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

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A B S T R A C T

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 $13.4 \pm 0.3\,^{\circ}C$ 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.

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

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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 center 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 de 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 de 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 de 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 van den 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