



Differentiation of the fossil leaves assigned to *Taeniopteris*, *Nilssoniopteris* and *Nilssonia* with a comparison to similar genera



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ARTICLE INFO

Article history:

Received 11 October 2016

Accepted 24 November 2016

Available online 6 December 2016

Keywords:

Nomenclature

Taxonomy

Typification

Taeniopteris

Nilssoniopteris

Nilssonia

ABSTRACT

Taeniopterid leaves are characterized by an entire margin and a midrib with secondary veins that may or may not bifurcate. This artificial group contains leaves that belong to ferns or, mainly cycadophyte, gymnosperms. If cuticle or reproductive structures are present, the leaves can be placed in natural groups and genera, such as *Nilssonia* and *Nilssoniopteris*. If not, they are placed in the fossil-genus *Taeniopteris*. However, nomenclatorial issues around these genera were complicated and most have only recently been solved. Here we briefly describe and differentiate between these three genera, including diagnoses and type species, all of which are figured. Other, similar but less well known or not often used genera are briefly discussed as well. Moreover we provide taxonomic keys to help determine the generic affiliation of such fossils.

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1. Introduction

Fossil sterile leaves with an entire margin, a midrib and secondary veins that may or may not be bifurcated are generally united in a larger group of sterile leaves commonly called Taeniopterides (or taeniopterids). This group contains leaves that belonged either to certain ferns (Marattiales) or to mainly cycadophyte gymnosperms (Cycadales, Bennettitales) and includes fossils of both Mesozoic and Palaeozoic age. If cuticle and/or reproductive structures are preserved, the fossils can usually be placed easily in these taxonomic groups. However, impression fossils of such leaves can be difficult to assign, although venation patterns may help (e.g., differentiation between the fern and cycadophyte leaves).

In the past, various genera have been used for such leaves (e.g., *Taeniopteris*, *Taeniozamites*, *Nilssoniopteris*, *Nilssonia*) but the nomenclatorial issues surrounding these generic names are often complicated and have remained unresolved. Several authors have misidentified their specimens, placed them in the wrong genera or indicated incorrect types for the generic names. All of these genera and their typifications have been recently discussed, and some proposals for conservation made (Gomolitzky, 1987; Cleal and Rees, 2003; Cleal et al., 2006; Zijlstra, 2016; Zijlstra et al., 2016), but the complicated nomenclatorial history is still causing confusion among palaeobotanists. In this paper

we will, therefore, briefly describe and differentiate between these genera, and provide taxonomic keys to help determine the generic affiliation of such fossils.

2. Material and methods

We briefly explain the typification of the various genera from the literature, their diagnoses (as published and emended), type specimens (providing, if possible, new photos of the holotypes and, when present, illustrations of the epidermal and cuticular characteristics). We also provide a very short history and discussion of each genus.

In our discussions we use the term 'midrib' rather than midvein or rachis, but when citing diagnoses we do not replace those words. The same applies to the use of the term bifurcating veins (rather than forking veins).

For some species, it was necessary to produce new cuticle slides. Rock pieces yielding cuticles were sampled directly from the specimen and processed according to the standard procedure as most recently outlined by Pott et al. (2016). The slides are stored in the collections of the Laboratory of Palaeobotany and Palynology, Utrecht University, Utrecht, The Netherlands, and of the Swedish Museum of Natural History, Stockholm, Sweden.

For some of the macrofossil specimens existing photographs were used, and others were photographed with a Nikon D80/Nikkor AF-S Mikro 60-mm 1:2.8G ED system digital camera. Oblique lighting and polarizing filters in front of both the camera lenses and the lights were

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used to enhance contrast and fine details. The cuticles were analysed with an Olympus BX51 light microscope, which was modified for epifluorescence microscopy, and photographed with an Olympus DP71 digital camera.

3. Systematic part

3.1. *Taeniopteris* Brongniart, 1828 *nom. cons. prop.*

Diagnosis (as emended by Cleal and Rees, 2003): “Leaves with a simple, entire-margined lamina. Midvein rigid, extending for entire length

of leaf. Lateral veins approximately perpendicular to midvein, simple or forking at base. Evidence of epidermal structure not known”.

Type: 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 (p. 61) and its type species *T. vittata* Brongniart, 1828 (Brongniart, 1828, p. 194) with a conserved type. This type specimen for *T. vittata* had already been proposed by Cleal and Rees (2003) (Oxford University Museum: OUM J23456 from Stonesfield, Oxfordshire, Great Britain, Middle Jurassic), albeit that they considered the species name to have been validly published only in 1831. It was briefly described and illustrated in

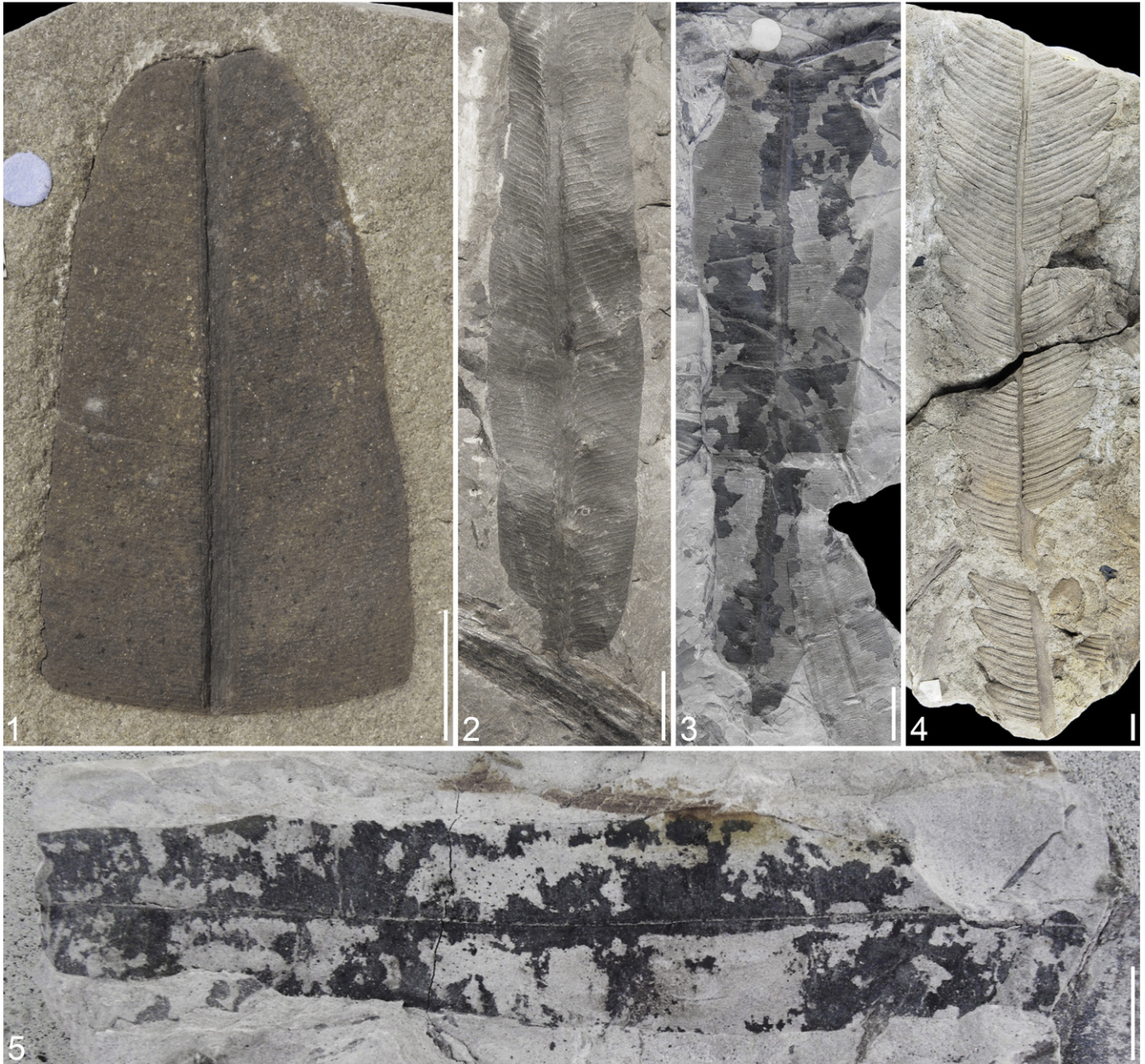


Plate I.

1. *Taeniopteris vittata*; holotype, OUM J23456, from Stonesfield, Oxfordshire, UK, Middle Jurassic (Bajocian); held in the Oxford University Museum, Oxford, UK.
2. *Danaeopsis lunzensis*; 1885/D/3061, from Lunz, Lower Austria, Austria, Upper Triassic (Carnian); held in the Natural History Museum, Vienna, Austria.
3. *Nilssoniopteris tenuinervis*; lectotype, S134241, from Cloughton Wyke, Yorkshire, UK, Middle Jurassic (Bajocian); held in the Swedish Museum of Natural History, Stockholm, Sweden.
4. *Nilsonia brevis*; holotype, S087452, from Höör, Scania, Sweden, Upper Triassic (Rhaetian); held in the Swedish Museum of Natural History, Stockholm, Sweden.
5. *Nilsonia gristhorpensis* sp. nov.; holotype, UU1293, from Cayton Bay, Yorkshire, UK, Middle Jurassic (Bajocian); held in the University Utrecht, Utrecht, The Netherlands. Scale bars – 1 cm.

Sternberg (1823), p. 42, pl. 37, fig. 2 as *Phyllites scitamineaeformis* Sternberg, 1823 and refigured in Cleal and Rees (2003), pl. 7, fig. 1; we here illustrate this specimen again on Plate I, 1.

Remarks: Such a taxon might be deemed to be artificial and thus of limited value. However, as so many of these leaves are preserved as impressions and so cannot be assigned to one of the more “natural” fossil-genera, it is in fact a useful taxonomic concept. This is especially important with the leaves of cycadophyte gymnosperms, many of which can only be reliably attributed to one of the higher taxonomic groups if cuticles are preserved. The proposal by Zijlstra et al. (2016) will, therefore, ensure stability as none of the cycadophyte foliage fossils from Stonesfield have yielded cuticles, and there is in practice little likelihood that additional, better preserved material could be collected from there; all of the known material from Stonesfield came from underground workings that are now abandoned (Cleal et al., 2001). Therefore, it is most unlikely that the generic type will ever be attributable to any of the candidate major plant groups.

Because *Taeniopteris vittata* is the type species of *Taeniopteris* and not of *Nilssoniopteris* as mentioned by many authors (see e.g., Harris, 1969), leaves identified as this species but yielding a bennettitalean cuticle should be referred to *Nilssoniopteris* under a name different from *N. vittata* (see below).

In the case of fossil marattialean fern leaf fragments, they are assigned to *Taeniopteris* if no fertile material is known. The presence of sporangia immediately distinguishes them from the gymnosperm taeniopterids. Such marattialean leaves were originally pinnate in architecture but, since the fossil material is almost always preserved as frond- or pinna fragments only, their attribution to *Taeniopteris* is often warranted. Good examples of marattialean ‘fern-type’ taeniopterids are sterile specimens of the genus *Danaeopsis* Heer ex Schimper, 1869 (Plate I, 2); before their fertile structures were known, such fossils were always placed in the genus *Taeniopteris*. In some cases, it is possible to recognize marattialean sterile material by its venation instead (in which case it is placed in the fossil-species for which the sporangia are known); the veins arise from the rachis under a narrow angle and then bend outwards to an almost perpendicular position. In gymnosperm taeniopterids, the veins directly arise (almost) perpendicularly from the rachis.

3.2. *Nilssoniopteris* Nathorst, 1909 (including *Taeniozamites* Harris, 1932)

Diagnosis (as emended by Pott et al., 2007): “Strap-shaped leaf falling from stem at maturity, petiolate, lamina undivided, lobed to completely dissected down to the rachis, attached laterally or to adaxial surface of midrib, leaving part of the upper surface of the midrib exposed. Veins free, simple or forked, ending at margin. Cuticle with syndetocheilic stomata; epidermal cell walls straight or usually sinuous”.

Type: Cleal and Rees (2003, p. 763) and Cleal et al. (2006, p. 219) demonstrated that the type species of the genus *Nilssoniopteris* is *N. tenuinervis* (Nathorst, 1880) Nathorst, 1909. Its lectotype is the specimen S134241 of the Swedish Museum of Natural History, Stockholm (Plate I, 3). Nathorst (1909) figured the specimen in his pl. 6, figs. 23, 25 and pl. 7, fig. 21. Cleal et al. (2006) illustrated its cuticular features in their text-fig. 1, which are figured here again (Plate II, 1, 2).

Remarks: Brongniart (1831) figured four specimens that he included in *Taeniopteris vittata*, three from Yorkshire and one from Scania (Cleal and Rees, 2003, p. 762; Pott and Launis, 2015, p. 23). Cleal and Rees (2003) already explained that if one considers the Stonesfield specimen as *T. vittata*, those four specimens require another name. They should 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 and Rees, 2003). However, Pott and Launis (2015) revealed that at least one of the specimens (Brongniart, 1831, pl. 82, fig. 2) is *Nilssoniopteris major* (Lindley and Hutton, 1833) Florin,

1934 based on its cuticle, whereas the others (Brongniart, 1831, pl. 82, figs. 1, 3) are most likely *N. solitaria*. Anyhow, the name “*Nilssoniopteris vittata* (Brongniart, 1828) Florin, 1934” should consequently not be used anymore.

Although Nathorst (1909) gave a good description of the differentiating characters of *Nilssoniopteris*, Harris (1969) still improved the brief diagnosis of that fossil-genus. Harris (1932a, p. 33) retained *Taeniopteris* Brongniart, 1828 for cases in which no cuticle is known or present. At the same time, he proposed (p. 33) the generic name *Taeniozamites* for those species of *Taeniopteris* that possess a bennettitalean cuticle. Harris (1932a, p. 101) placed only one species in this genus: ‘*Taeniozamites vittata*’ – with an epithet that must have been taken from *Taeniopteris vittata* Brongniart; however, that species is not mentioned as its basionym. More important is the synonym that Harris (1932a) gave for this species: *Nilssoniopteris tenuinervis*. This makes *Taeniozamites* a junior synonym of *Nilssoniopteris*. The combination “*Taeniozamites vittatus* (Brongniart, 1828) Harris, 1932” thus should not be used any more. Later, Harris (1932b): p. 34–40 placed several more species in *Taeniozamites*.

Gomolitzky (1987) proposed to conserve *Nilssoniopteris* Nathorst, 1909 against *Taeniozamites* Harris, 1932. This proposal was rejected because an earlier name never needs conservation against a later name and *Taeniozamites* should not be used. Thus, all species that Harris (1932b) added to *Taeniozamites*, were transferred to *Nilssoniopteris* as new combinations by Florin (1934); examples include *N. groenlandica* (Harris, 1926) Florin, 1934, *N. ajorpokensis* (Harris, 1932a) Florin, 1934 and *N. jourdyi* (Zeiller, 1903) Florin, 1934. Boyd (2000) emended the generic diagnosis to include lobed leaves, and Pott et al. (2007) and Pott and McLoughlin (2009) included leaves that were dissected, but irregularly and never in their basal and apical portions.

3.3. *Nilssonia* Brongniart, 1825

Diagnosis (as emended by Harris, 1964): “Leaf as a whole linear or oblanceolate, lamina gradually increasing in width from the base. Lamina attached to the upper edge of rachis, and entirely concealing it from above, lamina entire or cut transversely into segments. Veins simple, numerous, equal and ending at its distal margin; resin bodies often present between veins. Stomata confined to lower side, scattered between veins, guard cells lightly cutinised, exposed or sunken and surrounded and more or less protected by a more or less regular ring of subsidiary cells; subsidiary cells unspecialised or each bearing a papilla projecting over the aperture. Unicellular trichome bases occurring on the underside, at least on veins”.

NB 1. This type of stomata is generally called haplocheilic (Florin, 1933).

NB 2. In some leaves, the lamina does not completely conceal the midrib from above, (see e.g., Harris, 1932a, pl. 4, fig. 8; Harris, 1964, fig. 13A,C, 15B, 24G, H), but this might be due to preservation.

Type: The genus *Nilssonia* comprises pinnate species and unsegmented, entire-leaved species. The type specimen, provided by *N. brevis* from the Hettangian of Scania, is segmented, and housed in the Swedish Museum of Natural History, Stockholm, under accession number S087452. It was figured by Brongniart (1825), pl. 12, fig. 4 (here figured again on Plate I, 4) and its diagnosis included the segmented state of the leaf. However, it is well-documented that there is a gradation between species with such segmented leaves and entire-margined species such as *Nilssonia orientalis* Heer, 1878. In the latter’s diagnosis, Heer (1878) reported an entire-margined lamina that was incised in various ways in some specimens. However, most figured leaves in Heer’s (1878) plate 4, figs. 5–9, show entire leaves that are either not well-preserved or torn. Only one leaf (Heer, 1878, plate 4, fig. 6) may have been slightly incised.

Remarks: Brongniart (1825) instituted a genus that he named *Nilsonia*, and which included the pinnate *N. brevis* specimens. It was named after Swedish palaeontologist Sven Nilsson (1787–1883),

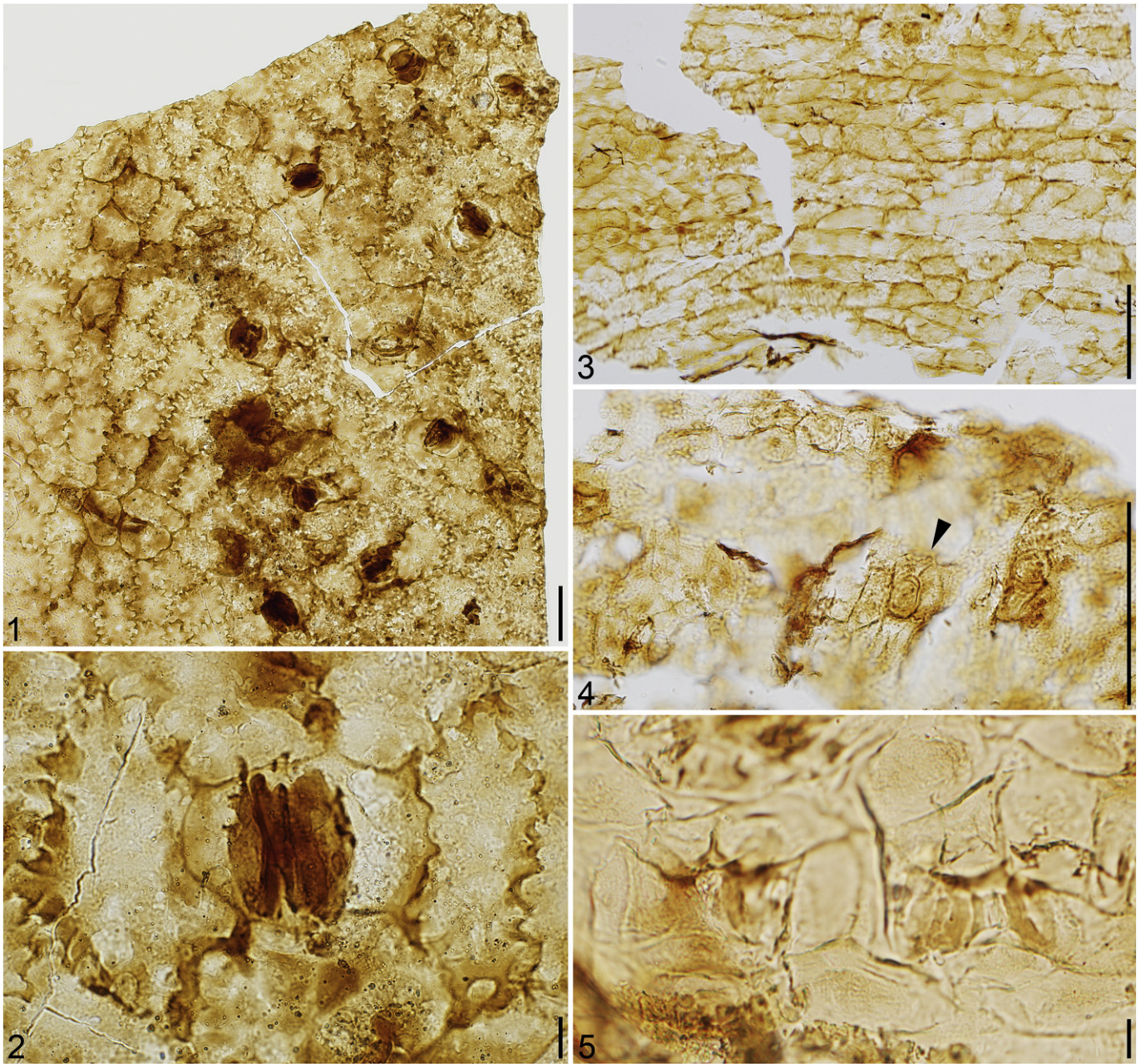


Plate II.

1. *Nilssoniopteris tenuinervis*, overview of abaxial cuticle with randomly oriented stomata; note the undulate anticlinal cell walls; lectotype, S134241, from Cloughton Wyke, Yorkshire, UK, Middle Jurassic (Bajocian); held in the Swedish Museum of Natural History, Stockholm, Sweden.
 2. *Nilssoniopteris tenuinervis*, brachyparacytic stoma; lectotype, S134241, from Cloughton Wyke, Yorkshire, UK, Middle Jurassic (Bajocian); held in the Swedish Museum of Natural History, Stockholm, Sweden.
 3. *Nilssonia gristhorpensis* sp. nov., overview of adaxial cuticle; note the typical *Nilssonia*-like shape and arrangement of epidermal cells; holotype, UU1293 slide C-7505, from Cayton Bay, Yorkshire, UK, Middle Jurassic (Bajocian); kept in the University Utrecht, Utrecht, The Netherlands.
 4. *Nilssonia gristhorpensis* sp. nov., aspects of abaxial cuticle; note the *Nilssonia*-typical papillae (arrowhead); holotype, UU1293 slide C-7504, from Cayton Bay, Yorkshire, UK, Middle Jurassic (Bajocian); kept in the University Utrecht, Utrecht, The Netherlands.
 5. *Nilssonia gristhorpensis* sp. nov.; two adjacent actinocytic (haplocheilic) stomata; paratype, cuticle slide C-194, obtained from specimen UU4761 (Hasty Bank, Yorkshire, UK, Middle Jurassic (Aalenian)); kept in the University Utrecht, Utrecht, The Netherlands.
- Scale bars – 100 μm (figs. 1, 3, 4), 10 μm (figs. 2, 5).

whose name Brongniart (1825) misspelled as 'Nilson'. Brongniart consistently used the spelling *Nilsonia* (with single 's') in later publications (e.g., Brongniart, 1831), as did other authors including Sternberg (1825) and Lindley and Hutton (1831–1833), p. xli, 189.

The *Nilssonia* spelling (with double 's') was introduced later (e.g., Bronn, 1835). Wang (2011) has proposed that *Nilssonia* should be conserved over *Nilsonia*, and this was accepted by the IAPT Nomenclature

Committee on Fossils (Herendeen, 2015) in the belief that it would benefit nomenclatural stability, including the avoidance of changing correlatively derived names (Nilssoniales, Nilssonaceae, Nilssoniocladus Kimura et Sekido, 1975, and even Nilssoniopteris). However, the initial use of the *Nilssonia* spelling by Bronn (1835) provided direct reference to Brongniart's *Nilsonia* and so can be treated as an orthographical variant (ICN Art. 61.2). The IAPT Nomenclature General Committee has

now unanimously agreed that the spelling *Nilssonia* is an error that may simply be corrected to *Nilssonia* and does not require conservation (Herendeen, pers. comm., May 2016). This issue will be decided in the nomenclatorial session that precedes the International Botanical Congress in Shenzhen, China, in 2017.

The entire-margined *Nilssonia tenuinervis* sensu Seward, 1900 is different from *Nilssonia tenuinervis* Nathorst, 1880 as originally described by Nathorst (1880). Nathorst's (1880) *N. tenuinervis* is the basionym of the type of *Nilssoniopteris* Nathorst, 1909 [= *Nilssoniopteris tenuinervis* (Nathorst, 1880) Nathorst, 1909] (see before). The species as described, but erroneously identified as *Nilssonia tenuinervis* (and thus misidentified) by Seward (1900) consequently is a different and thus new species, which requires a new name. Therefore, we present it here as a new species, for which we propose the name *Nilssonia gristhorpensis* sp. nov., named after the locality (Gristhorpe Bed, Cayton Bay, Yorkshire, UK), where the original material was found (Seward, 1900). Specimen UU1293 from that same locality is here designated as the holotype (Plates I, 5 and II, 3, 4).

Nilssonia gristhorpensis sp. nov.

Plates I, 5 and II, 3–5.

Synonymy:

This new species is based on: *Nilssonia tenuinervis* sensu Seward, 1900

1900 *Nilssonia tenuinervis* sensu Seward – Seward, p. 230, text-fig. 41

1964 *Nilssonia tenuinervis* sensu Seward – Harris, p. 33, cum syn., pl. 1, fig. 10, text-figs. 13, 14

not 1880 *Nilssonia tenuinervis* sensu Nathorst – Nathorst, p. 35, no illustration.

Holotype: Specimen UU1293 from the Gristhorpe Bed, Cayton Bay, Yorkshire, stored in the collections of the Laboratory of Palaeobotany and Palynology, University of Utrecht, The Netherlands, here figured on Plate I, 5 (and cuticles on Plate II, 3, 4). Here designated.

Paratype: Specimen UU4761 with cuticle slide C-194 (Plate II, 5). Here designated.

Type locality: Scarborough (Cayton Bay, Gristhorpe Bed), Yorkshire, UK.

Type horizon and age: Cloughton Formation, Gristhorpe Member, Bajocian (Middle Jurassic).

Diagnosis: Leaf linear, apex acute, petiole short or absent but rachis base expanded at its attachment. Lamina typically entire but sometimes irregularly dissected margins and midrib depressed, entirely covered on the upper side by attached lamina. Veins fine, simple, emerging typically at an angle of 85° from midrib, but curving forward to reach the margin at c. 70°. Lamina thin, with resin bodies between veins. Upper cuticle delicate, composed of elongated, straight-walled cells. Stomata and trichomes absent, cells along veins slightly narrower than cells between the veins. Lower cuticle delicate, cells along veins elongated, cells between veins isodiametric or irregular, outlines often indistinct. Stomata scattered in relatively broad strips between veins, haplocheilic, guard cells without papillae. Trichome bases frequent along veins, occasional between veins.

Discussion: The entire-margined *Nilssonia gristhorpensis* is distinguished from *Nilssoniopteris solitaria* by differences in gross morphology; these differences, however, are cryptic. Both species are similar on first view and often occur in the same localities and beds (e.g., Gristhorpe Bed at Cayton Bay and *Solenites* Bed at Cloughton Wyke). However, the venation is different: fine and simple, densely arranged secondary veins characterize *Nilssonia gristhorpensis*, while the secondary veins in *Nilssoniopteris solitaria* are commonly bifurcating and wider spaced. In addition, when cuticle is preserved, they can easily be distinguished by the different types of their stomata (haplocheilic versus syndetocheilic) and the straight versus sinuous anticlinal cell walls. A comparison with other entire-leaved *Nilssonia* genera is elaborately done by Harris (1964), and we have nothing to add.

The holotype of *Nilssonia gristhorpensis* (UU1293; Plate I, 5) is a good leaf, which also yielded small cuticle fragments (Plate II, 3, 4). However, the cuticle of UU4761 is much better (Plate II, 5) and hence it has been designated as paratype.

3.4. Other comparable Mesozoic genera

Various authors erected other genera for entire-margined cycadophyte leaves resembling *Nilssonia* due to the poorly circumscribed characterization of the latter by Brongniart (1825). Harris (1932a) established the genus *Doratophyllum* Harris, 1932 for entire-leaved species that have a cycad cuticle with haplocheilic stomata but in which the lamina is attached to the side of the rachis, contrary to those of *Nilssonia*, where the lamina is attached to the upper side of the rachis. According to Harris (1932a), lateral veins bifurcate in *Doratophyllum*, but almost never in *Nilssonia*. Barnard and Miller (1976) emphasized the cuticular features of *Doratophyllum* and its very typical, haplocheilic stomata, in which the epistomatal chamber is surrounded by up to eight subsidiary cells forming only a small external aperture. Kiritchkova and Esenina (2014) emended the diagnosis of *Doratophyllum* to include several species with amphistomatic cuticles. However, stomata on the upper epidermis are rare, while they are common on the lower epidermis. *Doratophyllum* is rare and so far restricted to Upper Triassic floras from Greenland, Sweden and Russia (Kiritchkova and Esenina, 2014). Some authors (e.g., Samylina, 1956) included it in *Nilssonia*.

Macrotæniopteris Schimper, 1869 is used for large *Tæniopteris*-like leaves, but many species have either been transferred to *Nilssoniopteris* based on their bennettitalean type of cuticle (e.g., *N. major* or *N. angustior* (Krasser, 1909) Pott et al., 2007; see Pott et al., 2007) or to the cycadalean genus *Bjuvia* Florin, 1933. Florin (1933) attributed the female organ *Palaeocycas integer* (Nathorst, 1878) Florin, 1933 to the genus based on association, but *Bjuvia* is generally used for large, entire-margined leaves with a cycadalean type of cuticle (see also Pott et al., 2007). Kustatscher and Van Konijnenburg-van Cittert (2010) emended the generic diagnosis of *Bjuvia* with more details on venation (lateral veins usually not or only rarely bifurcating) and the arrangement of stomata in longitudinal bands between veins on amphistomatic cuticles.

Jacutiella Samylina, 1956 is separated from *Nilssonia* by its bifurcating veins that arise perpendicularly from the midrib and the bennettitalean type of stomata, although the latter was not illustrated by Samylina (1956). Apart from its type, *J. amurensis* Samylina, 1956 from the Lower Cretaceous of Siberia, only one other species is known to us: Zhang and Zheng (1987) described *J. dentata* Zhang et Zheng, 1987 from the Upper Jurassic Lanqi (Tiaojishan) Formation of Shebudaigou close to Beipiao in Liaoning, PR China, which has recently also been identified among the specimens from the Upper Jurassic of the Daohugou Bed of Inner Mongolia (PR China) that are currently under study by CP. However, we will not discuss this genus any further due to its small number of species.

Many species nowadays assigned to *Yabeiella* Ôishi, 1931 have earlier been identified as *Tæniopteris* or *Macrotæniopteris*. *Yabeiella* includes *tæniopterid* leaves with a lamina inserted laterally to a strong midrib; the perpendicularly emerging lateral veins are simple or bifurcate basally and occasionally later to form anastomoses. Besides the latter, the most characteristic feature of *Yabeiella* is a marginal vein that runs parallel to the leaf margin and connects the ending of all lateral veins (Ôishi, 1931), separating it from all similar genera mentioned in the text.

Santaecruzia Gnaedinger et Herbst, 1998 is distinguished from all similar genera by its irregularly undulate, serrate or incised margin and regular anastomosing of its perpendicularly emerging lateral veins (Gnaedinger and Herbst, 1998).

Barnard and Miller (1976) emended *Rhabdotaenia* Pant, 1956 to comprise all *tæniopterid* leaves with haplocheilic stomata in which the lamina is attached in a way that at least a portion of the adaxial

side of midrib is exposed, in contrast to *Nilssonia*, where the midrib is entirely concealed by the lamina attached to a line along the centre of the rachis. Moreover, veins are commonly bifurcating in *Rhabdotaenia*. Barnard and Miller (1976, p. 86) recognized four “smaller groups” within *Rhabdotaenia*, which partly overlap, according to the authors; (1) *Bjuvia* (see above), (2) *Nipaniophyllum* Sahnii, 1948 (formerly included in *Taeniopteris* but belonging to the Pentoxylales), (3) *Doratophyllum* (see above) and (4) *Rhabdotaenia* s.s. However, recombining all these genera within one fossil-genus is a too general approach. All four genera provide prominent characters allowing them to be properly distinguished (see Table 2). Moreover, the fossil-genus *Rhabdotaenia* s.l. would then unite foliage of at least three different plant groups that are not closely related (viz. Cycadales, Pentoxylales, Glossopteridales).

Schimper (1869) erected another new genus, *Oleandridium* Schimper, 1869, to which he assigned the first three Yorkshire specimens of *Taeniopteris vittata* from Brongniart (1831) as “*Oleandridium vittatum* (Brongniart) Schimper, 1869”. The fourth specimen was not even considered by Schimper (1869); see also above. Moreover, Schimper (1869) did not mention the Prodrôme (Brongniart, 1828), nor the two elements mentioned in it: no reference to the Sternberg, 1823 plate (*T. vittata* cons. prop.), nor to Brongniart's (1828) p. 194 with its var. *major*, referring to *Marantoidea arenacea* Jaeger, 1827 (that until conservation made *T. vittata* a synonym of *Marantoidea* Jaeger, 1827, which is a nom. rej. against *Danaeopsis* Heer ex Schimper, 1869). In *Oleandridium*, however, Schimper (1869) included five more species, but the genus was not widely considered subsequently. No type species has been indicated; hence, we will not consider it any further. The name “*Oleandridium vittatum* (Brongniart) Schimper, 1869” should consequently not be used anymore.

3.5. Palaeozoic *Taeniopteris*

Taeniopteris has been used also for various Palaeozoic, mainly poorly understood, leaves (as summarised by Remy and Remy, 1975). Many have no cuticle or reproductive structures preserved and so may be retained in the fossil-genus *Taeniopteris* as defined here, but there are a few exceptions. *Taeniopteris jejuna* Grand'Eury, 1877 was transferred to a new fossil-genus *Ilfeldia* Remy, 1953 based on associated synangial structures (Remy, 1953), and subsequently, cuticles (Barthel, 1962) and attached putative ovules (Barthel et al., 1975; Barthel, 2006) have been reported. However, there has so far been no attempt to revise the definition of *Ilfeldia* to incorporate all of these characters into a generic or specific diagnosis.

Yan et al. (in press) have described cuticles as *Taeniopteris* cf. *T. multinervia* Weiss, 1869 from Permian specimens from north China. However, as the type of that species originated from Europe, the taxonomic attribution of these specimens remains uncertain. Kerp (1983) described cycad-like ovulate structures as *Sobernheimia* Kerp, 1983 associated with *T. multinervia* from Germany but no attachment was found.

4. Differentiating key for some common taeniopterid leaves

This paper is dealing with various types of taeniopterid leaves. To distinguish between them, we here provide a simple differentiating key (Table 1). The key is only informal and in many cases, a cuticle sample is inevitable for further discrimination (see Table 2).

A more elaborate key can be found in Table 2. Samylin (1956) also provided a key for taeniopterid leaves, but this key contained fewer genera than the present one, and is, in addition, published exclusively in Russian, a language not familiar to every palaeobotanist.

5. Conclusions

The present paper is a good example for using a ‘fossil-taxon’ such as *Taeniopteris* in terms of the International Code of Nomenclature

Table 1

Simple differentiating key for the main taeniopterid leaves discussed in this paper.

1. Species in which the cuticle is absent or unknown:
 - a. Species in which sporangia are present – ferns belonging to the Marattiales
 - b. Species without sporangia – *Taeniopteris*
2. Species with a definite cuticle:
 - a. Bennettitalean type of cuticle with syndetocheilic stomata – *Nilssoniopteris*
 - b. Cycadalean type of cuticle with haplocheilic stomata
 - a. Leaves in which the lamina is (almost) completely attached to the upper side of the rachis and with unforked veins – *Nilssonia*
 - b. Leaves in which the lamina is attached more to the side of the rachis, and in which the veins are commonly forked – *Rhabdotaenia* and a number of other genera, see Table 2 for more elaborate key.

(McNeill et al., 2012). Fossil leaves can easily be placed in this fossil taxon, when their gross-morphology (including venation) is known, but more details such as presence of sporangia and information on epidermal anatomy are unavailable. However, if the latter information is available, their attribution to a natural group of plants, such as ferns, cycads or bennettites, is warranted in most cases.

Table 2

Elaborate key to differentiate between taeniopterid-type leaves.

1	Lamina inserted to a central line on the adaxial side of the rachis, midrib (almost) completely covered, veins simple	<i>Nilssonia</i>
	Lamina inserted in two lines to the midrib, midrib exposed, veins simple or commonly basally bifurcating	2
2	Lamina inserted adaxially close to the centre of the midrib, veins bifurcating, arising perpendicularly	<i>Jacutiella</i>
	Lamina inserted laterally, leaving midrib exposed almost entirely	3
3	Lateral veins ending in a marginal vein running parallel to the leaf margin, leaving a distinct vein-free margin	<i>Yabeiella</i>
	Lateral veins ending at leaf margin	4
4	Lateral veins bifurcating, arising under pronounced narrow angle, then bending to perpendicular course	Marattialean ferns (e.g., <i>Danaeopsis</i>)
	Lateral veins simple or bifurcating, arising (almost) perpendicularly ^a	5 (gymnosperm foliage ^b)
5	Cuticle unknown	6
	Cuticle known	7
6	Small, slender leaves, lamina on each side of midrib up to as twice as wide as midrib	<i>Taeniopteris</i>
	Large, broad leaves, lamina on each side of midrib several times as wide as midrib	<i>Macrotaeniopteris</i>
7	Stomata of the syndetocheilic ^c type, subsidiary cells might be perpendicularly divided	8
	Stomata of the haplocheilic ^d type	9
8	Subsidiary cells lateral, 2, undivided	<i>Nilssoniopteris</i> (Bennettitales)
	Subsidiary cells lateral, 2, perpendicularly divided	<i>Nipaniophyllum</i> (Pentoxylales)
9	Subsidiary cells not forming a definite ring, irregular, identical to ordinary epidermal cells, guard cells exposed	<i>Rhabdotaenia</i>
	Subsidiary cells forming a complete ring, guard cells sunken	10
10	Subsidiary cells, thickly cutinized, overarching pit	<i>Doratophyllum</i>
	Polar subsidiary cells indistinct, subsidiary cells almost identical with ordinary epidermal cells	<i>Bjuvia</i>

^a Or under narrow angle (>45°) but immediately bending to a perpendicular course.

^b For further discrimination, a sample of the cuticle of the leaves is inevitable.

^c The two lateral subsidiary cells and the guard cells originate from the same mother cell, which by double division produces three cells, the central of which is the mother cell of the guard cells, and the lateral represent or produce the subsidiary cells by another cell division (Florin, 1933).

^d The guard cells originate from one mother cell; the more than two subsidiary cells are epidermal cells homogeneous to this mother cell or originate from such (Florin, 1933).

Acknowledgements

We want to thank Pat Herendeen for his advice on nomenclatural issues and his review of the paper, just as we are thankful to an anonymous reviewer.

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