**Thomas Denk**



Senior Curator.

**Contact**

Phone: +46 (0)8 519 541 43
E-mail: thomas.denk@nrm.se

**Billing and Mailing Address:**

[See the Staff and Contacts page.](https://www.nrm.se/english/researchandcollections/palaeobiology/staffandcontacts.9002710.html)

**Education**

**MSc** University of Vienna, 1995

**PhD** University of Vienna, Austria, 1998

**Responsibilities**

I am the contact person for the Cenozoic plant collections housed at the department and have been responsible for the registration of the large historical collections from the Arctic and Subarctic. I have been part of the *HIGH LAT* and *SYNTHESIS* evaluation panels at the museum since 2001. I have been supervising Master and PhD students since 2001 (four completed, one current). I have been teaching at Stockholm University since 2007. I taught as a visiting professor at the University of Vienna in 2011.

**Research Interests**

I am interested in the evolution of northern hemispheric terrestrial ecosystems during the Late Cretaceous and the Cenozoic. I want to understand how climate change and the re-arrangement of continents, both of which are strongly influenced by plate tectonics, shaped distributional patterns of organisms across the Northern Hemisphere.

To achieve this, I am exploring the evolutionary histories of selected genera of flowering plants using the fossil record and molecular phylogenetic data. I am particularly interested in biogeographic changes of clades and whether or not these were accompanied by ecological shifts (niche evolution).

Target groups of my current research are the Fagaceae (oak family) with a major focus on the genus *Quercus* (oaks), a north hemispheric genus of about 400-600 species, and other plant genera in different families (Aquifoliaceae, Rosaceae, Sapindaceae, etc.).

I am also investigating the vegetation development in the Mediterranean region during the Neogene (the past 23 million years) and in Arctic regions during the Cenozoic (the past 60 million years).

My overall research question is how various plant groups respond to changing climate and environments over different time scales.

**Projects**

[**Project I.** The evolution of distribution patterns in flowering plants](https://www.nrm.se/english/researchandcollections/palaeobiology/ourresearch/angiospermdistribution.9003802.html)

**Project II.** Evolution of the Madrean-Tethyan sclerophyllous vegetation and the onset of Mediterranean biotas (VR project 2013-16)

**Other Professional Roles**

* Subject Editor for the scientific journal *GRANA*
* Editorial Board member for *Turkish Journal of Botany*
* Editorial Board member for *Acta Palaeobotanica*

## 2021

**Denk, T.**, & Bouchal, J.M., 2021. Dispersed pollen and calyx remains of Dinospyros (Ebenaceae) from the middle Miocene “Plant beds” of Søby, Denmark. GFF. [https://doi.org/10.1080/11035897.2021.1907443](https://doi.org/10.1080/11035897.2021.1907443)

## 2020

Bouchal, J.M. & **Denk, T**., 2020. Low taxonomic resolution of papillate Cupressaceae pollen (former Taxodiaceae) impairs their applicability for palaeo-habitat reconstruction. Grana 59, 71–93. [https://doi.org/10.1080/00173134.2019.1701704](https://doi.org/10.1080/00173134.2019.1701704)

Bouchal, J.M. Güner, T.H., Velitzelos, D., Velitzelos, E. & **Denk, T**., 2020. Messinian vegetation and climate of the intermontane Florina–Ptolemais–Servia Basin, NW Greece inferred from palaeobotanical data: how well do plant fossils reflect past? Royal Society Open Science 7(5), 192067. [https://doi.org/10.1098/rsos.192067](https://doi.org/10.1098/rsos.192067)

Dagtekin, D., Şahan, E.A., **Denk, T**., Köse, N. & Dalfes, H.N., 2020. Past, present and future distributions of Oriental beech (Fagus orientalis) under climate change projections.PloS one 15, e0242280. [https://doi.org/10.1371/journal.pone.0242280](https://doi.org/10.1371/journal.pone.0242280)

**Denk, T**., Hipp, A.L., Manos, P.S., Hahn, M., Avishai, M. & Bodénès, C., 2020. Genomic landscape of the global oak phylogeny. New Phytologist 226: 1198–1212. [https://doi.org/10.1111/nph.16162](https://doi.org/10.1111/nph.16162)

Kvaček, Z. & Vasilis Teodoridis, V. & **Denk, T.,** 2020. The Pliocene flora of Frankfurt am Main, Germany: taxonomy, palaeoenvironments and biogeographic affinities. Palaeobiodiversity and Palaeoenvironments 100, 647–703. [https://doi.org/10.1007/s12549-019-00391-6](https://doi.org/10.1007/s12549-019-00391-6)

Sadowski, E.-M., Schmidt, A.R. & **Denk, T**., 2020. Staminate inflorescences with in situ pollen from Eocene Baltic amber reveal high diversity in Fagaceae (oak family). Willdenowia 50, 405–517. [https://doi.org/10.3372/wi.50.50303](https://doi.org/10.3372/wi.50.50303)

## 2018

Bouchal, J. M., Güner, T. H. and **Denk, T.,** 2018. Middle Miocene climate of southwestern Anatolia from multiple botanical proxies. Climates of the Past, Vol. 14: 1427–1440. [https://www.clim-past.net/14/1427/2018/](https://www.clim-past.net/14/1427/2018/)

**Denk, T**., Zohner, C. M., Grimm, G. W. & Renner, S. S. 2018. Plant fossils reveal major biomes occupied by the late Miocene Old-World Pikermian fauna. Nature Ecology & Evolution. [https://www.nature.com/articles/s41559-018-0695-z](https://www.nature.com/articles/s41559-018-0695-z)

Sadowski, E.-M., Hammel, J. U. & **Denk, T**. 2018. Synchrotron X- ray imaging of a dichasium cupule of Castanopsis from Eocene Baltic amber. American Journal of Botany 105 (12): 1-12. [doi:10.1002/ajb2.1202](http://dx.doi.org/10.1002/ajb2.1202)

Simeone, M. C., Cardoni, S., Piredda, R., Imperatori, F., Avishai, M., Grimm, G. W., **Denk, T**. 2018. Comparative systematics and phylogeography of Quercus Section Cerris in western Eurasia: inferences from plastid and nuclear DNA variation. PeerJ 6: e5793. [https://doi.org/10.7717/peerj.5793](https://doi.org/10.7717/peerj.5793)

## 2017

Bouchal, J. M., Mayda, S., Zetter, R., Grímsson, F. and **Denk, T**., 2017. Miocene palynofloras of the Tinaz lignite mine, Mugla, southwest Anatolia: Taxonomy, palaeoecology and local vegetation change. Review of Paleobotany and Palynology, Vol. 243: 1-36.

**Denk, T**., Güner, T. H., Kvaček, Z. and Bouchal, J. M., 2017. The early Miocene flora of Güvem (Central Anatolia, Turkey): a window into early Neogene vegetation and environments in the Eastern Mediterranean. Acta Palaeobotanica, Vol. 57 (no 2): 237-338. [Journal website](https://www.degruyter.com/view/j/acpa.2017.57.issue-2/acpa-2017-0011/acpa-2017-0011.xml)

**Denk, T**., Velitzelos, D., Güner, T. H., Bouchal, J. M., Grímsson, F. and Grimm, G., 2017. Taxonomy and palaeoecology of two widespread western Eurasian Neogene sclerophyllous oak species: Quercus drymeja Unger and Q. mediterranea Unger. Review of Palaeobotany and Palynology, Vol. 241: 98-128. [Journal website](http://www.sciencedirect.com/science/article/pii/S003466671630104X?via%3Dihub)

Güner, T. H., Bouchal, J. M., Köse, N., Göktas, F., Mayda, S., and **Denk, T**., 2017. Landscape heterogeneity in the Zatagan Basin (southwestern Turkey) during the middle Miocene inferred from plant macrofossils. Palaeobographica, Abt. B, Vol. 296 (no 1–6): 113-171. [Journal website](https://dx.doi.org/10.1127/palb/296/2017/113)

## 2016

Bouchal, J. M., Zetter. R., **Denk, T**., 2016. Pollen and spores of the uppermost Eocene Florissant Formation, Colorado: a combined light and scanning electron microscopy study. Grana 55 (3): 179-245.

Bouchal, J. M., Grímsson, F., Zetter, R., **Denk, T**., 2016. The middle Miocene palynoflora and palaeoenvironments of Eskihisar (Yatağan Basin, southwestern Anatolia): a combined LM and SEM investigation. Botanical Journal of the Linnean Society 182 (1): 14-19.

**Denk, T**. 2016. Palaeoecological interpretation of the late Miocene landscapes and vegetation of northern Greece: a comment to Merceron et al., 2016. Geobios, doi:10.1016/j.geobios.2016.01.004.

Grimm, G.W., Bouchal, J. M., **Denk, T**., Potts, A. 2016. Fables and foibles: A critical analysis of the Palaeoflora database and the Coexistence Approach for palaeoclimate reconstruction. Review of Palaeobotany and Palynology 223: 216-235. [http://dx.doi.org/10.1016/j.revpalbo.2016.07.001](http://dx.doi.org/10.1016/j.revpalbo.2016.07.001)

Renner, S. S., Grimm, G., Kapli, P., **Denk, T**., 2016. Species relationships and divergence times of beeches (Fagus): New insights from the inclusion of numerous fossil beech species in a birth-death clock approach. Philosophical Transactions of the Royal Society B 20150135. [http://rstb.royalsocietypublishing.org/content/371/1699/20150135](http://rstb.royalsocietypublishing.org/content/371/1699/20150135)

Simeone, M. C., Grimm, G. W., Papini, A., Vessella, F., Cardoni, S., Tordoni, E., Piredda, R., Franc, A., **Denk, T**., 2016. Plastome data reveal multiple geographic origins of Quercus Group Ilex. PeerJ 4:e 1897. DOI 10.7717/peerj.1897

## 2015

Grímsson, F., Zetter, R., Grimm, G. W., Pedersen, G. K., Pedersen, A. K., **Denk, T**. 2015. Fagaceae pollen from the early Cenozoic of West Greenland: revisiting Engler’s and Chaney’s Arcto-Tertiary hypotheses. Plant Systematics and Evolution 301: 809–832.

**Denk, T**., Velitzelos, D., Güner, H. T., Ferrufino-Acosta, L. 2015. Smilax from the Miocene of the eastern Mediterranean with Caribbean biogeographic affinities. American Journal of Botany 102: 423-438.

Grímsson, F., Zetter, R., **Denk, T**. Cenozoic vegetation and phytogeography of the sub-arctic North Atlantic. In: E. Panagiotakopulu (ed.), Biogeography in the Sub-Arctic: The Past and Future of North Atlantic Biotas. Wiley. ISBN: 978-1-118-56147-8. In press.

Grimm, G., **Denk, T**., Bouchal, J. M., Potts, A. J. 2015. Fables and foibles: a critical analysis of the Palaeoflora database and the Coexistence Approach for palaeoclimate reconstruction. bioRxiv, 016378

## 2014

Bouchal, J. M., Zetter, R., Grímsson, F., and **Denk, T.**, 2014. Evolutionary trends and ecological differentiation in early Cenozoic Fagaceae of western North America. American Journal of Botany 101: 1332–1349.

**Denk, T.**, Güner, H. T. and Grimm, G. W., 2014. From mesic to arid: Leaf epidermal features suggest preadaptation in Miocene dragon trees (Dracaena). Review of Palaeobotany and Palynology 200: 211-228.

**Denk, T.,** and Tekleva, M. V., 2014. Pollen morphology and ultrastructure of Quercus with focus on Group Ilex (=Quercus Subgenus Heterobalanus (Oerst.) Menitsky): implications for oak systematics and evolution. Grana 53: 255-282.

Grimm, G. W. and **Denk, T.,** 2014. The Colchic region as refuge for relict tree lineages: cryptic speciation in field maples. Turkish Journal of Botany 38: 1050–1066.

Grímsson, F., Zetter, R., Grimm, G. W., Krarup Pedersen, G., Pedersen, A. K. and **Denk, T.,** 2014. Fagaceae pollen from the early Cenozoic of West Greenland: revisiting Engler's and Chaney's Arcto-Tertiary hypotheses. Plant Systematics & Evolution doi: 10.1007/s00606-014-1118-5.

Velitzelos, D., Bouchal, J. M. and **Denk, T.,** 2014. Review of the Cenozic floras and vegetation of Greece. Review of Palaeobotany and Palynology 204: 56–117.

## 2013

**Denk, T.,** Grimm, G. W., Grímsson, F. and Zetter, R. in press. Effective heat transport of Gulf Stream to subarctic North Atlantic during Miocene cooling. Biogeosciences.

## 2012

**Denk, T.,** Grimm, G. W. and Röseler, A.-K., 2012. When field botany meets history: taxonomy of Platanus mexicana Moric. in Mexico. Willdenowia 42: 99-115.

**Denk, T.**, Grímsson, F. and Zetter, R., 2012. Fagaceae from the Early Oligocene of Central Europe: persisting New World and emerging Old World biogeographic links. Review of Palaeobotany and Palynology 169: 7-20.

Grimm, G. W. and **Denk, T.**, 2012. Reliability and resolution of the coexistence approach - a revalidation using modern-day data. Review of Palaeobotany and Palynology 172: 33-47.

Güner, T. and **Denk, T.,** 2012. The genus Mahonia in the Miocene of Turkey: taxonomy and biogeographic implications. Review of Palaeobotany and Palynology 175: 32-46.

Tekleva, M. V. and **Denk, T.,** 2012. Sporoderm ultrastructure of Platanus quedlinburgensis Pacltová emend. Tschan, Denk & von Balthazar from the Late Cretaceous of Germany. Acta Palaeobotanica 52(1): 177-191.

Tschan, G. F. and **Denk, T.,** 2012. Trichome types, foliar indumentum, and epicuticular wax in the Mediterranean ‘Gall Oaks´, Quercus subsectio Galliferae (Spach) Guerke; (Fagaceae): implications for taxonomy, ecology, and evolution. Botanical Journal of the Linnean Society 169: 611-644.

## 2011

**Denk, T.**, Grimsson, F., Zetter, R. and Símonarson, L. A., 2011.  Late Cainozoic Floras of Iceland. 15 Million Years of Vegetation and Climate History in the Northern North Atlantic. Topics in Geobiology 35. Springer. Dordrecht. 870 pp. ISBN 978-94-007-0371-1

Wappler, T. and **Denk T.**, 2011. Herbivory in early Tertiary Arctic forests. Palaeogeography, Palaeoclimatology, Palaeoecology 310: 283-295.

## 2010

**Denk, T.** and Grimm, G. W., 2010. The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers. Taxon 59: 351-366.

**Denk, T.**, Grímsson, F., Zetter, R.,  2010. Episodic migration of oaks to Iceland — Evidence for a North Atlantic “land bridge" in the latest Miocene. American Journal of Botany 97: 276-287.

Grimm, G. W. and **Denk, T.,** 2010. The reticulate origin of modern plane trees (Platanus, Platanaceae) - a nuclear marker puzzle. Taxon 59: 134-147.

Tekleva, M. V., Maslova, N. P. and  **Denk, T.**,2010. Evolution of pollen characters of the Platanaceae. Proceedings of the XII Moscow meeting on plant phylogeny. Moscow: KMK. P. 308-311.

## 2009

**Denk, T.** and Grimm, G. W., 2009. Significance of pollen characteristics for infrageneric classification and phylogeny in Quercus (Fagaceae). International Journal of Plant Science  170: 926-940.

**Denk, T.**and Grimm, G. W., 2009. The biogeographic history of beech trees. Review of Palaeobotany & Palynology 158: 83-100.

## 2008

Grimm, G. W. & **Denk, T.**, 2008. ITS Evolution in Platanus (Platanaceae): Homoeologues, Pseudogenes and Ancient Hybridization. Annals of Botany 101: 403-419.

Grímsson, F., **Denk, T.** & Zetter, R., 2008. Pollen, fruits, and leaves of Tetracentron (Trochodendraceae) from the Cainozoic of Iceland and western North America and their palaeobiogeographic implications. Grana 47: 1-14.

Tschan, G.F., **Denk, T**. & von Balthazar, M., 2008. Credneria and Platanus (Platanaceae) from the Late Cretaceous (Santonian) of Quedlinburg, Germany. Review of Palaeobotany and Palynology152: 211-236.

von Balthazar, M., Schönenberger, J. & **Denk, T**., 2008. In Search of the Earliest Flowers: Introduction. International Journal of Plant Sciences 169: 815-815.

## ****2007****

Grimm, G.W., **Denk, T**., Hemleben, V. 2007. Coding of intraspecific nucleotide polymorphisms: a tool to resolve reticulate evolutionary relationships in the ITS of beech trees (Fagus L., Fagaceae). Systematics and Biodiversity 5(3): 291-309.

Grimm, G.W., **Denk, T**., Hemleben, V. 2007. The Evolutionary History and Systematics of Acer section Acer − a case study of low-level phylogenetics. Plant Systematic and Evolution 267: 215-253.

Grímsson, F., **Denk, T**. 2007. Floristic turnover on Iceland 15 to 6 Ma - extracting biogeographic signals from fossil floral assemblages. Journal of Biogeography 34: 1490-1504.

Grímsson, F., **Denk, T**. and Símonarson, L.A. 2007. Middle Miocene floras of Iceland  - the early colonization of an island? Review of Palaeobotany and Palynology 144: 181-219.

Grímmson, F., Símonarson, L. A., **Denk, T**. 2007. Elstu gróðursamfélög íslenskrar jarðsögu. (Late Langhian to early Seravallian floras of Iceland. In Icelandic with English summary.) Náttúrufræðingurinn 75 (2-4): 85-106.

Uhl, D., Traiser, C., Griesser, U. and **Denk, T**., 2007. Fossil leaves as palaeoclimate proxies in the Palaeogene of Spitsbergen (Svalbard). Acta Palaeobotanica 47(1): 89—107.

## ****2006****

**Denk, T**. & Tekleva, M.V. 2006. Comparative pollen morphology and ultrastructure of Platanus: Implications for phylogeny and evaluation of the fossil record. Grana 45: 195-221.

**Denk, T**. 2006. Rhododendron ponticum var. sebinense in the Late Pleistocene flora of Hötting, Northern Calcareous Alps: witness of a climate warmer than today? Veröffentlichungen des Tiroler Landesmuseums Ferdinandeum 85: 5-30.

## 2005

**Denk, T**. & Dillhoff, R. M. 2005. Ulmus leaves and fruits from the Early-Middle Eocene of northwestern North America: Systematics and implications for character evolution within Ulmaceae. Canadian Journal of Botany, 83:.

**Denk, T.** & Grimm, G., 2005, Phylogeny and biogeography of Zelkova (Ulmaceae s.str.) as inferred from leaf morphology, ITS sequence data and the fossil record. Botanical Journal of the Linnean Society 147: 129-157.

**Denk, T**. & Oh, I.-C., 2005, Phylogeny of Schisandraceae based on morphological data: evidence from modern plants and the fossil record. Plant Systematics and Evolution 256:113-145.

**Denk, T.**, Grimm, G. & Hemleben, V., 2005. Patterns of molecular and morphological differentiation in Fagus: Phylogenetic implications. American Journal of Botany 92: 1006-1016.

**Denk, T.**, Grímsson, G. & Kvacek, Z., 2005. The Miocene flora of Iceland and its significance for late Cainozoic North Atlantic biogeography. Botanical Journal of the Linnean Society149: 369-417.

Grímsson, F. & **Denk, T.**, 2005. Fagus from the Miocene of Iceland: Systematics and biogeographical considerations. Review of Palaeobotany and Palynology134: 27-54.

## 2004

**Denk, T.** 2004 Revision of Fagus from the Cenozoic of Europe and southwestern Asia and its phylogenetic implications. Documenta Naturae 150: 1-72

## 2003

**Denk, T**., 2003. Phylogeny of Fagus L. (Fagaceae) based on morphological data. Plant Systematics & Evolution 240: 55-81.

Oh, I.-C., **Denk, T**., & Friis, E.-M., 2003. Phylogeny of Illicium (Illiciaceae): Mapping morphological characters on the molecular tree. Plant Systematics & Evolution240: 175-209.

Wang, Q., Hao, S.-G., Wang, D.-M., Wang, Y., & **Denk, T.**, 2003. A Late Devonian arborescent lycopsid Sublepidodendron songziense Chen emend. Sublepidodendraceae sensu Kräusel et Weyland, 1949 from China, with a revision of the genus Sublepidodendron (Nathorst) Hirmer, 1927. Review of Palaeobotany and Palynology :in press

## 2002

**Denk, T**. 2002. Revision of Tertiary Fagus cupules from Russia, Transcaucasia and western Siberia. Feddes Repertorium113: 193-210.

**Denk, T**., Grimm, G., Stögerer, K., Langer, M. & Hemleben, V. 2002. The evolutionary history of Fagus in western Eurasia: Evidence from genes,morphology and the fossil record. Plant Systematics and Evolution 232: 213-236.

**Denk, T**. & Velitzelos, D. 2002. First evidence of epidermal structures of Ginkgo from the Mediterranean Tertiary. Review of Palaeobotany and Palynology 120: 1-15.

Kottis, T., Chryssanthi, I., Velitzelos, E., Kvacek, Z., **Denk, T**., Velitzelos, D., 2002. Field guide to the Neogene of the island of Evvia- Early Miocene Flora of Kymi. 6th European Paleobotany - Palynology Conference. Athens, August 29 - September 2.

## 2001

**Denk, T.**, Frotzler, N. & Davitashvili, N. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). Biological Journal of the Linnean Society 72: 287-332.

**Denk, T**. & Meller, B. 2001. Systematic significance of the cupule/nut complex in living and fossil Fagus. International Journal of Plant Sciences 162(4): 869-897.

Wang, Y.-F., Ferguson, D. K., Zetter, R., **Denk, T**. & Garfi, G. 2001. Leaf architecture and epidermal characters in Zelkova, Ulmaceae. Botanical Journal of the Linnean Society 136: 255-265.

## 2000

**Denk, T**. 2000. Die Flora des Gumpenecks und des Walchengrabens in den Wölzer Tauern (Steiermark). Joannea Bot. 1: 27-114.

## 1999

**Denk, T**. 1999. The taxonomy of Fagus in western Eurasia, 1: Fagus sylvatica subsp. orientalis (=F. orientalis). Feddes Repertorium 110 (3-4): 177-200.

**Denk, T**. 1999. The taxonomy of Fagus in western Eurasia, 2: Fagus sylvatica subsp. sylvatica. Feddes Repertorium 110 (5-6): 381-412.

**Denk, T**. 1999. The taxonomy of Fagus in western Eurasia and the ancestors of Fagus sylvatica s. l. Acta Paleobotanica. Suppl. 2.: 633-641.

**Denk, T**., Wanntorp, L. & Manum, S. B. With the assistance of Haglund, O. 1999. Catalogue of the Tertiary plant fossils from Spitsbergen housed in the Swedish Museum of Natural History, Stockholm. Swedish Museum of Natural History, Stockholm. 184 pp.

Ferguson, D. K., Hoffmann, C.-C. & **Denk, T**. 1999. Taphonomy: field techniques in modern environments. I: Jones, T. P. & Rowe, N. P. (eds.). Fossil plants and spores: modern techniques: 210-213. Geological Society, London.

## 1998

**Denk, T**. 1998. Cystopteris regia (L.) Desvaux (Pteridophyta) - new for Iran. Iranian Journal of Botany 7(2): 259-264.

**Denk, T**. 1998. The beech (Fagus L.) in western Eurasia - an actualistic approach. Feddes Repertorium 109(5-6): 435-463.