



Phenotypic evolution in a venerid bivalve species lineage from the late Middle Miocene Central Paratethys Sea: a multi-approach morphometric analysis

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Received 18 March 2013; revised 10 April 2013; accepted for publication 10 April 2013

A morphometric analysis was performed for the late Middle Miocene bivalve species lineage of *Polititapes tricuspis* (Eichwald, 1829) (Veneridae: Tapetini). Specimens from various localities grouped into two stratigraphically successive biozones, i.e. the upper *Ervilia* Zone and the *Sarmatimactra* Zone, were investigated using a multi-method approach. A Generalized Procrustes Analysis was computed for 15 landmarks, covering characteristics of the hinge, muscle scars, and pallial line. The shell outline was separately quantified by applying the Fast Fourier Transform, which redraws the outline by fitting in a combination of trigonometric curves. Shell size was calculated as centroid size from the landmark configuration. Shell thickness, not covered by either analysis, was additionally measured at the centroid. The analyses showed significant phenotypic differentiation between specimens from the two biozones. The bivalves become distinctly larger and thicker over geological time and develop circular shells with stronger cardinal teeth and a deeper pallial sinus. Data on the palaeoenvironmental changes in the late Middle Miocene Central Paratethys Sea suggest the phenotypic shifts to be functional adaptations. The typical habitats for *Polititapes* changed to extensive, very shallow shores exposed to high wave action and tidal activity. Caused by the growing need for higher mechanical stability, the bivalves produced larger and thicker shells with stronger cardinal teeth. The latter are additionally shifted towards the hinge centre to compensate for the lacking lateral teeth and improve stability. The deepening pallial sinus is related to a deeper burrowing habit, which is considered to impede being washed out in the new high-energy settings. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **110**, 320–334.

ADDITIONAL KEYWORDS: Fast Fourier Transform – functional morphology – landmarks – late Sarmatian – relative warps.

INTRODUCTION

During the Sarmatian period the Paratethys Sea covered large regions of today's eastern and south-eastern Europe, reaching from the Pannonian Basin System in the west to the Turan Depression in the east (Rögl, 1998, 1999; Popov *et al.*, 2004; Piller & Harzhauser, 2005). In this late stage of its development, the Paratethys comprised the Central Paratethys (Fig. 1), restricted to the Pannonian Basin, and the vast, extensive Eastern Paratethys.

During the Sarmatian, seaways between these two seas allowed full exchange of the uniform, low-diversity, fully endemic Paratethyan fauna (Rögl, 1998, 1999; Piller & Harzhauser, 2005). The Alpidic and Dinaric mountain chains acted as barriers to separate the Central Paratethys from the Mediterranean Sea. This separation resulted in completely different faunal inventories, which are reflected in the regional biostratigraphical zonations (Fig. 2; Harzhauser & Kowalke, 2002; Harzhauser, Piller & Steininger, 2002; Piller & Harzhauser, 2005; Harzhauser, Gross & Binder, 2008).

Throughout the Sarmatian, distinct morphological evolution is recorded among several gastropod and bivalve species of the Central Paratethys (Papp, 1956,

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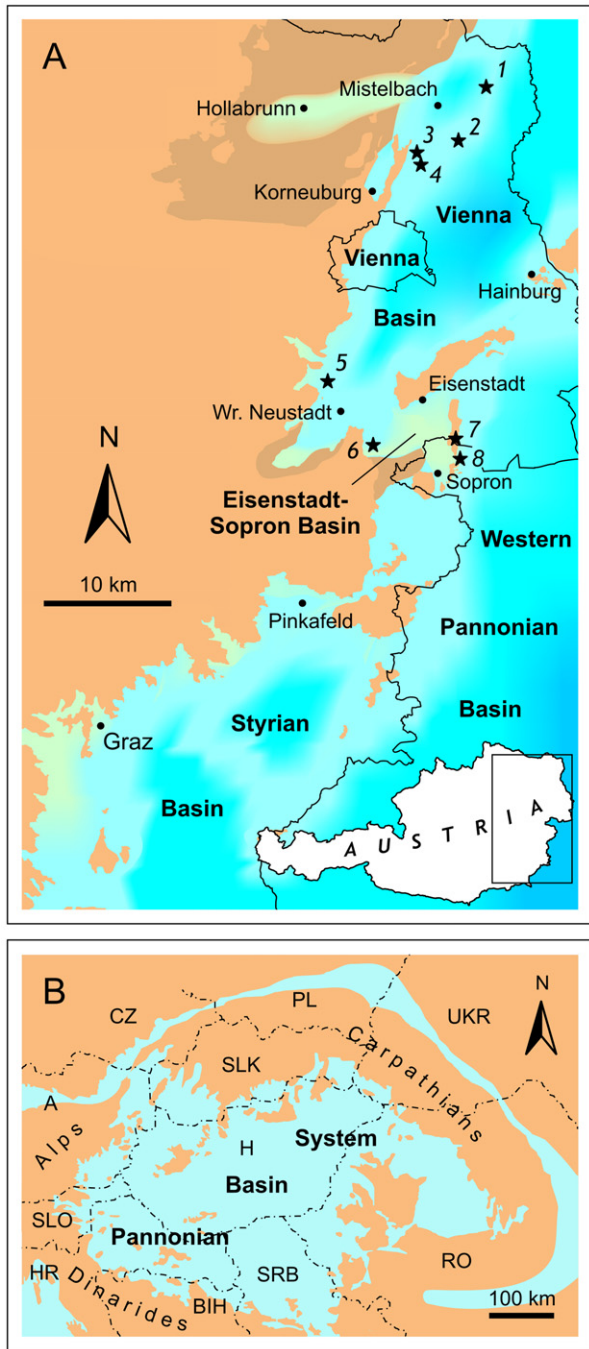


Figure 1. A, geographical overview of the western shores of the Central Paratethys Sea in the late Sarmatian with roughly estimated water depths (modified after Piller & Harzhauser, 2005). Investigated localities in the Vienna Basin and adjacent Eisenstadt–Sopron Basin are indicated with stars and numbered as follows: 1, Hauskirchen; 2, Nexing; 3, Hautzendorf; 4, Kronberg; 5, Hölles; 6, Wiesen; 7, St. Margarethen Zollhaus; 8, Fertőrákos. B, extent of the Central Paratethys in the Pannonian Basin System and the Alpine–Carpathian Foredeep during the Sarmatian (modified after Harzhauser, Mandic & Zuschin, 2003).

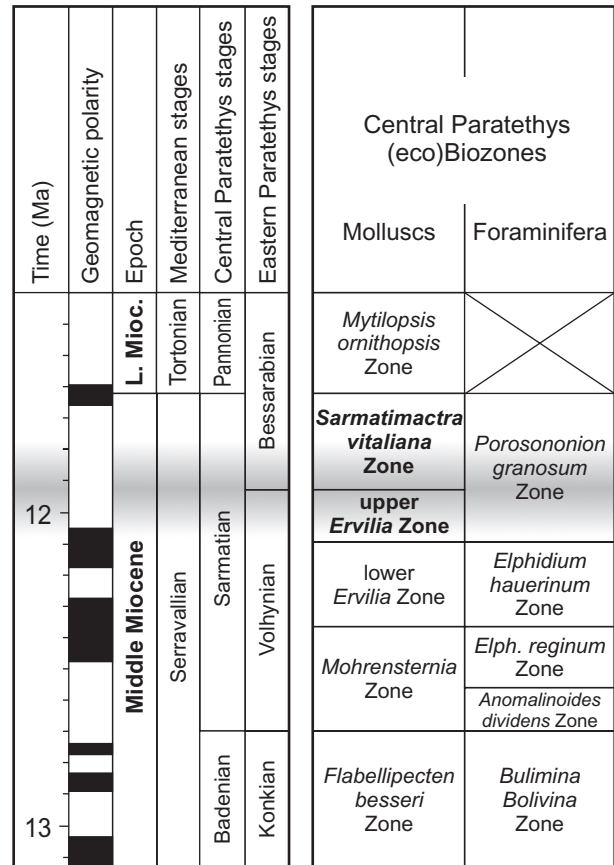


Figure 2. Biostratigraphy of the Sarmatian stage with correlation of Mediterranean and Eastern Paratethys stages (modified after Harzhauser & Piller, 2004, 2012). The grey bar roughly indicates the studied time slice (no precise data available). Polarity chrons were created with TimeScale Creator 6.0 (Ogg & Luginovskiy, 2012) following the current age model in Gradstein *et al.* (2012).

1958; Piller & Harzhauser, 2005). Papp (1958) was the first to provide studies on the morphological changes in these molluscs and tried to relate them to phyletic processes. Based on the rapid endemic evolution, Papp (1958) established a mollusc-based biozonation of the Sarmatian stage, starting with the *Mohrensternia* Zone from c. 12.7 to 12.4 Mya, followed by the lower and upper *Ervilia* Zones (c. 12.4–12.1 and 12.1–11.9 Mya, respectively) and the *Sarmatimactra* Zone from c. 11.9 to 11.6 Mya (dates after Harzhauser & Piller, 2004).

Being a very eye-catching example, we studied the phenotypic differentiation in the species lineage of *Polititapes tricuspidis* (Eichwald, 1829) (Veneridae: Tapetini) across the boundary between the upper *Ervilia* Zone and the *Sarmatimactra* Zone. Since the lower *Ervilia* Zone this species has been widespread over the entire Paratethys Sea (Fig. 2; Schneider,

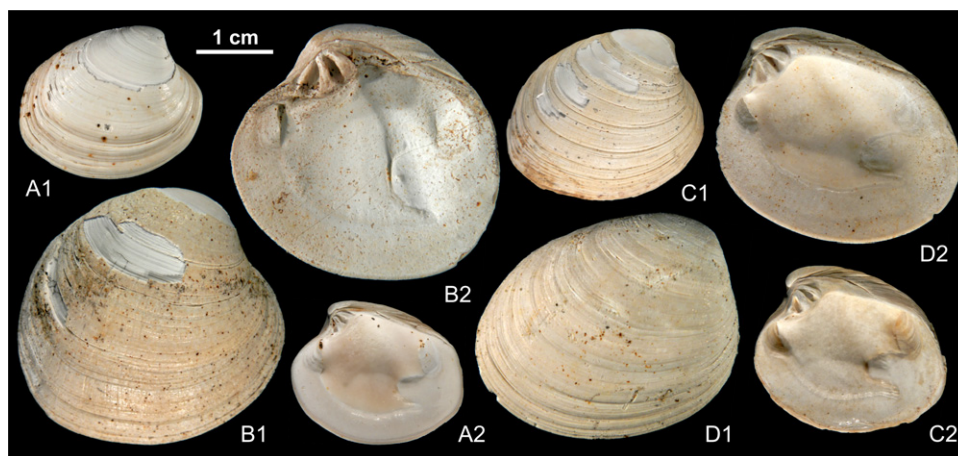


Figure 3. Representative specimens of the *Polititapes tricuspis* lineage illustrating the great morphological variety. A, classic triangular *Polititapes tricuspis* from Kronberg, upper *Ervilia* Zone (NHMW 2013/0022/0001). B, common ‘ponderosa-phenotype’ from Wiesen, *Sarmatimactra* Zone (NHMW 2013/0024/0001). C, *Polititapes tricuspis* from Hölles, upper *Ervilia* Zone (NHMW 2013/0023/0001). D, specimen from Wiesen, *Sarmatimactra* Zone (NHMW 2013/0024/0002).

Mandic & Harzhauser, 2013). It belongs to a genus that originated around the Early–Middle Miocene transition and is represented today in shallow-water settings of the Western Atlantic and the Mediterranean with species such as *Polititapes aureus* (Gmelin, 1791) (Goncharova, 1986). The complex taxonomic history of *Polititapes tricuspis*, including a whole host of names, was accurately reviewed by Kojumdgieva (1969), Nevesskaja *et al.* (1993), and Schneider *et al.* (2013). According to the taxonomic model established therein, *P. tricuspis* originated in the early Sarmatian, most probably from the Badenian–Sarmatian *P. vitalianus* (d’Orbigny, 1844), and gave rise to *P. ponderosa* (d’Orbigny, 1844) in the late Sarmatian *Sarmatimactra* Zone (Papp, 1974). The whole lineage became extinct by the end of the regional Bessarabian stage at *c.* 11.2 Mya (Papp, 1974; Nevesskaja *et al.*, 1993; Schultz, 2005; Schneider *et al.*, 2013).

In this study we focus on the morphological transition between the phenotypes ‘*P. tricuspis*’ and ‘*P. ponderosa*’ (Fig. 3). To avoid prejudiced categorization, the traditional taxonomic entities in this lineage are *a priori* ignored. We follow the definition of Simpson (1961), who defined the term ‘lineage’ as an ancestral–descendant sequence of populations forming an evolutionary species. While the ‘classical’ *P. tricuspis* has a small, roughly triangular shell, *P. ponderosa* develops large, thick and rounded shells. In between, a great variety of transitional shapes and sizes is observed (Papp, 1958, 1974), complicating an objective taxonomic classification in many cases. To prevent subjective interpretation of traditionally used taxonomic criteria, we applied geometric morphometric techniques based on various aspects of

the shell. The internal proportions of the shell were analysed with a Generalized Procrustes Analysis from a configuration of 15 landmarks. The shell outline was separately examined using the Fast Fourier Transform (FFT) method. Shell size and thickness were additionally recorded, since they were not covered by either analysis. This multi-approach investigation is considered to give a very detailed picture of the phenotypic changes at the transition of the two biozones. Together with comprehensive data on the regional palaeoenvironmental shifts occurring at the same time, this forms a solid base for a reliable ecological interpretation.

MATERIAL

Although the morphological evolution in *Polititapes* is known to occur to a similar extent throughout the entire Paratethys Sea (Kojumdgieva, 1969; Papp, 1974; Nevesskaja *et al.*, 1993; Ionesi *et al.*, 2005), we used exclusively material from the Vienna Basin and the adjacent Eisenstadt–Sopron Basin. For this rather restricted geographical region a considerable amount of material and more data on stratigraphy and the palaeoenvironment is available, allowing more detailed and reliable interpretations of the results.

To apply both types of morphometric analyses to the same set of shells, only well-preserved specimens showing internal features could be considered. Among the available shells, the right valves were more abundant and better preserved and were therefore selected. These limitations restricted the appropriate material. From several localities only a few specimens could be used. Usually such small sample sizes would

be statistically not meaningful and one could not presume a normal distribution. However, more material is available for each of these localities roughly falling into the same morphological ranges; it is simply insufficiently preserved to be used in the morphometric analyses.

Only shells from localities with reliable stratigraphic classifications were used for the analysis. As precise geological ages are wanting for most localities, they were grouped into biozones, namely the upper *Ervilia* Zone and the successive *Sarmatimactra* Zone. Most specimens were obtained from the collection of the Natural History Museum Vienna, stored under inventory numbers NHMW 2013/0018–0024. Material from Fertőrákos (Hungary) was kindly provided by Anton Breitenberger and Reinhold Kunz. Specimens from St Margarethen were collected and photographed by Simon Schneider. A total of 405 specimens were studied. The investigated localities comprise Hauskirchen ($n = 76$), Nexing ($n = 78$), Hautzendorf ($n = 45$), Kronberg ($n = 94$), Hölles ($n = 39$), and the lower layers of Wiesen ($n = 36$) for the upper *Ervilia* Zone, and the upper layers of Wiesen ($n = 29$), St Margarethen ($n = 2$), and Fertőrákos ($n = 6$) for the *Sarmatimactra* Zone (Fig. 1).

METHODOLOGY

To cover as many morphological details as possible, we applied two different morphometric methods. The first technique uses homologous points, i.e. landmarks, to shed light on internal features and their changes over time. The second approach analyses the shell outline and thus provides a picture of the general shape. Because both methods explore different shell characters, the results can only be discussed separately. This approach also allows a separate assessment of changes of internal and external morphology through time. However, both analyses disregard size differences. To test for changes of dimensions through time, size was recorded as centroid size. This is calculated as the sum of squared Euclidean distances of all landmarks to the geometric centroid (Bookstein, 1991; Roopnarine & Vermeij, 2000). In the absence of allometry it is the only size measure that is uncorrelated with shape (Bookstein, 1991). Unfortunately, it was not possible to test for allometric growth (e.g. Anderson & Roopnarine, 2005; Roopnarine, Signorelli & Laumer, 2008), as no juvenile shells were available for the *Sarmatimactra* Zone. To make the results of both biozones comparable, we excluded specimens of < 50% of the maximum shell length for each locality of the upper *Ervilia* Zone.

One parameter not covered by the aforementioned analyses is shell thickness, which is known to change over time in the *Polititapes tricuspis* lineage (Papp,

1958; Piller & Harzhauser, 2005). It was measured at the estimated shell centroid using a special caliper. As variation in shell thickness is negligible around the centroid, this approximate approach does not distort the results.

The shells were, where necessary, cleaned from sediment to ensure easy identification of the landmarks. Specimens were scanned with an Epson Perfection 4990 Photo flatbed scanner to guarantee uniformly plane alignment. Sediment particles around outlines were deleted with the rubber tool in Corel PhotoPaint 12. Likewise, small pieces of broken shell margins were digitally restored. Such edits were only performed when there was no doubt about the course of the original shell margin.

LANDMARK ANALYSIS

The shell of the venerid bivalve *Polititapes* has a complex hinge apparatus and distinct muscle scars, which allow a clear identification of homologous points that can be used as landmarks. Fifteen Type I and II landmarks were chosen (Bookstein, 1991; Slice *et al.*, 1996), describing the relative position of the umbo, the features of the cardinal teeth, the size of the muscle scars, and the pallial sinus (Fig. 4). Landmarks were set on digitized images with the program tpsDig 2.16 (Rohlf, 2010a). The resulting coordinates were subjected to tpsRelw 1.49 (Rohlf, 2010b). This program performs the generalized orthogonal least-squares Procrustes superimposition to compute the ‘consensus’ or reference configuration (Rohlf & Slice, 1990). For a detailed description of the methods see Bookstein (1991, 1996), Rohlf (1993), Rohlf & Marcus (1993), and Slice (2000). The affine/uniform component was not included in the analysis. To visualize shape differences between the two zones, a linear discriminant analysis (LDA) was performed on the relative warps including Hotelling’s T^2 test.

OUTLINE ANALYSIS

For the FFT method the same set of specimens was used. Details on the advantages of this method over other outline-based techniques are described by Haines & Crampton (2000) and briefly summarized in Neubauer, Harzhauser & Kroh (2013). Because the method is very sensitive to starting point (Haines & Crampton, 2000), images were orientated uniformly. They were rotated in Corel PhotoPaint 12 such that the ventral tips of the adductor/retractor muscle scars lie on a horizontal line (Fig. 4). As the method is also sensitive to outline irregularities, contrast, brightness, and intensity were increased by 100, and the tools ‘noise reduction’ (parameters: minimum, percentage 100, radius 1) and ‘dust and scratches’

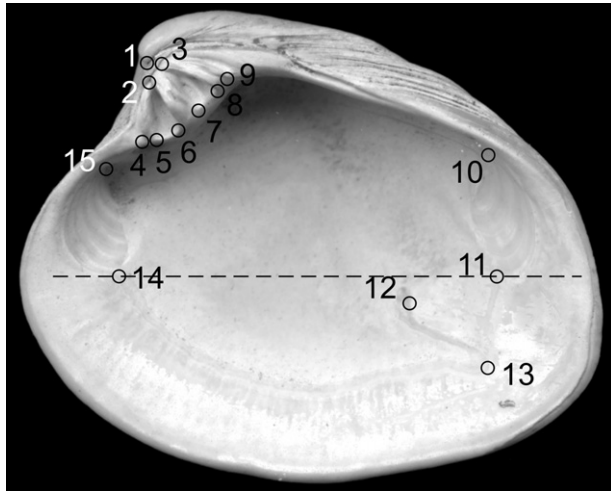


Figure 4. Landmark configuration. 1, umbo; 2, dorsal tip of anterior cardinal tooth; 3, dorsal tip of posterior cardinal tooth; 4, antero-ventral tip of anterior cardinal tooth; 5, postero-ventral tip of anterior cardinal tooth; 6, antero-ventral tip of middle cardinal tooth; 7, postero-ventral tip of middle cardinal tooth; 8, antero-ventral tip of posterior cardinal tooth; 9, postero-ventral tip of posterior cardinal tooth; 10, dorsal tip of posterior adductor/retractor muscle scar; 11, junction of ventral tip of posterior adductor/retractor muscle scar and pallial line; 12, deepest point of pallial sinus (when horizontally orientated); 13, postero-ventral tip of pallial sinus; 14, junction of ventral tip of anterior adductor/retractor muscle scar and pallial line; 15, dorsal tip of anterior adductor/retractor muscle scar. The dashed line indicates the horizontal orientation of the shell based on the ventral tips of the muscle scars.

(parameters: level 80, radius 5) were applied. This created sharp outlines that were captured with tpsDig 2.16 (Rohlf, 2010a). The starting point for outline tracing was the umbo as the most distinct outline feature. The resulting x,y -coordinates were subjected to the program Hangle, which employs the FFT (Crampton & Haines, 1996). Twelve harmonics were used to reproduce the outline, covering the main features of the outline but neglecting minor irregularities (tested with inverse Fourier decomposition using the program Hcurve; Crampton & Haines, 1996). Outlines were smoothed ten times in Hangle to reduce potential pixel noise. Subsequently, curves were matched for starting point using Hmatch (Crampton & Haines, 1996). A principal components analysis (PCA) was computed from the variance-covariance matrix of the resulting Fourier coefficients. As for the relative warps analysis (RWA), an LDA for the two biozones was performed on the principal components. All statistical analyses used in this paper were performed applying PAST 2.14 software (Hammer, Harper & Ryan, 2001).

RESULTS

The LDA of the relative warps obtained from the landmark analysis yielded a positive classification rate of 93.58% for a separation between specimens of the upper *Ervilia* Zone and *Sarmatimactra* Zone (Hotelling's $T^2 = 367.47$, $P < 0.001$) (Fig. 5A). The partial misclassification resulting from a morphological overlap is indeed expected rather than surprising with respect to phenotypic evolution. Best differentiation between both groups in the RWA is given along RW2 (17.08%) and RW4 (8.06%) (Fig. 6). Hence, the morphological variability of *P. tricuspis* within each biozone (e.g. along RW1, 27.34%) is larger than between the two zones. The RWA allows interpretation in a biological sense (e.g. Roopnarine & Vermeij, 2000; Roopnarine *et al.*, 2008). For each of the first four relative warps, thin-plate spline images for the approximate minimum and maximum occupied values per warp are provided in Figure 6. For RW1 negative values reflect very small cardinal teeth and a widening of the ventral margin (ventral tips of both adductor/retractor muscle scars drift outwards). RW1 is basically correlated with changes of relative shell length. Negative values for RW2 correspond to increasing size/strength of the cardinal teeth and a deep pallial sinus. Additionally, the ventral tip of the anterior adductor muscle scar lies more centrally, producing a shorter pallial line. Along RW3 (11.74%), negative values reflect large cardinal teeth, but a small sinus. Low values for RW4 correspond to a slight rotation of the cardinal teeth and a shift of the dorsal tip of the anterior muscle scar in posterior direction. In particular, the posterior cardinal tooth becomes distinctly elongate.

To sum up, the differentiation of specimens of the *Sarmatimactra* Zone, detected by the RWA, with small values for RW2 and high values for RW4 (Fig. 6), is based on (1) relatively large, roughly equally expressed cardinal teeth, (2) a short pallial line, as a consequence of a shortened ventral shell margin (shells become less triangular), and (3) a deep pallial sinus. The separation of both biozones should not be overestimated, however, as there is still a large morphological overlap. The shapes typical for *Sarmatimactra* Zone specimens are in part already present in the upper *Ervilia* Zone, yet do not dominate. However, it is evident from the RWA that the average shell shape changes over time, expressed as a shifted mean and a narrowing spread. The lower sample size for the *Sarmatimactra* Zone must have an effect on this, but the differences are still very distinct.

While the RWA considers proportions of the internal elements of the shell, the Fourier analysis covers properties of the outline. Comparable to the RWA, the

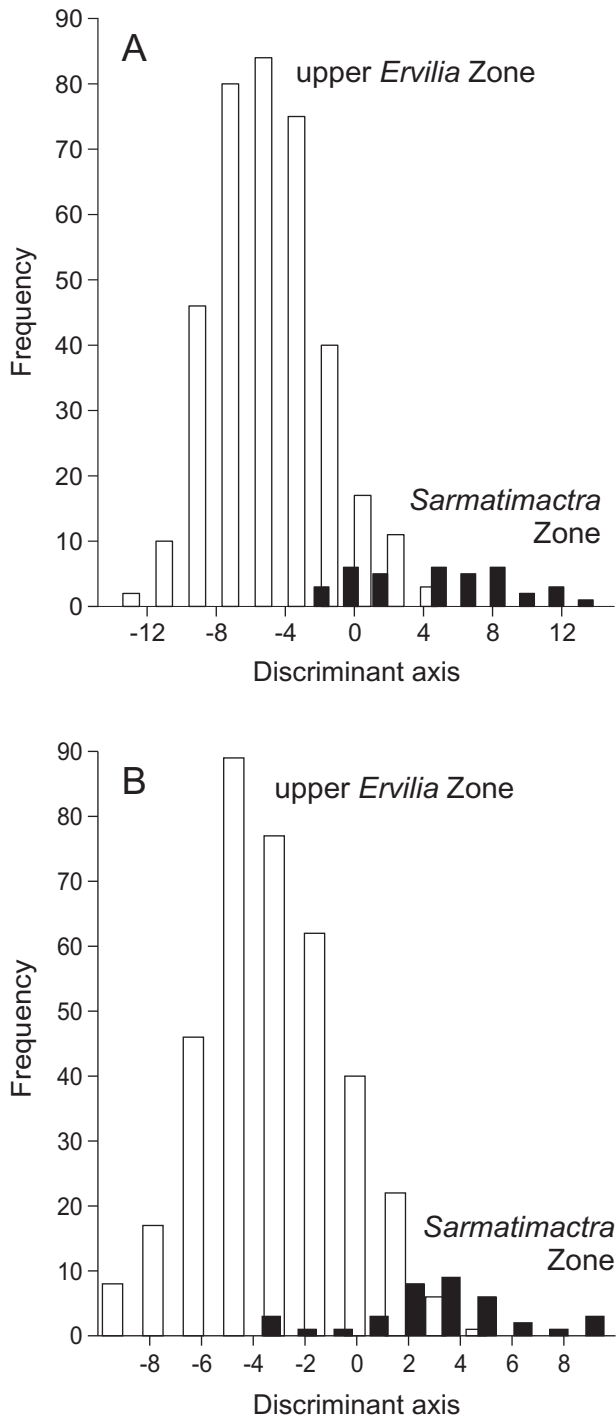


Figure 5. Linear discriminant functions showing the separation between the upper *Ervilia* Zone and the *Sarmatimactra* Zone, computed for the relative warps (A) and the principal components (B).

results are presented as PCA computed from the Fourier coefficients (Fig. 7). The LDA of the principal components yielded significant separation of both biozones (Hotelling's $T^2 = 250.04$, $P < 0.001$) with a

classification rate of 89.38% (Fig. 5B). The PCA of the Fourier coefficients showed best separation along PC2 (16.42%) and PC3 (10.56%) rather than PC1 (34.37%), proving again that the variability within the biozones is larger than between. The biplot indicates that the first four components are mainly controlled by harmonics 2 and 3, which describe length (anterior–posterior extension) and height (ventral–dorsal extension) (Fig. 7). In particular, length is the main parameter responsible for the variation along PC1 (as in the RWA). PC2 largely corresponds to changes in shell height. PC3 is best explained by a combination of height and length. Beginning with PC5, more detailed structures of the outline have an influence on the data spread. Thus, relative shell height obviously has a strong effect on the separation of the biozones. Shells in the *Sarmatimactra* Zone tend to be higher and slightly broader, resulting in relatively circular outlines.

Both analyses showed also slight differences between specimens from localities of the same biozone, which are not presented here. This regional variation cannot be reliably discussed with precise age classifications wanting. More information is needed to shed light on these small-scale differences.

SHELL SIZE AND THICKNESS

The RWA and FFT exclusively analyse shape and completely ignore size and thickness differences. Yet, both parameters are obviously important for differentiating shells of the two biozones. The box plots in Figure 8 clearly indicate considerable discrepancies for centroid size and shell thickness. Both factors are significantly correlated with each other (upper *Ervilia* Zone: $r = 0.608$, $P < 0.001$; *Sarmatimactra* Zone: $r = 0.683$, $P < 0.001$).

DISCUSSION

The entirety of all analyses indicates a distinct morphological shift in the *Polititapes tricuspis* lineage across the two biozones, involving changes in shell shape, size, and thickness. The differentiation of the *Sarmatimactra* Zone specimens from the upper *Ervilia* Zone specimens is essentially based on (1) larger and thicker shells, (2) rounder, less pointed outlines, (3) a deeper pallial sinus, and (4) larger, roughly equally expressed cardinal teeth. While size, thickness, and outline curvature produced good separation between the biozones, the internal features gave less clear results. The RWA showed solely a shifted mean and spread of the occupied morphospace, yet with no distinctly isolated clusters. Nevertheless, this shift, or rather the lack of certain former morphologies, requires an explanation. To

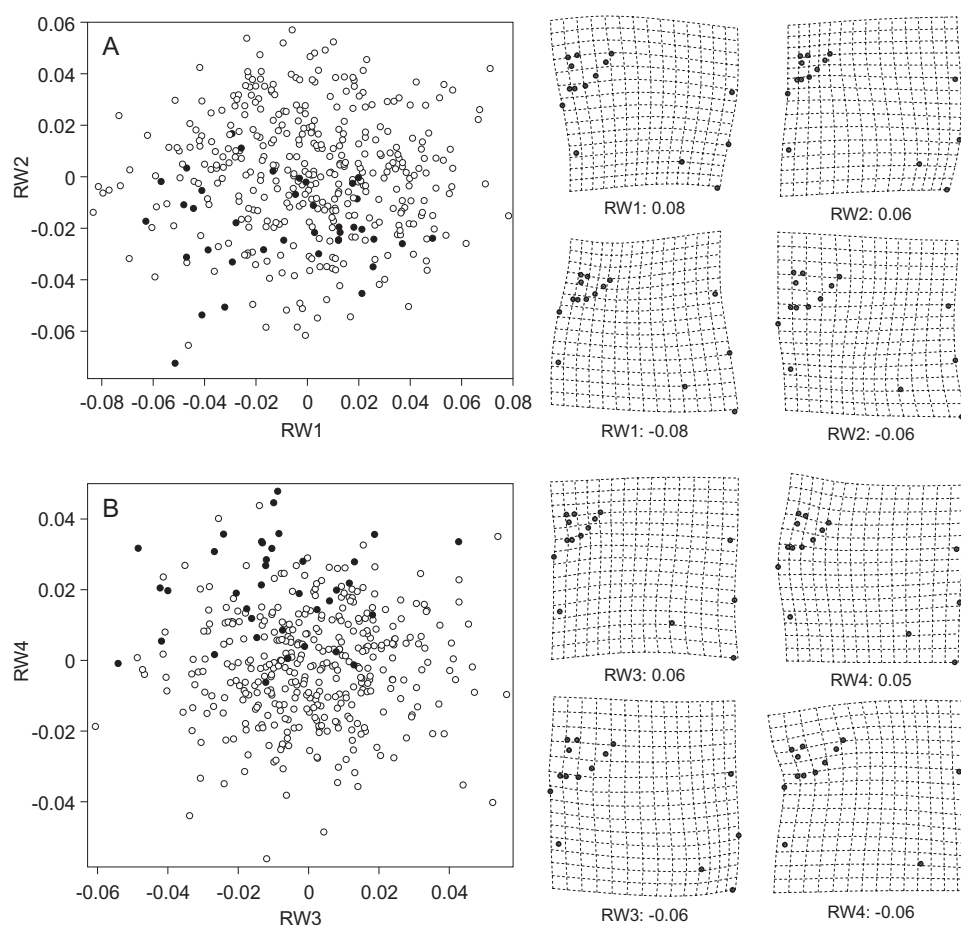


Figure 6. Relative warps analysis showing the first four warps and the associated deformation grids at the approximate minimal and maximal occupied values. Open circles correspond to upper *Ervilia* Zone specimens, and solid circles to *Sarmatimactra* Zone specimens.

provide a reliable interpretation of the biological significance of all the aforementioned changes, an environmental characterization of the two biozones is necessary.

ENVIRONMENTAL DESCRIPTION OF THE BIOZONES

In the upper *Ervilia* Zone massive carbonate sedimentation prevails, resulting in extensive ooid shoals throughout the Central Paratethys (Piller & Harzhauser, 2005; Lukeneder *et al.*, 2011). Together with thick cross-bedded successions, this indicates rather shallow, high-energy conditions. Based on sedimentological evidence, strong influence of tidal activity is suggested from the early Sarmatian up to the *Ervilia* Zone by Mandić *et al.* (2008) and Harzhauser & Piller (2012). Oolites and shell beds both show strong carbonate cementation, arguing for supersaturation of the water with calcium carbonate (Piller & Harzhauser, 2005).

The *Sarmatimactra* Zone is still dominated by carbonate sedimentation, with negligible siliciclastic input (Piller & Harzhauser, 2005). Carbonate cementation increases distinctly, commonly forming very thick radial-fibrous cement crusts on oolites and shell beds. Foraminiferal-microbial build-ups reach their optimum during this biozone, attaining up to 20 m in width. Stable isotope analyses of gastropod shells from the *Sarmatimactra* Zone document a distinct increase in salinity due to enhanced evaporation (Latal, Piller & Harzhauser, 2004; Tóth *et al.*, 2010). Uniform sediment bedding signals high water energy. Strong wave action, water currents, and the low input of siliciclastics impede the formation of sedimentary structures. All these environmental changes favoured the establishment of extensive, very shallow, tidal-dominated, high-energy areas along the entire Central Paratethys shores. Even in central parts of the Pannonian Basin System a shallowing-upward trend is recorded, with the establishment of warm,

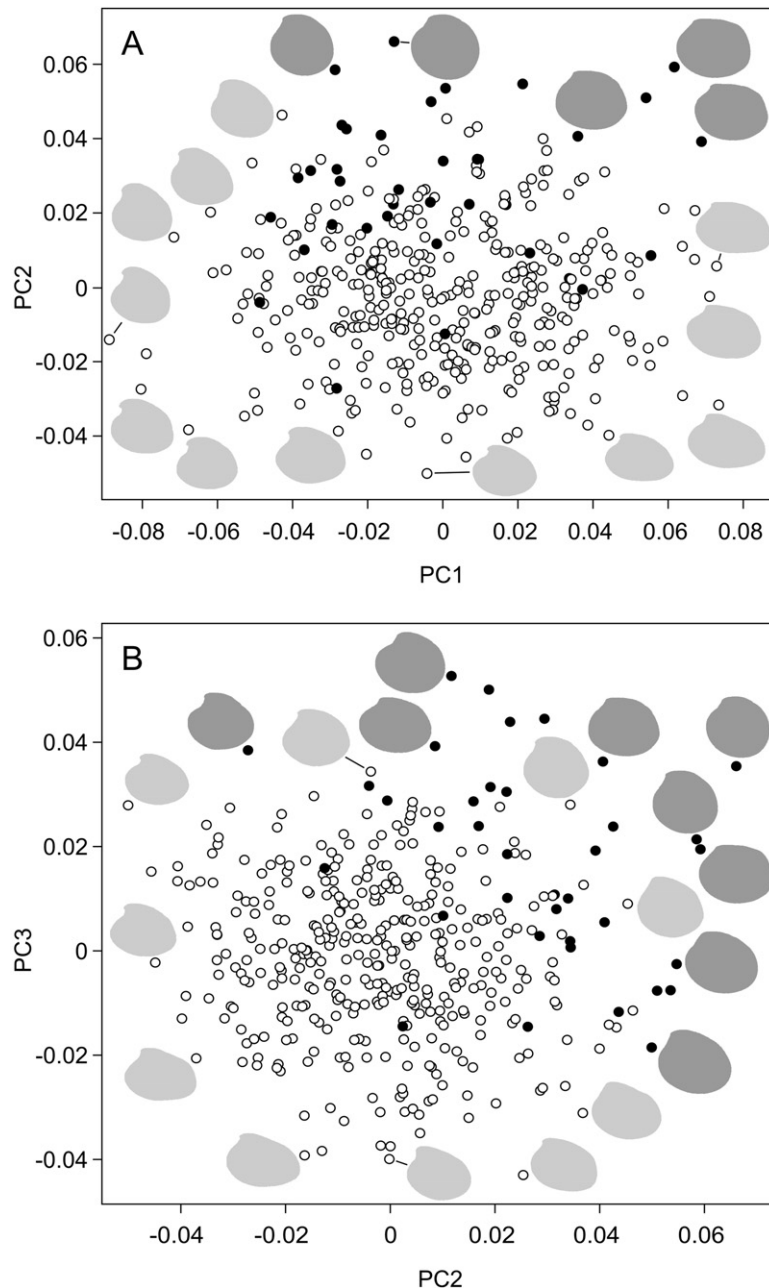


Figure 7. Principal components analysis of the Fourier coefficients with indication of several outlines in the plots. Open circles and light grey outlines correspond to upper *Ervilia* Zone specimens, and solid circles and dark grey to *Sarmatimactra* Zone specimens. The images are not to scale. Note the distinct increases of relative shell length along PC1 and relative shell height along PC2 and PC3.

shallow-water marine lagoons in the latest Sarmatian (Cornée *et al.*, 2009).

INTERPRETATION OF MORPHOLOGICAL CHANGES

Each of the morphological trends detailed above fits well to the environmental trends in a biologically functional way. In particular, the evolution of a larger,

thicker shell with a circular shape and the centralization and strengthening of the cardinal teeth might share the same environmental trigger. Because of the decreased water depth in the *Sarmatimactra* Zone, shells were more exposed to wave action and the influence of the tides. Deeper environments that might have served as a refuge were available only to a minor extent. The new high-energy habitats

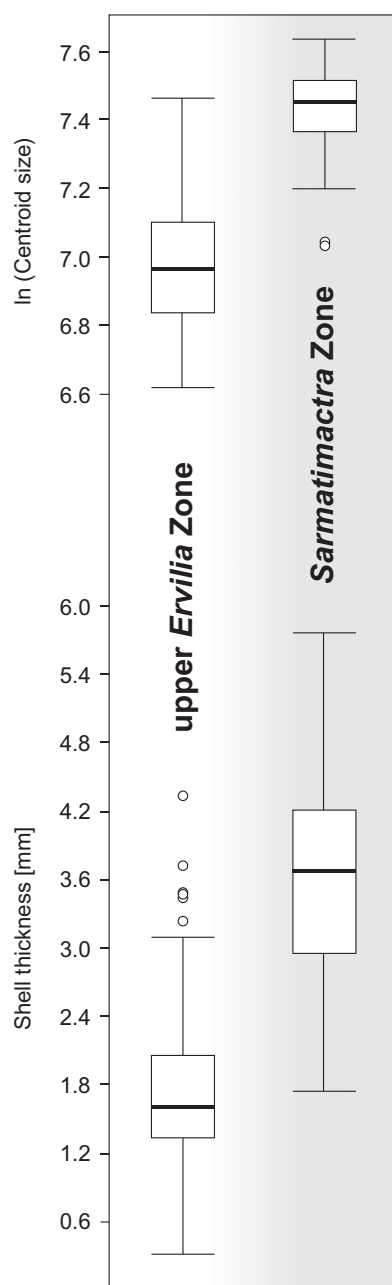


Figure 8. Box plots showing substantial differences for shell size (given as natural logarithm of centroid size) and shell thickness at the centroid between specimens of the upper *Ervilia* Zone and the *Sarmatimactra* Zone. The thick black lines indicate the median, white boxes the ranges from 25th to 75th percentile, horizontal lines outside boxes the minimal and maximal values, and circles the outliers (Hammer & Harper, 2006). For both shell size and thickness the two biozones overlap with respect to the total ranges, but the average (median) and majority of specimens (white boxes) indicate a considerable distinction.

required a higher degree of mechanical stability. In such settings larger and thicker shells are of course beneficial. Many species typically found among recent shores exposed to high wave action have comparably thick shell walls. Stanley (1970) noted that for non-attached bivalves thick shells are very typical among reclining and shallow-burrowing groups, being more prone to disruption by wave action and currents.

The adaptations of the hinge apparatus reflect the developmental restrictions of tapetine Veneridae. This bivalve group lacks lateral teeth (Moore, 1969), making the cardinal teeth (apart from the ligament) the main opponent to shearing stress. Therefore, strengthening and a more central position of the cardinal teeth are the two options to achieve higher constructional stability by lowering the possible influence of lateral shearing.

The size of the pallial sinus is usually associated with burrowing depth. Deeply burrowing bivalves need longer siphons to retain a connection with the bottom water, which consequently need more space in the mantle cavity leading to a deeper pallial sinus (e.g. Taylor & Lewis, 2005). Hence, the deepening of the pallial sinus in specimens from the *Sarmatimactra* Zone corresponds to a trend of deeper burrowing. Although most burrowing organisms develop elongate shapes, there are several examples of deep-burrowing bivalves with circular shells, especially among the Lucinidae or dosiniine Veneridae (Ansell, 1961; Stanley, 1970). According to the comprehensive survey of Stanley (1970) on the functional morphology of bivalve shells, species with distinctly circular shells burrow vertically downward into the sediment. In contrast to its triangular predecessor, the new phenotype in the *P. tricuspis* lineage with a circular to subcircular shape might therefore have been adapted to deeper, vertically bound burrowing. On the other hand, burrowing rate was supposedly reduced. Larger and rounder shells oppose the sediment with a greater surface area, so will experience higher resistance (Trueman, Brand & Davis, 1966; Trueman & Ansell, 1969; Stanley, 1970; Seilacher, 1984). In addition, thicker shells are heavier, requiring more energy to move (Stanley, 1970).

The changing burrowing habit may again be a result of environmental changes at the transition to the *Sarmatimactra* Zone. The possibility of being washed out by wave action is thus reduced. Beyond that, the ability to protrude deeper into the sediment might be advantageous in such settings, where deeper sediment layers are still saturated with water at low tide (Ott, 1988). In such a high-energy intertidal environment the sediments are highly permeable and show a high water throughput (Ott, 1988; Anschutz *et al.*, 2009). Therefore, water saturation in the sediment column readily decreases as the water level

retreats during ebb tides. The shallow burrowing *Polititapes tricuspis* was likely to have been affected by occasional exposure to desiccation and temperature variability (Bayne, 1976; Dame, 2012). Moreover, with regard to being washed out by waves and suffering from desiccation during low tide, a larger, stronger body might prove advantageous (e.g. Kurihara, 2003; see below).

Greater burrowing depth as a method to escape competition for settling space is unlikely in this context. Overall biodiversity is strongly reduced in the *Sarmatimactra* Zone as a result of a high rate of extinction at the end of the upper *Ervilia* zone (Harzhauser & Piller, 2007). Other infaunal bivalves recorded for the *Sarmatimactra* Zone comprise the small and rare *Donax lucidus* Eichwald, 1830, the small and rare *Solen subfragilis* Eichwald, 1853, the large, abundant *Sarmatimactra vitaliana* (d'Orbigny, 1844), and several cardiid species (Papp, 1954, 1974). The tellinid genus *Donax* is a rapid, shallow burrower, characteristic of shallow, wave-exposed sandy beaches (Trueman *et al.*, 1966; Stanley, 1970); solenids are rapid- and deep-burrowing bivalves (Trueman, 1967); cardiids have short siphons, indicating very shallow sediment penetration (Stanley, 1970). *Sarmatimactra* is interpreted to be a shallow water dweller in estuarine and lagoonal settings (Mandic *et al.*, 2008), comparable to recent examples of Mactridae from the Atlantic, where mass occurrences with densities of up to 400 individuals m⁻² are reported from inlets exposed to strong in-/outflow currents (Branch & Branch, 1981). As the fossil record is incomplete, especially concerning the great number of infaunal, purely soft-bodied species, we cannot fully exclude the competition–escape hypothesis.

The diminishing burrowing rate is not expected to have a negative effect, such as the reduced ability to escape potential predators. Escalation as a driving force behind any of the observed morphological changes is unlikely. Organisms that are able to predate on bivalves are rare during the late Sarmatian. There is only a single species of carnivore ocinebrid muricid gastropod in the Sarmatian, which rarely occurs in the *Sarmatimactra* Zone, and naticids are absent during this period (Papp, 1954, 1974). Starfish, many of which predate on bivalves (e.g. Carter, 1968; McClintock & Robnett, 1986), are also completely lacking in this late phase of the Central Paratethys (Piller & Harzhauser, 2005). The impact of other molluscivorous animals such as certain birds, crabs, or vertebrates (e.g. Vermeij & Covich, 1978; West, Cohen & Baron, 1991; West & Cohen, 1994; Zuschin, Stachowitsch & Stanton, 2003; Stempien, 2007), which can be quite considerable, is unknown. Not a single shell exhibits bore holes or any

sign of predational biological interaction or repair marks.

An effect of the hypersaline regime proposed for the *Sarmatimactra* Zone on any of the observed morphological changes could not be tested. Although the uniform Paratethyan fauna indicates largely uniform conditions for the entire sea, the degree of hypersalinity and potential geographical variation of such conditions are unknown (Latal *et al.*, 2004; Piller & Harzhauser, 2005). Moreover, *Polititapes tricuspis* is a fossil species, and its tolerance to salinity fluctuations is unknown. The few existing data on salinity requirements for tapetine venerids (e.g. Rasmussen, 1958; Nell & Paterson, 1997; Namaguchi, 1998) indicate wide ranges (from brackish to hypersaline) with large discrepancies between different species. This makes any estimation doubtful.

WHY LARGER?

One hypothesis usually discussed in the context of evolutionary size increase is Cope's Rule, i.e. the tendency for organisms in evolving lineages to increase in size over time (Cope, 1896; Stanley, 1973). This theory raised heated debates over the last century, but has been rarely demonstrated and lacks empirical data for most systematic groups (for a review see Hone & Benton, 2005). Many arguments for and against (or arguments against generalization) exist in the literature (e.g. Brown & Maurer, 1986; Jablonski, 1997; Kingsolver & Pfennig, 2004). The advantages of being larger, which are summarized by Hone & Benton (2005) and potentially applicable to bivalves, involve a greater range of acceptable foods, increased defence against predation, increased success in mating, intra- and interspecific competition, survival through lean times, and resistance to climatic variation. One often neglected factor is that individual body size is strongly dependent on the environmental conditions (Hunt & Roy, 2006). Changes in the ecological setting over geological time therefore have implications for body size evolution. This is probably the case for *P. tricuspis*. The greater exposure to water energy and tidal activity and supposedly also the increasing salinity in the *Sarmatimactra* Zone produced enhanced environmental pressure on the bivalves, which might have resulted in a shifting selection pressure towards larger shells. As stated above, predation and interspecific competition were probably negligible factors. Consequently, body size evolution in *P. tricuspis* is considered as a functional adaptation to increase individual fitness in a changing environment. In its broadest sense, this is in line with the idea of Cope's Rule.

To maintain larger bodies a certain availability of food is necessary. The increases of shell size and thickness caused an exponential augmentation of shell and body mass. Such developments, in addition to the expected energy loss by resisting higher mechanical stress, necessitate a highly elevated nutrient uptake. This relationship is non-linear as a bivalve's filtration efficiency decreases with increasing individual size (Wilbur & Owen, 1964). The feeding preferences in the fossil *P. tricuspis* are of course not easily determined. Recent tapetine venerids feed on various types of phytoplankton, bacteria, and particulate plant matter (e.g. Laing, Child & Janke, 1990; Stenton-Dozey & Brown, 1992; Coutteau, Curé & Sorgeloos, 1994; Laing & Child, 1996), with retention largely depending on particle size (Møhlenberg & Riisgård, 1978; Defosse & Hawkins, 1997). Although we cannot identify the main food sources of *P. tricuspis*, the extension of foraminiferal-microbial bioconstructions with thick carbonate crusts (Piller & Harzhauser, 2005), paired with evidence for high primary productivity at that time (for an overview see Cornée *et al.*, 2009), suggest high availability of nutrients.

IMPLICATIONS FOR TAXONOMY

Much effort has been expended to categorize the morphological variability in the *Polititapes tricuspis* lineage, resulting in the descriptions of many species, subspecies, phenotypes, and/or forms (e.g. Eichwald, 1830, 1852, 1853; Goldfuss, 1841; Papp, 1958, 1974). The strong morphological overlap between some of these entities (if recognizable as such) and the ongoing evolutionary trend, however, complicate such attempts. The plenitude of names was reduced to some extent in the taxonomic revisions by Kojumdzieva (1969), Nevesskaja *et al.* (1993), and Schneider *et al.* (2013). The temporal resolution of the fossil successions limits a more precise assessment of the evolutionary mechanisms and the possibility of deriving small-scale phylogenetic patterns. Whether speciation takes place, in whatever manner, cannot be evaluated from the present data. Therefore, and because of the high degree of morphological overlap, an assignment of a name to a specific morphology is avoided. Future investigations need to focus on the integration of material from other localities and on obtaining more precise knowledge of their stratigraphic ages. This would perhaps allow specifying trends in a more detailed way, to construct a reliable time frame, and to relate small-scale morphological tendencies to local environmental shifts.

MORPHOLOGICAL TRENDS IN THE LATE SARMATIAN

Interestingly, morphological evolution seems to be a common phenomenon in many mollusc species

passing the transition from the upper *Ervilia* Zone to the *Sarmatimactra* Zone. Papp (1958) recorded more or less gradual evolutionary tendencies in a series of bivalve and gastropod species. For example, *Sarmatimactra vitaliana* (d'Orbigny, 1844), the eponymous species of the respective biozone, shows a massive size increase. In contrast, the gastropod *Duplicatum duplicatum* (Sowerby, 1832) becomes gradually larger during the *Ervilia* Zone, but smaller in the *Sarmatimactra* Zone. Size variation plays a minor role in the snail *Gibbula poppelacki* (Hörnæs, 1855), which instead shows a trend towards more slender shells with reduced sculpture over time. The eponymous *Ervilia dissita* (Eichwald, 1830) shows a gradual size increase during the *Ervilia* Zone and goes extinct at its end.

These developments supposedly have their origin in the same palaeoenvironmental changes summarized above. Although an interpretation of each of these morphological alterations is beyond the scope of this paper, they indicate the massive impact of the ecological and climatic turnover on the late Sarmatian Sea. Comparable morphometric studies of each of these species would certainly increase our understanding of the environmental influence at that time.

CONCLUSIONS

This study displays a multi-method approach to the analysis of morphology. By including both a landmark- and an outline-based morphometric method, various aspects of the shell can be captured and a detailed picture of the evolutionary tendencies can be drawn. The morphometric analyses of the late Sarmatian *Polititapes tricuspis* lineage, including separate assessments of shell size, thickness, outline, and internal morphology, show distinct differences between the populations sampled from the upper *Ervilia* Zone and those from the subsequent *Sarmatimactra* Zone. RWA and FFT yield similar results. Both methods show that shape variation is higher within each biozone than between. Differentiation of the geologically younger specimens is based on larger and thicker shells, rounder, less pointed outlines, a deeper pallial sinus, and larger cardinal teeth.

Data on the palaeoenvironments of both biozones suggest the morphological trends to be functional adaptations to a changing ecological setting. Because of a decreased water depth followed by significant surface increase of intertidal flats in the *Sarmatimactra* Zone (Latal *et al.*, 2004; Piller & Harzhauser, 2005), shells were exposed to stronger wave action and a greater influence of the tides. The associated necessity for more mechanical stability resulted in the production of larger and thicker shells

with stronger cardinal teeth. Because of the lack of lateral teeth in tapetine venerids, another option to improve stability is to move the cardinal teeth towards the hinge centre. The deepening pallial sinus suggests deeper penetration into the sediment. Deep burrowing reduces the chances of being washed out in such high-energy settings and impedes desiccation during low tide.

The larger, rounder, and thicker shells supposedly diminished the burrowing rate considerably. A negative implication of this, however, is unlikely. Predators that might have exploited such an opportunity are extremely rare in the late Sarmatian; only a single, seldom occurring predatory gastropod species is known.

ACKNOWLEDGEMENTS

Our sincere thanks go to Simon Schneider (CASP, Cambridge), Reinhold Kunz (Vienna), and Anton Breitenberger (Gainfarn) for providing specimens. We are gratefully indebted to F. James Rohlf (State University of New York, Stony Brook) for helpful comments on the statistics. Martin Zuschin (University of Vienna) shared ideas on the functional morphology of bivalves and Andreas Kroh (Natural History Museum Vienna) helped with the graphical processing of the bivalve images. Many thanks go to Simon Schneider (CASP, Cambridge) and Peter D. Roopnarine (California Academy of Sciences, San Francisco) for their very constructive reviews and helpful comments that substantially improved the paper. The data are stored at <http://doi.pangaea.de/10.1594/PANGAEA.810115>.

REFERENCES

- Anderson LC, Roopnarine PD. 2005.** Role of constraint and selection in the morphologic evolution of *Caryocorbula* (Mollusca: Corbulidae) from the Caribbean Neogene. *Palaeontologia Electronica* **8**: 32A.
- Anschutz P, Smith T, Mouret A, Deborde J, Bujan S, Poirier D, Lecroart P. 2009.** Tidal sands as biogeochemical reactors. *Estuarine, Coastal and Shelf Science* **84**: 84–90.
- Ansell AD. 1961.** The functional morphology of the British species of Veneracea (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom* **41**: 489–517.
- Bayne BL. 1976.** *Marine mussels, their ecology and physiology*. Cambridge: Cambridge University Press.
- Bookstein FL. 1991.** *Morphometric tools for landmark data: geometry and biology*. Cambridge: Cambridge University Press.
- Bookstein FL. 1996.** Biometrics, biomathematics and the morphometric synthesis. *Bulletin of Mathematical Biology* **58**: 313–365.
- Branch M, Branch G. 1981.** *The living shores of southern Africa*. Cape Town: C. Struik.
- Brown JH, Maurer BA. 1986.** Body size, ecological dominance and Cope's Rule. *Nature* **324**: 248–250.
- Carter RM. 1968.** On the biology and palaeontology of some predators of bivalved mollusca. *Palaeogeography, Palaeoclimatology, Palaeoecology* **4**: 29–65.
- Cope ED. 1896.** *The primary factors of organic evolution*. Chicago: The Open Court Publishing Company.
- Cornée J-J, Moissette P, Saint Martin J-P, Kázmér M, Tóth E, Görög Á, Dulai A, Müller P. 2009.** Marine carbonate systems in the Sarmatian (Middle Miocene) of the Central Paratethys: the Zsámbék Basin of Hungary. *Sedimentology* **56**: 1728–1750.
- Coutteau P, Curé K, Sorgeloos P. 1994.** Effect of algal ration on feeding and growth of juvenile manila clam *Tapes philippinarum* (Adams and Reeve). *Journal of Shellfish Research* **13**: 47–55.
- Crampton JS, Haines AJ. 1996.** Users' manual for programs Hangle, Hmatch and Hcurve for the Fourier shape analysis of two-dimensional outlines. *Institute of Geological and Nuclear Sciences, Science Report* **96**: 1–28.
- Dame RF. 2012.** *Ecology of marine bivalves. An ecosystem approach*. Boca Raton: CRC Press.
- Defosse J-M, Hawkins AJS. 1997.** Selective feeding in shellfish: size-dependent rejection of large particles within pseudofaeces from *Mytilus edulis*, *Ruditapes philippinarum* and *Tapes decussatus*. *Marine Biology* **129**: 139–147.
- Eichwald E. 1829.** *Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilnensi habendarum. Pars prior propaedeuticam zoologiae atque specialem heterozoorum expositionem continens*. Vilnius: Joseph Zawadzki.
- Eichwald E. 1830.** *Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht*. Wilna: Voss.
- Eichwald E. 1852.** *Lethaea Rossica ou le monde primitive de la Russie. Atlas. Troisième volume. Période moderne*. Stuttgart: Schweizerbart.
- Eichwald E. 1853.** *Lethaea Rossica ou Paléontologie de la Russie 3, dernière période*. Stuttgart: Schweizerbart.
- Gmelin JF. 1791.** *Caroli a Linné, systema naturae. Tomus I. Pars VI*. Lipsiae: Beer.
- Goldfuss GA. 1841.** *Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmae rhenanae servantur quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata, II (4)*. Düsseldorf: Arnz & Co.
- Goncharova IA. 1986.** Sistema i istoria tapetin (Bivalvia: Veneridae, Tapetinae) neogenovih morei Zapadnoi Evrazii. In: Kafanov AI, ed. *Paleogen-neogenovye dvustvorcatye molljuzki Dal'nego Vostoka i Vostocnogo Paratetisa. Sbornik naucnykh trudov*. Vladivostok: DVNC AN SSSR, 75–100.
- Gradstein FM, Ogg JG, Schmitz MD, Ogg GM. 2012.** *The geologic time scale 2012, 2 volumes*. Oxford: Elsevier.

- Haines AJ, Crampton JS. 2000. Improvements to the method of Fourier shape analysis as applied in morphometric studies. *Palaeontology* **43**: 765–783.
- Hammer Ø, Harper DAT. 2006. *Paleontological data analysis*. Oxford: Blackwell Publishing.
- Hammer Ø, Harper DAT, Ryan PD. 2001. Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**: 1–9.
- Harzhauser M, Gross M, Binder H. 2008. Biostratigraphy of Middle Miocene (Sarmatian) wetland systems in an Eastern Alpine Intramontane Basin (Gratkorn Basin, Austria). The terrestrial gastropod approach. *Geologica Carpathica* **59**: 45–58.
- Harzhauser M, Kowalke T. 2002. Sarmatian (Late Middle Miocene) gastropod assemblages of the Central Paratethys. *Facies* **46**: 57–82.
- Harzhauser M, Mandic O, Zuschin M. 2003. Changes in Paratethyan marine molluscs at the Early/Middle Miocene transition – diversity, paleogeography and paleoclimate. *Acta Geologica Polonica* **53**: 323–339.
- Harzhauser M, Piller WE. 2004. Integrated stratigraphy of the Sarmatian (Upper Middle Miocene) in the western Central Paratethys. *Stratigraphy* **1**: 65–86.
- Harzhauser M, Piller WE. 2007. Benchmark data of a changing sea – palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **253**: 8–31.
- Harzhauser M, Piller WE. 2012. Molluscs as a major part of subtropical shallow-water carbonate production – an example from a Middle Miocene oolite shoal (Upper Serravallian, Austria). In: Mutti M, Piller WE, Betzler C, eds. *Carbonate systems during the Oligocene–Miocene climatic transition*. Oxford: Wiley-Blackwell, 185–200.
- Harzhauser M, Piller WE, Steininger FF. 2002. Circum-Mediterranean Oligo/Miocene biogeographic evolution – the gastropod's point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology* **183**: 103–133.
- Hone DWE, Benton MJ. 2005. The evolution of large size: how does Cope's Rule work? *Trends in Ecology and Evolution* **20**: 4–6.
- Hörnnes M. 1851–1856. Die fossilen Mollusken des Tertiär-Beckens von Wien. I. Univalven. *Abhandlungen der Geologischen Reichsanstalt* **3**: 1–736.
- Hunt G, Roy K. 2006. Climate change, body size evolution, and Cope's Rule in deep-sea ostracodes. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 1347–1352.
- Ionesi L, Ionesi B, Roșca V, Lungu A, Ionesi V. 2005. *Sarmatianul mediu și superior de pe Platforma Moldovenească*. București: Editura Academiei Române.
- Jablonski D. 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's Rule. *Nature* **385**: 250–252.
- Kingsolver JG, Pfennig DW. 2004. Individual-level selection as a cause of Cope's Rule of phyletic size increase. *Evolution* **58**: 1608–1612.
- Kojumdgieva E. 1969. *Les fossiles de Bulgarie. VIII. Sarmatien*. Sofia: Académie Bulgare des Sciences.
- Kurihara T. 2003. Adaptations of subtropical Venus clams to predation and desiccation: endurance of *Gafrarium tumidum* and avoidance of *Ruditapes variegatus*. *Marine Biology* **143**: 1117–1125.
- Laing I, Child AR. 1996. Comparative tolerance of small juvenile palourdes (*Tapes decussatus* L.) and Manila clams (*Tapes philippinarum* Adams & Reeve) to low temperature. *Journal of Experimental Marine Biology and Ecology* **195**: 267–285.
- Laing I, Child AR, Janke A. 1990. Nutritional value of dried algae diets for larvae of Manila clam (*Tapes philippinarum*). *Journal of the Marine Biological Association of the United Kingdom* **70**: 1–12.
- Latal C, Piller WE, Harzhauser M. 2004. Palaeo-environmental reconstructions by stable isotopes of Middle Miocene gastropods of the Central Paratethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* **211**: 157–169.
- Lukeneder S, Zuschin M, Harzhauser M, Mandic O. 2011. Spatiotemporal signals and palaeoenvironments of endemic molluscan assemblages in the marine system of the Sarmatian Paratethys. *Acta Palaeontologica Polonica* **56**: 767–784.
- Mandic O, Harzhauser M, Roetzel R, Tibuleac P. 2008. Benthic mass-mortality events on a Middle Miocene incised-valley tidal-flat (North Alpine Foredeep Basin). *Facies* **54**: 343–359.
- McClintock JB, Robnett TJ Jr. 1986. Size selective predation by the asteroid *Pisaster ochraceus* on the bivalve *Mytilus californianus*: a cost–benefit analysis. *Marine Ecology* **7**: 321–332.
- Møhlenberg F, Riisgård HU. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. *Ophelia* **17**: 239–246.
- Moore RC. 1969. *Treatise on invertebrate paleontology. Part N. Mollusca 6. Bivalvia, 2 volumes*. Lawrence: Geological Society of America and University of Kansas Press.
- Namaguchi K. 1998. Preliminary experiments on the influence of water temperature, salinity and air exposure on the mortality of Manila clam larvae. *Aquaculture International* **6**: 77–81.
- Nell JA, Paterson KJ. 1997. Salinity studies on the clams *Katylisia rhytiphora* (Lamy) and *Tapes dorsatus* (Lamarck). *Aquaculture Research* **28**: 115–119.
- Neubauer TA, Harzhauser M, Kroh A. 2013. Phenotypic evolution in a fossil gastropod species lineage: evidence for adaptive radiation? *Palaeogeography, Palaeoclimatology, Palaeoecology* **370**: 117–126.
- Nevesskaja LA, Goncharova IA, Paramonova NP, Popov SB, Babak EB, Bagdasarjan KG, Voronina AA. 1993. *Opredelitelj miocenovjeh dvustvorchatjih molljuskov Juzgo-Zapadnoi Evrazii*. Moscow: Nauka.
- Ogg JG, Lugowski A. 2012. *TSCreator visualization of enhanced Geologic Time Scale 2004 database* (Version 6.0). Available at: <http://www.tscreator.org>
- d'Orbigny A. 1844. Paléontologie du voyage de M. Hommaire de Hell. Dans les steppes de la Mer Caspienne, le Caucase, la Crimée et la Russie Méridionale. In: Hommaire De Hell

- X, ed. *Les steppes de la Mer Caspienne, le Caucase, la Crimée et la Russie Méridionale. Voyage pittoresque, historique et scientifique. Tome troisième*. Paris: Levraut, 419–450.
- Ott J. 1988. *Meereskunde. Einführung in die Geographie und Biologie der Ozeane*. Stuttgart: Verlag Eugen Ulmer.
- Papp A. 1954. Die Molluskenfauna im Sarmat des Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien* 45: 1–112.
- Papp A. 1956. Fazies und Gliederung des Sarmats im Wiener Becken. *Mitteilungen der Geologischen Gesellschaft in Wien* 47: 35–98.
- Papp A. 1958. Morphologisch-genetische Studien an Mollusken des Sarmats von Wiesen (Burgenland). *Wissenschaftliche Arbeiten aus dem Burgenland* 22: 5–39.
- Papp A. 1974. Die Molluskenfauna der Sarmatischen Schichtengruppe. In: Papp A, Marinescu F, Seneš J, eds. *M5 Sarmatien. Chronostratigraphie und Neostratotypen. Miozän der Zentralen Paratethys*. Bratislava: Vydavateľstvo Slovenskej Akadémie Vied, 4: 318–427.
- Piller WE, Harzhauser M. 2005. The myth of the brackish Sarmatian Sea. *Terra Nova* 17: 450–455.
- Popov SV, Rögl F, Rozanov AY, Steininger FF, Shcherba IG, Kováč M. 2004. Lithological–paleogeographic maps of Paratethys. 10 Maps. Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg* 250: 1–46.
- Rasmussen E. 1958. Past and present distribution of *Tapes (Venerupis) pullastra* (Montagu) in Danish waters. *Oikos* 9: 77–93.
- Rögl F. 1998. Paleogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien* 99A: 279–310.
- Rögl F. 1999. Mediterranean and paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (Short overview). *Geologica Carpathica* 50: 339–349.
- Rohlf FJ. 1993. Relative warp analysis and an example of its application to mosquito wings. In: Marcus LF, Garcia-Valdecasas AE, eds. *Contributions to morphometrics, Vol. 8*. Madrid: Museo Nacional de Ciencias Naturales (CSIC), 131–159.
- Rohlf FJ. 2010a. *tpsDig, digitize landmarks and outlines, version 2.16*. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at: <http://life.bio.sunysb.edu/morph>
- Rohlf FJ. 2010b. *tpsRelw, relative warps analysis, version 1.49*. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at: <http://life.bio.sunysb.edu/morph>
- Rohlf FJ, Marcus LF. 1993. A revolution in morphometrics. *Trends in Ecology and Evolution* 8: 129–132.
- Rohlf FJ, Slice DE. 1990. Extensions of the Procrustes method for the optimal superposition of landmarks. *Systematic Zoology* 39: 40–59.
- Roopnarine PD, Signorelli J, Laumer C. 2008. Systematic, biogeographic and microhabitat-based morphometric variation of the bivalve *Anomalocardia squamosa* (Bivalvia: Veneridae: Chioninae) in Thailand. *The Raffles Bulletin of Zoology, Supplement* 18: 95–102.
- Roopnarine PD, Vermeij GJ. 2000. One species becomes two: the case of *Chione cancellata*, the resurrected *C. elevata*, and a phylogenetic analysis of *Chione*. *Journal of Molluscan Studies* 66: 517–534.
- Schneider S, Mandic O, Harzhauser M. 2013. Preserved colour pattern in *Polititapes tricusps* (Eichwald, 1829) (Bivalvia: Veneridae) from the Sarmatian holotype at Nexing (Lower Austria). *Neues Jahrbuch für Geologie und Paläontologie* 268: 191–197, doi: 10.1127/0077-7749/2013/0326.
- Schultz O. 2005. Band 1, Teil 3. Bivalvia neogenica (Solenoida-Clavagelloidea). In: Piller WE, ed. *Catalogus Fossilium Austriae*. Wien: Österreichische Akademie der Wissenschaften, 691–1211.
- Seilacher A. 1984. Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology* 27: 207–237.
- Simpson GG. 1961. *Principles of animal taxonomy*. New York: Columbia University Press.
- Slice DE. 2000. The geometry of landmarks aligned by generalized Procrustes analysis. *American Journal of Physical Anthropology* 114: 283–284.
- Slice DE, Bookstein FL, Marcus LF, Rohlf FJ. 1996. Appendix I: a glossary for geometric morphometrics. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, eds. *Advances in morphometrics. NATO ASI series A: life sciences*. New York: Plenum Press, 284: 531–551.
- Sowerby GB. 1832. Table of fossils of lower Styria. *Transactions of the Geological Society of London, series 2* 3: 419.
- Stanley SM. 1970. Relation of shell form to life habit of the Bivalvia (Mollusca). *Geological Society of America, Memoir* 125: 1–296.
- Stanley SM. 1973. An explanation for Cope's Rule. *Evolution* 27: 1–26.
- Stempien JA. 2007. Detecting avian predation on bivalve assemblages using indirect methods. *Journal of Shellfish Research* 26: 271–280.
- Stenton-Dozey JME, Brown AC. 1992. Clearance and retention efficiency of natural suspended particles by the rock-pool bivalve *Venerupis corrugatus* in relation to tidal availability. *Marine Ecology Progress Series* 82: 175–186.
- Taylor PD, Lewis DN. 2005. *Fossil invertebrates*. London: Natural History Museum.
- Tóth E, Görög Á, Lécuyer C, Moissette P, Balter V, Monostori M. 2010. Palaeoenvironmental reconstruction of the Sarmatian (Middle Miocene) Central Paratethys based on palaeontological and geochemical analyses of foraminifera, ostracods, gastropods and rodents. *Geological Magazine* 147: 299–314.
- Trueman ER. 1967. The dynamics of burrowing in *Ensis* (Bivalvia). *Proceedings of the Royal Society B* 166: 429–476.
- Trueman ER, Ansell AD. 1969. The mechanisms of burrowing into soft substrata by marine animals. *Oceanography and Marine Biology Annual Reviews* 7: 315–366.
- Trueman ER, Brand AR, Davis P. 1966. The dynamics of burrowing of some common littoral bivalves. *The Journal of Experimental Biology* 44: 469–492.
- Vermeij GJ, Covich AP. 1978. Coevolution of freshwater

- gastropods and their predators. *The American Naturalist* **112**: 833–843.
- West K, Cohen A. 1994.** Predator–prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. In: Martens K, Goddeeris B, Coulter G, eds. *Speciation in ancient lakes. Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, 44: 267–283.
- West K, Cohen A, Baron M. 1991.** Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator–prey coevolution. *Evolution* **45**: 589–607.
- Wilbur KM, Owen G. 1964.** Growth. In: Wilbur KM, Yonge CM, eds. *Physiology of mollusca, Vol. 1*. New York: Academic Press, 211–242.
- Zuschin M, Stachowitsch M, Stanton RJ. 2003.** Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Science Reviews* **63**: 33–82.