



Two fossilized swamps containing in situ Sphenophyta stems, rhizomes, and root systems from the Middle Jurassic Hojedk Formation, Kerman area (Iran)

Hadis Khalilizadeh¹ · Ali Reza Ashouri² · Abbas Ghaderi³ · Maria Barbacka^{4,5}

Received: 27 July 2021 / Revised: 17 February 2022 / Accepted: 28 February 2022
© The Author(s), under exclusive licence to Senckenberg Gesellschaft für Naturforschung 2022

Abstract

Sphenophytes often occur in wet environments; examples include the many extant equisetaleans that grow along streams, lake banks, and marshes. In the northern part of Kerman Province in Central Iran, in sandstone beds of the Middle Jurassic Hojedk Formation, there are two wetland sites, Swamp 1 and Swamp 2, separated by ~160 m along the sequence. Large numbers of in situ stems of sphenophytes were recorded there. They are preserved as casts, with imprints of the external cortex and/or vascular bundles of the internal cylinder. The stems belonged to one genus, *Neocalamites*, represented by three morphotypes. In Swamp 1, all the stems are large, ~120–220 mm in diameter, and of arborescent habit, while in Swamp 2, they do not exceed 20 mm in diameter. Swamp 2 contains two stem morphotypes that significantly differ in the number of vascular bundle traces. Such a type of Sphenophyta stem found in situ has not been reported from other regions of Iran or other parts of the world. The deposits of both swamps indicate a meandering river system. The observed Sphenophyta colonies and trace fossils found in the same bed may indicate undisturbed life conditions occurring after cessation of environmental stress.

Keywords Fossilized swamp · Sphenophytes · Middle Jurassic · Hojedk formation · Kerman · Central Iran

Introduction

The first record of plant fossils (sphenophytes) from the Hojedk Formation in the study area (“Dogger, Bathonian–Callovian”) was given by Huckriede et al. (1962), who mentioned, among several other taxa, *Equisetites* sp.; the Middle Jurassic flora of Kerman was reported much

earlier (Tipper 1921). More recently, plant fossils of the Hojedk Formation in the Tabas Block were studied by Vaez-Javadi (2014, 2018) and treated in their palynological/ palaeobotanical aspects by Badihagh et al. (2019). Reports of sphenophytes in Iran were given by Kilpper (1964) and Barnard (1965), who determined some remains as *Neocalamites hoerensis* (Schimper) Halle and *Neocalamites* cf. *carrerei* (Zeiller) Halle from the Alborz Mountains in northern Iran (Shemshak Formation). The Shemshak Formation was first defined by Assereto (1966) and later gained Group status (Fürsich et al. 2009). Later, other authors reported the same and some different species of *Neocalamites* (Assereto et al. 1968; Corsin and Stampfli 1977; Fakhr 1977; Sadovnikov 1976). Some species of *Equisetites* (*Equisetum*) have also been described, mainly by Kilpper (1964) and Sadovnikov (1976, 1984). Lastly, Schweitzer et al. (1997) made detailed revisions of floras from Iran, considering all earlier-described species, which resulted in the retaining of three taxa of *Neocalamites* [*Neocalamites ishpustensis* Jacob et Shukla, *Neocalamites* cf. *meriani* (Brongniart) Halle, *Neocalamites* sp.] and seven species of *Equisetites* [*Equisetites arenaceus* (Jaeger) Schenk, *Equisetites conicus* Sternberg, *Equisetites eurasiaticus*

✉ Ali Reza Ashouri
ashouri@um.ac.ir

✉ Abbas Ghaderi
aghaderi@um.ac.ir

¹ Department of Geology, Faculty of Science, Ferdowsi University of Mashhad, Post Box. 9177948974, Mashhad, Iran

² Department of Geology, Faculty of Science, Ferdowsi University of Mashhad, Post Box. 9177948974, Mashhad, Iran

³ Department of Geology, Faculty of Science, Ferdowsi University of Mashhad, Post Box. 9177948974, Mashhad, Iran

⁴ W. Szafer Institute of Botany, Polish Academy of Sciences, ul. Lubicz 46, 31-512 Kraków, Poland

⁵ Hungarian Natural History Museum, Botanical Department, P.O. Box 137, Budapest 1431, Hungary

Schweitzer et al. *Equisetites laevis* Halle, *Equisetites columnaris* (Brongniart) Phillips, *Equisetites beanii* (Bunbury) Seward, *Equisetites ferganensis* Seward]. In Iran, remains of *Neocalamites* have been reported from lower Mesozoic strata (Norian–Rhaetian) in Kerman (Central Iran); most of the studied specimens were poorly preserved or too small to be identified precisely (Schweitzer et al. 1997). Species of *Neocalamites* confirmed by Schweitzer et al. (1997) originate from the Kerman region (Vaez-Javadi and Mirzaei-Ataabadi 2006). From the Hojedk Formation in Pabdana, four new equisetalean species, (*Equisetites pabdanaei* Ameri, Khalilizade and Zamani, *Equisetites sparseii* Ameri, Khalilizade and Zamani, *Equisetites hojedkii* Ameri, Khalilizade and Zamani, *Equisetites irregularii* Ameri, Khalilizade and Zamani) were reported by Ameri et al. (2014). Among the relatively large number of sphenophytes reported in Alborz and Central Iran, none have been found in situ, particularly in such an extensive colony.

Neocalamites is a fossil genus common from the late Permian to the Jurassic but prevalent in the Middle to Late Triassic, being a typical element of plant assemblages in many parts of the world (Shuqin et al. 2012). A significant reduction of equisetaleans was noticeable during the Jurassic, and only one phylogenetic line reached the Cenozoic. The generic difference between *Neocalamites* and *Equisetites* has been discussed; they belong to one evolutionary lineage (Elgorriaga et al. 2015). The giant Mesozoic stems of sphenophytes belong to *Equisetites arenaceus*, with a stem diameter of ~250 mm (Pott et al. 2008), and *Neocalamites* sp. from the Upper Triassic of western Colorado, with a stem diameter of ~300 mm (Holt 1947). Many localities containing plant fossils are known in the Kerman region, but the remains have not been studied so far due to the remoteness and inaccessibility of the Deh-Sheikh area.

Most Mesozoic sphenophytes are still poorly understood because of their apparently uniform vegetative morphology, the overall scarcity of detailed anatomical information, and the rarity of finds of reproductive structures (Bomfleur et al. 2013). Their life strategy is similar to that of recent horsetails, but fossil evidence confirming their actual habitat has not been so clear. This paper is the first report of Jurassic sphenophytes found in situ (including stems attached to rhizomes) in a relatively large accumulation from the Hojedk Formation (lower Bajocian) in Kerman Province, Central Iran. For the first time, Sphenophyta colonies are described along with their environment, adding to our knowledge of the palaeoecology of Jurassic horsetails. The character of this assemblage supports its association with a stable environment, confirmed by trace fossils; similar assemblages can be used as indicators of a specific type of palaeoenvironment (Naugolnykh and Mitta 2016).

Geological setting

The Upper Triassic to Middle Jurassic strata in northern and Central Iran are terrigenous and consist mainly of shale and sandstone (Ghorbani 2013). Continental sequences in the Kerman–Tabas Coal Basin vary significantly in thickness from a few meters to over 1000 m. The sequence is known as the Shemshak Group and includes the Nayband (Upper Triassic), Ab-e-Haji, Badamu (Tuarcian–Aalenian), and Hojedk formations (Middle Jurassic) (Huckriede et al. 1962; Aghanabati 1977; Fürsich et al. 2005, 2009; Wilmsen et al. 2009a). This Jurassic part of the Shemshak Group (Badamu Formation) was combined in the Ab-e-Haji Subgroup by Seyed-Emami et al. (2020). Hettangian–Sinemurian sediments in the foreland basin of a shallow continental marsh were deposited under the same conditions, forming coherent and homogeneous facies (Aghanabati 2006) of sand, silt, shale, and coal, with plant fossils. They belong to the Shemshak Group, extending from the Alborz to Central and eastern Iran (Stöcklin and Setudehnia 1971; Fürsich et al. 2009). Middle Jurassic strata (Bajocian) with alluvial, river, floodplain, wetland, and lake facies are known as the Hojedk Formation. The Hojedk Formation was named in 1964 by the Stratigraphic Names Committee of Iran (Stöcklin and Setudehnia 1971). It is separated by the Badamu (Limestone) Formation from the Lower Jurassic coal-bearing unit, i.e. the Ab-e-Haji Formation (Salehi et al. 2018). The overlying Badamu Formation comprises fossiliferous limestone and marl, including ammonites and bivalves in Kerman (Seyed-Emami 1971). The Badamu Formation is followed conformably by a thick, greyish siliciclastic succession (Hojedk Formation) containing the most workable coal seams of the Tabas Block. The marine influence increases towards the east, especially on the Lut Block (Wilmsen et al. 2009b). Based on the ammonite record of the underlying and overlying formations (Badamu and Parvadeh, respectively) the Hojedk Formation is dated early Bajocian to the earliest late Bajocian. (Seyed-Emami et al. 2020).

The Hojedk Formation (lower Middle Jurassic) is formed mainly by siliciclastic and rarely carbonate rocks (base unit) and is located in the Zarand region in the northwest part of Kerman province. Its thickness reaches ~1000 m along the Kuhbanan Fault. The Hojedk Formation is divided into three parts based on differences in lithology and facies. The lower part of this formation, with bioturbated ferruginous quartz arenite, litharnite, *feldspatic litharenite*, and shale facies, was deposited in lagoonal and beach environments. In the middle part of the Hojedk Formation, subchert arenite, fossiliferous phyllarenite, rarely bioclastic grainstone, and shale/mudstone facies represent a river-deltaic environment. With micritic quartz arenite facies, the upper part was deposited in a meandering river environment (Lasemi and Kheradmand 1999). The high thickness of the Hojedk Formation (More than 700 m (is related to land subsidence. Salehi et al. (2018) provided the subsidence curve to show the vertical

movement history of the southern Tabas Block sedimentary basin since the Early Jurassic. Accordingly, this part of the basin subsided along with block faulting from the Early Jurassic. The subsidence curves show a relatively high and rapid subsidence rate in the Early Jurassic that confirms the onset of extension in this time. In addition, the subsidence rates in the western part of southern Tabas Block (Ravar–Abkuh, and Zarand) was decreasing towards the east (Zarand–Eshkeli). During Toarcian–Aalenian ages, the tectonic subsidence rate was lower as the curves flattened in this interval. Finally, in the early Bajocian, when the Hojedk Formation strata were deposited, the subsidence rate dramatically increased again in the run-up to the Mid-Cimmerian Event.

The northern part of Kerman Province is one of the wealthiest regions in Iran for surveying plant fossils; more than 80 taxa have been reported from this area. The best sedimentary succession containing these plant fossils is the Hojedk Formation, and the outcrop of this formation near the village of Deh-Sheikh, 143 km north of Kerman, is very rich in these fossils (Fig. 1). The studied fossil stems preserved in the sandstone beds are located in the mid-upper part of the formation (deltaic–meandering river environment) of the Middle Jurassic (lower Bajocian, Vaez-Javadi 2018) (Fig. 2). The lithofacies of the Hojedk Formation in the Deh-Sheikh area are divided into three groups: conglomerate, sandstone, and mudstone. Fine to medium-grained sandstones with rippled sandstone facies are most widespread in the study area (Fig.

3a, b). The sorting and rounding of the grains are relatively advanced and show high textural maturity. Current linguoid ripple marks (Fig. 3d) represent the effects of unidirectional flows in river deposits (Allen 1963). The upward-fining of the whole continental succession from an alluvial fan to a meandering river system can be explained by a continuous sea-level rise and by contemporary degradation of the relief in the source area (Kędzior and Popa 2013). The dominance of coarse-grained deposits demonstrates a braided fluvial system within the whole section and by the lesser content of overbank fines (Kędzior and Popa 2018). The study area is commonly shown by the dominance of fine-grained deposits within the whole section, suggesting a meandering system. A low lateral extension of wedge-shaped or lenticular sandstone facies occurring at small intervals in the form of fining-upward cycles reflects the influence of point-bar depositional processes (Fig. 3c). According to Vaez-Javadi (2018), the floral gradient score of this area is 52.93. A comparison chart of floral gradients of other localities in Iran has been established in which the average scores of North Kouchekali, Mazino, Calshaneh, Jafar-Abad (Tabas Block), Rudbarak, Baladeh, Bazehowz (Alborz Mountains), and Kerman Basin are 56.2, 53.5, 58.5, 58.5, 63.4, 60.38, 53.57, and 62.1, respectively. Since the floral gradient scores are in the middle part of the Rees et al. (2000) table, it is concluded that the Tabas Block and Kerman Basin were located in the warm temperate biome. The floral gradient of the study area is 63.4 and is comparable to Baladeh (Alborz), Rudbarak, and Jafarabad (Tabas) areas.

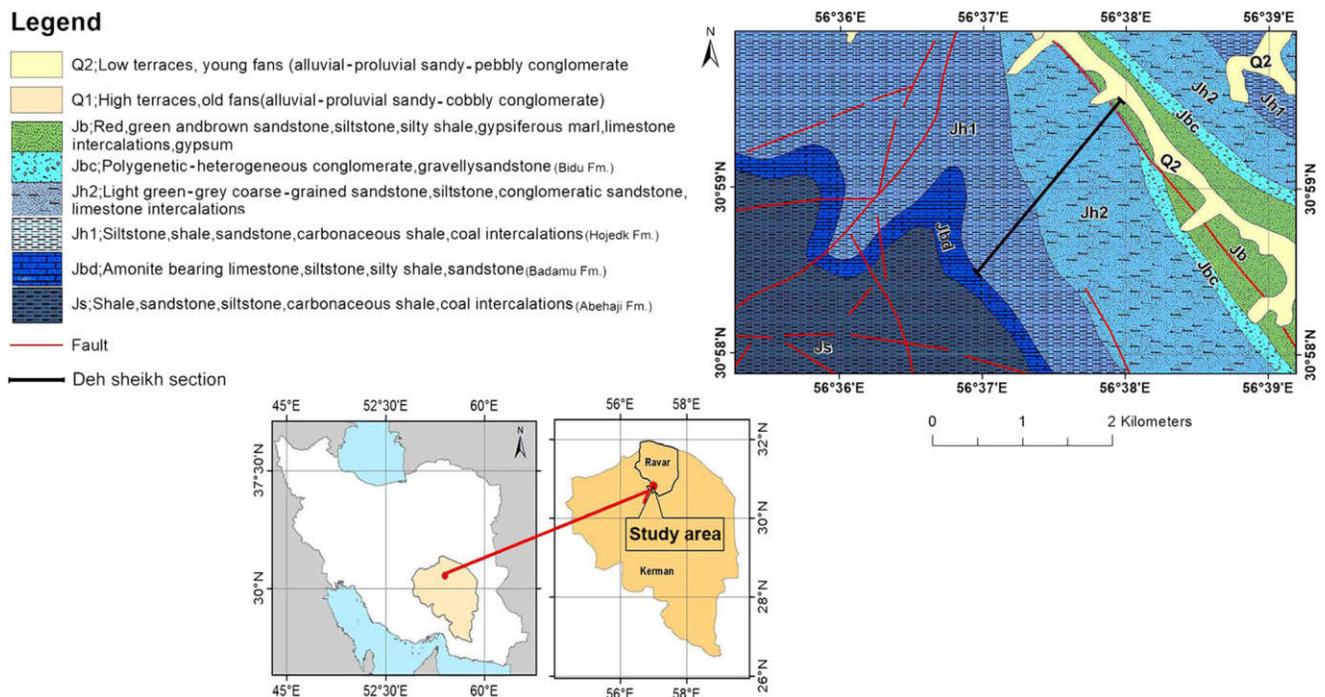


Fig. 1 Geological map of northern Kerman province, showing the position of the Deh-Sheikh section

Fig. 2 Vertical distribution of plant fossils and ichnofossils through the Hojedk Formation in the Deh-Sheikh section

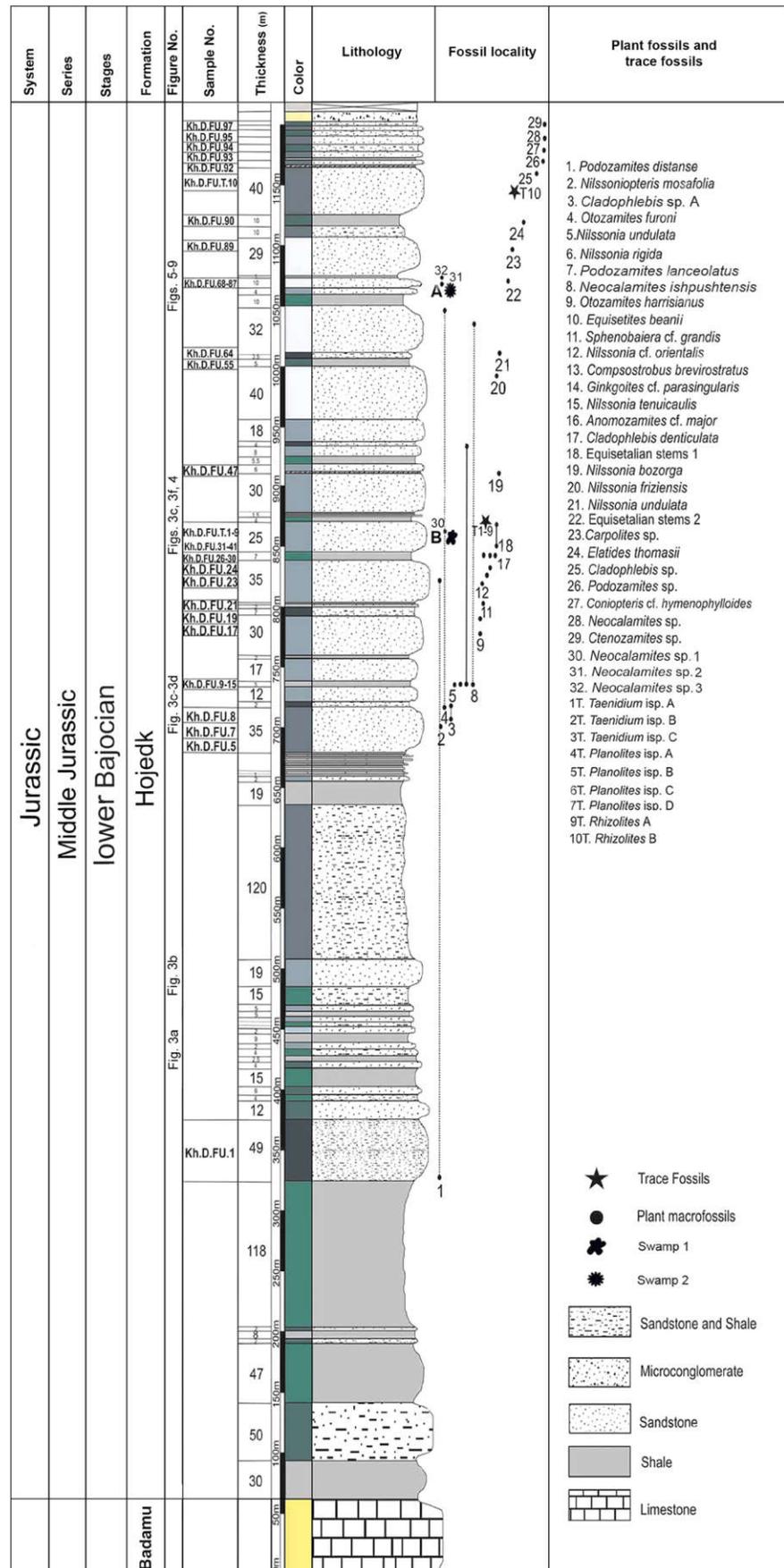




Fig. 3 Lithofacies and petrographic features of the Deh-Sheikh section. **a,b** Phyllarenite and feldspathic litearenite or feldspathic phyllarenite **c** Linguoid ripple marks represent the effects of unidirectional flows in river deposits **d** Lenticular cross-bedding structure at the base of upward-fining

cycles indicates channel-filling and decreasing energy **e** In situ Sphenophyta stems in the Hojedk Formation, large numbers of stems (12 adjacent stems indicated by black arrows) in cross-sections of beds. **f** Parts of mature plants and relatively robust stems

Locality, material, and methods

Two sites of fossil plants are located in the Deh-Narion Valley near Deh-Sheikh village, known as the Deh-Sheikh Geosite. The two sites are separated by ~160 m along the stratigraphic sequence (Fig. 2). The in situ Sphenophyta stems are preserved in hard, sandy, and silicified beds; it was difficult to access and isolate them, so our data are based on some specimens only. Most stems are embedded in the host rock, with only their surfaces observable. Large stems visible on the surface were damaged by erosion and tectonic effects and required removing rock to access them. Most observations were made in the field and were documented by photographs taken there. Some specimens were isolated from the rock and transferred to the laboratory for study. To separate the stem fragments from the beds, we used drills, hammers, and chisels. Stems and rhizomes were cleaned by removing the sediment using the chisel. Morphological details were observed using lenses and microscopes. Photographs were taken with a Nikon D 90 digital camera and schematically drawn using standard graphics software (Adobe Photoshop CS5). Specimens are stored in the Geology Museum, Faculty of Science, Ferdowsi University of Mashhad, Iran. Fifty specimens are labelled Kh.D.FU followed by consecutive specimen numbers. Distance from the bottom of the section is indicated for all specimens.

Systematic palaeontology; sites and material in situ

Swamp 1

This swamp is represented by a hard light-grey sandstone bed of quartz arenite, 25 m thick, with traces of wavy ripple marks visible on the lower bedding plane. This bed is located 726 m above the base of the Hojedk Formation (Fig. 2). Due to the thickness of the bed erosion and tectonics, which severely damaged the fossils, only a few stems were available for more detailed study. Stems are visible in large numbers across the beds (Fig. 3e, f). More than 12 specimens are exposed on a 3×3 m surface, all having almost the same diameter (~150–220 mm), suggesting that they were mature plants and had relatively robust stems (Figs. 3e, f, 4a, b). In addition to these 12 stems forming a compact group, a ~1 km² area of this bed is covered by a large number of widely scattered stems (Fig. 3e, f). Unfortunately, we could not access the root systems belonging to these stems.

Division Pteridophyta

Phylum (Equisetophyta Sinnott 1930) Sphenophytes

Class Equisetopsida Agardh, 1825

Equisetales Dumort, 1829

Family incertae sedis

Genus *Neocalamites* Halle 1908

Neocalamites sp. 1

(Figs. 3e, 3f, 4)

Material: Twelve specimens in situ in resistant sandstone (Deh-Narion Valley, Deh-Sheikh). Three of them, suitable for examination, are numbered. The described specimens are preserved in the sandstone as casts, with only ~100 mm of their length exposed. The full length of the plants cannot be estimated, but nodes and internodes are visible.

Hand specimens (all in situ): Kh.D.FU.31 (723 m), Kh.D.FU.38 (721 m), Kh.D.FU.41 (726 m);

Locality and horizon: Deh-Sheikh section; 726 m from the base of the Hojedk Formation and 171.5 m below Swamp 2 (Equisetlean Stem locality 2).

Description: Stems straight and cylindrical. At least 3 nodes and 3 internodes visible. Internodes 40 mm long, with clearly distinct grooves and ribs on surface. Grooves 7 mm deep, ribs prominent, 4 mm thick, at 10 mm intervals. Ribs alternate on two sides of node. Vascular bundles densely arranged (8–9.1 cm) at regular intervals of 1 mm, 3–4 vascular bundles seen on each rib. Node prominent and ~10 mm wider than internode. Leaf scars well-preserved and regular, sunken, circular to slightly horizontally oval, ~1 mm in diameter, each circle situated between vascular bundles, quite compact, visible as three concentric circles.

Hand specimen Kh.D.FU.41 is a stem fragment and is much better preserved than the other specimens (Fig. 4c, d): fragment length 190 mm, width 120 mm, 2 nodes and 3 internodes visible, internodes 40 mm long. Inner surface of outer cortex preserved with ribs and imprints of internal cylinder vascular bundles. Grooves and ribs prominent, 4 mm wide, sunken 7 mm into stem at regular intervals of 10 mm. Ribs subopposite to alternate on the two sides of node. Vascular bundles densely arranged (8–9/cm) at regular intervals of 1 mm, 0.25 mm thick, gradually narrowing from node to internodes. Most relief visible at ~10 mm from top of internode and reaching bottom of node. Node prominent, extent ~10 mm. Vascular bundles opposite both sides of node. Leaf scars well preserved and regular, in contact with each other, circular to slightly horizontal oval, ~1 mm in diameter, each circle situated between vascular bundles, quite compact, visible as three concentric circles. Leaves not preserved.

Specimen Kh.D.FU.31 is a robust stem, ± cylindrical, with internal diameter of 180 mm and external diameter of 220 mm. Visible internode 80 mm long. Traces of ribs of external cortex poorly preserved but visible, opposite both sides of node, distance between ribs almost the same, ~10 mm. Density of vascular bundles of internal cylinder 6/cm, spaced 1.6 mm apart. In one well preserved part of stem, 60 vascular bundles visible, their total number estimated at 240. Node ~5 mm thick. No trace of leaves observed, diaphragm flat.

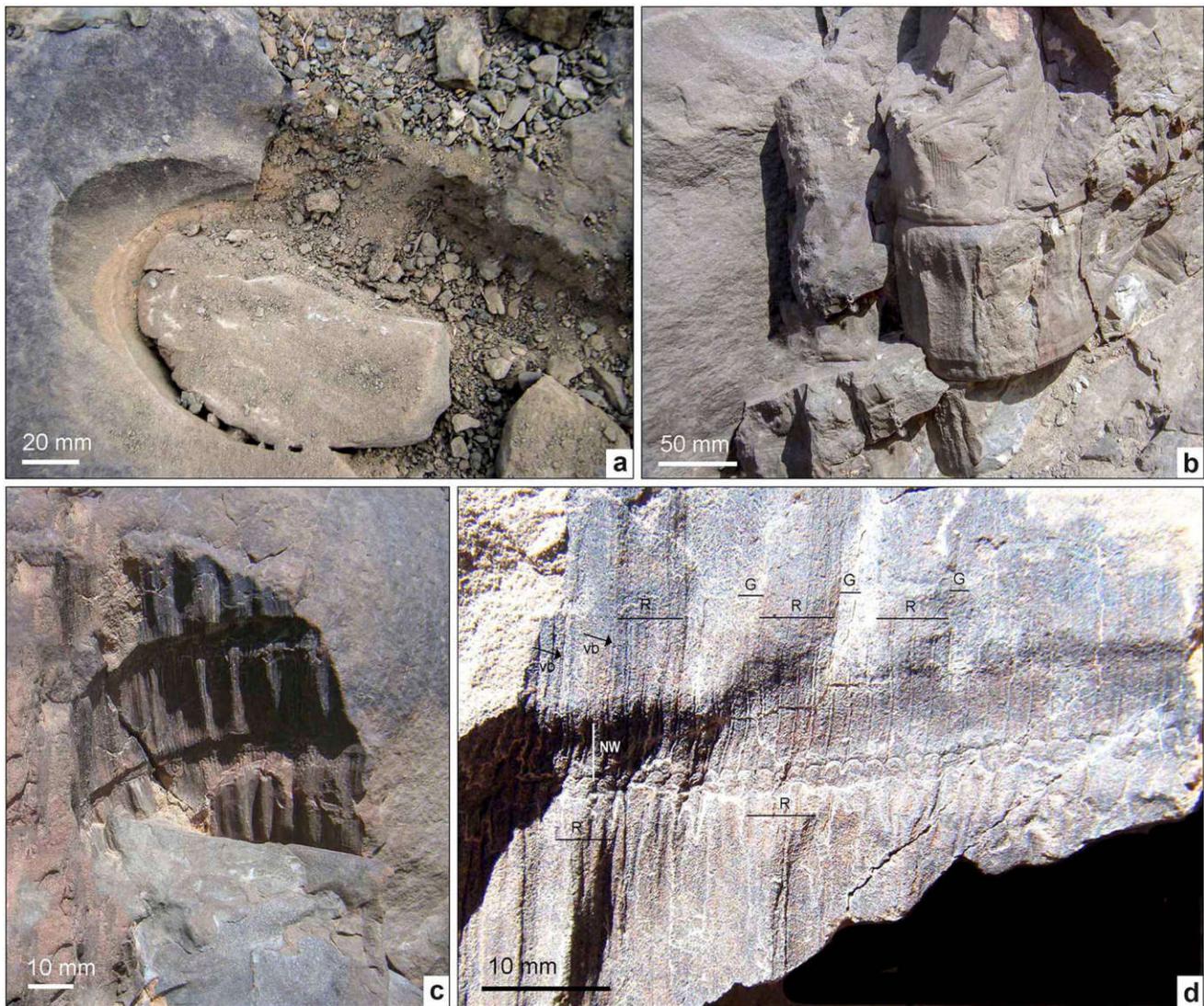


Fig. 4 In situ Sphenophyta stems (Swamp 2) in the Hojedk Formation. **a, b** Parts of mature plants and relatively robust stems. **c, d** Specimen Kh.D.FU.41: part of the stem, preserved much better than other specimens, leaf scars visible. *R* Ribs, *G* Grooves, *Vb* vascular bundles, *Nw* Node width

Specimen Kh.D.FU.38 closely resembles specimen Kh.D.FU.31 in internode length (80–90 mm), width (8 mm), and vascular bundle density (6/cm). Differences are seen in rib density: 1/cm in specimen Kh.D.FU.31 and 1/3 cm in specimen Kh.D.FU.38 (Fig. 4a, b). All three specimens show similar vascular bundle density. Unfortunately, the two figured specimens, Kh.D.FU.31 (Fig. 4d) and Kh.D.FU.38 (Fig. 4a), have poorly preserved leaf scars, so their shape is unknown and not comparable. Internode length slightly differs (80 mm in Kh.D.FU.31, 90 mm in Kh.D.FU.38); internode diameter varies as well (220 mm in Kh.D.FU.31, 120 mm in Kh.D.FU.38).

Discussion: The stems are of equisetalean type, possibly *Neocalamites* because of the characteristic leaf scars. In overall shape, diameter and dimensions correspond to specimens

reported by Naugolnykh and Mitta (2016) from the North Caucasus region of Russia, but the diaphragm, node, and vascular bundles are different. The equisetalean diaphragm reported from the Caucasus shows radial filaments, while our specimen's diaphragm surface is flat. In the Caucasus specimens, the nodes are unclear, whereas in the studied specimen, they are distinct and expanded, and the vascular bundles are thicker and denser.

The studied stems are narrower (diameter 110–120 mm), while the Caucasian stems' diameter was 110–200 mm. The Caucasian and the studied specimens show almost identical internode lengths (89 and 90 mm, respectively). They differ in the number and width of ribs and vascular bundles. This is a significant difference and we regard it as of diagnostic importance, following Jarzynka and Pacyna (2015).

The largest in situ *Neocalamites* stems, measuring ~300 mm in diameter, have been reported from the Upper Triassic of western Colorado (Holt 1947). The largest specimen we studied measured ~220 mm. Stem size is not a diagnostic character, but node shape and vascular bundle density differ between the Colorado specimen and ours. Unfortunately, a complete comparison cannot be made because the specimen from Colorado does not have more details preserved. Our specimens are similar to *N. ishpushtensis* and *N. lehmannianus* in leaf scar form and size, but they differ in leaf scar density and number. The compact form of the leaf scar in our material is also similar to that seen in *N. muratae*, but the leaf scars in *N. muratae* are larger than in ours (3 mm versus 1.3–1.5 mm in diameter (Enzo 1973).

Stratigraphic range: *Equisetites* Sandstone; 106 m below the *Nilssonia friziensis* horizon and 210 m below the *Elatides thomasi* horizon (Hojedk Formation, lower Bajocian).

Swamp 2

This is a relatively large area containing stems and rhizomes. A bed of light-coloured sandstone is ~10 m long and 45 cm thick and lies 1060 m above the base of the Hojedk Formation (Fig. 2). Erosion has exposed large parts of the swamp with stems and rhizomes. The primary swamp was much more extensive (exact extent unknown), and it seems that the plants had formed significant accumulations in their lifetime. The stems from this bed are much smaller in diameter (~10–20 mm) than the stems from Swamp 1. At first sight, the embedded stems look like dense cavities on the bed surface, with ~60–70 cavities/m² (Fig. 5a). The stems are partly visible, embedded in rock, and in some, the inner surface of the cortex is exposed (Fig. 7c). Some segments could be separated because the bed is relatively low in thickness. After transfer to the laboratory and separation from the rock, we could observe a complex root system. In this bed, we noted bioturbation effects and ichnofossils, including *Treptichnus aporum* Rindsberg and Kopaska-Merkel 2005 and Rhizoliths, the fossilized root tracks (Figs. 8, 9) caused by the burrowing of some organisms living and/or feeding in the swamp.

Neocalamites sp. 2
(Figs. 6, 7a)

Material: Sixty specimens were observed in situ. The described specimen (prepared) is fairly complete, with a rhizome and two aerial shoots, one of which has a lateral branch and is not compressed, showing the whole diameter. This is one of the most complete equisetalean stem specimens found in situ and attached to the rhizome.

Hand specimen: Kh.D.FU.70.

Locality and horizon: Deh-Sheikh section; 897 m above the base of the Hojedk Formation and 171.5 m above Swamp 1 (Equisetalian Stem locality 1).

Description aerial organs: Length of stem connected to rhizome ~130 mm. Some other fragments broken on the surface. Full-length specimens not known; based on stem diameter, inferred to be rather small. Two aerial shoots arise from rhizome 80 mm apart (Figs. 7a, 10). Lateral branch 22 mm long, rather poorly preserved; 2 incomplete leaf whorls visible (Fig. 6a, b). Stem 10 mm wide, at least 2 nodes visible but not prominent. Internode length 42 mm, internode length/width ratio 42/10=4.2. Ribs of the external cortex and vascular bundles of internal vascular cylinder well visible: 5 ribs and 41 internal vascular bundles at a density of 41/cm. Ribs and vascular bundles opposite on both sides of the node. Node 2 mm thick, not extended. Leaf scars preserved extremely poorly, but their triangular shape and position observable with a magnifying lens. Each scar corresponds to one vascular bundle (Figs. 6d, 11). In one stem, 36 well preserved leaf fragments 1 mm wide visible.

Description subterranean organs: Rhizome fragment 320 mm long, width varies along rhizome from 7 mm at join with aerial stem to 12 mm at some distance from it (Figs. 6e, 7a). At least 4 nodes and 3 internodes of various lengths visible: 55 mm, 45 mm, and 40 mm, length decreasing along rhizome from the base of aerial organs (Fig. 6e). Two large prominences in the nodal region visible, interpretable as rhizome scars according to Schweitzer et al. (1997). Roots interwoven along with rhizoids 30 mm long; each branched 2 or more times.

Discussion: The stem diameter of this specimen corresponds with that of *Equisetites muensteri*, which has stem diameter of 20 mm (Schweitzer et al. 1997). However, they differ in vascular bundle density, 24/cm in *E. muensteri* versus 41/cm in our specimen, and in internode length, 24 mm versus 42 mm. The form of our stems, with uniform node diameter and internodes, resembles *N. ishpushtensis* (Schweitzer et al. 1997), but that taxon differs in the number of grooves (5) and ribs (6), with 0.6 mm distance between ribs. Internode length in *N. ishpushtensis* is 25 mm, and the leaf scars are circular. Stem thickness in *N. carrei* is almost of the same, 21 mm, but it has 35 ribs and more prominent nodes (Schweitzer et al. 1997). Its rounded leaf scars (Kimura et al. 1982) also differ from the triangular scars of our specimen. Our material is most similar to *N. muratae*, in which the cylinder-like stem is 32 mm wide, but without the effect of compression, the real stem diameter was 20 mm. The outer surface of *N. muratae* is smooth at the node, and the internode length is ~60 mm.

Stratigraphic range: *Equisetites* Sandstone; 110 m below the *Coniopteris* cf. *hymenophylloides* horizon and 40 m below the *Elatides thomasi* horizon (Hojedk Formation, lower Bajocian).

Fig. 5 **a** General view of a fossiliferous bed whose surface appears to be covered by 60–70 cavities. **b** poor remnants of leaves were observed



Neocalamites sp. 3
(Figs. 7b, d, 12)

Material: Ten specimens in situ.

Hand specimens: Kh.D.FU.78, Kh.D.FU.82. (898 m)

Locality and horizon: Deh-Sheikh section; 898 m above the base of the Hojedk Formation and 172.5 m above Swamp 1 (Equisetian Stem locality 1).

Description: Specimen Kh.D.FU78 preserved as an impression (Fig. 7b). Stem fragment length 250 mm, width 12 mm. Node slightly wider, reaching ~14 mm. Three internodes and two nodes observed. Internode length 82 mm. Ten ribs

opposite on both sides of 2 mm thick node. Due to poor preservation, leaf scars not observed.

Specimen Kh.D.FU.82. Part of stem with recognisable vascular bundles, node, and lateral branch. Stem diameter 14 mm, length of preserved fragment 25 mm, vascular bundle density 19–21/cm. Total number of leaves unknown because only 10 preserved (Fig. 7d), but estimated at 20–21. Scars nearly circular 2.5 mm in diameter. Two nodes preserved, 2 mm thick, lateral extent ~2 mm. At least two lateral branches connected to stem (Fig. 12); 3–4 longitudinal grooves visible on their surface. Six vascular bundles on one of the lateral branches. Branch thickens towards distal end, maximum

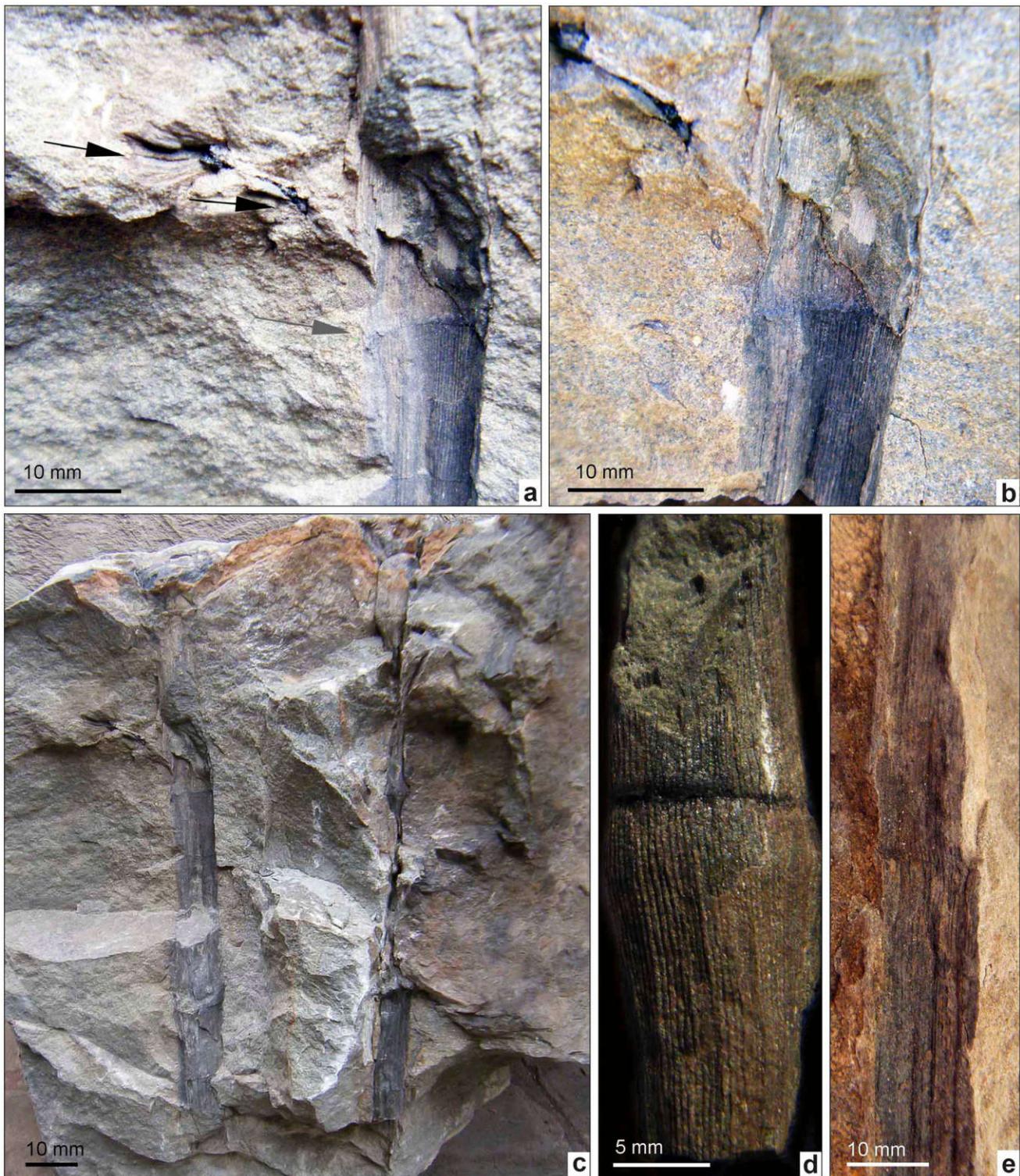


Fig. 6 Aerial organs of in situ equisetalean stem in the Hojedk Formation (Swamp 2). (Kh.D.FU.70): **a, b** One aerial stem with a node (grey arrows) and lateral branch (black arrows indicate two whorls; **c** Two aerial shoots arise from the rhizome 80 mm apart; **d** Triangular scar of the leaf with

diameter 4 mm. Branch connected to stem at 85–90° angle. Inner vascular cylinder of stem almost smooth but external cortex striated (Fig. 12).

very poor preservation at the bottom of the node. **e** Detail of rhizome, showing that internode distance decreases with increased distance from aerial organs

Discussion: The number of ribs of the above specimens corresponds with those of *N. ishpustensis*, in which rib density is 11–12/cm (versus 10/cm), but internode length significantly

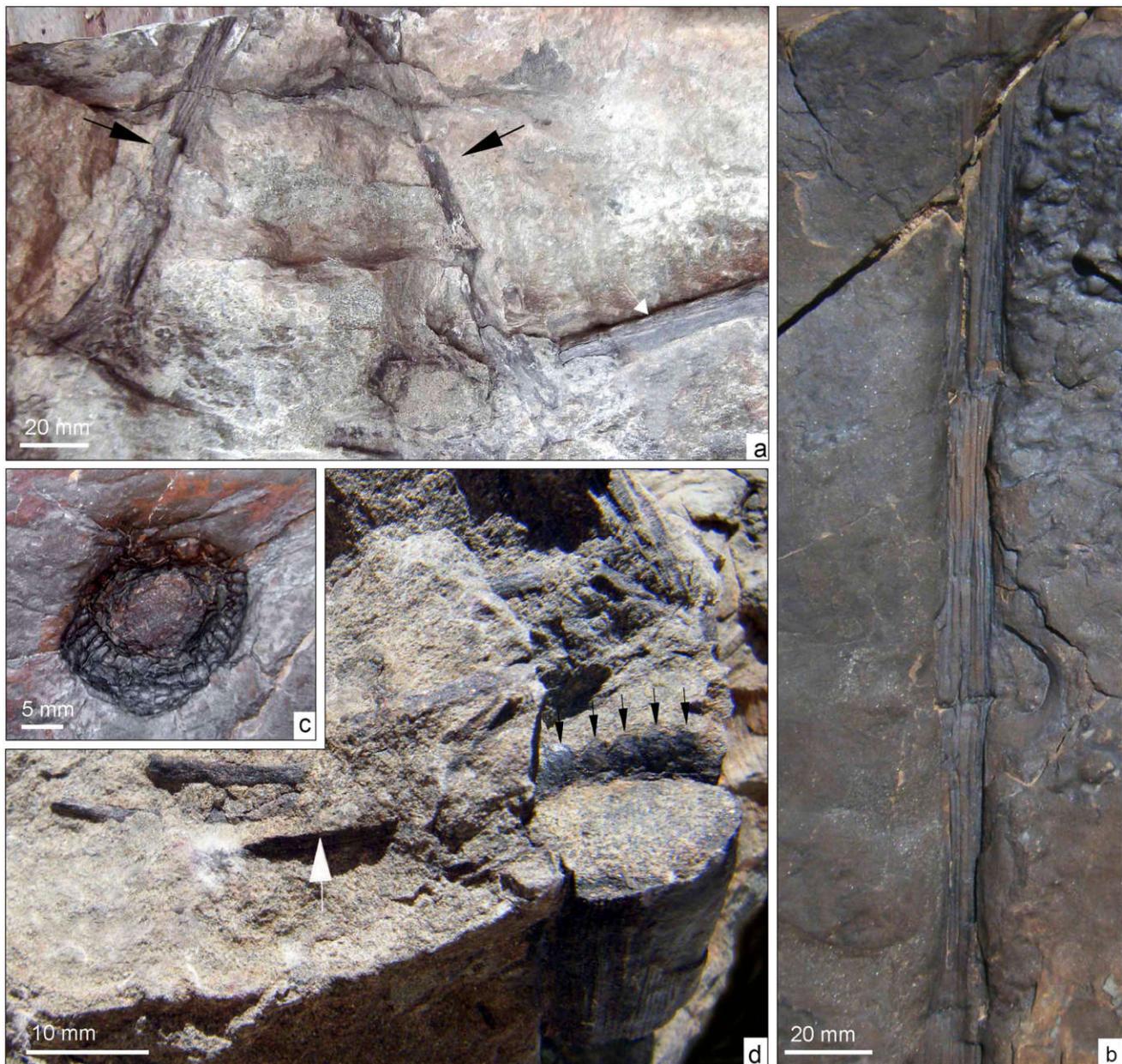


Fig. 7 **a** Two aerial shoots arise from the rhizome. Black arrows represent two aerial stems going upward from the rhizome (white arrow indicates rhizome); **b** Specimen Kh.D.FU.78: stem impression with three nodes

and four internodes. **c** Leaf-sheath around stems, easily countable. **d** Specimen Kh.D.FU.82: main (black arrows) and lateral stem (white arrow)

differs (in *N. ishpushtensis* 25 mm, against 82 mm in one of our specimens). Another difference is the node in *N. ishpushtensis*, which is not wider, while in our specimens, the node is ~2 mm wider than the internodes. The inner vascular cylinder of specimen Kh.D.FU.78 is similar to those of *Equisetites beanii*, described by Schweitzer et al. (1997). The differences are least in comparison with *N. hoerensis*, since the vascular bundle density is almost the same (in our specimen 10/cm, in *N. hoerensis* 12–20/cm), and internode length also fits in the same range (in our specimen 14–82 mm, in *N. hoerensis* more than 70 mm).

Stratigraphic range: *Equisetites* Sandstone; 109 m below the *Coniopteris* cf. *hymenophylloides* horizon and 39 m below the *Elatides thomasii* horizon (Hojedk Formation, lower Bajocian).

General remarks on taxonomy

Based on stem morphology, we assigned the sphenophytes found in Kerman to the genus *Neocalamites*. Stems of *Neocalamites* differ significantly from *Equisetites*, due to the

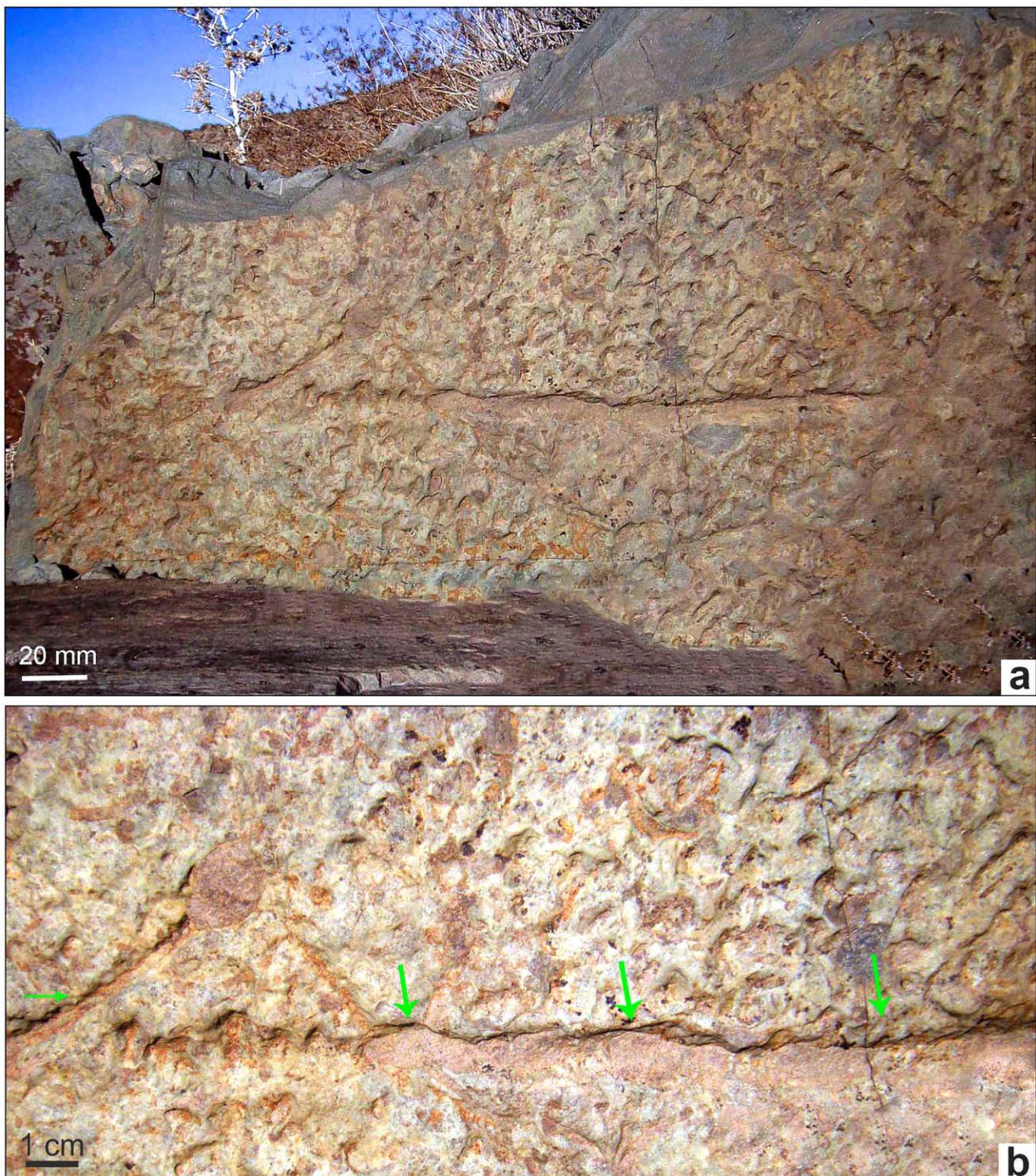


Fig. 8 **a** Ichnofossils from the Hojedk Formation (Swamp 2). *Treptichnus apsorum*, general view of the bed, **b** Magnified detail of *Treptichnus apsorum*

absence of the characteristic leaf sheaths that are usually preserved in *Equisetites*; instead, *Neocalamites* possess leaf scars on the nodes. *Neocalamites* may be confused with *Schizoneura*, although in *Neocalamites* the leaves are single-veined and entirely separate down to their base, as opposed to being fused in the sheath in *Schizoneura*. In *Schizoneura* the

number of leaves is considerably lower (by ‘at least half’) than the number of internode vascular bundles (Holmes 2001; Bomfleur et al. 2013). Also, the nodal area in *Schizoneura* is joined by a sizeable underground stem remnant of lateral root radiation and dome-shaped internal structure (Bomfleur et al. 2013). These all characters differ from those of our material.

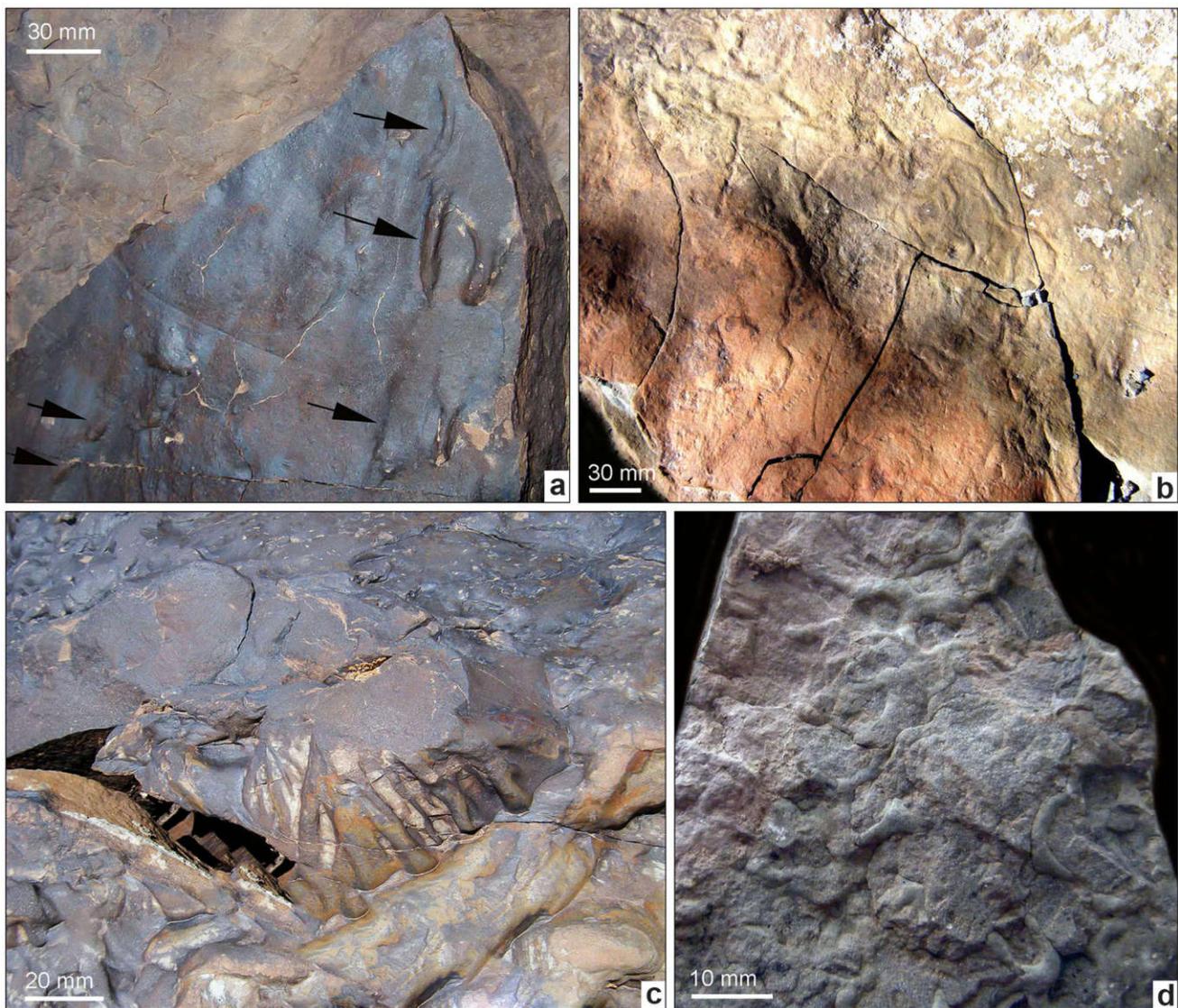


Fig. 9 Ichnofossils from the Hojedk Formation (Swamp 2). **a** undeterminable tunnel filling, **b** locomotion and feeding burrows, **c** Rhizoliths, **d** cylindrical burrows resembling the ichnogenus *Thalassinoides*

The problems in studying in situ specimens and the frequent loss of detail due to poor preservation in coarse-grained sedimentary beds often make it impossible to identify taxa accurately. Although stems and rhizomes were preserved in situ in a calm environment, leaves were not found. In fact, leaves or branches attached to neocalamitean stems are scarce due to their delicate and fragile attachment, a feature of recent forms. So possibly the event that buried the area together with the plants caused the loss of leaves, and the hardness of the recent host rock prevents finding detached fragments among the stems. The thick stems from Swamp 1 and the thin stems from Swamp 2 comprise two compact assemblages that differ significantly from each other. Based on the number of leaf scars or vascular bundles, the studied specimens represent three taxa, although they were not determined more exactly

(Table 1). Since the usual mode of growth of horsetail communities is clonal colonial, we assume that the number of taxa growing together in each of these two swamps was not much higher than what we saw. The community from Swamp 1 is mostly composed of one form (*Neocalamites* sp. 1) and Swamp 2 of two forms (*Neocalamites* sp. 2, *Neocalamites* sp. 3). These types were separated mainly by several vascular bundles (*Neocalamites* sp. 1, 6–9/cm, *Neocalamites* sp. 2, 41/cm, *Neocalamites* sp. 3, 19–21/cm) and leaf scar shape (circular-oval in *Neocalamites* sp. 1 and *Neocalamites* sp. 3, triangular in *Neocalamites* sp. 2). Other differences observed between specimens of particular taxa (e.g. internode length) were not significant and fit within natural intraspecific variability. Such uniformity is usual in colonies where plants spread mainly vegetatively.

Table 1 Comparison of biometric parameters in the studied specimens from the Hojedk Formation of the Kerman area

Hand specimen	length of internodes	width of internodes	width of nodes	shape of leaf scare	leaf scare density	leaf scare position	density of ribs	Ribs arrangement on both sides of the node	density of vascular bundles	Width of leaves
Kh.D.FU. 31.	80 mm	220 mm	5 mm	–	–	–	1/1 cm	opposite	6/1 cm	–
Kh.D.FU. 38.	90 mm	120 mm	8 mm	–	–	–	1/3 cm	opposite- sub opposite	6/1 cm	–
Kh.D.FU. 41.	40 mm	120 mm	1 mm	circular-slightly horizontal oval	8/1 cm	Under node	1/1 cm	alternate	8-9/1 cm	–
Kh.D.FU. 70.	40.2 mm	10 mm	2 mm	triangle shape	33/1 cm	Under node	5/1 cm	opposite	41/1 cm	–
Kh.D.FU. 78.	80.2 mm	10.2 mm	2 mm	–	–	–	9-10/1 cm	opposite	–	–
Kh.D.FU. 82.	10.4 mm	10.4 mm	2 mm	–	–	–	–	–	19-21/1 cm	20.5-30 mm

In situ Sphenophyta rhizomes were also reported from the Upper Triassic of Lunz, southern Austria, but these were single specimens, not a colony, and since they were not collected from the horizon, their palaeoecology was only inferred (Pott et al. 2008). In the case of the equisetalean stems from the Caucasus (Naugolnykh and Mitta 2016), their palaeoenvironment was evident and determined as nearshore shallows. This environment corresponded well with the gross morphology of the specimens.

Palaeoecology of horsetails

Horsetails are a particular group of vascular plants that survived from the Late Devonian up to recent times. Their high adaptability most probably enabled their persistence over a long time to a wide range of environmental conditions. As a group, they could live in very different, difficult, highly disturbed, or stressed (anoxic, metalliferous, saline, thermal spring) habitats (Husby 2013).

The survival power of horsetails lies in their life strategies, which are and were ecologically opportunistic, using their tolerance as a tool for survival in unfavourable conditions. They developed special anatomical features such as tubers, hydathodes, and ventilation systems (Husby 2013) or the whole unusual structure of Jurassic *Equisetum thermale* Channing, Zamuner, Edwards and Guido, Channing et al. 2011), and mechanisms facilitating extensive colonisation. First, they colonise mostly near-water ecotopes (Naugolnykh 2009) such as a stream or river banks or the margins of other water bodies. They also colonise disturbed places (Geertsema and Pojar 2007; Milner et al. 2007), damaged or newly created postvolcanic habitats (Siegel and Siegel 1982; Adams et al. 1987; Tsuyuzaki 1987, 1997; Coturel et al. 2016) or semi-arid conditions (Channing et al. 2011). The colonies are usually

clonal; this mode is often successful in settling new areas. In any case, an extensive rhizome and root system plays an important role in forming and expanding horsetail colonies. Horsetails structure and life tactics are very conservative, and the Mesozoic sphenophytes from the Iranian swamps had the same growth strategy.

The fossil record from the Hojedk Formation confirmed that the subterranean organs were relatively dense and extensive, forming a compact system (Fig. 10). The development of horizontally spread rhizomes in the ground ensured dominance and prevents the expansion of other plants via asexual reproduction (Kimura et al. 1982). The fragmentation of both the rhizomes and aerial stems allows new individuals and colonies to develop rapidly in highly disturbed conditions that would be lethal to other plants (Husby 2013). This is similar to the growth mode of recent ferns and certain angiosperms such as bamboo, but horsetails developed this mechanism further, as in recent *Equisetites arenaceus*, whose branches can be transported by water, creating a new colony elsewhere (Pott et al. 2008) and ensuring the growth of large numbers of new individuals (Rothwell et al. 1996). The rhizome system can be multi-story and can penetrate even 4 m deep in the soil (Husby 2013, with references), thus increasing the chance to reach the groundwater and nutrients in dry-surface areas and to survive extremely hard conditions such as damage to aboveground organs by wildfire or other factors (Husby 2013, with references).

In recent horsetails, aerial stems periodically branch from the rhizomes, reaching up to six feet (1.8 m) above the surface. In the *Equisetum* subgenus *Hippochaete*, the aerial branches are perennial, and any aerial branch can form reproductive organs. In other species of *Equisetum* the vegetative and reproductive branches are separate (Bold et al. 1987). It is thought that duplicated genes with functions enabling adaptation to be moist and disturbed habitats may have been

generated, allowing horsetails to specialise their physiology despite their overall remarkably stable morphology (Vanneste et al. 2015).

Extinct Sphenophyta, which included both herbaceous and arborescent forms, successfully dominated the vegetation during the Palaeozoic but became less diverse and more often took herbaceous forms during the Mesozoic; they also specialised in colonising disturbed and moist habitats (Husby 2013). The Late Triassic flora of the Quebrada de Los Fósiles Formation (Argentina), composed of potentially strategist taxa, stand out for their small size and their capacity for vegetative reproduction (especially the sphenopsids), allowing them to colonise new environments (Coturel et al. 2016) rapidly. The studied *Neocalamites* colonies, by analogy, probably developed in a stabilised post-stress habitat). As mentioned, the entire sphenophyte-covered swamp was much more extensive than the studied area. The occurrence of sphenophyte colonies in the swamps may be interpreted as colonisation after severe damage to the area (probably by flood) and suggests stabilisation of the environment, enabling such great vast expansion.

Based on studies conducted in the Jurassic successions of the Hojedk Formation (Tabas Block), the palynomorphs and parental flora indicate deposition in an oxygenated environment close to the shoreline in a deltaic system (Badighigh et al. 2019).

The size difference between the specimens from the two sites may be due to various factors: differences in population maturity and local conditions such as poorer nutrients, thinner soil, dry spells, and higher insolation. As the forms represent different taxa, the size difference may also be connected with their strategies: smaller taxa ensure faster colonisation of new territories after stressful environmental conditions.

Palaeoecology of invertebrate life tracks in the swamp

In Swamp 2, in the same bed as the fossil plants, 18 specimens with trace fossils were noted and are worth mentioning as an integral part of the swamp ecosystem at the same site as *Neocalamites*. Most of these trace fossils are tubular and cylindrical horizontal burrows preserved in full relief at the top of the bed. In most cases, they represent fodinichnia. One of them from Swamp 2 was determined as *Treptichnus apsorum* (Fig. 8). It is a horizontal, cylindrical, zigzag burrow with short side-protrusions. The burrow is ~ 10 mm in diameter and at least ~ 250 mm long, and the zigzag segments are 55–60 mm long. The longitudinal striae are not preserved. *T. apsorum* is produced by deposit feeders comparable in behaviour to recent arthropods, mainly dipteran larvae below the sediment surface (Uchman et al. 2005). Another trace fossil is represented by an undeterminable tunnel

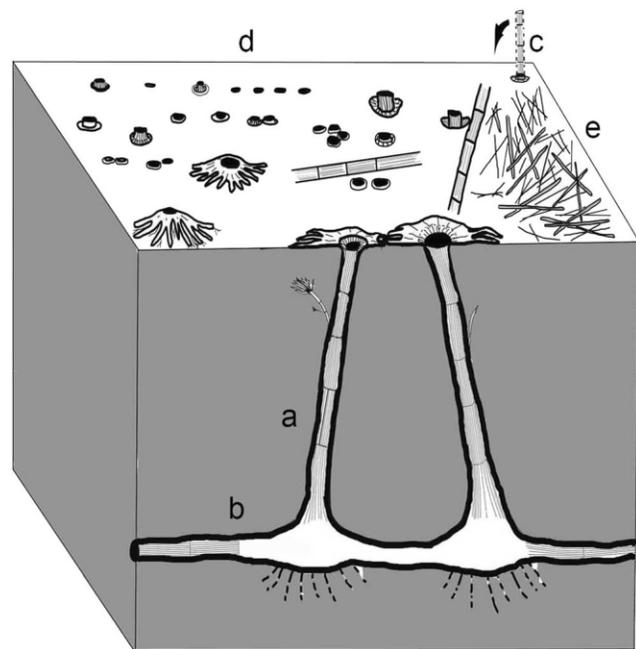


Fig. 10 Diagram of studied specimens, showing details. Specimen Kh.D.FU.70: Large area covered by stems and rhizomes (Swamp 2), showing root system; **a** Aerial stems, **b** Rhizome, rhizoid and root system, **c** Reconstruction of part of the stem in the habitat (pieces have fallen onto the bed surface), **d** Wide holes seen on the bed surface, along with stem sections inside the bed, **e** a large number of pinnules accumulating in one part of the bed surface

filling ~ 7.5 mm in diameter (Fig. 9a). It is preserved as a semi-relief, suggesting erosion caused by water flow. This confirms the periodic destabilisation of the environment. Another trace fossil from Swamp 2 is ~3.5 mm in diameter and shows a meandering course (Fig. 9b). It is probably a locomotion and feeding burrow, suggesting more stable conditions. Systematically branched cylindrical burrows resemble the ichnogenus *Thalassinoides* (Fig. 9d), which is basically a complete marine trace fossil but may occur in a marginal brackish, marine environment. This was an open burrow system used for a longer time by the trace maker. This suggests a stable environment. Environmental stabilisation is also indicated by rhizoliths, fossilised root traces found in the growing position (Fig. 9c).

Conclusion

1. The lower Middle Jurassic successions (lower Bajocian) north of Kerman (Central Iran) display alluvial, river, floodplain, wetland, and lake facies belonging to the Hojedk Formation. Based on lithofacies and petrography studies, ancient unimodal flow patterns reflect the impact of river flows on deposition. Point-bar cycles indicate channel-filling and decreasing energy (Figs. 3d).

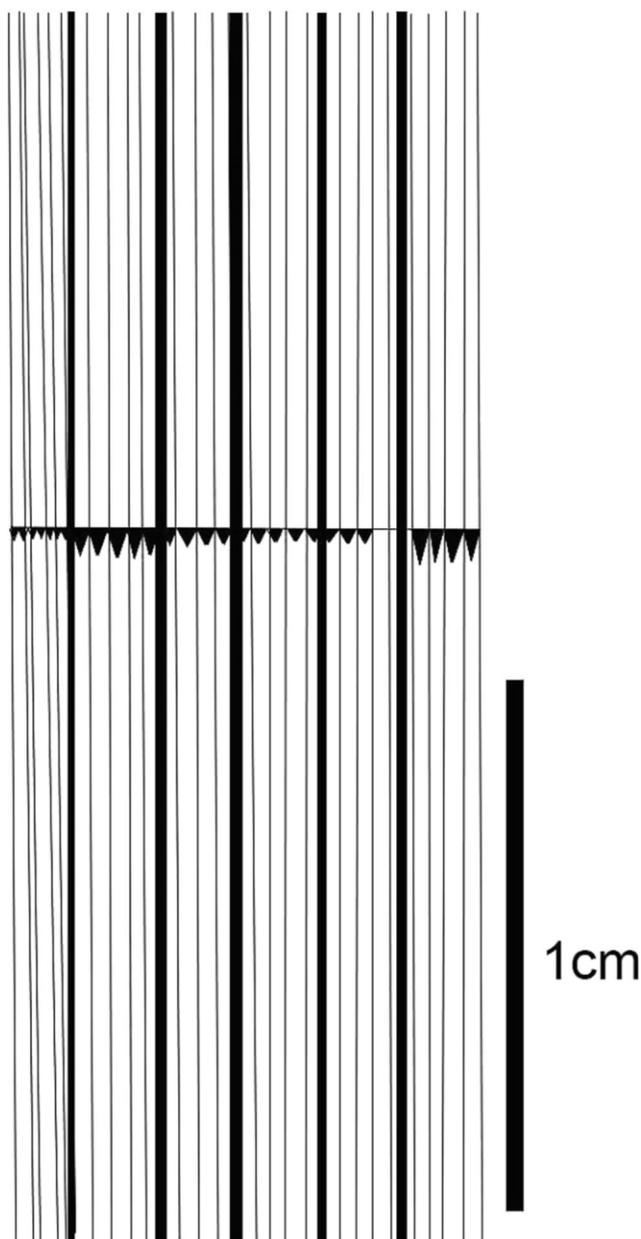


Fig. 11 Diagram of studied specimens, showing stem details. Specimen Kh.D.FU.71: Leaf scars, some enlarged to show the triangular shape

- Two fossil swamps are reported for the first time from Deh-Sheikh, northern Kerman Province (Central Iran), unique in their kind, with in situ sphenophyte stems. Among them are the giant sphenophyte fossil stems in Iran, which are also among the largest known far from other localities.
- In situ sphenophyte colonies were found in both swamps, preserved in their growth position. Swamp 1 contains large Sphenophyta stems (150–220 mm in diameter), and Swamp 2 has small ones (10–20 mm in diameter). Their unique preservation, with rhizomes and a developed root system in Swamp 2, helps reconstruct the life strategy

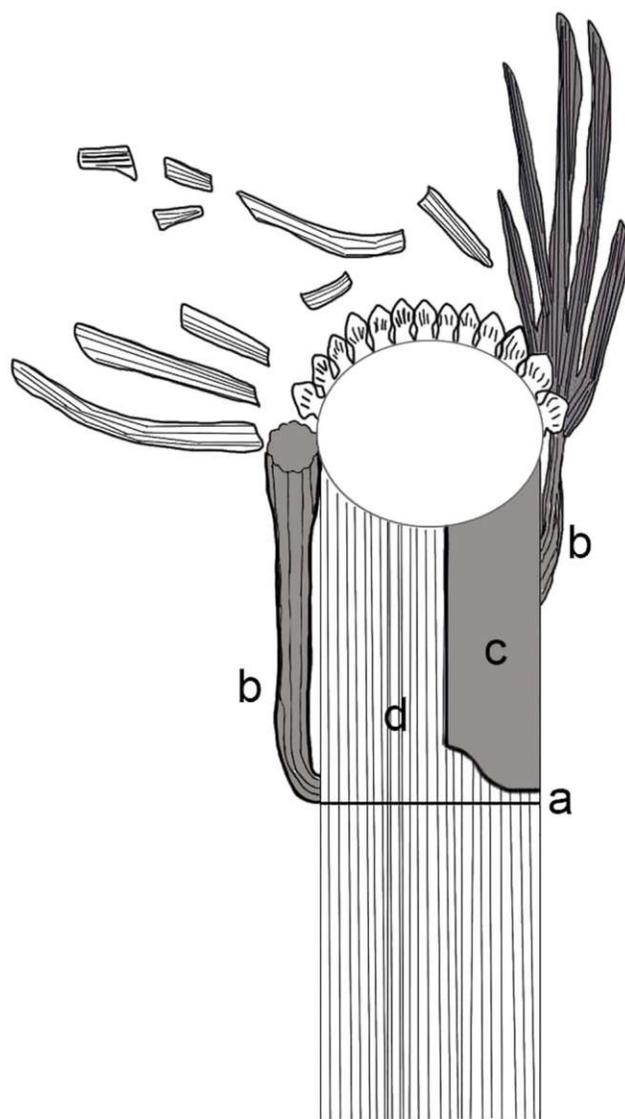


Fig. 12 Diagram of studied specimens, showing stem details. Specimen Kh.D.FU.82: **a** Node, **b** Two lateral branches connected to stem, **c** Inner vascular cylinder of stem almost smooth, **d** external cortex striated

of these plants, forming colonies that could effectively stabilise the plants after periods of flooding and erosion. The occurrence of trace fossils also confirms this environment stabilisation.

Acknowledgements We are grateful to Dr. Johanna H.A. van Konijnenburg-van Cittert (University of Utrecht) for her invaluable help, Mr. Thomas Good (University of Utah) for valuable suggestions about identifying ichnofossils, and Dr. Hamed Zand-Moghadam (Shahid Bahonar University of Kerman) for help in the sedimentological interpretation. This project was funded by the Ferdowsi University of Mashhad (grant number 3/40963 to H.Kh.). We thank Prof. Alfred Uchman (Institute of Geological Sciences, Poland) for his help in identifying and interpreting trace fossils. We also thank Mihai Emilian Popa (University of Bucharest) and an anonymous reviewer for their valuable comments and suggestions for improving the text.

Data availability All data used during this study are included in this published article. The data used during the current study include the plant macrofossils available in the Geology Museum repository hall of the Faculty of Science, Ferdowsi University of Mashhad, Iran (<https://sci.um.ac.ir>). These data are available via [aghaderi@um.ac.ir] as the Geology Museum curator at [Ferdowsi University of Mashhad].

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Adams, A. B., Dale, V. H., Smith, E. P., & Kruckeberg, A. R. (1987). Plant survival, growth form and regeneration following the 18 May 1980 eruption of Mount St. Helens, Washington. *Northwest Science*, 61, 160–170.
- Agardh, C. A. (1825). *Classes plantarum, quas, praeside* (pp. 1–34). Literis Berlingianis.
- Aghanabati, S. A. (1977). *Étude géologique de la région de Kalmard (W. Tabas). stratigraphie et tectonique*. Geological Survey of Iran Press.
- Aghanabati, S. A. (2006). *Geology of Iran* (pp. 1–603). Tehran: Geological survey of Iran.
- Allen, J. R. (1963). Asymmetrical ripple marks and the origin of waterlaid cosets of cross strata. *Geological Journal*, 3(2), 187–236.
- Ameri, H., Khalilzadeh, H., & Zamani, F. (2014). Four new *Equisetites* species (sphenophytes) from the Hojedk formation, middle Jurassic (Bajocian–Bathonian), the north of Kerman, Iran. *Journal of Sciences, Islamic Republic of Iran*, 25(3), 253–264.
- Assereto, R. (1966). The Jurassic Shemshak formation in central Elburz (Iran). *Rivista Italiana di Paleontologia e Stratigrafia*, 72, 1133–1182.
- Assereto, R., Riccardo, P., & Sestini, N. F. (1968). Jurassic stratigraphy of central Alburz (Iran). *Rivista Italiana di Paleontologia e Stratigrafia*, 74(1), 3–21.
- Badihagh, M. T., Sajjadi, F., Farmani, T., & Uhl, D. (2019). Middle Jurassic palaeoenvironment and palaeobiogeography of the Tabas block, Central Iran: Palynological and palaeobotanical investigations. *Palaeobiodiversity and Palaeoenvironments*, 99(3), 379–399.
- Barnard, P. D. W. (1965). The geology of the upper Djadjerud and Lar valleys (North Iran) II. Palaeontology. Flora of the Shemshak formation I. Liassic plants from Dorud. *Rivista Italiana di Paleontologia e Stratigrafia*, 71(4), 1123–1168.
- Bold, H. C., Alexopoulos, C. J., & Delevoryas, T. (1987). *Morphology of plants and Fungi* (5th ed.). New York: Harper Collins Publishers Inc.
- Bomfleur, B., Escapa, I. H., Serbet, R., Taylor, E. L., & Taylor, T. N. (2013). A reappraisal of *Neocalamites* and *Schizoneura* (fossil Equisetales) based on material from the Triassic of East Antarctica. *Alcheringa: An Australasian Journal of Palaeontology*, 37, 1–17.
- Channing, A., Zamuner, A., Edwards, D., & Guido, D. (2011). *Equisetum thermale* sp. nov. (Equisetales) from the Jurassic San Agustín hot spring deposit, Patagonia: Anatomy, paleoecology, and inferred paleoecophysiology. *American Journal of Botany*, 98(4), 680–697.
- Corsin, P., & Stampfli, M. G. (1977). La formation de Shemshak dans l'Elburz oriental (Iran) flore – stratigraphie – paléogéographie. *Geobios*, 10, 509–571.
- Coturel, E. P., Morel, E. M., & Ganuza, D. (2016). Lycopodiopsids and equisetopsids from the Triassic of Quebrada de los Fósiles formation, San Rafael Basin, Argentina. *Geobios*, 49(3), 167–176.
- Elgorriaga, A., Escapa, I., Bomfleur, B., Cúneo, R., & Ottone, G. (2015). Reconstruction and phylogenetic significance of a new *Equisetum* *Linnaeus* species from the lower Jurassic of Cerro Bayo (Chubut Province, Argentina). *Ameghiniana*, 52(1), 135–152.
- Enzo, K. N. (1973). New species of *Pleuromeia* and *Neocalamites* from the upper Scythian Bed in the Kitakami Massif. Japan. *Science Reports of the Tohoku University, Series 2, Geology*, 43(2), 99–115.
- Fakhr, M. S. (1977). Flore jurassique de l'Iran. Contribution a l'étude de la flore Rhéto Liasique de la formation de Shemshak de l'Elbourz (Iran). *Mémoires de la section des Sciences de Paris*, 5, 1–178.
- Fürsich, F. T., Hautmann, M. T., Senowbari-Daryan, B., & Seyed-Emami, K. (2005). The Upper Triassic Nayband and Darkuh formations of east Central Iran: Stratigraphy, facies patterns and biota of extensional basins on an accreted terrane. *Beringeria*, 35, 53–133.
- Fürsich, F. T., Wilmsen, M., Seyed-Emami, K., Majidifard, M. R., (2009). Lithostratigraphy of the Upper Triassic–Middle Jurassic Shemshak Group of Northern Iran. In M.-F. Brunet, M. Wilmsen, & J. W. Granath (Eds.), *South Caspian to Central Iran basins. The Geological Society of London*, 312(1), 129–160.
- Geertsema, M., & Pojar, J. J. (2007). Influence of landslides on biophysical diversity A perspective from British Columbia. *Geomorphology*, 89(1–2), 55–69.
- Ghorbani, M. (2013). *The economic geology of Iran: Mineral deposits and natural resources*. Springer Geology.
- Halle, T. G. (1908). Zur Kenntnis der Mesozoischen Equisetales Schwedens. *Kungliga Svenska Vetenskapsakademiens Handlingar*, 43(1), 1–56.
- Holmes, W. K. (2001). Equisetalean plant remains from the Early to Middle Triassic of New South Wales, Australia. *Records–Australian Museum*, 53(1), 9–20.
- Holt, E. (1947). Upright trunks of *Neocalamites* from the Upper Triassic of western Colorado. *The Journal of Geology*, 55(6), 511–513.
- Huckriede, R., Kürsten, M., & Venzlaff, H. (1962). Zur Geologie des Gebietes zwischen Kerman und Sagand. *Neues Jahrbuch für Geologie und Paläontologie*, 81, 237–276.
- Husby, C. (2013). Biology and functional ecology of *Equisetum* with emphasis on the giant horsetails. *The Botanical Review*, 79(2), 147–177.
- Jarzynka, A., & Pacyna, G. (2015). Fossil flora of middle Jurassic Grojec clays (southern Poland). Raciborski's original material reinvestigated and supplemented. I. Sphenophytes. *Acta Palaeobotanica*, 55(2), 149–181.
- Kędzior, A., & Popa, M. E. (2013). Sedimentology of the Early Jurassic terrestrial Steierdorf Formation in Anina, Colonia Cehă Quarry, South Carpathians, Romania. *Acta Geologica Polonica*, 63(2), 175–199.
- Kędzior, A., & Popa, M. E. (2018). An Early Jurassic braided river system from Mehadia, South Carpathians, Romania. *Geological Quarterly*, 62(2), 415–432.
- Kilpper, K. (1964). Über eine Rät/Lias-Flora aus dem nördlichen Abfall des Albus-Gebirges in Nordiran. I. Bryophyta und Pteridophyta. *Palaeontographica Abteilung B*, 114, 1–78.
- Kimura, T., Kim, B. K., & Tamiko, O. (1982). *Neocalamites carrerei* (Zeiller) Halle (Equisetales), found in situ from the Daedong Supergroup, Korea. *Proceedings of the Japan Academy, Series B*, 58(6), 156–159.
- Lasemi, Y., & Kheradmand, A. (1999). Facies, depositional environments and sandstone province of the Hojedk Formation in Zarand area, Northwest Kerman. *Journal of Geosciences*, 8(31–32), 50–63.
- Milner, A. M., Fastie, C. L., Chapin, F. S., Engstrom, D. R., & Shorman, L. C. (2007). Interactions and linkages among ecosystems during landscape evolution. *BioScience*, 57(3), 237–247.
- Naugolnykh, S. V. (2009). A new fertile *Neocalamites* from the upper Permian of Russia and equisetophyte evolution. *Geobios*, 42(4), 513–523.

- Naugolnykh, S., & Mitta, V. (2016). In situ preserved Equisetophyte stems in the upper Bajocian Parkinsoni zone (Middle Jurassic) of the northern Caucasus. *Palaeodiversity*, 9(1), 113–120.
- Pott, C., Kerp, H., & Krings, M. (2008). Sphenophytes from the Camian (upper Triassic) of Lunz am see (Lower Austria). *Jahrbuch der Geologischen Bundesanstalt*, 148(2), 183–199.
- Rees, PMCA, Ziegler, A.M., & Valdes, P.J. (2000). Jurassic phytogeography and climate: New data and model comparison. In B. T. Huber, K. G. Macleod, & S. L. Wing (Eds.), *Warm Climates in Earth History* (pp. 297–318.). Cambridge University Press.
- Rindsberg, A. K., & Kopaska-Merkel, D. C. (2005). *Treptichnus* and *Arenicolites* from the Steven C. Minkin paleozoic footprint site (Langsettian, Alabama, USA). *Pennsylvanian Footprints in the Black Warrior Basin of Alabama*, 1, 121–141.
- Rothwell, G. W., Mapes, G., & Mapes, R. H. (1996). Anatomically preserved voynovskyaean seed plants in upper Pennsylvanian (Stephanian) marine shales of North America. *Journal of Paleontology*, 70(6), 1067–1079.
- Sadovnikov, G. N. (1976). *The Mesozoic flora of Alborz and Central Iran and its stratigraphic importance*. National Iran Steel Company of Iran Press.
- Sadovnikov, G. N. (1984). *Die Flora der Kohleformation des Elburs. III. Gheslugh-Flora*. Atlas (pp. 1–83). Akademii Nauk SSSR, Institute of Geology, N 839–84 Dep., [in Russian]
- Schweitzer, H. J., van Konijnenburg-van Cittert, J., & Burg, J. van der (1997). The Rhaeto–Jurassic flora of Iran and Afghanistan. 10. Bryophyta, Lycophyta, sphenophytes, Pterophyta–eusporangiate and Protileptosporangiate. *Palaeontographica Abteilung B*, 243, 103–192.
- Salehi, M. A., Moussavi-Harami, R., Mahboubi, A., Fürsich, F. T., Wilmsen, M., & Heubeck, C. (2018). A tectono–stratigraphic record of an extensional basin: The Lower Jurassic Ab–Haji Formation of east Central Iran. *Swiss Journal of Geosciences*, 111(1), 51–78.
- Seyed-Emami, K. (1971). The Jurassic Badamu Formation in the Kenman region, with some remarks on the Jurassic stratigraphy of Iran. *Geological Survey of Iran, Report*, 19(1–80), 264.
- Seyed-Emami, K., Wilmsen, M., & Fürsich, F. T. (2020). A summary of the Jurassic system in north and east-Central Iran. *Zitteliana*, 99–156.
- Shuqin, Z., Axsmith, B., Escapa, I., Fraser, N., Xiang, L. F., & Xing, D. E. (2012). A new Neocalamites (sphenophytes) with prickles and attached cones from the Upper Triassic of China. *Palaeoworld*, 21(2), 75–80.
- Siegel, B. Z., & Siegel, S. M. (1982). Mercury content of *Equisetum* plants around Mount St. Helens one year after the major eruption. *Science*, 216(4543), 292–293.
- Sinnott, E. W. (1930). The morphogenetic relationships between cell and organ in the petiole of *Acer*. *Bulletin of the Torrey Botanical Club*, 57, 1–20.
- Stöcklin, J., & Setudehnia, A. (1971). Stratigraphic lexicon of Iran. *Geological Survey of Iran, Report* 18: 1–376.
- Tipper, G. H. (1921). The geology and mineral resources of eastern Persia. *Records of the Geological Survey of India*, 53, 51–80.
- Tsuyuzaki, S. (1987). Origin of plants recovering on the volcano Usu, northern Japan, since the eruptions of 1977 and 1978. *Vegetatio*, 73(1), 53–58.
- Tsuyuzaki, S. (1997). Wetland development in early stages of volcanic succession. *Journal of Vegetation Science*, 8(3), 353–360.
- Uchman, A., Buta, R. J., Rindsberg, A. K., & Kopaska-Merkel, D. C. (2005). *Treptichnus*-like traces made by insect larvae (Diptera: Chironomidae, Tipulidae). *Pennsylvanian Footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society Monograph*, 1, 143–146.
- Vaez-Javadi, F. (2014). *Triassic and Jurassic floras and climate of central East Iran*. Tehran: Geological Survey of Iran.
- Vaez-Javadi, F. (2018). Middle Jurassic flora from the Hojedk Formation of Tabas, central East Iran: Biostratigraphy and palaeoclimate implications. *Rivista Italiana di Paleontologia e Stratigrafia*, 124(2), 299–316.
- Vaez-Javadi, F., & Mirzaei-Ataabadi, M. (2006). Jurassic plant macrofossils from the Hojedk Formation, Kerman area, east-Central Iran. *Alcheringa*, 30(1), 63–96.
- Vanneste, K., Sterck, L., Myburg, A. A., Van de Peer, Y., & Mizrachi, E. (2015). Horsetails are ancient polyploids: evidence from *Equisetum giganteum*. *The Plant Cell*, 27(6), 1567–1578.
- Wilmsen, M., Fürsich, F. T., Seyed-Emami, K., & Majidifard, M. R. (2009a). An overview of the stratigraphy and facies development of the Jurassic system on the Tabas block, east–Central Iran. *Geological Society, London, Special Publications*, 312(1), 323–343.
- Wilmsen, M., Fürsich, F. T., Seyed-Emami, K., Majidifard, M. R., & Taheri, J. (2009b). The Cimmerian orogeny in northern Iran: Tectono-stratigraphic evidence from the foreland. *Terra Nova*, 21(3), 211–218.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.