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The bivalve *Glycymeris planicostalis* as a high-resolution paleoclimate archive for Rupelian (Early Oligocene) of Central Europe

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Abstract

Current global warming is likely to result in a unipolar glaciated world with unpredictable repercussions on atmospheric and oceanic circulation patterns. These changes are expected to affect seasonality as well as the frequency and intensity of decadal climate oscillations. To better constrain the mode and tempo of the anticipated changes, climatologists require high-resolution proxy data of time intervals in the past, e.g. the Early Oligocene during which boundary conditions were similar to those predicted for the near future. As demonstrated by the present study, pristinely preserved shells of the long-lived bivalve mollusk *Glycymeris planicostalis* from the late Rupelian of the Mainz Basin, Germany, provide an excellent archive to reconstruct changes of sea surface temperature on seasonal to inter-annual time scales. Their shells grew uninterruptedly during winter and summer and therefore recorded the full seasonal temperature amplitude that prevailed in the Mainz Basin 30 Ma ago. Absolute sea surface temperature data were faithfully reconstructed from $\delta^{18}O_{shell}$ values assuming a $\delta^{18}O_{water}$ signature that was extrapolated from coeval sirenian tooth enamel. Extreme values ranged between 12.3 and 22.0 °C and agree well with previous estimates based on planktonic foraminifera and shark teeth. However, summer and winter temperatures varied greatly on inter-annual time-scales. Winter and summer temperatures averaged over 40 annual increments of three specimens equaled 13.6 ± 0.8 °C and 17.3 ± 1.2 °C, respectively. Unless many samples are analyzed, this variability is hardly seen in foraminiferan tests. Our data also revealed decadal-scale oscillations of seasonal extremes which have – in the absence of appropriate climate archives – never been identified before for the Oligocene. This information can be highly relevant for numerical climate studies aiming to predict possible future climates in a unipolar glaciated or, ultimately, polar ice-free world.

1 Introduction

Current CO_2-induced global warming is likely to result in a unipolar glaciated world ultimately followed by one substantially without polar ice caps (e.g. Raper and Braithwaite, 2006). In light of these predicted boundary conditions, climate is expected to change profoundly, particularly at higher latitudes. According to numerical climate models, reduced meridional gradients will lead to substantial changes in atmospheric and oceanic circulation patterns (e.g. Cai and Chu, 1998; Hansen et al., 2004), thereby affecting seasonality as well as the frequency and intensity of decadal climate oscillations (e.g. Marshall et al., 2001; Solomon et al., 2007). In turn, this will alter surface temperature patterns, storm intensities and precipitation rates (Hurrell, 1995; Dai et al., 1997; Barbosa, 2009), all of which present a major challenge to densely populated coastal areas and coastal ecosystems, particularly in Central Europe (Ottersen et al., 2001; Stenseth et al., 2002).

To date, the mode and tempo of the environmental change anticipated for the near future have remained poorly constrained (e.g. Vellinga and Wood, 2002; Hátún et al., 2005). A promising avenue toward a better understanding of future climates is to investigate the short-term climate variability of time intervals in the past during which boundary conditions were similar to those predicted for the coming millennia. The last time a unipolar glaciated world occurred in Earth history was during the Early Oligocene when atmospheric CO_2 levels were slightly higher than today (Zachos et al., 2008) and the paleogeographic configuration on a global scale was at least broadly similar to the present-day situation (Lefebvre et al., 2013). Thus, the Oligocene world can serve as a natural laboratory for studying the possible effects of anthropogenic global warming. As yet, however, the Oligocene has remained a relatively poorly studied epoch of Earth history, which is at least partially attributed to the stratigraphic incompleteness of many Oligocene successions. In particular, shallow-water sequences of Oligocene age are often compromised by unconformities resulting from strong, glacially induced eustatic sea-level fluctuations (e.g. Miller et al., 2005; Pälike et al., 2006).

The epicontinental sedimentary archives from the Oligocene of Central Europe, notably the Rhenish triple junction system (e.g. Sissingh, 2003), can play a prime role in elucidating the short-term (i.e., seasonal to decadal) climate dynamics during that time. The significance of Oligocene sediments from the Rhenish triple junction system was first stressed by Beyrich (1954), whose work on strata from the Mainz and Kassel Basins ultimately led to the coinage of the term "Oligocene". These shallow marine successions exhibit much higher sedimentation rates and generally contain considerably more macrofossils than their open-marine counterparts. Moreover, their extremely proximal position with regard to the paleo-coastline and the low water-mass inertia as compared to the open ocean make them particularly sensitive to short-term paleoclimatic and paleoceanographic change. Furthermore, these strata contain well-preserved shells of long-lived bivalves (*Glycymeris planicostalis*, Lamarck 1819) whose modern representatives have recently been identified as highly promising tools for ultra-high-resolution climate reconstructions (Brocas et al., 2013; Royer et al., 2013; Bušelić et al., 2014). This species occurs worldwide in subtidal settings and lives infaunally in sandy and gravelly sediments (Ansell and Trueman, 1967; Thomas, 1978; Squires, 2010). Their fossil history dates back to the Aptian (Gillet, 1924; Casey, 1961) and besides some evolutionary innovations acquired during the Early Cenozoic, their fundamental bauplan remained largely unvaried until today (Thomas, 1975).

Bivalve shells serve as reliable recorders of ambient environmental conditions (e.g. Wanamaker et al., 2011). The production of shell material occurs on a periodic basis resulting in the formation of distinct growth lines which separate the growth pattern into time slices of equal duration, so-called growth increments. These growth patterns serve as a calendar which can be used to place each shell portion and each geochemical data point in a precise temporal context. Furthermore, the relative rate at which the shells grow is controlled by environmental variables. For example, warmer temperature and better food supply typically result in broader increments. In combination with geochemical analyses of the shell, increment width data can thus provide useful information on past environmental variables (e.g. Ivany and Runnegar, 2010; Mettam et al., 2014). Some bivalve species live for several centuries and can therefore provide uninterrupted environmental records covering hundreds of years such as the genera *Glycymeris* (Ramsay et al., 2000; Brocas et al., 2013), *Arctica* (e.g. Ropes, 1985; Butler et al., 2013) and *Panopea* (e.g. Strom et al., 2004; Black et al., 2008).

In the present study, we have sclerochronologically analyzed specimens of *G. planicostalis* from the upper Rupelian of the Mainz Basin, SW Germany, in order to assess their potential as "deep-time" paleoclimate archives. In particular, we focused on elucidating (i) whether the shells are sufficiently well preserved to permit reconstruction of water temperatures from oxygen-isotope data; (ii) what the timing and rate of seasonal shell growth of these specimens were; and (iii) how the seasonal $\delta^{18}O_{shell}$-derived water temperatures compare to existing temperature proxy data from that region. In order to assess a realistic oxygen isotope signature of the water ($\delta^{18}O_{water}$) during the Rupelian we measured the phosphate oxygen isotope ($\delta^{18}O_{PO_4}$) value of the tooth enamel of seven seacows (*Halitherium schinzii*) from the same formation as the *G. planicostalis* shells. The $\delta^{18}O_{PO_4}$ signature has been successfully exploited as a $\delta^{18}O_{water}$ proxy by many authors, e.g. Clementz and Koch (2001), Clementz et al. (2006), Thewissen et al. (2007) and Clementz and Sewall (2009). Our results demonstrate that – similar to their modern relatives – fossil *G. planicostalis* can be successfully employed for reconstructions of seasonal and decadal-scale environmental oscillations that prevailed during the Rupelian in Central Europe, i.e., data that as yet no other fossil archive could provide.

2 Study area

The Mainz Basin is located near the northwestern margin of the Upper Rhine Graben. Its formation dates back to the Middle Eocene and is related to the taphrogenesis of the European Cenozoic rift system (Dèzes et al., 2004; Ritzkowski, 2005; Grimm et al.,

2011) (Fig. 1). Its sedimentary succession, which was mainly deposited in shallow marine and brackish water settings, covers a time interval of ca. 20 Ma, from the Lutetian (~ 49.5 Ma) to the early Burdigalian (~ 18.5 Ma). During the late Rupelian (i.e. Early Oligocene; 33.9–28.4 Ma; Gradstein et al., 2004), central Europe experienced a period of extended marine transgressions due to local tectonic subsidence and eustatic sea level rise. As a consequence, the Mainz Basin became part of a marine strait, which extended from the paleo-North Sea Basin to the southernmost Upper Rhine Graben (Picot, 2002; Sissingh, 2003; Berger et al., 2005a). A possible southern connection with the western Molasse Basin has been controversially debated (Martini, 1982; Picot, 2002; Berger et al., 2005a, b; Grimm, 2006).

According to Berger et al. (2005b), marine conditions in the Mainz Basin lasted for about 2.5 Ma from the sea-level high stand Ru2/Ru3 (~ 32 Ma;) to Ru3/Ru4 (~ 29.5 Ma) of Haq et al. (1988). Nearshore deposits representing that time comprise coarse-grained (sand to gravel) siliciclastics of the Alzey Formation (from which the studied fossil material was collected – see below) and the overlaying Stadecken Formation. Contemporaneously deposited basinal sediments (pelites) belong to the Bodenheim Formation (Grimm et al., 2000; Sissingh, 2003; Berger et al., 2005b). Age control for the marine strata of the Mainz Basin is mainly based on calcareous nannoplankton (Martini and Müller, 1971; Martini, 1982), dinoflagellate cysts (e.g. Pross, 1997), and, to a lesser extent, benthic foraminifera (Grimm, 1998, 2002). With regard to the nannoplankton zonation, the Alzey and Bodenheim Formations comprise the upper part of nannoplankton zone NP23 and the lower part of nannoplankton zone NP24 (Grimm, 1994; Pross and Schmiedl, 2002; Berger et al., 2005b).

Paleoenvironmental reconstructions of the Alzey Formation are based on palynological and faunal data indicating an overall warm climate comparable to modern subtropical climate zones of the Mediterranean (Grimm et al., 2011). Reconstructed mean annual air temperature in the hinterland fluctuated between ~ 16 and ~ 17 °C, and mean annual precipitation was between 1000 and 1250 mm per year (Pross et al., 1998, 2000). The fully marine setting of the Mainz Basin was characterized by alternating dry and wet phases, which led to strong fluctuations of salinity levels (Pross and Schmiedl, 2002), and the episodic formation of water-mass stratification (Pross, 2001). Temperature estimates of the seawater have been derived from the δ^{18}O values of shark teeth and foraminiferan tests. These estimates yielded values of 6.9 to 23.3 °C (Tütken, 2003) for surface waters and 5.9 to 14.9 °C for bottom waters (Grimm, 1994).

3 Material and methods

3.1 Material

The studied shell material was collected by Jürgen Boy during the 70s and 80s of the last century, and has then been stored at the Paleontological collection of the Institute of Geosciences in Mainz. Samples originate from the outcrop "Trift" near Weinheim, the stratotype of the Alzey Formation (Grimm et al., 2000) (Fig. 1). Additional information about the precise stratigraphic position of the sampled layer is not available. The outcrop is ∼ 8 m thick and ∼ 40 m wide; it consists of fossiliferous middle to coarse sands and fine gravels. ^{87}Sr/^{86}Sr dating of a well-preserved *Glycymeris* sp. shell from the outcrop yielded an age of 30.1 ± 0.1 Ma (Grimm et al., 2003). The outcrop exhibits a highly diverse benthic fauna dominated by bivalves, gastropods and scaphopods that dwelled in shallow subtidal waters. Water-depth estimates, which are based on sedimentological features (Grimm et al., 2003) and ichnofossils (Schindler et al., 2005), range from ∼ 30 to ∼ 40 m. The teeth material originated from four localities located along the southwestern paleo-coastline of the Mainz Basin (Fig. 1; Table 1), and was also stored at the Paleontological collection. The samples were embedded in the siliciclastic deposits of the Alzey Formation. A more precise determination of their stratigraphic position was not possible in the field.

3.2 Methods

From the of *Glycymeris planicostalis* specimens collected at the outcrop "Trift", three large valves (~ 8 cm in height) that visually appeared well-preserved were selected for further investigations. These valves were labeled (MB-Wht-2, MB-Wht-4 and MB-Wht-7), mounted on Plexiglas cubes with GlueTec Multipower plastic welder and coated with WIKO metal epoxy resin to avoid fracture during cross-sectioning. From each valve, two ca. 3 mm-thick slabs were cut perpendicular to the growth lines and along the axis of maximum growth from the umbo to the commissure using a low-speed precision saw (Buehler Isomet 1000; at 200 rpm) equipped with a wafering-thin (0.4 mm), diamond coated blade. Both shell slabs were glued to glass slides with the mirroring sides facing up, ground on glass plates (320, 800, 1200 grit SiC powder) and polished with 1 µm Al_2O_3 powder. After each preparation step, the samples were ultrasonically rinsed in deionized water.

One polished slab of each specimen was firstly used for diagenetic screening. For this purpose, a set of different methods was employed including cathodoluminescence petrography, Raman spectroscopy and immersion of the shell slabs in Feigl solution. The presence of Mn^{2+} (> 10–20 ppm) in calcium carbonates produces an orange cathodoluminescence (Machel et al., 1991) and is typically regarded as an indicator of diagenetic neomorphism (Flügel, 2004) because biogenic aragonite is non-cathodoluminescent (Major, 1991). Like modern *Glycymeris* spp., shells of fossil representatives of this genus consisted of aragonite which is prone to change to calcite during diagenesis. Raman spectroscopy can yield detailed and spatially highly resolved information on the type of polymorphs of $CaCO_3$. Likewise, the Feigl test can distinguish between aragonite and calcite (Feigl, 1958). Feigl solution stains aragonite black and calcite pale grey. After diagenesis screening, the shell slabs were ground and polished again, and prepared for sclerochronological studies and subsequent scanning electron microscopic (SEM) analyses. For this purpose, polished cross-sections were immersed in Mutvei's solution for 40 min under constant stirring at 37–40 °C (Schöne et al., 2005a). After the staining process, the samples were gently rinsed in deionized water, air-dried and then photographed with a digital camera (Canon EOS 600D) mounted to a binocular microscope (Wild Heerbrugg M8). Growth increments were counted and their width measured with the image processing software Panopea (© Peinl and Schöne). Subsequently, samples were sputter-coated with a 2 nm thick gold layer and viewed under a scanning electron microscope (LOT Quantum Design Phenom Pro, 2nd generation) in order to describe the prevailing microstructures and identify possible neomorphic minerals that may have formed during diagenesis (Fig. 2).

The other polished slab of each specimen was used for the analysis of oxygen isotope values ($\delta^{18}O_{shell}$). Prior to the analysis, the outer ca. 0.5 to 1 mm thick chalky rim of the shell surfaces was physically removed. Then, 675 individual carbonate powder samples were micromilled from the outer shell layer of the three specimens (316, 193 and 166 samples from specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7, respectively) using a Rexim Minimo dental drill mounted to a stereomicroscope and equipped with a cylindrical, diamond-coated bit (1 mm diameter; Komet/Gebr. Brasseler GmbH and Co. KG, model no. 835104010). Individual milling steps contoured the shell growth patterns and measured between 100 and 200 µm in width. Carbonate powder samples weighing between 50 and 120 µg were reacted with 100 % phosphoric acid in He-flushed borosilicate exetainers at 72 °C. The resulting CO_2 was measured with a GasBench II-coupled Thermo Finnigan MAT 253 gas source isotope ratio mass spectrometer in continuous flow mode at the Institute of Geosciences of the University of Mainz. Oxygen isotope values are reported in δ-notation and given as parts per mil (‰). Data were calibrated against a NBS-19 calibrated IVA Carrara marble ($\delta^{18}O = -1.91$ ‰). On average, replicated internal precision (1σ) and accuracy (1σ) were better than 0.05 ‰, respectively.

If the bivalves formed their shell in oxygen isotopic equilibrium with the ambient water, the $\delta^{18}O_{shell}$ values can provide information on water temperature during growth (Epstein et al., 1953). For aragonitic shells, the paleothermometry equation of Grossman and Ku (1986) with a scale correction of −0.27 ‰ (see Dettman et al.,

1999) is typically employed:

$$T_{\delta^{18}\mathrm{O}}(^\circ\mathrm{C}) = 20.60 - 4.34 \cdot (\delta^{18}\mathrm{O}_{\mathrm{shell}} - (\delta^{18}\mathrm{O}_{\mathrm{water}} - 0.27)), \quad (1)$$

where $\delta^{18}O_{shell}$ is measured relative to VPDB and $\delta^{18}O_{water}$ relative to VSMOW. To compute reliable temperatures from $\delta^{18}O_{shell}$ values also requires knowledge of the $\delta^{18}O_{water}$ signature during shell formation. These data were estimated from the tooth enamel of sea cows, i.e., homoeothermic marine animals, from the same stratigraphic level. The precision errors of the mass spectrometric analyses of bivalve shells and sirenian teeth resulted in a combined average $T_{\delta 18O}$ error of ±0.3 °C (1σ).

3.3 Sea cow teeth

The oxygen isotope composition of tooth enamel from marine vertebrates can provide information on the $\delta^{18}O_{water}$ value of ambient seawater (e.g. Lécuyer et al., 1996a; Clementz and Koch, 2001; Clementz et al., 2006; Clementz and Sewall, 2009). Therefore, we measured the phosphate oxygen isotope composition ($\delta^{18}O_{PO_4}$) of the enamel from seven sirenian teeth of *Halitherium schinzii* recovered from the deposits of the Alzey Formation.

The surface of the teeth was physically cleaned and then sampled with a hand-held dental drill. A fraction of each enamel powder sample was then treated with 2 % NaOCl and 0.18 mL of 0.1 molar acetic acid to remove organics and potential diagenetic carbonates, respectively. Subsequently, ca. 4 mg of each sample were converted into silver phosphate (Ag_3PO_4) following the method of O'Neil et al. (1994) with modifications of Dettman et al. (2001) and Tütken et al. (2006). Triplicates of 500 µg of each Ag_3PO_4 sample were analyzed with a Thermo Fisher Delta Plus XL mass spectrometer coupled to a TC-EA, at the University of Tübingen, Germany. Measured values were normalized to in-house standards, Tu-1 and Tu-2 (Vennemann et al., 2002) and reported in δ-notation vs. VSMOW. Replicate ($n = 6$) analyses of NBS 120c resulted in an average $\delta^{18}O_{PO_4}$ value of 21.6 ± 0.13 ‰ which is well in the range of the average value (21.7 ‰) given by Lécuyer et al. (1993, 1996a) and O'Neil et al. (1994). The $\delta^{18}O_{PO_4}$ values of the *H. schinzii* teeth of the Mainz Basin were converted into $\delta^{18}O_{water}$ values using the equation determined for modern sirenians by Tütken (2003):

$$\delta^{18}O_{water} = \frac{\delta^{18}O_{PO_4} - 20.23}{0.86}, \qquad (2)$$

where $\delta^{18}O_{water}$ and $\delta^{18}O_{PO_4}$ are given relative to VSMOW.

In order to assess the possibility of diagenetic alteration of the enamel oxygen isotope composition, the carbonate ($\delta^{18}O_{CO_3}$) and the phosphate ($\delta^{18}O_{PO_4}$) group of the enamel were plotted against each other and compared to a compilation of $\delta^{18}O_{CO_3}$ vs. $\delta^{18}O_{PO_4}$ pairs from extant mammals published by Pellegrini et al. (2011). The $\delta^{18}O_{CO_3}$ values were determined in the remaining fraction of the pretreated *H. schinzii* enamel powders. About 800 µg of each enamel powder sample were analyzed with a Thermo Finnigan MAT 253 gas source isotope ratio mass spectrometer in continuous flow mode equipped with a GasBench II at the University of Mainz. The $\delta^{18}O_{CO_3}$ values were measured against VPDB and normalized to a NBS-18 and NBS-19 calibrated Laaser marble (−5.21 ‰; replicated precision, 1σ, better than 0.1 ‰). Afterward, the results were converted to the SMOW scale using the equation of (Coplen et al., 1983):

$$\delta^{18}O_{SMOW} = 1.03091 \cdot \delta^{18}O_{PDB} + 30.91. \qquad (3)$$

3.4 Mathematical resampling of intra-annual isotope data

In bivalves, shell growth rate declines during ontogeny resulting in increasingly narrow annual growth increments with increasing lifespan (Jones and Quitmyer, 1996). Since the isotope samples were taken at approximately equidistant intervals (100 to 200 µm), the number of samples per year decreases through lifetime and the time represented by each carbonate sample (= time-averaging) increases in ontogenetically older shell portions. To compensate for that bias and make the isotope samples from different ontogenetic years comparable to each other, the number of $\delta^{18}O_{shell}$ values per year was mathematically equalized by a re-sampling technique similar to that described in Schöne et al. (2004) and Hallmann et al. (2011). Following previous work (e.g. Schöne and Fiebig, 2008; Wanamaker et al., 2011), we fitted the isotope data of each annual increment with a 7-point cubic spline using the software Analyseries 1.1 (Paillard et al., 1996) and re-sampled each intra-annual curve so that the same number of isotope values were available for each annual increment, i.e., seven $\delta^{18}O_{shell}{}'$ values. Noteworthy, this re-sampling method slightly deviated from previous approaches (Schöne et al., 2004; Hallmann et al., 2011), because it was impossible to determine seasonal growth curves from microgrowth patterns. Hence, the $\delta^{18}O_{shell}{}'$ values within a given year most likely represented different amounts of time, but the first, second, third etc. $\delta^{18}O_{shell}{}'$ values of different years represented same amounts of time.

4 Results

4.1 Preservation of material

According to a set of different diagenesis screening tests outlined above, the studied shells of *Glycymeris planicostalis* from the Rupelian of the Mainz Basin consist of aragonite and were remarkably well preserved. This even applies to the chalky rims of the shells, i.e., the shell portions that were only pale blue stained by Mutvei's solution and lost almost all organics during taphonomy. Orange cathodoluminescence was only emitted from very few isolated spots, i.e., cracks containing neomorphic mineral phases. Most other portions of the shells were dark blue to non-luminescent. Moreover, both reflected light microscope and electron microscope analyses revealed the same shell microstructures that occur in modern representatives of this genus, i.e., crossed-lamellar structures (Fig. 2a–c). Alternately, the 1st order lamellae appear dark and bright because the higher order-lamellae are arranged in a fence-like manner and stand perpendicular to each other (compare Füllenbach et al., 2014). Furthermore, both shell layers are perforated by numerous hollow microtubuli (Fig. 2d), especially in the juvenile portion of the shells. On rare occasions, these tubuli (ca. 10 µm in diameter) are filled with pyrite crystals or iron oxides.

Like the bivalves, the studied sirenian teeth are pristinely preserved (Fig. 3). The $\delta^{18}O_{CO_3}$ vs. $\delta^{18}O_{PO_4}$ pairs of the seven specimens plot well within the 95 % prediction intervals of modern and other well-preserved fossil mammal enamel data compiled by Pellegrini et al. (2011) (Table 1; Fig. 3). Diagenetically altered tooth enamel would in the first place have affected the carbonate-bound oxygen (Iacumin et al., 1996) and resulted in $\delta^{18}O_{CO_3}$ vs. $\delta^{18}O_{PO_4}$ pairs plotting farther away from the regression line depicted in Pellegrini et al. (2011). Given the excellent preservation, $\delta^{18}O_{water}$ values were computed from $\delta^{18}O_{PO_4}$ values of the enamel using Eq. (2). On average, the $\delta^{18}O_{water}$ value of the water was -0.9 ± 0.3 ‰ (1σ).

4.2 Bivalve sclerochronology: $\delta^{18}O_{shell}$ and reconstructed water temperatures

The studied fossil *G. planicostalis* specimens show distinct growth lines in the ventral margin and the hinge plate of Mutvei-stained cross-sections (Fig. 2). These lines were previously identified as periodic annual features (Berthou et al., 1986; Royer et al., 2013; Bušelić et al., 2014) separating the growth pattern in annual time slices, i.e., annual growth increments. The annual growth lines are more distinctly developed and hence easier to discern in the hinge plate than in the ventral margin. Based on annual increment counts, it was possible to determine the ontogenetic ages of the specimens. Specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7 reached life spans of 77, 84 and 67 years, respectively.

Oxygen isotope curves of all three specimens exhibits distinct seasonal oscillations (16, 14 and 10 cycles in specimens MB-Wht-2, -4, and -7, respectively) with the annual growth lines occurring shortly after the most negative $\delta^{18}\mathrm{O}_{\mathrm{shell}}$ values of each cycle (Fig. 4; see the Supplement). In other words, the full seasonal amplitudes are preserved in the shells including winter and summer values. The annual growth line formation occurred in later summer/early fall.

The shells grew faster during the first half of the year than after summer. This is well reflected in the seasonal temperature curve based on the averaged $\delta^{18}\mathrm{O}'_{\mathrm{shell}}$ values of all 40 measured annual increments (Fig. 5). There are more data points in shell portions formed during spring than in shell portions formed during fall (Fig. 5). Accordingly, the reconstructed temperature curve is right-skewed.

The average annual $\delta^{18}\mathrm{O}_{\mathrm{shell}}$ values and seasonal $\delta^{18}\mathrm{O}_{\mathrm{shell}}$ ranges are fairly similar among the three studied specimens (Table 2). Seasonal extremes fluctuate between −1.48 ‰ (summer value) and 0.75 ‰ (winter value) in specimen MB-Wht-2, between −1.16 and 0.67 ‰ in specimen MB-Wht-4, and between −1.19 and 0.60 ‰ in specimen MB-Wht-7. Using the reconstructed $\delta^{18}\mathrm{O}_{\mathrm{water}}$ value, this translates into total temperature ($T_{\delta^{18}\mathrm{O}}$) ranges of 9.7, 7.6, and 7.8 °C in specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7, respectively. Taking the average value of the 40 seasonal cycles of all three specimens, the average annual temperature is 15.4 ± 0.7 °C (1σ), and the seasonal temperature range equals 3.7 °C with average minimum (winter) values of 13.6 ± 0.8 °C (1σ) and average maximum (maximum) values of 17.3 ± 1.2 °C (1σ).

Noteworthy, the seasonal amplitudes vary through time. In some years, the seasonal $T_{\delta^{18}\mathrm{O}}$ range was less than 2 °C (Fig. 6). Although the isotope time-series are too short to reliably identify lower-frequency oscillations, the seasonal ranges seem to vary on a quasi-decadal time-scale.

5 Discussion

As demonstrated by this study, shells of *Glycymeris planicostalis* provide an excellent archive to reconstruct climate dynamics – in particular changes of sea surface temperature – during the Oligocene on subseasonal to inter-annual time-scales. Shells of the studied species grew during both the coldest and warmest periods of the year and therefore contain information on the full seasonal temperature amplitude that prevailed in the Mainz Basin 30 Ma ago. Like modern *Glycymeris glycymeris* (e.g. Ramsay et al., 2000), the Oligocene representatives of this genus lived for several decades which make them excellent recorders of decadal-scale climate variability. Furthermore, the shells are pristinely preserved and their $\delta^{18}O_{shell}$ values reflect changes of ambient water temperature.

5.1 Preservation

The excellent preservation of the studied *G. planicostalis* shells is remarkable. Not only consisted the shells of aragonite, SEM analysis also revealed original delicate microstructures including the typical skeletal feature of glycymerids, i.e., microtubules. These cylindrical cavities perforate the inner and outer shell layers and are filled with organics during the lifetime of the animal (e.g. Waller, 1980; Crippa, 2013). The diagenetic loss of organic material leaves behind hollow cavities that potentially can be filled with neomorphic mineral phases. However, the microtubules of the studied specimens were typically hollow and only rarely contained pyrite. Noteworthy, pyrite crystals can even occur in shells of living bivalves and are possibly related to the bacterial degradation of organic matter (Clark and Lutz, 1980).

In fact, the recovery of pristinely preserved fossil glycymerids has been reported from many other localities and geological time intervals (e.g. Tsuboi and Hirata, 1935; Dorman and Gill, 1959; Crippa, 2013). Since *Glycymeris* spp. dwells in sandy to fine gravelly habitats, shells of this genus are usually embedded in coarse grained and highly porous sediments. In such type of host rock and stratigraphic age, one would not expect aragonitic shell preservation, particularly if the burial depth is shallow (few tens of meters) and the sediment is still unconsolidated such as weakly cemented sandstones of the Alzey Formation. Under surface conditions, aragonite is metastable and slowly turns into the more stable polymorph of $CaCO_3$, i.e., calcite (Boettcher and

Wyllie, 1967). This conversion into calcite can be expedited when a fluid is present (Putnis and Putnis, 2007) and when temperature is increased (Dasgupta, 1963). The resistance of glycymerid shells against diagenetic alteration likely resulted from low organic content and the dense crossed-lamellar microstructure (Taylor and Layman, 1972).

5.2 Timing and rate of shell growth

Pristine preservation is a major prerequisite for the reconstruction of environmental variables from geochemical properties of the shells including ambient water temperature from $\delta^{18}O_{shell}$ values. According to shell oxygen isotope data the studied shells grew during winter and summer and recorded the full seasonal amplitude of environmental variables. Such data are crucial for paleoclimate studies. Similar findings on shell growth during seasonal extremes were recently reported by for modern *Glycymeris bimaculata* from Croatia (Bušelić et al., 2014). The only difference is that the Oligocene shells formed annual growth lines in late summer/early fall, whereas the period of extremely slow or no shell growth in specimens from Croatia occurs during spring. Noteworthy, modern *G. glycymeris* from the North Atlantic form annual growth breaks in winter (Berthou et al., 1986; Royer et al., 2013). These findings suggest that the timing and rate of shell growth can vary greatly among different species of the same genus and most likely even among specimens of the same species alive at different localities. It is therefore required to conduct thorough calibration studies prior to using shells for environmental reconstructions.

Shell growth rates of the studied bivalves from the Early Oligocene of the Mainz Basin also varied during the main growing season. For example, shell production was faster during spring and summer than during winter. This finding has implications for geochemical sampling strategies. In order to obtain reliable information on the actual seasonal temperature spread, a higher sampling resolution has to be applied in slow-growing shell portions.

5.3 Temperatures of the Mainz Basin during the Rupelian

Only few temperature estimates of the Mainz Basin and adjacent regions during the Rupelian are currently available. For example, sediments of the Alzey Formation contain a diverse warm-water fauna including marine fish, mammals and crocodiles as well as terrestrial turtles. Based on this fossil assemblage, subtropical climate conditions – similar to the modern southeastern Mediterranean – were inferred for the Mainz Basin (Grimm et al., 2003, 2011). Furthermore, macroflora and palynological data from the Bodenheim Formation yielded winter and summer air temperatures of 7.1–10.2 °C and 25.7–28.1 °C, respectively (Pross et al., 1998, 2000). These estimates compare well with that at other contemporaneous localities in Central Europe (Mosbrugger et al., 2005; Erdei et al., 2012).

Knowledge on water temperatures of the Mainz Basin comes from oxygen isotope values of biogenic skeletons. Tütken (2003) reported the δ^{18}O values of shark teeth apatite that correspond to absolute temperatures between 6.9 and 23.3 °C (temperatures recalculated assuming a $\delta^{18}O_{water}$ value of −0.9 ‰; Table 3), using the thermometry equation of Longinelli and Nuti (1973). Grimm (1994) reported oxygen isotope data of planktonic and benthic foraminifera which can be converted into absolute temperatures using the paleothermometry equation by Anderson and Arthur (1983) and a $\delta^{18}O_{water}$ value of −0.9 ‰. Based on this calculation, sea surface temperatures of the Mainz Basin fluctuated between 11.7 and 21.3 °C (Table 4), whereas bottom water (up to 150 m depth; Grimm et al., 2011) temperatures were as cold as 5.9 to 14.9 °C during the Rupelian. Similar surface water temperatures were reconstructed from bivalve shells in the present study (12.3 and 22.0 °C), albeit the lowest temperatures were ∼ 5 °C higher than those obtained from the shark teeth (Fig. 7). Leaving aside the fact that it is rather unlikely that the studied bivalves, sharks and foraminifera lived during the exact same time interval, a direct comparison of temperature extremes derived from the different marine archives seems problematic for a variety of reasons:

(i) The temporal resolution provided by foraminifera is much higher than that of bivalves. Foraminiferan tests can grow within a few weeks (Bé et al., 1981). Thus, each specimen recorded environmental conditions during a very short time interval of the year. However, each sample taken from the bivalve shells represents, on average, about one month worth of growth. With a higher sampling resolution it would likely be possible to better capture the actual seasonal temperature extremes. This applies particularly to winter temperatures, because the shells grew slower during the cold season of the year than during summer (Fig. 5). Notably, the precise timing of the year when the foraminifera formed their skeletons remains unknown. Samples analyzed so far may not necessarily have grown when the most extreme seasonal temperatures occurred. Accordingly, actual winter temperatures may have been even colder and summers warmer than suggested by the foraminifera δ^{18}O values.

(ii) Seasonal temperature extremes given by sharks may not represent the actual temperatures where the bivalves lived. Sharks are highly mobile, nektonic organisms. Temporarily, they may have scavenged in the shallowest waters near the coast and at other times dived to the very bottom of the sea. In addition to vertical movements, they may have travelled large distances such as modern sharks (e.g. Domeier and Nasby-Lucas, 2008). Lowest temperatures recorded by sharks may thus represent conditions below the thermocline or settings much further north instead of winter temperatures in the Mainz Basin. In turn, those portions of the teeth that provided temperature estimates of 22 °C may actually have been formed while the animal lived in warmer waters much farther south or very near the coast.

(iii) Actual sea surface temperatures during winter and summer may have been underestimated by the planktonic foraminifera (and sharks while they resided in shallowest, coastal waters), because the assumed average $\delta^{18}\text{O}_{\text{water}}$ value did not reflect the actual isotope signature of the water. Planktonic foraminifera lived in the upper few meters of the water column in a narrow, shallow epicontinental sea. In such a habitat, seasonally varying riverine freshwater influx, precipitation and evaporation rates likely resulted in seasonal changes of the $\delta^{18}\text{O}_{\text{water}}$ value. Increased evaporation during summer may have shifted the $\delta^{18}O_{\text{water}}$ value toward more positive values resulting in lower than actual reconstructed water temperatures near sea surface. In contrast, higher precipitation rates during winter may have shifted the $\delta^{18}O_{\text{water}}$ value toward more negative values so that the oxygen isotope-derived temperatures appeared colder than they actually were. Implications for a seasonally varying $\delta^{18}O_{\text{water}}$ value come from sirenian teeth. Like their extant relatives, sea cows lived the upper ten meters of the ocean and near the coast (Louise Chilvers et al., 2004) and have thus recorded the isotope signature of the water in which the foraminifera lived. Reconstructed $\delta^{18}O_{\text{water}}$ values fluctuated between −0.2 and −1.4 ‰. If the latter value reflected conditions during winter and the former during summer, actual seasonal temperatures in the upper few meters of the Mainz Basin reconstructed from foraminifera ranged between ca. 11 and 27 °C.

(iv) Bivalve shell-based temperature estimates cannot be directly compared to those of planktonic foraminifera even if the fluctuating $\delta^{18}O_{\text{water}}$ values in the upper few meters of the ocean were precisely known. In ca. 30–40 m water depth, bivalves likely experienced a smaller seasonal temperature range than organisms in the upper few meters of the sea.

The robustness of temperature estimates derived from *G. planicostalis* shells is further supported by data on thermal regimes of the water column in modern semi-enclosed seas. According to hydrographical studies of the coastal regions in the northwestern Mediterranean (France) and southeastern Mediterranean (Lebanon), the water in 30–40 m water depth is still strongly influenced by surface conditions (Abboud-Abi Saab et al., 2004). At 35 m water depth the water temperatures in Lebanon ranged between 16.9 and 29.1 °C with an annual average of 22.5 ± 4.1 °C (1σ), whereas the coastal waters in France ranged between 21.8 and 12.3 °C with an annual average of 15.2 ± 2.2 °C (1σ). Temperatures recorded by *G. planicostalis* lay well in these thermal regimes suggesting paleoclimate conditions were more similar to regions in the northwestern Mediterranean than subtropical. However, the mean annual precipitation in the area of Marseille equals 751 ± 172 mm (Harris et al., 2014), which is considerably lower than 1000–1250 mm a^{-1} reconstructed precipitation rates in the Mainz Basin (Pross et al., 1998, 2000). A possible explanation for the high precipitation rates in Central Europe during the Oligocene has been provided by Pross and Schmiedl (2002). The deposition of the Alzey formation and its basinal counterparts, the Bodenheim formation, took place during sea-level highstands, which could have increased the moisture concentration in the atmosphere, and so, intensified rainfalls. Such linkage between sea level rise and precipitation has recently been postulated for the Early Holocene intensification of the Australian–Indonesian monsoon rainfall (Griffiths et al., 2009).

5.4 Advantages of using shells of *Glycymeris planicostalis* for reconstruction of the climate conditions during the Rupelian

The studied specimens of *G. planicostalis* offer a number of advantages over existing marine paleoclimate archives. As sessile organisms, bivalves faithfully recorded the water properties at a specific locality and depth throughout their lifetimes. Since their shells grew almost year-round, each isotope sample can be assigned to a particular season. If preservation permits, daily microgrowth increments can be employed to temporally contextualize the seasonal shell growth to the nearest week or so (e.g. Schöne et al., 2005b) Such an internal calendar is missing in foraminifera.

The studied *G. planicostalis* specimens lived for several decades and recorded seasonal temperature changes over the course of many consecutive years. This is a clear advantage over other climate archives that only provide very short temporal snapshots of unknown timing within the year such as foraminifera or shark teeth, or few consecutive years, such as fish otoliths. Otoliths are calcareous ossicles (usually aragonite) that grow in the inner ear of fish. Analogously to bivalve shells, they form growth lines, and their oxygen isotope composition can be used for seasonal paleotemperature reconstructions, for example, at the Eocene/Oligocene boundary (Ivany et al., 2000). Although fish otoliths are very common components of marine nektonic microfossil assemblages, their reduced size makes them difficult to sample, and analyses of their chemical composition usually cover only short time intervals.

Long proxy records offer the possibility to track decadal-scale variability of winter and summer temperatures. Although the $\delta^{18}O_{shell}$ chronologies of *G. planicostalis* are too short to conduct statistically reliable time-series analyses, the seasonal extremes, specifically winter temperatures, seem to have changed periodically through time. Such decadal climate dynamics are well known from modern settings in the Northeast Atlantic sector (Hurrell and Van Loon, 1997) and can be attributed, for example, to the North Atlantic Oscillation (Hurrell and Deser, 2009). Future studies should conduct isotope measurements of longer-lived specimens of *G. planicostalis* and generate time-series that are long enough to permit spectral analyses. Furthermore, these data should then be combined with numerical climate models for that time.

The $\delta^{18}O_{water}$ signature at 30–40 m water depth was most probably much less variable than near the sea surface. Seasonal changes in freshwater influx into the Mainz Basin likely did not have any effect on the isotope signature of the water in which the bivalves lived. In fact, modern *G. glycymeris* from the North Atlantic is most prolific in water with stable salinity of 34–35 PSU (Rombouts et al., 2012). If the same preference is true for the Oligocene relatives of this genus, water temperatures can be reconstructed with smaller error bars from oxygen isotope values of the bivalve shells than from skeletal hard parts of nektonic and planktonic organisms. Evidently, absolute temperature estimates from $\delta^{18}O$ values require knowledge of the oxygen isotope signature of the ambient water, which is rarely available for fossil environments. In the present study, the $\delta^{18}O_{water}$ value was reconstructed from the tooth enamel of sea cows from the same stratigraphic level. Although the bivalves and the sea cows did most certainly not live during the exact same time and the sphere of action of the sea cows was the upper ten meters of the ocean, the average $\delta^{18}O_{PO_4}$ value of the sirenian teeth serves as a reasonable estimate of the $\delta^{18}O_{water}$ signature (−0.9 ‰) of the Mainz Basin during the Rupelian. A similar value (−1 ‰) was also assumed by Grimm (1994). To test the temperature estimates obtained from $\delta^{18}O_{shell}$ values and circumvent uncertainties related to the precise $\delta^{18}O_{water}$ signature during shell formation, future studies should explore other potential temperature proxies such as Sr/Ca and Δ_{47} values.

6 Summary and conclusions

Shells of *Glycymeris planicostalis* provide faithful recorders of sea surface temperatures in the Mainz Basin during the Rupelian. Since the shells were preserved as pristine aragonite, the $\delta^{18}O_{shell}$ values can be used to reconstruct ambient water temperature. Although the exact oxygen isotope signature of the water is not known, it is highly likely to assume that the $\delta^{18}O_{water}$ value in 30–40 m water depth remained largely invariant through time. Attributed to its notable longevity, shells of this species can be used to study seasonal temperature changes over several consecutive years. As shown in the present study, summer and winter temperatures varied greatly on inter-annual time-scales. Unless many samples are analyzed, this variability is hardly seen in foraminiferan tests. Our data also revealed decadal-scale oscillations of seasonal extremes which have – in the absence of appropriate climate archives – never been identified before for the Oligocene. This information can be highly relevant for numerical climate studies aiming to predict possible future climates in a unipolar glaciated or polar ice-free world.

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Table 1. Enamel δ^{18} values (VSMOW) of the sea cows teeth from the Alzey Formation deposits of the Mainz Basin and $\delta^{18}O_{water}$ values calculated from the sea cow enamel $\delta^{18}O_{PO_4}$ values. See text for details..

Sample ID	$\delta^{18}O_{PO_4}$ [‰]	$\delta^{18}O_{CO_3}$ [‰]	$\delta^{18}O_{water}$ [‰]
Trai 01-1	19.36	25.79	−1.01
Trai 01-2	19.04	26.14	−1.38
Eck 01-1	19.29	26.40	−1.09
Wein 01-1	19.31	26.63	−1.07
Wein 01-2	19.36	26.64	−1.01
PW 2008/2-1	19.32	26.31	−1.06
PW 2008/2-2	19.55	26.74	−0.79
PW 2008-1B	20.03	27.05	−0.23
STS-BE 62-1	19.07	25.98	−1.35
PW 2008-1A	19.35	26.40	−1.02
PW 2005/5042-LS-1	19.75	26.67	−0.56
Eck 01-2	19.74	26.40	−0.57
Average ±1σ	19.43 ±0.29	26.43 ±0.35	−0.9 ±0.1
Min	19.04	25.79	−1.38
Max	20.03	27.05	−0.23

Table 2. Stable oxygen isotope values (VPDB) of the three *Glycymeris planicostalis* shells analyzed in this study. The table lists seasonal extremes ($\delta^{18}O_{min}$ and $\delta^{18}O_{max}$) as well as average summer ($\delta^{18}O'_{summer}$; re-sampled values; explanation see text) and winter extremes values ($\delta^{18}O'_{winter}$).

Sample ID	$\delta^{18}O_{min}$ [‰]	$\delta^{18}O'_{summer} \pm 1\sigma$ [‰]	$\delta^{18}O_{max}$ [‰]	$\delta^{18}O'_{winter} \pm 1\sigma$ [‰]	$\delta^{18}O_{mean} \pm 1\sigma$ [‰]
MB-Wht-2	−1.48	−0.66 ±0.21	0.75	0.38 ±0.23	−0.12 ±0.13
MB-Wht-4	−1.16	−0.40 ±0.31	0.67	0.28 ±0.14	−0.03 ±0.13
MB-Wht-7	−1.19	−0.61 ±0.23	0.60	0.24 ±0.19	−0.20 ±0.16

Table 3. Dentine and enamel $\delta^{18}O_{PO_4}$ values (VSMOW) of shark teeth recovered from the Lower Oligocene deposits of the Mainz Basin (Tütken, 2003). Values have been converted to temperature ($T\delta^{18}O_{PO_4}$) using the paleothermometry equation by Longinelli and Nuti (1973) assuming $\delta^{18}O_{water} = -0.9$‰.

Sample ID	Genus	$\delta^{18}O_{PO_4}$ [‰]	$T\delta^{18}O_{PO_4}$ [°C]
FD HAI MB 2	*Carcharias* sp.	22.9	9.1
FZ HAI MB 2	*Carcharias* sp.	22.8	9.5
FZ HAI MB 3	*Carcharias* sp.	19.6	23.3
FD HAI MB 4	*Carcharias* sp.	21.0	17.2
FZ HAI MB 4	*Carcharias* sp.	21.5	15.1
FZ HAI MB 8	*Carcharias* sp.	20.1	21.1
FZ HAI MB 9	*Carcharias* sp.	21.0	17.2
FZ HAI MB 10	*Carcharias* sp.	23.4	6.9
Average ± 1σ		21.5 ± 1.3	14.9 ± 5.9
Min		19.6	6.9
Max		23.4	23.3

Table 4. Stable oxygen isotope values (VPDB) of foraminiferan tests from the Bodenheim Formation (wells Kriegsfeld 5 and Bodenheim 65) reported by Grimm (1994). $\delta^{18}O_{Glob}$ = *Globigerina* sp. (planktonic foraminifera); $\delta^{18}O_{Bol}$ = *Bolivina* sp. (benthonic foraminifera). Values have been converted to temperature ($T\delta^{18}O_{Glob}$, $T\delta^{18}O_{Bol}$) using the equation by Anderson and Arthur (1983) assuming $\delta^{18}O_w = -0.9$‰.

Kriegsfeld 5 Depth [m]	$\delta^{18}O_{Glob}$ [‰]	$T\delta^{18}O_{Glob}$ [°C]	Bodenheim 65 Depth [m]	$\delta^{18}O_{Bol}$ [‰]	$T\delta^{18}O_{Bol}$ [°C]
15	−1.8	18.7	21.5	1.5	5.9
23	−2.4	21.3	70	−0.9	14.9
25	−0.1	11.7	80	1.0	7.6
28	−1.3	16.5	85	1.1	7.3
30	−2.0	19.5	90	0.7	8.7
32	−0.7	14.1	95	−0.03	11.4
34	−0.8	14.5	99	0.7	8.7
Average ±1σ	2.75 ±0.81	16.6 ±3.4	Average	0.6 ±0.8	9.5 ±2.9
Min	−2.4	11.7	Min	−0.9	5.9
Max	−0.1	21.3	Max	1.5	14.9

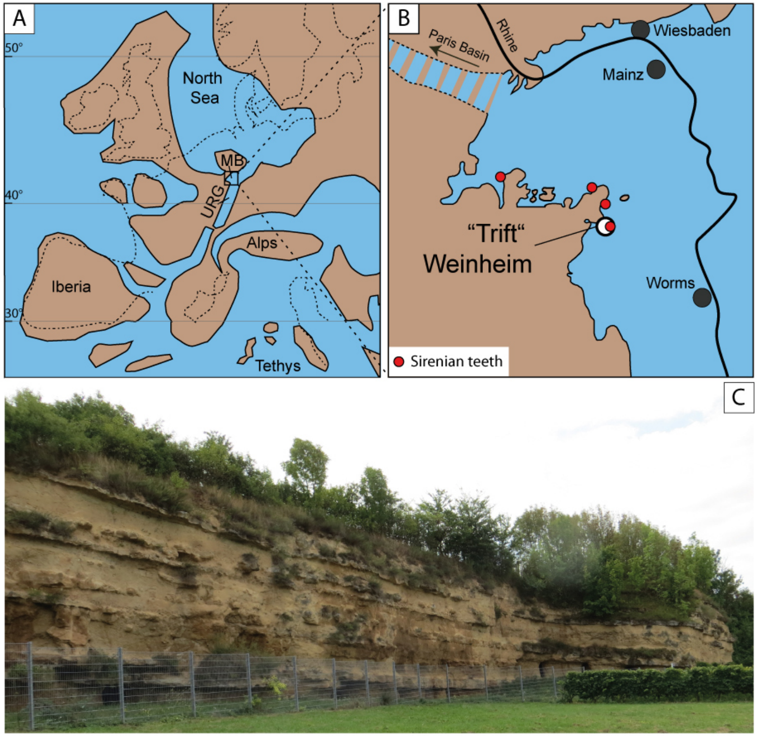

Figure 1. Map showing the paleogeography during the Rupelian and the sample locality in the Mainz Basin. **(a)** Position of the Mainz Basin (MB) in Central Europe. URG = Upper Rhine Graben. Emerged land areas are shown in brown and marine environments in blue. Modified from Spiegel et al. (2006). **(b)** Sample locality of the shells (outcrop "Trift" near Weinheim; open circle) and sea cow teeth (red dots). The presence of a western gateway (dashed area) connecting the Mainz Basin to the Paris Basin is unclear. Modified after Grimm et al. (2011). **(c)** Photograph of the outcrop "Trift" near Weinheim.

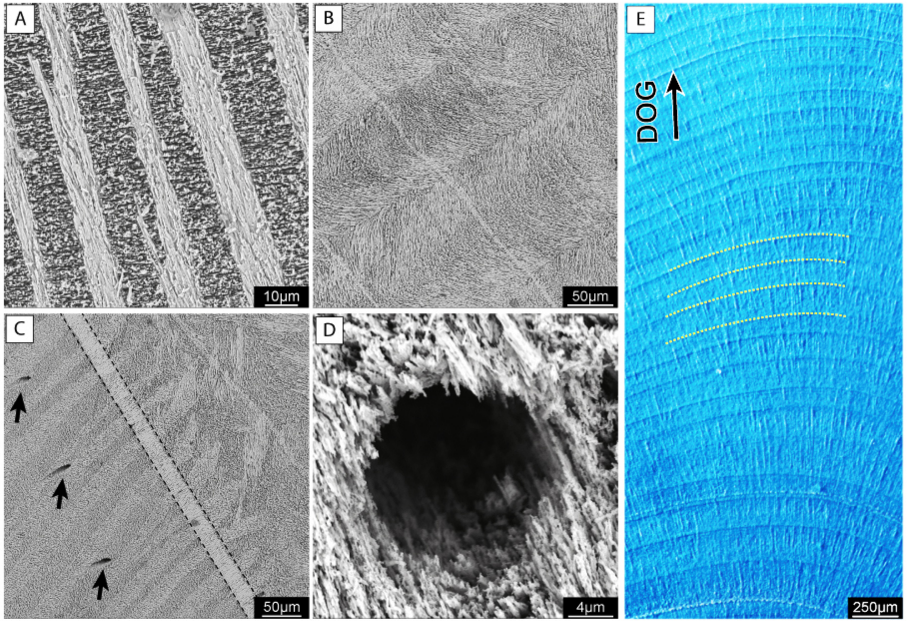

Figure 2. SEM images showing the extraordinary preservation state of the *Glycymeris planicostalis* shells from the Early Oligocene of the Mainz Basin. Primary microstructures are still present. **(a)** Outer crossed-lamellar layer, **(b)** inner complex crossed-lamellar layer and **(c)** transition zone between outer and inner shell layer (dotted lines). Arrows point to tubule openings. **(d)** Detailed view of a tubule. The lack of diagenetic fillings inside the cavity further supports the absence of any significant diagenetic overprint. **(e)** Distinct growth lines (yellow dotted lines) are visible in the hinge plate of Mutvei-stained cross-sections. DOG = direction of growth.

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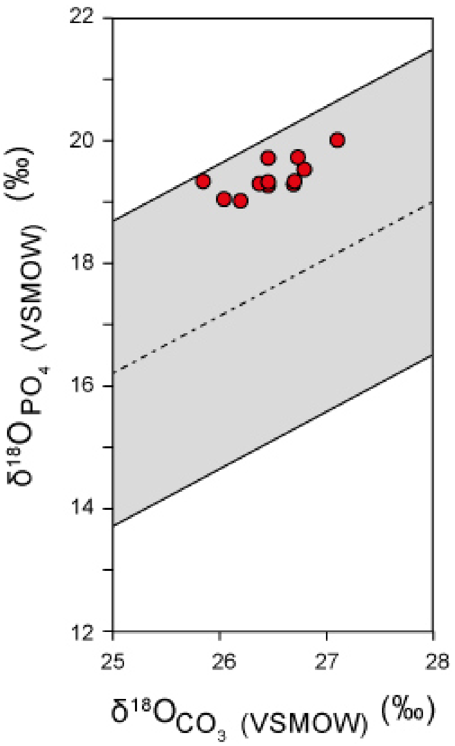

Figure 3. Cross-plot of mammal tooth enamel $\delta^{18}O_{PO_4}$ and $\delta^{18}O_{CO_3}$ pairs (dashed line = average; grey area = 95 % prediction intervals) compiled by Pellegrini et al. (2011) with respective data from the seven Oligocene sirenian teeth of the present study (red filled circles). Sea cow isotope data plot within the 95 % prediction intervals suggesting that diagenesis has not affected the isotope signature of the phosphate group.

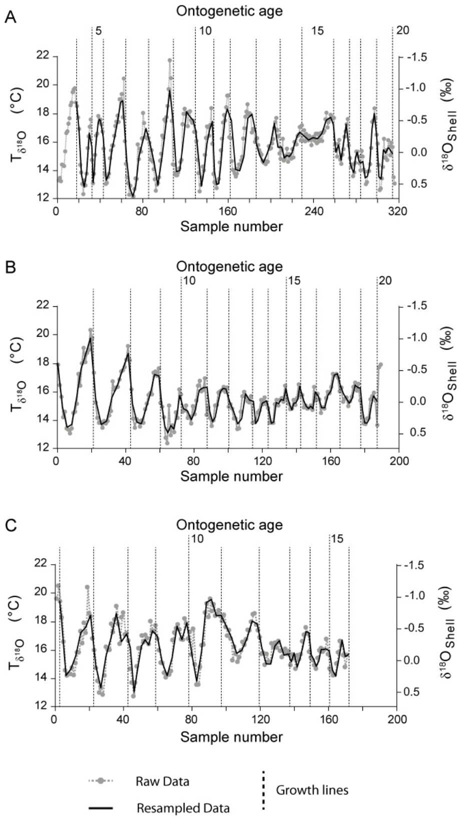

Figure 4. Raw (grey) and re-sampled (black) $\delta^{18}O_{shell}$ values for each of the three *Glycymeris planicostalis* shells used in this study (**a** = MB-Wht-2; **b** = MB-Wht-4; **c** = MB-Wht-7). Vertical dotted bars represent annual growth lines. Temperatures were calculated using Eq. (2) with a $\delta^{18}O_{water}$ value reconstructed from $\delta^{18}O_{PO_4}$ of sea cow tooth enamel (see text for description).

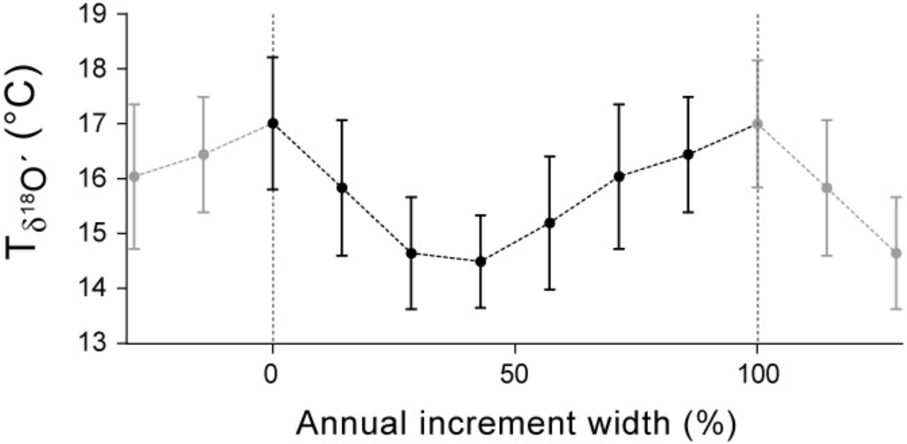

Figure 5. Average seasonal temperature changes (black dots, $\pm 1\sigma$) based on mathematically re-sampled shell oxygen isotope values ($\delta^{18}O'_{\text{shell}}$ values; see text for explanation) of 40 annual increments measured in three specimens of *Glycymeris planicostalis*. Note that the resultant temperature curve is not symmetric as one would expect, but right-skewed indicating slower shell growth occurred during fall and winter than during the remainder of the year. In other words, more shell material has been deposited during spring and summer than during fall and winter.

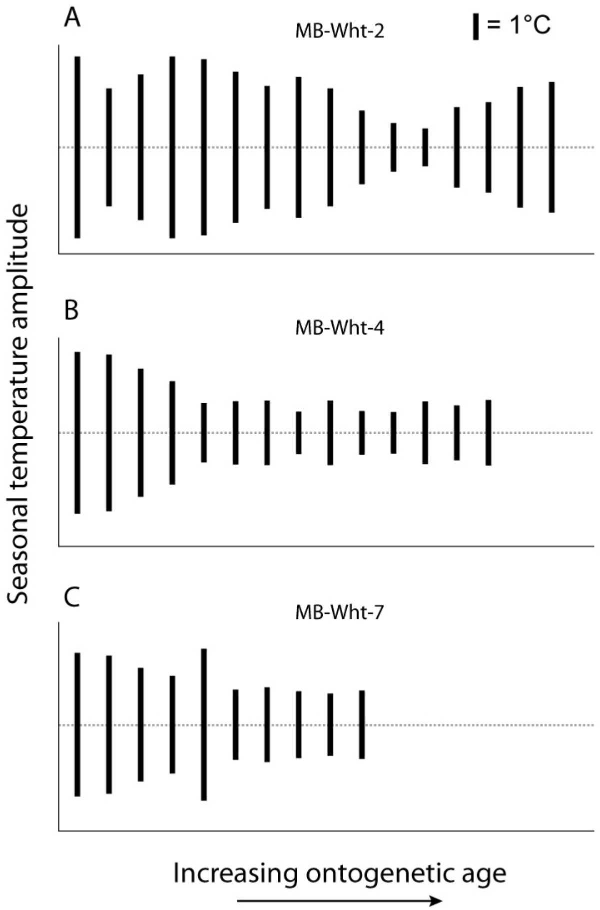

Figure 6. Seasonal shell oxygen isotope-derived temperature amplitudes (black bars) of *Glycymeris planicostalis* (**a** = MB-Wht-2; **b** = MB-Wht-4; **c** = MB-Wht-7) vary on quasi-decadal time-scales.

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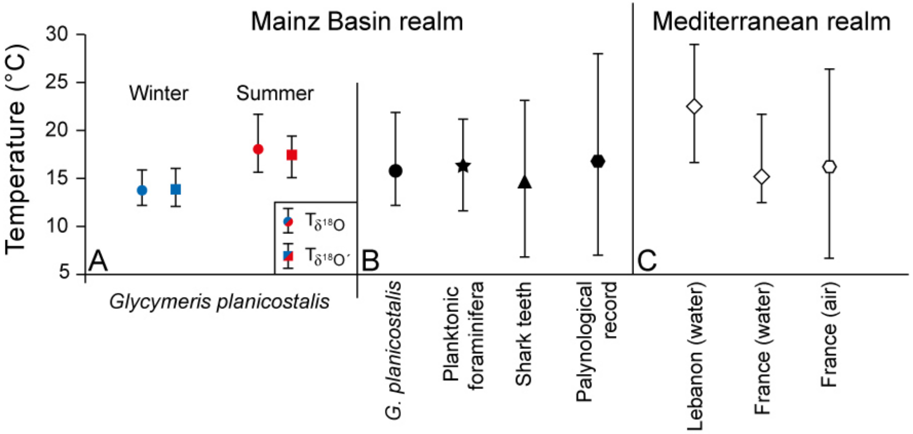

Figure 7. Seasonal temperature ranges. **(a)** Comparison between raw (circles) and mathematically re-sampled (squares) summer (red) and winter (blue) temperature data based on shell oxygen isotope data of three fossil *Glycymeris planicostalis* shells. Whereas mathematical re-sampling did not greatly affect average values and winter ranges, the summer temperature range of re-sampled data is truncated. **(b)** Comparison of the reconstructed temperature data based on $\delta^{18}O_{shell}$ values of the three studied bivalve shells (filled black circle) and previously published temperature data based on planktonic foraminifera (Grimm, 1994), shark teeth (Tütken, 2003), palynological associations (Pross et al., 1998, 2000). **(c)** Seawater temperatures in Lebanon and southern France at 35 m depth (Abboud-Abi Saab et al., 2004) and air temperatures in southern France (GHCN Montly Dataset; Lawrimore et al., 2011).