Late Triassic Plant Megafossils from Aghdarband (NE-Iran)\(^*)\)

By MIENTE BOERSMA & JOHANNA H.A. VAN KONIJNENBURG-VAN CITTERT\(^*)\)

With 1 Table and 10 Plates

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Zusammenfassung

Pflanzliche Megafossilien von verschiedenen Fundstellen in der Trias-Schichtfolge bei Aghdarband im Osten des Iran werden beschrieben. Eine Liste der identifizierten Reste enthält zwei neue Arten, Podozamites paucinervis und Pagiophyllum ruttneri.

Aus jeder Lokalität werden die bestimmmbaren Pflanzenreste beschrieben und biostratigraphische Implikationen diskutiert. Bestimmmbare Pflanzenreste lieferten nur das Aghdarband Coal Bed an der Basis der Miankuhi Formation und ein weiterer Kohlenhorizont an der Basis der Ghal’eh Qabri Shales.

Anhand der fossilen Reste wird versucht, das Alter dieser beiden Kohlenhorizonte festzustellen. Für die Basis der Ghal’eh Qabri Shales ist ein Rhät-Alter wahrscheinlich; für das Aghdarband Coal Bed ist eher ein Nor-Alter anzunehmen.

Die iranische fossile Flora wird verglichen mit anderen spät-triassischen Floren, besonders mit denen aus der zentralasiatischen Region der Euro-Chinesischen Provinz.

Abstract

Late Triassic plant megafossils are described from several sites within the Triassic sequence of beds exposed at Aghdarband, eastern Iran. A list is given of the taxa recognized, including two new species, viz. Podozamites paucinervis and Pagiophyllum ruttneri.

From each site the determinable fossil plant fragments are described. They belong either to the Aghdarband Coal Bed at the base of the Miankuhi Formation or to a coal horizon at the base of the Ghal’eh Qabri Shales. The biostratigraphic implications of the determinations are discussed, and an overall age interpretation is given. It seems realistic to consider the plant megafossils to be indicative for a Norian-Rhaetian age: the base of the Ghal’eh Qabri Shales is probably Rhaetian, the Aghdarband Coal Bed, if anything, Norian in age.

The Iranian florule is compared with other Late Triassic floras, especially with those from the Middle-Asian area of the Euro-Chinese province.

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\(^*)\) Authors’ address: MIENTE BOERSMA, JOHANNA H.A. VAN KONIJNENBURG-VAN CITTERT, Laboratory of Palaeobotany and Palynology, State University, Heidelberglaan 2 (De Uithof), NL-3584 Utrecht.
1. Introduction

As part of a multidisciplinary research-project in the Triassic of Aghdarband, eastern Iran, palaeobotanical and palynological investigations were carried out in the Laboratory of Palaeobotany and Palynology of the State University, Utrecht, The Netherlands.

The investigations were based on samples and a collection of plant megafossils from the Triassic rock-sequence of Aghdarband (RUTTNER, 1980, 1984 and this vol.). Unfortunately, palynological data remained inconclusive because of the strong carbonization of organic material. Part of the plant megafossils, on the other hand, are well enough preserved to be identified. In the present paper they are described and an age-interpretation is given in terms of Triassic standard stages.

2. Material

For a comprehensive account on the geology of the Aghdarband region as well as the lithological Triassic sequence, one is referred to the paper of A. W. RUTTNER in the present volume.

The material originates from the Sina and Miankuhi Formations of the Aghdarband Group and from the basal sandstone of the Ghal‘eq Qabri Shales. Thick tuffaceous marine sandstones and shales of the Sina Formation are overlain by the Aghdarband Coal Bed consisting of coals and coaly shales (1–3 m). The latter are in turn overlain by a thick sequence of shales; together with the Aghdarband Coal Bed they form the Miankuhi Formation of the Aghdarband Group. The folded and faulted rocks of this Group are unconformably overlain by the Ghal‘eq Qabri Shales which again have a thin coal bed and a layer of plant bearing sandstone at their base (compare lithological column in RUTTNER [this vol.], Table 1 and Text-Fig. 4).

The material collected consists of 40 specimens from various sampling sites. Several specimens (from sites 75/44, 76/58, 76/63, 76/64, 76/65, 76/68 and 76/98) are so badly preserved that, in our opinion, identification is impossible. From these, one sample (76/63) originates from the top of the Sandstone Member, one sample (76/58) from the base (Faqir Bed) and two samples (76/65 and 76/88) from upper parts of the Shale Member of the Sina Formation. Sample 76/64 was collected at the very top of this Formation at the site where the vertical standing tree trunk was found. Samples 76/82 and 76/98 originate from tectonical slices in Unit I of the Southern Frame, and No. 75/44 refers to questionable plant remains which were obtained from the Upper Devonian limestone of the Northern Frame.

The material from the remaining sites is better preserved: 76/94 contains two, 76/95 three, 75/19 eight and 75/3 eighteen specimens; samples 76/94, 76/95 and 76/19 (13 specimens in total) were obtained from the Aghdarband Coal Bed, whereas the 18 specimens of sample 76/3 were collected at the base of the Ghal‘eq Qabri Shales close to the village of the same name east of the mapped area. In about half of all these 31 specimens the plant material is preserved as impressions; in the other half as compressions. None of the compressions yielded a cuticle; most of the specimens show little or no venation.

In most cases the lack of detailed venation and cuticle renders accurate determination at the species level impossible.

The following taxa were recognized:

**Equisetophyta**
- *Neocalamites* sp. A

**Pteridophyta**
- *Cladophlebis* sp. A

**Cycadophyta**
- *Pterophyllum* sp. cf. *P. ptilum* HARRIS
- *Pterophyllum* sp. cf. *P. subangulare* HARTZ

*"Pteridophyllum" sensu NATHORST*
- *Taeniopteris* sp. A
- *Taeniopteris* sp. B

**Ginkgophyta**
- *Sphenobaiera* sp. A

**Coniferae**
- *Pagiophyllum ruttneri* nov. sp.
- *Podozamites paucerrivis* nov. sp.
- *Podozamites* sp.
- *Stachyolaxus elegans* NATHORST

**Incertae sedis**
- *Carpolithes* sp. cf. *C. cinctus* NATHORST
- *Seed scale*

The material is kept in the Paleontological Department of the Geological Survey (Geologische Bundesanstalt) in Vienna and is listed under the reference numbers 1991/1/1–16.

3. Descriptions

3.1. Site 76/94

The two specimens from this site both contain *Podozamites* sp. In addition, one also holds *Sphenobaiera* sp. A and *Taeniopteris* sp. A.

**Formgenus Taeniopteris** BRONGIART 1828

**Taeniopteris** sp. A

(Pl. 1, Fig. 4; GBA 1991/1/1)

The apex of a *Taeniopteris* leaf (see Pl. 1, Fig. 4) is preserved in one of the specimens. The fragment is 4.4 cm long and 1.8 cm broad. The midrib has a width of 2 mm. The apex is acute.

As there are no veins visible and the cuticle is absent, determination at the species level is impossible (compare remarks under *Taeniopteris* sp. B).

**Formgenus Sphenobaiera** FLORIN 1936

**Sphenobaiera** sp. A

(Pl. 1, Fig. 6; GBA 1991/1/1))

**Description**: The leaf fragment of *Sphenobaiera* sp. A has a length of 8.2 cm. It shows one dichotomy, and thus two segments. The basal, undivided portion is about 3 cm long. At the base the width is 2 mm, just below the dichotomy 7 mm and in the two segments 6 and 6.8 mm resp. The basal angle is about 20°, the angle of branching is 5°. Below the dichotomy the...
Discussion: This fragment is too small to be identified at the species level. It somewhat resembles Sphenobaiera parallelinervis STANISLAVSKI 1976. In the latter species, however, both the basal angle and the angle of branching are larger. The width of the segments and the number of veins in our fragment, though, agree with this species. Sphenobaiera parallelinervis is known from the Donets Basin, Protovipskaya suite. This suite is considered to be of Late Norian age by STANISLAVSKI (1976). VAHRAMEEV et al. (1976) believe it to be more likely Karpnovian in age. This belief, however, is based on the absence, in their opinion, of any comparable Norian flora.

Another Sphenobaiera species similar to our specimen, is Sphenobaiera paucipartita (NATHORST) FLORIN. In this case the basal angle and the angle of branching agree. However, in the segments more veins seem to be present than in our specimen. This species has, among other localities, been reported from the Norian deposits of the Amba river (SHOROKHOVA, 1975).

Genus Podozamites BRAUN 1843

**Podozamites sp.**

(GBA 1991/1/1,2)

Small Podozamites leaves are preserved in both specimens from this site, varying in size from 17 mm long and 3.5 mm broad to 37 mm long and 6 mm broad. The smallest leaf is part of a three-leaved apical portion of a shoot. The greatest width is at about \( \frac{1}{3} \) of the length of the leaf reckoned from the base. No venation is visible.

Broader leaves are preserved in the other two specimens. Three fragmentary leaves among them show venation (resp. 7 mm wide with nine parallel veins; 8 mm wide with ten veins and 11 mm wide with eleven veins). One entire leaf (partly shown on Pl. 4, Fig. 5) is 55 mm long, 10 mm wide and contains nine veins.

We are of the opinion that this material might belong to Podozamites paucinervis nov. sp. to be described in the paragraph on site 75/19, where most of the material of this species was found.

Incertae sedis

**Seed scale**

(Pl. 4, Fig. 5; GBA 1991/1/4)

In one specimen a seed scale is preserved. The upper part of the scale is slightly triangular. Near the apex an also slightly triangular scar is visible where the seed has been attached. The scale is 8 mm long, 3 mm wide at the base and 5.5 mm wide just below the scar. The absence of any detail makes determination impossible.

3.3. Site 75/19

Of the eight specimens from this site six preserve Podozamites only, one holds Podozamites and Carpolithes and one a fragment of Neocalamites. As in sites 76/94 and 76/95, Podozamites is the dominant form in this small collection.

Genus Neocalamites HALLE 1908

**Neocalamites sp. A**

(Pl. 1, Fig. 1; GBA 1991/1/5)

The slab holds several fragments of Neocalamites, the largest being 7.7 cm long and 1.2 cm broad. It shows one complete and several incomplete whorls of leaves. The internodia are rather short, ranging from 5–13 mm. The stem gives the impression of being rather scarcely ribbed, because of the obscurity of the major part of the ribs. The nodes are more clearly visible, they are slightly enlarged. The complete whorl has twelve leaves, about 2 mm wide with an expanded base (up to 3 mm). None of the leaves is complete, the longest fragment being 4.6 cm long.

Very probably the two fragments of Neocalamites from site 76/95 belong to the same species as the one preserved in this specimen.

At present the genus Neocalamites comprises three common and well-known species and a number of less common or ill-defined ones; the last-mentioned will not be discussed. The three well-known Neocalamites species have a number of characteristics in common. This accounts for the problems when dealing with the identification of small fragments.

Neocalamites carrerei (ZEILLER) HALLE occurs in the Upper Triassic (Norian and Rhaetian) and Jurassic of Asia.
(China – Tonkin flora –, Japan, U.S.S.R., etc.). It is reported to have slender leaves (max. width 1.3 mm at the base; see Kon'no, 1972). In this aspect it differs from our material.

Neocalamites meriani (Brongniart) Halle occurs in the "Keuper" and is smaller than the other two species; the maximum number of leaves per whorl is reported to be eight. The width of the leaves is about 1.5 mm (see Krausel, 1959–80). With regard to these characteristics it differs from our material.

Neocalamites lehmannianus Goepert (Weber) – including N. hoerensis (Schimper) Halle, see Weber (1968) – is known from the Rhaetian and Jurassic of Europe and Asia. It has been described from e.g. the Rhaetian horizons of the Donets Basin (Stanislawski, 1971). Our material is too fragmentary and too badly preserved to be assigned to any of these three species, but agrees best with N. lehmannianus.

Genus Podozamites Braun 1843

Podozamites paucinervis nov. sp.

(Pl. 3, Figs. 1–3; GBA 1991/1/6)

Holotype: The specimen without number, figured on Pl. 3, Figs. 2, 3.

Diagnosis: Ultimate shoots unbranched, main stems unknown. Axis of shoot with longitudinal ridges. Leaves borne singly, probably in a simple helix, at variable distances.

Leaf-blade lanceolate-ovate, typically 50–60 mm long and 10 mm wide at its broadest point. Optimum width below the middle, often at about 10 mm from the base. Leaf apex slightly obtuse. Leaf base strongly contracted to about 1.5 mm.

Veins typically 10–11 per cm at the broadest point, converging towards the apex. Cuticle unknown.

Description: This Podozamites species is one of the few taxa in this floro determinable at the species level:

- The number of specimens present is rather large, and
- The preservation of the material is, although cuticle is absent, fairly good.

The material consists of several fragments of ultimate shoots and about a hundred detached complete or fragmentary leaves. The axis of the shoots is at least 15.5 cm long; maximum width 4 mm, minimum 1.5 mm. Normally, the leaves are borne at an angle of 30–50° to the axis; some, however, at an angle of 90° (see Pl. 2, Figs. 1, 2: leaves attached to a broad axis). The leaf-blade is typically 5–6 cm long and has an optimum width of 1 cm; the leaves range from 7.1×1.3 cm to 2.5×0.7 cm. The number of veins per cm in the broadest part of the leaf is 8–12, in general 10–11. In all leaves the veins converge towards the apex.

In this description the one specimen from site 75/3 holding this species is included (Pl. 2, Figs. 1, 2). We believe the material of Podozamites described from the sites 76/94 and 76/95 to belong to this species, too. As fewer details are visible, the identification is not certain. The few leaves from these sites showing venation, have on the average 10–11 veins/cm in the broadest part, the same number as in the specimens from sites 75/19 and 75/3. The leaves from all sites have their optimum width distinctly below the middle.

Discussion: As for the diagnostic characters the species might as well be assigned to Lindleycladus Harris 1979. This genus, however, has been erected on cuticular features. As the cuticle is not preserved in the Iranian material the fossil fragments are attributed to Podozamites. See Harris (1979).

Podozamites paucinervis is distinguished from most Podozamites species as conventionally recognized by its low number of veins per cm (compare, e.g. Podozamites lanceolatus (Lindley et Hutton) Braun: 20–30 veins per cm). In the late Triassic Podozamites distans (Presl) Braun some sparcely veined forms are included, although, normally, the number of veins per cm is not less than 15 and often up to 30. Also in P. latissimus Stanislawski 1971 from the Rhaetian flora of Raiskoye (Donets) the venation is rather sparse (normally 12–14 veins per cm, sometimes more). However, in both P. distans and P. latissimus the leaves reach their maximum width in the middle region and not below the middle. The differences between the relevant Podozamites species are demonstrated in Table 1.

It should be noted that the conventional species concepts within Podozamites may need reconsideration. Rich material collected from the Rhaetian – Liassic of Franken (Germany) shows a wide variation in venation pattern of Podozamites specimens collected in a single site. The variation could well be intraspecific. A detailed study is, however, required to support this hypothesis before definite taxonomic conclusions can be drawn.

Formgenus Carpolithes Brongniart 1822

Carpolithes cf. cinctus Nathorst

(Pl. 4, Fig. 2; GBA 1991/1/7)

One slab of this site holds six seedlike structures, on the average 7 mm long and 4 mm wide. They resemble the well-known species C. cinctus Nathorst. This species has been recorded from several localities in Eurasia, e.g. from the Rhaetian flora of Raiskoye (Donets) – Stanislawski (1971) –; similar seeds have been reported from some probably Norian beds of the Donets Basin (Stanislawski, 1976).

Since C. cinctus is commonly believed to belong to Podozamites (compare e.g. Stanislawski, 1971), the material here described possibly belongs to Podozamites paucinervis.
Formgenus **Cladophlebis** BRONGNIART 1849

**Cladophlebis sp. A.**

(Pl. 5, Fig. 1; GBA 1991/1/8)

One small, only 3 cm long, sterile fragment of *Cladophlebis* is preserved, the only fern present in this florule.

**Description:** Rachis 2.5 mm broad with wrinkles and striations. Pinnae arising at 80–90°; pinna rachis less than 1 mm broad; first pinnule arising on basiscopic (katadromic) side. Pinnules arising at an angle of 40–70°, nearly straight or slightly falcate with rather abruptly narrowed apex which has a dentate margin. Pinnule length: 10–12 mm; width: 4–5 mm. Pinnule venation not clearly visible: a strong midrib gives off the pinnae. Pinna base contracted rather abruptly, lateral margins parallel, in terminal pinna being in line with the rachis. All pinnae of the pinnae.

**Discussion:** This fragment is of a very common type of *Cladophlebis*. It is somewhat comparable with *Cladophlebis denticulata* (BRONGNIART) FONTAINE, a throughout the Mesozoic geographically widely distributed species. The presence of this taxon, therefore, has no importance as to the dating of the source strata.

**Genus Pterophyllum BRONGNIART 1828**

**Pterophyllum sp. cf. P. ptilum HARRIS**

(Pl. 5, Fig. 3; GBA 1991/1/9)

**Description:** A single, 11 cm long fragment is preserved. It shows the apical part of a leaf. The rachis is 1.5 mm wide with fine, transverse wrinkles. In the basal part of the fragment pinnae arising at angles of 70–90°, in the subterminal part at smaller angles, the terminal pinna being in line with the rachis. All pinnae fragmentary, except for the 4.9 cm long terminal one. Width of pinnae 3–4.5 mm. Pinnae alternating, partly inserted close to one another, partly with intervals of various sizes. Scars on the rachis and detached pinnae indicate that there may have been more pinnae on the rachis than preserved. Pinna base contracted rather abruptly, lateral margins parallel, in terminal pinna slightly tapering to a truncate apex. Venation not visible, cuticle unknown.

**Discussion:** This specimen has been provisionally assigned to *Pterophyllum ptilum* HARRIS, first described from the Rhaetian of Greenland (HARRIS, 1935, 1937). Although our specimen is larger than those described by HARRIS (pinnae typically 3–4 cm long, and 3 mm wide) they are in close agreement, especially with regard to the typical, rather abruptly contracted base of the pinnae.

Similar leaf bases occur, to our knowledge, only in *P. zygotacticum* HARRIS which has also been described from the Rhaetian of Greenland by HARRIS (1935, 1937). The remaining *Pterophyllum* species have either a straight or an expanded base, e.g. *P. bavieri* ZEILLER (1902–03), known from Tonkin and Pamir. It only differs from *P. ptilum* in the straight or slightly expanded pinna base. Considering the form of the pinna base, *P. ptilum* might be placed in Zamites (see HARRIS, 1969; ASH, 1975), a formgenus for bennettitalean leaves with a symmetrically contracted pinna base. For convenience only it is here attributed to *Pterophyllum* (see also LUNDBLAD, 1950, on *Pterophyllum* cf. *ptilum* from Sweden).

In *P. zygotacticum* the pinna base is contracted gradually and not as abruptly as in *P. ptilum*. Moreover, *P. zygotacticum* has rather larger pinnae than *P. ptilum* (typically 6 cm long, 4–7 mm wide). As to the latter aspect our fragment is more like *P. zygotacticum* than *P. ptilum*. However, the form of the pinna is so characteristic that our specimen has been provisionally assigned to *P. ptilum*.

The cuticles of *P. ptilum* and *P. zygotacticum* are rather different. The lack of a cuticle in our material, however, makes identification on this basis impossible. Apart from the Rhaetian of Greenland, *P. ptilum* has been recorded from the Rhaetian of Sweden (*P. cf. ptilum*, see LUNDBLAD, 1950) and the Donets Basin, U. S. S. R., (*P. cf. ptilum*, see STANISLAVSKI, 1971). The species, therefore, seems to be confined to the Rhaetian.

**Pterophyllum sp. cf. P. subaequale HARTZ**

(Pl. 4, Figs. 1,3; Pl. 5, Figs. 2,4; Pl. 6, Figs. 1,2; Pl. 7, Figs. 1,2; GBA 1991/1/10–12)

**Description:** On five slabs 11 smaller and larger fragments of this taxon are preserved. Despite some variation the fragments are assigned to *Pterophyllum* while

- the lamina is attached laterally to the rachis and
- the pinna bases are either straight or slightly expanded but never contracted (see HARRIS, 1969).

One fragment (Pl. 4, Fig. 3) shows a leaf base; the petiole is 3.5–4.4 mm wide and at least 20 mm long. Rachis tapering to about 2 mm wide at the top of the fragment. Pinnae almost in contact laterally, straight or slightly falcate, apex obtuse. Venation not visible.

The remaining three slabs (Pl. 4, Fig. 1; Pl. 5, Figs. 2,4; Pl. 6, Figs. 1,2) hold fragments of nine very similar leaves. The width of the leaves is 4 cm; width of the pinnae 4–5 mm, base slightly expanded (6 mm wide), apex obtuse. Venation not visible.

The remaining three slabs (Pl. 4, Fig. 1; Pl. 5, Figs. 2,4; Pl. 6, Figs. 1,2) hold fragments of nine very similar leaves. The width of the leaves is 4 cm; width of the pinnae 4–5 mm, base slightly expanded (6 mm wide), apex obtuse. Venation not visible.
Discussion: Although our material is rather badly preserved, it fits in all major aspects the Rhaetian Pterophyllum subaequale HARTZ. Since the cuticle is absent, a provisional assignment has been made. In P. subaequale – in which HARRIS (1932, 1937) includes part of P. andraeanum SCHIMPER, known e.g. from Pamir – the dimensions of the pinnae vary considerably. The pinna base is usually expanded as in our material, the pinnae are straight or falcate, sometimes the apex is rounded-rectangular, more often it is obtuse. Since the aim of the present paper is to provide with data for the biostratigraphical positioning of the source strata, comparison will only be made with common, or well-defined species.

The Rhaetian P. aequale (BRONGNIART) NATHORST, known e.g. from the Rhaetian parts of the Donets Basin (STANISLAVSKY, 1971), is according to some authors an older synonym of P. schenkii ZEILLER from Tonkin (see e.g. LUNDBLAD, 1950).

Others, e.g. HARRIS (1932, 1969), however, consider them separate species, the main difference being the length of the pinna (in P. aequale longer than in P. schenkii) and the apex of the pinna (rectangular in P. aequale, more or less rounded-rectangular in P. schenkii). P. compressum LUNDBLAD 1950 has been erected for those specimens of P. aequale and P. schenkii in which the cuticle has been preserved. The here studied material differs from the three above mentioned species in the falcate pinna (instead of straight) and the obtuse pinna apex (instead of more or less rectangular). See also LUNDBLAD (1950).

Pterophyllum jaegeri BRONGNIART was widespread during the Middle and Late Triassic (e.g. Japan, Switzerland – Neuwelt near Basel). The same holds for P. longifolium BRONGNIART. According to KRÄUSEL & SCHAARSCHMIDT (1966) the main difference between the two species is the length/width ratio of the pinnae: 6–7–(10) in P. longifolium, (10)–12–(16) in P. jaegeri. Moreover, in P. jaegeri the absolute length and width of the pinnae are greater than in P. longifolium. Both the length/width ratio (7–10) and the absolute dimensions of the pinnae in our material agree more with P. longifolium. The differences are

- in our material all pinnae except at the very leaf base are falcate, and
- in our material the pinna base is expanded.

In both P. longifolium and P. jaegeri the pinnae, inserted at an angle of 70–90°, are usually straight, only rarely falcate; the pinna bases are, normally, not expanded. The Liassic Pterophyllum propinquum GOEPPEL – known from Sweden, Japan, etc. – resembles our specimens too, especially as to the expanded pinna base. In P. propinquum, however, the pinnae are straight and more distantly spaced (lateral margins of adjacent pinnae 1–5 mm apart, hardly ever touching).

The genus Pterophyllum is known from the Ladinian upwards into the Late Cretaceous. Its presence in our material indicates an age for the source strata not older than the Ladinian. The provisional assignments P. sp. cf. P. pilium and P. sp. cf. P. subaequale point towards a Rhaetian age.

**Formgenus Taeniopteris BRONGNIART 1828**

*Taeniopteris* sp. B

**Description:** In total 30 complete or fragmentary leaves are preserved in three slabs. Leaves linear, at least 12 cm long, on the average 1.1 cm wide (extremes noted 0.9–1.4 cm). Leaf margins in the middle portion parallel to one another, apical and basal portions somewhat tapering. Apex acute; base tapering more or less quickly; lamina ending rather abruptly, when reduced to about ⅓ of its optimum width; margins entire. Petiole stout; mid-rib 0.5–1 mm wide. Venation in most leaves not visible; if veins are discernable, they arise at an angle of 85–90°, at a concentration of 22–26 per cm, simple. Cuticle unknown.

**Discussion:** The formgenus *Taeniopteris* contains Mesozoic fossil leaves which, should the cuticle be known, might be attributed to various genera referred to the Bennettitales (e.g. *Nilssoniopteris*), Cycadales (e.g. *Nilsenia* – the undivided form –, *Bjuria, Doratophyllum*) or the Pentoxyleas (*Nipaniophyllum*). Without the support of the cuticle structure, however, most of these leaves can not be placed into a satisfying systematic position. They are thus assigned to the Late Palaeozoic/Mesozoic formgenus *Taeniopteris*, as has been done with our material.

The present material includes a basal portion of a leaf showing the petiole. This fragment precludes an attribution of the Iranian material to fern genera such as *Marattia*. The leaf base is of a type mainly found in *Nilsoniopteris* (e.g. *N. vittata*).

A great many similar *Taeniopteris* species occur all over the world, e.g. *T. tenuinervis* BRAUNS (see HARRIS, 1932). As our material lacks too much detail, it is impossible to make a definite assignment. The presence of *Taeniopteris* is of no importance with regard to a precise dating of the source strata.

**Formgenus Pagiophyllum HEER 1881**

*Pagiophyllum ruttneri* nov. sp.

**Description:** After Dr. A.W. RUTTNER, former Director of the Geologische Bundesanstalt, Vienna, Austria.

**Holotype:** The specimen without registration number, figured on Pl. 8, Fig. 1; Pl. 9, Fig. 1.

**Diagnosis:** Main shoot giving off alternating penultimate shoots; penultimate shoots alternately giving off numerous ultimate shoots all in one plane. Main shoot sparsely covered with leaves, penultimate and ultimate shoots covered with spirally arranged, falcate leaves. Leaves deciduous, inserted on a cushion about 1 mm wide and 1–3 mm long, gradually contracting towards the apex. Leaves slightly dimorphic, either falcate, free part (2)–5–(6) mm long, 1–1.5 mm wide, or only slightly falcate, free part 7–10 mm long, 1.5 mm wide. Apex usually acute, sometimes (in short leaves) obtuse. No cuticle known.
Description: The material consists of eight slabs on which smaller or larger shoots are preserved, and two slabs on which small fragments are preserved together with other species. It is by far the most common species in site 75/3. The largest specimen is shown in Pl. 8, Fig. 1. The total length of the shoot system is 23 cm. The main axis in the lower part of the fragment is 7.5 mm wide, tapering to 3 mm in the upper part. It is sparsely covered with leaves, about 5 mm long. It is alternately branched at angles of 30–70° to the main axis; distances between branches 1–2 cm. Width of the axes of penultimate and ultimate shoots varying between 1 and 2 mm. All shoots covered with spirally arranged leaves, normally arising at an angle of 30–50°, often falcate. Length of the free part of the leaf between 2 and 6 mm, width 1–1.5 mm, vertical thickness 0.25–0.5 mm. Apex acute. Decurrent leaves inserted on a cushion, about 1 mm wide and 1–2 mm long.

The material comprises several smaller shoots that despite some minor differences agree closely with the one described above. In one of the shoots the cushions on which the leaves are inserted are distinct (Pl. 4, Fig. 4): their length varies from 1 to 3 mm, their width is about 1 mm. The additional material shows a greater variability as to the length of the leaves: the shorter ones are only 1 mm long with an obtuse apex; most leaves are 2–6 mm long. A few shoots preserved in a coarser sandstone show leaves up to 10 mm long (on penultimate shoots), which are slightly falcate and inserted at an angle of 40–60°.

Discussion: The material described here is assigned to the form genus Pagiophyllum since no fructifications have been found to warrant an attribution to a more natural taxon. See Harris (1979).

In the Middle Triassic floras quite a few Voltzia species occur, e.g. V. heterophylla Brongniart, V. coburgensis Schauroth and some Pagiohyllum species, such as P. foetleri (Stur) Schütze, P. sandbergeri Schenk and P. weismannii (Kurn) Schenk. All are different from our species.

From the Liassic onwards, quite a lot of Pagiohyllum species are known, such as P. vernonense Wesley and P. revoltinum Wesley from the Liassic of northern Italy. See Wesley (1956). In general aspects these species resemble our material. However, as they are mainly based in cuticular characteristics, our material cannot be attributed to any of them. Foliage of the type here described is also found, among other genera, in the Jurassic genus Elatides (Taxodiaceae).

Only a few conifers of the type here described have until now been recorded from Late Triassic floras. From the Rhaetian – Liassic flora of the Chelabinsk Basin, eastern Urals (Kryshtofovich and Prinada, 1933b), and the Late Triassic (probably Rhaetian) floras of Armenia (Kryshtofovich and Prinada, 1933a) no conifers of this type have been described. The same holds for the Norian and Rhaetian floras of Japan, Pamir (U.S.S.R.), Afghanistan and East Greenland. In the probably Rhaetian flora of Son-kul only small fragments attributed to Brachphyllum and Pagiohyllum are present.

The flora of the Donets Basin from sediments that are, according to Stanislavski (1976) probably Early Norian in age, has yielded one species of the type here described, viz. Voltzia charkoviensis Stanislavski. This species, assigned to Voltzia because both the male and female cones are known, resembles our material in several aspects:

- The branches of ultimate order are all in one plane, a feature often found in conifers, and
- the slightly dimorphic, often falcate leaves have about the same dimensions.

The main differences are:

- In V. charkoviensis the leaves are much more crowd- ed on the shoots than in Pagiohyllum ruttneri.
- They are often inserted at wider angles: 60–90° in V. charkoviensis, 40–60° in P. ruttneri.
- In V. charkoviensis the dimorphism is stronger: the most commonly occurring small, falcate leaves are 3–4 mm long, in P. ruttneri 2–6 mm; the other leaf type is straight, 8–9 mm long, 1.5 mm wide, in P. ruttneri 7–10 mm long, 1.5 mm wide.
- In V. charkoviensis the apex of the leaf is always obtuse, in P. ruttneri normally acute.

Although in the present material no cuticle is preserved we have decided to erect a new species for the present material of Pagiohyllum. The decision has been based on the both geographically and stratigraphically interesting position of the Aghdarband material and the presence in this material of large fragments of well-preserved compressions, which add much to the minute fragments hitherto described and figured from time-stratigraphical comparable horizons.

Genus Podozamites Braun 1843

Podozamites paucinervis nov. sp.
(Pl. 2, Figs. 1, 2; GBA 1991/1/15)

In the material from site 75/3 one specimen is preserved. As P. paucinervis has been described and discussed to some extent in the paragraph on site 75/19, including the specimen from site 75/3, we refer to that paragraph.

Formgenus Stachyotaxus Nathorst 1886

Stachyotaxus elegans Nathorst
(Pl. 5, Fig. 4; Pl. 6, Fig. 1; Pl. 10, Fig. 1, 2; GBA 1991/1/11, 16)

Description: In four slabs fragments of branched shoots of Stachyotaxus elegans are preserved. The longest fragment is a 9 cm long, penultimate axis with three ultimate shoots (partly figured in Pl. 6, Fig. 1). On the reverse side of this slab, a 8.5 cm long penultimate shoot with two ultimate ramifications is preserved (Pl. 5, Fig. 4) as well as shorter fragments. Pl. 10, Fig. 2 shows a 7.9 cm long penultimate axis with four alternating ultimate shoots of which also the counterpart is present. The specimen on Pl. 10, Fig. 1 holds five shoots. In another specimen (not figured) two fragmentary shoots are preserved.
The rachis of the penultimate shoots is 2–4 mm wide with longitudinal ridges; the rachis of the undivided shoots, here interpreted as ultimate shoots, is 1–2 mm wide with longitudinal ridges.

The base of the ultimate shoots is over a length of at most 5 mm covered with slender scales, 3–5 mm long, probably persistent bud scales. Pl. 10, Fig. 2 shows both scales and ordinary leaves.

Both penultimate and ultimate shoots are covered with leaves, opposite or subopposite, inserted at an angle of 50–90° to the rachis, length on the average between 0.9 and 1.5 cm, in some specimens up to 2.1 cm, leaf base contracted, apex acute. Midrib in most leaves clearly visible. Cuticle unknown.

Discussion: Stachyotaxus elegans was first described from the Rhaetian of Sweden. Later it was also found in the Rhaetian of Greenland (HARRIS, 1935, 1937) together with the much less common forms identified as Stachyotaxus septentrionalis (AGARDH) NATHORST. The main difference between S. elegans and S. septentrionalis is that the latter has smaller shoots, leaves and cones (leaves of S. elegans are normally about twice as large as those of S. septentrionalis). According to HARRIS the Swedish material should be revised as it might prove to belong to one species only. In both species the persistent scale leaves are present. Stachyotaxus elegans has also been reported from a small Rhaetian flora in Afghanistan (JACOB and SHUKLA, 1955), the Rhaetian flora of Issyk-kul (U.S.S.R. near Pamir; VAKHRAMEEV et al., 1978) and a Karnian or Norian flora in Japan (KIMURA, 1980).

Other species of Stachyotaxus have been recorded from the Karnian floras of Lunz (Austria) – S. lipoldii (STUR KRAUSEL) – and Neuewelt (Switzerland) – S. sahnii KRAUSEL. See KRAUSEL (1955). Both species differ from S. elegans, especially in form and size of the leaves. In S. elegans the length/width ratio of the leaves is 10–11; in S. lipoldii and S. sahnii resp. 8–9 and 5.8. Moreover, the leaves in S. elegans are much larger.

A fossil conifer that also shows some resemblance with S. elegans is Dechellyia germanii ASH from the Chinle Formation of Arizona, U. S. A. (probably of Norian age). It has shoots with opposite branches (in S. elegans the branches alternate), with scale leaves in the lower third of the shoot (in S. elegans at most the basal 5 mm, being a minor portion of the shoot). The upper two thirds of the ultimate shoot have always opposite leaves (in S. elegans the leaves are opposite or subopposite). The main axis, normally, does not bear leaves (in S. elegans it does). See ASH (1972). Until now Stachyotaxus elegans has mainly been recorded from the Rhaetian. The presence of this species in the Aghdarband florule, therefore, adds to a Rhaetian age for at least site 75/3.

4. Age interpretation

Summarizing the discussion on the stratigraphical ranges of the taxa described, it may be concluded that, although representatives of the genus Pterophyllum show first occurrences in the Ladinian, the overall composition of the florule here investigated is indicative of a Late Triassic age. An assignment to the Jurassic can be excluded since at least three species have been encountered that disappear at the Rhaetian–Lias-sic boundary, viz. Stachyotaxus elegans, Pterophyllum sp. cf. P. subaequale and Pterophyllum sp. cf. P. pilum.

Notably site 75/3 allows for a more precise dating. Of the seven species recorded two occur in the Rhaetian only, viz. the two species of Pterophyllum. One species, viz., Stachyotaxus elegans, has been recorded from Rhaetian sediments in, e.g. East Greenland, Sweden, Afghanistan and U. S. S. R. (Issyk-kul), with only one Karnian/Early Norian occurrence in the Yamachuti Formation. The remaining four species are of a type commonly found in the Upper Triassic and Jurassic. Thus, a Rhaetian age for site 75/3 seems more probable than a Karnian or Norian one. The site is situated at the base of the Ghali‘eh Gabri Shales.

Sites 76/94, 76/95 and 75/19 have much in common; all of them are sites within the Aghdarband Coal Bed. The dominance of Podozamites paucinervis is striking. A comparable flora, also dominated by Podozamites is the Norian flora of the Amba river, southern Primorye, U. S. S. R. (SHOROKHOVA, 1975). The Sphenobaiera material present in both floras is of a type mainly recorded from the Norian. The seed attributed to the catch-all formgenus Carpotheca may have belonged to Podozamites. The species of Taeniopteris and Neocalamites are of a type mostly recorded from the Upper Triassic and the Lower Jurassic. So a Norian age seems more probable than a Karnian or a Rhaetian one.

In view of the small number of species present, a definite dating of the florule would be a hazardous undertaking. There are indications of a Norian age as far as the Aghdarband Coal Bed is concerned. The Base of the Ghali‘eh Gabri Shales is probably Rhaetian in age.

5. Comparison with other Late Triassic floras

In this paragraph Late Triassic floras from various localities will be briefly compared with the material here described and figured.

The Iranian florule holds a position at about the boundary of what HARRIS (1937) called the Northern Province (northern part of Europe, Siberia, Afghanistan and Japan) and the Middle Province (China, Indo-China, Iran, Armenia + Caucasus and Pamir). VAKHRAMEEV et al. (1978) distinguish within the Laurasian area a Siberian and a Euro-Chinese province, the latter being subdivided in a European, Middle-Asian and East-Asian area. According to VAKHRAMEEV et al. the florule here investigated would belong to the Middle-Asian area of the Euro-Chinese province. So comparison with Late Triassic floras from this area seems to be obvious.

In the Karnian the main floras have been described and figured from Europe (Austria – Lunz, Switzerland – Neuewelt) and East-Asia (China and Japan): they do not show any resemblance to our florule. The sediments in the lower part of the Mesozoic in the Donets Basin, which are by some authors believed to be of Karnian age (VAKHRAMEEV et al., 1978) and by others of Norian age (STANISLAVSKI, 1971, 1976) show some resemblance with the material from sites 76/94, 76/95 and 75/19.

Of the Norian time interval not many floras have so far become known. Among those the flora of Armenia
(Kryshtofovich and Prinada, 1933a) has not much in common with the one described here. The floras of the Amba river (southern Primorye, U. S. S. R.), described by Shorokhova (1975) and the famous Nariwa flora (Japan, e.g. Kimura, 1980) show in general aspects some resemblance with the material from sites 76/94, 76/95 and 75/19.

Of the Rhaetian time-interval many well-known floras have been recorded, such as those from East Greenland (Harris, 1931–1937), Sweden (Lundblad, 1950), part of the Mesozoic Donets sediments (Stanislavski, 1971), Son-kul (Aliév and Genkina, 1970), Issyk-Kul (Genkina, 1966), Pamir (Sikstel', 1960) and Afghanistan (Barnard, 1976b), which all show more or less resemblance to our florule, especially to the material from site 75/3. The famous floras of Tonkin (Zeiller, 1902–1903) and Malaysia (Kon'no, 1972), on the other hand, do not show very much similarity to our material.

From Iran some supposedly Rhaetian plants have been earlier described by Kilpper (1975), but most floras in this country are of Liassic age (Barnard, 1965, 1967a; Kilpper, 1964, 1968, 1971) and have nothing in common with the material described here.

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Plate 1

Fig. 1: *Neocalamites* sp. A.
GBA 1991/1/5.
Natural size.

Fig. 2: *Taeniapteris* sp. B.
Natural size.

Fig. 3: *Taeniapteris* sp. B.
GBA 1991/1/10.
Natural size.

Fig. 4: *Taenipteris* sp. A.
GBA 1991/1/1.
× 2.

Fig. 5: *Taeniapteris* sp. B.
GBA 1991/1/10.
× 2.

Fig. 6: *Sphenobaiera* sp. A.
GBA 1991/1/1.
Natural size.
Plate 2

Fig. 1: *Podozamites paucinervis* nov. sp.
GBA 1991/1/15.
Natural size.

Fig. 2: *Podozamites paucinervis* nov. sp.
Detail of specimen in Fig. 1.
GBA 1991/1/15.
× 2.
Plate 3

Fig. 1: *Podozamites paucinervis* nov. sp.
GBA 1991/1/6.
Natural size.

Fig. 2: *Podozamites paucinervis* nov. sp.
Detail of specimen in Fig. 3.
GBA 1991/1/6.
× 3.

Fig. 3: *Podozamites paucinervis* nov. sp.
GBA 1991/1/6.
Holotype.
Natural size.
Plate 4

Fig. 1: *Pterophyllum* sp. cf. *P. subaequale*.
GBA 1991/1/10.
× 2.

Fig. 2: *Carpolithes* sp. cf. *C. cinctus*.
GBA 1991/1/7.
× 3.

Fig. 3: *Pterophyllum* sp. cf. *P. subaequale*.
GBA 1991/1/10.
× 2.

Fig. 4: *Pagiophyllum ruttneri*.
GBA 1991/1/14.
× 2.

Fig. 5: Seed scale and *Podozamites* sp.
× 2.
Fig. 1: *Cladophlebis* sp. A.
× 2.

Fig. 2: *Pterophyllum* sp. *cf. P. subaequale*.
GBA 1991/1/12.
× 2.

Fig. 3: *Pterophyllum* sp. *cf. P. ptilum*.
Natural size.

Fig. 4: *Pterophyllum* sp. *cf. P. subaequale* and *Stachyotaxus elegans*.
GBA 1991/1/11.
Natural size.
Fig. 1: *Pterophyllum* sp. *cf. subaequale* and *Stachyotaxus elegans*.
GBA 1991/1/11.
Natural size.

Fig. 2: *Pterophyllum* sp. *cf. subaequale*.
GBA 1991/1/12.
× 2.
Plate 7

Fig. 1: *Pterophyllum* sp. cf. *subaequale*.
GBA 1991/1/12.
Natural size.

Fig. 2: *Pterophyllum* sp. cf. *subaequale*.
detail of specimen in Fig. 1.
GBA 1991/1/12.
× 2.
Fig. 1: *Pagiophyllum ruttneri*.
GBA 1991/1/14.
Holotype.
Natural size.
Plate 9

Fig. 1: *Pagiophyllum rattneri*.
GBA 1991/1/14.
Detail of Specimen in Pl. 8, Fig. 2.
$\times 3$. 

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Plate 10

Fig. 1: *Stachyotaxus elegans.*
GBA 1991/1/16.
Natural size.

Fig. 2: *Stachyotaxus elegans.*
GBA 1991/1/16.
× 2.
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