



Non-pollen palynomorphs notes: 2. Holocene record of Megalohypha aqua - dulces , its relation to the fossil form genus Fusiformisporites and association with lignicolous freshwater fungi

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Non-pollen palynomorphs notes: 2. Holocene record of *Megalohypha aqua-dulces*, its relation to the fossil form genus *Fusiformisporites* and association with lignicolous freshwater fungi

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ABSTRACT

The first Holocene record of the freshwater ascomycete *Megalohypha aqua-dulces* from the sediment core Kongor (NE Iran) is presented here. Based on the similarity of the spore morphology with the fossil form genus *Fusiformisporites*, we establish a link between extant and fossil taxa. Comparative analysis of morphological characteristics of fossil spores of *Fusiformisporites* indicates that several different fungal groups might be included in this form genus. At least five species of *Fusiformisporites* share similar morphology with spores of *Megalohypha aqua-dulces*: *Fusiformisporites annafrancescae*, *Fusiformisporites crabbii*, *Fusiformisporites keralensis*, *Fusiformisporites paucistriatus*, and *Fusiformisporites pseudocrabbii*. Based on *Fusiformisporites*, the evolution of *Megalohypha aqua-dulces* can be traced to the late Cretaceous, corresponding with diversification of the flowering plants and pointing to a co-evolution of both groups. *Megalohypha aqua-dulces* has a tropical to subtropical distribution but also occurs in the semi-arid steppe environments of Kongor together with other freshwater fungal genera such as *Xylomyces*, *Dictyosporium*, and *Sporoschisma*, which spores we describe here. The ecological requirements of *Megalohypha* indicate that its spores can be used for the palaeoecological sign of dead submerged wood as well as of tropical to subtropical conditions.

Keywords:
Palaeomycology
Xylomyces
Dictyosporium
Sporoschisma
Freshwater fungi
Lignicolous fungi
Fossil fungi

Contents

1.	Introduction	168
2.	Material and methods.	169
3.	Results	169
3.1.	Spore morphology of <i>Megalohypha aqua-dulces</i>	169
3.2.	Records of freshwater fungi in Kongor	169
4.	Discussion	173
4.1.	Taxonomic relationship between <i>Fusiformisporites</i> and <i>Megalohypha aqua-dulces</i>	173
4.2.	Ecology and palaeoecology	173
4.3.	Geological evidence for the evolution of aquatic ascomycetes.	174
5.	Conclusions	175
	Acknowledgements	175
	References	175

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1. Introduction

Morphologically distinctive fungal spores present in the geological record provide valuable information about a wide variety of environmental conditions, including climate, hydrological conditions, fire and erosion history, vegetation type, and organismal interactions (e.g. [Elsik, 1976](#); [Sherwood-Pike, 1988](#); [Pirozynski, 1989](#); [Van Geel and Aptroot, 2006](#); [Taylor et al., 2015](#)). The description of fossil fungal spores is usually carried out based on fossil material, which rarely provides identification to extant taxa ([Elsik, 1976](#); [Jansonius and Kalgutkar, 2000](#)). Studies on the relationship between extant and fossil taxa however deliver important information for geological and mycological research by combining geological records with known fungal ecology. For example, investigation of the monotypic genus *Potamomyces* indicate that it likely contains several species ([Schlütz and Shumilovskikh, 2013](#); [Nuñez Otaño et al., 2016](#)), or in

the case of *Caryospora callicarpa* led to the discovery of species thought to be extinct ([Hawksworth et al., 2016](#)). Further connections of fossil fungal spores to recent species are required for a deeper understanding of the history, evolution, ecology and (palaeo)geography of fungal taxa.

During palynological investigations of a sediment core from Kongor (NE Iran), covering the last 6000 years ([Shumilovskikh et al., 2016](#)), fungal spores of *Megalohypha aqua-dulces* Ferrer et Shearer were documented ([Plate 1](#)) and identified using mycological literature ([Ferrer et al., 2007](#)). These spores share similar characteristics to additional fossilised spores from geological records described as *Fusiformisporites* [Rouse, 1962](#). Continuing our series of “non-pollen palynomorphs notes” ([Schlütz and Shumilovskikh, 2017](#)), in this paper we provide the first Holocene record of the extant species *Megalohypha aqua-dulces* and discuss its relation to the fossil form genus *Fusiformisporites*.

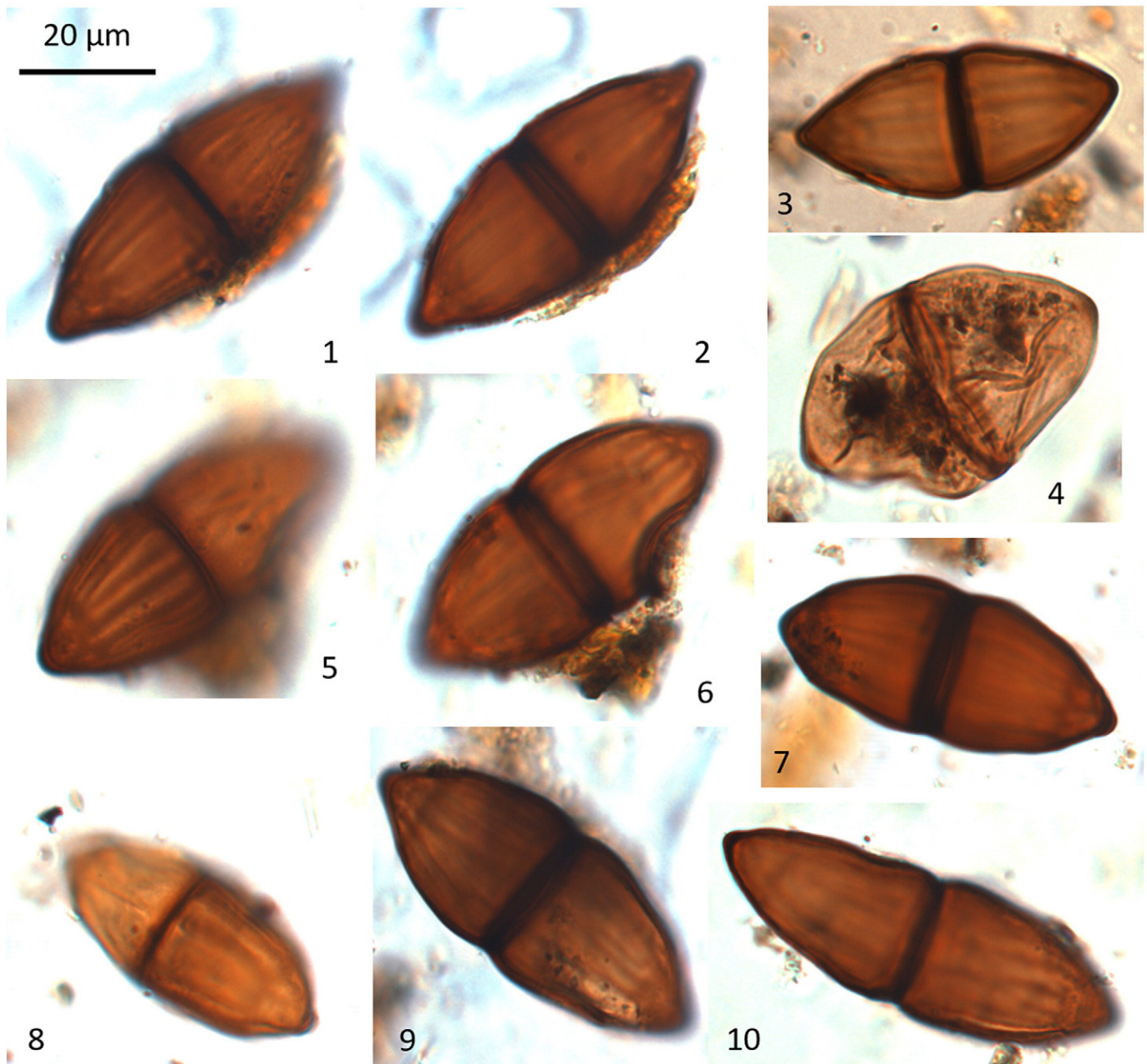


Plate 1. Spores of *Megalohypha aqua-dulces* (KNG 62) from the sediment core Kongor, NE Iran, showing variation in spore morphology and different preservation grade (1–2: 176 cm core depth, 3: 224 cm, 4: 64 cm, 5–6: 48 cm, 7–8: 96 cm, 9: 72 cm, 10: 80 cm). Photos at 500× magnification with oil immersion.

2. Material and methods

The Kongor core was obtained from the temporary lake Kongor, located in the *Artemisia*-steppe of the eastern Gorgan Plain, NE Iran. Samples from the core were treated with standard palynological laboratory procedures and studied for pollen and non-pollen palynomorphs including microscopic plant, animal and fungal remains (details in Shumilovskikh et al., 2016). For the purpose of this paper we present an abbreviated version of the palynological diagram with freshwater fungi, arboreal pollen and tree and shrub macroremains (Fig. 1). The description of the *Megalohypha aqua-dulces* spores (Plate I) and of the spores of other freshwater fungi (Plate III) from the sediment core Kongor follows the scheme of Elsik (1983) with an abbreviation KNG (Kongor) for the first described types. Spore measurements were carried out on 1000 $\times$ magnification.

The samples from Panama were collected from freshwater habitats at the Soberania National Park, which support lowland tropical forest. Samples of submerged partially decomposed wood were incubated in the laboratory in plastic boxes containing moistened paper towels at room temperature and examined with a dissecting microscope periodically over 12 months. Fungi were removed from the substrate and placed in a drop of distilled water on a glass slide. Measurements and photographs of the spores and fruiting bodies were made in material mounted in distilled water (Plate II; Ferrer et al., 2007).

3. Results

3.1. Spore morphology of *Megalohypha aqua-dulces*

Spores of *Megalohypha aqua-dulces* from the sediment core Kongor (KNG 62; Plate I): spores are fusiform, dark reddish-brown, dicellate, 47–60 $\times$ 21–27 μ m (average = 54.4 $\times$ 23.4 μ m, SD = 4.5 $\times$ 1.7 μ m, n = 10), inaperturate, slightly constricted at the septum, wall

thickness 1–1.5 μ m, up to 3 μ m at apices. The axis is straight, 2 symmetrical cells are separated by a septum 2–3 μ m thick. The sculpture is longitudinally striate with 5–7 ridges exposed on each flattened sector. The striate pattern merges to a coarse reticulum at the apices.

The morphology corresponds to the original description of spores of the extant fungus *Megalohypha aqua-dulces* (Ferrer et al., 2007): ascospores 40–55 $\times$ 19–22 μ m (mean = 48.3 $\times$ 18.8 μ m, SD = 2.8 $\times$ 0.91 μ m, n = 30), ellipsoidal, acutely tapered at apices, brown to dark brown, 1-septate, septum appearing as a dark band, both cells of equal shape and size, rough walled with longitudinal sulcate striations lacking appendages or a gelatinous sheath (Plate II).

In addition, the spores from Kongor resemble spores of the fossil form genus *Fusiformisporites* Rouse, 1962 with holotype *Fusiformisporites crabbii* Rouse, 1962 (Kalgutkar and Jansonius, 2000): spores are distinctly fusiform in outline. The unit is split into two equal halves by an equatorial wall that appears to be continuous, thus completely dividing the unit. Longitudinal grooves spread out along the wall from either pole like a spindle; some reach the equator, others stop short of it. Only occasionally is a groove continuous across the dividing wall. The wall is moderately thick, about 3 μ m. Ornamentation levigate. Size range 20–100 μ m. Size of *Fusiformisporites crabbii* is 45–52 μ m (Rouse, 1962).

According to Kalgutkar and Jansonius (2000), *Fusiformisporites* includes forms with less obvious parallel ornamentation elements (striations) (Table 1). The authors place it taxonomically into Fungi Imperfecti, Didymosporae.

3.2. Records of freshwater fungi in Kongor

In the Kongor sediment core, *Megalohypha aqua-dulces* occurs together with freshwater lignicolous fungi such as *Sporoschisma saccardoi*-type, *Dictyosporium heptasporum*, *Dictyosporium digitatum*, *Zopfiella* cf. *submersa*, and *Xylomyces chlamydosporus*-type (Fig. 1). Arboreal pollen varies between 5 and 20% throughout the record. Macroremains of trees and shrubs, including seeds, epidermis and wood, occur in the upper metre of the core.

Below we provide a description of the spores of freshwater fungi from the Kongor site.

Dictyosporium digitatum (KNG 27b; Plate III: 4–6)

Conidia are 58–62 $\times$ 28–32 μ m in size, reddish-brown, multiseptate, composed of 6–7 parallel arms, closely branched from the terminal cell, flattened in one plane. The wall is smooth, about 1 μ m thick. The spore morphology resembles *Dictyosporium digitatum* Chen, Hwang, Tzean, which is commonly found on submerged dead wood in Australia, Brunei Darussalam, Hong Kong, Seychelles, Taiwan, and Thailand (Goh et al., 1999). In Kongor, five spores were found from the Middle and Late Holocene (Fig. 1; Shumilovskikh et al., 2016).

Dictyosporium heptasporum (HdV 1053 by Van Geel et al., 2011; Plate III: 1–3)

Conidia are 62–68 $\times$ 22–26 μ m in size, with 7 parallel arms, branched from the terminal cell in form of a cylinder, apices of arms are incurved. The spore morphology resembles *Dictyosporium heptasporum* with conidia broad ellipsoidal, 42–71 $\times$ 21–25 μ m, branched, composed of ca. 7 rows of cells (Damon, 1952). Van Geel et al. (2011) described type HdV 1053 from Lake Challa in Africa and identified them as *Dictyosporium* cf. *heptasporum* (Garov.) Damon. Two species of *Dictyosporium* have similar size and cylindrical morphology of conidia: *D. heptasporum* and *Dictyosporium cocophilum* (Goh et al., 1999). However, the apex of the arms is straight by the latter species. Therefore, we identified our specimen as *D. heptasporum*. *Dictyosporium heptasporum* has been observed on dead wood and submerged wood in Australia, Belize, Brunei Darussalam, Cuba, Europe, Hong Kong, India, Ecuador, Mexico, Peru, Taiwan, Tanzania, Thailand, USA (Goh et al., 1999). Subfossil finds are known from the Late Holocene from Lake Challa (Africa, Van Geel et al., 2011) and the Middle and Late Holocene from Kongor (NE Iran, Shumilovskikh et al., 2016). Spores of another

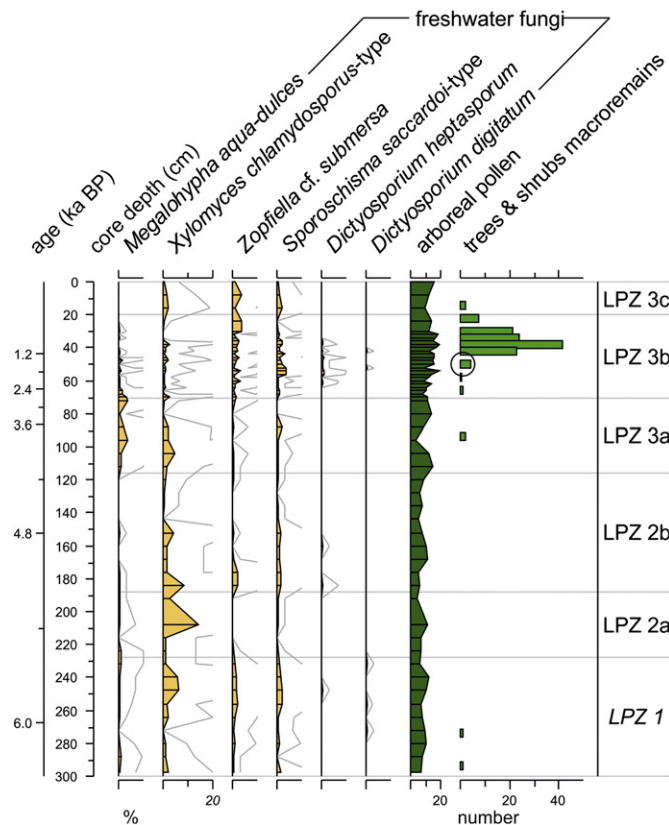


Fig. 1. Freshwater fungi in the palynological record of the Kongor sediment core. Grey lines show exaggeration line $\times$ 10. Circle indicates presence of *Morus alba* wood.

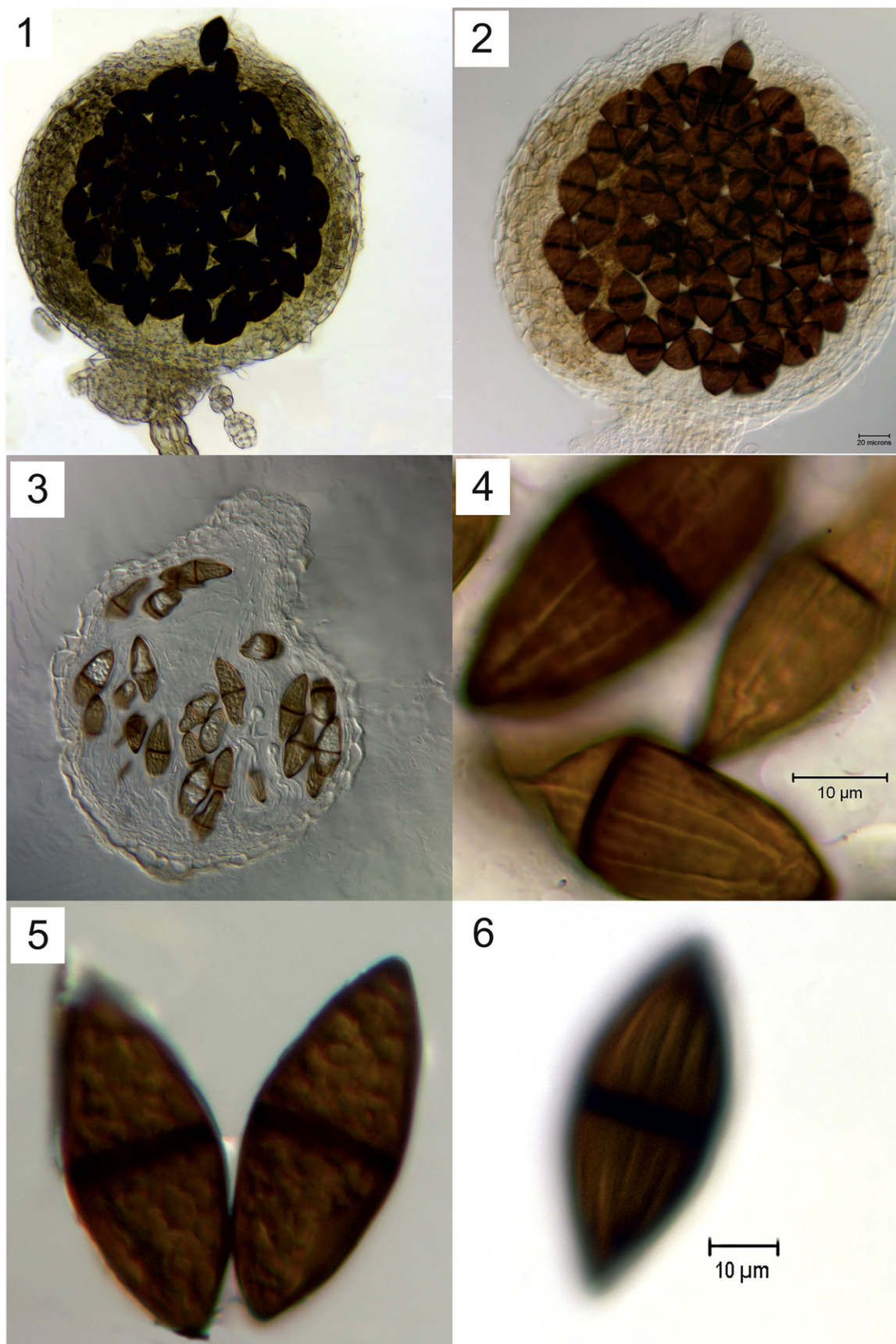


Plate II. *Megalohypha aqua-dulces* (1–2) grown in culture (Holotype AF005-2) and (3–6) collected from wood (Holotype AF005-1): 1–2: stalked ascomata, 3: longitudinal section through ascoma, 4: surface of ascospores with coarse reticulum at apices, 5: longitude section through ascospores, 6: surface of ascospores with sulcate striations. Further details in Ferrer et al. (2007).

Table 1Morphological characteristics of *Megalohypha aqua-dulces* and *Fusiformisporites* species (based on Kalgutkar and Jansonius, 2000; Ferrer et al. 2007).

Species	Length (µm)	Width (µm)	Wall	Septum	Striation	Apical ends	Form
<i>Megalohypha aqua-dulces</i> Ferrer & Shearer 2007	40–55	19–22	–	Dark band	Sulcate striations	Acutely tapered	Fusiform
Subfossil <i>M. aqua-dulces</i> (present study)	47–60	21–27	1–1.5 µm	2–3 µm	5–7 grooves with broader ridges	Facetted sectors	Fusiform
<i>Fusiformisporites annafrancescae</i> Norris 1997	44–55	19–24	0.25–0.5 µm (1 µm at apices)	1–2 µm	0.25–0.5 µm wide, spaced 0.5–1 µm	Facetted sectors	Fusiform
<i>F. crabpii</i> Rouse 1962	45–52	–	–	3 µm	5 grooves exposed on each flattened sector	–	Fusiform
<i>F. duenasii</i> Kalgutkar and Jansonius 2000	28–32	8–10	–	–	–	–	–
<i>F. elongatus</i> Ramanujam & Rao 1978	35–38.5	8–12	1 µm	2.5 µm	Fine striate with ridges as thick as grooves	Blunt ends	–
<i>F. foedus</i> Salujha, Kindra & Rehman 1974	43.2–46.4	24.5–27.2	1.2 µm	2–2.5 µm	10 ridges about 1.5 µm wide	Pointed ends	–
<i>F. keralensis</i> Ramanujam & Rao 1978	51–56	32–36	1.5 µm, much thicker at each end	4 µm	Striae numerous, ridges slightly broader than grooves	Ends truncate to broadly arched	Fusiform to rhomboidal
<i>F. lineatus</i> Rouse & Mustard 1997	58–62	23–29	0.75–1.0 µm uniform	–	3–5 in each cell with a uniform width of 0.3–0.9 µm	Polar cap readily detaches or hinges open	Fusiform
<i>F. lineolatus</i> Sheffy and Dilcher 1971	33.8	18.4	–	1 µm	6–7 ribs	–	Fusiform
<i>F. mackenziei</i> Parsons & Norris 1999	31–41	15.5–24	Thicker at apices	Incompl. septate	15 to 20 ribs	Rounded apices, slight apical nub	Fusiform
<i>F. marii</i> Elsik 1968	21	12	1 µm	Thicker than wall	Two ridges in one hemisphere rotated 90° from two ridges in the opposite hemisphere	–	Capsular to ovoid
<i>F. microstriatus</i> Hopkins 1969	42–49	–	Thick, granular	–	Fine longitudinal ribs	–	Oval
<i>F. paucistriatus</i> Rouse & Mustard 1997	39–42	15–22	0.25–0.5 µm	–	3–10 striae, very thin, irregular	1.5–2 µm thick at apices	–
<i>F. pseudocrabpii</i> Elsik 1968	40–45	25	Inner layer 0.5 µm, outer 0.5–1.5 µm	2 µm; two layers	Broad longitudinal ribs or folds	1.5–2 µm thick at apices	Fusiform
<i>F. rugosus</i> Sheffy and Dilcher 1971	43.5	19.3	–	2–3 µm	Folds and tears, 1 µm thick	Rounded at one apex, with flat basal attachment at other end	Fusiform
<i>F. striatus</i> (Ke & Shi) Kalgutkar and Jansonius 2000	46.4	29	1.5 µm two-layered, outer layer thicker	3 µm divided into two layers	Six sulci	–	Elliptical

species, *Dictyosporium australiense*, have been documented from Holocene peat sediments from Germany (Shumilovskikh et al., 2015).

***Sporoschisma saccardoi*-type** (UG 1002 by Gelorini et al., 2011; Plate III: 13–15)

Conidia are 45–50 × 15–17 µm in size, composed of 4 to 6 cells with dark central and hyaline short apical cells, subtruncate at both ends; the spore is slightly constricted at septa, with a smooth wall 1–2 µm thick. Inner dark septa 3–4 µm thick, distal septa 1–1.5 µm. Central cells are normally equal but sometimes unequal (compare Plate III: 13 and 14). Some spores were found within the conidiophore, showing production of 5 and 3-septate spores by the same fungus specimen (Plate III: 15). Gelorini et al. (2011) associated the type UG 1002 with *Sporoschisma* spp. possibly with *Sporoschisma saccardoi*. In addition, at least *Sporoschisma nigroseptatum* has similar morphology (Goh et al., 1997b) and may be another *Sporoschisma* species, therefore here the *Sporoschisma saccardoi*-type is erected. Both species have been observed on submerged dead wood from Australia, Brunei Darussalam, Ecuador, Europe, Hong Kong, Indonesia, Malaysia, Peru, South Africa, Taiwan (Goh et al., 1997b). Subfossil spore finds are known from African modern lake sediments (Gelorini et al., 2011), Holocene sediments from NE Iran (Shumilovskikh et al., 2016) and terrestrial surface samples from Nepal (Shumilovskikh, unpubl.). Prager et al. (2006) affiliated EMA 12 to *Sporoschisma* or *Chalara* or hyphae. Morphologically EMA 12 differs from conidia of *Sporoschisma saccardoi*-type, and it might be a part of hyphae.

***Xylomyces chlamydosporus*-type** (KNG 7; Plate III: 16–17)

Conidia are 145–255 × 35–40 µm in size, fusiform, straight or slightly curved, dark-brown with pale end cells. Spores have 6–14 septa, 2–5 µm

thick. Spores are constricted at septa. The wall is 2–4 µm thick with scarce irregular longitudinal ornamentation (rugulate to coarse striate). Based on similar morphology, the type KNG 7 is assigned to hyphomycete genus *Xylomyces*. According to mycobank database (www.mycobank.org), the genus *Xylomyces* consists of nine species but only four, *Xylomyces chlamydosporus* Goos, Brooks & Lamore, *Xylomyces giganteus* Goh, Ho, Hyde & Tsui, *Xylomyces rhizophorae* Kohlm. & Volkm.-Kohlm. and *Xylomyces acerosisporus* Oliveira, Malosso & Castañeda, produce large spores over 140 µm long with 6–14, 6–26, 11–43(–64) and 7–15 septa, respectively (Goos et al., 1977; Goh et al., 1997a; Kohlmeyer and Volkmann-Kohlmeyer, 1998; Oliveira et al., 2015). Morphologically, the type KNG 7 is the most close to *X. chlamydosporus* and *X. giganteus*. For this two and possibly upcoming species with same spore morphology the *X. chlamydosporus*-type is erected here.

Xylomyces chlamydosporus is the type species of *Xylomyces* and it was first described from dead, decaying wood submerged in freshwater in southern Rhode Island and Alabama (Goos et al., 1977). The fungus was found during all seasons at water temperature ranging from 1.7 to 23.8 °C; it grows well on laboratory media within temperature range 15 to 30 °C and at salinities of up to 22.15 ‰ (Goos et al., 1977). Its known distribution is from Brunei Darussalam, Hong Kong, Seychelles, and the United States (Goh et al., 1997a). *Xylomyces giganteus* was described from submerged wood in Australia and is also found in South Africa and United Kingdom (Goh et al., 1997a). Our findings reveal the presence of *X. chlamydosporus*-type during the Late Holocene in NE Iran. Campbell et al. (2007) refer *Xylomyces* to the order Jahnulales based on the wide mycelium and molecular evidence, while Sivichai et

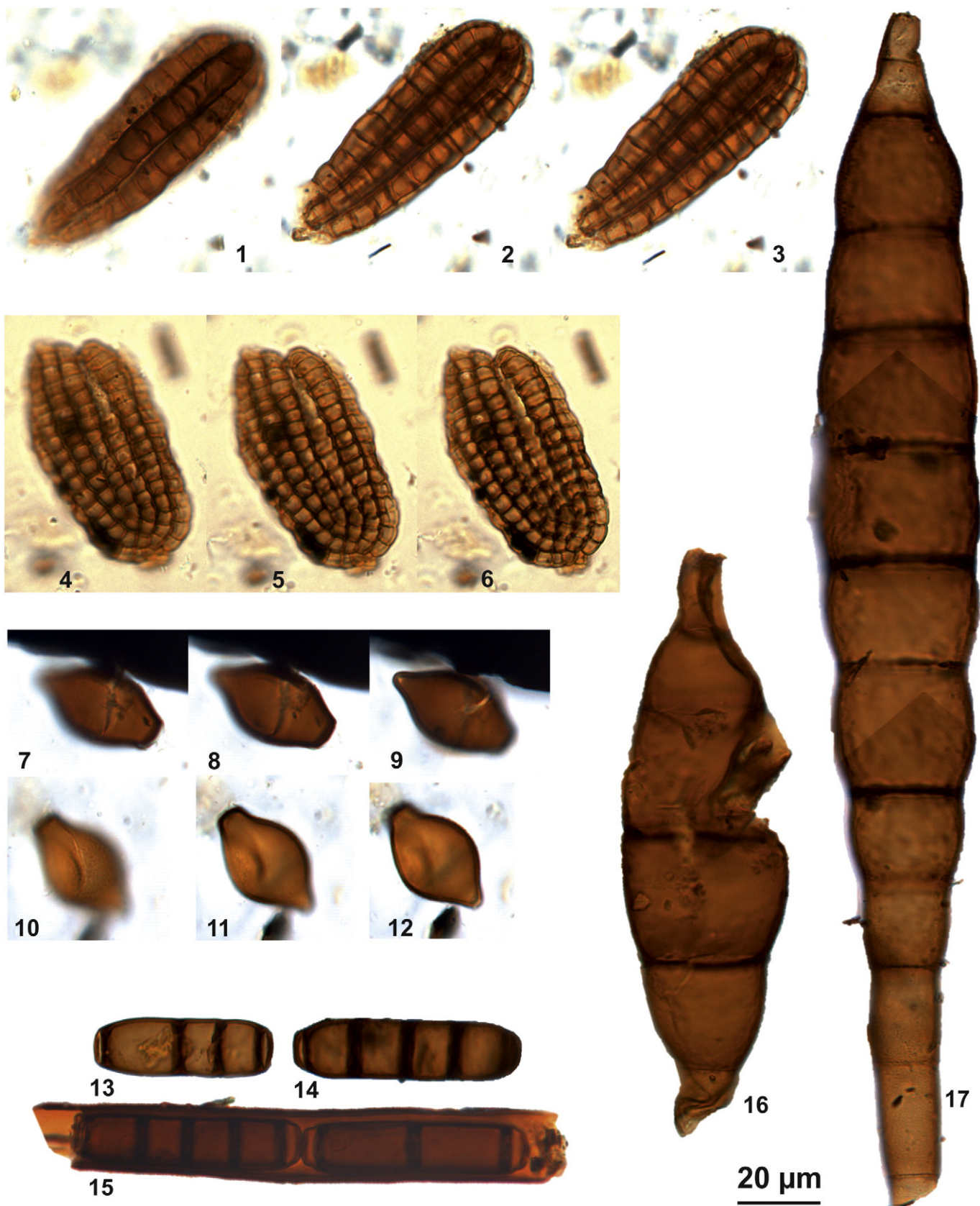


Plate III. Spores of freshwater fungi from the sediment Kongor, NE Iran: 1–3: *Dictyosporium heptasporum* (HdV 1053; core depth 56 cm); 4–6: *Dictyosporium digitatum* (KNG 27b; core depth 272 cm); 7–12: *Zopfiella cf. submersa* (KNG 60; core depth 7–9 – 0 cm, 10–12 – 32 cm); 13–15: single conidiospores (13–14) and conidiophore bearing spores (15) of *Sporoschisma saccardoi*-type (UG 1002; core depth 13 – 0 cm, 14 – 32 cm, 15 – 184 cm); 16–17: conidiospores of *Xylomyces chlamydosporus*-type (KNG 7; core depth 16 – 160 cm, 17 – 184 cm).

al. (2011) made a connection between *X. chlamydosporus* (anamorph) and *Jahnula aquatica* (teleomorph).

Goos et al. (1977) assigned *Xylomyces chlamydosporus* to the fossil fungus *Pluricellaesporites psilatus* Clarke known from late Cretaceous (Clarke, 1965). Recently, spores of *Xylomyces giganteus* are reported from the early Eocene formation Princeton Chert (Klymiuk et al., 2013).

Zopfiella* cf. *submersa (KNG 60; Plate III: 7–12)

Spores are $28\text{--}30 \times 18\text{--}20\ \mu\text{m}$ in size, limoniform, truncate at the base, dark-brown, with a subapical germ pore of $0.5\text{--}1\ \mu\text{m}$ diameter, umbonate at the apex. The wall is $2\text{--}3\ \mu\text{m}$ thick with a coarse scabrate surface. The spores resemble *Zopfiella submersa* Guarro, Al-Saadon, Gené et Abdullah, however its upper melanized cell is smaller ($13.0\text{--}20.5 \times 10\text{--}14\ \mu\text{m}$). It is possible to assume a change of the spore size due to fossilisation processes or laboratory preparations or appearance of other *Zopfiella* species. For example, *Zopfiella inermis* has the largest spores in the genus ($28\text{--}32 \times 18\text{--}21\ \mu\text{m}$) (Malloch and Cain, 1971), corresponding well to the size of KNG 60. Unfortunately, we could not access the original publication for comparison of all morphological characteristics. Therefore, KNG 60 is named *Zopfiella* cf. *submersa*. Although different *Zopfiella* species grow on a wide range of substrates such as herbaceous debris, rotten wood, dung, and soil in terrestrial and marine environments, *Z. submersa* was first described from the Euphrates River in Iran, on submerged dead culms of *Phragmites* and *Arundo donax* (Guarro et al., 1997).

4. Discussion

4.1. Taxonomic relationship between *Fusiformisporites* and *Megalohypha aqua-dulces*

Fusiformisporites has a long identification history. The fossil form genus *Fusiformisporites* was first described by Rouse (1962) from the Tertiary sediments of the Burrard Formation of western British Columbia. In describing the genus *Fusiformisporites* and *F. crabbii* as the holotype, Rouse (1962) suggested a relationship to algae such as *Desmatractum bipyramidatum* (Chodat) Pascher or oospores of *Oedogonium*, both are representatives of the Chlorococcaceae, or representatives of the Class Desmocontae (Division Pyrrophyta). However, this view was not supported.

Later Elsik (1968) recognised the fungal nature of *Fusiformisporites* and affiliated the genus to the extant fungus *Cookeina*, as illustrated by Wolf (1967). Indeed, describing fungal spores from East African lake sediments, Wolf (1967) drew a 2-celled fungal spore with striation and erroneously named it *Cookeina*, a wood inhabiting pantropical genus from the Pezizales. In fact, ascospores of *Cookeina* can bear striations but consist of only one-cell (Iturriaga and Pfister, 2006; Weinstein et al., 2002), contradicting Wolf's (1967) drawings and the morphology of *Fusiformisporites* spores. Nevertheless, *Fusiformisporites* affinity to *Cookeina* was used in further geological studies (Germeraad, 1979; Kalgutkar and Jansonius, 2000; Singh and Chauhan, 2008; Massini and Jacobs, 2011; Taylor et al., 2015). While referring to a personal communication of Elsik in 1996, Rull and Vegas-Villarúbia (1999) suggested that *Fusiformisporites* might be a dung fungus, indicating foraging and grazing animals. However, they did not affiliate it to any species. Carrión and van Geel (1999) and Carrión and Navarro (2002) note an absence of published connections to extant fungal taxa and suggest a possible affinity of *Fusiformisporites* to ascospores of *Nectria peziza*, *Herpotrichia lignicola*, *Parodiella perisporioides* or *Ceriophora palustris*. However, all these species have different spore morphology.

Studying Holocene sediments from salt marshes, Marsh and Cohen (2008) suggested correspondence of *Fusiformisporites duenasii* to *Atrorquata lineata* (Cainiaceae, Xylariales), which was described from standing culms of *Juncus roemerianus*. Similar spore morphology of both species supports this connection.

The morphology of spores from the Kongor sediment core is comparable to the morphology of *Megalohypha aqua-dulces*. The larger size of

the spores from the Kongor core (Table 1) can be explained by fossilisation processes or laboratory treatment or storing in glycerine. Influence of these processes on size is well-known for pollen, but similar studies have not been done for fungal spores. The spores share similar characteristics to some species of the fossil form genus *Fusiformisporites*. From 15 described fossil species of *Fusiformisporites* (Table 1), seven species have a similar size as *Megalohypha aqua-dulces*: *Fusiformisporites annafrancescae*, *Fusiformisporites crabbii*, *Fusiformisporites keralensis*, *Fusiformisporites paucistriatus*, *Fusiformisporites pseudocrabbii*, *Fusiformisporites rugosus*, and *Fusiformisporites striatus*. Apical thickness is described and seen on the drawings of four species: *F. crabbii*, *F. keralensis*, *F. paucistriatus*, and *F. pseudocrabbii*. Only *F. annafrancescae* has distinct faceted sectors in the description. The spore diversity of *Megalohypha aqua-dulces* from the Kongor core shows that faceted sectors are not easy to see in decomposed spores (Plate I: 4). Combining all morphological features, we suggest that *F. crabbii*, *F. keralensis*, *F. paucistriatus*, *F. pseudocrabbii* and *F. annafrancescae* can all be affiliated to *Megalohypha aqua-dulces*. Most likely other representatives of *Fusiformisporites* belong to different fungal taxa.

4.2. Ecology and palaeoecology

The fungus *Megalohypha aqua-dulces* A. Ferrer et Shearer is described from submerged wood in tropical forest streams in Panama and Thailand (Ferrer et al., 2007). Studies on 18S and 28S nuclear ribosomal DNA sequences supported its position in the order Jahnulales (Campbell et al., 2007). Molecular phylogeny places *Megalohypha aqua-dulces* within the *Jahnula* sensu stricto clade in the polyphyletic genus *Jahnula* (Suetrong et al., 2011). Similar to other freshwater ascomycetes, *Megalohypha aqua-dulces* is an important degrader of wood in fresh water, playing a key role in the process of carbon mineralization. It produces a wide spectrum of enzymes such as general cellulases, endoglucanase, β -glucosidase, xylanase, laccase, amylase, pectic lyase, and polygalacturonase, making the degradation of cellobiose, hemicellulose, lignin, starch and pectin possible (Simonis et al., 2008). Ferrer et al. (2007) suggested that the occurrence of soft rot cavities was caused by *Megalohypha aqua-dulces*, however further experimental studies did not support this conclusion (Simonis et al., 2008).

In general, freshwater ascomycetes grow in freshwater habitats and complete part or the whole of their lifecycle in water (Cai et al., 2006). They can be recorded in terrestrial and marine habitats and therefore are divided in four major groups according to their occurrence: 1) exclusively freshwater; 2) freshwater and terrestrial; 3) freshwater and marine; 4) freshwater, marine and terrestrial (Vijaykrishna et al., 2006). Since *Megalohypha aqua-dulces* was described from freshwater habitats, and the known Holocene occurrences are from freshwater environments, the species likely belongs to the first group. However, spores of *F. pseudocrabbii* were described from the Tertiary coastal to marginal marine environment in the Eastern Niger Delta in Nigeria (Ajaegwu et al., 2012), possibly suggesting the ability of *Megalohypha aqua-dulces* to occupy marine habitats.

While the entire group of freshwater fungi was highlighted for its importance in the palaeoecological studies (Sherwood-Pike, 1988), *Megalohypha aqua-dulces* has a potential to be used as palaeoecological indicator for presence of wood. In the Kongor sediment core, *Megalohypha aqua-dulces* represents a part of the freshwater fungal spore assemblage (Fig. 1). Being described from submerged wood, *Megalohypha aqua-dulces* indicates presence of decaying wood and therefore trees or shrubs growing on, or near the sampling site. This interpretation is supported by the presence of other wood decomposers such as conidia of *Xylomyces chlamydosporus*-type, *Dictyosporium digitatum* and *Dictyosporium heptasporum* (Cai et al., 2006). In addition, *Zopfiella* cf. *submersa* grows on herbaceous debris or wood while *Sporoschisma saccardoi*-type is saprobic on decaying wood and bamboo culms (Cai et al., 2006). Interestingly, the continuous presence of woody vegetation on the Kongor site is neither indicated by pollen nor by

macroremains (Fig. 1), but by insects, strongly suggesting the presence of riverine forests with *Alnus* or *Salix* close to the site (Shumilovskikh et al., 2016). In fact, pollen of woody vegetation is present in the pollen diagram (4–20%), but due to possible long-distance transport it is not possible to infer local vegetation (Fig. 1). Macroremains of trees and shrubs provide a very local signal but can rapidly become decomposed. Remains of *Rubus*, *Sambucus*, *Morus*, and *Viscum* occur in the upper 60 cm of the core, but are almost completely absent in the lower part (Fig. 1), possibly due to decomposition. Considering the biology of *Megalohypha aqua-dulces*, it is possible that wood of the above-mentioned trees and shrubs as well as of shrubby *Artemisia* or *Chenopodiaceae* might be the possible substrates for the development of freshwater lignicolous fungi at the Kongor site.

The presence of spores of freshwater fungi in sediments provides opportunities to infer the presence of woody vegetation development at a site. This can be used, for example, for testing of the gallery forest theory in South America. Our preliminary results on the sediment core São Francisco de Assis from southern Brazil (Behling et al., 2005) provides evidence for the first occurrence of *Megalohypha aqua-dulces* in association with *Potamomyces* spp. (Schlütz and Shumilovskikh, 2013; Nuñez Otaño et al., 2016) in the mid-Holocene while it is absent from the sediment during the late glacial and early Holocene. In contrast, a core from Aguas Claras near Porte Alegre (SE Brasil) shows the presence of *Megalohypha aqua-dulces* during the late glacial (Medeanic and Silva, 2010).

Freshwater ascomycetes have pan-tropical or pan-temperate distributions and may overlap in warm temperate or subtropical regions. The optimum temperature for tropical and temperate freshwater ascomycetes is 20–25 °C (Vijaykrishna et al., 2006). Recent documentation of *Megalohypha aqua-dulces* spores in Holocene peat cores from Indonesia (Fig. 2) confirms its pantropical distribution. Occurrence of the fungus in the peatland of Northern Iran and southern Brazil expands the known distribution of *Megalohypha aqua-dulces* to more arid subtropics, highlighting its ecological plasticity.

The modern distribution of *Megalohypha aqua-dulces* in the tropics, and its Holocene occurrence in the subtropics suggest that it is a good indicator of warm humid conditions in the Tertiary, as proposed from

geological records for *Fusiformisporites* (Elsik, 1968; Kumar, 1990; Oboh, 1992; Kalgutkar, 1997). Carrión and van Geel (1999) and Carrión and Navarro (2002) use *Fusiformisporites* sp. as indicators of organic matter decomposition and peaty layer formation in deposits of the Canal de Navarrés (Spain), whereas the presence of *Megalohypha aqua-dulces* provides evidence of decaying wood in the peat.

4.3. Geological evidence for the evolution of aquatic ascomycetes

Freshwater fungi colonise streams around the world, and thus they are not restricted by geographical barriers (Wood-Eggenschwiler and Bärlocher, 1985; Vijaykrishna et al., 2006). Hyde and Goh (2003) suggest that fungi 1) might have evolved before the split of the continents, or 2) have been carried between continents on plant substrates, or 3) fungal spores may have dispersed by animals or wind. Ecological and molecular data suggest that freshwater ascomycetes should have evolved from their terrestrial ancestors (Vijaykrishna et al., 2006) and may have multiple origins (Belliveau and Bärlocher, 2005). Molecular studies propose that the earliest divergence of freshwater species in Jahnulales occurred at 380 ± 100 MYA (Paleozoic period), however most of the freshwater lineages appear to have diverged during the Mesozoic period (66–245 MYA) (Vijaykrishna et al., 2006). In contrast, palaeontological studies reveal that fungal diversity increased after the Cretaceous–Tertiary boundary and that fungi underwent rapid specialisation during the Tertiary, connected with the evolution of angiosperms (Graham, 1962; Kalgutkar, 1993, 1997).

In the absence of the molecular data for the evolution of *Megalohypha aqua-dulces*, palaeontological data reveal the occurrence of *Fusiformisporites* since the Upper Cretaceous (Fig. 2), corresponding well with the diversification of flowering plants and pointing to a co-evolution of both groups. The first description of *Fusiformisporites*, *F. crabbii*, was made from Upper Cretaceous to the Middle Eocene sediments of the Burrard Formation of western British Columbia (Rouse, 1962). Further Upper Cretaceous finds of *Fusiformisporites* are known from NW Bolivia (Vajda-Santivanez, 1999), NW Ellesmere Island in Canada (Falcon-Lang et al., 2004) and the north-western desert in Egypt (El Beialy et al., 2010).

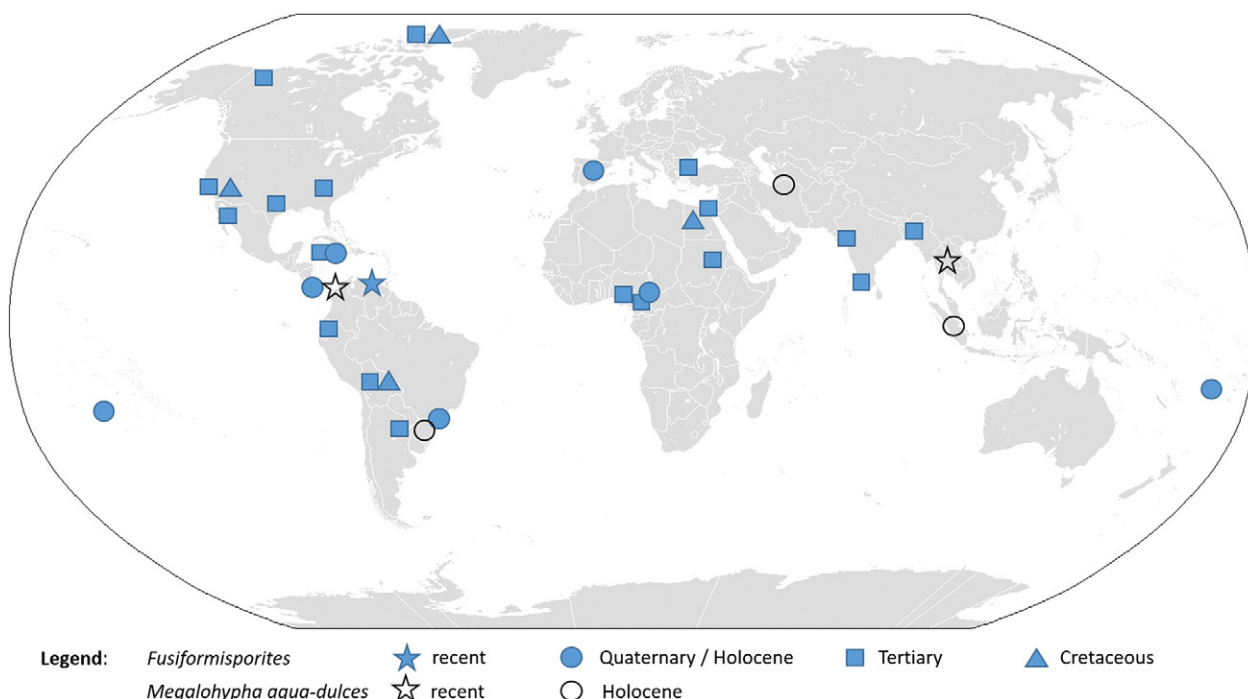


Fig. 2. Recent distribution and geological records of *Megalohypha aqua-dulces* and *Fusiformisporites*.

During the Tertiary, *Fusiformisporites* evolves further and becomes more diverse and abundant (Fig. 2, Elsik, 1976). In the Paleogene, *Fusiformisporites pseudocrabii*, *Fusiformisporites crabii*, *Fusiformisporites lineolatus*, *Fusiformisporites lineatus*, *Fusiformisporites annafrancescae*, *Fusiformisporites microstriatus*, *Fusiformisporites paucistriatus*, *Fusiformisporites rugosus* and other *Fusiformisporites* species are documented in the USA (Elsik, 1968; Sheffy and Dilcher, 1971), Canada (Kalgutkar, 1997; Norris, 1997), coasts of North America (Mustard and Rouse, 1994; Jansonius and Kalgutkar, 2000), Jamaica (Germeraad, 1979), central Ecuador (Jaillard et al., 2004), India (Saxena, 2006; Singh et al., 2011), Northern Taurus basin (Turkey) (Ediger and Alişan, 1989), Cameroon (Salard-Chebaldaff, 1979) and the Ethiopian Plateau (Massini and Jacobs, 2011). Neogene finds of *Fusiformisporites* are less diverse. *Fusiformisporites pseudocrabii* was found in the Eastern Niger Delta in Nigeria (Ajaegwu et al., 2012) and in the Parana Formation of Argentina (Garralla, 1989). *Fusiformisporites crabii* is known from the Niger Delta (Bankole et al., 2014) and in Mizoram of NE India (Nandi and Sinha, 2007; Kar et al., 2010). *Fusiformisporites acutus* is described from the Miocene Quilon Beds of Kerala State in India (Kumar, 1990). Other unidentified *Fusiformisporites* are documented in the Niger Delta (Obboh, 1992), Cameroon (Tchouatcha et al., 2010), the Gulf of Suez in Egypt (El Beialy et al., 2005), the Gulf of California (Helenes et al., 2009), and India (Singh and Chauhan, 2008).

During the Quaternary, *Fusiformisporites* was found in the late glacial sediments in southern Brazil (Medeanic and Silva, 2010) as well as in the Holocene sediments of the Changuinola peat deposit in Panama (Phillips, 1995), at Holland bay and Bowden in Jamaica (Germeraad, 1979), SW Pacific islands (Macphail and Stevenson, 2004) and in the late Quaternary – Holocene sediments of Spain (Carrión and van Geel, 1999; Carrión and Navarro, 2002). Rull and Vegas-Villarúbia (1999) found *Fusiformisporites* in surface samples from a coastal basin in Venezuela. Al-Ameri and Jassim (2011) indicated the presence of *Fusiformisporites* in the late Quaternary sediments of southern Iraq, but a photo of the hyaline spore does not correspond to *Fusiformisporites*. In addition, Holocene finds of *Fusiformisporites*, new records of *Megalohypha aqua-dulces* are documented for north-eastern Iran, southern Brazil and Indonesia (Fig. 2).

Based on *Fusiformisporites*, the evolution of *Megalohypha aqua-dulces* can be traced to the late Cretaceous, defining its divergence within Jahnulales (Vijaykrishna et al., 2006).

5. Conclusions

Several species of the form genus *Fusiformisporites* have been described from Cretaceous to Holocene times (Kalgutkar and Jansonius, 2000). Not all of them seem to fulfil the morphological criteria of the genus *Fusiformisporites* as erected by Rouse (1962). The type species *Fusiformisporites crabii* and the later erected *Fusiformisporites annafrancescae*, *Fusiformisporites keralensis*, *Fusiformisporites paucistriatus*, and *Fusiformisporites pseudocrabii* are in close morphological accordance to the extant fungi *Megalohypha aqua-dulces* (Ferrer et al., 2007). *Megalohypha aqua-dulces* is a lignicolous freshwater fungus from the tropics belonging to order Jahnulales. Its substrate and habitat preference is underlined by the co-occurrence of spores from additional lignicolous freshwater taxa as *Sporoschisma saccardoi*-type, *Dictyosporium heptasporum*, *Dictyosporium digitatum*, *Zopfiella cf. submersa*, *Xylomyces chlamydosporus*-type in the Holocene record from NE Iran (Shumilovskikh et al., 2016). Until now known recent and Holocene finds of *Megalohypha aqua-dulces* indicate that it can be expected in appropriate habitats of the tropics and subtropics including semi-arid regions. Its evolutionary history reaches back into the late Cretaceous and is most probably associated with the diversification of angiosperms. In the fossil context, *Megalohypha aqua-dulces* is a good indicator for decaying wood, even if macroremains of trees and shrubs do not appear in the sediment.

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