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Groenlandia pescheri sp. nov. (Potamogetonaceae) from the Late Oligocene Fossil-Lagerstätte Enspel (Westerwald, Germany)

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ABSTRACT. The new species *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., belonging to the family Potamogetonaceae, is described from the Late Oligocene Fossil-Lagerstätte Enspel (Westerwald, Germany). The species is characterized by sub-oppositely arranged leaves without observable stipule-like appendages at the leaf bases and a very thin exocarp (both characteristics of the aquatic genus *Groenlandia* J. Gay) with a spiked crest (which differs from the only other species included in this genus, the modern *Groenlandia densa* (L.) Four.). The taxon represents the first pre-Quaternary record of the genus *Groenlandia*, which is usually regarded as a basal sister group of all other Potamogetonaceae.

KEYWORDS: *Groenlandia*, Potamogetonaceae, Oligocene, crater lake, Enspel

INTRODUCTION

The Fossil-Lagerstätte Enspel (Fig. 1) offers a unique window into the Late Oligocene biota of Central Europe (for an overview see Poschmann et al. 2010). Besides the outstanding preservation of molecular fossils (Stankiewicz et al. 1997), as well as the occurrence of various microfossils (Köhler & Clausing 2000, Schiller & Wuttke 2014, 2015), palynomorphs (Herrmann et al. 2009, 2010), macro-plants (e.g. Köhler & Uhl 2014, Uhl 2014, 2015), arthropods (e.g. Wedmann et al. 2010) and traces of interactions of the latter two groups (Gunkel & Wappler 2015), some of the recorded vertebrates such as fish (Böhme 2000), amphibians (e.g. Rocek & Wuttke 2010), birds (e.g. Mayr et al. 2006, Mayr 2013) and mammals (e.g. Storch et al. 1996, Engler & Martin 2015) show soft-part preservation (cf. Toporski et al. 2002, Barden et al. 2015). The site has an excellent age control based not only on biostratigraphy (e.g. Storch et al. 1996, Engesser & Storch 1999) but also on absolute dating of basalts over- and underlying the lake sediments (Mertz et al. 2007). Hitherto, excavations at this site yielded almost 23 800 recorded fossils, including about 12 300 insects, 300 invertebrates (other than insects), 2600 vertebrates and 8600 plant specimens.

In their monograph on the macroflora of this locality, Köhler and Uhl (2014) described fruits of *Potamogeton corticosus* Nikitin in Dorofeev, as well as an isolated spike of putatively unripe fruits of *Potamogeton* sp., which could not be determined to species level. Additionally, Uhl (2014) discussed two morphologically slightly different types of enigmatic plant fossils from this locality, which both

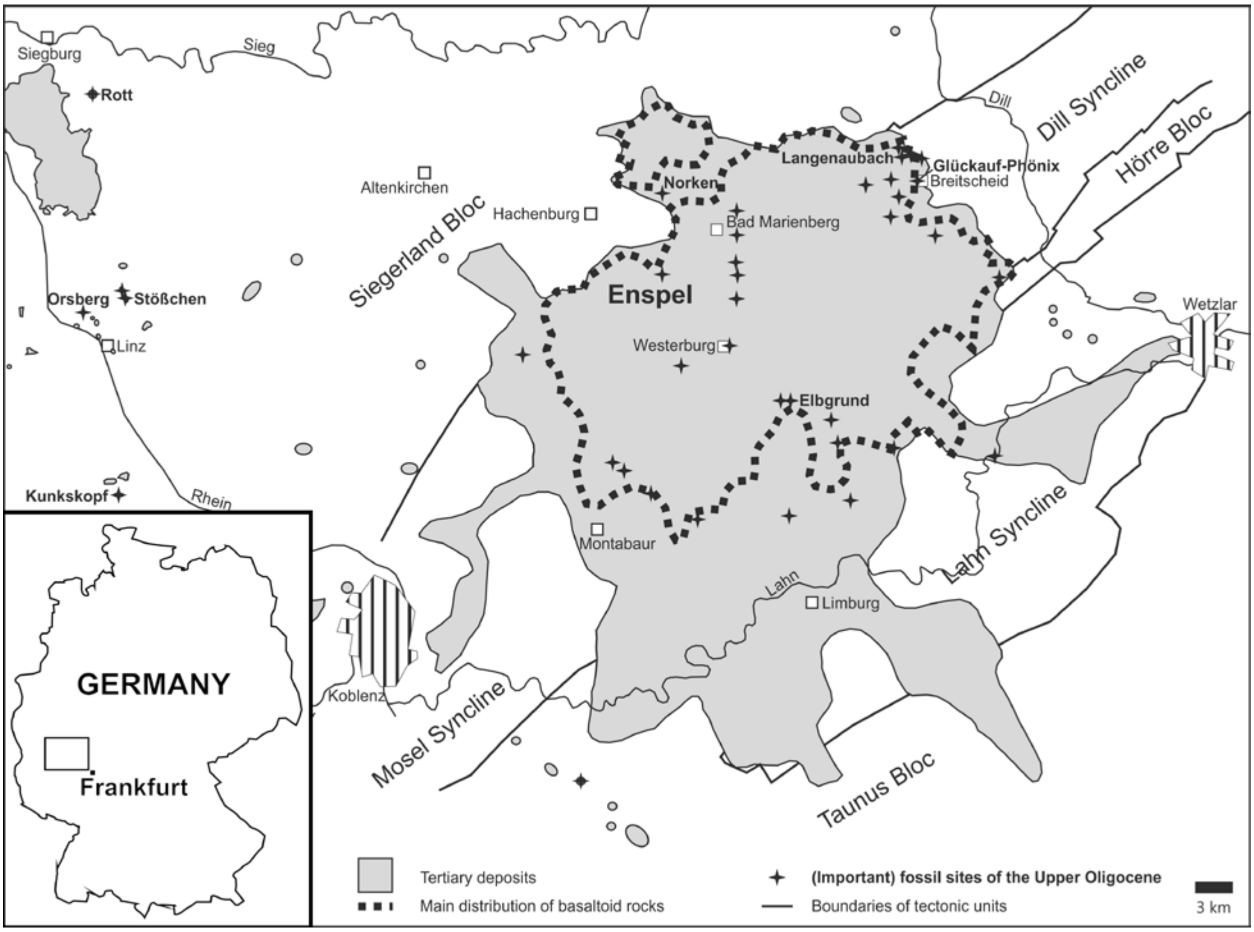

Fig. 1. Geological overview map of the Westerwald Tertiary; ✦ fossil localities (after Schindler & Wuttke 2010)

were characterized by slender axes divided in nodes and internodes. Those two morphotypes differ in the length of the internodes, width of the axis and mode of branching, but further morphological details were not visible due to initial decay which occurred prior to embedding of the specimens in the sediment. Thus it was even unclear whether the two problematic morphotypes belong to a single natural taxon or to two or more different taxa.

New material collected during excavations in 2014 and 2015 helped to elucidate this enigma. These new findings made it clear that the two morphotypes indeed belong to the same taxon, and it was also possible to identify this taxon as belonging to the aquatic genus *Groenlandia* J. Gay, today a monotypic genus of the family Potamogetonaceae. Based on the material discovered in 2014 and 2015, this taxon is described here as a new species of the genus *Groenlandia*.

MATERIAL AND METHODS

The "oilshales" excavated at Enspel represent the sedimentary infill of a crater lake (e.g. Felder et al. 1998, Pirrung et al. 2001, Schindler & Wuttke 2010, 2015). Biostratigraphically, the locality can be assigned to mammal zone MP28 (based on the occurrence of eomyid rodents; Storch et al. 1996, Engesser & Storch 1999). Radioisotopic dating of basalts on the base and top of the Enspel sedimentary sequence yielded an age of 24.79–24.56 Mya for the lake filling (Mertz et al. 2007). For further details about the geology of the Enspel locality see Schindler and Wuttke (2010, 2015) and Schäfer et al. (2011).

The material studied here comes from excavations conducted by GDKE RLP, Direktion Landesarchäologie/Erdgeschichte. It is part of the Landessammlung für Naturkunde Rheinland-Pfalz, with accession numbers PB 2006/5166-LS, PB 2011/5352-LS, PB 2012/5383-LS, PB 2012/5406-LS, PB 2012/5415-LS, PB 2015/5442-LS, PB 2015/5443-LS, PB 2015/5444-LS, PB 2015/5445-LS and PB 2015/5446-LS.

Specimens were photographed immersed in water using a Canon EOS 600D SLR camera equipped with a Canon EFS 60 mm macro lens. CombineZM image-stacking software (by Alan Hadley) was used to combine photographs of differing focal planes into a composite with enhanced depth of field.

All measurements were taken from calibrated images with the aid of the Fiji software package (Schindelin et al. 2012).

SYSTEMATIC PALAEOBOTANY

Magnoliophyta Brongn.

Monocotyledonae

Potamogetonales Dumortier

Potamogetonaceae Berchtold & Presl

Groenlandia J. Gay

Type species: ***Groenlandia densa***
(L.) Fourreau

Groenlandia densa, the only species included so far in the genus, is an aquatic plant, usually growing in rivers, streams, canals and ditches, occasionally in ponds and lakes (Akhani 2014). It is distributed in large parts of Europe, North Africa and the Middle East, reaching into the Caucasus. It reaches as far north as southern Scandinavia and in the east to the Baltic states and Iran (Akhani 2014). Fossil endocarps of this taxon are known from numerous Quaternary localities within Europe (e.g. Aalto 1970, Godwin 1975), but pre-Quaternary records are missing up to now.

Species ***Groenlandia pescheri***
D. Uhl & Poschmann sp. nov.

Synonymy.

2014? *Potamogeton* sp., Köhler & Uhl, p. 42, plate 12, fig. 15 (fertile remains)

2014 Problematikum, Uhl, p. 46, fig. 2–5 (vegetative remains)

Holotype. Large fertile specimen; PB 2015/5443-LS, Landessammlung für Naturkunde Rheinland-Pfalz in Mainz (Germany); Pl. 1, fig. 1.

Locus typicus. Enspel (Westerwald, Germany).

Stratum typicum. "Oilshale", basal part of layer S14, Enspel Formation, Late Oligocene (MP 28), Chattian (Schäfer et al. 2011) (Fig. 2).

Derivatio nominis. In honour of Dr. Michael Pescher (Adrian Basalt Company), for his continuous support of the early scientific excavations at Enspel during the 1990s.

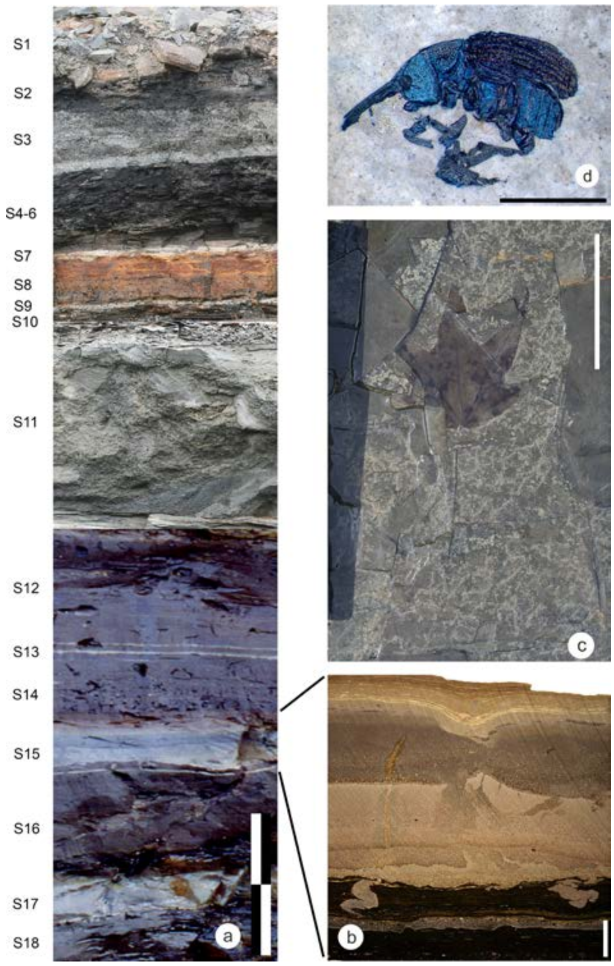

Fig. 2. Profile of the uppermost Enspel sequence; **a** – Standard profile of the uppermost Enspel sequence subjected to scientific excavations, compiled from photographs of various sites. Scale bar = 20 cm. Numbering of layers according to Schindler & Wuttke (2015); **b** – Event layer S15. Top shows finely laminated facies at the base of S14. Bottom: Top of "oilshale" S16. Scale bar = 10 mm; **c** – Bedding, plane view in basal part of S14, showing net-like filamentous microbial mats and well-preserved leaf of *Acer integerrimum* (Viviani) Massalongo. Scale bar = 10 cm; **d** – Well-preserved weevil from the base of S14, showing structural colours. Scale bar = 2 mm

Diagnosis. Species of the genus *Groenlandia*, characterized by a spiked crest on the keel of the thin exocarp. Number of drupe-like fruits (=flowers) per spike 2–4 [– 6]. Leaves amplexicaul and (sub-)oppositely arranged throughout the shoot, without observable stipule-like appendages.

Description. Shoot with slender axes, repeatedly branching (Pl. 1, fig. 1; Pl. 2, fig. 1). Leaves (sub-)oppositely arranged throughout shoot, amplexicaul, without observable stipule-like appendages (Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 3, figs 1–3; Pl. 4, figs 1–4). Leaves parallel-veined (Pl. 3, fig. 2), up to 16 mm long and 1.5–2 mm

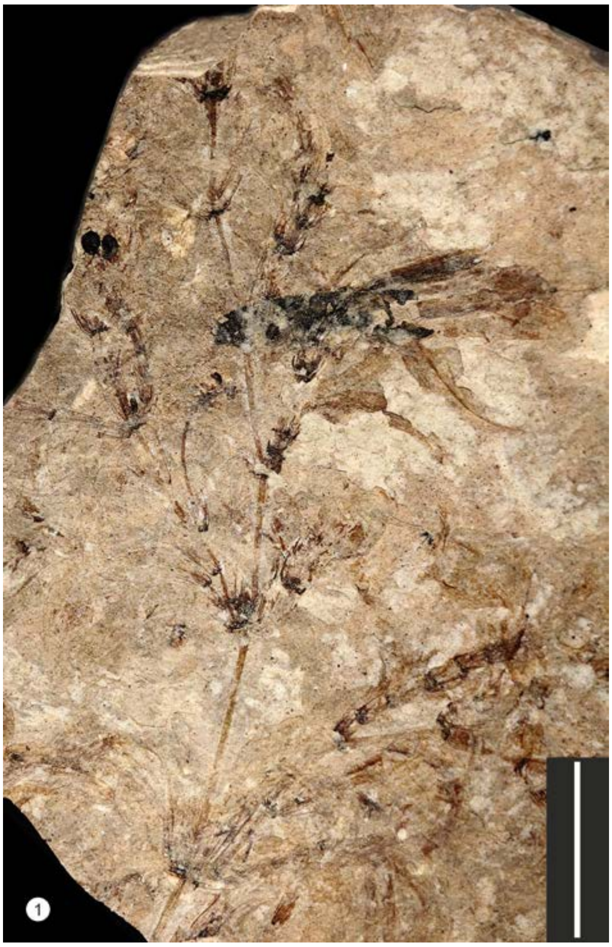

Plate 1. **1**. Holotype of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov.; PB 2015/5443-LS b. Scale bar = 10 mm

wide (Pl. 1, fig. 1; Pl. 2, fig. 1; Pl. 4, fig. 4), oblong and ± linear with rounded apex (Pl. 4, fig. 4). Shoot divided in nodes and internodes (Pl. 1, fig. 1; Pl. 2, fig. 1). Length of internodes variable, depending on position within plant (Pl. 1, fig. 1; Pl. 2, fig. 1). Internodes up to ca 0.5 mm wide (Pl. 2, fig. 1). Branches originate oppositely in nodal areas (Pl. 1, fig. 1; Pl. 2, fig. 1).

Fruits drupe-like, with spiked crest on keel of thin exocarp (Pl. 5, fig. 1; Pl. 6, figs 1–5). Number of fruits (=flowers) per spike 2–4 [– 6] (Pl. 5, fig. 1; Pl. 6, figs 1–5). Length of endocarps: average 1.42 mm, max. 1.71 mm, min. 1.14 mm (n=9); width of endocarps: average 1.12 mm, max. 1.35 mm, min. 0.92 mm (n=9); length : width ratio of endocarps: average 1.26, max. 1.48, min. 1.13 (n=9). Endocarps with large distinct furrow marking partition wall (Pl. 6, figs 1–3, 5).

Remarks. Based on the habitus of the plants discovered at Enspel, as well as the general morphology of the fruits, the new taxon can be assigned to Potamogetonaceae (e.g. Les & Haynes 1996, Wiegleb & Kaplan 1998). This family includes the three genera *Potamogeton* L. (with 72 modern species and 99 hybrids), *Stuckenia* Börner (with 7 modern species and 6 hybrids) and monotypic *Groenlandia* J. Gay (Kaplan et al. 2013). This high diversity, together with reduced morphology as well as high phenotypic variability, makes this family one of the taxonomically most difficult families of modern aquatic plants (Wiegleb & Kaplan 1998, Kaplan 2002, Kaplan et al. 2013). Additionally, a large number of fossil species assigned to *Potamogeton,* as well as *Stuckenia* (in the literature often recognized as *Potamogeton* subgen. *Coleogeton*) are known from a variety of Palaeogene and Neogene localities (e.g. Kirchheimer 1957, Dorofeev 1963, 1977, Knobloch 1977, Collinson 1982, Mai 1985, 1987, 1995, Teodoridis 2007, Doweld 2015, 2016). In contrast, fossils

Plate 2. **1**. Large vegetative specimen of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., showing mode of branching as well as opposite attachment of leaves; PB 2015/5445-LS a. Scale bar = 10 mm

Plate 3. **1**. Two partly decayed axes of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., showing opposite attachment of amplexicaul leaves; PB 2015/5444-LS a. Scale bar = 10 mm; **2**. Leaf bases of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., exhibiting parallel venation; PB 2015/5442-LS a. Scale bar = 5 mm; **3**. Leaf bases of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov.; one of the leaves is moderately well preserved; the other (upper) leaf is almost completely missing, with only part of the amplexicaul leaf base preserved; PB 2006/5166-LS. Scale bar = 10 mm

assigned to *Groenlandia*, that is, the modern species *Groenlandia densa*, have so far only been reported from Holocene and Pleistocene deposits (e.g. Aalto 1970, Godwin 1975, Hoffmann et al. 1998, Mania et al. 2010) but not from older periods.

Groenlandia differs from *Potamogeton* and *Stuckenia* in a number of aspects (cf. Les & Haynes 1996, Wiegleb & Kaplan 1998, Kaplan et al. 2013, Tab. 1). Not all of these aspects, such as chromosome number, can be observed in the fossil specimens described here. Nevertheless, it is possible to assign the new species to the genus *Groenlandia* as other characters of the specimens from Enspel are in agreement with this taxon but not with the other two genera included in Potamogetonaceae:

1) All leaves in the specimen from Enspel are arranged (sub-)oppositely throughout the stem and not only in the floral region as in *Potamogeton* and *Stuckenia* (?).

2) No stipule-like appendages could be observed in the material from Enspel.

3) The fruit type seems to be drupe-like, with a thin exocarp.

4) The number of fruits (=flowers) per spike is 2–4 [– 6].

The new species differs from *Groenlandia densa* primarily in the form of the crest on the keel of the exocarp, which is spiked in the Oligocene species, in contrast to the sharp but smooth keel in the modern species. Thus it seems justified to erect a new species belonging to the genus *Groenlandia*. Additionally, no stipule-like appendages could be observed in the fossil specimen, not even on involucral leaves as in modern *G. densa*. However, these stipules are sometimes difficult to detect in

Table 1. Selected differences between the genera *Groenlandia, Potamogeton* and *Stuckenia* (based on Les & Haynes 1996, Wiegleb & Kaplan 1998, Kaplan et al. 2013)

Fruit type	*Groenlandia*	*Potamogeton*	*Stuckenia*
	drupe-like	achene-like	achene-like
leaf arrangement	predominantly sub-opposite throughout stem	alternating throughout stem, subopposite only in floral region	alternating throughout stem, subopposite only in floral region
stipule-like appendages	absent on most leaves, lateral ones being produced only on involucral leaves	axillary or adnate (< 1/2 length of stipule) stipules on all leaves	adnate (≥ 2/3 length of stipule) stipules on all leaves
number of flowers per spike	(1–)2(–4)	4 to many	4 to many
submersed leaves	translucent, flat and without grooves or channels	translucent, flat and without grooves or channels	opaque, channeled and turgid
chromosome number	n = 15	n = 13–14	n = 13

fresh and herbarium specimens of *G. densa*, so it is not clear whether this character can be used for separation of the fossil species from the modern species.

Endocarps of *Groenlandia pescheri* are morphologically very similar to endocarps of *Potamogeton pygmaeoides* Mai from the Late Oligocene of Mockrehna in Saxony, Germany, described by Mai (1987). The form of the endocarp (which is, however, slightly more elongated in *P. pygmaeoides*) and especially the presence of a large distinct furrow marking the partition wall (also occurring in modern *Groendlandia densa* endocarps; Aalto 1970), are similar in both taxa. They differ in size, as shed and thus probably ripe fruits of *Potamogeton pygmaeoides* are consistently smaller than the largest, unshed (probably unripe) seeds of *Groenlandia pescheri* (cf. Mai 1987).

However, as the exocarp is largely missing or heavily eroded in the specimens of *Potamogeton pygmaeoides* described and figured by Mai (1987), it is not possible at the moment to decide whether *Potamogeton pygmaeoides and Groenlandia pescheri* sp. nov. might in fact be congeneric or even conspecific. The morphological similarities between endocarps of *Groenlandia pescheri* and *Potamogeton pygmaeoides*, as well as the modern *Groenlandia densa*, make it at least likely that all three taxa are closely related and may in fact belong to the same genus.

Groenlandia represents a basal sister group of other Potamogetonaceae (e.g. Lindqvist et al. 2006), and members of the genus *Potamogeton* are known since at least the Palaeocene (Knobloch 1977, Mai 1995). Besides a large number of fossil taxa attributed to *Potamogeton* and *Stuckenia* based on carpological remains from Paleogene and especially Neogene deposits of Europe and Northern Asia (e.g. Kirchheimer 1957, Dorofeev 1963, 1977, Knobloch 1977, Collinson 1982, Mai 1985, 1987, 1995, Teodoridis 2007, Doweld 2015, 2016), a number of vegetative remains attributed to Potamogetonaceae or especially *Potamogeton* have been described in the literature:

Potamogeton seifhennersdorfensis Engelhardt from the Oligocene of Seifhennersdorf in Saxony is known from vegetative and carpological remains (Mai 1963, Walther & Kvaček 2007). According to Mai (1963) the leaves are alternating and possess “stipules”, and the leaves have five veins with a larger central vein, leaves up to 2.2 mm wide and rarely up to 3 cm long. In contrast, Walther and Kvaček (2007) stated that this taxon has sub-oppositely arranged leaves throughout the stem, but figured specimens show that the leaves have a more alternating arrangement than in *Groenlandia pescheri* sp. nov. Additionally, the venation pattern, with a clear mid-rib in *Potamogeton seifhennersdorfensis,* is different from the new taxon. The same is true for isolated leaves of *Potamogeton* sp. described Walther and Kvaček (2007), which have a venation pattern resembling *Potamogeton seifhennersdorfensis*.

Sitár (1969) described leaves of *Potamogeton martinianus* Sitár from the Miocene of the Turiec basin in the Western Carpathians. These leaves are wide-elliptic with a constricted base, clearly differing from the oblong and ± linear leaves in the new taxon described here. Additional occurrences of *P. martinianus* are also known from other Miocene deposits, for example the Styrian basin in Austria (Kovar-Eder & Krainer 1990, 1991).

Heer (1855) decribed specimens of *Potamogeton bruckmanni* A. Braun based on leaves from Öhningen, which seem to be very similar to *Potamogeton martinianus* but with a more

Plate 4. 1. Axes of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., showing opposite attachment of amplexicaul leaves as well as opposite attachment of branches; PB 2012/5415-LS. Scale bar = 10 mm; **2**. Axes of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., showing opposite attachment of amplexicaul leaves as well as opposite attachment of branches; PB 2015/5444-LS b. Scale bar = 10 mm; **3**. Axis of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., showing opposite attachment of amplexicaul leaves; PB 2012/5383-LS. Scale bar = 10 mm; **4**. Axes of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., showing opposite attachment of amplexicaul leaves and also leaf morphology (right axis); PB 2015/5442-LS a. Scale bar = 10 mm

slender leaf base. *Potamogeton geniculatus* A. Braun mentioned by Heer (1855) from Öhningen is certainly not a *Potamogeton* (Kirchheimer 1957). Many other vegetative remains of putative Potamogetonaceae have been described from Palaeogene and Neogene deposits, such as *Frimmersdorfia natans* (Weyland 1959) or *Wackersdorfia dubia* (Peters 1963) from Miocene deposits, but these are generally too fragmentarily preserved to be assigned reliably to the family.

TAPHONOMY AND PALAEOECOLOGY

Although remains of aquatic plants are less frequently preserved in most localities, due to a number of taphonomic factors, there are

Plate 5. 1. Fertile specimen of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., exhibiting several spikes with up to six (?) seeds per spike; PB 2015/5446-LS a. Scale bar = 5 mm

several examples of excellent preservation of (almost) entire plants from a number of localities (e.g. Collinson 1988, Kvaček 2007a). There are also examples of numerous plants or organs of single taxa of water-plants occurring within individual horizons, such as leaves of *Potamogeton martinianus* Sitár which occur packed together in a few layers at the late Miocene localities at Würth near Kirchberg/Raab and Reith near Unterstorcha in Austria (Kovar-Eder & Krainer 1990, 1991, Kovar-Eder 1992).

Groenlandia fossils from Enspel are generally rare and occur (almost) exclusively in the basal part of black pelite or "oilshale" unit S14 of lithozone C/D of palaeolake Enspel, or within the uppermost Enspel Formation, respectively (see Schindler & Wuttke 2015 for a standard profile and the numbering of layers). The basal part of layer S14 (bS14) is ca 2 centimeters thick and represents a distinct facies characterized by extraordinarily fine lamination and light colour (especially when dry), the latter attributable to the abundance of siliceous microfossils such as diatoms. In the upper part of bS14, filamentous cyanobacterial mats are present, forming observable net-like structures by trapping of siliceous microfossils (cf. Wuttke & Radtke 1993; Fig. 2). The basal part of S14 has attracted special attention because it has yielded a wealth of well-preserved fossil leaves and insects (Poschmann & Wedmann 2005; Fig. 2) including lightly sclerotized specimens such as insect larvae. On the other hand, vertebrate remains are very scarce. For example, sampling of 0.5 m^2 restricted to bS14 in excavation site G30/2015 yielded a total of 237 plant remains (including 83 leaves, 61 leaf fragments, 27 seeds) and 100 insect remains (including 16 beetles, 22 hymenopterans [mainly ants], 10 aquatic larvae), but only one vertebrate fossil (a tadpole) was found. This sample included five remains attributable to *Groenlandia pescheri* sp. nov. As mentioned above, the latter is restricted almost exclusively to the basal part of layer S14, with very few specimens recorded from the basal part of layer S16, which shows some similarities to bS14, namely the lack of coarse siliciclastic/pyroclastic input and deposition on top of a tuffitic debris flow or turbidite (S15 and S17, respectively).

Fine-grained matrix probably is a prerequisite for the preservation of an obviously very delicate plant like *Groenlandia*, which in some cases already shows signs of initial decay. However, the reasons for its occurrence in bS14 (and rarely in bS16) cannot be explained by the high preservation potential of fine-grained host matrix alone. *Groenlandia* has not been recorded in other equally fine-grained "oilshale" layers (which also yielded insect larvae, for example). Its extraordinary (relative) abundance may be seen as an indication that the time represented by deposition of bS14 reflects environmental conditions that allowed *Groenlandia* to flourish in Lake Enspel. Some extant Potamogetonaceae, such as *Potamogeton coloratus*, are pioneer plants that prefer to colonize open spaces and tend to disappear when competition pressure increases (Kohler et al. 1974). The phenomenon of submersed hydrophytic plants being driven out by helophytic plants entering the water from banks in times of environmental stability is well documented (e.g. Kohler et al. 1974). Therefore, one possible explanation for the occurrence of *Groenlandia* in bS14 is erosion and destruction (i.e. clearing) of shallow water habitats reflected in the (re)deposition of S15 (and S17) (e.g. Gaupp & Wilke 1998). Assuming that *Groenlandia pescheri* sp. nov. was such

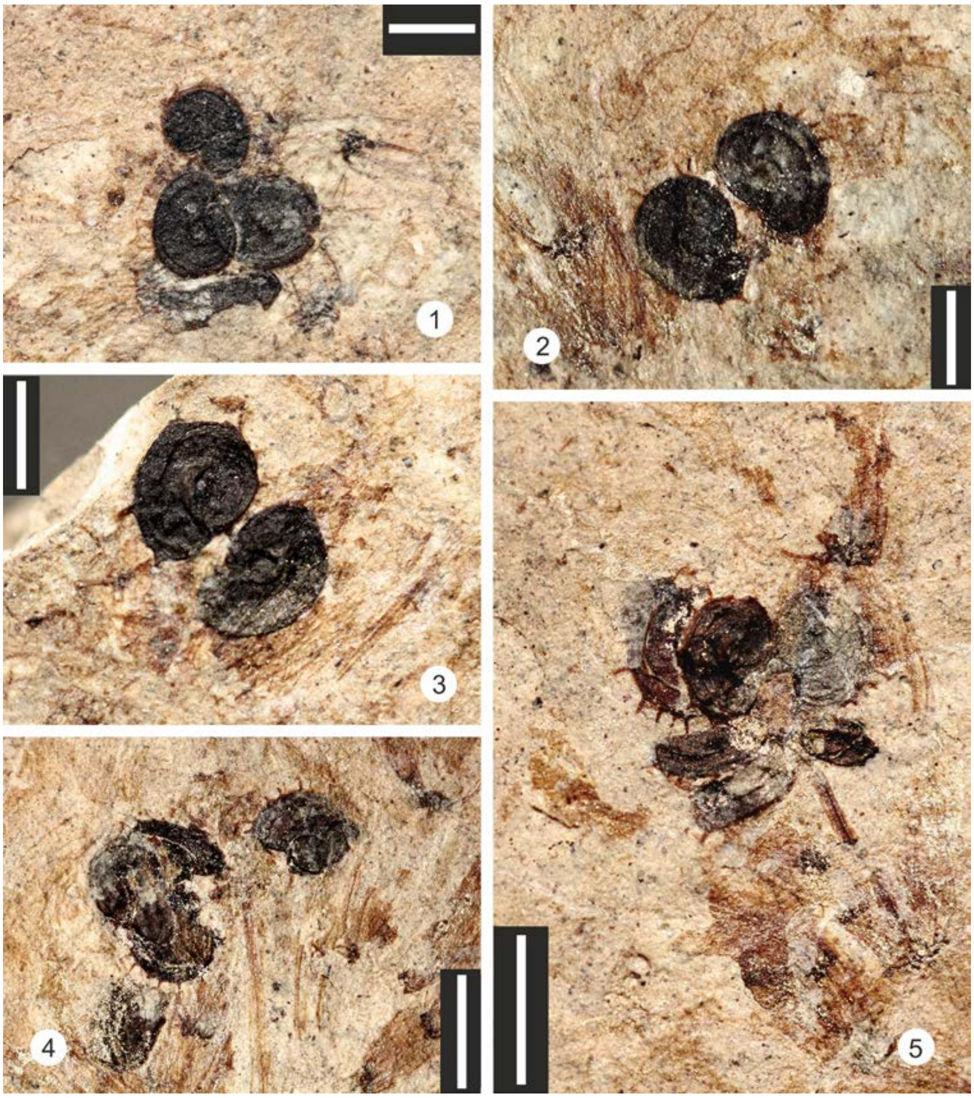

Plate 6. 1. Spike of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., with four seeds; Holotype (counterpart); PB 2015/5443-LS a. Scale bar = 1 mm; **2**. Spike of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., exhibiting two seeds; note large distinct furrow, marking partition wall on specimen at right; Holotype (counterpart); PB 2015/5443-LS a. Scale bar = 1 mm; **3**. Spike of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., exhibiting two seeds; Holotype; PB 2015/5443-LS b. Scale bar = 1 mm; **4**. Spike of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., exhibiting four seeds; PB 2015/5446-LS a. Scale bar = 2 mm; **5**. Spike of *Groenlandia pescheri* D. Uhl & Poschmann sp. nov., exhibiting six (?) seeds: PB 2015/5446-LS a. Scale bar = 2 mm

a pioneer plant, it may well have colonized such empty spaces, flourishing for some time in Lake Enspel and subsequently declining at times of environmental stability and growing competition from other plants. Self-sedimentation of aggregated mats of diatoms (algal blooms) following the introduction of nutrients by the (re) sedimentation of tuffites (like S15) may have contributed to the preservation of the biota by shrouding it on the lakebed (Allison et al. 2008).

According to Mai (1985), the occurrence of *Groendlandia densa* endocarps in Quaternary sediments is commonly regarded as an indicator of flowing water. However, as pointed out by various authors (e.g. Kvaček 2007b), it is always difficult to use modern monotypic taxa to deduce palaeoenvironmental or palaeoclimatic conditions for their fossil precursors, as it is never clear whether or not such taxa may have changed their environmental preferences during evolution. Thus, it needs to be clarified that the occurrence of *Groenlandia* in the sediments of Lake Enspel certainly cannot be regarded as a reliable indicator of inflow into the lake.

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