The Palaeoflora Database - Documentation and Data

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Introduction

The Palaeoflora database has been designed to provide essential information about fossil taxa, their related nearest living relatives (NLRs), and their climatic requirements. The database was established in 1990 to foster quantitative palaeoclimate reconstructions and has been continually growing, as well as being updated and corrected on a regular basis. As of March 2024, Palaeoflora includes ca. 7000 macrobotanical and 3300 microbotanical taxa, and ca. 1900 modern taxonomical units (species, genera, families) for which climate data are available.

The **NLR concept** proposed in the Palaeoflora refers to published palaeobotanical literature resources and kind advice of numerous colleagues. Being maintained in the context of the international scientific network NECLIME (www.neclime.de), Palaeoflora profits immensely from cooperations and the activities within NECLIME, especially of the working groups on palynology and plant macrofossils. **Climatic** ranges for extant plant taxa in the Palaeoflora Database are mainly based on records of meteorological stations located within the plant distribution area of the respective taxon and refer to a global context. Climate data of the Palaeoflora database are most suitable to **reconstruct past regional climates** based on palaeobotanical records. They are primarily designed for the application of the Coexistence Approach (CA, Mosbrugger and Utescher, 1997; Utescher et al., 2014), but are also useful sources for any discussion of past climates.

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Data collected in the Palaeoflora database

Compilation of palaeobotanical taxa and NLR assignments

The identification of palaeobotanical remains and their NLRs depends on organ type and preservation status. Depending on morphological traits displayed by the fossil taxon and closeness of phylogenetic relations to modern species, the taxonomic level of NLR identification varies from species, genera to family and even higher levels.

For pollen, the introduction of a standardised terminology of recent and fossil pollen micromorphology by Punt et al. (2007) and Hesse et al (2009) improved the possibility to compare and correctly identify NLRs. Moreover, the publication of several important pollen atlases, especially the Atlas of Pollen and Spores of the Polish Neogene (Stuchlik, 2001, 2002, 2009) for the Cenozoic of Central Europe, provide not only highly valuable light and scanning electronic microscopic pictures for comparison, but also important remarks on the pollen taxon's NLRs.

With plant macrofossil remains, major progress has been made in the identification of fossil organs and related NLRs within the past two decades of palaeobotanical research by using classical techniques such as comparative morphology, and leaf and wood anatomy (e.g., Manchester, 1994; Mai and Walther, 2000; Kunzmann and Mai, 2005; Kovar-Eder et al., 2006; Erdei et al., 2007; Teodoridis et al., 2009; Barrón et al., 2010; Collinson et al., 2012; Kvaček and Walther, 2012; Denk et al., 2012; Mehrotra et al., 2014; Martinetto, 2015; Pigg and DeVore, 2016; Kovar-Eder, 2016; Averyanova et al., 2022). Moreover, recent advances in combining morphotypes of different organs ("whole plant approach") and the introduction of complex taxa have proven beneficial for developing sound NLR concepts and unravelling true palaeobiodiversity (e.g., *Craigia bronnii* Ung. complex (Worobiec et al., 2010), and *Reevesia hurnikii* Kvaček complex (Worobiec et al., 2012)).

Compilation of climate data

The first step to obtain data on climate space for NLRs is to define the spatial distribution of each taxon of interest. Several sources of distribution maps are available online, e.g., at The Global Biodiversity Information Facility (GBIF) (http://www.gbif.org/), The Atlas of United States Trees (http://esp.cr.usgs.gov/data/atlas/little/), and Flora Europaea (http://www.luomus.fi/english/botany/afe/index.htm). Additionally, various books give printed maps for plant distributions in specific regions like China (Fang et al., 2009, 2011), SW Asia (e.g., Browicz and Zielinski 1982; 1984), and the former Soviet Union (Sokolov et al., 1977; 1980; 1986).

Palaeoflora climate data are mainly based on meteorological stations, which are carefully chosen in order to represent the climatic space of a modern taxon with respect to various climate variables. In order to avoid bias introduced by specific microclimates high altitudinal stations usually are not considered. As regards the selection of suitable stations, we follow the procedure described in Mosbrugger and Utescher (1997). Using GIS, a considerable number of stations of the Müller and Hennings (2000) selection of global station data (long-time means 1961 – 1990), or regional compilations (e.g., for China: State Bureau of Meteorology, 2002), can be effectively checked for extremes. The use of station data accommodates the lack of digital data on plant distribution, coarse raster data (e.g., Flora Europaea) and/or incomplete point data (e.g., GBIF). Moreover, station data can be retrieved easily also for analogue plant distribution maps (e.g., Meusel et al., 1965) and to some extent mere descriptions of plant distribution. For some taxa distributed in regions with a poor station cover, WORLDCLIM datasets (Hijmans et al., 2005) are used to complement their climatic requirements.

For a detailed discussion of uncertainties and the accuracy of Palaeoflora climate data, please refer to Utescher et al. 2014.

How to use the data

Palaeoflora data published here replace the data that have been available on the former Palaeoflora Website which is no longer operational. Please ensure to cite this publication if using any climatic information on modern plant taxa. The Palaeoflora data are published in their present state, however it is planned to update the information provided in the tables on occasion. Please note that unauthorized copies of Palaeoflora contents provided elsewhere in the WEB may contain erroneous entries or may be outdated.

Palaeoflora data have been compiled over decades and may contain fossil taxa that are no more valid. Also, the citations of first describing authors provided for species entries are inconsistent regarding their formatting or may be completely missing. The user should also take in account that the taxonomical information provided is not synonymized and entries on synonyms are incomplete. Authors cited in the context of NLR assignment refer to palaeobotanical literature and/or personal communications of colleagues mentioning the respective fossil taxon, but in most cases not to the first describing publication. Therefore, it is recommended to consult additional recent palaeobotanical literature resources in the case of uncertainties regarding the NLR concept of a newly studied fossil assemblage.

It is planned to update the herein published tables on a regular basis. Thus, input from Palaeoflora users is highly welcome. Please contact the corresponding author if you find any data needing revision.

Main contributors to the database

Data compilation for the Palaeoflora database immensely profited from kind advice of numerous colleagues, mainly from the NECLIME network and works conducted in the frame of meetings of the NECLIME working groups on palynology, plant macrofossils and climate.

Taxonomy and NLRs of the Neogene macrobotanical record and complex taxa (Whole-plant-approach) were specifically discussed with Eduardo Barrón, Olesya Bondarenko, Vladimir Bozukov, Desa Dordjevic-Milutinovic, Boglarka Erdei, Lilla Hably, Lutz Kunzmann, Zlatko Kvacek, Edoardo Martinetto, Svetlana Popova, Su Tao, Jakub Sakala, Gaurav Srivastava, Vasilis Teodoridis, Dieter Uhl, Zhou Zhe-Kun.

Taxonomy and NLRs of the Neogene microbotanical record were discussed with Funda Akgün, Serkan Akkiraz, Rahman A. Ashraf, Adele Bertini, Nela Dolakova, Ewa Durska, Dimiter Ivanov, Mine Sezgül Kayseri, Marianna Kovacova, Vandana Prasad, Ulrich Salzmann, Barbara Slodkowska, Leon Stuchlik, Jean-Pierre Suc, Svetlana Syabryaj, Wang Wei-Ming, Elzbieta Worobiec.

Discussions on climate data for extant taxa profited greatly from David Greenwood, Arata Momohara, Robert A. Spicer, Christopher Traiser, and Zhou Zhe-Kun.

In addition, Palaeoflora immensely profited from numerous contributors submitting results of their most recent research. Their help and advice is gratefully acknowledged.

The database structure and content

The following tables describe the structure and content of the three main tables of the Palaeoflora database. Each table below gives the list of attributes of one database table, their format, and a short description. Each attribute is described individually in detail.

Table Palaeoflora_2024_NLR_plant macrofossils

field name	short description	entry
MACRO_NAME	name of fossil taxon	string, key field
STATUS	synonyms, if applicable	string
ТҮРЕ	C=Fruits or Seeds, L=Leaves, W=Wood, etc.	string
COMPLEX	taxa defining the complex	string
NLR_TAXON	nearest living relative taxa as proposed in literature	string, linked with
		Table climate data
NLR_FAMILY		string
NLR_CLASS	D dicotyledon, M monocotyledon, G gymnosperm, etc.	string
NLR_SOURCE	source of NLR assignment	string
NLR_REMARKS	extinct genus, differing opinions on NLRs, etc.	string

The table <u>Palaeoflora 2024_NLR plant macrofossils connects</u> a plant macrofossil taxon with one or more nearest living relatives (NLRs). The table contains **7033** macrobotanical taxa as of version 2024.

The attribute MACRO_NAME contains the name of the fossil taxon of interest. If the table is incorporated into a database the attribute MACRO_NAME is a key to connect to a list of fossil taxa under consideration for analysis.

The attribute **STATUS** gives information about synonyms or other taxonomic concepts. Note that synonym names are also listed as MACRO_NAME to facilitate the connection to NLRs.

The attribute **TYPE** lists one or several plant organs, which document the taxon in the fossil record. Abbreviations are C carpological remain (fruit or seed), L leaf, W wood, while more rare plant parts are given in full, e.g. endocarp, flower, cuticle.

The attribute **COMPLEX** refers to other plant fossils that are assigned to the same plant in the frame of the whole plant approach.

The attribute **NLR_TAXON** provides the suggested assignment of the respective fossil taxon to a nearest living relative (NLR). One fossil taxon can be assigned to one or more NLRs depending on the

author. This attribute is connected to table Palaeoflora_2024_climate data, but not all NLRs have climate data entries.

The attribute **NLR_FAMILY** gives the plant family of the NLR, if applicable.

The attribute **NLR_CLASS** gives information on the higher taxonomic level of the NLR, if applicable. Those 'classes' are abbreviated as D dicotyledon, M monocotyledon, G gymnosperm, P Polypodiopsida (true ferns), E Equisetidae, B bryophyte (mosses, liverworts, hornworts), L lycophyte (clubmosses, spikemosses, quillworts).

The attribute NLR_SOURCE gives short references to the source of the NLR assignment.

The attribute **NLR_REMARKS** can contain comments regarding different opinions on NLRs, or other information.

Table Palaeoflora 2024 NLR palynomorphs

field name	short description	entry
MICRO_NAME	name of fossil taxon	string, key field
STATUS	synonyms, if applicable	string
ТҮРЕ		string
NLR_TAXON	nearest living relative taxa as proposed in literature	string, linked with
		Table climate data
NLR_FAMILY		string
NLR CLASS	D dicotyledon, M monocotyledon, G gymnosperm, etc.	string
NLR_SOURCE	source of NLR assignment	string
NLR_REMARKS	extinct genus, differing opinions on NLRs etc.	string

The table <u>Palaeoflora 2024 NLR palynomorphs</u> connects a plant palynomorph taxon with one or more nearest living relatives (NLRs). The table contains **3279** microbotanical taxa as of version 2024.

The attribute MICRO_NAME contains the name of the fossil taxon of interest. If the table is incorporated into a database the attribute MICRO_NAME is a key to connect to a list of fossil taxa under consideration for analysis.

The attribute **STATUS** gives information about synonyms or other taxonomic concepts. Note that synonym names are also listed as MICRO_NAME to facilitate the connection to NLRs.

The attribute **TYPE** lists the plant organ, which document the taxon in the fossil record. Abbreviations are P pollen, S spore, while more rare cases are given in full, e.g. cuticle.

The attribute **NLR_TAXON** provides the suggested assignment of the respective fossil taxon to a nearest living relative (NLR). One fossil taxon can be assigned to one or more NLRs depending on the author. This attribute is connected to table Paleoflora_2024_climate data, but not all NLRs have climate data entries.

The attribute **NLR_FAMILY** gives the plant family of the NLR, if applicable.

The attribute **NLR_CLASS** gives information on the higher taxonomic level of the NLR, if applicable. Those 'classes' are abbreviated as D dicotyledon, M monocotyledon, G gymnosperm, P Polypodiopsida (true ferns), E Equisetidae, B bryophyte (mosses, liverworts, hornworts), L lycophyte (clubmosses, spikemosses, quillworts).

The attribute **NLR SOURCE** gives short references to the source of the NLR assignment.

The attribute **NLR_REMARKS** can contain comments regarding different opinions on NLRs, or other information.

Table Palaeoflora_2024_climate data

field name	short description	entry
NLR_TAXON	name(s) of nearest living relatives	string, key field
MATmin	minimum value of the range of MAT in [°C]	float
MATmax	maximum value of the range of MAT in [°C]	float
CMTmin	minimum value of the range of CMT in [°C]	float
CMTmax	maximum value of the range of CMT in [°C]	float
WMTmin	minimum value of the range of WMT in [°C]	float
WMTmax	maximum value of the range of WMT in [°C]	float
MAPmin	minimum value of the range of MAP in [mm]	integer
MAPmax	maximum value of the range of MAP in [mm]	integer
MPWETmin	minimum value of the range of LMP in [mm]	integer
MPWETmax	maximum value of the range of LMP in [mm]	integer
MPDRYmin	minimum value of the range of HMP in [mm]	integer
MPDRYmax	maximum value of the range of HMP in [mm]	integer
MPWARMmin	minimum value of the range of WMP in [mm]	integer
MPWARMmax	maximum value of the range of WMP in [mm]	integer
CLIMATE_SOURCE	Gallagher et al., 2003; Greenwood et al., 2003	string

The table <u>Palaeoflora 2024 climate data gives</u> the climatic ranges of seven climate parameters for nearest living relative (NLR). Not all NLRs listed here do occur in the tables above. Moreover, not all taxa listed as NLRs in the tables above have climate data entries. The values were mainly obtained from meteorological stations within the distribution area of the modern taxa. The table contains **1899** datasets.

The attribute **NLR_TAXON** contains the name of the nearest living relative (NLR) as given in tables <u>Palaeoflora 2024 NLR plant macrofossils and Palaeoflora 2024 NLR palynomorphs</u>, thus linking all three tables.

The attribute **MATmin** gives the minimum value of the range of mean annual temperature in the distribution area of the given NLR. The value is given in [°C].

The attribute **MATmax** gives the maximum value of the range of mean annual temperature in the distribution area of the given NLR. The value is given in [°C].

The attribute **CMTmin** gives the minimum value of the range of mean temperature of the coldest month in the distribution area of the given NLR. The value is given in [°C].

The attribute **CMTmax** gives the maximum value of the range of mean temperature of the coldest month in the distribution area of the given NLR. The value is given in [°C].

The attribute **WMTmin** gives the minimum value of the range of mean temperature of the warmest month in the distribution area of the given NLR. The value is given in [°C].

The attribute **WMTmax** gives the maximum value of the range of mean temperature of the warmest month in the distribution area of the given NLR. The value is given in [°C].

The attribute **MAPmin** gives the minimum value of the range of mean annual precipitation in the distribution area of the given NLR. The value is given in [mm].

The attribute **MAPmax** gives the maximum value of the range of mean annual precipitation in the distribution area of the given NLR. The value is given in [mm].

The attribute **MPWETmin** gives the minimum value of the range of mean monthly precipitation of the wettest month in the distribution area of the given NLR. The value is given in [mm].

The attribute **MPWETmax** gives the maximum value of the range of mean a monthly precipitation of the wettest month in the distribution area of the given NLR. The value is given in [mm].

The attribute **MPDRYmin** gives the minimum value of the range of mean monthly precipitation of the driest month in the distribution area of the given NLR. The value is given in [mm].

The attribute **MPDRYmax** gives the maximum value of the range of mean a monthly precipitation of the driest month in the distribution area of the given NLR. The value is given in [mm].

The attribute **MPWARMmin** gives the minimum value of the range of mean monthly precipitation of the warmest month in the distribution area of the given NLR. The value is given in [mm].

The attribute **MPWARMmax** gives the maximum value of the range of mean a monthly precipitation of the warmest month in the distribution area of the given NLR. The value is given in [mm].

The attribute **CLIMATE_SOURCE** gives short references where climate data are taken from external sources (i.e. Gallagher et al., 2003; Greenwood et al., 2003).

References

- Averyanova, A., Tarasevich, V.F., Popova, S., Su, T., Mosbrugger, V., 2022. Late Rupelian flora of the Zaissan Depression (Eastern Kazakhstan). Review of Palaeobotany and Palynology 304, 104721.
- Barrón, E., Rivas-Carballo, E., Postigo-Mijarra, J., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., Valle-Hernandez, M., 2010. The Cenozoic vegetation of the Iberian Peninsula: A synthesis. Rev. Palaeobot. Palynol 162 (3), 382–402.
- Browicz, K., Zielinski, J., 1982. Chorology of Trees and Shrubs in South-West Asia and Adjacent Regions, vol. I. Polish Academy of Sciences, Institute of Dendrology, Kórnik.
- Browicz, K., Zielinski, J., 1984. Chorology of Trees and Shrubs in South-West Asia and Adjacent Regions, vol. IV. Polish Academy of Sciences, Institute of Dendrology, Kórnik.
- Collinson, M.E., Manchester, S.R., Wilde, V., 2012. Fossil fruits and seeds of the Middle Eocene Messel biota. Abh. Senckenb. Ges. Naturforsch. 570, 1–251.
- Denk, T., Grímsson, F., Zetter, R., 2012. Fagaceae from the Early Oligocene of Central Europe: persisting New World and emerging Old World biogeographic links. Rev. Palaeobot. Palynol. 169, 7–20.
- Erdei, B., Hably, L., Kázmér, M., Utescher, T., Bruch, A.A., 2007. Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography. Palaeogeogr. Palaeoclimatol. Palaeoecol. 253, 115–140.
- Fang, J., Wang, Z., Tang, Z., 2009. Atlas of Woody Plants in China. Vol. 1 and Index. Higher Education Press, Beijing.
- Fang, J., Wang, Z., Tang, Z., 2011. Atlas of Woody Plants in China. Vol. 2 and Index. Higher Education Press, Beijing.
- Gallagher, S.J., Greenwood, D.R., Taylor, D., Smith, A.J., Wallace, M.W., & Holdgate, G.R. 2003. The Pliocene climatic and environmental evolution of southeastern Australia: evidence from the marine and terrestrial realm. Palaeogeography, Palaeoclimatology, Palaeoecology, 193:349-382.
- Greenwood, D.R., Moss P.T., Rowett, A.I., Vadala, A.J., & Keefe, R.L., 2003. Plant communities and climate change in southeastern Australia during the early Paleogene. pp. 365–380, In, Wing, S.L., Gingerich, P.D., Schmitz, B., and Thomas, E. (eds.) Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America Special Paper 369.
- Hesse, M., Halbritter, H., Zetter, R., Weber, M., Buchner, R., Frosch-Radivo, A., Ulrich, S., 2009. Pollen Terminology An Illustrated Handbook. Springer, Wien.
- Kovar-Eder, J., Kvaček, Z., Martinetto, E., Roiron, P., 2006. Late Miocene to Early Pliocene vegetation of southern Europe (7–4 Ma) as reflected in the megafossil plant record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 321–339.
- Kovar-Eder, J. 2016. Early Oligocene plant diversity along the Upper Rhine Graben: The fossil flora of Rauenberg, Germany. Acta Palaeobotanica 56(2), 329–440.

- Kunzmann, L., Mai, D.H., 2005. Die Koniferen der Mastixioideen-Flora von Wiesa bei Kamenz (Sachsen, Miozän) unter besonderer Berücksichtigung der Nadelblätter. Palaeontogr. Abt. B 272, 67–135.
- Kvaček, Z., Walther, H., 2012. European Tertiary Fagaceae with chinquapin-like foliage and leaf epidermal characteristics. Feddes Repertorium 121, 248–267.
- Mai, D.H., Walther, H., 2000. Die Fundstellen eozäner Floren des Weißelster-Beckens und seiner Randgebiete Altenburger Naturwiss. Forsch. 13, 1–59.
- Manchester, S.R., 1994. Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, north central Oregon. Palaeontogr. Am. 58, 1–205.
- Martinetto, E., 2015. Monographing the Pliocene and early Pleistocene carpofloras of Italy: methodological challenges and current progress. Palaeontographica B 293, 57–99.
- Mehrotra, R.C., Shukla, A., Srivastava, G., Tiwari, R.P., 2014. Miocene megaflora of peninsular India: Present status and future prospect. Spec. Pub. Palaeont. Soc. India 5, 273–281.
- Meusel, H., Jäger, E., Weinert, E., 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Band 1 (Text und Karten)Fischer-Verlag, Jena.
- Mosbrugger, V., Utescher, T., 1997. The coexistence approach amethod for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 134, 61–86.
- Müller, M.J., Hennings, D., 2000. The Global Climate Data Atlas on CD Rom. University Flensburg, Institute für Geografie, Flensburg.
- Pigg, K.B., DeVore, M.L., 2016. A review of the plants of the Princeton chert (Eocene, British Columbia, Canada). Botany 94, 661–681.
- Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., Le Thomas, A., 2007. Glossary of pollen and spore terminology. Rev. Palaeobot. Palynol. 143, 1–81.
- Sokolov, S., Svjseva, O., Kubli, V., 1977. Ranges of Trees and Shrubs of the USSR, Volume 1. Nauka, Leningrad.
- Sokolov, S., Svjseva, O., Kubli, V., 1980. Ranges of Trees and Shrubs of the USSR, Volume 2. Nauka, Leningrad.
- Sokolov, S., Svjseva, O., Kubli, V., 1986. Ranges of Trees and Shrubs of the USSR, Volume 3. Nauka, Leningrad.
- State Bureau of Meteorology, 2002. Climate Observation of China (1971–2000). Chinese Meteorological Publishing House, Beijing.
- Stuchlik, L. (Ed.), 2001. Atlas of pollen and spores of the Polish Neogene, Spores, vol. 1. Polish Academy of Sciences, W. Szafer Institute of Botany, Kraków.
- Stuchlik, L. (Ed.), 2002. Atlas of pollen and spores of the Polish Neogene, Gymnosperms, vol. 2. Polish Academy of Sciences, W. Szafer Institute of Botany, Kraków.
- Stuchlik, L. (Ed.), 2009. Atlas of pollen and spores of the Polish Neogene, Angiosperms, vol. 3. Polish Academy of Sciences, W. Szafer Institute of Botany, Kraków,
- Teodoridis, V., Kvaček, Z., Uhl, D., 2009. Pliocene palaeoenvironment and correlation of the Sessenheim–Auenheim floristic complex (Alsace, France). Palaeodiversity 2, 1–17.
- Utescher, T., Bruch, A.A., Erdei, B., François, L., Ivanov, D., Jacques, F.M.B., Kern, A.K., Liu, Y.S., Mosbrugger, V., Spicer, R.A., 2014. The Coexistence Approach—Theoretical background and practical considerations of using plant fossils for climate quantification. Palaeogeography, Palaeoclimatology, Palaeoecology 410, 58-73.

- Worobiec, G., Worobiec, E., Kvaček, Z., 2010. Neogene leafmorphotaxa of Malvaceae s.l. in Europe. Int. J. Plant Sci. 171, 892–914.
- Worobiec, G., Worobiec, E., Szynkiewicz, A., 2012. Plant assemblage from the Upper Miocene deposits of the Bełchatów Lignite Mine (Central Poland). Acta Palaeobotanica 52, 369–413.