Zamites (Bennettitales) from the Minjir Formation (Norian) of Saudi Arabia – a unique record from the Late Triassic palaeotropics of Gondwana

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ABSTRACT
Late Triassic plant macro-remains are extremely rare in an equatorial belt stretching across the North of Gondwana from northern South America to Arabia. Located between the Laurussian floral province to the North and the Gondwana floral province to the South, this large area, is almost entirely lacking palaeobotanical data. Thus, this region is of special interest to our knowledge of Late Triassic floral provincialism and plant distribution. Based on impressions from ferruginous crusts, the first record of identifiable plant macro-remains from the Late Triassic (Norian-Rhaetian) Minjur Formation is described, as belonging to the bennettitalean taxon Zamites aff. persicus. This new finding at least tentatively supports palynological data, which indicated similarities between the Late Triassic (Norian) palynoflora of the Minjur Formation of the Arabian Peninsula on the southern shores of the Tethys and the Norian palynoflora of Iran, during this time located in the northern part of the Tethys.

Introduction
Triassic macrofloras from the northern regions of Gondwana (i.e. the northern parts of South America and Africa, as well as Arabia) are virtually unknown (e.g. Dobruskina 1994; Kustatscher et al. 2018). Focussing on the eastern part of the region, so far only a few plant macro-remains (mostly consisting of charred and permineralized wood, as well as dispersed cuticles) have been described in some detail from Middle Triassic (Anisian-Ladinian) deposits of Jordan (e.g. Abu Hamad et al. 2013, 2014, 2019). Additionally, the rare occurrence of plant macro-remains (including permineralized wood) has repeatedly been mentioned in studies focusing on other subjects related to the Triassic geology of this region (e.g. Jordan: Bandel and Salameh 2013; Saudi Arabia: Powers et al. 1966; Issautier et al. 2019). Besides these few, more or less detailed, reports on Triassic macrofloras mentioned above, as well as palynological studies dealing with early Triassic deposits (e.g. Esset and Cousminer 1986; Esset 1990; Abu Hamad 2004; Powell et al. 2016), there is a limited number of studies dealing with middle to late Triassic palynofloras from the Middle East, as well as the Arabian Peninsula, which were mostly conducted for biostratigraphic purposes (e.g. Powers et al. 1966; Abu Hamad 2004; Issautier et al. 2019; and citations therein).

This lack of (macro)floristic data from an equatorial (tropical) belt stretching from northern South America to Arabia across the entire North of Gondwana left a large geographical gap in our knowledge about the worldwide floral zonation during the Late Triassic (Kustatscher et al. 2018). This gap lies between the Gondwana floral province (comprising the Onslow and Ipswich subprovinces) and the Laurussian floral province, which can be divided into a number of subprovinces (cf. Dobruskina 1994; Kustatscher et al. 2018).

Recently, targeted fieldwork, as suggested by Kustatscher et al. (2018), led to the discovery of the first determinable foliage remains from a locality within this large geographic gap. Based on this material occurring in ferruginous crusts the first record of the bennettitelean genus Zamites can be described from the Late Triassic Minjur Formation of Saudi Arabia.

Geological setting and lithostratigraphy
From the Permian to the Early Jurassic, the Arabian plate drifted from south of the equator northwards, reaching the equator by the Early Jurassic (Stampfl and Borel 2002; Golonka 2007), accompanied by a transition from semi-arid to warm-humid climate (Issautier et al. 2019). This climatic change contributed to a lithological variation from carbonate and evaporites to clastics. However, the whole period is marked by tectonic activity related to the pre-breakup of Pangaea (Sharland et al. 2001).
After an early Middle Permian rifting phase, Late Permian subsidence was mainly driven by post-rift thermal super-cycle, during the rest of the Permo-Triassic super-cycle, the contribution of sediment loading is thought to have been the dominant mechanism driving subsidence (Bishop 1995), despite local structural control.

During the Early Triassic, a period of basin restriction led to a widespread accumulation of shale and evaporite deposits, i.e. the Sudair Shale, in a broad intrashelf basin extending up to the Arabian Gulf. The overlying mid-Late Triassic Jilha Formation consists of sandstone, shales with evaporites, and carbonate, which correspond to periodic clastic input, alternating with three brief marine transgressive cycles over the platform during the Ladinian and the Carnian (Issautier et al. 2019). The overlying facies resemble alternating intertidal carbonate flats and siliciclastic littoral deposits that display an aggrading trend. The Triassic-Jurassic boundary in Arabia witnessed a clear discontinuity which reflects a piece of evidence for the sudden lowering in the sea level as resulted of depositing fluvial to continental facies represented by the Upper Triassic Rukhman Formation in northern Saudi Arabia and its equivalent Minjur Sandstone in southern areas (Khalifa 2007).

The Minjur Sandstone, which hosts the plants studied here, was named for Khashm al Minjur (lat. 23° 31’ N, long 46° 10’) where the lower part of the formation is exposed in surface outcrops (Figures 1–2). The term was originally proposed by Bramkamp (unpublished report, 1950) as a replacement for Upper Es Sirr sandstone (discarded) and henceforth raised to formation rank. The type section of the Minjur Sandstone (315 m thick) extends from the top bed of the Jilha Formation (at lat. 23°34’33”N, long. 46° 07’ 15” E) up to the base of the Marrat Formation in the face of Khashm al Khalta (lat. 23° 35’24” N, long. 46° 10’ 36” E). The Minjur Formation shows thinning north of the type locality (Powers et al. 1966). The boundary between the Minjur Sandstone and Marrat Formation is located at the contact of grey, friable, cross-bedded sandstone of the Minjur Sandstone below and the tan-brown limestone above (Khalifa 2007).

Lithologically, the Minjur Formation is a thick continental siliciclastic rock unit, showing minor variation in composition and essentially comprises littoral

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**Figure 1.** Simplified geological map of Saudi Arabia; based on Al-Husseini (2009). Red star refers to the sampling locality.
sandstone, buff, commonly cross-bedded, locally calcareous with multiple zones of red, purple, and blue-grey shale, sandy shale, and shaly sand; black to brown ironstone at several levels forms thin layers and concretions with few conglomeratic lenses that encompass stem impressions, tree trunks and silicified wood of unknown affinity (Powers et al. 1966; Sharief 1986). Moreover, it was documented from outcrop studies as an interbedded succession of sandstone and shale with minor evaporites and dolomite that were originally assigned to a dominantly fluvial-deltaic system (Le Nindre 1987). In surface exposures, unidentifiable fossil plant remains (i.e. axes, stems and foliage remains [the determination of such remains as Calamites foliage by Issautier et al. (2019) is most likely a misidentification]) have been reported from the base and the top of the Minjur Formation (Issautier et al. 2019). Based on the stratigraphic position, Steineke et al. (1958) considered the Minjur to be Upper Triassic or Lower Jurassic. In surface exposures, it was dated as Norian near the base by conodonts (Vrielynck et al. 1986). However, in subsurface sections, the palynological investigations of Jones and Hooker (2011) assumed a Norian-Rhaetian age. In addition, a fourfold biostratigraphic subdivision extending from the latest Carnian-early Norian to
the latest Rhaetian-Pliensbachian (Triassic-Early Jurassic), was recently suggested based on palynological studies of core samples (Issautier et al. 2019). Moreover, the Minjur Formation is informally subdivided into a lower and an upper unit, their depositional environments ranging from alluvial to marginal marine with tidally influenced channels (Issautier et al. 2019).

The lower member starts with unsorted, gravely, cross-beded sandstone containing fairly steep sets and a channeled surface, and displays traces of leached silty palaeosoils and ferruginization. It is topped by medium-grained, well-beded sandstone with ferruginous crusts at various levels (Al-Husseini 2009). The plants analysed in the present study were retrieved from one of these crusts of the lower member of the Minjur Formation (Figure 2(a-c)). This fossiliferous crust consists of a lower, (non-fossiliferous) coarse-grained sandstone and an upper, very fine-grained claystone, which exhibit a thick, secondary (?) mineralization with iron minerals. Large parts of the surface of the crust, which was exposed in the outcrop, is covered with a kind of rather glossy “desert varnish”. Those ferruginous crusts are usually interbedded with mustard-yellow, coarse channel-fill sandstone. Here, we follow the dating of Viélyncx et al. (1986) who dated the Minjur Formation as Norian, as this is so far the only available reliable dating for surface exposures as in our case.

**Material and methods**

The studied material has been collected from an outcrop in the vicinity of Hunaydhel Village (lat. 26° 59’ 62” N, long. 44° 06’ 19” E), north Wadi Al-Rumah, north Al-Qassim region, where the lower part of the Al-Minjur Formation is exposed in the form of scattered hills (Figure 2(a,b)). Besides the remains of Zamites the ferruginous crusts contain also abundant impressions and “steinkerns” of unidentified plant axes (Figure 2(c-g)). The specimens described here are curated in the palaeobotanical collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, under accession numbers SM.B 22252 – SM.B 22257. Photographic images were taken with a NIKON Z7, with a AF-S Micro Nikkor 60 mm 1:2.8 G ED objective, a Leica M80 stereo microscope equipped with a Leica EC3 camera, as well as a Nikon SMZ 25 microscope equipped with a Nikon DS-Ri2 camera. As the surfaces of the specimens (fossils and rock), which were exposed in the outcrop, are covered by a kind of rather glossy “desert varnish” photographing the specimens proved to be rather difficult. Standard techniques which can often be applied to reduce such reflections (e.g. Kerp and Bomfleur 2011) did not work in this particular case: Photographs taken under liquid did not result in a reduction of the reflections on the glossy surface of the “varnish”, and photographs taken under polarized light or after whitening of the fossils, did not show enough details of the fossils to allow for the observation of most of the morphological details.

**Systematic palaeontology**

Order Bennettitales Engler 1892
Family Williamsoniaceae Carruthers 1870
Genus Zamites Brongniart 1828

**Zamites aff. persicus** Boureau 1950 (Figures 3–7)

**Nomenclatural remark**

Boureau (in Boureau et al. 1950) described the new Zamites species *Z. persica* from Triassic-Jurassic strata of the Shemshak region in Iran. According to 626.4 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018), all plant genera ending with – *ites* are treated as masculine. Thus, the specific epithet of this taxon is here corrected to *persicus*.

**Description**

Fragments of pinnate fronds, with base and apex of fronds missing (Figure 3–5). Pinnae arranged oppositely to sub-oppositely or even alternating (Figure 3–5). Bases of pinnae sometimes overlapping (Figure 5). Insertion angles between rachis and pinnae vary from 41° to 76°, decreasing apically (Figure 3–5). Distance between insertion points of pinnae varies from ~6.5 mm to 11 mm (Figure 3–5). Base of pinnae more or less rounded (constricted), symmetric, latero-adaxially attached with a relatively small area of attachment (approx. 2.5 mm wide) (Figure 4, 6(a)). Pinnae apex not preserved. Length of the complete pinnae ranges from ~4 to >8 cm, width from ~6 to 10.5 mm (Figure 3–5). Length to width ratio varies from ~5.8 to 8. Venation parallel, individual veins bifurcating only near the base of the pinnae (Figure 6(b)). Venation density ~37–42 veins/cm. On the adaxial surfaces of various pinnae, more or less isodiamic epidermal cells are visible, which are arranged in longitudinal rows (Figure 7). No details of the stomata, etc., could be detected. Rachis with slight longitudinal striation and transverse “wrinkles” (Figure 6(a)), diameter of the rachis ~1.8–2.2 mm.

**Remarks**

The affiliation to the genus *Zamites* is based on the latero-adaxially attachment of the pinnae with a more or less rounded (constricted) and symmetric base (see Watson and Sincock 1992; Schweitzer and Kirchner 2003). Many *Zamites* species have been described from numerous Mesozoic, mainly Jurassic, deposits.
of the northern hemisphere (Zijlstra and van Konijnenburg-van Cittert 2020). Only few Zamites taxa are known from the Middle and Late Triassic (e.g. Ash 1975; Dobruskina 1994; Lucas 2001; Schweitzer and Kirchner 2003; Kustatscher et al. 2018). The best-known Triassic taxa occur in Iran and North America (e.g. Boureau et al. 1950; Ash 1975; Fakhr 1977; Schweitzer and Kirchner 2003; Vaez-Javadi 2006), whereas for other taxa from Europe and Asia the intra-specific variability is less well known.

Two Late Triassic Zamites species are known from the Norian–Rhaetian Shemshak Formation in Iran (e.g. Boureau et al. 1950; Corsin and Stampfli 1977; Fakhr 1977; Schweitzer and Kirchner 2003; Vaez-Javadi 2006). These species, Zamites persicus Boureau 1950 and Zamites boureaui (Fakhr 1977), are morphologically very similar to the material analysed here. However, Schweitzer and Kirchner (2003) synonymized Zamites boureaui with Zamites persicus based on Iranian specimens that exhibited characters originally used to differentiate between both taxa. Zamites

Figure 3. Zamites aff. persicus from the Minjur Formation. a) Zamites aff. persicus; scalebar = 1 cm; specimen SM.B 22255; b) Zamites aff. persicus, exhibiting the longest pinnae observed so far in the material from Saudi Arabia; scalebar = 1 cm; specimen SM.B 22256.

Figure 4. Zamites aff. persicus from the Minjur Formation in adaxial view exhibiting constricted pinnae bases. Enlargement from Figure 3; scalebar = 1 cm; specimen SM.B 22255.
persicus (Zamites boureaui) is characterized by the following characters according to Schweitzer and Kirchner (2003), those characters that agree with the material described here are printed in bold:

1. Rachis with slight longitudinal striation and transverse “wrinkles”.
2. Length to width ratio of pinnae up to 18x.
3. Pinnae apices rounded to slightly acute.
4. Distance between insertion points of pinnae on the rachis ranging from less than 7.5 mm to 10 mm.

5. Insertion angles of pinnae decrease from 70° in the centre of a frond to 45° near the apex.

The pinnae dimensions, which vary considerably between individual specimens of Zamites persicus, are considered unsuitable for taxonomic purposes by Schweitzer and Kirchner (2003), as these may just represent differences between sun- and shade leaves within an individual taxon. Such a differentiation into sun- and shade leaves seems unlikely considering the assumed divaricate growth form or plant architecture and common occurrence.

Figure 5. Zamites aff. persicus from the Minjur Formation in abaxial view, bases of pinnae thus covered partly by the rachis. Enlargement from Figure 3; arrow points to basally overlapping pinnae; scalebar = 1 cm; specimen SM.B 22255.

Figure 6. Zamites aff. persicus from the Minjur Formation. a) Overview of a constricted pinna base and the rachis with transverse “wrinkles” (arrow); scalebar = 2 mm; specimen SM.B 22255; b) detail of the basal venation of a pinna, arrow points to a bifurcation; scalebar = 2 mm; specimen SM.B 22255.
in more open habitats of many taxa belonging to Williamsoniaceae (e.g. Pott and McLoughlin 2014). In fact, several studies have repeatedly demonstrated that leaf size, as well as a number of other morphological characters like venation density, of many angiosperms but also gymnosperms, are sensitive to a wide variety of environmental parameters that may act as stressors for plants (e.g. Uhl and Walther 2000; Uhl and Mosbrugger 1999, 2002; Uhl et al. 2002; Zhang et al. 2018; and citations therein). Such environmentally influenced characters should therefore only be used with great care for taxonomic purposes, especially in extinct plant groups with no modern representatives. Additionally, it should be considered that pinnae dimensions could also be related to the age of a plant with leaves of younger plants being smaller than those of older plants, as it was suggested previously for other bennettitalean taxa (Pott et al. 2007; Pott and Krings 2007; and citations therein).

The material from Saudi Arabia exhibits many similarities to Zamites persicus specimens described from Iran, but due to the fragmentary preservation of the material described here many characters must remain uncertain for the time being (i.e. the form of the pinna apex) and there are even characters which differ from all Zamites persicus specimens described so far in the literature (i.e. the diameter of the rachis, which is smaller in the material described here [~2 mm] than in the type material [~4 mm] as described by Boureau et al. 1950). Based on our observations, the Saudi material cannot be assigned to Zamites persicus, although it seems to have a close affinity to this taxon. It seems possible that this material even represents a so far undescribed new species of the genus Zamites, but more complete and better-preserved material is needed to clarify the affilia
tion of this material.

The also well-known and widely distributed North American “Zamites” powellii differs considerably from the Saudi Arabian material, as this material is characterized by the occurrence of basiscopic and acroscopic auricles at the base of the broadly attached pinnae bases (e.g. Ash 1975). This character, which also occurs in several Jurassic taxa from Mexico, was used as one character to establish the genus Laurozamites for such material by Weber and Zamudio-Varela (1995). These authors also included “Zamites” powellii into this new genus, a combination not accepted by all subsequent authors (e.g. Lucas 2001).

**Preliminary palaeoecological and palaeobiogeographic considerations**

Based on the divaricate growth form of many members of the Williamsoniaceae and the ecology of modern taxa exhibiting such a growth form, as well as the depositional environments in which many members of this family have been preserved (i.e. coastal and delta-plain settings, including floodplains), Pott and McLoughlin (2014) tried to reconstruct the habitats of plants belonging to this family. These authors came to the conclusion that members of the Williamsoniaceae may have inhabited preferentially open vegetation types on floodplains in deltaic and/or coastal settings, favouring low-nutrient sites on sandy plains or in peat mires. As the Minjur Formation has been deposited under alluvial to marginal marine conditions including tidally influenced channels (Issattier et al. 2019), it seems possible that the habitat(s) of Zamites recovered
from this formation were also within the area of an alluvial or coastal plain. However, as stated above for the taxonomic affiliation, more complete and better-preserved material is needed to evaluate such a preliminary palaeoecological interpretation.

So far Late Triassic plant macro-remains are extremely rare in an equatorial belt stretching across the North of Gondwana from northern South America to Arabia (e.g. Dobruskina 1994; Kustatscher et al. 2018). The here described plant remains come from a region that is located within this vast belt from which so far palaeobotanical and thus palaeobiogeographical data are missing (Figure 8) (Kustatscher et al. 2018). Although it is difficult to provide a meaningful palaeobiogeographical interpretation based on a single occurrence we try to provide a preliminary interpretation based not only on this new occurrence of Zamites, but also on the rare, previously published palynological data from the Minjur Formation (i.e. Powers et al. 1966; Issautier et al. 2019).

During the Norian, the composition of palynofloras from the Nayband Formation in Iran shows great affinities to Gondwana floras (e.g. Eastern Australia and New Zealand) and after the collision of the Iranian microplate with Eurasia the flora became more similar to Eurasian floras during the Rhaetian, mostly by an enrichment of cosmopolitan taxa (e.g. Cirilli et al. 2005). It has been noted by previous authors, that the palynoflora of the Minjur Formation also shows some similarities to the palynoflora of the Shemshak Group in Iran (Powers et al. 1966; Issautier et al. 2019). Unfortunately, the interpretation of the palynological data from the Minjur Formation is hampered by the fact that so far only selected biostratigraphic data have been published from cores and cuttings drilled by the oil industry (e.g. Powers et al. 1966; Issautier et al. 2019) and thus only limited data are available for any interpretation that goes beyond biostratigraphy.

Many different species of the genus Zamites have been described from Mesozoic strata of different continents, especially Europe, Asia, and the Americas (e.g. Zijlstra and van Konijnenburg-van Cittert 2020). Although the majority of these taxa has so far been described from Jurassic deposits (see Zijlstra and van Konijnenburg-van Cittert 2020), a few taxa were already known from Triassic strata (e.g. Dobruskina 1994; Kustatscher et al. 2018 [and citations therein]). The plants described here from Saudi Arabia exhibits a morphological affinity to Zamites persicus from the Norian-Rhaetian part of the Shemshak Group in Iran (e.g. Schweitzer and Kirchner 2003). Although this must be seen with great care, it seems possible that these morphological similarities also imply a more or less close "phylogenetic" relationship between Zamites persicus from the Norian-Rhaetian of Iran and Zamites aff. persicus from Saudi Arabia. This assumed relationship, together with previously published palynological data from the Late Triassic of Iran and Saudi Arabia may point to a certain biogeographic relationship between both regions and the rest of Gondwana. However, more data from plant macro-remains from the Minjur Formation will be necessary to test this preliminary interpretation and we expect that ongoing fieldwork may help to clarify this and other problems related to the Late Triassic flora of the tropics in the eastern part of Gondwana.
Acknowledgments

The authors gratefully thank Prof. Abdulaziz Al-Laboun (Saudi Geologists Society) for his support during fieldwork and Michael Ricker as well as Robin Kunz (Senckenberg Frankfurt) for help with taking the photographs of the specimens. H. El Atfy acknowledges financial support from Alexander von Humboldt Foundation (Germany – EGY – 1190326 - GF-P). S. Abu Alkhayl thanks the Saudi Geologists Society for their help and continuous support. The authors thank Johanna H.A. van Konijnenburg-van Cittert and Christian Pott for their constructive reviews of an earlier version of the manuscript, which helped to improve the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Alexander von Humboldt Foundation [Germany – EGY-1190326-GF-P].

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Data availability

Non-digital data supporting this study (i.e. fossil specimens) are curated at the palaeobotanical collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, under accession numbers SM.B 22252 – SM.B 22257.

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