Final author comments

Response to Reviewer 1:
Referee comment 1:
The manuscript submitted by Bouchal et al. is of very high quality. I fully agree with the methods and conclusions. This will be a very useful paper on the mid-Miocene climate change according to floras in the Eastern Mediterranean.

Author's response:
Thank you very much.

Referee comment 2:
I have just two suggestions: - the nearby Catakbagyaka Langhian pollen flora of (Jiménez-Moreno, 2005 - phd thesis pp. 109 and 212) should be used in the discussion because it contains several mega or mega-mesothermal taxa and 20 to 50% of herbs.

Author's response:
Thank you for drawing our attention to the Çatakbagyaka flora/fauna. The uncertain age of the Çatakbagyaka vertebrate fauna (MN5-MN8) has recently been revised to MN7-8 (see references in our changed manuscript). We refer to this locality in the revised text, considering it roughly coeval with Yeni Eskihisar and mentioning that the increased AP pollen ratios of the Çatakbagyaka flora fit with the general trend observed by us in the Yatagan Basin.

Author's changes in manuscript
The following lines concerning the Çatakbagyaka locality have been inserted in section "3.4 Changes in ratios arboreal to non-arboreal pollen", line 272 in revised manuscript.

…..shows again a higher proportion of arboreal taxa (67%). *Similarly, from the vertebrate locality Çatakbagyaka (revised age MN7+8, 12 km south of the Yatagan Basin) AP percentages range from c. 50% to c. 80% (Jiménez-Moreno, 2005; Mayda et al., 2016; Bouchal et al. 2017; Aiglstorfer et al. 2018).*

and in section "4.4 Detection of Miocene global climatic changes in the terrestrial fossil record", line 458 in revised manuscript.

…Eskihisar pollen assemblage clearly belongs to MN7+8. Here, *and in the nearby locality Çatakbagyaka* woody taxa *(including some warmth-loving taxa)* are again more prominent. Thus, although the correlation…..

Referee comment 3:
The herbs are often under-evaluated in pollen records that causes an significant bias to the ratio 'arboreal taxa/non-arboreal taxa' (see: Favre et al., 2008, Review of Palaeobotany and Palynology, 148, 13-35).

Author's response:
We use the threshold values given by Favre et al. (2008) in the revised manuscript. In

addition, we use the threshold values for local presence of European tree taxa (Lisitsyna et al., 2011 – reference in revised manuscript) to evaluate those pollen floras that are indicated as reflecting "herb-prevalent" environments based on the values given by Favre et al.

Author's changes in manuscript
The following lines concerning this comment have been inserted under "3.4 Changes in ratios arboreal to non-arboreal pollen", line 278 in revised manuscript.

We used the threshold (AP/NAP = 3.85) proposed by Favre et al. (2008) to separate between tree- and herb-prevalent environments. This ratio translates into AP percentages of close to 80% to predict reliably tree-prevalent landscapes. As can be seen in Supplementary Material S6, pollen zones 1 and 2 are largely dominated by forested environments. In the upper part of PZ2 (Tinaz, Eskihisar), PZ2/3 and PZ3 (Tinaz) herb-prevalent landscapes are inferred. However, it is noteworthy, that although NAP taxa are more abundant in these pollen zones, AP taxa remain to have fairly high percentages as well (Bouchal et al., 2016, 2017). For example, Fagus, Quercus deciduous and evergreen type, still are above the threshold values indicative of local tree presence (Lisitsyna et al., 2011). Hence, the opening of the vegetation in the upper parts of PZ2, and in PZ2/3, PZ3 may actually represent a coexistence of forest and open vegetation.

Referee comment 4:
- Beerling & Royer (2011) and Mai (1995) are not in the Reference list;

Author's response:
Have been added.

Referee comment 5:
 - I do not understand the reference to 'table S1' on lines 55 and407.

Author's response:
We apologize. This has been misleading. We meant table S1 in the paper of Beerling & Royer, 2011. This has been clarified in the revised manuscript.

Response to Reviewer 2:
Referee comment 1:
Bouchal et al. present a paleobotanic study from middle Miocene Anatolia using different approaches to reconstruct climate changes from existing data of the middle Miocene climate transition, ca. 15-13 Ma. The beauty of the study lies in the combination of three different reconstruction techniques, each with different underlying assumptions.
The authors combine the results of two taxonomical approaches – one relying on the nearest-living-relative principle and the other on biogeography of floras - with leaf physiognomy, which does not rely on taxonomy. The authors conclude that the climate of middle Miocene Anatolia could not have been tropical but would have been fully humid warm temperate. This result is important in the discussion about global latitudinal temperature gradients. The study also reveals increase of herbal vegetation in the mainly forested landscape of Anatolia during the global cooling after the mid-Miocene climate optimum. Moreover, the results of the study

concerning vegetation structure are important in the discussion about the landscape of Anatolia in relation with fossil faunas. Thus, the paper presents an elegant study with interesting results for a wide research spectrum.

Author's response:
Thank you very much.

Referee comment 2:
I would like, however, to give some suggestions that may help reaching that broader audience.
Primarily, the paper needs clear conclusions, which now are missing. I strongly urge the authors to provide them in a separate section.

Author's response:
A concluding paragraph has been added in the revised manuscript.

Author's changes in manuscript:
The following lines have been inserted in section "5. Conclusion" in Line 478 in the revised manuscript.

5. Conclusion
Here we used three proxies to infer climate, palaeoenvironments and biogeographic affinities of three middle Miocene floras of southwestern Anatolia. We showed that the palaeobotanical record resolves transitions from the warm MCO (16.8–14.7 Ma) into the MMCT (14.7–13.9 Ma), and a more pronounced cooling at 13.9–13.8 Ma, mainly expressed in the changing and fluctuating ratios between AP and NAP taxa. Using threshold percentages for main tree taxa, we further show that although NAP values significantly increased during the MMCT, AP taxa remained relatively abundant, signifying the coexistence of forested and open landscapes during this transition. In addition, the biogeographic analysis indicates mainly northern hemispheric biogeographic affinities of the middle Miocene flora of southwestern Anatolia and thus invalidates previous comparisons with tropical environments. Tropical climate conditions are also rejected by the Köppen signatures of the investigated floras and by the CLAMP analysis. Finally, the CLAMP data readily distinguish between strongly seasonal Cs and Cw and fully humid Cf climate types. More combined macrofossil and microfossil studies are needed for the Neogene of Turkey in order to establish a robust framework of terrestrial climate evolution in this important region.

Referee comment 3:
Secondly, the explanation of the Köppen signatures unfortunately hides in the supplementary information. I suggest fitting S2 into a table in the main text.

Author's response:
File S2 has been moved from the supplementary material to the main manuscript as Table 3.

Author's changes in manuscript:
Table 3 and table caption is now included in the main text.

Referee comment 4:
Please, also summarize CLAMP protocols and leaf characteristics (lobbing and tooth form, leaf size, apex form, base form, length-to-width ratio and shape) instead of referring to the website, only.

Author's response:
Additional text concerning this has been included in the final manuscript.

Author's changes in manuscript:
The following lines concerning the CLAMP have been inserted in section "2.4 CLAMP**",** line 172ff in the revised manuscript.

Referee comment 5:
I suggest plotting the CLAMP results of Tinaz and Eskihisar together in Figure 6. (The separate scores can be found in the supplementary material.)

Author's response:
This has been done in the revised manuscript.

Referee comment 6
Please explain explicitly what you mean with the question marks to 'marginal???' (line 194) and 'increased summer rainfall???' (line 363).

Author's response:
These were old edits not removed before submission. We apologize for this.

1 **Middle Miocene climate of southwestern Anatolia from multiple botanical proxies**

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Abstract

The middle Miocene climate transition (MMCT) was a phase of global cooling possibly linked to decreasing levels of atmospheric CO_2. The MMCT coincided with the European Mammal Faunal Zone MN6. From this time, important biogeographic links between Anatolia and eastern Africa include the hominid *Kenyapithecus*. Vertebrate fossils suggested mixed open and forested landscapes under (sub)tropical seasonal climates for Anatolia. Here, we infer the palaeoclimate during the MMCT and the succeeding cooling phase for a middle Miocene (14.8–13.2 Ma) intramontane basin in southwestern Anatolia using three palaeobotanical proxies: (i) Köppen signatures based on the nearest-living-relative principle. (ii) Leaf physiognomy analysed with the Climate Leaf Analysis Multivariate Program (CLAMP). (iii) Genus-level biogeographic affinities of fossil floras with modern regions. The three proxies reject tropical and hot subtropical climates for the MMCT of southwestern Anatolia and instead infer mild warm temperate *C* climates. Köppen signatures reject summer-dry *Cs* climates but cannot discriminate between fully humid *Cf* and winter-dry *Cw*; CLAMP reconstructs *Cf* climate based on the low X3.wet/X3.dry ratio. Additionally, we assess whether the palaeobotanical record does resolve transitions from the warm Miocene Climatic Optimum (MCO, 16.8–14.7 Ma) into the MMCT (14.7–13.9 Ma), and a more pronounced cooling at 13.9–13.8 Ma, as reconstructed from benthic stable isotope data. For southwestern Anatolia, we find that arboreal taxa predominate in MCO floras (MN5), whereas in MMCT floras (MN6) abundances of arboreal and non-arboreal elements strongly fluctuate indicating higher structural complexity of the vegetation. Our data show a distinct pollen zone between MN6 and MN7+8 dominated by herbaceous taxa. The boundary MN6 and MN7+8, roughly corresponding to a first abrupt cooling at 13.9–13.8 Ma, might be associated with this herb-rich pollen zone.

Keywords: Miocene; plant fossil; climate proxy; Köppen signatures; CLAMP; biogeography

1 Introduction

The middle Miocene (15.97–11.63 Ma, ICS-chart 2017/02, Cohen, 2013) is characterized by a warm phase lasting until ca. 15 Ma that was followed by a gradual cooling and the restoration of a major Antarctic ice sheet and first northern hemispheric glaciations (Holbourn et al., 2014). It has been suggested that the final closure of the Mediterranean gateway connecting the Mediterranean with the Indian Ocean and the resulting changes in ocean circulation might have been one of the reasons for the final expansion of the East Antarctic ice sheet around 14.8 Ma (Flower & Kennett, 1993). During the middle Miocene climate transition (MMCT) at 14.7 to 13.8 Ma a drop of sea surface temperatures of 6–7°C occurred (Shevenell et al., 2004). At the same time, different proxies to reconstruct atmospheric CO_2 levels for the Miocene Climatic Optimum (MCO), MMCT, and the succeeding more pronounced cooling, do not concur (Beerling & Royer, 2011). Specifically, stable isotope data from phytoplankton infer stable CO_2 levels for the Neogene, with minor fluctuations (MCO, 227–327 ppm, MMCT, 265–300 ppm; see table S1 of Beerling & Royer, 2011), while stomata densities from fossil leaves suggest a pronounced drop of CO_2 after the MCO (see table S 1 of Beerling & Royer, 2011).

The European Mammal Faunal Zone MN6 (14.8–13.8 Ma; Neubauer et al., 2015) coincides with the MMCT. From this period world-famous vertebrate faunas are known from western Anatolia (e.g. Andrews & Tobien, 1977; Mayda et al., 2015) including the hominoids *Griphopithecus alpani* in Çandır and Paşalar, and *Kenyapithecus kizili* in Paşalar (Stringer & Andrews, 2011). Geraads et al. (2003) investigated the depositional environment and large mammal fauna of Çandır close to Ankara and inferred open landscapes for this locality. Bernor et al. (1979, p. 86) analysed community structure of Turkish and European middle Miocene faunas and suggested that "*faunas adapted to woodland conditions were present …*

at localities such as Paşalar and Yeni Eskihisar [MN7+8]" while the "*Çandır fauna has a community structure more suggestive of closed woodland conditions*". This interpretation is

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74 the exact opposite of that by Geraads et al. (2003). Recent investigations using carnivore guild

75 structure suggest a "*mixed environment between tropical forest and open savannah*

76 *landscape*s" for Çandır and Paşalar (Mayda et al., 2015). Strömberg et al. (2007) investigated

77 phytoliths (plant silica bodies) from early to late Miocene deposits of Turkey and suggested

78 that open, grass-dominated habitats had become common in Turkey and adjacent areas by the

79 early Miocene (c. 20 Ma). In contrast, Kayseri-Özer (2017) using 'integrated plant record'

80 (IPR) analysis (Kovar-Eder et al., 2008) suggested that various forest types covered most of

81 western and Central Anatolia during the middle Miocene (*broad-leaved evergreen* and *mixed*

82 *mesophytic forests* and ecotones between these forests).

83 Here we use a large data set from recently published macrofossils and pollen, spores and cysts

84 from a well-dated middle Miocene basin in western Anatolia to infer palaeoclimate and

85 palaeoenvironments using three palaeobotanical proxies: climate affinity of modern analogues

86 ('nearest living relatives'; taxon-based approach), leaf physiognomy (a-taxonomic), and

87 biogeographic affiliation of plant communities (also taxon-based). The following research

88 questions are addressed: How do the three approaches resolve local climate conditions of

89 Anatolia during a phase of global cooling, ca. 15–13 million years ago? Do different proxies

90 agree on climate inference? Where do modern climates occur that correspond to middle

91 Miocene climates of western Anatolia? Can the palaeobotanical record resolve transitions

92 between MCO, MMCT, and the succeeding more pronounced cooling during the middle

93 Miocene?

94

95 **2 Material and methods**

96 **2.1 Geological setting**

97 The Yatağan Basin is a southeast trending graben (50 km long, 15 km wide) in the province

98 of Muğla, southwestern Turkey (Fig. 1). The Neogene basin fill is up to 600 m thick and

99 divided into the Eskihisar Formation (early to middle Miocene), the Yatağan Formation (late

Miocene to early Pliocene), and the Milet Formation (middle to late Pliocene; Alçiçek, 2010). The Eskihisar Formation comprises the Turgut Member (reddened alluvial-fan deposits followed by fluviatile deposits and lignites) and the Sekköy Member (fossiliferous limnic marls and limestones); all economically exploited lignite seams of the Yatağan Basin are confined to the transition zone of these two members (Atalay, 1980; Becker-Platen, 1970). For the present study, we investigated the palaeobotanical content (pollen and plant macrofossils) of the upper Turgut and the Sekköy members exposed at the lignite mines of Eskihisar, Salihpaşalar, and Tınaz (Fig. 1.2). The age of the investigated sediments is well constrained by mammal fossils (Eskihisar lignite gallery locality, MN6, *Gomphotherium angustidens* Cuvier 1817, *Percrocuta miocenica* Pavlov et Thenius 1965, Bouchal et al., 2017; Yeni Eskihisar vertebrate locality, MN 7/8, The NOW Community, 2018), and by radiometric dates from the upper Sekköy Member (13.2 Ma ± 0.35, Becker-Platen et al., 1977). Hence, the investigated pollen zones (PZ) 1, 2, 2/3, and the Yeni Eskihisar pollen assemblage represent the Neogene mammal zones MN6 and MN7+8, 14.8–13.2 Ma; Neubauer et al., 2015). The layers from which most of the leaf fossils originate correspond to PZ 2. A ~20 m section comprised of limestone and clayey limestone between PZ 2/3 and the Yeni Eskihisar assemblage is barren of palynological content (Fig. 2).

2.2 Plant material

The investigated plant material comprises roughly 1800 macrofossils (mainly leaf fossils) collected between 2010 and 2017. Macrofossils represent 77 taxa, of which five belong to gymnosperms and 72 to angiosperms. Pollen, spores and cysts from five pollen zones (Fig. 2) represent 182 taxa, of which one is a fungus, 9 are algae, 17 moss or fern allies spores, 15 gymnosperms, and 140 angiosperms (Supplementary Material S1; for taxonomic descriptions of the plant taxa see Yavuz-Işık et al., 2011; Bouchal et al., 2016, 2017; Bouchal, in press; Güner et al., 2017).

126

2.3 Köppen signatures

Fossil taxa that are resolved to genus or sectional level were represented by extant members

of the genera and sections as modern analogues. First, for accepted taxa (IPNI,

http://www.ipni.org/index.html; most recent regional floras and monographs) their

distribution ranges were determined. Then, 26 Köppen-Geiger climate types (see Table 3 for

detailed explanation of Köppen-Geiger climate types, and Kottek et al., 2006; Peel et al.,

2007; Rubel et al., 2017; Global_1986-2010_KG_5m.kmz) were mapped on modern

distribution ranges using Google Earth to establish 'Köppen signatures' (Denk et al. 2013) for

each modern analogue. Representation of different climate types was first scored for each

species within a genus as present (1)/absent (0). To summarize preferences for climate types

of all modern analogues, we used an implicit weighting scheme to discriminate between

modern analogues that are highly decisive (climatically constrained) vs. those that can be

found in many climate zones. The sum of each modern species' Köppen signature is always

one. For example, *Tilia chingiana* is present in two Köppen-Geiger climate types, *Cfa* and

*Cfb,*which count as 0.5 for each type , while *Tilia americana* is present in ten Köppen-Geiger

climate types (*As*, *Aw*, *Cfa*, *Cfb*, *Dfa*, *Dfb*, *Cwa*, *Cwb*, *BSk*, *BWh*), all counting as 0.1. The

Köppen signature of a genus or section, the modern analogue of a fossil taxon, is the sum of

its species' Köppen signatures for each climate type divided by the total number of scored

species for this genus. By this, the percentage representation of each Köppen-Geiger climate

type was determined for a genus/ section. In case of *Tilia*, the distribution ranges of 26 species

resulted in a genus Köppen signature as follows: *Cfa*, 22.1%, *Cfb*, 14.7%, *Cwa*, 19.9%, *Cwb*,

9.1%, *Dfb*, 5.7%, for the five most common climate types. Fig. 3.1 shows all climate types

realized in genus *Tilia*; Fig. 3.2 shows that the genus occurs predominantly in *Cf* and *Cw*

Köppen-Geiger climate types and that tropical and desert climates are nearly absent (see

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153   Supplementary Material S3 for genus-level scoring of Köppen-Geiger climate types for all

154   plant taxa encountered in the Yatağan basin fossil assemblages).

155   For taxa that are resolved to family-level only, mainly pollen taxa of herbaceous and a few

156   woody angiosperm groups, the distributions of extant members of the family were combined

157   into a general family distribution range and the corresponding Köppen-Geiger climate types

158   determined.

159   Genus-level Köppen-Geiger signals were used to account for possible niche evolution within

160   lineages/ species groups of a genus. For example, modern species of *Quercus* section *Ilex* are

161   typical members of sclerophyllous, evergreen Mediterranean forest and shrubland vegetation

162   thriving under a *Cs* (summer-dry warm temperate) climate in western Eurasia and to the south

163   of the eastern Hindu Kush and Karakorum ranges, but also occur in humid, mesophytic

164   forests from Afghanistan to East Asia (*Cf* and *Cw* climates). To account for this climate niche

165   variability, all species of sect. *Ilex* were scored for the general Köppen signature of sect. *Ilex*.

166   Hence, the entire section was used as modern analogue, the nearest living relative (NLR), for

167   several fossil species of *Quercus* sect. *Ilex*.

168

169   **2.4 CLAMP**

170   We inferred quantitative palaeoclimate parameters for the three Yatağan Basin floras using

171   the Climate Leaf Analysis Multivariate Program (CLAMP) (Yang et al., 2011). CLAMP

172   makes use of the relationship between leaf physiognomy of dicotyledonous flowering plants

173   and climate and, hence, is a non-taxonomic approach to palaeoclimate inference (Spicer,

174   2008). CLAMP calibrates the numerical relations between leaf physiognomy of woody

175   dicots and meteorological parameters in modern terrestrial environments. With this

176   calibration, past climatic data can be determined from leaf fossil assemblages if the

177   sampling of the fossil assemblage represents well the characteristics of the living source

178   vegetation (http://clamp.ibcas.ac.cn). Modern and fossil leaf physiognomic data are

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positioned in multidimensional physiognomic space using canonical correspondance analysis (CANOCO; Ter Braak, 1986). CANOCO orders vegetation sites based on a set of attributes (leaf physiognomic characters).

For modern sites, climate variables are known from long-term observations of climate stations or from high-resolution gridded climate data (New et al., 1999, 2002; Spicer et al., 2009). Vectors for each of the measured climate variables can be positioned in physiognomic space and calibrated. Palaeoclimate variables can then be quantified by scoring a fossil assemblage in the same manner as for the modern vegetation and positioning the fossil site in physiognomic space (http://clamp.ibcas.ac.cn).

For the present study, 36 different leaf characters (including leaf shape and size, apex shape, base shape, and leaf margin characteristics) were scored for 61, 63, and 14 dicotyledonous leaf morphotypes from three localities, Tınaz, Eskihisar, and Salihpaşalar (see Supplementary Material S3 for scoring of morphotypes), following the CLAMP protocols (http://clamp.ibcas.ac.cn). At genus level, the floras of the Yatağan Basin show highest similarity with Eurasian extant woody angiosperms (Table 1), thus the PhysgAsia1 Calibration files dataset of CLAMP was used to position the fossil data.

2.5 Genus level biogeographic affinities

For all fossil taxa determined to genus level, the present distribution was tabulated indicating presence/absence of a genus in western Eurasia, East Asia, eastern North America, western North America, and Africa (Table 1).

3 Results

3.1 Climate inference from Köppen signatures (Fig. 5, Supplementary Materials S4, S5)

For the fossil plant assemblages warm temperate to temperate *C* and *D* climates accounted for almost 80% of the realized Köppen-Geiger climate types of all taxa in a fossil plant

217 assemblage (using genus-level NLR). The sum of *Cf*, *Df*, *Cw* and *Dw* climates amounted to

218 60–70% in all assemblages (highest scores in macrofossil assemblages).

219 Overall, the best represented Köppen-Geiger climate types when using genus-level NLR were

220 *Cfa* (warm temperate, fully humid, hot summer), followed by *Cfb* (warm temperate, fully

221 humid, warm summer), *Cwa* (warm temperate, winter-dry, hot summer), and *Cwb* (warm

222 temperate, winter-dry, warm summer). Summer-dry *Cs* climates were represented by 9–13%

223 and arid (generally dry) *B* climates by 6–11% (Table 3, Supplementary Materials S4).

224 Tropical (equatorial) climates (*A*) are represented by 9–11% in older assemblages, and 7–8%

225 in the two youngest assemblages (PZ 2/3 and Yeni Eskihisar). Of 1555 modern species used

226 to inform the Köppen signatures of the NLRs for the fossil taxa, 119 show marginal range

227 extensions into *Af* climate, 168 into *Am* (heavy monsoon), 85 into *As*, and 295 into *Aw*

228 (Supplementary Material S2). Taxa extending in tropical climates are mainly species of *Pinus*,

229 *Celtis*, *Smilax*, and *Viburnum*, *Quercus* sections *Quercus* and *Lobatae*, Juglandaceae

230 subfamily Engelhardioideae, Oleaceae, and Sapotaceae. Exclusion of Köppen-Geiger climate

231 signals extracted from cosmopolitan and/or gymnospermous taxa did not change the general

232 trends (Supplementary Material S5).

233

234 **3.2 CLAMP**

235 Sixty-three morphotypes were scored for Eskihisar (Fig. 6; see Supplementary Material S3 for

236 score sheets and other reconstructed climate parameters). Inferred values for mean annual

237 temperature (MAT) were (11.2–) 12.6 (–14) °C, for coldest month mean temperature

238 (CMMT) (0.3–) 2.3 (–4.4) °C, and for the three wettest months (X3.wet) (410–) 666 (–936)

239 mm and for the three driest months (X3.dry) (148–) 204 (–262) mm. The ratio X3.wet/X3.dry

240 was between 2.9 and 3.6. For Tınaz, the reconstructed MAT was (12.3–) 13.8 (–15.2) °C,

241 CMMT (1.5–) 3.6 (–5.6) °C, X3.wet (420–) 700 (–980) mm, and X3.dry (146–) 205 (–260)

242 mm. The ratio X3.wet/X3.dry was between 2.9 and 3.8. Values for Salihpaşalar are not

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248 considered here as they are based on a too small set of morphotypes (see Supplementary

249 Material S3).

250

251 **3.3 Genus level biogeography**

252 The genus-level biogeographic analysis of the four Yatağan Basin floras ranging in age from

253 14.8 to 13.2 Ma (MN6 into MN7+8; Table 1) shows that closest biogeographic relationships

254 are with the modern East Asian flora (54 of 59 taxa shared with East Asia), 48 and 44 genera

255 are shared with the modern western Eurasian and eastern North American floras, respectively.

256 Among modern tropical floras, closest relationships are with South America (21), followed by

257 Africa (16) and northern/ north-eastern Australia (13). Most taxa extending to tropical regions

258 are cosmopolitan (e.g. *Euphorbia*, *Drosera*, *Phragmites*), hence, of little discriminative

259 power. This is also true for higher taxa such as Polygalaceae and Valerianoideae. The fossil

260 species *Smilax miohavanensis* belongs to a subtropical-tropical clade of extant species (Denk

261 et al., 2015) and is the only member of this group in Eurasia; it has its last occurrence in the

262 middle Miocene floras of the Yatağan Basin. Overall, the dominating biogeographic signal is

263 a northern hemispheric one.

264

265 **3.4 Changes in ratios arboreal to non-arboreal pollen**

266 Ratios of arboreal pollen (AP) to non-arboreal pollen (NAP) change considerably among and

267 within pollen zones of the Yatağan Basin assemblages (Table 2, Supplementary Material S6).

268 Pollen zone 1 (main lignite seam) consistently has high percentages of AP (94–70%). In

269 contrast, AP percentage values fluctuate throughout pollen zone 2, with values from 89 to 29.

270 Pollen zone 2-3, only covered in the Tınaz section, records AP percentages of 50 to 19.

271 Above, the MN7+8 assemblage of Yeni Eskihisar shows again a higher proportion of arboreal

272 taxa (67%). Similarly, from the vertebrate locality Çatakbağyaka (revised age MN7+8, 12 km

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276 south of the Yatağan Basin) AP percentages range from c. 50% to c. 80% (Jiménez-Moreno,

277 2005; Mayda et al., 2016; Bouchal et al. 2017; Aiglstorfer et al. 2018).

278 We used the threshold (AP/NAP = 3.85) proposed by Favre et al. (2008) to separate between

279 tree- and herb-prevalent environments. This ratio translates into AP percentages of close to

280 80% to predict reliably tree-prevalent landscapes. As can be seen in Supplementary Material

281 S6, pollen zones 1 and 2 are largely dominated by forested environments. In the upper part of

282 PZ2 (Tınaz, Eskihisar), PZ2/3 and PZ3 (Tınaz) herb-prevalent landscapes are inferred.

283 However, it is noteworthy, that although NAP taxa are more abundant in these pollen zones,

284 AP taxa remain to have fairly high percentages as well (Bouchal et al., 2016, 2017). For

285 example, *Fagus*, *Quercus* deciduous and evergreen type, still are above the threshold values

286 indicative of local tree presence (Lisitsyna et al., 2011). Hence, the opening of the vegetation

287 in the upper parts of PZ2, and in PZ2/3, PZ3 may actually represent a coexistence of forest

288 and open vegetation.

289

290 **4 Discussion**

291 **4.1 Climate inference using Köppen signatures and CLAMP**

292 Using Köppen signatures, we made a semi-quantitative reconstruction of the palaeoclimate of

293 the Yatağan Basin during the middle Miocene. All Köppen signatures used here rely on the

294 nearest-living-relative principle (Denk et al., 2013). Such approaches are prone to error

295 because niche evolution may have occurred in lineages, the morphologically nearest living

296 relatives (NLRs), a species or group of morphologically similar species, of fossil taxa may

297 have different niches, and the shift is difficult to quantify (Ackerly, 2004; Grimm & Potts,

298 2016; Denk et al., 2017). Hence, we opted against applying quantitative NLR methods and

299 determined Köppen signatures for fossil taxa using information from all extant species of a

300 genus used as NLR to avoid bias from undetected niche shifts.

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302   It is important to keep climatic niche shift in mind when using NLR based approaches to

303   palaeoclimate inference and interpreting their results (cf. Grimm & Potts, 2016; Denk et al.,

304   2017). In our dataset of 1555 modern species, 295 also occur in tropical *Aw* climates. Most of

305   them belong to clades (monophyletic sections, genera, families) that occur in a wide range of

306   climate types (e.g. Amaranthaceae, *Celtis*, white and red oaks). Others, such as *Engelhardia*

307   are usually interpreted as tropical-subtropical evergreen element (Kvaček, 2007) based on the

308   distribution range of the extant genera of the comprising subfamily, the Engelhardoideae.

309   However, '*Engelhardia*' of the western Eurasian Cenozoic belongs to its own (extinct)

310   section or genus *Palaeocarya* (Kvaček, 2007) with a stratigraphic range from Eocene to

311   Pliocene. Pollen, foliage, and reproductive structures of fossil material clearly belong to

312   subfamily Engelhardioideae but cannot be assigned to just a single modern genus *Engelhardia*

313   (tropical Southeast Asia). Instead the fossil-taxon is a mosaic taxon having characteristics of

314   both American and Asian members of the subfamily. Kvaček (2007) noted that the fossil

315   genus/subgenus flourished in subtropical climates during the Eocene but in distinctly

316   temperate climates with coldest month mean temperatures close to the freezing point in the

317   Neogene, in stark contrast to the surviving four, likely relict genera of the Engelhardioideae.

318   Hence, this extinct lineage of Engelhardioideae is not well represented by a single or the

319   combination of all extant genera and their constituent species. Similarly, representatives of

320   *Smilax havanensis* and allied species are part of a New World clade with most species

321   occurring in tropical climates. However, the single Old World member of the clade, the fossil

322   species *S. miohavanensis*, is known from early to middle Miocene strata of Anatolia and

323   Central Europe (Denk et al., 2015). This fossil species formed part of plant assemblages that

324   rule out tropical climates. In this case, inferring palaeoclimate from extant distribution data

325   only inevitably will produce noise to the climatic signal.

326   Overall, the most common Köppen-Geiger climate types of NLR taxa of the Yatağan floras

327   were warm temperate *C* types, and among *C* types fully humid *Cf* climates were better

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329 represented than more seasonal *Cw* and *Cs* types (Fig. 5; Supplementary Material S4). *Cs*

330 types played only a minor role; however, there was no clear preference of *Cf* over *Cw*

331 climates in the representation of Köppen-Geiger climate types. Removing azonal taxa, or taxa

332 commonly associated with higher elevations (conifers) did not affect the general signal.

333 In contrast, CLAMP is not based on NLR and hence not potentially biased by taxonomic

334 error. Its combination with the Köppen signature analysis provides a powerful tool for climate

335 inference and to discern between seasonal *Cw* (winter dry) and *Cs* (summer dry) and fully

336 humid *Cf* climates can be made. Specifically, the ratio of the wettest and the driest month

337 clearly distinguishes strongly seasonal summer rain (monsoon) climates (*Cw*; precipitation

338 wettest month > 10x precipitation driest month, $[P_{wdry/sdry} < P_{wet/wwet}/10]$; Peel et al., 2007)

339 from weakly seasonal, fully humid climates (*Cf*; precipitation wettest month << 10x

340 precipitation driest month). Precipitation values for X3.wet and X3.dry inferred by CLAMP,

341 and the ratio between these ranges being between 2.9 and 3.8 thus largely rules out a *Cw*

342 climate (X3.wet and X3.dry are closely correlated to $P_{dry/wet}$). In conjunction with the Köppen

343 signature results ruling out summer-dry conditions, the CLAMP precipitation and temperature

344 estimates point towards cold subtropical to mild temperate *Cfa* climates at the margin to fully

345 temperate *Cfb* climates.

346

347 **4.2 Comparison to palaeoclimate and palaeoenvironment inferences from other proxies**

348 A further refinement of previous climate and vegetation inferences can be made regarding the

349 distinction between tropical ($T_{min} \equiv CMMT \geq 18$ °C), subtropical (8–12 months with $T \geq 10°$

350 C; ~ MAT 12–18 °C, and CMMT <18 °C) and temperate climates. CLAMP consistently

351 resolves MAT < 18 ºC and CMMT < 6 °C for the localities Eskihisar and Tınaz, and this

352 agrees with the results from Köppen signatures and a previous qualitative assessment of

353 palaeoenvironments in the Yatağan Basin (Güner et al., 2017). Both these results, rejecting

354 strongly seasonal *Cw* climates, summer dry *Cs,* and tropical *A* climates (at least for non-

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357   coastal areas) for the middle Miocene of western Anatolia, have implications for the

358   reconstruction of palaeoenvironments of famous vertebrate localities in Anatolia that are

359   assigned to MN6. The δ^{13}C composition from fossil tooth enamel at Paşalar, western

360   Anatolia, MN6, indicates that animals were feeding on C_3 vegetation (Quade et al., 1995).

361   The palaeoenvironment for this locality was determined as closer to Indian subtropical

362   forests, with seasonal summer rainfalls (i.e. warm *Cwa* climates), semi-deciduous forest and

363   dense ground vegetation (Stringer & Andrews, 2011; Mayda et al., 2015). Using carnivore

364   guild structures Morlo et al. (2010) inferred open (Serengeti type, *Aw* climate) landscapes for

365   the Central Anatolian MN6 vertebrate locality Çandır. Also, the NOW database

366   (http://www.helsinki.fi/science/now/; The NOW Community, 2018) refers to Çandır as more

367   open ("woodland biome", "open vegetation structure", "grassland with mosaic of forests")

368   and to Paşalar as more forested landscapes ("subtropical", "closed vegetation structure",

369   "semi-deciduous forests"). Bernor et al. (1979) using community structure of vertebrate

370   faunas inferred densely wooded environments for Çandır. In a later study based on a

371   taxonomic revision of carnivores, Mayda et al. (2015) proposed a mixed environment

372   between tropical forests and open savannah landscapes for Çandır. It is important to note that

373   these carnivore guild structure studies used only two modern calibration faunas to estimate

374   palaeoenvironments, one tropical rainforest fauna in Guyana, and one savannah (tropical)

375   fauna in the Serengeti (Morlo et al., 2010). Thus, using this proxy, only two environments can

376   be reconstructed, tropical savannah or rainforest.

377   Our plant-proxy based climate reconstruction unambiguously rejects a tropical climate for the

378   middle Miocene Yatağan Basin and major biogeographic patterns strongly suggest northern

379   hemispheric affinities. Similar environmental conditions as reconstructed in our study have

380   been inferred for most of western Anatolia during the late early and middle Miocene

381   (Kayseri-Özer, 2017). Most proxies currently used to infer climate and vegetation in western

382   Anatolia during the middle Miocene (carnivore guild structures, vertebrate community

383 structure, plant functional types, plant macrofossils, pollen and spores; Mayda et al., 2015,

384 2016; Kayseri-Özer, 2017; Güner et al., 2017; Bouchal et al. 2016, 2017; Bouchal, 2018)

385 clearly infer forested vegetation with varying contributions of open vegetation. In contrast,

386 Strömberg et al. (2007) found that "*all Miocene phytolith assemblages point to relatively open*

387 *vegetation, such as savanna or open woodland dominated by open-habitat grasses, or a*

388 *mixture of grassland and wooded areas*". This result may be biased (see Jokela, 2015, p. 44)

389 and increased diversity of grass types in the phytolith record may not necessarily indicate the

390 presence of widespread open, grass-dominated landscapes.

391

392 **4.3 Modern climate analogues**

393 The inferred climate for the middle Miocene Yatağan Basin plant assemblages is

394 characterized by MAT 11–15 °C, coldest month mean temperature (CMMT) 0–6 °C, MAP

395 ca. 1000–2000 mm, and ratios of X3.wet/X3.dry 2.9–3.8. A non-exhaustive search for climate

396 stations with this combination of climate parameters (Supplementary Material S7) identified a

397 single closest match, Pacific central Honshu of Japan. X3.wet/X3.dry ratios and MAT are

398 similar to the upper limits of the ranges reconstructed for the middle Miocene Yatağan Basin.

399 East Asian *Cf* climates are generally characterized by distinct summer rain maxima. The

400 modern vegetation of Japan is home to many plant taxa that are currently absent from western

401 Eurasia but were abundant in Neogene plant assemblages of western Eurasia (e.g.

402 *Cephalotaxus*, *Cryptomeria*, *Torreya*, *Alangium*, *Camellia*, *Castanopsis*, *Cercidiphyllum*,

403 *Daphniphyllum*, *Eurya*, *Fatsia*; Mai, 1995; Miyawaki, 1984; see also Milne, 2004). These

404 taxa require warm and humid equable climates.

405 A further close match is the area from northern Turkey via Georgia to northern Iran, the

406 Euxinian-Hyrcanian region (Supplementary Material S7). Climates at the transition between

407 *Csa* and *Cfa/b* of the region north of Istanbul have up to 1166 mm MAP (Ustaoğlu, 2012) and

408 other climate parameters in this area match the Miocene climate of southwestern Turkey

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413 inferred by CLAMP. Towards the humid north-eastern part of Turkey, X3.wet/X3.dry ratios

414 are lower (2.4 for Rize, Hopa and Poti and Kobuleti in adjacent western Georgia). Further to

415 the east, south of the Caspian Sea, Rasht and Kiashahr have *Cfa* and borderline *Csa* to *Cfa*

416 climates with slightly more pronounced seasonality than the reconstructed climate for the

417 Miocene of southwestern Turkey (X3.wet/X3.dry ratios 4.4 and 4.2). In contrast,

418 X3.wet/X3.dry ratios in modern Mediterranean western and southwestern Turkey amount to

419 25 (Izmir) and 21.8 (Muğla, Yatağan Basin). It is noteworthy that modern *Cf* climates of the

420 Euxinian-Hyrcanian region differ markedly from those of the Pacific part of Honshu by their

421 summer minima in rainfall (Supplementary Material S7). This feature indicates a (weak)

422 Mediterranean influence in this region. According to Biltekin et al. (2015) the Anatolian

423 refugium emerged after the retreat of the Parathethys Sea in the Pliocene and increasing

424 monsoon influence (increased summer rainfall) over the north-eastern Mediterranean region

425 (the latter accounting for the much higher summer precipitation in the Euxinian-Hyrcanian

426 than in the Mediterranean region). The Mediterranean climate type in Europe appeared first

427 during the late Pliocene and early Pleistocene (ca. 3.2–2.3 Ma; Suc, 1984) coinciding with

428 first large-scale north hemispheric glaciation in the North Atlantic (Denk et al., 2011).

429

430 **4.4 Detection of Miocene global climatic changes in the terrestrial fossil record**

431 High-resolution benthic stable isotopic data provide a detailed chronology of (global) climatic

432 changes across the Miocene Climatic Optimum (MCO), the middle Miocene Climatic

433 transition (MMCT), and the subsequent more pronounced cooling (Holbourn et al., 2014).

434 The terrestrial record usually does not provide the same temporal resolution but allows

435 focussing on regional patterns. The transition from MCO to MMCT has previously been

436 documented in high-resolution palynological analyses. For example, Jiménez-Moreno et al.

437 (2005) investigated a core from the Pannonian Basin and observed a decline of megathermic

438 taxa at the transition MCO to MMCT. Also Ivanov & Worobiec (2017) reported a decrease of

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thermophile taxa for the transition for Bulgaria and Poland. In southwestern Anatolia, Kayseri et al. (2014) investigated three localities in the Muğla-Ören area south of the Yatağan Basin, which are dated by vertebrate fossils as early and late MN5 and thus correspond to the MCO. These authors report a few warmth-loving elements (palms, *Avicennia*) that are missing in the younger strata of the Yatağan Basin. This could be due to the deltaic setting of these floras as opposed to the intramontane setting of the Yatağan Basin floras. In general, the floras of the Muğla-Ören area are very similar to the floras of the Yatağan Basin (Bouchal. et al., 2017). However, a striking difference with the MN6 and MN7+8 assemblages of the Yatağan Basin is the almost entire absence of herbaceous taxa (non-arboreal pollen) in the MN5 assemblages of Ören (see figs 7–9 in Kayseri et al. 2014). This may indicate the presence of more closed forest vegetation of the laurisilva type. The extant laurisilva or laurel forest is a type of subtropical forest found in areas with high humidity and relatively stable, mild temperatures. The assemblages of the Yatağan Basin, show fluctuating arboreal to non-arboreal pollen (AP:NAP) ratios with a peak of NAP in the transition zone MN6 to MN7+8 (pollen zone PZ 2–3). This peak could possibly correspond to a sharp cooling detected in the benthic stable isotopic data at 13.9–13.8 Ma (Holbourn et al., 2014). In the European mammal stratigraphy (Neubauer et al., 2015) the boundary MN6 to MN7+8 is at 13.9 Ma. Above PZ 2–3, the radiometrically dated Yeni Eskihisar pollen assemblage clearly belongs to MN7+8. Here, and in the nearby locality Çatakbağyaka woody taxa (including some warmth-loving taxa) are again more prominent. Thus, although the correlation of pollen zone 2–3 with the cooling event at 13.9–13.8 Ma is highly speculative, it is clear that the MCO in southwestern Anatolia was characterized by laurisilva vegetation with little contribution of herbaceous taxa. During the MMCT the main woody taxa did not change much, but herbaceous taxa played a much greater role. This indicates higher structural complexity of the vegetation. The presence of early hominids in western Anatolia during this time might be connected to this more complex vegetation. It is unclear at present, whether these changes were accompanied by changes in

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concentrations of atmospheric CO_2. The compilation of reconstructed CO_2 values across the Cenozoic from hundreds of proxy data (Beerling & Royer, 2011) shows that there is no agreement between different proxies for the MCO and the subsequent middle Miocene climate cooling. Phytoplankton stable isotopic data suggest nearly stable CO_2 concentrations (MCO, 227–327 ppm, MMCT, 265–300 ppm; see table S 1 of Beerling & Royer, 2011). In contrast, stomata densities from fossil leaves suggest a pronounced decline of CO_2 across this interval.

5. Conclusion

Here we used three proxies to infer climate, palaeoenvironments and biogeographic affinities of three middle Miocene floras of southwestern Anatolia. We showed that the palaeobotanical record resolves transitions from the warm MCO (16.8–14.7 Ma) into the MMCT (14.7–13.9 Ma), and a more pronounced cooling at 13.9–13.8 Ma, mainly expressed in the changing and fluctuating ratios between AP and NAP taxa. Using threshold percentages for main tree taxa, we further show that although NAP values significantly increased during the MMCT, AP taxa remained relatively abundant, signifying the coexistence of forested and open landscapes during this transition. In addition, the biogeographic analysis indicates mainly northern hemispheric biogeographic affinities of the middle Miocene flora of southwestern Anatolia and thus invalidates previous comparisons with tropical environments. Tropical climate conditions are also rejected by the Köppen signatures of the investigated floras and by the CLAMP analysis. Finally, the CLAMP data readily distinguish between strongly seasonal Cs and Cw and fully humid Cf climate types. More combined macrofossil and microfossil studies are needed for the Neogene of Turkey in order to establish a robust framework of terrestrial climate evolution in this important region.

Author contribution

JMB and TD designed the study. TD wrote the first draft of the manuscript. TG made the

CLAMP analysis, JMB made the Köppen signature analysis. All authors discussed the data

and contributed to the final version of the manuscript.

Acknowledgements

This work was supported by the Swedish research Council [grant no. 2015-03986 to TD]. We

thank G. W. Grimm for his comments on the first version of the manuscript. Valuable

suggestions by the reviewers L. M. Dupont and J.-P. Suc are highly appreciated.

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Supplementary Material.

S1: A. Number of fossil-taxa (macrofossils and microfossils) from four middle Miocene

localities (including one macrofossil horizon and four pollen zones - PZ) in the Yatağan

Basin.

B. All fossil-taxa recorded from four Yatağan Basin floras (14.8–13.2 Ma; MN6 into MN7–

8).

S2: Köppen-Geiger climate type signatures of all genera represented in micro and macrofloras

of the Yatağan Basin.

S3: Coding of leaf physiognomic characters for morphotypes from three macrofloras. Output

pdf files from online CLAMP analysis (http://clamp.ibcas.ac.cn).

S4: Heat maps showing precise representation of different Köppen-Geiger climate types for

all fossil assemblages.

S5: Köppen signature diagrams excluding cosmopolitan and gymnospermous taxa.

S6: Arboreal to non-arboreal pollen ratios for three sections, of the Yatağan Basin.

S7: Modern climate stations comparable to the middle Miocene climate of the Yatağan Basin,

southwestern Anatolia. Climate data from CLIMATE-DATA.ORG (https://sv.climate-

data.org/info/sources/) and Ustaoğlu (2012). Selected Walter-Lieth climate diagrams illustrate

qualitative difference between Euxinian-Hyrcanian and Japanese (Honshu) *Cf* climates.

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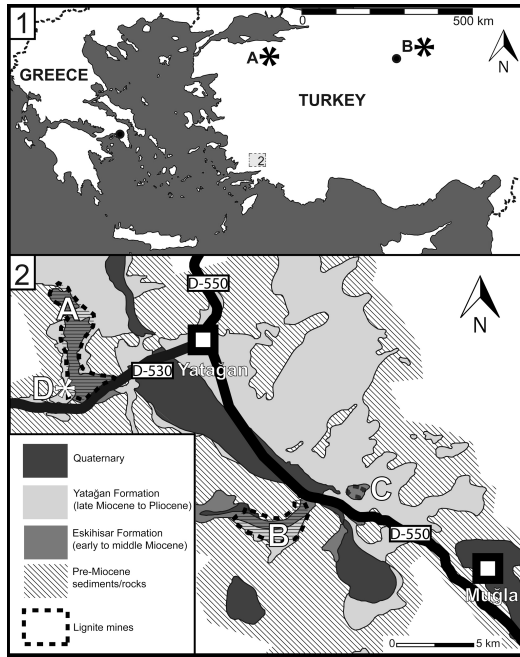
Figure 1. Geographic and regional geologic setting of the Yatağan basin. **1.** Map showing the

geographical position of the Yatağan Basin (2) and the MN6 vertebrate fossil localities (*)

Paşalar (A) and Çandir (B). **2.** Simplified regional geological map of the Yatağan Basin based

on Becker-Platen (1970) and Atalay (1980); lignite mines Eskihisar (A), Tınaz (B),

Salihpaşalar (C); vertebrate fossil locality (*) Yeni Eskihisar MN7/8 (D).

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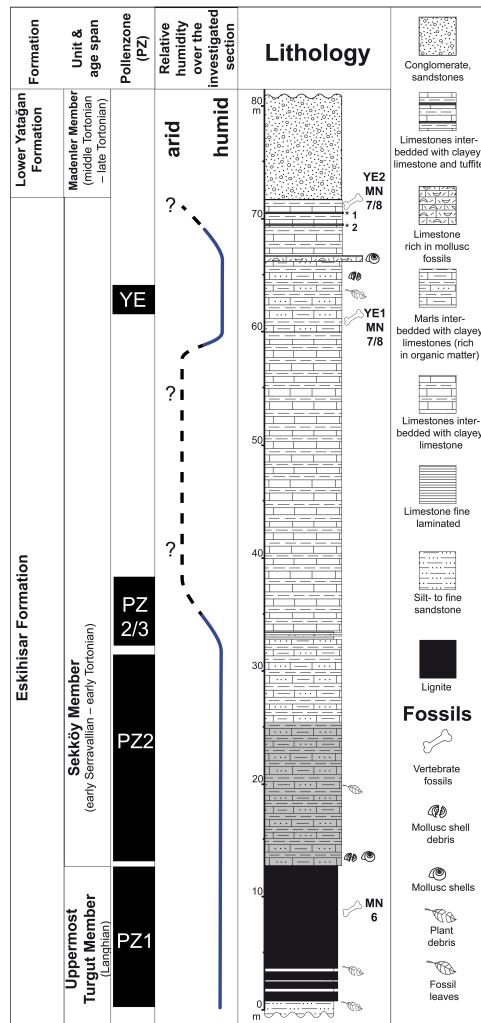
Figure 2. Generalized lithostratigraphic column for the Eskihisar lignite mine and pollen

zones (PZ). The main part of the investigated plant macrofossils originates from ca 10 m thick

deposits overlying the exploited lignite seams (part of the section highlighted in grey

corresponding to PZ 2). Yeni Eskihisar 2 (YE2) and Yeni Eskihisar 1 (YE1) vertebrate fossil

localities (Becker-Platen et al. 1977). Radiometrically dated tuff layers (*), 1* 11.2 ± 0.2 Ma,

2* 13.2 ± 0.35 Ma (Becker-Platen et al. 1977).

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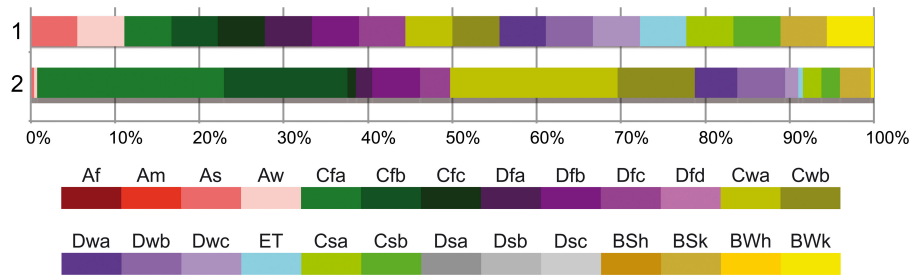
Figure 3. Köppen signal for genus *Tilia* extracted from 26 extant species. **1**. Köppen-Geiger

climates in which *Tilia* is present. **2**. Combined Köppen signature of all 26 extant *Tilia*

species.

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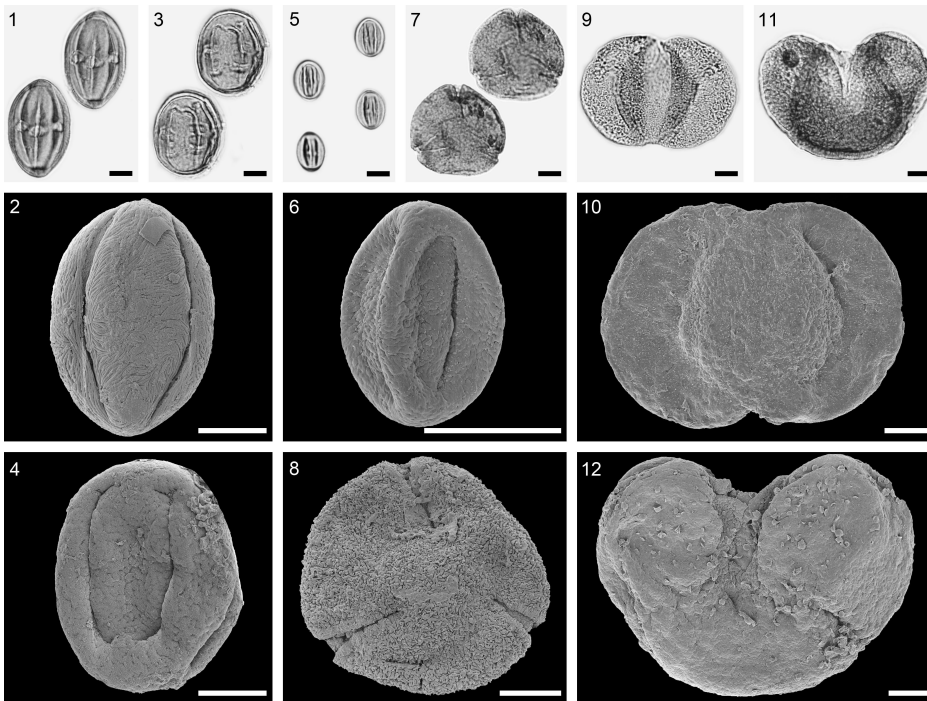
Figure 4. Selected pollen grains LM (1, 3, 5, 7, 9, 11) and SEM (2, 4, 6, 8, 10, 12)

micrographs of the same fossil pollen grain of the Eskihisar (E), Tınaz (T), and Salihpaşalar

(S) sections. **1–2**. *Nitraria* sp., EV (E, S153567). **3–4**. Sapotaceae gen. indet., EV (T,

S143604). **5–6**. *Decodon* sp., EV (S, S153635). **7–8**. *Fagus* sp., PV (T, S143621). **9–10**.

Cathaya sp., (9) PV, (10) PRV (S, S153632). **11–12**. *Cedrus* sp., EV (E, S153590).

EV = equatorial view, PV = polar view, PRV = proximal view. Scale bar = 10μm (1–12).

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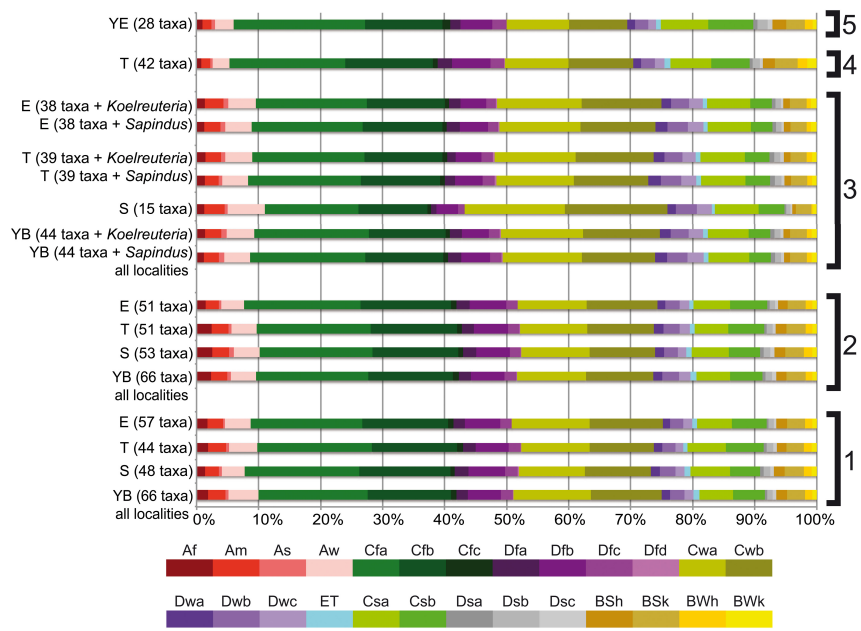
Figure 5. Köppen signals for the Yatağan Basin floras. **1.** Pollen zone (PZ) 1 (MN6; 14.95–
13.9 Ma) of the Eskihisar (E), Tınaz (T), and Salihpaşalar (S) localities and the combined
signal of all present taxa from PZ 1 of the three Yatağan Basin localities (YB). **2.** PZ 2 (MN6)
of E, T, S, YB. **3.** Macrofossil (MF) assemblages (same level as PZ 2) of E, T, S. **4.** PZ 2/3 of
T. (younger than Yeni Eskihisar vertebrate locality). **5.** Yeni Eskihisar vertebrate locality
pollen assemblage (MN7/8, younger than radiometric age 13.2 Ma).

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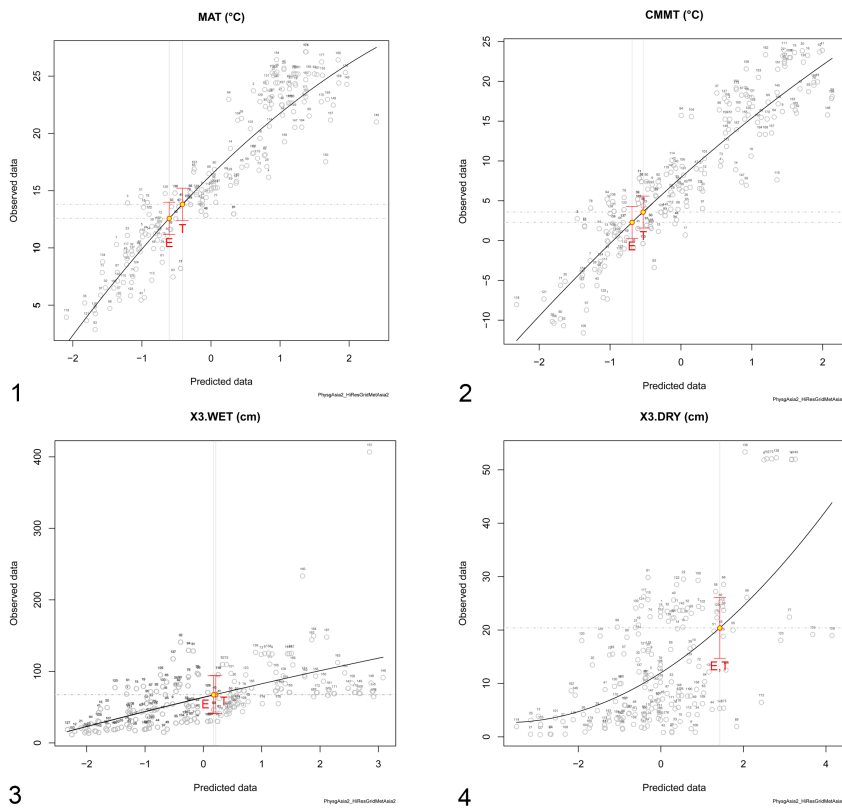
Figure 6. CLAMP climate inference for the macrofossil assemblage of (E) Eskihisar and (T) Tınaz (same level as PZ 2). **1.** Mean annual temperature (MAT). **2.** Coldest month mean temperature (CMMT). **3.** Precipitation of the three wettest months. **4.** Precipitation of the three driest months.

Table 1

Latest occurrence W Eurasia	Fossil-taxon (genus level)	wEUR[f]	EA	eNA	wNA	SA	AF	AUS
	Ephedra	+	+	+	+	+	+	
Pliocene?[a]	*Glyptostrobus*		+					
Taxodium-type, < 0.1 Ma[a]	*Taxodium*			+	+			
0.5-0.4 Ma[a]	*Cathaya*		+					
	Cedrus	+	+					
	Picea	+	+	+	+			
	Pinus	+	+	+	+			
0.4-0.3 Ma[a]	*Tsuga*		+	+	+			
	Acer	+	+	+	+			
late Pliocene[b]	*Ailanthus*		+					
	Alnus	+	+	+	+	+		
no data	*Apios*		+	+				
	Betula	+	+	+	+			
	Buxus	+	+	+	+	+	+	
	Buxus (balearica type)	+	+					
	Carpinus	+	+	+				
< 0.1 Ma[a]	*Carya*		+	+				
	Castanea	+	+	+				
Pliocene[c]	*Cedrelospermum*†	+	+		+			
	Celtis	+	+	+	+	+	+	+
	Centranthus	+	+					
	Corylus	+	+	+	+			
Pleistocene[d]	*Decodon*			+				
	Drosera	+	+	+	+	+	+	+
	Erica	+					+	
	Erodium	+	+	+	+	+	+	+
0.6 Ma[a]	*Eucommia*		+					
	Euphorbia	+	+	+	+	+	+	+
	Fagus	+	+	+				
	Fraxinus	+	+	+	+			
	Ilex	+	+	+	+	+	+	+
	Juglans	+	+	+	+	+		
	Linum	+	+	+	+	+	+	+
	Liquidambar	+	+	+				
	Lonicera	+	+	+	+			
	Ludwigia	+	+	+	+	+	+	+
Pliocene[d]	*Mahonia*		+					
	Nitraria	+	+				+	+
	Ostrya	+	+	+				
	Parrotia	+						
	Persicaria	+	+	+	+	+		
	Phragmites	+	+	+	+	+	+	+
no data	*Picrasma*		+	+	+	+		
Pleistocene[e]	*Podocarpium* †	+	+					
	Polygonum	+	+	+	+			
	Populus	+	+	+	+			
	Pterocarya	+	+					
	Quercus	+	+	+	+	+		
	Rumex	+	+	+	+	+	+	+
	Salix	+	+	+	+	+		
	Scabiosa	+					+	
	Smilax	+	+	+	+	+	+	+
14.8-13.8 Ma	*Smilax (havanensis* group*)*			+		+		
	Sorbus	+	+	+	+			
	Sparganium	+	+	+	+			+
	Tilia	+	+	+	+			
	Typha	+	+	+	+	+	+	+
	Ulmus	+	+	+	+			
	Viburnum	+	+	+	+	+		
	Zelkova	+	+					
No. of genera/region		48	54	44	36	21	16	13
		wEUR[f]	EA	eNA	wNA	SA	AF	AUS

Table 1. Genus-level biogeographic affinities of fossil-taxa of the Yatağan Basin floras.

[a]Magri et al., 2017; [b]Corbett & Manchester, 2004; [c]Jia et al., 2015; [d]Martinetto, 2001; [e]Wang et al., 2007; [f]including northern Africa; † extinct genus.

800   wEUR = western Eurasia, EA = East Asia, eNA = eastern North America, wNA = western

801   North America, SA = South America, AF = Africa (excluding northern Africa), AUS =

802   Australia.

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Table 2

Pollen Zone	AP	NAP	
Hüssamlar	90	10	16.8 Ma
Kultak	90	10	MN5
Karacaağaç	96	4	
Tınaz PZ1	75,00	25,00	14.8 Ma
	94,20	5,80	MN6
	0,00	0,00	
	0,00	0,00	
	75,58	24,42	
	85,00	15,00	
	0,00	0,00	
Tınaz PZ2	54,13	45,87	
	89,22	10,78	
	62,04	37,96	
	86,82	13,18	
	28,66	71,34	
	46,04	53,96	
	0,00	0,00	13.9 Ma
Tınaz PZ2-3	19,01	80,99	(?)MN7+8 *
	0,00	0,00	
	50,44	49,56	MN7+8
Yenieskihisar	67,00	33,00	13.2 Ma

* = perhaps linked with 13.9-13.8 Ma cooling event
(Holbourn et al., 2014)
AP = arboreal pollen (angiosperms)
NAP = non-arboreal pollen (angiosperms)
wavy line = profiles separated by tens of meters
of sediment barren of pollen

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805 **Table 2**. Arboreal to non-arboreal pollen ratios in southwestern Anatolia across the MCO,

806 MMCT and subsequent cooling phase.

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Table 3

Descripton of Köppen-Geiger climate symbols and defining criteria			
1st	2nd	3rd	Description and criteria
A			equatorial / tropical ($T_{cold} \geq 18°C$)
	f		rainforest, fully humid ($P_{dry} \geq 60mm$)
	m		monsoonal (not Af & $P_{dry} \geq 100\text{-}MAP/25$)
	s		savannah with dry summer ($P_{sdry} < 60$ mm)
	w		savannah with dry winter($P_{wdry} < 60$ mm)
B			arid (MAP <10 x $P_{threshold}$)
	W		desert (MAP <5 x $P_{threshold}$)
	S		steppe (MAP ≥5 x $P_{threshold}$)
		h	hot arid (MAT ≥18°C)
		k	cold arid (MAT <18°C)
C			warm temperate/temperate (T_{hot} >10°C & 0°C< T_{cold} <18°C)
D			snow / cold (T_{hot} >10°C & T_{cold} ≤0°C)
		s	summer dry (P_{sdry} <40 & P_{sdry} <P_{wwet}/3)
		w	winter dry (P_{wdry} < P_{swet}/10)
		f	fully humid / without a dry season (not s or w)
		a	hot summer (T_{hot} ≥22°C)
		b	warm summer (not a & 1≤ T_{mon}10 <4)
		c	cool / cold summer (not a or b & T_{mon}10 ≥4)
		d	extremely continental / very cold winter (not a or b & T_{cold} <-38°C)
E			polar (T_{hot} <10°C)
	T		polar tundra (T_{hot} ≤10°C)

Table 3 Description of Köppen-Geiger climate symbols and defining criteria (Kottek et al., 2006; Peel et al. 2007). MAP = mean annual precipitation, MAT = mean annual temperature, T_{hot} = temperature of the hottest month, T_{cold} = temperature of the coldest month, T_{mon10} = number of months where the temperature is above 10°C, P_{dry} = precipitation of the driest month, P_{sdry} = precipitation of the driest month in summer, P_{wdry} = precipitation of the driest month in winter, P_{swet} = precipitation of the wettest month in summer, P_{wwet} = precipitation of the wettest month in winter, $P_{threshold}$ = varies according to the following rules (if 70% of MAP occurs in winter then $P_{threshold}$ = 2 x MAT, if 70% of MAP occurs in summer then $P_{threshold}$ = 2 x MAT + 28°, otherwise $P_{threshold}$ = 2 x MAT + 14). Summer (winter) is defined as the warmer (cooler) six months period of ONDJFM and AMJJAS.

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