Comparative investigation of modern and fossil *Toricellia* fruits – a disjunctive element in the Miocene and Eocene of Central Europe and the USA

by

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Abstract

The genus *Toricellia* DC. includes two extant species in the eastern Himalaya and in central China: *T. tiliifolia* DC. and *T. angulata* OLIV. Up to now, fossil occurrences have been restricted to the Eocene of Oregon and Washington (USA) and Messel (Germany). Here, fruits from the Austrian Early Miocene locality Oberdorf are described in detail, proving the generic identity through similarities in the fruit morphology to the modern species: globose endocarps with two wide holes in the lateral wall; three chambers, the two larger ones being empty; the smaller embryo-bearing chamber opens with a triangular germination valve. The fossil habitat, inferred from the sediments, taphonomy, the associated plant assemblage and modern habitats, could have been a Mixed Mesophytic Forest in the hinterland or a disturbed area, possibly near a fluvial system. The occurrence and recognition of these fossils build a substantial part in the reconstruction of the distribution areas and potential routes of migration.

Keywords: Toricelliaceae, fruit morphology - anatomy, palaeoecology, taphonomy, palaeobiogeography

Zusammenfassung

Die Gattung *Toricellia* kommt heute mit zwei Arten im östlichen Himalaya und in Zentralchina vor: *T. tiliifolia* DC. und *T. angulata* OLIV.. Fossilnachweise waren lange unbekannt und dann auf einzelne eozäne Fundstellen in N-Amerika (Clarno, Ronald) und Deutschland (Messel) beschränkt. Aus dem österreichischen Unter-Miozän werden hier nun *Toricellia* Früchte ausführlich beschrieben und mit den rezenten Früchten verglichen. Charakteristische Merkmale sind eine kugelige Gestalt mit zwei rundlichen Öffnungen in der lateralen Endokarp-Wand.

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Im Querschnitt zeigen sie drei Fächer, von denen die zwei größeren leer sind und jeweils eine Öffnung in der Endokarp-Wand aufweisen. Das kleine, schmale, umlaufende, dritte Fach enthält den Embryo und öffnet sich unterhalb des Apex durch eine dreieckige Keimklappe. Aufgrund der sedimentären Fazies, taphonomischer Überlegungen, der fossilen Begleitflora und des heutigen Habitats ist zu schließen, dass es sich um ein akzessorisches Element im Mixed Mesophytic Forest handelte oder eine Pionierpflanze auf gestörten Standorten in Flussnähe war. Diese Fossilnachweise bilden einen wichtigen Beitrag für die Rekonstruktion der Verbreitungsgebiete und Migrationswege.

1. Introduction

The genus *Toricellia* DC. was unknown in the fossil record up to 1999, when MANCHESTER (1999:476) described material from the Eocene of the USA and Germany. At the same time, but quite independently, endocarps from the Miocene of Austria were recognized as *Toricellia* (MELLER, 1998a). The modern genus *Toricellia* is not very well known by botanists or palaeobotanists, due to its restricted distribution in the Himalaya and China, low species number and isolated systematic position. In the past, the genus was mentioned in the palaeobotanical literature for comparative purposes only. EYDE (1988:312-313) had discussed the systematic position in comparison to the Cornaceae, SZAFER (1963:17-19) and NIKITIN (1965:86) in comparison to *Carpolithus rosenkjaeri* HARTZ, a diaspore taxon of still uncertain systematic-taxonomic position (Onagraceae: *Hartziella rosenkjaeri* (HARTZ) SZAFER or Cornaceae: *Hartzia rosenkjaeri* (HARTZ) NIKITIN). Fossil *Toricellia* endocarps have previously been regarded as a probable Lythraceae (COLLINSON, 1988), as an organ genus *Tripartisemen* MANCHESTER 1994 and as *Swida* sp. (type B) (KOVAR-EDER & MELLER, 2003:294). The manuscript by KOVAR-EDER & MELLER (2003) was submitted in March 1998, but due to the long time-span between submission and publication, an additional sentence with the revised determinations was added to the manuscript. The significance of the Austrian endocarps, which are the only known record of *Toricellia* from the Neogene and connect
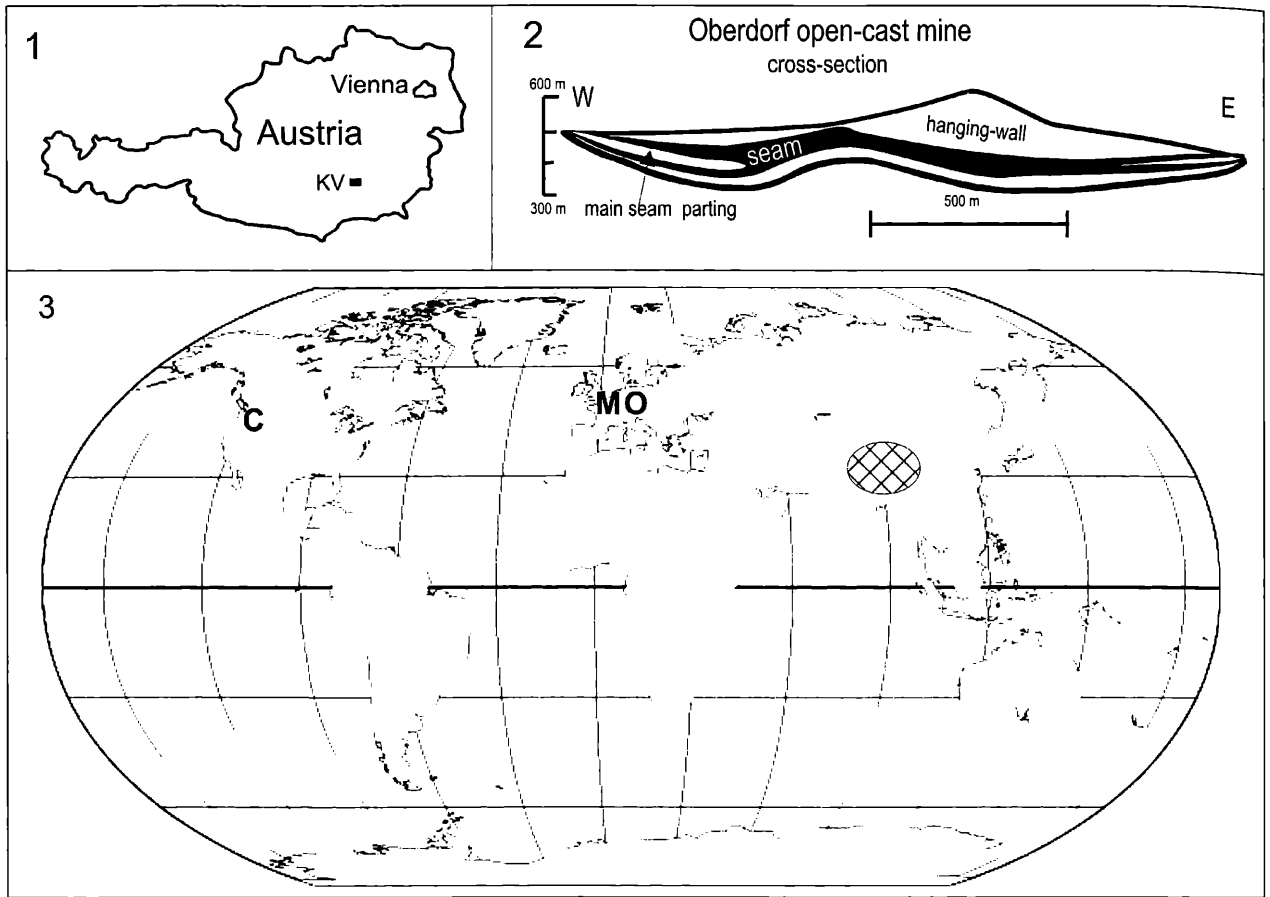
Figure 1: Geographic position of the Köflach-Voitsberg lignite mining area (KV) in Austria.

Figure 2: W-E cross-section through the Oberdorf open-cast mine; samples with *Toricellia* derive from the western margin of the main seam parting and from the hanging wall sequence at the northeastern margin of the outcrop (for the detailed sedimentary profile see MELLER, 1998b: fig. 4).

Figure 3: Geographic position of the modern (crossed lines), Miocene (O = Oberdorf) and Eocene (M = Messel, C = Clarno, Ronald) occurrences of *Toricellia*.

the Eocene records with the modern distribution area, affords a detailed comparison with the fruits of the modern species. The aim of this paper is to document and compare the morphology and anatomy of the *Toricellia* fruits from Oberdorf with the two modern species (*T. angulata* OLIV. and *T. tiliifolia* DC.). Furthermore, the palaeoenvironment, in comparison to the extant habitat and to the sedimentological results has been tentatively reconstructed.

The paper is dedicated to my colleague Gudrun Daxner-Höck, with thanks for her long cooperation in investigating the Neogene deposits of Austria.

2. Material and methods

Endocarps of *Toricellia* were obtained in several samples from different sedimentary layers in the Oberdorf open-cast mine in the Köflach-Voitsberg lignite mining area, about 200 km southwest of Vienna, in SE Austria (Fig. 1; compare also MELLER, 1998b: fig. 4). In particular, numerous endocarps were found in the sandy main seam parting at the western margin of the western sub-basin

(Fig. 2). In the eastern sub-basin only a few specimens were found in the upper part of the hanging-wall sequence in sandy and marly sediments. The carpological preparation methods used follow MELLER (1998b). The Oberdorf specimens are preserved as coalified three-dimensional endocarps which were sometimes secondarily compressed during diagenesis.

Endocarps of the modern species were provided by the herbarium of the Royal Botanical Garden, Edinburgh (see appendix). Some of these specimens were partly soaked in KOH or Schulz solution to remove the outer skin layer or divided and broken mechanically. For SEM-analysis, they were also coated with gold und studied with a Jeol scanning electron microscope.

The Oberdorf specimens are stored in the palaeobotanical collection of the Natural History Museum Vienna and in the collection of the Geological Survey of Austria in Vienna. The latter includes also some modern fruits and some Eocene specimens from the Clarno type locality in the western USA, most of which are stored in the Florida Museum of Natural History of the University of Florida in Gainesville.

The descriptive terminology (e.g. dorsal, ventral) is used in

an arbitrary way because of the lack of botanical developmental investigations. Abbreviations of author names follow MABBERLY (1997).

3. Toricelliaceae

The spelling of the name as well as the family author seems to be a source of inconsistency. In some monographs *Toricellia* is written with double r: *Torricellia*. Despite the probable origin of the name (the Italian physian E. Torricelli), de CANDOLLE (1830) has written the genus name and the name of the physian with only one r. In DIELS (1901) and WANGERIN (1910) it is written *Torricellia* DC., without any explanation about the changed spelling. However it seems to be not sure, that the writing with one r is really an orthographic error (compare International Code of Botanical Nomenclature, Saint Louis Code, Art. 60). Therefore, the original spelling is used here. However, in the following sentences, the spelling of the cited authors is used. The mentioned authors of the family are: Toricelliaceae (WANG.) HU corr. AIRY SHAW, used in WATSON & DALLWITZ (1992 onwards), Torricelliaceae (WANGENHEIM) H.H. HU, used in STEVENS (2001 onwards), and Toricelliaceae fam. nov., written in HU (1934). WANGERIN (1910:31) had introduced a new tribe Torricellieae within the subfamily Cornoideae, but not a new family. The family Torricelliaceae has been introduced by HU (1934:311) due to morphological differences to the Cornaceae and Araliaceae. AIRY SHAW (in WILLIS, 1966) has corrected the spelling used by HU (1934) and has written Toricelliaceae with one r. WANGENHEIM was already dead (1749-1800) when *Toricellia* was described and his authorship is probably a wrong interpretation of an abbreviation.

The systematic relationship of *Toricellia* has been reinvestigated during recent decades. In the past, the genus was regarded as either a Cornaceae, or an Araliaceae, or as a distinct family. However, molecular investigations (PLUNKETT et al., 1996) placed *Toricellia* into the Apiales, as a separate family (APG II 2003: Torricelliaceae HU). Most recently the family has been expanded to also include *Melanophylla* BAKER and *Aralidium* MIQ. (STEVENS, 2001 onwards; PLUNKETT et al., 2004). The former is an endemic genus of Madagascar with seven species; the latter is a monospecific genus in western Malaysia.

Only two living species of *Toricellia* have been documented, growing in restricted areas in the eastern Himalaya and central China at 900 to 2600 m above sea level. Their distribution areas overlap partly; *Toricellia tiliifolia* DC. occurs in Bhutan, Burma, Nepal, N. India (Sikkim), and western China (Xizang, Yunnan) whilst *Toricellia angulata* OLIV. grows in western and central China (XIANG & BOUFFORD, 2005; WANG, 1961). The distribution area of *T. angulata* var. *intermedia* (HARMS) HU is wider than the extremes of the two species in China according XIANG & BOUFFORD (2005:234). This variation, at first recognized as a separate species, has been discussed by XIANG & BOUFFORD (2005:234) as a hybrid or an "introgression from *T. tiliifolia* into *T. angulata*" There is little information about the associated vegetation

types and the habitats; *T. tiliifolia* has been documented from broad-leaved forests, forest margins, open dry slopes, partially cleared forest on steep roadside banks (XIANG & BOUFFORD, 2005; data from the herbarium sheets in Edinburgh). In Bhutan, occurrences on disturbed areas have also been mentioned (GRIERSON & LONG, 1991). *Toricellia angulata* has been observed at forest margins and streamsides (XIANG & BOUFFORD, 2005). The herbarium sheets provided no additional information for this species.

The *Toricellia* species grow as small deciduous trees and shrubs of about 2.5-12 m height and are distinguishable by leaf morphology; *T. tiliifolia* has nonlobate leaves with serrate margins, *T. angulata* shows lobed leaves with entire margins, *T. angulata* var. *intermedia* is characterized by lobed leaves with dentate margins. The infructescences are organized as panicles, with numerous fruits.

4. Fruit morphology of the extant Toricellia tiliifolia DE CANDOLLE and T. angulata OLIVER

The fruits are 4-6 mm in diameter; the fruit shape is globose or slightly pyriform with three apical style remnants and a basal peduncle attachment. In lateral view, the peduncle is in a supra-basal dorsal position (Pl. 1, figs. 1, 2, 4). The fruit is built from a lignitic endocarp and a skinny exocarp, probably with only a thin mesocarp layer (no fresh fruits were available for investigation). The exocarp surface is distinctly wrinkled (Pl. 1, fig. 8). After removing the exocarp, the endocarp wall shows two wide (1.5-2 mm in diameter) holes in a dorsal-lateral position (Pl. 1, figs. 9, 18.). Two distinct ridges mark the ventral surface of the endocarp surface (Pl. 1, figs. 5-7); initially, these diverge from the apex, then run parallel to each other down to the base and join again directly at the peduncle attachment. A third ridge, generally less strongly developed, runs between and parallel to the others, but often joining one or other before the base. A transversal bridge links the ridges in the upper part. The sub-apical area, between the transversal and lateral ridges and apex, represents the germination valve (Pl. 1, figs. 5-6). In *T. tiliifolia* the germination valve is less distinct (Pl. 1, fig. 7). Vascular bundles have been observed on the endocarp surface, on top of the ridges (Pl. 1, fig. 19). The outer surface of the endocarp bears cells of cuboid shape with thin, slightly undulate anticlines, probably representing meso-exocarp remnants (Pl. 1, figs. 19, 20). In cross-section (Pl. 1, fig. 12-13), three chambers have been observed: two large ones are symmetrically arranged to each other, the third, smaller one lies marginal between them. The position of the smaller embryo chamber is indicated by the two strong ridges on the endocarp surface but is more extended onto the dorsal side than the ridges. In a longitudinal section, the whole length of the fertile embryo chamber is clearly exposed (Pl. 1, figs. 10-11); this is about 2/3 of the whole perimeter. The endocarp walls are composed of regular rows of isodiametric, partly irregularly built cells (Pl. 1, figs. 14, 16-17), the walls of which are thickenened, but with small and wide pits. A thin layer of more or less parallel-orientated cell rows covers the inner side of the walls (Pl. 1, fig. 15).

According the available fruit material (see appendix) the endocarps of both extant species show few morphological differences. *Toricellia tiliifolia* fruits are larger (5-6 mm), the holes are also slightly larger and their surface ridges are often weakly developed in contrast to the smaller endocarps (4-4.5 mm) with strong ridges in *T. angulata*. The endocarp wall and the septa between the large locules of *T. tiliifolia* are about 0,2-0,25 mm thick (Pl. 1, fig. 17) and in *T. angulata* about 0.3-0.4 mm (Pl. 1, fig. 16); the walls between the small and large chambers are about 0.1-0.15 mm thick in *T. tiliifolia* and 0.2-0.25 mm in *T. angulata*. More fruit collections, especially of the latter species, would be useful to improve these preliminary data.

5. Systematic palaeontology

Toricellia bonesii (Manchester 1994?) Manchester 1999
(Plate 2, figs. 1-11)

Material: 75 endocarps from the Oberdorf open-cast mine; the material is listed in table 1, which also includes the inventory numbers of the collections respectively.

Synonyms:
?1988 ?Lythraceae – Collinson:192, pl. 1, fig. 11 (Messel, Germany, Eocene).
?1989 ?Lythraceae – Collinson:238 (Messel, Germany, Eocene).
?v1994 *Tripartisemen bonesii* sp. nov. – Manchester:113, pl. 62, figs. 8-15 (Clarno, USA, Eocene).
1998 *Toricellia* – Meller (Oberdorf, Austria, Miocene) (abstract).
?1999 *Toricellia bonesii* (Manchester) Manchester comb. nov. – Manchester:476, figs. C-G (Clarno, Ronald, USA, Eocene).
1999 *Toricellia* – Meller & Collinson (Oberdorf, Austria, Miocene; Messel, Germany; Eocene, Clarno, USA, Eocene) (abstract).
?2002 *Toricellia* fruit – Pigg & Wehr:4, pl.1, figs.1 (Ronald, USA, Eocene).
2003 *Swida* sp. (type B) – Kovar-Eder & Meller:294, pl. 5, figs. 19-25 (Oberdorf, Austria, Miocene).
2003 *Toricellia bonesii* (Manchester) Manchester – Kovar-Eder & Meller:299 (Oberdorf, Austria, Miocene).

Description: The endocarps are mainly compressed and often incomplete, which causes a distinct morphological variability (Pl. 2, figs. 1-6, see also in Kovar-Eder & Meller, 2003, pl. 5, figs. 19-24). They were originally of globose shape with two wide holes in a lateral-dorsal position (Pl. 2, figs. 1, 2, 4). The diameters vary between 2.5-3.5 mm. The endocarp surfaces bear two distinct ridges ventrally (Pl. 2, figs. 5, 6), starting and diverging from the apex, then running parallel, crossing the basal area and joining again at the dorsal side. In the upper part, the two ridges are linked by a transversal ridge. The sub-apical triangular area between apex and the transversal ridge forms the germination valve. Sometimes, another ridge divides the valve in two sym-

Sample Number	Inventory Number	No. of specimens
Me-Ob-89-8	NHMW 1992/0275/0006	1
Me-Ob-89-12	NHMW 1992/0278/0007	5
Me-Ob-89-13	NHMW 1992/0279/0010	9
Me-Ob-89-14	NHMW 1992/0280/0009	1
Me-Ob-89-17	NHMW 1992/0283/0006	2
Me-Ob-89-22	NHMW 1992/0287/0014	2
Me-Ob-89-25	GBA 2006/005/0001-4	4
Me-Ob-89-26	NHMW 1992/0291/007	2
Me-Ob-90-5-1	GBA 2006/005/0008	1
Me-Ob-90-9a	GBA 2006/005/0005	1
Me-Ob-90-20	NHMW 1992/0361/0005	1
Me-Ob-90-33	NHMW 1992/0365/0015	13
Me-Ob-90-36	NHMW 1992/0368/007	1
Me-Ob-90-52	NHMW 1992/0383/0019	30
Me-Ob-90-52	GBA 2006/005/0006-7	2

Table 1: The number of specimens from the Oberdorf open-cast mine samples and their inventory number in the collections (NHMW = Natural History Museum Vienna, GBA = Geological Survey of Austria).

metrical parts (Pl. 2, figs. 5-6). If the endocarps are laterally compressed, the ridges can appear as furrows and the wall of the small fertile chamber can build a distinct ridge (Pl. 2, fig. 2). Cell structures are generally not observable on the endocarp surface because of the strong degradation. Only one specimen shows cell outlines with undulate anticlines, probably representing meso-exocarp remnants (Pl. 2, fig. 11). In a horizontal cross-section, three chambers, separated by septum with a Y-shape (fertile locule above) are visible (Pl. 2, fig. 3). The two laterally arranged larger chambers are not totally enclosed by the endocarp because of the wide holes in the wall. The endocarp wall comprises isodiametric cells. A thin layer of long, parallel-orientated wrinkles covers the inner surface of the endocarp (Pl. 2, fig. 7). The thickness of the endocarp wall and the septum is variable, in part due to the poor state of preservation. One specimen shows endocarp wall thicknesses of less than 0.1 mm (Pl. 2, fig. 3), another of 0.1-0.2 mm.

Discussion of the systematic position: Comparisons of the fossil fruits from Oberdorf and the modern *Toricellia* fruits show identical features, which led to the generic determination. The main characteristic features of the genus are the three chambers, two big ones, each with a large hole in the lateral-dorsal endocarp wall, and one small one, the fertile chamber, with a triangular sub-apical germination valve. Moreover, the anatomy of the endocarp walls, including the innermost layer, which form the surface in the big locules, seems to be similar. The Madagascan genus *Melanophylla* has fruits which look similar in cross-section, and have similar isodiametric cells composing the endocarp, but the fruit shape is more elliptic and the endocarp surface is not smooth.

The identification of the species is slightly complicated. At a first glance, the endocarp holes seem a distinct difference when compared to the fossil type specimens from Clarno.

However, this is probably only because of the type of preservation. The Clarno specimens are nearly all silicified casts, with only thin petrified remains of the endocarp wall (MANCHESTER, 1994). As both MANCHESTER (1994:113, 1999: 476) and COLLINSON (1986, 1988) confirmed the conspecifity of the Clarno and Messel specimens and COLLINSON (1989: 238) described lateral-dorsal holes in the endocarp wall (originally interpreting them as bite marks), it seems that their absence in the Clarno specimens is only a matter of preservation. Although specimens from the Clarno type locality have been checked by the author for traces of these endocarp holes, the observed features (very thin or missing endocarp wall, sometimes no distinct separation between the filling and the outer sediment where the holes could have been located) have not been unequivocally seen. Since the sediment in which the casts are formed is found both inside and outside the endocarps, MANCHESTER (oral comm.) assumed that the sediment entered the endocarps through the lateral endocarp holes. The coalified specimens from Messel apparently show another distinguishing feature: the smaller endocarp size of about 1-2 mm (COLLINSON, 1989:238) in contrast to the 2.8-4.4 mm of the Clarno specimens and 2.5-3.5 mm of the Oberdorf specimens. Different fruit sizes might be a diagnostic feature, especially bearing the difference in the modern *Toricellia* species in mind. However, this must be checked with populations from other localities and with extant populations of varying maturity, to establish whether these differences are caused by different degrees of fruit maturity or by different ecological conditions (nutrient availability, local annual climate) of the habitats. The studied herbarium material seems to be nearly mature. The fruits of *T. tiliifolia* from Bhutan, Burma, and Nepal were collected in April (flowering period November-March according XIANG & BOUFFORD, 2005) and the fruits of *T. angulata* from Hupeh in June (flowering period April according XIANG & BOUFFORD 2005). Additionally, when comparing fossils from different sites, the taphonomic aspects (such as repeated soaking and drying during transport, see below) and diagenetic processes have also to be taken into account, as well as slightly different ecological conditions of the fossil habitat. Considering all these different aspects, the specimens from Oberdorf probably belong to the same species as the Eocene specimens from Clarno. However, this could not been proven because of the one feature, which is not preserved in the type material. Therefore a question mark has to be made (according the rules in RICHTER, 1948: 49) and question marks in the list of synonyms.

6. Palaeoecology, taphonomy and the palaeogeographic pattern

The associated elements in the different samples from Oberdorf vary slightly, although the assemblages are nearly all of allochthonous origin, with a variable amount of autochthonous elements. The samples from the seam parting are generally not very rich in species (Tab. 2). Common elements are *Pterocarya*, *Alnus* et/vel *Betula* sp. (catkins), *Cephalotaxus*, *Prunus*, and *Sequoia*. All the other elements occur less regularly and are often represented by a single specimen only. The sedimentary facies indicate a fluvial system, crossing a lignite-forming area. The two samples from the hanging-wall sequence, which also yielded *Toricellia*, vary slightly. The sample from the sandy layer of the hanging wall sequence is relatively rich in species and contains a high amount of *Mastixia* and *Cephalotaxus* endocarps as well one cupule of *Trigonobalanopsis exacantha* (MELLER, 1998b:637, sample Me-Ob-90-5-1, KOVAR-EDER & MELLER, 2001: tab. 3). The other sample, from more fine-grained sediment, is species poor, with numerous *Glyptostrobus* remains (MELLER, 1998: 638, sample Me-Ob-90-9a).

If modern *Toricellia* grows in dense forests as accessory elements, and the same can be also assumed for the fossil plants, the chances of both the fruits and also the leaves being fossilized seems to be astronomically small. If they grew in a riparian forest, then, given their rare record, it would have been either as accessory elements, or for a very short time as a pioneer plant. From their modern occurrence on disturbed areas or along streams (see above), one could infer both that *Toricellia* might be a pioneer plant and that it can grow in different habitats. This may have been the reason for the survival of this rare plant. It might be an epibiotic element, as suggested by WANG (1961:225-226), which will not radiate or spread anymore, although it seems to be able to survive changing environments.

The dispersal mechanism of the modern *Toricellia* fruits has not been described. The fruit exocarps show a black colour, which might be attractive for birds, although a fleshy mericarp does not seem to develop. If the two big chambers are indeed empty, then only the embryo remains as food. On the other hand, empty chambers covered with a strong exocarp could serve as floating mechanism. Simple experiments have shown that the exocarp does not become easily damaged in water or with other chemical solutions, but only by mechanical influences. The globose shape of the endocarps would also enable them to roll around on the floor. These observations support the idea that *Toricellia* is an accessory element in mesophytic forests or on drier places within a riparian forest. A pollen grain record for this element is still lacking, but this might be due to the fragility of the pollen grains, as observed in the modern plants (oral comm. ZETTER). The lack of leaves might be explained by the rareness of this element in this vegetation or that they have not been recognized yet. Considering the sedimentological and palaeogeographic situation, it is probable that the neighbourhood of the swampy Köflach-Voitsberg lignite area was hilly (MELLER, 1998b) and that *Toricellia* lived in the hinterland and the neighbourhood of the lignite environment.

The sedimentary conditions at the Eocene localities are only in part similar. The Eocene Clarno nut beds comprise volcanic deposits with siltstones and conglomerates, interpreted as a fluvial sucession in a lake delta (MANCHESTER, 1994). The flora is a very rich, with about 170 species and abundant *Toricellia* fruit casts. The casts from the Ronald site in Washington have been found in shales associated with a coal mine. In Messel, the fruits

Taxa \ Samples	Me-Ob-89-8	Me-Ob-89-12	Me-Ob-89-13	Me-Ob-89-14	Me-Ob-89-17	Me-Ob-89-22	Me-Ob-89-25	Me-Ob-89-26	Me-Ob-90-20	Me-Ob-90-33	Me-Ob-90-36	Me-Ob-90-52	Me-Ob-90-5-1	Me-Ob-90-9a
Cephalotaxus miocenica	1	x		1	1		1			x	1	xx		
Glyptostrobus europaeus (seeds)	1		1				x			1	1	1		xx
Glyptostrobus europaeus (cones)			1			1								1
Pinaceae gen. et sp.indet.										1	1			
Sequoia abietina (seeds)							x			x				
Sequoia abietina (cones)	x				1		1	1						
cf. *Acer* sp.													1	
Actinidia spp.							x				1		x	
Alnus spp.	x						1					1	xx	
Alnus vel *Betula* sp. (male catkins)	x						x				xx	xx	xx	
Ampelopsis cf. *malvaeformis*											1			
Araliaceae gen. et sp. indet.														
Arbutoideae div. gen. et spp. indet							1							
Carpinus sp.														1
Carya ventricosa					1									1
Decodon gibbosus														
Eurya stigmosa														
Fagus cf. *deucalionis*												1		
Fagus spp.						1				1				
cf. *Fagus* sp.	1													
Gironniera verrucata	x		x				1		1		x			
Hamamelidaceae gen. et sp. indet.			1								x			
Ilex spp.											1			
Lauraceae gen. et sp. indet.														
Liquidambar sp.														
Magnolia burseracea			1					1		1				
Magnolia sp. (cf. cor)														
Magnolia spp.														
Mastixia amygdalaeformis											1			
Mastixia cf. *lusatica*														
Meliosma pliocaenica						1				1				
Moehringia spp.							1							
Myrica boveyana et/vel *M. ceriferiformoides*														
Nyssa ornithobroma									1			1		
Prunus spp.	x						x	1	1		1	xx	x	1
Pterocarya s.l. spp.	xx		x	1			x	x	x		x	xx	xx	
Rubus spp.			1				1						1	
Sabia europaea														x
Salix sp.														1
Sambucus spp.						1		1		x		1		
Staphylea sp.											1		x	
Swida sp.									1	1			xx	
Symplocos cf. *schereri*						1								
Symplocos lignitarum			1			1							1	
Symplocos salzhausensis			x			1						x	x	1
Symplocos sp.												xx		
Ternstroemia sp.												1		
Tetrastigma cf. *lobata*													1	
Toddalia latisiliquata													1	
Toricellia bonesii ?	1			1						1	1		1	1
Trigonobalanopsis exacantha													1	
cf. *Trigonobalanopsis exacantha*											x			
Ulmaceae/ Lauraceae											1			
Viscum vel *Loranthus* sp.						1								
Vitaceae gen. et sp. indet.										1			x	
Vitis cf. *teutonica*													1	
Vitis cf. *globosa*													x	
cf. *Zanthoxylum* sp.		1												
Sparganium spp.										x				
Urospathites cf. *visimense*										1				

Table 2: List of associated taxa in the different samples from the main seam parting and from the two samples of the hanging wall sequence (last two); (x = 2-10 specimens, xx = 11-100, xxx = > 100).

derive from a sandy lens within the oil shale and are also common (COLLINSON, 1988, tab. 1). The fruit and seed assemblage is still under investigation by Collinson. The Messel maar deposit represents lake sediments within a zonal forest, indicating that the plants were part of the zonal vegetation.

There are few climate data available for exactly those areas from which *Toricellia* has been described (MÜLLER, 1982; WANG, 1961, herbarium sheets). The data for Hupeh (WANG, 1961:97) derives from lower altitudes (469 m above sea level) than the reported occurrence of *Toricellia* (about 1000-1100 m above sea level). The mean annual temperature there is 16.4 °C, the mean annual precipitation 1400 mm. The mean temperature of the coldest month is >0°C although temperatures down to -4.7 °C occur. These data should not be accepted as the full range of conditions for extant *Toricellia* in general, but fit the reconstructed climate of the Oberdorf area during Early Miocene times surprisingly well (MELLER, 1998b:575; MELLER et al., 1999:171, BRUCH & KOVAR-EDER, 2003). MANCHESTER (1994:23) proposed a MAT above 20 °C for the Clarno locality during Eocene times, based on the occurrence of *Ensete*, cycads and palms. Thus from the Eocene to the Miocene and up to the present, *Toricellia* has been adapted to slightly cooler conditions. There might be also some local conditions, which influence the settling of the plants. However, considering the sparse fossil record, the rare extant occurrences and the lack of ecological data, any assumption must be considered very speculative.

The palaeogeographic and modern distributions of *Toricellia* (Fig. 3) show a pattern which is visible in several plants growing today in Asia (e.g. *Tapiscia*, *Platycarya*, *Mahonia*; MANCHESTER, 1999; TIFFNEY, 1985, 2000). MANCHESTER (1999:476, 507) inferred a crossing of the North Atlantic during Eocene times, but called the timing of the arrival in Asia a mystery. The Miocene fossil occurrence of *Toricellia* in Austria closes a gap to the modern occurrences which might be considered as refugial or relictual in distribution. Just recently (during improving the manuscript after the review) a silicified fruit of *Toricellia* has been recognized from the Palaeocene Almont flora in North Dakota (pers. comm. MANCHESTER & PIGG). The promising research about *Toricellia* will be continued.

7. Acknowledgements

8. References

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Appendix:

Studied extant fruits, derving from the following herbarium sheets of the Royal Botanical Garden Edinburgh:

Species	No. of fruits	Country	Collector	Date of collection
Toricellia angulata OLIV.	8	China, Hupeh	Ho-Ch'ang Chow no. 648,	15th June 1934
T. tiliifolia dC.	12	Burma	F.G. Dickason 7266,	2nd April 1938
T. tiliifolia dC.	10	Nepal	Stainton, Sykes & Willimas 132	23rd April 1954
T. tiliifolia dC.	20	Bhutan	Grieson & Long 4538	20th April 1982

PLATE 1

Toricellia angulata OLIVER

Fig. 1   Fruit in dorsal view; the attachment of the peduncel (P) is supra-basal (GBA 2006/005/0016).

Fig. 2   Fruit in lateral view with the peduncle (GBA 2006/005/0017).

Fig. 5   Lateral-apical view on a fruit; the embryo chamber and the germination valve (GV) are very distinct; remnants of the styles (S) are present (GBA 2006/005/0019).

Fig. 6, 9 The same specimen in different views (GBA 2006/005/0020)

Fig. 6   Ventral view showing the distinct embryo chamber and the germination valve in the sub-apical area.

Fig. 9   Dorsal view exposing the holes of the endocarp wall.

Fig.10   Endocarp in lateral view exposing the long open embryo chamber (GBA 2006/005/0021).

Fig. 13, 14, 16 All pictures from the same specimen (GBA 2006/005/0018);

Fig. 13   Cross-section of the endocarp showing the three chambers; the upper one is the embryo chamber (EC) with remnants of the embryo; the lateral ones show the holes in the wall.

Fig. 14   Detail of the endocarp wall.

Fig. 16   Septum in detail.

Toricellia tiliifolia DE CANDOLLE

Fig. 3, 4 The same fruit in ventral (fig. 3) and dorsal view (GBA 2006/005/0026)

Figs. 7, 19 show the same specimen (GBA2006/005/0022)

Fig. 7   Endocarp in ventral view, a few remnants of the exocarp are visible at the apex (A). The arrows point to weak dentations, indicating the lower margin of the germination valve.

Fig. 19   Detail of the endocarp surface; on the left, a part of the longitudinal ridge along the margin of the fertile chamber is visible; in the right part of the picture, cell outlines of the meso-exocarp are observable.

Figs. 8, 12, 15, 17 show the samen specimen (GBA2006/005/0025)

Fig. 8   Exocarp surface.

Fig. 12   Cross-section of the fruit.

Fig. 15   Inner surface of the endocarp wall with distinct parallel ridges.

Fig. 17   Detail of the septa.

Fig. 11   Endocarp in a longitudinal cross-section, exposing the long embryo chamber (GBA 2006/005/0024).

Fig. 18   Dorsal view of an endocarp with the large holes (GBA 2006/005/0023).

Fig. 20   Detail of the endocarp surface with probable meso-exocarp cell remnants (GBA 2006/005/0023).

Toricellia bonesii (MANCHESTER) MANCHESTER from the Eocene of Oregon

Fig. 21   One of the paratypes in lateral-ventral view; the imprint of the sub-apical triangular germination valve is visible; the arrows mark the outline (FLMNH 9295).

Fig. 22   Cross-section of a silicified specimens; one of the rare examples, where the endocarp has been preserved (GBA 2006/005/0010).

Scales show 1 mm unless otherwise mentioned; figures have been taken with the SEM apart from figs. 1-5, 21, 22.
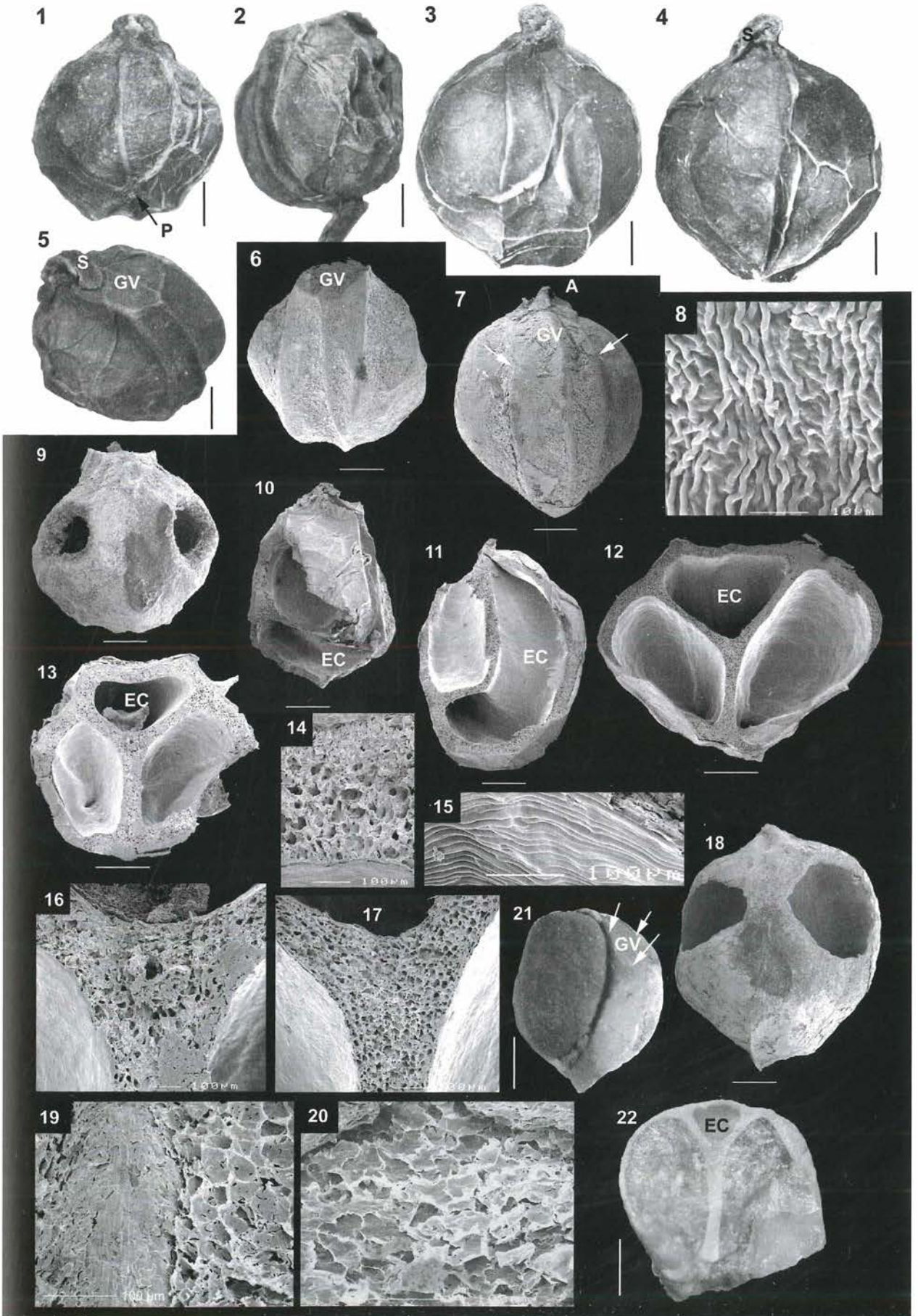
PLATE 1

PLATE 2

Toricellia bonesii (MANCHESTER ?) MANCHESTER from the Oberdorf open-cast mine
(Styria, Austria, Early Miocene)

Fig. 1   Endocarp in lateral-apical view, showing the endocarp hole and the sub-apical germination valve (GBA 2006/005/0008).

Fig. 2   Oblique compressed and flattened endocarp in lateral-ventral view; the endocarp holes are visible as well as the germination valve (GBA 2006/005/0005).

Fig. 3   Cross-section of one endocarp, exposing the three chambers (NHMVienna 1992/0279/0010/3; the specimen is also figured in KOVAR-EDER & MELLER, 2003: pl. 5, fig. 25).

Fig. 4-5   One specimen in ventral (fig. 5) and dorsal (fig. 4) view; the embryo chamber and the sub-apical germination valve are very distinct (GBA 2006/005/0001).

Fig. 8   Detail of the endocarp wall (GBA 2006/005/0001).

Fig. 11   Endocarp surface with irregular undulate cell outlines (GBA 2006/005/0001).

Fig. 6, 9   Compressed and dorso-ventrally flattened specimen; note the large germination valve with a cordate lower margin; the arrow point to the area, shown in fig. 9, where traces of the vascular bundles at the junction of the ridges are observable (NHMVienna 1992/0279/0010/3; the specimen is also figured in KOVAR-EDER & MELLER, 2003: pl. 5, fig.23).

Fig. 7   Inner surface of an endocarp with distinct wrinkles (NHMVienna 1992/0383/0019/3; an overview of this specimen is figured in KOVAR-EDER & MELLER, 2003: pl. 5, fig. 24).

Fig. 10   Endocarp wall of a thick-walled fragmentary specimen (NHMVienna 1992/0287/0014/1).

Toricellia bonesii (MANCHESTER) MANCHESTER from the Eocene of Oregon

Fig. 12   The wrinkles of the inner surface of the endocarp are indicated by these surface structures of the cast (GBA 2006/005/0009).

Fig. 13   Dorsal view of one of the paratypes; the bright fill of the longitudinal furrow represent indicate the septa between the big lateral chambers (the same specimen as on Pl. 1 fig. 21).

Fig. 14   Specimen in ventral view, the longitudinal furrows mark the margins of the embryro chamber; in the upper part, also the germination valve is indicated; parts of the sediment are still attached to the cast at the upper lateral part (GBA 2006/005/0009).

Scales of the overview pictures are always 1 mm; the scales of the details 10 μm. Apart from figs. 1, 13, 14, all pictures have been taken with the SEM.

PLATE 2