***Taeniopteris novomundensis* sp. nov. – “cycadophyte” foliage from the Carnian of Switzerland and Svalbard reconsidered: How to use *Taeniopteris*?**

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With 5 figures.

Abstract: Recent findings of *Taeniopteris*-like foliage from the Carnian of Hopen, Svalbard, necessitated the re-evaluation of cycadophyte foliage from the Carnian flora of Neuwelt, Basel, Switzerland, revealing the illegitimate status of *Taeniopteris angustifolia*. The specimen from the Ladinian or Carnian (Lower Keuper) of Lower Franconia, Germany, on which the identification was based, was recently identified as the holotype of the marattialean fern *Danaeopsis angustifolia*, whereof *Taeniopteris angustifolia* is the basionym. This implies that the Neuwelt specimens lack any type and basionym, and a new species name is required. The specimens from Hopen as well as specimens elsewhere from Svalbard are identified as conspecific with the specimens from Neuwelt, and we here assign all specimens to *Taeniopteris novomundensis* sp. nov., which is thus known from the Carnian of Switzerland and Svalbard. Information on epidermal anatomy is not available, and the affinity of the species can, therefore, not be elucidated further, but is here interpreted as a cycadophyte. Several specimens from the Carnian of Franconia assigned to *Taeniopteris angustifolia* belong to a species different from *Taeniopteris novomundensis*, i.e. *Taeniopteris kelberi*. Earlier inclusion of some of the specimens now assigned to *Taeniopteris novomundensis* in *Taeniopteris kelberi* is unsupported. The typification and use of *Taeniopteris* are discussed in this framework.

Key words: *Nilssoniopteris*, *Taeniopteris vittata*, *Taeniopteris angustifolia*, *Danaeopsis*, Keuper, Lunz, Franconia, Bennettitales, Cycadales

1. Introduction

The Carnian flora from Neuwelt close to Basel, Switzerland (Fig. 1A), comprises well-preserved compression plant fossils and is, moreover, coeval with the excellently preserved flora from Lunz-am-See, Austria. The latter is currently being revised in detail (e.g. POTT 2007; POTT et al. 2007a, 2007b, 2008, 2010). Both floras share a high number of species, but there are a number of species, which occurred only in either flora. One of these species is a foliage type from Neuwelt attributed to *Taeniopteris angustifolia*, which, according to current perception, appears to be a common representative of Ladinian–Norian floras of the southern German Basin. The foliage is of unknown affinity and is mentioned in a number of older and recent publications (i.a. SCHENK 1864; SCHENK in SCHÖNLEIN 1865; COMPTON 1874, 1894, 1912; HEER 1877; LEUTHARDT 1904; KRÄUSEL & SCHAARSCHMIDT 1966; KELBER & HANSCH 1995; KELBER & NITSCH 2005).

From Neuwelt, *Taeniopteris angustifolia* was first reported by HEER (1877), who based the identification of his specimens on an illustration of a specimen from the Ladinian or Carnian (Lower Keuper) of Lower Franconia, published by SCHENK (1864, pl. 2, fig. 5) as *Taeniopteris angustifolia*. The specimen of SCHENK (1864) shows a compound fern-like leaf and HEER (1877) interpreted the single leaves from Neuwelt as isolated pinnae of such a frond.

The specimen of SCHENK (1864), however, was recently identified as the holotype of the marattialean fern *Danaeopsis angustifolia* (KUSTATSCHER et al. 2012), whereof the name *Taeniopteris angustifolia* is consequently the basionym. The leaves from Neuwelt are, in contrast, not only completely different in their appearance, their anatomy (shape, outline, venation) from *Danaeopsis angustifolia*, but also more likely to interpret as single, entire-margined leaves than as leaflets of a compound leaf or frond, due to their symmetrical shape, their prominent petiole and the fact that they apparently are shed individually. Therefore, we regard the leaves from Neuwelt attributed to *Taeniopteris angustifolia* not conspecific with *Danaeopsis angustifolia*. This implies that all specimens, which were identified as *Taeniopteris angustifolia* based on HEER (1877) need reconsideration.

Recent findings of well-preserved identical leaves from Carnian strata on the islands of Hopen and Edgeøya, Svalbard (Fig. 1A), raised interest in this species and, in consequence of the study by KUSTATSCHER et al. (2012), necessitated the revision of *Taeniopteris angustifolia sensu* HEER (1877) and its taxonomic status. In the present study, we re-

evaluated the original material from Neuwelt together with the new specimens from Hopen and Edgeøya. As no holotype is available and *Taeniopteris angustifolia* is the basionym for *Danaeopsis angustifolia*, a new species name with a new type is required.

2. Material and methods

The original material of *Taeniopteris angustifolia* from Neuwelt comprises eleven specimens (HEER 1877; KRÄUSEL & SCHAARSCHMIDT 1966), whereof eight are still present in the paleontological collections of the Natural History Museum of Basel, Switzerland, and available under accession numbers NHMB B635–640, B641/2, B722/2; two additional specimens (B633 and B1376) were mentioned by KRÄUSEL & SCHAARSCHMIDT (1966). From a recent geological excursion to Hopen (LAUNIS et al. 2014), three specimens yielding *Taeniopteris* leaves were obtained at Gåsskaret on Kollerfjellet. Those specimens are stored in the paleontological collections of the Natural History Museum, Oslo, Norway, under accession numbers PMO 227.556A, 227.561 and 227.573. Nineteen specimens from Kvalpynten on Edgeøya, yielding 20 leaves, were identified in the palaeobotanical collections of the Laboratory of Palaeobotany and Palynology (LPP), University Utrecht, The Netherlands (accession numbers 24210, 24215, 24216, 24218, 15 specimens without number), on a recent visit of CP. In addition to these specimens, a few specimens from Kapp Lee on Edgeøya (Svalbard; Fig. 1A) and Kollerfjellet on Hopen have been considered, which have earlier been published by VASILEVSKAYA (1972, 1983) (cf. POTT 2012). These specimens are stored in the A. P. Karpinsky Russian Geological Research Institute VSEGEI, St. Petersburg, Russian Federation, under accession numbers 10979-24, 10979-25, 10979-52, 10979-65, 10979-71, 4/12163, 18/12163–20/12163 and were examined during a visit of CP in 2011.

The specimens from Neuwelt (Münchenstein) come from the Carnian Schilfsandstein Member of the Mergelkeuper Formation (SCHMASSMANN 1953; BITTERLI-BRUNNER 1987; JORDAN 2008); the specimens from Hopen and Edgeøya have been obtained from two beds within the lower part of the Carnian–Norian De Geerdalen Formation (see POTT 2012; LAUNIS et al. 2014; VIGRAN et al. 2014, and references therein).

The hand specimens were analysed under a dissecting microscope and photographed with Nikon D80/Nikkor AF-S Mikro 60mm 1:2.8G ED and Nikon D300/Sigma 50mm F2.8 EX DG Macro system digital cameras; in order to enhance contrast, cross-

polarisation and oblique lighting were used. Some specimens were analysed with an Olympus BX51 microscope under fluorescent light at the Palaeobiology Department of the Swedish Museum of Natural History, Stockholm, by CP, but no fluorescent cuticles were observed, and cuticles, if they were present, did not survive maceration by standard techniques (cf. POTT & MCLOUGHLIN 2009).

3. Systematic palaeobotany

Class Cycadophyta

Order Incerti ordinis

Family Incertae familiae

Genus *Taeniopteris* BRONGNIART 1828.

Diagnosis: Leaves with a simple, entire-margined lamina. Midvein rigid, extending for the entire length of the leaf. Lateral veins approximately perpendicular to the midvein, simple or forking at the base. Epidermal anatomy not known (after BRONGNIART 1828; CLEAL & REES 2003).

Type species: *Taeniopteris vittata* BRONGNIART 1828; from the Middle Jurassic of Stonesfield, Oxfordshire, UK (STERNBERG 1823; MILLER 1889).

Remarks: *Taeniopteris* is traditionally used as a morpho-taxon for entire-margined leaves with a cycadophyte appearance, whose affinity cannot entirely be ascertained due to the lack of epidermal details (i.e. the architecture of the stomata), which are necessary for an unequivocal assignment (THOMAS & BANCROFT 1913; POTT 2007). The use of *Taeniopteris* and the debate concerning its affinity and typification is addressed in the 'Discussion' section below.

Taeniopteris novomundensis C.POTT et A.LAUNIS sp. nov.

Figs. 2–5

Records

1828	<i>Taeniopteris vittata</i> , <i>pro parte</i> . BRONGNIART, p. 263, no illustration (specimens of MERIAN).
1835	<i>Taeniopteris vittata</i> var. <i>minor</i> . MERIAN, p. 37, no illustration.
1877	<i>Taeniopteris angustifolia</i> SCHENK. HEER, p. 72, pl. 24, figs. 2–3, 3c, pl. 30, fig. 3e.
1966	<i>Taeniopteris angustifolia</i> . KRÄUSEL & SCHAARSCHMIDT, p. 29, pl. 10, figs. 2–8.

- 1972 *Taeniopteris* sp. VASILEVSKAYA, p. 51, pl. 15, fig. 3b, pl. 16, figs. 1–2a, 3–5.
- 1983 *Taeniopteris* sp. VASILEVSKAYA, p. 143, pl. 6, figs. 2–4.
- 2010 *Taeniopteris kelberi* KUSTATSCHER et VAN KONIJNENBURG-VAN CITTERT 2010, *pro parte*. KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT, p. 14 (specimens of HEER, LEUTHARD and KRÄUSEL & SCHAARSCHMIDT).
- 2012 *Nilssoniopteris angustior* (STUR ex KRASSER 1909) POTT, KRINGS et KERP 2007, *pro parte*. POTT, p. 38, no illustration.
- 2014 *Taeniopteris* sp. LAUNIS et al., p. 39, fig. 4C, E–F.

Rejected records

- non 1864 *Taeniopteris angustifolia*. SCHENK, p. 53, pl. 2, fig. 5.
- non 1865 *Taeniopteris angustifolia* SCHENK. SCHENK in SCHÖNLEIN, p. 16, pl. 7, fig. 1, pl. 8, fig. 9.
- non 1874 *Danaeopsis angustifolia* (SCHENK). COMPTEUR, p. 6, no illustration.
- non 1874 *Pterophyllum jaegeri* var. *brevifolia* KURR. COMPTEUR, p. 6, pl. 1, fig. 1.
- non 1894 *Taeniopteris angustifolia* SCHENK. COMPTEUR, p. 207, pl. 2, fig. 2.
- non 1904 *Taeniopteris angustifolia* SCHENK (var. *siliquosa* LEUTHARDT). LEUTHARDT, p. 28, pl. 12, fig. 1, pl. 21, fig. 3.
- non 1912 *Taeniopteris angustifolia* SCHENK. COMPTEUR, p. 82, no illustration.
- non 1995 *Taeniopteris angustifolia*. KELBER & HANSCH, p. 70, text-figs. 145–149, 287, 296.
- non 2005 *Taeniopteris angustifolia*. KELBER & NITSCH, text-fig. 8e.

See also KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT (2010), p. 14: *Taeniopteris kelberi*.

Etymology: After the locality name Neuwelt (literally translated: ‘new world’, ‘*mundus novus*’), where the first specimens of the new species have been obtained.

Holotype: Slight difficulties appear when tracing the specimens figured by HEER (1877) on pl. 24, figs. 2 and 3, which can be regarded as the type specimens (syntypes). KRÄUSEL & SCHAARSCHMIDT (1966) state that the specimen in fig. 2 is lost, but the specimen in fig. 3 is still present in the collections under accession number B722/2, the illustration of which by HEER (1877), as KRÄUSEL & SCHAARSCHMIDT (1966) state, does not entirely depict the specimen because it has been modified by the illustrator. However, when comparing the illustrations of HEER (1877) and the photographs of KRÄUSEL & SCHAARSCHMIDT (1966), it appears to us that the specimens in pl. 10, figs. 2 and 3 of KRÄUSEL & SCHAARSCHMIDT (1966) are those illustrated by Heer (1877) on plate 24, figs. 2 and 3, respectively. Still, it is not completely unambiguous, and, therefore, a new type is designated here. The specimen serving this best is NHMB B640, figured here on fig. 2A; we here agree with KRÄUSEL & SCHAARSCHMIDT (1966).

Paratypes: Specimens figured by HEER (1877) on pl. 24, figs. 2 and 3, and on pl. 30, fig. 3e; and by KRÄUSEL & SCHAARSCHMIDT (1966) on pl. 10, figs. 2–3, 5–8.

Deposition of types: Palaeontological collections of the Natural History Museum Basel (NHMB), Basel, Switzerland.

Type locality and horizon: Neuwelt (Münchenstein), Basel-Land, Switzerland; Mergelkeuper Formation, Schilfsandstein Member, Carnian (SCHMASSMANN 1953; BITTERLI-BRUNNER 1987; JORDAN 2008).

Material studied: NHMB B635–B640, B641/2, B722/2; VSEGEI 10979-24, 10979-25, 10979-52, 10979-65, 10979-71, 4/12163, 18/12163–20/12163; PMO 227.556A, 227.561, 227.573; LPP 24210, 24215, 24216, 24218, 15 specimens without number.

Diagnosis: Cycadophyte foliage of unknown affinity; leaves long and slender, fusiform to lanceolate; lamina robust, entire-margined, with straight margins, tapering towards extended and pointed apex and base; rachis prominent, retaining its width throughout the whole leaf; veins delicate, dense, parallel, emerging laterally from the rachis in angles of $\sim 80^\circ$, occasionally bifurcating close to the rachis and proceeding straight to the leaf margin; epidermal anatomy unknown.

Description: Leaves of *Taeniopteris novomundensis* are up to 15 cm long and 21 mm wide at their widest point (Fig. 2A–B), which is in the middle portion of the leaf. Most leaves are incomplete; some of them suggest a leaf length even up to 22–25 cm. The leaves taper continuously towards their apex and base (Figs. 2A, C–D, 3B, 5); the apex is acutely rounded (Fig. 2A, C) and the base contracted. The entire-margined lamina was apparently very robust and is characterised by straight margins and a central, 2–4 mm wide, slightly depressed rachis (Figs. 3A, C, F, 4A–E) that proceeds into a short, 10–15 mm long petiole up to 3 mm wide (Figs. 3C–D, 5). The rachis widens slightly when entering the petiole, but retains its width throughout the course of the whole leaf and gives off delicate, densely spaced, parallel lateral veins at angles of $75\text{--}80^\circ$ (Figs. 2B, 3B, E, 4A, B, D, 5), occasionally bifurcating close to the rachis and proceeding straight to the leaf margin (Figs. 3F, 4A). No information on epidermal anatomy is available.

Occurrence: Carnian of Switzerland (Neuwelt) and Svalbard (Edgeøya and Hopen).

Remarks: *Taeniopteris novomundensis* is discussed below in more detail.

4. Discussion

4.1. Remarks on the typification and use of *Taeniopteris*

The typification of *Taeniopteris* is still a matter of debate and a consensus has not yet been reached. CLEAL & REES (2003) recommended *Taeniopteris vittata* as the type species following MILLER (1889), and came to the conclusion that the specimen figured by STERNBERG

(1823, pl. 37, fig. 2; refigured by CLEAL & REES 2003, pl. 7, fig. 1) is the “only sensible choice as lectotype” (CLEAL & REES 2003, p. 762). This specimen originated from the Middle Jurassic of Stonesfield, Oxfordshire, UK, and has no cuticles preserved. Therefore, it is unknown whether *Taeniopteris* is a cycad (comparable to *Bjuvia*), a bennettite (comparable to *Nilssoniopteris*) or even a member of the Nilssoniales (comparable to *Nilssonia*). CLEAL & REES (2003) and CLEAL et al. (2006) also clarified that *Taeniopteris vittata* is certainly not the type of *Nilssoniopteris* in contrast to earlier views (e.g. FLORIN 1933; HARRIS 1969). More or less entire-margined bennettitalean leaves from the Yorkshire Jurassic that are superficially similar to *Taeniopteris vittata*, but where cuticles are preserved, should be more correctly referred to as *Nilssoniopteris solitaria* (CLEAL & REES 2003; CLEAL et al. 2006).

It is rather questionable that the specimens published by BRONGNIART (1831, pl. 82, figs. 1–4) in the protologue of *Taeniopteris vittata* are conspecific with the type specimen of *Taeniopteris vittata* from Stonesfield. The specimen in BRONGNIART’s figure 1 comes from the Aalenian of Whitby, Yorkshire, UK, and is certainly a *Nilssoniopteris solitaria*, whereas the specimens in figures 2 and 3 are from the Bathonian of Scarborough, Yorkshire, and could either be *Nilssoniopteris major* (fig. 2) or *Nilssoniopteris solitaria* (fig. 3) (cf. HARRIS 1969) or, less likely, a *Nilssonia tenuinervis* (nom. illeg., CLEAL et al. 2006) (HARRIS 1964); the fourth specimen comes from the Hettangian of Höör, Scania, Sweden, and lacks cuticle (CP, own observation) (personal communication with J.H.A. VAN KONIJNENBURG-VAN CITTERT, April 2014).

A recent proposal to conserve the name *Taeniopteris* with a conserved type (DOWELD 2013) also regards *Taeniopteris vittata* as the type but with one of the specimens published by BRONGNIART (1831, pl. 82, fig. 2) as the type specimen, which is more likely attributable to *Nilssoniopteris major* (based on its epidermal anatomy and the presence of brachyparacytic [=syndetocheilic] stomata). DOWELD (2013) most likely overlooked STERNBERG’s specimen, which certainly is a *Taeniopteris*, and did not consider the works of MILLER (1889) and CLEAL & REES (2003), where the typification of *Taeniopteris* is assessed in detail. The author, moreover, refers to differences in epidermal anatomy between *Taeniopteris* and *Marantoidea* outlined in BORNEMANN (1856) and WEBB (2001). In the cited works, however, no information on epidermal anatomy of any of the species is given at all; and the epidermal anatomy of *Taeniopteris* is still unknown.

We here agree with CLEAL & REES (2003) that the specimen of STERNBERG (1823, pl. 37, fig. 2) is the best choice as a lectotype of *Taeniopteris vittata* and, therefore, of *Taeniopteris*.

The affinity of the genus can consequently not be clarified based on the type species/specimen, which was regarded as a leaf portion of a *Scitaminea* (modern Zingiberales) by STERNBERG (1823). After considerable personal discussion with J.H.A. VAN KONIJNENBURG-VAN CITTERT (Leiden & Utrecht, The Netherlands) and G. ZIJLSTRA (Utrecht, The Netherlands), we all came to the conclusion that the best and simplest option is to leave *Taeniopteris* as an illegitimate genus and not to support to conserve it at all. STAFLEU (1987) in an editorial note in *Taxon* 36, p. 648, already gave comments on the difficulties concerning the genus. However, even if the genus is illegitimate, the various species are validly published (if done according to the rules of that time) and can, therefore, be legitimate (Art. 55 in the *International Code of Nomenclature for algae, fungi, and plants [Melbourne Code]*; MCNEILL et al. 2012). So we can continue to use *Taeniopteris* as a fossil genus for leaves of a certain shape and venation, of which no cuticle is known. As soon as epidermal anatomy becomes available, the material can then be transferred to e.g. *Nilssoniopteris*, *Nilssonia*, etc. or, in the case of a fertile fern, to *Danaeopsis*.

4.2. Remarks on *Taeniopteris novomundensis* sp. nov.

HEER (1877) identified the Neuwelt leaves using a specimen documented by SCHENK (1864, pl. 2, fig. 5) as *Taeniopteris angustifolia* from Franconia. As mentioned above, this specimen has recently been identified as the holotype of *Danaeopsis angustifolia* (KUSTATSCHER et al., 2012), a marattialean [tree] fern characterised by large, once-pinnate fronds, whose individual pinnae resemble *Taeniopteris novomundensis*, but they display an entirely different venation and leaf outline (see KUSTATSCHER et al., 2012). *Taeniopteris novomundensis*, furthermore, represents individual single leaves that are, in our opinion, not leaflets of compound leaves. This implies that all specimens based on HEER's (1877) identification assigned to *Taeniopteris angustifolia* had to be reconsidered. We here include most specimens in the new species *Taeniopteris novomundensis* that have been identified earlier as *Taeniopteris angustifolia* based on HEER's report (1877).

The specimens identified by HEER (1877) as *Taeniopteris angustifolia* are most likely those that MERIAN (1835) collected and reported from Neuwelt as *Taeniopteris vittata* var. *minor*. From MERIAN's report (1835, p. 37), it is evident that BRONGNIART was aware of the fossils and included them in his *Histoire des végétaux fossiles* (BRONGNIART 1831, p. 263), but lat-

er authors disregarded MERIAN's report. We disagree with KRÄUSEL & SCHAARSCHMIDT (1966) that the fossils known to BRONGNIART were most likely what was later identified as *Taeniopteris angustifolia* var. *siliquosa* by LEUTHARDT (1904; =*Leguminanthus siliquosus*), bennettitalean microsporophylls that resemble *Taeniopteris* leaves folded along their rachis (see below). HEER (1877) only figured 'true' *Taeniopteris angustifolia* leaves and did not mention or describe the 'siliquosa' leaves at all. The 'siliquosa' leaves most likely came only later to the museum collections through the private collection of LEUTHARDT, which were acquired in 1910, and were thus unknown to MERIAN, BRONGNIART and HEER. LEUTHARDT (1904, p. 28), moreover, stated that "this character [the 'folded' lamina] is present in all my specimens ... while the other leaves represent a much more slender form", which gives the impression that he regarded the 'true' specimens different. Later, he also stated that the specimens collected by MERIAN were assigned to *Taeniopteris vittata* by BRONGNIART (1831). The inclusion of MERIAN's or HEER's specimens in *Leguminanthus siliquosus* by LEUTHARDT (1904) was consequently unjustified (see also KRÄUSEL & SCHAARSCHMIDT 1966).

Besides Neuwelt, leaves now assigned to *Taeniopteris novomundensis* are so far only known from different localities on Svalbard, originally reported as *Taeniopteris* sp. (VASILEVSKAYA, 1972, 1983; POTT 2012; LAUNIS et al. 2014). VASILEVSKAYA (1972) compared the leaves from Svalbard with specimens from Neuwelt, but refrained from assigning the Svalbard specimens to any species and left the taxonomic issue unresolved. POTT (2012) included a number of Svalbard specimens with entire-margined *Taeniopteris*-like foliage comprising those of VASILEVSKAYA (1972, 1983) in *Nilssoniopteris angustior* (POTT et al. 2007b), but the new fossils found in 2011 on Hopen (LAUNIS et al. 2014) revealed that the specimens VSEGEI 10979-24, 10979-25, 10979-52, 10979-65, 10979-71, 4/12163, 18/12163–20/12163 from Edgeøya and Hopen (cf. VASILEVSKAYA 1972, 1983) belong to a different species instead and thus have to be separated from the *Nilssoniopteris angustior* of POTT (2012). The findings also revealed the conspecificity of the fossils from Hopen and Edgeøya with the Neuwelt specimens and prompted the here presented re-evaluation of the latter.

The material published by SCHENK in SCHÖNLEIN (1865) as *Taeniopteris angustifolia* has partly been assigned to *Danaeopsis angustifolia* by KUSTATSCHER et al. (2012). The remaining figured specimens and those reported by COMPTON (1874, 1894, 1912), KELBER & HANSCH (1995) and KELBER & NITSCH (2005) from the Carnian (Keuper) of Franconia, Germany, belong to a species different from *Taeniopteris novomundensis* as they have a different venation

and a tapering rachis that is much wider basally (typically 8–12 mm wide). Those records were attributed to *Taeniopteris kelberi* by KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT (2010), a species, which is very similar to *Taeniopteris novomundensis*, but easily recognised by its different, tapering rachis. KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT (2010) included the *Taeniopteris* specimens of HEER (1877) and KRÄUSEL & SCHAARSCHMIDT (1966) as well as the *Leguminanthus siliquosus* leaves of LEUTHARDT (1904) in *Taeniopteris kelberi*, which is, as outlined above, incorrect and consequently rejected here. Superficially similar specimens from the Upper Triassic of Franz Josef Land, Russian Federation, assigned to different *Taeniopteris* species by VASILEVSKAYA (1985) are better placed in *Nilssoniopteris angustior* (cf. POTT et al. 2007b; POTT 2012).

A species very close if not conspecific with *Taeniopteris novomundensis* was reported from the Lower Cretaceous of Franz Josef Land by SVESHNIKOVA & BUDANTSEV (1969) as *Nilssoniopteris polymorpha*. The similar appearance is striking, but considering these species conspecific would make it a rather long-ranging taxon, which is unreliable given the number of similar but differing species from Jurassic to Cretaceous deposits of the Northern Hemisphere (e.g. *Nilssonia resoluta*, *N. tenuinervis*, *N. bluebirdii* or *Jacutiella amurensis*; SAMYLINA 1956; HARRIS 1964; WATSON & CUSACK 2005; POTT et al. 2014).

All specimens including those from Svalbard and Switzerland lack organic remains and information on epidermal anatomy is, consequently, unavailable. This would be evident to assign the species confidently either to Bennettitales (e.g. *Nilssoniopteris*), Cycadales (e.g. *Bjuvia*) or Nilssoniales (e.g. *Nilssonia*). In our opinion, a bennettitalean affinity of the species is most likely given its similarity to other *Nilssoniopteris* foliage types reported from Svalbard, Lunz and Neuwelt, the absence of any cycad remains (inclusive reproductive structures) from Svalbard and Neuwelt, and the different leaflet morphology of all so far known Mesozoic cycad remains. *Nilssoniopteris* foliage from Lunz was previously classified as *Taeniopteris*, which was, at that time, regarded as a genus of marattialean ferns (KRASSER 1909), but has recently been identified as bennettitalean foliage based on its epidermal anatomy (POTT et al. 2007b). An affinity of *Taeniopteris novomundensis* to any fern family has been ignored per se by previous authors, but is not impossible given that *Taeniopteris* also included foliage specimens that were later identified as ferns.

4.3. Remarks on *Leguminanthus siliquosus*

The previous assignment of the *Taeniopteris novomundensis* leaves to *Leguminanthus siliquosus* (as *Taeniopteris angustifolia* var. *siliquosa*) by Leuthardt (1904) reveals the close resemblance of both species. *Leguminanthus siliquosus* organs are, however, much wider (up to 30 mm, 'folded' form) and longer (up to 24 cm) and connate at the ventral joint (KRÄUSEL & SCHAARSCHMIDT 1966), with a much more prominent midvein (dorsal joint) and more bluntly rounded apices and broader bases. The veins of *Leguminanthus siliquosus* always bifurcate once close to the rachis while in *Taeniopteris novomundensis*, not all veins bifurcate when they enter the lamina. A closer look into their internal anatomy revealed that the previous assumption, they could just be folded *Taeniopteris* leaves (e.g. LEUTHARDT 1904), is unsupported. KRÄUSEL & SCHAARSCHMIDT (1966) elucidated that *Leguminanthus siliquosus* is, instead, a bennettitalean microsporophyll with numerous pollen sacks attached to the 'inner' surface of the pod-like organs; it occurred in both the Neuwelt and Lunz floras. In addition, the macroscopic and epidermal anatomies of the lamina of *Leguminanthus siliquosus* are strikingly similar to that of *Nilssoniopteris angustior* from Lunz (lamina < 52 mm wide, > 29 cm long; identical venation pattern) (POTT et al. 2007b). POTT et al. (2010), however, suggested that *Nilssoniopteris angustior* might be the sterile foliage of a plant bearing bennettitalean reproductive structures comprising *Bennetticarpus* seed cones and *Haitingeria* microsporophylls. This concept might have to be re-evaluated as it appears more likely that *Nilssoniopteris angustior* leaves and *Leguminanthus siliquosus* 'pods' belonged to the same parent plant. The anatomical differences make it rather unlikely that *Taeniopteris novomundensis* belonged to *Leguminanthus siliquosus*. The fertile organs of the plant bearing *Taeniopteris novomundensis* leaves are consequently still unknown.

It is interesting to note that *Nilssoniopteris angustior* has not yet been found at Neuwelt, whereas *Taeniopteris novomundensis* has not yet been found in the flora from Lunz, while *Leguminanthus siliquosus* 'pods' occurred in both floras. Both foliage types, however, co-occurred in the flora from Svalbard, together with *Leguminanthus siliquosus* on Kapp Lee, Kvalpynten and Kollerfjellet (POTT 2012; LAUNIS et al. 2014). In our opinion, it is more likely that *Nilssoniopteris angustior* was present in Neuwelt as well, but has not yet been found. Unfortunately, new material from Neuwelt will not emerge, since all localities are no longer accessible, because the area is now completely covered by concrete due to the construction of a power plant.

4.4. Palaeoecology and palaeogeography

Recent re-evaluation of the Carnian flora from Svalbard (POTT 2012; LAUNIS et al. 2014) could substantiate the earlier assumed resemblance to the Neuwelt and Lunz floras from the Northern Calcareous Alps (VASILEVSKAYA 1972). A comparatively high number of taxa are shared by both floras and the Svalbard flora (cf. POTT 2007, 2012; POTT et al. 2008; POTT & KRINGS 2010; LAUNIS et al. 2014) despite their separation by more than 5000 km (or more than 30 degrees of latitude) already during the Carnian (Fig. 1B). At the same time, minor local differences in the composition of the floras occurred as well: cycad-like Nilssoniales (POTT et al. 2007a) have, for example, not been noted from Neuwelt or Svalbard, whereas putative pteridosperms such as *Paratatarina* are so far 'endemic' to Svalbard (POTT 2012). The Carnian flora in deltaic environments in the central part of Laurasia with its northern and southern shores was consequently rather uniform and poor in diversity with minor local differences or adaptations, which led POTT (2012) hypothesise that the floristic North Atlantic sub-province, which was well-established at the close of the Triassic (POTT & MCLOUGHLIN 2011), might have been developing much earlier. Ongoing collecting and concurrent analyses of the Svalbard, Lunz and Neuwelt floras are continuously producing new findings that substantiate this view (e.g. POTT et al. 2007a, 2007b; MELLER 2009; LAUNIS et al. 2014; this study; CP, own observation).

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Figure captions

Fig. 1. **A** – Map of northern Europe depicting the present day locations of the Neuwelt, Edgeøya and Hopen fossil localities. **B** – Map of the same area during the Late Triassic (220 mya) with the contemporary locations of the Neuwelt and Svalbard floras. Palaeomap based on reconstructions by Ron Blakey, Colorado Plateau Geosystems, Inc., Flagstaff, AZ, USA. Scale bars – 500 km.

Fig. 2. *Taeniopteris novomundensis* sp. nov. from the Carnian of Neuwelt, Münchenstein, Basel-Land, Switzerland. **A** – Lectotype, depicting the upper portion of a leaf; note the pointed apex; specimen NHMB B640. **B** – Close-up of the lower portion of the specimen in A, depicting details of the venation. **C** – Another leaf on the lectotype specimen; note the pointed apex, the tapering leaf lamina and the venation. **D** – Upper portion of a leaf; specimen NHMB B636. Scale bars – 1 cm.

Fig. 3. *Taeniopteris novomundensis* sp. nov. from the Carnian of Kapp Lee, Edgeøya, and Kollerfjellet, Hopen, Svalbard. **A** – Well-preserved middle portion of a leaf; specimen PMO 227.573. **B** – Almost complete leaf; note the lamina tapering towards base and apex; specimen PMO 227.556A. **C** – Complete leaf, of which the apex is bent down into the rock matrix; note the central rachis keeping its width throughout the course of the leaf; specimen VSEGEI 4/12163. **D** – Almost entire leaf; note the petiole; specimen VSEGEI 10797-52. **E** – Upper portion of a leaf; note the rachis and the secondary veins; specimen VSEGEI 10797-25. **F** – Close-up of the middle portion of the specimen in A depicting the venation in detail. Scale bars – 1 cm.

Fig. 4. *Taeniopteris novomundensis* sp. nov. from the Carnian of Kvalpynten, Edgeøya, Svalbard. Well-preserved middle portions of different leaves. **A** – Specimen LPP 24210. **B** – Specimen LPP 24215. **C** – Specimen LPP 24216. **D** – Specimen LPP 24216. **E** – Specimen LPP 24218. Scale bars – 1 cm.

Fig. 5. Restoration of an entire leaf of *Taeniopteris novomundensis* sp. nov. based on different specimens from Neuwelt, Edgeøya and Hopen. Scale bar – 1 cm.