




Influence of abiotic and biotic factors on benthic marine community composition, structure and stability: a multidisciplinary approach to molluscan assemblages from the Miocene of northern Germany

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Abstract: The Miocene mica-clay deposits of Groß Pampau (northern Germany) are well known for their diverse assemblages of marine mammals. Despite numerous systematic and biostratigraphic studies, an in-depth palaeoecological analysis of its molluscan assemblages and a comprehensive palaeoenvironmental reconstruction are lacking. Here, we integrate new faunal, sedimentological and geochemical data to reconstruct the marine palaeoecosystem of the Upper Miocene sedimentary succession of Groß Pampau, and to identify the drivers controlling the composition, ecological structure and temporal dynamics of its macrobenthic molluscan assemblages. Fossil evidence, coupled with analyses of clay mineral composition, grain size distribution and geochemical data (total organic carbon, total nitrogen, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, $\delta^{15}\text{N}$ of sediment and shells), suggests a warm-temperate, mesotrophic, low-energy, offshore marine setting mostly below storm wave base and a pronounced surface-to-bottom water temperature gradient. Low variability in sedimentological and geochemical signals indicates generally

stable physicochemical conditions, whereas the occurrence of the opportunistic species *Varicorbula gibba* suggests occasionally unfavourable bottom conditions, possibly related to transient hypoxia. Canonical correspondence analysis indicates that the distribution of molluscan assemblages correlates with total organic carbon and nitrogen content, suggesting organic matter availability at the sea floor as a controlling factor. A pattern of repetitive punctuated stasis of molluscan assemblages is defined by the temporal persistence in taxonomic and ecological composition, occasionally interrupted by shifts to a different faunal configuration. We suggest that both stable environmental conditions and biotic interactions (i.e. the top-down control exerted by carnivorous gastropods and environmental modification by ubiquitous burrowing deposit feeders) probably contributed to the observed temporal stability.

Key words: Late Miocene, North Sea Basin, palaeoenvironment, molluscan fauna, stable isotopes.

OFTEN referred to as ‘the whales’ graveyard’, the locality of Groß Pampau in northern Germany is famous for its fossil whale remains. The fossils are derived from fully marine mica-clay deposits, which developed in the southeast of the North Sea Basin during the Middle–Late Miocene, and are found today at Groß Pampau, in the commercial gravel and clay pit of the company Kieswerke Ohle & Lau GmbH (Hinsch 1990). Over the past 40 years, excavations yielded highly diverse marine fossil assemblages, which include marine mammals (mainly mysticetes, odontocetes and pinnipeds), remains of chelonid and dermochelyid sea turtles, teeth and skeletal

elements of elasmobranchs, teleost otoliths, and more than 140 species of mollusc (Moths 1989, 1990, 1992, 1994, 1995, 1998, 2003; Höpfner 1991, 2014; Behrmann 1995; Lierl 1995; Hampe 1999, 2006; Kazár & Hampe 2014; Kriwet *et al.* 2015; Montañez-Rivera & Hampe 2020).

Despite numerous studies on the systematics and biostratigraphy of the Groß Pampau succession, an in-depth reconstruction of the Late Miocene marine palaeoenvironment and of the importance of abiotic and biotic parameters that primarily governed the composition and dynamics of its species-rich molluscan assemblages is

lacking. To fill this gap, we used a multidisciplinary approach, comprising palaeoecological, sedimentological and geochemical analyses. Based on new quantitative bed-by-bed sampling, we analysed the taxonomic composition, diversity and ecological structure of macrobenthic assemblages and their dynamic fluctuations through time. For a regional perspective, we compared the Groß Pampau assemblages with contemporaneous benthic molluscan assemblages in the North Sea Basin, in particular those from the Late Miocene of Denmark (Rasmussen 1966). Coupled with new sedimentological analyses of grain size distributions and clay mineral composition, and utilizing geochemical proxy data (total organic carbon, total nitrogen, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $\delta^{15}\text{N}$ of bulk sediment and selected shells), we provide a detailed view of the Late Miocene palaeoenvironmental conditions of the Groß Pampau area. Specifically, we address the following questions: (1) which were the prevailing physicochemical conditions, and how stable or dynamic were these over time; (2) how are benthic molluscan assemblages characterized in terms of species diversity, taxonomic composition, and life-habit and trophic structure, and how stable or variable were they; (3) are there correlative, and thus potentially causative, links between abiotic ecosystem components and the characteristics of molluscan assemblages; and (4) how important were biotic parameters, such as predation pressure, for molluscan assemblage composition and structure and their dynamics.

GEOLOGICAL SETTING

The study area ($53^{\circ} 31' 47.8''$ N, $10^{\circ} 33' 55.4''$ E) is located in the commercial gravel and clay pit of the company Kieswerke Ohle & Lau GmbH in Groß Pampau, northern Germany (Fig. 1). The sedimentary succession of the Pampau area developed south-east of the North German Cenozoic troughs in the North Sea Basin and geographically represents the largest area of pre-Quaternary outcrops in the state of Schleswig-Holstein (Hinsch 1990).

The development of the Miocene sedimentary succession of the North Sea Basin was influenced by tectonic events and marked climatic changes (Jordt *et al.* 1995; Clausen *et al.* 1999; Rasmussen 2004a, 2004b; Larsson *et al.* 2011). At the end of the Early Miocene and beginning of the Middle Miocene, the global warming known as the Miocene Climate Optimum coincided with a distinct sea level rise and deposition of silts and marine sands of the Arnium Formation (Hinsch 1986a; Rasmussen 2004a, 2004b; Rasmussen *et al.* 2010). Meanwhile, in the eastern part of the North Sea Basin, tectonism and uplift of the hinterland led to a major increase of sediment supply and consequent progradation of the

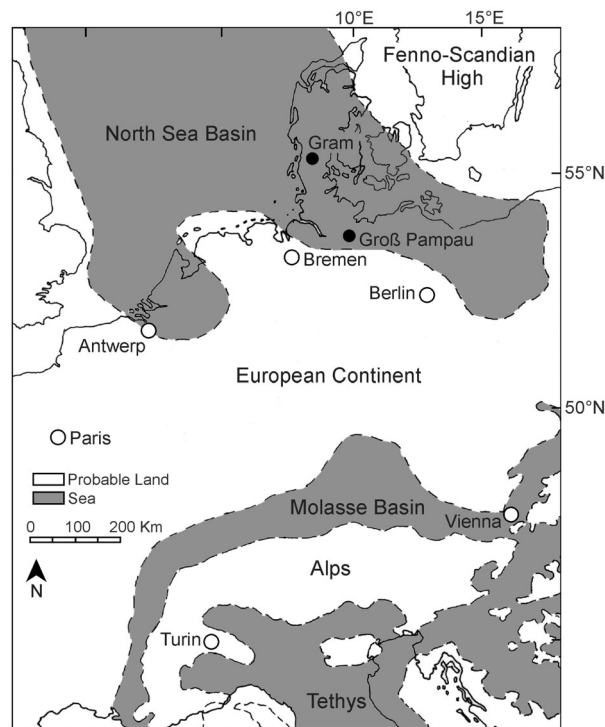


FIG. 1. Palaeogeographical reconstruction of west-central Europe during the Middle–Late Miocene showing the geographical position of the localities of Groß Pampau and Gram (modified from Kriwet *et al.* 2015).

shoreline with the development of the fluvial Upper Brown Coal Sand Formation (Gripp 1964; Hinsch 1986a; Rasmussen 2004a, 2004b; Gibbard & Lewin 2016). Despite the global climatic cooling of the Middle Miocene Climate Transition (13.9 Ma; Westerhold *et al.* 2005), deposition of fine-grained marine sediments (Hodde and Gram formations) dominated the late Middle Miocene to early Late Miocene as a result of increased subsidence of the eastern North Sea Basin (Hinsch 1986a; Rasmussen 2004a, 2004b). Progradation of the coastline continued during the Late Miocene to Early Pliocene, leading to the deposition of shoreface sediments (Morsum Member) and fluvial deposits (Oldesloe Formation) (Hinsch 1986a; Rasmussen 2004a, 2004b). In the Groß Pampau pit, below *c.* 1–3-m-thick Pleistocene deposits, *c.* 17-m-thick mica-rich clay and silt layers of the so-called ‘Oberer Glimmertön’ (Upper Mica-Clay Formation) are exposed (Spiegler & Gürs 1996). Two cored sections (Pampau I and II), drilled in the pit by the Geological Survey of Schleswig-Holstein, showed that the fully marine deposits developed during the late Langhian (Middle Miocene) to early Tortonian (Late Miocene) (Hinsch 1990; Spiegler & Gürs 1996). According to litho- and biostratigraphical comparisons with the adjacent southern Denmark successions, the lower and upper

deposits of the ‘Oberer Glimmerton’ of Schleswig-Holstein are usually referred to respectively as the Hodde and the Gram formations. As a result of transgressive events, the boundary between the Hodde and Gram formations is diachronous and corresponds approximately to a glauconitic clay unit in the upper part of the cored section Pampau I (King *et al.* 2016).

The cores were studied biostratigraphically using benthic and planktonic molluscs (Hinsch 1990; Spiegler & Gürs 1996; Gürs 2002; Gürs & Janssen 2002) and bolboforms (Spiegler & Gürs 1996; Gürs & Spiegler 1999). The benthic molluscan assemblages define the regional sub-stages of the upper Reinbekian to upper Langenfeldian (Hinsch 1990; Spiegler & Gürs 1996). The *Bolboforma* biostratigraphy enabled an accurate calibration of the regional stages, and correlation with the nannoplankton (Spiegler & Gürs 1996) and the planktonic gastropod biozonations (Gürs & Janssen 2002). Additional biostratigraphical studies on the Groß Pampau boreholes and sedimentary succession included calcareous nannoplankton (Martini 2001), and dinoflagellate cysts and foraminifera (Daniels *et al.* 1990). However, due to the absence of key species (Martini 2001) and lack of stratigraphical order in sampling (Daniels *et al.* 1990), correlation with the studied section remains unresolved.

The succession studied herein corresponds to the lower part of the Gram Formation and biostratigraphically correlates with the upper 5–6 m of the borehole Pampau I, as presented in Hinsch (1990). The presence of *Astarte vetula* and *Astarte gleuei* in the lower and upper part of the section, respectively, correlates with the upper Langenfeldian substage (*sensu* Hinsch 1986b, 1990) and the *Bolboforma fragori–subfragoris* and *B. capsula–laevis* zones. Occurrence of the planktonic gastropods *Limacina valvatina*, *Limacina gramensis* and *Limacina ingridae* support the biostratigraphic inferences based on benthic molluscs. In particular, the presence of *L. ingridae* and the concomitant absence of *L. gramensis* in the upper 2 m restrains this part of the section to the *B. capsula–laevis* Zone (Gürs & Janssen 2002). In conclusion, based on the benthic and planktonic molluscs and correlation with the *Bolboforma* biozonation, we infer an approximately early Tortonian age for the studied succession.

MATERIAL AND METHOD

Field work

The 6-m-thick sedimentary succession is located in the north-eastern part of the pit on a south-facing wall (Fig. 2). To investigate the taxonomic and ecological composition of the benthic molluscan fauna, 30 bulk samples of *c.* 20 kg each were collected from uniform

layers of sandy silt at intervals of 20 cm (Fig. 2). Additionally, 30 sediment samples of *c.* 500 g each were taken for sedimentological and stable isotope analyses from the same levels as the faunal samples.

Sedimentological analysis

Grain size analysis was carried out with a combined sieve and areometer analysis. Samples were washed through a sieve with a 63 µm mesh size. The sand fraction was dry sieved in quarter-phi steps. The grain size distribution of the silt and clay fractions was determined by areometer analysis on sub-samples weighing *c.* 30–50 g. The results of the combined sieve and areometer analysis were evaluated using the programs GGU-SIEVE (<https://www.ggu-software.com/geotechnik-software/laborversuche/ggu-sieve-kornverteilung>) and GRADISTAT (Blott & Pye 2001).

To determine the clay mineralogy of the samples, the clay fractions were separated using a centrifuge and smeared onto slides. Each sample was measured three times in a Bruker D2 Phaser x-ray diffractometer with Cu-K α radiation from 3 to 300 2 θ , first after air drying, then after ethylene glycol treatment and finally after heating at 550°C for 1 h. Clay minerals were identified by comparing the three x-ray diffractometer runs. Quantification of the clay mineralogy was performed on the ethylene glycol runs, with the areas of mineral-specific peaks measured with Rigaku’s SmartLab software and converted to relative weight fractions using the weighting factors of Biscaye (1965). We also calculated the clay mineral ratio illite + kaolinite/smectite + chlorite (IK/SC). Variation in this ratio can indicate shifting contributions of clay minerals from different source areas, climatic variations such as those induced by orbital forcing (e.g. Milankovitch cycles), or a combination of both.

Faunal samples

All samples were dried, soaked in water and washed over a 0.5 mm mesh sieve. Residues were treated with 10% H₂O₂ solution and wet-sieved through a 0.5 mm mesh screen. Taxa were identified to the lowest possible taxonomic rank (species or genus). The total dataset consists of 6810 individuals representing 112 benthic taxa of gastropods, bivalves, scaphopods and one brachiopod (Carobene *et al.* 2023, datasheet 1). The benthic fauna occasionally included remains of echinoids and cupulidrid bryozoans. Owing to their fragmentary condition, it was unclear how many complete specimens they represented and thus were not considered further in the quantitative analyses. A total of 3090 occurrences of three planktonic gastropod species were used for biostratigraphical

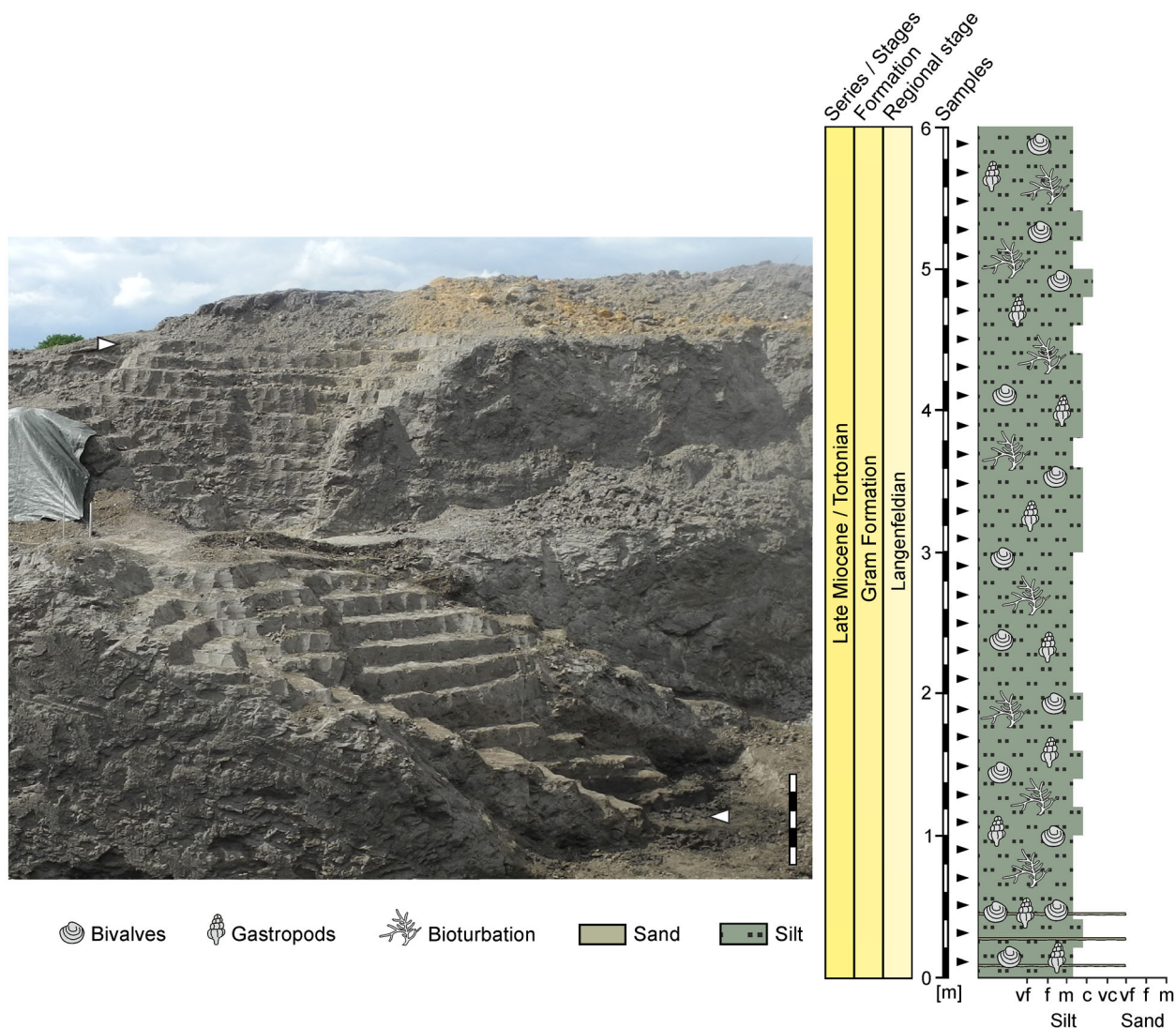


FIG. 2. Field photograph and stratigraphy of the Upper Miocene clay pit of Groß Pampau. Photograph provides view of the north-eastern part of the Ohle & Lau clay pit with sampled section. Note that sampling proceeded from top to bottom, which is reflected in the numbering of the samples. White arrowheads at top left and bottom right indicate the position of quantitative palaeoecological sample S1 and S30, respectively. Stratigraphic log of the sampled section shows position of faunal and sediment samples (black arrowheads). *Abbreviations:* c, coarse; f, fine; m, medium; vc, very coarse; vf, very fine. Scale bar represents 1 m.

placement. We inferred the number of individuals of bivalves and brachiopods by adding the most numerous valves (left–right or dorsal–ventral respectively) to the number of articulated specimens. For gastropods, complete specimens and individual apices were counted as single individuals. For scaphopods, the number of individuals was estimated by counting the number of discrete posterior apertures. To assess whether the faunal assemblages are likely to be (par-)autochthonous relics of former living communities and shells buried in their original habitat, we also calculated the percentage of articulated shells of the six most abundant bivalve species in samples in which a species reached at least 20 individuals

(Table 1). Specimens were deposited at the Museum für Natur und Umwelt Lübeck under the sample inventory numbers MNUL.Pal.100.725–754.

Taxonomy

Taxonomic identifications were based on previous studies (Moths 1989, 1990, 1992, 1994, 1995; Spiegler & Gürs 1996) and relevant literature on stratigraphically coeval and/or geographically close deposits (Ravn 1907; Kautsky 1925; Gilbert 1945; Hinsch 1952; Rasmussen 1956, 1968; Sorgenfrei 1958; Anderson 1964; Janssen 1984;

TABLE 1. Percentage of articulated specimens of the most abundant Late Miocene bivalve species of Groß Pampau, northern Germany.

| Taxon | Samples | Specimens | Articulated specimens (%) |
|-------------------------------------|---------|-----------|---------------------------|
| <i>Yoldiella</i> cf. <i>pygmaea</i> | 25 | 892 | 88.79 |
| <i>Yoldiella spiegleri</i> | 27 | 1108 | 63.63 |
| <i>Astarte gleuei</i> | 2 | 44 | 9.09 |
| <i>Astarte vetula</i> | 4 | 130 | 3.08 |
| <i>Alveinus nitidus</i> | 8 | 293 | 77.82 |
| <i>Varicorbula gibba</i> | 7 | 295 | 32.20 |

Wienrich 1999, 2001, 2007; Schnetler 2005; Janssen & Wienrich 2007; Moths *et al.* 2010; Stein *et al.* 2016). We used open nomenclature qualifiers in the case of poor preservation, insufficient number of individuals to evaluate morphological variability or uncertainty of taxonomic status. The taxonomic position of several groups of the Groß Pampau molluscan fauna will be clarified in a forthcoming revision (R. Janssen & G. Stein, pers. comm. 2020).

Ecological categorization

We categorized the benthic taxa according to three fundamental ecological parameters: mobility level, tiering position relative to the sediment–water interface, and feeding mechanism (Bambach *et al.* 2007; Table 2). We also assign their specific mode of life (MOL): taxon-specific unique combinations of these three ecological parameters that describe the realized ecospace of a community (Bambach *et al.* 2007; Carobene *et al.* 2023, datasheet 2). The ecological classification is based on the Neogene Marine Biota of Tropical America (NMITA) database (<https://nmita.rsmas.miami.edu/>), the Paleobiology Database (<https://paleobiodb.org/>) and the available literature (Table 2). Out of 112 taxa, only one species (the gastropod *Diaphana moerchi* represented by a single specimen) could not be categorized ecologically and was excluded from the MOL-based analyses. Before performing cluster analyses, MOLs represented by only one or two individuals were removed from the database because they have no ecological relevance (non-motile semi-infaunal byssate suspension feeders: *Modiolula* cf. *phaseolina*, one specimen; non-motile epifaunal pedically attached suspension feeders: *Cryptopora nysti*, two specimens).

Statistical analysis

To investigate taxonomical and functional biodiversity through time, we calculated richness and Simpson's index

of diversity for each faunal assemblage. To standardize for differences in sample size, species richness was calculated as rarefied richness, with samples rarefied to 91 individuals (i.e. the size of the smallest faunal sample) and using the *rarefy* function in the *vegan* package in R (Oksanen *et al.* 2019). Simpson's index considers both richness and evenness and is defined as $1-D$, where $D = \sum p_i^2$ and p is the proportional abundance of species i . Simpson's index was computed with the *diversity* function in *vegan*.

To detect recurring faunal and MOL associations, we performed two-way cluster analyses. Q-mode hierarchical clustering (*hclust* function in the *stats* package) identifies groups of faunal assemblages with similar composition and abundance of species or MOLs, here termed faunal associations and MOL associations, respectively. R-mode clustering groups the species or MOLs that tend to co-occur. Clustering was performed on Bray–Curtis distance matrices (*vegdist* function in *vegan*) using Ward's clustering criterion. We applied the similarity profile test (SIMPROF) to determine the number of statistically distinct clusters, calculated with the R package *clustsig* (Clarke *et al.* 2008) and used the default significance level of $p < 0.05$ unless stated otherwise. Illustrations of the two-way cluster analyses applied the *heatmap()* function of the *heatmap* R package. Data were also ordinated using non-metric multidimensional scaling (NMDS) to verify the groupings of species and MOLs identified with cluster analyses. Ordinations were carried out on Bray–Curtis distance matrices, using the *metaMDS* function from *vegan*, with two dimensions and 100 attempts. The fit of the NMDS ordinations was estimated using the stress value: the higher the stress values, the less reliable the NMDS representation, with values lower than 0.2 considered acceptable.

To explore the relationship between species occurrence and the environmental variables measured in this study, we conducted a canonical correspondence analysis (CCA) with the function *cca* (*vegan* package). The isotopic composition of benthic gastropod shells was excluded from the correspondence analysis because the values were not normally distributed. The outputs were displayed in a species-conditional triplot. Sample 5 was excluded from the final dataset given that no total organic content measurement was available. To minimize the influence of rare species, the dataset included only species with a total relative abundance $>0.5\%$. The significance of CCA dimensions and environmental variables was tested using analysis of variance (ANOVA) with 999 permutations, applying the function *anova.cca* (*vegan* package, Legendre *et al.* 2011).

We used Spearman's rank to measure the correlation between the species accounting for most of the variability in faunal associations and the environmental variables. Given that time series can be often spuriously correlated

TABLE 2. Benthic marine macroinvertebrates from the Late Miocene of Groß Pampau, northern Germany and their ecological classification[†]

| Class | Taxon | Mobility | Feeding | Tiering | Remarks and Source |
|-------|--------------------------------------------------|--------------|----------|----------|-----------------------------------------|
| B | <i>Nucula georgiana</i> | Reg-mov | Sub-dep | Shal-inf | Based on <i>Nucula</i> [1;30] |
| B | <i>Yoldia</i> cf. <i>glaberrima</i> | Reg-mov | Sub-dep | Shal-inf | Based on <i>Yoldia</i> [1;2;43] |
| B | <i>Yoldiella</i> cf. <i>pygmaea</i> | Reg-mov | Sub-dep | Shal-inf | Based on <i>Yoldiella</i> [1;2;43] |
| B | <i>Yoldiella spiegleri</i> | Reg-mov | Sub-dep | Shal-inf | Based on <i>Yoldiella</i> [1;2;43] |
| B | <i>Modiolula</i> cf. <i>phaseolina</i> | Non-mot(bys) | Susp | Semi-inf | Based on Modiolinae [1;10] |
| B | <i>Anadara</i> cf. <i>diluvii</i> | Fac-mob(un) | Susp | Semi-inf | Based on <i>Anadara</i> [1;47] |
| B | <i>Bathyarca</i> cf. <i>pectunculoides</i> | Fac-mob(at) | Susp | Epi | Based on <i>Bathyarca</i> [29] |
| B | <i>Limopsis aurita</i> | Fac-mob(at) | Susp | Semi-inf | Based on <i>Limopsis</i> [32] |
| B | <i>Korobkovia</i> sp. | Fac-mob(un) | Susp | Epi | Based on Pallioliinae [1;4] |
| B | <i>Pallolium</i> sp. | Fac-mob(un) | Susp | Epi | Based on <i>Pallolium</i> [1] |
| B | <i>Pecten</i> sp. | Fac-mob(un) | Susp | Epi | Based on <i>Pecten</i> [1;4] |
| B | <i>Pseudamussium clavatum</i> | Fac-mob(un) | Susp | Epi | Based on <i>Pseudamussium</i> [1;4] |
| B | <i>Limatula</i> sp. | Fac-mob(un) | Susp | Epi | Based on <i>Limatula</i> [1;13;47] |
| B | <i>Astarte gleuei</i> | Fac-mob(un) | Susp | Shal-inf | Based on <i>Astarte</i> [40;43] |
| B | <i>Astarte vetula</i> | Fac-mob(un) | Susp | Shal-inf | Based on <i>Astarte</i> [40;43] |
| B | <i>Goodallia waeli</i> | Fac-mob(un) | Susp | Shal-inf | Based on <i>Astarte</i> [40;43] |
| B | <i>Cyclocardia</i> sp. | Fac-mob(un) | Susp | Shal-inf | Based on <i>Cyclocardia</i> [1] |
| B | <i>Axinulus</i> sp. | Fac-mob(un) | Chem | Deep-inf | Based on other Thyasiridae [1;11;22] |
| B | <i>Parvicardium</i> cf. <i>scabrum</i> | Fac-mob(un) | Susp | Shal-inf | Based on <i>Parvicardium</i> [43] |
| B | <i>Abra</i> cf. <i>antwerpiensis</i> | Fac-mob(un) | Surf-dep | Shal-inf | Based on <i>Abra</i> [1;26;50] |
| B | <i>Abra</i> cf. <i>sorgenfrei</i> | Fac-mob(un) | Surf-dep | Shal-inf | Based on <i>Abra</i> [1;26;50] |
| B | <i>Glossus olearii</i> | Fac-mob(un) | Susp | Shal-inf | Based on <i>Glossus</i> [34] |
| B | <i>Alveinus nitidus</i> | Fac-mob(un) | Susp | Shal-inf | Based on <i>Alveinus</i> [1;5] |
| B | <i>Spisula</i> sp. | Fac-mob(un) | Surf-dep | Shal-inf | Based on Mactridae [1] |
| B | <i>Varicorbula gibba</i> | Fac-mob(at) | Susp | Shal-inf | Based on <i>Corbula</i> [1;49] |
| B | <i>Cuspidaria</i> sp. | Reg-mov | Pred | Shal-inf | Based on <i>Cuspidaria</i> [1;39] |
| G | <i>Turritellinella tricarinata</i> | Reg-mov | Susp | Semi-inf | Based on Turritellidae [1;6;48] |
| G | <i>Hemiacirsa lanceolata</i> | Reg-mov | Par | Epi | Based on <i>Acirsa</i> [1;17;23;27] |
| G | <i>Turriscala</i> cf. <i>borealis</i> | Reg-mov | Par | Epi | Based on other Epitoniidae [1;17;23;27] |
| G | <i>Euspira helicina</i> auct. | Reg-mov | Pred | Shal-inf | Based on <i>Euspira</i> [1;7;19] |
| G | <i>Norephora fritschi</i> | Reg-mov | Par | Epi | Based on Triphoridae [1] |
| G | <i>Alvania</i> sp. | Reg-mov | Herb | Epi | Based on <i>Alvania</i> [1] |
| G | <i>Cingula inusitata</i> | Reg-mov | Herb | Epi | Based on <i>Cingula</i> [1] |
| G | <i>Obtusella gottscheana</i> | Reg-mov | Herb | Epi | Based on <i>Obtusella</i> [1] |
| G | <i>Solariorbis pulchralis</i> | Reg-mov | Herb | Epi | Based on <i>Solariorbis</i> [1] |
| G | <i>Circulus</i> cf. <i>hennei</i> | Reg-mov | Herb | Epi | Based on <i>Circulus</i> [1;41] |
| G | <i>Circulus</i> sp. | Reg-mov | Herb | Epi | Based on <i>Circulus</i> [1;41] |
| G | <i>Aclis minor</i> | Reg-mov | Par | Epi | Based on <i>Acirsa</i> [1;38] |
| G | <i>Eulima glabra</i> | Reg-mov | Par | Epi | Based on <i>Eulima</i> [1;38] |
| G | <i>Melanella</i> sp. | Reg-mov | Par | Epi | Based on other Eulimidae [1;38] |
| G | <i>Aporrhais</i> sp. | Reg-mov | Surf-dep | Shal-inf | Based on <i>Aporrhais</i> [24;35] |
| G | <i>Galeodea bicatenata marqueti</i> | Reg-mov | Pred | Shal-inf | Based on <i>Galeodea</i> [2;3;20;47] |
| G | <i>Semicassis</i> cf. <i>laevigata</i> | Reg-mov | Pred | Shal-inf | Based on <i>Semicassis</i> [2;3;20;47] |
| G | <i>Xenophora</i> sp. | Reg-mov | Herb | Epi | Based on Xenophoridae [1;36] |
| G | <i>Calcarata mioparva</i> | Reg-mov | Par | Epi | Based on Cancellariidae [1;33] |
| G | <i>Sveltia</i> cf. <i>lyrata</i> | Reg-mov | Par | Epi | Based on Cancellariidae [1;33] |
| G | <i>Pseudobabylonella</i> cf. <i>fusififormis</i> | Reg-mov | Par | Epi | Based on Cancellariidae [1;33] |
| G | <i>Pseudobabylonella</i> sp. 1 | Reg-mov | Par | Epi | Based on Cancellariidae [1;33] |
| G | <i>Pseudobabylonella</i> sp. 2 | Reg-mov | Par | Epi | Based on Cancellariidae [1;33] |
| G | <i>Pseudobabylonella pampauensis</i> | Reg-mov | Par | Epi | Based on Cancellariidae [1;33] |
| G | <i>Colus gregarius</i> | Reg-mov | Pred | Epi | Based on <i>Colus</i> [1;25;46] |
| G | <i>Liomesus</i> sp. | Reg-mov | Pred | Epi | Based on other Buccinidae [1;25;46] |

(continued)

TABLE 2. (Continued)

| Class | Taxon | Mobility | Feeding | Tiering | Remarks and Source |
|-------|-----------------------------------------------|----------|---------|---------|-------------------------------------|
| G | <i>Macrurella nassoides</i> | Reg-mov | Pred | Epi | Based on <i>Mitrella</i> [1] |
| G | <i>Aquilofusus lüneburgensis</i> | Reg-mov | Pred | Epi | Based on other Fasciolaridae [1;45] |
| G | <i>Latirulus rothi</i> | Reg-mov | Pred | Epi | Based on <i>Latirulus</i> [1;45] |
| G | <i>Tritia mothsii</i> | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Tritia</i> sp. 1 | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Tritia</i> sp. 2 | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Tritia</i> sp. 3 | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Tritia</i> cf. <i>spectabilis</i> | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Tritia sylvensis</i> | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Tritia wienrichi</i> | Reg-mov | Sca | Epi | Based on Nassaridae [1;16] |
| G | <i>Murex spinicosta</i> | Reg-mov | Pred | Epi | Based on <i>Murex</i> [1;45] |
| G | <i>Lyrotyphis</i> cf. <i>sejunctus</i> | Reg-mov | Pred | Epi | Based on other Muricidae [1;45] |
| G | <i>Pagodula semperi</i> | Reg-mov | Pred | Epi | Based on other Muricidae [1;45] |
| G | <i>Amalda</i> cf. <i>obsoleta</i> | Reg-mov | Pred | Epi | Based on Olivoidea [44;45] |
| G | <i>Conilithes poulsenii</i> | Reg-mov | Pred | Epi | Based on <i>Conus</i> [1;45] |
| G | <i>Aphanitoma</i> sp. | Reg-mov | Pred | Epi | Based on Borsoniidae [1;37;45] |
| G | <i>Bathytoma jugleri</i> | Reg-mov | Pred | Epi | Based on <i>Bathytoma</i> [1;37;45] |
| G | <i>Microdrillia serratula</i> | Reg-mov | Pred | Epi | Based on Borsoniidae [1;37;45] |
| G | <i>Pleurotomoides biconicus</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Pleurotomoides mariae</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Nitidiclavus maitrejus</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Spirotropis gramensis</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Haedropleura miocaenica</i> | Reg-mov | Pred | Epi | Based on Conoidea [1] |
| G | <i>Benthomangelia</i> aff. <i>obtusangula</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Oenopta kochi</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Sorgenfreispira tenella</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;45] |
| G | <i>Inquisitor</i> (s.l.) <i>borealis</i> | Reg-mov | Pred | Epi | Based on Conoidea [1;21;45] |
| G | <i>Raphitoma spinosoreticulata</i> | Reg-mov | Pred | Epi | Based on Conoidea [45] |
| G | <i>Teretia anceps</i> | Reg-mov | Pred | Epi | Based on Conoidea [45] |
| G | <i>Teretia</i> sp. | Reg-mov | Pred | Epi | Based on Conoidea [45] |
| G | <i>Pseudotoma</i> sp. | Reg-mov | Pred | Epi | Based on Conoidea [1;18;45] |
| G | <i>Gemmula</i> sp. 1 | Reg-mov | Pred | Epi | Based on <i>Gemmula</i> [1;18;45] |
| G | <i>Gemmula</i> sp. 2 | Reg-mov | Pred | Epi | Based on <i>Gemmula</i> [1;18;45] |
| G | ' <i>Gemmula</i> ' sp. 3 | Reg-mov | Pred | Epi | Based on <i>Gemmula</i> [1;18;45] |
| G | <i>Unedogemmula</i> (s.l.) <i>hanseata</i> | Reg-mov | Pred | Epi | Based on <i>Gemmula</i> [1;18;45] |
| G | <i>Acteon</i> sp. | Reg-mov | Pred | Epi | Based on <i>Acteon</i> [1;51] |
| G | <i>Ringicula promarginata</i> | Reg-mov | Pred | Epi | Based on <i>Ringicula</i> [1;14] |
| G | <i>Ringicula tiedemanni</i> | Reg-mov | Pred | Epi | Based on <i>Ringicula</i> [1;14] |
| G | <i>Pyrunculus</i> cf. <i>elongatus</i> | Reg-mov | Pred | Epi | Based on other Retusidae [1;42;47] |
| G | <i>Volvulella acuminata</i> | Reg-mov | Herb | Epi | Based on <i>Volvulella</i> [1;28] |
| G | <i>Cylichna pseudoconvoluta</i> | Reg-mov | Pred | Epi | Based on <i>Cylichna</i> [1;28] |
| G | <i>Diaphana moerchi</i> | Reg-mov | - | Epi | Based on Diaphanidae [2;31] |
| G | <i>Scaphander</i> sp. | Reg-mov | Pred | Epi | Based on <i>Scaphander</i> [1;12] |
| G | <i>Roxania</i> sp. | Reg-mov | Pred | Epi | Based on Philinoidea [1;2] |
| G | <i>Chrysallida</i> sp. | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Eulimella</i> cf. <i>acicula</i> | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Eulimella</i> cf. <i>scillae</i> | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Eulimella</i> sp. 1 | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Eulimella</i> sp. 2 | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Eulimella</i> sp. 3 | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Megastomia tuexeni</i> | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Odostomia</i> sp. | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Parthenina</i> cf. <i>indistincta</i> | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |

(continued)

TABLE 2. (Continued)

| Class | Taxon | Mobility | Feeding | Tiering | Remarks and Source |
|-------|--------------------------------------|--------------|---------|----------|--------------------------------------|
| G | <i>Turbonilla</i> cf. <i>koeneni</i> | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| G | <i>Turbonilla</i> sp. | Reg-mov | Par | Epi | Based on Pyramidellidae [1;15] |
| S | <i>Fissidentalium floratum</i> | Fac-mob(un) | Sub-dep | Shal-inf | Based on <i>Fissidentalium</i> [2;9] |
| S | <i>Fissidentalium twistringense</i> | Fac-mob(un) | Sub-dep | Shal-inf | Based on <i>Fissidentalium</i> [2;9] |
| S | <i>Laevidentalium</i> sp. | Fac-mob(un) | Sub-dep | Shal-inf | Based on <i>Fissidentalium</i> [2;9] |
| S | <i>Polyschides weinbrechti</i> | Fac-mob(un) | Sub-dep | Shal-inf | Based on <i>Polyschides</i> [2;47] |
| Br | <i>Cryptopora nysti</i> | Non-mot(ped) | Susp | Epi | Based on <i>Cryptopora</i> [8] |

†Numbers in brackets refer to the source of information listed in Appendix S1. B, Bivalvia; Br, Brachiopoda; G, Gastropoda; S, Scaphopoda. *Mobility level*: Fac-mob(at), facultative mobile, attached; Fac-mob(un), facultative mobile, unattached; Non-mot(bys), non-motile, byssate; Non-mot(ped), non-motile, pedically attached; Reg-mov, regularly moving. *Tiering*: Deep-inf, deep-infaunal; Epi, epifaunal; Semi-inf, semi-infaunal; Shal-inf, shallow-infaunal. *Feeding mechanism*: Chem, chemosymbiosis, deposit feeder; Herb, herbivore/grazer; Par, carnivore/parasitic; Pred, carnivore/predator; Sca, carnivore/scavenger; Sub-dep, subsurface deposit feeder; Surf-dep, surface deposit feeder; Susp, suspension feeder.

due to the presence of trends, we detrended the data by applying generalized differencing (McKinney 1990) with the R script by Graeme T. Lloyd (http://www.graemetlloyd.com/pubdata/functions_2.r). All analyses were computed in R (RStudio Team 2020).

Comparison of benthic molluscan faunas from the North Sea Basin

To assess the variability of benthic molluscan faunas in the North Sea Basin that existed penecontemporaneously with the Groß Pampau fauna, we focused on the Late Miocene faunal assemblages of the locality of Gram (stratotype of the Gram Formation) in southwestern Denmark that were documented with quantitative data.

In the borehole Gram BH I (Geological Survey of Denmark, File No. 141.277), Rasmussen (1966) recognized five zones defined by the composition of the benthic molluscan assemblages. Applying the regional benthic molluscs zonation, molluscan zones I and II belong to the *Astarte vetula*–*Aquilofusus luneburgensis* (= Langenfeldian regional stage) Zone, while zones III–V correspond to the *A. reimersi*–*A. semiglaber* (= Gramian regional stage) Zone (Rasmussen 1966). The correlation of molluscan zones I and II with the studied section of Groß Pampau is supported by biostratigraphical evidence, that is, the occurrence of the index fossil *Aquilofusus luneburgensis* and the planktonic gastropods *Limacina valvatina*, *L. gramensis* and *L. ingridae* (Rasmussen 1966; Gürs & Janssen 2002).

To circumvent taxonomic uncertainties at the species level, the faunal comparison was conducted at the genus level, and the original taxonomic assignments in Rasmussen (1966, 1968) were updated following Schnetler (2005)

and Wienrich (2007). Given that quantitative data of the Gram BH I were sampled in a similar way to the data from Groß Pampau, we selected 20 bulk samples from zones I–IV that comprise 2373 individuals (54% bivalves, 42% gastropods, 4% scaphopods) belonging to 78 different genera (52 gastropods, 23 bivalves, 3 scaphopods). The final database consists of 50 samples with a total of 9181 individuals belonging to 101 molluscan genera (Carobene *et al.* 2023, datasheets 3, 4). Bulk samples with less than 28 individuals (samples 6 and 7 from Zone I) and MOLs contributing less than 2% of the overall functional variability (non-motile semi-infaunal byssate suspension feeders; non-motile epifaunal pedically attached suspension feeders) were excluded from the quantitative analyses. The Q-mode cluster analyses were performed with the same distance matrix and clustering criteria as applied in the faunal and functional analyses of the Groß Pampau benthic fauna. To prevent oversplitting of data, we chose a lower significance level ($p < 0.005$) for the SIMPROF test.

Geochemical analysis

To detect potential changes in environmental parameters during the study interval, we carried out geochemical analyses of both bulk sediment (concentrations and stable isotopes of organic carbon and nitrogen) and shells (stable isotopes of carbon and oxygen). For $\delta^{13}\text{C}$ analysis of bulk sedimentary organic matter, c. 50 mg of bulk sediment powder was weighed into a silver foil cup and treated with 2 molar HCl until bubbling ceased. After drying the decalcified samples at 40°C, stable isotope analysis and concentration measurements of nitrogen and carbon were performed simultaneously with a THERMO/

Finnigan MAT V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyser via a THERMO/Finnigan Conflo IV interface in the stable isotope laboratory of the Museum für Naturkunde, Berlin. Standard deviation for repeated measurements of laboratory standard material (peptone) was $<0.15\text{‰}$ for both nitrogen and carbon. Standard deviations of concentration measurements of replicates of our laboratory standard are $<3\%$ of the concentration analysed. Additionally, we calculated the molar total organic carbon to nitrogen ratio (TOC/TN).

We measured the stable carbon and oxygen isotope compositions of shells of four molluscan species: two benthic (*Gemmula* sp.1 and sp.2) and two planktonic gastropods (*Limacina valvatina* and *L. ingridae*). Due to their discontinuous temporal distribution, specimens of *Gemmula* sp.2 and *L. valvatina* were selected from the lower part of the section (600–300 cm and 600–200 cm, respectively), while individuals of *Gemmula* sp.1 and *Limacina ingridae* were picked from the remaining part of the section. To assess interspecies variations in isotopic composition and potential vital effects, we analysed respective congeneric specimens from two samples: S16 for *Gemmula* spp. and S11 for *Limacina* spp.

The analyses include a total of 31 and 158 well-preserved specimens of *Gemmula* spp. and *Limacina* spp., respectively. Owing to their small shell size, on average five specimens of *Limacina* spp. were analysed for each sample. Shells were cleaned with ethanol in an ultrasonic bath. Entire single shells (*Gemmula* spp.) and multiple shells (*Limacina* spp.) were reduced to a fine powder with an agate mortar and pestle. Approximately 100–400 μg of powdered material was put into a clean 10 ml exetainer and sealed with a septum cap (caps and septa for LABCO exetainer 438b). The remaining air was removed by flushing the exetainer with He (grade 4.6) for 6 min at a flow of 100 ml per minute. After flushing, c. 30 μl of anhydrous, phosphoric acid was injected through the septum into the sealed exetainer using a disposable syringe. After c. 1.5 h of reaction time at 50°C, the samples were ready for isotope measurement.

The oxygen and carbon isotope composition in the CO_2 in the headspace was measured using a Thermo Finnigan GASBENCH II coupled online with a Thermo Finnigan Delta V isotope ratio mass spectrometer. Reference gas was pure CO_2 (laboratory grade 4.5) from a cylinder calibrated against the VPDB (Vienna PeeDee Belemnite) standard using IAEA (International Atomic Energy Agency) reference materials (NBS 18, NBS 19). Reproducibility of replicate measurements of laboratory standards (limestone) was $<0.10\text{‰}$ (one standard deviation). All stable isotope ratios are expressed in the conventional delta notation ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$, $\delta^{15}\text{N}$) in per mil (‰) versus AIR nitrogen and VPDB standard.

RESULTS

Sedimentological analysis

The mean grain size of the sediment samples is 5.3 phi (range 4.9–5.7 phi). Most samples can be classified as coarse silt and only a few as very coarse silt. In the Folk (1954) silt-sand-clay triangle diagram, all samples are classified as sandy silt (Fig. 3). The mean level of sorting is 1.5 (range, 1.1–1.9), reflecting poor sorting. Many samples show a bimodal, and some a polymodal grain size distribution. In the field, distinct primary sedimentary structures were not observed in the studied section, which suggests mixing of sediment by bioturbators. Trace fossils occurred throughout the section, except for the lowermost samples (samples 30–28).

The clay mineral composition of the clay fraction of the samples consists of illite (mean, 45%; range, 31–60%), smectite (mean, 31%; range, 21–45%), kaolinite (mean, 21%; range, 11–30%) and chlorite (mean, 2%; range, $<1\text{--}4\%$). Along the section, clay mineral composition and the IK/SC ratio vary irregularly with no trend or cyclicity discernible. A correlation test of clay mineral content and grain size parameters (mean, sorting, skewness, kurtosis) did not show any significant correlations.

Faunal composition and preservation

The macrobenthic fauna of Groß Pampau (Carobene et al. 2023, datasheet 1) is dominated by bivalves (3619 individuals, 26 taxa) in terms of number of individuals

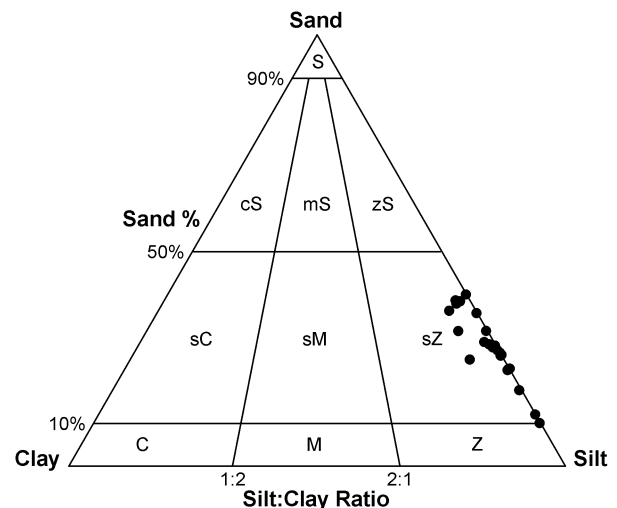


FIG. 3. Position of the Upper Miocene sediment samples of Groß Pampau in the silt-sand-clay triangle diagram of Folk (1954). Abbreviations: C, clay; cS, clayey sand; M, mud; mS, muddy sand; S, sand; sC, sandy clay; sM, sandy mud; sZ, sandy silt; zS, silty sand; Z, silt.

and by gastropods (2816 individuals, 81 taxa) in terms of number of taxa, followed by scaphopods (373 individuals, 4 taxa) and brachiopods (2 individuals, 1 species). Figure 4 shows representative examples of the numerically most abundant molluscan species considered in this study. With regard to life habit and mobility, infaunal taxa (63.3% of the total number of individuals) and regularly moving taxa (75.4%) are most abundant, while sessile species are extremely scarce (0.04%). As to feeding mode, the fauna is composed of deposit feeders (40.8%), carnivores (36.0%) and suspension feeders (18.4%), with herbivores and chemosymbiotic taxa being very rare (4.3%). Except for the two species of *Astarte*, which have moderate values for

valve articulation, the percentage of articulated shells of infaunal bivalves is very high (Table 1). Hence, the high degree of articulation and frequently preserved micro-ornamentation on larval and adult shells suggest that reworking and transport of shells was insignificant, and shells were deposited in their original habitat.

Faunal associations

Cluster analysis resulted in two groups of faunal assemblages separated from each other at a high hierarchical level, here termed cluster A and cluster B, with the latter

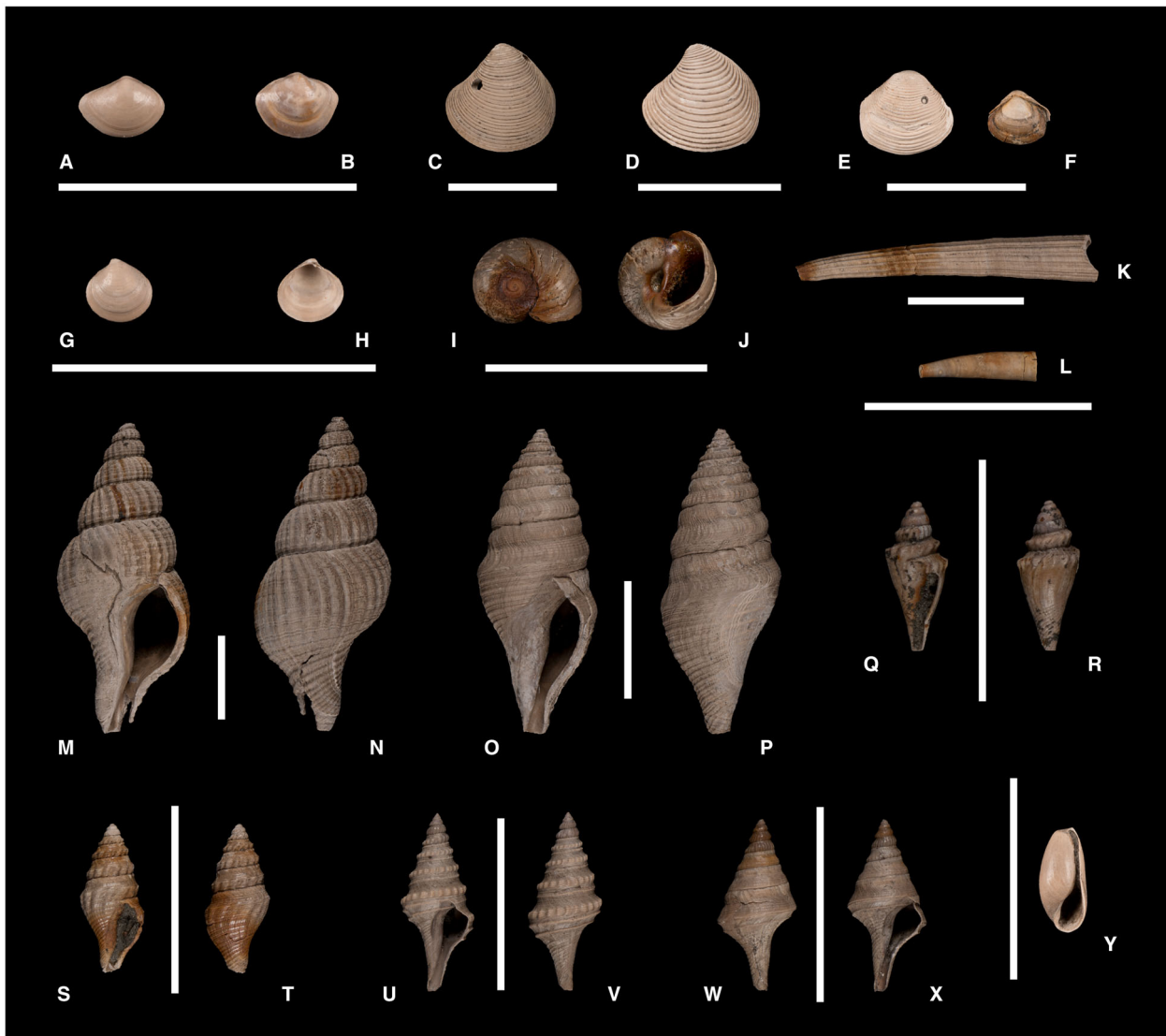


FIG. 4. Illustrations of numerically abundant macrobenthic molluscs from the Upper Miocene of the studied Groß Pampau section. A, *Yoldiella* cf. *pygmaea*. B, *Yoldiella* *spiegleri*. C, *Astarte* *gleuei*. D, *Astarte* *vetula*. E–F, *Varicorbula* *gibba*. G–H, *Alveinus* *nitidus*. I–J, *Euspira* *helicina* auct. K, *Fissidentalium* *floratum*. L, *Polyschides* *weinbrechti*. M–N, *Aquilofusus* *luneburgensis*. O–P, *Bathytoma* *jugleri*. Q–R, *Conilithes* *poulsenii*. S–T, *Benthomangelia* aff. *obtusangula*. U–V, *Gemmula* sp.1. W–X, *Gemmula* sp.2. Y, *Pyrunculus* cf. *elongatus*. All scale bars represent 1 cm.

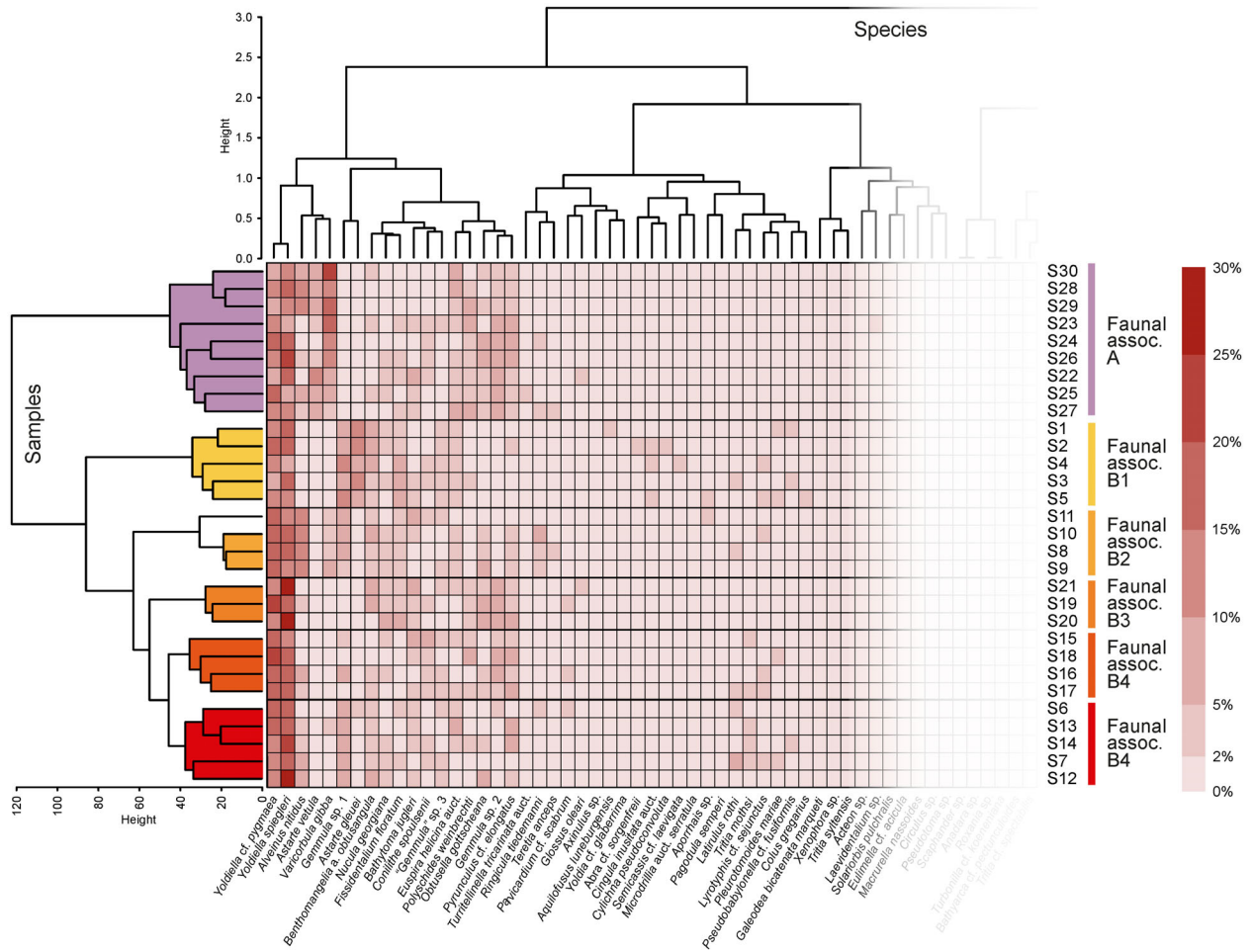


FIG. 5. Heat-map diagram of a two-way hierarchical cluster analysis of Late Miocene faunal assemblages (Q-mode) and benthic macroinvertebrate species (gastropods, bivalves, scaphopods, and brachiopods) (R-mode) from Groß Pampau based on the relative abundance of species. Statistically distinct clusters of faunal assemblages S1–S30 define six faunal associations. Colour coding indicates the relative abundance of species. This figure shows only the segment with species attaining at least 5% relative abundance in any faunal assemblage. The complete two-way cluster diagram, comprising 112 species, is provided in Figure S1.

being subdivided into five statistically significantly different subclusters B1–B5 (Fig. 5). One individual assemblage (S11), statistically distinct from any other assemblage according to the similarity profile test, was included in faunal association B2 upon visual inspection because of its high similarity with the other assemblages of B2 (Fig. 5; Fig. S1, Table S1). NMDS ordination confirms the separation of the six faunal associations along NMDS axis 1 (Fig. 6A). The only overlap in NMDS space occurs for B2 and B5, and is generated by including the isolated assemblage S11 in B2.

Comparison of the faunal associations shows that differences in the relative abundance of the most common taxa are only moderate between assemblages, indicating a fairly even taxonomic composition of the fauna (Fig. 5; Fig. S1, Table S1). None of the species reaches more than 30% relative abundance in any assemblage. Two small-

sized yoldiid bivalve species, *Yoldiella cf. pygmaea* and *Yoldiella spiegeleri*, are the most abundant faunal elements in all associations (Fig. 5; Table S1). At the highest hierarchical level, cluster A differs from B by having relatively high abundances of the bivalves *Varicorbula gibba* and *Astarte vetula*. In contrast, the gastropod *Gemmula sp.1* is a common constituent of most assemblages in cluster B (except for B3), whereas it is absent from A. In cluster B, faunal association B1 has relatively high proportional abundances of the bivalve *Astarte gluei*, whereas this species is absent or rare in other assemblages. The bivalve *Alveinus nitidus* reaches fairly high abundances in B2, and the gastropod *Gemmula sp.2* is common in faunal association B3. Otherwise, although being statistically distinct, the differences between faunal associations in cluster B are small, amounting to only minor differences in the abundance of a few species.

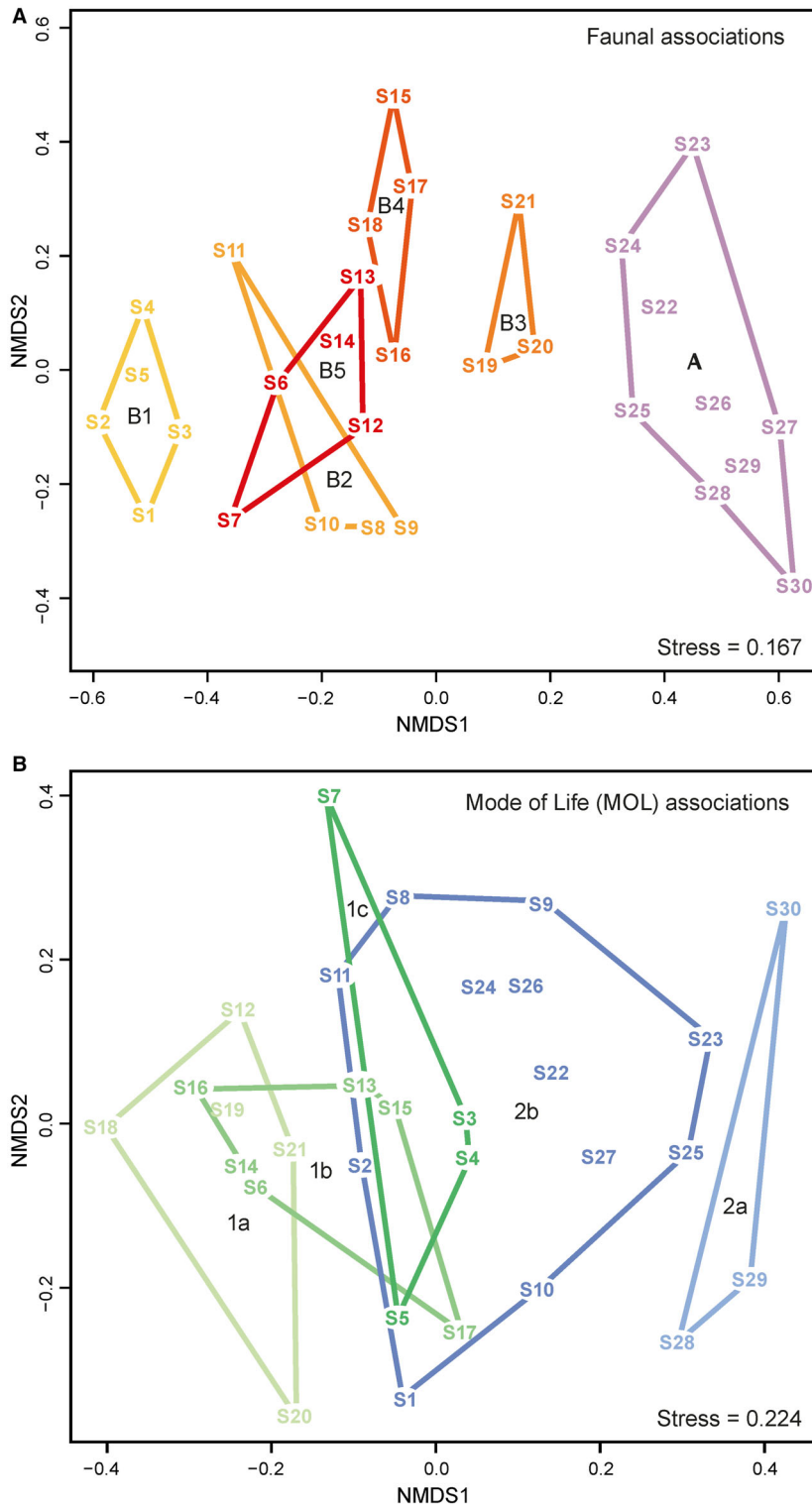


FIG. 6. Ordination analyses on faunal and functional composition of Late Miocene faunal assemblages from Groß Pampau. A, non-metric multidimensional scaling ordination (NMDS) using species composition; colour coding and convex-hull outlines reflect Q-mode clusters of faunal assemblages in Figure 5. B, NMDS of modes of life (MOLs). Colour coding and convex-hull outlines reflect grouping of assemblages in Figure 7.

MOL associations

We identified 10 distinct modes of life (Fig. 7; Table S2), of which three are especially abundant: regularly moving infaunal deposit feeders (MOL1), regularly moving epifaunal carnivores (MOL2) and facultatively mobile infaunal suspension feeders (MOL3). MOL-based cluster analysis shows separation of faunal assemblages into two groups at a high hierarchical level, referred to as MOL clusters 1 and 2, respectively (Fig. 7). MOL cluster 1

differs from 2 by having particularly high abundances of infaunal deposit feeders and epifaunal carnivores, whereas in MOL cluster 2 infaunal suspension feeders constitute an important additional functional component. At lower hierarchical levels, each of the two main clusters is subdivided into statistically distinct subgroupings (MOL associations 1a, b, c and 2a, b). However, differences between subgroupings in each of the main MOL clusters, while evident in the ranking of the constituent MOLs, are fairly minor (Fig. 7; Table S2). In MOL association 1a, infaunal

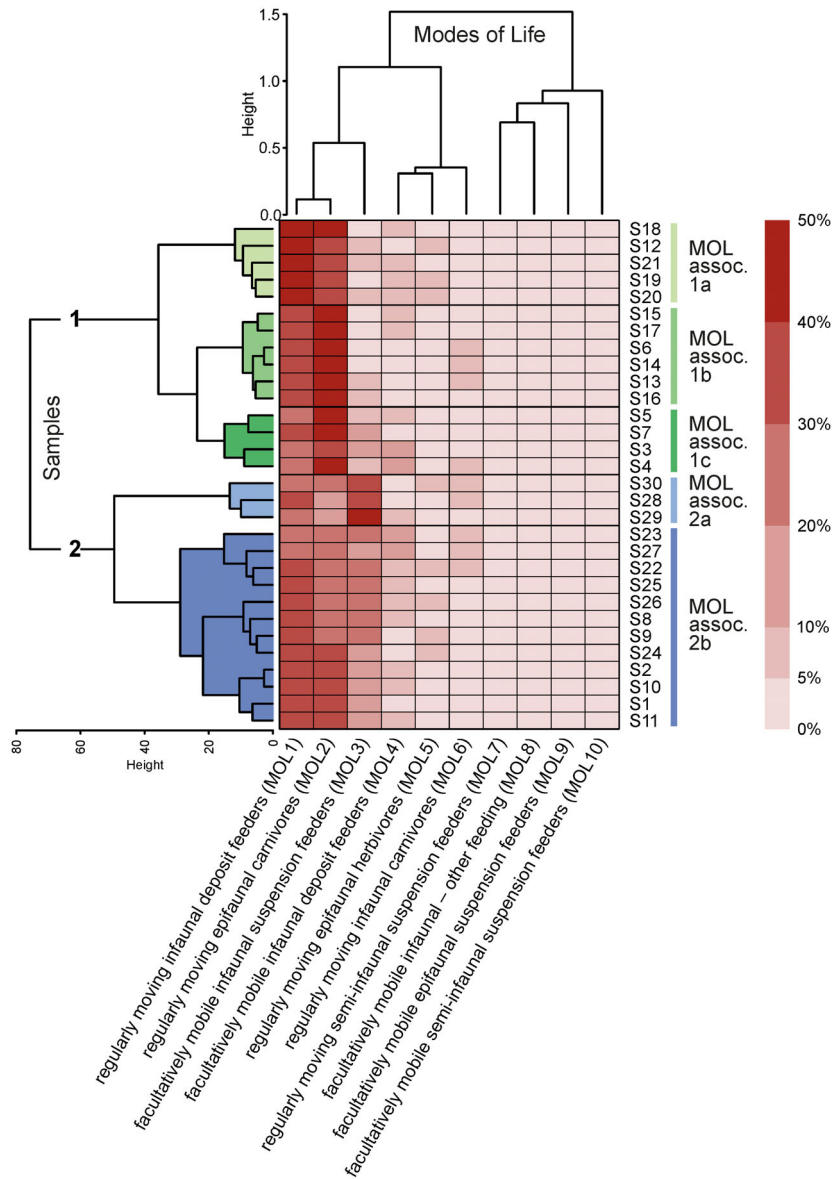


FIG. 7. Heat-map diagram of a two-way hierarchical cluster analysis of Late Miocene assemblages (Q-mode) and benthic macroinvertebrate species (R-mode) from Groß Pampau based on the relative abundances of modes of life (MOLs). Statistically distinct clusters of faunal assemblages S1–S30 define five MOL associations. Colour coding indicates the relative abundance of modes of life. In MOL8, ‘other feeding’ comprises chemosymbionts and surface deposit feeders.

deposit feeders (*Yoldiella* spp.) are most abundant and are followed by epifaunal carnivores, typified by the gastropods *Bathytoma jugleri*, *Benthomangelia* aff. *obtusangula*, *Gemmula* sp.2 and *Pyrunculus* cf. *elongatus*. In MOL associations 1b and 1c, epifaunal carnivores are dominant, mainly consisting of *Conilithes poulsenii*, *Bathytoma jugleri*, *Benthomangelia* aff. *obtusangula* and *Gemmula* spp., whereas infaunal deposit feeders are ranked second. The relatively high proportions of infaunal suspension feeders in MOL associations 2a and 2b are partitioned between several bivalve species, particularly *Varicorbula gibba*, *Alveinus nitidus*, *Astarte gleuei* and *Astarte vetula*.

NMDS ordination based on functional groups supports the separation of MOL clusters 1 and 2 along NMDS axis 1 with some overlap around axis scores of 0.0 (Fig. 6B). Functional similarity between associations of MOL cluster 1 is also evident from the overlap of the convex-hull polygon of MOL association 1b with both 1a and 1c. The arrangement of their faunal assemblages reflects the shift in dominance from infaunal deposit feeders in 1a to epifaunal carnivores in 1b, which is even more pronounced in 1c. Separation of MOL associations 2a and 2b is generated by the prevalence of infaunal suspension feeders in 2a, a feature unique to this MOL association.

Temporal patterns

The two dominant *Yoldiella* species are well represented throughout the succession, whereas distinct temporal changes in relative abundance between common species are observed in four bivalve species (*Astarte gleuei*, *Astarte vetula*, *Alveinus nitidus* and *Varicorbula gibba*) and two gastropod taxa (*Gemmula* sp.1 and *Gemmula* sp.2) (Fig. 8). *Alveinus nitidus* and *Varicorbula gibba* show similar temporal abundance fluctuations, with relatively high values in the lower part of the succession (c. 600–440 cm height) and again from c. 240 to 140 cm. *Astarte vetula* and *Astarte gleuei* occur in the lower and the upper part of the section, respectively. Likewise, *Gemmula* sp.2 becomes rare in the upper half of the section, where *Gemmula* sp.1 is prominent.

The temporal distribution of the six faunal associations exhibits a pattern of general stability in faunal composition across several consecutive assemblages before shifting to a new faunal configuration (Fig. 9). Recurrence of a faunal association at different levels of the succession is evident only in faunal association B5, occurring from 280 to 220 cm and again from 140 to 100 cm. Given the hierarchical nature of clusters, the main shift in species

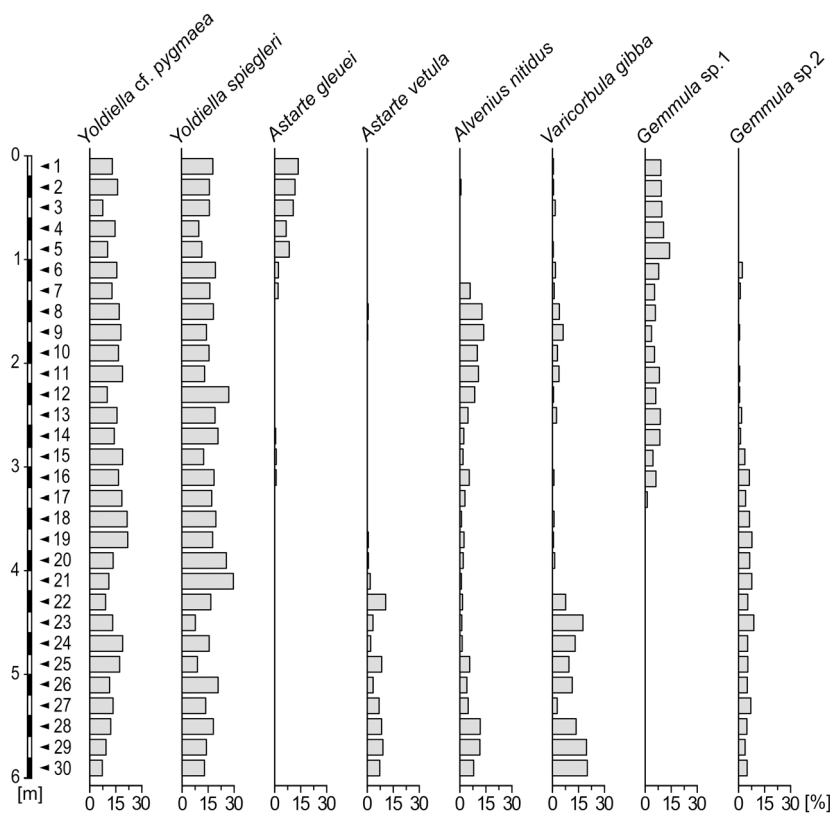


FIG. 8. Relative abundances of the most common Late Miocene bivalve and gastropod species at Groß Pampau.

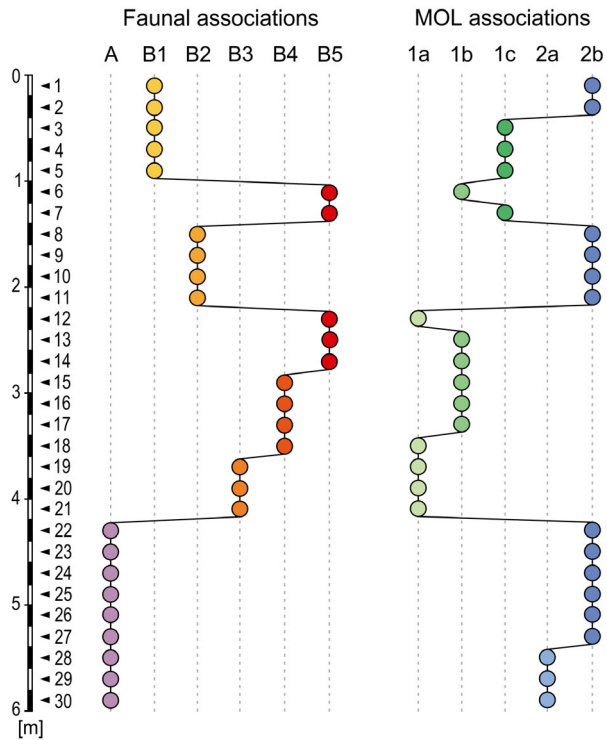


FIG. 9. Stratigraphical distribution of Late Miocene benthic macroinvertebrate associations at Groß Pampau based on species composition (left) and their modes of life (MOLs, right). See cluster analyses in Figures 5 and 7, and Tables S1 and S2, for assignment of faunal assemblages to associations.

composition and abundance is from faunal association A to cluster B and occurs only once: from S22 to S21 at 420 cm.

Assemblage-level rarefied richness fluctuates moderately in a narrow band of 20–30 species without any distinct temporal trend (Fig. 10). Richness appears to fluctuate somewhat more in the lower third of the succession compared with younger parts (Fig. 10). Similarly, Simpson's index is very stable and indicates fairly consistent, very even species abundance distributions.

Temporal changes in the relative abundance of MOLs are apparent in regularly moving infaunal deposit feeders (MOL1), regularly moving epifaunal carnivores (MOL2) and facultatively mobile infaunal suspension feeders (MOL3). The increases in relative abundance of MOL1 and MOL2 in the lower third of the section correspond to a decrease of MOL3 (Fig. 11A). Thereafter, the percentage of MOL1 remains fairly stable whereas MOL2 und MOL3 exhibit a longer-term undulation in opposing directions. Considering the three main ecological categories (mobility level, tiering, and feeding mechanism) separately, we noticed that changes in feeding habits account for most of the MOLs' temporal variability (Fig. 11B). Deposit feeders gradually increase in the lower third of

the section, becoming relatively abundant and stable thereafter. Carnivores show a similar increasing trend, but fluctuate considerably in relative abundance in the upper part of the section. Suspension feeders are abundant in the lowermost samples but then decline across the lower third of the section, stay fairly stable in the middle third, and slightly fluctuate in the upper third of the section.

The temporal distribution pattern of the MOL associations resembles that of the faunal associations, suggesting ecological stability punctuated by shifts to a different functional composition that again remains stable for several consecutive assemblages (Fig. 9). According to cluster hierarchy, the main shift in species composition and abundance from faunal association A to cluster B occurs simultaneously with an ecological shift from MOL cluster 2 to cluster 1 at 420 cm. Also, most other shifts among associations B1–B5 occur contemporaneously or in close temporal proximity with shifts of MOL associations. Similar to taxonomic diversity, functional diversity indices are also fairly constant with no long-term trend and without any abrupt shifts anywhere in the studied interval (Fig. 10).

Comparison of molluscan associations of Groß Pampau and Gram, Denmark

Using genus composition, the Q-mode cluster analysis combining faunal samples from Groß Pampau and Gram resulted in 11 faunal associations (Fig. 12A; Table S3). The associations for Gram mirror the molluscan assemblages already identified by Rasmussen (1966). Cluster analysis shows a complete separation between the benthic molluscan assemblages of Gram and Groß Pampau. This pattern also holds when the clustering is based on presence–absence data (not shown). The bivalve *Yoldiella* dominates most faunal associations at both sites, except for Gram associations 1 and 6 (Table S3). In addition, quantitatively important faunal elements in Gram are the bivalve genera *Limopsis*, *Cyclocardia*, *Astarte* and *Goodallia*, and the gastropods *Tritia* and *Obtusella*, while in Groß Pampau the faunal associations are characterized by the numerically abundant bivalve genera *Astarte*, *Varicorbula*, *Alveinus* and a few prominent gastropod genera (Table S3).

In terms of ecological composition, the MOL-based cluster analysis recognized two main clusters, A and B, the latter being composed of three subclusters, labelled MOL associations B1, B2, and B3 (Fig. 12B). In all four MOL associations the same three modes of life prevail albeit in variable relative abundances (Table S4). At the highest hierarchical level, cluster A is unique in being dominated by infaunal suspension feeders, whereas in B1–B3 infaunal deposit feeders and epifaunal carnivores

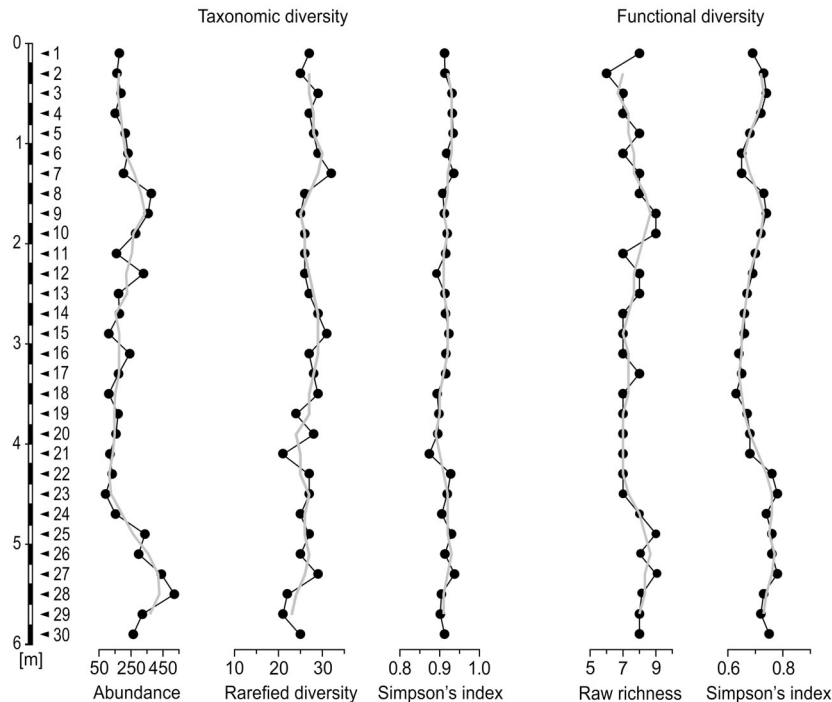


FIG. 10. Macrobenthic abundance and diversity through the Upper Miocene succession of Groß Pampau. Absolute abundance (number of individuals per constant amount of sediment) and various biodiversity metrics of Late Miocene molluscan assemblages based on their taxonomic and ecological composition. Grey lines represent the three-point moving average.

occupy first or second rank. As evident from the assemblages assigned to MOL associations A, B2 and B3, the functional variability of Gram associations closely reflects the one recorded in the lower third of the Groß Pampau section. MOL associations A and B2, which include most of the Gram samples (73% and 85% of each association, respectively), are dominated by infaunal suspension feeders (39.1%) and epifaunal carnivores (33.4%), respectively. In contrast, MOL association B3, mainly represented by Groß Pampau samples (70%), yields a high percentage of infaunal deposit feeders (33.6%) and similar abundances of epifaunal carnivores (25.9%) and infaunal suspension feeders (21.8%). MOL association B1, solely consisting of Groß Pampau samples, is dominated by epifaunal carnivores (39.7%) and infaunal deposit feeders (37.5%).

Stable carbon and nitrogen isotope signatures of bulk sediment, TOC and TOC/TN

The concentration of TOC and TN, the TOC/TN ratio, and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope composition of bulk sediment are shown in Figure 13 and listed in Carobene *et al.* (2023, datasheet 5). All geochemical profiles are relatively stable and consistent over time (Fig. 13). Nitrogen varies between 0.06% and 0.08%, with an average of

$0.07 \pm 0.01\%$, while TOC ranges from 0.92% to 1.76%, with a mean of $1.26 \pm 0.23\%$. The TOC/TN ratio varies from 11.39 to 23.95, with a mean of 15.95 ± 2.90 (Fig. 13). The $\delta^{13}\text{C}$ composition of organic carbon varies between -24.61‰ and -23.48‰ , with a mean of $-24.03 \pm 0.32\text{‰}$. The $\delta^{15}\text{N}$ signature of organic matter ranges from 3.05‰ to 5.31‰ , with a mean of $4.19 \pm 0.44\text{‰}$.

Stable carbon and oxygen isotope signatures of benthic and planktonic gastropod species

The stable isotope compositions of both benthic and planktonic gastropod species are given in Figure 14 and Carobene *et al.* (2023, datasheets 6, 7). Except for two outliers (samples S16 and S26), the $\delta^{18}\text{O}$ composition of *Gemmula* sp.1 and sp.2 is relatively similar and constant throughout the section (*G. sp.1*: mean, $1.82 \pm 0.14\text{‰}$; *G. sp.2*: mean, $1.80 \pm 0.62\text{‰}$). The outliers of *Gemmula* sp.2 in S26 and S16 are most likely to represent false measurements rather than true signals of environmental change (S26) or species-specific vital effects (S16). In the lower part of the section, the $\delta^{13}\text{C}$ composition of *Gemmula* sp.2 ranges from 0.36‰ to 1.56‰ with two outliers (S30 and S27), while in the upper part the $\delta^{13}\text{C}$ values of *Gemmula* sp.1 remain more stable ($0.10\text{--}1.04\text{‰}$). Overall, the

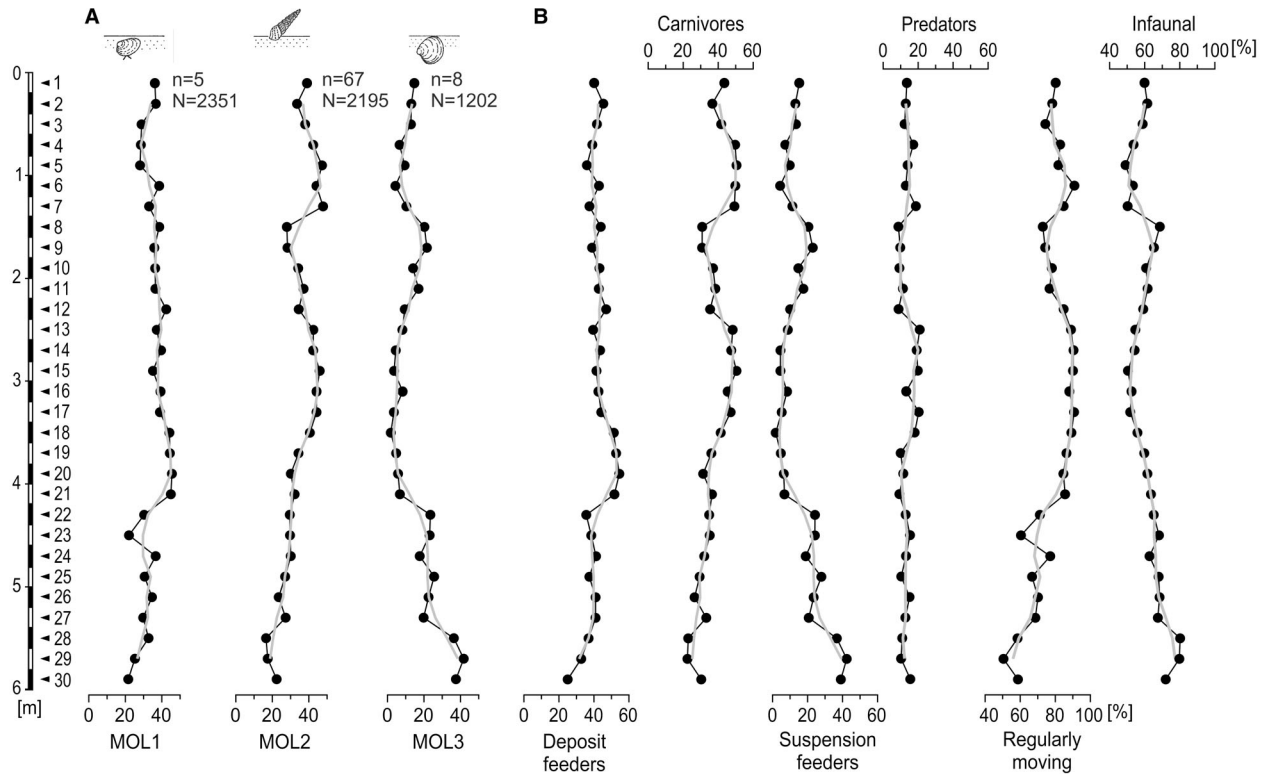


FIG. 11. Abundance of macrobenthic functional groups through the Upper Miocene succession of Groß Pampau. A, relative abundance (%) of the most important modes of life (MOLs). B, relative abundance of the major ecological parameters: feeding mechanism (deposit feeders, carnivores, suspension feeders, predators), mobility level (regularly moving) and tiering (infaunal). Grey lines represent the three-point moving average. *Abbreviations:* n, number of species; N, number of individuals; MOL1, regularly moving, infaunal, deposit feeder; MOL2, regularly moving, epifaunal, carnivore; MOL3, facultatively mobile, infaunal, suspension feeder. For less abundant MOLs see Figure 7.

$\delta^{13}\text{C}$ profile shows a gradual decrease, followed by a slight increase towards the top of the section.

No measurements could be obtained for *L. ingridae* in S4, while the isotopic composition of specimens from samples 1, 2 (*L. ingridae*), 21, 23 and 25 (*L. valvatina*) were not considered further because sample sizes were inadequate for isotope analyses. The $\delta^{18}\text{O}$ values of *L. valvatina* and *L. ingridae* display a slightly greater variability than those of the benthic *Gemmula* species with values ranging from -1.84‰ to 1.32‰ and from -2.41‰ to 0.50‰ , respectively. Except for outliers in samples 17, 12 and 11, the stable oxygen values of both species are fairly similar, suggesting the lack of species-specific isotopic fractionation. This is further supported by the concomitantly low $\delta^{18}\text{O}$ value of *L. valvatina* in S11, indicating an environmental change as the source of the signal. The composite $\delta^{18}\text{O}$ profile exhibits a fluctuating pattern shortly interrupted by a negative shift at 2.1–1.9 m. The $\delta^{13}\text{C}$ composition of *Limacina* species records a single outlier in S11 and a fluctuating pattern with mean values of $1.82 \pm 0.31\text{‰}$ for *L. valvatina* and $1.57 \pm 0.50\text{‰}$ for *L. ingridae*.

Palaeotemperature reconstructions

For the interval from the Middle–Late Miocene boundary into the early Late Miocene, the $\delta^{18}\text{O}$ values of seawater are estimated to range between -0.5‰ and -0.25‰ standard mean ocean water (SMOW) (Lear *et al.* 2000; Billups & Schrag 2002). Palaeotemperature estimates from the $\delta^{18}\text{O}$ composition of benthic and planktonic species, derived from the equation of Böhm *et al.* (2000), along with estimated $\delta^{18}\text{O}$ values of seawater, are presented in Figure 14 and Carobene *et al.* (2023, datasheets 6, 7).

While inferred bottom-water temperatures remain relatively stable throughout the succession, sea surface temperatures oscillate slightly around the mean, with a transient increase in samples 11 and 10. Except for these two samples and disregarding the dubious $\delta^{18}\text{O}$ values of *Gemmula* in S26 and S16 (see above), the bottom and surface temperatures calculated from the remaining samples (and assuming a $\delta^{18}\text{O}_{\text{seawater}}$ value of -0.5‰ SMOW), have mean values of $9.7 \pm 0.7^\circ\text{C}$ and $18.7 \pm 2.6^\circ\text{C}$, respectively. When using a $\delta^{18}\text{O}_{\text{seawater}}$ of -0.25‰ SMOW, palaeotemperature estimates simply

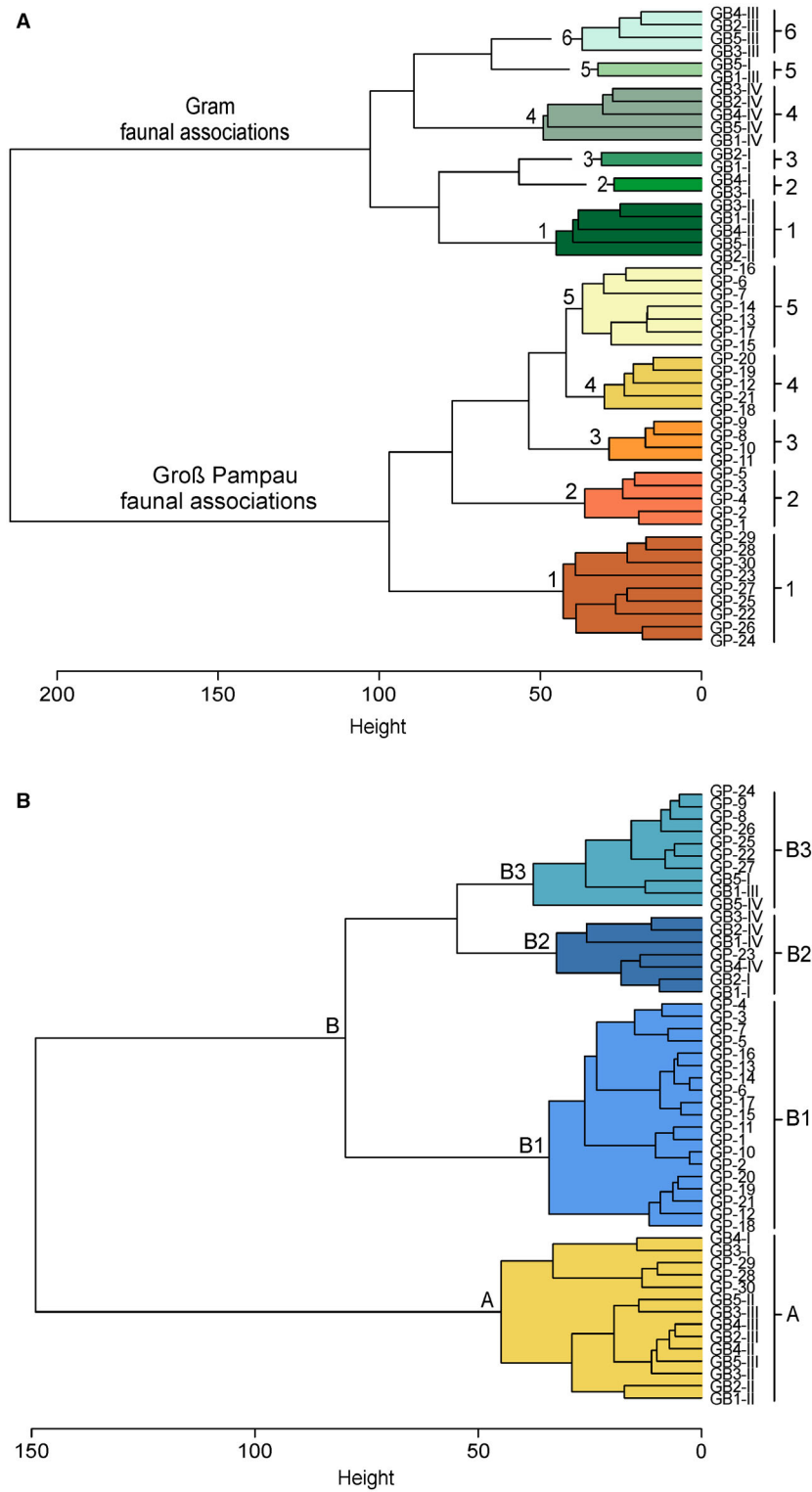


FIG. 12. Q-mode cluster analyses based on the genus-level composition of quantitative samples of benthic macroinvertebrates from Groß Pampau and Gram (Denmark) considering the relative abundances of: A, species; B, ecological groups. *Sample coding:* GB, Gram borehole I; GB-I, Gram borehole, Zone I; GB-II, Gram borehole, Zone II; GB-III, Gram borehole, Zone III; GB-IV, Gram borehole, Zone IV; GP, Groß Pampau. Zones numbered after Rasmussen (1966).

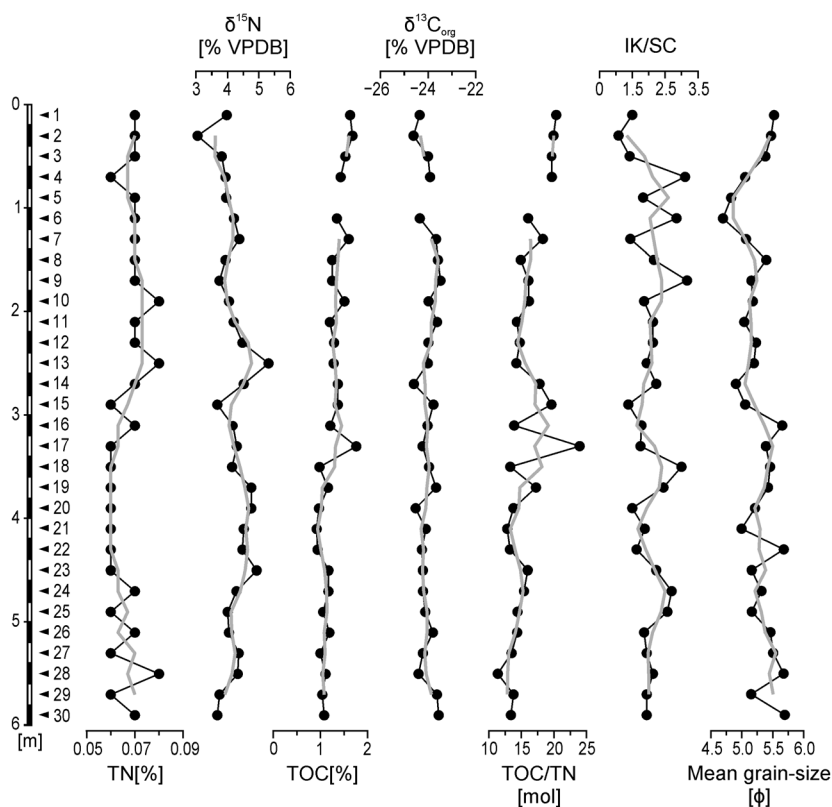


FIG. 13. Geochemical and sedimentological data of Upper Miocene bulk rock samples from the Groß Pampau section. Shown are relative abundances of total organic carbon (TOC) and nitrogen (TN), their isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), the molar total organic carbon to total nitrogen ratio (TOC/TN), the clay mineral ratio (IK = illite + kaolinite; SC = smectite + chlorite), and the mean grain size distribution. Grey lines represent the three-point moving average.

increase by 1.1°C . The offset between surface- and bottom-water temperatures shows a mean value of $8.8 \pm 2.6^\circ\text{C}$.

Canonical correspondence analysis and Spearman's rank-order correlation

CCA axis 1 (CCA1) and CCA axis 2 (CCA2) explain 31.3% of the total variance in the observed species abundances (total inertia = 0.64) and 76.9% of the variance in weighted averages and class total of species with respect to the environmental variables (Fig. 15; Table S5). As shown in Table 3, assemblage structure is significantly associated with TOC (CCA dimension 1, biplot score = 0.97, Eigenvalue = 0.14, F-value = 8.14, $p = 0.001$, Table S5) and marginally influenced by TN content (CCA dimension 2, biplot score = 0.72, Eigenvalue = 0.02, F-value = 3.16, $p < 0.1$, Table S5). In contrast, neither the grain size and clay mineral ratio of the sediment nor the stable isotope ratios of nitrogen and of organic carbon were significantly correlated with assemblage patterns. Taxa and faunal samples clustering at the centre of the

ordination are either not correlated to any of the environmental variables or occur throughout the section, as in the case of *Yoldiella spiegelri* and *Y. pygmaea* (Fig. 15). In contrast to *Gemmula* sp.2 and *A. vetula*, *Gemmula* sp.1 and *A. gleuei* were abundant at the higher TOC values in the upper part of our studied section. *Alveinus nitidus* and *R. tiedemanni* are found at intermediate positive CCA2 values, while *V. gibba* plots at negative CCA1 scores.

When analysing the temporal distributions of the abundant species separately, Spearman's rank-order correlations indicated no significant correlations of *Y. spiegelri*, *Y. cf. pygmaea*, *A. vetula*, the two species of *Gemmula*, and *F. floratum* with any of the analysed environmental factors (Table S6). A significant positive correlation was found between the distribution of *A. nitidus* and $\delta^{18}\text{O}$ ($\rho = 0.46$, $p = 0.01$), and *V. gibba* and the TN content ($\rho = 0.37$, $p = 0.05$), and a negative correlation exists between *A. gleuei* and the clay mineral ratio ($\rho = -0.38$, $p = 0.05$). Thus, with the exception of *V. gibba*, no other species was significantly linked to the variables that dominated assemblage variation (i.e. TOC and TN). However, assemblage structure showed variation along these

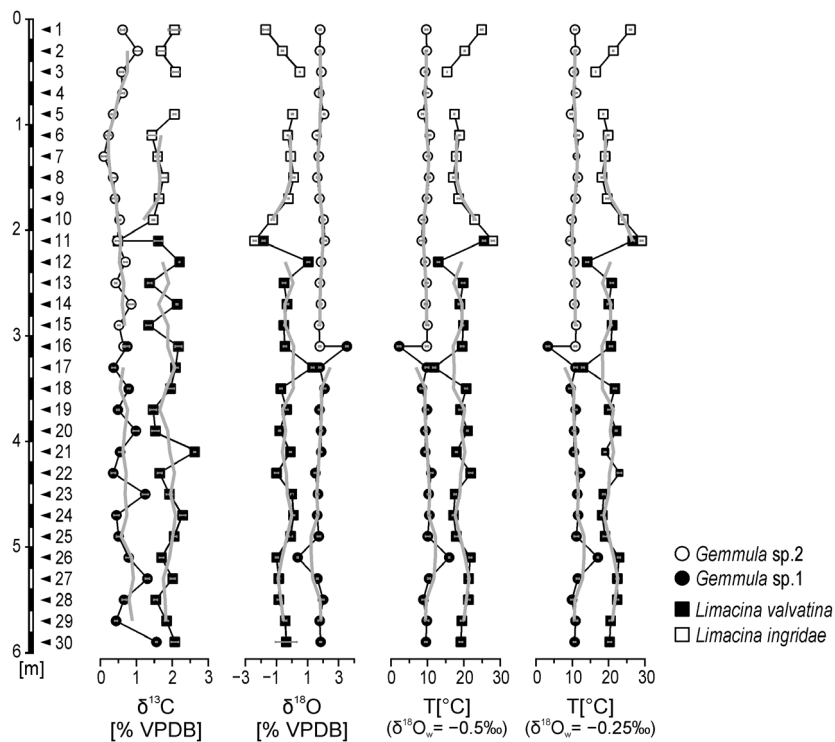


FIG. 14. Carbon and oxygen isotopic composition of the shells of benthic (*Gemmula* sp.1 and *Gemmula* sp.2) and planktonic gastropods (*Limacina valvatina* and *L. ingridae*) from the Upper Miocene of Groß Pampau. Palaeotemperature estimates (T) are calculated from the $\delta^{18}\text{O}$ composition of benthic and planktonic species for two different $\delta^{18}\text{O}$ values of seawater ($\delta^{18}\text{O}_{\text{seawater}} = -0.5\text{‰}$ and $\delta^{18}\text{O}_{\text{seawater}} = -0.25\text{‰}$), and from the absolute temperature, which was computed using the oxygen isotope thermometer of Böhm *et al.* (2000). Grey lines represent the three-point moving average. *Abbreviation:* VPDB, Vienna PeeDee Belemnite.

environmental gradients (Fig. 15). The earliest faunal assemblages S30–S28 are associated with relatively low TOC and high TN values. Faunal assemblages S27–S24 correspond to a fall in TN to lower values, which is continued for assemblages S23–S18. Assemblages S12–S7 are found at higher TN (and $\delta^{13}\text{C}$) values, while S4–S1 are associated with the highest TOC values. Although these changes are not large, they correspond to the subtle temporal changes in TN and TOC, showing that assemblages and environmental conditions are slowly drifting in concert over time.

DISCUSSION

Reconstruction of the Late Miocene benthic ecosystem of Groß Pampau

Our combined sedimentological, geochemical and faunal evidence allows for a reconstruction of the environmental conditions during deposition of the Groß Pampau succession. Overall, the relatively monotonous sedimentary succession, coupled with low variability in geochemical proxy data and relatively high and fairly stable values of

both species richness and evenness, point to fairly uniform environmental conditions, which were generally favourable for molluscan communities. In the following, we reconstruct the Groß Pampau ecosystem in more detail in terms of depositional processes, water depth and water energy, oxygenation, substrate conditions, water temperature and productivity.

Depositional processes and sediment sources. Poor sorting and the often bimodal, partly polymodal grain size distribution suggest differently transported sediment fractions. Although clay and silt were likely to have been deposited by the background settling of suspension load, the sand fraction of the sandy silts might be transported by events such as storms or turbidity currents.

The clay mineral composition of the sediment samples reflects different source areas as well as a climatic influence. Illite, which dominates the clay fractions of most samples, is most likely to have originated predominantly from physical weathering of gneisses and granites of the Precambrian Fennoscandian Shield and was transported to the North Sea by the west-flowing Eridanos River (Gibbard & Lewin 2016). Illite formation was probably favoured by the relatively cooler climate in the Late

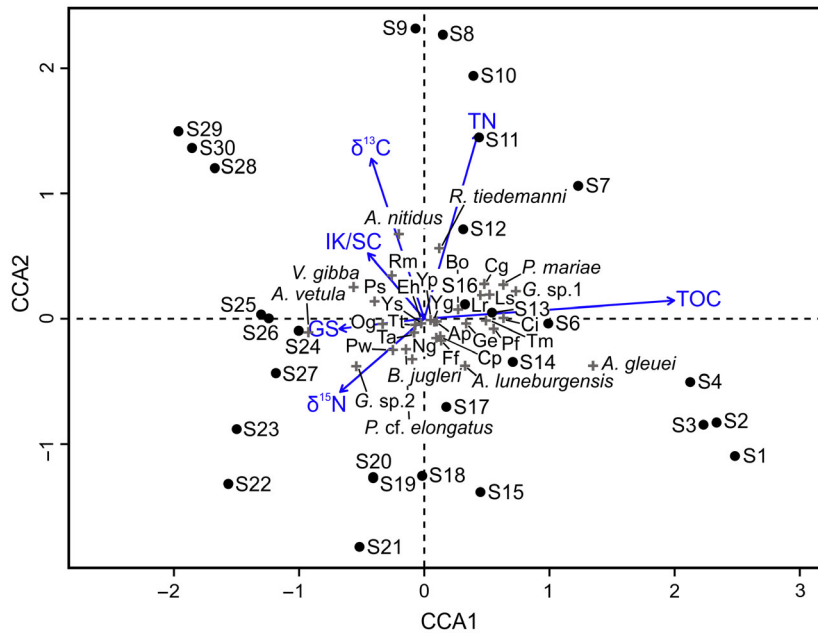


FIG. 15. Results of the canonical correspondence analysis in a species-conditional triplot showing the distribution of Late Miocene assemblages (circles) and species (crosses) from Groß Pampau along the environmental gradients (blue arrows). *Species abbreviations:* Ap, *Aporrhais* sp.; Bo, *Benthomangelia* aff. *obtusangula*; Ci, *Cingula inusitata* auct.; Cg, *Colus gregarius*; Cp, *Conilithes poulsenii*; Eh, *Euspira helicina* auct.; Ff, *Fissidentalium floratum*; G. sp.1, *Gemmula* sp.1; G. sp.2, *Gemmula* sp.2; Ge, ‘*Gemmula*’ sp.3; Lr, *Latirulus rothi*; Ls, *Lyrotypis* cf. *sejunctus*; Ng, *Nucula georgiana*; Og, *Obtusella gottscheana*; Pf, *Pseudobabylonella* cf. *fusiformis*; Ps, *Parvicardium* cf. *scabrum*; Pw, *Polyschides weinbrechti*; Rm, *Ringicula promarginata*; Ta, *Teretia anceps*; Tm, *Tritia mothsii*; Tt, *Turritellina tricarinata* auct.; Yg, *Yoldia* cf. *glaberrima*; Yp, *Yoldiella* cf. *pygmaea*; Ys, *Yoldiella spiegelri*. *Environmental gradient abbreviations:* $\delta^{13}\text{C}_{\text{org}}$, organic carbon isotope composition; $\delta^{15}\text{N}$, nitrogen isotope composition; GS, mean grain size; IK/SC, clay mineral ratio; TN, total nitrogen content; TOC, total organic carbon content.

TABLE 3. Biplot scores of environmental variables against CCA dimensions 1 (CCA1) and 2 (CCA2), followed by the significance of the environmental variables tested using ANOVA-like permutation and the setting ‘by margin’.

| Environmental variables | CCA1 | CCA2 | d.f. | Chi-squared | F-value | p-value |
|------------------------------------|-------|-------|------|-------------|---------|---------|
| TOC | 0.97 | 0.07 | 1 | 0.08412 | 4.868 | 0.001 |
| TN | 0.21 | 0.72 | 1 | 0.03464 | 2.004 | 0.077 |
| $\delta^{15}\text{N}$ | -0.33 | -0.28 | 1 | 0.02463 | 1.425 | 0.184 |
| $\delta^{13}\text{C}_{\text{org}}$ | -0.21 | 0.62 | 1 | 0.02348 | 1.359 | 0.205 |
| IK/SC | -0.22 | 0.25 | 1 | 0.01319 | 0.763 | 0.595 |
| Mean grain size | -0.33 | -0.04 | 1 | 0.01721 | 0.996 | 0.409 |
| Residual | | | 22 | 0.38018 | | |

$\delta^{13}\text{C}_{\text{org}}$, stable carbon isotope composition of organic matter; $\delta^{15}\text{N}$, stable nitrogen isotope composition; IK/SC, clay mineral ratio (illite + kaolinite/smectite + chlorite); Mean grain size, mean grain size distribution; TN, total nitrogen content; TOC, total organic carbon content.

Miocene (Nielsen *et al.* 2015). The Neogene uplift of the Rhenish Slate Mountains and the Carpathians could have created another source of illite (Nielsen *et al.* 2015). It is most likely that smectite was formed primarily by onshore weathering of Palaeogene volcanic ash derived from pyroclastic activity associated with the opening of the North Atlantic (Huggett & Knox 2006) or by its halmyrolysis in seawater (Nielsen *et al.* 2015). Kaolinite

probably originated mainly from the chemical weathering of the Fennoscandian Shield and, as a relatively coarse clay mineral, was preferentially deposited near the coast (Biscaye 1965). Chlorite originated mainly from physical erosion of the Caledonides on both sides of the northern North Sea (Nielsen *et al.* 2015). Being susceptible to chemical weathering, its occurrence was most likely to have been promoted by the cooling of the Late Miocene

climate. The clay mineral composition of the samples roughly corresponds to the clay mineral composition of sediments from offshore areas of the northern North Sea Basin in the Late Miocene (Nielsen *et al.* 2015). This indicates the dominance of supra-regional sediment sources and an offshore depositional environment for the Groß Pampau sediments.

Water depth and energy. Assessment of the water depth of the Groß Pampau benthic environment can be obtained via sedimentological evidence; the proportion of organisms depending on photosynthetic plants as a food source; and by the preferred habitat depth of species that still exist today or that of closely related living species. The monotonous silty facies of the succession indicates that deposition occurred in a low energy environment, mostly below storm wave base. Only the occasional very thin layers (5 mm thick) of very fine-grained sand and thin shell accumulations at the base of the section indicate possible proximity to storm wave base and are interpreted as distal storm beds. Low energy conditions mostly below storm wave base are supported by the high percentage of deposit feeders suggesting that calm water conditions enabled the accumulation of particulate organic matter at the sea floor. Furthermore, the high percentages of articulated bivalves corroborate the calm bottom conditions and the general lack of reworking. The scarcity of herbivores (eight taxa, 4.3% of the total number of individuals) suggests a habitat at the limit of or beyond the photic zone.

Accurate bathymetric preferences are available only for the extant species *Varicorbula gibba*, which commonly thrives on muddy sand bottoms at 10–40 m depth, and occasionally reaches greater depths (down to 250 m; Hrs-Brenko 2006). The living species *Yoldiella philippina* (Nyst), morphologically similar to *Yoldiella cf. pygmaea*, usually lives at depths of 100–300 m and occasionally has been found in shallower habitats up to 25 m (Warén 1989). The preferred habitat depths of the extinct *Astarte vetula* and *Astarte gleuei* are unknown but living astartids usually thrive at depths of 10–150 m. *Alveinus nitidus* is an extinct species of the bivalve family Kelliellidae, the representatives of which inhabit a wide range of habitats, from the continental shelf down to 1000 m depth (Krylova *et al.* 2018). *Gemmula* species are also ubiquitous inhabitants of rather deep environments, ranging from 50 to 500 m depth (Heralde *et al.* 2010). The bathymetric preferences of common Miocene species at Groß Pampau are thus consistent with a water depth of several tens of metres. This estimation agrees with the minimum depth of 40–60 m inferred by Moths (1994) based on the occurrence of elasmobranch species.

Oxygenation of bottom waters and the upper sediment layer. The dominance of shallow infauna and high

diversity and abundances of epifaunal carnivores indicate that oxygenated conditions prevailed at the sediment–water interface and in the uppermost layers of the sediment. However, increased abundances of the opportunistic bivalve *Varicorbula gibba* in the lower third of the section hint at intermittently less favourable conditions, possibly related to transient hypoxia (see below). A position of the redox boundary at relatively shallow depth might explain the absence of deep infaunal burrowers.

Substrate conditions. The burrowing activity of the abundant deposit-feeding nuculanids (*Yoldiella* spp.) probably resulted in a moderately soft substrate and a turbid boundary layer. The fairly soft and potentially turbid bottom conditions and the lack of adequate hard parts may have prevented the settlement and growth of a diverse sessile suspension-feeding epifauna (trophic group amensalism, Rhoads & Young 1970). Likewise, a soft substrate and poor penetration of daylight, as suggested by the scarcity of herbivorous gastropods, may have hampered the growth of macrophytes and algal mats. Nevertheless, a soupy consistency of the substrate is unlikely because morphological adaptations, such as a snowshoe strategy among epifaunal gastropods, are missing, and many mobile epifaunal species were able to colonize the sea floor.

Sea surface and bottom water palaeotemperatures. Stable isotope composition of molluscan shells is a reliable proxy for palaeoenvironmental reconstruction (Kobashi & Grossmann 2003; Lécuyer *et al.* 2004; Latal *et al.* 2006a, 2006b; Reich *et al.* 2015). Given that secretion of the calcareous shell by molluscs usually occurs over several years and in isotopic equilibrium with the ambient water, their shells are likely to record changes in the isotopic composition of ambient water due to global and local palaeoenvironmental factors (Grossman & Ku 1986; Wefer & Berger 1991). The $\delta^{18}\text{O}$ of marine mollusc shells is related to both the temperature and $\delta^{18}\text{O}$ of the seawater (Leng & Lewis 2016). Rather than an increase in temperature, the shift toward isotopically lighter $\delta^{18}\text{O}$ values of *Limacina* spp. at 2.1–1.9 m is more likely to indicate a change in surface water salinity, while $\delta^{18}\text{O}$ values in benthic *Gemmula* suggest that bottom water salinity (and temperature) remained constant. Although freshwater exhibits a wide range of isotopic composition, their values are clearly lower than in marine settings (Latal *et al.* 2006b). A temporary increase in the discharge of freshwater from land (e.g. by a shifting river mouth) is expected to lower the oxygen isotope ratio of surface water, and would explain the isotopically lower $\delta^{18}\text{O}$ values of *Limacina* spp.

With the sampling technique adopted here, the $\delta^{18}\text{O}$ values represent averaged isotopic compositions recorded

throughout the growth of a single shell (*Gemmula* spp.) or multiple shells (*Limacina* spp.). Thus, the conversion of $\delta^{18}\text{O}$ values into seawater temperatures provides corresponding estimates of multi-annual temperatures of both the mixed surface layer and bottom waters, averaged over the growth season. The calculated sea surface temperatures of 18.7°C and 19.8°C, depending on the SMOW values used, are consistent with the continental mean annual temperature of *c.* 17–19°C estimated for the Middle to early Late Miocene of northern Europe using palynological proxies (Larsson *et al.* 2011) and correspond to warm temperate climatic conditions. The pronounced difference in temperature of *c.* 8.8°C between the mixed surface layer and bottom waters implies the presence of a strong seasonal thermocline. An example of a similar present-day oceanographic situation seems to be the Gulf of Lions (France) in the western Mediterranean Sea. Here, a summer thermocline forms at 10–20 m water depth and separates the bottom water with a minimum temperature of 13.5°C from the surface water with a mean temperature of 20°C (Millot 1990; Requena *et al.* 2013). It should be kept in mind that, owing to the geochemical sampling of whole shells, the estimated sea surface temperatures result from a mixed signal of temperature values realized during the whole period of shell growth. Accordingly, surface temperatures during the summer months were probably higher than the calculated average temperatures, and winter temperatures were lower. Consequently, also the temperature differences between surface and bottom waters represent mixed signals. It is quite plausible that a strong thermocline with a marked temperature gradient developed during summer, while ocean mixing occurred during winter, and surface and bottom water temperatures converged.

Biogeochemical cycles and trophic conditions. Although the $\delta^{15}\text{N}$ of sinking organic nitrogen may be altered by contamination with low- $\delta^{15}\text{N}$ bacterial biomass and by diagenetic processes, bulk sedimentary $\delta^{15}\text{N}$ is often used for understanding past and present changes in the ocean cycle of nitrogen (Galbraith *et al.* 2008; Robinson *et al.* 2012). The stability of the bulk $\delta^{15}\text{N}$ signal throughout the studied section excludes any diagenetic alteration.

The $\delta^{15}\text{N}$ signature and TOC concentrations indicate that mesotrophic open marine conditions and a relatively well oxygenated sea-floor environment prevailed during the deposition of the studied succession (Struck 2012). $\delta^{15}\text{N}$ values between 3‰ and 8‰ and relatively low TOC concentrations are usually associated with a nitrogen cycle dominated by nitrate production, in which primary producers are provided with nutrients, influencing the flux of organic matter to the sea floor. The high abundances of deposit feeders in the macrobenthic assemblages and the frequent findings of baleen whales point towards a

relatively high productivity rate, sustaining a diverse food web that also includes carnivores, suspension-feeders and a few herbivores. An indicator of constant primary production is provided by the offset in $\delta^{13}\text{C}$ composition between the shells of benthic and planktonic species. Benthic *Gemmula* species have on average a *c.* 1‰ more depleted $\delta^{13}\text{C}$ composition than the planktonic *Limacina* species, suggesting an isotopic offset between surface and bottom waters. The $\delta^{13}\text{C}$ of the surface water dissolved inorganic carbon was probably ^{13}C enriched, resulting from ^{12}C assimilation by photosynthetic organisms, while bottom waters were ^{13}C depleted due to decomposition of isotopically lighter organic matter on the sea floor (Kobashi & Grossmann 2003).

The sedimentary organic $\delta^{13}\text{C}$ composition and the TOC/TN ratio accurately reflect the source of organic matter preserved in coastal environments (Twichell *et al.* 2002; Mackie *et al.* 2005; Lamb *et al.* 2006). The $\delta^{13}\text{C}$ of marine particulate organic carbon and marine algae is higher compared with that of terrestrial particulate organic carbon (Fig. 16; Lamb *et al.* 2006 and references therein). When analysed together, the relatively low $\delta^{13}\text{C}$ composition of the organic carbon and the TOC/TN of the samples suggest that the organic matter mainly consisted of marine organic carbon with a partial contribution of land-derived material (Fig. 16).

Abiotic drivers of faunal variability

Canonical correspondence analysis combines quantitative species abundance data and environmental data at sites to obtain environmental gradients that maximize the niche separation among species (Ter Braak 1986; Ter Braak & Verdonschot 1995). Our CCA results reveal the influence of two abiotic environmental variables, TOC content and, less distinctly, TN content, on the distribution of the Groß Pampau molluscan fauna (Fig. 15, Table 3). As proxies of productivity and terrestrial runoff, TOC and TN are closely related to each other and reflect changes in organic matter availability at the sea floor, which can affect the composition and ecological structure of macrobenthic communities. Notably, as geochemical conditions remained fairly stable across the section, the TOC and TN gradients in the CCA represent narrow ranges of variation. Nevertheless, this slight variation may have changed the balance of assemblage membership over time in an ecologically meaningful way, such as by altering competition dynamics.

The clustering of the most common species in the middle of the ordination plot indicates the similarity in core members of the Groß Pampau benthic molluscan fauna and its probable ecosystem functioning over time (Fig. 15). The distribution of faunal assemblages along

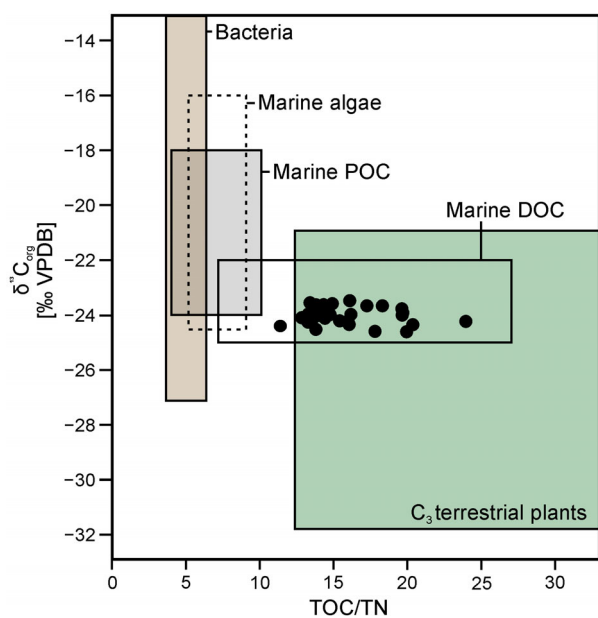


FIG. 16. Organic carbon isotopic composition ($\delta^{13}\text{C}_{\text{org}}$) vs molar total organic carbon to total nitrogen ratio (TOC/TN) for the bulk rock samples of Groß Pampau, showing the partial contribution of land-derived material in the total organic matter of Groß Pampau. Ranges of $\delta^{13}\text{C}$ and TOC/TN compiled after Lamb *et al.* (2006). Abbreviations: DOC, dissolved organic carbon; POC, particulate organic carbon.

the TOC gradient does not correspond to any substantial increase in functional groups usually related to organic enriched sediments, such as deposit feeders or opportunistic species, and is most likely to reflect the generally low variability in total organic matter content. The position of a few species (i.e. *Astarte vetula*, *Gemmula* sp.2, *Gemmula* sp.1 and *Astarte gleuei*) along CCA1 suggests slightly different preferences for organic carbon concentrations that are indicative of subtle but statistically significant assemblage change.

As for CCA2 and the corresponding TN gradient, several species, namely *Ringicula tiedemanni*, *Alveinus nitidus* and *Varicorbula gibba*, were found at intermediate positive CCA2 axis values and low to negative CCA1 values (Fig. 15). Thus, part of the faunal assemblages in faunal association A and those belonging to faunal association B2, in which these species are common constituents, apparently co-vary with the small-scale variation in nitrogen content. The Spearman correlation test yields only one positive and significant covariance: between *V. gibba* and nitrogen concentration, which is consistent with the opportunistic character of this species. The dominance of *V. gibba* in both recent and fossil communities is usually associated with unfavourable environmental conditions and re-colonization of devastated areas (Bernasconi & Robba 1993; Dominici 2001; Mandić & Harzhauser 2003;

Dominici & Kowalke 2007; Zuschin *et al.* 2007; Schneider 2008; Tomašových *et al.* 2018). This species tolerates a wide range of environmental disturbances: seasonal oxygen depletion, chemical pollutants and increased turbidity (Yonge 1946; Hrs-Brenko 2006). In Groß Pampau, the individual abundances of up to c. 20% of *V. gibba* in the lower part of the section (faunal association A) coincide with slightly higher and fluctuating TN proportions (Fig. 13). Nevertheless, both taxonomic (richness and evenness) and functional diversity in this part of the section show variable but relatively high values (Fig. 10). Thus, unlike the monospecific assemblages described from stressful environments, the proliferation and distribution of *V. gibba* were probably controlled by short-term, or low-level environmental stress, such as transient hypoxia or elevated turbidity. Regarding the other concurrent species, low-oxygen tolerance was detected in some extant species of astartids and ringiculids (Diaz & Rosenberg 1995; Dominici 2001). Hence, the co-occurrence of *V. gibba* with *A. vetula*, ringiculids and the generalist *Alveinus nitidus* (Schneider 2008) in faunal association A, and of *V. gibba* with *A. nitidus* and *Ringicula tiedemanni* in faunal association B2, supports the occasional occurrence of less favourable bottom conditions. The positive correlation of *A. nitidus* with the $\delta^{18}\text{O}$ composition of the benthic gastropods and the negative correlation of *A. gleuei* with the clay mineral ratio cannot be explained in terms of ecological requirements of the species. Given the low variation in $\delta^{18}\text{O}$ composition of *Gemmula* spp. and the lack of any significant correlation between the clay mineral ratio and the temporal distribution of faunal assemblages, we consider these correlations as spurious.

Punctuated stasis of faunal associations

The temporal distribution of faunal associations describes a pattern of punctuated stasis, characterized by temporal persistence in taxonomic and functional composition, interrupted by occasional shifts to a different species and MOL composition (Fig. 9). Both external environmental factors and internal ecological interactions have been proposed to underlie the patterns of stability and shifts in community structure over time (Miller 1986, 1997; Brett & Baird 1995; Brett *et al.* 1996; Ivany 1996; Jablonski & Sepkoski 1996; DiMichele *et al.* 2004; Ivany *et al.* 2009). The stabilizing effect that constant ecological conditions exert on communities derives from the observation that taxa with similar environmental preferences tend to occupy the same habitat for as long as that habitat persists (Ivany 1996 and references therein). Thus, it is very likely that the stable physical environmental conditions that occurred throughout the studied succession, as shown by the sedimentological and geochemical data,

contributed to the pattern of species consistency in faunal associations.

As major drivers of community structure, biotic interactions are important in promoting temporal stability of communities (Connell & Slatyer 1977; Morris *et al.* 1995; Ivany 1996; Miller 1997). According to recent studies, it is the diversity of interaction types that determines the ecological structure of communities in nature (Mougi & Kondoh 2012; Quian & Akcay 2020). The effects of predation and competition on community organization have received the majority of attention (Paine 1966; Menge & Sutherland 1976; Pearson & Rosenberg 1987; Chase *et al.* 2002; Holt 2009). Predation can positively or negatively affect community assembly by either enhancing or hampering competition within the same guilds of prey (Bodini 1991; Chase *et al.* 2002; Holt 2009). Community stability and species diversity usually increase when predators promote the coexistence of competing prey species (Chase *et al.* 2002 and references therein). For example, predation on competing prey can alter the diversity and abundance of the prey's resources and increase the probability of coexistence by supporting differences in resource consumption (Chase *et al.* 2002).

In Groß Pampau, the overall functional structure of the fauna is characterized by a great diversity and abundance of carnivorous gastropods. These include predatory species of the shell-drilling families Naticidae (*Euspira*) and Muricidae (*Lyrotyphis*, *Murex* and *Pagodula*), which on average reach 4.7% relative abundance in faunal assemblages. The importance of successful drilling predation can be assessed by the frequency of drillholes. We recorded the frequency of individuals bearing circular boreholes of millimetric size as typically produced by naticids and muricids (Fig. 4 and Carobene *et al.* 2023, datasheet 8). The most abundant species at Groß Pampau, the two species of *Yoldiella*, exhibit very low drilling frequencies (Carobene *et al.* 2023, datasheet 8), although their mobile and infaunal lifestyle itself can be seen as an antipredator strategy (Vermeij 1987; Aberhan *et al.* 2006). Similarly, drilling frequencies for most other species with at least one bored specimen are mostly low (less than 3%). Among the highest drilling frequencies are those found in the two abundant species of *Astarte* (8.7% and 8.1% on average, respectively). An even higher frequency is associated with *Turritellinella tricarinata* (17.1%), although the sample size of this species (35 specimens) is relatively small. Other, mostly non-drilling predatory gastropods that are common in Groß Pampau, and are known to have molluscs among their prey in modern communities (Table 2 and references therein), belong to the neogastropod clades Buccinidae (*Colus*), Conidea (*Conilithes*), Fascioliidae (e.g. *Aquilofusus* and *Latirulus*) and to Retusidae (*Pyrunculus*). However, owing to the lack of distinct signatures of predation in the prey's shells,

it is not feasible to estimate the predation intensity exerted by non-drilling predatory gastropods from the fossil record. We tentatively infer that it is quite likely that the continuous and frequent presence of predatory gastropods (Fig. 11B) exerted appreciable predation pressure on the Miocene molluscan assemblages of Groß Pampau, albeit at a level that cannot be assessed more precisely. Owing to the stabilizing role of predators, we hypothesize that predatory gastropods exerted a top-down control on the communities, contributing to the relatively high taxonomic diversity and stability of the Groß Pampau faunal associations.

An alternative or additional mechanism that would explain the stable species composition is ecological incumbency. Ecological incumbency or priority effects consist of competitive interspecies-level interactions, in which the incumbent taxa are advantaged over newly entering taxa because their population is numerically stronger than that of the invading species (Jablonski & Sepkoski 1996). This is especially the case when priority effects derive from niche pre-emption (i.e. the reduction of resources available to other potentially invading species by early arriving species; Fukami 2015). Given that predators can weaken the competitive ability of prey, high predation pressure is usually related to decreased priority effects (Chase *et al.* 2009; Fukami 2015). However, priority effects can also prevent invasion by niche modification. In niche modification, incumbent species directly or indirectly modify the type of niches available in a local site with negative effects on the ecological conditions required by the newly arriving species (Fukami 2015). For the Late Miocene benthic ecosystem at Groß Pampau, a physical modification of the environment by the ubiquitous burrowing deposit feeders might have led to ecological incumbency effects on suspension feeders (trophic group amensalism), thereby favouring the temporal persistence of faunal associations.

The stability of faunal associations over longer time-spans is from time to time interrupted by changes to a somewhat different taxonomic and functional composition (Fig. 9). These occasional shifts to differently composed faunal associations and, for example, the conspicuous stratigraphic distribution of the two species of *Gemmula* and the two species of *Astarte* (Fig. 8), cannot be explained by any obvious change in the abiotic environment, be it grain size or clay mineral composition of the substrate or in the geochemical proxy data (Figs 13, 14). This also holds for the most pronounced shift in species composition from faunal association A to those of cluster B in assemblage S21 (Fig. 9). Only the inferred ecological adaptations of the bivalves *Varicorbula gibba* and *Astarte vetula*, both common elements of A but rare thereafter, hint at a somewhat less favourable environment, possibly with transient hypoxic conditions or elevated turbidity (see above). Thus, the higher proportions

of infaunal suspension feeders in MOL cluster 2 than in cluster 1 would only be an epiphenomenon, brought about by two stress-resistant bivalve species that happen to be suspension feeders. For the other shifts in taxonomic and ecological composition we can only speculate on whether the observed pattern is related to subtle changes in environmental conditions, such as the low variation in TOC content. Alternatively, deterministic ecological processes (e.g. driven by variations in the abundance of predatory gastropods; Fig. 11B) may have been important (Chase *et al.* 2009), although no statistically significant relationship is evident. Finally, shifts to a different faunal association might derive from stochastic biological processes such as vagaries in the recruitment and dispersal of larvae.

Comparison of Late Miocene molluscan assemblages of the southern North Sea Basin

Given the similar low-energy offshore settings of Groß Pampau (northern Germany) and Gram (southwestern Denmark) and marine connectivity between both sites, it seems surprising that cluster analysis at the genus level showed total separation of their molluscan assemblages (Fig. 12A). Many molluscan genera, mostly gastropods, were found only at Groß Pampau (23 genera) or at Gram (14 genera) (Carobene *et al.* 2023, datasheet 3). Although these 37 genera tend to be rare, differences are also evident in the relative abundance of genera common to both localities. Among the abundant genera, *Yoldiella* is ubiquitous, whereas the percentages of a few prominent bivalve genera (*Limopsis*, *Cyclocardia*, *Goodallia*, *Varicorbula* and *Alveinus*) differ distinctly within and between the two localities.

While *Limopsis* and/or *Cyclocardia* are important faunal elements of Gram associations 1–3, composed entirely of samples from Gram, they only rarely occur in the assemblages of Groß Pampau (0.5% of the total number of individuals). However, literature and field observations confirm the presence of *Limopsis* and *Cyclocardia* in the metacommunity of Groß Pampau (Hinsch 1990; Spiegler & Gürs 1996). In the Middle–Upper Miocene mica-clay deposits of Schleswig-Holstein and Mecklenburg-Vorpommern, *Limopsis* and *Cyclocardia* assemblages are usually associated with the deepest water conditions (Hinsch 1987, 2000, 2001). Therefore, we infer that, at the time of deposition of the sampled part of the Groß Pampau succession, the bathymetric position at Gram was probably slightly deeper than in Groß Pampau. Furthermore, the decrease of *Limopsis* and *Cyclocardia* in Gram associations 4–6, and the concurrent increase of comparatively shallower water taxa such as *Yoldiella*, *Goodallia* and *Astarte*, are consistent with a shallowing-

upwards trend in the Gram Formation (Rasmussen 1966; Piasecki 2005).

The peak abundances of *Varicorbula* and *Alveinus* in Groß Pampau associations 1 and 3 are in contrast to their virtual absence in Gram BH I. Owing to the opportunistic character of *Varicorbula gibba* (Yonge 1946; Hrs-Brenko 2006), this difference suggests that those assemblages in the lower part of the Groß Pampau section that yielded abundant *Varicorbula* experienced some degree of oxygen depletion, whereas oxygenated conditions prevailed throughout at Gram. For the early Gram clay deposits at Måde (Jutland, Denmark) belonging to the *A. vetula* Zone, Rasmussen (1966) inferred unfavourable reducing environmental conditions on the basis of the high pyrite content and the small-sized shells of molluscan assemblages. However, no similar qualitative observations were reported from the molluscan zones of Gram BH I. If the low values of raw richness at the base of Gram BH I are due to unstable conditions, their subsequent increase suggests that more favourable ecological conditions were eventually established at Gram as proposed by Piasecki (2005). Regarding ecologically defined associations (Fig. 12B), all assemblages from Gram occur in MOL associations that also contain assemblages from Groß Pampau. This ecological congruence shows that despite differences in genus composition and abundances, the benthic molluscan ecosystems at both sites operated in a very similar manner.

CONCLUSION

Our multidisciplinary approach, integrating quantitative sedimentological, geochemical and faunal analyses, provides an in-depth reconstruction of the ‘Glimmerton’ palaeoenvironment at Groß Pampau and the biotic and abiotic factors controlling its diverse molluscan assemblages. The studied 6-m-thick upper part of the fully marine succession is early Tortonian in age. Small grain size and clay mineral composition indicate an offshore depositional setting. The monotonous silty facies and faunal evidence suggest a low-energy habitat, mostly below storm wave base, at a water depth of several tens of metres. Constant and relatively high rates of primary production are supported by nitrogen isotope values, the offset in $\delta^{13}\text{C}$ composition between benthic and planktonic species and the high proportion of deposit feeders in the macrobenthic assemblages. Along with land-derived organic matter, high primary productivity apparently maintained a complex marine food web. The $\delta^{18}\text{O}$ composition of planktonic gastropod shells indicates a mean surface water temperature of 18.7°C and 19.8°C depending on the value used for standard mean ocean water, which is in accordance with the warm temperate climate conditions estimated for the Middle to early Late

Miocene of northern Europe. By contrast, bottom water temperatures determined from the $\delta^{18}\text{O}$ composition of benthic gastropods were *c.* 9°C lower on average, resulting in a pronounced thermal gradient from surface to bottom waters and a marked summer thermocline.

Low variability in sedimentological and geochemical proxies coupled with the relatively uniform taxonomic and functional composition of the fauna indicate generally stable and favourable ecological conditions for benthic molluscan communities. Although correlation does not necessarily indicate causation, statistical analyses suggest that the most important abiotic environmental factors influencing the distribution of faunal assemblages seem to be total organic carbon content and total nitrogen content. In terms of individual responses of species to environmental factors, the positive correlation between the opportunistic bivalve species *Varicorbula gibba* and total nitrogen concentration suggests occasionally less favourable bottom conditions, possibly related to transient hypoxia.

The temporal distribution of faunal associations defines a pattern of punctuated continuity, with taxonomic and functional composition persisting over time before shifting to a somewhat different configuration, which in turn remains stable for some time before shifting again. Prevailing stable environmental conditions most likely were not the only prerequisite for taxonomic and ecological consistency. We envisage top-down control by numerous predatory gastropods and/or niche modification by incumbent deposit feeders as an important additional factor for faunal stability, whereas the causes of faunal shifts remain speculative.

Comparison with the Late Miocene molluscan assemblages of the palaeoenvironmentally similar succession at Gram, Denmark, indicates differences in the composition and relative abundance of constituent genera. However, the pronounced ecological congruence of their molluscan assemblages indicates that the offshore macrobenthic ecosystems of the southern North Sea Basin functioned very similarly.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0p2ngf253>.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1496>):

Appendix S1. Data sources for Table 2.

Fig. S1. Heat-map diagram of a two-way hierarchical cluster analysis of Late Miocene faunal assemblages (Q-mode) and 112 benthic macroinvertebrate species (gastropods, bivalves, scaphopods, and brachiopods) (R-mode) from Groß Pampau based on the relative abundances of species. Statistically distinct clusters of assemblages S1–S30 define six faunal associations. Colour coding indicates the relative abundance of species.

Table S1. Late Miocene macrobenthic associations of Groß Pampau based on cluster analysis (Fig. 5) with relative abundance and presence percentage of species attaining at least 1% relative abundance.

Table S2. Late Miocene functional associations of Groß Pampau based on cluster analysis (Fig. 7) with relative abundance and presence percentage of modes of life.

Table S3. Late Miocene molluscan associations of Gram borehole I zones I–IV (GB) and Groß Pampau (GP) based on cluster analysis (Fig. 12A) with relative abundance and presence percentage of genera attaining at least 1% relative abundance.

Table S4. Late Miocene functional associations of Gram borehole I zones I–IV (GB) and Groß Pampau (GP) based on cluster analysis (Fig. 12B) with relative abundance and presence percentage of modes of life.

Table S5. The top six rows show the biplot scores of the environmental variables against the CCA dimensions, followed by eigenvalues and cumulative proportions explained by the CCA

dimensions and their significance as tested by the ANOVA-like permutation test.

Table S6. Spearman's rho and significance level of the correlation between the most abundant species and environmental variables.

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