Taxonomical and palaeogeographic considerations on the seedfern genus Ptilozamites with some comments on Anomozamites, Dicroidium, Pseudoctenis and Ctenozamites

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Taxonomical and palaeogeographic considerations on the seedfern genus *Ptilozamites* with some comments on *Anomozamites, Dicroidium, Pseudoctenis* and *Ctenozamites*

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With 6 figures and 3 tables

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Abstract: A detailed study of the original (Nathorst and Antevs) material of the genus *Ptilozamites* was undertaken, both using macromorphology and epidermal anatomy. The 9 species present in the original collection (*Ptilozamites blasii* (BRAUNS) NATHORST, *P. carlsonii* NATHORST, *P. heeri* NATHORST, *P. falcatus* NATHORST, *P. fallax* NATHORST, *P. linearis* NATHORST, *P. nilssonii* NATHORST, *P. oldhamii* NATHORST, *P. triangularis* NATHORST) have been reduced to three species (*P. blasii* (BRAUNS) NATHORST, *P. heeri* NATHORST, *P. nilssonii* NATHORST). Moreover, the new combination *Ptilozamites sandbergeri* (SCHENK) nov. comb. was made together with an emended diagnosis. Various other species are now omitted from the genus *Ptilozamites*; *P. acuminatus* NATHORST and *P. acutangulatus* NATHORST are conspecific and belong unequivocally, due to the cuticular pattern, to the genus *Anomozamites*. *Ptilozamites chinensis* HSÜ has been transferred to *Pseudoctenis chinensis* (HSÜ) n. comb. Also some other species, sometimes attributed to *Ptilozamites*, are discussed and their attributions to other genera such as *Dicroidium* and *Ctenozamites*. The genus *Ptilozamites*, once considered restricted to the Rhaeto-Liassic is now reported also from the Middle Triassic, but the largest distribution of the genus remains in the Rhaeto-Liassic and is restricted to the Northern Hemisphere. Finally, the relationships with the macromorphologically related genera *Anomozamites*, *Dicroidium*, *Pseudoctenis* and *Ctenozamites* are discussed.

Key words: fossil seed ferns, *Ptilozamites,* Scania, Sweden, Dolomites, Italy, Triassic.

1. Introduction

NATHORST (1878b) established the genus *Ptilozamites* on material from Scania in southern Sweden. The genus has historically been regarded as typical for the Swedish Rhaeto-Liassic (NATHORST 1886: 40). Later, further species of *Ptilozamites* have been described from Rhaeto-Liassic localities elsewhere in the Northern Hemisphere. However, the discovery of *Ptilozamites* in various Middle and early Late Triassic plant localities of the Southern Alps (e.g. WACHTLER & VAN KONIJNENBURG-VAN CITTERT 2000a, b; KUSTATSCHER, 2004; KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT 2005; ROGHI et al., in press) casted doubt on the temporal distribution of the genus. In order to accurately identify the new findings, it became necessary to restudy the original material especially with regard to the typespecific variability. However, this was sometimes difficult as NATHORST published one series of plates for his paper-series of

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"Om floran i Skånes kolförande bildningar – Floran vid Bjuf" (1878a - 1886). In these papers, the figures are variously assigned to different species, e.g. in NATHORST (1879) the figure of pl. 13, fig. 8 is described as *Ptilozamites* sp. on p. 65, while in the plate captions it is defined as *Ptilozamites blasii* (BRAUNS) NATHORST.

As a result, a detailed study of the original collection became important, including cuticle analyses. These helped to distinguish the studied material on generic and sometimes on specific level, confirming also similarities in macromorphology. In one case (*Anomozamites acuminatus* (NATHORST) nov. comb.) it permitted also to attribute the specimens to a different group of plants, from the seed ferns to the bennettitaleans.

The results of this study are discussed in this paper. Additionally, further species attributed to the genus *Ptilozamites* are considered, including their present taxonomical position. All material identified as *Ptilozamites* sp. is not included. Finally, the palaeogeographical and temporal distribution of *Ptilozamites* and related genera are discussed.

2. Material and methods

The material was studied under dissecting microscope, and, where possible, the original cuticle slides were analysed as well. When necessary, new cuticle preparations were made by maceration in Schulze's reagent ($KClO_3$ and 30 % HNO_3), neutralisation in ammonium hydroxide (5 %), mounted in glycerine jelly and sealed with paraplast (see also BATTEN 1999). The cuticle photos have been taken at the Naturhistoriska Riksmuseet in Stockholm with a Zeiss Axioskop 2 with digital image capture. Some of the cuticles were studied by scanning electron microscope (SEM) at the Naturhistoriska Riksmuseet in Stockholm.

The original material of NATHORST (S0 prefix) is stored in the paleobotanical collection of the Naturhistoriska Riksmuseet in Stockholm, the Anisian and Ladinian plant remains from the Dolomites (PAL and KÜH prefix) at the Naturmuseum Südtirol in Bolzano (Italy), the Carnian plant remains from Raibl at the Geologische Bundesanstalt (GBA prefix) and at the Naturhistorisches Museum in Vienna (Austria). A few historical specimens from the Ladinian of the Dolomites are stored in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (Germany), at the Naturhistorisches Museum in Vienna (Austria), at the Museo delle Regole "Rinaldo Zardini" in Cortina (CoAz prefix) and at the "Museum de Gherdëina" in Ortisei (M prefix; both Italy).

3. Systematic palaeontology

Division Pteridospermatophytes
Order indet.
Family indet.
Genus Ptilozamites NATHORST 1878 b

NATHORST (1878 b: 21-23) introduced this genus for elongated, pinnate and petiolate leaves from the Rhaeto-Liassic of Sweden. The pinnae are attached to the rachis with their entire base and possess straight to slightly concave distal and rounded proximal margin. Veins dichotomise and radiate in the direction of the posterior margin. The author interpreted the genus as a transitional form between *Ptilophyllum* and *Anomozamites*. *Ptilozamites* differs from *Ptilophyllum* in that the decurrent basal part of the pinnae is absent and from *Anomozamites* by the parallel veins and proximally rounded margin. Moreover, *Ptilozamites* differs from *Otozamites* in that the upper margin of the pinnae is auriculate in the latter, and from *Ctenozamites* by being bi- or tripinnate and not just once pinnate. Although NATHORST did not designate types, but described *Ptilozamites nilssonii* first; SCHIMPER & SCHENK (in: ZITTEL 1890: 225) and SEWARD (1910: 546 f.) considered *Ptilozamites heeri* being the type species of this genus.

ANTEVS (1914: 3-8) emended the original diagnosis and also described the epidermal anatomy "The fronds are pinnate, from broadly or narrowly lanceolate to linear with stout, often forked rachis. The square, rhomboidal, linear, triangular or falcate pinnae are densely placed or imbricate. They are attached with the whole base laterally on the rachis with a straight to concave distal margin and a first parallel then apically bending proximal margin. Numerous veins arise from the rachis, bifurcate at least once and procede more or less radiating or parallel to the margin. The thick cuticle is characterised by irregular to isodiametric epidermis cells, which become elongated and organised in regular rows above the veins and on the rachis. The epidermis cells are often papillate, with straight or somewhat undulating walls. The cuticle is amphistomatic or hypostomatic, with stomata concentrated in the areas between the veins of the lower cuticle. The guardian cells are sunken and surrounded by irregularly shaped subsidiary cells, which form a ring-like thickening."

Discussion: The systematic affinity of *Ptilozamites* has been discussed by various authors. SEWARD (1910: 548) and NATHORST (1880) regarded *Ptilozamites* as a cycad. Together with *Ctenis*, *Nilssonia,* and *Ctenopteris* (= *Ctenozamites*), SEWARD (1917: 511) referred it to the Nilssoniales group, as did THOMAS & BANCROFT (1913: 194, 196), WIELAND (1916: 26, 183), and GOTHAN & WEYLAND (1954, *Ptilozamites-Ctenopteris* series), while EMBERGER (1968: 446) assigned it to the Caytoniales. SEWARD later attributed *Ptilozamites* (1931: 317) to the "fern-like plants which are probably pteridosperms", DARRAH (1939: 199) to the "Rhaetian-mid-Jurassic *Dictyophyllum* series", while HARRIS (1931: 144) and FRENGUELLI (1943: 233 f., 271-276, fig. 17A, B) grouped it into into the Triassic-Jurassic "*Thinnfeldia* Series".

GOTHAN (1920: 84) suggested that a relationship exists between *Ptilozamites* and *Ctenopteris* (= *Ctenozamites*) based on the presence of bifurcate leaves in both genera, and POTONIÉ (1921: 146) noted similarities in the epidermis of both genera. HARRIS (1931: 145) related both genera with *Dicroidium*, *Johnstonia* and *Thinnfeldia* (sunken stomata, ring of subsidiary cells). HARRIS (1964) also noted similarities between the genera *Ptilozamites*, *Dicroidium* and *Ctenozamites* with regard to epidermal anatomy, while the differences where mostly in gross morphology; e.g. how many times the leaves were pinnate and the various types of pinna bases. In addition to the differences discussed by HARRIS (1964), ZHOU (1981: 26) marked a difference in the pinna attachment between *Ctenozamites* and *Ptilozamites*. According to the latter author, the pinnae in *Ctenozamites* extend from the upper side of the rachis, while they are attached laterally to the rachis in *Ptilozamites*. Moreover, we found that in the latter genus stomata occur on the upper side of the rachis, while the lower side lacks stomata. In *Ctenozamites*, the rachis cuticle is similar to that of the pinna, but more heavily cutinized.

Today, *Ptilozamites* is considered a pteridospermous morpho-taxon, but Order and Family remain unknown due to the lack of fructifications in organic connection.

HARRIS (1932b, 1937) considered *Hydropteridangium* (capsules with pollen sacs inside; pollen bisaccate) the male fructification of *Ptilozamites*, and related *Hydropteridangium marsilioides* to *P. nilsonii*. The supposed relationship between these two species is based on the co-occurrence of *H. marsilioides* and *P. nilsonii* in certain beds in Greenland and Sweden, along with similarities in epidermal anatomy and structure of the axis. However, no material showing the two structures in organic connection has become available to date and LUNDBLAD (1950: 72 f.) did not consider the specimens from Greenland and Sweden conspecific. Therefore, only a further detailed study may produce evidence that substantiates the supposed relationship between *Ptilozamites* and *Hydropteridangium*.

Species belonging to the genus *Ptilozamites*

Ptilozamites heeri NATHORST 1878
Fig. 1A-L

Selected synonymy:

1878a *Ptilozamites heeri* NATHORST, p. 11 (nomen nudum).
1878a *Ptilozamites linearis* NATHORST, p. 11 (nomen nudum).
1878a *Ptilozamites oldhamii* NATHORST, p. 11 (see NATHORST, 1879: 15) (nomen nudum).
1878a *Ptilozamites carlsonii* NATHORST, p. 11 (nomen nudum).
1878a *Ptilozamites triangularis* NATHORST, p. 11 (nomen nudum).
1878b *Ptilozamites heeri* NATHORST. – NATHORST, p. 7, 24, pl. 3, fig. 9.
1879 *Ptilozamites heeri* NATHORST. – NATHORST, p. 60, pl. 12, figs. 1a-c, 7.
1879 *Ptilozamites carlsonii* NATHORST. – NATHORST, p. 61, pl. 11, figs. 12-13a; pl. 12, fig. 8; pl. 13, fig. 18.
1879 *Ptilozamites linearis* NATHORST. – NATHORST, p. 63, pl. 13, fig. 3.
1879 *Ptilozamites triangularis* NATHORST. – NATHORST, p. 62, pl. 12, fig. 2.
non 1879 *Ptilozamites triangularis* NATHORST. – NATHORST, p. 62, pl. 12, fig. 3.
1880 *Ptilozamites heeri* NATHORST. – NATHORST, p. 66.
1880 *Ptilozamites linearis* NATHORST. – NATHORST, p. 66.
1880 *Ptilozamites triangulatus* NATHORST. – NATHORST, p. 66.
1880 *Ptilozamites carlsonii* NATHORST. – NATHORST, p. 66.
1886 *Ptilozamites heeri* NATHORST. – NATHORST, p. 122, pl. 12, fig. 5.
1886 *Ptilozamites heeri* f. *angustior* NATHORST. – NATHORST, p. 122, pl. 13, fig. 3.
1886 *Ptilozamites carlsonii* NATHORST. – NATHORST, p. 122.
1886 *Ptilozamites linearis* NATHORST. – NATHORST, p. 122.
1886 *Ptilozamites triangulatus* NATHORST. – NATHORST, p. 122.
1910 *Ptilozamites heeri* NATHORST. – SEWARD, fig. 361.

1914 *Ptilozamites heeri* NATHORST. – ANTEVS, p. 12-14, pl. 2, fig. 2; pl. 3 figs. 1-3, 12.
1914 *Ptilozamites carlsonii* NATHORST. – ANTEVS, p. 14, pl. 2, figs. 4-5; pl. 3, fig. 11.
1917 *Ptilozamites heeri* NATHORST. – SEWARD, p. 511.
1932a *Ptilozamites heeri* NATHORST. – HARRIS, p. 74.
1932a *Ptilozamites carlsonii* NATHORST. – HARRIS, p. 74.
1933 *Ptilozamites heeri* NATHORST. – FLORIN, text-fig. 16.
1943 *Ptilozamites heeri* NATHORST. – FRENGUELLI, p. 274, 329, fig. 17B.
1943 *Ptilozamites carlsonii* NATHORST. – FRENGUELLI, p. 276, 329.
1950 *Ptilozamites heeri* NATHORST. – KRÄUSEL, pl. 58, fig. 4.

NATHORST introduced this species in 1878 as a *nomen nudum*, in a list of species from the Rhaeto-Liassic of Scania (1878a: 11). The diagnosis and first figures of the species followed the same year, however, in a different publication (1878b: 24, pl. 3, fig. 9). According to these notes, *Ptilozamites heeri* is characterised by coriaceous, long and pointed leaves. The pinnae display a truncate distal and angular-rounded proximal margin, are of equal or more length than width and attached laterally to a striate rachis. The dichotomising veins are delicate and arise perpendicular to the rachis, or slightly radiating. Nathorst stated that pinnules on the left side of the leaves are smaller from those on the right side and concluded that the fragments could be parts of bifurcated leaves.

The first description of *P. heeri* cuticles was given by ANTEVS (1914: 12-14), together with an emended diagnosis: "The narrow pinnate fronds of varying size are characterised by a strong, undivided rachis terminating basally in a petiole. The short and broad but not imbricated pinnae are basally crescent-shaped and apically rhombic to triangular, with blunt to rounded apex. The distal margin is straight; the proximal margin is first parallel to the distal one, then bending apically or is curved from its base. The more or less distinct forked veins are parallel to slightly radiating. The thick cuticle is characterised by polygonal to isodiametric epidermal cells, not showing any variations above the veins. The upper cuticle misses almost completely stomata, on the lower side few stomata are equally distributed over the whole lamina."

FLORIN (1933: 46) regarded the ring-like thickening of the outer wall of the subsidiary cells as one of the most important features of the *Ptilozamites* cuticle.

Description: The holotype (S054946, Fig. 1A-B) is represented by an almost complete leaf, 530 mm long and 21 mm wide, with a 30 mm long and 7 mm wide petiole. The pinnae are, usually without imbricating, laterally and broadly attached to the rachis that reduces apically to 1 mm. The basal pinnae are crescent-shaped (4.3 x 10.5 mm, Fig. 1B), more apically the pinnae become rhomboidal to subrectangular and increase in width (13-14 x 8-10 mm). At the apex (Fig. 1D) they become slightly imbricated and narrower (7.8 x 6.3 mm), terminally almost falcate of 4.2 x 2.5 mm. The distal margin of the pinnae is truncate or slightly apically inclined; the proximal margin is first parallel to the distal one and then curved or inclined (60-80°) reaching the distal margin with a rounded apex. Veins arise perpendicularly to the rachis or at a more acute angle. They bifurcate somewhere in the middle portion of the pinnae and reach the margin almost parallelly (15-17/cm, Fig. 1C).

The abaxial and adaxial epidermis are similar, but there are some differences with regard to the number of stomata and dimensions of the isodiametric to polygonal cells. On neither side costal and intercostal areas are distinguishable (Fig. 1F-G). The epidermal cells of the rachis are elongate to rectangular, up to 2-3 times longer than wide, becoming most elongated near the margin (Fig. 1I, K). The epidermal cells of the pinnae are protected by solid papillae; stomata are irregularly scattered and guard cells sunken (Fig. 1J). The 6-7 subsidiary cells form a ring-like thickening around the stomatal pit. On the upper side, stomata are very rare on the pinnae but abundant on the rachis (Fig. 1F, I). On the lower side, the number of stomata on the pinnae is high – sometimes they even share individual subsidiary cells – while there are almost no stomata on the rachis (Fig. 1G, K). The upper cuticle (c. 5-7 µm) is usually thicker than the lower cuticle (1-3 µm).

Material from the Rhaetian of Wüstenwelsberg (Bavaria, Germany; private collection of Mr. STEFAN SCHMEISSNER) shows small (5-7 cm long and 0.8-1.7 cm wide) leaf fragments of *Ptilozamites heeri* (Fig. 1H). Crescent-shaped and slightly imbricating pinnae (0.6-1.2 x 0.5-0.8 mm) arise laterally from a 2 mm wide rachis. The delicate venation is difficult to see. The hypostomatic leaf is characterised by uniformely distributed epidermal cells. The epidermal cells,

Fig. 1. *Ptilozamites heeri* NATHORST 1878 (scale = 10 mm if not otherwise indicated).
A. Almost entire leaf, holotype (S054946), scale = 20 mm. **B.** Basal part of the leaf, detail of the holotype (S054946). **C.** Apical leaf fragment (S054944b). **D.** Leaf fragment with clear venation pattern (S055829). **E.** Cuticle showing the venation pattern (S079836), scale = 5 mm. **F.** General view of the upper cuticle with part of rachis and lamina (S057091-01), scale = 500 µm. **G.** General view of the lower cuticle with part of rachis and lamina (S057091-02), scale = 500 µm. **H.** Leaf fragment from the Rhaetian of Wüstenwelsberg (Q383-04), scale = 5 mm. **I.** Upper cuticle of the rachis (S057091-01), detail of Fig. 1F, scale = 200 µm. **J.** Lower cuticle of the pinnae with detail of the stomata (S057091-01), detail of Fig. 1F, scale = 60 µm. **K.** Lower cuticle of the rachis (S057091-01), detail of Fig. 1G, scale = 200 µm. L. SEM, inner view of a stoma from the lower cuticle (S057091-01), scale = 30 µm.

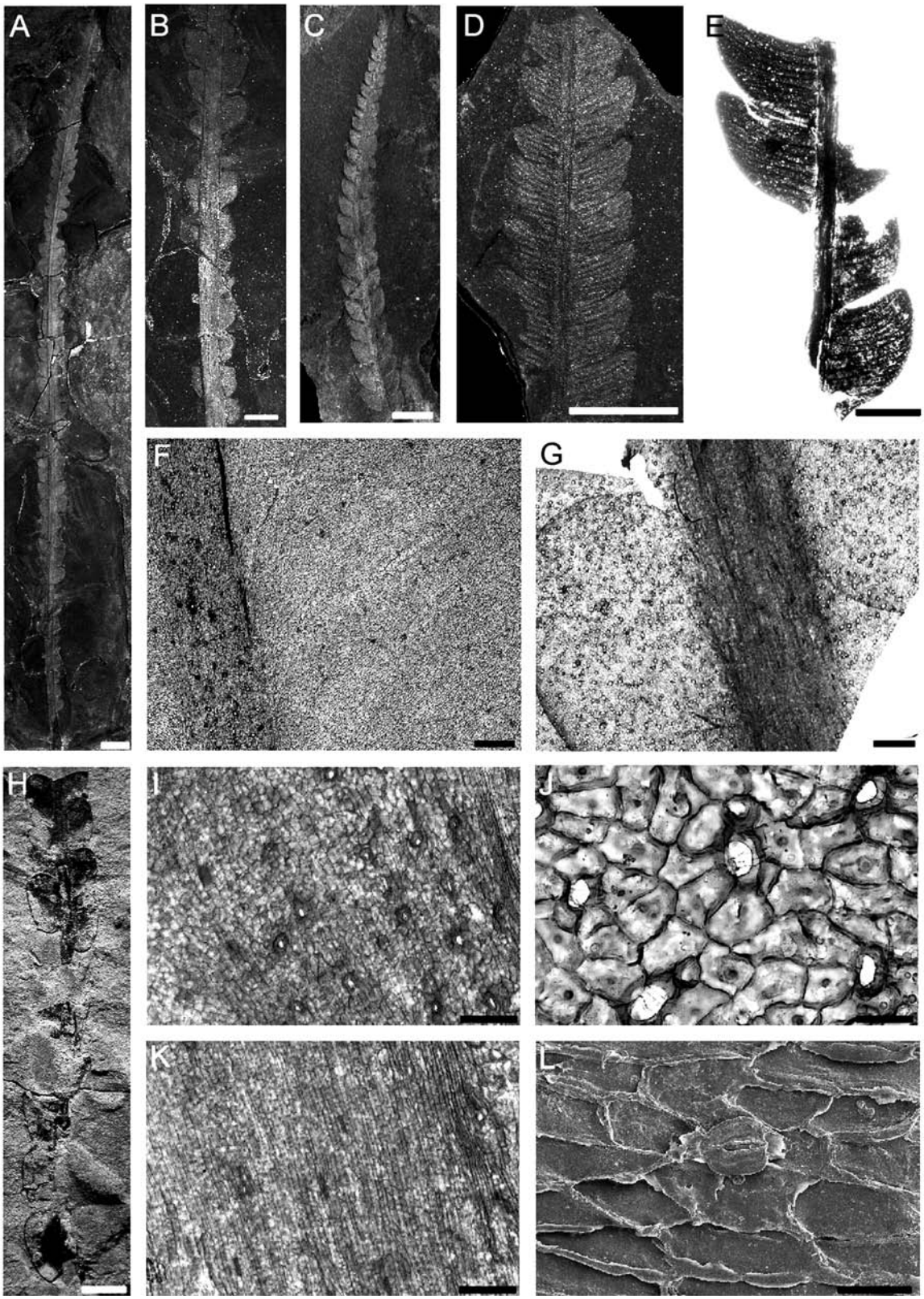

Fig. 1 (Legend see p. 74)

particularly of the abaxial side are protected by papillae. The scattered stomata are sunken and surrounded by a ring-like structure, typical for *P. heeri*. The upper cuticle is c. 5-8 µm thick, the lower cuticle measures 2-4 µm.

Distribution of the species: Rhaetian – Liassic from Bjuv and Höganäs (Scania, S Sweden); Rhaetian of Wüstenwelsberg (Bavaria, Germany).

Discussion: Nathorst (1880: 66) proposed to include some of his former species into *Ptilozamites heeri,* especially *P. triangulatus* and *P. linearis*; at first respectively as "f. *latior*" and "f. *angustior*" (1886: 122), afterwards (1886: 123) including them completely into this species. Furthermore, he discussed the option that *P. acuminatus* and *P. acutangulatus* also might belong to *Ptilozamites heeri*, the latter confirmed by Antevs (1914: 12-14) and Frenguelli (1943: 274). Moreover, Antevs considered *P. carlsonii* Nathorst and *P. zuberi* (Szajnocha) Nathorst closely related to *P. heeri*.

While the conspecificy of *Ptilozamites linearis* and *P. triangularis* with *P. heeri* has generally been accepted, the one with *P. carlsonii* Nathorst is still debated in literature. In fact, Harris (1932a: 74) considered the two taxa synonyms, since these two species apparently differ only in leaf size and pinnule shape. On the other hand, Antevs (1914) and Frenguelli (1943) regarded them as separate species because of the smaller dimensions of pinnae and fronds as well as the (imbricate) attachment of the pinnae in *P. carlsonii*. Since *P. carlsonii* shows the same basic pinna morphology as *P. heeri*, especially in the apical portion of the frond of the latter, the dimensional differences may also be explained by a difference in position in the frond. The pinna remains attributed to *P. carlsonii* might be apical fragments of *P. heeri* or even parts of young leaves.

Antevs stated also a difference in the cuticle pattern and in the epidermal structure above and between the veins. The study of the cuticle slides stored at the Naturhistoriska Riksmuseet in Stockholm, however, showed that all slides related to still existing macrofossils correspond to the cuticle of *P. heeri* as do also some dispersed cuticles labelled *P. carlsonii*. On the other hand, some slides with dispersed cuticles show a different epidermal pattern, which rather corresponds to e.g. *P. nilssonii*.

P. acuminatus and *P. acutangulatus* are not considered conspecific with *P. heeri*, but are transferred to *Anomozamites* and will be discussed in another paragraph of this paper.

The material from the Rhaetian of Wüstenwelsberg (Germany) slightly varies from the general macromorphological structure of *Ptilozamites heeri* from Scania. Crescent-shaped pinnae are however already observed from juvenile leaves or basal pinnae of this species. In these cases they may also be slightly more imbricate than usual, as observed in the German material. The particularly well-protected (with many papillae) cuticle from the German material may, however, also suggest, that these leaf fragments belong to plants growing in a more xerophytic environment (or climate) than the Swedish plants. The general macro- and cuticular patterns establish that the German material belongs to *P. heeri* and indisputably distinguishes the specimens from all other species discussed in this paper.

Ptilozamites blasii (Brauns 1862) Nathorst 1879
Fig. 2 A-I

Selected synonymy:

1862 *Nilssonia blasii* Brauns, p. 56 f., pl. 14, fig. 1a-c.
1866 *Nilssonia blasii* Brauns. – Brauns, p. 11.
1867 *Pterophyllum blasii*. – Schenk, p. 168, pl. 40, fig. 1.
1869 *Pterozamites blasii* (Brauns). – Schimper, p. 146.
1876 *Otozamites blasii* (Brauns). – Nathorst, p. 35, 40.
1878a *Ptilozamites blasii*. – Nathorst, p. 11.
non 1878a *Ptilozamites oldhamii* Nathorst, p. 11 (see Antevs 1914: 15).
1878a *Sphenozamites* ? *braunsii* Nathorst, p. 11 (nomen nudum).
1879 *Ptilozamites blasii* (Brauns). – Nathorst, p. 64, pl. 13, figs. 4-7.
1879 *Ptilozamites blasii* (Brauns) Nathorst (*Ptilozamites* sp.). – Nathorst, p. 65, pl. 13, fig. 8.
?1879 *Ptilozamites* sp. – Nathorst p. 60, pl. 15, fig. 16.
?1879 *Pterophyllum* ? *oldhamii* Nathorst, p. 71, pl. 13, fig. 15.
1880 *Ptilozamites blasii* (Brauns) Nathorst. – Nathorst, p. 66.
1886 *Ptilozamites blasii* (Brauns) Nathorst. – Nathorst, p. 123.
1914 *Ptilozamites blasii* (Brauns) Nathorst. – Antevs, p. 15 f., pl. 1, figs. 9-10; pl. 2, fig. 1; pl. 3, fig. 10.

Fig. 2. *Ptilozamites blasii* (Brauns 1862) Nathorst 1879 (scale = 10 mm if not otherwise indicated). **A.** Biggest specimen, (S055414). **B.** Apical leaf fragment (S055416). **C.** Single pinna (S054961). **D.** Single pinna with clear venation (S055417). **E.** Overview of the upper cuticle with small part of rachis and lamina (S079818), scale = 500 µm. **F.** Detailed view of the lower cuticle with stomata (S054966-02), scale = 20 µm. **G.** Detailed view of the upper cuticle with elongated epidermal cells over the veins (S055418-01), scale = 100 µm. **H.** Lower cuticle, outer view of stomata with the distinct ring, SEM (S057084-01), scale = 15 µm. **I.** Lower cuticle, outer view of a stoma, SEM (S 057084-01), scale = 15 µm.

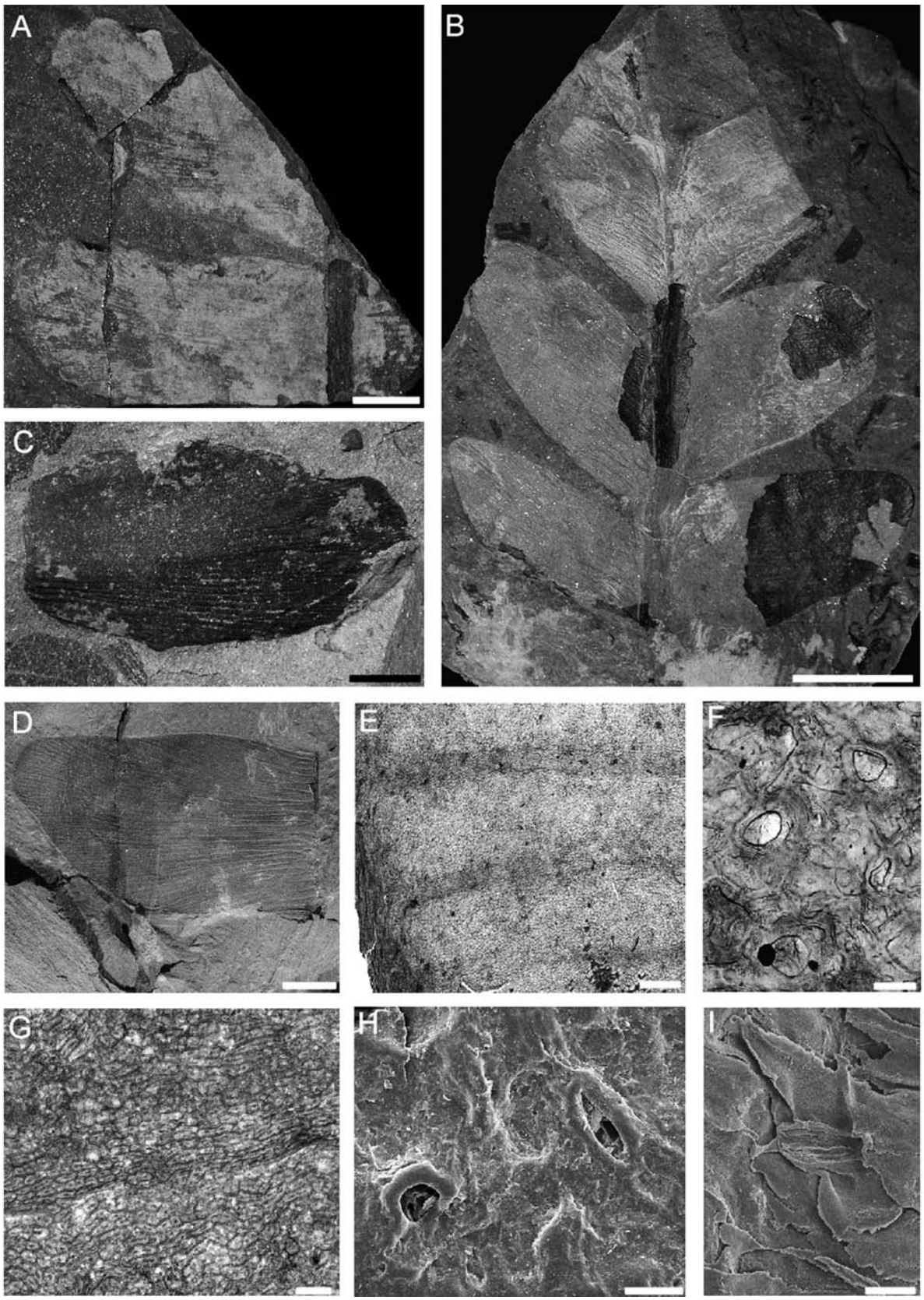

Fig. 2 (Legend see p. 76)

1943 *Ptilozamites blasii* (Brauns) Nathorst. – Frenguelli, p. 276, 329.
1950 *Ptilozamites blasii* (Brauns) Nathorst. – Lundblad, p. 49, pl. 7, fig. 1.

Brauns (1862: 56 f.) introduced this species for a few leaf fragments from the Rhaetian Sandstone of Seinstedt in Germany. The species, attributed to the sub-genus *Hisingera* Miquel of *Nilssonia* Brongniart, is characterised by a strong rachis and rhomboedral to slightly falcate pinnae that touch each other at their base. The veins are almost radiating, and the proximal part of the pinna is covered by veins curved slightly backwards.

Schenk (1867: 168) assigned this species, together with *Odontopteris laevis* Brauns 1862 (Schenk 1867: 170), to the genus *Pterophyllum* Schenk with the following emended diagnosis: "Pinnate leaves with perpendicularly, alternately and closely inserted pinnae. The wide oval pinnae with obtuse or slightly falcate apex reduce basally in dimension; the lowermost are shortened and almost ovoidal. Numerous delicate, but equally strong, veins cover the pinnae and run parallel to each other."

Schimper (1869: 146) attributed this species to the genus *Pterozamites*, but commented on its *Nilssonia*-like features, while Nathorst assigned the material from Bjuv first to the genus *Otozamites* (1876: 35) and finally to the new genus *Ptilozamites* (1878a: 11). He considered it, together with *Nilssonia acuminata* Goeppert, *Pterophyllum acuminatum* Morris, *Taeniopteris tenuivervis* Brauns, and *Asplenites ottonis* Goeppert, as a typical Rhaetian species (1876: 40).

Antevs (1914: 15 f.) described the cuticle of this species. According to the author, the cuticles of the lower and upper side differ only by the occurrence of elongate cells over the veins on the lower leaf-side. The epidermal cells are polygonal, sometimes with undulating anticlinal walls, and show thickenings only on the upper cuticle. Stomata are rare and sunken. Lundblad (1950: 49) compared the cuticle of *Ptilozamites blasii* with that of *Pseudoctenis florinii*, and evidenced a higher number of stomata than that recorded by Antevs (1914: 15).

Description: The most complete specimen is 56 mm long and 65 mm wide (S055414, Fig. 2A). The rachis is striate and decreases from 6 mm at base to 1 mm at the apex. Slightly falcate to lobate pinnae with a rounded apex, up to 60 mm long and 35 mm wide, arise from the rachis (S054961, Fig. 2C). The proximal margin is apically curved; the distal margin is straight or slightly concave. The pinnae are laterally and with their whole base attached to the rachis (S055414, Fig. 2A). The marked veins arise parallel to slightly radiating from the rachis, bifurcating at the base or within the first third of the pinnae, and sometimes a second time in the apical part, reaching the margin of the pinnae at a concentration of 18-20/cm.

An apical leaf-fragment (S055415 / S055416, Fig. 2B) shows four pairs of lobate to slightly falcate pinnae of 15 x 12-15 mm. The pinnae are imbricate and inserted with their whole base. Veins arise from the rachis apically inclinated, and then curve outwards, becoming almost perpendicular to the axis; in the proximal part of the pinnae they may also curve slightly backwards. The veins bifurcate immediately after the attachment area and at least once or twice toward the apex of the pinnae.

The upper and lower side of the cuticles show very similar features. On both sides, the epidermal cells are isodiametric to rectangular and show more elongate epidermal cells over the veins (Fig. 2E). The upper cuticle (c. 5-7 µm thick) is stomata-free and characterised by slightly smaller epidermal cells (40-60 µm against 50-70 µm) protected by frequent thickenings (Fig. 2E). On the lower cuticle (c. 2-4 µm thick) stomata sporadically occur both on and between the elongated cell bands over the veins. The stomata are sunken and surrounded by 7 subsidiary cells, forming a strong ring of c. 20-30 µm diameter around the stomata (Fig. 2F, H-I).

Distribution of the species: Rhaetian of Seinstedt (Germany); Rhaetian-Liassic of Bjuv (Scania, S Sweden).

Discussion: This species includes a few taxa originally described as separate species by Nathorst, and later attributed by himself to *P. blasii*, in detail the material previously assigned to *Pterophyllum oldhamii* Nathorst (Nathorst 1880: 66), *Ptilozamites* sp., *Ptilozamites oldhamii* and *Sphenozamites ?braunsii* (Nathorst 1886: 123).

This species is easily distinguishable from the others, especially when preserved with basal pinnae, based on the dimension and shape, as well as the venation pattern. Some particularly large isolated pinnae could be confused with smaller leaves of *Sphenozamites,* as has already been observed by Nathorst (1876: 35, 1879: 65). *Sphenozamites*, however, differs from *Ptilozamites* in the cuticle and the attachment to the rachis, broad and lateral in *Ptilozamites blasii* and restricted in *Sphenozamites*.

Ptilozamites nilssonii Nathorst 1878
Fig. 3A-I, L-M

Selected synonymy:

1878a *Ptilozamites falcatus* Nathorst, p. 11 (nomen nudum).
1878a *Ptilozamites fallax* Nathorst, p. 11 (nomen nudum).
1878a *Ctenopteris falcata* Nathorst, p. 11 (nomen nudum).
1878b *Ptilozamites nilssonii* Nathorst, p. 7, 23-24, pl. 3, figs. 1-5, 8.
1878b *Ptilozamites nilssonii* var. *longior* Nathorst, p. 23, pl. 3, figs 6-7.
1878b *Ptilozamites fallax* Nathorst. – Nathorst, p. 7, 24, pl. 3, fig. 18.
?1878b *Ptilozamites ? latior* Nathorst, p. 7, 25, pl. 3, fig. 10.
1879 *Ptilozamites fallax* Nathorst. – Nathorst, p. 59, pl. 7, fig. 10.
1879 *Ptilozamites falcatus* Nathorst. – Nathorst, p. 63, pl. 11, fig. 14; pl. 12, fig. 9.
1879 *Ptilozamites nilssonii* Nathorst. – Nathorst, p. 64.

1880 *Ptilozamites nilssonii* NATHORST. – NATHORST, p. 64-6, table p. 83.
1880 *Ptilozamites falcatus* NATHORST. – NATHORST, p. 66.
1880 *Ptilozamites fallax* NATHORST. – NATHORST, p. 66.
1886 *Ptilozamites fallax* NATHORST. – NATHORST, p. 122.
1886 *Ptilozamites nilssonii* NATHORST. – NATHORST, p. 123, pl. 12, fig. 9.
1886 *Ptilozamites falcatus* NATHORST. – NATHORST, p. 123.
1886 *Ctenopteris ? falcate*, NATHORST, p. 120, 123.
1914 *Ptilozamites nilssonii* NATHORST. – ANTEVS, p. 8-10, pl. 1, figs. 1-7; pl. 2, figs. 8-9; pl. 3, figs. 4-9.
1914 *Ptilozamites fallax* NATHORST. – ANTEVS, p. 10 f., pl. 1, fig. 8; pl. 2, figs. 6-7.
1917 *Ptilozamites fallax* NATHORST. – SEWARD, p. 511.
1917 *Ptilozamites nilssonii* NATHORST. – SEWARD, p. 511.
1922 *Ptilozamites nilssonii* NATHORST. – JOHANSSON, p. 35 f., pl. 1, figs. 18-21; pl. 6, figs. 9-11; pl. 8, fig. 19.
1922 *Ptilozamites fallax* NATHORST. – JOHANSSON, p. 36 f., pl. 6, figs. 12-13.
1926 *Ptilozamites nilssonii* NATHORST. – HARRIS, p. 69, text-fig. 8A, B, E.
1932a *Ptilozamites nilssonii* NATHORST. – HARRIS, p. 71-75, pl. 8, fig. 7; text-figs. 29-30.
1932b *Ptilozamites nilssonii* NATHORST. – HARRIS, p. 126.
?1932 ?*Ptilozamites nilssonii* NATHORST. – OISHI, p. 322 f., pl. 43 (25), fig. 4.
1934 *Ptilozamites nilssonii* NATHORST. – HOFMANN, p. 128, 239.
1937 *Ptilozamites nilssonii* NATHORST. – HARRIS, p. 35 f.
?1940 *Ptilozamites nilssonii* NATHORST – OISHI, p. 175, 364.
1943 *Ptilozamites fallax* NATHORST. – FRENGUELLI, p. 274, 329.
1943 *Ptilozamites nilssonii* NATHORST. – FRENGUELLI, p. 274, 329, fig. 17A.
1950 *Ptilozamites nilssonii* NATHORST. – LUNDBLAD, p. 38 f.
1950 *Ptilozamites fallax* NATHORST. – LUNDBLAD, p. 38 f.
1959 *Ptilozamites nilssonii* NATHORST. – KIMURA, tab. 3.
1960 *Ptilozamites nilssonii* NATHORST. – ANDREWS, p. 360, fig. 12-6E.
1968 *Ptilozamites nilssonii* NATHORST. – EMBERGER, p. 446, fig. 527.
1987 *Ptilozamites nilssonii* NATHORST. – SHUYING, p. 182, tab. 1.

NATHORST (1878a: 23-24) introduced the taxon *Ptilozamites nilssonii* for linear, dichotomising leaves with widely falcate pinnae from the Rhaetian of Höganäs. This species is characterised by a tuberculate rachis and imbricate, falcate pinnae with obtuse apex. Numerous distinct veins radiate slightly towards the distal and the proximal margins of the pinnae. Nathorst distinguished a "var. *longior*" with slightly more imbricated pinnae of up to 22 mm long from the normal form, with up to 15 mm long and 6-7 mm wide pinnae.

Later, ANTEVS (1914: 8-10) withdrew NATHORST's "var. *longior*" and discussed some additional characters of this species: the high variation in leaf-size, the straight to concave distal and convex proximal margin and the bifurcation of the veins. He described the cuticle as thick and composed of irregular to isodiametrical polygonal cells. The upper uniform epidermis lacks stomata, while the abaxial epidermis is characterised by elongated cells over the veins and numerous stomata in the intercostals fields.

HARRIS (1926: 69-70) provided additional information about this species, including the sometimes sinuous thickenings of the cell walls and papillae on the upper epidermis. He also notes the presence of a cutinised lamella with a round-oval pore around the stomatal pit, which is partially occlused by the fused papillae of the five subsidiary cells.

Description: The collection of the Naturhistoriska Riksmuseet in Stockholm houses a few hundreds of leaf fragments (several of them bifurcated) and single pinnae belonging to this species.

The most complete specimen is an almost entire leaf, 315 mm long and 87 mm wide, formerly designated as *Ptilozamites fallax* (S055423, Fig. 3A). The bifurcate leaf shows a stout, tuberculate rachis, 4.5 mm wide below and 2.5 mm wide above the bifurcation, decreasing apically to less then 1 mm width. The slightly falcate pinnae of 13 x 13 mm do not imbricate at the base. They increase (30 x 13 mm) up to the bifurcation point decreasing again apically. Due to the preservation, veins are not visible. This specimen is, however, exceptional in dimension, both of the leaf and the pinnae. Most of the bifurcate leaf fragments do not reach more than 150 mm in length and are characterised by smaller pinnae from 3.5 x 4 mm up to 14 x 5 mm (Fig. 3B). The falcate pinnae with a more or less obtuse apex possess a straight to concave distal and a curved proximal margin. The veins arise from the rachis slightly inclined apically at an angle of c. 80°, less frequently perpendicular. They can be slightly sinuous, bifurcate at least once in the lower part and often a second time in the upper part of the pinnae, close to the margin. In small leaf fragments (S055404, S055408, Fig. 3C) small falcate, slightly imbricating to not even touching, pinnae (3.3 x 3.5 mm) arise above the petiole (8 mm long and 2 mm wide). An apical leaf fragment (S055409, Fig. 3D) of 32 mm long and 10 mm wide shows, above the alternately inserted apical pinnae (7.5 x 3.5 mm), a terminal pinna of 11 x 5.4 mm. The veins bifurcate several times. Several pinna fragments (i.e. S059632, S059639, Fig. 3E) are, however, smaller as mentioned above, with a tuberculate rachis less than 1 mm wide, and falcate, slightly imbricate pinnae of 2.5-5 x 2.5-5 mm. The veins bifurcate at the base and reach the margin almost parallely. The upper cuticle (c. 3-5 µm) is thicker than the lower cuticle (1-3 µm). Both the lower and upper cuticles display costal and intercostals fields, the

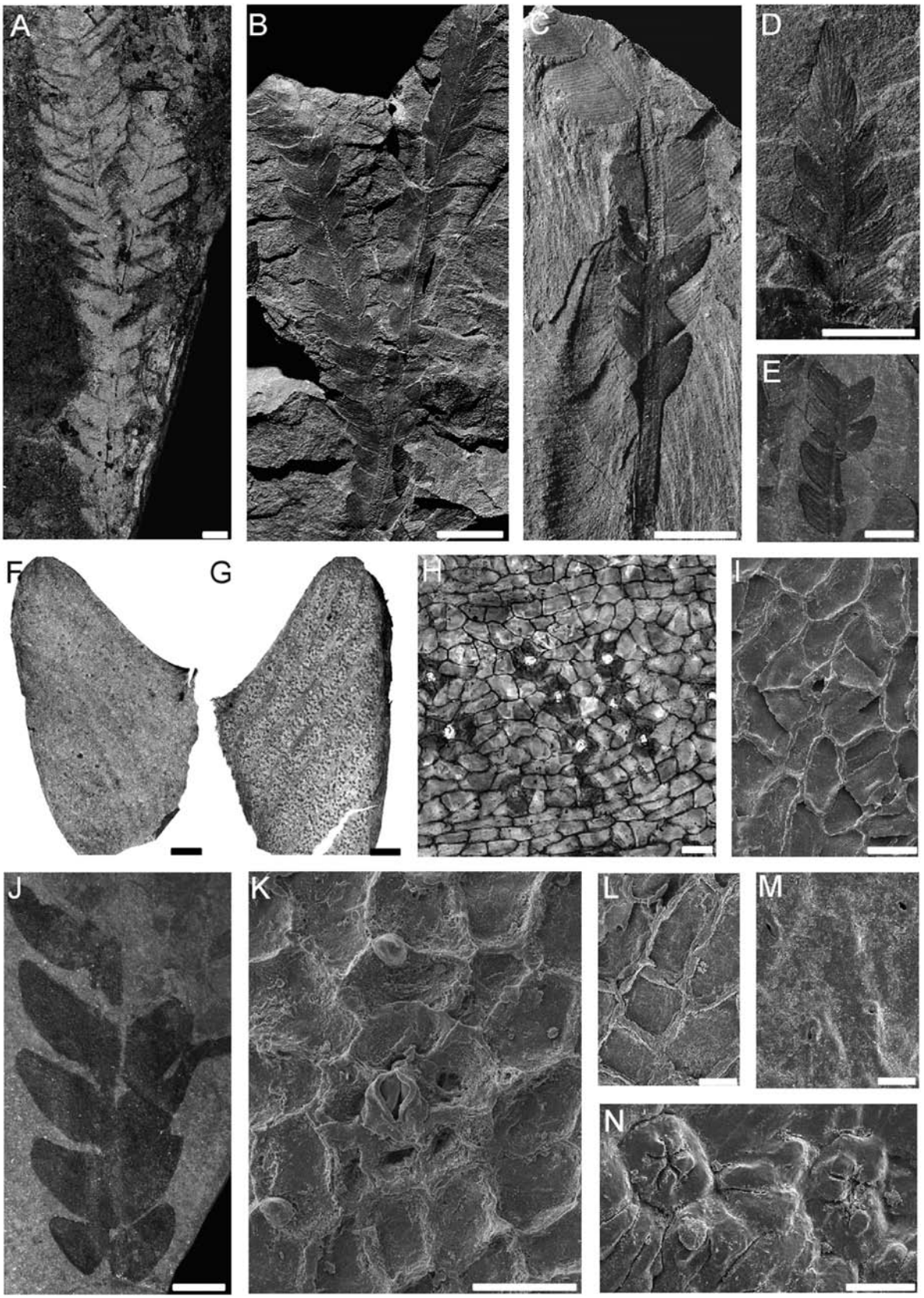

Fig. 3 (Legend see p. 81)

latter characterised by 3-4 rows of elongated epidermal cells (Fig. 3F-H). This difference is less prominent on the upper side with a thicker cuticle. The isodiametric to polygonal epidermal cells have straight anticlinal walls, which can show, depending on the preservation of the cuticle, "twisted-cord"-like thickenings (Fig. 3L). Sometimes, epidermal cells, especially of the lower cuticle, may bear papillae or thickenings. The rachis is covered by elongate (2 to 3 times longer than wide) epidermal cells and a few stomata. The stomata are generally more numerous on the upper than on the lower side of the leaf, but always sunken and sometimes small ringlike structures surround the stomatal pit. Stomata occur in the intercostals fields on the lower side, sometimes sharing individual subsidiary cells (Fig. 3H). Each stomatal apperature consists of six, less often five or seven, subsidiary cells; the typical ring-like structure seen in *Ptilozamites heeri* is not well developped in this species (Fig. 3H, I, M). In very small pinnae (e.g. S059639, S059665-01, Fig. 3E), the cuticle of the rachis does not differ much from the cuticle of the imbricating pinnae.

Distribution of the species: Rhaetian of Scania (S-Sweden), Scoresby Sound (E-Greenland), ?Alborz (Iran), Qinghe flora (S-China) and Okayama (Japan); Liassic of Scania (S-Sweden) and Nishihata, Nariwa, Okayama (Japan).

Discussion: Antevs (1914) and Johansson (1922) grouped *Ptilozamites falcatus* with *P. nilsonii*, since the former differed only by less radiating veins and lackes imbricating pinna. Both authors considered, however, *P. fallax* a different species, although noticing its close resemblance, while Harris (1926) included also this third species into *P. nilssonii*. We agree with Harris (1926), since the previously noted differences between *P. nilsonii* and *P. fallax* were the different size of the pinnae and the more distinct veins, while pinnae shape, rachis and cuticle pattern remain the same.

A leaf fragment described by Nathorst (1878a) as *Ptilozamites ?latior* could also belong to this species. The material, however, is too badly and fragmentarily preserved to permit a definite specific attribution. The specimen, compared by Nathorst with *Phyllopteris bifida* Heer from Jurassic layers of Spitsbergen at Cap Boheman, could, however, belong to *Ptilozamites nilssonii*, based on its pinna shape and dimension.

The study of some material from Stabbarp (S078804) and Bjuv (S060383, Fig. 3J) permitted to evidence the sometimes close relationship with regard to the macromorphology of *Ptilozamites nilssonii* and *Lepidopteris ottonis*. Some of the falcate pinnae attributed to *Ptilozamites nilssonii* show a remarkably different epidermis, characterised by five subsidiary cells with 5 distinctive papillae covering the stomatal pit almost completely (Fig. 3K, N). A similar epidermal anatomy has been described by Harris (1926: 69-70), although he figured the papillae-covered stomata correctly as belonging to *Lepidopteris ottonis* (Harris 1926, fig. 8D).

Ptilozamites tenuis Oishi 1932

1931 *Pterophyllum contiguum* Oishi (non Schenk), p. 359.
1932 *Ptilozamites tenuis* Oishi, p. 321, pl. 43 (25), figs. 1-3.
1938 *Ptilozamites tenuis* Oishi & Huzioka, p. 93, pl. 6, figs. 2-2a.
1940 *Ptilozamites tenuis* Oishi. – Oishi, p. 147, 175, 365.
1943 *Ptilozamites tenuis* Oishi. – Frenguelli, p. 276, 329.
1959 *Ptilozamites nilssonii* Nathorst. – Kimura, p. 90 f., tab. 3.

Oishi (1932, 1940) established this species for pinnate slender fronds with thin, delicate and tuberculate rachis that forks at least once. The pinnules are alternately attached with their entire base, closely inserted or slightly spaced and at a wide angle. The pinnae (1.5-2 x 1 mm) are parallel-sided and with an obtuse to rounded apex. The 4-7 veins of each pinna are parallel, simple or forked.

The attribution to *Ptilozamites* was based on the presence of a forked rachis, although Oishi (1932) evidenced also the close resemblance of the material to *Pterophylum aequale* Brongniart and *P. contiguum* Schenk. He distinguished the species from *Ptilozamites nilssonii* due to the pointed apex of the pinnae and the parallel-sided margin.

Fig. 3. A-I, L-M: *Ptilozamites nilssonii* Nathorst 1878. J, K, N: *Lepidopteris ottonis* (scale = 10 mm if not otherwise indicated). **A.** Most complete specimen with bifurcated axis (S055423). **B.** Leaf fragment with bifurcated axis (S055404). **C.** Basal leaf fragment with short petiole (S059649). **D.** Apical leaf fragment with terminal pinnae (S055409). **E.** Leaf fragment with small pinnae (S059639), scale = 5 mm. **F.** Upper cuticle with small part of rachis and almost entire pinna lamina (S059632-01), scale = 500 µm. **G.** Lower cuticle with small part of rachis and almost entire pinna lamina (S059632-01), scale = 500 µm. **H.** Detail of the lower cuticle with areas between and above the veins (S059632-01), scale = 50 µm. **I.** Stomata seen from the inner side (S054729-01), SEM, scale = 30 µm. **J.** Specimen of *Lepidopteris ottonis* assigned previously to *Ptilozamites nilssonii* Nathorst 1878 (S060383), scale = 5 mm. **K.** Cuticle, inner view with stoma (S078804-01), SEM, scale = 30 µm. **L.** Detail of epidermal cells with "twisted-cord"-like thickenings, inner view (S075476-01), SEM, scale = 15 µm. **M.** Outer view with numerous sunken stomata, protected by a ringlike thickening (S075476-01), SEM, scale = 30 µm. **N.** Cuticle, outer view with two, clearly papillate, stomata (S078804-01), SEM, scale = 30 µm.

Distribution of the species: Rhaetian (*Lepidopteris* zone) of Kamihina, Okayama (Japan).

Discussion: The material closely resembles the species *Ptilozamites nilssonii* NATHORST. The description and figures seem to confirm the attribution to *Ptilozamites*, but cannot resolve the question if or not this form represents a distinct species or has to be included into the intraspecific variability of *Ptilozamites nilssonii*.

Ptilozamites sandbergeri (SCHENK) n. comb.
Fig. 4A-J

non 1825 *Pterophyllum minus* BRONGNIART, p. 219, pl. 12, fig. 8.
1858 *Pterophyllum minus* BRONGNIART. – BRONN, p. 56 f., pl. 9, fig. 2.
1866 *Pterophyllum sandbergeri* SCHENK, p. 17 f., pl. 1, fig. 9.
1868 *Pterophyllum sandbergeri* SCHENK. – STUR, p. 103.
1869 *Pterophyllum sandbergeri* SCHENK. – SCHIMPER, p. 138.
1885 *Pterophyllum sandbergeri* SCHENK. – STUR, p. 10.
1927 *Pterophyllum brevipenne* KURR. – OGILVIE-GORDON, p. 66, pl. 8, fig. 1.
1980 cfr. *Pterophyllum venetum* DE ZIGNO. – ZARDINI, pl.1, fig. 8.
1999 *Ptilozamites heeri* NATHORST. – KUSTATSCHER, p. 26 ff., 45, 48.
2000a *Ptilozamites heeri* NATHORST. – WACHTLER & VAN KONIJNENBURG-VAN CITTERT, p. 108, pl. 2, figs. 2-9.
2000b *Ptilozamites heeri* NATHORST. – WACHTLER & VAN KONIJNENBURG-VAN CITTERT, p. 118, pl. 2, figs. 2-9.
2001 *Pterophyllum sandbergeri* SCHENK. – DOBRUSKINA et al., fig. 2.
2001 *Pterophyllum bronnii* SCHENK. – DOBRUSKINA et al., pl. 9, figs. 4-5, 7-10, 14.
2004 *Ptilozamites heeri* NATHORST. – KUSTATSCHER, p. 163 f., pl. 11, fig. 5; pl. 12, fig. 1.
2004 *Ptilozamites heeri* NATHORST. – KUSTATSCHER et al., p. 64 f.
2005 *Ptilozamites heeri* NATHORST. – KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT, p. 35 f.

SCHENK (1866-1867: 17-18) established *Pterophyllum sandbergeri* for pinnate leaves with a stout rachis and alternately inserted pinnae. The short pinnae are elongate to equidimensional, with an entire margin, a narrow vein-free band and rounded apex. Their base is broadly attached; the veins are distinct and parallel. It differs from *Pterophyllum minus* Brongniart due to the rounded apex of the pinnae and the distinct and more numerous veins.

Description: The leaf fragments, up to 11.5 cm long and 15 mm wide, are characterised by oppositely to subopposite arranged pinnae (Fig. 4A). The subrectangular to subquadrate pinnae with rounded apex are laterally attached to the striate rachis and decrease in size towards the apex (8 x 6-8 mm, Fig. 4A). The veins arise perpendicularly from the rachis, with a concentration of 7-9/cm and run parallelly and almost completely without forking up to the margin (Fig. 4D-F). Sometimes bifurcations can be observed at the base of the pinnae. The margin shows a narrow vein-free band (Fig. 4C, E, G).

The cuticle is rather thick (upper side c. 4-6 µm, lower side c. 2-4 µm) and composed of irregular polygonal epidermal cells (Fig. 4H). Stomata are scattered on the upper side and more frequent on the lower side of the leaf (Fig. 4J). On the upper side the venation is not recognizable. The epidermal cells of the lower cuticle are more elongate over the veins; stomata are concentrated in bands between the veins. They are irregulary distributed and never share subsidiary cells. Stomata are numerous on the upper side of the rachis and almost completely absent on the lower side.

Distribution of the species: Upper Ladinian of the Dolomites (N-Italy); Carnian of Raibl and Dogna (Julian Alps).

Discussion: Part of the material discussed here (that from the Carnian of Raibl) has previously been attributed to various *Pterophyllum* species: i.e. *Pterophyllum minus* BRONGNIART, *Pterophyllum brevipenne* KURR, cf. *Pterophyllum venetum* DE ZIGNO and *Pterophyllum bronnii* SCHENK, but both the pinna morphology and especially the cuticular features make an attribution to *Pterophyllum* incorrect.

The findings of plant fossils in the Middle Triassic (Ladinian) of the Dolomites, apparently belonging to the genus *Ptilozamites*, was the immediate cause of our in depth study of *Ptilozamites*. The specimens from the Dolomites were first attributed to *Ptilozamites heeri*, due to pinna morphology (WACHTLER & VAN KONIJNENBURG-VAN CITTERT 2000a, b; KUSTATSCHER 2004; KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT 2005), but then the find of the old material of *Pterophyllum sandbergeri* SCHENK from Raibl in the collections in Vienna made a specific attri-

Fig. 4. *Ptilozamites sandbergeri* (SCHENK) n. comb. (scale = 10 mm if not otherwise indicated). **A.** One of the most complete specimens (GBA, XV 46 13). **B.** Basal leaf fragment (GBA Raibl 1986-3-113). **C.** Leaf fragment with short petiole (PAL 014). **D.** Leaf fragment (MDG M18). **E.** Leaf fragment with evident venation (PAL 009), scale = 5 mm. **F.** Leaf fragment with basal pinnae (PAL 223). **G.** Leaf fragment (PAL 114). **H.** Upper cuticle with polygonal epidermal cells (CoAz 2655), scale = 50 µm. **I.** cf.-specimen, leaf fragment (KÜH 906). **J.** Detail of the lower cuticle with areas between and above the veins (M 14), scale = 50 µm. **K.** Slightly damaged cuticle, lower cuticle (KÜH 906), scale = 30 µm.

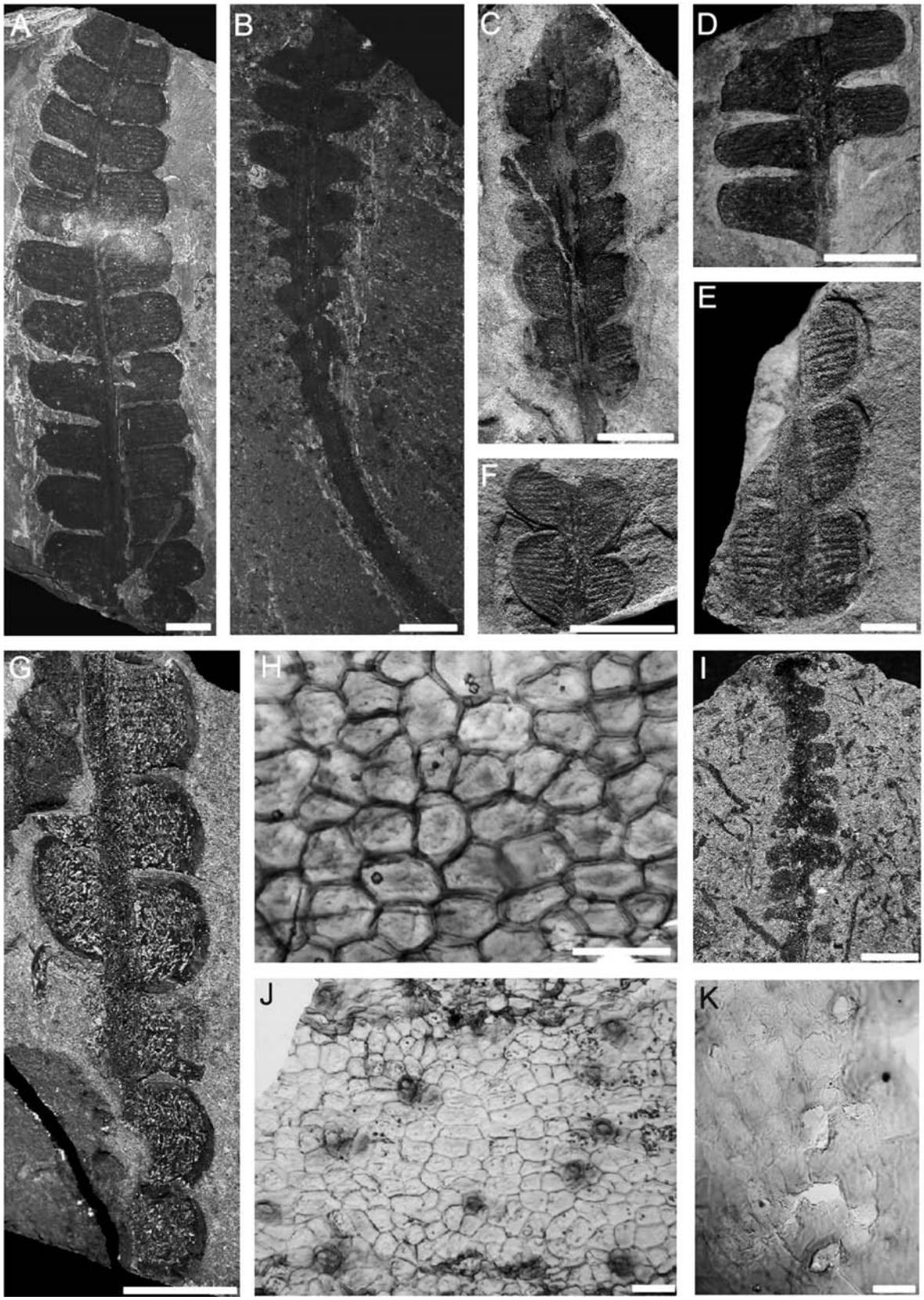

Fig. 4 (Legend see p. 82)

bution to *P. heeri* rather doubtful. Macromorphologically, the material from the Dolomites was comparable to that of *Pterophyllum sandbergeri*.

Our re-examination of the historical collections in Sweden and Vienna, along with that of original and new cuticular slides indicated differences to *Ptilozamites heeri*. The shape of *P. heeri* pinnae is generally rhomboidal with rounded apex, although basally it can be crescent-shaped and apically sub-falcate, while *P. sandbergeri* has sub-rectangular to subquadrate pinnae with rounded apex. The veins of *P. heeri* are delicate, bifurcate in the middle part, and reach the margin parallely with a concentration of 15-17/cm. In *P. sandbergeri*, the distinct veins, when only bifurcate close to the base of the pinnae. They end slightly before the margin at a concentration of 7-9/cm, leaving a narrow marginal band devoid of veins. The lower side of the pinnae of both species is covered by stomata, which are losely scattered in *P. heeri* and distributed between the veins in *P. sandbergeri*.

Emended diagnosis: Rachis striate. Simple pinnate leaves with laterally attached, subrectangular – subquadrate pinnae with rounded apex. Pinnae decreasing in size apically. Margin characterised by a narrow vein-free band. Veins distinct, arising perpendicularly from the rachis, rarely forking at the base of the pinnae and ending with a concentration of 7-9/cm slightly before the margin. Cuticle thick (5-7 µm) displaying polygonal epidermal cells with straight anticlinal walls. Upper cuticle with rare stomata and no evident vein pattern. Lower epidermis distinguished into stomatal-free bands above the veins and stomatal bands with irregularly scattered haplocheilic stomata. Stomatal-free bands characterised by more elongated epidermal cells. Rachis covered by elongated epicermal cells, upper side bearing numerous well protected stomata, lower side almost devoid of stomata.

Basionym: *Pterophyllum sandbergeri* Schenk 1866.

Type: *Pterophyllum sandbergeri* Schenk, p. 17-18, pl. 1, fig. 9.

Ptilozamites sp. cf. Pt. *sandbergeri* (Schenk) n. comb.
Fig. 4 I, K

2004 ?*Ptilozamites* sp. – Kustatscher, p. 145, pl. 6, fig. 1.

Description: A few frond fragments of up to 15 cm in length have been attributed to the genus *Ptilozamites* and provisionally to the species *Ptilozamites sandbergeri*. The frond-fragments are characterised by rectangular pinnae with rounded angles, attached with the whole base to a rachis of 1-2 mm width. The pinnae vary from 5 x 5 mm to 6 x 6.5 mm in dimension, although a very small leaf fragment shows even smaller pinnae (2-2.5 x 2 mm, Fig. 4I). Unfortunately, the preservation of the material does not permit to distinguish macroscopically more details.

From one leaf fragment (Küh 906) also small cuticle fragments have been isolated (Fig. 4K). These show polygonal epidermal cells with straight anticlinal cell walls. The badly preserved stomatal apparati are characterised by a variably thick ring-like thickening and 4-6 subsidiary cells.

Distribution of the species: Upper Anisian of the Dolomites (N Italy).

Discussion: The lack of detailed information regarding the gross-morphology (i.e. venation pattern) and cuticle (i.e. stomatal distribution) impede the definitive attribution of these specimens to any of the above-discussed *Ptilozamites* species. The attachment of the pinnae to the rachis, the thick cuticle, displaying isodiametric-polygonal epidermal cells and the ringlike thickenings around the stomatal pit with 4-6 irregularly distributed subsidiary cells, however, allows us to assign the specimens to the genus *Ptilozamites*. Nevertheless, as there are no real macromorphological and cuticular differences to the Ladinian-Carnian species *Ptilozamites sandbergeri*, we provisionally place our Anisian material in this taxon.

?Ptilozamites bartangensis Prinada 1934

1934 Ptilozamites bartangensis Prinada, p. 23, 78, pl. 1, fig. 3.

This species has been introduced by Prinada (1934: 23 f.) for simple, pinnate leaves. The pinnae are sublanceolate to falcate and slightly subcrenulate with an obtuse apex and acute proximal margin. They are attached to the rachis with their whole base and close one another. Apically, the pinnae gradually decrease in size; in the middle part of the leaves they are 23 mm long and 8 mm wide. The loosely spaced and thin veins are simple or bifurcating, sometimes also slightly radiating.

Distribution of the species: Mesozoic of Bartang River (Pamir, Tatjikistan).

Discussion: Prinada (1934) compared his specimen with the genus *Pterophyllum* stating, however, its difference from all Mesozoic species of this genus, due to the coarse venation which arches within the pinnae and runs parallel to the distal margin. The author evidenced also similarities with *Ctenozamites cycadea* Brongniart as figured by Schenk (1887) from the Rhaetian of Iran from which it is distinguished, though, by its shorter segments. Actually the fragmentary nature of the specimen does not permit to observe if the leaves are pinnate like in *Ctenopteris* (= *Ctenozamites*, see same article), or simple to once bifurcate as in *Ptilozamites*.

The strong resemblance with *Ptilozamites*, especially *Ptilozamites nilssonii* as pictured by Johansson (1922), convinced the author to attribute it to this genus, although not without doubts. The thick and leathery consistence of the leaves, the whole-base attachment of the sublanceolate to falcate pinnae and the parallel to bifurcating veins seem to support this attribution. The attachment of the pinnae is not very clear, not even to Prinada (1934). The latter reported a closer to the upper side or perhaps upper-side attachment, stating however the lower-side vision of the

leaf. Due to the difficulty to distinguish this very important feature, the species has to remain in *Ptilozamites*, at present, although its generic attribution is still not determined.

Species no longer considered as belonging to Ptilozamites

Various authors have erroneously attributed several species the genus *Ptilozamites*. According to SCHWEITZER & KIRCHNER (1998), the species *Ptilozamites* (*Pterophyllum*) *ctenoides* (OISHI 1932) SADOVNIKOV 1991 and the material from the Norian and Rhaetian of the Alborz attributed to *Ptilozamites nilssonii* and *Ptilozamites nilssonii* cf. *confluens* SADOVNIKOV by SADOVNIKOV (1991: 99, 102), do not belong to this genus; the latter two taxa represent probably specimens of *Nilssonia* (SCHWEITZER & KIRCHNER 1998: 62). *Ptilozamites abiekensis* FAKHR 1977 is considered conspecific with *Ctenozamites iranica* FAKHR 1977 (SCHWEITZER & KIRCHNER 1998: 63).

Moreover, *Ptilozamites shirakii* KAWASAKI 1939 (p. 31, pl. 7, figs. 29-30) does not belong to this genus because of the restricted pinnae bases and the upper-side-attachment of the pinnae to the rachis. The orbiculate shape with constricted base could rather attribute the material described and figured by KAWASAKI to the genera *Zamites* or *Otozamites*.

Some additional species enlisted in the Fossilium Catalogus (JONGMANS & DIJKSTRA 1960, 1963) in the genus *Ptilozamites* are here removed to different seedfern or bennettitalean genera as discussed below.

Anomozamites SCHIMPER 1869

This genus, as described by SCHIMPER (1869: 140) and emended by HARRIS (196: 79), is characterised by "long-lanceolate leaves with a lamina divided into segments, typically as long as broad. The base of the segments is not constricted; the numerous veins are parallel, simple or forked and ending at the distal margin. The midrib is partly exposed on the upper side of the leaf. The cuticle shows syndetocheilic stomata with two lateral subsidiary cells. The guard cells have a crescent-shaped dorsal thickening of cutin."

Anomozamites acuminatus (NATHORST 1879) n. comb.
Fig. 5A-I

Selected synonymy:

non 1871 *Nilssonia neuberi* STUR, p. 464.
non 1867 *Nilssonia acuminatum* SCHENK, p. 125.
1876 *Pterophyllum acuminatum* MORRIS. – NATHORST, p. 31.
1879 *Ptilozamites heeri* NATHORST (*Ptilozamites triangularis* NATHORST). – NATHORST, p. 62, pl. 12, fig. 3.
1879 *Ptilozamites acuminatus* NATHORST, p. 62, pl. 12, figs. 4, 6.
1879 *Ptilozamites acutangulatus* NATHORST, p. 63, pl. 18, fig. 2.
?1879 *Ptilozamites* sp. – NATHORST, pl. 18, fig. 1.
1886 *Ptilozamites acuminatus* NATHORST. – NATHORST, p. 122 f.
1886 *Ptilozamites acutangulatus* NATHORST. – NATHORST, p. 123.
non 1908 *Ptilozamites acuminatus* NATHORST. – KRASSER, p. 449 f.
?1971 *Anomozamites* sp. 1. – STANISLAVSKI, p. 70 f., fig. 33.

NATHORST (1876: 32) assigned a leaf fragment from the sandstone of Bjuv to the species *Pterophyllum acuminatum* MORRIS based on macromorphology, although SCHENK (1867: 125) had previously assigned the latter species to the genus *Nilssonia*. In 1879 (p. 62), NATHORST created for his specimens a new species (*Ptilozamites acuminatus*), characterised by a longitudinally striated rachis and veins, which fork near the pinna base but proceed converging or parallel rather than diverging. According to the author, *P. acuminatus* differs from the original material of *Pterophyllum acuminatum* MORRIS by the symmetrical subdivision of the leaves.

Description: The most complete specimen is 77 mm long and up to 8 mm wide (S054948, Fig. 5A). Alternate or opposite triangular pinnae with an acute (45-50°) proximal and straight distal margin and rounded apex arise from the striate axis (1-3 mm wide). The basis of each pinna is broadly attached, touching the base of the following one, but not imbricating (Fig. 5B). The pinnae reach a maximal width of 13 mm and a maximal length of 10 mm (S054949, Fig. 5B). The delicate veins arise at a slightly acute angle and sometimes bifurcate once at the base, reaching the margin of the pinnae parallel to each other. In apical fragments, the pinnae decrease in dimension (7 x 2.5 mm) and become slightly more inclined and narrower (S054951/2, Fig. 5C).

The cuticle is relatively thin (upper side c. 2-4 µm, lower side c. 1-2 µm). The upper epidermis is characterised by rectangular cells with straight anticlinal walls. The lower cuticle is distinguished into bands above the veins with elongated epidermal cells with straight walls and devoid of stomata, and stomatal bands (Fig. 5E). Within the stomatal bands the epidermal cells show clearly undulating anticlinal walls (Fig. 5D-E, H-I). Numerous slightly sunken, syndetocheilic stomata are irregularly oriented. The guard cells are large and butterfly-shaped (Fig. 5H).

Distribution of the species: Rhaetian of Bjuv and Höganäs (Scania, S Sweden).

Discussion: NATHORST (1880: 66; 1886: 122 f.) grouped this species with *Ptilozamites acutangulatus* and discussed

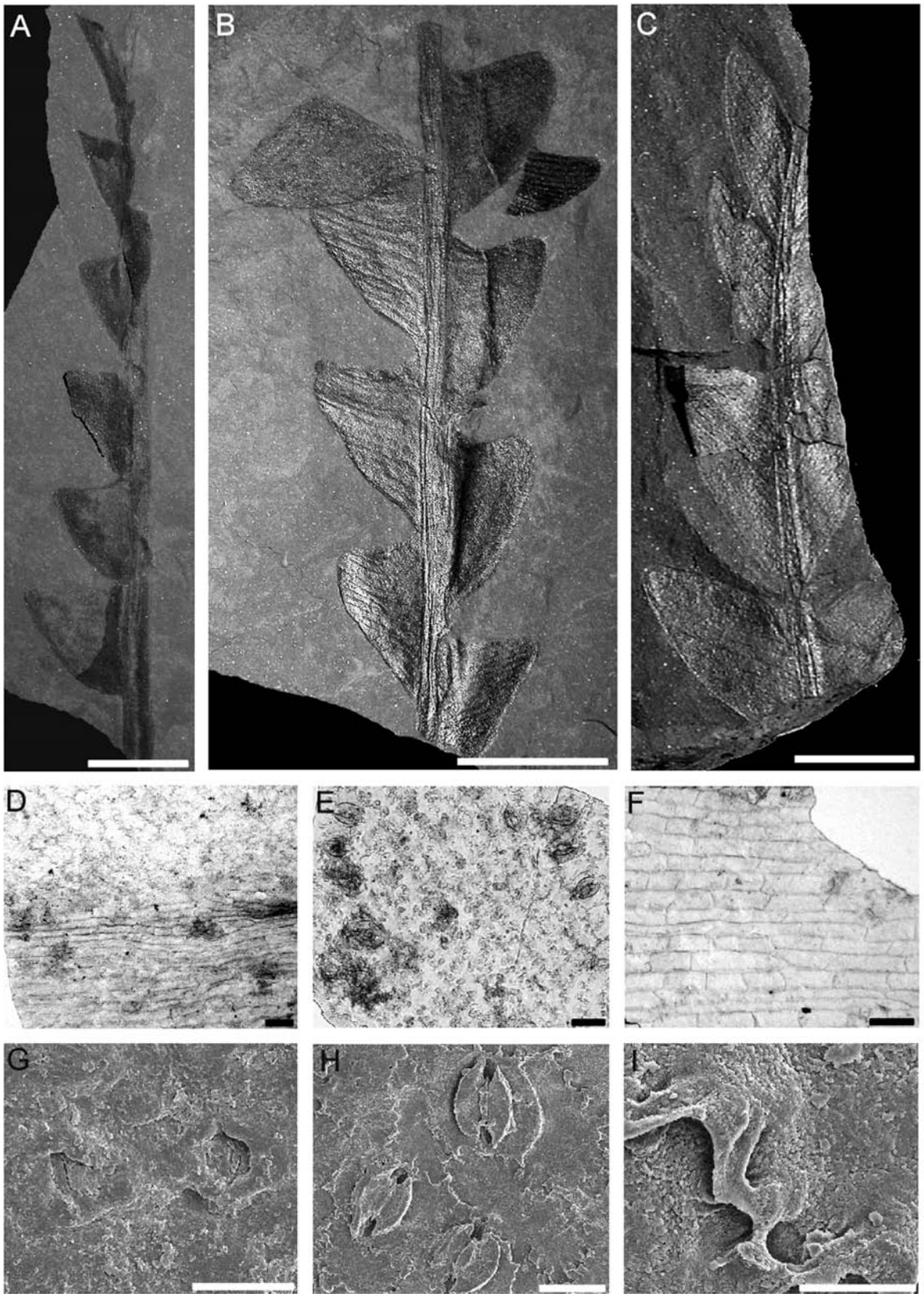

Fig. 5 (Legend see p. 87)

whether these two species may represent junior synonyms of *P. heeri*, an opinion confirmed later by ANTEVS (1914: 13). Afterwards, KRASSER (1908: 449 f.) attributed also the specimens from the Grestener Schichten of Bernreuth (Austria), described by STUR as *Nilssonia neuberi*, to this species (1871: 464).

In our opinion *Ptilozamites acutangulatus* and *Pt. acuminatum* are conspecific but not synonym of *Pt. heeri* since the pinnae of *Ptilozamites heeri* are never triangular in shape. Regarding the specimens mentioned by KRASSER, the latter belong to the genus *Nilssonia*. This is demostrated by the attachment of the pinnae (to the upper side of the rachis) and the epidermal anatomy (pers. comm. CHRISTIAN POTT, 2005).

The cuticle, described here for the first time, unequivocally shows that this species does not belong to the genus *Ptilozamites*. *Ptilozamites* species are characterised by a thick cuticle with haplocheilic stomata, surrounded by 6-7 indistinct subsidiary cells and characterised by a distinct ring around the stomatal pit. The cuticle of "*Ptilozamites" acuminatus*, however, is thin with undulating epidermal cells and typical bennettitalean syndetocheilic stomata.

According to the keys for bennettitalean leaves provided by HARRIS (1969: 3) and WATSON & SINCOCK (1992) we propose to include this species in the genus *Anomozamites*, since it shows the broad attachment of the pinnae with approximately the same width as length (in our case just slightly shorter than wide). The species does not show the standard rectangular shape of the pinnae, but this character has not been considered typical for the species (see also *Anomozamites nilssonii* e.g. in HARRIS 1969, figs. 37-38). This species, with S054949 (NATHORST 1879, pl. 12, fig. 4) as the most complete specimen of the two syntypes, is characterised by triangular pinnae with an acute proximal and straight distal angle that are attached laterally and with their whole base to a striate axis. The pinnae touch one another slightly but do not imbricate. The weak veins arise at a slightly acute angle, fork at the base and continue parallel to each other up to the margin of the pinnae.

Specimens S054951 and S054952 are part and counterpart of the second syntype; it shows the morphological characters well and moreover yielded a good cuticle.

The basal leaf fragment of *Anomozamites* described by STANISLAVSKI (1971: 70 f.) could also belong to this species. This specimen shows the typical triangular shape with an obtuse apex of the pinnae, attached laterally to the rachis. The distal margin is straight; the proximal one is widely oblique. The veins are thin, fork occasionally and run more or less parallel to each other. No cuticle is known to date.

Emended diagnosis: Leaves pinnate. Triangular pinnae (slightly shorter than wide) with a rounded apex, alternately or oppositely arising from a longitudinally striate rachis. Pinnae broadly attached and closely inserted with an acute (45-50°) proximal and straight distal margin. Pinnae reduced in dimension in apical fragments, becoming more inclined and narrower. Veins delicate, arising at a slightly acute angle, sometimes forking once at the base, reaching the margin of the pinnae parallel to each other. Cuticle delicate. Rectangular epidermal cells with straight anticlinal wall on the upper side. Lower epidermis distinguished into stomata-free bands above the veins, with elongated epidermal cells and straight walls, and stomatal bands with strongly undulating epidermal cell walls and irregularly scattered syndetocheilic stomata with two large, butterfly-shaped guard cells.

Basionym: *Ptilozamites acuminatus* NATHORST 1879.

Types: As no types where indicated by NATHORST, two syntypes were chosen from his original material, one because it is the best specimen and one because it gave the best cuticle preparation: *Ptilozamites acuminatus* NATHORST, p. 62, pl. 12, fig. 4. (S054949), our Fig. 5B. *Ptilozamites acuminatus* NATHORST, p. 62, pl. 12, fig. 6. (S054951-2), our Fig. 5C, cuticle Fig. 5F-I).

Ptilophyllum MORRIS 1840

The emended diagnosis of HARRIS (1969: 55) includes in this genus "simply pinnate leaves with elongated pinnae attached to the upper side of the rachis, having a pointed, asymmetric base, a decurrent proximal and a contracted distal margin, forming a rounded angle but angle scarcely forming an auricle. Veins parallel arising from the whole region of attachment, forking and ending near apex. Cuticle developed, syndetocheilic stomata with one subsidiary cell beside each guard cell; normally confined to lower surface; cell walls of the epidermis normally sinuous."

"*Ptilozamites acutifolia* FEISTMANTEL 1877", listed in the "Fossilium Catalogus" (JONGMANS & DIJKSTRA 1963) in the genus *Ptilozamites* probably belongs to this genus. On the referred page of FEISTMANTEL (1877: 65), however, the described species is just *Ptilophyllum acutifolium*. The description and figures

Fig. 5. *Anomozamites acuminatus* (NATHORST 1879) n. comb. (scale = 10 mm if not otherwise indicated). **A.** Most complete specimen (S054948). **B.** Leaf fragment (S054949). **C.** Apical leaf fragment (S054952), scale = 5 mm. **D.** Lower cuticle with small part of rachis (S055036), scale = 50 µm. **E.** Lower cuticle with undulating epidermal walls (S059632-01), scale = 50 µm. **F.** Detail of the lower cuticle of the rachis (S054951), scale = 30 µm. **G.** Outer view with sunken stomata, protected by a ringlike thickening (S054951-01), scale = 30 µm. **H.** Cuticle, inner view with stomata (S054951-01), SEM, scale = 30 µm. **I.** Lower cuticle, detail of epidermal cells with distinctly undulating anticlinal walls, inner view (S054951-01), SEM, scale = 12 µm.

of this species (with a decurrent basal angle of the pinnae) confirms the original attribution.

Ptilophyllum bengalensis (Oldham 1862) Schimper 1869

Selected synonymy:

1862 *Palaeozamia bengalense* Oldham in Oldham & Morris, p. 27, pl. 19, figs. 1-2, 6.
1867 *Otopteris bengalense* (Oldham). – Schenk, p. 138.
1869 *Ptilophyllum bengalense* (Oldham). – Schimper, p. 166.
1876 *Otozamites abbreviatus* Feistmantel, p. 10.
1877 *Otozamites abbreviatus* Feistmantel, p. 65, 67 f.
1878b *Ptilozamites bengalense* (Oldham). – Nathorst, p. 22.
1913 *Otozamites abbreviatus* Feistmantel. – Halle, p. 67, pl. 7, fig. 17.
1914 *Ptilozamites bengalense* (Oldham) Nathorst. – Antevs, p. 8.
1917 *Ptilophyllum bengalense* (Oldham) Schimper. – Seward, p. 521 f.
1943 *Ptilophyllum bengalense* (Oldham) Schimper. – Frenguelli, p. 276, 329.
1968a *Ptilophyllum bengalense* (Oldham) Schimper. – Kilpper, p. 550.
non 1968b *Ptilophyllum bengalense* [non (Oldham) Schimper]. – Kilpper, p. 129, pl. 1, figs. 1-4; pl. 2, figs. 3-4; text-figs. 2-3, 6. (see Schweitzer & Kirchner 2003: 115, 118).

This species has been described by Oldham for long, linear and narrow pinnate fronds with short rhomboidal pinnae. The pinnae with a falcate apex are slighltly imbricate and inserted by almost the whole base and obliquely to the striate rachis, often with a slight auricle. The prominent veins radiate from the base and fork toward the margin of the pinnae. Oldham described also a "var. *obtuse*", differing from the species due to its obtuse apex, while sharing the other characters of the species.

Later, this species has been transferred to various genera, first by Schimper (1869: 166) to *Ptilophyllum* Morris, then by Schenk (1867: 138) to *Otopteris* Lindley et Hutton and by Nathorst (1878: 22) to *Ptilozamites*. Feistmantel (1876: 10) attributed this species to the genus *Otozamites*, as De Zigno in an early, unpublished manuscript (1861) had also done, according to Feistmantel. Since the name *Otozamites bengalense* was already occupied by Schimper (1869: 169) for another *Otozamites* species, Schimper introduced a new name, *Otozamites abbreviatus*, due to the shortness of the leaflets. This attribution of the species to the genus *Otozamites* had been made under the assumption that the shape of the pinnae seems to be different from that of *Ptilophyllum* Morris and the pinnae are auriculate. Halle (1913: 67) marked on the weakness of the auricles in this species but assigned the material, on the authority of Feistmantel and Schenk, in the end to the genus *Otozamites*.

Distribution of the species: Jurassic of Jamkoondih, Soorujbera (Bengala).

Discussion: Schimper (1869: 166) assigned this species to the genus *Ptilophyllum*. Nathorst (1878: 22), later placed it in *Ptilozamites*, due to the shape of leaves and pinnae as well as due to the attachment of the pinnae. He considered it closely resembling the species *Ptilozamites nilssonii*.

The attachment of the pinnae with their entire base mentioned in the original diagnosis (Oldham 1862: 28) is, however, contradicted by the description of this species. There, the author stated that "…in most cases it is not easy to say certainly whether the pinnulae were truly auriculate, or were inserted by a portion only or by the whole of the base. But in one or two specimens, the front of the pinnae is preserved, and these show that there was a very slight auriculation, and that the pinnules were attached by nearly their whole breadth."

The species can, therefore, not been attributed to the genus *Ptilozamites*, where the pinnae are attached laterally to the rachis, as already discussed by Frenguelli (1943: 276).

As discussed by Seward (1917: 522) the attribution of some species to the genera *Ptilophyllum* or *Otozamites* is difficult. *Otozamites* indicates "fronds with pinnae characterised by an auriculate base, a broader lamina then in *Ptilophyllum* and more spreading veins." Due to the similarity of the Indian species *O. hislopi* and *O. abbreviatus* of Halle (1913: 67) to the English *Ptilophyllum pecten* or the material from India described by Feistmantel and Morris as *P. cutchense* and *P. acutifolium*, Seward (1917: 522) proposed to include these into the genus *Ptilophyllum*.

We attribute this species to the genus *Ptilophyllum*, in agreement with Schimper (1869), since the auricles seem to be only weakly developed, while the genus *Otozamites* is generally distinctly auriculate. No information of the epidermal anatomy of this species is known; therefore, the specific attribution cannot be established.

Dicroidium Gothan 1912

Gothan distinguished *Dicroidium* from *Thinnfeldia* based on the fact that the rachis is forked in *Dicroidium*. Each side of the leaf is again once to twice pinnate. The pinnules are characterised by odontopterid, sometimes alethopterid venation. The cuticle is thin, the epidermal anticlinal walls are thin and undulating and the stomata irregularly scattered.

According to Anderson & Anderson (1983) the genus is characterised by "a single dichotomy (angle of 25-30°) dividing fronds into lower 1/3 and upper 2/3. The frond is petiolate, simple to tripinnate. The pinnae of variable shape arise oppositely to alternately at ± 35° and have a constricted to decurrent base. The venation varies from taeniopterid, odontopterid to sphenopterid. The thin cuticle is characterised by

epidermal cells with straight cell walls and 0-4 papillae or trichome per cell. The cuticle is generally amphistomatic, sometimes hypostomatic. The stomata are haplocheilic with 4-5 subsidiary cells forming an ill defined ring."

Dicroidium (*Cardiopteris*) *zuberi***,** listed in the "Fossilium Catalogus" (JONGMANS & DIJKSTRA 1963) in the genus *Ptilozamites*, belongs to this genus.

Dicroidium zuberi (SZAJNOCHA) ARCHANGELSKY 1968

Selected synonymy (for a detailed list see ARCHANGELSKY 1968; ANDERSON & ANDERSON 1983).

1888 *Cardioperis zuberi* SZAJNOCHA, p. 233, pl. 2, fig. 1.
1889 *Ptilozamites zuberi* (SZAJNOCHA). – NATHORST, p. 202.
1914 *Ctenopteris zuberi* (SZAJNOCHA). – ANTEVS, p. 8.
1943 *Zuberia feistmanteli* (JOHNSTON). – FRENGUELLI, p. 308, fig. 25.
1943 *Zuberia barrealensis* FRENGUELLI, p. 310.
1943 *Zuberia sahni* SEWARD. – FRENGUELLI, p. 310, fig. 26.
1943 *Zuberia zuberi* (SZAJNOCHA). – FRENGUELLI, p. 300-310, 329.
1957 *Hoegia papillata* TOWNROW, p. 49, pls. 2C, 3; text-figs. 8B-D, G, K, 10 C-J, 11A-C.
?1957 *Hoegia antevsiana* TOWNROW, p. 50, pl. 3C, text-figs. 8E, 9L, 10K, 11D.
1968 *Dicroidium zuberi* (SZAJNOCHA). – ARCHANGELSKY, p. 502 f., pl. 98, figs. 1-2; text-figs. 1a, 2d-e.
1983 *Dicroidium zuberi* (SZAJNOCHA) ARCHANGELSKY. – ANDERSON & ANDERSON, p. 89, 108, p. 122, fig. 18; p. 193 f., tab. 14.3; p. 200, fig. 6.4; pls. 36-37, 101-2.
2003 *Dicroidium zuberi* (SZAJNOCHA). – ARCHANGELSKY et al., p. 257, fig. 1.

SZAJNOCHA (1888: 15) created this species for large linear, pinnate leaves with a stout, and sometimes slightly striate rachis. The rhomboidal pinnae with an acute apex and delicately rounded base are oppositely attached. The base of the pinnae is broadly inserted to the rachis; lateral pinnae never touch one another. The delicate, simple veins arise in groups and radiate.

NATHORST (1889: 202) positioned this species within the genus *Ptilozamites*, due to the thick leathery consistence of the leaves and the shape of the pinnae. Also the typical structure of the veins is, according to that author, closely related especially to the species *Pt. nilssonii* NATHORST and *Pt. blasii* (BRAUNS) NATHORST.

Later, ANTEVS (1914: 8) proposed to assign this species, due to its probably bipinnate frond, to the genus *Ctenopteris* (= *Ctenozamites*).

FRENGUELLI (1943: 301-10, 329) created the new genus *Zuberia* for big bifurcated and bipinnate (pinnatifide or pinnate) fronds with short pinnules of broad base and wide, odontopterid venations. He assigned *Cardiopteris zuberi* SZAJNOCHA, *Thinnfeldia feistmanteli* JOHNSTON, *Thinnfeldia sahni* SEWARD and *Zuberia barrealensis* FRENGUELLI to this genus, and considered the new genus different from *Dicroidium* due to the bifurcate but monopinnate fronds of *Dicroidium* and from *Thinnfeldia* due to the bifurcations of the aletopterid venation of *Thinfeldia*.

ARCHANGELSKY (1968: 502), however, did not agree with the removal of this species from *Dicroidium* and attribution to the new genus *Zuberia* since "the shape of the pinnules and the venation are identical". He attributed this species to *Dicroidium*, due to this identical shape of the pinnules and venation.

Finally, ANDERSON & ANDERSON (1983, 2003), regarded the species *Zuberia feistmanteli* (JOHNSTON) FRENGUELLI, *Zuberia barrealensis* FRENGUELLI, *Zuberia sahni* FRENGUELLI, *Hoegia papillata* TOWNROW and *Hoegia antevsiana* TOWNROW as junior synonyms of *Dicroidium zuberi*.

Distribution of the species: Early Triassic of Australia (Canning Basin, Sydney Basin, New England Foldbelt); Late Anisian of North Argentina; Ladinian of North Argentina, Antarctica, Australia (New Zealand, South Australia, Clarence-Moreton Basin); Carnian of North Argentina, South-Africa (Karoo Basin), India, Australia (Clarence-Moreton Basin); Norian of Chile; Rhaetian of South-America, S-Africa, Queensland and Tasmania (FRENGUELLI 1943; ANDERSON & ANDERSON 1983).

Discussion: From the original figures and descriptions it is not clear if this species could belong to the simple pinnate genus *Ptilozamites* as proposed by NATHORST and listed in the "Fossilium Catalogus" (JONGMANS & DIJKSTRA 1963). The bifurcate and bipinnate frond figured and discussed by ARCHANGELSKY (1968: 502) and ANDERSON & ANDERSON (1983, 2003), however, confirm the placement of this species in *Dicroidium*.

Pseudoctenis SEWARD 1911

According to the emended diagnosis given by HARRIS (1964: 70 f.) the genus *Pseudoctenis* is characterised by "large, simple pinnate leaves. Pinnae broad or narrow and elongated, lanceolate or parallel-sided, arising laterally on the rachis. Pinna margins entire, apex truncate or contracted, the base expanded or contracted. Veins nuomerous, parallel, simple or forked, not anastomousing. Lamina thick, hypostomatic. Haplocheilic stomata scattered, orientation variable or longitudinal. Guard cells sunken in a cutinised pit formed by a ring of haplocheilic subsidiary cells. Cell walls straight or nearly straight."

Pseudoctenis chinensis (HSÜ) n. comb.

Selected synonymy (for a detailed list see ZHOU 1981, 1989).

1950 *Ptilozamites chinensis* Hsü, p. 20, pl. 1, fig. 4.
1954 *Ptilozamites chinensis* Hsü. – Sze & Hsü, p. 54, pl. 48, fig. 6; pl. 53, fig. 1.
1965 *Ptilozamites chinensis*. – Cao, p. 518; pl. 3, fig. 2; pl. 4, figs. 1-4; pl. 6, fig. 1.
1978 *Ptilozamites chinensis* Hsü. – Zhou, p. 106, pl. 20, figs. 1-4; text-fig. 3.
1980 *Ptilozamites chinensis* Hsü. – He & Shen, p. 13, pl. 6, figs. 2, 5; pl. 8, fig. 1.
1981 *Ptilozamites chinensis* Hsü. – Zhou, p. 19 f., pl. 2, figs. 1-7; pl. 3, figs. 1-6.
1984 *Ptilozamites chinensis* Hsü. – Duan & Chen, p. 501, pl. 9 figs. 5-6.
1989 *Ptilozamites chinensis* Hsü. – Zhou, p. 140 f., pl. 4, fig. 5; pl. 5, figs. 1-8.

In 1950 Hsü (pl. 1, fig. 4) figured a specimen of *Ptilozamites chinensis*. The author discriminated the new species from *Pt. tenuis* Oishi due to 2 (or rarely 4) veins in the pinnae of *Pt. tenuis*, but without describing the venation pattern of *Pt. chinensis*. In 1954 (p. 54, in Sze & Hsü) he described the species as characterised by lanceolate leaves with a branched axis covered by small knob-like projections. The linear-falcate pinnae with 3-4 parallel veins arise alternately with an acute apex and 2-4 apical teeth.

A more detailed emended diagnosis is provided in Zhou (1981): "The lanceolate leaves with branched axis are covered by numerous small knobs-like projections. Linear to falcate pinnae (6-25 x 3 mm) arise with an angle of 40°-50° from the pinna axis. They are attached with the whole base and with slightly decurrent margin on the lateral side of the axis. The apex is acute and characterised by 2-4 (commonly 3) apical teeth. The fine veins arise in pairs or bifurcate at the base of the segments, afterwards moving on parallely, 2-6 (commonly 4) within each segment. The upper cuticle (2-3 μm) is slightly thicker than or similar to the lower one, with rectangular epidermal cells covered by papilla-like thickenings on the surface walls. Sometimes epidermal cells are elongated above the veins. Stomata are missing or very rare. In the lower cuticle (1-2.5 μm) the veins are distinct and composed of rectangular cell files. Cells in the intravenal zones are irregulare in shape and arrangement, and the stomata are randomly distributed. The haplocheilich stomata are polycyclic or incomplete dicyclic and share occasionally subsidiary cells. Guard cells are sunken and form bow-shaped to crescent thickenings. Subsidiary cells, 4-7 (5-6 common) in number, are irregular in shape and size. On the rachis the cuticle is thick, epidermal cells are elongated and regularly arranged. Stomata are rare and longitudinally arranged."

Distribution of the species: Late Triassic of Hunan Province (China).

Discussion: Zhou (1989) remarked on the close resemblance of this species with *Ptilozamites tenuis* (Oishi 1932: 321) and *Keraiaphyllum brevifolium* (Kilpper 1975), suspecting that at least the first could belong to the same species. To verify this theory is however impossible for us, due to the limited information available on the morphological variation of both species. The species differs, however, according to Zhou (1989), in pinna shape and epidermis from *Ptilozamites nilssonii* Nathorst).

The pinnate axis and side-ways attachment of the pinnae to the rachis resemble characters shown by various species of *Ptilozamites*, but they also agree with the generic diagnosis of *Pseudoctenis*. The attachment of the pinnae (with decurrent base and acute angle of 40 - 50°), shape (linear-falcate) and apex (dentate) of the pinnae, along with the small number of veins (2-6) within each pinna, are characters that suggest the new combination *Pseudoctenis chinensis*. This is confirmed also by the cuticle, especially the polycyclic or incomplete dicyclic stomata, sharing occasionally subsidiary cells and the bow- to crescent-shaped thickenings around the stomatal pits, which are longitudinally arranged.

Basionym: *Ptilozamites chinensis* Hsü 1950.

Type: *Ptilozamites chinensis* Hsü, p. 20, pl. 1, fig. 4.

Ctenozamites Nathorst 1886

This genus is based on the diagnosis in Saporta (1873: 351 f.) for *Ctenopteris*. Nathorst (1886: 122) realised the improper use of the previous name since it is a homonym of the extant fern *Ctenopteris* described much earlier (see also Antevs 1914; Harris 1964). He proposed, therefore, to use *Ctenozamites* for "species with compound leaves (*Ctenozamites bergeri* Goeppert and *Ctenozamites leckenbyi* Bean), while the single or dichotomously divided leaves should be assign to *Ptilozamites*."

Later, Nathorst (1897: 5), Seward (1900: 237), and Möller (1903: 19-21) used *Ptilozamites* and *Ctenozamites* (= *Ctenopteris*) as palaeobotanical subgenera of the same genus, distinguished only by the number of subdivisions of the fronds. Zeiller (1900: 101), Seward (1910: 548), Antevs (1914: 5) and Frenguelli (1943: 261 ff.) refused the use of the genus *Ctenozamites* in favor of *Ctenopteris*. This is, however, nomenclatorially incorrect.

The emended diagnosis of Harris (1964: 89) includes into this genus (summarised) "large, elongated leaves, with simple or forking rachis bearing simple pinnae both above and below the forking point. The proximal margin of the rhomboidal, triangulate or falcate pinnae is decurrent and broadly attached on the upper side of the rachis. The veins are parallel or slightly divergent, bifurcating and reaching the margin. The cuticle is thick, stomata are confined on the lower epidermis and scattered in areas between the veins, variably scattered."

The following species sometimes listed in the "Fossilium Catalogus" (JONGMANS & DIJKSTRA 1963) for the genus *Ptilozamites* belong to *Ctenozamites*.

According to HARRIS (1964: 90), the only difference between *Ptilozamites* and *Ctenozamites* is that the latter is bipinnate and the first simply pinnate. This difference separates them easily but is unlikely to have botanical importance, and it seems possible that they might be no more than two sections of a single natural genus".

Ctenozamites cycadea (BERGER) NATHORST 1886

Selected synonymy (for a detailed list see HARRIS 1961, 1964):

1832 *Odontopteris cycadea* BERGER, p. 23 f., pl. 3, figs. 2-3.
1835 (?1836) *Filicites cycadea*. – BRONGNIART, p. 387, pl. 129, figs. 2-3.
1836 *Odontopteris bergeri* GOEPPERT, p. 215.
1873 *Ctenopteris cycadea* (BRONGNIART). – SAPORTA, p. 355, pl. 40, figs. 1-2.
1876 *Ctenopteris cycadea* (BRONGNIART). – NATHORST, p. 37.
1878 *Ptilozamites cycadea* (BRONGNIART). – NATHORST, p. 51.
1884 *Ptilozamites bergeri* (GOEPPERT). – RICHARDS, p. 2.
1886 *Ctenozamites cycadea* (BRONGNIART). – NATHORST, p. 122.
1887 *Ctenozamites cycadea* (BRONGNIART) NATHORST. – SCHENK, p. 5, pl. 3, figs. 11-16a; pl. 4, fig. 18; pl. 6, fig. 30; pl. 7, fig. 36; pl. 8, fig. 43; pl. 9, fig. 54.
1922 *Filicites cycadea* BRONGNIART. – KRASSER, p. 46-8.
1961 *Ctenozamites cycadea* (BERGER) SCHENK. – HARRIS, p. 151, pls. 31-32; text-figs. 1-2.
1964 *Ctenozamites cycadea* (BERGER) SCHENK. – HARRIS, p. 95, pl. 4, figs. 3, 7; text-figs. 41-2.
1997 *Ctenozamites cycadea* (BERGER) SCHENK. – BARBACKA, p. 82, pl. 1, fig. 1.
1998 *Ctenozamites cycadea* (BERGER) SCHENK. – SCHWEITZER & KIRCHNER, p. 48, pl. 11, figs. 1-6; text-figs. 19-21, 25a.
2000 *Ctenozamites cycadea* (BERGER) SCHENK. – POPA, p. 144, pl. 64, fig. 3, pl. 101, figs. 3-4.

The species has been instituted by BERGER (1832: 23) for pinnate leaves with thick, elongated pinnae with entire margin and obtuse apex. The pinnae are inserted (sub)alternately, at an acute angle and with a broad base to the thick rachis. No midrib is visible, but delicate and sometimes dichotomising veins arise from the leaf-base.

BRONGNIART (1835-1836) added the closely inserted pinnae, which are however not basally fused, and the indistinct primary and secondary veins to the description.

HARRIS (1964: 95 f.) described this species as having sometimes once bifurcated but further simply pinnate leaves with rhomboidal to triangular pinnae arising at an angle of more than 45°. The apex of the pinnae is obtuse; the veins are nearly parallel and fork once or twice. The cuticle is moderately thick, with polygonal epidermal cells, which become elongate above the veins. The incompletely dicyclic stomata are characterised by c. 6 subsidiary cells forming a pit with strongly thickened sides and irregular encircling cells.

Distribution of the species: Lower Liassic of Lyme Regis (England), Germany, France, Hungary, Waidhofen an der Ybbs (Austria), Romania, Hör (Sweden), Middle-Upper Liassic of Alborz (Iran), Middle Jurassic of England.

Discussion: Brongniart attributed the species described in his "*Histoire des végétaux fossiles, ou Recherches botaniques et géologiques sur les Végétaux renfermes dans les divers couches du globe*" to the genus *Filicites*, enlisting however as synonymy the species *Odontopteris cycadea* BERGER 1832. Although BRONGNIART's work is often considered published in 1828, actually it was published in several parts between 1828 and 1836. HARRIS (1961) indicated 1835 or 1836 for the "Livre 10" where *Filicites cycadea* is discussed. The latter fact explains why BRONGNIART could discuss a species described – according to the general reference lists – by BERGER in 1832. A detailed systematic discussion on this account was published by HARRIS (1961: 169-171).

GOEPPERT (1936, p. 215) established a new species for this material, *Odontopteris bergeri*, which is however nomenclatorially incorrect. Later, SAPORTA (1873: 355) assigned the species to *Ctenopteris* and NATHORST first to *Ptilozamites* (1878: 21) and finally to the new genus *Ctenozamites* (1886: 122).

Ctenozamites leckenbyi (BEAN) NATHORST 1886

Selected synonymy (for a detailed list see HARRIS 1964):

1864 *Ctenis leckenbyi* LECKENBY (ex BEAN MS), p. 78, pl. 10, fig. 1a-b.
1867 *Odontopteris leckenbyi*. – DE ZIGNO, p. 111 f.
1869 *Cycadopteris leckenbyi* (BEAN). – SCHIMPER, p. 487.
1875 *Odontopteris leckenbyi* DE ZIGNO. – PHILLIPS, p. 218, fig. 41.
1880 *Ptilozamites leckenbyi* (BEAN). – NATHORST, p. 64 ff., plate on p. 83.
1884 *Ptilozamites leckenbyi* (BEAN). – RICHARDS, p. 2.
1892 *Ptilozamites leckenbyi* (BEAN). – FOX-STRANGWAYS, p. 141.
1900 *Ptilozamites* (*Ctenozamites*) *leckenbyi* (BEAN). – SEWARD, p. 238 f..
1903 *Ptilozamites* (*Ctenozamites*) *leckenbyi* (BEAN) NATHORST. – MÖLLER, p. 20 f., pl. 2, fig. 19.
1919 *Ptilozamites leckenbyi* (BEAN) NATHORST. – KNOWLTON, p. 518.
1934 *Ctenozamites leckenbyi* (BEAN) GOTHAN. – HOFMANN, p. 212.

1943 *Ctenopteris leckenbyi* (Bean) Gothan. – Frenguelli, p. 263, 329.
1964 *Ctenozamites leckenbyi* (Bean) Gothan. – Harris, p. 91, pl. 4, figs. 6, 10; text-figs. 35E, 39, 40.
1998 *Ctenozamites leckenbyi* (Leckenby) Nathorst. – Schweitzer & Kirchner, p. 53, pl. 12, figs. 1-10.
2000 *Ctenozamites leckenbyi* (Leckenby) Nathorst. – Popa, p. 145, pl. 65, fig. 1; pl. 113, figs. 1, 3.

Leckenby (1864: 78) described and figured for the first time *Ctenis leckenbyi*, dedicated to him by Bean in an unpublished manuscript. The species is characterised by bipinnate leaves, with a stout, grooved primary and delicate secondary rachis. The pinnae are attached with the entire base to the rachis; veins are forked, almost parallel.

De Zigno (1867: 111 f.) moved the species to the genus *Odontopteris*, adding the opposite attachment of the elongate-falcate pinnae, the pointed to rounded apex and the subparallel but twice or three times forking veins. Phillips (1875) independently also transferred the species to *Odontopteris*, but since then no other authors considered this attribution to this Palaeozoic genus as correct.

Harris (1964: 91) separated *C. cycadea* from *C. leckenbyi* based on the length/width ratio of the pinnules (1-2 in *C. cycadea* and 2-5 in *C. leckenbyi*) and especially the shape of the pinnule-apex (obtuse or occasionally acute in *C. cycadea*, and acute-mucronate with some small additional teeth in *C. leckenbyi*). Moreover, the cell walls are straight in *C. cycadea* and slightly wavy in *C. leckenbyi*.

Distribution of the species: Liassic of Lyme Regis (England), the Vicentinian Alps (Italy) and Romania; Middle Jurassic of Yorkshire (England) and Afghanistan.

Discussion: As already said above, De Zigno (1867: 111 f.) and Phillips (1875: 218) both moved the species to *Odontopteris*, mainly based on venation. Schimper (1869: 487) attributed the species to the genus *Cycadopteris*. Nathorst (1880: 64 ff.) considered "*Ctenis leckenbyi*" close to his *Ptilozamites nilssonii* (see also *Ptilozamites heeri* in Nathorst 1879: 60) due to some bifurcated leaf-fragments of the latter taxon. Therefore, he assigned the English form to the genus *Ptilozamites*, just as Richards (1884: 2), not knowing Nathorst's previous consideration. Later on, however, Nathorst (1886: 122) distinguished between the once forked leaves of *Ptilozamites* and composed leaves of *Ctenozamites* (= *Ctenopteris*), assigning both *Ctenozamites bergeri* Göppert and *Ctenozamites leckenbyi* Bean to this new genus. Harris (1964: 91) finally discussed the species in detail and assigned it to *Ctenozamites*.

4. Palaeogeographic and biochronostratigraphic distribution of the various *Ptilozamites* species

The genus *Ptilozamites* was introduced by Nathorst (1878b) for a plant group he considered of limited stratigraphic range; i.e. restricted to the Rhaeto-Liassic. This consideration has recently been questioned because specimens belonging to this genus, were discovered in sediments from the Middle and lower Upper Triassic of the Alps (e.g. Wachtler & Van Konijnenburg-Van Cittert 2000a, b; Kustatscher 2004; Kustatscher et al. 2004; Kustatscher & Van Konijnenburg-Van Cittert 2005; Roghi et al., in press). The systematic revision of the original collection and taxonomic revision of all species attributed to this genus, revealed an interesting biochronostratigraphic and palaeogeographic distribution of the genus (Fig. 6A-F).

The earliest evidence for this genus comes from the Upper Anisian (lower Middle Triassic) of the Dolomites (N Italy) (Fig. 6B). The leaf fragments closely resemble the general pattern of *Ptilozamites*, in particular *P. sandbergeri*, with regard to attachment of pinnae (lateral, whole-basely) to the rachis and epidermal anatomy (polygonal epidermal cells, ring-like stomatal thickenings, 4-6 polygonal subsidiary cells). However, detailed information on the stomatal pattern is missing; therefore it has been attributed only on a cf. level to this species.

The first persuasive fossil evidence of *Ptilozamites sandbergeri* (Fig. 6C) comes from the Ladinian (upper Middle Triassic) of the Dolomites. This species, present also in the Carnian (lower Upper Triassic, Fig. 6D) of the Dolomites and the Julian Alps (both N Italy), is characterised by a simple morphology. The laterally attached pinnae are square to rectangular with rounded angles. The simple, unforked veins are parallel and end close to the margin thus resulting in a c. 1 mm wide marginal rim. The leaf is hypostomatic, with elongate epidermal cells above the veins of the lower side.

During the Norian-Rhaetian, the presence of dolomitic sediments in the alpine area inhibits preservation of plant material. In other localities of the Northern Hemisphere, however, this genus reaches an ample palaeogeografic and taxonomic distribution in the Rhaeto-Liassic (Fig. 6E). Several species can be distinguished, also in the same locality, as for example in Scania, S-Sweden, where during the Rhaeto-Liassic at least 3 different species co-existed: *Ptilozamites heeri*, *P. blasii* and *P. nilssonii*. *Ptilozamites heeri* has been recorded from Sweden, but has recently also been recorded from the southern Germany (see p. 76). *Ptilozamites blasii* has also been described from Germany and Sweden (p. 78). *Pilozamites nilssonii* showes the widest palaeogeographic distribution. It

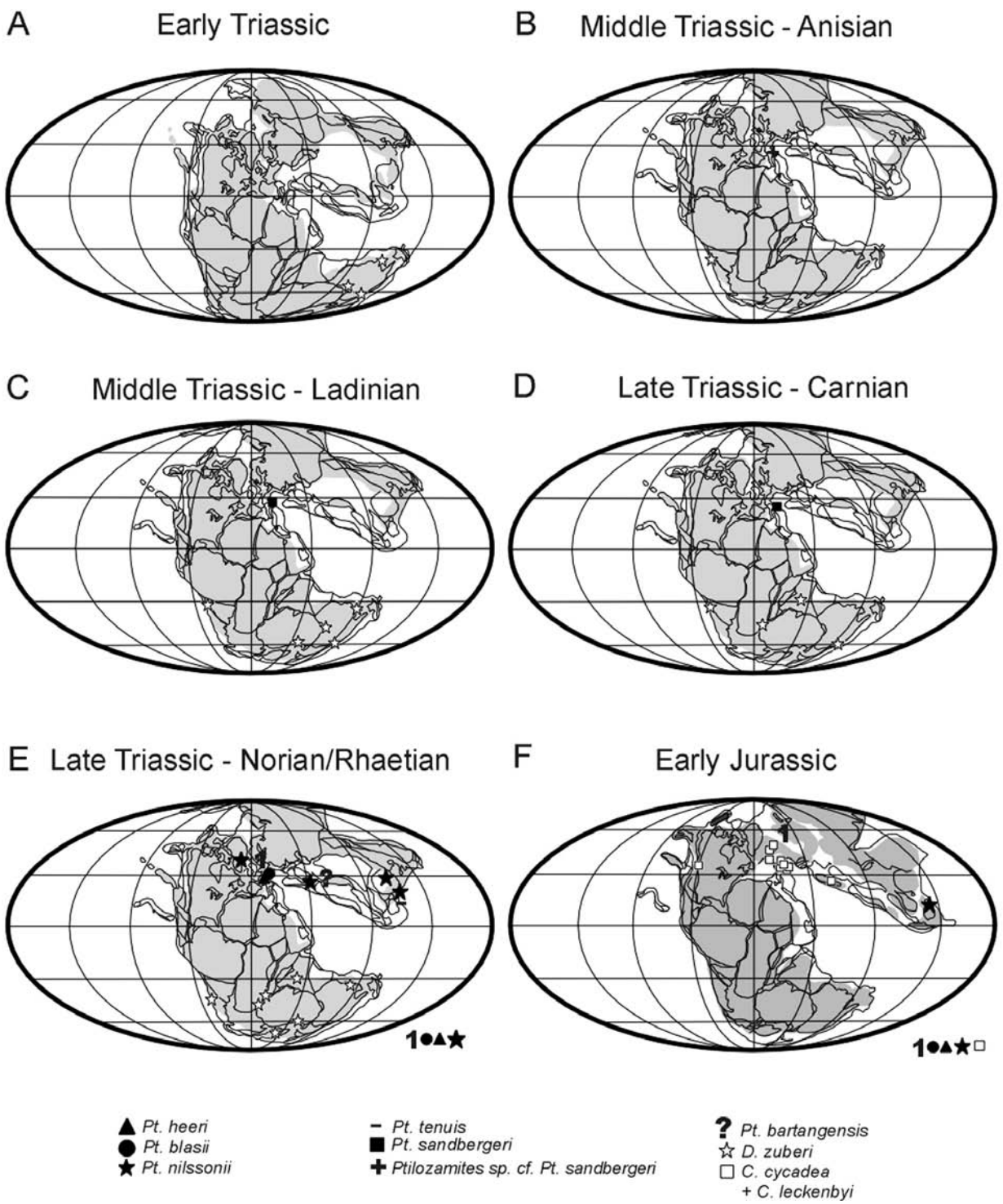

Fig. 6. The palaeogeographical distribution of the *Ptilozamites* species and some related taxa during the Early Mesozoic.

has been collected from Rhaetian sediments of Sweden, E Greenland, Romania and China, perhaps also from Iran (p. 81). Additionally, *P. nilssonii* has been recorded, together with *P. tenuis* (p. 81 f.) from Rhaeto-Liassic sediments of Japan. Perhaps *P. bartangensis,* which has been described from Pamir (Tatjikistan) (p. 84), also belongs to the genus. No specimens are known to date from sediments younger than the Liassic (Early Jurassic, Fig. 6F).

In the Southern Hemisphere, *Ptilozamites* is completely absent. The only species historically attributed to this genus is *Dicroidium zuberi* (SZAJNOCHA) ARCHANGELSKY, once assigned to *Ptilozamites* by NATHORST (1889: 202), due to the leatherly consistence of the leaves, its pinnae shape and the venal pattern. The bipinnate leaf-structure of the specimens resulted, however, in the attribution of the species first to the genus *Ctenopteris* (= *Ctenozamites*) (ANTEVS 1914: 8) and then to *Dicroidium* (ARCHANGELSKY 1968: 502). This species shows an ample distribution in the Southern Hemisphere during the Middle-Late Triassic, from the Olenekian – lower Carnian of Australia (Fig. 6A-D), the upper Ladinian of the Antarctica (Fig. 6C), the lower Carnian of South-Africa and India (Fig. 6D) and the Norian-Rhaetian of South America (Fig. 6E).

In this context the close affinities between the genera *Ptilozamites*, *Ctenozamites* and *Dicroidium* can be observed, as has been discussed by HARRIS (1964) for the first two genera. *Ptilozamites* is characterised by simple pinnate leaves, sometimes (i. e. *P. nilssonii*) displaying a bifurcate rachis. The difference between *Ptilozamites* and *Dicroidium* and *Ctenozamites* lies mostly in gross morphology. *Ctenozamites* leaves (also sometimes forked) are bi- to tripinnate with pinnae broadly attached on the upper side, while *Dicroidium* is always forked, simple to tripinnate and pinnae with constricted to decurrent base. The epidermal anatomy is very similar in all three genera. They are all characterised by amphistomatic to hypostomatic leaves with sunken guard cells surrounded by subsidiary cells forming a more or less complete and distinct ring. This latter feature has been considered as typical for *Ptilozamites* cuticles by FLORIN (1933). The close resemblance between the epidermal anatomies of these three genera, not only renders it difficult to assign ill preserved and/or small leaf fragments to any of these genera, but also suggests a close relationship between these three morphogenera.

Stratigraphically, *Dicroidium* is the first genus to appear (i.e. Late Permian) and also to disappear. *Ptilozamites* has been first recorded from the Middle Triassic and has its last occurrence in the Liassic, while *Ctenozamites* only first appears in the Liassic.

5. Conclusions

A detailed study of the original *Ptilozamites* material of NATHORST and ANTEVS showed a large variability in the genus and within the individual species.

Material attributed to *Ptilozamites heeri* NATHORST, *Ptilozamites linearis* NATHORST, *Ptilozamites carlsonii* NATHORST (pro parte), *Ptilozamites oldhamii* NATHORST, *Ptilozamites heeri* f. *angustior* NATHORST and *Ptilozamites triangularis* NATHORST has been combined into the genus *Ptilozamites heeri* NATHORST together with new, unpublished specimens from the Rhaetian of Germany (first record outside of Sweden).

Material attributed to *Ptilozamites nilssonii* NATHORST, *Ptilozamites falcatus* NATHORST, *Ptilozamites fallax* NATHORST, *Ptilozamites nilssonii* var. *longior* NATHORST, *Ptilozamites ?latior* NATHORST has been combined into the genus *Ptilozamites nilssonii* NATHORST.

Material attributed to *Pterophyllum sandbergeri* SCHENK, *Pterophyllum minus* BRONGNIART (pro parte), *Pterophyllum brevipenne* KURR (pro parte), cfr. *Pterophyllum venetum* DE ZIGNO, *Pterophyllum bronnii* SCHENK (pro parte) and *Ptilozamites heeri* NATHORST (pro parte) have been assigned to the new combination *Ptilozamites sandbergeri* (SCHENK) n. comb., with an emended diagnosis including the first description of its cuticular pattern. Additional specimens have been assigned to this species at a cf. level.

Ptilozamites bartangensis PRYNADA is considered doubtfully attributed to the genus.

Various species are excluded from *Ptilozamites*; *Ptilozamites acuminatus* (NATHORST 1979) and *Ptilozamites acutangulatus* are conspecific and unequivocally belong to *Anomozamites*, *Ptilozamites chinensis* HSÜ has been transferred to *Pseudoctenis chinensis* (HSÜ) n. comb. due to the attachment of the pinnae, as well as the cuticular pattern.

The genus *Ptilozamites*, once considered restricted to the Rhaeto-Liassic is now reported also from the Middle Triassic. During that time there was one species (*P. sandbergeri*) from the Alpine area, but in the Rhaetian and Liassic there was a large increase in both diversity and spatial distribution.

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Table 1. Comparison between the leaf-morphology of four *Ptilozamites* species.

	Pt. heeri	*Pt. blasii*	*Pt. nilssoniii*	*Pt. sandbergeri*
Leaf	Simple	Simple	Simple-dichotomising	simple
Axis	Striate	Striate	Tuberculate, small acute bumps	Striate
Pinnae	Romboidal with rounded apex; basally crescent-shaped apically sub-falcate	Falcate- lobate, rounded apex	Wide falcate with obtuse apex and imbricate to subimbricate margin	Subrectangulare - subquadrate with rounded apex
Pinna dimensions base	Max. 8-10 x 13-14 mm; apically 2.5 x 4.2 mm, basally 4.3 x 10.5 mm;	Max. 60 x 35 mm; apical 15 x 12-15 mm	Max. 15 x 6-7 mm (var. longior –22 mm length)	Max. 8 x 6-8 mm, apically 2,8 x 3,5 mm, basally 6 x 11 mm
Prox. margin	Parallel to the distal margin, then curved or inclined	Apically curved	First parallel with the front, then rounded	First parallel with the front, then curved
Distal margin	Truncate to apically inclined	Straight to slightly concave	Concave, sometimes straight	Straight to slightly curved
Veins	Delicate to distinct veins	Distinct veins	Distinct veins	Distinct veins
Veins arise	Perpendicularly to slightly apically inclined	Slightly acute angle	Slightly acute angle	Perpendicularly
Veins bifurcations	In the middle part	At the base, and once in the apical part	Bifurcating in the lower-middle parte	Rare bifurcations at the base
Veins at the margin	Parallel with 15-17/cm	Slightly radiating	Radiating towards the prox. Margin - almost parallel	Parallel, with 7-9/cm small vein-free band

Table 2. Comparison of the epidermal anatomy of four *Ptilozamites* species (e.c = epidermal cells).

	Pt. heeri	*Pt. blasii*	*Pt. nilssoniii*	*Pt. sandbergeri*
Epidermal cells	Isodiametric polygonal, small thickenings	Isodiametric - rectangular, with thickenings	Irregular to isodiametric polygonal	Irregular polygonal
Epidermal cell walls	Straight	Straight	Straight, with "twisted-cord"-like thickenings	Straight
Pinnae - upper epidermis	Stomata rare	Stomata absent	Stomata absent	Stomata rare
Pinnae – u. e. venal pattern	No distinction	Elongate e.c.	Elongate e.c.	No
Pinnae - lower epidermis	Stomata abbundant on pinnae, sharing subsidiary cells	Stomata rare on and between the veins; e.c. 50-70 µm	Numerous stomata between the veins	Stomata scattered between veins, thickenings on e.c. of the veins
Pinnae – l. e. venal pattern	No distinction	Elongate e.c.	More or less disting strips of oblong cells	Elongate e.c.
Rachis - upper epidermis	Elongate e.c.; Stomata abbundant	Elongate e.c.	Elongate e.c.; Stomata abbundant	Slightly elongate e.c.
Rachis - lower epidermis	Elongate e.c.; stomata absent or few	Elongate e.c.	Elongate e.c.; stomata few	Elongate e.c.; stomata few
Stomata	Sunken, just lower side or both sides	Sunken, only on the lower side	Sunken, only on the lower leaf surface and rachis	Sunken, irregularly distributed, never share subsidiary cells
Subsidiary cells	Strong ring formed by 6-7 subsidiary cells	Strong ring formed by 7 subsidiary cells	6 subsidiary cells (less often 5, 7)	Ring formed by 6-8 subsidiary cells

Table 3. Synopsis of the leaf-morphology of the genera *Ptilozamites, Dicroidium* and *Ctenozamites.*

	Ptilozamites	***Dicroidium***	***Ctenozamites***
Leaf	Pinnate	Simple to tripinnate	Pinnate to bipinnate
Rachis	Stout, often forked	Bifurcated	Simple or forking
Pinnae shape	Square, rhomboidal, linear, triangular or falcate	Variable in shape	Rhomboidal, triangular or falcate
Pinnae attachment	Whole base laterally to the rachis	Constricted to decurrent base	Broadly attached on upper side of rachis
Veins	Bifurcate at least once, more or less radiating or parallel	Taeniopterid, odotopterid to sphenopteroid veins	Parallel or slightly divergent bifurcating, reach the margin
Epidermis	Thick, amphistomatic or hypostomatic	Thin, generally amphistomatic, sometimes hypostomatic	Thick, hypostomatic
Stomata	Guard cells sunken; irregular subsidiary cells forming ring-like thickenings	Monocyclic stomata with sunken guard cells, 4-5 subsidiary cells forming an ill defined ring	6 subsidiary cells forming a rounded or irregular group forming a thick ring