



Turritelline mass accumulations from the Lower Miocene of southern Germany: implications for tidal currents and nutrient transport within the North Alpine Foreland Basin

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The mass occurrence of turritelline gastropod shells from the Lower Miocene of southern Germany allows for detailed studies of their palaeoecology, transport mechanisms, preservation potentials and the reconstruction of nutrient regimes. Changes in the fabric of the gastropod-dominated beds are used to reconstruct a generally deepening environment corresponding to the Lower Miocene transgression within the Upper Molasse Sea of the North Alpine Foreland Basin. The sedimentary succession ranges from chaotically arranged, densely packed and near-shore transported; wave-influenced deposits showing bimodal shell orientations; more widely dispersed shells showing a uni-directional orientation; and dispersed shells showing diverse orientations. The shells often show damage to the apex and aperture though it is not clear whether this is due to predation events, pagurisation or abrasion due to transport. An outstanding feature is the replacement of aragonite shells by calcite leading to internal vugs as well as modulating the outer shell surface morphology. The high density of turritelline gastropods indicates a nutrient-rich palaeoenvironment at the northern edge of the Molasse Sea. □ *Molasse, orientation data, palaeoecology, taphonomy, turritelline gastropods.*

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Mass accumulations of fossils are useful indicators of both local and regional environmental conditions during deposition. In this study, a classic locality, the Ermingen Turritellenplatte (Fig. 1), with mass accumulations of turritelline gastropod from the Miocene of the Upper Marine Molasse, is studied in detail. The purpose of this investigation is to show changes in sedimentation, orientation and other taphonomic features of the fossil assemblage from the base to the top of the accumulation; to use these data to interpret water movement and relative depth; and to draw possible inferences with respect to basin-wide water movement within the North Alpine Foreland Basin.

The North Alpine Foreland Basin

The locality is Early Miocene in age (Fig. 2) and lies within the North Alpine Foreland Basin (NAFB)

(Fig. 3), an asymmetric, peripheral foreland basin produced by alpine tectonics during the Palaeogene. It extends from the Rhone Valley in France across Switzerland, southern Germany and Austria to what is now the Vienna Basin (Fig. 3). The NAFB was formed in the Eocene by the Alpine orogeny with the underthrusting of the European Plate beneath the Adriatic-African Plate (Kuhlemann & Kempf 2001; Bieg 2005; Bieg *et al.* 2008). The NAFB has a complex history of sedimentation resulting from global eustatic sea-level changes, climate oscillations, isostatic reaction to the overthrusting Alpine chain to the south and variations in sediment input primarily from the emerging Alps, as well as sediment transport along its axis (see discussion in Pippèr & Reichenbacher 2017). These variations in sea level and sedimentation patterns led to two major transgressive–regressive cycles, and thus repetitious transitions between marine and non-marine conditions.

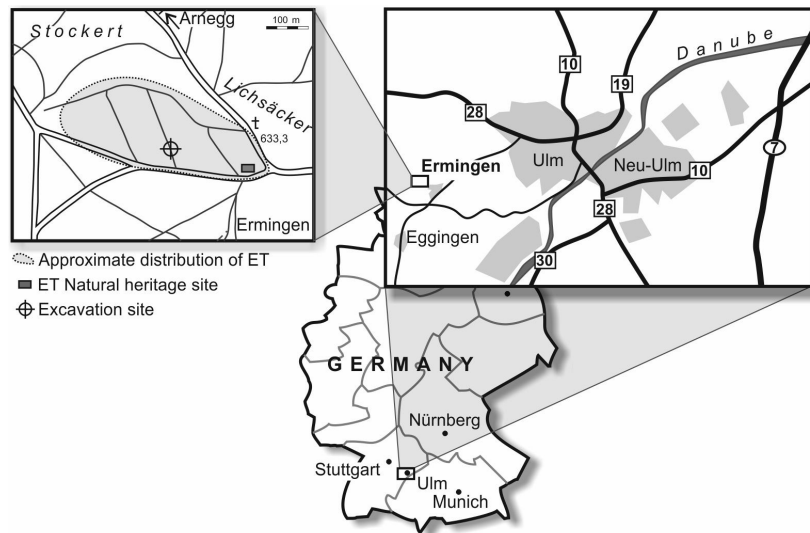


Fig. 1. Geographical location of the Ermingen Turritellenplatte in SW Germany.

In southern Germany, this led to the well-known succession of the Lower Marine Molasse, Lower Freshwater Molasse, Upper Marine Molasse and, following a brackish water phase, the Upper Freshwater Molasse which essentially continues to the present-day.

Sedimentological data and modelling have shown that the Upper Marine Molasse in southern Germany was a macrotidally influenced shallow marine basin

(Homewood & Allen 1981; Allen & Homewood 1984; Allen *et al.* 1985; Roetzel *et al.* 2006; Bieg *et al.* 2008; Frieling *et al.* 2011), connecting the Mediterranean to the more extensive, and in part deeper water basinal configuration towards the east in Austria. Marginal marine sediments are preserved on the northern rim of the basin. These can be highly fossiliferous, yielding microfossils, trace fossils, invertebrates and vertebrate faunas (Pippèr & Reichenbacher 2009; Schneider *et al.*

| MA | Epochs | Stages | Paratethyan Stratigraphy | NAFB |
|----|----------------|-------------|--------------------------|--------------------------|
| 15 | Middle Miocene | Langhian | Badenian | Upper Freshwater Molasse |
| | | | Karpatian | |
| 20 | Early Miocene | Burdigalian | Ottnangian | Upper Brackwater M. |
| | | | Eggenburgian | -- ETP -- |
| | | | | Upper Marine Molasse |
| 25 | Late Oligocene | Aquitanian | Egerian | Lower Freshwater Mollase |
| | | Chattian | | |

Fig. 2. Stratigraphical position of the Ermingen Turritellenplatte (ETP) within the Upper Marine Molasse of the North Alpine Foreland Basin (NAFB). M., Molasse. Stratigraphical boundaries following Schneider *et al.* (2011a, fig. 1).

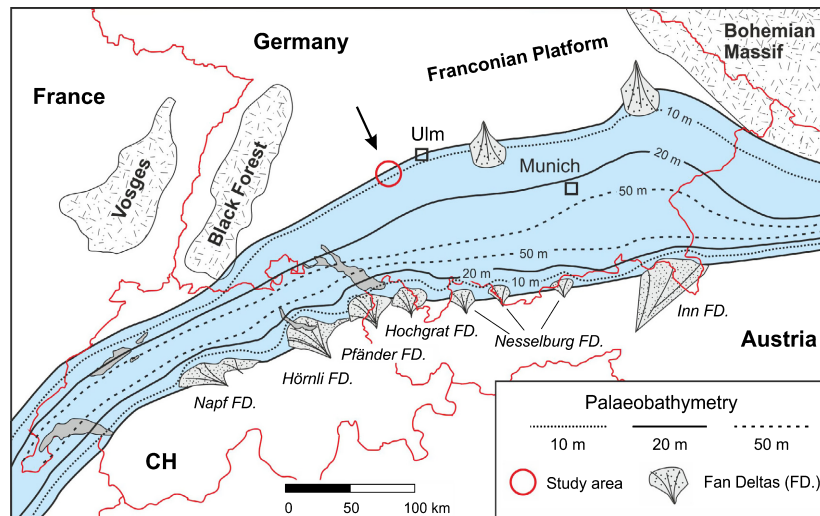


Fig. 3. Central part of the North Alpine Foreland Basin with palaeogeographical and bathymetric reconstruction of the Upper Marine Molasse during the Early Miocene (after Bieg *et al.* 2008, fig. 4).

2011b), primarily in siliciclastic settings. In some restricted areas, however, the high contributions of bioclastic material have led to the production of bryomol-type carbonates (Nebelsick 1989, 1992; Kaiser *et al.* 2001; Bieg *et al.* 2007). Tidal currents and amplitudes have been reconstructed within this basin using non-linear, three-dimensional hydrodynamic modelling (Bieg *et al.* 2008) indicating a complex system of convergent and divergent currents in the seaway within a high mesotidal ranges and current velocities reaching up to 8 ms^{-1} (Fig. 4).

Fossil orientation data

The orientation of components and their inclusion in directional statistical analysis have been shown to be useful for reconstructing transport mechanisms and palaeocurrent directions (Nagle 1967; Futterer 1978a,b; Wendt 1995 and literature therein). Orientation is influenced by numerous factors including the shape, density and ornamentation of the biogenic components, as well as coarseness and traction of the substrate over which the shells are transported. As shown by flume experiments and field observation, the movement of even simple shapes can be complex depending on current velocity, grain size characteristic and bed forms resulting in a variety of transport phenomena (Trussheim 1931; Menard & Boucot 1951; Ager 1963; Nagle 1967; Futterer 1978a,b). Various elongate and cone-shaped biotic components have been used as current indicators including crinoid stems (Schwarzacker 1963), belemnites (Futterer 1978a; Vörös 2011), bivalves and brachiopods (Nagle 1967), orthocerid cephalopods (Wendt 1995)

and others. Directional data for turrilline gastropods have also been measured and interpreted with ambient current directions (Allmon & Dockery 1992; Allmon & Knight 1993; Crawford *et al.* 2008; Anderson *et al.* 2017).

Mass occurrences of gastropods and palaeoecology of *Turritella*

Mass occurrences of gastropods are known from both marine and non-marine settings (Price *et al.* 1985; Cohen 1989; Geary & Allmon 1990; Waite *et al.* 2008; Waite & Strasser 2011) as well as turrilline gastropods as in this study. *Turritella* is a highly speciose taxon present on or in mobile substrates in fully marine, normal salinity conditions (see Allmon 2011). These gastropods represent semi-infaunal suspension feeders which use a modified operculum to acquire food (Yonge 1946; Waite & Allmon 2013) though some are deposit feeders. They can occur in very high numbers either buried in the substrate with the apertures exposed or lying on the sediment surface. Studies on recent (Allmon 1988; Allmon *et al.* 1992; Teusch *et al.* 2002; Waite & Allmon 2013) and fossil (Allmon *et al.* 1995; Allmon 2007; Crawford *et al.* 2008; Anderson *et al.* 2017) turrilline gastropods have stressed their importance as indicative of high nutrient conditions such as shallow water areas with coastal upwelling and increased phytoplankton, though there are exceptions (Allmon *et al.* 1994; Allmon 2011). They are also sensitive to disturbance and hypoxia conditions (Gallmetzer *et al.* 2017; Tomašových *et al.* 2018). In turrilline gastropod-dominated assemblages (Allmon 2007), local

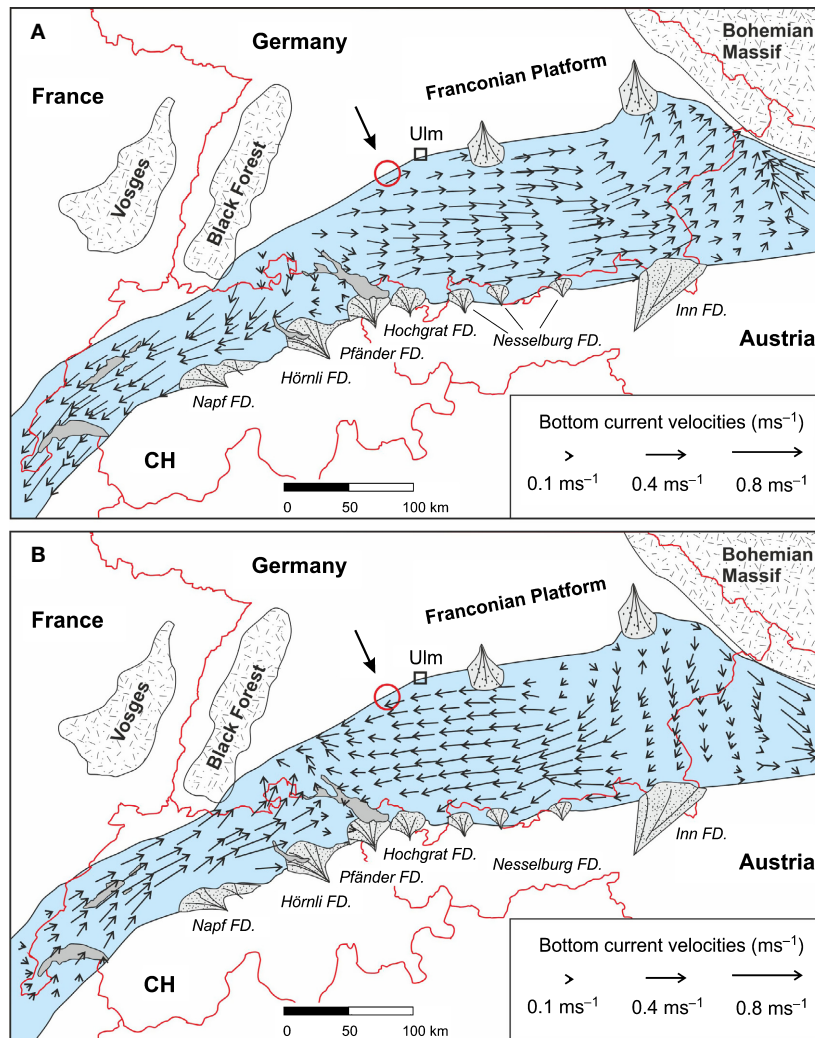


Fig. 4. Central part of the North Alpine Foreland Basin. A, simulated bottom velocities during incoming flood. B, simulated bottom velocities during incoming ebb. Key: FD = fan delta; red circle = study area (after Bieg *et al.* 2008, fig. 11).

concentrations can occur at such high densities as to exclude the presence of other benthic taxa. Predation on *Turritella* has been reported from various predators including naticid gastropods, crabs and starfish in some cases leading to recognizable traces (Dudley & Vermeij 1978; Allmon *et al.* 1990; Tull & Bohning-Gaese 1993; Cadée *et al.* 1997; Hagadorn & Boyajian 1997; Allmon 2011). In living specimens of *Turritella*, the thin outer lip is seldom complete, even in mature examples (Bosch *et al.* 1995).

Materials and methods

The Erminger Turrیتellenplatte (ETP) locality is well known as a collection site and source of museum specimens (Baier *et al.* 2004; Baier 2008), but has not been studied in detail with respect to taphonomy and

sedimentology. It occurs close to the northern boundary of the NAFB (Figs 3, 4), which transgressed across sediments of the Lower Freshwater Molasse and Late Jurassic limestones at its northern border. These Lower Miocene sediments have been correlated with the Ottnangian (Fig. 2) of the regional Paratethys stages (Vennemann & Hegner 1998).

The turrیتelline gastropod from this locality has been identified as *Turritella* cf. *eryna communiformis* Voorthuysen 1944 (Fig. 5C). It possesses 13 weakly convex whorls that increase steadily in size. The whorls are separated by a clear suture. The number of spiral lines increases from 3 to 5 to 7 in the last whorls. Finer sculpturing is commonly difficult to ascertain due to poor preservation (see below). The aperture is slightly oval in shape. See Höltker (2009) for discussion of species identification and historical treatment of the molluscan fauna found in this locality.

An excavation was conducted at the edge of a quarry wall of the ETP, using a mini-excavator (Fig. 5 A), and then cleaned (Fig. 5B). Sedimentological features were assessed, and samples were taken for fossil material and thin sections. Taphonomic features were noted and snails were measured for length if complete from the apex to aperture (Fig. 6). The compass bearings of apex direction, as well as horizontal inclinations of turritelline gastropod specimens, were measured in situ as well as on excavated, oriented

blocks using a geological compass to collect orientation data (Fig. 7). An unlithified clay deposit underlying the ETP was drilled using a manual piston core. Thin sections measuring 48×48 mm. were studied for detailed sedimentary, fabric and component analysis (Figs 8, 9). Microfacies photographs were taken using a Wild Microscope and digital Nikon VI camera and processed using Adobe Photoshop CC2018.

Specimen orientations were plotted, and statistical tests of uniformity were run using the Circular

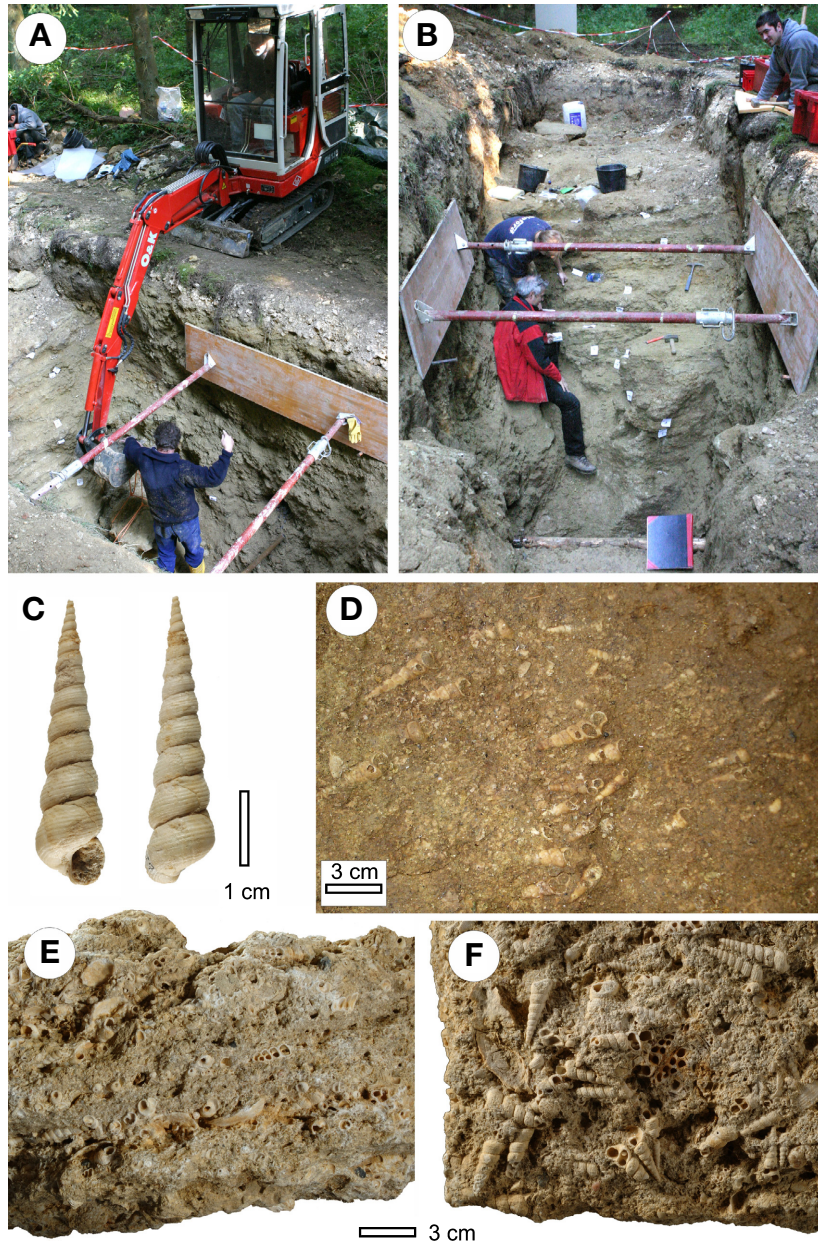


Fig. 5. A, excavation and recovery of sedimentary blocks of the Erminger Turritellenplatte using a mini-excavator. B, overview and sampling within the exposed section. C, isolated *Turritella* cf. *eryna communiformis*. D, typical preservation and sedimentary context of fossils from the Erminger Turritellenplatte from Bed 17 showing generally isolated, uni-directionally orientated specimens. E, F, side and plan views of Bed 5 with densely packed, variously orientated and slightly dipping specimens.

package (Agostinelli & Lund 2013) in the statistical computing software R (R Core Team 2015). Trend measurements for specimens in each of the measured beds were plotted using rose diagrams with bin size equal to 20° and fried egg plots using kernel density estimation with a bandwidth of 25 (Fig. 7). Rao's spacing test, with results shown in Table 1, was used to determine whether the orientation data were not uniformly distributed. Size and orientation data were plotted and analysed in R. The length of complete specimens was plotted for all bedding planes pooled together (Fig. 6) and for each bed (Fig. 10). Additionally, for the three beds with more than twenty individuals, a Kruskal–Wallis test was used to assess whether or not the length–frequency distribution of individuals in the beds were significantly different.

Results

Fossils and stratigraphical succession

The ETP is dominated by the turritelline gastropod *Turritella* cf. *eryna communiformis* Voorthuysen 1944, which occurs in rock-forming quantities (Fig. 5). Thick-shelled ostreids and the venerid bivalve *Tapes helvetica* Mayer 1853, can also occur, though less common (see Höltnke 2009). Other molluscs, including both gastropods and bivalves, are rare and occur along with vertebrate remains, including shark teeth, abraded bone fragments and scarce teeth of cervids. The recovered turritelline specimens range between 10 and 70 mm in length with a mean of 36 mm. (Fig. 6). The distribution of lengths for the three beds where more than twenty complete individuals were measured (Beds 11, 17 and 18) were not shown to be significantly different (Kruskal–Wallis test, $\chi^2 = 0.78$, two degrees of freedom, $P = 0.68$).

The excavated succession of the ETP is ca. 3.5 m thick (Fig. 7) and consists of poorly consolidated

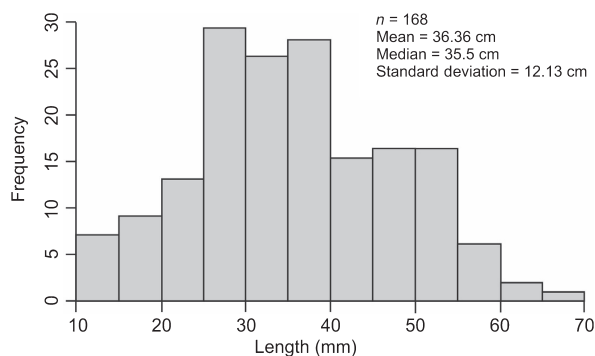


Fig. 6. Histogram of length measurements of complete turritelline gastropod specimens.

sediments and rocks including coarse-grained fossiliferous sandstones and mass occurrences of turritelline gastropods. Isolated fossil specimens can be recovered, but most specimens are firmly cemented within a bioclastic sandstone with calcareous matrix which can pass into quartz-rich limestones. The fossiliferous sandstones of the ETP are underlain by unconsolidated, light blue to grey calcareous muds, lacking macrofossils with a thickness of 190 cm, preceded by an impenetrable, hard, calcareous horizon. The ETP starts abruptly with thin beds consisting of a basal gravel layer with well-rounded quartzitic pebbles, silty marlstone (Bed 2), well-rounded, coarse-grained sandstone (Bed 3) and an oblique thin layer of silty marls with sands. These thin beds, which include isolated turritelline specimens and bivalves, are followed by more massive, coarse-grained, poorly consolidated rocks (Beds 5–14) rich in fossils, which make up the bulk of the ETP.

The turritelline specimens are concentrated in and mostly accumulated along distinct, several cm thick layers that represent bedding planes. Areas with densely packed components occur adjacent to or laterally grade into clean sandstones. The gastropods can also completely dominate the sedimentary succession in decimetre thick accumulations (especially Bed 8) where the specimens are often bunched together sometimes with opposing, though parallel orientations. The coarse-grained bioclastic sandstone succession is interrupted by thin discontinuous mudstone intercalations, as well as by a 30-cm-thick sedimentary layer dominated by isolated oyster valves. Some beds are slightly inclined (Beds 11, 15). Towards the top of the succession, more unconsolidated sandstones rich in isolated gastropods are present (Beds 16, 17) followed by large blocks *in situ*. Among the non-carbonate components, rounded coarse quartz grains up to 40 mm also occur along with dark siliciclastic pebbles up to several cm size. Well-rounded mudstone clasts composed of the material from the above-mentioned silty mudstone layers are distributed throughout the section, reaching sizes up to 100 mm in Bed 6.

Microfacies analysis and taphonomy

Thin section analysis shows sedimentary rocks dominated by poorly sorted, angular to subrounded quartz with an admixture of bioclasts (Figs 8, 9). The most common bioclastic components are high-spired gastropods attributed to turritellines (Figs 8, 9) which totally dominates the macrofauna. Bivalves are disarticulated and can be highly fragmented. Oyster fragments are typically highly rounded while balanid barnacles are present as disarticulated single wall

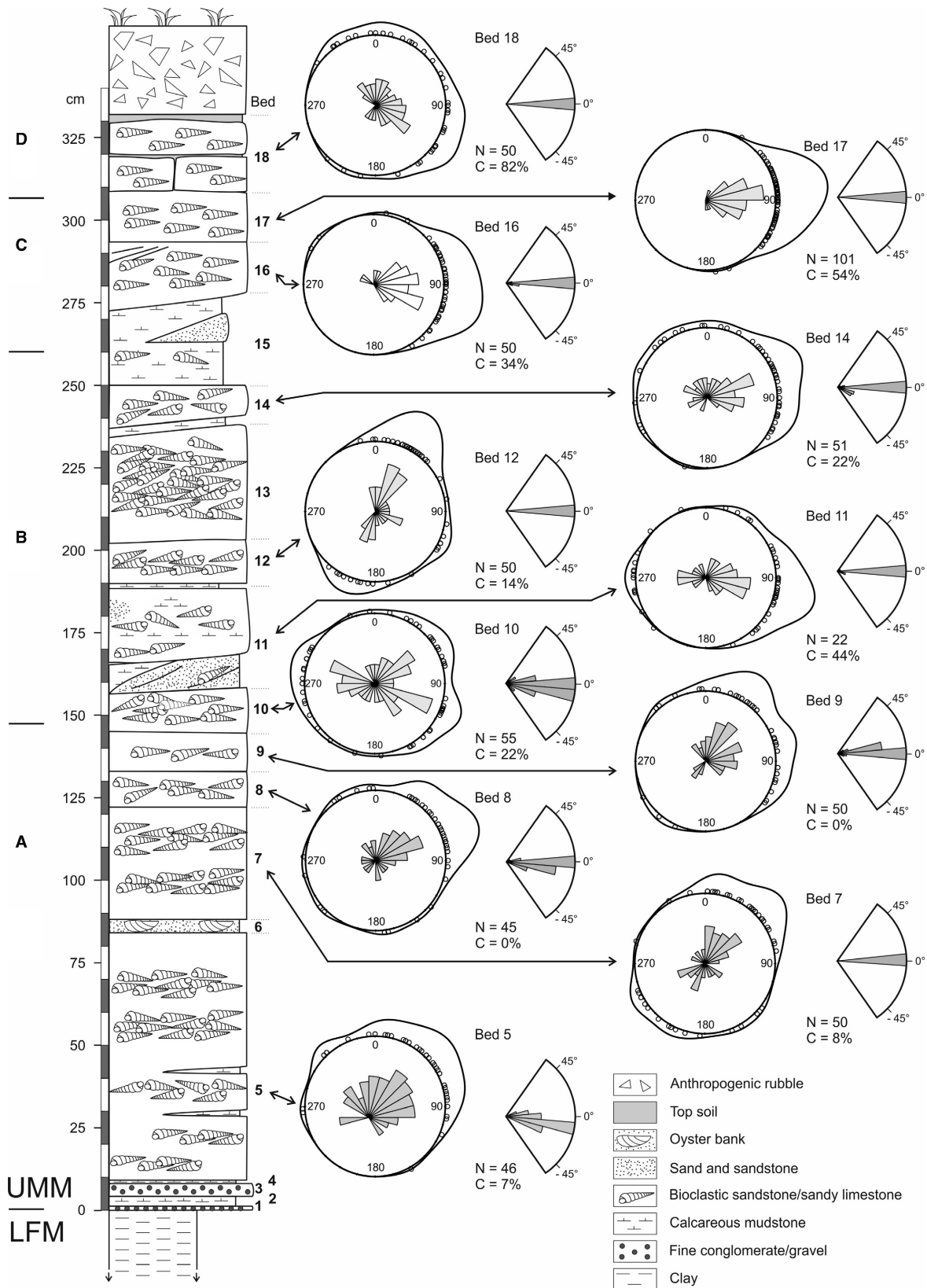


Fig. 7. Stratigraphical section of the ETP with orientation data and schematic representation of turritelline gastropod presence within the section. Orientation data include azimuth ('fried egg' diagram) and dip directions. Key: N = number of measured specimens; C = % complete specimens; LFM = Lower Freshwater Molasse; UMM = Upper Marine Molasse. A-D = palaeoenvironmental associations (see Fig. 11).

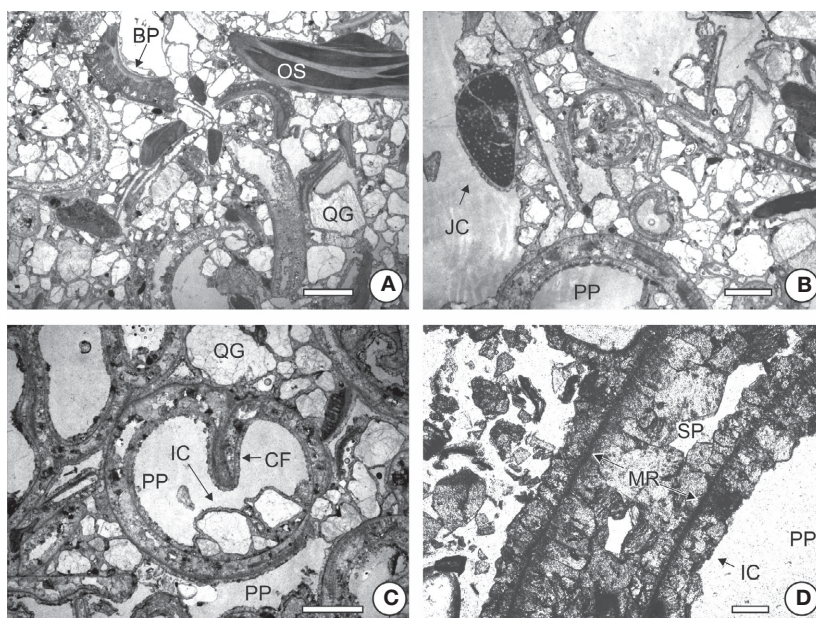


Fig. 8. Thin sections: A, ERMBX-6, Bed 7. B–D, ERMBX-6, Bed 5. Key: BP = Barnacle plate; CF = columellar fold; IC = isopachous calcitic cement; JC = Jurassic component; MR = micritized rim; OS = oyster shell; PP = primary porosity; QG = quartz grains; SP = secondary porosity. A, overview showing poorly quartzose sandstone rich in bioclasts including mollusc shells replaced by calcite, rounded calcitic oyster shell fragments and isolated balanid barnacle plates showing tree-like structures and growth lines. The angular to sub-rounded quartz grains are poorly sorted. Thin section, scale bar = 2 mm. B, overview showing cross-sections of gastropods and a well-rounded, upper Jurassic clast consisting of a sponge limestone. Scale bar = 0.5 mm. C, circular cross-section of snail shell showing prominent columellar fold. Thin rim of isopachous sparite covers both the shell surface and quartz grains. Scale bar = 2 mm. D, close up of Figure 5C showing prominent micritization on both the outer and inner surface of the shell. Incomplete infilling of calcite leads to secondary porosity. Isopachous sparite grown both into the shell volume and away from the surface. The interior of the shell is incompletely filled by sparite leading to secondary porosity. Scale bar = 0.2 mm.

plates (Fig. 8A). Rare echinoid spines, bryozoans and isolated fish teeth are also present. Well-rounded clasts of Jurassic limestone consisting either of mudstones or sponge limestones are present, though rare (Fig. 8B).

The highly spired shells are often broken at both the aperture and the apex, especially at the base of the section with more complete shells towards the top (Table 1). Cylindrical, bevelled boreholes typical for naticid predation can be present (*Oichnus paraboloides* Bromley 1981), but were not quantified as most specimens recovered during the excavation could not be readily extracted from the sedimentary matrix. The surface preservation of the turrilline gastropod shells often is somewhat irregular with respect to surface sculpturing.

Sediment infilling of the high-spired shells is mostly incomplete and often restricted to the whorls closest to the aperture (Fig. 9A). Whorls in the middle part of the shells show geopetal distribution of sediment grains, while the apical whorls are mostly empty of sediment. These apical whorls either remain empty or are filled by sparite. The lithified sediment within the shells, when present, shows the same characteristics as the sedimentary matrix

between components, consisting predominately of poorly sorted, angular to subrounded quartz grains (Figs 8, 9).

As revealed by optical microscopy, there is a complex diagenetic pathway which includes the dominant turrilline shells and other primarily aragonitic components such as infaunal bivalves. The shells are micritized, which is visible as a thin, opaque layer (Figs 8D, 9C). This micritized layer is present on the outer shell surface, but can be missing within more inner whorls of the snail as seen in longitudinal sections (Fig. 9A). Otherwise, the shell is replaced by sparite crystals, though faint growth lines parallel to the shell surface can, in part, still be preserved (Figs 8C, 9B). In addition, the replacement by sparite is often incomplete leading to the production of secondary vugs (Figs 8D, 9B). Coarse calcite crystals can also grow into the primary pore space of the shell interior as well as on the exterior of the shell if not blocked by matrix. This crystal growth is often irregular and does not necessarily faithfully follow the fine sculpturing of the outer shell surface (Fig. 9C). Both former shell surfaces as well as quartz grains can be covered by a thin layer of equant sparite crystals (Fig. 9C).

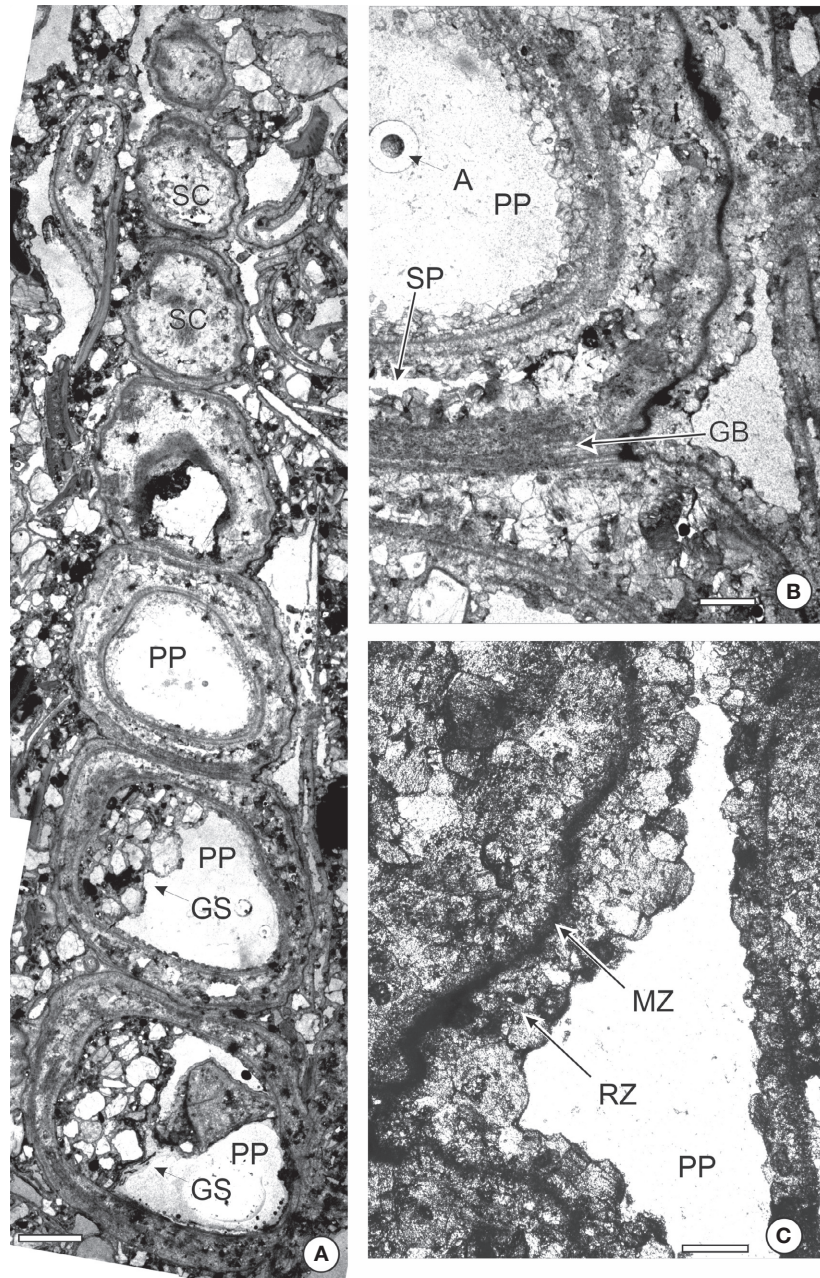


Fig. 9. Thin section ERMBX-26, Bed 9. Key: A = Artefact; GB = Growth bands; GS = Geopetal infill; MZ = micritized rim; PP = primary porosity; SP = secondary porosity; RZ = rim cement; SC = sparite cement. A, longitudinal section of an elongate, many-whorled turritelline gastropod shell. Anterior whorls filled with sparite cement, followed by a whorl free of both sediment and cement, followed by posterior whorls partially filled with geopetal quartz grains, otherwise showing primary porosity. Scale bar = 2 mm. B, detail of Figure 9A showing shell preservation. Growth bands within the shell are partially preserved. Outer shell surface shows micritization present as a dark band, which is missing from the inner surface. Primary porosity is present within the empty whorl of the snail, secondary porosity within the shell. Scale bar = 0.5 mm. C, detail showing growth of sparite crystals away from the micritized rim. Differential growth of the sparite obscures ornamental details of the shell surface. Scale bar = 0.25 mm.

Analysis of directional data and size–frequency distribution

Rose diagrams and fried egg plots showing the distribution of specimen trends in each bed are shown in Figure 7. In all cases, the null hypothesis of uniformly distributed data is rejected (Table 1),

and, indeed, the non-uniformity of the data is evident in the rose diagrams, which show clear directionality (Fig. 7). The directional data show a shift of shell orientations and dip from the base to the top of the section (Beds 5 to 17). A broader distribution of orientations is often accompanied by a wider distribution of dip directions. The main direction of snail

Table 1. Results of Rao's spacing test to determine if orientation data is not uniformly distributed; number of measured taxa and % recorded complete specimens

| | U | Null.Hypothesis | Measured | Complete | % Complete |
|--------|---------------------|-----------------|----------|----------|------------|
| Bed 5 | 206.739.130.434.783 | Rejected | 46 | 3 | 6.52 |
| Bed 7 | 172.8 | Rejected | 50 | 4 | 8.00 |
| Bed 8 | 197.8 | Rejected | 45 | 0 | 0.00 |
| Bed 9 | 209.6 | Rejected | 50 | 0 | 0.00 |
| Bed 10 | 162.636363636364 | Rejected | 55 | 12 | 21.82 |
| Bed 11 | 185 | Rejected | 50 | 22 | 44.00 |
| Bed 12 | 198 | Rejected | 50 | 7 | 14.00 |
| Bed 14 | 176.411764705882 | Rejected | 51 | 11 | 21.57 |
| Bed 16 | 230.4 | Rejected | 50 | 17 | 34.00 |
| Bed 17 | 266.920792079208 | Rejected | 101 | 55 | 54.46 |
| Bed 18 | 160.090909090909 | Rejected | 44 | 36 | 81.82 |

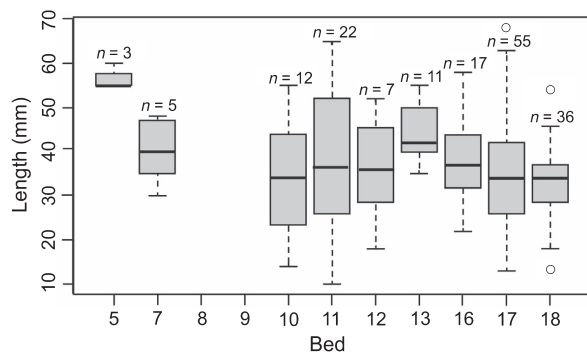


Fig. 10. Box plots showing the distribution of shell lengths from each bed.

apices varies between south-east to north-east (and corresponding opposite orientations). The base of the section is dominated by poorly constrained orientations, varying dip directions and often poorly preserved specimens. In the middle part of the section, more bimodal distributions are present with major axis 180° to one another (Beds 7, 11 to 14). Some of these beds also contain a few shells with a 90° offset (especially Bed 12). These shells also show high dips and are generally poorly preserved. Clear unimodal orientations are in Beds 16 and 17 where the snail shells are loosely distributed and show flattened dip directions. These shells are well preserved, and most specimens are complete as in Bed 17. Bed 18 reverts to a wide distribution of orientations, while the specimens are well separated from one another as well as showing only very slight inclination, if at all. As in Bed 17, there are numerous well-preserved specimens.

Discussion

Preservation and diagenesis

The shells often show damage to the apex and aperture. It is not clear whether damage to the aperture is

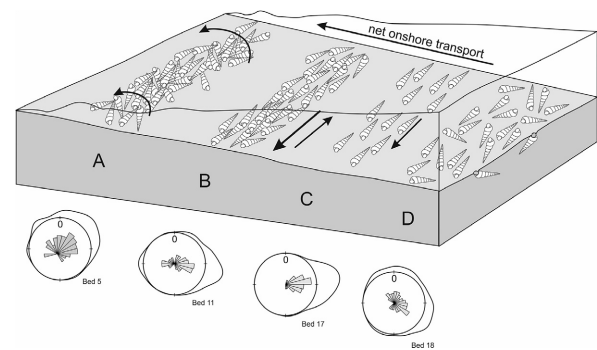


Fig. 11. Reconstruction of depositional environments of turritelline gastropods in the ETP along a depth gradient with representative orientation data (see Fig. 4). A, jumbled, poorly preserved, inclined shells indicating strong transport. B, bidirectional, poorly preserved, inclined shells on lee surfaces of cross-bedded sandstones indicating stronger current conditions. C, uniform orientation of disjunct, well-preserved, flat-lying shells indicating moderate uniform current. D, disjunct, well-preserved, autochthonous, flat-lying shells on the sedimentary bed surface with no clear orientation.

due to predation, pagurisation or abrasion due to transport (compare with Tull & Bohning-Gaese 1993; Cadée *et al.* 1997; Hagadorn & Boyajian 1997; Allmon 2011). In general, however, the preservation of specimens is better towards the top of the section. Clear predatory events are seen in rare borehole (*O. paraboloides*) interpreted as the result of naticid gastropod predation, but could not be quantified as specimens were well cemented within the rock and could not be removed without destroying the shell.

An outstanding feature of the ETP is the preservation of originally aragonitic components as calcitic replacements in highly permeable, coarse-grained, siliciclastic sedimentary rocks. This is interpreted as a neomorphic transformation of aragonite by calcite, resulting in replacement of the original aragonitic skeleton by drusy calcite while maintaining, to a large extent, the original morphology of the skeleton (see discussion in Perrin *et al.* 2014). An important role is played by the micritization of the shell surface which serves as a template for drusy calcite crystals growing both into the internal space and on the

outside of the shell (Flügel 2010). The transformation of aragonite to calcite was rapid as reflected by the preservation of growth lines within the sparite crystals. A further implication of the presence of drusy calcite growing outward from the shell surface is the masking of surface details. This may have implications for the identification of fossil turritelline species, which are often differentiated based on fine sculpturing of the outer shell surface.

The observed characteristics of transformation of aragonite to calcite are functions of climate and hydrology (Dodd 1966) with the calcium carbonate derived from aragonite dissolution reprecipitated as calcite either in the mixed marine/freshwater zone or in freshwater lenses (Budd 1988; Brachert & Dullo 2000). This rapid transformation of gastropod shells and other aragonitic molluscs in three dimensions was most probably aided by the impermeable layers of the muddy sediments below the ETP.

Palaeoenvironmental gradient within the ETP

A polymodal origin of shell accumulations is present in the ETP and can be interpreted with respect to sedimentary structures, orientation data and shell preservation. The basal clays can be correlated with sediments of the Lower Freshwater Molasse (LFM), which are represented by isolated occurrences on the slope south of the excavation site. The basal gravels represent a transgression horizon over the preceding muds of the LFM. This succession of the ETP, dominated by turritelline gastropods, ranges from four different associations (Fig. 7) including (from bottom to top):

- A High energy, chaotically arranged, densely packed, transported assemblages possibly representing storm deposits. These represent the thickest and most highly dense shell beds.
- B Tidally influenced deposits showing bimodal shell orientations, in a cross-bedded sandstone texture, with concentrated, transported gastropod shells following the sedimentary inclination.
- C Lower energy conditions with slightly fine-grained sedimentary rocks and widely dispersed, parautochthonous, flat-lying shells which were subjected to enough water energy to result in a uni-directional orientation.
- D Flat-lying, dispersed specimens showing a poorly constrained orientation representing the lowest energy conditions which were not high enough to substantially influence shell orientation. The reduction in energy conditions is accompanied by the presence of better-preserved, complete specimens.

These developments point to a generally deepening of palaeoenvironment in line with the ongoing transgression of the Upper Marine Molasse as reconstructed in Figure 11. The turritelline gastropods are interpreted to have lived as semi-infaunal suspension-feeding gastropods in associations C and D (see above). The shells were then transported to shallower, higher energy environments where they were then concentrated at higher densities.

Current directions and origin of nutrients

The high density of turritelline gastropods together with the presence of other filter-feeding molluscs (bivalves), bryozoans and barnacles of the ETP are indicative of nutrient-rich palaeoenvironments. This is present despite the fact that sediments of the Molasse Sea generally transgressed over a karstified Upper Jurassic limestone landscape, represented by rounded components, from which little nutrient input could be expected. Upwelling conditions in the North Alpine Foreland Basin have been reported for various time-slices of the Paratethys Sea, notably during the formation of the Paratethys at the Eocene/Oligocene transition (Schulz *et al.* 2005) as well as during the Late Oligocene and Early Miocene (Wagner 1996, 1998). Upwelling systems driven by wind leading to oxygen deficiency and resulting oxygen-poor sediments were suggested by Wagner (1996) on the northern margin of the North Alpine Foreland basin. Grunert *et al.* (2010, 2012) used dinoflagellates and planktonic foraminifera to reconstruct upwelling conditions along the Bohemian Massif of the Central Paratethys during the Mid-Burdigalian with a sea surface temperature between 10° and 14° related to north-east trade winds and strong tidal currents. Nutrient-rich conditions at the northern NAFB margin are also reflected by bryomol-type carbonates dominated by filter-feeding organisms along with coralline algae and a restricted larger foraminiferal fauna (Nebelsick 1989, 1992; Kaiser *et al.* 2001; Bieg *et al.* 2007).

The present study confirms the high degree of water movement within the Molasse Sea with nutrients either derived from Central Paratethyan upwelling some 400 km to the east or from the emerging alpine chain on the southern coastline of the North Alpine Foreland Basin. Caution must be exerted in making any general conclusion on the general direction of basinal water movement from the directional data as near-coastal water movements can differ highly from that of more offshore currents. Bieg *et al.* (2008) reconstructed tidal generated water movements within the Molasse Sea, whereas current movements change responding to tidal cycles. This

study shows that there are differences in current velocities at different depths, although, at least in the study area, a general direction from the east is assumed.

Conclusions

The following conclusions can be drawn:

- 1 Detailed investigations of a mass occurrence of turritelline gastropods in the Lower Miocene Ermingen Turriteltenplatte from the North Alpine Foreland Basin shows 3.5-m-thick sections dominated by coarse-grained sandstones containing variously packed fossils. This succession follows directly over unconsolidated muds of the Lower Marine Molasse.
- 2 Aragonitic shells have been completely replaced by calcite resulting in vugs within the shells. In some specimens, calcite growth from the surface outward has resulted in a slight modulation of surface morphologies.
- 3 Sedimentary characteristics, shell preservation and orientation data of the gastropod specimens indicate a shallowing-upward sequence ranging from the following: A) high energy, storm-induced and winnowed sediments with variously dipping, densely packed non-directional shells; B) variously dipping, commonly bimodal-distributed shells in cross-bedded sands; C) tidally influenced, strictly uni-directional, isolated, well-preserved, flat-lying specimens; and finally D) variously oriented, loosely distributed, flat-lying specimens in depths not affected by strong current.
- 4 Possible sources of nutrients are seen as being transported from the east where deeper water upwelling has been reconstructed or coastal input from the emerging Alps to the south.

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References

Ager, D.V. 1963: *Principles of Paleoecology*, 371 pp. McGraw Hill, New York.

- Agostinelli, C. & Lund, U. 2013: R package ‘circular’: Circular Statistics, 0.4-7 edition.
- Allen, P.A. & Homewood, P. 1984: Evolution and mechanics of a Miocene tidal sandwave. *Sedimentology* 31, 63–81.
- Allen, P.A., Mange-Rajetzky, M., Matter, A. & Homewood, P. 1985: Dynamic palaeogeography of the open Burdigalian seaway, Swiss Molasse basin. *Eclogae Geologicae Helvetiae* 78, 351–381.
- Allmon, W.D. 1988: Ecology of Recent turritelline gastropods (Prosobranchia, Turritellidae): Current knowledge and paleontological implications. *Palaios* 3, 259–284.
- Allmon, W.D. 2007: Cretaceous marine nutrients, greenhouse carbonates, and the abundance of turritelline gastropods. *Journal of Geology* 115, 509–524.
- Allmon, W.D. 2011: Natural history of turritelline gastropods (Cerithioidea, Turritellidae): A status report. *Malacologica* 54, 159–202.
- Allmon, W.D. & Dockery III, D.T. 1992: A turritelline gastropod-dominated bed in the Byram Formation (Oligocene) of Mississippi. *Mississippi Geology* 13, 29–35.
- Allmon, W.D. & Knight, J.L. 1993: Paleocological significance of a turritelline-dominated layer in the Cretaceous of South Carolina. *Journal of Paleontology* 67, 355–360.
- Allmon, W.D., Nieh, J.C. & Norris, R.D. 1990: Drilling and peeling of Turritelline gastropods since the late Cretaceous. *Palaeontology* 33, 595–611.
- Allmon, W.D., Jones, D.S. & Vaughan, N. 1992: Observations on the biology of *Turritella gonostoma* Valenciennes (Prosobranchia, Turritellidae) from the Gulf of California. *The Veliger* 35, 52–63.
- Allmon, W.D., Jones, D.S., Aiello, R.L., Gowlett-Holmes, K. & Probert, P.K. 1994: Observations on the biology of *Maoricolpus roseus* (Quoy & Gaimard) (Prosobranchia: Turritellidae) from New Zealand and Tasmania. *The Veliger* 37, 267–279.
- Allmon, W.E., Spizuco, M.P. & Jones, D.S. 1995: Taphonomy and paleoenvironment of two turritellid-gastropod-rich beds, Pliocene of Florida. *Lethaia* 28, 75–83.
- Anderson, M., Hendy, A., Johnson, E.H. & Allmon, W.D. 2017: Paleocology and paleoenvironmental implications of turritelline gastropod-dominated assemblages from the Gatun Formation (Upper Miocene) of Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology* 470, 132–146.
- Baier, J. 2008: Ein Beitrag zur Erminger Turriteltenplatte (Mittl. Schwäb. Alb, SW Deutschland). *Jahresbericht und Mitteilungen des oberrheinischen geologischen Vereins, Neue Folge* 90, 9–17.
- Baier, J., Schmitt, K.-H. & Mick, R. 2004: Notizen zur unter-miozänen Hai- und Rochenfauna der Erminger Turriteltenplatte (Mittlere Schwäbische Alb, SW-Deutschland). *Jahresbericht und Mitteilungen des oberrheinischen geologischen Vereins, Neue Folge* 86, 361–371.
- Bieg, U. 2005: *Palaeoceanographic Modeling in Global and Regional Scale: An Example from the Burdigalian Seaway, Upper Marine Molasse (Early Miocene)*. PhD thesis, 108 pp. University of Tübingen, Tübingen. <https://publikationen.uni-tuebingen.de/xmlui/handle/10900/48865>
- Bieg, U., Nebelsick, J.H. & Rasser, M. 2007: North Alpine Foreland Basin (Upper Marine Molasse) of southwest Germany: Sedimentology, stratigraphy and palaeontology. *Geo. Alp* 4, 149–158.
- Bieg, U., Süß, M.P. & Kuhlemann, J. 2008: Simulation of tidal flow and circulation patterns in the Early Miocene (Upper Marine Molasse) of the Alpine foreland basin. In de Boer, P., Postma, G., van der Zwan, K., Burgess, P. & Kukla, P. (eds): *Analogue and Numerical Modelling of Sedimentary Systems: From Understanding to Prediction. International Association of Sedimentologists, Special Publications* 40, 145–169. Wiley-Blackwell, Hoboken.
- Bosch, D.T., Dance, S.P., Moolenbeek, R.G. & Oliver, P.G. 1995: *Seashells of Eastern Arabia*, 296 pp. Motivate Publishing, Dubai.
- Brachert, T.C. & Dullo, W.-C. 2000: Shallow burial diagenesis of skeletal carbonates: selective loss of aragonite shell material (Miocene to Recent, Queensland Plateau and Queensland Trough, NE Australia) — implications for shallow cool-water carbonates. *Sedimentary Geology* 136, 169–187.

- Bromley, R.G. 1981: Concepts in ichnology illustrated by small round holes in shells. *Acta Geologica Hispanica* 16, 55–64.
- Budd, D.A. 1988: Aragonite-to-calcite transformation during fresh-water diagenesis of carbonates: Insights from pore-water chemistry. *Geological Society of America* 100, 1260–1270.
- Cadée, G.C., Walker, S.E. & Flessa, K.W. 1997: Gastropod shell repair in the intertidal of Bahía la Choya (N. Gulf of California). *Palaeogeography, Palaeoclimatology, Palaeoecology* 136, 67–78.
- Cohen, A.S. 1989: The taphonomy of gastropod shell accumulations in large lakes: An example from Lake Tanganyika, Africa. *Paleobiology* 15, 26–45.
- Crawford, R.S., Casadio, S., Feldmann, R.M., Griffin, M., Parras, A. & Schweitzer, C.E. 2008: Mass mortality of fossil decapods within the Monte León Formation (Early Miocene), southern Argentina: victims of Andean volcanism. *Annals of Carnegie Museum* 77, 259–287.
- Dodd, J.R. 1966: Processes of conversion of aragonite to calcite with examples from the Cretaceous of Texas. *Journal of Sedimentary Research* 36, 733–741.
- Dudley, E.C. & Vermeij, G.J. 1978: Predation in time and space: drilling in the gastropod *Turritella*. *Paleobiology* 4, 436–444.
- Flügel, E. 2010: *Microfacies of Carbonate Rocks: Analysis, Interpretation and Application*, 984. Springer-Verlag, Berlin.
- Frieling, D., Mazumder, R. & Reichenbacher, B. 2011: Tidal sediments in the Upper Marine Molasse (OMM) of the Allgäu area (Lower Miocene, Southwest Germany). In Nebelsick, J.H., Rasser, M. & Bieg, U. (eds): *The North Alpine Foreland Basin: special volume of the 2008 Molasse Meeting. Neues Jahrbuch für Geologie und Paläontologie* 254, 151–163. Schweizerbart Science Publishers, Stuttgart.
- Futterer, E. 1978a: Studien über die Einregelung, Anlagerung und Einbettung biogener Hartteile im Strömungskanal. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 155, 87–131.
- Futterer, E. 1978b: Untersuchungen über die Sink- und Transportgeschwindigkeit biogener Hartteile. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 155, 318–359.
- Gallmetzer, I., Haselmair, A., Tomašových, A., Stachowitsch, M. & Zuschin, M. 2017: Responses of molluscan communities to centuries of human impact in the northern Adriatic Sea. *PLoS ONE* 12, e0180820.
- Geary, D.H. & Allmon, W.D. 1990: Biological and physical contributions to the accumulation of strombid gastropods in a Pliocene shell bed. *Palaiois* 5, 259–272.
- Grunert, P., Soliman, A., Harzhauser, M., Müllegger, S., Piller, W.E. & Rögl, F. 2010: Upwelling conditions in the Early Miocene Central Paratethys Sea. *Geologica Carpathica* 61, 129–145.
- Grunert, P., Soliman, A., Ćorić, S., Roetzel, R., Harzhauser, M. & Piller, W.E. 2012: Facies development along the tide-influenced shelf of the Burdigalian Seaway: An example from the Otnnangian stratotype (Early Miocene, middle Burdigalian). *Marine Micropaleontology* 84–85, 14–36.
- Hagadorn, J.W. & Boyajian, G.E. 1997: Subtle change in manure predator-prey systems; an example from Neogene *Turritella*, (Gastropoda). *Palaiois* 12, 372–279.
- Höltke, O. 2009: Die Molluskenfauna der Oberen Meeresmolasse (Untermiozän) von Ermingen und Ursendorf (SW-Deutschland) The mollusc fauna of the 'Obere Meeresmolasse' (Lower Miocene) from Ermingen and Ursendorf (SW Germany). *Palaeodiversity* 2, 67–95.
- Homewood, P. & Allen, P.A. 1981: Wave-, tide-, and current-controlled sandbodies of Miocene Molasse, Western Switzerland. *Bulletin of the American Association of Petroleum Geologists* 65, 2534–2545.
- Kaiser, D., Rasser, M.W., Nebelsick, J.H. & Piller, W.E. 2001: Late Oligocene Algal Limestones on a Mixed Carbonate-Siliciclastic Ramp at the Southern Margin of the Bohemian Massif (Upper Austria). In Piller, W.E. & Rasser, M.W. (eds): *Paleogene of the Eastern Alps Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommission* 14, 197–224. Verlag der österreichischen Akademie der Wissenschaften, Vienna.
- Kuhlemann, J. & Kempf, O. 2001: Post-Eocene evolution of the North Alpine Foreland Basin and its response to Alpine tectonics. *Sedimentary Geology* 152, 45–78.
- Mayer, K. 1853: Verzeichnis der in der marinen Molasse der schweizerisch-schwäbischen Hochfläche enthaltenen fossilen Mollusken. *Mitteilungen der naturforschenden Gesellschaft Bern* 1853, 76–106.
- Menard, J.W. & Boucot, A.J. 1951: Experiments on the movements of shells by water. *American Journal of Science* 249, 131–151.
- Nagle, J.S. 1967: Wave and current orientation of shells. *Journal of Sedimentary Petrology* 37, 1124–1138.
- Nebelsick, J.H. 1989: Temperate water carbonate facies of the Early Miocene Paratethys (Zogelsdorf Formation, Lower Austria). *Facies* 21, 11–40.
- Nebelsick, J.H. 1992: Components analysis of sediment composition in Early Miocene temperate carbonates of the Zogelsdorf Formation, Lower Austria. *Palaeogeography, Palaeoclimatology, Palaeoecology* 91, 59–69.
- Perrin, C., Prestimonaco, L., Servelle, G., Tilhac, T., Maury, M. & Cabrol, P. 2014: Aragonite–calcite speleothems: identifying original and diagenetic features. *Journal of Sedimentary Research* 84, 245–269.
- Pippèr, M. & Reichenbacher, B. 2009: Biostratigraphy and paleoecology of benthic foraminifera from the Eggenburgian 'Ortenburger Meeressande' of southeastern Germany (Early Miocene, Paratethys). In Nebelsick, J.H., Rasser, M. & Bieg, U. (eds): *The North Alpine Foreland Basin: special volume of the 2008 Molasse Meeting. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 254, 41–61. Schweizerbart Science Publishers, Stuttgart.
- Pippèr, M. & Reichenbacher, B. 2017: Late Early Miocene palaeoenvironmental changes in the North Alpine Foreland Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 468, 485–502.
- Price, B.A., Killingley, J.S. & Berger, W.H. 1985: On the pteropod pavement of the eastern Rio Grande Rise. *Marine Geology* 64, 217–235.
- R Core Team 2015: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Roetzel, R., Ćorić, S., Galović, I. & Rögl, F. 2006: Early Miocene (Otnnangian) coastal upwelling conditions along the southeastern scarp of the Bohemian Massif (Parisdorf, Lower Austria, Central Paratethys). *Beiträge zur Paläontologie* 30, 387–413.
- Schneider, S., Pippèr, M., Frieling, D. & Reichenbacher, B. 2011a: Sedimentary facies and paleontology of the Otnnangian Upper Marine Molasse and Upper Brackish Water Molasse of eastern Bavaria: A field trip guide. In Carena, S., Friedrich, A.M. & Lammerer, B. (eds): *Geological Field Trips in Central Western Europe: Fragile Earth International Conference, Munich, September 2011*, Geological Society of America Field Guide 22, 35–50.
- Schneider, S., Berning, B., Bitner, M.A., Carriol, R.-P., Jäger, M., Kriwet, J., Kroh, A. & Werner, W. 2011b: A parautochthonous shallow marine fauna from the Late Burdigalian (early Otnnangian) of Gurlarn (Lower Bavaria, SE Germany): Macrofaunal inventory and paleoecology. In Nebelsick, J.H., Rasser, M. & Bieg, U. (eds): *The North Alpine Foreland Basin: special volume of the 2008 Molasse Meeting. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 254, 63–103. Schweizerbart Science Publishers, Stuttgart.
- Schulz, H.-M., Bechtel, A. & Sachsenhofer, R.F. 2005: The birth of the Paratethys during the Early Oligocene: From Tethys to an ancient Black Sea analogue? *Global and Planetary Change* 49, 163–176.
- Schwarzacker, W. 1963: Orientation of crinoids by current action. *Journal of Sedimentary Petrology* 33, 580–586.
- Teusch, K.P., Jones, D.S. & Allmon, W.D. 2002: Morphological variations in turritellid gastropods from the Pleistocene to Recent of Chile: Association with upwelling intensity. *Palaiois* 17, 366–377.
- Tomašových, A., Gallmetzer, I., Haselmair, A., Kaufman, D.S., Kralj, M., Cassin, D., Zonta, R. & Zuschin, M. 2018: Tracing the effects of eutrophication on molluscan communities in sediment cores: outbreaks of an opportunistic species coincide with reduced bioturbation and high frequency of hypoxia in the Adriatic Sea. *Paleobiology* 44, 575–602.

- Trussheim, F. 1931: Versuche über Transport und Ablagerung von Mollusken. *Senckenbergiana* 13, 124–139.
- Tull, D.S. & Bohning-Gaese, K. 1993: Patterns of drilling predation on gastropods of the family Turritellidae in the Gulf of California. *Paleobiology* 19, 476–486.
- Vennemann, T.W. & Hegner, E. 1998: Oxygen, strontium and neodymium isotope composition of fossil shark teeth as a proxy for the palaeoceanography and palaeoclimatology of the Miocene northern Alpine Paratethys. *Palaeogeography, Palaeoclimatology Palaeoecology* 98, 107–121.
- Voorthuysen, J.H. 1944: Miozäne Gastropoden aus dem Peelgebiet (Niederlande) (Rissoidea-Muricidae, nach Zittels Einteilung, 1924). *Mededeelingen van de geologische Stichting, Serie C-IV-1* 5, 1–65.
- Vörös, A. 2011: Episodic sedimentation on a peri-Tethyan ridge through the Middle-Late Jurassic transition (Villány Mountains, southern Hungary). *Facies* 58, 425–443.
- Wagner, L.R. 1996: Stratigraphy and hydrocarbons in Upper Austrian Molasse Foredeep (active margin). In Wessely, G. & Liebl, W. (eds): *European Association of Geoscientists and Engineers Special Publication* 5, 217–235. The Alden Press, Oxford.
- Wagner, L.R. 1998: Tectono-stratigraphy and hydrocarbons in the Molasse Foredeep of Salzburg, Upper and Lower Austria. *Geological Society, London, Special Publications* 134, 339–369.
- Waite, R. & Allmon, W.D. 2013: Observations on the Biology and Sclerochronology of *Turritella leucostoma* (Valenciennes, 1832; Cerithioidea: Turritellidae) from the Gulf of California. *American Malacological Bulletin* 31, 297–310.
- Waite, R. & Strasser, A. 2011: A comparison of recent and fossil large, high-spired gastropods and their environments: the Nopparat Thara tidal flat in Krabi, South Thailand, versus the Swiss Kimmeridgian carbonate platform. *Facies* 57, 223–248.
- Waite, R., Wetzel, A., Meyer, C.A. & Strasser, A. 2008: The paleoecological significance of nerineoid mass accumulations from the Kimmeridgian of the Swiss Jura Mountains. *Palaios* 23, 548–558.
- Wendt, J. 1995: Shell directions as a tool in palaeocurrent analysis. *Sedimentary Geology* 95, 161–186.
- Yonge, C.M. 1946: On the habits of *Turritella communis* Risso. *Journal of Marine Biological Association of the UK* 26, 377–380.