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ORIGINAL PAPER

The biodiversity of the Eocene Messel Pit

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Abstract

The Messel Pit is a *Konservat-Lagerstätte* in Germany, representing the deposits of a latest early to earliest middle Eocene maar lake, and one of the first palaeontological sites to be included on the list of UNESCO World Heritage Sites. One aspect of Messel that makes it so extraordinary is that its sediments are rich in different fossilised organisms – microfossils, plants, fungi, invertebrate animals and vertebrates – that are rarely preserved together. We present an updated list of all taxa, named or not, that have been documented at Messel, comprising 1409 taxa, which represent a smaller but inexactly known number of biological species. The taxonomic list of Labandeira and Dunne (2014) contains serious deficiencies and should not be used uncritically. Furthermore, we compiled specimen lists of all Messel amphibians, reptiles and mammals known to us. In all, our analyses incorporate data from 32 public collections and some 20 private collections. We apply modern biodiversity-theoretic techniques to ascertain how species richness tracks sampling, to estimate what is the minimum asymptotic species richness, and to project how long it will take to sample a given proportion of that minimum richness. Plant and insect diversity is currently less well investigated than vertebrate diversity. Completeness of sampling in aquatic and semiaquatic, followed by volant, vertebrates is higher than in terrestrial vertebrates. Current excavation rates are one-half to two-thirds lower than in the recent past, leading to much higher estimates of the future excavation effort required to sample species richness more completely, should these rates be maintained. Species richness at Messel, which represents a lake within a paratropical forest near the end of the Early Eocene Climate Optimum, was generally higher than in comparable parts of Central Europe today but lower than in present-day Neotropical biotopes. There is no evidence that the Eocene Messel ecosystem was a "tropical rainforest."

Keywords Messel · Eocene · Biodiversity · Species richness · Extrapolation · Sampling · Fossil · Greenhouse climates

Introduction

The early Palaeogene, particularly the time interval recognised as the Early Eocene Climate Optimum (EECO), is widely considered a time of extraordinary warmth in Earth history, on land and in the oceans (e.g. Clyde et al. 2001; Zachos et al. 2001; Westerhold et al. 2020). Continental fossiliferous areas in high latitudes preserve remains of taxa that no longer exist anywhere near the poles (e.g. Estes and Hutchison 1980; Eberle et al. 2010), and even middle latitude sites commonly preserve taxa that today are restricted to more tropical climes, a pattern seen amongst plants (e.g. Collinson et al. 2012), fungi (e.g. Taylor et al. 2015), insects (e.g. Wedmann et al. 2007), amphibians, reptiles (e.g. Smith 2009b), birds (e.g. Mayr 2011; Saupe et al. 2019), and mammals (e.g. Bown and Rose 1987).

Documenting palaeodiversity and its covariation with palaeoenvironmemt is a core goal in palaeobiology. *Konservat-Lagerstätten* (Seilacher 1970; Kimmig and Schiffbauer 2024), or "conservation deposits," play an important role in this context. They are defined by the exceptional preservation of the fossils they contain, typically due to anoxic conditions and a stable sediment-water interface, as may occur in isolated basins (Muscente et al. 2017). These localities preserve more complete specimens with more anatomical detail than at other sites, and so allow deeper insights into palaeobiology and biotic interactions. They can

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also preserve a broader taxonomic spectrum, such that soft-bodied organisms, including animals without mineralised skeletons, are found together with skeletonised animals like vertebrates.

Three continental *Konservat-Lagerstätten* provide extraordinary insight into biodiversity around the EECO, which ended c. 47 Ma (Westerhold et al. 2020): the Fossil Butte Member of the Green River Formation of Wyoming in North America (Grande 1984, 2013) at a palaeolatitude of 47 °N, and in Germany Geiseltal (Krumbiegel 1959; Krumbiegel et al. 1983; Georgalis et al. 2021), at a palaeolatitude of 47 °N, and the Messel Pit (Schaal and Ziegler 1988; Gruber and Micklich 2007; Smith et al. 2018a), at a palaeolatitude of 45 °N. At Messel – more precisely the Messel Pit Fossil Site – fossils are excavated from the "oil-shale" of the Middle Messel Formation, which represents the stable, meromictic phase of a maar lake that formed 48.06 Ma (Mertz and Renne 2005; Lenz et al. 2015; Kaboth-Bahr et al. 2024) and persisted until at least 47.22 Ma (Kaboth-Bahr et al. 2024). Older strata (the Lower Messel Formation) are mostly clastic sediments deposited during stabilisation of the land surface following the eruptive phase and accessible only in the 2001 Messel research drill-core. Younger fine-grained clastic sediments with minor occurrences of lignite (the Upper Messel Formation) were mostly eroded (Büchel and Schaal 2018) or destroyed by subsequent mining from c. 1859–1961 (Schaal and Schneider 1995; Felder and Harms 2004). The Senckenberg Research Institute and Natural History Museum in Frankfurt (SMF) and the Hessisches Landesmuseum Darmstadt (HLMD) continue to conduct annual scientific excavations in the Middle Messel Formation.

In this paper we give for the first time an accounting of Messel collections scattered throughout over 50 repositories. We provide estimates of the species richness of Messel using biodiversity-theoretic techniques. These estimates serve two strictly scientific purposes. First, they provide a point of comparison with modern biotopes at the same and more tropically situated latitudes. Second, they provide the first extrapolations of the species richness of undersampled higher taxa. Furthermore, we show how these data can be used in the management of palaeontological resources by providing estimates of the time remaining to sample any given proportion of extrapolated taxonomic richness. Finally, we present an updated taxonomic list for Messel.

Material and methods

We use the term "taxon" (rather than "species") to mean the lowest-level taxonomic entity that can be identified for a particular organ or fossil type (e.g. body fossil, trace fossil). In many cases, it is to be expected that a given biological species could be represented by multiple taxa in our data set (e.g. pollen-, seed-, flower-, wood- and leaf-based taxa for plants), or that different biological species can be represented by a single fossil taxon (e.g. pollen, wood), yet in most cases it is not clear how they are associated. Furthermore, in a number of cases, a taxon has not yet formally been identified to the species level; it has merely been noted that some unknown representative of a certain higher taxon is present, possibly with the use of open nomenclature. We think the term "taxa" is therefore the least ambiguous way to describe what we mean. We note that a taxon need not be named formally (International Commision on Zoological Nomenclature 2024).

In our quantitative analyses of richness, in contrast, we generally (except for palynomorphs and insect damage types) write of "species richness." The reason for the difference is that all these analyses are restricted to a particular kind of fossil, and for seed plants (based on fruit and seed fossils) and vertebrates (based on body fossils) we believe that the units are close to biological species.

Tabulation of taxon occurrence records

All methods that seek to estimate species richness rely on the frequency distributions in an adequate sample of the diversity to be estimated. Thus, all phenomena that influence the frequency distribution of species in a sample introduce biases, which may be more or less remediable, but should always be borne in mind. For instance, in a palaeobiological context, it is normally accepted that taphonomic filters have distorted taxon representation, such that one cannot assume that the abundances of fossil taxa in a death assemblage (thanatocoenosis) or burial assemblage (taphocoenosis) represent their abundances in the live assemblage (biocoenosis). In the case of Messel, for instance, lepidopteran insects are rare, which is thought to result from their large wing surface area and the surface tension of water, preventing them from sinking readily (Wagner et al. 1996). As a further example, isolated feet of Messel birds could represent the feeding remains of crocodylians (Mayr 2016), with the potential for distortion of bird abundances. Taphonomic filters are not always severe, and death assemblages can fairly closely reflect live assemblages (e.g. Kidwell 2001, 2013; Terry 2010).

Of particular relevance to Messel is its complex administrative history (Schaal and Schneider, 1995). This has resulted in collections that are highly heterogeneous: both private persons and public institutions have excavated in the Messel Pit, with varying degrees of intensity; some persons dug alternately for their private collections and for a public institution; many privately held specimens have subsequently been acquired by public institutions, or changed hands; and excavations have been conducted in different horizons, often at a time when there was no stratigraphic control due to a dearth of recognised marker beds.

Whitaker and Kimmig (2020) recently reviewed a number of anthropogenic biases that can creep in, starting with field work, where collection bias can arise for different reasons (e.g. Ifrim et al. 2010; Eck 2018). At Messel, collection bias toward more complete specimens is a concern for the plant macrofossils, insects, and fishes. Particularly in the early years, plant and insect remains were rarely collected by private persons and less intensively by institutional scientific teams. Within the tetrapod vertebrate groups analysed here (Amphibia, "reptiles", Mammalia, Aves) we do not believe that collection bias is significant, as institutional staff collect all such specimens, and interaction with persons once engaged in private collecting at Messel convinces us that they too would have taken all tetrapod skeletal remains. Preparation and curation biases are not likely to be a serious problem for any group. Study or publication bias is a potentially greater concern, but much less so now than in the past (when the greatest effort was on mammal fossils). Moreover, we focus on collections that have been comprehensively examined, and therefore we have reason to believe that no subgroup has been excluded from scientific attention.

The data sets we analysed quantitatively are summarised as follows (Supplementary Information, Supplementary Data S1):

Seed plants based on fruits and seeds (Supplementary Data S2, S14). We used the comprehensive data set of Collinson et al. (2012), which is based on the HLMD and especially the SM.B Me collections. Most taxa in the data set are fruits or seeds, but it includes a cone scale taxon from a conifer, which was included because it is certain that seeds would have been attached to the cone scales; this is not a carpological taxon, strictly speaking. Note also that one taxon in this data set, *Equisetum* sp., is excluded because it is not a seed- but a spore-bearing plant and because it is not a reproductive organ but a vegetative survival organ (bulbil). We are aware that during the intervening years additional, so far undescribed, fruit and seed taxa have been discovered during annual excavations (DU, unpublished observation).

Palynomorphs (Supplementary Data S15). We used the comprehensive data set of Lenz et al. (2011, 2017) for the Middle Messel Formation (Messel 2001 research drill-core), which consists of 517 samples, each with several hundred palynomorphs identified by light microscopy (mean: 241; standard deviation: 12.8; range: 210–304).

Insects and damage types (Supplementary Data S3, S16). Most insect groups have not been comprehensively studied, so we do not analyse most in detail, but for two exceptions: the click-beetle family Elateridae, published by Tröster (1991, 1993, 1994, 1999), and the poneromorph ants, published by Dlussky and Wedmann (2012). For insect-induced damage types on leaves, our taxonomic list is based on 9334 leaves in Messel collections (SM.B Me and HLMD), which were examined for traces of insect damage by Wappler et al. (2012) and Albrecht et al. (2023) and recorded using the system of Labandeira et al. (2007).

Fishes (Supplementary Information, Supplementary Data S17–S21). We used the comprehensive data set of Micklich (2012).

Amphibia (Supplementary Information, Supplementary Data S4, S22). We tabulated all fossils known to us.

"Reptiles" (Supplementary Information, Supplementary Data S5–S8, S23–S26). We tabulated all fossils known to us. "Reptilia" is no longer a formally recognised group, so we also list and analyse the constituent groups Squamata, Testudines, and Crocodylia separately.

Aves (Supplementary Information, Supplementary Data S9, S27). We used the comprehensive data set of Mayr (2017).

Mammalia (Supplementary Information, Supplementary Data S10, S28). We tabulated all fossils known to us.

We assume that rare isolated body parts never come from the same individual, i.e. that each specimen, even when partial, is independent of any other. In general, we believe that this assumption is secure, given the broad scattering of the excavation sites within the Messel Pit and their individually small spatial extent. There are, however, rare cases in which the assumption of a Bernoulli process (each draw of an individual is independent of the others) might be violated (Gotelli and Chao 2013). In the case of mating turtles (Joyce et al. 2012), two individuals are found together. Here, it is clear that the second individual must be of the same species as the first individual, which will bias counts of that species higher. Consequently, we counted only one individual of the pair. In the case of gut contents, one individual is found inside another. Here, the consumer does not choose food species randomly (for instance, a crocodile will not be found in the gut of an aphid), but a broad spectrum is still possible, especially as cannibalism is not excluded (e.g. Micklich 2012). Hence, we count rare individuals identified in gut contents.

In the early days of collecting in Messel – at a time when the pit was slated to become a landfill (Schaal and Schneider 1995) – sometimes hundreds of private persons at a time were engaged in collecting, especially on the weekends. Of these, some dozen or so were especially active and became well known for their collections. Some of these private collections (e.g. Behnke, Feist, Irle, Perner, Sommer, Tandler) have since been acquired, at least in part, by public institutions. Major remaining private collections, if left unexamined, could potentially form a significant lacuna or bias in the data with the potential to alter our conclusions (Whitaker and Kimmig 2020). Hence, we sought to include them wherever possible, although we conducted separate analyses for 'publicly held' and 'all' specimens.

Collections examined

Altogether our study encompassed 32 public collections holding Messel fossils, as listed below. We tabulated all amphibian, "reptile" or mammal fossils (Supplementary Materials), insofar as these were present in said collections. Our lists are almost certain to be incomplete and to contain inaccuracies (especially as we intended no taxonomic revisions to be part of this work), but they nevertheless should provide a reasonable first approximation of known diversity and a solid basis for quantitative studies.

1. American Museum of Natural History, New York, U.S.A. (AMNH)
2. Bayerische Staatssammlung für Paläontologie, Munich, Germany (SNSB-BSPG)
3. Bürgermeister-Müller-Museum, Solnhofen, Germany (BMMS)
4. Geologisches und Paläontologisches Institut, Universität Hamburg, Germany (GPIH)
5. Hessisches Landesmuseum, Darmstadt, Germany (HLMD)
6. Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB)
7. Johannes Gutenberg University Mainz, Germany (JGU)
8. Museum für Naturkunde, Berlin, Germany (MfN)
9. Museum National d'Histoire Naturelle, Paris, France (MNHN)
10. Museumsverein Messel, Germany (MVM)
11. Natural History Museum, London, U.K. (NHMUK)
12. Naturalis Biodiversity Centre, Leiden, Netherlands (RGM)
13. Naturhistorisches Museum, Basel, Switzerland (NMB)
14. Naturhistorisches Museum, Mainz, Germany (NHMMZ)
15. Naturhistorisches Museum, Vienna, Austria (NHMW)
16. Naturhistorisk Museum Oslo, Norway (PMO)
17. Naturmuseum Dortmund, Germany (MNNW)
18. Paläontologische Sammlung der Universität Tübingen, Germany (GPIT-TV)
19. Paläontologisches Museum Nierstein, Germany (SSN)
20. Paleontological Museum of Liaoning, Shenyang, China (PMOL)
21. Senckenberg Research Institute, Historical Geology and Paleontology Collection, Frankfurt am Main, Germany (SMF R)
22. Senckenberg Research Institute, Mammalogy Collection, Frankfurt am Main, Germany (SMF M)
23. Senckenberg Research Institute, Messel Invertebrate Collection, Senckenberg Research Station Grube Messel, Messel, Germany (SMF-MeI)
24. Senckenberg Research Institute, Messel Paleobotany Collection, Dept. of Historical Geology and Paleontology, Frankfurt am Main, Germany (SM.B Me)
25. Senckenberg Research Institute, Messel Vertebrate Collection, Frankfurt am Main, Germany (SMF-ME)
26. Senckenberg Research Institute, Messel Vertebrate Cast Collection, Frankfurt am Main, Germany (SMF-MEA)
27. Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK)
28. Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS)
29. Stiftung Ruhr Museum, Essen, Germany (RE)
30. Urzeithof, Stolpe, Germany (no acronym)
31. Urzeitmuseum, Taufkirchen, Germany (no acronym)
32. Wyoming Dinosaur Center, Thermopolis, U.S.A. (WDC)

Where possible we also examined specimens in private collections known to us and counted specimens in private collections previously surveyed, amounting to about 20 private collections in total. Accessibility to private collections is variable, but some collectors welcome scientific research on their holdings. While we recognise that sometimes limited specimen accessibility in private collections makes these observations less reproducible, we have attempted, wherever possible, to buttress our observations with citation to casts, photographs, and CT scans.

Interpolation and extrapolation of taxonomic richness

In order to examine the relationship between sampling and richness in different taxonomic groups, we conducted rare–faction–extrapolation using Colwell et al.'s (2012) system with unconditional variance. Individual-based rarefaction is the classic method for interpolation of species richness – that is, for estimating how many species one can expect to have found if the sample size of individual organisms had been smaller (Heck et al. 1975). Since then, a number of different approaches have been developed for interpolation (e.g. Alroy 2010a, b; Chao and Jost 2012) and extrapolation (e.g. Chao 1984; Colwell and Coddington 1994; Colwell et al. 2012; Starrfelt and Liow 2016; Alroy 2017). The Colwell et al. (2012) system has the advantage of seamlessly uniting interpolation/rarefaction and extrapolation. We conducted rarefaction-extrapolation analyses using the iNEXT function in the iNEXT package (Hsieh et al. 2016) v4.2.3 for R (R Core Team 2023) with three exceptions, in which sample size is large: EstimateS v9 (Colwell 2013) was used for sample-based rarefaction-extrapolation of palynomorphs and insect damage types and for individual-based rarefaction-extrapolation of actinopterygian fishes.

While we created taxon accumulation curves for the two insect clades for the sake of completeness (Fig. S1), we otherwise used coverage estimators to estimate minimum total species richness in each taxonomic group (Colwell et al. 2012; Gotelli and Chao 2013). In the context of diversity studies, the term coverage refers to "what percentage of individuals in the original population belong to species included in the sample" (Close et al. 2018, p. 1387). These asymptotic richness estimators – the abundance-based coverage estimator (ACE) for individuals and the incidence-based coverage estimator (ICE) for samples – seek to estimate minimum species richness based on the frequency of rare species (where 'rare' is defined by an arbitrarily low frequency cutoff, κ, typically 10 individuals/samples or fewer). ACE and ICE are generalisations of the Chao1 and Chao2 estimators (Chao et al. 2005), respectively, which were concerned only with $\kappa < 3$ (i.e. singletons and doubletons). The two estimators are considered non-biased and non-parametric (Gotelli and Chao 2013), although they assume that the underlying frequencies of rare taxa are identical (Gotelli and Chao 2013; Close et al. 2018). Diversity estimates made using these coverage estimators are considered to be *minima* in that estimates using different abundance distributions will be *at least* as high (Chao et al. 2009). In a previous study of Palaeogene snakes it was found that richness estimates were essentially stable for $\kappa \geq 3$ (Smith and Georgalis 2022). To ascertain whether ACE has reached a plateau, we also ran diversity analyses in EstimateS v9 (Colwell 2013). For seed plants and other vertebrate groups other than Actinopterygii, we took the iNEXT estimate of ACE.

We also divided vertebrate taxa according to broad habitat preference, viz., aquatic, semiaquatic, volant and terrestrial (Supplementary Data S11–S13, S29–S31). We were aiming here to test a taphonomic hypothesis: that completeness of our sample declines with decreasing proximity to water. That is, aquatic taxa are always in the water, and semiaquatic taxa spend at least part of their time in water, increasing their chances of being sampled; volant taxa can travel over water, and so will be better sampled than taxa that neither swim nor fly. Hence, "terrestrial" here includes substrate-bound tetrapods, including ground-dwelling, fossorial and arboreal taxa. For maximum comparability, we aimed to include all taxa in both sets of analyses (taxonomic, ecological). This made it necessary to make decisions in a couple of cases of uncertainty. Specifically, the incomplete "Mammalia taxon nov." and "Testudines taxon nov." were tentatively concluded to be terrestrial rather than semiaquatic. Our overall results are insensitive to these decisions.

Excavation effort

We aim to relate the number of (identified) specimens discovered to excavation effort. To estimate total excavation effort (in person-days), we need to know how many persons were actively participating in the excavations and for how long. We took two approaches, as applied to excavations by Senckenberg: a theoretical approach based on the planned number of excavators (including employees and students/interns) and the length of the excavation season, and a data-driven approach based on the actual number of excavators recorded each day. The former is far less labour-intensive. Our estimates begin in 1975, the first year of Senckenberg excavations. The year 2016 was the last year we examined, as there was a radical change in the procedures that affected subsequent excavations (see below).

Theoretical approach. For the period 1975–1985, when the average number of excavators was reported, we simply multiplied the number of excavators by the number of weeks of excavation. For the period 1986–2016, the average number of excavators was not reported and so the number of employees participating regularly in the excavation ("employees") and of students/interns had to be included separately. Effort was calculated as the sum of two products: (1) number of employees × number of weeks of excavation + (2) number of students/interns × 4 weeks, four weeks being the typical internship period.

Data-driven approach. The number of excavators per day was tabulated from field books for every excavated day from 1975–2016. It is to be expected that the actual excavation effort, as reflected by the data-driven approach, will differ from the theoretical excavation effort, and normally be lower, because excavations can be suspended due to necessary fossil preparation, holidays, rain or heat, and sickness, and sometimes internship periods are for less than 4 weeks.

We emphasise here that we focus exclusively on the Senckenberg excavations because extensive data were available linking excavation effort to the number of identified specimens, which enables us to make projections about how quickly new specimens will be discovered. Notably, Senckenberg has also been the most active institution in excavating. This is especially important in view of the fact that it is impossible to give any remotely accurate estimate of excavation effort on the part of private persons. We anticipate that, if estimates of past excavation effort are made for other institutions (especially other members of the "big four" in Brussels, Darmstadt, and Karlsruhe), similar results will be obtained. That, of course, is a hypothesis that could be tested in the future.

Future sampling effort

Chao et al. (2009) developed a means of estimating the additional sampling effort (number of additional specimens, m) required to discover a given proportion (g) of estimated species richness (S_{est}). We set $S_{est} = S_{ACE}$. We calculated m with $g = 0.8$, 0.9, and 0.95 using equation 12 in Chao et al. (2009), setting $\hat{f}_0 = S_{ACE} - S_{obs}$ (cf. Gotelli and Chao 2013). In other words, we assume that the number of species remaining to be discovered (i.e. species currently represented by 0 specimens) is equal to the difference between the ACE asymptotic richness estimator and observed species richness. To the extent that S_{ACE} is a minimum, our estimates of future excavation effort are also minima.

Finally, we estimated the number of years of excavation to which this additional sampling effort corresponds. We made separate calculations of additional sampling effort using the excavation rate estimated for the period 1975–2016 and the years 2022–2023. The reasoning behind this division is that a moratorium on excavation was imposed in 2017 by the state government regulatory agency (Landesamt für Denkmalpflege), and normal excavations could resume only in 2019 after the agency enacted new regulations, with which all institutions active in Messel must now comply. These regulations have had the effect of significantly slowing the excavation rate. Thus, whereas we estimated that a reference team (size: 9.4 persons) was able to excavate 1–1.5 m^3 per day in the interval up to 2016 (Smith et al. 2024, this issue), the rate for Senckenberg teams has dropped precipitously (to 0.46 m^3 per day in 2022, 0.41 m^3 per day in 2023, and 0.39 m^3 per day in 2024, scaled in each case to reference team size). In other words, if we conservatively take the current average as 0.5 m^3 per day, the current rate is 1/2 to 1/3 of the recent historical rate, and it will take 2× to 3× as long to find the same number of specimens. Note that we discounted lower rate estimates based on the years 2019–2021, as Senckenberg and HLMD teams were in the process of learning and optimising the new regulations.

Results

Excavation effort

Both theoretical and data-driven approaches to estimating excavation effort yield qualitatively similar results (Table 1). There is furthermore a strong and highly statistically significant correlation between estimates based on the two approaches ($r^2 = 0.85$, $p < 1\times10^{-15}$). Only for the first year (1975) is there a major discrepancy. Excluding that year, the ratio of actual (data-driven) to theoretical excavation effort (summed for all years) is 36,494 person-days / 48,050 person-days = 0.760. If we calculate the ratio for each year separately, the ratio shows neither a positive nor a negative trend over the period we examined (1976–2016), with an average of 0.763 (Figure 1). Thus, we take a ratio of 0.76 to have predictive validity.

In the first year (1975), as excavations were ramping up, actual excavation effort was low (because the season was only 8 weeks long; Table 1), but it increased substantially thereafter (Figure 2). From 1976–1990, effort was very high, with an actual average of 1360 person-days per year. Starting in 1991, it decreased by over half, averaging 619 person-days per year from 1991–2016, owing both to decreased excavation season length (mean of 25.3 weeks from 1976–1990, and 19.2 weeks from 1991–2016) and to decreased average team size (mean of 13.7 persons from 1976–1990 and 8.8 persons from 1991–2016). Still, there is a slight but noticeable upward trend over 1991–2016.

Taxonomic diversity

A full list of the 1409 taxa documented thus far at Messel is found in Appendix 1 (references are in Supplementary Materials). A summary of this table by higher taxon is found in Table 2. Note that these tables should not be misinterpreted as a list of biological species documented at Messel, which would require substantial new work on "whole-organism reconstruction" (cf. Kvaček 2008).

Diatoms and dinoflagellates

Of the common aquatic clades Bacillariophyceae (diatoms) and Dinoflagellata (dinoflagellates), only *Melosira* sp. and *Messelodinium thielepfeifferae*, respectively, have been documented at Messel. The former are difficult to identify because their siliceous frustules are mostly dissolved (Goth 1990); the latter are represented by resting stages (Lenz et al. 2007a). The diatom taxa listed by Labandeira and Dunne (2014) are from the modern Great Lakes of North America and have not been documented at Messel (see below).

Green plants

In all 813 taxa of green plants (Viridiplantae) have been documented at Messel (Table 2, Appendix 1). Of these taxa, four are green algae and one is a charophyte, and the remaining 808 taxa are embryophytes. Of the latter, 259 are pollen or spore taxa (141 from Lenz et al. 2007b, 2011), 182 are fruit and seed taxa (156 from Collinson et al. 2012), 349 are taxa of foliage (mostly leaves), 1 is a bulbil, and 15 are flower taxa. Wood is rare but known (e.g. in MNNW, RE, SMF), and one piece has been attributed to the boxwood family, probably *Buxus*, a group otherwise unknown at Messel (Wilde and Süß 2001). However,

Table 1 Excavation effort by Senckenberg teams, 1975–2016. Both theoretical and actual estimates of excavation effort are included (see text)

Year	Theoretical excavation effort								Actual excavation effort	
	Nr. of weeks excavated	Average Nr. of personnel (for 1975–1985, ave. team size)	Person-weeks: personnel	Students & Interns	Person-weeks: students/interns	Person-weeks (total)	Person-days (total)	Average team size	Person-days	Person-weeks
1975	8	11	88	NA	NA	88	440	11.0	43	8.6
1976	14	10	140	NA	NA	140	700	10.0	670	134
1977	25	15	375	NA	NA	375	1875	15.0	1464	292.8
1978	33.5	13	435.5	NA	NA	435.5	2178	13.0	1466	293.2
1979	30.5	14	427	NA	NA	427	2135	14.0	1480	296
1980	28	13	364	NA	NA	364	1820	13.0	1211	242.2
1981	27	15	405	NA	NA	405	2025	15.0	1583	316.6
1982	26	17	442	NA	NA	442	2210	17.0	1224	244.8
1983	26	15.5	403	NA	NA	403	2015	15.5	2012	402.4
1984	25	13	325	NA	NA	325	1625	13.0	1509	301.8
1985	20.5	15	307.5	NA	NA	307.5	1538	15.0	1330	266
1986	24	4	96	65	260	356	1780	14.8	1500	300
1987	24	4	96	55	220	316	1580	13.2	1228	245.6
1988	24	4	96	61	244	340	1700	14.2	1206	241.2
1989	24	4	96	47	188	284	1420	11.8	1403	280.6
1990	27.5	4	110	47	188	298	1490	10.8	1107	221.4
1991	16	4	64	30	120	184	920	11.5	618	123.6
1992	19	4	76	31	124	200	1000	10.5	526	105.2
1993	13	4	52	10	40	92	460	7.1	272	54.4
1994	18	3	54	40	160	214	1070	11.9	624	124.8
1995	16	3	48	21	84	132	660	8.3	490	98
1996	18	3	54	18	72	126	630	7.0	481	96.2
1997	20	3	60	30	120	180	900	9.0	703	140.6
1998	20	3	60	39	156	216	1080	10.8	781	156.2
1999	20	3	60	25	100	160	800	8.0	666	133.2
2000	20	3	60	25	100	160	800	8.0	751	150.2
2001	19	3	57	22	88	145	725	7.6	556	111.2
2002	20	3	60	18	72	132	660	6.6	645	129
2003	21	3	63	21	84	147	735	7.0	470	94
2004	20	3	60	31	124	184	920	9.2	611	122.2
2005	20	3	60	17	68	128	640	6.4	550	110
2006	16	3	48	28	112	160	800	10.0	601	120.2
2007	20	3	60	13	52	112	560	5.6	451	90.2
2008	20	3	60	38	152	212	1060	10.6	752	150.4

Table 1 (continued)

Year	Theoretical excavation effort								Actual excavation effort	
	Nr. of weeks excavated	Average Nr. of personnel (for 1975–1985, ave. team size)	Person-weeks: personnel	Students & Interns	Person-weeks: students/interns	Person-weeks (total)	Person-days (total)	Average team size	Person-days	Person-weeks
2009	20	3	60	19	76	136	680	6.8	562	112.4
2010	20	3	60	36	144	204	1020	10.2	555	111
2011	20	3	60	20	80	140	700	7.0	659	131.8
2012	20	3	60	39	156	216	1080	10.8	772	154.4
2013	20	3	60	33	132	192	960	9.6	697	139.4
2014	20	3	60	47	188	248	1240	12.4	854	170.8
2015	20	3	60	22	88	148	740	7.4	572	114.4
2016	24	2	48	44	176	224	1120	9.3	882	176.4
						9698	48490		36537	7307.4

three-dimensional preservation of wood remains is often not good enough to allow for any meaningful anatomical analysis or interpretation of such material from Messel (DU, unpublished data). Wilde (2018) figured excellently preserved charred angiosperm wood from the Lower Messel Formation, subsequently identified as a splinter of oleaceous wood (Haag and Wilde 2024).

There are two key limitations on interpretation concerning these counts and lists, which should be emphasised here. First, because plant organs (pollen grains and spores, leaves, fruits and seeds, flowers, wood) are typically preserved separately and given different names, there may be considerable overlap of taxonomic names on biological species. That is, the number of biological species represented by these nominal taxa may be lower than 808. Work on *in situ* pollen in flowers from Messel (e.g. Schaarschmidt and Wilde 1986; Geier et al. 2023) and other approaches to “whole-plant reconstructions” (Kvaček 2008) can help to reduce this limitation.

Second, revisions of many taxa are lacking and will likely lead to a reduction in valid leaf taxa recognised at Messel. Engelhardt (1922) described a large number of taxa from the Middle Messel Formation based on predominantly leaf remains. With a few exceptions like Lauraceae (Sturm 1971) and Malvales (Kvacek and Wilde 2010), most of these taxa have not yet been revised. Revision of Engelhardt’s specimens is made much more difficult by the poor state of preservation of most remains on which original descriptions were based (Wilde 1989), because methods of preservation were not yet optimised. The supposed occurrence of three families in particular in the Eocene of Central Europe (Gingkoaceae, Proteaceae, and Casuarinaceae) has repeatedly been disproven in other localities. Nevertheless, Engelhardt (1922) identified a large number of not only species but also higher taxa that were not present in Wilde’s (1989) sample (Appendix 1), including taxa currently known or suspected only from other organ types: pollen (e.g. Oleaceae; the recent description of oleaceous wood is from the Lower Messel Formation), flower and pollen (e.g. Nyctaginaceae), or infructescences (e.g. *Ailanthus*, *Berchemia*).

Asymptotic richness, S_{ACE}, of fruit and seed taxa is 254.0 species (95% C.I. 176.6–331.4 species). Accordingly, we have sampled a maximum of 61% of estimated species richness. Asymptotic richness has also not levelled off (Fig. 3a), indicating that it will continue to rise with increased sampling.

Our quantitative analyses of the taxonomic diversity of palynomorphs is based on the data set of Lenz et al. (2011, 2017), which identified 141 taxa. That count is considerably lower than the 259 palynomorph taxa identified at Messel in all studies (see above). According to our data set, the ICE estimate of asymptotic diversity is 148.8 taxa (Fig. 3b). The Chao2 estimate is nearly identical: 148.3 taxa (95% C.I. 142.9–169.0 taxa).

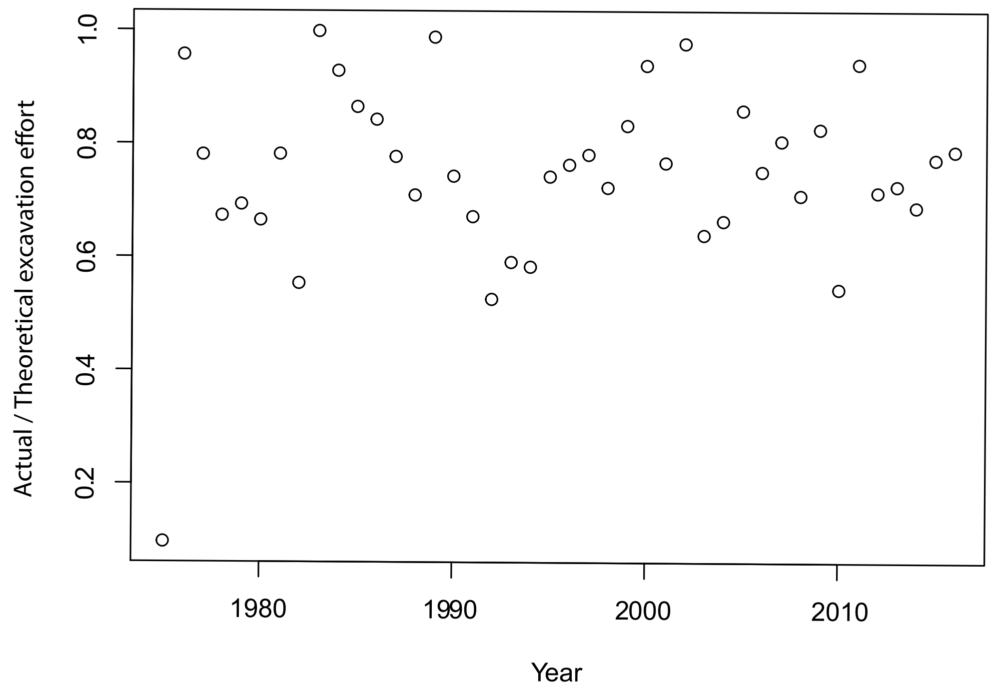

Fig. 1. Comparison of actual to theoretical excavation effort by Senckenberg teams in the 42 years from 1975–2016. It is to be expected that actual effort will lag theoretical effort. Excluding the first year (1975) with a short field season, the ratio of actual to theoretical effort is stochastically constant at 0.76

Fig. 2. Excavation effort by Senckenberg teams from 1975–2016 in person-days. Effort ramped up in 1975–1976, remained high until 1990, then dropped by more than one-half from 1990 to 1991. Since then, the trend has been increasing slightly

Fungi

Fungi have been documented at Messel as body fossils both microscopically (Weitzel 1933; OL, pers. obs.) and macroscopically (Schaarschmidt 1988), but a detailed study of these is wanting (Wilde 1989). Nevertheless, at least four orders of epiphyllous fungal pathogens have been identified on Messel leaves (Appendix 1; FH, pers. obs.), and further microfossils are present in the sediment of the Middle Messel Formation (Weitzel 1933).

The "death-grip" marks on a leaf caused by so-called "zombie ants" are also known (Hughes et al. 2011). Entomopathogenic fungi of the genus *Ophiocordyceps* are widespread in tropical climates, and they only parasitise ants of the genus *Camponotus*. They reproduce asexually via spores. One spore (= conidium) is sufficient to infect an ant. The germinating spore forms a hypha, which enters the ant host through its cuticle. The fungus develops in the host and feeds on it. The fungus changes ant behaviour to induce climbing up a plant and affixing itself with its mandibles on the underside of the leaf (or, in temperate climates, twig: Loreto et al. 2018) of the affected plant, leaving behind characteristic bite marks. The ant dies about three days post-infection. *Camponotus* has not been documented by body fossils at Messel (Appendix 1), but recent studies showed a higher host range within the myrmecophilic clade of fungi (Araújo and Hughes 2019).

Invertebrate animals

Two freshwater sponge taxa are documented at Messel (Table 2, Appendix 1), and it is worth pointing out here that sponge spicules are so abundant in some horizons that the rock is referred to as a "spiculite" (Richter and Baszio 2009). Additionally, four taxa of freshwater gastropods are documented together with a coprolite ichnofossil taxon, *Toxocoprulus weitzeli*, that was referred to an unknown freshwater gastropod (Rietschel 1988).

By far the most abundant and species-rich group of invertebrate animals are the arthropods, which are documented by 273 taxa of body fossils at Messel together with 117 ichnofossil taxa (principally damage types).

Table 2 Documented taxonomic diversity in major groups. Indented groups in parentheses represent subsets of superordinate groups. Where appropriate, estimates of minimum taxonomic or species richness (S_{ACE} or S_{ICE}; see text) are included, as well as the fraction of documented to (minimum) estimated richness. Because of said comparisons, the numbers of taxa for some Viridiplantae (seeds/fruit and pollen/spores) and Vertebrata (Actinoptyerygii) differ from those given in the text, because the extrapolations are based on samples, rather than all known specimens. The seeds/fruit counts are based only on Collinson et al. (2012), the pollen/spores only on Lenz et al. (2011, 2017), and the ray-finned fishes only on Micklich (2012). See text for details

	Total number of documented taxa	(of those)	Number of documented taxa (S_{obs}) used for extrapolation of species richness	Extrapolated species richness (S_{ACE} or S_{ICE})	Fraction of extrapolated richness documented (upper bound)
Unicellular	2		–	–	–
Viridiplantae	813		–	–	–
(non-embryophytes)		5	–	–	–
(seeds + fruit)		182	156	254	0.61
(foliage + shoots)		349	–	–	–
(bulbil)		1	–	–	–
(pollen + spores)		259	141	148.8	0.95
(flowers)		15	–	–	–
(wood)		2	–	–	–
Fungi	7		–	–	–
Invertebrates	397		–	–	–
(body fossils)		279	–	–	–
(trace fossils)		118	–	–	–
Vertebrata	190		–	–	–
(Actinopterygii)		8	7	7	1.00
(Amphibia)		6	6	10.5	0.57
(reptiles)		34	34	44.1	0.77
(Aves)		72	72	114.6	0.63
(Mammalia)		51	51	65	0.78
(coprolites)		19	–	–	–
TOTAL	1409				

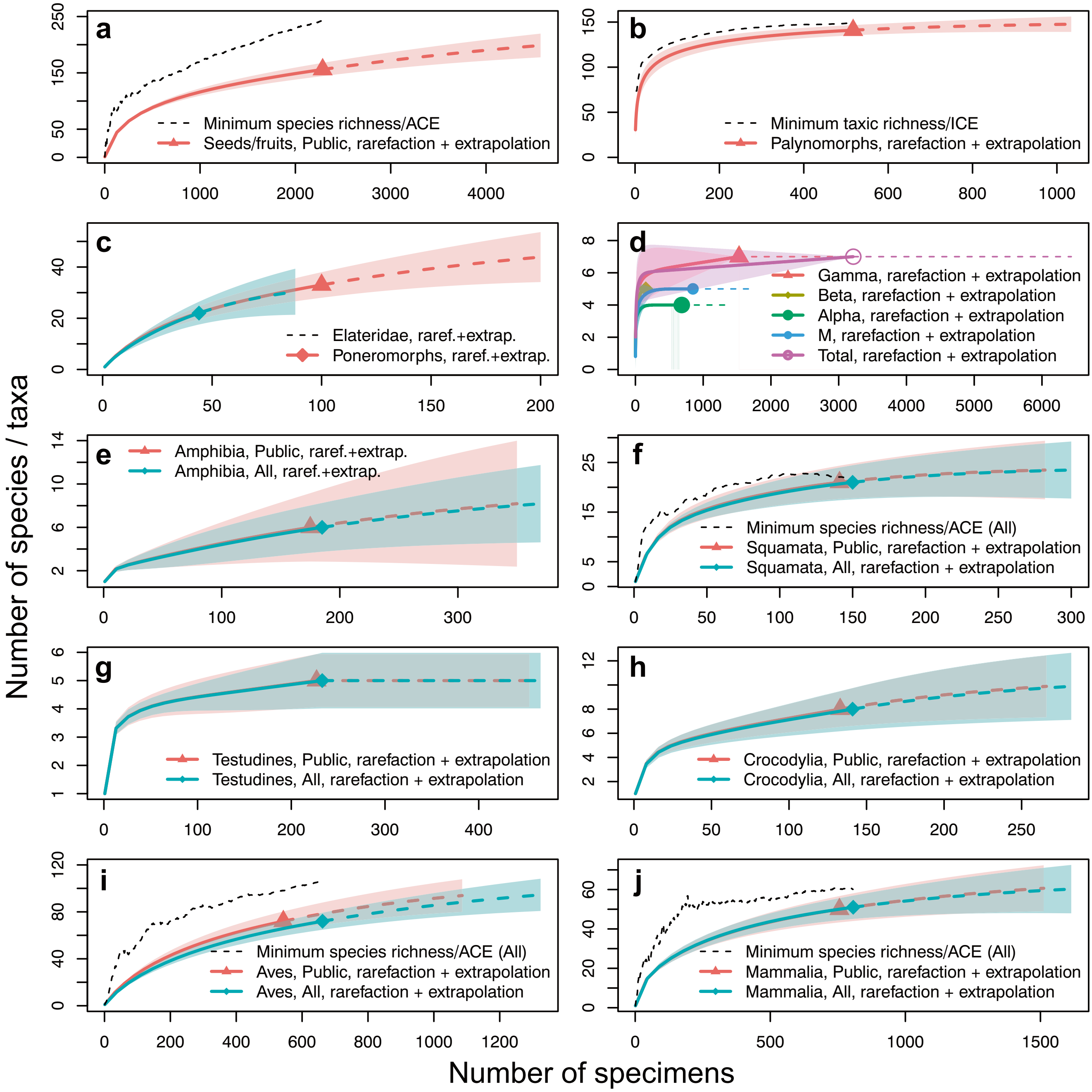

Fig. 3. Estimates of species or taxonomic richness in dependency on sample size, using rarefaction/interpolation (solid line to left of symbol) and extrapolation (dashed line to right of symbol), for eight major groups. Shaded areas are 95% confidence envelopes. **a** Seed plants (Spermatophyta) based on fruit and seed taxa. **b** Palynomorph taxa. **c** Two clades of Insecta: click-beetles (Elateridae) and poneromorph ants. **d** Actinopterygian fishes from the vicinity of four major marker beds (Gamma, Beta, Alpha, and M) as well as combined ("total") data. **e** Amphibia. **f** Squamata. **g** Testudines. **h** Crocodylia. **i** Aves. **j** Mammalia. *ACE* abundance-based coverage estimator (of minimum species/taxic richness). *ICE* incidence-based coverage estimator (of minimum species/taxic richness). Where appropriate, separate analyses were conducted for specimens housed in publicly available collections and those in "all" collections (i.e. publicly available and private collections)

Unfortunately, as with the plants (see above), original descriptions by Meunier (1921) are based on specimens that have degraded due to the inadequate conservation methods of the time.

Amongst poneromorph ants (Fig. 3c), 22 species have been described, and asymptotic richness, S_{ACE}, is 35.8 species (95% C.I. 22.0–89.2 species). Accordingly, 61% of poneromorph ant species richness had been sampled

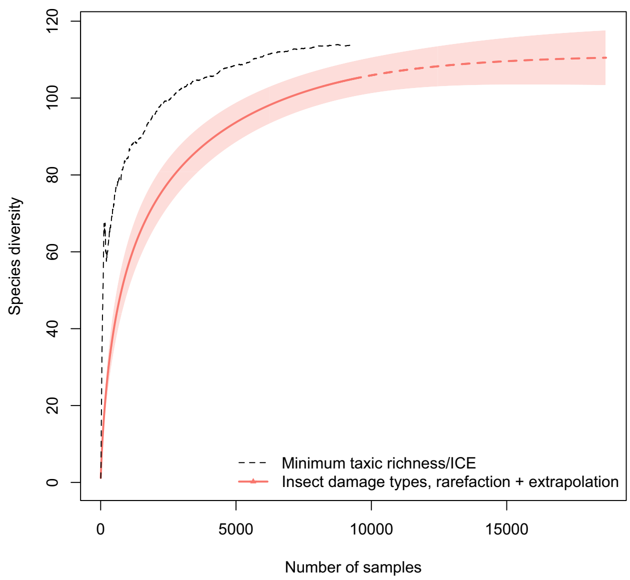

Fig. 4. Rarefaction-extrapolation of insect damage types on fossil leaves from the Messel Pit (Albrecht et al. 2023). Number of samples is equated with number of leaves. Shaded areas are 95% confidence envelopes. ICE = incidence-based coverage estimator (of minimum taxic richness)

up to the year 2012. ACE is not rising. Amongst click-beetles, Elateridae (Fig. 3c), 33 taxa have been described, and asymptotic richness, S_{ACE}, is 55.3 species (95% C.I. 33.0–92.4 species). Accordingly, 64% of elaterid species richness had been sampled up to the year 1999.

The study of plant-insect interactions yields important information on functional diversity (e.g. Labandeira and Wappler 2023). 113 damage types were documented (Albrecht et al. 2023; TW, pers. obs.), of which 41 could be assigned to an insect family. Many of those represent families or even higher taxa not recorded as body fossils. Particularly in Lepidoptera, there are more ichnofossil than body fossil taxa, and most of the latter are only known from feeding remains in gut contents. For the 105-taxon sample in Albrecht et al.'s (2023) data set, asymptotic taxic richness of insect damage types, S_{ICE}, has plateaued at around 113.8 taxa (Fig. 4). The Chao1 estimator is 110.4 (95% C.I. 106.5–124.6 taxa). Potential associations between body and trace fossil taxa amongst arthropods are poorly explored.

Vertebrata

In all, 171 taxa of vertebrate body fossils are now documented (Table 2, Appendix 1). This number is probably robust and unlikely to decrease significantly as a result of future taxonomic revision given currently available methods and concepts, although the reality of a couple of taxa is questionable (e.g. Hooker 2013; Rose et al. 2014). Additionally, 19 coprolite morphotypes have been documented (Schmitz 1991; Richter and Baszio 2001), which have been ascribed to fishes, reptiles, and birds (Appendix 1). Most unexpected of these is the heteropolar spiral morphotype, found only in upper "coaly" strata that were completely mined away, which might be referable to Dipnoi (Schmitz 1991). There are no records of lungfish body fossils at any stratigraphic level (Schmitz 1991). It is unclear how remains like tooth plates could have been overlooked, or not reported, by 19th century miners.

Eight ray-finned fish taxa are currently recognised by body fossils at Messel. One of them, *Anguilla ignota*, is known from a single individual that was discovered decades ago by a private collector (Bettag 1977) and subsequently acquired by two museums (the main part housed at NHMMZ, and the counterpart at SMF). It does not occur in our (very large) fish sample, and our rarefaction-extrapolation curves therefore peak at 7 species. We separately calculated curves for stratigraphic packages closely associated with the marker beds Gamma, Beta, Alpha and M, and the curves are all qualitatively similar, reaching a plateau rapidly. Only one taxon in the data set is considered 'rare' by any definition, *Masillosteus kelleri*, the short-snouted gar, which was found around Gamma and contributes to a slightly less flat curve for this sediment package and for the fish assemblage as a whole. (Another specimen of the same species that was originally found by MNNW, and is now in the collection of HLMD, is probably from layers around Alpha.) Asymptotic richness, S_{ACE}, is identical to known species richness, 7 species (Fig. 3d).

Six amphibian taxa have been identified at Messel (Fig. 3e). The most common is the primitive, terrestrial spadefoot toad, *Eopelobates wagneri*, for which there is no evidence of a spadefoot or of fossoriality (Roček et al. 2014), its extant relatives notwithstanding. Three rarer frog taxa are known, one (*Lutetiobatrachus gracilis*) from a single individual, and the two salamander taxa also are singletons. Asymptotic richness, S_{ACE}, is 10.5 species (95% C.I. 6.0–18.6 species). Accordingly, we have sampled no more than 57% of estimated species richness.

Thirty-four "reptile" taxa have been identified at Messel based on body fossils, including seven squamate taxa that have yet to be described. ACE has not yet levelled off (results not shown). Asymptotic richness, S_{ACE}, is 44.1 species (95% C.I. 34.0–68.0 species). Accordingly, we have sampled no more than 77% of estimated species richness, and probably less. Thus, we can expect at least 10 species in addition to the undescribed taxa already documented. When individual "reptile" clades (Squamata, Testudines, Crocodylia) are examined individually, slightly different results are obtained (Fig. 3f–h). S_{ACE} has levelled off for Squamata and Testudines but not yet for Crocodylia. At least 3 additional species are expected for Squamata and Crocodylia, but none for Testudines. It will be noted that these additional species ($S_{ACE} - S_{obs}$) do not add up to the 10 additional species when considering "reptiles" as a whole, which results from the fact that the number of "rare" taxa interacts in complex ways with coverage estimates (Gotelli and Chao 2013), such that S_{ACE} is not distributive (Smith and Georgalis 2022).

Seventy-two bird taxa have been identified at Messel based on body fossils, making birds the most species-rich major clade of vertebrates at Messel (Mayr 2018). One species, *Messelornis cristata*, is hyperabundant, accounting for 62% or 66% of identified specimens (for public and all collections, respectively). ACE appears to be levelling off (Fig. 3i). Asymptotic richness, S_{ACE}, is 114.6 species (95% C.I. 84.3–144.9 species). Accordingly, we have sampled no more than 63% of estimated species richness.

Fifty-one mammal taxa have been identified at Messel. The most abundant of these is the bat species *Palaeochiropteryx tupaiodon*, but even the primitive "horse" taxa *Eurohippus messelensis* and *Propalaeotherium hassiacum* are each known by >50 specimens. ACE appears to be levelling off (Fig. 3j). Asymptotic richness, S_{ACE}, is 65.0 species (95% C.I. 51.0–86.9 species). Accordingly, we have sampled no more than 78% of estimated species richness, and we can expect at least another 14 species in addition to the undescribed taxa already documented. Amongst bats (Chiroptera) specifically, S_{ACE} is 10.0 species (95% C.I. 9.0–14.8 species).

Grouping of vertebrates by habitat

When we group vertebrates not taxonomically but according to broad habitat preference, we find that the number of specimens is greatest amongst the fully aquatic species (i.e. fishes). Volant species are more abundant than terrestrial species. These observations are consistent with the hypothesis that proximity to water is important for fossilization. However, semiaquatic species do not fit this pattern, because they form the least abundant group. We suggest that one reason for this is that, comprising most crocodylians and turtles, they are on average much larger than the members of other groups, and larger animals are typically rarer (Peters and Wassenberg 1983). Additionally, the boundary region between fully aquatic and fully terrestrial landscape compartments is geographically smaller than either.

Estimated taxonomic richness as well as sampling thereof rises from aquatic to semiaquatic to volant to terrestrial (including arboreal). According to our analyses, aquatic organisms are best sampled, with S_{obs} = 7, and ACE is not expected to rise further (Fig. 5a). If the same slope is maintained, a doubling of sample size might lead to an increase in ACE of 1 species, but the model behaves poorly with low species richness and almost no rare species, and the only reason ACE rises at all is because there one singleton species (*Masillosteus kelleri*) amongst thousands of specimens in the sample.

Richness of semiaquatic taxa (principally frogs, turtles and crocodiles) has levelled off strongly (Fig. 5b), with S_{obs} = 14 and S_{ACE} = 16.0 (95% C.I. 14.0–20.7 species). The data suggest that further sampling will increase species richness by no more than about 14%. Richness of volant taxa (birds and bats) has levelled off strongly (Fig. 5d), but the difference between S_{obs} = 76 and S_{ACE} = 110.3 (95% C.I. 84.3–136.3 species) is much greater, so we have sampled no more than 69% of estimated minimum diversity. For terrestrial taxa (principally mammals and squamates, with a few amphibians, crocodiles and birds), sampling is poorest (Fig. 5c). S_{obs} = 73 and S_{ACE} = 106.8 (95% C.I. 73.0–158.1 species), whereby we note that S_{ACE} has not levelled off, and we expect it to rise further. Thus, so far we have sampled no more than 68% of estimated diversity, probably substantially less.

Future sampling effort

To estimate the amount of time required to sample a given percentage of the (minimum) estimated richness of most groups, we first calculated the total counts of identified specimens in the SMF collection (up to a cut-off year; Table 3) and the actual excavation effort (number of person-days) required to achieve this count. The specimen counts exclude specimens that had been purchased, which, however, make a negligible contribution. The total actual excavation effort of SMF from 1975–2016 is 36,537 person-days (Table 1). Average actual excavation effort of SMF from 1991–2016 (Fig. 2) is 16,101 person-days / 26 yr = 619.3 person-days/yr. We assume that HLMD increases this effort to 880 person-days/yr (SMF averaged 19 weeks field work/yr, HLMD 8 weeks/yr).

Accordingly, at 1991–2016 excavation rates it will take a number of generations to more completely sample plant and animal species richness (Table 3). For fruit and seed taxa, 42.1 yr and 130.9 yr (after the cut-off year 2010) will be required to sample 80% and 95%, respectively, of minimum richness. Because the S_{ACE} estimate has not yet levelled off, we expect that these estimates will rise with further sampling. Since the comprehensive monograph on Messel fruits and seeds by Collinson et al. (2012), a number of morphologically distinct taxa, new to Messel, have been excavated, which have so far not been formally described and named (K. Schmidt / Senckenberg, pers. comm., 2024).

For amphibians, these figures are 70.6 yr and 199.0 yr, respectively. For reptiles, these figures are 15.8 yr and 177.5 yr, respectively. For birds, these figures are 135.9 yr and

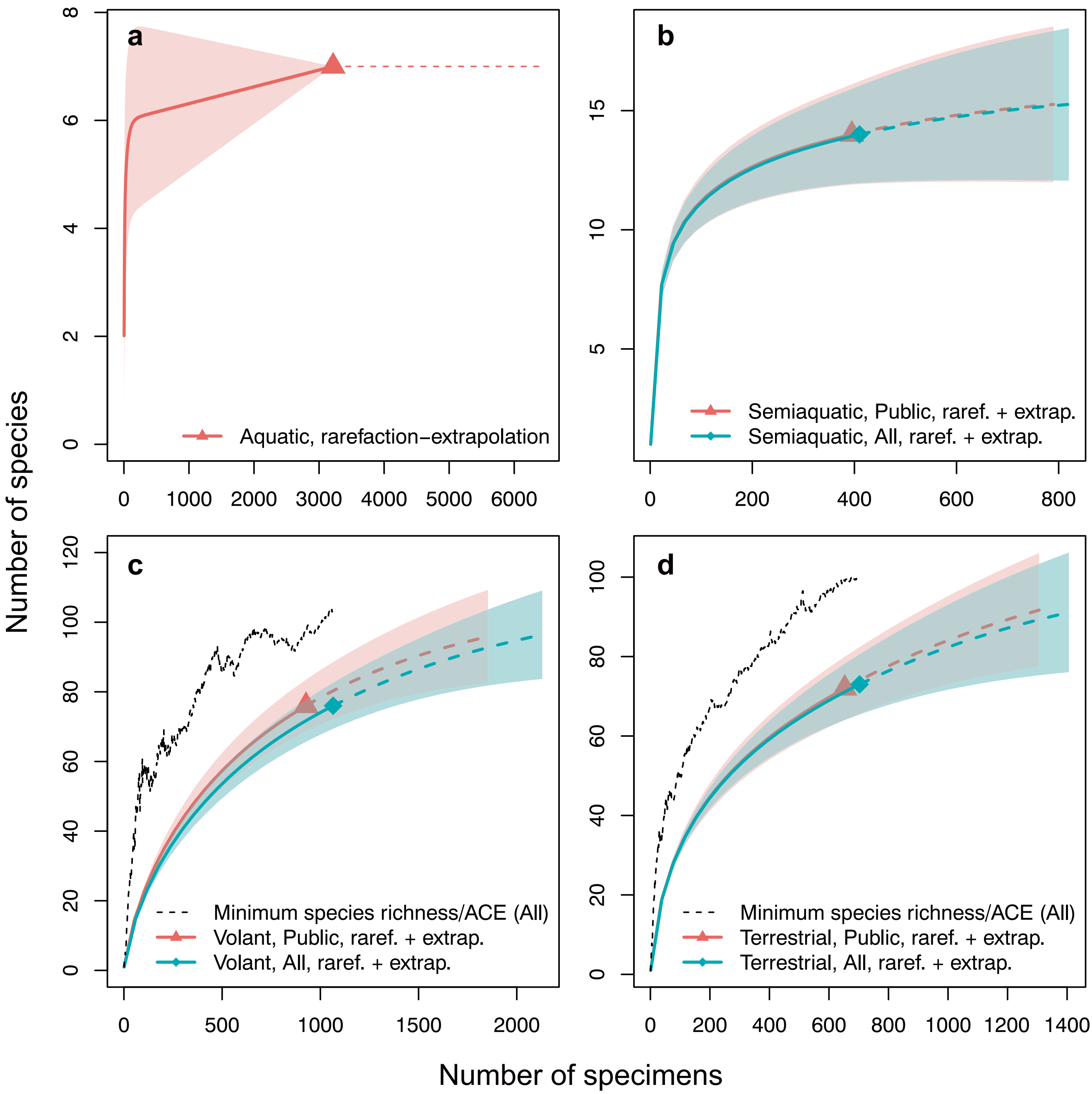

Fig. 5. Estimates of species or taxonomic richness in dependency on sample size, using rarefaction/interpolation and extrapolation, for four categories of vertebrates that were hypothesised to differ taphonomically due to their varying proximity to water. **a** Fully aquatic taxa (Actinopterygii). **b** Semiaquatic taxa. **c** Volant taxa (i.e. those that can fly, including over the surface of Palaeolake Messel). **d** Terrestrial taxa (i.e. those obliged to locomote on a substrate, including fossorial and arboreal forms)

439.8 yr. It may be noted that, if all the undescribed Messel bird taxa are excluded from consideration, S_{ACE} remains high (93.0 species, 95% C.I. 65.0–120.9 species), and the time needed to discover them is at least 50% higher than for other groups; this might reflect a higher proportion of rare taxa amongst birds. For mammals, these figures are 8.4 yr and 166.4 yr, respectively. The mammal estimates are lower, which might reflect – at least in part – the higher rate of discovery of identified mammal specimens (Table 3). That being said, the rate of discovery of identified amphibian specimens is substantially lower than that of "reptiles" or birds.

If the post-2016 actual excavation rate is maintained (one-half to one-third of the historical rate above), then it will take

Table 3 Estimates of future excavation effort needed to recover a given proportion of estimated species richness for fruit and seed taxa, amphibians, reptiles, birds, and mammals. Separate estimates are given of future excavation effort for Senckenberg's past excavation rates (pre-2016) and current excavations rates (post-2016), which are one-half to one-third lower. Abbreviations: n, total sample size of specimens analysed quantitatively; S_{obs}, observed species richness of that sample; f_1, number of singletons, or those species known from only one specimen; f_2, number of doubletons, or those species known from only two specimens; S_{ACE}, asymptotic abundance-based coverage estimator of minimum species richness; g, proportion of estimated species richness; m, number of additional specimens required to discover said proportion of estimated species richness. To estimate the time t required to discover m specimens, it was necessary to link the number of identified specimens in the SMF collections with SMF excavation effort (see Table 1). A cut-off year was employed (i.e. we counted the number of specimens identified, n (SMF), and compared that with excavation effort up until said year). Then, using the fossil discovery rate (fossils/person-day of excavation) and our projection of future excavation effort based on the historical rate (see text), we calculated how many years of excavation will be required to sample the fraction g of estimated richness. Additionally, we made the same calculation for an excavation rate that is one-half to one-third of the historical rate, based on recent excavation years during which new regulations (imposed by the state government agency) were implemented

							m (specimens)			Fossil discovery rate			t to m (yr) @historical excavation rate			t to m (yr) @one-half historical excavation rate			t to m (yr) @one-third historical excavation rate		
Group	n	S_{obs}	f_1	f_2	S_{ACE}	f_0	$g = 0.8$	$g = 0.9$	$g = 0.95$	Year cut-off	Cumulative person-days	n (SMF)	$g = 0.8$	$g = 0.9$	$g = 0.95$	$g = 0.8$	$g = 0.9$	$g = 0.95$	$g = 0.8$	$g = 0.9$	$g = 0.95$
Seed/fruit taxa	2286	156	56	16	254	98	2628.6	5401.5	8174.5	2010	32101	2278	42.1	86.5	130.9	84.2	173.0	261.8	126.3	259.5	392.7
Amphibia	158	6	3	1	10.5	4.5	180.6	344.9	509.2	2014	35083	102	70.6	134.8	199.0	141.2	269.6	398.0	211.8	404.4	597.0
Reptiles	416	34	9	4	44.1	10.1	63.4	387.8	712.2	2014	35083	160	15.8	96.6	177.5	31.6	193.3	354.9	47.4	289.9	532.4
Aves	664	72	32	12	114.6	42.6	548.8	1162.4	1776.1	2014	35083	161	135.9	287.8	439.8	271.8	575.7	879.6	407.7	863.5	1319.4
Mammalia	701	51	15	8	65	14	48.7	504.2	959.8	2014	35083	230	8.4	87.4	166.4	16.9	174.8	332.7	25.3	262.2	499.1

2× to 3× as long to find the same number of specimens. The corresponding values for future excavation effort under this scenario are included as well in Table 3.

Discussion

Taxonomic lists

Taxonomic lists for Messel have been presented at irregular intervals. Harrassowitz (1922) listed 2 fish, 1 lizard, 4 turtle, 2 crocodylian, 1 bird, and 5 mammal taxa. Matthess (1966) listed 3 types of sponge needles, 18 insect taxa, the gastropod family Hydrobiidae, and 34 vertebrate taxa (plus unidentified snakes and birds). Heil et al. (1979) listed 36 plant taxa, the sponge family Spongillidae, the gastropod family Hydrobiidae, 18 insect taxa, and 38 vertebrate taxa (including at least one unidentified snake and one lizard taxon), noting that further taxa were present in existing collections, citing specifically Bettag (1977). Franzen (1982) gave a family-level overview for non-vertebrates, including 9 plant families, the sponge family Spongillidae, the gastropod family Viviparidae (but questioning Hydrobiidae), and 11 insect families, and 47 vertebrate taxa plus several undescribed frog, lizard and snake taxa. Behnke et al. (1986) listed 3 bacterial taxa, 48 plant taxa, 1 sponge taxon, questionably 2 gastropod taxa, 23 insect taxa, and 55 vertebrate taxa (over half of them mammals). Heil et al. (1987) listed only animals: 23 invertebrate and 59 vertebrate taxa (over half of them mammals), as well as an unknown number of snake taxa. An enormous jump in the number of plant (Schaarschmidt 1988), squamate (Keller and Schaal 1988) and bird (Peters 1988) taxa, most of them not formally published, occurred with the publication of the first major review book (Schaal and Ziegler 1988). By the mid-2000s, the number of taxa had expanded again: in plants (Wilde 2004), invertebrate animals (Wedmann 2005) and vertebrates (Morlo et al. 2004). The latter two works include a more in-depth literature review, and the last lists 132 vertebrate species.

Most recently, Dunne et al. (2014) presented a list from the literature that included a total of 700 taxa, amongst them 189 plant taxa and 316 arthropod taxa (including trace fossils). They wrote (p. 2) that their "Messel data-set (Labandeira and Dunne 2014) includes all documented species deposited within the small maar lake basin, including taxa from the lake's water column and benthos and from the immediately surrounding paratropical forest". (In a number of cases, their taxonomic list plausibly unites plant pollen and macrofossils, such as *Osmunda lignitum* and *Baculatisporites primarius*, but without supporting justification.) The data set had the potential to be the most comprehensive ever assembled for Messel – and perhaps for any other fossil ecosystem – but unfortunately, on closer examination both the taxonomic list and the list of trophic interactions show severe deficiencies. For instance, the distinction between taxonomic and biological species was not addressed; the taxonomic list contains numerous serious errors (see below); and reported evidence concerning gut contents often has no basis in fact.

We concern ourselves here only with the taxonomic list of Labandeira and Dunne (2014). The reference for the first four listed diatom taxa (taxa #22–25) is the same: the Great Lakes Diatoms webpage (https://websites.umich.edu/-phytolab/GreatLakesDiatomHomePage/top.html). In the year 2024 it includes the listed genera but only one of the listed species and in any case provides no information about the Messel Pit. There is no evidence that these diatom taxa occurred at Messel. We now turn to the plants that follow, and specifically the plants exclusive of angiosperms (36 taxa, #33–68). The first four taxa (#33–36) cover orders (Charales, Dicraniales, Jungermanniales, Muscales) that the cited references documented at Eckfeld and/or Geiseltal, but not Messel (see also under invertebrate animals below). The documentation of the family ?Marattiaceae (taxon #39) was referenced to Labandeira et al. (2007), which, however, mentions Messel only in passing reference to the future publication of Dunne et al. ("in prep.") and provides no new taxonomic data on plants, including Marattiaceae. *Lygodium kaulfussi* is listed twice (as part of taxon #40, together with *Leiotriletes maxoides*, and as #52). In the former case, Lenz et al. (2007b) in fact list *Leiotriletes maxoides*, but neither Lenz et al. (2007b) nor Schaarschmidt (1992), supporting taxon #52, list *Lygodium kaulfussi*, although it has since been documented by Wilde (2018). Schaarschmidt (1992) is given as an exclusive reference for three spore taxa (#43–45) of Polypodiaceae; he listed none specifically, although he summarised that 11 are present. Of the taxa, #43 and #44 are in fact listed by Lenz et al. (2007b), but #45 ["*Verrucatosphorites" (sic*, for *Verrucatosporites*) *tenellis*] is not documented at Messel. "Polypodiaceae (gen. et sp. indet.)" (taxon #47) is unclear, but the entry might possibly refer to "*Polypodiaceoisporites* sp." of Lenz et al. (2007b). There is no record of *"Schizaea* sp." (taxon #54) in Schaarschmidt (1992), nor has this taxon clearly been documented in other works, although the spore taxon *Microfoveolatosporis granuloides* of Thiele-Pfeiffer (1988) might be attributable to that genus. Undetermined members of three further fern families are listed (#55–57), all given as documented by Franzen (1994). In fact, Franzen (1994) did not list any fern taxa in that work focused on bacterial remains in gut contents. Blechnaceae (#55) was actually documented by Wilde (1989), but Gleicheniaceae (#56) was only subsequently documented by Lenz and Wilde (2018) and Wilde (2018). To our knowledge, Parkeriaceae (#57) has never clearly been documented. The conifer pollen taxon *Libocedrites "salicorniodes"* [*sic*, for *salicornioides*; now

Tetraclinis salicornioides] (#60) is not documented at Messel, including in Schaarschmidt (1992), as given. The taxon *Glyptostrobus* (#62) is listed as being documented by pollen; in fact, it was Thiele-Pfeiffer (1988) who documented it, and the pollen taxon has a different name: *Inaperturopollenites concedipites*. Inexplicably, taxon #63 is *Inaperturopollenites concedipites*, the pollen taxon associated with *Glyptostrobus* and the only record of that lineage at Messel; it was not given by Schaarschmidt (1992). (Identification of *Glyptostrobus* by means of pollen is, according to current knowledge, not possible in any case, as there is too much overlap in pollen morphology with taxodioid Cupressaceae.) We cannot understand what taxon "Sciadopityoideae" (#65) refers to, and it was not documented by Franzen (1994), as stated. The gnetalean family Ephedraceae (taxon #68) has never been documented at Messel, including by Schaarschmidt (1992), as stated. Thus, at least 11 of these 36 taxa were not documented at Messel at the time (2 have been documented subsequently), and a further 3 listed taxa cannot clearly be associated with documented taxa. In other words, about one-third of the taxa are incorrect.

We refrain here from examining the rest of the plant taxa, or the vertebrate taxa (which were taken from Morlo et al. 2004), but we note that problems are also common in the records of invertebrate animals given in this data set. For example, Labandeira and Dunne's (2014) invertebrate taxa #235, #236 and #237 have not been recorded from Messel. There are no records either of "Entoprocta" (taxon #235) or of "Unionoida" (taxon #236) or "Mytiloidea" (taxon #237) in Collinson and Gregor (1988), nor do Martini and Richter (1996) make any mention of "Unionoida" or "Mytiloidea." In fact, bivalves have never been documented at Messel. As another example, taxa #264 (the termite species *Mastotermes krishnorum*) and #499 (the bee species *Eckfeldapis electrapoides*) are recorded from Eckfeld (Lutz 1993; Wappler and Engel 2006), but not from Messel. Because of the time difference of about 3 million years between Messel and Eckfeld (e.g. Uhl et al. in review, this issue), it cannot be assumed that the same taxonomic species occur at both sites. To be sure, this is true in some cases (e.g. Tröster 1992; Wappler 2003; Katzke et al. 2018). However, when insects from Eckfeld and Messel which belong to the same genus have been compared closely, often different species have been described for the two sites (Tröster 1993; Dlussky et al. 2008, 2009), or major differences were found (e.g. Katzke et al. 2018). Moreover, all taxa were specifically stated as being recorded at Messel.

It is not possible in the framework of this paper to review exhaustively all taxa and all linkages, i.e. the entire data set of Labandeira and Dunne (2014). For the present, however, we must conclude that the taxonomic list should not be used uncritically, and for this reason alone the linkage data set should also not be used uncritically. An updated and complete list of taxa – not biological species – was one goal of the present work (Appendix 1).

Species diversity at Messel

Taphonomy plays a role in the study of any palaeontological collection. The richness and abundance of preserved taxa is influenced not only by their richness and abundance in life but also by taphonomic factors that govern which species make it into the assemblage, and how. For many collections, it may be that diversity in a taphocoenosis closely mirrors that in the corresponding biocoenosis (Kidwell 2001, 2013), but this cannot be assumed for any particular case. Therefore, we emphasise that we are discussing the diversity of the taphocoenosis, where taxon abundance reflects both life abundance and taphonomic factors.

Amongst vertebrates in our taphocoenosis, both species richness and sampling thereof rise with proximity to water. The aquatic species are best sampled, followed by semiaquatic species. Volant species, which are capable of flying over the lake, remain undersampled, but at least our estimate of minimum species richness (S_{ACE}) is plateauing. Richness of terrestrial species, which do not normally enter water or fly over it, and whose carcasses therefore must be transported from water's edge out into the lake, is least well sampled, so much so that S_{ACE} is not clearly plateauing yet.

Amongst insects it is the other way around. Terrestrial taxa are far more abundant than aquatic taxa, and winged taxa are much more abundant than wingless ones. However, it must be pointed out that the composition of the insect taphocoenosis likely does not reflect the original insect biocoenosis, but is influenced by a whole series of taphonomic processes (e.g. surface drift, filter effects of the riparian vegetation, size of the lake, surface tension of the water). This is particularly evidenced by the high abundance of Coleoptera individuals and the very low abundance of (for example) Diptera and Lepidoptera individuals in Messel.

These observations concerning sampling are consistent with Smith et al.'s (2024, this issue) calculations that >700 fishes became fossilised in the Middle Messel Formation annually but only about 6.3–9.5 bats. Calculations based on birds would be somewhat higher than those of bats, but calculations based on mammals, turtles, crocodylians and squamates would be much lower. Still, snakes seem to be curiously abundant at Messel, with 134 specimens collected by SMF teams from 1975–2016, i.e. only one-quarter the number of bats (Smith et al. 2024, this issue). The virtually limbless lizard *Ophisauriscus quadrupes* is also one of the most abundant lizards. If a tube-like body shape combined with uninterrupted alpha and beta keratin layers leads to a longer flotation time for carcasses (because there are fewer places where they could rupture), this could increase the probability of such fossils being transported out into the lake. However, osteoderms invest the skin of *O. quadrupes*, like in other anguids, crocodylians and Palaeovaranidae, which could also increase the density of these animals and hence influence buoyancy of carcasses; this factor has not been studied yet.

There is a discrepancy between total taxonomic richness of palynomorphs and the data set analysed quantitatively here. This is mainly due to the fact that the large number of palynomorph taxa of Thiele-Pfeiffer (1988), like *Tricolporopollenites* sp. 1–25, which only occurred as single specimens in individual samples, were included in the tabulation of taxonomic diversity (Appendix 1) but were not quantitatively recorded by Lenz et al. (2011, 2017). At the same time, extrapolation of taxic richness of all plants based on palynomorphs (Fig. 3b) has plateaued at a level lower than the observed richness of fruit and seed taxa and much lower than the extrapolated species richness of fruit and seed taxa, which has not even plateaued yet (Fig. 3a).

Studies on palynomorphs from Messel have thus far relied on light microcopy, but several studies have demonstrated that many biological taxa cannot be reliably identified with light microscopy only. Combining light microscopy with scanning electron microscopy can add a wealth of additional data on surface structures preserved in pollen and spores and help to refine the taxonomic resolution of such palynomorphs (e.g. Bouchal et al. 2024). An ongoing study of Messel palynomorphs combining both techniques has already revealed 26 new types of pollen, demonstrating that the taxic richness of the palynoflora is definitely higher than assumed so far (Bouchal et al. 2024) and potentially helping to resolve the discrepancy between the taxic richness of palynomorphs and fruit and seed taxa.

Many of the leaf remains from Messel have so far only been described and determined based on macro-morphological data (Engelhardt 1922; Wilde 1989). Several studies also analysed different leaf taxa by means of cuticular analysis, which adds taxonomic information and allows for a more precise taxonomic affiliation in many groups of higher plants (e.g. Sturm 1971; Wilde 1989). However, for many of the leaf fossils, cuticular analysis has so far not been performed, because suitable cuticles have not been preserved or discovered. A large number of the leaf remains in the collections remain unstudied with regard to preservation of suitable cuticles, and this may be a rich area for further study.

For fruit and seed taxa, there is potential for a taphonomic bias to depress species richness estimates. It is probable that very small fruits or seeds are less likely to be perceived during excavation. Furthermore, fruits and seeds from low-growing plants such as herbaceous plants, except those growing very near the lake, are less likely to be dispersed far enough to be transported out into the lake compared, for example, to those produced by tall plants such as trees. These factors are consistent with the fact that most of the taxa documented by fruits and seeds at Messel are thought to have been woody (Collinson et al. 2012). Also seeds and fruits of zoochorous plants will certainly be underrepresented as compared to anemochorous plants. Therefore, there may be a part of seed plant diversity (as documented by fruits and seeds) that is largely missing in studied samples.

For flowers so far only a few preliminary determinations have been published, but an ongoing project on flowers and their in situ pollen, again combining light-microscopy and scanning electron microscopy, will certainly add a number of reliably identified taxa to the list in the near future (e.g. Geier et al. 2024).

Amongst birds, a particular problem arises from the fact that most vertebrate specimens from Messel are compression fossils that often do not allow the assessment of subtle osteological details. These issues are exemplified by a recent study of three-dimensionally preserved fossils of the Halcyornithidae from the early Eocene deposits of the British London Clay, which revealed a high taxonomic diversity of very similar species that would be much more difficult to recognise in Messel fossils (Mayr and Kitchener 2024). Thus, the relationship between taxonomic and biological species will retain an element of uncertainty even for some vertebrate body fossils, yet this uncertainty is unlikely to affect the interpretations that follow.

The fruits of excavation

Biodiversity encompasses more than species richness and is further addressed using concepts like phylogenetic diversity, functional diversity, and disparity (i.e. diversity of form). Insofar as insect damage types on plants are not necessarily species-specific, and a given type may be caused by a variety of insect species, they may be seen as a measure of the diversity of insect use of plants. In this context, it is noteworthy that the data from Messel show a significantly higher proportion of highly diverse insect feeding traces for the period after the EECO than is known from comparable periods in North or South America (Wappler et al. 2012).

Further, new specimens inevitably yield new data on palaeobiology. The exceptional preservation of Messel fossils allows for accurate reconstructions of anatomy and behaviour, with insights into locomotion, feeding, reproductive strategies, sensory systems, and more. For instance, specimens of the booid snake *Eoconstrictor fischeri* with stomach contents showed how its diet changed with ontogeny (Smith and Scanferla 2016), and reconstruction of neurovascular anatomy in an exceptional specimen suggested the early evolution of infrared detection as part of the visual system (Scanferla and Smith 2020). Combining information from stomach contents and wing shape, it was inferred that the bats of Messel occupied different aerial niches for foraging, e.g. closer to the ground or higher in the canopy, but without specialisations in echolocation, as indicated by the inner ear (Habersetzer et al. 1994). Thus, we don't stop learning about the biology of ancient species once we've put a name on them. These discoveries underscore the huge potential for understanding the interactions between form, function, and sensory ecology in Messel ecosystems.

Variation is the fuel of evolution, burned by the motor of selection. Investigations of individual and ontogenetic variation help to fill in missing pieces of anatomical puzzles. High-resolution computed tomography (μCT) of multiple individuals can also be used to generate 3D composites (e.g. Habersetzer et al. 2018), informing on the whole area of interest. The study of variation can provide information on phylogenetic patterns and processes, such as identifying "zones of variability" that might allow organisms to explore extensive areas of morphospace, increasing opportunities for ecological diversification (e.g. Bever et al. 2011). Such analyses require both detailed 3D anatomical investigation and large-scale scanning projects that are now possible by harnessing high-throughput μCT scanning, digital extraction, and rapid quantification of delicate external and internal structures.

Yearly excavations at Messel cost the state of Hesse, Germany, a considerable amount every year, which historically funded 5 scientific positions, 4 technical assistants, 1 lab manager, 3 excavation/preparation positions, and 1 facility caretaker at Senckenberg alone, along with substantial costs related to site management. This investment yields a plethora of invaluable scientific data in the form of fossils and their associated stratigraphic and geologic data. Adequate management of palaeontological resources requires some understanding of future needs and expectations. If a fuller understanding of species richness is considered a worthy research object, then our work shows that scientific excavations at Messel will continue to produce significant new results for generations to come. Furthermore, investigation of patterns in individual, interspecific, and ontogenetic variation (e.g. Micklich 2012) relies on large sample sizes, as will large-scale studies of ecosystem structure and function.

Future excavation effort

Our quantitative estimates of future excavation effort (Table 3) have three critical dependencies:

(1) *Abundance distribution of taxa with respect to stratigraphic distribution*. While a full analysis is not available for all higher taxa, fine-scale analysis has clearly shown that fish species abundances vary considerably in the profile (Micklich 2012). The same appears to be true of at least one squamate taxon (Smith and Wuttke 2012) and for certain plankton (e.g. Lenz et al. 2007a) and plants (Lenz and Wilde 2018). In our estimates of additional sampling effort, we have implicitly assumed that future excavations will exactly mirror the collecting effort devoted in the past to the different horizons. This may not be the case, and different horizons may be examined in the future. Therefore, it is likely that excavations will reveal more species than estimated here, or reveal them more quickly. Specifically, if merely abundance fluctuations within a fixed species pool are recorded, then excavating different horizons should decrease the future excavation effort required to reach a given proportion of estimated species richness. If the species pool itself changes through time, then excavating different horizons should increase both total species richness and the excavation effort required to sample it.

(2) *Coverage-based estimators (ACE/ICE) of minimum species richness*. These are asymptotic and tend to rise with increased sampling, especially in the early sampling stages (Chao et al. 2009), which is typical of diversity estimators (Gotelli and Colwell 2001). In a number of cases examined here (most notably seed and fruit taxa and, less so, "reptiles"), ACE has not yet plateaued. Thus, we expect ACE and the additional sampling effort required to reach a given proportion thereof, to rise further over time.

(3) *Excavation rate*. If annual excavation effort rises above 1991–2016 levels, which we took as our baseline, the time required to reach a given proportion of estimated species richness will decrease, and vice versa. Current excavation rates are in fact one-half to two-thirds lower than the recent historical (1991–2016) rates. More specifically, after 2016, new regulations were imposed (see above), with which all institutions working in Messel must comply. They require the photographic documentation of the site at the beginning and end of each day, photographic documentation of each excavated sediment block, GPS-based measurement with cm-scale precision of the location of certain fossils (despite known and ongoing mass-wasting phenomena in some areas), and the recording of a vast number of data concerning fossils of unproven significance (e.g. indeterminable "insect" remains, indeterminable "plant" remains, fish scales, etc., in total up to c. 8,000 entries per week per team). As a result,

the actual excavation rate decreased from 1–1.5 m^3/day (see Smith et al. 2024, this issue) to c. 0.5 m^3/day (see above). This decrease in excavation rate, in turn, doubles or triples our estimates of future excavation effort (Table 3).

In sum, our estimates of future excavation effort are dependent on a number of factors whose uncertainties are difficult to quantify. Changing the locations of excavation within the stratigraphic column could increase or decrease our estimates of future excavation effort. Better sampling of diversity is likely to increase estimates of future excavation effort for groups in which coverage-based estimators of minimum total richness have not yet plateaued. Finally, any increase in excavation rate will decrease our estimates of future excavation effort.

Messel compared to other mid-latitude, early-middle Eocene sites

There is no single early Palaeogene, terrestrial site whose fossil content has been so thoroughly investigated as has Messel. Furthermore, the macrofossils from Messel – a maar lake deposit – generally represent the lake itself and its immediately environs, whereas the areal extent of other sites is often much larger. Finally, the taphonomy of Messel as a maar lake is to a large degree different from the majority of continental fossil-bearing localities in fluvial or non-volcanogenic lacustrine settings (cf. Uhl et al. 2024). Thus, comparisons of Messel with other roughly early-middle Eocene sites is complicated for a number of reasons, and comparisons will necessarily remain piecemeal for some time to come. At the same time, even limited comparisons can be revealing.

Messel and the EECO in North America

The Fossil Butte Member of the Green River Formation, from early Eocene zone Wa7 (beginning of the EECO), hence older than Messel, represents a much larger lake than the ancient maar of Messel (e.g. Grande 1984, 2013; Roehler 1993; Smith et al. 2008; Buchheim et al. 2015). Its documented richness of fish species is substantially higher (c. 3× greater) than at Messel, but richness in both is consistent with lake size (see Grande 1984: fig. II.100). On the other hand, its documented richness of birds is substantially lower (about one-half) than at Messel, and documented richness of amphibians (2) and reptiles (13) is lower still. Only 8 species of mammal in total are known from the Fossil Butte Member, almost one order of magnitude lower than at Messel. For further comparison, 30–50 bat specimens, representing three species, have been found at Fossil Butte in half a century (Grande 2013; Rietbergen et al. 2023). Detailed quantitative comparisons are not available for the Fossil Butte Member, but there are many more terrestrial and volant vertebrate fossils known from Messel. This could relate to both ecological and taphonomic conditions, such as the overall greater distance between basin centre and shores in typical Green River localities than at Messel.

Insects and other invertebrates from the different members of Green River have not been studied comprehensively in recent decades, but in some cases closely related species in the same genera have been recorded from both Messel and Green River

(e.g. Archibald et al. 2011; Wedmann et al. 2021; de Mazancourt et al. 2022). For giant ants, the former dispersal possibilities between North America and Europe have been related to hyperthermal events (Archibald et al. 2011).

Messel and coeval European localities

Concerning insects, the beetle taphocoenoses of Messel and the Geiseltal have been compared, and – a few similarities notwithstanding – they are most conspicuous for their taxonomic differences (Hörnschemeyer et al. 1995). A well-investigated group in both sites is the jewel beetles (Buprestidae). Fossils of this group are common in both sites, but their species richness is significantly higher in Messel than in Geiseltal (Hörnschemeyer et al. 1995), despite the broader age range probably covered by Geiseltal (Georgalis et al. 2021).

Similarly, total vertebrate species richness of Geiseltal is notably lower than at Messel. In some cases diversity is comparably low (Actinopterygii, Amphibia) even if the taxonomic composition is somewhat different (Krumbiegel et al. 1983). Birds are far richer at Messel (Mayr 2020). Interestingly, mammals as a whole are richer at Geiseltal than at Messel, especially due to the richness of primates, perissodactyls and artiodactyls, and in spite of a lower richness of bats (Krumbiegel et al. 1983).

Reptiles are somewhat richer at Messel than at Geiseltal, especially the squamates, although it must be acknowledged that sample size is probably higher at Messel. The squamates show similarities, with species like *Ophisauriscus quadrupes* and *Eolacerta robusta* considered to be in common (Kuhn 1940; Nöth 1940; Sullivan et al. 1999; Müller 2001). However, recent work also highlights taxonomic differences (Smith 2009a; Smith and Habersetzer 2021; Villa et al. 2022; Palci et al. 2024), and there is nothing quite like the large carnivorous lizard *Eosaniwa koehni* at Messel. There is great taxonomic similarity between the crocodylians of Messel and of Geiseltal (Berg 1966; Hastings and Hellmund 2017).

The Messel avifauna shows close taxonomic similarities to that of the somewhat older fossil sites of the London Clay and Green River (Mayr 2022). The birds fossils from Geiseltal also show close taxonomic similarities to those from Messel, although the relative abundance of certain groups is different, notably with flightless terrestrial birds predominating in Geiseltal (Mayr 2020).

Messel then and now

Geopolitical borders as such are of no relevance for natural biological diversity, yet administrative record-keeping is frequently closely tied to them. Hence, in the following we focus on Germany, although our interest is the central, mid-latitude part of the European continent. For many groups, asymptotic species richness at Messel is estimated to be much higher than in the same area at present.

For the fossil insects from Messel, the present state of the art of research does not allow for faunal comparisons at species level. For example, intensive studies at Messel have revealed 19 species of click beetle (Elateridae) and 14 additional elaterid "groups," which represent at least one species each (Appendix 1). So at least 33 elaterid species were documented among the fossils from Messel by 1999, with $S_{ACE} = 55.3$. For comparison, today's elaterid fauna for the whole of Germany comprises about 150 elaterid species (Rupp and Schmidt 2022).

Altogether 20 native species of Amphibia (6 Caudata, 14 Anura) occur in Germany today (Kühnel et al. 2009; Glandt 2018), all but one of which occur in the state of Hesse (Kühnel et al. 2009) that encompasses Messel. With $S_{ACE} = 10.5$, asymptotic amphibian species richness at Messel is about half that in Hesse and Germany today.

There are 13 species of squamate in all of Germany today (Rote-Liste-Gremium Amphibien und Reptilien 2020), so the currently documented richness at Messel (21) is nearly twice that. Furthermore, most squamate taxa at Messel – with the exception of stem members of Lacertidae (Čerňanský and Smith 2018) and the glass lizard *Ophisauriscus quadrupes* – are not closely related to any extant European group (like birds; see below). Rather, Messel squamates – both lizards and snakes – have closer relations to coeval North American faunas and extant tropical to subtropical regions (Smith 2017; Smith et al. 2018b). Finally, in all of Germany there is 1 species of turtle and no crocodylians (Glandt 2018; Rote-Liste-Gremium Amphibien und Reptilien 2020), in contrast to the 13 species of these large reptiles at Messel.

Altogether 98 native, established mammal species occur in Germany today (Meinig et al. 2020), and asymptotic species richness of mammals at Messel, S_{ACE}, is two-thirds of that value. The correspondence of the two figures would be somewhat closer if bats were excluded. Bats show a very strong latitudinal diversity gradient (e.g. Wilson 1974), and bat diversity in all of Germany is only 25 species, including the extirpated *Miniopterus schreibersii* (Meinig et al. 2020). Remarkably, the number of fossil bat species in the Middle Messel Formation (9) is comparable to the number (10–11) observed in the Messel Pit today, all of which pertain to the clade Vespertilionidae (Rabenstein et al. 2010).

Altogether 248 native and regularly breeding bird species in Germany were assessed by Grüneberg et al. (2015), and remarkably the asymptotic species richness of birds at Messel is nearly one-half of that value. The Messel avifauna includes stem group representatives of a few taxa that still occur in Central Europe (Apodidae, Coraciidae), but most groups represent extinct clades with no close relatives, or taxa whose extant ranges are in the tropical or subtropical regions (e.g. Trogoniformes, Coliiformes).

Messel compared to the modern tropics

Detailed comparison of Messel with modern tropical biotopes is hardly easier than with other fossil assemblages. Neotropical rainforests are better studied overall than African or Asian rainforests (Voss 2024), limiting comparison to the former. Even here, few areas have been studied with respect to all organismic groups (Gentry 1990). Furthermore, most well-studied areas, like the Maroni-Oyapock interfluve in French Guiana and Yavarí-Ucayali interfluve in Amazonian Peru, have a geographic extent of 10^4 km^2. A higher species richness (180 and 199 documented species of mammals, respectively; Voss 2024) is expected, because species richness rises with increased area sampled (e.g. Rosenzweig 1995).

Messel and its immediate environs were a small piece of the geography of Central Europe at the time. One of the best comparisons to draw, therefore, would be with La Selva, Costa Rica (McDade et al. 1994; Anonymous 2017), a tiny,

Table 4 Minimum species richness at Messel (asymptotic species richness estimator, S_{ACE}) compared to observed species richness (S_{obs}) at modern La Selva, Costa Rica. Amongst ants, only poneromorphs have been studied at Messel, but the La Selva tally includes all. *Amongst ray-finned fishes, one species is known at Messel (*Anguilla ignota*) that has not otherwise been documented in large subsequent samples, including those analysed quantitatively here

	S_{ACE} at Messel Pit	S_{obs} at La Selva
Vascular plants	258.5	2087
Insects	?	10^4
(of those, ants)	35.8 (poneromorph only)	>450
Fishes	7*	45
Amphibia	10.5	48
Reptiles	44.1	87
Aves	114.6	470
Mammalia	65	125
(of those, Chiroptera)	10	72

well-studied fragment (c. 15 km^2) of tropical rainforest in modern Costa Rica (Table 4). Vascular plant species richness (essentially, number of gymnosperm and angiosperm species) is one order of magnitude higher at La Selva than at Messel. Amongst animals, ant species diversity is also an order of magnitude higher at La Selva than at Messel. Fish and amphibian richness too is higher at La Selva, but less extremely so. Reptile species richness at La Selva is perhaps twice that estimated at Messel. Mammal species richness at La Selva – exclusive of bats, which were in the early phase of their diversification in the Eocene – is nearly the same as that of Messel. Bird species richness is substantially higher at La Selva than at Messel (about five times as high), but as at Messel bird species richness is substantially higher than mammal species richness. Overall the comparison suggests that species richness for most extant clades is substantially higher at La Selva than at Messel at the time of deposition.

A further relevant comparison with the modern tropics concerns biogeography (e.g. Rossmann 2000; Wappler 2006; Wedmann et al. 2007; Dlussky et al. 2008; Smith et al. 2018a, b). For instance, the Messel birds and squamates includes stem group representatives of some extant taxa that today occur in the Neotropics. On the other hand, amongst birds there are taxa, whose closest relatives are today in the tropics of the African region (the Madagascan Leptosomidae), and in the tropical regions of Southeast Asia and Australia (Podargidae). South America and Madagascar were geographically isolated during most of the Cenozoic, which may account for the relictual occurrence of avian groups that had larger ranges in the early Cenozoic (Mayr 2011).

Conclusions

Messel is sometimes compared to a "tropical rainforest" (e.g. Mangel 2011; Schaal 2017), but the evidence for this assertion is wanting. Messel is not tropical with respect to its geographic position (at c. 45° N palaeolatitude). Its climate may have been warmer and more equable than at present in Central Europe (Grein et al. 2011; Kaboth-Bahr et al. 2024; Schmitt et al. 2024), but there were still substantial seasonal differences in temperature (Grein et al. 2011) and day length (Storch and Schaarschmidt 1988). A rainforest, if we accept a definitional threshold of 2000 mm precipitation per year (e.g. Morley 2000), has not yet been proven. The term "paratropical forest" used frequently in the palaeobotanical literature to refer to forest types with mean annual temperature of 20–25 °C and mean annual range of temperature up to 20 °C (e.g. Wolfe 1987) might be more apt and was already employed in Collinson et al. (2012). The biodiversity of Messel comports with these observations. Overall, species richness is higher than in Central Europe today, but lower than in well-surveyed modern Neotropical biotopes, especially La Selva, Costa Rica.

Detailed comparisons with both other fossil localities and other modern biotopes are difficult due to data insufficiency, taphonomic differences, and the varying geographic extent of sites. Therefore, our comparisons have necessarily been unsystematic. Allotemporal comparisons (Smith and Gauthier 2013) between Messel and modern biotopes presents a further difficulty where diversity dynamics may not be equilibrial (cf. Alroy 1998; Cantalapiedra et al. 2017). Namely, many modern groups were in the process of diversification, and it is unclear to what extent this may influence diversity patterns independently of environmental or purely geographic factors. For instance, of the 180 and 199 mammal species documented in the Maroni-Oyapock and Yavarí-Ucayali interfluves, respectively, some 50% or more are bats (Voss 2024). Bats have a much higher net diversification rate than most other mammal groups, and Messel existed early in their history (Teeling et al. 2005).

With its abundance and diversity of fossils, Messel has a vital role to play in understanding how ecosystems as a whole might respond to anthropogenic global warming. In Messel, for instance, evergreen plant taxa, especially within the laurel and walnut families, were particularly heavily attacked by herbivorous insect taxa (Wappler et al. 2012; Albrecht et al. 2023). This is most likely due to the up to 3× higher atmospheric CO_2 (Rae et al. 2021; Cenozoic CO_2 Proxy Integration Project Consortium 2023), which also has a direct effect on plants and can stimulate plant growth (so-called "CO_2 fertilisation effect"). This also means that the C/N ratio in the tissue increases under increased CO_2, which de facto leads to a reduction in the quality of the food source for herbivorous insect taxa. The latter react to the reduced quality of the food supply with an increase in consumption. Overall, it is apparent that at the time of the Eocene, the functional diversity and intensity of exploitation of herbivorous insects in middle latitudes were many times higher than today.

Epistemic ironies are embedded in biology. In phylogenetic systematics, the more we understand about a group's history, the less confident we become of individual steps, because the size of those steps and so the amount of evidence that can bear witness to them decreases. In the study of species richness, the better we sample a group, the harder we have to work to complete it, because diversity curves are concave downward. Thus, going forward we should not rest on our laurels but redouble our efforts.

Appendix 1

Complete list of all currently valid taxa documented thus far at the Eocene Messel Pit, beginning with unicellular autotrophic forms, followed by plants, fungi and animals. Nearly all of them are known from the Middle Messel Formation (but many palynomorph taxa and taxa from fish coprolites are also known from the Lower Messel Formation). Not all taxa have been formally named: some are given in open nomenclature, for some a genus but not species was specified (e.g. Equisetum sp., and still others are referred to informally (e.g. insect damage types, vertebrate coprolites). As explained in the text, this list should not be misinterpreted as a list of biological species present at Messel, especially for plants and insects, as the associations between different taxa or morphospecies (e.g. between pollen, leaf and fruit/seed taxa, or of insect damage types to body fossils) are poorly understood. Furthermore, in some cases (especially for plant leaf taxa), revision of many groups is outstanding and, when accomplished, will probably reduce the number of recognised taxa. In other cases, further taxonomic study is likely to reveal new taxa (especially for pollen and flower taxa). The taxonomy is as current as possible. Thus, previously described taxa that have been synonymised are omitted. Referenes for Appendix 1 are found in the Supplementary information. Taxa referenced are addressed in Bouchal et al. (in prep.) Qualitative LM and SEM study of the Messel palynoflora: Part II. Fabales to Caryophyllales.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Dinoflagellata					
Peridiniaceae	*Messelodinium thielepfeifferae*	resting cyst	Lenz, Wilde, Riegel & Heinrichs, 2007b	Lenz et al. 2007a, 2011	
Diatomophyceae / Bacillariophyceae					
Melosiraceae	*Melosira* sp.	body fossil		Goth 1990	
Viridiplantae: Chlorophyta					
Botryococcaceae	*Botryococcus* sp. cf. *B. braunii*	body fossil		Goth 1990; Lenz et al. 2007a, 2011; Bouchal et al. 2024	
Chlorophyceae	*Coelastrum* sp.	body fossil		Richter & Baszio 2001b; Richter et al. 2013	
Hydrodictyaceae	*Tetraedron minimum*	body fossil	(Braun, 1855) Hansgirg, 1889	Goth 1990	
Algae Incertae sedis					
Incertae sedis	Taxon indet.	body fossil		Bouchal et al. 2024	Algae fam. indet. sp. of Bouchal et al. (2024)
Viridiplantae: Charophytes					
Zygnemataceae	*Spirogyra* sp.	resting cyst		Lenz et al. 2007a, 2011; Bouchal et al. 2024	Previously *Ovoidites* sp.
Viridiplantae: Lycophytes					
Lycopodiaceae, *Lycopodium*	*Camarozonosporites eocaenicus*	spore	Krutzsch & Vanhoorne, 1977	Lenz & Wilde 2018	
Lycopodiaceae, *Lycopodiella*	*Camarozonosporites decorus*	spore	(Wolff, 1934) Krutzsch, 1963a	Bouchal et al. 2024	*Lycopodiella* sp. 1 of Bouchal et al. (2024)
Lycopodiaceae, *Lycopodiella*	*Hamulatisporites helenensis*	spore	(Krutzsch, 1963a) S. K. Srivastava, 1975	Bouchal et al. 2024	*Lycopodiella* sp. 2 of Bouchal et al. (2024)
Selaginellaceae, *Selaginella*	*Echinatisporis hungaricus*	spore	Kedves, 1973	Krutzsch 1963; Thiele-Pfeiffer 1988; Lenz et al. 2011	
Selaginellaceae, *Selaginella*	*Tegumentisporis sculpturoides*	spore	(Krutzsch, 1959) Krutzsch, 1963b	Thiele-Pfeiffer 1988; Lenz et al. 2011	
Selaginellaceae, *Selaginella*	*Tegumentisporis tegumentis*	spore	(Krutzsch, 1959) Krutzsch, 1963b	Thiele-Pfeiffer 1988; Lenz et al. 2011; Bouchal et al. 2024	*Selaginella* sp. 2 of Bouchal et al. (2024)
Selaginellaceae, *Selaginella*	*Tegumentisporis villosoides*	spore	(Krutzsch, 1959) Krutzsch, 1963b	Thiele-Pfeiffer 1988; Lenz et al. 2011; Bouchal et al. 2024	*Selaginella* sp. 1 of Bouchal et al. (2024)
Incertae sedis	*Tegumentisporis corrugatius*	spore	(Krutzsch, 1959) Krutzsch, 1963b	Thiele-Pfeiffer 1988	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Viridiplantae: Ferns					
Blechnaceae	?*Blechnum dentatum*	pinnule	(Goeppert, 1836) Braun, 1852	Wilde 1989	
Dryopteridaceae	cf. *Rumohra recentior*	pinnule	(Unger, 1841-1847) Barthel, 1976	Wilde 1989	
Equisetaceae	*Equisetum* sp.	tuber		Collinson et al. 2012	
Gleicheniaceae	*Gleicheniidites* sp.	spore		Lenz & Wilde 2018	
Gleicheniaceae	*Gleichenia* sp.	frond		Wilde 2018	
Osmundaceae, *Osmunda*	*Baculatisporites major*	spore	(Raatz, 1937) Krutzsch, 1959	Bouchal et al. 2024	Possibly only 1 species of *Osmunda* (Bouchal et al. 2024)
Osmundaceae, *Osmunda*	*Baculatisporites nanus*	spore	(Wolff, 1934) Krutzsch, 1959	Bouchal et al. 2024	Possibly only 1 species of *Osmunda* (Bouchal et al. 2024)
Osmundaceae, *Osmunda*	*Baculatisporites primarius*	spore	(Wolff, 1934) Thomson & Pflug, 1953	Krutzsch 1967a; Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Possibly only 1 species of *Osmunda* (Bouchal et al. 2024)
Osmundaceae	*Osmunda lignitum*	pinnule	(Giebel, 1857) Stur, 1870	Wilde 1989	
Polypodiaceae	*Verrucatosporites favus*	spore	(R. Potonié, 1931d) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Polypodiaceae gen. indet. sp. 1 of Bouchal et al. (2024)
Polypodiaceae	*Verrucatosporites microfavus*	spore	Thiele-Pfeiffer, 1988	Lenz et al. 2007a, 2011; Bouchal et al. 2024	Polypodiaceae gen. indet. sp. 3 of Bouchal et al. (2024)
Polypodiaceae	*Verrucatosporites pseudoregulatius*	spore	Krutzsch, 1967	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Polypodiaceae, *Polypodium*?	*Verrucatosporites cellarius*	spore	(Krutzsch, 1959) Krutzsch, 1967	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Polypodiaceae	*Verrucatosporites* sp.	spore		Lenz & Wilde 2018	
Polypodiaceae	Polypodiaceae gen. indet. sp. 2	spore		Bouchal et al. 2024	
Polypodiaceae	*Microfoveolatosporis granuloides*	spore	(Krutzsch, 1959) Krutzsch, 1967	Thiele-Pfeiffer 1980, 1988; Bouchal et al. 2024	Polypodiaceae gen. indet. sp. 4 of Bouchal et al. (2024)
Pteridaceae	*Acrostichum ?aureum*	pinnule	Linnaeus, 1753	Wilde 1989	
Pteridaceae	*Bifacialissporites ornatus*	spore	Nagy, 1963	Bouchal et al. 2024	cf. *Cosentinia* sp. of Bouchal et al. (2024)
Pteridaceae	*Cryptogrammasporis magnoides*	spore	(Krutzsch, 1963b) Skawińska in Ziembińska-Tworzydło et al. 1994	Bouchal et al. 2024	*Cryptogramma* sp. of Bouchal et al. (2024)
Pteridaceae	*Polypodiaceoisporites boerzsoenyensis*	spore	Nagy, 1985	Bouchal et al. 2024	*Pteris* vel *Jamesonia* sp. of Bouchal et al. (2024)
Pteridaceae	*Bifacialissporites murensis*	spore	Nagy, 1963	Bouchal et al. 2024	*Pteris* sp. 1 of Bouchal et al. (2024)

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Pteridaceae	*Polypodiaceoisporites marxheimensis*	spore	(Mürriger & Pflug, 1952 ex Thomson & Pflug, 1953) Krutzsch, 1959	Bouchal et al. 2024	*Pteris* sp. 3 of Bouchal et al. (2024)
Pteridaceae, *Pteris*	*Polypodiaceoisporites gracillimus*	spore	Nagy, 1963	Krutzsch 1967a; Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011	
Pteridaceae, *Pteris*	*Polypodiaceoisporites lusaticus*	spore	Krutzsch, 1967	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011 Bouchal et al. 2024	*Pteris* sp. 2 of Bouchal et al. (2024)
Pteridaceae, *Pteris*	*Polypodiaceoisporites* sp.	spore		Lenz et al. 2007a, 2011	
Pteridaceae, *Pteris*	*Verrucingulatisporites undulatus*	spore	Nagy, 1963	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	*Pteris* sp. 4 of Bouchal et al. (2024)
Schizaeaceae, *Lygodium*	*Trilites solidus*	spore	(R. Potonié 1934) Krutzsch 1959	Thomson & Pflug 1953; Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Schizaeaceae	*Lygodium kaulfussi*	pinnule	Heer, 1861	Wilde 2018	
Schizaeaceae	*Ruffordia subcretaceae*	pinnule	(Saporta, 1868) Barthel, 1976	Engelhardt 1922; Wilde 1989	
Schizaeaceae	*Cicatricosisporites dorogensis*	spore	R. Potonié & Gelletich 1933	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	cf. *Ruffordia* sp. 1 of Bouchal et al. (2024)
Schizaeaceae	*Cicatricosisporites paradorogensis*	spore	Krutzsch, 1959	Barthel 1976; Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	cf. *Ruffordia* sp. 2 of Bouchal et al. (2024)
Schizaeaceae	Taxon indet.	spore		Bouchal et al. 2024	Schizaeaceae gen. indet. sp. of Bouchal et al. (2024)
Thelypteridaceae	*Thelypteris* sp.	pinnule		Wilde 1989	
Incertae sedis	*Concavisporites (Obtusisporis) minimus*	spore	Krutzsch, 1962a	Lenz et al. 2011	
Incertae sedis	*Foveotriletes rueterbergensis*	spore	Krutzsch, 1962a	Bouchal et al. 2024	Trilete spore ord. indet. sp. 4 of Bouchal et al. (2024)
Incertae sedis	*Intrapunctisporis gracilioides*	spore	Krutzsch & Vanhoorne, 1977	Lenz et al. 2007a	
Incertae sedis	*Ischyosporites tertiarius*	spore	Krutzsch, 1967 ex Roche, 1973	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Incertae sedis	*Laevigatosporites discordatus*	spore	Pflug, 1953a	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Monolete spore ord. indet. sp. 2 of Bouchal et al. (2024)
Incertae sedis	*Laevigatosporites haardtii*	spore	(R. Potonié & Venitz, 1934) Thomson & Pflug, 1953	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Monolete spore ord. indet. sp. 1 of Bouchal et al. (2024)

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	Monolete spore ord. indet. sp. 3	spore		Bouchal et al. 2024	
Incertae sedis	*Leiotriletes kopecki kopecki*	spore	Kedves, 1973	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Trilete spore ord. indet. sp. 1 of Bouchal et al. (2024)
Incertae sedis	*Leiotriletes maxoides maxoides*	spore	Krutzsch, 1962a	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Trilete spore ord. indet. sp. 2 of Bouchal et al. (2024)
Incertae sedis	*Leiotriletes microadriennis*	spore	Krutzsch, 1959	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Trilete spore ord. indet. sp. 2 of Bouchal et al. (2024)
Incertae sedis	*Leiotriletes triangulus*	spore	(Mürriger & Pflug, 1952) Krutzsch, 1962a	Thiele-Pfeiffer 1988; Lenz et al. 2023; Bouchal et al. 2024	Trilete spore ord. indet. sp. 2 of Bouchal et al. (2024)
Incertae sedis	*Leiotriletes wolfii wolfii*	spore	Krutzsch, 1962a	Bouchal et al. 2024	Trilete spore ord. indet. sp. 3 of Bouchal et al. (2024)
Incertae sedis	*Punctatisporites* sp.	spore		Lenz & Wilde 2018	
Incertae sedis	*Retitriletes belgicus*	spore	Krutzsch & Vanhoorne, 1977	Lenz et al. 2011	
Incertae sedis	*Toroisporis arealis*	spore	Krutzsch, 1959	Lenz et al. 2023	
Incertae sedis	*Toroisporis irregularis*	spore	Krutzsch, 1959	Lenz et al. 2023	
Incertae sedis	*Trilites menatensis*	spore	Kedves, 1982	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Incertae sedis	*Toripunctisporis* sp.	spore		Thiele-Pfeiffer 1988; Bouchal et al. 2024	Triolete spore ord. indet. sp. 2 of Bouchal et al. (2024)
Viridiplantae: Gymnosperms					
Cephalotaxaceae	*Cephalotaxus messelensis*	shoot	Wilde, 1989	Wilde 2018	
Cupressaceae, *Sciadopitys*	*Sciadopityspollenites eocaenicus*	pollen	Krutzsch, 1971	Thiele-Pfeiffer 1988	
Cupressaceae	*Cupressacites insulipapillatus*	pollen	(Trevesian, 1967) Krutzsch, 1971	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Non-papillate Cypressaceae
Cupressaceae	*Inaperturopollenites concedipites*	pollen	(Wodehouse, 1933) Krutzsch, 1971	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Papillate Cupressaceae
Cupressaceae	*Inaperturopollenites verrupapillatus*	pollen	Trevesian, 1967	Krutzsch 1971; Thiele-Pfeiffer 1988	
Cupressaceae	*Inaperturopollenites dubius*	pollen	(R. Potonié & Venitz, 1934) Thomson & Pflug, 1953	Lenz et al. 2023	
Cupressaceae	*Inaperturopollenites magnus*	pollen	(R. Potonié, 1934) Thomson & Pflug, 1953	Lenz et al. 2023	
Cupressaceae	*Athrotaxis* (?) *subulata*	branch	Gardner, 1883	Engelhardt 1922	
Cupressaceae	*Callitris* sp.	cone		Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Cupressaceae	*Sequoia couttsiae*	branch	Heer, 1862	Engelhardt 1922	
Cupressaceae	*Sequoia langsdorfii*	branch	Heer, 1877	Engelhardt 1922	
Cupressaceae	*Doliostrobus sternbergii*	branch	Marion, 1888	Engelhardt 1922	
Cycadales fam. indet.	*Monocolpopollenites crassiexinus* (in part)	pollen	Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2011; Bouchal et al. 2024	Bouchal (pers. comm. 2024) suggests that pollen of Cycadales and Nymphaeales look very similar under light microscopy
Doliostrobaceae	*Doliostrobus taxiformis*	cone-scale	(Sternberg, 1833) Kvaček, 1971 emend. Kunzmann, 1999	Collinson et al. 2012	
Doliostrobaceae	*Doliostrobus* cf. *certus*	shoots, bract-scale	Bůžek, Holý & Kvaček, 1969	Wilde 1989	Same as *D. taxiformis*? Kunzmann synonymized. However, Wilde (1989) indicates that it is similar to *D. certus*. Further study should be done of these specimens.
“Ginkgoaceae”	*“Ginkgo* sp.”	leaf		Engelhardt 1922	Most likely *Lygodium kaulfussi*; this mistake was common during this time and there is no evidence for Eocene *Ginkgo* in Central Europe
Pinaceae, *Abies*	*Abiespollenites maximus*	pollen	Krutzsch, 1971	Bouchal et al. 2024	
Pinaceae, *Picea*	*Piceapollis praemarianus*	pollen	Krutzsch, 1971	Bouchal et al. 2024	
Pinaceae, *Pinus* (*Pinus*)	*Pityosporites labdacus*	pollen	(R. Potonié, 1931c) Thomson & Pflug, 1953	Krutzsch 1971; Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Pinaceae, *Pinus* (*Strobus*)	*Pinuspollenites pseudocristatus*	pollen	(Doktorowicz-Hrebnicka, 1960 in Krutzsch, 1971 ex Ziembińska-Tworzydło, 1974) Grabowska & Ważyńska in Stuchlik et al. 2002	Bouchal et al. 2024	
Pinaceae, *Cathaya*	*Pityosporites microalatus*	pollen	(R. Potonié, 1931c) Thomson & Pflug, 1953	Thiele-Pfeiffer 1980, 1988	
Podocarpaceae	*Podozamites eocaenica*	foliage	Engelhardt, 1922		
Viridiplantae: Angiosperms: Nymphaeales					
Nymphaeaceae?	*Monocolpopollenites crassiexinus* (in part)	pollen	Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2011; Bouchal et al. 2024	?Nymphaeaceae gen. indet. of Bouchal et al. 2024
Nymphaeaceae	taxon indet.	seed		Collinson et al. 2012	
Nymphaeaceae	*Nelumbium* (sic) *buchi*	leaf	Ettingshausen, 1855	Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Nymphaeaceae	*Nuphaea engelhardtii*	leaf	Gee & Taylor, 2019	Engelhardt 1922 [as *Nymphaea* sp.]; Wilde 1989	
Nymphaeaceae	*Cabomba* sp.	leaf		Wilde 1989	
Nympheaeceae	taxon indet.	flower		Schaarschmidt 1988; Wilde 2018	
Viridiplantae: Angiosperms: Chloranthales					
Chloranthaceae, *Ascarina*	*Emmapollis pseudoemmaensis*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	*Ascarina* sp. 1 of Bouchal et al. (2024)
Chloranthaceae, *Ascarina*	*Emmapollis pseudoemmaensis*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	*Ascarina* sp. 2 of Bouchal et al. (2024)
Viridiplantae: Angiosperms: Magnoliales					
Annonaceae	*Anona* (sic) *elliptica*	leaf	Unger, 1850	Engelhardt 1922	
Magnoliaceae	*Magnolipollis magnolioides*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1988	
Magnoliaceae	*Magnolia dianae*	leaf	Unger, 1850	Engelhardt 1922	
Magnoliaceae	*Magnolia inaequalis*	leaf	Engelhardt, 1922	Engelhardt 1922	
Magnoliaceae	*Magnolia grandifolia*	leaf	Engelhardt, 1922		
Magnoliaceae	*Magnolia pristina*	leaf	Engelhardt, 1922		
Magnoliaceae	*Magnolia multinervis*	leaf	Engelhardt, 1922		
Magnoliaceae	*Magnolia laurioides*	leaf	Engelhardt, 1922		
Magnoliaceae	*Magnolia* spp.	seed		Collinson et al. 2012	Probably multiple distinct taxa are present here (Collinson et al. 2012)
Magnoliaceae	*Magnolia* sp. 1	fruit		Collinson et al. 2012	
Myristicaceae	*Knema* (*Myristica*) *tertiaria*	leaf	Engelhardt, 1922		
Myristicaceae	*Myristicacarpum* sp.	seed		Collinson et al. 2012	
Incertae sedis	“Magnoliales flower”	flower		Schaarschmidt 1984	
Viridiplantae: Angiosperms: Piperales					
Piperaceae	*Macropiper rotundifolium*	leaf	Engelhardt, 1922		
Viridiplantae: Angiosperms: Laurales					
Atherospermataceae	*Laurelia tertiaria*	leaf	Engelhardt, 1922		
Lauraceae	*Daphnogene crebrigranosa*	leaf	(Unger, 1850) Wilde, 1989	Wilde 2018	
Lauraceae	*Daphnogene cryptostoma*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Daphnogene leptohuephe*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Daphnogene eocaenica*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Daphnogene multipora*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Daphnogene* sp. 1	leaf		Wilde 1989	
Lauraceae	*Daphnogene* sp. 2	leaf		Wilde 1989	
Lauraceae	*Daphnogene* sp. 3	leaf		Wilde 1989	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Lauraceae	*Laurophyllum lanigeroides*	leaf	(Engelhardt, 1922) Wilde, 1989	Sturm 1971	
Lauraceae	*Laurophyllum hirsutum*	leaf	(Bandulska, 1926) Wilde, 1989	Sturm 1971	
Lauraceae	*Laurophyllum ovosimilis*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Laurophyllum schottleri*	leaf	(Engelhardt, 1922) Wilde, 1989	Sturm 1971	
Lauraceae	*Laurophyllum weylandii*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Laurophyllum lutetium*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Laurophyllum glaphyre*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Laurophyllum streble*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Laurophyllum natistomum*	leaf	(Sturm, 1971) Wilde, 1989		
Lauraceae	*Laurophyllum tertiarium*	leaf	(Engelhardt, 1922) Wilde, 1989	Sturm 1971	
Lauraceae	*Laurophyllum ebenoides*	leaf	(Engelhardt, 1922) Wilde, 1989	Sturm 1971	
Lauraceae	*Laurophyllum alatum*	leaf	Sturm ex Wilde, 1989		
Lauraceae	*Laurophyllum* sp. 1	leaf		Wilde 1989	
Lauraceae	*Laurophyllum* sp. 2	leaf		Wilde 1989	
Lauraceae	gen. indet.	fruit		Collinson et al. 2012	
Lauraceae	*Laurocarpum* sp. 1	fruit		Collinson et al. 2012	
Lauraceae	*Laurocarpum* sp. 2	fruit		Collinson et al. 2012	
Lauraceae	*Laurocarpum* sp. 3	fruit		Collinson et al. 2012	
Viridiplantae: Angiosperms: Alismatales					
Araceae	*Araciphyllites tertiarius*	leaf	(Engelhardt, 1922) Wilde, Kvaček & Bogner, 2005	Wilde 1989, 2018	
Araceae	*Araciphyllites schaarschmidtii*	leaf	Wilde, Kvaček & Bogner, 2005	Wilde 1989	
Araceae	*Caladiosoma messelense*	leaf	Wilde, Kvaček & Bogner, 2005	Wilde 1989	
Hydrocharitaceae	*Hydrocharis* sp.	leaf		Wilde 1989	
Hydrocharitaceae, *Stratiotes*	*Stratiotes* sp.	pollen		Bouchal et al. 2024	
Potamogetonaceae	*Potamogeton speciosus*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Viridiplantae: Angiosperms: Pandanales					
Cyclanthaceae	*Cyclanthus messelensis*	fruiting head	S. Y. Smith et al. 2008	Collinson et al. 2012; Wilde 2018	
Pandanaceae	Pandanaceae sp.	leaf		Wilde 1989	
Viridiplantae: Angiosperms: Liliales					
Smilacaceae	*Smilax grandifolia*	leaf	Unger, 1847	Engelhardt 1922	
Smilacaceae	*Smilax lingulata*	leaf	Heer, 1869	Engelhardt 1922	
Smilacaceae	*Smilax ovata*	leaf	Wessel, 1856	Engelhardt 1922	
Smilacaceae	*Smilax reticulata*	leaf	Heer, 1869	Engelhardt 1922	
Smilacaceae	cf. *Smilax* sp. 1	leaf		Wilde 1989	
Smilacaceae	cf. *Smilax* sp. 2	leaf		Wilde 1989	
Smilacaceae	cf. *Smilax* sp. 3	leaf		Wilde 1989	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Viridiplantae: Angiosperms: Arecales					
Arecaceae	*Dicolpopollis kockeli*	pollen	Pflanzl, 1956	Lenz et al. 2007a; Bouchal et al. 2024	Calamoideae gen. indet. sp. 1 of Bouchal et al. (2024)
Arecaceae	*Dicolpopollis kockeli*	pollen	Pflanzl, 1956	Lenz et al. 2007a; Bouchal et al. 2024	Calamoideae gen. indet. sp. 2 of Bouchal et al. (2024)
Arecaceae	*Monocolpopollenites verrucatus*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Arecoideae gen. indet. sp. of Bouchal et al. (2024)
Aracaceae	*Punctilongisulcites microechinatus*	pollen	Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1980; Lenz et al. 2007a, 2011; Bouchal et al. 2024	Arecaceae gen. indet. sp. of Bouchal et al. (2024)
Aracaceae	cf. *Calamopsis bredana*	leaf	Heer, 1859	Engelhardt 1922	
Arecaceae	*Phoenicites lepidocaryoides*	leaf	Wilde, 1989		
Arecaceae	*Friedemannia messelensis*	fruit	Collinson et al. 2012		
Arecaceae	Type A	flower		Schaarschmidt & Wilde 1986	
Arecaceae	Type B	flower		Schaarschmidt & Wilde 1986	
Arecaceae	Type C	flower		Schaarschmidt & Wilde 1986	
Arecaceae	Type D	flower		Schaarschmidt & Wilde 1986	
Arecaceae	Type E	flower		Schaarschmidt & Wilde 1986	
Viridiplantae: Angiosperms: Poales					
Cyperaceae	*Cyperaceaepollis germanicus*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1980, 1988; Bouchal et al. 2024	Cyperaceae gen. indet. sp. 2 of Bouchal et al. (2024)
Cyperaceae	*Cyperaceaepollis neogenicus*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1988; Bouchal et al. 2024	Cyperaceae gen. indet. sp. 1 of Bouchal et al. (2024)
Cyperaceae	*Volkeria messelensis*	infructescence	S. Y. Smith et al. 2009	Collinson et al. 2012; Wilde 2018	
Poaceae	*Phragmites oeningensis*	stalk/reed	Braun, 1845	Engelhardt 1922	
Poaceae	Poaceae gen. indet. sp. 1	pollen		Bouchal et al. 2024	
Poaceae	Poaceae gen. indet. sp. 2	pollen		Bouchal et al. 2024	
Restionaceae	*Milfordia minima*	pollen	Krutzsch, 1970a	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a	
Restionaceae	*Milfordia incerta*	pollen	(Thomson & Pflug, 1953) Krutzsch, 1961	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a	
Typhaceae	*Sparganiaceaepollenites* cf. *cuvilleri*	pollen	(Gruas-Cavagnetto, 1966) Krutzsch & Vanhoorne,1977	Thiele-Pfeiffer 1988	
Typhaceae	*Typha* sp.	stalk		Engelhardt 1922	
Viridiplantae: Angiosperms: Asparagales					
Iridaceae	*Iris latifolia*	leaf	Heer, 1869	Engelhardt 1922	
Iridaceae	*Iris* (?) sp.	leaf		Engelhardt 1922	
Viridiplantae: Angiosperms: Zingiberales					

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Zingiberaceae	*Amomum tertiarium*	leaf	Engelhardt, 1922		
Zingiberaceae	*Musophyllum* sp.	leaf		Engelhardt 1922	
Zingiberaceae	Zingiberaceae sp.	leaf		Wilde 1989	
Viridiplantae: Angiosperms: Ranunculales					
Menispermaceae	Menispermaceae sp.	leaf		Wilde 1989	
Menispermaceae	*Tinomiscoidea jacquesii*	fruit	Collinson et al. 2012		
Menispermaceae	*Parabaena* cf. *europaea*	fruit		Collinson et al. 2012	
Menispermaceae	Tinosporeae sp. 1	fruit		Collinson et al. 2012	
Menispermaceae	Tinosporeae sp. 2	fruit		Collinson et al. 2012	
Menispermaceae	Tinosporeae sp. 3	fruit		Collinson et al. 2012	
Menispermaceae	*Diploclisia rugulosa*	fruit	Collinson et al. 2012		
Menispermaceae	*Stephania hootae*	fruit	Collinson et al. 2012		
Menispermaceae	*Martinmuellera tuberculata*	fruit	Collinson et al. 2012		
Menispermaceae	*Palaeosinomenium ornamentum*	fruit	Collinson et al. 2012		
Menispermaceae	*Palaeosinomenium venablesii*	fruit	Chandler, 1961	Collinson et al. 2012	
Menispermaceae	*Palaeosinomenium* sp.	fruit		Collinson et al. 2012	
Menispermaceae	Unnamed Menispermaceae	fruit		Collinson et al. 2012	
Menispermaceae	unnamed taxon	fruit		Collinson et al. 2012	
Menispermaceae	*Wardensheppeya* sp.	fruit		Collinson et al. 2012	
Menispermaceae	*Karinschmidtia rotulae*	fruit	Collinson et al. 2012	Wilde 2018	
Menispermaceae	*Cocculus lottii*	fruit	Collinson et al. 2012		
Menispermaceae	?*Pericampylus* sp.	fruit		Collinson et al. 2012	
Ranunculaceae	*Tricolporopollenites* sp. 1	pollen		Thiele-Pfeiffer 1988; Bouchal et al. 2024	Ranunculaceae gen. indet. of Bouchal et al. (2024)
Viridiplantae: Angiosperms: Buxales					
Buxaceae	?*Buxus* sp.	wood		Wilde & Süß 2001	
Viridiplantae: Angiosperms: Proteales					
Platanaceae, *Platanus*	*Platanipollis ipelensis*	pollen	(Pacltová, 1966) Grabowska in Ziembińska-Tworzydło et al. 1994	Bouchal et al. 2024	
Platanaceae	cf. *Platanus neptuni* morphoforma *fraxinifolia*	leaf	(Johnson & Gilmore, 1921) Walther, 1985	Wilde 1989; Kvaček and Manchester 2004	
“Proteaceae”	*“Banksia haeringiana”*	leaf	Ettingshausen, 1851	Engelhardt 1922	The presence of Proteaceae in the European Cenozoic floras has repeatedly been invalidated. A revision of the taxa at Messel remains to be done.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
"Proteaceae"	*"Banksia dillenioides"*	leaf	Ettingshausen, 1851	Engelhardt 1922	The presence of Proteaceae in the European Cenozoic floras has repeatedly been invalidated. A revision of the taxa at Messel remains to be done.
"Proteaceae"	*"Persoonia daphnes"*	leaf	Ettingshausen, 1851	Engelhardt 1922	The presence of Proteaceae in the European Cenozoic floras has repeatedly been invalidated. A revision of the taxa at Messel remains to be done.
"Proteaceae"	*"Persoonia laurina"*	leaf	Heer, 1856	Engelhardt 1922	The presence of Proteaceae in the European Cenozoic floras has repeatedly been invalidated. A revision of the taxa at Messel remains to be done.
Sabiaceae	*Meliosma* sp.	fruit		Collinson et al. 2012	
Viridiplantae: Angiosperms: Saxifragales					
Altingiaceae	*Steinhauera subglobosa*	fruiting head	Collinson et al. 2012	Wilde 2018	
Cercidiphyllaceae	*Cercidiphyllum* sp.	leaf		Wilde 1989	
Hamamelidaceae	cf. *Chunia* sp.	pollen		Bouchal et al. 2024	
Hamamelidaceae	*Tricolpopollenites vegetus*	pollen	(R. Potonié, 1934) Krutzsch, 1959	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	cf. *Fortunearia* sp. of Bouchal et al. 2024
Hamamelidaceae	*Tricolpopollenites vegetus*	pollen	(R. Potonié, 1934) Krutzsch, 1959	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. 2024	*Corylopsis* vel. *Maingaya* sp. of Bouchal et al. (2024)
Hamamelidaceae	Taxon indet.	pollen		Bouchal et al. 2024	Hamemelidaceae gen. indet. sp. of Bouchal et al. (2024)
Hamamelidaceae	*Hamamelites fothergilloides*	leaf	Saporta, 1865	Engelhardt 1922	
Hamamelidaceae	*Mytilaria boglei*	infructescence	Collinson et al. 2012		
Hamamelidaceae	*Corylopsis maii*	infructescence	Collinson et al. 2012		
Hamamelidaceae	*Corylopsis waltheri*	seed	Collinson et al. 2012		
Viridiplantae: Angiosperms: Vitales					
Vitaceae	*Parthenopollenites marcodurensis*	pollen	(Thomson & Pflug, 1953) Traverse, 1994	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011	= *Tricolporopollenites marcodurensis*; *Parthenocissus* sp. 1 of Bouchal et al. (2024)
Vitaceae	*Parthenocissus* sp. 2	pollen		Bouchal et al. 2024	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Vitaceae	*Parthenocissus* sp. 1	pollen		Wedmann et al. 2021b; Bouchal et al. 2024	Bouchal (pers. comm. 2024) states that *Parthenocissus* sp. 1 of Bouchal et al. (2024) is identical to *Parthenocissus* sp. of Wedmann et al. (2021b)
Vitaceae, *Vitis*	*Vitispollenites tener*	pollen	Thiele-Pfeiffer, 1980	Thiele-Pfeiffer 1988	
Vitaceae	Vitaceae sp. (cf. *Ampelopsis*)	leaf		Wilde 1989, 2018	
Vitaceae	*Vitis messelensis*	seed	Collinson et al. 2012		
Vitaceae	*Parthenocissus britannica*	seed	(Heer, 1862) Chandler, 1957	Collinson et al. 2012	
Vitaceae	*Cayratia jungii*	seed	(Gregor, 1957) Chen & Manchester, 2011	Collinson et al. 2012	
Vitaceae	*Palaeovitis* sp.	seed		Collinson et al. 2012	
Vitaceae	cf. *Ampelopsis* sp.	seed		Collinson et al. 2012	
Vitaceae	*Crassivitisemen wildei*	fruit	(Chen & Manchester, 2007) Collinson et al. 2012		
Vitaceae	unnamed taxon	seed		Collinson et al. 2012	
Viridiplantae: Angiosperms: Oxalidales					
Cunoniaceae	*Callicoma* (?) *microphylla*	leaf	Ettingshausen, 1869	Engelhardt 1922	
Cunoniaceae	*Ceratopetalum haeringianum*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Cunoniaceae	*Ceratopetalum myricinum*	leaf	de la Harpe in Heer, 1859	Engelhardt 1922	
Cunoniaceae	*Ceratopetalum* sp.	leaf		Engelhardt 1922	
Cunoniaceae	*Cunonia formosa*	leaf	Friedrich, 1883	Engelhardt 1922	
Elaeocarpaceae	*Sloanea messelensis*	fruit	Collinson et al. 2012	Wilde 2018	
Elaeocarpaceae	*Sloanea peolai*	leaf	(Principi, 1916) Hably et al. 2007	Engelhardt 1922	Originally described as *Elaeodendron degener* by Engelhardt (1922)
Viridiplantae: Angiosperms: Celastrales					
Celastraceae	*Tricolporopollenites crassiexinus*	pollen	Krutzsch & Vanhoorne, 1977	Lenz et al. 2023	
Celastraceae	*Elaeodendron obovatifolium*	leaf	Engelhardt, 1922		
Celastraceae	*Elaeodendron dryadum*	leaf	Ettingshausen, 1869	Engelhardt 1922	
Celastraceae	*Evonymus heerii*	leaf	Ettingshausen, 1877	Engelhardt 1922	
Viridiplantae: Angiosperms: Malpighiales					
Euphorbiaceae	*Tricolporopollenites splendidus*	pollen	Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1988; Bouchal et al. In prep.	Euphorbiaceae gen. indet. sp. 1 of Bouchal et al. In prep.
Euphorbiaceae	Euphorbiaceae gen. indet. sp. 2	pollen		Bouchal et al. In prep.	
Euphorbiaceae	*Tricolporopollenites* cf. *quercioides*	pollen		Thiele-Pfeiffer 1988; Lenz et al. 2011; Bouchal et al. In prep.	In the absence of SEM, it is not fully clear that the taxon of Thiele-Pfeiffer is the same as that of Bouchal et al. In prep.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Euphorbiaceae	*Tricolporopollenites* cf. *fraudulentes*	pollen		Thiele-Pfeiffer 1988; Bouchal et al. In prep.	In the absence of SEM, it is not fully clear that the taxon of Thiele-Pfeiffer is the same as that of Bouchal et al. In prep.
Euphorbiaceae	Euphorbiaceae gen. indet. sp. 5	pollen		Bouchal et al. In prep.	
Euphorbiaceae	Euphorbiaceae gen. indet. sp. 6	pollen		Bouchal et al. In prep.	
Euphorbiaceae	Euphorbiaceae gen. indet. sp. 7	pollen		Bouchal et al. In prep.	
Euphorbiaceae	Euphorbiaceae gen. indet. sp. 8	pollen		Bouchal et al. In prep.	
Euphorbiaceae	*Euphorbiotheca gothii*	fruit	Collinson et al. 2012	Wilde 2018	
Malpighiaceae	*Banisteria* (*Heteropteris*) *tertiaria*	leaf	Engelhardt, 1922		
Malpighiaceae	*Malpighiastrum coriaceum*	leaf	Unger, 1850	Engelhardt 1922	
Malpighiaceae	*Malpighiastrum procrustrae*	leaf	Unger, 1850	Engelhardt 1922	
Malpighiaceae	*Malpighiastrum rotundifolium*	leaf	Ettingshausen, 1885	Engelhardt 1922	
Malpighiaceae	*Tetrapteris* (sic) *minuta*	leaf	Ettingshausen, 1888	Engelhardt 1922	
Malpighiaceae	*Tetrapteris* (sic) *messelensis*	leaf	Engelhardt, 1922		
Salicaceae, *Salix*	*Tricolpopollenites retiformis*	pollen	Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Salix* sp. 1 of Bouchal et al. In prep.
Salicaceae, *Salix*	Taxon indet.	pollen		Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Salix* sp. 2 of Bouchal et al. In prep.
Salicaceae	*Populus latior*	leaf	Braun, 1836	Engelhardt 1922	
Salicaceae	*Samyda europaea*	leaf	Unger, 1866	Engelhardt 1922	
Viridiplantae: Angiosperms: Cucurbitales					
Coriariaceae	*Coriaria longaeva*	leaf	Saporta, 1866	Engelhardt 1922	
Viridiplantae: Angiosperms: Fabales					
Fabaceae	cf. *Erythrina* sp.	pollen		Bouchal et al. In prep.	
Fabaceae	*Acacia sotzkiana*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Bauhinia europaea*	leaf	Engelhardt, 1922		
Fabaceae	*Caesalpinia mediocrifoliola*	leaf/leaflet	Engelhardt, 1922		
Fabaceae	*Cassia berenices*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Cassia hyperborea*	leaf/leaflet	(Unger) Heer, 1859	Engelhardt 1922	
Fabaceae	*Cassia fischeri*	leaf/leaflet	Heer, 1859	Engelhardt 1922	
Fabaceae	*Cassia phaseolites*	leaf/leaflet	Unger, 1851	Engelhardt 1922	
Fabaceae	*Cassia feroniae*	leaf/leaflet	Ettingshausen, 1853	Engelhardt 1922	
Fabaceae	*Cassia zephyri*	leaf/leaflet	Ettingshausen, 1853	Engelhardt 1922	
Fabaceae	*Cassia lignitum*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Cassia pseudoglandulosa*	leaf/leaflet	Ettingshausen, 1853	Engelhardt 1922	
Fabaceae	*Cassia ambigua*	leaf/leaflet	Unger, 1850	Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Fabaceae	*Cercis parvifolia*	leaf	Engelhardt, 1922		
Fabaceae	*Copaifera tenuifolia*	leaf/leaflet	Engelhardt, 1922		
Fabaceae	*Dalbergia haeringiana*	leaf/leaflet	Ettingshausen, 1853	Engelhardt 1922	
Fabaceae	*Dalbergia primaeva*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Dalbergia nostratum*	leaf/leaflet	(Kováts, 1856) Heer, 1859	Engelhardt 1922	
Fabaceae	*Dalbergia bella*	leaf/leaflet	Heer, 1859	Engelhardt 1922	
Fabaceae	*Dolichos* (?) *pristina*	leaf	Engelhardt, 1922		
Fabaceae	*Erythrina ungeri*	leaf	Ettingshausen, 1876	Engelhardt 1922	*E. phaseolites* synonymized with *Byttneriopsis daphnogenes* by Kvaček & Wilde (2010)
Fabaceae	*Erythrina daphnoides*	leaf	Unger, 1850	Engelhardt 1922	
Fabaceae	*Hardenbergia macrophylloides*	leaf	Engelhardt, 1922		
Fabaceae	*Leguminosites cassioides*	leaf/leaflet	Engelhardt, 1922		
Fabaceae	*Machaerium muticoides*	leaf/leaflet	Engelhardt, 1922		
Fabaceae	*Palaeolobium sotzkianum*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Palaeolobium radobojense*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Palaeolobium heterophyllum*	leaf/leaflet	Unger, 1850	Engelhardt 1922	
Fabaceae	*Palaeolobium haeringianum*	leaf	Unger, 1851	Engelhardt 1922	
Fabaceae	*Piscidia erythrophyllum*	leaf	Unger, 1864	Engelhardt 1922	
Fabaceae	*Sophora europaea*	leaf	Unger, 1850	Engelhardt 1922	
Fabaceae	Leguminosae sp. 1	leaf/leaflet		Wilde 1989	
Fabaceae	Leguminosae sp. 2	leaf/leaflet		Wilde 1989	
Fabaceae	Leguminosae sp. 3	leaf/leaflet		Wilde 1989	
Fabaceae	Leguminosae sp. 4	leaf/leaflet		Wilde 1989	
Fabaceae	Leguminosae sp. 5	leaf/leaflet		Wilde 1989	
Fabaceae	*Mimosites spiegeli*	fruit	Engelhardt, 1922	Collinson et al. 2012; Wilde 2018	
Fabaceae	*"Gleditschia* (sic) *wesseli"*	fruit	Weber, 1852	Engelhardt 1922; Collinson et al. 2012	Collinson et al. (2012) suggest this might be *Leguminocarpon* sp. 1 or *Mimosites spiegeli*; the specimen described and illustrated by Engelhardt cannot be located, and this record should therefore be treated with the caution
Fabaceae	*Leguminocarpon herendeenii*	fruit	Collinson et al. 2012	Wilde 2018	
Fabaceae	*Leguminocarpon* sp. 1	fruit		Collinson et al. 2012	
Fabaceae	*Leguminocarpon* sp. 2	fruit		Collinson et al. 2012	
Fabaceae	*Mimosites spiegeli*	fruit	Engelhardt, 1922		
Loranthaceae	*Viscophyllum* cf. *septemnervium*	leaf	Rüffle, Müller-Stoll & Litke, 1976	Wilde 1989	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Loranthaceae	*Viscophyllum pinnatum*	leaf	Rüffle, Müller-Stoll & Litke, 1976	Wilde 1989	
Viridiplantae: Angiosperms: Rosales					
Cannabaceae, *Celtis*	*Celtipollenites intrastructurus*	pollen	(Krutzsch & Vanhoorne, 1977) Thiele-Pfeiffer, 1980	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Celtis* vel *Pteroceltis* sp. 1 of Bouchal et al. In prep.
Cannabaceae, *Celtis*	*Celtipollenites laevigatus*	pollen	Thiele-Pfeiffer, 1988	Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Celtis* vel *Pteroceltis* sp. 2 of Bouchal et al. In prep.
Cannabaceae	*Aphananthe* cf. *tenuicostata*	fruit		Collinson et al. 2012	
Elaeagnaceae	*Elaeagnus acuminata*	leaf	Weber, 1852	Engelhardt 1922	
Moraceae	Gen. et sp. indet.	pollen		Bouchal et al. In prep.	
Moraceae	*Ficus apocynoides*	leaf	Ettingshausen, 1858	Engelhardt 1922	Many *Ficus* spp. of Engelhardt (1922) synonymized with *Byttneriopsis daphnogenes* by Kvaček & Wilde (2010)
Moraceae	*Ficus atlantidis*	leaf	Ettingshausen, 1866	Engelhardt 1922	
Moraceae	*Ficus banisteriaefolia*	leaf	Ettingshausen, 1885	Engelhardt 1922	
Moraceae	*Ficus dalmatica*	leaf	Ettingshausen, 1855	Engelhardt 1922	
Moraceae	*Ficus giebeli*	leaf	Heer, 1861	Engelhardt 1922	
Moraceae	*Ficus jynx*	leaf	Unger, 1850	Engelhardt 1922	
Moraceae	*Ficus laneolata*	leaf	Heer, 1856	Engelhardt 1922	
Moraceae	*Ficus lanceolato-acuminata*	leaf	Ettingshausen, 1872	Engelhardt 1922	
Moraceae	*Ficus laurifolioides*	leaf	Engelhardt, 1922		
Moraceae	*Ficus lauroides*	leaf	Engelhardt, 1922		
Moraceae	*Ficus multinervis*	leaf	Heer, 1856	Engelhardt 1922	
Moraceae	*Ficus orbicularis*	leaf	Engelhardt, 1922		
Moraceae	*Ficus penninervia*	leaf	(Unger, 1850) Ettingshausen, 1870	Engelhardt 1922	
Moraceae	*Ficus planicostata*	leaf	Lesquereux, 1872	Engelhardt 1922	
Moraceae	*Protoficus insignis*	leaf	Saporta, 1868	Engelhardt 1922	
Rhamnaceae	*Paliurus sismondanus*	leaf	Heer, 1859	Engelhardt 1922	
Rhamnaceae	*Pomaderris acuminata*	leaf	Ettingshausen, 1869	Engelhardt 1922	
Rhamnaceae	*Pomaderris lanigeroides*	leaf	Engelhardt, 1922		
Rhamnaceae	*Pomaderris grandifolia*	leaf	Engelhardt, 1922		
Rhamnaceae	*Rhamnus rossmässleri*	leaf	Unger, 1859	Engelhardt 1922	
Rhamnaceae	*Rhamnus aizoon*	leaf	Unger, 1847	Engelhardt 1922	
Rhamnaceae	*Rhamnus acuminatifolius*	leaf	Weber, 1852	Engelhardt 1922	
Rhamnaceae	*Rhamnus gaudini*	leaf	Heer, 1859	Engelhardt 1922	
Rhamnaceae	*Rhamnus decheni*	leaf	Weber, 1852	Engelhardt 1922	
Rhamnaceae	*Rhamnus eridani*	leaf	Unger, 1850	Engelhardt 1922	
Rhamnaceae	*Zizyphus tiliaefolius* (*sic*, for *Ziziphus tiliifolia*)	leaf	(Unger, 1847) Heer, 1859	Engelhardt 1922	
Rhamnaceae	*Zizyphus ovatus* (*sic*, for *Ziziphus ovata*)	leaf	Weber, 1852	Engelhardt 1922	
Rhamnaceae	*Berchemia multinervis*	leaf	Braun, 1836	Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Rhamnaceae	*Berchemia mellerae*	fruit	Collinson et al. 2012		
Rosaceae	*Tricolporopollenites solé de portai*	pollen	Kedves, 1965	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Rosaceae gen. indet. sp. of Bouchal et al. In prep.; see also Anacardiaceae and Sapindaceae
Rosaceae	*Amygdalus pereger*	leaf	Unger, 1850	Engelhardt 1922	
Rosaceae	Rosaceae sp.	leaf		Wilde 1989	
Ulmaceae?	*Subtriporopollenites constans microrugulatus*	pollen	Pflug, 1953a; Kedves, 1970	Thiele-Pfeiffer 1988	
Ulmaceae	*Polyporopollenites eoulmoides*	pollen	Krutzsch & Vanhoorne, 1977	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Cedrelospermum* sp. of Bouchal et al. In prep.
Ulmaceae, *Ulmus*	*Polyporopollenites verrucatus*	pollen	Thiele-Pfeiffer, 1980	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Ulmus* sp. of Bouchal et al. In prep.
Ulmaceae, *Zelkova*	*Ulmipollenites undulosus*	pollen	Wolff, 1934 ex R. Potonié, 1960	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	= *Polyporopollenites undulosus*; *Zelkova* sp. of Bouchal et al. In prep.
Ulmaceae	*Tremophyllum* sp.	leaf		Wilde and Manchester 2003	
Ulmaceae	*Cedrelospermum leptospermum*	fruit	Wilde and Manchester, 2003	Collinson et al. 2012; Wilde 2018	
Ulmaceae	*Ulmus longifolia*	leaf	Unger, 1847	Engelhardt 1922	
Ulmaceae	*Ulmus antiquissima*	leaf	Saporta, 1868	Engelhardt 1922	
Ulmaceae	Mophotypes 1	leaf		Wilde 1989	
Ulmaceae	Mophotypes 2	leaf		Wilde 1989	
Urticaceae	*Cecropoia europaea*	leaf	Ettingshausen, 1866		
Incertae sedis	*Subtriporopollenites subporatus subporatus*	pollen	Krutzsch & Vanhoorne, 1977	Bouchal et al. In prep.	
Viridiplantae: Angiosperms: Fagales					
Betulaceae, *Alnus*	*Polyvestibulopollenites verus*	pollen	(R. Potonié, 1931a) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988	
Betulaceae, Coryloideae	*Triporopollenites rhenanus*	pollen	(Thomson in R. Potonié, Thomson & Thiergart, 1950) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Coryloideae gen. indet. of Bouchal et al. In prep.
Betulaceae	*Carpinus suessionensis*	leaf	Watelet, 1866	Engelhardt 1922	
"Casuarinaceae"	*"Casuarina haidingeri"*	branch	Ettingshausen, 1853	Engelhardt 1922	The presence of Casuarinaceae in the European Cenozoic floras has repeatedly been invalidated. A revision of the taxon at Messel remains to be done.
Fagaceae, Castanoideae	*Tricolporopollenites cingulum fusus*	pollen	(R. Potonié, 1931b) Thomson & Pflug, 1953; (R. Potonié, 1931a) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Castanoideae gen. indet. sp. 1 of Bouchal et al. In prep.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Fagaceae, Castanoideae	*Tricolporopollenites cingulum pusillus*	pollen	(R. Potonié, 1931b) Thomson & Pflug, 1953; (R. Potonié, 1934) Thomson & Pflug, 1953	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Castanoideae gen. indet. sp. 1 of Bouchal et al. In prep.
Fagaceae, Castanoideae	*Tricolporopollenites cingulum oviformis*	pollen	(R. Potonié, 1931b) Thomson & Pflug, 1953; (R. Potonié, 1931a) Thomson & Pflug, 1953	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011	
Fagaceae, Castanoideae	*Tricolpopollenites liblarensis liblarensis*	pollen	(Thomson in R. Potonié, Thomson & Thiergart, 1950) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Castanoideae gen. indet. sp. 2 of Bouchal et al. In prep.
Fagaceae, Castanoideae	*Tricolpopollenites liblarensis fallax*	pollen	(Thomson in R. Potonié, Thomson & Thiergart, 1950) Thomson & Pflug, 1953; (R. Potonié, 1934) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Castanoideae gen. indet. sp. 2 of Bouchal et al. In prep.
Fagaceae	*Tricolpopollenites microhenrici*	pollen	(R. Potonié, 1934) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988	
Fagaceae	*Tricolpopollenites quisqualis*	pollen	(R. Potonié, 1934) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2011; Bouchal et al. 2024	*Trigonobalanopsis* sp. of Bouchal et al. 2024
Fagaceae, *Quercus?*	*Tricolpopollenites asper*	pollen	Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Fagaceae	*Castanea atavia*	leaf	Unger, 1850	Engelhardt 1922	
Fagaceae	*Castanopsis sagoriana*	leaf	Ettingshausen, 1868	Engelhardt 1922	
Fagaceae	*Dryophyllum dewalquei*	leaf	Saporta et Marion, 1873	Engelhardt 1922	
Fagaceae	*Dryophyllum palaeocastanea*	leaf	Saporta, 1868	Engelhardt 1922	
Fagaceae	*Dryophyllum curticellense*	leaf	(Watelet, 1866) Saporta et Marion, 1873	Engelhardt 1922	
Fagaceae	*Dryophyllum* sp.	leaf		Engelhardt 1922	
Fagaceae	*Quercus nereifolia*	leaf	(Braun, 1845) Braun in Unger, 1850	Engelhardt 1922	
Fagaceae	*Quercus chlorophylla*	leaf	Unger, 1850	Engelhardt 1922	
Fagaceae	*Quercus myrtilloides*	leaf	Unger, 1850	Engelhardt 1922	
Fagaceae	*Quercus lineari-lanceolata*	leaf	Engelhardt, 1922		
Fagaceae	*Quercus lyelli*	leaf	Heer, 1856	Engelhardt 1922	
Fagaceae	*Quercus valdensis*	leaf	Heer, 1856	Engelhardt 1922	
Fagaceae	*Quercus lonchitis*	leaf	Unger, 1850	Engelhardt 1922	
Fagaceae	*Quercus axonensis*	leaf	Watelet, 1866	Engelhardt 1922	
Fagaceae	*Quercus sprengeli*	leaf	Heer, 1869	Engelhardt 1922	
Fagaceae	*Quercus gmelini*	leaf	Unger, 1847	Engelhardt 1922	
Fagaceae	*Cruciptera schaarschmidtii*	fruit	Manchester, Collinson & Goth, 1994	Collinson et al. 2012; Wilde 2018	
Fagaceae	*Hooleya* sp.	fruit		Collinson et al. 2012	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Fagaceae	"*Palaeocarya* sp."	fruit		Collinson et al. 2012; Wilde 2018	
Juglandaceae, *Carya*	*Caryapollenites triangulus*	pollen	(Pflug, 1953a) Krutzsch, 1961	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Juglandaceae, *Carya*	*Caryapollenites circulus*	pollen	(Pflug, 1953a) Krutzsch, 1961	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Carya* sp. of Bouchal et al. In prep.
Juglandaceae, Engelhardioideae	*Momipites punctatus*	pollen	(R. Potonié, 1931a) Nagy, 1969	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Engelhardioideae gen. indet. sp. 2 of Bouchal et al. In prep.
Juglandaceae, Engelhardioideae	*Momipites quietus*	pollen	(R. Potonié, 1931d) Nichols, 1973	Thomson & Pflug 1953; Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Engelhardioideae gen. indet. sp. 1 of Bouchal et al. In prep.
Juglandaceae, *Engelhardia*?	*Labraferoidaepollenites menatensis*	pollen	Kedves, 1982	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Juglandaceae	*Engelhardia brongniartii*	fruit	Saporta, 1865	Engelhardt 1922; Collinson et al. 2012: 33	
Juglandaceae, *Platycarya*	*Platycaryapollenites anticyclus*	pollen	Krutzsch & Vanhoorne, 1977	Lenz et al. 2023; Bouchal et al. In prep.	*Platycarya* sp. 3 of Bouchal et al. In prep.
Juglandaceae, *Platycarya*	*Platycaryapollenites miocaenicus*	pollen	Nagy, 1969	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Platycarya* sp. 1 of Bouchal et al. In prep.
Juglandaceae, *Platycarya*	*Platycaryapollenites platycaryoides*	pollen	(Roche, 1969) Kedves, 1982	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Platycarya* sp. 2 of Bouchal et al. In prep.
Juglandaceae, *Platycarya*	*Platcacaryapollenites semicyclus*	pollen	(Krutzsch & Vanhoorne, 1977) Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Juglandaceae, *Pterocarya*	*Pterocaryapollenites stellatus*	pollen	(R. Potonié, 1931b) Thiergart, 1937	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	*Platycarya* sp. of Bouchal et al. In prep.
Juglandaceae	*Plicatopollis plicatus*	pollen	(R. Potonié, 1934) Krutzsch, 1962b	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Juglandaceae gen. indet. sp. 3 of Bouchal et al. In prep.
Juglandaceae	*Plicatopollis hungaricus*	pollen	Kedves, 1974	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Juglandaceae gen. indet. sp. 4 of Bouchal et al. In prep.
Juglandaceae	*Plicatopollis lunatus*	pollen	Kedves, 1974	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Juglandaceae gen. indet. sp. 1 of Bouchal et al. In prep.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Juglandaceae	*Plicatopollis tetraporus*	pollen	Nickel, 1996	Bouchal et al. In prep.	Juglandaceae gen. indet. sp. 2 of Bouchal et al. In prep.
Juglandaceae	*Plicatopollis* sp. 1	pollen		Thiele-Pfeiffer 1988	
Juglandaceae	*Subtriporopollenites anulatus nanus*	pollen	Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Juglandaceae gen. indet. sp. 5 of Bouchal et al. In prep.
Juglandaceae	*Subtriporopollenites constans*	pollen	Pflug, 1953a	Krutzsch & Vanhoorne, 1977; Bouchal et al. In prep.	cf. Juglandaceae gen. indet. sp. of Bouchal et al. In prep.
Juglandaceae	*Juglans acuminata*	leaf	Braun, 1845	Engelhardt 1922	
Juglandaceae	*Juglans bilinica*	leaf	Unger, 1850	Engelhardt 1922	
Juglandaceae	*Juglans vetusta*	leaf	Heer, 1859	Engelhardt 1922	
Juglandaceae	*Juglans ungeri*	leaf	Heer, 1859	Engelhardt 1922	
Juglandaceae	*Pterocarya denticulata*	leaf	(Weber, 1852) Heer, 1859	Engelhardt 1922	
Juglandaceae	Mophotype 1	leaf		Wilde 1989	
Juglandaceae	Mophotype 2	leaf		Wilde 1989	
Juglandaceae	Mophotype 3	leaf		Wilde 1989	
Juglandaceae	Mophotype 4	leaf		Wilde 1989	
Juglandaceae	*"Carya" ventricosa*	fruit	(Sternberg 1825) Unger, 1850	Engelhardt 1922; Collinson et al. 2012: 32	
Juglandaceae	*"Carya" hickoryaeformis*	fruit	Engelhardt, 1922	Collinson et al. 2012: 32	
Myricaceae, *Myrica*	*Myricipites rurensis*	pollen	(Thomson & Pflug, 1953) Nagy, 1969	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	= *Triatriopollenites rurensis*
Myricaceae, *Myrica*	*Myricpites bituitus*	pollen	(R. Potonié, 1931d) Nagy, 1969	Lenz et al. 2011	= *Triatriopollenites bituitus*
Myricaceae	*Myricipites robustus*	pollen	(Pflug, 1953a) Casas-Gallego & Barrón, 2020	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	= *Triporopollenites robustus*
Myricaceae	*Triporopollenites megagranifer*	pollen	(R. Potonié, 1931a) Thomson & Pflug, 1953	Lenz et al. 2023	
Myricaceae	*Nudopollis terminalis*	pollen	(Thomson & Pflug, 1953) Pflug, 1953b	Thiele-Pfeiffer 1988; Lenz et al. 2007a; Bouchal et al. In prep.	Normapolles element; Myricaceae gen. indet. sp. 1 of Bouchal et al. In prep.
Myricaceae	*Plicapollis pseudoexcelsus turgidus*	pollen	(Krutzsch, 1957) Krutzsch, 1961; Pflug, 1953a	Lenz et al. 2023	Normapolles element; see cf. *Myricamentum* type 2 of Bouchal et al. In prep.
Myricaceae	*Plicapollis pseudoexcelsus semiturgidus*	pollen	(Krutzsch, 1957) Krutzsch, 1961; Pflug, 1953a	Lenz et al. 2023	Normapolles element; see cf. *Myricamentum* type 2 of Bouchal et al. In prep.
Myricaceae	*Plicapollis pseudoexcelsus microturgidus*	pollen	(Krutzsch, 1957) Krutzsch, 1961; Pflug, 1953a	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	Normapolles element; see cf. *Myricamentum* type 2 of Bouchal et al. In prep.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Myricaceae	*Triatriopollenites excelsus*	pollen	(R. Potonié, 1931c) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	cf. *Myricamentum* type 1 of Bouchal et al. In prep.
Myricaceae	*Triatriopollenites excelsus minor*	pollen	(R. Potonié, 1931c) Thomson & Pflug, 1953; Pflug, 1953a	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Myricaceae gen. indet. sp. 2 of Bouchal et al. In prep.
Myricaceae	"*Comptonia*" *difformis*	leaf	(Sternberg 1825) Berry, 1906	Wilde & Frankenhäuser 1999	
Myricaceae	*Myrica hakeaefolia* (*sic*, for *Myrica hakeifolia*)	leaf	(Unger, 1850) Brongniart, 1861	Engelhardt 1922	
Myricaceae	*Myrica lignitum*	leaf	(Unger, 1857) Saporta, 1865	Engelhardt 1922	
Myricaceae	*Myrica laevigata*	leaf	(Heer, 1856) Brongniart, 1861	Engelhardt 1922	
Myricaceae	*Myrica banksiaefolia* (*sic*, for *Myrica banksiifolia*)	leaf	Unger, 1845	Engelhardt 1922	
Myricaceae	*Myrica salicina*	leaf	Unger, 1850	Engelhardt 1922	
Myricaceae	Myricaceae sp.	leaf		Wilde 1989	
Incertae sedis	*Labrapollis labraferus*	pollen	(R. Potonié, 1931c) Krutzsch, 1968a	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Fagales fam. indet. sp. 1 of Bouchal et al. In prep.
Incertae sedis	Taxon indet.	pollen		Bouchal et al. In prep.	Fagales fam. indet. sp. 2 of Bouchal et al. In prep.
Viridiplantae: Angiosperms: Myrtales					
Combretaceae	*Getonia macroptera* (?)	leaf	Unger, 1850	Engelhardt 1922	
Combretaceae	*Terminalia radobojensis*	leaf	Heer, 1859	Engelhardt 1922	
Lythraceae?	*Tricolporopollenites* sp. 12	pollen		Thiele-Pfeiffer 1988	
Lythraceae, *Rotala, Ammania*	*Lythraceaepollenites minimus*	pollen	Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1988	
Lythraceae, *Rotala, Lawsonia, Woodfordia*	*Lythraceaepollenites* sp.	pollen		Thiele-Pfeiffer 1988	
Lythraceae	Lythraceae gen. indet. sp. 1	pollen		Bouchal et al. In prep.	
Lythraceae	Lythraceae gen. indet. sp. 2	pollen		Bouchal et al. In prep.	
Lythraceae	*Decodon* sp.	pollen		Wedmann et al. 2021b	
Lythraceae	cf. *Decodon*	infructescence		Collinson et al. 2012	
Melastomataceae	*Melastoma tertiarium*	leaf	Engelhardt, 1922		
Myrtaceae	*Acmena floribundoides*	leaf	Engelhardt, 1922		
Myrtaceae	*Callistemon lanceolatum*	leaf	Engelhardt, 1922		
Myrtaceae	*Callistemophyllum melaleucaeforme*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Myrtaceae	*Eucalyptus oceanica*	leaf	Unger, 1850	Engelhardt 1922	
Myrtaceae	*Eugenia haeringiana*	leaf	Unger, 1850	Engelhardt 1922	
Myrtaceae	*Eugenia aizoon*	leaf	Unger, 1850	Engelhardt 1922	
Myrtaceae	*Eugenia apollinis*	leaf	Unger, 1850	Engelhardt 1922	
Myrtaceae	*Eugenia heerii*	leaf	Engelhardt, 1922		

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Myrtaceae	*Metrosideros calophyllum*	leaf	Ettingshausen,1851	Engelhardt 1922	
Myrtaceae	*Myrtophyllum incertum*	leaf	Engelhardt, 1922		
Myrtaceae	*Myrtophyllum myraciaefolium*	leaf	Engelhardt, 1922		
Myrtaceae	*Myrtus syncarpifolia*	leaf	Friedrich, 1883	Engelhardt 1922	
Myrtaceae	*Rhodomyrtophyllum reticulosum*	leaf	(Rossmaessler, 1840) Knobloch & Kvaček in Knobloch et al. 1996	Wilde 1989; Glinka & Walther, 2003	
Myrtaceae	*Tristania laurinoides*	leaf	Engelhardt, 1922		
Myrtaceae	*Tristania tertiaria*	leaf	Engelhardt, 1922		"n. sp." not specifically invoked in text but in caption to pl. XXXVI fig. 10
Oenotheraceae (Onagraceae), *Oenothera?*, *Epilobium*?	*Corsinipollenites oculus-noctis*	pollen	(Thiergart, 1940) Nakoman, 1965	Lenz et al. 2023	
Viridiplantae: Angiosperms: Crossosomatales					
Staphyleaceae	*Celastrus lanceolatus*	leaf	Friedrich, 1883	Engelhardt 1922	
Staphyleaceae	*Celastrus elaenus*	leaf	Unger, 1850	Engelhardt 1922	
Staphyleaceae	*Celastrus oxyphyllus*	leaf	Unger, 1850	Engelhardt 1922	
Staphyleaceae	*Celastrus illicinoides*	leaf	Engelhardt, 1922		
Viridiplantae: Angiosperms: Sapindales					
Anacardiaceae	*Tricolporopollenites solé de portai*	pollen	Kedves, 1965	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Anacardiaceae gen. indet. sp. 1 of Bouchal et al. In prep.; see also Rosaceae and Sapindaceae
Anacardiaceae	Anacardiaceae gen. indet. sp. 2	pollen		Bouchal et al. In prep.	
Anacardiaceae	*Tricolporopollenites solé de portai*	pollen	Kedves, 1965	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Anacardiaceae gen. indet. sp. 3 of Bouchal et al. In prep.; see also Rosaceae and Sapindaceae
Anacardiaceae	Anacardiaceae gen. indet. sp. 4	pollen		Bouchal et al. In prep.	
Anacardiaceae	*Anaphrenium europaeum*	leaf	Engelhardt, 1922		
Anacardiaceae	*Anaphrenium lanceolatum*	leaf	Engelhardt, 1922		
Anacardiaceae	*Mangifera tertiaria*	leaf	Engelhardt, 1922		
Anacardiaceae	*Rhus saportana*	leaf	Pilar, 1883	Engelhardt 1922	
Anacardiaceae	*Rhus ternata*	leaf	Engelhardt, 1922		
Anacardiaceae	*Rhus juglandogene*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Anacardiaceae	*Rhus meriani*	leaf	Heer, 1859	Engelhardt 1922	
Anacardiaceae	*Rhus longifolia*	leaf	Engelhardt, 1922		
Anacardiaceae	*Lannea hessenensis*	fruit	Collinson et al. 2012		
Anacardiaceae	*Pleiogynium mitchellii*	fruit	Collinson et al. 2012		
Anacardiaceae	*Pentoperculum minimus*	fruit	(Reid & Chandler, 1933) Manchester, 1994	Collinson et al. 2012	

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Anacardiaceae	*Anacardium germanicum*	fruit	Manchester, Wilde & Collinson, 2007	Collinson et al. 2012; Wilde 2018	
Burseraceae	*Tricolporopollenites vancampoae*	pollen	Kedves, 1964	Thiele-Pfeiffer 1988; Bouchal et al. In prep.	cf. *Garuga* sp. of Bouchal et al. In prep.
Burseraceae	*Bursericarpum* sp.	fruit		Collinson et al. 2012	
Burseraceae	*Canarium* sp.	fruit		Collinson et al. 2012	
Rutaceae	Rutaceae gen. indet. sp. 1	pollen		Bouchal et al. In prep.	
Rutaceae?	*Tricolporopollenites* sp. 7	pollen		Thiele-Pfeiffer 1988	
Rutaceae?	*Tricolporopollenites* sp. 10	pollen		Thiele-Pfeiffer 1988	
Rutaceae	*Tricolporopollenites* sp. 11	pollen		Thiele-Pfeiffer 1988	
Rutaceae	*Tricolporopollenites reticingulum*	pollen	Krutzsch & Vanhoorne, 1977	Bouchal et al. In prep.	Rutaceae gen. indet. sp. 3 of Bouchal et al. In prep.
Rutaceae	*Tricolporopollenites* sp. 21	pollen		Bouchal et al. In prep.	Rutaceae gen. indet. sp. 4 of Bouchal et al. In prep.
Rutaceae	*Tricolporopollenites messelensis*	pollen	Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Rutaceae gen. indet. sp. 5 of Bouchal et al. In prep.
Rutaceae	Rutaceae gen. indet. sp. 6	pollen		Bouchal et al. In prep.	
Rutaceae	*Tricolporopollenites microreticingulum*	pollen	Krutzsch & Vanhoorne, 1977	Thiele-Pfeiffer 1988; Bouchal et al. In prep.	Rutaceae gen. indet. sp. 2 aff. *Zanthoxylum* of Bouchal et al. In prep.
Rutaceae	*Zanthoxylon* (sic) *haeringianum*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Rutaceae	*Toddalia ovata*	leaf	Wilde, 1989		
Rutaceae	*Rutaspermum messelense*	seed	Collinson & Gregor, 1988	Collinson et al. 2012	
Rutaceae	*Rutaspermum chandleri*	seed	Collinson & Gregor, 1988	Collinson et al. 2012	
Rutaceae	Rutaceae undetermined A	seed		Collinson et al. 2012	
Rutaceae	Rutaceae undetermined B	seed		Collinson et al. 2012	
Rutaceae	cf. *Toddalia* sp.	seed		Collinson et al. 2012	
Rutaceae? ("probably")	Incertae sedis	flower		Schaarschmidt 1988	
Sapindaceae	*Tricolporopollenites solé de portai*	pollen	Kedves, 1965	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Sapindaceae gen. indet. sp. of Bouchal et al. In prep.; see also Rosaceae and Anacardiaceae
Sapindaceae	*Acer* sp.	leaf		Wilde 1989	
Sapindaceae	*Cupania neptuni*	leaf	Unger, 1850	Engelhardt 1922	
Sapindaceae	*Cupania juglandina*	leaf	Ettingshausen, 1858	Engelhardt 1922	
Sapindaceae	*Dodonaea salicites*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Sapindaceae	*Sapindus falcifolius*	leaf	(Braun in Unger, 1850) Braun in Stizenberger, 1851	Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Sapindaceae	*Sapindus pythii*	leaf	Unger, 1860	Engelhardt 1922	
Sapindaceae	*Sapindus basilicus*	leaf	Unger, 1850	Engelhardt 1922	
Sapindaceae	*Sapindus dubius*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Sapindaceae	*Sapindus cupanoides*	leaf	Ettingshausen, 1869	Engelhardt 1922	
Sapindaceae	*Sapindus heliconius*	leaf	Unger, 1850	Engelhardt 1922	
Sapindaceae	*Sapindus undulatus*	leaf	Braun in Walchner, 1851	Engelhardt 1922	
Sapindaceae	*Sapindus lanceolatus*	leaf	Engelhardt, 1922		
Sapindaceae	*Sapindus firmifolius*	leaf	Engelhardt, 1922		
Simaroubaceae	*Ailanthus dryandroides*	leaf	Heer, 1859	Engelhardt 1922	
Simaroubaceae	*Ailanthus confucii*	fruit	Unger, 1850	Collinson et al. 2012; Wilde 2018	
Incertae sedis	"Sapindales inflorescence"	flower		Schaarschmidt 1984	
Viridiplantae: Angiosperms: Huerteales					
Tapisciaceae	*Tapiscia pusilla*	fruit	(Reid & Chandler, 1933) Mai, 1976	Collinson et al. 2012	
Viridiplantae: Angiosperms: Malvales					
Malvaceae, *Craigia*	*Intratriporopollenites maxoides*	pollen	Krutzsch, 1970b	Thiele-Pfeiffer 1988; Lenz et al. 2023; Bouchal et al. In prep.	*Craigia* sp. of Bouchal et al. In prep.
Malvaceae, *Mortoniodendron*	*Intratriporopollenites minimus*	pollen	Mai, 1961	Thiele-Pfeiffer 1988; Lenz et al. 2023; Bouchal et al. In prep.	*Mortoniodendron* sp. of Bouchal et al. In prep.
Malvaceae, *Tilia*	*Intratriporopollenites microinstructus*	pollen	Krutzsch & Vanhoorne, 1977	Lenz et al. 2023	
Malvaceae, *Tilia*	*Intratriporopollenites microreticulatus*	pollen	Mai, 1961	Lenz et al. 2023	
Malvaceae, Tilioideae	cf. *Intratriporopollenites medioinsculptus*	pollen	Krutzsch & Vanhoorne, 1977	Bouchal et al. In prep.	Tilioideae gen. indet. sp. 1 of Bouchal et al. In prep.
Malvaceae, Tilioideae	Tilioideae gen. indet. sp. 2	pollen		Bouchal et al. In prep.	
Malvaceae, Bombacoideae	*Bombacacidites tilioides*	pollen	Krutzsch, 1970b	Thiele-Pfeiffer 1988; Lenz et al. 2023	
Malvaceae, Bombacoideae	*Bombacacidites reticulatus*	pollen	Krutzsch, 1961	Lenz et al. 2023	
Malvaceae, Bombacoideae	*Bombacacidites eckfeldensis*	pollen	Krutzsch, 2004	Lenz et al. 2007a	
Malvaceae, Bombacoideae	*Bombacacidites messelensis*	pollen	Krutzsch, 2004	Lenz et al. 2007a	
Malvaceae, Bombacoideae	*Bombacacidites* sp. 1	pollen		Thiele-Pfeiffer 1988; Bouchal et al. In prep.	Bombacoideae gen. indet. sp. of Bouchal et al. In prep.
Malvaceae, Bombacoideae	*Bombacacidites* sp. 2	pollen		Thiele-Pfeiffer 1988	
Malvaceae, Malvoideae	*Compositoipollenites rhizophorus burghasungensis*	pollen	(Mürriger & Pflug, 1952) Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Malvoideae gen. indet. sp. 1 of Bouchal et al. In prep.
Malvaceae, Malvoideae	Malvoideae gen. indet. sp. 2	pollen		Bouchal et al. In prep.	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Malvaceae, Malvoideae	*Porocolpopollenites rarobaculatus*	pollen	Thiele-Pfeiffer, 1980	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	Malvoideae gen. indet. sp. 3 of Bouchal et al. In prep.
Malvaceae, Malvoideae	Malvoideae gen. indet. sp. 4	pollen		Bouchal et al. In prep.	
Malvaceae	*Compositoipollenites minimus*	pollen	Krutzsch & Vanhoorne, 1977	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011; Bouchal et al. In prep.	aff. Malvaceae gen. indet. sp. 1 of Bouchal et al. In prep.
Malvaceae	aff. Malvaceae gen. indet. sp. 2	pollen		Bouchal et al. In prep.	
Malvaceae	*Bombax chorisioides*	leaf	Friedrich, 1883	Engelhardt 1922	
Malvaceae	*Bombax lepsii*	leaf	Engelhardt, 1922		
Malvaceae	*Byttneriopsis spiegelii*	leaf	Kvaček & Wilde, 2010		
Malvaceae	*Byttneriopsis steuerii*	leaf	Kvaček & Wilde, 2010		
Malvaceae	*Byttneriopsis daphnogenes*	leaf	Kvaček & Wilde, 2010		
Malvaceae	*Pterospermum chattanum*	leaf	Engelhardt, 1922		
"Sterculiaceae"?, *Mansonia*?	*Subtriporopollenites geiseltalensis*	pollen	Krutzsch, 1968b	Thiele-Pfeiffer 1988	
Sterculiaceae	*Sterculia labrusca*	leaf	Unger, 1850	Engelhardt 1922	*S. grandifolia* synonymized with *Byttneriopsis daphnogenes* by Kvaček & Wilde (2010)
Sterculiaceae	*Sterculia cinnamomifolia*	leaf	Engelhardt, 1922		
Sterculiaceae	*Sterculia modesta*	leaf	Saporta,1868	Engelhardt 1922	
Sterculiaceae	*Sterculia variabilis*	leaf	Saporta, 1868	Engelhardt 1922	
Thymelaeaceae, *Wikstroemia, Stellera*	*Pseudospinaepollis pseudospinosus*	pollen	Krutzsch, 1966	Thiele-Pfeiffer 1980, 1988	
Thymelaeaceae	*Daphne aquitanica*	leaf	Ettingshausen, 1853		
Incertae sedis	"Tiliaceous flower"	flower		Schaarschmidt 1984	
Viridiplantae: Angiosperms: Santalales					
Olacaceae, *Anacolosa*	*Anacolosidites efflatus*	pollen	(R. Potonié, 1934) Erdtman, 1954	Thiele-Pfeiffer 1988; Bouchal et al. In prep.	cf. *Anacolosa* sp. of Bouchal et al. In prep.
Olacaceae, *Olax*	*Olaxipollis* cf. *matthesi*	pollen	Krutzsch, 1962b	Thiele-Pfeiffer 1980, 1988; Bouchal et al. In prep.	cf. *Olax* sp. 1 of Bouchal et al. In prep.
Olacaceae, *Olax*	*Olaxipollis* cf. *matthesi*	pollen	Krutzsch, 1962b	Thiele-Pfeiffer 1980, 1988; Bouchal et al. In prep.	cf. *Olax* sp. 2 of Bouchal et al. In prep.
Santalaceae	*Leptomeria distans*	branch	Ettingshausen, 1853	Engelhardt 1922	
Santalaceae	*Leptomeria flexuosa*	branch	Ettingshausen, 1853	Engelhardt 1922	
Viridiplantae: Angiosperms: Caryophyllales					
Nyctaginaceae, *Bougainvillea*	*Reticulataepollis intergranulatus*	pollen	(R. Potonié, 1934) Krutzsch, 1959	Thiele-Pfeiffer 1988; Bouchal et al. In prep.	cf. *Bougainvillea* sp. of Bouchal et al. In prep.
Nyctaginaceae	*Pisonia eocaenica*	leaf	Ettingshausen, 1853	Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Nyctaginaceae	Taxon indet.	flower		Wilde & Schaarschmidt 1993	
Viridiplantae: Angiosperms: Cornales					
Alangiaceae	*Alangium* sp.	fruit		Collinson et al. 2012	
Cornaceae	*Tricolporopollenites satzveyensis*	pollen	Pflug, 1953a	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011	
Cornaceae	*Tricolporopollenites edmundii*	pollen	(R. Potonié, 1931b) Thomson & Pflug, 1953	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011	
Cornaceae	*Cornus orbifera*	leaf	Heer, 1853	Engelhardt 1922	
Cornaceae	*Cornus rhamnifolia*	leaf	Weber, 1852	Engelhardt 1922	
Nyssaceae, *Nyssa*	*Nyssapollenites kruschii analepticus*	pollen	(R. Potonié, 1931c) Nagy, 1969; (R. Potonié, 1934) Nagy, 1969	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Nyssaceae, *Nyssa*	*Nyssapollenites kruschii accessorius*	pollen	(R. Potonié, 1931c) R. Potonié, Thomson & Thiergart, 1950; (R. Potonié, 1934) R. Potonié, Thomson & Thiergart, 1950 ex Simoncsics, 1969	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Nyssaceae	*Eomastixia* cf. *rugosa*	fruit		Collinson et al. 2012	
Nyssaceae	?*Mastixia* sp.	fruit		Collinson et al. 2012	
Nyssaceae	*Mastixiopsis nyssoides*	fruit	Kirchheimer, 1936	Collinson et al. 2012	
Nyssaceae	Nyssaceae sp. 1	fruit		Collinson et al. 2012	
Nyssaceae	Nyssaceae sp. 2	fruit		Collinson et al. 2012	
Nyssaceae	*Nyssa disseminata*	fruit	(R. Ludwig, 1857) Kirchheimer, 1937	Collinson et al. 2012	
Nyssaceae	*Nyssa ornithobroma*	fruit	Unger, 1860	Engelhardt 1922; Collinson et al. 2012	Specimens illustrated by Engelhardt (1922, pl. 18, figs. 1 and 2) appear to show variable characters. Fig. 2 seems more like *N. ornithobroma* (obovoid), whilst fig. 1 is more like *N. disseminata* (see details in Collinson et al. 2012). In Engelhardt the extent of the margin of the germination valve is not clear on the figures and the germination valve is not mentioned in the text. These specimens are considered to belong to the genus *Nyssa* but the species attribution is unconfirmed. Therefore, it is uncertain how many species of *Nyssa* fruit are present at Messel.

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Nyssaceae	*Nyssa* sp.	leaf		Wilde 1989	
Nyssaceae	*Nyssa europaea*	leaf	Unger, 1845	Engelhardt 1922	
Viridiplantae: Angiosperms: Ericales					
Cyrillaceae	*Cyrillaceaepollenites megaexactus*	pollen	(R. Potonié, 1931b) R. Potonié, 1960	Thiele-Pfeiffer 1980, 1988	= *Tricolporopollenites megaexactus*
Ebenaceae	*Diospyros brachysepala*	leaf	Braun, 1836	Engelhardt 1922	
Ebenaceae	*Diospyros lotoides*	leaf	Unger, 1866	Engelhardt 1922	
Ebenaceae	*Diospyros ebenoides*	leaf	Engelhardt, 1922		
Ericaceae	*Ericipites callidus*	pollen	(R. Potonié, 1931a) Krutzsch, 1970c	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Ericaceae	*Ericipites ericius*	pollen	(R. Potonié, 1931a) R. Potonié, 1960	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Ericaceae	*Andromeda* (*Leucothoë*) *protogaea*	leaf	Unger, 1851	Engelhardt 1922	
Ericaceae	*Andromeda vacciniifolia*	leaf	Unger, 1850	Engelhardt 1922	
Ericaceae	*Gaultheria germanica*	leaf	Engelhardt, 1922		
Ericaceae	*Rhododendron* (?) *alcyonidum*	leaf	Unger, 1866	Engelhardt 1922	
Ericaceae	*Rhododendron flos saturni*	leaf	Unger, 1866	Engelhardt 1922	
Lecythidaceae	Taxon indet.	flower		Wilde & Schaarschmidt 1993	
Pentaphylacaceae	*Cleyera* sp.	fruit		Collinson et al. 2012	
Primulaceae	*Myrsine centarorum*	leaf	Unger, 1850	Engelhardt 1922	
Primulaceae	*Myrsine eumelaena*	leaf	Unger, 1866	Engelhardt 1922	
Primulaceae	*Myrsine endymionis*	leaf	Unger, 1850	Engelhardt 1922	
Primulaceae	*Myrsine doryphora*	leaf	Unger, 1850	Engelhardt 1922	
Primulaceae	*Myrsine caronis*	leaf	Unger, 1866	Engelhardt 1922	
Primulaceae	*Myrsine clethrifolia*	leaf	Saporta, 1867	Engelhardt 1922	
Primulaceae	*Myrsine semiserrulata*	leaf	Engelhardt, 1922		
Primulaceae	*Maesa europaea*	leaf	Engelhardt, 1922		
Sapotaceae	*Sapotaceoidaepollenites manifestus contractus*	pollen	(R. Potonié, 1931c) R. Potonié, 1960; Pflug, 1953a	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	= *Tetracolporopollenites manifestus contractus*
Sapotaceae	*Tetracolporopollenites kirchheimeri*	pollen	Thomson & Pflug, 1953	Lenz et al. 2023	
Sapotaceae	*Tetracolporopollenites obscurus*	pollen	Thomson & Pflug, 1953	Lenz et al. 2023	
Sapotaceae	*Tetracolporopollenites sapotoides*	pollen	Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Sapotaceae	cf. *Sapotispermum* sp.	seed		Collinson et al. 2012	
Sapotaceae	*Achras protosapota*	leaf	Engelhardt, 1922		
Sapotaceae	*Achras pithecobroma*	leaf	Unger, 1851	Engelhardt 1922	
Sapotaceae	*Bumelia ambigua*	leaf	Ettingshausen, 1851	Engelhardt 1922	
Sapotaceae	*Chrysophyllum sagorianum*	leaf	Ettingshausen, 1877	Engelhardt 1922	
Sapotaceae	*Chrysophyllum elongatum*	leaf	Engelhardt, 1922		
Sapotaceae	*Chrysophyllum reticulosum*	leaf	(Rossmaessler, 1840) Heer in Giebel, 1859	Engelhardt 1922	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Sapotaceae	*Chrysophyllum palaeo-cainito*	leaf	Ettingshausen, 1868	Engelhardt 1922	
Sapotaceae	*Mimusops ballotaeoides*	leaf	Engelhardt, 1922		
Sapotaceae	*Mimusops* (?) *verisimilis*	leaf	Engelhardt, 1922		
Sapotaceae	*Sapotacites sideroxyloides*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Sapotaceae	*Sapotacites eocaenicus*	leaf	Engelhardt, 1922		
Sapotaceae	*Sapotacites mimusops*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Sapotaceae	*Sapotacites euphemes*	leaf	Unger, 1850	Engelhardt 1922	
Sapotaceae	*Sapotacites schlottleri*	leaf	Engelhardt, 1922		
Sapotaceae	*Sapotacites sideroxylonoides*	leaf	Engelhardt, 1922		
Sapotaceae	*Sapotacites minor*	leaf	Ettingshausen, 1853	Engelhardt 1922	
Styracaceae	*Styrax stylosa*	leaf	Ettingshausen, 1868	Engelhardt 1922	
Styracaceae	*Styrax eocaenica*	leaf	Engelhardt, 1922		
Styracaceae	*Styrax ovatifolia*	leaf	Engelhardt, 1922		
Symplocaceae, *Symplocos?*	*Porocolpopollenites vestibulum*	pollen	(R. Potonié, 1931a) Thomson & Pflug, 1953	Lenz et al. 2011	
Symplocaceae, *Symplocos?*	*Symplocospollenites orbis*	pollen	(Thomson & Pflug, 1953) R. Potonié, 1960	Lenz et al. 2011	
Symplocaceae	cf. *Symplocos* sp.	leaf		Wilde 1989	
Symplocaceae	*Symplocos gregaria*	leaf	(Bronn in Leonhard, 1832) Unger, 1866	Engelhardt 1922	
Theaceae	*Polyspora hassiaca*	leaf	Wilde, 1989		
Theaceae	*Polyspora saxonica*	leaf	Kvaček & Walther, 1984	Wilde 1989	
Theaceae	*Ternstroemites engelhardtii*	leaf	Wilde, 1989		
Theaceae	*Ternstroemites dentatus*	leaf	Wilde, 1989		
Theaceae	*Camelliacarpoidea messelensis*	fruit	Collinson et al. 2012		
Viridiplantae: Angiosperms: Icacinales					
Icacinaceae, *Gomphandra*	*Brosipollis striatobrosus*	pollen	(Krutzsch, 1961) Krutzsch, 1968a	Thiele-Pfeiffer 1988	
Icacinaceae	*Palaeohosiea* sp.	fruit		Collinson et al. 2012	
Icacinaceae	*Icacinicarya tiffneyi*	fruit	Collinson et al. 2012		
Icacinaceae	cf. *Natsiatum* sp.	fruit		Collinson et al. 2012	
Icacinaceae	*Palaeohosiea bilinica*	fruit	(Ettingshausen, 1869) Kvaček & Bůžek, 1995	Collinson et al. 2012	
Icacinaceae	*Palaeophytocrene* sp.	fruit		Collinson et al. 2012	
Icacinaceae	*Pyrenacantha* sp. 1	fruit		Collinson et al. 2012	
Icacinaceae	*Pyrenacantha* sp. 2	fruit		Collinson et al. 2012	
Icacinaceae	cf. *Pyrenacantha*	fruit		Collinson et al. 2012	
Icacinaceae	*Icacinicarya densipunctata*	fruit	Collinson et al. 2012		
Icacinaceae	*Icacinicarya* sp.	fruit		Collinson et al. 2012	
Icacinaceae	*Phytocrene punctilinearis*	fruit	Collinson et al. 2012		
Viridiplantae: Angiosperms: Garryales					

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Eucommiaceae, *Eucommia*	*Tricolporopollenites parmularius*	pollen	(R. Potonié, 1934) Krutzsch in Krutzsch, Pchalek & Spiegler, 1960	Krutzsch & Vanhoorne 1977; Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Viridiplantae: Angiosperms: Gentianales					
Apocynaceae	*Alstonia eocaenica*	leaf	Engelhardt, 1922		
Apocynaceae	*Apocynophyllum amsonia*	leaf	Unger, 1850	Engelhardt 1922	
Apocynaceae	*Apocynophyllum wetteravicum*	leaf	Unger, 1866	Engelhardt 1922	
Apocynaceae	*Apocynophyllum ellipticum*	leaf	Engelhardt, 1922		
Apocynaceae	*Apocynophyllum longe-petiolatum*	leaf	Ettingshausen, 1877	Engelhardt 1922	
Apocynaceae	*Apocynophyllum helveticum*	leaf	Heer, 1859	Engelhardt 1922	
Apocynaceae	*Apocynophyllum sessile*	leaf	Unger, 1866	Engelhardt 1922	
Apocynaceae	*Apocynophyllum plumeriaefolium*	leaf	Ettingshausen, 1857	Engelhardt 1922	
Apocynaceae	*Echites* (?) *tenuifolia*	leaf	Engelhardt, 1922		
Apocynaceae	*Echitonium sezannense*	leaf	Watelet, 1866	Engelhardt 1922	
Apocynaceae	*Neritinium dubium*	leaf	Unger, 1850	Engelhardt 1922	
Apocynaceae	*Neritinium majus*	leaf	Unger, 1850	Engelhardt 1922	
Apocynaceae	*Neritinium ungeri*	leaf	Engelhardt, 1922		
Apocynaceae	*Neritinium minus*	leaf	Ettingshausen, 1872	Engelhardt 1922	
Apocynaceae	*Nerium eocaenicum*	leaf	Engelhardt, 1922		
Apocynaceae	*Nerium germanicum*	leaf	Engelhardt, 1922		
Apocynaceae	*Cypselites* sp.	seed		Collinson et al. 2012	
Rubiaceae	*Cinchonidium bilinicum*	leaf	Ettingshausen, 1868	Engelhardt 1922	
Rubiaceae	*Cinchonidium angustifolium*	leaf	Ettingshausen, 1891	Engelhardt 1922	
Rubiaceae	*Cinchonidium acuminatofolium*	leaf	Engelhardt, 1922		
Rubiaceae	*Morinda tertiaria*	leaf	Engelhardt, 1922		
Rubiaceae	*Ixora tertiaria*	leaf	Engelhardt, 1922		
Rubiaceae	taxon indet.	flower		Schaarschmidt 1986	
Viridiplantae: Angiosperms: Lamiales					
Bignoniaceae	*Darmstadtia biseriata*	fruit	Collinson et al. 2012		
Lamiaceae	*Vitex* (?) *pentamera*	leaf	Engelhardt, 1922		
Lamiaceae	*Clerodendron serratifolium*	leaf	Friedrich, 1883	Engelhardt 1922	
Oleaceae	*Oleoidearumpollenites microreticulatus*	pollen	(Thomson & Pflug, 1953) Ziembińska-Tworzydło in Ziembińska-Tworzydło et al. 1994	Thiele-Pfeiffer 1980, 1988; Lenz et al. 2007a, 2011	= *Tricolporopollenites microreticulatus*
Oleaceae	*Ligustrum priscum*	leaf	Ettingshausen, 1868	Engelhardt 1922	
Oleaceae	*Notelaea eocaenica*	leaf	Ettingshausen, 1858	Engelhardt 1922	
Oleaceae	*Notelaea prisca*	leaf	Engelhardt, 1922		
Oleaceae	*Oleoxylon* sp.	wood		Haag & Wilde 2024	Single known specimen from the Lower Messel Formation
Viridiplantae: Angiosperms: Solanales					

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Convulvulaceae	*Porana ungeri*	leaf	Heer, 1856	Engelhardt 1922	
Solanaceae?	*Tricolporopollenites crassostriatus*	pollen	Nickel, 1996	Lenz et al. 2023	
Viridiplantae: Angiosperms: Aquifoliales					
Aquifoliaceae, *Ilex*	*Ilexpollenites iliacus*	pollen	(R. Potonié, 1931d) Thiergart, 1937 ex R. Potonié, 1960	Thiele-Pfeiffer 1988; Lenz et al. 2007a	
Aquifoliaceae, *Ilex*	*Ilexpollenites margaritatus*	pollen	(R. Potonié, 1931a) Thiergart, 1937 ex R. Potonié, 1960	Thiele-Pfeiffer 1988; Lenz et al. 2007a	
Aquifoliaceae	*Ilexpollenites propinquus*	pollen	(R. Potonié, 1934) R. Potonié, 1960	Thiele-Pfeiffer 1988	
Aquifoliaceae	cf. *Apocynophyllum helveticum*	leaf	Heer, 1859	Wilde 1989	
Aquifoliaceae	cf. *"Stemonurus" spiculata*	leaf	(Bandulska, 1923) Rüffle, 1976	Wilde 1989	
Viridiplantae: Angiosperms: Apiales					
Araliaceae	*Araliaceoipollenites euphorii*	pollen	(R. Potonié, 1931a) R. Potonié, 1951	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Araliaceae, *Hedera*	*Araliaceoipollenites reticuloides*	pollen	Thiele-Pfeiffer, 1980	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Araliaceae	*Hedera pristina*	leaf	Engelhardt, 1922		
Araliaceae	*Hedera* sp.	leaf		Wilde 1989	
Araliaceae	*Panax longissimum*	leaf	Unger, 1850	Engelhardt 1922	
Araliaceae	Araliaceae sp. (?cf. *Fatsia*)	leaf		Wilde 1989	
Pittosporaceae	*Pittosporum eocaenicum*	leaf	Engelhardt, 1922		
Toricelliaceae	*Toricellia bonesii*	fruit	(Manchester, 1994) Manchester, 1999	Collinson et al. 2012	
Viridiplantae: Angiosperms: Incertae sedis					
Incertae sedis	Taxon indet.	flower		Wilde & Schaarschmidt 1993	
Incertae sedis	Taxon indet.	flower		Wilde 2018	
Hamamelidaceae?, Verbenaceae?, Oleaceae?	*Tricolporopollenites microporitus*	pollen	Thomson & Pflug, 1953	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Rhizophoraceae?, Solanaceae?, Verbenaceae?, Rutaceae?, Euphorbiaceae?	*Tricolporopollenites mansfeldensis*	pollen	Krutzsch, 1969	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Incertae sedis	*Zircipollenites globosus*	pollen	Kedves, 1974	Thiele-Pfeiffer 1988	
Incertae sedis	*Pompeckjoidaepollenites subhercynicus*	pollen	(Krutzsch, 1954) Krutzsch in Góczán, Groot, Krutzsch & Pacltová, 1967	Thiele-Pfeiffer 1988	Normapolles element
Incertae sedis	*Subtriporopollenites magnoporatus*	pollen	(Thomson & Pflug, 1953) Krutzsch, 1961	Lenz et al. 2023	
Incertae sedis	*Pistillipollenites mcgregorii*	pollen	Rouse, 1962	Lenz et al. 2023	
Incertae sedis	*Pentapollenites pentangulus pentangulus*	pollen	(Pflug, 1953a) Krutzsch, 1957; Krutzsch, 1962c	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	*Pentapollenites pentangulus foveostriatus*	pollen	(Pflug, 1953a) Krutzsch, 1957; Krutzsch, 1962c	Thiele-Pfeiffer 1988; Lenz et al. 2007a, 2011	
Incertae sedis	*Pentapollenites punctoides*	pollen	Krutzsch, 1962c	Thiele-Pfeiffer 1988	
Incertae sedis	*Pentapollenites* sp. 1	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Multiporopollenites microreticulatus*	pollen	Krutzsch, 1961	Thiele-Pfeiffer 1988	
Incertae sedis	*Multiporopollenites* sp. 1	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Multiporopollenites* sp. 2	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolpopollenites pudicus*	pollen	(R. Potonié, 1934) Thomson & Pflug, 1953	Lenz et al. 2023	
Incertae sedis	*Tricolpopollenites* sp. 1	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolpopollenites* sp. 2	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites pseudocingulum*	pollen	(R. Potonié, 1931a) Thomson & Pflug, 1953	Thiele-Pfeiffer 1980	
Incertae sedis	*Tricolporopollenites pseudoiliacus*	pollen	Krutzsch & Vanhoorne, 1977	Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites eofagoides*	pollen	Krutzsch & Vanhoorne, 1977	Thiele-Pfeiffer 1988	
Incertae sedis	*Tricoloropollenites setarius*	pollen	(R. Potonié, 1934) Thiele-Pfeiffer, 1988	Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 2	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 3	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 4	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 5	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 6	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 8	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 14	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 15	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 16	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 17	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 18	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 19	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 20	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 22	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 23	pollen		Thiele-Pfeiffer 1988	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	*Tricolporopollenites* sp. 24	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites* sp. 25	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tricolporopollenites belgicus*	pollen	Krutzsch & Vanhoorne, 1977	Lenz et al. 2007a	
Incertae sedis	*Tricolporopollenites abbreviatus*	pollen	(R. Potonié, 1934) Krutzsch, 1961	Lenz et al. 2007a, 2011	
Incertae sedis	*Tricolporopollenites eocaenicus*	pollen	Krutzsch & Vanhoorne, 1977	Lenz et al. 2007a	
Incertae sedis	*Tricolporopollenites megaporatus*	pollen	Krutzsch & Vanhoorne, 1977	Lenz et al. 2023	
Incertae sedis	*Tetracolporopollenites sculptatus*	pollen	Pacltová, 1958	Thiele-Pfeiffer 1988	
Incertae sedis	*Tetracolporopollenites* sp. 1	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Tetracolporopollenites* sp. 2	pollen		Thiele-Pfeiffer 1988	
Incertae sedis	*Phyllites cytisoides*	leaf	Engelhardt, 1922		
Incertae sedis	*Phyllites asymmetrica*	leaf	Engelhardt, 1922		
Incertae sedis	*"Anona* (sic) *cacaoides"*	seed	(Zenker, 1833) Poppe, 1866	Engelhardt 1922	One of the specimens illustrated by Engelhardt (1922, pl. 25, fig. 1) shows longitudinal patterning, which is also noted in the text. In contrast, in Anonaceae seeds, wrinkling or paterning is typically oriented transversely (e.g., Collinson 1983). Hence, attribution of these seeds to Anonaceae cannot be confirmed and is unlikely to be correct.
Incertae sedis	*Bacca diospyroides*	fruit	Engelhardt, 1922		No characters are illustrated or stated in text by Engelhardt that can be used to identify this specimen. Specimen is likely to be indeterminate.
Incertae sedis	*Carpolithus callosaeoides*	fruit	(Engelhardt, 1922) Collinson et al. 2012	Collinson et al. 2012	
Incertae sedis	*"Juglans troglodytarum"*	fruit	Heer, 1859	Engelhardt 1922	Neither the illustration by Engelhardt nor his text contains any character diagnostic of *Juglans* or of Juglandaceae

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	*Leguminosites trigonellaeformis*	fruit	Engelhardt, 1922		An elongate pod-like fruit containing seeds is illustrated by Engelhardt, but the text gives no informative characters; family and generic attribution unconfirmed.
Incertae sedis	*Pinus* sp.	cone		Engelhardt 1922	
Incertae sedis	*Saportaspermum kovacsiae*	fruit	Kvaček & Wilde, 2010	Collinson et al. 2012	
Incertae sedis	*Spirellea* sp.	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithes* (sic) *aristolochiae*	fruit	Engelhardt, 1922		Insufficient characters stated in the text or shown in the illustration in Engelhardt to confirm the family attribution.
Incertae sedis	*Carpolithes* (sic) *aroideus*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *ficoides*	fruit	Engelhardt, 1922		A fruit on a stalk is illustrated in Engelhardt, but no characters are shown or stated that are diagnostic of *Ficus* or of Moraceae.
Incertae sedis	*Carpolithes* (sic) *leguminosae*	fruit	Engelhardt, 1922		"n. sp." not specifically invoked in text but in caption to pl. XL fig. 17; no informative characters stated in text or shown in the illustration; specimen likely to be indeterminate; family attribution unconfirmed.
Incertae sedis	*Carpolithes* (sic) *myristicoides*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *drupaceus*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *anacardiaceus*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *sapindoides*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *euphoriaeoides*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *rhamnoides*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *globosus*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *ovatus*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *palaeolobioides*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithes* (sic) *dispermus*	fruit	Engelhardt, 1922		
Incertae sedis	*Carpolithus* sp. 1	fruit		Collinson et al. 2012	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	*Carpolithus* sp. 2	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 3	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 4	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 5	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 6	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 7	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 8	disseminule		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 9	disseminule		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 10	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 11	uncertain		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 12	fruiting head		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 13	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 14	seed cluster		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 15	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 16	fruiting head		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 17	fruiting head		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 18	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 19	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 20	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 21	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 22	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 23	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 24	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 25	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 26	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 27	fruiting raceme		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 28	disseminule		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 29	fruiting head		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 30	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 31	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 32	disseminule		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 33	fruiting head		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 34	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 35	seed/endocarp		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 36	fruiting head		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 37	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 38	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 39	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 40	uncertain		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 41	fruit with seeds		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 42	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 43	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 44	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 45	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 46	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 47	uncertain		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 48	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 49	fruiting head		Collinson et al. 2012	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	*Carpolithus* sp. 50	seed		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 51	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 52	disseminule		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 53	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 54	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 55	nutlet/pyrene		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 56	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 57	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 58	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 59	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 60	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 61	fruit		Collinson et al. 2012	
Incertae sedis	*Carpolithus* sp. 62	fruit		Collinson et al. 2012	
Fungi: Ascomycota					
?Ophiocordycipitaceae	?*Ophiocordyceps* sp.	ichnofossil		Hughes et al. 2011	No formal assignment of trace fossils on leaves, but identity strongly indicated in text
Incertae sedis	mushroom or lichen	body fossil		Richter 1981; Franzen & Richter 1988	As gut contents
Incertae sedis	Rhytismatales indet.	body fossil		Schaarschmidt 1988	Damage on *Laurophyllum lanigeroides*; F. Hennicke, pers. obs.
Incertae sedis	Meliolales indet.	body fossil			F. Hennicke, pers. obs.
Fungi: Basidiomyctes					
Incertae sedis	Uredinales indet.	body fossil			F. Hennicke, pers. obs.
Incertae sedis	Ustilaginales indet.	body fossil			F. Hennicke, pers. obs.
Fungi: Incertae sedis					
Incertae sedis	Indet.	body fossil		Weitzel 1933a	It was strongly suggested by Weitzel (1933a) that fungal microfossils occur in the sediment of the Middle Messel Formation; OL has also observed them; they have not yet been studied in detail
Porifera					
Spongillidae	*Ephydatia gutenbergiana*	body fossil	(Müller, Zahn & Maidhoff, 1982)	Richter & Wuttke 1999	Matthess (1966) indicated 3 types of sponge spicules
Spongillidae	*Lutetiospongilla heili*	body fossil	Richter & Wuttke, 1999		
Mollusca: Gastropoda					
Hydrobiidae	Hydrobiidae gen. et sp. indet.	body fossil		Weitzel 1933b; Neubert 1999	Only in literature
Planorbidae	*Australorbis* cf. *pseudoammonius*	body fossil	(Schlotheim, 1820)	Martin & Munk 1992	The species is now in the genus *Headonia*.
Pleuroceridae	?Pleuroceridae gen. et sp. indet.	body fossil		Neubert 1999	
Viviparidae	"*Viviparus*" sp. indet.	body fossil		Neubert 1999	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	*Toxocoprulus weitzeli*	supposed ichnofossil	Rietschel, 1988	Neubert 1999	Possibly the same as type 7b of Schmitz (1991)
Arthropoda: Chelicerata: Araneae					
Araneidae	?*Singa* or ?*Zygiella*	body fossil		Wunderlich 1986	
?Cybaeidae	*Lutetiana neli*	body fossil	Selden & Wappler, 2019		
Hersiliidae	Gen. et sp. indet.	body fossil		Wedmann 2018	
Arthropoda: Chelicerata: Trombidiformes					
Eriophyidae	Damage type 117	ichnofossil		Albrecht et al. 2023	
Eriophyidae	Damage type 149	ichnofossil		Albrecht et al. 2023	
Eriophyidae	Damage type 283	ichnofossil			T. Wappler, pers. obs.
Arthropoda: Chelicerata: Opiliones					
Sclerosomatidae	*?Leiobunum messelense*	body fossil	Bartel, Dunlop & Wedmann, 2024		
Sclerosomatidae	?*Leiobunum schaali*	body fossil	Bartel, Dunlop & Wedmann, 2024		
Sclerosomatidae	Leiobuninae / Gagrellinae, gen. indet.	body fossil		Bartel et al. 2024	
Incertae sedis	Opiliones indet.	body fossil		Bartel et al. 2024	
Arthropoda: Crustacea: Branchiopoda					
Incertae sedis	Branchiopoda indet.	body fossil		Richter & Baszio 2001a	
Arthropoda: Crustacea: Cladocera					
Daphniidae	*Daphnia pulex*-type ephippia	body fossil		Lutz 1991; Richter & Wedmann 2005	
Daphniidae	*Ctenodaphnia magna*-type ephippia	body fossil		Richter & Wedmann 2005	
Moinidae	*Moina macrocopa*-type ephippia	body fossil		Lutz 1991; Richter & Wedmann 2005	
Incertae sedis	Cladocera indet.	body fossil		Richter & Baszio 2002	
Arthropoda: Crustacea: Conchostraca					
Incertae sedis	Conchostraca indet.	body fossil		Richter & Baszio 2001a	
Arthropoda: Crustacea: Ostracoda					
Incertae sedis	Ostracoda indet.	body fossil		Goth 1990	
Arthropoda: Crustacea: Decapoda					
?Palaemonoidea	*Bechleja brevirostris*	body fossil	Mazancourt, Wappler & Wedmann, 2023	Mazancourt et al. 2022	
Arthropoda: Insecta: Ephemeroptera					
Baetidae or Siphlonuridae	Baetidae or Siphlonuridae gen. et sp. indet.	body fossil		Richter & Krebs 1999; Richter & Baszio 2001a	
Arthropoda: Insecta: Odonata					
?Aeshnidae	?Aeschnidae gen. et sp. indet.	ichnofossil		Hellmund & Hellmund 1996	
?Aeshnidae; ?Corduliidae	?Aeschnidae ?Corduliidae gen. et sp. indet.	body fossil		Lutz 1990	
Coenagrionidae	Coenagrionidae gen. et sp. indet.	ichnofossil		Hellmund & Hellmund 1996	
Dysagrionidae	*Petrolestes messelensis*	body fossil	Garrouste & Nel, 2015		
Gomphidae	Gomphidae indet.	body fossil		Wedmann 2018	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Megapodagrionidae	Megapodagrionidae gen. et sp. indet.	body fossil		Petrulevicius et al. 2008	
Pseudostenolestidae	*Pseudostenolestes bechlyi*	body fossil	Garrouste & Nel, 2015		
Arthropoda: Insecta: Plecoptera					
Perlidae	Perlidae gen. et sp. indet.	body fossil		Wedmann 2018	
Plecoptera	Plecoptera indet.	body fossil		Lutz 1987, 1990	
Arthropoda: Insecta: Dermaptera					
Incertae sedis	Dermaptera indet.	body fossil		Wedmann 2005, 2018	
Arthropoda: Insecta: Orthoptera					
Acrididae	Damage type 314	ichnofossil			T. Wappler, pers. obs.
?Gryllacrididae	?Gryllacrididae gen. et sp. indet.	body fossil		Lutz 1990	
Tetrigidae	Gen. et sp. nov. 1	body fossil		Wedmann 2018; Kasalo et al. 2024 (in press)	
Tetrigidae	Gen. et sp. nov. 2	body fossil		Kasalo et al. 2024 (in press)	
Tettigoniidae	Tettigoniidae gen. et sp. indet.	body fossil		Lutz 1988	
Arthropoda: Insecta: Phasmatodea					
Phylliinae	*Eophyllium messelense*	body fossil	Wedmann, Bradler & Rust, 2007		
Incertae sedis	Phasmatodea indet.	body fossil		Lutz 1990	
Arthropoda: Insecta: Blattodea					
Blaberidae	*Morphna cenozoica*	body fossil	Šmídová, Vidlička & Wedmann, 2022		
Blattidae	*Periplaneta eocaenica*	body fossil	Meunier, 1921		
Blattidae	*Periplaneta relicta*	body fossil	Meunier, 1921		
Arthropoda: Insecta: Isoptera					
?Hodotermitidae	?Hodotermitidae gen. et sp. indet.	body fossil		Lutz 1990	
Arthropoda: Insecta: Hemiptera					
Aphididae	Damage type 150	ichnofossil		Albrecht et al. 2023	
Aradidae	*Aneurus*? *incertus*	body fossil	Wappler et al. 2015a		
Aradidae	*Mezira eocenica*	body fossil	Wappler & Heiss, 2006		
Aradidae	*Mezira parapetrificata*	body fossil	Wappler et al. 2015a		
Aradidae	*Mezira petrificata*	body fossil	Wappler et al. 2015a		
Aradidae	*Neuroctenus kotejai*	body fossil	Wappler & Heiss, 2006		
Aradidae	*Neuroctenus messelensis*	body fossil	Wappler & Heiss, 2006		
Belostomatidae	Belostomatidae gen. et sp. indet.	body fossil		Wedmann 2018	
Coccidae	Damage type 183	ichnofossil			T. Wappler, pers. obs.
Coreidae	Damage type 213	ichnofossil		Albrecht et al. 2023	
Cydnidae	*Cydnopsis meunieri*	body fossil	Kinzelbach, 1970a		
Cydnidae	*Cydnopsis nana*	body fossil	Kinzelbach, 1970a		
Diaspididae	Damage type 157	ichnofossil		Albrecht et al. 2023	
Diaspididae	Damage type 191	ichnofossil		Albrecht et al. 2023	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Gerridae	*Cylindrobates messelensis*	body fossil	Wappler & Andersen, 2004		
Phylloxeridae	Damage type 147	ichnofossil		Albrecht et al. 2023	
?Lygaeidae	?Lygaeidae indet.	body fossil		Kinzelbach 1970a	
Miridae	Miridae gen. indet.	body fossil		Lutz 1990	
Notonectidae	Notonectidae gen. et sp. indet.	body fossil		Lutz 1991	
Pemphigidae	Damage type 169	ichnofossil		Albrecht et al. 2023	
Pentatomidae	*Eospinosus peterkulkai*	body fossil	Wedmann, Kment, Campos & Hörnschemeyer, 2021	Wedmann et al. 2021a	
Psyllidae	Damage type 205	ichnofossil		Albrecht et al. 2023	
Reduviidae	*Amphibolus disponsi*	body fossil	Kinzelbach, 1970a		
Ricaniidae	Damage type 216	ichnofossil		Albrecht et al. 2023	
Tingidae	*Chorotingioites priscus*	body fossil	Wappler, 2003		
Tingidae	*Exmesselensis disspinosus*	body fossil	Wappler, 2003		
Tingidae	*Oblongomorpha lutetia*	body fossil	Wappler, 2003		
Tingidae	*Lutetiacader petrefactus*	body fossil	Wappler, 2006		
Arthropoda: Insecta: Sternorrhyncha					
Aphidina	Aphidina gen. et sp. indet.	body fossil		Wedmann 2018	
Diaspididae	Aspidiotinae gen. et sp. indet. 1	body fossil		Wappler & Ben-Dov 2008	
Diaspididae	Aspidiotinae gen. et sp. indet. 3	body fossil		Wappler & Ben-Dov 2008	
Arthropoda: Insecta: Auchenorrhyncha					
?Cercopidae	?Cercopidae gen. et sp. indet.	body fossil		Lutz 1990	
Cicadidae	Cicadidae gen. et sp. indet.	body fossil		Lutz 1990	
Dictyopharidae	*Wedelphus dichopteroides*	body fossil	Szwedo & Wappler, 2006	Wappler 2004	
Eurybrachidae	*Amalaberga ostrogothiorum*	body fossil	Szwedo & Wappler, 2006		
?Flatidae or ?Ricaniidae	?Flatidae or ?Ricaniidae	body fossil		Lutz 1990	
Lophopidae	*Baninus thuringiorum*	body fossil	Szwedo & Wappler, 2006		
cf. Membracidae	cf. Membracidae gen. et sp. indet.	body fossil		Lutz 1990	
Arthropoda: Insecta: Thysanoptera					
Incertae sedis	Thysanoptera indet.	body fossil		Wedmann 2018	
Arthropoda: Insecta: Neuropterida					
Mantispidae	*Symphrasites eocenicus*	body fossil	Wedmann & Makarkin, 2007		
Incertae sedis	Neuroptera indet.	body fossil			S. Wedmann, pers. obs.
Arthropoda: Insecta: Coleoptera					
Apionidae	Apionidae	body fossil		Lutz 1990	
Brenthidae	Brenthidae	body fossil		Lutz 1990; Tröster 1993b	
Buprestidae	Agrilinae? gen. et sp. indet. 1	body fossil		Wedmann & Hörnschemeyer 1994	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Buprestidae	Agrilinae? gen. et sp. indet. 2	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilinae? gen. et sp. indet. 3	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilinae? gen. et sp. indet. 4	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilinae? gen. et sp. indet. 5	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilinae? gen. et sp. indet. 6	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilinae? gen. et sp. indet. 7	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilini? gen. et sp. indet. 1	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilini? gen. et sp. indet. 2	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilini? gen. et sp. indet. 3	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Agrilini? gen. et sp. indet. 4	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Buprestini gen. et sp. indet., 1 species	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	*Anthaxia?* sp. 1	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	*Anthaxia?* sp. 2	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	*Eurythyrea* sp.	body fossil		Meunier 1921	
Buprestidae	*Eurythyrea*? sp., 1 species	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	*Eurythyrea*? cf. *bilyi*	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 1	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 2	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 3	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 4	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 5	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 6	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 7	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 8	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Coroebini? gen. et sp. indet. 9	body fossil		Wedmann & Hörnschemeyer 1994	
Buprestidae	Psilopterini gen. et sp. indet., 1 species	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera transversovittata*	body fossil	(Haupt, 1950)	Hörnschemeyer & Wedmann 1994	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Buprestidae	*Psiloptera cf. transversovittata*	body fossil	(Haupt, 1950)	Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera weigelti*	body fossil	(Pongracz, 1935)	Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera* sp.	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera*? sp. 1	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera*? sp. 2	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera*? sp. 3	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Touzalinia / Psiloptera*, indet.	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera / Dicercomorpha* sp. 1	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera / Dicercomorpha* sp. 2	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera / Dicercomorpha* sp. 3	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Touzalinia / Dicercomorpha*, indet.	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera / Dicerca* sp. 1	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Psiloptera / Dicerca* sp. 2	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	Psilopterini / Dicercini, gen. et sp. indet. 1	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	Psilopterini / Dicercini, gen. et sp. indet. 2	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	Psilopterini / Dicercini, gen. et sp. indet. 3	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Dicerca*? sp.	body fossil		Hörnschemeyer & Wedmann 1994	
Buprestidae	*Perotis messelensis*	body fossil	Meunier, 1921	Wedmann 2005	
Buprestidae	*Sphenoptera eocaenica*	body fossil	Meunier, 1921	Wedmann 2005	
Buprestidae	*Sphenoptera metallica*	body fossil	Meunier, 1921	Wedmann 2005	
Carabidae	*Scarites*? sp. indet.	body fossil		Lutz 1990	
Carabidae	*Harpalus*? sp. indet.	body fossil		Meunier 1921	
Cerambycidae	Prioninae gen. et sp. indet.	body fossil		Lutz 1988	
Cerambycidae	Lamiinae gen. et sp. indet.	body fossil		Lutz 1988	
Chrysomelidae	*Lina titana*	body fossil	Meunier, 1921		
Chrysomelidae	Sagrinae, *Eosagra*? sp.	body fossil		Lutz 1990	
Chrysomelidae	Damage type 200	ichnofossil		Albrecht et al. 2023	
Chrysomelidae	Damage type 222	ichnofossil		Albrecht et al. 2023	
Colydiidae	Colydiidae gen. et sp. indet	body fossil		Tröster 1993b	
Cupedidae	*Tenomerga*? *messelense*	body fossil	Tröster, 1993a		
Curculionidae	Curculionidae	body fossil		Lutz 1990; Rheinheimer 2007	
Curculionidae	*Palaeoalatorostrum schaali*	body fossil	Rheinheimer, 2007		

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Curculionidae	*Palaeocneorhinus messelensis*	body fossil	Rheinheimer, 2007		
Curculionidae	*Palaeocrassirhinus rugosithorax*	body fossil	Rheinheimer, 2007		
Curculionidae	*Palaeocrassirhinus messelensis*	body fossil	Rheinheimer, 2007		
Curculionidae	Damage type 143	ichnofossil		Albrecht et al. 2023	
Curculionidae	Damage type 171	ichnofossil		Albrecht et al. 2023	
Curculionidae	Damage type 223	ichnofossil		Albrecht et al. 2023	
Curculionidae	Damage type 348	ichnofossil			T. Wappler, pers. obs.
?Dytiscidae	?Dytiscidae gen. et sp. indet.	body fossil		Lutz 1991	
Elateridae	“*Ancylochira*” *minuta*	body fossil	(Meunier, 1921)	Lutz 1990	
Elateridae	*Agrypnus*? sp. 1	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 2	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 3	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 4	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 5	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 6	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 7	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 8	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? sp. 9	body fossil		Tröster 1994a	
Elateridae	*Agrypnus*? aff. ?*costipennis*	body fossil		Tröster 1994a	
Elateridae	*Lacon*? sp.	body fossil		Tröster 1994a	
Elateridae	*Lanelater verae*	body fossil	Tröster, 1993c		
Elateridae	*Lanelater* sp. 1	body fossil		Tröster 1993c	
Elateridae	*Lanelater* sp. 2	body fossil		Tröster 1993c	
Elateridae	*Lanelater* sp. 3	body fossil		Tröster 1993c	
Elateridae	*Macropunctum angulosum*	body fossil	Tröster, 1999		
Elateridae	*Macropunctum angustiscutellum*	body fossil	Tröster, 1994b		
Elateridae	*Macropunctum eocaenicum*	body fossil	(Meunier, 1921)	Tröster 1991; Lutz 1990	
Elateridae	*Macropunctum latiscutellum*	body fossil	Tröster, 1994b		
Elateridae	*Macropunctum messelensis*	body fossil	Tröster, 1991		
Elateridae	*Macropunctum meunieri*	body fossil	Tröster, 1991		
Elateridae	*Macropunctum promptum*	body fossil	(Meunier, 1921)	Tröster 1991; Lutz 1990	
Elateridae	*Macropunctum rebugense*	body fossil	Tröster, 1994b		
Elateridae	*Macropunctum senckenbergi*	body fossil	Tröster, 1994b		
Elateridae	Elateridae gen. et sp. indet. 1	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 2	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 3	body fossil	Tröster, 1994a		

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Elateridae	Elateridae gen. et sp. indet. 4	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 5	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 6	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 7	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 8	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 9	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 10	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 11	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 12	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 13	body fossil	Tröster, 1994a		
Elateridae	Elateridae gen. et sp. indet. 14	body fossil	Tröster, 1994a		
Eucnemidae	Eucnemidae gen. sp. indet	body fossil		Wedmann 1994	
Hydrophilidae	*Hydrobiomorpha eopalpalis*	body fossil	Fikácek, Wedmann & Schmied, 2010		
Hydrophilidae	*Hydrobiomorpha* sp. 1	body fossil		Fikácek et al. 2010	
Hydrophilidae	*Hydrochara* sp.	body fossil		Fikácek et al. 2010	
Hydrophilidae	*Hydrophilus* sp.	body fossil		Fikácek et al. 2010	
Histeridae	Histeridae indet.	body fossil		Tröster 1993b	
Lucanidae	*Protognathinus spielbergi*	body fossil	Chalumeau & Brochier, 2001		
Psephenidae	Eubrianacinae gen. et sp. indet.	body fossil		Wedmann et al. 2011	
Scarabaeidae	*Geotrupes*? sp.	body fossil		Lutz 1990	
Scarabaeidae	*Geotrupes messelensis*	body fossil	Meunier, 1921	Krell 2007	
Scarabaeidae	*Gymnopleurus eocaenicus*	body fossil	Meunier, 1921	Krell 2007	
Scarabaeidae	*Onthophagus*? sp.	body fossil		Lutz 1990	
Scarabaeidae	*Onitis*? sp.	body fossil		Lutz 1990	
Scarabaeidae	Scarabaeidae indet.	body fossil		Lutz 1990; Krell 2007	
Staphylinidae	Staphylinidae gen. et sp. indet.	body fossil		Lutz 1987, 1990	
Tenebrionidae	*Ceropria*? *messelense*	body fossil	Hörnschemeyer, 1994		
Throscidae	Throscidae gen. et sp. indet.	body fossil		Wedmann 1994	
Trogossitidae	*Trogosita eocaenica*	body fossil	Meunier, 1921	Wedmann 2005	
Incertae sedis	*Ancylochira agilis*	body fossil	Meunier, 1921	Lutz 1990	
Arthropoda: Insecta: Strepsiptera					
Myrmecolacidae	*Stichotrema* sp.	body fossil		Kinzelbach & Pohl 1994; Lutz 1990	
Arthropoda: Insecta: Hymenoptera					
Agaonidae	Damage type 204	ichnofossil		Albrecht et al. 2023	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Anthophoridae	Anthophoridae gen. et sp. indet.	body fossil		Lutz 1990	
Apidae	*Electrapis* sp. indet.	body fossil		Wappler et al. 2015b	
Apidae	*Protobombus messelensis*	body fossil	Engel & Wappler, 2003	Wappler & Engel 2003	
Apidae	*Pygomelissa lutetia*	body fossil	Engel & Wappler, 2003	Wappler & Engel 2003	
Apidae	*Xylocopa* (*Apocolyx*) *primigenia*	body fossil	Engel & Wappler, 2024	Geier et al. 2024	
Braconidae	Braconidae gen. et sp. indet.	body fossil		Lutz 1990	
Chalcididae	Chalcididae gen. et sp. indet.	body fossil		Lutz 1990	
Cimbicidae	Cimbicidae gen. et sp. indet.	body fossil		Wedmann 2018	
Cynipidae	Damage type 145	ichnofossil		Albrecht et al. 2023	
Cynipidae	Damage type 148	ichnofossil		Albrecht et al. 2023	
Cynipidae	Damage type 217	ichnofossil			T. Wappler, pers. obs.
Eumenidae	Eumenidae gen. et sp. indet.	body fossil		Lutz 1990	
Evaniidae	Evaniidae gen. et sp. indet.	body fossil		Wedmann 2018	
Formicidae	*Archimyrmex wedmannae*	body fossil	Dlussky, 2012		
Formicidae	*Casaleia eocenica*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Cephalopone grandis*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Cephalopone potens*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Cyrtopone striata*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Cyrtopone elongata*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Cyrtopone curiosa*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Cyrtopone microcephala*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Gesomyrmex curiosus*	body fossil	Dlussky, Wappler & Wedmann, 2009		
Formicidae	*Gesomyrmex breviceps*	body fossil	Dlussky, Wappler & Wedmann, 2009		
Formicidae	*Gesomyrmex pulcher*	body fossil	Dlussky, Wappler & Wedmann, 2009		
Formicidae	*Messelepone leptogenoides*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Oecophylla longiceps*	body fossil	Dlussky, 2008	Dlussky et al. 2008	
Formicidae	*Pachycondyla eocenica*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Pachycondyla lutzi*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Pachycondyla? messeliana*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Pachycondyla minuta*	body fossil	Dlussky & Wedmann, 2012		

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Formicidae	*Pachycondyla petrosa*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Pachycondyla petiolosa*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Protopone vetula*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Protopone sepulta*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Protopone oculata*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Protopone magna*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Protopone? dubia*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Protopone germanica*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Pseudectatomma eocenica*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Pseudectatomma striatula*	body fossil	Dlussky & Wedmann, 2012		
Formicidae	*Titanomyrma giganteum*	body fossil	(Lutz, 1986)	Archibald et al. 2011	
Formicidae	*Titanomyrma simillimum*	body fossil	(Lutz, 1986)	Archibald et al. 2011	
Formicidae	Damage type 212	ichnofossil		Albrecht et al. 2023	
Formicidae	Damage type 214	ichnofossil		Albrecht et al. 2023	
Ichneumonidae	*Mesornatus markovici*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Ichneumonidae	*Polyhelictes bipolarus*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Ichneumonidae	*Trigonator macrocheirus*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Ichneumonidae	*Rhyssella vera*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Ichneumonidae	*Xanthopimpla praeclara*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Ichneumonidae	*Xanthopimpla messelensis*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Ichneumonidae	*Scambus fossilobus*	body fossil	Spasojevic, Wedmann & Klopfstein, 2018		
Megachilidae	*Friccomelissa schopowi*	body fossil	Wedmann, Wappler & Engel, 2009		
Megachilidae	*Phagophytichnus* sp. indet.	ichnofossil		Wedmann et al. 2009	
Pompilidae	Pompilidae gen. et sp. indet.	body fossil		Lutz 1988	
Proctotrupoidea	Proctotrupoidea gen. et sp. indet.	body fossil		Lutz 1990	
Scoliidae	Scoliidae gen. et sp. indet.	body fossil		Lutz 1990	
Siricidae	*Xoanon? eocenicus*	body fossil	Wedmann, Pouillon & Nel, 2014		
Sphecidae	Sphecidae gen. et sp. indet.	body fossil		Lutz 1990	
Stephanidae	Stephanidae gen. et sp. indet.	body fossil		Wedmann 2018	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Tenthredinidae	Tenthredinidae gen. et sp. indet.	body fossil		Wedmann 2018	
Tenthredinidae	Damage type 146	ichnofossil		Albrecht et al. 2023	
Tenthredinidae	Damage type 187	ichnofossil		Albrecht et al. 2023	
Tenthredinidae	Damage type 197	ichnofossil		Albrecht et al. 2023	
Tenthredinidae	Damage type 209	ichnofossil		Albrecht et al. 2023	
Tiphiidae	Tiphiidae gen. et sp. indet.	body fossil		Lutz 1990	
Vespidae	*Vespula? hassiaca*	body fossil	Abels & Wedmann, 2022		
Arthropoda: Insecta: Mecoptera					
Incertae sedis	Mecoptera indet.	body fossil		Wedmann 2018	
Arthropoda: Insecta: Diptera					
Agromyzidae	Damage type 207	ichnofossil		Albrecht et al. 2023	
Asilidae	Asilidae gen. et sp. indet.	body fossil		Tröster 1992	
Bibionidae	*Plecia* aff. *acourti*	body fossil	Cockerell, 1921	Skartveit & Wedmann 2015	
Bibionidae	*Plecia hoffeinsorum*	body fossil	Skartveit, 2009	Skartveit & Wedmann 2015	
Bibionidae	*Plecia* sp. indet. 1	body fossil		Skartveit & Wedmann 2015	
Bombyliidae	*Comptosia pria*	body fossil	Wedmann & Yeates, 2008		
Cecidomyiidae	Damage type 55	ichnofossil			T. Wappler, pers. obs.
Cecidomyiidae	Damage type 142	ichnofossil		Albrecht et al. 2023	
Cecidomyiidae	Damage type 206	ichnofossil		Albrecht et al. 2023	
Cecidomyiidae	Damage type 215	ichnofossil		Albrecht et al. 2023	
Cecidomyiidae	Damage type 218	ichnofossil		Albrecht et al. 2023	
Ceratopogonidae	Ceratopogonidae gen. et sp. indet.	body fossil		Wedmann 2018	
Chaoboridae	Chaoboridae gen. et sp. indet.	body fossil		Richter & Baszio 2001a; Richter & Wedmann 2005	
Chironomidae	Tanypodinae gen. et sp. indet.	body fossil		Richter & Wedmann 2005	
Chironomidae	Chironomidae gen. et sp. indet.	body fossil		Richter & Baszio 2001a	
Culicidae	Culicidae gen. et sp. indet.	body fossil		Richter & Baszio 2001a	
Mycetophilidae	Mycetophilidae gen. et sp. indet.	body fossil		Wedmann 2018	
Nemestrinidae	cf. *Hirmoneura* sp. indet.	body fossil		Wedmann 2007	
Nemestrinidae	*Hirmoneura messelense*	body fossil	Wedmann, Hörnschemeyer, Engel, Zetter, & Grimsson, 2021	Wedmann et al. 2021b	
Nematocera	Nematocera larvae	body fossil		Lutz 1991	
Rhagionidae or Athericidae	cf. Rhagionidae or Athericidae gen. et sp. indet.	body fossil		Lutz 1990	
Sciaridae	Sciaridae gen. et sp. indet.	body fossil		Wedmann 2018	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Stratiomyidae	Stratiomyidae gen. et sp. indet.	body fossil		Tröster 1992	
Syrphidae	Syrphidae gen. et sp. indet.	body fossil		Lutz 1990	
Tabanidae	cf. Tabanidae gen. et sp. indet.	body fossil		Lutz 1991	
Tipulidae	Tipulidae gen. et sp. indet.	body fossil		Lutz 1990	
Arthropoda: Insecta: Trichoptera					
Limnephilidae	Limnephilidae gen. et sp. indet.	body fossil		Martini & Richter 1996	
Incertae sedis	Trichoptera indet.	body fossil		Lutz 1990; Habersetzer et al. 1994	
Arthropoda: Insecta: Lepidoptera					
Agonoxenidae	Damage type 317	ichnofossil			T. Wappler, pers. obs.
?Cosmopterigidae	?Cosmopterigidae	ichnofossil		Schaarschmidt & Wilde 1986	
Gracillariidae	Damage type 185	ichnofossil		Albrecht et al. 2023	
Lyonetiidae	Damage type 210	ichnofossil		Albrecht et al. 2023	
Macrolepidoptera	Macrolepidoptera indet.	body fossil		Habersetzer et al. 1994	
Micropterigidae	Micropterigidae indet.	body fossil		Habersetzer et al. 1994	
Nepticulidae	Damage type 208	ichnofossil		Kinzelbach 1970b; Albrecht et al. 2023	
Nymphalidae	Damage type 220	ichnofossil		Albrecht et al. 2023	
Psychidae	Damage type 224	ichnofossil			T. Wappler, pers. obs.
?Zygaenidae	gen. et sp. indet. 1	body fossil		McNamara et al. 2011	
?Zygaenidae	gen. et sp. indet. 2	body fossil		McNamara et al. 2011	
Incertae sedis	Lepidoptera indet.	body fossil		Lutz 1990; Richter & Baszio 2001a	
Arthropoda: Insecta: Incertae sedis					
Incertae sedis	Damage type 1	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 2	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 3	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 4	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 5	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 6	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 7	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 8	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 9	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 12	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 13	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 14	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 15	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 16	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 17	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 19	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 22	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 25	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 26	ichnofossil		Albrecht et al. 2023	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	Damage type 29	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 30	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 31	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 32	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 33	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 34	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 36	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 37	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 38	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 41	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 43	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 45	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 49	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 50	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 53	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 54	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 57	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 61	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 62	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 68	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 76	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 78	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 79	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 80	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 81	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 84	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 85	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 90	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 91	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 92	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 105	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 106	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 109	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 119	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 120	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 137	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 152	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 163	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 164	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 165	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 168	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 176	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 188	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 189	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 190	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 194	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 195	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 196	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 198	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 201	ichnofossil		Albrecht et al. 2023	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	Damage type 203	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 211	ichnofossil		Albrecht et al. 2023	
Incertae sedis	Damage type 219	ichnofossil		Albrecht et al. 2023	
Actinopterygii: Holostei					
Amiidae	*Cyclurus kehreri*	body fossil	(Andreae, 1893)	Micklich 1985; Grande & Bemis 1998	
Lepisosteidae	*Atractosteus messelensis*	body fossil	Grande, 2010	Kinkelin 1884; Micklich 1985	
Lepisosteidae	*Masillosteus kelleri*	body fossil	Micklich & Klappert, 2001	Grande 2010	
Incertae sedis	Coprolite type 4	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite type 5	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite type 6	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite type 11	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite type 12	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite type 13	ichnofossil		Schmitz 1991	
Actinopterygii: Incertae sedis					
Thaumaturidae	*Thaumaturus intermedius*	body fossil	Weitzel, 1933a	Micklich 1985; Micklich & Arratia 2022	
Incertae sedis	Coprolite Type A	ichnofossil		Richter & Baszio 2001b	Possibly the same as Type 7a of Schmitz (1991); see below
Incertae sedis	Coprolite Type B	ichnofossil		Richter & Baszio 2001b	Reportedly same as Type 7b of Schmitz (1991) (Richter & Baszio, 2001b: 78), but size clearly wrong
Incertae sedis	Coprolite Type C	ichnofossil		Richter & Baszio 2001b	
Incertae sedis	Coprolite Type 7a	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite Type 14	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite Type 15	ichnofossil		Schmitz 1991	
Actinopterygii: Elopomorpha					
Anguillidae	*Anguilla ignota*	body fossil	Micklich, 1985	Micklich 1983	
Actinopterygii: Centrarchiformes					
Centrarchidae?	*Rhenanoperca minuta*	body fossil	Gaudant & Micklich, 1990		
Actinopterygii: Perciformes					
Moronidae	*Palaeoperca proxima*	body fossil	Micklich, 1978	Micklich 1985	
Percichthyidae?	*Amphiperca multiformis*	body fossil	Weitzel, 1933a	Micklich 1985, 1987	
Sarcopterygii?: Dipnoi?					
Incertae sedis	Coprolite Type 3	ichnofossil		Schmitz 1991	Heterpolar spiral type known only from upper "coaly facies," now completely mined away; attribution to Dipnoi considered by Schmitz (1991) more probable than to Selachii, in part due to abundant plant remains in one such coprolite
Amphibia: Anura					

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Palaeobatrachidae	*Messelobatrachus tobieni*	body fossil	Wuttke in Sanchiz, 1998		
Palaeobatrachidae	Taxon nov.	body fossil		Morlo et al. 2004	
Pelobatidae	*Eopelobates wagneri*	body fossil	(Weitzel, 1938)	Wuttke 2012a; Rocek et al. 2014	
Incertae sedis	*Lutetiobatrachus gracilis*	body fossil	Wuttke in Sanchiz, 1998	Wuttke 2012b	
Amphibia: Caudata					
Salamandridae	*Chelotriton robustus*	body fossil	Westphal, 1980		
Salamandridae	*Chelotriton* sp. nov.	body fossil		Wuttke 2018	
“reptiles”: Squamata					
Anguidae	*Ophisauriscus quadrupes*	body fossil	Kuhn, 1940	Sullivan et al. 1999	
Anguidae	*Placosauriops abderhaldeni*	body fossil	(Kuhn, 1940)	Keller 2009	
Corytophanidae	*Geiseltaliellus maarius*	body fossil	K.T. Smith, 2009	Rossmann 2000a, 2001; K.T. Smith & Scanferla 2016	
Eolacertidae	*Eolacerta robusta*	body fossil	Nöth, 1940	Müller 2001; Čerňanský & Smith 2018, 2019	
Eolacertidae	*Stefanikia siderea*	body fossil	Čerňanský & Smith, 2017	Čerňanský & Smith 2018	Print publication in 2018
Eolacertidae	*Cryptolacerta hassiaca*	body fossil	Müller et al. 2011	Longrich et al. 2015	
Helodermatidae	*Eurheloderma* sp.	body fossil		K.T. Smith et al. 2018	
Lacertoidea	Taxon nov.	body fossil			K.T. Smith, pers. obs.
Palaeovaranidae	Taxon nov. (‘necromin’)	body fossil		K.T. Smith et al. 2018	Small ‘necrosaur’
Palaeovaranidae	*Paranecrosaurus feisti*	body fossil	(Stritzke, 1983)	K.T. Smith & Habersetzer 2021	
Polychrotidae	Taxon nov.	body fossil		K.T. Smith et al. 2018	
Shinisauridae	Taxon nov.	body fossil		K.T. Smith 2017	
Incertae sedis	Taxon nov. (‘curly-tail’)	body fossil		K.T. Smith et al. 2018	Originally suspected to be a lacertoid, now being re-described as an anguimorph (Čerňanský & Smith, in preparation)
Incertae sedis	Gekkota Taxon nov.	body fossil		K.T. Smith et al. 2018	
Incertae sedis	*Ornatocephalus metzleri*	body fossil	Weber, 2004		
“reptiles”: Squamata: Serpentes					
Boidae	*Eoconstrictor fischeri*	body fossil	(Schaal, 2004)	Smith & Scanferla 2016; Scanferla & Smith 2020	
Charinaidae	*Rageryx schmidi*	body fossil	K.T. Smith & Scanferla, 2021		
Messelopythonidae	*Messelopython freyi*	body fossil	Zaher & Smith, 2020	Szyndlar & Böhme 1993	
Messelopythonidae	*Palaeopython schaali*	body fossil	K.T. Smith & Scanferla, 2022		
Ungaliophiidae	*Messelophis variatus*	body fossil	Baszio, 2004	Scanferla et al. 2016; Scanferla & Smith 2020	
Ungaliophiidae	*Rieppelophis ermannorum*	body fossil	(Schaal & Baszio, 2004)	Scanferla et al. 2016; Scanferla & Smith 2020	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
"reptiles": Testudines					
Carettochelyidae	*Allaeochelys crassesculptata*	body fossil	(Harrassowitz, 1922)	Joyce et al. 2012	
Geoemydidae	*Palaeoemys messeliana*	body fossil	(Staesche, 1928)	Hervet 2004; Claude & Tong 2004; Ascarrunz et al. 2021	Includes *Francellia*
Geoemydidae?	"ptychogasterid" ?	body fossil		Ascarrunz & Joyce 2024	
Podocnemididae	*Neochelys franzeni*	body fossil	Schleich, 1993	Cadena 2015	
Trionychidae	*"Trionyx" messeliana*	body fossil	Reinach, 1900	Cadena 2016; Georgalis & Joyce 2017	
"reptiles": Crocodylia					
Alligatoridae	*Allognathosuchus gracilis*	body fossil	Rauhe & Rossmann, 1995		Not yet fully evaluated
Alligatoridae	*Hassiacosuchus haupti*	body fossil	Weitzel, 1935	Berg 1966; Brochu 2004	
Bergisuchidae	*Bergisuchus dietrichbergi*	body fossil	Kuhn, 1968	Berg 1966	
Crocodylidae	*Asiatosuchus germanicus*	body fossil	Berg, 1966		
Leidyosuchidae	*Diplocynodon darwini*	body fossil	Ludwig, 1977	Berg 1966; Rauhe & Rossmann 1995; Brochu 1999	
Leidyosuchidae	*Diplocynodon deponiae*	body fossil	(Frey et al. 1987)	Rauhe & Rossmann 1995; Delfino & Smith 2012	
Planocraniidae	*Boverisuchus magnifrons*	body fossil	Kuhn, 1938	Berg 1966; Rossmann 1999, 2000b, 2000c; Rossmann et al. 2000; Brochu 2012	
Tomistominae	Taxon indet.	body fossil		Rossmann 2002	
Incertae sedis	Coprolite type 1	ichnofossil		Schmitz 1991	
Incertae sedis	Coprolite type 2	ichnofossil		Schmitz 1991	
"reptiles": Diapsida indet.					
Incertae sedis	Coprolite type 8	ichnofossil		Schmitz 1991	Carnivorous turtles have not been excluded
Incertae sedis	Coprolite type 9	ichnofossil		Schmitz 1991	Carnivorous turtles have not been excluded
Incertae sedis	Coprolite type 10	ichnofossil		Schmitz 1991	Carnivorous turtles have not been excluded
Aves: Palaeognathae					
Lithornithidae	*Lithornis* sp.	body fossil		Mayr 2008a, 2009a	
Palaeotididae	*Palaeotis weigelti*	body fossil	Lambrecht, 1928	Houde & Haubold 1987; Peters 1988	
Aves: Galloanseres					
Gallinuloididae	*Paraortygoides messelensis*	body fossil	Mayr, 2000a	Mayr 2006a	
Gastornithidae	*Gastornis* cf. *geiselensis*	body fossil	(K. Fischer, 1978)		
Perplexicervicidae	*Perplexicervix microcephalon*	body fossil	Mayr, 2010	Mayr 2007	
Aves: Mirandornithes					
Juncitarsidae	*Juncitarsus merkeli*	body fossil	(Peters, 1987a)	Mayr 2014	
Aves: Charadriiformes					

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
cf. Jacanidae	*Vanolimicola longihallucis*	body fossil	Mayr, 2017a		
Charadriiformes	gen. et sp. indet.	body fossil		Mayr 2000e	
Aves: Gruiformes					
Messelornithidae	*Messelornis cristata*	body fossil	Hesse, 1988	Hesse 1990	
Aves: Aequornithes					
Threskiornithidae	*Rhynchaeites messelensis*	body fossil	Wittich, 1898	Peters 1983; Mayr 2022	
Incertae sedis	*Masillastega rectirostris*	body fossil	Mayr, 2002a		
Aves: Otidimorpha					
cf. Foratidae	cf. *Foro*	body fossil		Mayr 2016a	
Aves: Incertae sedis					
Eopachypterygidae	*Eopachypteryx praeterita*	body fossil	Mayr, 2015a		
Eopachypterygidae	*Eopachypteryx* sp.	body fossil		Mayr 2015a	
Incertae sedis	*Palaeopsittacus* cf. *georgei*	body fossil	Harrison, 1982	Mayr 2003a	
Incertae sedis	*Lapillavis incubarens*	body fossil	Mayr, 2016a		
Aves: Strisores					
Apodidae	*Scaniacypselus szarskii*	body fossil	(Peters, 1985)	Mayr 2015c	
Archaeotrogonidae	*Hassiavis laticauda*	body fossil	Mayr, 1998a	Mayr 2004	
Nyctibiidae	*Paraprefica major*	body fossil	Mayr, 1999a	Mayr 2005a	
Nyctibiidae	*Paraprefica kelleri*	body fossil	Mayr, 1999a		
Podargidae	*Masillapodargus longipes*	body fossil	Mayr, 1999a	Mayr 2015b	
?Pan-Trochilidae	*Parargornis messelensis*	body fossil	Mayr, 2003b		
Incertae sedis	*Protocypselomorphus manfredkelleri*	body fossil	Mayr, 2005b		
Incertae sedis	*Cypseloramphus dimidius*	body fossil	Mayr, 2016a		
Aves: Strigiformes					
Palaeoglaucidae	*Palaeoglaux artophoron*	body fossil	Peters, 1992		
Aves: Coliiformes					
Pan-Coliidae	*Masillacolius brevidactylus*	body fossil	Mayr & Peters, 1998		
Coliidae	*Selmes absurdipes*	body fossil	Peters, 1999	Mayr 2001	
Coliidae	*Chascacocolius cacicirostris*	body fossil	Mayr, 2005c		
Sandcoleidae	*Eoglaucidium pallas*	body fossil	K. Fischer, 1987	Mayr & Peters 1998	
Sandcoleidae	*Eoglaucidium* sp.	body fossil		Mayr & Peters 1998	
Aves: Leptosomiformes					
Incertae sedis	*Plesiocathartes kelleri*	body fossil	Mayr, 2002b		
Aves: Trogoniformes					
Incertae sedis	*Masillatrogon pumilio*	body fossil	(Mayr, 2005d)	Mayr 2009b	
Aves: Picocoraciades					
Eocoraciidae	*Eocoracias brachyptera*	body fossil	Mayr & Mourer-Chauviré, 2000		
Gracilitarsidae	*Gracilitarsus mirabilis*	body fossil	Mayr, 1998b		
Primobucconidae	*Primobucco frugilegus*	body fossil	Mayr, Mourer-Chauviré & Weidig, 2004		

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Primobucconidae	*Primobucco perneri*	body fossil	Mayr, Mourer-Chauviré & Weidig, 2004		
Incertae sedis	*Quasisyndactylus longibrachis*	body fossil	Mayr, 1998b		
Aves: Bucerotiformes					
Messelirrisoridae	*Messelirrisor grandis*	body fossil	Mayr, 2000b		
Messelirrisoridae	*Messelirrisor halcyrostris*	body fossil	Mayr, 1998b		
Messelirrisoridae	*Messelirrisor parvus*	body fossil	Mayr, 1998b	Mayr 2006b	
Aves: Cariamiformes					
Ameghornithidae	*Strigogyps sapea*	body fossil	(Peters, 1987b)	Mayr 2005e	
Ameghornithidae	*Strigogyps* sp.	body fossil		Mayr 2005e	
?Idiornithidae	*"Dynamopterus" tuberculatus*	body fossil	(Peters, 1995)		
Idiornithidae	*Dynamopterus* cf. *itardiensis*	body fossil	(Mourer-Chauviré, 1983)	Mayr 2000c	
Salmilidae	*Salmila robusta*	body fossil	Mayr, 2000d	Mayr 2002c	
Aves: Eufalconimorphae Incertae sedis					
Vastanavidae	*Avolatavis* sp.	body fossil		Mayr 2016b; Mayr & Kitchener 2023	
cf. Vastanavidae	*Eurofluvioviridavis robustipes*	body fossil	Mayr, 2005f		
Aves: Falconiformes					
Masillaraptoridae	*Masillaraptor parvunguis*	body fossil	Mayr, 2006c	Mayr 2009c; Mayr & Kitchener 2022	
Aves: Psittacopasseres					
Halcyornithidae	*Serudaptus pohli*	body fossil	Mayr, 2000c		
Halcyornithidae	gen. et sp. indet.	body fossil		Mayr 1998c, 2017b	
Halcyornithidae	*Pseudasturides* sp.	body fossil		Mayr 1998c	
Halcyornithidae	*Pseudasturides macrocephalus*	body fossil	(Mayr, 1998c)		
cf. Psittacopedidae	*Pumiliornis tessellatus*	body fossil	Mayr, 1999b	Mayr 2008b; Mayr & Wilde 2014	
Psittacopedidae	*Psittacopes lepidus*	body fossil	Mayr & Daniels, 1998		
Zygodactylidae	*Primozygodactylus ballmanni*	body fossil	Mayr, 1998b		
Zygodactylidae	*Primozygodactylus major*	body fossil	Mayr, 1998b		
Zygodactylidae	*Primozygodactylus danielsi*	body fossil	Mayr, 1998b		
Zygodactylidae	*Primozygodactylus longibrachium*	body fossil	Mayr, 2017c		
Zygodactylidae	*Primozygodactylus quintus*	body fossil	Mayr, 2017c		
Zygodactylidae	*Primozygodactylus eunjooae*	body fossil	Mayr & Zelenkov, 2009	Mayr 2017c	
Incertae sedis	*Messelastur gratulator*	body fossil	Peters, 1994	Mayr 2011	
Aves: Incertae sedis					
Incertae sedis	sp. 1	body fossil	Mayr, 2017b		
Incertae sedis	sp. 2	body fossil	Mayr, 2017b		
Incertae sedis	sp. 3	body fossil	Mayr, 2017b		
Incertae sedis	sp. 4	body fossil	Mayr, 2017b		

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Incertae sedis	sp. 5	body fossil	Mayr, 2017b		
Incertae sedis	sp. 6	body fossil	Mayr, 2017b		
Incertae sedis	sp. 7	body fossil	Mayr, 2017b		
Incertae sedis	sp. 8	body fossil	Mayr, 2017b		
Incertae sedis	sp. 9	body fossil	Mayr, 2017b		
Incertae sedis	sp. 10	body fossil	Mayr, 2017b		
Incertae sedis	sp. 11	body fossil	Mayr, 2017b		
Incertae sedis	Coprolite type 9	ichnofossil		Schmitz 1991	
Mammalia: Marsupialia					
Herpetotheriidae	*Amphiperatherium* sp.	body fossil		Filhol 1879; Storch 1993a; Kurz 2007	First described as *A.* aff. *maximum* or *A.* cf. *maximum* (Storch 1993a), the specific attribution of this large specimen remains doubtful (Kurz 2018)
Herpetotheriidae	*Amphiperatherium goethei*	body fossil	Crochet, 1979	Storch 1993a; Kurz 2007	
Herpetotheriidae	Herpetotheriidae indet.	body fossil		Kurz 2007	Since the teeth of that single specimen could not be studied in details yet, the attribution remains unspecific
Peradectidae	*"Peradectes"*	body fossil		Matthew & Granger 1921; Koenigswald & Storch 1988; Kurz 2007	Initially described as *Peradectes* sp. by Koenigswald & Storch (1988), the exact taxonomic identification of these 3 specimens remains unclear.
Mammalia: Eutheria Incertae sedis					
Apatemyidae	*Heterohyus nanus*	body fossil	Teilhard de Chardin, 1921	Koenigswald & Schierning 1987; Koenigswald 1990; Kalthoff et al. 2004	Since the occlusal surface of the teeth could not yet be studied, the attribution to *H. nanus* is only based on size
Pantolestidae	*Buxolestes piscator*	body fossil	Koenigswald, 1980	Koenigswald 1987; Pfretzschner 1993	
Pantolestidae	*Buxolestes minor*	body fossil	Pfretzschner, 1999	Rose et al. 2014	According to Rose et al. (2014), it is possible that the only known specimen of *B. minor* is actually a juvenile individual of *B. piscator*.
Paroxyclaenidae	*Kopidodon macrognathus*	body fossil	(Wittich, 1902)	Weitzel 1933b; Koenigswald 1983; Clemens & Koenigswald 1993	
Pseudorhyncocyonidae	*Leptictidium tobieni*	body fossil	Koenigswald & Storch, 1987	Frey et al. 1993; Christian 1999	
Pseudorhyncocyonidae	*Leptictidium nasutum*	body fossil	Storch & Lister, 1985	Maier et al. 1986; Koenigswald & Wuttke 1987	

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Pseudorhyncocyonidae	*Leptictidium auderiense*	body fossil	Tobien, 1962	Hooker 2013; Ruf et al. 2016	
Mammalia: Lipotyphla					
Amphilemuridae	*Macrocranion tenerum*	body fossil	(Tobien, 1962)	Storch 1993b, 1996	
Amphilemuridae	*Macrocranion tupaiodon*	body fossil	Weitzel, 1949	Maier 1977, 1979	
Amphilemuridae	*Pholidocercus hassiacus*	body fossil	Koenigswald & Storch, 1983	MacPhee et al. 1988	
Incertae sedis	Taxon nov.	body fossil		Gunnell et al. 2018	The stomach content of *Lesmesodon edingeri* SMF-ME 3843a includes the partial remains of a lipotyphlan mammal yet unknown to Messel. Its study is in progress.
Mammalia: Hyaenodontida					
Hyaenodontidae	*Lesmesodon edingeri*	body fossil	(Springhorn, 1982)	Springhorn 1988; Morlo & Habersetzer 1999	
Hyaenodontidae	*Lesmesodon behnkeae*	body fossil	Morlo & Habersetzer, 1999		
Mammalia: Pholidotamorpha					
Eomanidae	*Eomanis waldi*	body fossil	Storch, 1978	Gaudin et al. 2009; Gunnell et al. 2018	
Incertae sedis	*Euromanis krebsi*	body fossil	(Storch & Martin, 1994)	Gaudin et al. 2009; Gunnell et al. 2018	
Incertae sedis	*Eurotamandua joresi*	body fossil	Storch, 1981	Gaudin et al. 2009; Gunnell et al. 2018	The systematic position of this species was heavily debated. We follow the current state of research that seems to support the inclusion of *E. joresi* in Pholidotamorpha
Mammalia: Rodentia					
Ailuravidae	*Ailuravus macrurus*	body fossil	Weitzel, 1949	Tobien 1954; Gwosdek 1996	
Gliridae	*Eogliravus wildi*	body fossil	Hartenberger, 1971	Storch & Seiffert 2007	
Incertae sedis	*Masillamys parvus*	body fossil	Tobien, 1954	Vianey-Liaud et al. 2019	
Incertae sedis	*Masillamys beegeri*	body fossil	Tobien, 1954	Vianey-Liaud et al. 2019	
Incertae sedis	*Masillamys krugi*	body fossil	Tobien, 1954	Vianey-Liaud et al. 2019	
Mammalia: Chiroptera					
Archaeonycterididae	*Archaeonycteris trigonodon*	body fossil	Revilliod, 1917		
Archaeonycterididae	*Archaeonycteris pollex*	body fossil	Storch & Habersetzer, 1988		
Emballonuridae	*Tachypteron franzeni*	body fossil	Storch, Sigé & Habersetzer, 2002		
Hassianycterididae	*Hassianycteris messelensis*	body fossil	J.D. Smith & Storch, 1981		

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Hassianycterididae	*Hassianycteris magna*	body fossil	J.D. Smith & Storch, 1981		
Hassianycterididae	*Hassianycteris*? *revilliodi*	body fossil	(Russell & Sigé, 1970)	Morlo et al. 2004	
Palaeochiropterygidae	*Palaeochiropteryx* sp. nov.	body fossil			R. Rabenstein & J. Habersetzer, pers. obs.
Palaeochiropterygidae	*Palaeochiropteryx spiegeli*	body fossil	Revilliod, 1917		
Palaeochiropterygidae	*Palaeochiropteryx tupaiodon*	body fossil	Revilliod, 1917		
Mammalia: Primates: Adapiformes					
Cercamoniinae	*Europolemur koenigswaldi*	body fossil	Franzen, 1987		
Cercamoniinae	*Europolemur kelleri*	body fossil	Franzen, 2000		
Cercamoniinae	*Darwinius massilae*	body fossil	Franzen et al. 2009		
Mammalia: Carnivora					
Miacidae	*Messelogale kessleri*	body fossil	(Springhorn, 1982)		
Miacidae	*Paroodectes feisti*	body fossil	Springhorn, 1980		
Mammalia: Perissodactyla					
Hyrachyidae	*Hyrachyus minimus*	body fossil	(J. B. Fischer, 1829)	Franzen 1981a; Hellmund 2016	
Lophiodontidae	*Lophiodon* sp.	body fossil		Tobien 1988	Presence based on a single tooth published by Tobien (1988) and the unpublished complete skeleton of a juvenile individual (SMF-ME 1931)
Palaeotheriidae	*Eurohippus messelensis*	body fossil	(Haupt, 1925)	Franzen 2006, 2007	*E. messelensis* is sometimes alternatively considered a sub-species of *E. parvulus* (Laurillard 1849)
Palaeotheriidae	*Propalaeotherium hassiacum*	body fossil	Haupt (1925)	Franzen 2007	
Palaeotheriidae	*Propalaeotherium voigti*	body fossil	(Matthes, 1977)	Franzen 2007, 2018	
Incertae sedis	*Hallensia matthesi*	body fossil	Franzen & Haubold, 1986	Franzen 1990, 2007	
Mammalia: Artiodactyla					
Choeropotamidae	*Masillabune martini*	body fossil	Tobien, 1980	Tobien 1985; Erfurt & Haubold 1989	
Dichobunidae	*Messelobunodon schaeferi*	body fossil	Franzen, 1981b	Franzen 1983; Erfurt & Sudre 1996	
Dichobunidae	*Aumelasia* cf. *gabineaudi*	body fossil	Sudre, 1980	Franzen 1988; Erfurt & Métais 2007	
Dichobunidae	*Eurodexis* sp.	body fossil		Franzen 1983; Erfurt & Sudre 1996; Erfurt & Métais 2007	
Mammalia: cf. Dermoptera					

Family-group affiliation	Taxon	Organ/Part	Taxonomic Authority	Major additional references	Notes
Plagiomenidae?	Indet.	body fossil		Szalay & Schrenk 2002	The single known specimen, a partial skeleton, shows similarities to modern dermopterans and is linked to the only known (from dental remains) possibly dermopteran Eocene family: Plagiomenidae
Mammalia: Incertae sedis					
Incertae sedis	Gen. et sp. indet.	body fossil			T. Lehmann, pers. obs.

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Data availability Our new compilation of specimen data on amphibians, reptiles, and mammals are found in Supplementary Information together with lists summarising fishes, birds, palynomorphs, and fruit and seed taxa from existing literature. Input/output files for species richness analyses (Supplementary Data S1–S49) are available at: https://dataportal.senckenberg.de/dataset/a5d74b47-1dac-45fd-8465-1be5a79863ea.

Code availability R code for species richness analyses (Supplementary Data S1) is available at: https://dataportal.senckenberg.de/dataset/a5d74b47-1dac-45fd-8465-1be5a79863ea.

Declarations

Conflict of Interest KS is a member of the editorial board, and DU is editor-in-chief of the journal *Palaeobiodiversity and Palaeoenvironments*. KS, TL, DU, SW and MW are guest editors of the special issue on "Pre-Quaternary maar/volcanogenic lakes as *Konservat Lagerstätten*—Messel and beyond." None was involved in the peer review and decision process for this contribution. All other authors declare no competing interests.

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