Fossil amphibians and reptiles from Tegelen (Province of Limburg) and the early Pleistocene palaeoclimate of The Netherlands

(Article begins on next page)

23 April 2024

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22 **Fossil amphibians and reptiles from Tegelen (Province of Limburg) and the early Pleistocene**

23 **palaeoclimate of The Netherlands**

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36 **Abstract**

37 Few Quaternary herpetofaunas have been recovered from The Netherlands. Among these, the one

38 coming from the early Pleistocene site of the Russel-Tiglia-Egypte pit near Tegelen is of particular

39 interest, because it is the type locality of the recently described, last western European

40 palaeobatrachid anuran, *Palaeobatrachus eurydices*. The large number of fossil remains of

41 amphibians and reptiles found in the pit are representative of a very diverse fauna, including at least

42 17 taxa: *Triturus* gr. *T. cristatus*, *Lissotriton* sp., *Pelobates fuscus*, *Bufo bufo*, *Bombina* sp.,

43 *Pelophylax* sp., *Rana* sp., *Hyla* gr. *H. arborea*, *Pelodytes* sp., *Mauremys* sp., *Lacerta* sp., Lacertidae

44 indet., *Anguis* gr. *A. fragilis*, cf. *Pseudopus* sp., "colubrines" indet., *Natrix natrix* and *Vipera* sp.

Emys orbicularis, previously reported from a different Tegelen pit, is not present in this

assemblage. Palaeoclimatic conditions reconstructed based on the herpetofaunistic association

indicate a humid subtropical climate (Cfa according to the Köppen-Geiger classification of

climates) for Tegelen during the TC5 section of the Tiglian, with low, but fairly regular rainfalls

during the year. Mean annual temperature was $13.4 \pm 0.3°C$ and mean annual precipitation was 542

$\pm$ 50 mm. Moreover, three dry months were present during summer and early autumn, resulting in a

much drier climate than the one present at Tegelen today. Nevertheless, the occurrence of the water-

dwelling *P. eurydices* suggests the persistence of suitable permanent water bodies during the whole

year, and the survival of this taxon in this part of Europe might have been allowed by the generally

humid climate.

Keywords

Mutual Ecogeographic Range method; *Palaeobatrachus eurydices*; Tiglian; Western Europe;

Quaternary; Paleoclimatology; Data treatment, data analysis.

1. Introduction

The distribution of amphibians and reptiles is strictly dependent on environmental conditions such

as temperature and pluviometry (among others, Antúnez et al. 1988; Currie 1991; Rage and Roček

2003; Vitt and Caldwell 2009). Amphibians are ectothermic vertebrates with a permeable skin that

plays an important role in their respiration. In order not to impede the respiration and other

physiological processes, the skin needs to be maintained in moist conditions and temperatures

interfering with the correct rate of chemical reactions should be avoided (Vitt and Caldwell 2009).

Moreover, both in the case of permanent water-dwellers and of terrestrial species, amphibians need

suitable water bodies for their reproductive habits and for larval development. The main

environmental feature influencing the distribution of reptiles, and squamates in particular, is

temperature, since they are ectothermic and, with few exceptions, thermophilous animals. As for the

amphibians, thermal conditions are also a key factor in the regulation of physiological processes in

70 reptiles, but, because of them being active thermoregulators rather than simply temperature-

71 dependent organisms, temperature also has a direct effect on their activity patterns (Sears and

72 Angilletta 2004). The thermoregulatory behaviour, and specifically minimizing its cost, is also at

73 the origin of the propensity of some reptiles to select densely vegetated environments, since the

74 vegetation cover offers protection against predators and a mosaic of shaded and sunny areas that

75 ease the activities of these animals (Díaz 1997; Díaz and Carrascal 1991: Huey 1974; Huey and

76 Slatkins 1976). Vegetation is strictly linked to the pluviometry of a specific area and therefore this

77 latter factor has an indirect effect on the distribution of reptiles too, including those species that are

78 tied to arid environments.

79 Given this strong relationship with the environment, fossil amphibians and reptiles have been

80 largely used as indicators of the palaeoclimate (e.g., Agustí et al. 2009; Bailon and Blain 2007;

81 Blain et al. 2013, 2014; Böhme 2003; Böhme et al. 2006). Pleistocene fossils are particularly useful

82 in this sense, because they largely belong to extant species or species groups of which the

83 ecological requirements are well known (Blain et al. 2008). Given that, they represent suitable

84 material for the application of the Mutual Ecogeographic Range Method (Blain et al. 2009, 2016c

85 among others).

86 We here describe a herpetological assemblage from the early Pleistocene site of Tegelen (Province

87 of Limburg, The Netherlands) and use these data to reconstruct the climatic conditions present in

88 the locality during the time of deposition of the remains. The outcome is compared to those of

89 earlier environmental reconstructions based on other groups.

90 *1.1. The Tegelen pits*

91 The village of Tegelen has been an important centre for the production of ceramics since Roman

92 times because of the high-quality clay that was quarried from the various pits in the surroundings

93 (Van den Hoek Ostende and Vos 2006). During the 20th century, a large number of fossil bones

94 were collected as a byproduct of the quarry activity and soon Tegelen became famous also for its

95 fossil mammal fauna (Van den Hoek Ostende and Vos 2006 and references therein). Most of the

96 fossils from Tegelen were just picked up by workers as they encountered them, but during the

97 1970s a field campaign aimed at collecting small mammals was organized (Freudenthal et al. 1976).

98 The target of this campaign was the Russel-Tiglia-Egypte pit (Fig. 1), and it also resulted in the

99 collection of remains of fish (Gaudant 1979), amphibians and reptiles (Van den Hoek Ostende and

100 Vos 2006; Villa et al. 2016). These remains come from a stream gully infill located near the top of

101 the Russel-Tiglia-Egypte pit section (Kortenbout van der Sluys and Zagwijn 1962) and deposited

102 during the warm TC5 section of the Tiglian (Zagwijn 1963), which can be correlated with part of

103 the Gelasian (Drees 2005). The small mammal fauna from the infill, described by Van den Hoek

104 Ostende (2003), Reumer (1984), Reumer and Hoek Ostende (2003), Rümke (1985) and Tesakov

105 (1998) among others, is correlated with the *Borsodia newtoni–Mimomys pliocaenicus* Biozone,

106 dated to 2.26–2.1 Ma (Mayhew 2015).

107 **2. Material & Methods**

108 The herein-studied remains include all the amphibian and reptile fossil material recovered from the

109 Russel-Tiglia-Egypte pit, except for the palaeobatrachid remains that were recently described as the

110 new species *Palaeobatrachus eurydices* (Villa et al. 2016). The remains are stored in the collections

111 of Naturalis Biodiversity Center in Leiden, under the acronym RGM. A complete list and detailed

112 descriptions of the fossil remains are presented in the electronic supplementary material. The best

113 preserved and most significant skeletal elements have been photographed at the University of

114 Torino using a Leica M205 microscope equipped with the Leica application suite V 3.3.0. The

115 identification are based on both criteria found in the literature and direct comparisons with

116 skeletonized specimens of extant taxa. The comparative material is stored in the Department of

117 Earth Science of the University of Torino, in the Muséum national d'Histoire naturelle in Paris and

118 in the Naturhistorisches Museum in Wien.

119   The anatomical terminology follows Vater (2003), Ratnikov and Litvinchuk (2007, 2009), Wu et al.

120   (2012) and Villa et al. (2014) for caudates, Špinar (1972), Sanchiz (1998a) and Bailon (1999) for

121   anurans, Hervet (2000) for chelonians, Evans (2008), Barahona and Barbadillo (1997) and

122   Klembara et al. (2010) for lizards and Szyndlar (1984) for snakes.

123   *2.1. Palaeoclimatic reconstruction*

124   Early Pleistocene palaeoclimate reconstruction from Tegelen based on its herpetofaunal content has

125   been done using a quantitative climate reconstruction method, the Mutual Ecogeographic Range

126   (MER; Blain et al. 2009, 2016c). Analysis of the MER for the Tegelen fossil assemblage is based

127   on the distribution atlas of the European herpetofauna (Sillero et al. 2014), with 50×50 km

128   resolution maps in the Universal transverse Mercator (UTM) georeferenced system. Climatic

129   parameters have been estimated for each 50×50 km UTM square, using the climatic database from

130   Climate-Data.org.

131   **3. Results**

132   *3.1. Systematic palaeontology*

133   Amphibia Linnaeus, 1758

134   Caudata Scopoli, 1777

135   Salamandridae Goldfuss, 1820

136   *Triturus* Rafinesque, 1815

137   *Triturus* gr. *T. cristatus* (Laurenti, 1768) (Fig. 2A-L)

138   Material: 1 parasphenoid; 4 atlases; 88 trunk vertebrae; 7 caudal vertebrae; 10 humeri; 6 femora.

139   Identification: Combined, the fairly thin, gutter-shaped odontoid process, the presence of the

140   neurapophysis rather than of a bulge on the dorsal surface of the neural arch, the fairly robust dorsal

141   portion of the arch and the postzygapophyses that extend beyond the posterior margin are all

142 diagnostic features of the atlas of members of the family Salamandridae (Ratnikov and Litvinchuk

143 2009). Trunk vertebrae can be assigned to the same family based on the combination of

144 opisthocoelous condition, presence of wide subcentral foramina, of a foramen placed near the base

145 of the parapophyses and of a notch in the middle of the posterior margin of the neural arch

146 (Ratnikov and Litvinchuk 2007). Atlases and trunk vertebrae can be referred to the genus *Triturus*

147 based on a combination of characters. The subcircular neural canal, the presence of foramina on the

148 ventral surface of the centrum and of the lateral processes, the well-developed lateral crests, the

149 inclined dorsal margin of the arch, the slightly wavy posterior margin and the roughly parallel,

150 fairly separated secondary dorsal crests are features of the *Triturus* atlases (Ratnikov and

151 Litvinchuk 2009). Together, the flat and sometimes slightly ventrally inclined anterior surface of

152 the condyle, the weakly or well-developed neck, the straight or concave anterior margin of the

153 neural arch, the concavity of the anterior margin which never extends posteriorly to the anterior half

154 of the prezygapophyses, the posterior margin of the neural arch which extends up to the posterior

155 margin of the postzygapophyses or slightly beyond it, the low depth of the notch located in the

156 middle of the posterior margin and the prominent laminae allow to attribute the trunk vertebrae to

157 the same genus (Ratnikov and Litvinchuk 2007). The attribution to *Triturus* gr. *T. cristatus*, the

158 species complex comprising *Triturus arntzeni*, *T. carnifex*, *T. cristatus*, *T. dobrogicus*, *T. karelinii*

159 and *T. macedonicus* (Sillero et al. 2014), is based on: the combination of the absence of a triangular

160 surface posteriorly to the neurapophysis of the atlases, possible presence of grooves on the lateral

161 processes, low secondary dorsal crests which reach the posterior margin of the neural arch,

162 trapezoidal posterior portion of the neural arch in the atlases, height and development of the

163 neurapophysis and of the posterior ventral crests of the trunk vertebrae and the sizes of both atlases

164 and trunk vertebrae (Ratnikov and Litvinchuk 2007, 2009). It should be noticed, however, that

165 fairly developed anterior ventral crests and zygapophyseal crests are unusual in the vertebrae of the

166 genus *Triturus*, in which they are usually low developed or lacking. The morphological similarity

167 between trunk and caudal vertebrae permits the attribution of the latter to the same species complex.

168   Humeri and femora are referred to the same complex and not to *Lissotriton* sp. based on the larger

169   size and because of the more elongated, less inclined crista ventralis and the more robust shaft for

170   the humeri and because of the more elongated area included between the trochanter and the caput

171   femoris, the wider shaft and the wider distal epiphysis provided with a more convex margin for the

172   femora (Holman 1998). The identification of the parasphenoid is based partially on the large size,

173   but it also differs from the parasphenoid of *Salamandra lanzai* in the absence of processes on the

174   margines prooticum and on the margo otooccipitalis, the presence of the very low developed

175   processus lateralis superioris, the presence of the crista muscularis, the anteriorly open and

176   undivided lacuna cerebelli and the foramen located posteriorly to the crista prootica (see Villa et al.

177   2014). It differs from the one of *Ichthyosaura alpestris* because of the absence of cristae

178   vomeropalatinis and of processes on the margines prooticum and on the margo otooccipitalis, the

179   anteriorly-wider prominentia parasphenoidea, the straight crista muscularis provided with a three-

180   pointed process and the foramen located posteriorly to the crista prootica (see Vater 2003) and from

181   the one of *Lissotriton vulgaris* because of the absence of processes on the margines prooticum and

182   on the crista prootica, the anteriorly-wider prominentia parasphenoidea, the presence of the three-

183   pointed process on the crista muscularis, the well-defined sulci carotis and the foramen located

184   posteriorly to the crista prootica (AV, pers.obs). It is interesting to notice that it apparently differs

185   also from the parasphenoid of *Triturus carnifex* in the absence of processes on the margines

186   prooticum and on the margo otooccipitalis, the three points of the process located in the middle of

187   the crista muscularis, the lower development of the processus lateralis superioris and the foramen

188   located posteriorly to the crista prootica (AV, pers.obs).

189   *Lissotriton* Bell, 1839

190   *Lissotriton* sp. (Fig. 2M-V)

191   Material: 1 atlas; 32 trunk vertebrae; 2 caudal vertebrae; 7 humeri; 6 femora.

192   Identification: The atlas and the trunk vertebrae herein belong to the Salamandridae by the same

193   features discussed above in the identification of *Triturus* gr. *T. cristatus*. The atlas is assigned to the

194   genus *Lissotriton* because of the low ridges on the ventral surface of the centrum, the condyle wider

195   than the cotyle but narrower than the neural canal, the subcircular neural canal, the well-developed

196   lateral crests, the inclined neural arch, the shallow notch in the middle of the anterior margin of the

197   dorsal surface of the arch, the low neurapophysis visible in the anterior half of the arch only, the

198   secondary dorsal crests contacting posteriorly the triangular area formed by the two posteriorly-

199   directed ridges, the medial notch crossed by a well-developed ctenoid prominence located in the

200   middle of the posterior margin of the neural arch and the subtriangular posterior portion of the arch

201   (Ratnikov and Litvinchuk 2009). The attribution of the trunk vertebrae to the genus is based on the

202   combination of: the anterior surface of the condyle that can be slightly ventrally inclined, well-

203   developed ventral and zygapophyseal crests, deep notch in the middle of the posterior margin of the

204   neural arch, very high neurapophysis always reaching the posterior margin and flat or concave

205   laminae (Ratnikov and Litvinchuk 2007). The atlas differs from that of the two species of

206   *Lissotriton* considered by Ratnikov and Litvinchuk (2009), *L. montandoni* and *L. vulgaris*, because

207   its lateral crests start from the occipital joints, whereas theirs start near the posterior margin and

208   near the joints, respectively. Trunk vertebrae differ from those of *L. vulgaris* in the inclined or

209   straight anterior margin of the neurapophysis and from those of *L. montandoni* and *L. vulgaris* in

210   the anterior margin of the neural arch that can be slightly concave or slightly convex (Ratnikov and

211   Litvinchuk 2007). The size of the atlas is clearly smaller than the maximum values reported by

212   Ratnikov and Litvinchuk (2009) for *L. montandoni* and *L. vulgaris*, whereas trunk vertebrae are

213   smaller than the biggest ones of *L. montandoni* and reach higher values than those of *L. vulgaris*

214   (Ratnikov and Litvinchuk 2007). Given that, it is not possible to confidently identify these skeletal

215   elements at the species level. The attribution of the caudal vertebrae to *Lissotriton* sp. is based on

216   the morphological similarity with the trunk vertebrae. Humeri and femora that are smaller than

217   those assigned to *Triturus* and have a thinner shaft and a more inclined, less elongated crista

218   ventralis (humeri) or with a thinner shaft, a less elongated area between the trochanter and the caput

219   femoris and a less wide distal epiphysis with a less convex distal margin (femora) can be also

220   assigned to the genus *Lissotriton* (Holman 1998).

221   Caudata indet.

222   Material: 18 dentaries; 1 oto-occipital complex; 5 atlases; 11 trunk vertebrae; 3 caudal vertebrae; 6

223   humeri; 5 radii; 1 ulna; 3 ilia; 8 femora; 2 tibiae; 1 fibula.

224   Identification: A number of skeletal elements that are badly preserved or lack diagnostic features

225   have been identified only as indeterminate caudates.

226   Anura Fischer, 1813

227   Palaeobatrachidae Cope, 1865

228   *Palaeobatrachus* Tschudi, 1838

229   *Palaeobatrachus eurydices* Villa, Roček, Tschopp, Van den Hoek Ostende, Delfino, 2016

230   Material: Remains of *P. eurydices* from Tegelen are listed in Villa et al. (2016).

231   Identification: For the identification of these remains, the reader is referred to Villa et al. (2016).

232   Pelobatidae Bonaparte, 1850

233   *Pelobates* Wagler, 1830

234   *Pelobates fuscus* (Laurenti, 1768) (Fig. 3A-H)

235   Material: 32 maxillae; 7 sphenethmoids; 9 nasals; 8 frontoparietals; 49 fragments of frontoparietal;

236   8 squamosals; 1 atlas; 49 trunk vertebrae; 10 sacral vertebrae fused with the urostyle; 6 scapulae; 63

237   humeri; 26 ilia; 6 femora.

238   Identification: The following combinations of features (see Bailon, 1999, and Blain et al., 2016b)

239   allow to assign maxillae, sphenethmoids, frontoparietals, squamosals, sacral vertebrae fused with

240   the urostyle and ilia to *Pelobates fuscus.* Maxillae have teeth, little or fairly dense dermal

241   ornamentation composed by osseous keels and tubercles on the lateral surface and a slightly

242   concave margo orbitalis. Sphenethmoids are elongated and dorso-ventrally compressed, and are

243   provided with well-developed lateral processes, a long anterior process with an expansion at its

244   anterior end and a triangular dermal ossification on the dorsal surface. Frontoparietals are unpaired

245   and have a dorsal surface provided with fairly-dense dermal ornamentation, an undivided and

246   anteriorly-pointed incrassatio frontoparietalis, low developed and fairly-pointed squamosal

247   processes and foramina of the occipital arteries that can be seen in dorsal view. Squamosals have an

248   alary blade provided with sparse dense dermal ornamentation composed by osseous keels and

249   tubercles on the lateral surface. Sacral vertebrae are fused with the urostyle and have an anterior

250   cotyle and sacral apophyses strongly expanded antero-posteriorly. Ilia lack crista dorsalis and tuber

251   superior and are provided with a slightly curved shaft and little or fairly-marked lines on the

252   postero-medial surface of the body. Nasals, fragments of frontoparietal, atlas, trunk vertebrae,

253   scapulae, humeri and femora are assigned to the genus *Pelobates* on the basis of the following

254   combination of features (Bailon 1999). Nasals and fragments of frontoparietal are provided with

255   dermal ornamentation on the dorsal surface. The atlas has a posterior condyle, a long neural arch

256   and a well-developed posterior point. Procoelous trunk vertebrae have circular cotyle and condyle,

257   an elongated neural arch, a developed posterior point and cylindrical transverse apophyses which

258   are placed under the prezygapophyses and are antero-laterally directed. Scapulae are longer than

259   they are wide and display a processus glenoidalis partially hidden by the pars acromialis in ventral

260   view and a joint with the humerus composed by both processus glenoidalis and pars acromialis.

261   Humeri have a curved diaphysis, a laterally-shifted eminentia capitata, a crista paraventralis and a

262   fossa cubitalis ventralis that opens toward the lateral margin. Femora have a low crista femoris and

263   a very wide distal epiphysis. Following Bailon (1999), tibiofibulae are assigned to the genus

264   because of their overall shape and that of their epiphyses (see supplementary material). Given that a

265   single species of *Pelobates* has been identified in the studied material, also the bones that could be

266   identified at generic level only have been assigned to *P. fuscus*. The amphicoelous vertebral

267   centrum of RGM 817265 suggests that it was a trunk vertebra of a young individual (Bailon 1999).

268   Bufonidae Gray, 1825

269   *Bufo* Laurenti, 1768

270   *Bufo bufo* (Linnaeus, 1758) (Fig. 3I-N)

271   Material: 4 premaxillae; 3 frontoparietals; 13 trunk vertebrae; 1 sacral vertebra; 1 urostyle; 1

272   clavicle; 14 scapulae; 37 humeri; 19 ilia; 14 femora; 1 tibiofibula.

273   Identification: Frontoparietal, sacral vertebrae, scapulae, ilia and femora can be assigned to *B. bufo*

274   on the basis of the following combinations of features (Sanchiz 1977; Bailon 1999). Frontoparietals

275   are paired and not fused with the prootic-exoccipital; they are provided with a flat dorsal surface

276   and a long and wide occipital canal. The sacral vertebra has an anterior cotyle, a carina neuralis and

277   moderately wide sacral apophyses, but no fossae. Scapulae are elongated and display a strong

278   processus glenoidalis well visible in ventral view, a strong pars acromialis, no supraglenoidal fossa

279   and a crista anterior that is either absent or low. Ilia lack crista dorsalis, lamina calamita and

280   preacetabular fossa, but are provided with unilobed or bilobed and dorsally rounded tuber superior

281   and short pars ascendens. Femora are robust and display a triangular area formed by the splitting of

282   the crista femoris. Premaxillae, trunk vertebrae, the urostyle, the clavicle, humeri and the tibiofibula

283   can be identified only at the genus level, but the presence of a single species of *Bufo* in the studied

284   material allows their attribution to the same species. Combined features allowing the attribution of

285   the above-mentioned elements to *Bufo* are as follows (Bailon 1999). Premaxillae are toothless.

286   Trunk vertebrae are robust and procoelous, provided with a short neural arch, a well-developed

287   centrum and laterally directed transverse apophyses located posteriorly to the prezygapophyses. The

288   urostyle lacks transverse apophyses, but is provided with a well-developed crista dorsalis and two

289   slightly stretched anterior cotyles. The clavicle is large and straight. Humeri have no crista

290 paraventralis, but display a straight diaphysis, a laterally shifted and distally eroded eminentia

291 capitata, deep fossa cubitalis ventralis and moderately developed epicondyles. The tibiofibula is

292 robust and have the tibial portion strongly wider than the fibular portion. The robustness of all

293 skeletal elements is also in agreement with the assignment to *Bufo*. Because of the slightly curved

294 diaphysis, the humerus RGM 817096 could belong to a female (Bailon 1999).

295 Bombinatoridae Gray, 1825

296 *Bombina* Oken, 1816

297 *Bombina* sp. (Fig. 4A-H)

298 Material: 1 atlas; 36 trunk vertebrae; 4 sacral vertebrae; 3 urostyles; 27 humeri; 21 ilia; 2

299 tibiofibulae.

300 Identification: The morphology of these skeletal elements allows their attribution to the genus

301 *Bombina* on the basis of the combination of characters described by Bailon (1999). The atlas is

302 provided with a posterior cotyle, dorso-laterally inclined anterior cotyles, smooth ventral surface

303 and no carina neuralis. The trunk vertebrae have an opisthocoelous centrum, a moderately long

304 neural arch, carina neuralis absent or faint, no posterior point, cylindrical transverse apophyses (at

305 least in some specimens) and pseudo-zygosphene. The sacral vertebrae display an anterior condyle,

306 a single posterior condyle and the antero-posterior extension of the apophyses. Urostyles have short

307 and proximally widening transverse apophyses, no crista dorsalis and a single anterior cotyle.

308 Humeri are straight, lack a developed crista paraventralis and show a strongly laterally shifted

309 eminentia capitata and an absent or very shallow fossa cubitalis ventralis. Ilia have no crista

310 dorsalis, low or moderately developed tuber superior and low developed and scarcely visible pars

311 descendens. Tibiofibulae are straight and show slightly concave margins and moderately dorso-

312 ventrally compressed epiphyses. The presence of a low crista paraventralis in the humeri RGM

313 817135, 817179, 817180 and 817183 might suggest that they could belong to either *Discoglossus* or

314   *Pelodytes* (Bailon 1999), but the crista lateralis not bending ventrally excludes the former and the

315   absence of a distinct fossa cubitalis ventralis excludes the latter. These humeri have been therefore

316   assigned to *Bombina*, since their general morphology is fully comparable with that of the other

317   humeri attributed to this taxon.

318   Ranidae Rafinesque, 1814

319   *Pelophylax* Fitzinger, 1843

320   *Pelophylax* sp. (Fig. 4I-M)

321   Material: 1 sphenethmoid; 1 squamosal; 22 trunk vertebrae; 88 humeri; 69 ilia; 1 ilium fused with

322   the ischium.

323   Identification: These specimens are attributed to the group of the green frogs based on the following

324   combinations of features (Bailon 1999). The sphenethmoid is slightly longer than wide, not dorso-

325   ventrally compressed in its posterior portion, devoid of sella amplificans and provided with

326   moderately deep incisura semielliptica and short and well-individualized lateral processes. The

327   squamosal is T-shaped, lacks alar lamina and ornamentation and is provided with a low ridge on the

328   medial surface and a transverse branch the posterior portion of which is shorter than the anterior

329   one. Trunk vertebrae are either procoelous or amphicoelous, displaying a short neural arch, thin

330   lateral walls, poorly individualized centrum, carina neuralis, well-developed posterior point and

331   transverse apophyses not located ventrally to the prezygapophyses and laterally directed. Humeri

332   are provided with straight and robust diaphyses, eminentia capitata aligned with the diaphysis,

333   medially-directed crista medialis not as proximally developed as in brown frogs and lacking a

334   developed crista paraventralis. Ilia are provided with a high and vertical crista dorsalis, a well-

335   developed and robust tuber superior, high ileo-ischiadic junction and angle composed by tuber and

336   pars ascendens measuring 90°. The well-developed crista medialis identifies all the above-listed

337   humeri as belonging to male individuals (Bailon 1999).

338   *Rana* Linnaeus, 1758

339   *Rana* sp. (Fig. 4N-R)

340   Material: 24 trunk vertebrae; 1 trunk vertebra fused to the sacral vertebra; 45 humeri; 81 ilia.

341   Identification: The attribution of these trunk vertebrae to the brown frogs is based on the procoelous

342   or amphicoelous and poorly individualized vertebral centrum, the short neural arch with thin lateral

343   walls, the laterally directed and posteriorly located transverse apophyses, the very low carina

344   neuralis and the absent or low developed posterior point. The humeri are identified based on the

345   thin and straight diaphysis, the absence of a crista paraventralis, the unshifted eminentia capitata

346   and the very proximally elongated and dorsally bending crista medialis. Ilia are assigned to *Rana*

347   based on the presence of a crista dorsalis, the tuber superior less robust than in green frogs and the

348   angle composed by the tuber posterior and the pars ascendens exceeding 90°. All these

349   combinations of features are described by Bailon (1999). The presence of a crista paraventralis is an

350   unusual feature in brown frogs (Bailon 1999), but some humeri showing this feature clearly belong

351   to the genus *Rana* based on the presence of other diagnostic features of the group. Because of the

352   well-developed crista medialis, the above-listed humeri belong to males (Bailon 1999). Bailon

353   (1999) defines some diagnostic feature of the ilia of three different species of *Rana*: *Rana*

354   *dalmatina*, *R. arvalis* and *R. temporaria*. However, the ilia from Tegelen differ more or less

355   significantly from all these species. Ilia from Tegelen are distinguishable from those of *R.*

356   *dalmatina* and *R. arvalis* because of the medially bending crista dorsalis and the moderately high

357   ileo-ischiadic junction, whereas their attribution to *R. temporaria* is uncertain due to the variable

358   height of the crista dorsalis (low in *R. temporaria*, but sometimes moderately high in the Tegelen

359   specimens). Given these differences, we classify the fossil material as *Rana* sp.

360   Ranidae indet.

361   Material: 4 frontoparietals; 1 atlas; 18 trunk vertebrae; 71 sacral vertebrae; 29 urostyles; 4 clavicles;

362   64 scapulae; 2 scapulae fused to the clavicle; 1 shoulder girdle; 75 humeri; 111 ilia; 5 femora; 19

363   tibiofibulae.

364   Identification: The following combination of features allow the identification of the above-

365   mentioned remains as pertaining to undetermined ranids (Bailon 1999). Frontoparietals are not

366   medially fused, devoid of occipital canal, provided with an incrassatio frontoparietalis composed by

367   two portions, of which the posterior one is circular and medially closed, and with a low medial

368   ridge on the dorsal surface. The atlas has a posterior condyle, a short neural arch with thin lateral

369   walls; its carina neuralis and posterior point are not much developed and the poorly individualized

370   centrum is small and dorso-ventrally compressed. The fragmentary trunk vertebrae are either

371   procoelous or amphicoelous, with a short neural arch, thin lateral walls, a more or less developed

372   carina neuralis and transverse apophyses not located ventrally to the prezygapophyses. Sacral

373   vertebrae have an anterior condyle, two posterior condyles and cylindrical sacral apophyses.

374   Urostyles have no transverse apophyses, but are provided with a moderately high crista dorsalis and

375   two circular anterior cotyles. Clavicles are straight and thin. Scapulae are elongated, without crista

376   anterior, and have a pars acromialis hiding the pars glenoidalis in ventral view and not participating

377   in the articulation surface with the humerus. Humeri have a straight diaphysis aligned with the

378   eminentia capitata, but lack a crista paraventralis. Fragmentary ilia display a crista dorsalis and a

379   moderately developed tuber superior. Femora lack a crista femoris. Tibiofibulae have a straight

380   anterior margin, elliptical portions of the proximal epiphysis and fibular portion of the distal

381   epiphysis larger than the tibial portion. Due to the preservational status and to the lack of diagnostic

382   features on the elements, a more precise identification is not possible. Nevertheless, it could be

383   supposed that they belong to one of the two ranids identified in Tegelen: namely, either *Pelophylax*

384   or *Rana*. As written above for the humeri of *Rana* sp., the presence of a hint of the crista

385   paraventralis is unusual in Ranidae, but the above mentioned humeri showing it are here assigned to

386   this family because of the overall ranid morphology. The absence of a developed crista medialis

387   suggests that the above-listed humeri belonged to either juveniles or females (Bailon 1999).

388   Hylidae Rafinesque, 1815

389   *Hyla* Laurenti, 1768

390   *Hyla* gr. *H. arborea* (Linnaeus, 1758) (Fig. 5A-E)

391   Material: 4 trunk vertebrae; 2 sacral vertebrae; 12 scapulae; 7 humeri; 19 ilia; 6 femora.

392   Identification: The attribution of these specimens to *Hyla* is based on a combination of features

393   originally described by Bailon (1999). The diagnostic combination of features for the trunk

394   vertebrae includes the small and procoelous centrum, the short neural arch with thin lateral walls,

395   the transverse apophyses located posteriorly to the prezygapophyses and the absence of carina

396   neuralis. Sacral vertebrae are identified based on the presence of an anterior cotyle, the apparently

397   not much extended sacral apophyses and the absence of carina neuralis. Scapulae of *Hyla* are

398   characterized by the elongated and thin shape, the absence of a crista anterior, the straight and well-

399   visible processus glenoidalis and the straight pars acromialis. Significant features for the humeri are

400   the straight diaphysis, the absence of crista paraventralis, the laterally-shifted eminentia capitata, the

401   presence of the fossa cubitalis ventralis and the moderate development of the epicondyles.

402   Identification of the ilia is based on the absence of a crista dorsalis, the presence of a bulbous and

403   laterally curved tuber superior and the antero-ventral expansion of the preacetabular area. These

404   femora from Tegelen share with *Hyla* the thin morphology, the thin crista femoris and the

405   morphology of the epiphyses. Despite some attempt based either on the inclination of the

406   prezygapophyses on the sacral vertebra (Sanchiz 1998b) or on the morphology of the tuber superior

407   (Gleed-Owen 1998; Holman 1992), many authors consider it impossible to discriminate the

408   different European species of *Hyla* (Bailon 1999; Sanchiz 1981; Sanchiz and Mlynarski 1979;

409   Sanchiz and Sanz 1980). Therefore, we assign these fossils only to the species complex named after

410 the most widespread European species, *H. arborea* (Sillero et al. 2014). Furthermore, it has to be

411 noted that the Tegelen specimens differ from *H. savignyi* in lacking the supraglenoidal fossa

412 (Vasilyan et al. 2017).

413 Pelodytidae Bonaparte, 1850

414 *Pelodytes* Bonaparte, 1838

415 *Pelodytes* sp. (Fig. 5F-N)

416 Material: 1 trunk vertebra; 1 sacral vertebra.

417 Identification: RGM 817240, the trunk vertebra, is assigned to *Pelodytes* because of the

418 combination of a procoelous centrum with subelliptical cotyle and condyle, the moderately long

419 neural arch, the cylindrical and antero-laterally-directed transverse apophyses located ventrally to

420 the prezygapophyses and the poorly-developed posterior point (Bailon 1999). The attribution of the

421 sacral vertebra, RGM 817270, is based on the combined presence of an anterior cotyle, strongly

422 extended sacral apophyses, lack of fusion with the urostyle and two poorly-individualized posterior

423 condyles (Bailon 1999).

424 Anura indet.

425 Material: 20 premaxillae; 101 maxillae; 2 sphenethmoids; 2 parasphenoids; 11 exoccipitals; 9

426 prootic-exoccipitals; 3 columellae; 27 squamosals; 16 pterygoids; 3 quadratojugals; 127 angulars;

427 25 atlases; 833 trunk vertebrae; 1 atlas fused to the first trunk vertebra; 46 sacral vertebrae; 18

428 urostyles; 5 clavicles; 89 coracoids; 3 scapulae; 231 humeri; 643 radioulnae; 56 ilia; 6 ischia; 205

429 femora; 182 tibiofibulae; 1198 undetermined elements.

430 Identification: A large number of fragmentary or poorly taxonomically significant skeletal elements

431 are identified only as undetermined anurans.

432 "Reptilia" Laurenti, 1768

433 Testudines Batsch, 1788

434 Cryptodyra Cope, 1868

435 Geoemydidae Theobald, 1868

436 *Mauremys* Gray, 1869

437 *Mauremys* sp. (Fig. 6)

438 Material: 1 nuchal.

439 Identification: The wide area covered by the cervical scute distinguishes nuchals of *Mauremys* from

440 those of *Testudo* and *Emys* (Hervet 2000). Moreover, in contrast with the nuchal of *Emys*, the one of

441 *Mauremys* does not have the groove marking the contact between vertebral I and left pleural I

442 scutes (Hervet 2000). Because of that, we can assign the nuchal RGM 816718 to *Mauremys*.

443 Testudines indet.

444 Material: 1 fragment of plastron; 1 shell fragment.

445 Identification: A fragment of plastron and an undetermined shell fragment have been identified only

446 at order level because of the lack of diagnostic features allowing a more precise identification.

447 Squamata Oppel, 1811

448 "Lacertilia" Owen, 1842

449 Lacertidae Batsch, 1788

450 *Lacerta* Linnaeus, 1758

451 *Lacerta* sp. (Fig. 7A-C)

452 Material: 1 dentary.

453   Identification: The dentary RGM 816720 can be referred to a lacertid because of the presence of

454   cylindrical, pleurodont, mono-, bi- and tricuspid teeth, the medially-opened, wide Meckel's groove

455   and the convex ventral margin (Delfino 2002; Delfino et al. 2011). The length of the alveolar shelf

456   (11.5 mm) falls within the range of the largest species of the genus *Lacerta* and of *Timon lepidus*

457   (Barahona and Barbadillo 1997). *Timon*, however, reaches much higher dimensions than *Lacerta*:

458   up to 60 cm in total length, with documented specimens measuring 80/90 cm in length (Delfino

459   2002 and reference therein). Thus, it is possible to assign RGM 816720 to a large *Lacerta* species.

460   Lacertidae indet.

461   Material: 1 parietal; 1 maxilla; 1 pterygoid; 3 dentaries; 2 cervical vertebrae; 14 trunk vertebrae; 4

462   cloacal vertebrae; 11 caudal vertebrae.

463   Identification: All the above listed specimens are small-sized, suggesting the presence of a small

464   lacertid taxon in the fossil material from Tegelen. However, it has to be noted that the only skeletal

465   elements that can possibly have a diagnostic significance (namely, the parietal and the pterygoid,

466   since the tooth-bearing bones are too fragmentary) do not show clear adult features, and therefore

467   they can simply represent juveniles of a larger taxon. Because of this, this fossils are here attributed

468   only to undetermined lacertids.

469   Anguidae Gray, 1825

470   Anguinae Gray, 1825

471   *Anguis* Linnaeus, 1758

472   *Anguis* gr. *A. fragilis* Linnaeus, 1758 (Fig. 7M-V)

473   Material: 1 parietal; 1 maxilla; 56 trunk vertebrae; 2 cloacal vertebrae; 34 caudal vertebrae; 143

474   osteoderms.

475   Identification: The dorso-ventrally compressed centrum of presacral vertebrae devoid of

476   precondylar constriction is a feature of the subfamily Anguinae according to Estes (1983). The size

477   of the skeletal elements suggest their attribution to a small-sized taxon. Because of the parallel

478   margins in the posterior portion of the centrum, they can be assigned to *Anguis* (Holman 1998;

479   Klembara 1981). Maxilla and parietal can be attributed to the same genus because of the presence

480   of large, canine-like, unstriated and curved teeth on the former (Klembara et al. 2014) and the deep

481   parietal notch on the latter (Delfino et al. 2011). The identification of the osteoderms is based on the

482   small size, the rounded shape, the thin morphology and the absence of keels on the external surface

483   (Delfino et al. 2011; Holman 1998). Since a comparative osteological study of the different *Anguis*

484   species is still missing, the material has been identified only at the level of species complex

485   (including *Anguis cephallonica*, *Anguis colchica*, *Anguis fragilis*, *Anguis graeca* and *Anguis*

486   *veronensis*; Gvoždík et al. 2013).

487   *Pseudopus* Merrem, 1820

488   cf. *Pseudopus* sp. (Fig. 7W-X)

489   Material: 1 osteoderm.

490   Identification: The large size (about 4.3 mm of total length) of the osteoderm RGM 816716

491   suggests the presence of a large-sized anguid. Size, thickness and the ridge on the external surface

492   preclude the attribution of this osteoderm to *Anguis* (Delfino et al. 2011; Holman 1998). In the

493   European Pleistocene, findings confidently attributable to *Ophisaurus* are reported only from Spain

494   (Bailon and Blain 2007; Blain 2009; Blain et al. 2016a), whereas *Pseudopus* is the only non-*Anguis*

495   anguid known from northern countries. Moreover, the Spanish fossils represent much smaller

496   animals than the osteoderm found at Tegelen. Thus, RGM 816716 can be tentatively attributed to

497   cf. *Pseudopus* sp., the only large-sized anguid genus certainly identified from northern European

498   Pleistocene localities so far.

499   "Lacertilia" indet.

500   Material: 2 dentaries; 1 trunk vertebra; 1 caudal vertebra; 1 fragment of vertebra; 4 ribs; 1

501   scapulocoracoid; 5 humeri; 1 ulna; 3 ilia; 4 femora.

502   Identification: A number of poorly preserved or non-diagnostic skeletal elements have been

503   identified only as indeterminate lizards.

504   Serpentes Linnaeus, 1758

505   Colubridae Oppel, 1811

506   "Colubrines" Szyndlar, 1991a

507   "Colubrines" indet. (Fig. 8A-E)

508   Material: 6 trunk vertebrae.

509   Identification: "Colubrines" include members of the family Colubridae with no hypapophysis on the

510   trunk vertebrae (Szyndlar 1991a). Because of the presence of an hemal keel on the ventral surface

511   of the centrum of the herein-considered vertebrae, it is possible to attribute them to undetermined

512   colubrines (Szydlar 1984), but the poor preservational status hinders a more precise identification.

513   Natricinae Bonaparte, 1838 (sensu Szyndlar, 1991b)

514   *Natrix* Laurenti, 1768

515   *Natrix natrix* (Linnaeus, 1758) (Fig. 8F-J)

516   Material: 58 trunk vertebrae.

517   Identification: These trunk vertebrae are assigned to the genus *Natrix* because of the following

518   combination of features (Szyndlar 1984): their elongation, the presence of a sigmoid hypapophysis,

519   the well-developed and rounded prezygapophyseal processes, the horizontal prezygapophyses, the

520   vaulted neural arch and the high neural spine. The rounded end of the hypapophysis and of the

521 parapophyses allow the attribution to *N. natrix* (Szyndlar 1984; Szyndlar 1991b). Among the

522 diagnostic features distinguishing *N. natrix* from *N. tessellata* and *N. maura*, Szyndlar (1984) also

523 mentioned the thickness of the parapophyses, which are more robust in *N. natrix* than in the other

524 species. However, this features is highly variable both in the fossil and in the comparative material,

525 and therefore it is not enough to sustain an attribution either to *N. tessellata* or *N. maura*.

526 Natricinae indet.

527 Material: 60 trunk vertebrae.

528 Identification: These vertebrae show features of Natricinae as reported by Szyndlar (1984). Due to

529 the scarce preservational status, this fossil material is identified only as undetermined natricines, but

530 it might reasonably pertain to *N. natrix*, the only natricine identified in Tegelen.

531 Viperidae Oppel, 1811

532 *Vipera* Laurenti, 1768

533 *Vipera* sp. (Fig. 8K-O)

534 Material: 1 trunk vertebra.

535 Identification: Combined, the elongation, the presence of a non-sigmoid hypapophysis, the thin and

536 well antero-ventrally-directed parapophyses, the acute prezygapophyseal processes and the

537 tectiform posterior margin of the neural arch identify RGM 816823 as a trunk vertebra of a member

538 of the Viperidae (Szyndlar 1984; Szyndlar 1991b). The inclined zygapophyses and the wide cotyle

539 allow the attribution to an undetermined species of the genus *Vipera* (Delfino et al. 2011). The

540 small size (centrum length is 3.2 mm) and the rather lightly-constructed morphology distinguish

541 this vertebra from trunk vertebrae of the oriental vipers, indicating it rather represents one of the

542 smaller species of the *Vipera aspis* and *Vipera berus* complexes (Bailon et al. 2010).

543 Serpentes indet.

544   Material: 1 premaxilla; 2 maxillae; 1 dentary; 4 isolated tooth; 2 atlases; 1 axis; 8 cervical vertebrae;

545   109 trunk vertebrae; 66 caudal vertebrae; 2 fragments of vertebra; 22 ribs.

546   Identification: A number of poorly preserved or presumed undiagnostic skeletal elements are

547   identified only as undetermined snakes.

548   "Reptilia" indet.

549   Material: 2 vertebral centra.

550   Identification: Two small vertebral centra provided with subelliptical cotyle and condyle and a well-

551   developed keel on the ventral surface are attributed to undetermined reptiles. RGM 817472 has a

552   low and thin keel, whereas in RGM 817471 it is robust and, although broken, it was probably more

553   developed in ventral direction in origin.

554   *3.2. Palaeoclimatic reconstruction*

555   The fossil assemblage from Tegelen in its entirety has no modern analogue, because its extant taxa

556   do not co-occur in the present-day fauna. Nevertheless, overlap of the ranges of most of the taxa is

557   possible if we exclude from the analysis the extinct *P. euridyces* and the extant genus *Pelodytes*,

558   which currently has a disjoined distribution in southern Europe that seems not to be climate-related

559   (Pearman et al. 2010). In addition, we should take into account that the modern distribution of *P.*

560   *fuscus* in the Balkan area is probably influenced by the competition with *Pelobates syriacus* (Iosif et

561   al. 2014; Tarkhnishvili et al. 2009). To resolve the last point, an overlap with the modern fauna has

562   been obtained by merging the present distribution of both *P. fuscus* and *P. syriacus*. In doing so, an

563   analogue of the fauna can be found in three UTM squares (Fig. 9A). These 50 x 50 km UTM

564   squares occur in a relatively similar climatic environment in southern Bulgaria at the border with

565   Greece and Turkey (cities of Burgas, Svilengrad and Sandanski). Such an overlap corresponds to a

566   mean value of 13.4 ± 0.3ºC of mean annual temperature and 542 ± 50 mm of mean annual

567   precipitation (Tab. 1). The climate can be characterized as temperate, with a very high atmospheric

568   temperature range. The summer is warm and the winter is cold. Rainfall is low, but its distribution

569   is fairly regular, with the highest amount during winter and to a lesser extent spring. Three months

570   during summer and early autumn (from July to September) are considered to be dry, according to

571   the Gaussen Index (Fig. 9B). According to the Köppen-Geiger classification of climates, such an

572   overlap corresponds to the humid subtropical climate (Cfa). The Lautensach-Mayer and De

573   Martonne Indices suggest a semi-humid continental Mediterranean climate with three dry months in

574   summer (Fig. 9B; Tab. 2). By contrast, the Dantin-Revenga Aridity Index classifies the climate as

575   semi-arid (Tab. 2).

576   In comparison to the current climatic data from Tegelen area (Oceanic climate, Cfb) the MER-

577   estimated MAT is much higher (+3.4ºC) than at present (Tab. 1). Such warmer climatic conditions

578   during the early Pleistocene are mainly linked with a greater increase in temperature in summer

579   (between +5.1ºC and +6.0ºC) than in winter (+0.4ºC and +1.7ºC). The total amount of rainfall is

580   somewhat lower (-227 mm) than at present in the Tegelen area, leading to three months of aridity,

581   whereas today the Oceanic climate from Tegelen shows no dry month (Fig. 9B). This is

582   corroborated by the value of the Aridity Indices, suggesting that, at the time of deposition,

583   conditions in Tegelen were much drier than today, especially during summer.

584   **4. Discussion**

585   *4.1. The herpetofaunistic assemblage of the Russel-Tiglia-Egypte pit*

586   The very large amount (more than 6000 remains) of fossils of amphibians and reptiles coming from

587   the Russel-Tiglia-Egypte pit in Tegelen reveals a well diversified herpetofauna, a list of preliminary

588   identifications of which was provided by Van den Hoek Ostende and De Vos (2006). Now that we

589   have completed the entire study of the fauna, at least 17 taxa have been identified, including two

590   caudates (*Triturus* gr. *T. cristatus* and *Lissotriton* sp.), seven anurans (*P. fuscus*, *B. bufo*, *Bombina*

591   sp., *Pelophylax* sp., *Rana* sp., *Hyla* gr. *H. arborea* and *Pelodytes* sp.), one chelonian (*Mauremys*

592   sp.), four lizards (*Lacerta* sp., Lacertidae indet., *Anguis* gr. *A. fragilis* and cf. *Pseudopus* sp.) and

593   three snakes ("colubrines" indet., *Natrix natrix* and *Vipera* sp.). In addition, the locality yielded the

594   recently described new species of palaeobatrachid anuran *Palaeobatrachus eurydices* Villa et al.,

595   2016, the only extinct taxon so far known among amphibians and reptiles from Tegelen.

596   The only reptile previously reported from the Tegelen clay pits was a single specimen donated to

597   the Natuurhistorisch Museum of Maastricht by the owner of the Russel-Tiglia pit and attributed to

598   *Emys orbicularis* by Schreuder (1946). That specimen is currently lost and therefore it is not

599   possible to whether confirm or not its attribution to the European pond turtle. Nevertheless, another

600   specimen found in the Canoy-Herfkens pit and currently stored in the Naturalis Biodiversity Center

601   in Leiden, RGM 75114, clearly displays features of *E. orbicularis*, such as the presence on the

602   nuchal of the grooves marking the contact between the vertebral I scute and the left and right

603   pleural I scutes and the narrow and elongated area being covered by the cervical scute (see

604   diagnostic characters in Hervet 2000). The presence of *E. orbicularis* in Tegelen during the Tiglian

605   can therefore be actually confirmed, but since fossil remains coming from different pits might have

606   slightly different ages (Van den Hoek Ostende and Vos 2006) and the precise stratigraphical

607   position of both Schreuder's specimen and the Leiden one is not known, it is still not possible to

608   state that this species was coeval with the herein-described assemblage.

609   Tegelen represents one of the few Pleistocene herpetofaunas found in The Netherlands (Böhme and

610   Ilg 2003; Holman 1998; Schouten 2016), and is by far the most diverse known thus far. The only

611   other Dutch locality that is comparable in terms of number of taxa retrieved is the younger (Middle

612   Pleistocene) site of Maastricht-Belvédère 4 (Holman 1998; Schouten 2016), the herpetofauna of

613   which includes at least 11 amphibians and reptiles. Compared to Tegelen, the latter locality lacks

614   those taxa strictly linked to a warm climate such as *Mauremys*, and displays an assemblage that is

615   more similar to the extant herpetofauna of The Netherlands. A second significant absence in

616   Maastricht-Belvédère 4, as well as in all other quaternary Dutch localities, is *P. eurydices* (and

617   palaeobatrachids in general). This might suggest that the suitable conditions that allowed this water-

618   dwelling anurans to survive in the southern part of The Netherlands until the Gelasian disappeared

619   after the early Pleistocene, causing their definitive extinction in Western Europe. Nevertheless, it is

620   not possible to completely exclude that this absence might simply be a result of the scarce

621   knowledge we have of Dutch Pleistocene herpetofaunas. Only new data from other fossil-bearing

622   sites of the region will allow to shed more light on this issue.

623   *4.2. The climate of Tegelen and the survival of palaeobatrachids in Western Europe*

624   In The Netherlands, the Pleistocene is characterized by a marked palaeoclimatic cyclic nature,

625   involving alternating glacial and interglacial phases (Drees 2005 and references therein). After a

626   first glacial period, the Pretiglian, interglacial conditions set up during the Tiglian stage, even

627   though cool oscillations were still present (Drees 2005; Reid and Reid 1915; Vlerk and Florschütz

628   1953; Zagwijn 1963). Based on palynological analyses, the Tiglian stage was separated by Zagwijn

629   (1963) into three different substages (TA, TB and TC), the latter of which is further composed by

630   six sections (TC1 to TC6). According to the palaeoclimatic quantitative reconstructions of the

631   Dutch pollen sequence (Kasse 1988, 1993; Kasse and Bohncke 2001; Zagwijn 1963, 1989), the

632   TC5 section of the Tiglian is separated in three phases: warm-cold-warm. The deciduous vegetation

633   of the warm periods (TC5a and c) indicates that the mean summer temperature was around 18ºC

634   (mean temperature of the warmest month = 18 to 20ºC according to Pross and Kloss 2002), the

635   mean winter temperature above -1ºC (mean temperature of the coldest month = -2 to 0ºC according

636   to Pross and Kloss 2002) and the mean annual temperature circa 10ºC (i.e., similar to current value).

637   The German pollen record from Lieth (zone E5; Pross and Kloss 2002) provides for the TC5 a

638   mean January temperature estimate of -1ºC and mean July temperatures between 14 and 21.5 ºC

639   consistent with the estimation by Zagwijn (1963, 1989) for Tegelen. The palaeoclimatic

640   reconstruction based on the amphibian and reptile assemblage from Tegelen thus suggests that some

641   of these early Pleistocene interglacial periods in northern Europe would have been somewhat

642   warmer than previously reconstructed with mean temperature of the warmest month reaching up to

643   23.7 ± 0.6ºC and mean temperature of the coldest month 2.6 ± 0.1ºC.

644   The light degree of dryness based on herpetological evidence is apparently in contrast with the

645   palaeoenvironmental information given by some components of the fauna. For one, the best

646   represented group in the fauna are the beavers (Schreuder 1929), to the point that the Tegelen Clay

647   was sometimes referred to as the *Trogontherium* Clay, because of the numerous finds of this extinct

648   beaver. However, the herpetofauna stems from a stream gully cutting into the palustrine sequence,

649   which could be seen as confirmation that we are indeed dealing with a dryer period. Nevertheless,

650   the micromammal fauna, which was retrieved together with the herpetofauna, refutes overly dry

651   conditions. Desmans are numerous (Rümke 1985) and the diverse shrew fauna indicates a humid

652   environment. Among the voles, typical steppe elements of the era, such as *Borsodia*, are

653   conspicuously absent and the presumably semi-aquatic *Mimomys pliocaenicus* is numerous. In

654   addition, the assemblage show a high proportion of various forest and shrub dwellers, such as

655   *Apodemus*, *Clethrionomys* and the glirids, *Muscardinus* and *Glirulus*.

656   Part of the apparent inconsistency in the palaeoenvironmental reconstructions based on different

657   groups can be explained by the absence of recent analogues of the conditions in the Villafranchian.

658   As we noted, there is no strict present-day analogue of the herpetofauna, which is not surprising as

659   the same hold true for the flora and the mammal fauna. The former still contains a number of

660   Tertiary elements, whereas the dormouse *Glirulus* is now restricted to Japan. In finding a modern

661   analogue, we had discarded the only extinct member of the herpetofauna, *Palaeobatrachus*

662   *euridyces*. As a palaeobatrachid, *P. euridyces* is considered to have been extremely adapted to a

663   water-dwelling life (Villa et al. 2016), therefore needing permanent water bodies to survive. The

664   combination of increasing drought and periglacial areas with low temperatures during winter

665   leading to a freezing of the water bodies is thought to have caused the definitive extinction of

666   palaeobatrachid anurans during the Middle Pleistocene, and the aridization is usually singled out as

the cause for their extirpation from Western Europe (Wuttke et al. 2012). The presence at Tegelen

of a member of this group is evidence of the persistence of suitable water bodies during the whole

year, without a significant period of freezing during winter (as confirmed by our palaeoclimatic

results) and despite the relatively arid months during summer. The fairly regular pluviometric

regime might have contributed to maintain the availability of wet environments and, in addition, the

vicinity to the Rhine river would also have ensured the presence of permanent water bodies. A

similarly moist landscape might have been present in another, slightly older locality not so far from

Tegelen, in which rare palaeobatrachid remains have been found: Hambach 11 (late Pliocene, MN

16) in northwestern Germany (Mörs 2002). Hambach 11 shows a lower diversity in the amphibians

and reptiles assemblage compared to Tegelen (Cernanský et al. 2016; Mörs 2002), but also a

striking difference in the composition of the fauna, which includes cryptobranchids, proteids,

discoglossids and chelydrids. The presence of an anguid related with *Pseudopus pannonicus*, which

is considered to be linked with sub-humid/humid climates (Cernanský et al. 2016), might be an

evidence of moist conditions in Hambach during the late Pliocene. This seems to be further

confirmed by the fish remains (Mörs 2002). It can, therefore, be supposed that a rather humid

climate might have somehow persisted in this part of Western Europe, favouring the survival of

palaeobatrachids. Nevertheless, given our current knowledge of Dutch climate and herpetofaunas at

the early/Middle Pleistocene transition, it is not possible to state whether the following

disappearance of these anurans from this region could be linked with decreasing temperature,

increasing aridization, a combination of both or even with other, still unrecognised reasons.

5. Conclusions

The fossil herpetofauna of Tegelen contributes to fill the gap of knowledge we have of the

evolutionary history of Dutch amphibians and reptiles throughout the Quaternary, representing a

moment of high herpetological diversity at least in the South of The Netherlands. On the whole, the

association indicates a temperate climate, which allowed some warm-adapted taxa (as e.g.,

692 *Mauremys*) to live in the area. This climate can be linked to a warm phase of the Tiglian interglacial

693 stage. In comparison to previous climate reconstructions, the herpetofauna indicates slightly warmer

694 and, somewhat surprisingly, dryer conditions than previously assumed.

695 Most probably, the presence at Tegelen of humid or sub-humid conditions are directly correlated

696 with the survival of the water-dwelling frog *P. eurydices*, the last representative of the family

697 Palaeobatrachidae in Western Europe. However, more findings in other northwestern European

698 localities are needed in order to understand how palaeobatrachids escaped extinction due to

699 aridization after the Miocene/Pliocene boundary in the western portion of the European continent

700 and when and why they ultimately disappeared from the area.

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955 **Figures and figure captions**

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957
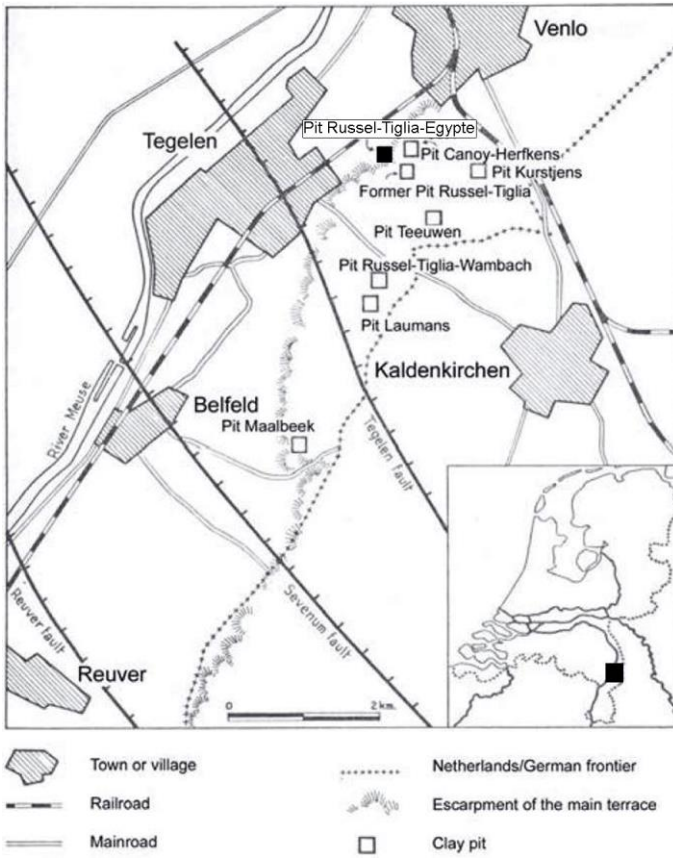
Fig. 1. Location of the Russel-Tiglia-Egypte pit and other clay pits near Tegelen (map modified

from Van den Hoek Ostende & Vos 2006).

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Fig. 2. Caudates from the Russel-Tiglia-Egypte pit. *Triturus* gr. *T. cristatus*: parasphenoid (RGM 816926) in ventral (A) and dorsal (B) views; atlas (RGM 816893) in dorsal (C), anterior (D), left lateral (E), ventral (F) and posterior (G) views; trunk vertebra (RGM 816912) in dorsal (H), ventral (I), anterior (J), posterior (K) and left lateral (L) views. *Lissotriton* sp.: atlas (RGM 816955) in anterior (M), posterior (N), left lateral (O), dorsal (P) and ventral (Q) views; trunk vertebra (RGM 816960) in ventral (R), dorsal (S), anterior (T), posterior (U) and left lateral (V) views. Scale bars = 1 mm.

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Fig. 3. Pelobatids and bufonids from the Russel-Tiglia-Egypte pit. *Pelobates fuscus*: right maxilla (RGM 817237) in lateral (A) and medial (B) views; sphenethmoid (RGM 817192) in dorsal (C) and ventral (D) views; frontoparietal (RGM 817226) in ventral (E) and dorsal (F) views; right ilium (RGM 817200) in medial (G) and lateral (H) views. *Bufo bufo*: left frontoparietal (RGM 817028) in dorsal (I) and ventral (J) views; right scapula (RGM 817020) in ventral (K) and dorsal (L) views; right ilium (RGM 817761) in lateral (M) e medial (N) views. Scale bars = 1 mm.

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Fig. 4. Bombinatorids and ranids from the Russel-Tiglia-Egypte pit. *Bombina* sp.: trunk vertebra (RGM 817141) in anterior (A), right lateral (B), ventral (C) and dorsal (D) views; left humerus (RGM 817145) in ventral (E) and lateral (F) views; right ilium (RGM 817104) in lateral (G) and medial (H) views. *Pelophylax* sp.: left humerus (RGM 817351) in dorsal (I), medial (J) and ventral (K) views; right ilium (RGM 817376) in lateral (L) and medial (M) views. *Rana* sp.: left humerus (RGM 817435) in dorsal (N), medial (O) and ventral (P) views; left ilium (RGM 817455) in lateral (Q) and medial (R) views. Scale bars = 1 mm.

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Fig. 5. Hylids and pelodytids from the Russel-Tiglia-Egypte pit. *Hyla* gr. *H. arborea*: left humerus (RGM 817187) in dorsal (A), medial (B) and ventral (C) views; right ilium (RGM 817150) in lateral (D) and medial (E) views. *Pelodytes* sp.: trunk vertebra (RGM 817240) in anterior (F), dorsal (G), left lateral (H), ventral (I) and posterior (J) views; sacral vertebra (RGM 817270) in dorsal (K), anterior (L), posterior (M) and ventral (N) views. Scale bars = 1 mm.

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998 **Fig. 6.** *Mauremys* sp. from the Russel-Tiglia-Egypte pit. Nuchal (RGM 816718) in dorsal (A) and

999 ventral (B) views. Scale bar = 5 mm.

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1003 **Fig. 7.** Lizards from the Russel-Tiglia-Egypte pit. *Lacerta* sp.: left dentary (RGM 816720) in dorsal

1004 (A), lateral (B) and medial (C) views. Lacertidae indet.: parietal (RGM 816758) in dorsal (D) and

1005 ventral (E) views; right pterygoid (RGM 816743) in ventral (F) and dorsal (G) views; trunk vertebra

1006   (RGM 816739) in anterior (H), posterior (I), right lateral (J), dorsal (K) and ventral (L) views.

1007   *Anguis* gr. *A. fragilis*: parietal (RGM 816693) in dorsal (M) and ventral (N) views; left maxilla

1008   (RGM 816701) in lateral (O) and medial (P) views; trunk vertebra (RGM 816676) in dorsal (Q),

1009   ventral (R), anterior (S), posterior (T) and left lateral (U) views; osteoderm (RGM 816699) in

1010   external view (V). cf. *Pseudopus* sp.: osteoderm (RGM 816716) in external (W) and internal (X)

1011   views. Scale bars = 1 mm.
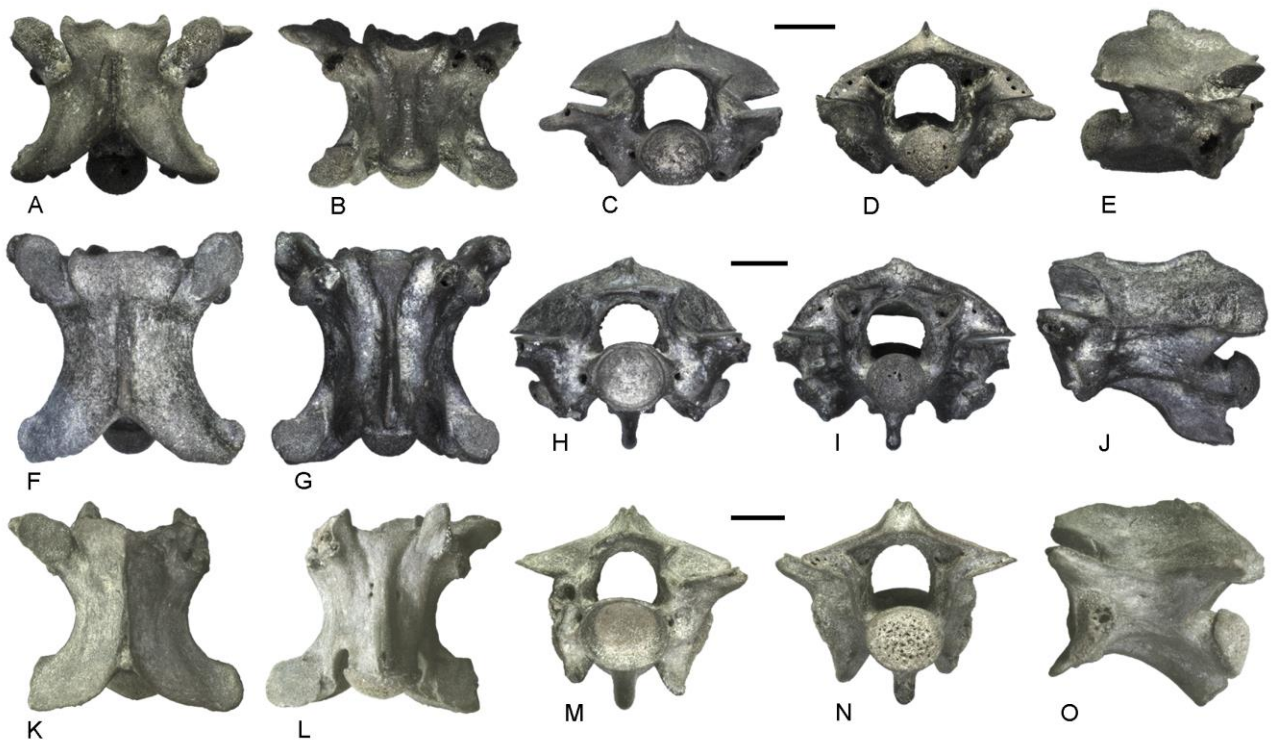
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1013   **Fig. 8.** Snakes from the Russel-Tiglia-Egypte pit. "Colubrines" indet.: trunk vertebra (RGM

1014   816817) in dorsal (A), ventral (B), anterior (C), posterior (D) and right lateral (E) views. *Natrix*
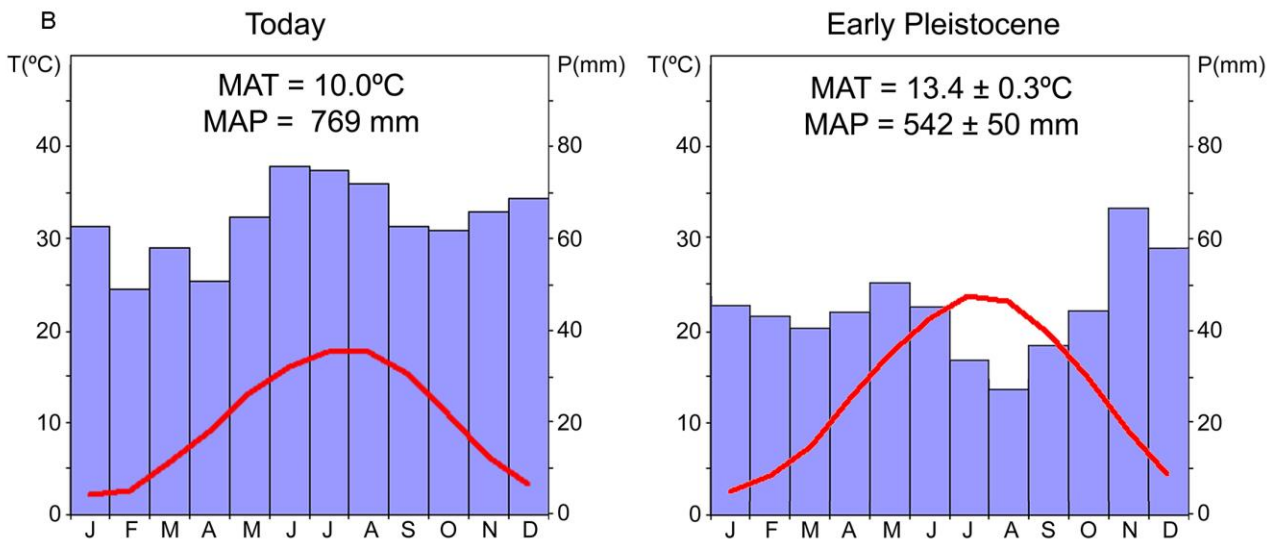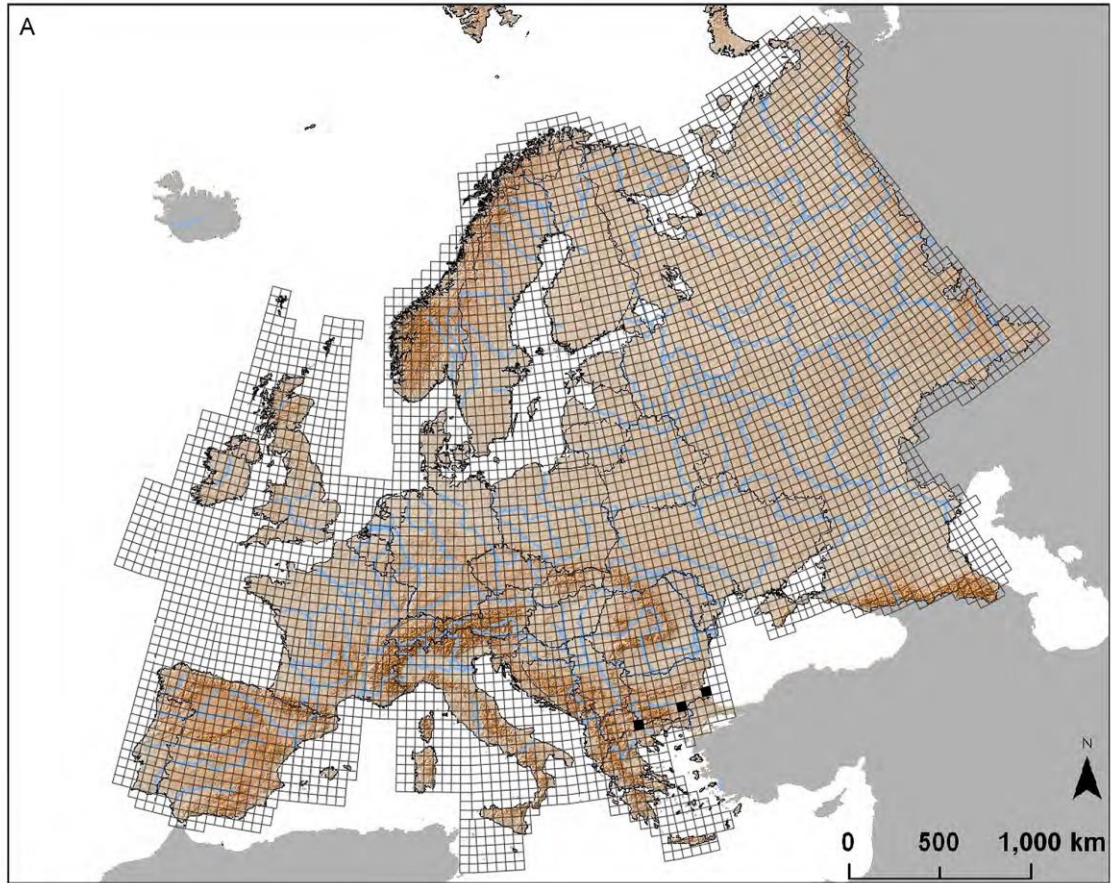
1015   *natrix*: trunk vertebra (RGM 816780) in dorsal (F), ventral (G), anterior (H), posterior (I) and left

1016   lateral (J) views. *Vipera* sp.: trunk vertebra (RGM 816823) in dorsal (K), ventral (L), anterior (M),

1017   posterior (N) and left lateral (O) views. Scale bars = 1 mm.

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Fig. 9. Monthly palaeoclimatic reconstructions for Tegelen based on its fossil herpetofaunal

assemblage. A: overlaps of the current distribution done in 50 × 50 km UTM squares; B:

quantitative reconstruction according to the Mutual Ecogeographic Range method compared with

current data.

						Temperature (in ºC)							
	MAT	J	F	M	A	M	J	J	A	S	O	N	D
MEAN	13.4	2.6	4.4	7.5	12.5	17.3	21.3	23.7	23.1	19.8	14.9	9.2	4.5
SD	0.3	0.1	0.4	0.7	0.6	0.6	0.5	0.6	0.7	0.6	0.8	0.6	0.6
Today	10.0	2.2	2.7	5.8	9.1	13.2	16.2	17.7	17.6	15.2	10.9	6.2	3.4
Δ	+3.4	+0.4	+1.7	+1.7	+3.4	+4.1	+5.1	+6.0	+5.5	+4.6	+4.0	+3.0	+1.1
						Precipitation (in mm)							
	MAP	J	F	M	A	M	J	J	A	S	O	N	D
MEAN	542	46	44	41	45	51	46	34	28	37	45	67	59
SD	50	9	6	7	5	1	3	4	4	11	7	6	9
Today	769	63	49	58	51	65	76	75	72	63	62	66	69
Δ	-227	-17	-5	-17	-6	-14	-30	-41	-44	-26	-17	1	-10

1025 **Tab. 1.** Climatic parameters calculated with the Mutual Ecogeographic Range method for the early

1026 Pleistocene of Tegelen and current climatic values from the Tegelen area. MAT: mean annual

1027 temperature; MAP: mean annual precipitation; SD: standard deviation; Δ: difference between Early

1028 Pleistocene estimated and current values.

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		Today		Early Pleistocene	
Temperature	Mean annual temperature	10.0°C	temperate	13.4°C	temperate
	Atmospheric temperature range	15.5°C	medium	21.1°C	very high
	Summer temperature	0 months>22°C	temperate	2 months>22°C	warm
	Winter temperature	MTC = 2.2°C	cold	MTC = 2.6°C	cold
Rainfall	Mean annual precipitation	769 mm	low	542 mm	low
	Distribution of rainfall	no month<30 mm	regular	1 month<30 mm	fairly regular
	Type of precipitation	rain		rain	
Aridity	Gaussen Index	0	Oceanic	3	Mediterranean
	Lautensach-Mayer Index	0	humid	3	semi-humid
	Dantin-Revenga Index	1.3	humid	2.5	semi-arid
	De Martonne Index	38.5	humid	23.2	semi-humid

1030 **Tab. 2.** Climatic interpretation of the modern and Early Pleistocene climatograms of Tegelen.

1031 MTC: mean temperature of the coldest month.