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EPIDERMAL ANATOMY OF *GLYPTOSTROBUS EUROPAEUS* (BRONGN.) UNGER FROM THE LATE OLIGOCENE OF THE WESTERWALD (RHINELAND-PALATINATE, W-GERMANY)

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Abstract: Details of the epidermal anatomy of *Glyptostrobus europaeus* (Brongn.) Unger from the Late Oligocene locality Norken in the Westerwald (Rhineland-Palatinate, W-Germany) are documented and described by means of scanning electron microscopy of in situ cuticles. The taxon had a wide distribution over the entire Northern Hemisphere during the Oligocene and it is considered to represent the most common conifer during the Cenozoic of Europe, but cuticles from this taxon are rarely figured in the literature. The cuticles from Norken exhibit cellular patterns and details (e.g. of stomatal complexes) typical for taxodioid Cupressaceae. Anatomical observations are in close agreement with results for this taxon from other Central European localities. The in situ cuticles had already fragmented into very small pieces, and this explains why it was so far impossible to retrieve cuticles from this locality by means of standard cuticular analytic techniques.

Key words: Late Oligocene, Westerwald, Norken, cuticles, SEM

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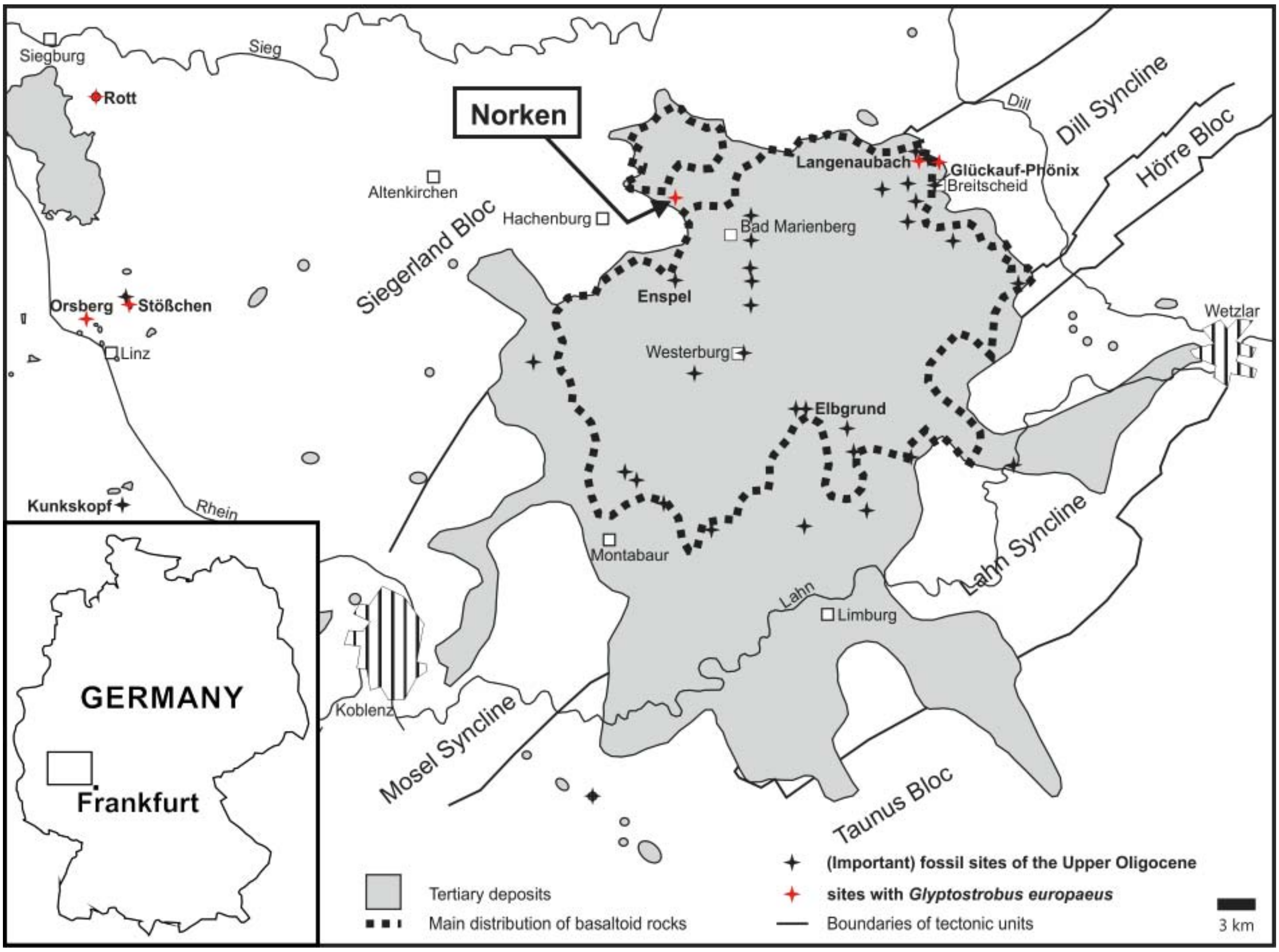
Introduction

Late Oligocene macrofloras from the Westerwald region in W-Germany have been known since at least the middle of the 19th century (e.g. Weber 1852, Ludwig 1859 – 1860). Most of these floras were discovered during lignite mining but due to fast disintegration of the excavated specimens during drying, the described plants were neither abundant nor diverse. However, many studies on geology and mining the lignites and basalts of this region cited the occurrence of fossil plants at a large number of localities (e.g. Casselmann 1853, Selbach 1867, Steckhan 1973). The Oligocene macroflora from the Westerwald is thus less well known when compared to other Central European floras from this period (e.g. Central German lignite basins: Mai and Walther 1978, 1991, Mai 1995, Walther 1999, Kvaček and Walther 2001; Czech České středohoří Mts.: Walther and Kvaček 2007, Akhmetiev et al. 2009; Siebengebirge in Germany: Weber 1852, Winterscheid 2006, Winterscheid and Kvaček 2014, Winterscheid et al. 2018).

Only during recent decades have some of the macrofloras from the Westerwald gained increased scientific interest. In particular the diverse macro-flora from the Late Oligocene maar or crater lake of Enspel has been studied in some detail (e.g. Uhl and Herrmann 2010, Köhler and Uhl 2014, Uhl 2014, 2015, Uhl and Poschmann 2018). Another flora that came under the focus of current research originates from the former Lignite mine "Späth" near Norken (Müller 1997, Uhl et al. 2011, Krüger et al. 2017), located only a few kilometres north of Enspel. Whereas the Enspel flora represents a species rich mixed mesophytic forest (Köhler and Uhl 2014), the more or less contemporary macro-flora from Norken probably represents a riparian forest dominated by *Acer tricuspidatum* Bronn and *Glyptostrobus europaeus* (Brongn.) Unger, with only rare constituents (leaves and seeds) from other vegetation types (Müller 1997, Uhl et al. 2011, Krüger et al. 2017).

Up to now it had not been possible to extract cuticles from this flora, as the cuticles fragment into tiny, taxonomically meaningless pieces during standard preparation procedures (Krüger et al. 2017). Attempts to analyse cuticles in situ by means of Scanning Electron Microscopy (SEM) were successful for a few twig fragments, assignable to *Glyptostrobus europaeus*. This taxon had a wide distribution over the entire Northern Hemisphere during the Oligocene (e.g. LePage 2007) and it is considered to represent the most common conifer in the Cenozoic of Europe (Kvaček 2007),



Text-fig. 1. Geological overview map of the Westerwald Tertiary; ✦ fossil localities (after Schindler and Wuttke 2010).

but cuticles from this taxon are rarely figured in the literature (cf. Kovar-Eder 1996, Sakala 2000, Vikulin et al. 2003, Ma et al. 2013, Winterscheid and Kvaček 2014, 2016b).

Geology and stratigraphy

The village of Norken is located at the western border of the High Westerwald (Text-fig. 1). This region is part of the Rhenish Slate Mountains, which were formed during the Variscan orogeny in the late Palaeozoic. After the Variscan orogeny until the beginning of the Cenozoic, the Devonian rocks from this region experienced intensive weathering and erosion (Baumann 1993). During the Oligocene the area was subject to tectonic upheavals, resulting in the formation of numerous depressions, small basins and tectonic graben structures, which were subsequently filled with up to 100 m thick sediments, including claystones, black shales and lignites rich in fossils (e.g. Schäfer et al. 2011, Uhl et al. 2011). There was also an intensive volcanism in this area during the Oligocene, which led to the deposition of massive basaltic tuff/tuffite deposits, as well as basalt sheets (e.g. Schäfer et al. 2011).

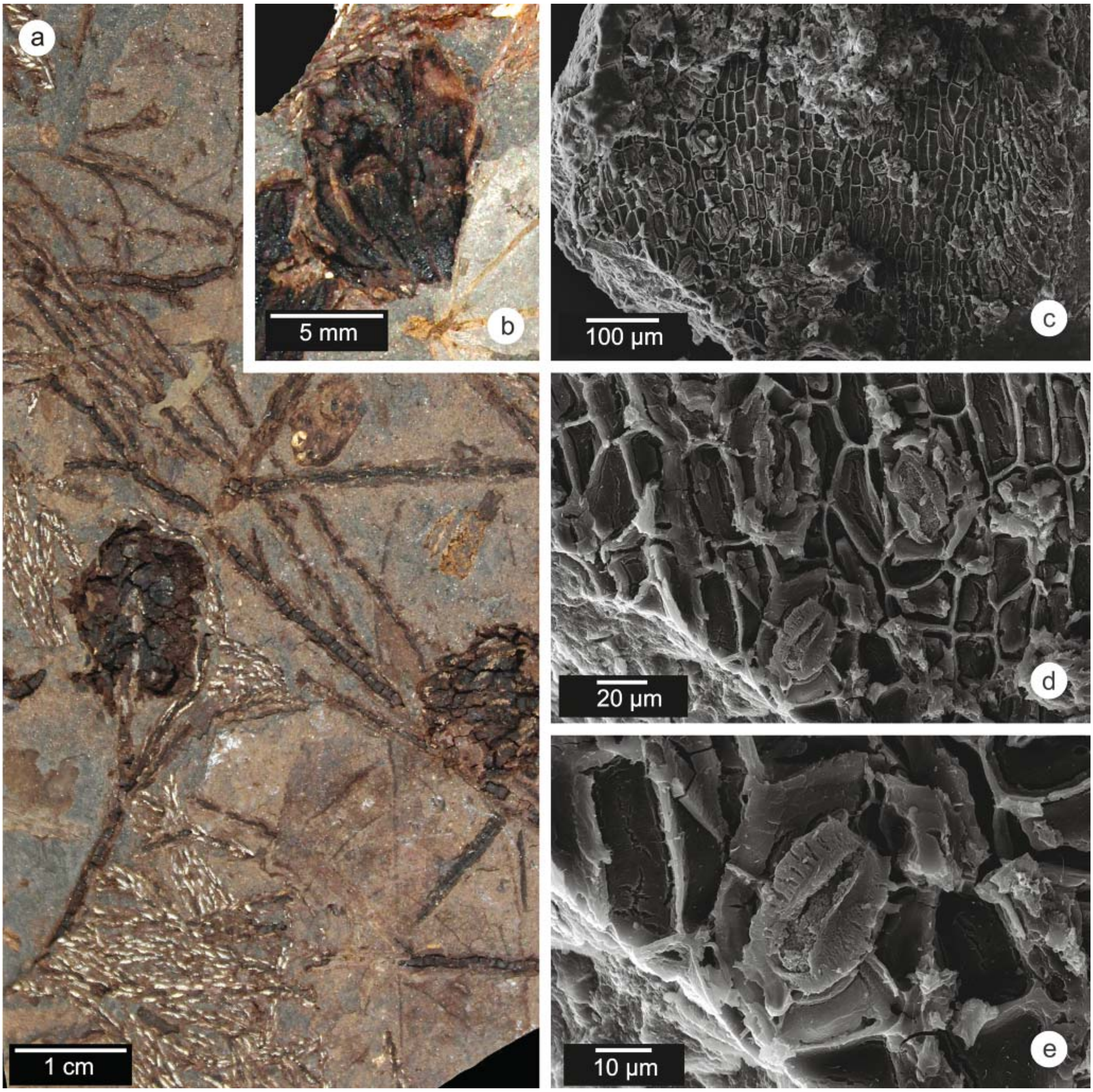
The fossil bearing deposits from Norken can be assigned to the Breitscheid Formation (cf. Uhl et al. 2011) This formation is of Late Oligocene age and consists of tuffs, tuffites, siliciclastic deposits as well as lignites (e.g. Schäfer et al. 2011). The Breitscheid Formation includes three main lignite seams, of which the uppermost seam has been mined in Norken (Steckhan 1973). This seam overlies lacustrine sediments consisting of fine grained, laminated black shales, as well as coarse re-sediments probably originating from the banks of the lake (Uhl et al. 2011). For more details on the geology of the Norken locality see Steckhan (1973) as well as Uhl et al. (2011).

Material and methods

The material analysed here was collected from the spoil tips of the former lignite mine "Späth" in Norken in the Westerwald, W-Germany (Text-fig. 1). It is stored in the collections of the Maarmuseum Manderscheid (cf. Krüger et al. 2017).

Small fragments of selected pieces of the laminated black shale ("Schwarzpelit" sensu Uhl et al. 2011) exhibiting twig remains of *Glyptostrobus europaeus* were mounted on standard stubs with LeitC-Tabs (Plano, Münster, Germany), and subsequently examined with the aid of a JEOL JSM 6490 LV Scanning Electron Microscope (SEM; accelerator current 20 kV) at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Germany.

Measurements of anatomical details were obtained using the software ImageJ (W. S. Rasband 1997 – 2016: ImageJ.



Text-fig. 2. ***Glyptostrobus europaeus*** **from Norken. a) Overview of slab with twigs and two cones attached to twigs (MMM-2012-059). b) Cone exhibiting flabellate seed-scales (MMM-2012-022). c) SEM-image of the cuticle near the base of a needle (MMM-2012-059). d) Detail of c) showing stomata and fragmented cuticle. e) Detail of d) showing the cuticle around a single stomatal apparatus.**

U. S. National Institutes of Health, Bethesda, Maryland, USA; http://imagej.nih.gov/ij/, last accessed: September 7th, 2018) with calibrated digital images.

Systematic palaeobotany

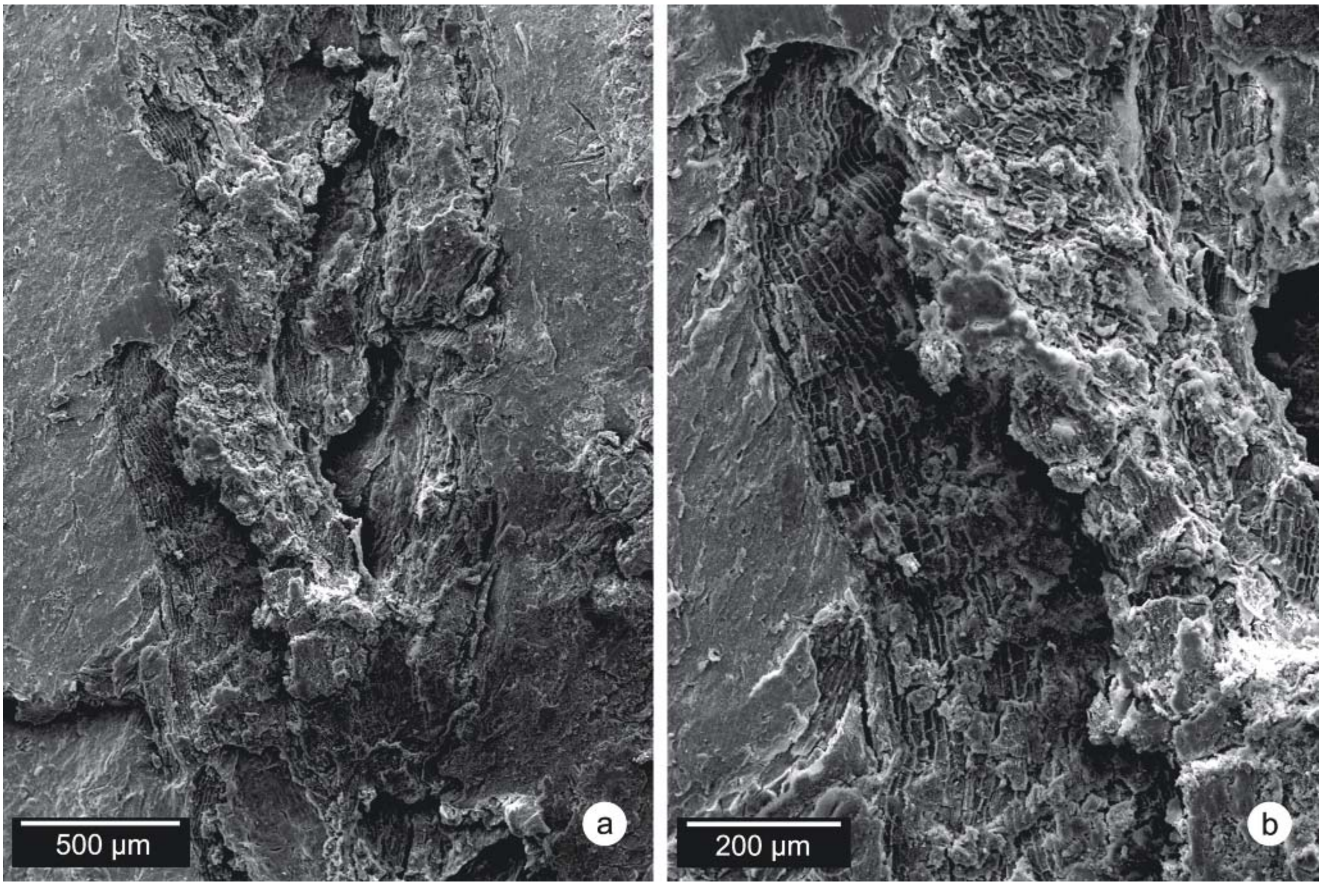
Family Cupressaceae Gray, nom. cons.
Subfamily Taxodioideae Endl. ex K.Koch

Genus *Glyptostrobus* Endl.

The genus *Glyptostrobus* has been known from the Cretaceous onwards and had a wide distribution over the entire Northern Hemisphere during much of the Cenozoic (LePage 2007). Today only a single species, *Glyptostrobus pensilis* (Staunton ex D.Don) K.Koch exists, occurring in Vietnam and southeast China, within the vegetation of river deltas, floodplains and lowland swamps (LePage 2007). Fossil members of this genus are also generally interpreted to represent members of swamp or riparian vegetation. However, such generalized interpretation of monotypic genera should be viewed with considerable care, as such taxa might have changed their climatic and ecological demands over time (cf. Kvaček 2007).

Glyptostrobus europaeus **(Brongn.) Unger**
Text-figs 2–3

Selected synonymy. Only references which are important for nomenclature and refer to occurrences in the



Text-fig. 3. SEM-images of *Glyptostrobus europaeus* from Norken. a) Detail of a split short shoot (MMM-2012-059). b) Detail of a), showing the apical part of a needle with stomatal-free zone and only a few stomata towards the base of the needle.

Westerwald or its direct vicinity; for more comprehensive lists of synonymies see LePage (2007) and Winterscheid et al. (2018).

1833 *Taxodium europaeum* Brongn., pp. 168–176.
1850 *Glyptostrobus europaeus* (Brongn.) Unger, pp. 434–435.
1851 *Cupressites brongniartii* Göpp.; Weber, p. 161.
1937 *Glyptostrobus europaeus* Heer; Weyland, p. 74.
1997 *Glyptostrobus* sp.; Müller, p. 46.
2011 *Glyptostrobus europaeus* (Brongn.) Unger; Uhl et al., p. 121, fig. 4.
2006 *Glyptostrobus europaeus* (Brongn.) Unger; Winterscheid, p. 74; pl. 18, fig. 1, pl. 22, fig. 8, pl. 23, fig. 9, pl. 24, figs 1– 2.
2014 *Glyptostrobus europaeus* (Brongn.) Unger; Winterscheid and Kvaček, pp. 7– 8, pl. 1, figs 3–5, pl. 8, fig. 26, pl. 9, fig. 1.
2016b *Glyptostrobus europaeus* (Brongn.) Unger; Winterscheid and Kvaček, pp. 117–118, pl. 1, fig. 7, pl. 4, fig. 2.
2017 *Glyptostrobus europaeus* (Brongn.) Unger; Krüger et al., p. 68, pl. 1A–B.
2018 *Glyptostrobus europaeus* (Brongn.) Unger; Winterscheid et al., pp. 124–125, pl. 4, figs 9–11.

Material. 38 twig remains of which 15 bear one or more cones at the end of the twigs (marked in **bold**): MMM-2012-009, **-018**, **-021**, **-022**, **-046**, **-049**, **-050**, -053, -054, -057, **-059 (SEM samples were taken from this specimen)**, -062, **-063**, -064, **-065**, -067, **-076**, **-077**, -080, -081, -082, **-084**, -085, -086, -088, **-090**, -093, -105, -107, -110, -113, -116, -121, **-150**, -156, **-189**, -196, -197.

Description. Long slender twig fragments, with cupressoid needles, up to 3 mm long and up to 1 mm wide. 15 specimens bear one or more elliptical to obovate cones at the end of the twigs (Text-fig. 2a–b). Seed-scales elongated, flabellate, thinning-out towards the base and with semi-circular (abraded?) apex (Text-fig. 2b).

Only abaxial cuticles could be analysed. Normal epidermal cells in stomata free zones (Text-fig. 3a–b) are usually elongated, orientated more or less parallel to the axes of the needles, 22–72 µm (average 39.8 µm) long and 9–24 µm (average 16.0 µm) wide. The length to width ratio of these cells is 1.3–5.2 (average 2.6). Stomatal complexes are elliptical, with (4–)5 subsidiary cells (Text-fig. 2d–e). The long-axis of the stomata are usually orientated oblique or parallel to the long axis of the needles (Text-fig. 2c). Outer walls of guard cells forming prominent lateral lamellae (Text-fig. 2d–e).

Remarks. The taxon can be identified by the characteristic form and arrangement of the needles, together with the occurrence of typical cones attached to twigs (cf. Uhl et al. 2011, Krüger et al. 2017), however the finer details of the seed-scales could not be observed in this material (cf. Text-fig. 2b). The form and arrangement of epidermal cells, as well as the stomatal complexes, clearly correspond to the published data for this taxon from other sites, as well as the only modern species *G. pensilis* (Tab. 1). Only small areas of the needle surfaces however could be analysed by means of SEM, due to incomplete splitting of the needles. Over all there is considerable variability in certain morphological features (e.g. size of epidermal cells), between cuticles from different fossil localities,

Table 1. Comparison of morphological data of cuticles of (cupressoid) *Glyptostrobus europaeus* needles from different fossil localities in comparison to modern *G. pensilis*. Data derived from descriptions in the text and figured cuticles.

	Fushun, Eocene, Ma et al. 2013	Orsberg, Late Oligocene, Winterscheid and Kvaček 2014	Stößchen, Late Oligocene, Winterscheid and Kvaček 2016b	**Norken, Late Oligocene, This study**	Kazakhstan, Early Miocene, Vickulin et al. 2003	Köflach, Early Miocene, Kovar-Eder 1996	Bílina, Early Miocene, Kovar-Eder 1996, Sakala 2000	Bükkábrány, Late Miocene, Erdei and Magyari 2011	Modern *G. pensilis*, Ma et al. 2004
Form of normal epidermal cells	elongated	quadrangular to elongated	quadrangular to elongated*	**usually elongated**	quadrangular to elongated	elongated	elongated, quadrangular to polygonal	elongated	quadrangular to elongated
Length of normal epidermal cells	91.9 ± 25.5 µm**	20–50 µm	20–50 µm*	**22–72 µm**	?	44–144 µm	25–55 µm	25–100 µm	131.6 ± 31.1 µm**
Width of normal epidermal cells	18.6 ± 2.4 µm**	7–20 µm	7–20 µm*	**9–24 µm**	?	11–20 µm	11–20 µm	20–40 µm	31.6 ± 5.4 µm**
Length to width ratio of normal epidermal cells	4.9 ± 1.1**	?	?	**1.3–5.2**	2–3	2.5–11.1	1.4–4.1	?	1.7–13.5**
Orientation of elongated epidermal cells in stomatal free areas	± parallel to needle axes	± parallel to needle axes	± parallel to needle axes	**± parallel to needle axes**	± parallel to needle axes	± parallel to needle axes	± parallel to needle axes	± parallel to needle axes	± parallel to needle axes
Form of stomatal complexes	elliptical	broad elliptical	broad elliptical*	**elliptical**	broad elliptical	elliptical	(broad) elliptical	elliptical	elliptical
Number of subsidiary cells	5–6	5–6	5–6*	**(4–)5**	(4–)5(–6)	?	6	?	(4–)5–6(–7)
Orientation of stomata in relation to needle axis	mostly parallel or oblique	oblique or parallel	?	**mostly oblique or parallel**	± parallel or oblique	parallel or perpendicular	mostly oblique or parallel	mostly oblique	oblique or perpendicular
Prominent lateral lamellae on outer walls of guard cells	?	guard cells not preserved	guard cells not preserved*	**present**	present	?	?	?	present

* data only from adaxial cuticles
** data from linear needles

ranging from Eocene up to Late Miocene, as well as in any comparison with modern *G. pensilis* (Tab. 1). However, as a number of cuticular features (such as cell size and orientation of stomatal complexes) varies considerably in modern *G. pensilis*, depending on needle type (linear, linear-subulate and scale-line [cuppressoid]), and even position within a needle (adaxial vs. abaxial) (Ma et al. 2004) it is difficult to interpret the variability of fossil cuticles as most come from only a few (or even single) needles. Thus it is not clear whether the observed variability in the fossil taxon may reflect ecological, climatic or even evolutionary differences between different populations of *G. europaeus*.

Attempts to isolate cuticles of a number of plants species from the fossiliferous sediments of Norken using standard preparation techniques have so far been unsuccessful as the cuticles fragmented into rather small and taxonomically meaningless pieces during preparation (Krüger et al. 2017). When looking at the in situ cuticles of *Glyptostrobus* from Norken it becomes obvious that this is due to the fact that the cuticles had already fragmented within the sediment (Text-fig. 2c–d). It is not clear whether this is due to long term diagenetic processes which affected the cuticles after deposition and before the material was mined or whether this is simply an effect of drying out and maybe oxidation after the material had been dumped on the spoil tips or even after it had been collected.

Conclusions

The occurrence of *Glyptostrobus europaeus* has previously been reported from a number of Late Oligocene localities in the Westerwald and adjacent areas (e.g. Müller 1997, Winterscheid 2006, Uhl et al. 2011, Winterscheid and Kvaček 2014, 2016a, b, 2018, Krüger et al. 2017). However, most of these reports were purely based on macroscopic characteristics, only Winterscheid and Kvaček (2014, 2016b) provided data on the cuticular anatomy of this taxon. The cuticular anatomy of *Glyptostrobus europaeus* remains from Norken clearly correspond with data from other localities, although only small areas of in situ cuticle could be analysed by SEM. Our results demonstrate that at least for the locality of Norken, SEM analysis of in situ cuticles can provide some anatomical information, adding to the purely morphological data available so far.

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