimen: three from Yorkshire, UK, and one from Scania, Sweden (Cleal & Rees 2003, Pott & Launis 2015). Cleal and Rees (2003) already explained that if one considers the Stonesfield specimen as *Taeniopteris vittata*, those four other specimens require another name, as their epidermal anatomy is available. The specimens should therefore, be placed in *Nilssoniopteris*, and Cleal and Rees (2003) found that a legitimate basionym already exists with *Scolopendrium solitarium* Phillips 1829, necessitating the new combination *Nilssoniopteris solitaria* (Phillips 1829) Cleal et P.M.Rees 2003 (Cleal & Rees 2003). However, Pott and Launis (2015) showed that at least one of the Brongniart specimens (Brongniart 1831, pl. 82, fig. 2) could be identified as *Nilssoniopteris major* (Lindley et Hutton 1833) Florin 1934, based on its cuticle, whereas two specimens (Brongniart 1831, pl. 82, figs 1, 3) are most likely *Nilssoniopteris solitaria*. The specimen from Scania does not yield any cuticle, and therefore further assignment is not possible; it consequently should be considered as *Taeniopteris*. Independent of the specific assignment of these four specimens, Van Konijnenburg-van Cittert et al. (2017) came to the conclusion that the name "*Nilssoniopteris vittata* (Brongniart 1828) Florin 1934" should no longer be used.

Also, the combination "*Taeniozamites vittatus* (Brongniart 1828) Harris 1932" should no longer be used. Harris (1932a, p. 33) retained *Taeniopteris* for cases in which no cuticle is known or present. At the same time, the author proposed the generic name *Taeniozamites* for species of *Taeniopteris* that possess a bennettitalean cuticle, disregarding that Nathorst (1909) had already erected a valid name (viz. *Nilssoniopteris*) for such fossil leaves (Florin 1934). Harris (1932a, p. 101) placed only one species in this genus: "*Taeniozamites vittata*", with an epithet that must have been taken from Brongniart's (1828, 1831) *Taeniopteris vittata*; however, that species is not mentioned as its basionym. More important is the synonym that Harris (1932a) gave for this species: *Nilssoniopteris tenuinervis* (Nathorst 1880) Nathorst 1909. This makes *Taeniozamites* a junior synonym of *Nilssoniopteris*.

Nilssoniopteris tenuinervis was identified as the type of *Nilssoniopteris* by Cleal and Rees (2003, p. 763) and Cleal et al. (2006, p. 219). Its lectotype is specimen S134241 of the Swedish Museum of Natural History, Stockholm. Cleal et al. (2006) clearly demonstrated that what was published by Nathorst (1909) under the name *Nilssonia tenuinervis* is in fact a bennettitalean leaf and thus cannot belong to the genus *Nilssonia*. Already the cuticle of *Nilssoniopteris tenuinervis* described and figured by Nathorst (1909, pl. 7, fig. 21) proved the bennettitalean nature of the specimen (Nathorst 1909). *Nilssonia tenuinervis sensu* Nathorst (1909), however, was identified by Cleal et al. (2006) as a later taxonomic synonym of *Scolopendrium solitarium*, and the correct name of the species is consequently not *Nilssoniopteris tenuinervis* but *Nilssoniopteris solitaria*. The latter can therefore be considered the type species of *Nilssoniopteris*, although the genus had at the moment of its erection *Nilssoniopteris tenuinervis sensu* Nathorst (1909) as its type species; the correct name of that species is *Nilssoniopteris solitaria*.

Until now, the new combination *Nilssoniopteris solitaria* (Phillips 1829) Cleal et P.M.Rees 2003 proposed by Cleal and Rees (2003) had not been confirmed by the necessary epidermal features, as (a) the base specimen had not been identified as such earlier and (b) no attempt had been made previously to locate the specimen that served Phillips (1829) in erecting *Scolopendrium solitarium*. During their above-mentioned study on taeniopterid leaves, Van Konijnenburg-van Cittert et al. (2017) could identify this base (=type) specimen. It was located in the Oxford University Museum of Natural History, Oxford, UK, under accession number OUMNH J.29628. The specimen appeared to yield cuticle and the authors were allowed to borrow the specimen and were permitted destructive sampling for cuticle analysis. The results show that the cuticle is of the bennettitalean type, confirming the new combination *Nilssoniopteris solitaria* as valid and also its conspecificity with most specimens assigned to *Nilssoniopteris tenuinervis* by Nathorst (1909) and to "*Nilssoniopteris vittata*" by Harris (1969).

MATERIAL AND METHODS

Specimen OUMNH J.29628 identified as *Scolopendrium solitarium* by Phillips (1829) from the palaeontological collections of the Oxford University Museum of Natural History (OUMNH), Oxford, Oxfordshire, UK, was photographed with a Nikon D750/Nikkor AF-S Mikro 60-mm 1:2.8G ED system digital camera. Oblique lighting and polarising filters in front of both the camera lenses and the lights were used to enhance contrast and fine details. The cuticles were analysed with an Olympus BX51 light microscope modified for epifluorescence microscopy, and photographed with an Olympus DP71 digital camera.

For cuticle preparation, organic matter yielding cuticles was sampled directly from the specimen and processed according to the standard procedure as outlined recently by, among others, Pott and McLoughlin (2009) and Pott et al. (2014, 2016). In order to remove sediment, cuticles were treated with 40% HF for one day. Subsequently, the organic remains were bathed in Schulze's reagent (30% HNO_3 with a few crystals of $KClO_4$) for 2–3 days for maceration, and the coaly layer was then removed using 5% potassium hydroxide (KOH) for a few seconds and neutralisation in water. The remaining water was removed by storing the cuticle remains in glycerine for a few days; the cuticles were then mounted on permanent microscopic slides with Kaiser's glycerine jelly.

The specimen and the produced slides are stored in the palaeontological collection of OUMNH under accession numbers OUMNH J.29628 and OUMNH J.29628/p1–p4.

RESULTS AND DISCUSSION

Nilssoniopteris solitaria (J.Phillips 1829) Cleal et P.M.Rees 2003

Plate 1, figs 1–5

B a s i o n y m. *Scolopendrium solitarium* J.Phillips 1829

non 1823 *Phyllites scitamineaeformis* (or '*Scitaminearum folium*' [Blattstück einer *Scitaminea*, p. 37]), Sternberg (1/III), p. 39, pl. 37, fig. 2 (Stonesfield specimen).
1829 *Scolopendrium solitarium*, Phillips, p. 147/153, pl. 8, fig. 5.
1831 *Taeniopteris vittata pro parte*, Brongniart, p. 263, pl. 82, figs 1, 3 (without synonymy).
non 1831 *Taeniopteris vittata pro parte*, Brongniart, p. 263, pl. 82, fig. 2, 4.
non 1831 *Taeniopteris vittata pro parte*, Brongniart, p. 263 (synonymy).
1831–1833 *Taeniopteris vittata pro parte*, Lindley and Hutton, p. 175, pl. 62 (without synonymy to '*Scitaminearum folium*').
non 1837 *Taeniopteris vittata*, Lindley and Hutton, p. 70, pl. 176, fig. B (Stonesfield specimen).
1838 *Taeniopteris vittata*, Presl in Sternberg (2/VII), p. 139, no illustration.
non 1838 *Taeniopteris scitaminea*, Presl in Sternberg (2/VII), p. 139, no illustration.
1869 *Oleandridium vittatum* (Brongnt.) Sch., Schimper, p. 607, no illustration.
1909 *Nilssoniopteris tenuinervis* Nathorst, p. 29, pl. 6, figs 23, 25, pl. 7, fig. 21.
1913 *Tæniopteris vittata*, Thomas and Bancroft, p. 188, pl. 19, figs 10–12, pl. 20, figs 5, 6
1932a *Taeniozamites vittata* (*Taeniopteris vittata*), Harris, p. 101, text-fig. 39F, G.
1932a *Nilssoniopteris tenuinervis*, Harris, p. 101, no illustration.
1932b *Taeniozamites vittata*, Harris, p. 34, no illustration.
1934 *Nilssoniopteris vittata* (*non* Brongniart), Florin, p. 4, no illustration.
1969 *Nilssoniopteris vittata pro parte*, Harris, p. 68, text-figs 32, 34E (most of the specimens mentioned under '1. Yorkshire specimens').
2003 *Nilssoniopteris solitarium* (Phillips) Cleal and Rees, p. 764, no illustration.
2006 *Nilssoniopteris tenuinervis* (Nathorst 1909), Cleal et al., p. 220, text-fig. 1.
2015 *Nilssoniopteris solitaria*, Pott and Launis, p. 23, no illustration.
2017 *Nilssoniopteris tenuinervis*, Van Konijnenburg-van Cittert et al., p. 102, pl. 1, fig. 3, pl. 2, figs 1, 2.
2017 *Nilssoniopteris solitaria*, Van Konijnenburg-van Cittert et al., p. 102, no illustration.

T y p e . OUMNH J.29628, here figured on Pl. 1, figs 1–5.

T y p e r e p o s i t o r y. Oxford University Museum of Natural History, Oxford, Oxfordshire, UK.

T y p e l o c a l i t y. White Nab near Scarborough (Yorkshire), Yorkshire, UK.

T y p e s t r a t u m a n d a g e. Gristhorpe Member, Cloughton Formation, Bajocian, Middle Jurassic.

D i a g n o s i s. Petiolate, entire-margined, linear-lanceolate leaves with prominent midvein; middle region of even width, upper and lower parts somewhat narrowed; apex obtuse or truncate, base tapering more or less quickly; lamina entire, laterally inserted; substance of lamina thick; secondary veins moderately conspicuous, emerging at almost right angles from midvein, bifurcating once close to rachis and proceeding straight to margin, some with additional bifurcations in their distal portion, rarely simple; leaves hypostomatic; cuticle heavily cutinised; elongate rectangular epidermal cells arranged in long rows above veins, unordered and polygonal within intercostal fields, anticlinal cell walls prominent and strongly undulate; stomata syndetocheilic, restricted to abaxial epidermis, randomly scattered in bands between veins, irregularly oriented; intercostal fields equalling or slightly broader than veins; periclinal walls smooth; trichomes present on abaxial epidermis, commonest along veins (modified from diagnosis published by Harris [1969] for "*Nilssoniopteris vittata*").

R e m a r k s. Phillips (1829, pl. 8, fig. 5 – a "rough sketch" according to Harris [1969]) originally identified his specimen with the specimen from Stonesfield figured by Sternberg (1823, pl. 37, fig. 2) under the name *Phyllites scitamineaeformis* or "*Scitaminearum folium*", who regarded it as a zingiberalean rather than a fern. Phillips (1829), however, placed his specimen in a different genus (and species), probably recognising that *Phyllites* was pre-occupied for fossil magnoliophyte foliage from the Miocene of Switzerland (Brongniart 1822), probably a later illegitimate synonym of *Populus* (see, e.g., Kvaček 2008). As mentioned above, the Stonesfield specimen does not provide information on its epidermal anatomy and was consequently retained in *Taeniopteris* (Zijlstra et al. 2016), while Phillips' (1829) specimen can, due to its cuticle, confidently be assigned to *Nilssoniopteris*. This does not, however, exclude the

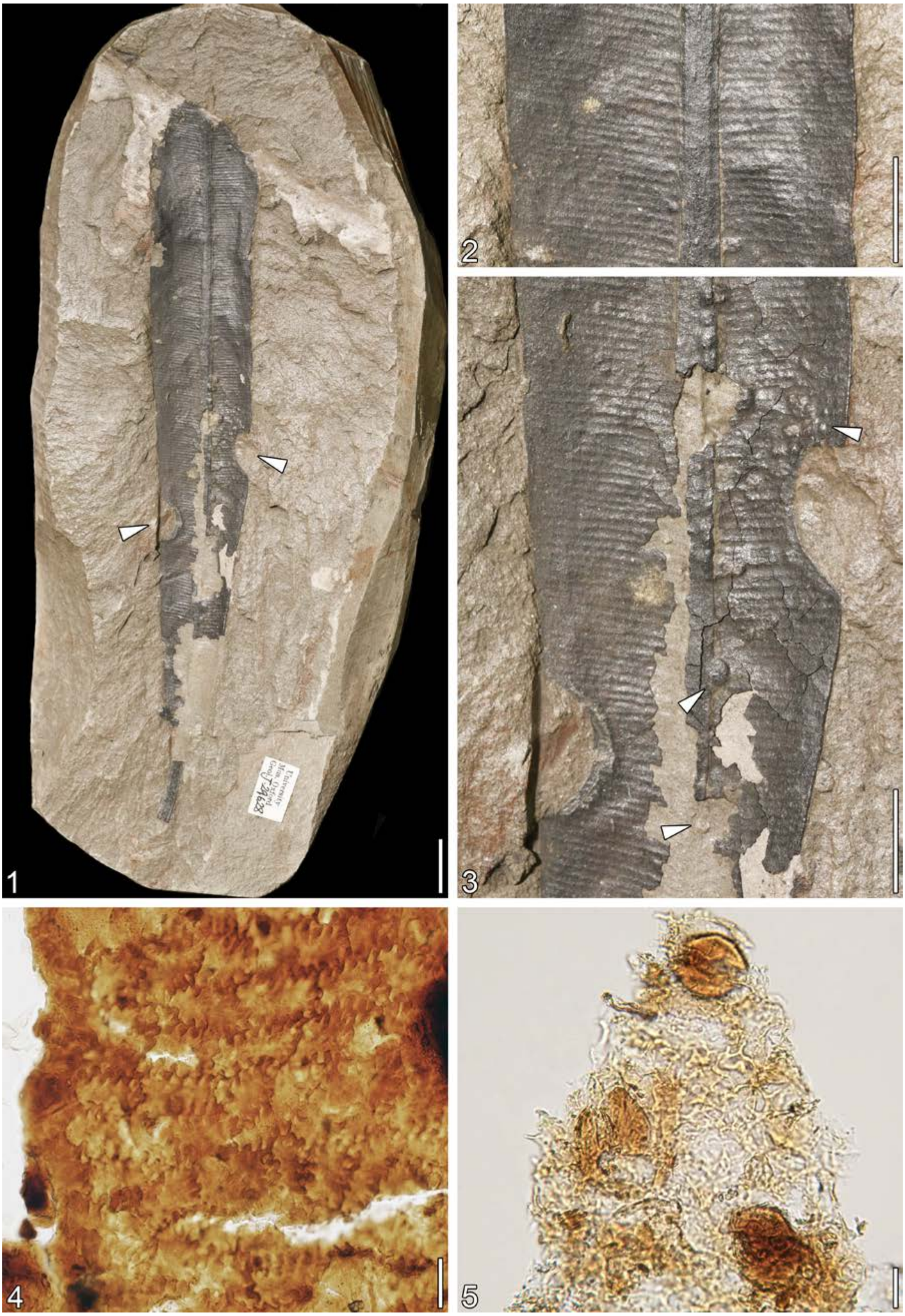

Plate 1. Holotype specimen of *Nilssoniopteris solitaria* (Phillips 1829) Cleal et P.M.Rees 2003 (OUMNH J.29628) from the Middle Jurassic (Bajocian) Gristhorpe Member of the Cloughton Formation at White Nab near Scarborough, Yorkshire, UK. **1**. Entire aspect of the holotype specimen OUMNH J.29628; note the feeding damage on both lateral margins of the leaf (arrowheads); scale bar – 10 mm; **2**. Enlargement of the apical portion of the leaf, showing venation details; scale bar – 5 mm; **3**. Enlargement of the middle portion of the leaf, showing margin feeding marks, putative galls (arrowheads) and venation details; scale bar – 5 mm; **4**. Overview of adaxial cuticle; note the almost rectangular epidermal cells with strongly undulate anticlinal cell walls; scale bar – 20 µm; **5**. Portion of the abaxial cuticle, with the guard cells of three stomata; scale bar – 20 µm

possibility that both specimens belong to the same natural species and that Phillips (1829) may have been right in identifying his specimen with the Stonesfield one, as they also are in the same collection at OUMNH. Neither Sternberg (1823) nor Phillips (1829) or Cleal and Rees (2003) provided any description or diagnosis of the species, but the diagnosis and description of Harris (1969) given for "*Nilssoniopteris vittata*" can be regarded as appropriate for this species.

Description of the holotype specimen. The specimen contains an almost complete leaf, whose preserved portion is 139 mm long and 19 mm wide at the widest expansion of the lamina, which is in the uppermost part of the preserved portion (Pl. 1, fig. 1). The basally 2.7 mm wide and 12 mm long petiole continues into a prominent, up to 2 mm wide midvein (or rachis) that keeps its width through the entire length of the leaf. The lamina evenly tapers in the lower half of the leaf towards its proximal end; in the preserved distal half, the leaf is more or less parallel-sided, while the apical portion is not preserved. The midvein gives rise to fine secondary veins that emerge at angles of ca 80–85° (Pl. 1, figs 2–3); the veins bifurcate once close to the rachis and some bifurcate again in their distal half. Marginal vein density is 22–26 veins/cm. In the proximal–middle portion, each lamina margin shows a semi-circular feeding damage 6.5 × 3.0 mm and 7.0 × 2.5 mm in size, respectively. In several places, small circular elevations or bulges of up to 1.2 mm in diameter are visible (Pl. 1, fig. 3), which probably represent insect galls. Harris (1942) described identical features on leaves of *Anomozamites nilssonii* and *Nilssoniopteris major* from the Gristhorpe plant bed that he earlier interpreted as sporangia of the bennettitalean microsporophylls *Wonnacottia crispa*, but the interpretation as microsporophyll was abandoned later (Harris 1969).

The leaves are hypostomatic; the adaxial cuticle is devoid of stomata. Epidermal cells are more or less rectangular in outline and arranged in long rows above the veins, while they tend to be more polygonal and unordered between veins. Anticlinal cell walls are heavily cutinised and strongly undulate, with 18–20 arcs per 100 µm (Pl. 1, fig. 4). Of the abaxial cuticle only a small portion could be retrieved from the holotype (Pl. 1, fig. 5), which was studied by epifluorescence and light microscopy. Although small and less well-preserved, the cuticle portion was sufficient to prove its agreement with cuticles of *Nilssoniopteris solitaria* published by Harris (1969, text-figs 32, 34E; as "*Nilssoniopteris vittata*") and Van Konijnenburg-Cittert (2017, pl. II, figs 1, 2; as *Nilssoniopteris tenuinervis*), in combination with epifluorescence microscopy.

Harris (1969) gives measurements for full-sized leaves as 250 × 25 mm, rarely up to 30 mm in width. According to Harris (1969), vein density lies between 12 and 24 veins per centimetre; the type specimen is thus at the upper end of this range, but we measured at the margin. Given text-figure 32B in Harris (1969), it can be assumed that Harris probably calculated once close to the rachis (12 veins/cm) and once at the margin (24 veins/cm). According to Harris (1969), stomatal density is ca 40–50/mm^2 and the stomata are ca 39–45 µm in diameter (Harris 1969, text-fig. 32), whereas the pore is 22 µm wide.

Comparison. The Yorkshire Jurassic flora (Harris 1969, Van Konijnenburg-van Cittert & Morgans 1999) yields two other strap-shaped sterile foliage species assigned to *Nilssoniopteris*. They can easily be differentiated from *Nilssoniopteris solitaria*.

The more ovate leaves of *Nilssoniopteris major* are sufficiently different from the linear-lanceolate leaves of *Nilssoniopteris solitaria* in lamina shape and size (width and length), but some leaves are smaller and might be mistaken for each other. Vein density is not a good indicator, although stated by Harris (1969) as such, but the vein densities of the two species overlap and the numbers given by Harris (1969: *Nilssoniopteris solitaria* 12–24; *Nilssoniopteris major* 7–14) cannot be verified based on the figured material. However, the species can be discriminated by epidermal details which include stomata that are less densely arranged and much smaller (only 20–33 µm in diameter) with subsidiary cells not overhanging the pit mouth in *Nilssoniopteris major* (see Harris [1969] and Pott and Launis [2015] for further details).

Nilssoniopteris pristis is easily discriminated by its toothed margin, where the teeth represent the ends of the secondary veins. Its epidermal anatomy is quite similar to that of *Nilssoniopteris solitaria* but the lamina is much longer and more slender than that of *Nilssoniopteris solitaria* (see Harris [1969] for further details).

CONCLUSIONS

In the present note we have shown that the specimen identified as the type specimen for *Scolopendrium solitarium* of Phillips (1829) is of bennettitalean nature and, in consequence, that the taxonomic treatment proposed earlier is correct. The specimen can be considered the holotype of *Nilssoniopteris solitaria*, which is a senior synonym of *Nilssoniopteris tenuinervis*, the original type of *Nilssoniopteris*. The name "*Nilssoniopteris vittata*" should no longer be used for this species because its basionym *Taeniopteris vittata* is the type of *Taeniopteris*, which is based on a specimen from Stonesfield, UK, that yields no information on epidermal anatomy. Specimens in which the latter is known and is of the bennettitalean type should be referred to *Nilssoniopteris solitaria* instead. This is the case for the specimen of Phillips (1829) and the specimen serving Nathorst (1909) in erecting *Nilssoniopteris tenuinervis*, as well as for two of the specimens figured by Brongniart (1831) under the name *Taeniopteris vittata* and most of the Yorkshire specimens mentioned by Harris (1969) under the name *Nilssoniopteris vittata*.

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