

A MONOTYPIC STAND OF *NEOCALAMITES IRANENSIS* N. SP. FROM THE CARNIAN PLUVIAL EPISODE (LATE TRIASSIC) OF THE AGHDARBAND AREA, NE IRAN (TURAN PLATE)

MINA MAZAHERI-JOHARI¹, EVELYN KUSTATSCHER²³, GUIDO ROGHI⁴, EBRAHIM GHASEMI-NEJAD⁵ & PIERO GIANOLLA¹

¹Department of Physics and Earth Sciences, University of Ferrara, Via G. Saragat 1, Ferrara 44100, Italy. E-mail: mzhmni@unife.it, piero.gianolla@unife.it

³SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 München, Germany. E-Mail: Evelyn.Kustatscher@naturmuseum.it

To cite this article: Mazaheri-Johari M., Kustatscher E., Roghi G., Ghasemi-Nejad E. & Gianolla P. (2021) - A monotypic stand of *Neocalamites iranensis* n. sp. from the Carnian Pluvial Episode (Late Triassic) of the Aghdarband area, NE Iran (Turan Plate). *Riv. It. Paleontol. Strat.*, 127(2): 189-209.

Keywords: Kopeh-Dagh Range; Triassic; coal deposits; sphenophytes; fossil plants; CPE.

Abstract. The Aghdarband Basin in the Kopeh-Dagh Range (NE Iran) is one of the most important areas for unraveling the evolution of the Turan plate (southern margin of Eurasia) during the last phase of the closure of the Paleotethys and to reconstruct the history of the Cimmerian blocks just before their collision with Eurasia during the early Late Triassic. The youngest sediments affected by the Early Cimmerian orogeny are those of the Upper Triassic Miankuhi Formation, which covers unconformably the Upper Triassic (lower Carnian) marine beds of the Sina Formation by an interval of continental facies including local conglomerates, cross-bedded sandstones, mudstone layers, silty shales, an up to one-meter thick coal layer with plant remains, and shales. The plant assemblages represent a relatively wide variety of different forms (sphenophytes, ginkgophytes, conifers, and incertis sedis), documenting wetlands with lush vegetation typical of warm and humid environments. In this study, we describe a plant fossil assemblage from the base of the Miankuhi Fm., dominated by roots and vegetative organs of Neocalamites iranensis n. sp., with few plant fossils of uncertain botanical affinity. Palynological investigations of the basal part of the Miankuhi Formation confirm a latest early Carnian to late Carnian age for this interval and reveal, for the first time, a clear link between this plant-bearing bed, and a time of global environmental changes, the Carnian Pluvial Episode. This is the first report of the Carnian Pluvial Episode in the Turan plate (southern margin of Eurasia) and Iran.

Introduction

Plant macrofossils are common in Iran, although most plant remains are of Rhaetian or Jurassic age (e.g., Vaez-Javadi 2013a and refs. therein). Among the first authors to describe and enlist Late Triassic to Middle Jurassic plant fossils from

Iran were Göppert (1861), Stur (1886), Schenk (1887), and Krasser (1891). The best studied area is the Alborz Mountains (e.g., Krasser 1891; Kilpper 1971, 1975; Bernard & Miller 1976; Schweitzer 1978; Vassiliev 1984; Schweitzer & Kirchner 1995, 1996, 1998, 2003; Schweitzer et al. 1997, 2000, 2009; Vaez-Javadi & Syooki 2002; Vaez-Javadi 2004, 2008; Vaez-Javadi & Abbasi 2012) as the Rhaeto-Liassic successions of Dorud (e.g., Barnard 1965, 1976),

²Department of Earth and Environmental Sciences, Paleontology & Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 München, Germany. E-mail: Evelyn.Kustatscher@naturmuseum.it

⁴Institute of Geosciences and Earth Resources - CNR, Via Gradenigo 6, Padova 35131, Italy. E-mail: guido.roghi@jgg.cnr.it

Department of Geology, Faculty of Science, University of Tehran, Enghelab Square, Tehran, Iran. E-mail: eghasemi@khayam.ut.ac.ir

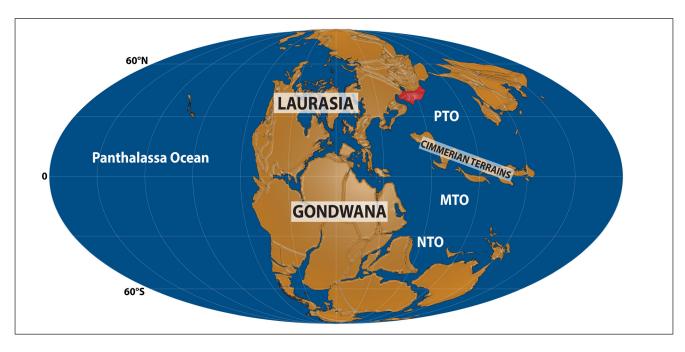


Fig. 1 - Late Triassic paleogeography (about 230 Ma, redrawn from Matthews et al. 2016; Cao et al. 2017). The red area corresponds to the studied location (Turan Plate). NTO: Neotethys Ocean; MTO: Mesotethys Ocean; PTO: Paleotethys Ocean.

Amol area (Popa et al. 2012), Karmozd, and Zirab (e.g., Kilpper 1964, 1968, 1971; Kimyai 1972), located in the Central Alborz Mountains, are rich in plant fossils.

Most studies describe diverse and abundant plant fossil assemblages that were mainly collected close to mined coal seams. The Aghdarband Coal Bed (Miankuhi Formation) from the Aghdarband area is an example of such a plant-bearing horizon in the Kopeh-Dagh Range, Northeast Iran. Boersma & Van Konijnenburg-van Cittert (1991) were so far the first and only ones to describe Triassic plant fossils from the Aghdarband area. The authors recognized a variety of sphenophytes (Neocalamites), ginkgophytes (Sphenobaiera), conifers (Podozamites), and incertis sedis (Taeniopteris, Carpolithes), including the new species Podozamites paucinervis. The plant fossils were collected at several outcrops either from the Aghdarbad Coal Bed at the base of the Miankuhi Formation, or from a coal horizon at the base of the Ghal'eh Qabri Shales. In situ trunks in vertical, standing position were mentioned (Ruttner 1991), but not described. The composition of the plant fossil assemblages from the basal coal layer of Miankuhi Formation (Boersma & Van Konijnenburg-van Cittert 1991) and the poorly preserved marine palynomorphs (dinoflagellate cysts; Ghasemi-Nejad et al. 2008) suggested a Norian age for the coal bed, whereas our palynological analyses yielding terrestrial palynomorphs support a Carnian age for the base of the Miankuhi Formation (see below). The plant-bearing basal part of the Ghal'eh Qabri Shales were assigned putatively to the Rhaetian (Boersma & Van Konijnenburg-van Cittert 1991).

This study aims to provide an overview of the fossiliferous horizon yielding in situ plant fossils from the coal layer of the Miankuhi Formation, to discuss plant fossils previously found in the area, and to describe the first plant fossils of Iran dated confidentially as Carnian, representing the Carnian Pluvial Episode (CPE).

GEOLOGICAL SETTING

Cimmeria as an extended deformed zone comprising several microcontinent blocks, rifted from Gondwana at the end of the Paleozoic (e.g., Sengör 1979, 1984, 1990; Stampfli & Borel 2002; Angiolini et al. 2007) and collided with Eurasia during the Triassic (e.g., Stöcklin 1974; Sengör 1979, 1984, 1990; Ricou 1994; Stampfli & Borel 2002; Wilmsen et al. 2009; Zanchi et al. 2009a, 2009b) (Fig. 1). The collision of the Iranian microplate as part of the Cimmerian blocks with the southern margin of Eurasia (Turan Plate) during the Late Triassic/Early Jurassic defines one of the

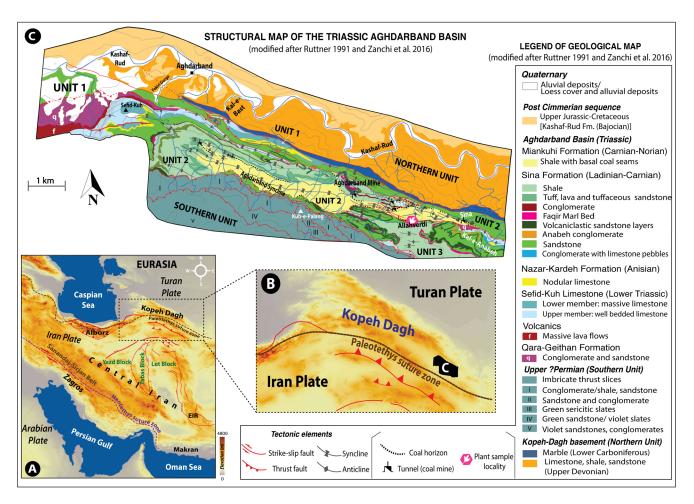


Fig. 2 - A) Main structural zones of the area (after Stöcklin & Nabavi 1973; Berberian & King 1981; Allen et al. 2004, 2011; Morley et al. 2009; Nozaem et al. 2013; Calzolari et al. 2016): EIZ: Eastern Iran zone. B) Detail of the Kopeh-Dagh Range and the location of the studied area (Aghdarband Basin). C) Geological map of the Aghdarband Area showing the three tectonic units and the various formations of the Aghdarband Basin (modified after Ruttner 1991; Zanchi et al. 2016).

major compressional events of the Iranian platform, named as Cimmerian collision, which caused the closure of the Paleotethys Ocean (e.g., Stöcklin 1974; Sengör 1979, 1984; Stampfli & Borel 2002; Wilmsen et al. 2009; Zanchi et al. 2009a, 2009b). The Eo-Cimmerian orogeny affected the Kopeh-Dagh Basin in the southern margin of the Eurasian Plate (NE Iran) and subsequent Middle Jurassic rifting led to the development of more than 7 km thick sequence of gently folded rocks of Jurassic to Paleogene sediments in this basin (e.g., Afshar-Harb 1979; Davoudzadeh & Schmidt 1985; Milanovsky 1991; Afshar-Harb 1994; Brunet et al. 2003; Garzanti & Gaetani 2002; Mahboubi et al. 2010; Robert et al. 2014). The Kopeh-Dagh intracontinental range stretches for about 700 kilometers in a WNW-ESE direction east of the Caspian Sea, and lies in the northeast of Iran and south of Turkmenistan (Fig. 2A, B). The basement of the Kopeh-Dagh Range (pre-Jurassic sediments) crops

out in the eastern part of the belt and within the Aghdarband erosional window due to the erosion of the gently folded overlying Jurassic-Paleogene beds by the river Kashaf-Rud and other drainage systems to the south (Ruttner 1984, 1991). The Aghdarband area occupied the southern part of the Kopeh-Dagh Range which was located at about 35–45°N during the Late Triassic (~230 Ma) (Mattei et al. 2014; Muttoni et al. 2015; Matthews et al. 2016; Cao et al. 2017) and its sediments are principally Triassic in age (e.g., Ruttner 1984, 1988, 1991; Baud et al. 1991a; Boersma & Van Konijnenburg-van Cittert 1991; Donofrio 1991; Alavi et al. 1997; Ghasemi-Nejad et al. 2008; Balini et al. 2009, 2019) (Fig. 2C). The well-dated Triassic successions of Aghdarband were deposited in a back-arc setting associated with the northward subduction of the Paleotethys Ocean along the southern margin of Eurasia and are strongly deformed as a result of the Cimmerian orogeny (Ruttner 1991; Alavi

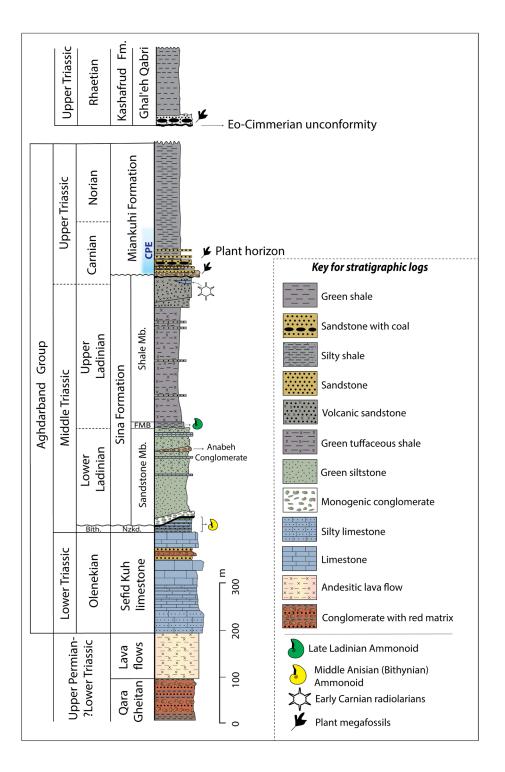
et al. 1997; Zanchi et al. 2009a; Sheikholeslami & Kouhpeyma 2012; Zanchetta et al. 2013). There is still considerable ambiguity about the precise time of deformation of the Aghdarband area although extensive field analyses by Zanchi et al. (2016) proposed a pre-Bajocian age for the deformation. This basin, formed within the framework of an extensional-transtensional tectonic regime, is subdivided into three main structural units named unit 1, 2, and 3 from north to south (Ruttner 1991; Zanchi et al. 2016). Unit 1 is characterized by folding and faulting deformation while thrusting characterizes the units 2 and 3 (Zanchi et al. 2016). A substantial systematic study on the central and eastern part of the Aghdarband Basin (units 1-3) was performed by Ruttner (1991), who represented a detailed geological map at 1:12,500 scale (Ruttner 1991: pl. 1). The present study was carried out in unit 2 of the Aghdarband Basin, where the most complete stratigraphic succession of the area is recorded.

REVISED STRATIGRAPHY

The Triassic stratigraphy of the tectonic unit 2 is represented by four distinct formations which are, in ascending stratigraphic order, the Sefid-Kuh Limestone, the Nazar-Kardeh Formation, the Sina Formation, and the Miankuhi Formation (Fig. 3). The Lower Triassic Sefid-Kuh Limestone (Baud et al. 1991a; Balini et al. 2019) overlies the ?late Permian-Early Triassic volcanoclastic conglomerates of the Qara-Qeitan Formation (Ruttner 1991; Eftekharnezhad & Behroozi 1991; Baud et al. 1991a; Alavi et al. 1997; Balini et al. 2009; Zanchi et al. 2016). Up-section, the relatively deep-water fossiliferous cherty limestones of the Nazar-Kardeh Formation were deposited due to a sudden deepening at the end of the Olenekian in the units 1 and 2. The Nazar-Kardeh Formation with a Bithynian age (Krystyn & Tatzreiter 1991; Balini et al. 2019) is unconformably capped by a relatively thick sequence of volcaniclastic-turbiditic units, named Sina Formation, which is divided into two members (Ruttner 1991; Baud et al. 1991b): the Sandstone Member comprises conglomerates and green tuffaceous sandstones, and the overlying Shale Member contains red ammonoid-bearing marls (Faqir Marl Bed) and tuffaceous shales. A quick change to a coarsening upward succession, combined with the end of volcanic activity during early Carnian times, is recorded in the uppermost Sina Formation. The age of the Sina Formation spans from the early Ladinian to the early Carnian (Ruttner 1991; Krystyn & Tatzreiter 1991; Donofrio 1991). The Sina Formation is separated from the overlying Miankuhi Formation by an unconformity documented by continental sediments resting on the marine shale. The base of the Miankuhi Formation is characterized by conglomerates, cross-bedded sandstones, mudstones with minor sandstone lenses, sandstone layers, silty shales, and an up to one-meter thick coal layer documenting a wet alluvial plain environment. Upwards, the Miankuhi Formation is composed of brown-colored shales with some interbedded siltstone and/or fine-grained sandstone (Ruttner 1991, fig. 12b). These shales were thought to be completely barren of fossils (Ruttner 1984, 1991), but a poor assemblage of benthonic foraminifers has been found at the base of the monotonous shales (Oberhauser 1991), reflecting extremely adverse living conditions. Furthermore, the lowermost Miankuhi Formation yielded plant megafossils (Boersma & Van Konijnenburg-van Cittert 1991) and poorly preserved marine palynomorphs (Ghasemi-Nejad et al. 2008) considered of Norian age. The described dinoflagellate cyst assemblage (Hebecysta, Heibergella, Rhaetogonyaulax, Sverdrupiella) is, however, not restricted to the Norian and has also been reported from the Carnian (e.g., Bucefalo Palliani & Buratti 2006).

Zanchetta et al. (2013) proposed a U-Pb zircon age of 217.1 ± 1.8 Ma for a magmatic intrusion (Torbat-e-Jam Granite) into the deformed coal-bearing terrigenous successions of the Miankuhi Formation in the north of Torbat-e-Jam, suggesting a minimum age of middle Norian and probably a Carnian to middle Norian age for this formation. The results of our palynological investigations on the basal part of the Miankuhi Formation confirm a latest early Carnian (Julian 2) to late Carnian (Tuvalian) age for this part of the succession (see Age assignments for details). This composition of the terrestrial palynomorph assemblages and their age indications, along with the stratigraphical and sedimentological observations, change the position of the unconformable contact between the Miankuhi Fm. and the underlying Sina Fm. from its traditional place (Ruttner 1984, 1991;

Fig. 3 - General lithostratigraphic column of the Triassic sequence of the Aghdarband Basin (modified from Ruttner 1991, 1993; Zanchi et al. 2016; Balini et al. 2019).



Baud et al. 1991b; Zanchi et al. 2016; Balini et al. 2019) immediately below the coal bed to the base of the conglomerate layers. Additionally, records of plant fossils below and above the coal bed provide adequate proof for the existence of a continuous continental succession and a clear wet interval at the base of the Miankuhi Formation starting with the conglomerate layers. Nevertheless, the contact between the two formations is often tectonized due to active faulting and syn-sedimenta-

ry tectonic control over short distances in the area during the Triassic (Zanchi et al. 2016). Up-section, the Miankuhi Formation is separated from the basal black shales (Ghal'eh Qabri Shales) of the Kashaf-Rud Formation by an angular unconformity representing the Eo-Cimmerian orogeny (Ruttner 1991). A transgressive white sandstone layer at the base of the Ghal'eh Qabri Shales contains another coal level with Rhaetian plant remains (Boersma & Van Konijnenburg-van Cittert 1991).

Table 1 - Comparison of the new species Neocalamiles iranensis n. sp. with the other Neocalamiles species from the Triassic and Jurassic of Iran and Afghanistan.

Boersma & Van Konijnenburg-van Cittert (1991)	Corsin & Stampfli (1977)	Khalilizade et al. (2020)	Saadat-Nejad et al. (2010)	Schweitzer et al. (1997)	Jacob & Shukla (1955)	Schweitzer et al. (1997)	Vaez-Javadi (2016)	Vaez-Javadi (2012a)	Vaez-Javadi (2013)	Vaez-Javadi (2013)	Corsin & Stampfli (1977)	Vaez-Javadi (2016)	Sadovnikov (1986)	Sadovnikov (1976)	Parvacideh & Vaez Javadi (2015)	Fakhr (1977)	Kilpper (1964)	Kilpper (1964)	This paper	
Neocalamites sp. A	Neocalamites sp.	Neocalamites ishpushtensis	Neocalamites ishpushtensis	Neocalamites ishpushtensis	Neocalamites ishpushtensis	Neocalamites cf. merianii	Neocalamites cf. merianii	Neocalamites cf. merianii	Neocalamites cf. merianii	Neocalamites merianii	Neocalamites merianii	?Neocalamites hoerensis	Neocalamites hoerensis	Neocalamites hoerensis	Neocalamites cf. hoerensis	Neocalamites hoerensis	Neocalamites hoerensis	Neocalamites cf. carrerei	Neocalamites iranensis	
12	40–50		4	3-21	ū	2	4	2-2.5	2-2.5	20–25	10–35	9	<50		14.7–15.7	25–30	15	20	up to 55 mm wide	stem width (mm)
5-13			25	20–50	20	20		19	19	19	18–26		<110	>50	24	up to 90	>20		35–90	internode length (mm)
				costate	n.a.	n.a.													smooth	cortex
scarcely ribbed			present		pronounced	pronounced, at 0.6 mm distance		3–4 ribs	3–4 ribs	distinct, 8–10 mm wide	pronounced								absent	costae
slightly enlarged		slightly swollen		no thickening	swollen	swollen					slightly swollen		expanded in branches						no thickening	nodes
			at 0.5 mm distance	distinct, straight								20–21/cm	10-25/cm	10-20/cm		14–16/cm	16/cm	20/cm	18/cm	vascular bundles
12				>25	6?	12–14	10		6	6			<50					25	at least 40	leaves/ whorl
			linear, narrow	slightly lanceolate, maximum width at the middle part	linear	straight, parallel margins, arise perpendicularly	linear, parallel margins	linear, parallel margins	linear, parallel margins	linear, parallel margins			linear	narrow, thin					straight, linear	leaf shape
>46			>25	50–120	50-60		>15	>20	>20	>20	>35		120						>85	leaf length (mm)
2			0.5–1	2-5	2	1		1-1.5	1–1.5	1–1.5	1.5–2		0.5–2.5 mm						0.4-1.4	leaf width (mm)
expanded (up to 3 mm)			free, base slightly restricted	free to the basis, restricted in width	free	broad							free to the bases						free, consistent with leaf width	leafbases
				acute															unknown	leafapex
				circular, 0.5–1 mm diameter							2 mm		rounded–e longated					1 mm diameter	unknown	leaf apex leaf traces
				distinct midrib	clear midrib	indistinct							single	indistinct					unknown	veins
				vascular bundles are probably described as costae	vascular bundles are probably described as costae	vascular bundles are probably described as costae						just stem with vascular bundles, not well enough to describe the species								annotations

MATERIALS AND METHODS

The studied macroflora is from a stratigraphic section called Allahverdi (35.98°N, 60.87°E; Fig. 2C). The plant fossil assemblage comprises 28 specimens, generally preserved as compressions or impressions. Sphenophytes are very delicate; their remains are mostly preserved as internal casts and impressions. The fossils are stored in the paleontological collection of Piero Leonardi Museum of Paleontology and Prehistory (MPL: Museo di Paleontologia e Preistoria Piero Leonardi) in Ferrara, Italy. Hand specimens were photographed with a Nikon 3200D digital camera and palynomorphs with a Leica 165C microscope equipped with Leica 170HD camera.

THE MACROFLORA OF THE AGHDARBAND AREA

At least four taxa were distinguished based on macromorphological analyses of the macroremains; they belong to the sphenophytes and to plant groups of unknown botanical affinity.

Division SPHENOPHYTA

Order **Equisetales** Dumortier, 1829 Family Equisetaceae Michaus, ex DC, 1804 Genus *Neocalamites* Halle, 1908

Neocalamites iranensis Kustatscher, Mazaheri-Johari et Roghi n. sp. Pl. 1, figs. A–E; Pl. 2, figs. A–D

Etymology: Named after the country where the remains were discovered for the first time, Iran.

Holotype: MPL 9303 (Pl. I, fig. A), showing a stem fragment with at least two nodes from which arise a whorl of leaves, here designated

Paratype: MPL 9304 (Pl. I, fig. B), showing the distribution and length of the leaves, here designated.

Additional material: Seven specimens, MPL 9305, 9306, 9307, 9308, 9309, 9310, 9311.

Type locality: Allahverdi outcrop, 35.98°N, 60.87°E, Aghdarband Basin, Iran.

Type horizon: Miakuhi Formation, Julian 2 to Tuvalian, Carnian, Late Triassic.

Repository: Museum of Paleontology and Prehistory Piero Leonardi, Ferrara, Italy.

Diagnosis: Stem articulated, with a smooth surface and distinct closely arranged vascular bundles. Lateral branches arising in whorls from non-swollen nodes. Leaves linear, entire-margined arranged in whorls of very numerous leaves; leaf bases consistent with leaf width, free up to the attachment at the nodal level. One to two internode vascular bundles per vallecular canal and leaf; no distinct midrib in leaves.

Description. The plant assemblage is dominated by leafless and leafy stems and putative branches, leaf whorls, and internal casts belonging to the

sphenophyte genus Neocalamites. The stem fragments are up to 112 mm long and 55 mm wide in compression (MPL 9312-9313, Pl. 1, figs. C-D), straight, with no evidence of tapering, and with densely disposed longitudinal grooves (corresponding to the vascular bundles) at a concentration of up to 18/cm (MPL 9313, Pl. 1, fig. D). Some internodes are 35 mm long (MPL 9303, Pl. 1, fig. A) but the maximum length of internodes exceeds 90 mm since in some fragments no complete internodes are observed (MPL 9313, Pl. 1, fig. D). Smaller fragments have been interpreted as lateral branches (MPL 9314, Pl. 1, fig. E). Nor lateral branches nor stems show any evidence of thickening at the nodal level. The internodes of the lateral branches are 3-5 mm wide and up to 15 mm long. When three-dimensionally preserved the stems appear secondarily compressed, with the vascular bundles of two successive internodes alternating (MPL 9315-9316, Pl. 2, figs. A–B). Leaves are long, linear, straight, entire-margined, 0.8-1.4 mm wide, at least 85 mm long with no distinct vein (MPL 9304, Pl. 1, fig. B; MPL 9317, Pl. 2, fig. C). The leaf bases are consistent in width with the leaf width and free up to the attachment to the node (MPL 9303, Pl. 1, fig. A, MPL 9318, Pl. 2, fig. D). The leaves radiate evenly from the node; they are attached to the stem in a whorl. Information on leaf traces is missing since no cortex with leaf traces has been found. Each whorl consists of at least 40 leaves since in the most complete specimens more than 20 leaves were counted in up to half of a whorl (MPL 9318, Pl. 2, fig. D). The number of vascular bundles corresponds to twice to three times the number of leaves in each whorl.

Comparisons with specimens from Iran. The stem fragments from the Rhaetian and Jurassic sediments of Iran assigned to Neocalamites meriani are in most cases very narrow, 3-15 mm in diameter (e.g., Schweitzer et al. 1997; Vaez-Javadi 2013a), although a maximum diameter of 35 mm is possible (e.g., Corsin & Stampfli 1977), and the number of leaves per whorl is very few (6–14 leaves; Tab. 1). This makes an assignment to Neocalamites merianii questionable (for discussion see below). Neocalamites iranensis resembles the specimens described by Kilpper (1964, pl. I, fig. 5) as Neocalamites sp. cf. N. carrerei (Zeiller) Halle in the distance between the vascular bundles (0.5 mm) but differs in the presence of distinct leaf bases and the higher number of leaves (more than 40 against \sim 25).

The specimens assigned by Kilpper (1964, pl. I, fig. 4) and Parvacideh & Vaez Javadi (2015, pl. I, fig. 2) putatively to *Neocalamites hoerensis* (Schimper) Halle are not well-enough preserved for a comparison with our specimens. The specimens described by Sadovnikov (1976, pl. I, figs. 5-7) as Neocalamites hoerensis from the Rhaetian-Middle Jurassic of Ziran (Iran) differs in having narrower stems and less vascular bundles (Tab. 1). The specimens are too badly preserved to permit a better comparison. Neocalamites iranensis n. sp. differs from Neocalamites sp. A sensu Boersma & Van Konijnenburg-van Cittert (1991) in having a narrower stem diameter (up to 12 mm wide), shorter internodes (5-13 mm), enlarged nodes, twelve leaves per whorl and the expanded base of the leaves in the latter (Tab. 1).

Neocalamites iranensis n. sp. resembles Neocalamites ishpushtensis Jacob et Shukla from the Jurassic of northern Afghanistan in the linear shape and the free attachment of the leaves at nodal level (Tab. 1). They differ, however, because of the narrower stems (5 mm), the swollen nodes, the lower number of leaves (6) per node, and the shorter but wider leaves (2 x 50-60 mm). Our specimens resemble Neocalamites ishpushtensis as described by Schweitzer et al. (1997) from the lower Middle Jurassic of Iran and Afghanistan in the non-thickened nodes and the long leaves that are not basally fused. However, the specimens from Schweitzer et al. (1997) differ from our specimens in the lower number of leaves, the smaller width and length of the stems, the costate outer surface, and the slightly lanceolate leaf shape with a pointed apex and a restricted basis (Tab. 1). Neocalamites iranensis n. sp. can be distinguished from the specimens assigned by Saadat-Nejad et al. (2010) to Neocalamites ishpushtensis by the much narrower stem (4 mm against up to 55 mm), and the shorter length (maximum 25 mm against minimum 85 mm) and narrower width (0.5–1 mm against 0.8–1.4 mm) of the leaves. The specimen figured by Khalilizadeh et al. (2020; fig. 10E, 12E) as Neocalamites ishpushtensis differs in the distinct thickening of the nodes; the missing of a description does not enable us to make a more detailed comparison. It has, however, to be noted that what Jacob et al. (1955) and Schweitzer et al. (1997) described as ridges and furrows correspond rather to the vascular bundles, and thus to characters of the inner structure of the stem, than to the costae of the outer surface (Tab. 1).

Comparisons with other species of Neocalamites. Neocalamites iranensis n. sp. differs from the type species Neocalamites lehmannianus (Goeppert) Weber from the Rhaetian-Lower Jurassic of Germany in the single or opposite attachment of the branches, the narrower but longer internodes, the swollen nodes, the lower number (12–48) of leaves per whorl, the broader leaves (1-2.5 mm) and the distinct midrib of the latter. The most closely resembling species is Neocalamites horridus Zan et al. from the Upper Triassic of China because of its abundant, linear leaves with a free base and the only slightly swollen nodes but it differs because of the unbranched stems, the striations and prickles on the outer surface and the distinct midrib on the leaves. It resembles also Neocalamites carrerei (Zeiller) Halle from the Rhaetian of Tonkin (North Vietnam), but well-known also from the Ladinian-Carnian of China (e.g., Sze, 1933, 1949, 1956; Xingxue, 1995), because of the linear to filiform leaves with a free attachment to the node and a similar frequency of vascular bundles. The type material differs, however, because of the lower vascular bundles vs. leaf scars ratio (1–2 times against 2–3 times in Neocalamites iranensis n. sp.), and the distinctly higher number (80-100 against >40 in our specimens) and wider (1–1.5 against 0.4–1.4 mm) leaves each whorl. Moreover, the leaves have a distinct vein in the Rhaetian type species. Neocalamites iranensis n. sp. differs from most Neocalamites species in missing a swelling of the nodes. One of the few exceptions that does not show swellings either is Neocalamites virginensis (Fontaine) Berry from the Triassic of USA but the lat-

PLATE 1

Neocalamites iranensis n. sp. - A) Stem fragment with at least two nodes from which arise a whorl of leaves, holotype (MPL 9303).
B) Distribution and length of the leaves of a half whorl, paratype (MPL 9304).
C) Stem fragments with impressions of the vascular bundles (MPL 9312).
D) Largest stem fragment with impressions of the vascular bundles (MPL 9313).
E) Small lateral branch fragments with leaves (MPL 9314).
Scale bars: A-E= 2 cm.

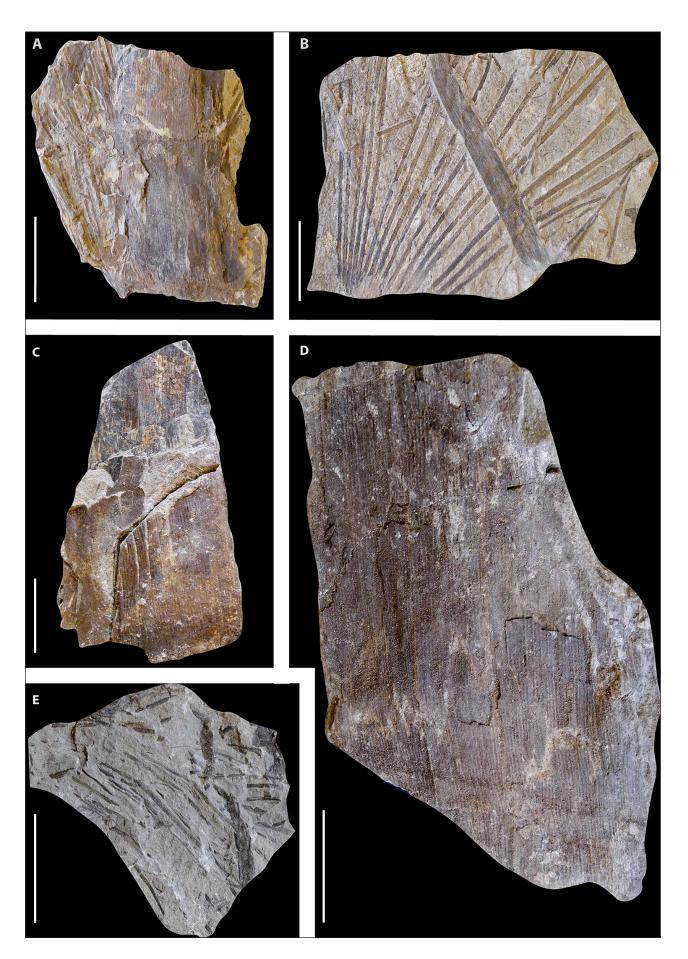


PLATE 1

ter has much narrower (5 mm) and shorter (15-20 mm) internodes, a lower number of leaves per node (<24) and wider leaves (1–2.5 mm) with a broad midvein (3-4 mm). Another main character of Neocalamites iranensis n. sp. is the indistinct midrib, which it has in common with Neocalamites minutus Gee et al. from the Upper Jurassic of Switzerland and Neocalamites suberosus (Artabe et Zamuner) Bomfleur et al. from the Middle Triassic of Argentina. It differs, however, in the slightly swollen nodes, the narrower and shorter internodes, and the higher number of narrower and shorter leaves. The new species differs from Neocalamites suberosus in having wide and shallow grooves on the external surface resulting in a costate external structure of the stem, and the shorter (> 30 mm) but broader (2-4 mm) leaves. The only other Triassic species, Neocalamites merianii from the Middle-lower Upper Triassic of Europe, resembles the new species in the arrangement in whorls of the branches and the general dimensions of the internodes, although the lateral branches are much thicker in the specimens from Germany. The two species differ, however, because the outer surface can be costate and the node is generally swollen in Neocalamites merianii. Moreover, in the latter species, the leaves are present only on the lateral shoots (see Pott et al. 2008), whereas both the primary and lateral shoots are covered by leaves in the new species, and the leaves are broader and have a distinct midrib in Neocalamites merianii.

Genus Radicites Potonié, 1893

Radicites sp. Pl. 2, fig. E

Material: Five specimens

Description. The main root axis is up to 50 mm long and 4 mm wide (MPL 9319, Pl. 2, fig. E). The secondary roots of 11–20 mm length and 1 mm width arise at an angle of 50–55°. The secondary roots do not show any rootlets or ramifications.

Discussion. Radicites is a genus used generally for compound root remains of unknown sphenophyte affinity with typically a mm thick main root and several secondary roots. Heer (1877, pl. 75, fig. 3; pl. 26, fig. 3) identified similar structures as roots of Equisetites arenaceus (Jaeger) Schenk from the Carnian of Neue Welt (Switzerland) because of their

frequent association with the latter. Linck (1943) described a stratigraphic section with several in situ "Wurzelböden" [root horizons] in the Schilfsandstein of Mühlbach (Germany), Kräusel & Leschik (1959, pl. 10, text-fig. 2; pl. 5, fig. 37) even described roots and stems arising from a rhizome. Kelber (1990, pl. 56, fig. 96; 1999, pl. 364, fig. 9) and Kelber & Hansch (1995, pl. 131, figs. 281-2) described horizons with several generations of Equisetites roots in the Erfurt Formation (Ladinian) of Germany. Sometimes the younger generation penetrates the "fossils" of the older, sediment-covered organic remains. These structures were interpreted as various successive root horizons representing several generations evolving in an ever-changing deltaic area of the Lower Keuper. Bock (1969, pl. 72–74) described Anabacaulus duplicatus Emmons as root systems of equisetaleans associated with, but not anatomically connected to, Neocalamites delewarensis Bock.

The simple structures of the roots, as well as a comparison with remains from the Triassic of Europe (e.g., Kelber & Hansch 1995; Kustatscher & Van Konijnenburg-van Cittert 2008) suggest a sphenophyte affinity. Since the only sphenophyte so far described in these fossiliferous horizons, is *Neocalamites iranensis* n. sp., an affinity with this species is most likely. Although the roots do not show holes that perforate older fossils, an autochthonous origin of the remains is postulated since the root fragments are distributed three-dimensionally and at various levels within the rock slabs (e.g. MPL 9319, Pl. 2, fig. E).

P_{LATE} 2

Neocalamites iranensis n. sp. - A) Three-dimensional preservation of a compressed stem (MPL 9315). B) Three-dimensional preservation of a compressed stem showing the vascular bundles at the nodal level (MPL 9316). C) Parallel arising linear leaves (MPL 9317). D) Whorl of leaves arising at nodal level (MPL 9318). E) Radicites sp., compound roots (MPL 9319). F) Triangular structures of unknown botanical affinity (MPL 9320). G) Three roundish structures in various sections (MPL 9321). G1–G2: Details of the structures showing the dessication structures of the organic material. Scale bars: A–G= 2 cm, G1–G2= 0.5 cm.

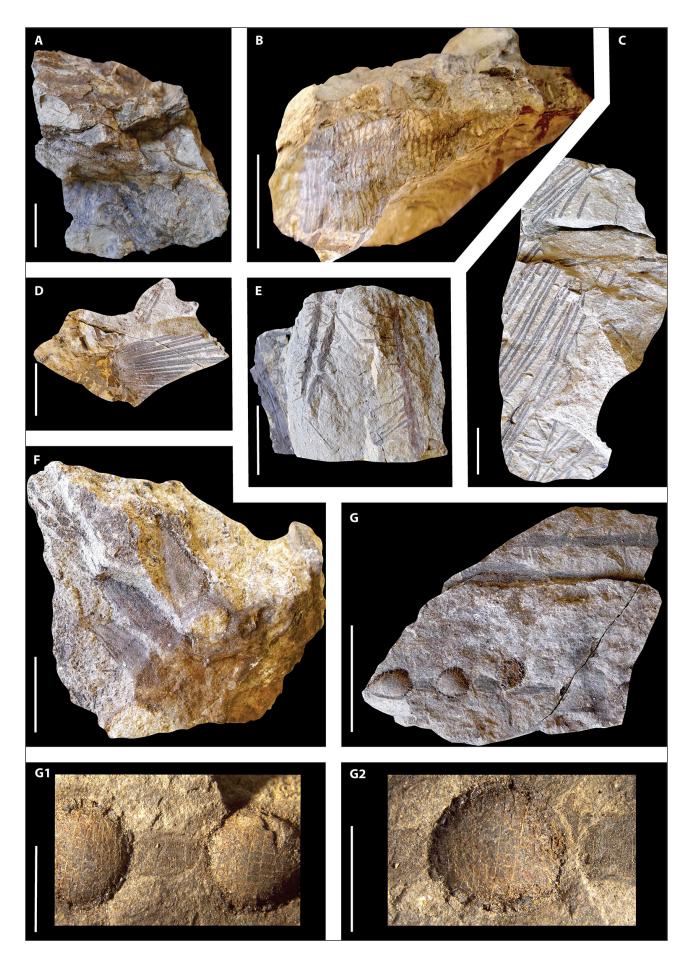


PLATE 2

The genus *Radicites* has been reported repeatedly from Rhaetian and Jurassic sediments of Iran and Afghanistan (e.g., Sadovnikov 1976; Schweitzer et al. 1997, 2009; Vaez-Javadi 2013a). The typical longitudinal striate structure of *Radicites sulcatus* Sadovnikov has not been observed in our specimens. Since the fragments are small, we prefer not to assign them to any species.

Additional material (Pl. 2, fig. F–G)

Two specimens are not assignable to any species but are here figured since they could represent the only non-sphenophyte remains in the assemblage. Specimen one (MPL 9320, Pl. 2, fig. F) is 50 mm long and 53 mm wide. It is composed of three elongated structures of 38-42 mm length and 9-11 mm width; the basal part of each element is enlarged and has a diameter of 12-13 mm. At least one of the elements seems subdivided in longitudinal striae and could show also a transversal line. The specimen seems composed of three shoots or axes that are basally connected or fused. These structures appear hollow. The possible longitudinal and transversal interruptions could suggest it to belong to some sphenophytes. It cannot be excluded that it could be a part of a sphenophyte axis with lateral shoots arising from a nodal element. In this case, it could be a part of a sphenophyte axis with lateral shoots arising from a nodal element. In this case, it could perhaps belong to Neocalamites iranensis and represent the proof that this species was articulated with a whorl of lateral axes arising at nodal level. Since the fragment is not well-preserved, we prefer to keep it for now distinguished from the Neocalamites iranensis.

Another rock slab (MPL 9321, Pl. 2, figs. G1-2) contains three elements with an elliptical (9.3 x 6.3 mm) to roundish section (6–7 mm) with a 0.8–1 mm thick coaly layer characterized by cracks with a quadrangular, blocky pattern filled by mineral layers. The latter structure can occur during the conservation of thick coaly layers, especially if the organic material is transformed in vitrinite. These structures could represent remains of seeds, considering the general shape and dimension; a clear integument and seed structure, is however, missing. Similar structures were also observed for root nodules, such as for example in Equisetites burchardtii Schimper from the Wealden near Bückeburg, northern Germany (Schenk, 1871), where they occur in large masses in palaeosols associated with Equisetites roots. Putative root nodules assigned to Equisetites renaceous of the Middle–Late Triassic of Germany are, however, generally bigger in dimension, up to 10 cm in diameter (EK, pers. observ.). In case these structures are isolated root nodules, this would support the presence of the monotypic sphenophyte stand. In case these would be seeds, they could belong to plants growing closely nearby or could have been transported over some distance to the depositional environment, and belong, thus, to allochthonous elements.

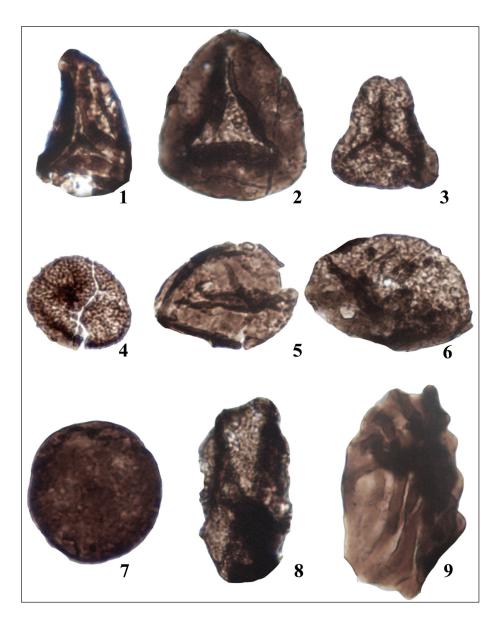
AGE ASSIGNMENT

Ruttner (1991) decribed coal seams and "hanging sandstone" with well-preserved plant remains. A distinct plant assemblage was described from the outcrops 76/94, 76/95, and 75/19, including Neocalamites sp. A sensu Boersma & Van Konijnenburg-van Cittert (1991), Sphenobaiera sp. A, Taeniopteris sp. A, Podozamites paucinervis Boersma et Van Konijnenburg-van Cittert, Podozamites sp., Carpolithes cf. cinctus Nathorst, and undetermined seed scales. The plant assemblage was interpreted as putatively Norian in age (Boersma & Van Konijnenburg-van Cittert 1991). Balini et al. (2019) proposed a general Late Triassic age for the Miakuhi Formation based on the stratigraphical position of the unit which overlies unconformably the Sina Formation.

Palynological analyses were carried out for the first time both in the Sina and Miankuhi formations and the better-preserved specimens are presented on Plate 3. The terrestrial sporomorph assemblage of the Upper Sina Formation (Shale Member) is dominated by cycads (Cycadopites sp.; Pl. 3, fig. 8), conifers (Triadispora sp., Lunatisporites sp., Araucariacites sp.) as well as sporadic ferns (Concavisporites sp., Dictyophyllidites mortonii, Trachysporites sp., Todisporites minor, Deltoidospora sp.; Pl. 3, figs. 1-3, 7) and sphenophytes (Calamospora sp.). The sporomorph assemblage of the lowermost part of the Miankuhi Formation is characterized by the co-occurence of Aulisporites astigmosus (Pl. 3, figs. 5-6), Spiritisporites sp. (Pl. 3, fig. 4), Equisetosporites sp. (Pl. 3, fig. 9), Chasmatosporites sp., and Annulispora sp. which allows us to define a latest early Carnian to late Carnian age, corresponding to the Carnian Pluvial Episode, for the lower part of the formation containing the coal levels and thus for both the new outcrop as well as for the outcrops 76/94, 76/95, and 75/19 of Boersma & Van Koniinenburg-van Cittert (1991).

PLATE 3

Sporomorphs of the plant yielding horizon. Each taxon name is followed by the section name, sample number, slide number, length of specimens, and stage coordinates for a Leica DM750 light microscope. 1) Concavisporites sp.; Kal-e-Bast section; KB 4 I; slide I; length 36.8 μm; K16/1; 2) Dictyophyllidites mortonii (de Jersey) Playford et Dettman, 1965; Kal-e-Bast section; KB 4 I; slide I; length 43.2 µm; H52; 3) Trachysporites sp.; Kal-e-Bast section; KB 4 I; slide I; length 30.4 µm; F25/4; 4) Spiritisporites sp.; Kal-e-Bast section; KB2; slide I; length 25.2 μm; M71/1; 5-6) Aulisporites astigmosus (Leschik) Klaus, 1960; Kal-e-Bast section: KB 4 I: slide I; N. 5: length 35 µm; N. 6: length 43.2 µm; N.5: W65, N.6: R40; 7) Todisporites minor Couper, 1958; Kal-e-Bast section; KB 4 II; slide II; length 32 µm; Q4; 8) Cycadopites sp.; Kal-e-Bast section; KB 4 I; slide II; length 49.6 μm; O54; 9) Equisetosporites sp.; Kal-e-Jom'eh section; MKJ 13; slide III; length 54.4 µm; G56/254.4 µm; G56/2.



DISCUSSION

Comparison between micro- and macrofloras of the Miankuhi Formation

Although the plant fossil assemblage described in this study represents a monotypic stand of sphenophytes (*Neocalamites iranensis* n. sp.), the surrounding coeval plant fossil localities 76/94, 76/95, and 75/19 of Boersma & Van Konijnenburg-van Cittert (1991), yielded a wider range of plant remains, including sphenophytes, ferns, and a variety of gymnosperms. Additional information on the regional flora, present during this moment, is given by the sporomorphs. Comparing the composition of the terrestrial sporomorphs with that of the macroplant assemblage from the same layer in the Miankuhi Formation, it becomes evident that for most of the identified spores and pollen there

is a good relationship. In the microflora the genera Aulisporites, Spiritisporites and Chasmatosporites have been produced by Bennettitales, Cycadales or Ginkgoales (Kräusel and Schaarschmidt 1966; Balme 1995; Paterson et al. 2016), which are also known from the macroplant remains due to the presence of the genera Pterophyllum (Bennettitales), Taeniopteris (Bennettitales or Cycadales), and Sphenobaiera (Ginkgoales). The conifer pollens are of unknown botanical affinity; among the macroremains the shoots of Podozamites are the only representatives of this plant group. The sphenophyte, monotypic in our assemblages but also present in the surrounding outcrops by Neocalamites, correspond to Calamospora in the microflora.

There are, however, also elements among the sporomorphs, belonging to taxa that are not found so far among the macroremains. To these belong

Annulispora, a typical bryophyte spore (e.g., Koppelhus 1991; Paterson et al. 2016). Their missing in the macrofossil record is, however, not very surprising considering the low preservation potential of mosses in the fossil record (e.g., Taylor et al. 2009; Heinrichs et al. 2018). Conifers and seed ferns must have been more abundant and diverse in the flora, considering the presence of the genera Triadispora, Lunatisporites and Araucariacites among the palynomorphs. Also, Equisetosporites belongs putatively to a group of plants not represented in the macroplant assemblage, the gnetophytes, ephedrales, or angiospermids (e.g., Pocock & Vasanthy 1988; Osborn et al. 1993; Lindström et al. 2016). The typical spore genera, *Todisporites*, and other baculate/ apiculat forms could be linked to the macroremains by Cladophlebis. The recorded microflora, therefore, represents a much more luscious vegetation during the deposition time of the fossiliferous horizon of the Miankuhi Formation than shown so far by the macrofossil record only, because it reflects the regional flora.

PALEOENVIRONMENTAL CONSIDERATIONS

The occurrence of sphenophytes is connected with humid habitats in the vicinity of rivers and lakes (Batten 1974; Abbink et al. 2004). Many of the arborescent Carboniferous taxa (*Calamites*) were important components of the peat-forming vegetation; they colonized, however, also riverbanks or disturbed areas (DiMichele & Hook 1992). Extant *Equisetum* plants colonize a broad spectrum of habitats, ranging from humid to dry, although most taxa prefer humid habitats or areas in which sufficient groundwater is available. It is, therefore, reasonable to conclude that Mesozoic sphenophytes probably grew in the more humid habitats.

The fact that most sphenophytes are clonal permits them to form more or less extensive (monotypic) stands along the margins of water bodies, where clonal plants are often especially successful. Rhizomes are effective in sustaining the plants during periods of flooding, erosion, or sediment accumulation since the resources stored in the rhizomatous system facilitate aerial shoot regeneration if the aerial parts of the plant are destroyed (Pott et al. 2008). Vegetative reproduction by means of fragmentation, as suggested for example for the

Triassic sphenophyte *Equisetites arenaceus*, may have been advantageous under these conditions (Pott et al. 2008). The branch fragments may have been transported by water, and ultimately started new clones in other areas.

Zan et al. (2012) described *Neocalamites hor*ridus as growing in large, closely packed stands consisting of completely monopodial aerial stems, which would have provided an interlocking support similar to that of modern-day stands of large *Equi*setum species or bamboo. Similar considerations can be made also on *Neocalamites iranensis* n. sp. considering their monotypical occurrence in our fossiliferous levels.

It is believed that *Neocalamites*-type plants prefer moist habitats but could stand slightly drier conditions than *Equisetites*-type of plants (Barbacka 2009, 2011), although *Neocalamites* remains were also found in sediments deposited under swamp conditions. This makes them swamp dwellers during the Jurassic (Barbacka et al. 2015, 2016; Popa, pers. comm. 2021). The presence of a monotypic stand of (autochtonous) sphenophytes of the *Neocalamites* type supports the hypothesis that these plants grew in a rather humid environment and could have been among the primary producers of the coal layers at the base of the Miankuhi Formation, similarly to their Carboniferous relatives.

Comparisons with coeval floras

Floras of the Carnian Pluvial Episode (CPE) are generally characterized by diverse plant assemblages that reflect floras growing under generally humid conditions and in swampy fluvial to deltaic depositional environments (e.g., Dobruskina 1994; Kelber & Hansch 1995; Pott et al. 2008; Kustatscher et al. 2018). The Lunz flora, the most famous European flora of the CPE, has been deposited in a swampy, paralic environment, which gave origin to thick coal layers. It is characterized by a rich and very diverse flora with plant fossils referable to a great diversity of species belonging to numerous plant groups. Ferns and cycads/bennettitaleans are very abundant, whereas sphenophytes, conifers, and putative ginkgophytes are less common (e.g., Dobruskina 1994, 1998; Pott et al. 2008; Pott & Krings 2010; Kustatscher et al. 2018 and references therein). The coeval Schilfsandstein flora of Germany is dominated by sphenophytes and ferns; conifers and bennettitaleans are locally rare to common. The

stratigraphic sequence hosting this flora includes multiple paleosol layers with consecutive generations of in situ sphenophyte (*Equisetites*) shoots and rhizomes (Kelber & Hansch 1995), which grew in a fluvio-deltaic setting (Franz et al. 2019; Kustatscher et al. 2018). These monotonous associations of ferns and sphenophytes as well as the occurrences of in situ sphenophytes, together with their sporomorph assemblages, suggest that these floras grew under humid conditions (e.g., Kelber & Hansch 1995; Kustatscher et al. 2018).

The base of the Stockton Formation in North Carolina and Pennsylvania (USA) could also correspond to the CPE. The plant assemblages of this formation are not associated with coal deposits (e.g., Kustatscher et al. 2018). They are diverse and abundant in conifers and cycads/bennettitaleans, whereas ferns and sphenophytes are rare (e.g., Wanner & Fontaine, in Ward, 1900; Bock 1969; Axsmith et al. 1995 and references therein). The paleogeographic position (about 25–30°N) of the European and Northern America floras is, however, much closer to the Equator than the plant assemblage from the Aghdarband Basin and the inner-continental setting of the America floras could account for the missing coal layers.

Paleolatitudinally closer are the Carnian floras of the De Geerdalen Formation in the Scandinavia-Greenland region. The CPE successions are represented by non-marine delta plain deposits (Klausen & Mørk 2014) yielding a rich flora dominated by ferns, bennettitaleans, and seed ferns, whereas sphenophytes and ginkgophytes are also well represented (e.g., Pott 2012; Kustatscher et al. 2018). The Protopivskaya Formation of the Donets Basin and the Kalachevskaya Formation of the Middle and Eastern Asian sub-provinces (north and central Asia; e.g., Kustatscher et al. 2018 and references therein) are dominated by seed ferns (mostly Peltaspermales; up to 30%) and Glossophyllum-type leaves (Dobruskina 1994). Marattiales are the dominant ferns in the Urals, Caucasus, and Central Asia, whereas the Dipteridaceae spread at lower latitudes of the East Asian Subprovince (e.g., Sad-Gorod Formation of the Primorye; Volynets & Shorokhova 2007). Sphenophytes are numerous but taxonomically not diverse and occupy a subordinate position in relation to other plant groups in these subprovinces (Kustatscher et al. 2018). They are, however, a significant component of several assemblages in the northern part of the Chelyabinsk Basin and the Southern Urals (Kirichkova 1969) and in the Bukobay Formation of the Ilek River Basin (Brick 1952), where the plants grew in rather humid environments of alluvial plains, delta plains and shallow lacustrine environments during the Carnian (Kochnev 1934; Brick 1936; Sixtel 1961, 1962; Dobruskina 1995). The CPE-deposited layers of the Madygen flora yielded both seed ferns but also various spore-producing plants including lycophytes and bryophytes, typical for humid environments (e.g., Dobruskina 1995; Moisan et al. 2011, 2012; Moisan & Voigt 2013).

The Carnian deposits of the Southern East Asia Subprovince (Kustatscher et al. 2018) include plant assemblages from the Daqiaodi Formation of the Yongren, Yunnan, and Yunnan-Sichuan border area, the Jiuligang Formation of Nanzhang, Hubei, and the Jiapeila Formation of Tibet (Zhou & Zhou 1983; Fansong 1983, 1990). The flora is abundant in sphenophytes, ferns, seed ferns, and cycads/bennettitaleans and resembles the Schilfsandstein flora of Western Europe (Zhou & Zhou 1983; Kustatscher et al. 2018). The Indonesian Carnian flora is dominated by sphenophytes, ferns, and cycads/ bennettitaleans (Kon'no 1972; Vakhrameev et al. 1978). Carnian floras from Japan; i.e., the Yamaguti plant assemblages from the Momonoki and Aso formations of the Mine Group (Oishi 1932a, 1932b, 1940; Ôishi & Takahashi 1936; Takahashi 1951) are abundant in ferns, conifers, and cycads/bennettitaleans, whereas sphenophytes are rare (Volynets & Shorokhova 2007).

This shows how diverse the plant fossil assemblages are generally during the Carnian and especially during the Carnian Pluvial Episode. Moreover, local conditions in Germany (e.g., Kelber & Hansch 1995) and Russia (e.g., Brick 1952) during the CPE gave origin to similar monotypic stands of sphenophytes, mostly in fluvio-deltaic settings.

CONCLUSIONS

The Carnian Pluvial Episode was a time of global environmental changes. The extent of the biological turnover in marine and terrestrial ecosystems associated with these events is, however, still not well understood, although a substantial reduction in genus and species richness in many marine

groups with the disappearance of up to 33% of all marine genera is proposed (Dal Corso et al. 2020). Within the terrestrial ecosystems, a major turnover is observed during the CPE, associated with a major radiation and diversification event (Bernardi et al. 2018; Dal Corso et al. 2020). Plant fossils evidence a shift of plant associations towards elements more adapted to humid conditions at different latitudes (e.g., Roghi et al. 2010; Preto et al. 2010; Mueller et al. 2016; Kustatscher et al. 2018), and extensive resin production (Gianolla et al. 1998; Roghi et al. 2006; Schmidt et al. 2012; Seyfullah et al. 2018). The onset of the CPE is very well constrained in many stratigraphic sections from Tethys domain to Panthalassa or, inside Pangea, from western Eurasia to South America (e.g., Dal Corso et al. 2012, 2015, 2018; Barany et al. 2018; Jin et al. 2020; Fu et al. 2020; Mancuso et al. 2020). There are, however, several areas where this event has not been documented as clearly as along the southern margin of Eurasia. The latest early Carnian to late Carnian age assigned to the basal part of the Miankuhi Formation using palynological associations allows to date the fluvial sediments, the coal layer and the plant levels to the CPE. This is the first record of Carnian plant fossils from the NE Iran, and also the first record for the Carnian Pluvial Episode in the Turan Plate, Kopeh-Dagh Range (NE Iran). The monotypic stand of Neocalamites iranensis n. sp. gives a glimpse into a peculiar microenvironment established under local conditions, during a period characterized by a high abundance in precipitation. The plant fossils from the surrounding areas (Boersma & Van Konijnenburg-van Cittert 1991) and the palynological record from the Miankuhi Formation give some ideas of the composition of the regional flora, including other plant groups, such as bryophytes, lycophytes, ferns, cycads, bennettitaleans, ginkgoaleans, and conifers, typical for the Carnian Pluvial Episode.

Acknowledgments: We are very grateful to Natalia Zavialova (Moscow) for her help with the Russian species of Neocalamites (translations and identification of the various characters). Mihai Popa (Bucharest, Romania), Zhuo Feng (Kunming, China) and Elke Schneebeli-Hermann (Zürich, Switzerland) helped with the literature research. Thanks also to Giovanni Muttoni (Milano) for the discussion about the paleolatitude position of the Turan plate during the Triassic and Angela Bertinelli (Perugia) for information about radiolarians. We also gratefully acknowledge the cooperation of colleagues from the Geological Survey of Iran, Mashhad branch, particularly Jafar Taheri, Abradat Maafi, and Maryam Hosseiniyoon for assistance in fieldwork. Mine Engineer Hajiyan (from the company of Maadan Khavar) is also acknowledged for providing hospitality at

the Aghdarband Coal mine during our fieldwork. Mihai Popa (Budapest) and an anonymous reviewer are thanked for their very helpful and constructive remarks. Sadly, we recently learned of the untimely and unexpected death of our dear colleague and co-author Ebrahim Ghasemi-Nejad. The painful news left us dismayed and saddened, with him we lost a talented scientist, a great friend who introduced us to the outstanding geology of Iran. We will miss him, as will his students, his colleagues and above all his family.

REFERENCES

- Abbink O.A., Van Konijnenburg-van Cittert J.H.A. & Visscher H. (2004) A sporomorph ecogroup model for the Northwest European Jurassic Lower Cretaceous: Concepts and framework. Geologie en Mijnbouw/ Netherlands Journal of Geosciences, 83(1): 17-38.
- Afshar-Harb A. (1979) The Stratigraphy, Tectonics and Petroleum Geology of the Koppeh-Dagh Region, Northern Iran. Unpublished Ph.D. thesis. Imperial College of Science and Technology, London (1979), 316 pp.
- Afshar-Harb A. (1994) Geology of Kopet Dagh. Treatise on the Geology of Iran, 11: 1-275.
- Alavi M., Vaziri H., Seyed-Emami K. & Lasemi Y. (1997) The Triassic and associated rocks of the Nakhlak and Aghdarband areas in central and northeastern Iran as remnants of the southern Turanian active continental margin. *Bulletin of the Geological Society of America*, 109(12): 1563-1575.
- Allen M., Jackson J. & Walker R. (2004) Late Cenozoic reorganization of the Arabia-Eurasia collision and the comparison of short-term and long-term deformation rates. *Tectonics*, 23(2).
- Allen M.B., Kheirkhah M., Emami M.H. & Jones S.J. (2011)
 Right-lateral shear across Iran and kinematic change in the Arabia-Eurasia collision zone. *Geophysical Journal International*, 184(2): 555-574.
- Angiolini L., Gaetani M., Muttoni G., Stephenson M.H. & Zanchi A. (2007) Tethyan oceanic currents and climate gradients 300 m.y. ago. *Geology*, 35(12): 1071-1074.
- Axsmith B.J., Taylor T.N., Delevoryas T. & Hope R.C. (1995)

 A new species of *Eoginkgoites* from the Upper Triassic of North Carolina, USA. *Review of Palaeobotany and Palynology*, 85(3-4): 189-198.
- Balini M., Nicora A., Berra F., Garzanti E., Levera M., Mattei M., Muttoni G., Zanchi A., Bollati I., Larghi C., Zanchetta S., Salamati R. & Mossavvari F. (2009) - The Triassic stratigraphic succession of Nakhlak (central Iran) a record from an active margin. Geological Society Special Publication, 312(1): 287-321.
- Balini M., Nicora A., Zanchetta S., Zanchi A., Marchesi R., Vuolo I., Hosseiniyoon M., Norouzi M. & Soleimani S. (2019) Olenekian to Early Ladinian stratigraphy of the western part of the Aghdarband window (Kopeh-Dag, NE Iran). Rivista Italiana di Palaeontologia e Stratigrafia, 125(1): 283-315.
- Balme B.E. (1995) Fossil in situ spores and pollen grains: an annotated catalogue. Review of Palaeobotany and Palynology, 87: 81-323.
- Baranyi V., Kürschner W.M., Ruffell A., Mark W. & Miller C.S. (2018) A continental record of the Carnian Pluvial Episode (CPE) from the Mercia Mudstone Group

- (UK). palynology and climatic implications. *Journal of the Geological Society*, 176: 149-166.
- Barbacka M. (2009) Sphenophyta from the Early Jurassic of the Mecsek Mts., Hungary. *Acta Palaeobotanica*. 49(2): 221-231.
- Barbacka M. (2011) Biodiversity and the reconstruction of Early Jurassic flora from the Mecsek Mountains (southern Hungary). *Acta Palaeobotanica*, 51(2): 127-179.
- Barbacka M., Püspöki Z., Bodor E., Forgács Z., Hámor-Vidó M., Pacyna G. & McIntosh R.W. (2015) -Palaeotopography related plant succession stages in a coal forming deltaic succession in early Jurassic in Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 440: 579-593.
- Barbacka M., Popa M.E., Mitka J., Bodor E., Puspoki Z. & McIntosh R.W. (2016) A quantitative approach for identifying plant ecogroups in the Romanian early Jurassic terrestrial vegetation. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 446: 44-54.
- Barnard P.D.W. (1965) Flora of the Shemshak Formation. Part 1. Liassic plants from Dorud. Rivista Italiana di Paleontologia e Stratigrafia, 71(4): 1123-1168.
- Barnard P.D.W. & Miller J.C. (1976) Flora of the Shemshak Formation (Elburz, Iran). 3. Middle Jurassic (Dogger) Plants from Katumbargah, Vasek Gah and Imam Manak. *Palaeontographica B*, 155: 31-117.
- Batten D.J. (1974) Wealden palaeoecology from the distribution of plant fossils. Proceedings of the Geologists' Association, 85(4): 433-458.
- Baud A., Brandner R. & Donofrio D.A. (1991a) The Sefid Kuh Limestone-A late Lower Triassic Carbonate Ramp (Aghdarband, NE-Iran). In: Ruttner A.W. (Ed.) - The Triassic of Aghdarband (AqDarband), NE-Iran, and its Pre-Triassic Frame. Abhandlungen der Geologischen Bundes-Anstalt, 38: 111-123.
- Baud A., Stampfli G. & Stephen D. (1991b) The Triassic Aghdarband Group: Volcanism and geological evolution.
 In: Ruttner A.W. (Ed.) The Triassic of Aghdarband (AqDarband), NE-Iran, and its Pre-Triassic Frame.
 Abhandlungen der Geologischen Bundes-Anstalt, 38: 125-137.
- Berberian M. & King G.C.P. (1981) Towards a Paleogeography and Tectonic Evolution of Iran. *Canadian Journal of Earth Sciences*, 18(2): 210-265.
- Bernardi M., Gianolla P., Petti F.M., Mietto P. & Benton M.J. (2018) Dinosaur diversification linked with the Carnian Pluvial Episode. *Nature Communications*, 9: 1499.
- Bock W. (1969) The American Triassic flora and global distribution. *Geological Center Research Series*, 3: 1-357.
- Boersma M. & Van Konijnenburg-van Cittert J.H.A. (1991)

 Late Triassic plant megafossils from Aghdarband (NE-Iran). In: A.W. Ruttner (Ed.) The Triassic of Aghdarband (AqDarband), NE-Iran, and its pre-Triassic frame. Abhandlungen der Geologischen Bundes-Anstalt, 38: 223-252.
- Brick M.I. (1936) The first finding of the Lower Triassic flora in Middle Asia. *Transactions of Geological Institute of the USSR Academy of Sciences*, 5: 161-174.
- Brick M.I. (1952) Iskopaemaja flora i stratigrafija nižnemezozojskich otloženij bassejna srednego tečenija r. Ilek v Zapadnom Kazachstane. *Gosudarstvennoe Izd. Geologičeskoj Literatur*: 1-116.
- Brunet F.F., Korotaev M.V., Ershov A.V. & Nikishin A.M. (2003) The South Caspian Basin: A review of its evolution from subsidence modelling. *Sedimentary*

- Geology, 156(1-4): 119-148.
- Bucefalo Palliani R. & Buratti N. (2006) High diversity dinoflagellate cyst assemblages from the Late Triassic of southern England: new information on early dinoflagellate evolution and palaeogeography. *Lethaia*, 39: 305-312.
- Calzolari G., Rossetti F., Seta M., Della Nozaem R., Olivetti V., Balestrieri M.L., Cosentino D., Faccenna C., Stuart F.M. & Vignaroli G. (2016) Spatio-temporal evolution of intraplate strike-slip faulting: The Neogene-Quaternary Kuh-e-Faghan Fault, central Iran. *Bulletin of the Geological Society of America*, 128(3-4): 374-396.
- Cao W., Zahirovic S., Flament N., Williams S., Golonka J. & Müller D.R. (2017) - Improving global paleogeography since the late Paleozoic using paleobiology. *Biogeosciences*, 14(23): 5425-5439.
- Corsin P. & Stampfli G. (1977) La Formation de Shemshak dans l'Elburz Oriental (Iran) Flore-Stratigraphie-Paléogéographie. *Geobios*, 10: 509-571.
- Dal Corso J., Mietto P., Newton R.J., Pancost R.D., Preto N., Roghi G. & Wignall P.B. (2012) Discovery of a major negative δ¹³C spike in the Carnian (Late Triassic) linked to the eruption of Wrangellia flood basalts. *Geology*, 40(1): 79-82.
- Dal Corso J., Gianolla P., Newton R.J., Franceschi M., Roghi G., Caggiati M., Raucsik B., Budai T., Haas J. & Preto N. (2015) Carbon isotope records reveal synchronicity between carbon cycle perturbation and the "Carnian Pluvial Event" in the Tethys realm (Late Triassic). Global and Planetary Change, 127: 79-90.
- Dal Corso J., Gianolla P., Rigo M., Franceschi M., Roghi G., Mietto P., Manfrin S., Raucsik B., Budai T., Jenkyns H.C., Reymond C.E., Caggiati M., Gattolin G., Breda A., Merico A. & Preto N. (2018) Multiple negative carbonisotope excursions during the Carnian Pluvial Episode (Late Triassic). Earth-Science Reviews, 185: 732-750.
- Dal Corso J., Bernardi M., Sun Y., Song H., Seyfullah L.J., Preto N., Gianolla P., Ruffell A., Kustatscher E., Roghi G., Merico A., Hohn S., Schmidt A.R., Marzoli A., Newton R.J., Wignall P.B. & Benton M.J. (2020) - Extinction and dawn of the modern world in the Carnian (Late Triassic). Science Advances, 6(38): eaba0099.
- Davoudzadeh M. & Schmidt K. (1985) Contribution to the paleogeography, stratigraphy and tectonics of the Cretaceous and Paleocene of Iran. *Neues Jahrbuch für* Geologie und Paläontologie. Abhandlungen, 169(3): 284-306.
- DiMichele W.A., Hook R.W., Beerbower R., Boy J.A., Gastaldo R.A., Hotton, N., Phillips T.L., Scheckler S.E., Shear W.A.
 & Sues H.D. (1992) Paleozoic terrestrial ecosystems.
 Terrestrial Ecosystems through Time. University of Chicago Press, Chicago: 205-325.
- Dobruskina I.A. (1994) Triassic Floras of Eurasia. Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommissionen, 10: 1-422.
- Dobruskina I.A. (1995) Keuper (Triassic) Flora from Middle Asia (Madygen, Southern Fergana). *Bulletin New Mexico Museum of Natural History and Science*, 5: 1-49.
- Dobruskina I.A. (1998) Lunz flora in the Austrian Alps A standard for Carnian floras In: *Palaeogeography, Palaeoclimatology, Palaeoecology*, 143(4): 307-345.
- Donofrio D.A. (1991) Radiolaria and Porifera (spicula) from the Upper Triassic of Aghdarband (NE-Iran). *Abhandlungen der Geologischen Bundes-Anstalt*, 38: 205-222.
- Eftekharnezhad J. & Behroozi A. (1991) Geodynamic

- significance of recent discoveries of ophiolites and late Paleozoic rocks in NE-Iran (including Kopet Dagh). *Abhandlungen der Geologischen Bundes-Anstalt*, 38: 89-100.
- Fakhr M. S. (1977) Contribution a l'Étude de la flore rhétoliassique de la formation de Shemshak de l'Elbourz (Iran). *Mémoires de la section des Sciences*. 5: 178 pp.
- Fansong M. (1983) New materials of fossil plants from the Jiuligang Formation of Jingmen-Dangyang Basin, W. Hubei. Professional Papers of Stratigraphy and Palaeontology, 10: 223-238.
- Fansong M. (1990) Some Pteridosperms from Western Hubei in Late Triassic and Their Evolutionary Tendency. *Journal of Integrative Plant Biology*, 32(4).
- Franz M., Kustatscher E., Heunisch C., Niegel S. & Röhling H.G. (2019) The Schilfsandstein and its flora; arguments for a humid mid-Carnian episode? *Journal of the Geological Society*, 176(1): 133-148.
- Fu X., Jian Wang J., Wen H., Wang Z., Zeng S., Song C., Chen W. & Wan J. (2020) A possible link between the Carnian Pluvial Event, global carbon-cycle perturbation, and volcanism: New data from the Qinghai-Tibet Plateau. Global and Planetary Change, 194: 103300.
- Garzanti E. & Gaetani M. (2002) Unroofing history of late Paleozoic magmatic arcs within the "Turan Plate" (Tuarkyr, Turkmenistan). Sedimentary Geology, 151(1-2): 67-87.
- Ghasemi-Nejad E., Head M.J. & Zamani M. (2008) Dinoflagellate cysts from the Upper Triassic (Norian) of northeastern Iran. *Journal of Micropalaeontology*, 27(2): 125-134.
- Gianolla P., Ragazzi E. & Roghi G. (1998) Upper Triassic amber from the Dolomites (Northern Italy). A paleoclimatic indicator? *Rivista Italiana di Paleontologia e Stratigrafia*, 104(3): 381-390.
- Göppert H.R. (1861) Ueber das Vorkommen von Lias-Pflanzen im Kaukasus und der Alborus-Kette: Abhandlungen der Schlesischen Gesellschaft für vaterländische Literatur. Abtheil. für Naturwissenschaften u. Medicin. 1861:Vol 2, 189-194.
- Heer O. (1876-1877). Flora fossilis Helvetiae. Die vorweltliche Flora der Schweiz. Verlag J. Wurster & Comp., Zürich. 182 p. Parts 1,2 (1876):1-90; Parts 3, 4 (1877): 91-182.
- Heinrichs J., Feldberg K., Bechteler J., Regalado L., Renner M.A.M., Schäfer-Verwimp A., Gröhn C., Müller P., Schneider H. & Krings M. (2018) A Comprehensive Assessment of the Fossil Record of Liverworts in Amber. In: Krings M., Harper C.J., Cúneo N.R. & Rothwell G.E. (Eds.) Transformative Paleobotany: Academic Press, Amsterdam, pp. 213-252.
- Jacob K., Shukla B.N. & West W.D. (1955) Jurassic Plants from the Saighan Series of northern Afghanistan and their paleoclimatological and paleogeographical significance. *Memoirs of the Geological Survey of India, Palaeontographica Indica*, 33 (2): 1-64.
- Jin X., Gianolla P., Shi Z., Franceschi M., Caggiati M., Du Y. & Preto N. (2020) - Synchronized changes in shallow water carbonate production during the Carnian Pluvial Episode (Late Triassic) throughout Tethys. Global and Planetary Change, 184: 103035.
- Kelber K.P. (1990) Die versunkene Pflanzenwelt aus den Deltasümpfen Mainfrankens vor 230 Millionen Jahren: Beringeria, 1: 1-67.
- Kelber K.P. & Hansch W. (1995) Keuperpflanzen Die Enträtselung einer über 200 Milionen Jahre alten Flora.

- Museo 11: 1-157.
- Khalilizadeh H., Ghaderi A., Ashouri A.R. & Zand-Moghadam H. (2020) Plant macrofossils, ichnofossils, facies analysis and palaeoenvironment interpretation of the Hojedk Formation in the north of Kerman (Central Iran). *Journal of Stratigraphy and Sedimentology Researches University of Isfahan*, 35 (4): 1-38.
- Kilpper K. (1964) Über eine Rät/Lias-Flora aus dem nördlichen Abfall des Alburs-Gebirges in Nord-Iran. Teil 1: Bryophyta und Pteridophyta. *Palaeontographica*, 114B: 1-78.
- Kilpper K. (1968) Einige Bennettiteen-Blätter aus dem Lias von Karmozd-Zirab (N-Iran). Journal of the Linnean Society of London. *Botany*, 61(384): 129-135.
- Kilpper K. (1971) Über eine Rät/Lias-Flora aus dem nördlichen Abfall des Alburs-Gebirges in Nord-Iran. Teil 2: Ginkgophyten-Belaubung. *Palaeontographica Abteilung* B: 89-102.
- Kilpper K. (1975) Paläobotanische untersuchungen in Nord-Iran. I. Nachweis nichtmariner Obertrias am Nordabfall des Alburs-Gebirges. 1. Grossform der Pflanzenfunde von seltenen Gattungen. Review of Palaeobotany and Palynology, 19(2): 139-153.
- Kimyai A. (1972) Fossil flora of Shemshak Formation, Garmabdar area. *Journal of Science, Tehran University*, 3(2): 7-25.
- Kirichkova A.I. (1969) Materials for the study of the Lower Mesozoic flora of the Eastern Urals. *Trudy V sesoyuznogo Neftjanogo Geologo Razved Instituta*, 268: 270-349.
- Klausen T.G. & Mørk A. (2014) The Upper Triassic paralic deposits of the De Geerdalen Formation on Hopen: Outcrop analog to the subsurface Snadd Formation in the Barents Sea. *AAPG Bulletin*, 98(10): 1911-1942.
- Kochnev E.A. (1934) On the study of Jurassic coal-bearing deposits of Fergana. *Materials on Geology of Coal Deposits of Middle Asia*: 5-6.
- Kon'no E. (1972) A new Chiropteris and other fossil plants from the Heian System, Korea. Japanese Journal of Geology and Geography, 16(1-2): 105-114.
- Koppelhus E. (1991) Palynology of the Lower Jurassic Rønne Formation on Bornholm, eastern Denmark. Bulletin of the Geological Society of Denmark, 39: 91-110.
- Krasser F. (1891) Über die fossile Flora der rhätischen Schichten Persiens. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, 100: 413-432.
- Kräusel R. & Leschik G. (1959) Die Keuperflora von Neuewelt bei Basel. III. Equisetaceen. Schweizerische Paläontologische Abhandlungen, 77: 5-19.
- Kräusel R. & Schaarschmidt F. (1966) Die Keuperflora von Neuewelt bei Basel; 4/5: Pterophyllen und Taeniopteriden. Schweizerische Paläontologische Abhandlungen, 84: 1-64.
- Krystyn L. & Tatzreiter F. (1991) Middle Triassic ammonoids from Aghdarband (NE-Iran) and their paleobiogeographical significance. *Abhandlungen der Geologischen Bundes-Anstalt*, 38: 139-165.
- Kustatscher E. & Van Konijnenburg-van Cittert J.H.A. (2008) Lycophytes and horsetails from the Triassic flora of Thale (Germany). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 250(1): 65-77.
- Kustatscher E., Ash S.R., Karasev E., Pott C., Vajda V., Yu J. & McLoughlin S. (2018) Flora of the Late Triassic. In: Tanner L. (Ed.) The Late Triassic World. Springer,

- Cham, pp. 545-622.
- Linck O. (1943) Fossile Wurzelböden aus dem Mittleren Keuper. *Natur und Volk*, 73: 226-234.
- Lindström S., Irmis R.B., Whiteside J.H., Smith N.D., Nesbitt S.J. & Turner A.H. (2016) - Palynology of the upper Chinle Formation in northern New Mexico, U.S.A.: Implications for biostratigraphy and terrestrial ecosystem change during the Late Triassic (Norian-Rhaetian). Review of Palaeobotany and Palynology, 225: 106-131
- Mahboubi A., Moussavi-Harami R., Carpenter S.J., Aghaei A. & Collins L.B. (2010) Petrographical and geochemical evidences for paragenetic sequence interpretation of diagenesis in mixed siliciclastic-carbonate sediments: Mozduran Formation (Upper Jurassic), south of Agh-Darband, NE Iran. Carbonates and Evaporites, 25(3): 231-246.
- Mancuso A.C., Benavente C.A., Irmis R.B. & Mundil R. (2020) - Evidence for the Carnian Pluvial Episode in Gondwana: New multiproxy climate records and their bearing on early dinosaur diversification. *Gondwana* Research, 86: 104-125.
- Mattei M., Muttoni G. & Cifelli F. (2014) A record of the Jurassic massive plate shift from the Garedu Formation of central Iran. *Geology*, 42(6): 555-558.
- Matthews K.J., Maloney K.T., Zahirovic S., Williams S.E., Seton M. & Müller R.D. (2016) Global plate boundary evolution and kinematics since the late Paleozoic. *Global and Planetary Change*, 146: 226-250.
- Milanovsky E.E. (1991) Rifting and its role in the tectonic structure of the Earth and its Mezo-Cenozoic geodynamics. *Geotektonika (Geotectonics)*, 1: 3-20.
- Moisan P. & Voigt S. (2013) Lycopsids from the Madygen Lagerstätte (Middle to Late Triassic, Kyrgyzstan, Central Asia). Review of Palaeobotany and Palynology, 192: 42-64.
- Moisan P., Voigt S., Pott C., Buchwitz M., Schneider J.W. & Kerp H. (2011) - Cycadalean and bennettitalean foliage from the Triassic Madygen Lagerstätte (SW Kyrgyzstan, Central Asia). Review of Palaeobotany and Palynology, 164(1-2): 93-108.
- Moisan P., Voigt S., Schneider J.W. & Kerp H. (2012) New fossil bryophytes from the Triassic Madygen Lagerstätte (SW Kyrgyzstan). Review of Palaeobotany and Palynology, 187: 29-37.
- Morley C.K., Kongwung B., Julapour A.A., Abdolghafourian M., Hajian M., Waples D., Warren J., Otterdoom H., Srisuriyon K. & Kazemi H. (2009) Structural development of a major late Cenozoic basin and transpressional belt in central Iran: The Central Basin in the Qom-Saveh area. *Geosphere*, 5(4): 325-362.
- Mueller S., Hounslow M.W. & Kürschner W.M. (2016) Integrated stratigraphy and palaeoclimate history of the Carnian Pluvial Event in the Boreal realm; new data from the Upper Triassic Kapp Toscana Group in central Spitsbergen (Norway). *Journal of the Geological Society, London,* 173(1): 186-202.
- Muttoni G., Tartarotti P., Chiari M., Marieni C., Rodelli D., Dallanave E. & Kirscher U. (2015) - Paleolatitudes of Late Triassic radiolarian cherts from Argolis, Greece: Insights on the paleogeography of the western Tethys. Palaeogeography, Palaeoclimatology, Palaeoecology, 417: 476-490.
- Nozaem R., Mohajjel M., Rossetti F., Della Seta M., Vignaroli G., Yassaghi A., Salvini F. & Eliassi M. (2013) Post-

- Neogene right-lateral strike-slip tectonics at the north-western edge of the Lut Block (Kuh-e-Sarhangi Fault), Central Iran. *Tectonophysics*, 589: 220-233.
- Oberhauser R. (1991) Triassic foraminifera from the Faqir Marl Bed of the Sina Formation (Aghdarband Group, NE-Iran). *Abhandlungen der Geologischen Bundesanstalt*, 38: 201-204.
- Ôishi S. (1932a) Rhaetic plants from Province Nagato (Yamaguchi Prefecture), Japan. Journal of the Faculty of Science, Hokkaido Imperial University. Ser. 4, Geology and Mineralogy, 2(1): 51-68.
- Ôishi S. (1932b) The Rhaetic Plants from the Nariwa District, Prov. Bitchû (Okayama Prefecture), Japan. Journal of the Faculty of Science, Hokkaido Imperial University. Ser. 4, *Geology and Mineralogy*, 1(3-4): 257-380.
- Ôishi S. (1940) The Mesozoic Floras of Japan. Journal of the Faculty of Science, Hokkaido Imperial University. Ser. 4, *Geology and Mineralogy*, 5(2-4): 123-480.
- Ôishi S. & Takahashi E. (1936) The Rhaetic Plants from Province Nagato. A Supplement. Journal of the Faculty of Science, Hokkaido Imperial University. Ser. 4, Geology and Mineralogy, 3(2): 113-133.
- Osborn J.M., Taylor T.N. & de Lima M.R. (1993) The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. *Review of Palaeobotany and Palynology*, 77(3-4): 171-184.
- Parvacideh A. & Vaez Javadi F. (2015) Plant Macrofossils from the Takht Coal Mine, Minoodasht and its Dating, Relative abundance and Sörensen index in comparison with the other Florizones in Iran and Eurasia. *Journal of Stratigraphy and Sedimentology Researches*, 30(4): 59-86.
- Paterson N.W., Mangerud G., Cetean C.G., Mørk A., Lord G.S., Klausen T.G. & Mørkved P.T. (2016) A multidisciplinary biofacies characterisation of the Late Triassic (late Carnian-Rhaetian) Kapp Toscana Group on Hopen, Arctic Norway. *Palaeogeography, Palaeoclimatology, Palaeoceology*, 464: 16-42.
- Pocock S.A.J. & Vasanthy G. (1988) Cornetipollis reticulata, a new pollen with angiospermid features from Upper Triassic (Carnian) sediments of Arizona (U.S.A.), with notes on Equisetosporites. Review of Palaeobotany and Palynology, 55(4): 337-356.
- Pott C. (2012) The Upper Triassic flora of Svalbard. *Acta Palaeontologica Polonica*, 59(3): 709-740.
- Pott C. & Krings M. (2010) Gymnosperm foliage from the Upper Triassic of Lunz, Lower Austria: an annotated check list and identification key. *GeoAlp*, 7: 19-38.
- Pott C., Kerp H. & Krings M. (2008) Sphenophytes from the Carnian (Upper Triassic) of Lunz am See (Lower Austria). *Jahrbuch der Geologischen Bundes-Anstalt*, 148(2): 183-199.
- Preto N., Kustatscher E. & Wignall P.B. (2010) Triassic climates State of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeocology*, 290(1-4): 1-10.
- Ricou L.E. (1994) La Thétys reconstruite: plaques, blocs continentaux et leurs limites depuis 260 Ma de l'Amérique centrale à l'Asie du sud-est. *Geodinamica Acta*, 7(4): 169-218.
- Robert A.M.M., Letouzey J., Kavoosi M.A., Sherkati S., Müller C., Vergés J. & Aghababaei A. (2014) Structural evolution of the Kopeh Dagh fold-and-thrust belt (NE Iran) and interactions with the South Caspian Sea Basin and Amu Darya Basin. *Marine and Petroleum Geology*, 57: 68-87.

- Roghi G., Ragazzi E. & Gianolla P. (2006) Triassic Amber of the Southern Alps (Italy). *Palaios*, 21(2): 143-154.
- Roghi G., Gianolla P., Minarelli L., Pilati C. & Preto N. (2010) Palynological correlation of Carnian humid pulses throughout western Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290(1-4): 89-106.
- Ruttner A.W. (1984) The pre-Liassic basement of the eastern Kopet Dagh Range. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 168: 256-268.
- Ruttner A.W. (1988) The coal deposits of Agdarband (Aq Darband) NE-Iran and its geological frame In: Second Mining Symposium Iran (Kerman). Ministry of Mines and Metals, Tehran: 183-202.
- Ruttner A.W. (1991) Geology of the Aghdarband Area (Kopet Dag, NE-Iran). In: Ruttner A.W. (Ed) The Triassic of Aghdarband (AqDarband), NE-Iran and its pre-Triassic frame. *Abhandlungen der Geologischen Bundes-Anstalt*, 38: 7-79.
- Ruttner A.W. (1993) Southern borderland of Triassic Laurasia in north-east Iran. Geologische Rundschau, 82(1): 110-120.
- Saadat Nejad J., Ghaderi A. & Naeemi Ghasabian N. (2010) Study and presentation of Toarcian- Bajocian plant macrofossils of Gorakhk- Shandiz Region, North East of Iran. *Sedimentary Facies*, 2(2): 173-203.
- Sadovnikov G.N. (1976) The Mesozoic flora of Alborz and central Iran and its stratigraphic importance. National Iran Steel Company of Iran, Tehran: 1-118.
- Schenk A. (1871) Die fossile Flora der norddeutschen Wealdenformation. Theodor Fischer, 66 pp, Cassel.
- Schenk A. (1887) Fossile Pflanzen aus der Albourskette, gesammelt von E. Tietze, Chefgeologe der k.k. geologischen Reichsanstalt. In: Uhlworm O. & Haenlein F.H. (Eds.) - Bibliotheca botanica, Abhandlungen aus dem Gesamtgebiete der Botanik: 1-12.
- Schmidt A.R., Jancke S., Lindquist E.E., Ragazzi E., Roghi G., Nascimbene P.C., Schmidt K., Wappler T. & Grimaldi D.A. (2012) Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences*, 109(37): 14796-14801.
- Schweitzer H.J. (1978) Die rhäto-jurassischen Floren des Iran und Afghanistan. 5. Todites princeps, Thaumatopteris brauniana und Phlebopteris polypodioides. Palaeontographica Abteilung B, 168(1-3): 17-60.
- Schweitzer H.J. & Kirchner M. (1995) Die rhäto-jurassischen Floren des Iran und Afghanistans: 8. Ginkgophyta. *Palaeontographica Abteilung* B, 237: 1-58.
- Schweitzer H.J. & Kirchner M. (1996) Die rhäto-jurassischen Floren des Iran und Afghanistans: 9. Coniferophyta. *Palaeontographica Abteilung* B: 77-139.
- Schweitzer H.J. & Kirchner M. (1998) Die rhätojurassischen Floren des Iran und Afghanistans. 11. Pteridospermophyta und Cycadophyta I. Cycadales. Palaeontographica B, 248 (1-3): 1-85.
- Schweitzer H.J. & Kirchner M. (2003) Die rhäto -jurassischen Floren des Iran und Afghanistans. 13. Cycadophyta III. Bennettitales. *Palaeontographica Abteilung B*, 264(1-6): 1-166.
- Schweitzer H.J., Van Konijnenburg-van Cittert J.H.A. & Van der Burgh J. (1997) The Rhaeto-Jurassic flora of Iran and Afghanistan. 10. Bryophyta, Lycophyta, Sphenophyta, Pterophyta-Eusporangiatae and -Protoleptosporangiatae. *Palaeontographica Abteilung B*: 103-192.

- Schweitzer H.J., Kirchner M. & Van Konijnenburg-van Cittert J.H.A. (2000) The Rhaeto-Jurassic flora of Iran and Afghanistan. 12. Cycadophyta II. Nilssoniales. *Palaeontographica Abteilung B*, 254(1-3): 1-63.
- Schweitzer H.J., Schweitzer U., Van Konijnenburg-van Cittert J.H.A, van der Burgh J. & Ashraf R.A. (2009)

 The Rhaeto-Jurassic flora of Iran and Afghanistan.
 14. Pterophyta Leptosporangiatae. *Palaeontographica Abteilung B*, 279(1-6): 1-108.
- Şengör A.M.C. (1979) Mid-Mesozoic closure of Permo-Triassic Tethys and its implications. *Nature*, 279: 590-593.
- Şengör A.M.C. (1984) The Cimmeride orogenic system and the tectonics of Eurasia. *Geological Society of America* Special Paper, 195: 82.
- Şengör A.M.C. (1990) A new model for the late Palaeozoic-Mesozoic tectonic evolution of Iran and implications for Oman. Geological Society Special Publication, 49(1): 797-831.
- Seyfullah L.J., Beimforde C., Dal Corso J., Perrichot V., Rikkinen J. & Schmidt A.R. (2018) Production and preservation of resins-past and present. *Biological Reviews*, 93(3): 1684-1714.
- Sheikholeslami M.R. & Kouhpeyma M. (2012) Structural analysis and tectonic evolution of the eastern Binalud Mountains, NE Iran. *Journal of Geodynamics*, 61: 23-46.
- Sixtel T.A. (1961) The representatives of the *Gigantopteris* and some accompanying plants from the Madygen Formation of Fergana. *Paleontological Journal*, 1: 151-158.
- Sitel T.A. (1962) Flora of the Late Permian and Early Triassic in Southern Fergana. Stratigraphy and Palaeontology of Uzbekistan and Adjacent Areas. Akademia Nauk USSR, Tashkent: 271-414 [In Russian].
- Stampfli G.M. & Borel G.D. (2002) A plate tectonic model for the Paleozoic and Mesozoic constrained by dynamic plate boundaries and restored synthetic oceanic isochrons. *Earth and Planetary Science Letters*, 196(1-2): 17-33
- Stöcklin J. (1974) Possible Ancient Continental Margins in Iran In: Chreighton A.B & Drake C.L. (Eds.) - The Geology of Continental margins: 873-887. Springer Berlin Heidelberg.
- Stöcklin J. & Nabavi M.H. (1973) Tectonic map of Iran. Geological Survey of Iran, 1: 5.
- Stur D. (1886) Vorlage der von Dr. Wähner aus Persien mitgebrachten fossilen Pflanzen. Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt, 16: 431-436.
- Sze H.C. (1933) Fossile Pflanzen aus Shensi, Szechuan und Kneichow. *Palaeontologica Sinica*, 1: 1-32.
- Sze H.C. (1949) Die Mesozoische Flora aus der Hsiangchi Kohlen Serie in Westupeh. *Palaeontologia Sinica*, 2: 1-71.
- Sze H.C. (1956) Older Mesozoic plants from the Yengchang Formation, Northern Shensi. *Palaeontologica Sinica*, 139:
- Takahashi E. (1951) Descriptive Notes on Some Mesozoic Plants from Province Nagato (Yamaguchi Prefecture). The Journal of the Geological Society of Japan, 57(664): 29-33.
- Taylor T.N., Taylor E.L. & Krings M. (2009) Paleobotany: the biology and evolution of fossil plants. Academic Press.
- Vaez-Javadi F. (2004) *Persicostrobus* Vaez-Javadi n. gen. a new Equisetalean strobilus from the Triassic of Iran. *Rivista Italiana di Paleontologia e Stratigrafia*, 110: 715-718.
- Vaez-Javadi F. (2008) Plant macrofossils of Iran. Department of Environment Press (in Persian), Tehran, 236 pp.

- Vaez-Javadi F. (2013) Triassic and Jurassic floras and climate of central-east Iran. Geological Survey of Iran, Rahi Pub., 261 pp.
- Vaez-Javadi F. & Syooki M.G. (2002) Plant megafossil remains from Shemshak Formation of Jajarm area, NE Alborz, Iran. *Paleobotanist*, 51(1-3): 57-72.
- Vaez-Javadi F. & Abbasi N. (2012) Study of plant macrofossils from Baladeh area (Central Alborz): dating and biostratigraphy. *Journal of Stratigraphy and Sedimentology Researches*, 28(3): 37-64.
- Vakhrameev V.A., Dobruskina I.A. & Meyen S.V. (1978) -Paläozoische und mesozoische Floren Eurasiens und die Phytogeographie dieser Zeit. VEB Gustav Fischer Verlag, Jena.
- Vassiliev I. (1984) Mesozoic plant fossils from coal areas in Iran. V. II. Atlas of Ministry of Mine and Netal, 2(2), 97 pp., 47 plates.
- Volynets E.B. & Shorokhova S.A. (2007) Late Triassic (Mongugai) flora of the Primorye region and its position among coeval floras of Eurasia. Russian Journal of Pacific Geology, 1(5): 482-494.
- Ward L.F., Fontaine W.M., Wanner A. & Knowlton F.H. (1900) - Status of the Mesozoic floras of the United States: First paper: the older Mesozoic: Vol. 20. US Government Printing Office.
- Wilmsen M., Fürsich F.T., Seyed-Emami K., Majidifard M.R. & Taheri J. (2009) The Cimmerian Orogeny in northern Iran: Tectono-stratigraphic evidence from the foreland. *Terra Nova*, 21(3): 211-218.

- Xingxue L. (1995) Fossil floras of China through the geological ages. Guangzhou: Guangdong Science and Tehnology Press, 144.
- Zan S., Axsmith B.J., Escapa I., Fraser N.C., Liu F.X. & Xing D.H. (2012) A new *Neocalamites* (Sphenophyta) with prickles and attached cones from the Upper Triassic of China. *Palaeoworld*, 21(2): 75-80.
- Zanchetta S., Berra F., Zanchi A., Bergomi M., Caridroit M., Nicora A. & Heidarzadeh G. (2013) The record of the Late Palaeozoic active margin of the Palaeotethys in NE Iran: Constraints on the Cimmerian orogeny. *Gondwana Research*, 24(3-4): 1237-1266.
- Zanchi A., Zanchetta S., Berra F., Mattei M., Garzanti E., Molyneux S., Nawab A. & Sabouri J. (2009a) The Eo-Cimmerian (Late? Triassic) orogeny in North Iran. In Brunet M.-F., Wilmsen M. & Granath J.W. (Eds.) South Caspian, northern and central Iran sedimentary basins. Geological Society Special Publication, 312(1): 31-55.
- Zanchi A., Zanchetta S., Garzanti E., Balini M., Berra F., Mattei M. & Muttoni G. (2009b) The Cimmerian evolution of the Nakhlak-Anarak area Central Iran and its bearing for the reconstruction of the historyof the Eurasian margin. Geological Society Special Publication, 312(1): 261-286.
- Zanchi A., Zanchetta S., Balini M. & Ghassemi M.R. (2016)

 Oblique convergence during the Cimmerian collision:
 Evidence from the Triassic Aghdarband Basin, NE Iran.
 Gondwana Research, 38: 149-170.
- Zhou T.S. & Zhou H.Q. (1983) Triassic nonmarine strata and flora of China. *Bulletin of Chinese Academy of Geological Sciences*, 5: 95-110.