Villa, Andrea; Blain, Hugues-Alexandre; Van Den Hoek Ostende, L.W.; [et al.]. «Fossil amphibians and reptiles from Tegelen (Province of Limburg) and the early Pleistocene palaeoclimate of The Netherlands». Quaternary Science Reviews, Vol. 187 (May 2018), p. 203-219. DOI 10.1016/j.quascirev.2018.03.020

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

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Abstract

Few Quaternary herpetofaunas have been recovered from The Netherlands. Among these, the one coming from the early Pleistocene site of the Russel-Tiglia-Egypte pit near Tegelen is of particular interest, because it is the type locality of the recently described, last western European palaeobatrachid anuran, *Palaeobatrachus eurydices*. The large number of fossil remains of amphibians and reptiles found in the pit are representative of a very diverse fauna, including at least 17 taxa: *Triturus* gr. *T. cristatus*, *Lissotriton* sp., *Pelobates fuscus*, *Bufo bufo*, *Bombina* sp., *Pelophylax* sp., *Rana* sp., *Hyla* gr. *H. arborea*, *Pelodytes* sp., *Mauremys* sp., *Lacerta* sp., Lacertidae 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 ± 0.3ºC and mean annual precipitation was 542 ± 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 reptiles, but, because of them being active thermoregulators rather than simply temperature-dependent organisms, temperature also has a direct effect on their activity patterns (Sears and Angilletta 2004). The thermoregulatory behaviour, and specifically minimizing its cost, is also at the origin of the propensity of some reptiles to select densely vegetated environments, since the vegetation cover offers protection against predators and a mosaic of shaded and sunny areas that ease the activities of these animals (Díaz 1997; Díaz and Carrascal 1991: Huey 1974; Huey and Slatkins 1976). Vegetation is strictly linked to the pluviometry of a specific area and therefore this latter factor has an indirect effect on the distribution of reptiles too, including those species that are tied to arid environments.

Given this strong relationship with the environment, fossil amphibians and reptiles have been largely used as indicators of the palaeoclimate (e.g., Agustí et al. 2009; Bailon and Blain 2007; Blain et al. 2013, 2014; Böhme 2003; Böhme et al. 2006). Pleistocene fossils are particularly useful in this sense, because they largely belong to extant species or species groups of which the ecological requirements are well known (Blain et al. 2008). Given that, they represent suitable material for the application of the Mutual Ecogeographic Range Method (Blain et al. 2009, 2016c among others).

We here describe a herpetological assemblage from the early Pleistocene site of Tegelen (Province of Limburg, The Netherlands) and use these data to reconstruct the climatic conditions present in the locality during the time of deposition of the remains. The outcome is compared to those of earlier environmental reconstructions based on other groups.

1.1. The Tegelen pits

The village of Tegelen has been an important centre for the production of ceramics since Roman times because of the high-quality clay that was quarried from the various pits in the surroundings (Van den Hoek Ostende and Vos 2006). During the 20th century, a large number of fossil bones were collected as a byproduct of the quarry activity and soon Tegelen became famous also for its fossil mammal fauna (Van den Hoek Ostende and Vos 2006 and references therein). Most of the fossils from Tegelen were just picked up by workers as they encountered them, but during the 1970s a field campaign aimed at collecting small mammals was organized (Freudenthal et al. 1976). The target of this campaign was the Russel-Tiglia-Egypte pit (Fig. 1), and it also resulted in the collection of remains of fish (Gaudant 1979), amphibians and reptiles (Van den Hoek Ostende and Vos 2006; Villa et al. 2016). These remains come from a stream gully infill located near the top of the Russel-Tiglia-Egypte pit section (Kortenbout van der Sluys and Zagwijn 1962) and deposited during the warm TC5 section of the Tiglian (Zagwijn 1963), which can be correlated with part of the Gelasian (Drees 2005). The small mammal fauna from the infill, described by Van den Hoek Ostende (2003), Reumer (1984), Reumer and Hoek Ostende (2003), Rümke (1985) and Tesakov (1998) among others, is correlated with the *Borsodia newtoni–Mimomys pliocaenicus* Biozone, dated to 2.26–2.1 Ma (Mayhew 2015).

2. Material & Methods

The herein-studied remains include all the amphibian and reptile fossil material recovered from the Russel-Tiglia-Egypte pit, except for the palaeobatrachid remains that were recently described as the new species *Palaeobatrachus eurydices* (Villa et al. 2016). The remains are stored in the collections of Naturalis Biodiversity Center in Leiden, under the acronym RGM. A complete list and detailed descriptions of the fossil remains are presented in the electronic supplementary material. The best preserved and most significant skeletal elements have been photographed at the University of Torino using a Leica M205 microscope equipped with the Leica application suite V 3.3.0. The identification are based on both criteria found in the literature and direct comparisons with skeletonized specimens of extant taxa. The comparative material is stored in the Department of Earth Science of the University of Torino, in the Muséum national d’Histoire naturelle in Paris and in the Naturhistorisches Museum in Wien.

The anatomical terminology follows Vater (2003), Ratnikov and Litvinchuk (2007, 2009), Wu et al. (2012) and Villa et al. (2014) for caudates, Špinar (1972), Sanchiz (1998a) and Bailon (1999) for anurans, Hervet (2000) for chelonians, Evans (2008), Barahona and Barbadillo (1997) and Klembara et al. (2010) for lizards and Szyndlar (1984) for snakes.

2.1. Palaeoclimatic reconstruction

Early Pleistocene palaeoclimate reconstruction from Tegelen based on its herpetofaunal content has been done using a quantitative climate reconstruction method, the Mutual Ecogeographic Range (MER; Blain et al. 2009, 2016c). Analysis of the MER for the Tegelen fossil assemblage is based on the distribution atlas of the European herpetofauna (Sillero et al. 2014), with 50 × 50 km resolution maps in the Universal transverse Mercator (UTM) georeferenced system. Climatic parameters have been estimated for each 50 × 50 km UTM square, using the climatic database from Climate-Data.org.

3. Results

3.1. Systematic palaeontology

Amphibia Linnaeus, 1758

Caudata Scopoli, 1777

Salamandridae Goldfuss, 1820

Triturus Rafinesque, 1815

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

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

Identification: Combined, the fairly thin, gutter-shaped odontoid process, the presence of the neurapophysis rather than of a bulge on the dorsal surface of the neural arch, the fairly robust dorsal portion of the arch and the postzygapophyses that extend beyond the posterior margin are all diagnostic features of the atlas of members of the family Salamandridae (Ratnikov and Litvinchuk 2009). Trunk vertebrae can be assigned to the same family based on the combination of opisthocoelous condition, presence of wide subcentral foramina, of a foramen placed near the base of the parapophyses and of a notch in the middle of the posterior margin of the neural arch (Ratnikov and Litvinchuk 2007). Atlases and trunk vertebrae can be referred to the genus *Triturus* based on a combination of characters. The subcircular neural canal, the presence of foramina on the ventral surface of the centrum and of the lateral processes, the well-developed lateral crests, the inclined dorsal margin of the arch, the slightly wavy posterior margin and the roughly parallel, fairly separated secondary dorsal crests are features of the *Triturus* atlases (Ratnikov and Litvinchuk 2009). Together, the flat and sometimes slightly ventrally inclined anterior surface of the condyle, the weakly or well-developed neck, the straight or concave anterior margin of the neural arch, the concavity of the anterior margin which never extends posteriorly to the anterior half of the prezygapophyses, the posterior margin of the neural arch which extends up to the posterior margin of the postzygapophyses or slightly beyond it, the low depth of the notch located in the middle of the posterior margin and the prominent laminae allow to attribute the trunk vertebrae to the same genus (Ratnikov and Litvinchuk 2007). The attribution to *Triturus* gr. *T. cristatus*, the species complex comprising *Triturus arntzeni, T. carnifex, T. cristatus, T. dobrogicus, T. karelinii* and *T. macedonicus* (Sillero et al. 2014), is based on: the combination of the absence of a triangular surface posteriorly to the neurapophysis of the atlases, possible presence of grooves on the lateral processes, low secondary dorsal crests which reach the posterior margin of the neural arch, trapezoidal posterior portion of the neural arch in the atlases, height and development of the neurapophysis and of the posterior ventral crests of the trunk vertebrae and the sizes of both atlases and trunk vertebrae (Ratnikov and Litvinchuk 2007, 2009). It should be noticed, however, that fairly developed anterior ventral crests and zygapophyseal crests are unusual in the vertebrae of the genus *Triturus*, in which they are usually low developed or lacking. The morphological similarity between trunk and caudal vertebrae permits the attribution of the latter to the same species complex.

Humeri and femora are referred to the same complex and not to *Lissotriton* sp. based on the larger size and because of the more elongated, less inclined crista ventralis and the more robust shaft for the humeri and because of the more elongated area included between the trochanter and the caput femoris, the wider shaft and the wider distal epiphysis provided with a more convex margin for the femora (Holman 1998). The identification of the parasphenoid is based partially on the large size, but it also differs from the parasphenoid of *Salamandra lanzai* in the absence of processes on the margines prooticum and on the margo otooccipitalis, the presence of the very low developed processus lateralis superioris, the presence of the crista muscularis, the anteriorly open and undivided lacuna cerebelli and the foramen located posteriorly to the crista prootica (see Villa et al. 2014). It differs from the one of *Ichthyosaura alpestris* because of the absence of cristae vomeropalatinis and of processes on the margines prooticum and on the margo otooccipitalis, the anteriorly-wider prominentia parasphenoidea, the straight crista muscularis provided with a three-pointed process and the foramen located posteriorly to the crista prootica (see Vater 2003) and from the one of *Lissotriton vulgaris* because of the absence of processes on the margines prooticum and on the crista prootica, the anteriorly-wider prominentia parasphenoidea, the presence of the three-pointed process on the crista muscularis, the well-defined sulci carotis and the foramen located posteriorly to the crista prootica (AV, pers.obs). It is interesting to notice that it apparently differs also from the parasphenoid of *Triturus carnifex* in the absence of processes on the margines prooticum and on the margo otooccipitalis, the three points of the process located in the middle of the crista muscularis, the lower development of the processus lateralis superioris and the foramen located posteriorly to the crista prootica (AV, pers.obs).

Lissotriton Bell, 1839

Lissotriton sp. (Fig. 2M-V)

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

Identification: The atlas and the trunk vertebrae herein belong to the Salamandridae by the same features discussed above in the identification of *Triturus* gr. *T. cristatus*. The atlas is assigned to the genus *Lissotriton* because of the low ridges on the ventral surface of the centrum, the condyle wider than the cotyle but narrower than the neural canal, the subcircular neural canal, the well-developed lateral crests, the inclined neural arch, the shallow notch in the middle of the anterior margin of the dorsal surface of the arch, the low neurapophysis visible in the anterior half of the arch only, the secondary dorsal crests contacting posteriorly the triangular area formed by the two posteriorly-directed ridges, the medial notch crossed by a well-developed ctenoid prominence located in the middle of the posterior margin of the neural arch and the subtriangular posterior portion of the arch (Ratnikov and Litvinchuk 2009). The attribution of the trunk vertebrae to the genus is based on the combination of: the anterior surface of the condyle that can be slightly ventrally inclined, well-developed ventral and zygapophyseal crests, deep notch in the middle of the posterior margin of the neural arch, very high neurapophysis always reaching the posterior margin and flat or concave laminae (Ratnikov and Litvinchuk 2007). The atlas differs from that of the two species of *Lissotriton* considered by Ratnikov and Litvinchuk (2009), *L. montandoni* and *L. vulgaris*, because its lateral crests start from the occipital joints, whereas theirs start near the posterior margin and near the joints, respectively. Trunk vertebrae differ from those of *L. vulgaris* in the inclined or straight anterior margin of the neurapophysis and from those of *L. montandoni* and *L. vulgaris* in the anterior margin of the neural arch that can be slightly concave or slightly convex (Ratnikov and Litvinchuk 2007). The size of the atlas is clearly smaller than the maximum values reported by Ratnikov and Litvinchuk (2009) for *L. montandoni* and *L. vulgaris*, whereas trunk vertebrae are smaller than the biggest ones of *L. montandoni* and reach higher values than those of *L. vulgaris* (Ratnikov and Litvinchuk 2007). Given that, it is not possible to confidently identify these skeletal elements at the species level. The attribution of the caudal vertebrae to *Lissotriton* sp. is based on the morphological similarity with the trunk vertebrae. Humeri and femora that are smaller than those assigned to *Triturus* and have a thinner shaft and a more inclined, less elongated crista ventralis (humeri) or with a thinner shaft, a less elongated area between the trochanter and the caput femoris and a less wide distal epiphysis with a less convex distal margin (femora) can be also assigned to the genus *Lissotriton* (Holman 1998).

Caudata indet.

Material: 18 dentaries; 1 oto-occipital complex; 5 atlases; 11 trunk vertebrae; 3 caudal vertebrae; 6 humeri; 5 radii; 1 ulna; 3 ilia; 8 femora; 2 tibiae; 1 fibula.

Identification: A number of skeletal elements that are badly preserved or lack diagnostic features have been identified only as indeterminate caudates.

Anura Fischer, 1813

Palaeobatrachidae Cope, 1865

Palaeobatrachus Tschudi, 1838

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

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

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

Pelobatidae Bonaparte, 1850

Pelobates Wagler, 1830

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

Material: 32 maxillae; 7 sphenethmoids; 9 nasals; 8 frontoparietals; 49 fragments of frontoparietal; 8 squamosals; 1 atlas; 49 trunk vertebrae; 10 sacral vertebrae fused with the urostyle; 6 scapulae; 63 humeri; 26 ilia; 6 femora.

Identification: The following combinations of features (see Bailon, 1999, and Blain et al., 2016b) allow to assign maxillae, sphenethmoids, frontoparietals, squamosals, sacral vertebrae fused with the urostyle and ilia to *Pelobates fuscus*. Maxillae have teeth, little or fairly dense dermal ornamentation composed by osseous keels and tubercles on the lateral surface and a slightly concave margo orbitalis. Sphenethmoids are elongated and dorso-ventrally compressed, and are provided with well-developed lateral processes, a long anterior process with an expansion at its anterior end and a triangular dermal ossification on the dorsal surface. Frontoparietals are unpaired and have a dorsal surface provided with fairly-dense dermal ornamentation, an undivided and anteriorly-pointed incrassatio frontoparietalis, low developed and fairly-pointed squamosal processes and foramina of the occipital arteries that can be seen in dorsal view. Squamosals have an alary blade provided with sparse dense dermal ornamentation composed by osseous keels and tubercles on the lateral surface. Sacral vertebrae are fused with the urostyle and have an anterior cotyle and sacral apophyses strongly expanded antero-posteriorly. Ilia lack crista dorsalis and tuber superior and are provided with a slightly curved shaft and little or fairly-marked lines on the postero-medial surface of the body. Nasals, fragments of frontoparietal, atlas, trunk vertebrae, scapulae, humeri and femora are assigned to the genus *Pelobates* on the basis of the following combination of features (Bailon 1999). Nasals and fragments of frontoparietal are provided with dermal ornamentation on the dorsal surface. The atlas has a posterior condyle, a long neural arch and a well-developed posterior point. Procoelous trunk vertebrae have circular cotyle and condyle, an elongated neural arch, a developed posterior point and cylindrical transverse apophyses which are placed under the prezygapophyses and are antero-laterally directed. Scapulae are longer than they are wide and display a processus glenoidalis partially hidden by the pars acromialis in ventral view and a joint with the humerus composed by both processus glenoidalis and pars acromialis. Humeri have a curved diaphysis, a laterally-shifted eminentia capitata, a crista paraventralis and a fossa cubitalis ventralis that opens toward the lateral margin. Femora have a low crista femoris and a very wide distal epiphysis. Following Bailon (1999), tibiofibulae are assigned to the genus because of their overall shape and that of their epiphyses (see supplementary material). Given that a single species of *Pelobates* has been identified in the studied material, also the bones that could be identified at generic level only have been assigned to *P*. *fuscus*. The amphicoelous vertebral centrum of RGM 817265 suggests that it was a trunk vertebra of a young individual (Bailon 1999).

Bufonidae Gray, 1825

Bufo Laurenti, 1768

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

Material: 4 premaxillae; 3 frontoparietals; 13 trunk vertebrae; 1 sacral vertebra; 1 urostyle; 1 clavicle; 14 scapulae; 37 humeri; 19 ilia; 14 femora; 1 tibiofibula.

Identification: Frontoparietal, sacral vertebrae, scapulae, ilia and femora can be assigned to *B*. *bufo* on the basis of the following combinations of features (Sanchiz 1977; Bailon 1999). Frontoparietals are paired and not fused with the prootic-exoccipital; they are provided with a flat dorsal surface and a long and wide occipital canal. The sacral vertebra has an anterior cotyle, a carina neuralis and moderately wide sacral apophyses, but no fossae. Scapulae are elongated and display a strong processus glenoidalis well visible in ventral view, a strong pars acromialis, no supraglenoidal fossa and a crista anterior that is either absent or low. Ilia lack crista dorsalis, lamina calamita and preacetabular fossa, but are provided with unilobed or bilobed and dorsally rounded tuber superior and short pars ascendens. Femora are robust and display a triangular area formed by the splitting of the crista femoris. Premaxillae, trunk vertebrae, the urostyle, the clavicle, humeri and the tibiofibula can be identified only at the genus level, but the presence of a single species of *Bufo* in the studied material allows their attribution to the same species. Combined features allowing the attribution of the above-mentioned elements to *Bufo* are as follows (Bailon 1999). Premaxillae are toothless. Trunk vertebrae are robust and procoelous, provided with a short neural arch, a well-developed centrum and laterally directed transverse apophyses located posteriorly to the prezygapophyses. The urostyle lacks transverse apophyses, but is provided with a well-developed crista dorsalis and two slightly stretched anterior cotyles. The clavicle is large and straight. Humeri have no crista paraventralis, but display a straight diaphysis, a laterally shifted and distally eroded eminentia capitata, deep fossa cubitalis ventralis and moderately developed epicondyles. The tibiofibula is robust and have the tibial portion strongly wider than the fibular portion. The robustness of all skeletal elements is also in agreement with the assignment to *Bufo*. Because of the slightly curved diaphysis, the humerus RGM 817096 could belong to a female (Bailon 1999).

Bombinatoridae Gray, 1825

Bombina Oken, 1816

Bombina sp. (Fig. 4A-H)

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

Identification: The morphology of these skeletal elements allows their attribution to the genus *Bombina* on the basis of the combination of characters described by Bailon (1999). The atlas is provided with a posterior cotyle, dorso-laterally inclined anterior cotyles, smooth ventral surface and no carina neuralis. The trunk vertebrae have an opisthocoelous centrum, a moderately long neural arch, carina neuralis absent or faint, no posterior point, cylindrical transverse apophyses (at least in some specimens) and pseudo-zygosphene. The sacral vertebrae display an anterior condyle, a single posterior condyle and the antero-posterior extension of the apophyses. Urostyles have short and proximally widening transverse apophyses, no crista dorsalis and a single anterior cotyle. Humeri are straight, lack a developed crista paraventralis and show a strongly laterally shifted eminentia capitata and an absent or very shallow fossa cubitalis ventralis. Ilia have no crista dorsalis, low or moderately developed tuber superior and low developed and scarcely visible pars descendens. Tibiofibulae are straight and show slightly concave margins and moderately dorso-ventrally compressed epiphyses. The presence of a low crista paraventralis in the humeri RGM 817135, 817179, 817180 and 817183 might suggest that they could belong to either *Discoglossus* or

Pelodytes (Bailon 1999), but the crista lateralis not bending ventrally excludes the former and the absence of a distinct fossa cubitalis ventralis excludes the latter. These humeri have been therefore assigned to *Bombina*, since their general morphology is fully comparable with that of the other humeri attributed to this taxon.

Ranidae Rafinesque, 1814

Pelophylax Fitzinger, 1843

Pelophylax sp. (Fig. 4I-M)

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

Identification: These specimens are attributed to the group of the green frogs based on the following combinations of features (Bailon 1999). The sphenethmoid is slightly longer than wide, not dorso-ventrally compressed in its posterior portion, devoid of sella amplificans and provided with moderately deep incisura semielliptica and short and well-individualized lateral processes. The squamosal is T-shaped, lacks alar lamina and ornamentation and is provided with a low ridge on the medial surface and a transverse branch the posterior portion of which is shorter than the anterior one. Trunk vertebrae are either procoelous or amphicoelous, displaying a short neural arch, thin lateral walls, poorly individualized centrum, carina neuralis, well-developed posterior point and transverse apophyses not located ventrally to the prezygapophyses and laterally directed. Humeri are provided with straight and robust diaphyses, eminentia capitata aligned with the diaphysis, medially-directed crista medialis not as proximally developed as in brown frogs and lacking a developed crista paraventralis. Ilia are provided with a high and vertical crista dorsalis, a well-developed and robust tuber superior, high ileo-ischiadic junction and angle composed by tuber and pars ascendens measuring 90°. The well-developed crista medialis identifies all the above-listed humeri as belonging to male individuals (Bailon 1999).

Rana Linnaeus, 1758

Rana sp. (Fig. 4N-R)

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

Identification: The attribution of these trunk vertebrae to the brown frogs is based on the procoelous or amphicoelous and poorly individualized vertebral centrum, the short neural arch with thin lateral walls, the laterally directed and posteriorly located transverse apophyses, the very low carina neuralis and the absent or low developed posterior point. The humeri are identified based on the thin and straight diaphysis, the absence of a crista paraventralis, the unshifted eminentia capitata and the very proximally elongated and dorsally bending crista medialis. Ilia are assigned to *Rana* based on the presence of a crista dorsalis, the tuber superior less robust than in green frogs and the angle composed by the tuber posterior and the pars ascendens exceeding 90°. All these combinations of features are described by Bailon (1999). The presence of a crista paraventralis is an unusual feature in brown frogs (Bailon 1999), but some humeri showing this feature clearly belong to the genus *Rana* based on the presence of other diagnostic features of the group. Because of the well-developed crista medialis, the above-listed humeri belong to males (Bailon 1999). Bailon (1999) defines some diagnostic feature of the ilia of three different species of *Rana*: *Rana dalmatina*, *R. arvalis* and *R. temporaria*. However, the ilia from Tegelen differ more or less significantly from all these species. Ilia from Tegelen are distinguishable from those of *R. dalmatina* and *R. arvalis* because of the medially bending crista dorsalis and the moderately high ileo-ischiadic junction, whereas their attribution to *R. temporaria* is uncertain due to the variable height of the crista dorsalis (low in *R. temporaria*, but sometimes moderately high in the Tegelen specimens). Given these differences, we classify the fossil material as *Rana* sp.

Ranidae indet.

Material: 4 frontoparietals; 1 atlas; 18 trunk vertebrae; 71 sacral vertebrae; 29 urostyles; 4 clavicles; 64 scapulae; 2 scapulae fused to the clavicle; 1 shoulder girdle; 75 humeri; 111 ilia; 5 femora; 19 tibiofibulae.

Identification: The following combination of features allow the identification of the above-mentioned remains as pertaining to undetermined ranids (Bailon 1999). Frontoparietals are not medially fused, devoid of occipital canal, provided with an incrassatio frontoparietalis composed by two portions, of which the posterior one is circular and medially closed, and with a low medial ridge on the dorsal surface. The atlas has a posterior condyle, a short neural arch with thin lateral walls; its carina neuralis and posterior point are not much developed and the poorly individualized centrum is small and dorso-ventrally compressed. The fragmentary trunk vertebrae are either procoelous or amphicoelous, with a short neural arch, thin lateral walls, a more or less developed carina neuralis and transverse apophyses not located ventrally to the prezygapophyses. Sacral vertebrae have an anterior condyle, two posterior condyles and cylindrical sacral apophyses. Urostyles have no transverse apophyses, but are provided with a moderately high crista dorsalis and two circular anterior cotyles. Clavicles are straight and thin. Scapulae are elongated, without crista anterior, and have a pars acromialis hiding the pars glenoidalis in ventral view and not participating in the articulation surface with the humerus. Humeri have a straight diaphysis aligned with the eminentia capitata, but lack a crista paraventralis. Fragmentary ilia display a crista dorsalis and a moderately developed tuber superior. Femora lack a crista femoris. Tibiofibulae have a straight anterior margin, elliptical portions of the proximal epiphysis and fibular portion of the distal epiphysis larger than the tibial portion. Due to the preservational status and to the lack of diagnostic features on the elements, a more precise identification is not possible. Nevertheless, it could be supposed that they belong to one of the two ranids identified in Tegelen: namely, either *Pelophylax* or *Rana*. As written above for the humeri of *Rana* sp., the presence of a hint of the crista paraventralis is unusual in Ranidae, but the above mentioned humeri showing it are here assigned to this family because of the overall ranid morphology. The absence of a developed crista medialis suggests that the above-listed humeri belonged to either juveniles or females (Bailon 1999).

Hylidae Rafinesque, 1815

Hyla Laurenti, 1768

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

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

Identification: The attribution of these specimens to *Hyla* is based on a combination of features originally described by Bailon (1999). The diagnostic combination of features for the trunk vertebrae includes the small and procoelous centrum, the short neural arch with thin lateral walls, the transverse apophyses located posteriorly to the prezygapophyses and the absence of carina neuralis. Sacral vertebrae are identified based on the presence of an anterior cotyle, the apparently not much extended sacral apophyses and the absence of carina neuralis. Scapulae of *Hyla* are characterized by the elongated and thin shape, the absence of a crista anterior, the straight and well-visible processus glenoidalis and the straight pars acromialis. Significant features for the humeri are the straight diaphysis, the absence of crista paraventralis, the laterally-shifted eminentia capitata, the presence of the fossa cubitalis ventralis and the moderate development of the epicondyles. Identification of the ilia is based on the absence of a crista dorsalis, the presence of a bulbous and laterally curved tuber superior and the antero-ventral expansion of the preacetabular area. These femora from Tegelen share with *Hyla* the thin morphology, the thin crista femoris and the morphology of the epiphyses. Despite some attempt based either on the inclination of the prezygapophyses on the sacral vertebra (Sanchiz 1998b) or on the morphology of the tuber superior (Gleed-Owen 1998; Holman 1992), many authors consider it impossible to discriminate the different European species of *Hyla* (Bailon 1999; Sanchiz 1981; Sanchiz and Mlynarski 1979; Sanchiz and Sanz 1980). Therefore, we assign these fossils only to the species complex named after the most widespread European species, *H. arborea* (Sillero et al. 2014). Furthermore, it has to be noted that the Tegelen specimens differ from *H. savignyi* in lacking the supraglenoidal fossa (Vasilyan et al. 2017).

Pelodytidae Bonaparte, 1850

Pelodytes Bonaparte, 1838

Pelodytes sp. (Fig. 5F-N)

Material: 1 trunk vertebra; 1 sacral vertebra.

Identification: RGM 817240, the trunk vertebra, is assigned to *Pelodytes* because of the combination of a procoelous centrum with subelliptical cotyle and condyle, the moderately long neural arch, the cylindrical and antero-laterally-directed transverse apophyses located ventrally to the prezygapophyses and the poorly-developed posterior point (Bailon 1999). The attribution of the sacral vertebra, RGM 817270, is based on the combined presence of an anterior cotyle, strongly extended sacral apophyses, lack of fusion with the urostyle and two poorly-individualized posterior condyles (Bailon 1999).

Anura indet.

Material: 20 premaxillae; 101 maxillae; 2 sphenethmoids; 2 parasphenoids; 11 exoccipitals; 9 prootic-exoccipitals; 3 columellae; 27 squamosals; 16 pterygoids; 3 quadratojugals; 127 angulars; 25 atlases; 833 trunk vertebrae; 1 atlas fused to the first trunk vertebra; 46 sacral vertebrae; 18 urostyles; 5 clavicles; 89 coracoids; 3 scapulae; 231 humeri; 643 radioulnae; 56 ilia; 6 ischia; 205 femora; 182 tibiofibulae; 1198 undetermined elements.

Identification: A large number of fragmentary or poorly taxonomically significant skeletal elements are identified only as undetermined anurans.

“Reptilia” Laurenti, 1768

Testudines Batsch, 1788

Cryptodyra Cope, 1868

Geoemydidae Theobald, 1868

Mauremys Gray, 1869

Mauremys sp. (Fig. 6)

Material: 1 nuchal.

Identification: The wide area covered by the cervical scute distinguishes nuchals of *Mauremys* from those of *Testudo* and *Emys* (Hervet 2000). Moreover, in contrast with the nuchal of *Emys*, the one of *Mauremys* does not have the groove marking the contact between vertebral I and left pleural I scutes (Hervet 2000). Because of that, we can assign the nuchal RGM 816718 to *Mauremys*.

Testudines indet.

Material: 1 fragment of plastron; 1 shell fragment.

Identification: A fragment of plastron and an undetermined shell fragment have been identified only at order level because of the lack of diagnostic features allowing a more precise identification.

Squamata Oppel, 1811

“Lacertilia” Owen, 1842

Lacertidae Batsch, 1788

Lacerta Linnaeus, 1758

Lacerta sp. (Fig. 7A-C)

Material: 1 dentary.

Identification: The dentary RGM 816720 can be referred to a lacertid because of the presence of cylindrical, pleurodont, mono-, bi- and tricuspid teeth, the medially-opened, wide Meckel’s groove and the convex ventral margin (Delfino 2002; Delfino et al. 2011). The length of the alveolar shelf (11.5 mm) falls within the range of the largest species of the genus *Lacerta* and of *Timon lepidus* (Barahona and Barbadillo 1997). *Timon*, however, reaches much higher dimensions than *Lacerta*: up to 60 cm in total length, with documented specimens measuring 80/90 cm in length (Delfino 2002 and reference therein). Thus, it is possible to assign RGM 816720 to a large *Lacerta* species.

Lacertidae indet.

Material: 1 parietal; 1 maxilla; 1 pterygoid; 3 dentaries; 2 cervical vertebrae; 14 trunk vertebrae; 4 cloacal vertebrae; 11 caudal vertebrae.

Identification: All the above listed specimens are small-sized, suggesting the presence of a small lacertid taxon in the fossil material from Tegelen. However, it has to be noted that the only skeletal elements that can possibly have a diagnostic significance (namely, the parietal and the pterygoid, since the tooth-bearing bones are too fragmentary) do not show clear adult features, and therefore they can simply represent juveniles of a larger taxon. Because of this, this fossils are here attributed only to undetermined lacertids.

Anguidae Gray, 1825

Anguinae Gray, 1825

Anguis Linnaeus, 1758

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

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

Identification: The dorso-ventrally compressed centrum of presacral vertebrae devoid of precondylar constriction is a feature of the subfamily Anguinae according to Estes (1983). The size of the skeletal elements suggest their attribution to a small-sized taxon. Because of the parallel margins in the posterior portion of the centrum, they can be assigned to *Anguis* (Holman 1998; Klembara 1981). Maxilla and parietal can be attributed to the same genus because of the presence of large, canine-like, unstriated and curved teeth on the former (Klembara et al. 2014) and the deep parietal notch on the latter (Delfino et al. 2011). The identification of the osteoderms is based on the small size, the rounded shape, the thin morphology and the absence of keels on the external surface (Delfino et al. 2011; Holman 1998). Since a comparative osteological study of the different *Anguis* species is still missing, the material has been identified only at the level of species complex (including *Anguis cephallonica*, *Anguis colchica*, *Anguis fragilis*, *Anguis graeca* and *Anguis veronensis*; Gvoždík et al. 2013).

Pseudopus Merrem, 1820

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

Material: 1 osteoderm.

Identification: The large size (about 4.3 mm of total length) of the osteoderm RGM 816716 suggests the presence of a large-sized anguid. Size, thickness and the ridge on the external surface preclude the attribution of this osteoderm to *Anguis* (Delfino et al. 2011; Holman 1998). In the European Pleistocene, findings confidently attributable to *Ophisaurus* are reported only from Spain (Bailon and Blain 2007; Blain 2009; Blain et al. 2016a), whereas *Pseudopus* is the only non-*Anguis* anguid known from northern countries. Moreover, the Spanish fossils represent much smaller animals than the osteoderm found at Tegelen. Thus, RGM 816716 can be tentatively attributed to cf. *Pseudopus* sp., the only large-sized anguid genus certainly identified from northern European Pleistocene localities so far.

“Lacertilia” indet.

Material: 2 dentaries; 1 trunk vertebra; 1 caudal vertebra; 1 fragment of vertebra; 4 ribs; 1 scapulocoracoid; 5 humeri; 1 ulna; 3 ilia; 4 femora.

Identification: A number of poorly preserved or non-diagnostic skeletal elements have been identified only as indeterminate lizards.

Serpentes Linnaeus, 1758

Colubridae Oppel, 1811

“Colubrines” Szyndlar, 1991a

“Colubrines” indet. (Fig. 8A-E)

Material: 6 trunk vertebrae.

Identification: “Colubrines” include members of the family Colubridae with no hypapophysis on the trunk vertebrae (Szyndlar 1991a). Because of the presence of an hemal keel on the ventral surface of the centrum of the herein-considered vertebrae, it is possible to attribute them to undetermined colubrines (Szydlar 1984), but the poor preservational status hinders a more precise identification.

Natricinae Bonaparte, 1838 (sensu Szyndlar, 1991b)

Natrix Laurenti, 1768

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

Material: 58 trunk vertebrae.

Identification: These trunk vertebrae are assigned to the genus *Natrix* because of the following combination of features (Szyndlar 1984): their elongation, the presence of a sigmoid hypapophysis, the well-developed and rounded prezygapophyseal processes, the horizontal prezygapophyses, the vaulted neural arch and the high neural spine. The rounded end of the hypapophysis and of the parapophyses allow the attribution to *N. natrix* (Szyndlar 1984; Szyndlar 1991b). Among the diagnostic features distinguishing *N. natrix* from *N. tessellata* and *N. maura*, Szyndlar (1984) also mentioned the thickness of the parapophyses, which are more robust in *N. natrix* than in the other species. However, this features is highly variable both in the fossil and in the comparative material, and therefore it is not enough to sustain an attribution either to *N. tessellata* or *N. maura*.

Natricinae indet.

Material: 60 trunk vertebrae.

Identification: These vertebrae show features of Natricinae as reported by Szyndlar (1984). Due to the scarce preservational status, this fossil material is identified only as undetermined natricines, but it might reasonably pertain to *N. natrix*, the only natricine identified in Tegelen.

Viperidae Oppel, 1811

Vipera Laurenti, 1768

Vipera sp. (Fig. 8K-O)

Material: 1 trunk vertebra.

Identification: Combined, the elongation, the presence of a non-sigmoid hypapophysis, the thin and well antero-ventrally-directed parapophyses, the acute prezygapophyseal processes and the tectiform posterior margin of the neural arch identify RGM 816823 as a trunk vertebra of a member of the Viperidae (Szyndlar 1984; Szyndlar 1991b). The inclined zygapophyses and the wide cotyle allow the attribution to an undetermined species of the genus *Vipera* (Delfino et al. 2011). The small size (centrum length is 3.2 mm) and the rather lightly-constructed morphology distinguish this vertebra from trunk vertebrae of the oriental vipers, indicating it rather represents one of the smaller species of the *Vipera aspis* and *Vipera berus* complexes (Bailon et al. 2010).

Serpentes indet.

Material: 1 premaxilla; 2 maxillae; 1 dentary; 4 isolated tooth; 2 atlases; 1 axis; 8 cervical vertebrae; 109 trunk vertebrae; 66 caudal vertebrae; 2 fragments of vertebra; 22 ribs.

Identification: A number of poorly preserved or presumed undiagnostic skeletal elements are identified only as undetermined snakes.

“Reptilia” indet.

Material: 2 vertebral centra.

Identification: Two small vertebral centra provided with subelliptical cotyle and condyle and a well-developed keel on the ventral surface are attributed to undetermined reptiles. RGM 817472 has a low and thin keel, whereas in RGM 817471 it is robust and, although broken, it was probably more developed in ventral direction in origin.

3.2. Palaeoclimatic reconstruction

The fossil assemblage from Tegelen in its entirety has no modern analogue, because its extant taxa do not co-occur in the present-day fauna. Nevertheless, overlap of the ranges of most of the taxa is possible if we exclude from the analysis the extinct *P. euridyces* and the extant genus *Pelodytes*, which currently has a disjoined distribution in southern Europe that seems not to be climate-related (Pearman et al. 2010). In addition, we should take into account that the modern distribution of *P. fuscus* in the Balkan area is probably influenced by the competition with *Pelobates syriacus* (Iosif et al. 2014; Tarkhnishvili et al. 2009). To resolve the last point, an overlap with the modern fauna has been obtained by merging the present distribution of both *P. fuscus* and *P. syriacus*. In doing so, an analogue of the fauna can be found in three UTM squares (Fig. 9A). These 50 x 50 km UTM squares occur in a relatively similar climatic environment in southern Bulgaria at the border with Greece and Turkey (cities of Burgas, Svilengrad and Sandanski). Such an overlap corresponds to a mean value of 13.4 ± 0.3ºC of mean annual temperature and 542 ± 50 mm of mean annual precipitation (Tab. 1). The climate can be characterized as temperate, with a very high atmospheric temperature range. The summer is warm and the winter is cold. Rainfall is low, but its distribution is fairly regular, with the highest amount during winter and to a lesser extent spring. Three months during summer and early autumn (from July to September) are considered to be dry, according to the Gaussen Index (Fig. 9B). According to the Köppen-Geiger classification of climates, such an overlap corresponds to the humid subtropical climate (Cfa). The Lautensach-Mayer and De Martonne Indices suggest a semi-humid continental Mediterranean climate with three dry months in summer (Fig. 9B; Tab. 2). By contrast, the Dantin-Revenga Aridity Index classifies the climate as semi-arid (Tab. 2).

In comparison to the current climatic data from Tegelen area (Oceanic climate, Cfb) the MER-estimated MAT is much higher (+3.4ºC) than at present (Tab. 1). Such warmer climatic conditions during the early Pleistocene are mainly linked with a greater increase in temperature in summer (between +5.1ºC and +6.0ºC) than in winter (+0.4ºC and +1.7ºC). The total amount of rainfall is somewhat lower (-227 mm) than at present in the Tegelen area, leading to three months of aridity, whereas today the Oceanic climate from Tegelen shows no dry month (Fig. 9B). This is corroborated by the value of the Aridity Indices, suggesting that, at the time of deposition, conditions in Tegelen were much drier than today, especially during summer.

4. Discussion

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

The very large amount (more than 6000 remains) of fossils of amphibians and reptiles coming from the Russel-Tiglia-Egypte pit in Tegelen reveals a well diversified herpetofauna, a list of preliminary identifications of which was provided by Van den Hoek Ostende and De Vos (2006). Now that we have completed the entire study of the fauna, at least 17 taxa have been identified, including two caudates (*Triturus* gr. *T. cristatus* and *Lissotriton* sp.), seven anurans (*P. fuscus*, *B. bufo*, *Bombina* sp., *Pelophylax* sp., *Rana* sp., *Hyla* gr. *H. arborea* and *Pelodytes* sp.), one chelonian (*Mauremys* sp.), four lizards (*Lacerta* sp., Lacertidae indet., *Anguis* gr. *A. fragilis* and cf. *Pseudopus* sp.) and three snakes (“colubrines” indet., *Natrix natrix* and *Vipera* sp.). In addition, the locality yielded the recently described new species of palaeobatrachid anuran *Palaeobatrachus eurydices* Villa et al., 2016, the only extinct taxon so far known among amphibians and reptiles from Tegelen.

The only reptile previously reported from the Tegelen clay pits was a single specimen donated to the Natuurhistorisch Museum of Maastricht by the owner of the Russel-Tiglia pit and attributed to *Emys orbicularis* by Schreuder (1946). That specimen is currently lost and therefore it is not possible to whether confirm or not its attribution to the European pond turtle. Nevertheless, another specimen found in the Canoy-Herfkens pit and currently stored in the Naturalis Biodiversity Center in Leiden, RGM 75114, clearly displays features of *E. orbicularis*, such as the presence on the nuchal of the grooves marking the contact between the vertebral I scute and the left and right pleural I scutes and the narrow and elongated area being covered by the cervical scute (see diagnostic characters in Hervet 2000). The presence of *E. orbicularis* in Tegelen during the Tiglian can therefore be actually confirmed, but since fossil remains coming from different pits might have slightly different ages (Van den Hoek Ostende and Vos 2006) and the precise stratigraphical position of both Schreuder’s specimen and the Leiden one is not known, it is still not possible to state that this species was coeval with the herein-described assemblage.

Tegelen represents one of the few Pleistocene herpetofaunas found in The Netherlands (Böhme and Ilg 2003; Holman 1998; Schouten 2016), and is by far the most diverse known thus far. The only other Dutch locality that is comparable in terms of number of taxa retrieved is the younger (Middle Pleistocene) site of Maastricht-Belvédère 4 (Holman 1998; Schouten 2016), the herpetofauna of which includes at least 11 amphibians and reptiles. Compared to Tegelen, the latter locality lacks those taxa strictly linked to a warm climate such as *Mauremys*, and displays an assemblage that is more similar to the extant herpetofauna of The Netherlands. A second significant absence in Maastricht-Belvédère 4, as well as in all other quaternary Dutch localities, is *P. eurydices* (and palaeobatrachids in general). This might suggest that the suitable conditions that allowed this water-dwelling anurans to survive in the southern part of The Netherlands until the Gelasian disappeared after the early Pleistocene, causing their definitive extinction in Western Europe. Nevertheless, it is not possible to completely exclude that this absence might simply be a result of the scarce knowledge we have of Dutch Pleistocene herpetofaunas. Only new data from other fossil-bearing sites of the region will allow to shed more light on this issue.

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

In The Netherlands, the Pleistocene is characterized by a marked palaeoclimatic cyclic nature, involving alternating glacial and interglacial phases (Drees 2005 and references therein). After a first glacial period, the Pretiglian, interglacial conditions set up during the Tiglian stage, even though cool oscillations were still present (Drees 2005; Reid and Reid 1915; Vlerk and Florschütz 1953; Zagwijn 1963). Based on palynological analyses, the Tiglian stage was separated by Zagwijn (1963) into three different substages (TA, TB and TC), the latter of which is further composed by six sections (TC1 to TC6). According to the palaeoclimatic quantitative reconstructions of the Dutch pollen sequence (Kasse 1988, 1993; Kasse and Bohncke 2001; Zagwijn 1963, 1989), the TC5 section of the Tiglian is separated in three phases: warm-cold-warm. The deciduous vegetation of the warm periods (TC5a and c) indicates that the mean summer temperature was around 18ºC (mean temperature of the warmest month = 18 to 20ºC according to Pross and Kloss 2002), the mean winter temperature above -1ºC (mean temperature of the coldest month = -2 to 0ºC according to Pross and Kloss 2002) and the mean annual temperature circa 10ºC (i.e., similar to current value). The German pollen record from Lieth (zone E5; Pross and Kloss 2002) provides for the TC5 a mean January temperature estimate of -1ºC and mean July temperatures between 14 and 21.5 ºC consistent with the estimation by Zagwijn (1963, 1989) for Tegelen. The palaeoclimatic reconstruction based on the amphibian and reptile assemblage from Tegelen thus suggests that some of these early Pleistocene interglacial periods in northern Europe would have been somewhat warmer than previously reconstructed with mean temperature of the warmest month reaching up to 23.7 ± 0.6ºC and mean temperature of the coldest month 2.6 ± 0.1ºC.

The light degree of dryness based on herpetological evidence is apparently in contrast with the palaeoenvironmental information given by some components of the fauna. For one, the best represented group in the fauna are the beavers (Schreuder 1929), to the point that the Tegelen Clay was sometimes referred to as the *Trogontherium* Clay, because of the numerous finds of this extinct beaver. However, the herpetofauna stems from a stream gully cutting into the palustrine sequence, which could be seen as confirmation that we are indeed dealing with a dryer period. Nevertheless, the micromammal fauna, which was retrieved together with the herpetofauna, refutes overly dry conditions. Desmans are numerous (Rümke 1985) and the diverse shrew fauna indicates a humid environment. Among the voles, typical steppe elements of the era, such as *Borsodia*, are conspicuously absent and the presumably semi-aquatic *Mimomys pliocaenicus* is numerous. In addition, the assemblage show a high proportion of various forest and shrub dwellers, such as *Apodemus*, *Clethrionomys* and the glirids, *Muscardinus* and *Glirulus*.

Part of the apparent inconsistency in the palaeoenvironmental reconstructions based on different groups can be explained by the absence of recent analogues of the conditions in the Villafranchian. As we noted, there is no strict present-day analogue of the herpetofauna, which is not surprising as the same hold true for the flora and the mammal fauna. The former still contains a number of Tertiary elements, whereas the dormouse *Glirulus* is now restricted to Japan. In finding a modern analogue, we had discarded the only extinct member of the herpetofauna, *Palaeobatrachus euridyces*. As a palaeobatrachid, *P. euridyces* is considered to have been extremely adapted to a water-dwelling life (Villa et al. 2016), therefore needing permanent water bodies to survive. The combination of increasing drought and periglacial areas with low temperatures during winter leading to a freezing of the water bodies is thought to have caused the definitive extinction of 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., *Mauremys*) to live in the area. This climate can be linked to a warm phase of the Tiglian interglacial stage. In comparison to previous climate reconstructions, the herpetofauna indicates slightly warmer and, somewhat surprisingly, dryer conditions than previously assumed.

Most probably, the presence at Tegelen of humid or sub-humid conditions are directly correlated with the survival of the water-dwelling frog *P. eurydices*, the last representative of the family Palaeobatrachidae in Western Europe. However, more findings in other northwestern European localities are needed in order to understand how palaeobatrachids escaped extinction due to aridization after the Miocene/Pliocene boundary in the western portion of the European continent and when and why they ultimately disappeared from the area.

Acknowledgements

Project supported by Fondi di Ateneo (2015-2016). Visits to the collections of the Muséum national d'Histoire naturelle, Paris and of the Naturhistorisches Museum Wien were supported by two Synthesys grants (SYNTHESYS FR-TAF-5007 and AT-TAF-4591, respectively) to AV. We thank Eelco Kruidenier and Anneke Madern (Naturalis Biodiversity Center, Leiden) for having provided photos of the turtle shell from the Canoy-Herfkens pit. This paper is also part of the projects CGL2016-76431-P (Generalitat de Catalunya/CERCA Programme, Agencia Estatal de Investigación (AEI) from Spain / European Regional Development Fund of the European Union), CGL2016-80000-P (Spanish Ministry of Economy and Competitiveness) and SGR2014-901 (Generalitat de Catalunya). The editor Danielle Schreve and the reviewer Jean-Claude Rage are also thanked for their comments on a previous version of this paper. We are grateful to Steve Donovan for his linguistic corrections.

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Figure captions

Fig. 1. Location of the Russel-Tiglia-Egypte pit and other clay pits near Tegelen (map modified from Van den Hoek Ostende & Vos 2006). [planned for single column width]

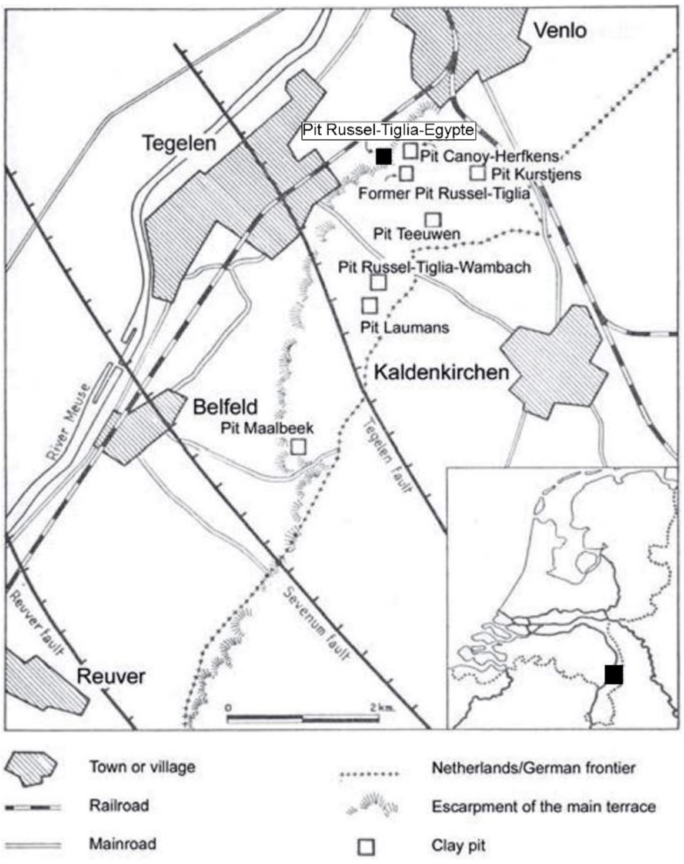

Fig. 2. Caudates from the Russel-Tiglia-Egypte pit. *Triturus* gr. *T. cristatus*: parasphenoid (RGM 816926) in ventral (A) and dorsal (B) views; atlas (RGM 816893) in dorsal (C), anterior (D), left lateral (E), ventral (F) and posterior (G) views; trunk vertebra (RGM 816912) in dorsal (H), ventral (I), 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. [planned for double column width]

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. [planned for double column width]

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. [planned for double column width]

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. [planned for double column width]

Fig. 6. *Mauremys* sp. from the Russel-Tiglia-Egypte pit. Nuchal (RGM 816718) in dorsal (A) and ventral (B) views. Scale bar = 5 mm. [planned for single column width]

Fig. 7. Lizards from the Russel-Tiglia-Egypte pit. *Lacerta* sp.: left dentary (RGM 816720) in dorsal (A), lateral (B) and medial (C) views. Lacertidae indet.: parietal (RGM 816758) in dorsal (D) and ventral (E) views; right pterygoid (RGM 816743) in ventral (F) and dorsal (G) views; trunk vertebra (RGM 816739) in anterior (H), posterior (I), right lateral (J), dorsal (K) and ventral (L) views. *Anguis* gr. *A. fragilis*: parietal (RGM 816693) in dorsal (M) and ventral (N) views; left maxilla (RGM 816701) in lateral (O) and medial (P) views; trunk vertebra (RGM 816676) in dorsal (Q), ventral (R), anterior (S), posterior (T) and left lateral (U) views; osteoderm (RGM 816699) in external view (V). cf. *Pseudopus* sp.: osteoderm (RGM 816716) in external (W) and internal (X) views. Scale bars = 1 mm. [planned for double column width]


A
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Fig. 8. Snakes from the Russel-Tiglia-Egypte pit. “Colubrines” indet.: trunk vertebra (RGM 816817) in dorsal (A), ventral (B), anterior (C), posterior (D) and right lateral (E) views. *Natrix natrix*: trunk vertebra (RGM 816780) in dorsal (F), ventral (G), anterior (H), posterior (I) and left lateral (J) views. *Vipera* sp.: trunk vertebra (RGM 816823) in dorsal (K), ventral (L), anterior (M), posterior (N) and left lateral (O) views. Scale bars = 1 mm. [planned for double column width]

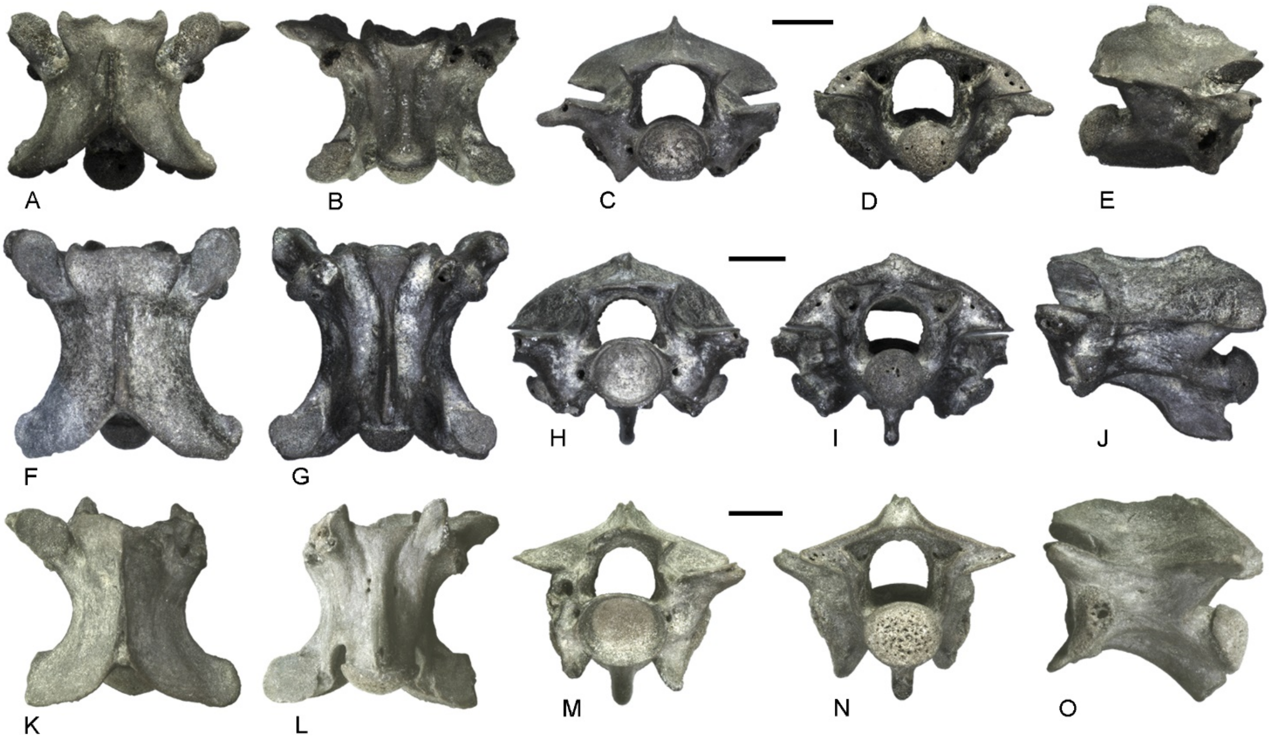
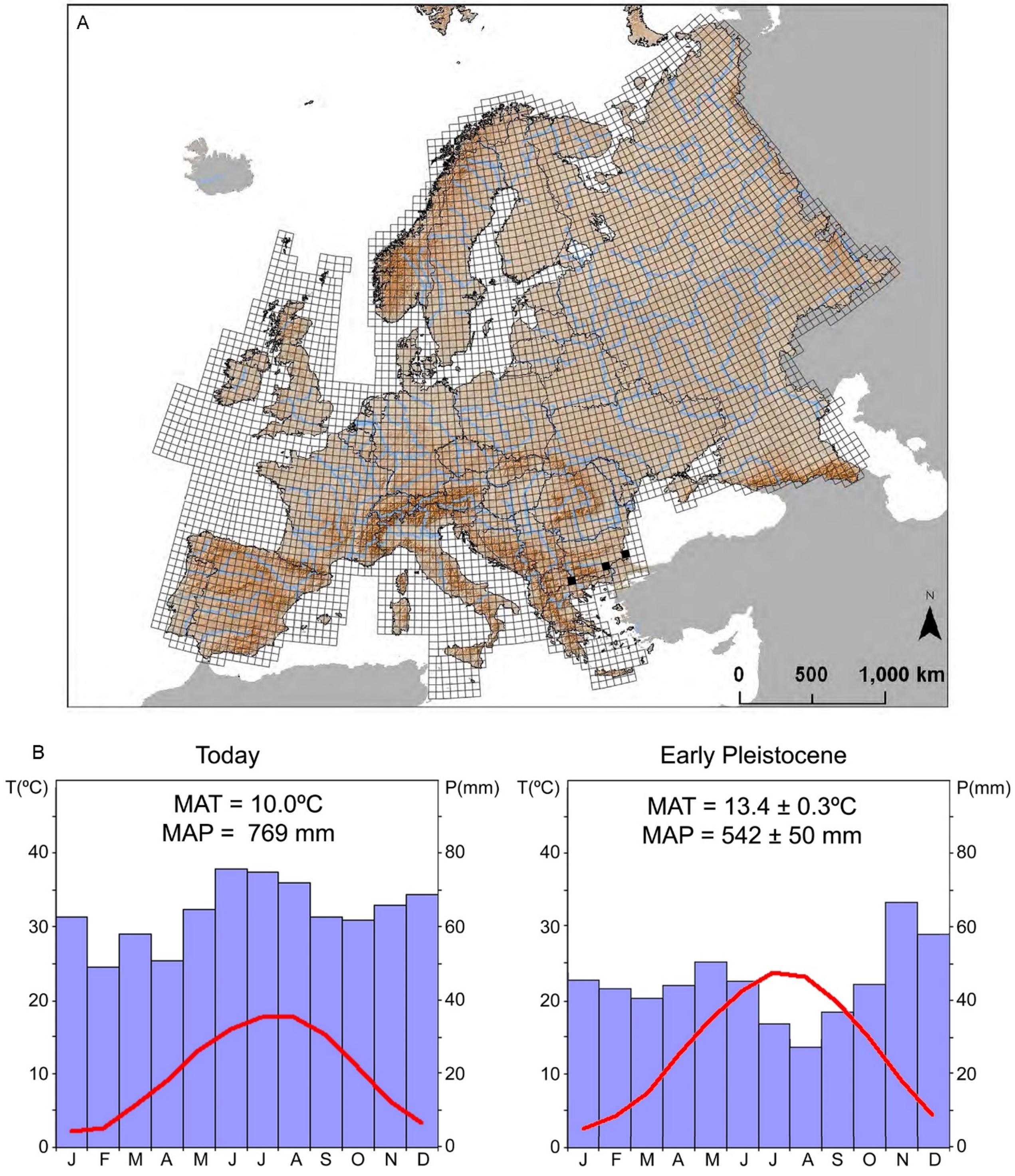


Fig. 9. Monthly palaeoclimatic reconstructions for Tegelen based on its fossil herpetofaunal assemblage. A: overlaps of the current distribution done in 50 × 50 km UTM squares; B: quantitative reconstruction according to the Mutual Ecogeographic Range method compared with current data. [planned for double column width]


A
N
0
500
1,000 km
B
Today
T(ºC)
P(mm)
MAT = 10.0ºC
MAP = 769 mm
40
30
20
10
0
80
60
40
20
0
J F M A M J J A S O N D
Early Pleistocene
T(ºC)
P(mm)
MAT = 13.4 ± 0.3ºC
MAP = 542 ± 50 mm
40
30
20
10
0
80
60
40
20
0
J F M A M J J A S O N D

	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

Tab. 1. Climatic parameters calculated with the Mutual Ecogeographic Range method for the early Pleistocene of Tegelen and current climatic values from the Tegelen area. MAT: mean annual temperature; MAP: mean annual precipitation; SD: standard deviation; Δ: difference between Early Pleistocene estimated and current values.

		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

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

MTC: mean temperature of the coldest month.