Palaeogeography, Palaeoclimatology, Palaeoecology 414 (2014) 116–128

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Population bottleneck triggering millennial-scale morphospace shifts in endemic thermal-spring melanopsids

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ARTICLE INFO

Article history:
Received 25 June 2014
Received in revised form 8 August 2014
Accepted 14 August 2014
Available online 27 August 2014

Keywords:
Phenotypic evolution
Genetic drift
Morphometric analysis
Fast Fourier Transform
Stable isotopes

ABSTRACT

For more than hundred years the thermal spring-fed Lake Pețea near Oradea, Romania, was studied for its highly endemic subfossil and recent fauna and flora. One point of focus was the species lineage of the melanopsid gastropod *Microcolpia parreyssii*, which exhibited a tremendous diversity of shapes during the earlier Holocene. As a consequence many new species, subspecies, and variety-names have been introduced over time, trying to categorize this overwhelming variability. In contrast to the varied subfossil assemblage, only a single phenotype is present today. We critically review the apparent "speciation event" implied by the taxonomy, based on the presently available information and new data from morphometric analyses of shell outlines and oxygen and carbon isotope data. This synthesis shows that one turning point in morphological evolution coincides with high accumulation of peaty deposits during a short time interval of maximally a few thousand years. The formation of a small, highly eutrophic swamp with increased input of organic matter marginalized the melanopsids and reduced population size. The presented data make natural selection as the dominating force unlikely but rather indicates genetic drift following a bottleneck effect induced by the environmental changes. This claim contrasts the "obvious trend" and shows that great morphological variability has to be carefully and objectively evaluated in order to allow sound interpretations of the underlying mechanisms.

1. Introduction

Microcolpia parreyssii (Philippi, 1847) is a thermophilic melanopsid species presently restricted to a single locality, the small thermal spring-fed Lake Pețea (*Rom.* Băile 1 Mai, Băile Episcopale; *Hung.* Püspökfürdő; *Germ.* Bischofsbad; Fig. 1), situated about 9 km SE of Oradea in W Romania. It is a morphologically well-defined taxon comprising distinctly stepped and ribbed shells. The morphological history of this species, however, draws a completely different picture. Shells from late Pleistocene to Holocene deposits of the thermal spring exhibit an extreme variability and a distinctly wider range of morphologies as present in the lake today. This range includes smooth, slender, and elongate shapes, stepped and non-ribbed forms, slender and keeled phenotypes, as well as subfossil representatives of typical *M. parreyssii* (Brusina, 1903; Kormos, 1903, 1904, 1905a,b; Paucă, 1937; Sümegi et al., 2012a,b; Fig. 2). This led to the introduction of a large number of names, trying to categorize this vast variability (Brusina, 1903; Kormos, 1905b). In total, 43 species-, subspecies-, variation- and forma-names have been introduced since then. Still, the taxonomic concepts applied by Brusina (1903) and Kormos (1905b) are unfortunately not clear from their descriptions — and illustrations are available only for a few phenotypes. Moreover, the taxon delimitations of both authors diverge considerably. Brusina (1903) himself recognized the strong over-splitting and suggested alternatively a series of synonymizations. The fluent morphological transitions, however, make splittings as well as synonymizations highly subjective anyway.

It has been demonstrated that the many phenotypes do not equally occur within the same time intervals, but rather show morphological changes over time (Kormos, 1905b; Sümegi et al., 2012a,b). The available data suggest that the succession of phenotypes is coupled with changes in the paleoenvironment. In former times Lake Pețea, which originated during the late stages of the Würmian glaciation, had a much larger extent (Sümegi et al., 2012a). Up to present the lake has shrunken to a size of a few hundred square meters and temperature has dramatically declined, what has a severe impact on the rich fauna, including several species of fish (Telcean and Cupşa, 2013), amphibians (Covaciu-Marcov et al., 2003), and gastropods (e.g., Brusina, 1903; Kormos, 1905b; Harzhauser and Mandic, 2008; Fehér et al., 2009;

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http://dx.doi.org/10.1016/j.palaeo.2014.08.015

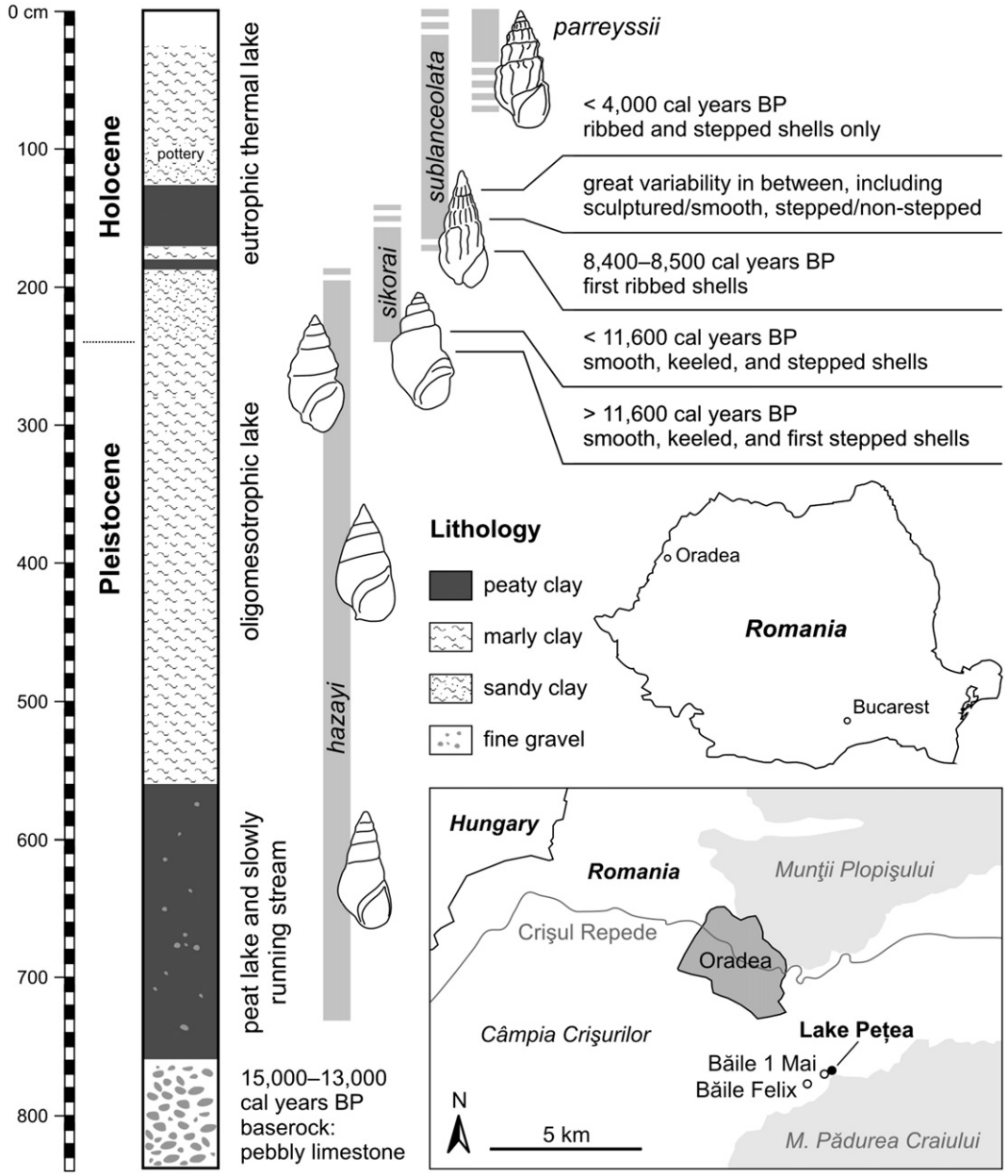

Fig. 1. Geographic overview of the studied locality and section. The morphological succession and the phenotype names were adopted from Kormos (1905b). For a revised taxonomic concept see Chapter 5.6. and the Appendix. The dating as well as the paleoecological interpretation to the right of the section is correlated following the data of Sümegi et al. (2012b).

Sîrbu et al., 2013). Some of these are entirely endemic to this small environment and are critically endangered (Sîrbu and Sárkány-Kiss, 2002; Fehér, 2011; Sîrbu et al., 2013).

The aim of this paper is an objective quantification of shell shapes to document and elucidate the morphological variability in the recent and past melanopsids of Lake Peţea by means of a morphometric analysis. Additional information is provided by stable isotope analyses to reconstruct paleo-water conditions. Together with existing data on lake's development a detailed picture of the evolutionary pattern and its causes is drawn.

2. Materials

The entire material derives from the collections of the Natural History Museum of Vienna. The subfossil Holocene specimens are stored in the Geological-Paleontological Department (coll. nos. NHMW 1903/0001, 1908/0012, 2013/0414), the recent specimens in the 3rd Zoological Department (Malacology section, referred to as NHMW Moll.). The whole material displays a compound of several independent collection surveys and fully covers the morphological variability described in the literature. Unfortunately, it was not possible to obtain material from stratified collections to provide information on the morphospace evolution through time. Only adult and subadult specimens were analyzed, which can be detected over the slightly thickened inner lip; juveniles were excluded from the analysis.

A total number of 327 specimens were analyzed (Table 1). As to the subfossil part, 245 *Microcolpia* specimens from Băile 1 Mai, Romania (= Püspökfürdő, Bischofsbad) were selected. To keep an objective position any preliminary attribution to a species, subspecies, or phenotype was avoided before the morphological analyses. However, in the discussion we refer to the ribbed forms (recent and subfossil) as *Microcolpia parreyssii parreyssii* (Philippi, 1847) and to the remaining subfossil ones as *Microcolpia parreyssii sikorai* (Brusina, 1903). Although we do not want to anticipate the taxonomic implications of the present work