

A clarification of the type of *Nilssoniopteris* Nathorst (fossil *Gymnosperma*, *Bennettitales*)

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INTRODUCTION

Nilssoniopteris Nathorst, 1909 is a widely used name for a morphogenus of Mesozoic foliage consisting of undivided or only weakly divided leaves, with the characteristic syndetocheilic stomata of the *Bennettitales* (Harris, 1969). The genus has a world-wide distribution during Late Triassic to Late Cretaceous times, and 29 species have been published up until 1983 (Jongmans & Dijkstra, 1961, 1968; Dijkstra & van Amerom, 1983).

The type of the name is normally given as *Nilssoniopteris vittata* (Brongniart) Florin, 1933 (Basionym: *Taeniopteris vittata* Brongniart, 1831, type of *Taeniopteris* Brongniart, 1828) mainly following Harris (1969). If Harris (1969) was correct in this, *Nilssoniopteris* and *Taeniopteris* would have the same type. However, no mention of the species name *N. vittata* is made in the protologue of *Nilssoniopteris*. Nathorst (1909: 28–29) assigns only one species to the genus, *Nilssoniopteris tenuinervis* (Nathorst) Nathorst (basionym *Nilssononia tenuinervis* Nathorst, 1880), and so following Art. 10.2 of the *ICBN* (Greuter & al., 2000) this must be taken as the type. This raises a problem in the application of the generic name as *Nilssononia tenuinervis* Nathorst is widely interpreted as a cycadalean species (Harris, 1964).

The nomenclatural problems surrounding *Nilssoniopteris* have been recognised for some time. Gomolitzky (1987) attempted to overcome them by proposing to conserve *Nilssoniopteris*, but this was rejected by the Committee for Fossil Plants (Traverse, 1993). The solution, we believe, does not require the name to be conserved, but rather that the issue of the typification of *Nilssoniopteris* is settled. In this paper, we show that Harris (1964) misinterpreted *Nilssononia tenuinervis* and that it is in fact a bennettitalean foliage morphospecies. *Nilssoniopteris* may thus continue to be used legitimately as a morphogenus for bennettitalean foliage, without the need for conservation.

TYPIFICATION AND AUTHORSHIP OF *NILSSONIA TENUINERVIS* NATHORST

Harris (1943) regarded *Nilssononia tenuinervis* Nathorst, 1880 as a *nomen nudum*, being merely a name given in a field guide. He therefore took *Nilssononia tenuinervis* as having been first validly published by Seward (1900) and designated the specimen in Seward's fig. 41 as the "holotype". However, this is incorrect. The problem may have arisen because Nathorst's (1880) paper was written in Swedish. The translation of Nathorst's (1880) text shows that an unequivocal diagnosis is given for *Nilssononia tenuinervis*: "In addition *Nilssononia* n. sp., which because of its extremely fine venation should be called *tenuinervis*. It appears to resemble very much *Taeniopteris*, with which it has also been confused up to now in England, but firstly the veins are here and there branched, and (secondly) the typical *Nilssononia* like shape of the apex show what type of plant this really was".

Although brief, it mentions critical details of the venation and leaf shape, and is a sufficient diagnosis for valid publication under the *Code*. It certainly gives no less detail than in Seward (1900), which Harris (1943, 1964) regarded as the first valid publication of the species. Furthermore, Nathorst (1880) clearly stated that he based the species on specimens that he had collected from Cloughton Wyke in Yorkshire, and so his collections from this locality may be taken to be the syntypes. Nathorst (1909) later figured some of these specimens, including a cuticle preparation. The most obvious choice for a lectotype is specimen S 134241 in the Swedish Museum of Natural History, Stockholm. This is the specimen figured by Nathorst (1909: Pl. 6, Fig. 23) that according to its cuticle characters and morphology agrees most closely with the diagnosis. Although Nathorst (1909) described the cuticular features it is unclear from his publication which specimen it was

derived from. Furthermore Nathorst (1909) stated the importance of cuticular features in being able to distinguish *Nilssonia* from *Nilssoniopteris*. Hamshaw Thomas re-examined the specimens in Stockholm and stated that the material figured by Nathorst (1909) in Pl. 6 (Figs. 23, 25) is the material that the cuticle illustrated on pl. 7 (Fig. 21) in the same publication is derived from. These slides have been remounted in the past, and we could not relocate the cuticle fragment illustrated by Nathorst (1909), due to fragmentation in the remounting process. New cuticular preparations from this specimen (S 134241) were made to confirm the features, as amongst the material from Cloughton Wyke is a similar leaf form with cycadalean cuticle (see below). The following description adopts the terminology recommended by Sincock and Watson (1988) and modified by Watson and Sincock (1992). Leaves are hypostomatic, adaxial cuticle thicker than abaxial, epidermal cells square to rectangular (Fig. 1A, B, D), up to 60 μm long by 41 μm wide, anticlinal cell walls sinuous and buttressed. Abaxial cuticle thinner (Fig. 1C), epidermal cells square to rectangular, up to 57 μm long by 30 μm wide, anticlinal walls sinuous and buttressed (Fig. 1D). Stomata scattered, oriented obliquely with respect to leaf length (Fig. 1C). Stomatal pit small, stomatal aperture up to 20 μm long, slit-like, dorsal epidermal flange of guard cells butterfly-shaped (Fig. 1E, F). Subsurface bodies present (Fig. 1B).

The features described above are consistent with the description of Nathorst (1909) and indicate placement in the Bennettitales. As specimen S 134241 conforms most closely to the diagnosis given in Nathorst (1909), both in gross morphology and cuticular features, it is designated as the lectotype.

■ TYPIFICATION OF *NILSSONIOPTERIS* NATHORST

It has been widely accepted (e.g., Florin, 1933; Harris, 1943, 1969) that most of the syntypes of *N. tenuinervis*, including the specimen designated here as lectotype, are conspecific with the species widely referred to as *Nilssoniopteris vittata* (Brongniart) Florin (basionym: *Taeniopteris vittata* Brongniart). This is why Harris (1969) incorrectly designated *N. vittata* as the type of *Nilssoniopteris*. However, the lectotype of *Taeniopteris vittata* Brongniart is an impression fossil from a macroflora that never yields cuticles (the Middle Jurassic of Stonesfield, Oxfordshire, U.K.) and whose systematic position is thus uncertain (Cleal & Rees, 2003). Since the type of *T. vittata* is in a different preservational state to the type of *N. tenuinervis*, the two morphospecies cannot be considered as synonyms (ICBN Article 1.2, Greuter & al., 2000).

Cleal & Rees (2003) have shown that more or less entire bennettitalean leaves, superficially similar to *T. vittata* but where cuticles are preserved, should be more correctly referred to as *Nilssoniopteris solitaria* (Phillips) Cleal & Rees, 2003 (basionym: *Scolopendrium solitarium* Phillips, 1829). *Nilssonia tenuinervis* is thus a later taxonomic synonym of *Scolopendrium solitarium* and so *Nilssoniopteris tenuinervis* is no longer the correct name of the species. However, this does not make *N. solitaria* the type of *Nilssoniopteris*; the generic type remains *N. tenuinervis*.

Although most of the syntypes of *Nilssoniopteris tenuinervis* are undoubtedly bennettitalean, one of the figured specimens (Nathorst, 1909, Pl. 6, Fig. 24) is different, having a cycadalean epidermal structure and venation. This was first pointed out by Thomas & Bancroft (1913), who argued that, as the syntypes with bennettitalean characters belong to what they called *Taeniopteris vittata*, the species epithet *tenuinervis* should be linked to the one cycadalean syntype. Consequently, most subsequent authors have used the name *Nilssonia tenuinervis* for cycadalean leaves, most notably Harris (1943, 1964). This is perverse, however, as it clearly conflicts with Nathorst's concept of the species. In 1880, Nathorst clearly stated that the veins fork, whereas *Nilssonia tenuinervis* sensu Thomas & Bancroft (1913) has simple veins. It also conflicts with Nathorst's (1909) revision of the species, which is unequivocally linked with the distinctive bennettitalean cuticles. Thomas & Bancroft's (1913) emendation of *Nilssonia tenuinervis* must therefore be rejected.

■ NOMENCLATURE OF *NILSSONIA TENUINERVIS* SENSU THOMAS & BANCROFT

The correct name for *Nilssonia tenuinervis* sensu Thomas & Bancroft involves taxonomic issues that are beyond the scope of this paper. Thomas & Bancroft (1913) regarded it as conspecific with *Nilssonia orientalis* Heer, 1878 but the latter species is quite different, having shorter and broader leaves, less dense and more oblique veins, and a transversely-waved lamina (Harris, 1943, 1964). *Nilssonia obtusa* (Nathorst) Harris, 1932 also bears some similarity to *N. tenuinervis* sensu Thomas & Bancroft in the shape of the leaves and features of the epidermis but, as pointed out by Harris (1964), the veining is much less dense and almost certainly is a different species. Harris (1964) listed a number of other species, which morphologically resemble the Yorkshire specimens but for which epidermal anatomy is unknown. These cannot be assessed relative to the Yorkshire material until this epidermal evidence becomes

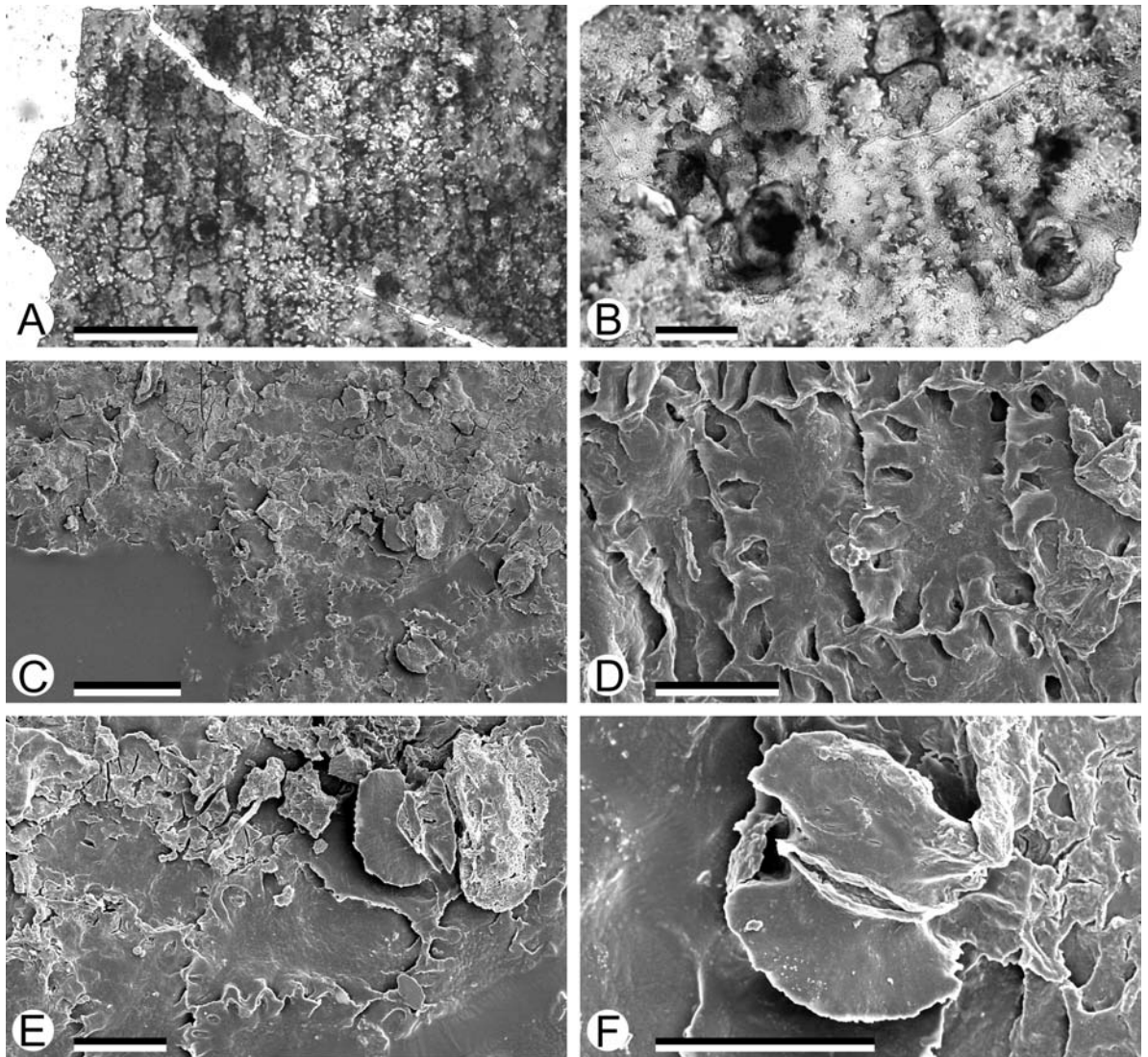


Fig. 1. Cuticular features of S 134241, the proposed lectotype of *Nilssoniopteris tenuinervis*. A–B, light micrographs of cuticle. A, overview of epidermal cell arrangement on the upper leaf surface; B, details of epidermal cells and poorly preserved subsurface body and stomata. C–F, scanning electron micrographs of cuticle; C, overview of lower leaf surface with randomly orientated stomatal complexes; D, details of the sinuous epidermal cell walls of upper surface; E, stomata and epidermal cells; F, details of stomata with distinct dorsal cuticular flanges over the guard cells. Scale bars as follows: A, C = 100 μm , B, D–F = 25 μm .

known. Whatever the outcome of this taxonomic problem, the Yorkshire cycadalean leaves cannot be referred to correctly as *Nilssonia tenuinervis*.

CONCLUSIONS

1. The lectotype of *Nilssoniopteris tenuinervis* (Nathorst) Nathorst is designated here as specimen S. 134241 in the Swedish Museum of Natural History, Stockholm. It is the specimen figured by Nathorst (1909: Pl. 6, Figs 23, 25, Pl. 7, Fig. 21).

2. The type of *Nilssoniopteris* Nathorst is not

Nilssoniopteris vittata (Brongniart) Florin, but *N. tenuinervis*. The above-designated lectotype of *N. tenuinervis* is thus also the type of the generic name.

3. The cycadalean foliage fossils from the Yorkshire Jurassic, incorrectly referred to *Nilssonia tenuinervis* by Harris (1943, 1964), require an alternative species name.

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