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Bipinnate *Ptilozamites nilssonii* from Jameson Land and new considerations on the genera *Ptilozamites* Nathorst 1878 and *Ctenozamites* Nathorst 1886

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ABSTRACT

Newly collected Rhaetian plant compressions of the seed fern *Ptilozamites nilssonii* Nathorst 1878 from Jameson Land, Eastern Greenland, revealed both simple and forked, unipinnate and bipinnate morphologies, indicating a closer relationship between the genera *Ptilozamites* Nathorst 1878 and *Ctenozamites* Nathorst 1886 than previously documented. Cuticle analysis revealed micromorphological traits typical of simply pinnate *P. nilssonii* on bipinnate leaf forms, yet up until the discovery of this material *Ptilozamites* has never been considered bipinnate. In 1886, the genus *Ctenozamites* was erected for species similar in epidermal characters to *Ptilozamites*, but presenting a typical bipinnate character, rarely or never unipinnate. As the new Greenland material collected from South Tancrediakløft and Astartekløft have shown, both genera are now very strongly related anatomically, and therefore identical from a systematic point of view. We therefore propose the use of the genus *Ptilozamites* as *Ctenozamites* Nathorst 1886 is a synonym of *Ptilozamites* Nathorst 1878.

1. Introduction

Gymnosperms with uncertain affinities such as the group represented by the genera *Ptilozamites* Nathorst, 1878a,b, *Ctenozamites* Nathorst, 1886, and *Raphidopteris* Barale 1972 include pteridosperm foliage with a high degree of morphological variation. They often show unclear systematic and stratigraphic status. The Jameson Land basin in Eastern Greenland includes a diverse assemblage of Late Triassic–Early Jurassic seed ferns with uncertain systematic affinities (Harris, 1964). Among them, *Ptilozamites nilssonii* Nathorst, 1878a,b is a frequent Rhaetian species, with highly variable and well preserved foliage.

The Triassic–Jurassic compressive flora of Jameson Land (formerly known as Scoresby Sound), Eastern Greenland was first described by Hartz (1896, 1902), and studied extensively by T.M. Harris (1926, 1931a,b, 1932a,b, 1935, 1937, 1946, 1961). This flora is one of the most diverse and well preserved floras in the Northern Hemisphere, which has received increasing attention over the last decade owing to its potential for elucidating paleoecological and paleoclimatic changes associated with the Triassic–Jurassic mass extinction event (McElwain et al., 1999; Beerling and Berner, 2002; McElwain et al., 2007). Harris produced a classical monographical series on all groups of fossil Triassic–Jurassic plants from Jameson Land, including bryophytes, pteridophytes and gymnosperms. Later publications by Pedersen (1976, 1984), Pedersen and Lund (1980), and Pedersen et al. (1989) provided further details on the Triassic–Jurassic macroflora and microflora of the basin. The basin of Jameson Land includes the Triassic–Jurassic continental Kap Stewart Group (Dam and Surlyk, 1993; Surlyk, 2003), yielding rich assemblages of Rhaetian–Hettangian aged fossil plants.

Ptilozamites nilssonii Nathorst, 1878a,b is the only *Ptilozamites* species reported from Greenland (Harris, 1926, 1932a, 1937), its foliage being common in the Rhaetian beds of Jameson Land. The material discussed in this paper was collected in 2002 and 2004 during the first paleobotanical field trips in this area after those of Hartz, Harris and Pedersen.

2. Occurrence and stratigraphy

The fossil material was collected from Jameson Land (Scoresby Sound), Eastern Greenland, from two representative localities of the Triassic–Jurassic flora: Astartekløft and South Tancrediakløft (Fig. 1). The Triassic–Jurassic Kap Stewart Group is well outcropped in these two plant localities, permitting precise and detailed sampling. The material

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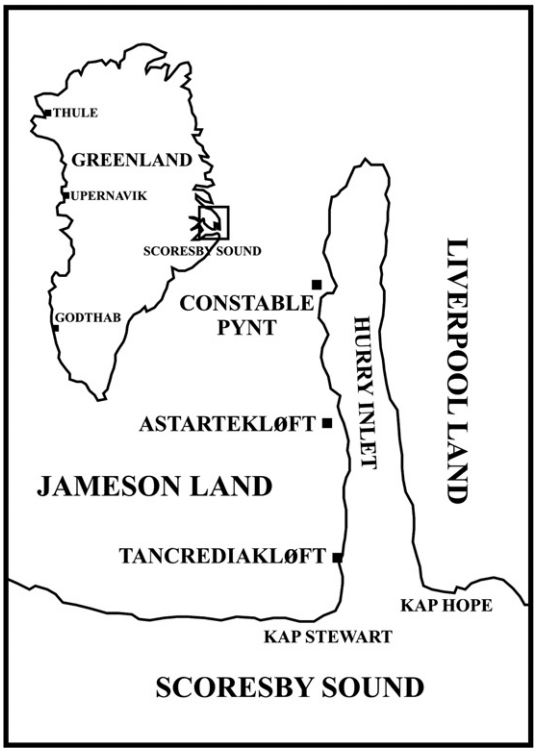

Fig. 1. Occurrence of Triassic–Jurassic plant localities Tancrediakløft and Astartekløft in Jameson Land, Eastern Greenland.

discussed here is Rhaetian in age, and has been collected from Bed 1 at a height of 21 m (which occurs below the *Lepidopteris* Bed of T.M. Harris) from South Tancrediakløft in 2004, and Bed 5 which occurs at a height of 46.4 to 46.9 m (Bed D of T.M. Harris) from Astartekløft in 2002.

Harris (1926, 1932a, 1937) reported *Ptilozamites nilssonii* from 8 localities in Jameson Land: Ryder River (*Nilssonia* Bed), Zamiteselv, Primulaelv, Astartekløft (*Lepidopteris* Bed, Bed B, Bed D), Vardekløft (*Dictyophyllum* Bed, *Anomozamites* Bed), Tancrediakløft (*Lepidopteris* Bed), Neill Cliffs (*Neocalamites* Bed, *Lepidopteris* Bed), and Kap Stewart (*Anomozamites minor* Bed). All these occurrences include *P. nilssonii* associated with taxa belonging to the *Lepidopteris ottonis* Assemblage Zone, marker for the Late Triassic (Rhaetian) interval. The latest field trips in Jameson Land (2002, 2004) and the collected material confirmed the constant Rhaetian age of *P. nilssonii* foliage.

3. Materials and methods

The material is compressed, represented by more than 73 leaf fragments including petioles, pinnae, pinnules, primary and secondary rachises. The leaf compressions are often found in very dense accumulations, where both unipinnate and bipinnate types occur, especially in South Tancrediakløft. The taphonomy of the plant material in their occurrence beds indicate a lack of transport, the leaves being probably shed in situ, with minimal or no transport at all. The leaf fragments are large, sometimes reaching 20–30 cm in length, but usually the fragments are 10–15 cm long. The preservation of the plant material is variable, ranging from very well preserved presenting a black, thick lamina with well preserved cuticles, to poorly preserved showing a very thin, brown lamina and collapsed, eroded cuticles. The *Ptilozamites* material is often associated with *Lepidopteris ottonis* material within the same beds.

In the field, the fossil material was collected using paleoecological protocols (McElwain et al., 2007), at cm by cm resolution within the plant beds. In the laboratory, the compressions were macerated using Schulze's Reagent, a mixture of $KClO_3$ and HNO_3, with 40% and 60% HNO_3. In some cases, cuticles were slightly heated to accelerate the oxidizing process. After oxidation, the material was washed, neutralized with KOH (5%) for a short time interval, washed again, and mounted on microscope (biological) slides, or on SEM stubs, in order to study in detail the cuticle anatomy of leaf compressions. The biological slides were studied and photographed using a Leica DLMB microscope with a mounted digital camera permitting serial microphotos using Automontage© for increased depth of field.

Macrophotos were taken using a Canon Powershot S3IS with both macro and supermacro modes, the latter mode permitting significant close-up of the fossils. Artificial lights were used with a copy stand in UCD, using lateral illumination, with one or two lateral light sources, depending on the material. Some material was photographed submersed in water, in order to enhance specimen contrast. Digital photographs were converted to grayscale and contrast enhanced using Corel Photopaint 11. Natural illumination was also used in various cases when artificial light did not induce the necessary contrast, especially in the case of poorly preserved but significant leaf material. The material is curated within the Paleobotany collections at the Field Museum, Chicago (the 2002 field trip material), and at the University College Dublin, in Dublin (the 2004 field trip material).

Systematics

Class Pteridospermopsida

Order unknown

Family unknown

Genus *Ptilozamites* Nathorst, 1878a,b emend.

The genus *Ptilozamites* was erected by Nathorst (1878b) for unipinnate, coriaceous, simple forked or unforked leaf fragments with odontopteroid pinnules from Upper Triassic–Lower Jurassic coal bearing sediments in Scania, without indicating a type species for this denomination. The type species was later considered without any explanation as *Ptilozamites heeri* (Seward, 1910), although *Ptilozamites nilssonii* was the first described in Nathorst's original paper. Antevs (1914) added cuticular descriptions for this genus, identifying the sunken stomata and the fused, raised, ring-like structure of the subsidiary cells as typical characters for *Ptilozamites*. Harris (1926, 1932a, 1937) described in detail the material collected from Jameson Land belonging to *P. nilssonii*, by both microscopical and macroscopical approaches.

The affinities of *Ptilozamites* probably lie with the pteridosperms (Harris, 1931a, 1961; Kustatscher and Van Konijnenburg-Van Cittert, 2007) although it was suggested by earlier authors that they were related to the cycadophytes (Nathorst, 1878b; Seward, 1910). Harris (1932b, 1937) considered, based on cuticle analysis that *Hydropterangium* Halle 1910 (misspelled sometimes as *Hydropteridangium marsilioides*) represents the male reproductive structures of *Ptilozamites nilssonii*, and Lundblad (1961) considered a different denomination for them, as *Harrisotheca marsilioides* Lundblad 1961. Unfortunately, no supplementary *H marsiliodies* material was collected recently from Greenland, and the type material is missing from the Geological Museum in Copenhagen, where the Harris collection is stored and curated. *Ptilozamites* species were described from Sweden, Greenland, Germany, China, Japan, where they range from Middle Triassic to Rhaetian in age (Kustatscher and Van Konijnenburg-Van Cittert, 2007).

Ptilozamites is currently defined on unipinnate, forked or unforked leaf fragments, with triangular, falcate or rounded pinnules inserted laterally to the rachis. Pinnules are inserted to the rachis both before and after the dichotomy, in forked leaves. They are amphystomatic or hypostomatic, with sunken stomata and subsidiary cells having part of their walls fused in a ring structure covering partially the ostiole. The unipinnate feature of the leaf was considered until now as a constant character for *Ptilozamites* species, the most significant feature separating *Ptilozamites* species from those belonging to *Ctenozamites*. To this character, two additional characters were added: the insertion of pinnules laterally to the rachis in *Ptilozamites*, versus the adaxial insertion