

Article

The environmental factors limiting the distribution of shallow-water terebratulid brachiopods

Diego A. García-Ramos , Stjepan Čorić , Michael M. Joachimski , and Martin Zuschin 

Abstract.—The Cenozoic genus *Terebratula* seems to be an exception to the post-Permian trend in brachiopod retreat to offshore habitats, because it was species rich and numerically abundant in warm-temperate shallow-water environments in the Mediterranean and the Paratethys realms. This was so despite the general dominance of bivalves and the pervasive bioturbation and predation pressure during the Neogene. *Terebratula*, however, went extinct in the Calabrian (Pleistocene). The optimal environmental conditions for *Terebratula* during its prime are poorly known. The Águilas Basin (SE Spain) is an ideal study area to investigate the habitat of *Terebratula*, because shell beds of this brachiopod occur there cyclically in early Pliocene deposits. We evaluate the paleoecological boundary conditions controlling the distribution of *Terebratula* by estimating its environmental tolerances using benthic and planktic foraminiferal and nannoplanktic assemblages and oxygen isotopes of the secondary layer brachiopod calcite. Our results suggest that *Terebratula* in the Águilas Basin favored oligotrophic to mesotrophic, well-oxygenated environments at water depths of 60–90 m. Planktic foraminiferal assemblages and oxygen isotopes point to sea-surface temperatures between ~16°C and 22°C, and bottom-water temperatures between 17°C and 24°C. The analyzed proxies indicate that *Terebratula* tolerated local variations in water depth, bottom temperature, oxygenation, productivity, and organic enrichment. *Terebratula* was probably excluded by grazing pressure from well-lit environments and preferentially occupied sediment-starved, current-swept upper offshore habitats where coralline red algae were absent. Narrow temperature ranges of *Terebratula* species might have been a disadvantage during the high-amplitude seawater temperature fluctuations that started about 1 Ma, when the genus went extinct.

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Introduction

Brachiopods were the most successful benthic marine animals during the Paleozoic (Thayer 1986), with about 400 species remaining today (Emig et al. 2013). In Recent seas, terebratulids are by far the most successful of all brachiopod clades (Lee 2008). Like other representatives of the subfamily Terebratulinae, such as *Pliothyridina* and *Maltaia*, some species of “*Terebratula*” appear to stand as an exception to the general progressive trend of brachiopod retreat to deep and/or cryptic habitats after the Permian–Triassic mass extinction (Tomašových 2006). This is because Terebratulinae were numerically abundant above the storm-

weather wave base (Kroh et al. 2003; Gramigna et al. 2008; Pervesler et al. 2011), much like other Terebratulida can dominate in present-day, shallow-water hard-bottom environments (Logan and Noble 1971; Richardson 1981; Försterra et al. 2008; Tomašových 2008). European Terebratulinae, however, went extinct in the Calabrian (approximately during or shortly after the Jaramillo Subchron), not surviving beyond the Sicilian (D’Alessandro et al. 2004; Taddei Ruggiero and Taddei 2006; La Perna and Vazzana 2016; Crippa et al. 2019), with the last species being *Terebratula terebratula* and *Terebratula scillae*. Although Neogene and Pleistocene *Terebratula* had to cope with specialized predators, niche competitors (bivalves),

and bulldozing and grazing marine organisms (Thayer 1983), it thrived mainly in warm-temperate shallow-water detritic-bottom habitats in the Paratethys and the Mediterranean realms (Pedley 1976; Bitner and Pisera 2000; Reolid et al. 2012). There are also reports from subtropical environments, where species of *Terebratula* infilled cavities in *Porites*–*Tarbellastraea* reefs during the Tortonian (Barbera et al. 1995) or were present on the distal slope of *Porites* fringing reefs during the lower Messinian (Llompart and Calzada 1982; Obrador et al. 1983; Videt 2003). Little is known, however, about the paleoecology of *Terebratula* (Benigni and Robba 1990; Pavia and Zunino 2008). Narrowing down the factors that led European Terebratulinae to extinction calls for improving our knowledge about the habitats and the ecological niche occupied by these terebratulids in their prime. This study is designed to help fill this gap by evaluating the environmental conditions in the subenvironments where the *Terebratula* populations were at their optimum in the Pliocene outcrops of the Águilas Basin (SE Spain), as well as the paleoecological boundary conditions onshore and offshore of this optimum. More specifically, we estimate environmental tolerances of this brachiopod with respect to water depth, bottom oxygenation, bottom temperature, productivity, and organic enrichment. This study area is among the most suitable for this purpose, because abundant and almost monospecific shell beds of *Terebratula* occur here cyclically in a mixed temperate carbonate–siliciclastic system (García-Ramos and Zuschin 2019).

Study Area and Paleoenvironmental Setting

The Águilas Basin (SE Spain) is located in the southwestern inner sector of the tectonic Águilas Arc (Fig. 1A,B), in the Internal Betic Zone (Coppier et al. 1989). The Águilas Basin was a small embayment (about 14 km wide) during the early Pliocene (Fig. 1C) (García-Ramos and Zuschin 2019).

The studied brachiopods belong to a sequence of late Zanclean age (MPI3 planktic foraminiferal biozone of the Mediterranean Pliocene; for the biozonation, see Iaccarino et al. [2007] and Corbí and Soria [2016]). The present study also yielded scarce specimens of the nannoplankton species *Reticulofenestra* cf. *cisnerosi* at the base of the sequence. This occurrence, together with the absence of *Discoaster tamalis* and the association with *Globorotalia puncticulata* and *Globorotalia margaritae*, constrains the age of the base of the sequence to the older part of Subchron C3n.1r (between 4.52 and 4.42 Ma), according to the biostratigraphic scheme of Lancis et al. (2015).

The studied strata define originally inclined units that were deposited on a slope (termed “clinobeds”), which were interpreted to reflect high-frequency and low-amplitude relative sea-level changes (García-Ramos and Zuschin 2019). Sedimentologically, these clinobedded units are consistent with sand-prone subaqueous delta-scale clinofolds (sensu Patruno et al. 2015), which developed entirely below sea level. The most proximal deposits are bioturbated coarse sands, followed distally by

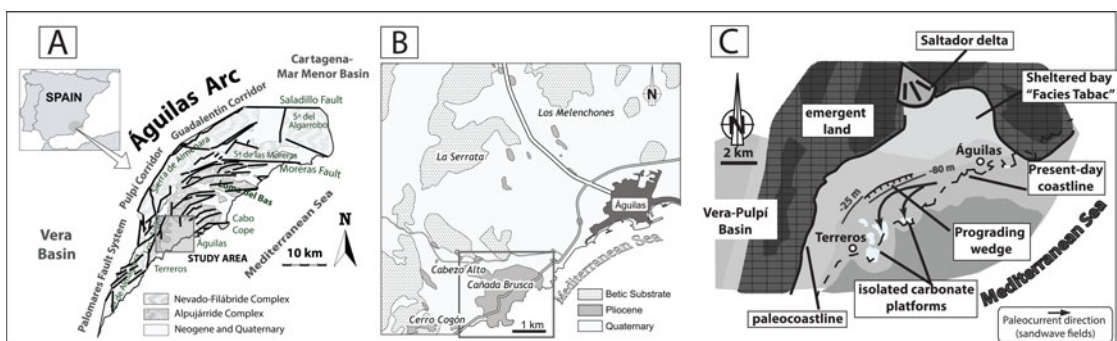


FIGURE 1. A, Location of the Águilas Arc in southeast Spain (adapted from Bardají et al. 2001). B, Location of the Cabezo Alto–Cañada Brusca area in the Águilas Basin. C, Paleogeographic map of the Águilas Basin during the Zanclean (adapted from García-Ramos and Zuschin 2019).

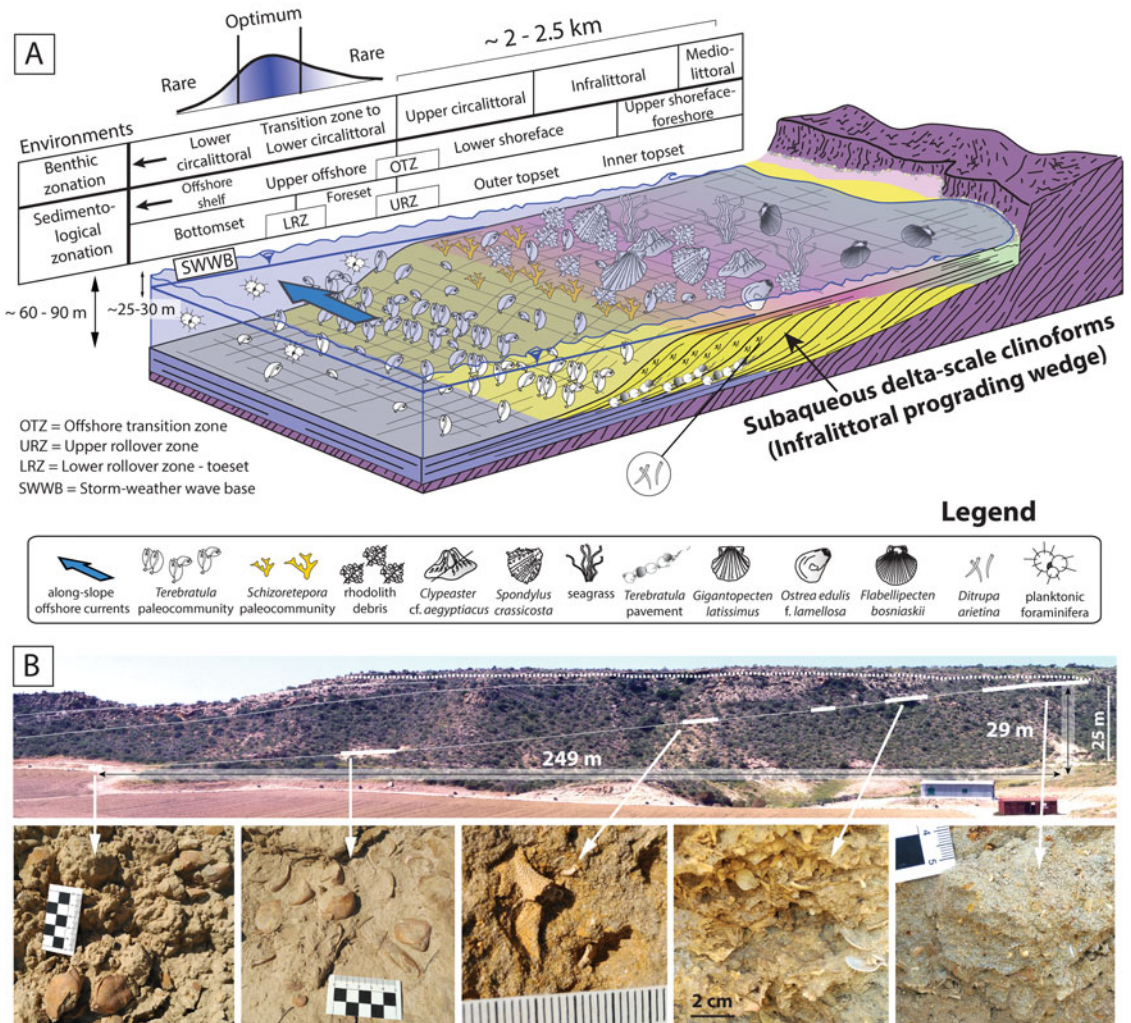


FIGURE 2. A, Depositional setting of the late Zanclean sediments in the study area and the paleoenvironmental distribution of *Terebratulina* across the depositional profile. Included are a biological benthic zonation slightly modified from Gili et al. (2014) and a sedimentological zonation based on Pomar and Tropeano (2001) and García-Ramos and Zuschin (2019). The depositional profile is adapted from Pomar et al. (2015). B, Field photo of subaqueous delta-scale clinofolds, with out-crop photos of biofacies along a proximal–distal gradient: *Schizoretopora*-rhodolith debris, *Schizoterepora* and *Terebratulina* biofacies (adapted from García-Ramos and Zuschin 2019).

rhodolith-rich finer-grained sediments (rhodalgal facies). Both facies correspond to the topset of the clinofolds (Fig. 2A). Following a biological benthic zonation (i.e., Gili et al. 2014), these environments were interpreted as mediolittoral to infralittoral (foreshore to upper shoreface) and lower infralittoral to upper circalittoral (lower shoreface) (García-Ramos and Zuschin 2019). The rhodolith debris disappears gradually toward the basin, giving way to fine-grained sands rich in the polychaete *Ditrupa arietina* along with benthic and planktic

foraminifera. The disappearance of the rhodoliths distally can be interpreted as a transition zone from the upper circalittoral to the lower circalittoral (Basso 1998; Cameron and Askew 2011; Gili et al. 2014). This facies transition between rhodalgal and *Ditrupa*-rich deposits was also interpreted as the offshore transition zone (OTZ) based on sedimentological evidence; it coincides with the topset–foreset transition (i.e., upper rollover) of the clinofolds (García-Ramos and Zuschin 2019). The *Ditrupa* facies in this transition zone to the lower

circularittoral corresponds to the foreset of the clinofolds (Fig. 2A). The most distal facies in our area is fine-grained muddy sands with the characteristic pectinid *Costellamussiopecten cristatum* occurring as dispersed, disarticulated shells (Fig. 2A, bottomset of the clinofolds). These deposits can be interpreted as formed

in upper offshore environments, also within the transition zone to the lower circularittoral.

In the above facies, 5- to 20-cm-thick mono-specific pavements of *Terebratula calabra* (Figs. 2B and 3A,B) are interspersed cyclically (Fig. 2A). Locally the pavements also yield rare specimens of the rhynchonellid *Aphelesia*

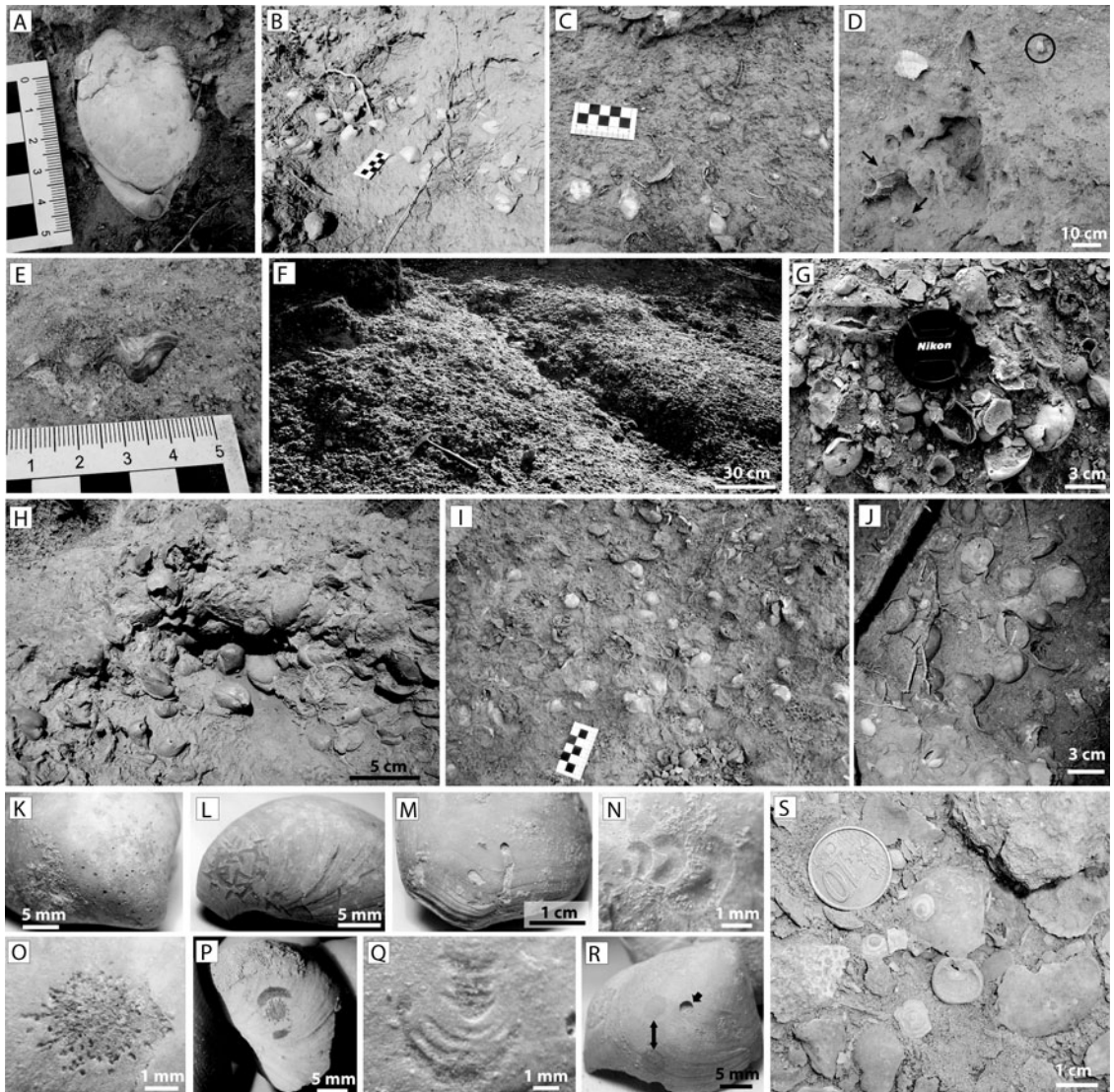


FIGURE 3. Paleoenvironmental features of *Terebratula calabra* outcrops in the Águilas Basin. A, An articulated specimen of *T. calabra*. B, Densely packed pavement TP1 at the toeset subenvironment. C, Loosely packed biofabrics on a plane bed at the bottomset. D, E, isolated *Terebratula* specimens in the rhodolithic hybrid floatstone facies. The arrows in D pinpoint typical shoreface taxa: *Gigantopecten latissimus*, *Spondylus crassicosta*, and *Aequipecten opercularis*, while the circle in D highlights a *Terebratula* specimen. F–J, Densely packed biofabrics from the *Terebratula* biostrome. K–R, Macrobioerosion traces on specimens from the biostrome: *Entobia* isp. (K), *Gnathichnus pentax* (L), *Caulostrepsis taeniola* (M), *Renichnus arcuatus* (N), *Podichnus obliquus* (O), same ichnospecies with abrasion marks from the foramen rims (P), *Centrichnus eccentricus* (Q), *Anellusichnus* isp. and *Oichnus simplex* indicated by arrows (R), specimens of *Novocrania anomala* from the biostrome (S).

bipartita. As a rule, the greatest *Terebratula* concentrations occur in the transition between the foreset and the bottomset (the lower rollover zone) (Fig. 2A,B), where the *Terebratula* pavements show loosely to densely packed biofabrics (Figs. 2B and 3B). The density of *Terebratula* decreases toward more proximal (foreset) and more distal positions (bottomset) (Figs. 2A and 3C) in the depositional profile. The rhodalgal facies (lower shoreface) also contains rare, isolated specimens of *Terebratula* (Fig. 3D,E). The shells in the pavements are mostly complete, articulated, and minimally encrusted by epizoans or bioeroded (recording rare traces of *Podichmus obliquus* produced by conspecifics). These concentrations were interpreted as parautochthonous assemblages in relatively shallow-water but offshore (circalittoral) environments during stages of reduced sedimentation rates (for details, see García-Ramos and Zuschin 2019). A recognizable 1.5- to 2-m-thick bed dominated by *Terebratula* in the study area shows loose to densely packed biofabrics (Fig. 3F–J). The taxonomic richness in this bed is distinctly higher than in the pavements. In this bed, the “*Terebratula* biostrome,” highly altered shells occur admixed with clusters of well-preserved terebratulids, some of which can be interpreted as biological clumps (sensu Kidwell et al. 1986). This suggests that the terebratulids were autochthonous (García-Ramos and Zuschin 2019). Many shells in the biostrome are bioeroded by clionaid sponges (Fig. 3K), although other traces also occur in low abundance (Fig. 3L–R). The rasping trace *Gnathichnus pentax* (Fig. 3L) is represented, whereas the rasping trace *Radulichnus* isp. is absent (García-Ramos and Zuschin 2019). Molinu et al. (2013), who studied microbioerosion traces affecting *Terebratula* specimens from the biostrome at the Cañada Brusca E-2 section, reported that the traces produced by fungi were dominant, although the microendolith trace *Rhopalia clavigera* (the product of chlorophytes) is also represented. The *Terebratula* biostrome, compared with the pavements, yields additional brachiopod taxa: the craniid *Novocrania anomala* (Fig. 3S), often encrusting disarticulated shells of *Terebratula*, is relatively common. In contrast, *Megathiris detruncata*, *Megerlia truncata*, *Terebratulina*

retusa, *A. bipartita*, and *Maltaia moysae* are rare or very rare.

From a morpho-sedimentary viewpoint, these clinoform systems have also been referred to as “infralittoral prograding wedges” (Hernández-Molina et al. 2000; Pomar and Tropeano 2001). Assuming the latter genetic model, the transition between the topset and the foreset of the clinoforms (i.e., the upper rollover) is coincident with the storm-weather wave base (lower shoreface–offshore transition) (Fig. 2A). A minimum water depth for this environment was probably about 25–30 m, in line with data from Recent examples from the Western Mediterranean (Hernández-Molina et al. 2000; Betzler et al. 2011) and the coralline algal assemblage (García-Ramos and Zuschin 2019). The vertical distance between the lower and upper rollover in the clinoform between clinothems 5 and 6 (García-Ramos and Zuschin 2019) is 29 m (Fig. 2B). This suggests a water depth of 54–59 m for the foreset–bottomset transition of the clinoforms (i.e., the lower rollover), without considering lithostatic compaction. During stages of low-amplitude (~15–20 m) relative sea-level rise pulses (García-Ramos and Zuschin 2019), the water depth of the lower rollover and bottomset was an estimated 70–80 m (Fig. 2A).

Material and Methods

Brachiopod assemblages are well represented, and crop out cyclically, in the Águilas Basin (SE Spain) (Fig. 1A,B). To evaluate the range of paleoenvironmental conditions, we studied the micropaleontological content of 26 bulk samples of friable sediment from the Cabezo Alto (CA) section (Fig. 4). The CA section was chosen because it records a vertical succession continuously exposing the main facies in the study area (including two *Terebratula* pavements: samples CA10 and CA15) (Fig. 4). The CA section is a suitable template for comparison with other *Terebratula* outcrops from the same stratigraphic sequence (three additional samples from *Terebratula* pavements [TP1, TP2, and TP3] and one from the *Terebratula* biostrome [sample TB]). Comparison between CA and other outcrops helps assess the variability of the environmental conditions

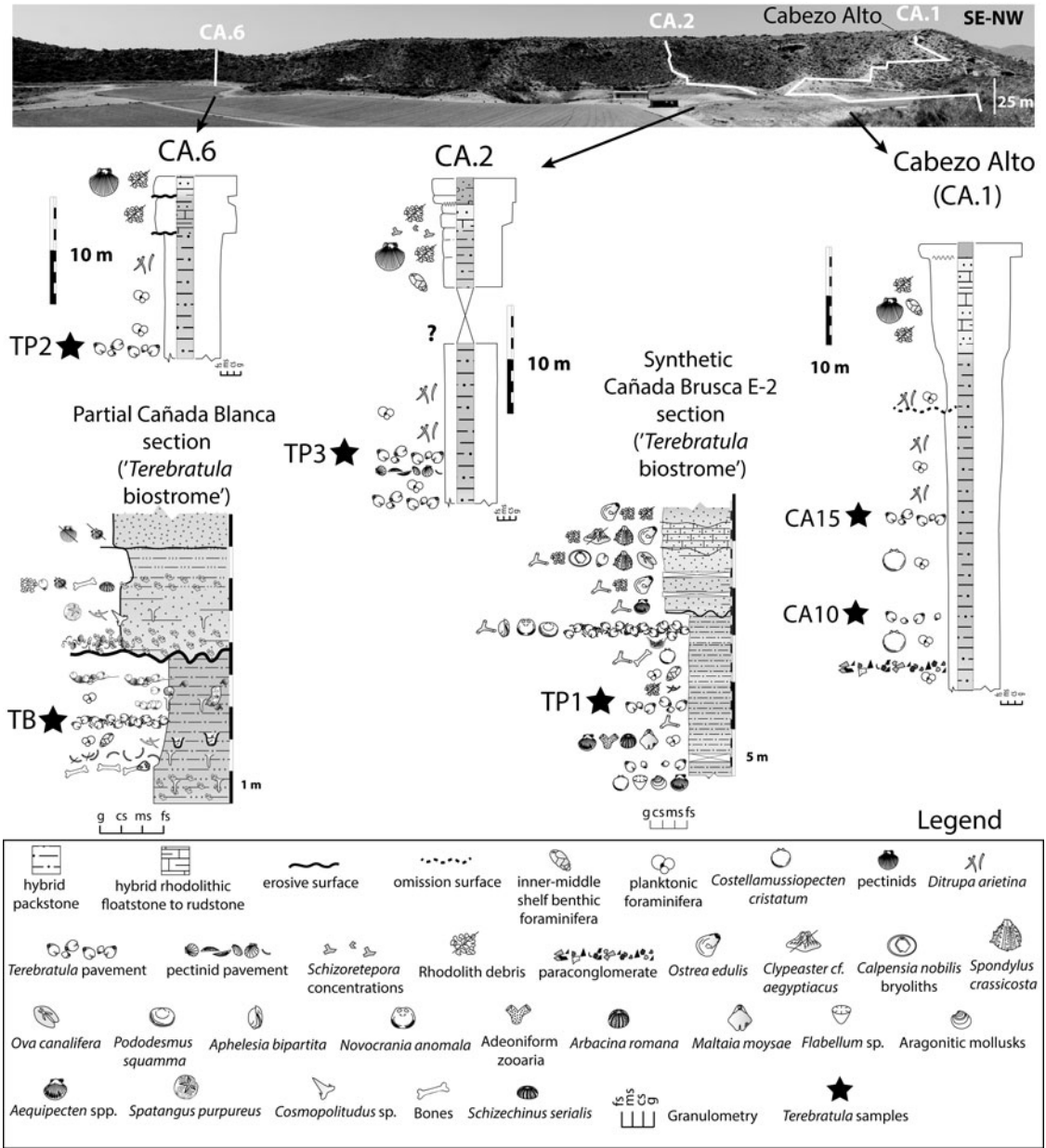


FIGURE 4. Synthetic sections from the Cabezo Alto, Cañada Brusca, and Cañada Blanca areas (adapted from García-Ramos and Zuschin 2019). The Cabezo Alto section, the focus of this study, is also indicated as CA.1. The studied *Terebratula* samples are indicated with black stars. fs = fine sand; ms = medium sand; cs = coarse sand; g = gravel.

associated with the presence and absence of *Terebratula* in the studied localities.

The samples were screened to study benthic and planktic foraminifera and calcareous nannoplankton. Each of the three taxonomic groups was studied and analyzed as separate data sets. For each sample, >200 specimens of

benthic foraminifera (>100 in the case of planktics) in the 125–500 µm fraction (Weinkauff and Milker 2018) were identified to species level whenever possible and counted. Only tests >50% complete, which included diagnostic features, were considered. For calcareous nannoplankton, smear slides were prepared using

standard procedures and examined under the light microscope (cross and parallel nicols) at 1000× magnification. The occurrence of ascidian spicules was noted. Quantitative data were obtained by counting at least 300 specimens from each smear slide. A further 100 view squares were checked for important species to interpret the biostratigraphy and paleoecology of the calcareous nannoplankton. Among reticulofenestrids, we followed the general distinction based on size (Young 1998): *Reticulofenestra minuta* (<3 µm), *Reticulofenestra haqii* (3–5 µm), *Reticulofenestra pseudoumbilica* (5–7 µm), and *R. pseudoumbilica* (>7 µm).

Before subsequent analyses, differences in sample size were accounted for by rarefying the Q × R matrix with count abundance data of benthic foraminifera so that each sample contained 200 specimens (100 specimens in the planktic foraminiferal data set). This was accomplished using the function *rrarefy* of the package *vegan* (Oksanen et al. 2018). All subsequent analyses were conducted in the R statistical environment, v. 3.5 (R Development Core Team 2018). The resampling process was repeated 100 times, and the mean data set was used for further analysis. For benthic foraminifera, species with relative abundances below 3% were discarded. The variability of the environmental parameters is shown in box plots by comparing samples where *Terebratula* was abundant, rare, or formed the biostrome. Samples lacking *Terebratula* were segregated between bottomset and foreset sub-environments (both in the transition zone from upper to lower circalittoral) (Fig. 2A) based on facies analysis conducted by García-Ramos and Zuschin (2019).

Benthic Foraminiferal Assemblages and Bathymetry

We used a Q-mode nonmetrical multidimensional scaling (NMDS) as an ordination method to visualize in the Bray-Curtis multivariate space the position of the samples containing *Terebratula* along the environmental gradient encompassing bottomset and foreset subenvironments at the CA section. Differences in the composition of benthic foraminiferal assemblages among bottomset, foreset, and *Terebratula* samples were additionally evaluated with

a test of permutational multivariate analysis of variance (PERMANOVA, function *adonis* in package *vegan*). The variation in composition of such assemblages was examined with a permutational analysis of multivariate dispersions (PERMDISP, function *betadisper* in package *vegan*). Facies occurring in shallower environments (e.g., the rhodalgal facies) were excluded from the analysis, because this facies consists of hardened rock that hampers the extraction of foraminiferal tests. The composition of benthic foraminifera in the samples containing *Terebratula* is shown in bar plots. The composition of the remaining samples can be checked in a two-way cluster analysis (Supplementary Fig. 1).

Additionally, we provide estimates for bathymetry using the transfer function proposed by Báldi and Hohenegger (2008). This approach was applied using benthic foraminiferal species with both non-overlapping and overlapping depth ranges. The depth ranges of benthic foraminifera were mainly compiled from Sgarrella and Moncharmont Zei (1993), Altenbach et al. (2003), Hohenegger (2005), Rasmussen (2005), Spezzaferri and Tamburini (2007), Sen Gupta et al. (2009), Phipps et al. (2010), and Milker and Schmiedl (2012). The same transfer function, weighted by the mean, was applied on the vertical distribution range of planktic foraminiferal species to estimate minimum water-column depth. The depth ranges of planktic foraminifera were compiled from Rebotim et al. (2017). For comparison, we also computed depth estimates based on the plankton/benthic ratio (P/B) using the regression function by van der Zwaan et al. (1990).

Ecological Groups of Benthic Foraminifera as Proxies for Oxygenation and Organic Enrichment

Changes in organic matter content are often coupled with reduced oxygen concentrations at the seafloor (Jorissen et al. 1995; Koho et al. 2008). An increase in organic matter is evaluated by analyzing changes in the proportional abundance of foraminiferal species assigned to five ecological groups (EG1 to EG5). These groups were proposed based on different degrees of opportunistic species' response to varying levels of organic matter enrichment

(Alve et al. 2016; Jorissen et al. 2018). We used only species whose proportional abundance was >3%, because ecological information on rare species is often not available. For visualization in box plots, percentages were recalculated after discarding rare species (Dominici et al. 2008). For some quantitatively important species (e.g., *Planulina ariminensis*) not listed by Alve et al. (2016) and Jorissen et al. (2018), a tentative attribution to a category of EG was attempted based on literature evidence (e.g., Rasmussen 2005). In this study, for each EG, we report the proportion of taxa, including unlisted species that were tentatively attributed to a corresponding group. We denoted this as the “aggregated ecological group” (AEG). To visualize the results, we used the conceptual TROX model (Jorissen et al. 1995), representing the *Terebratula* samples in a scheme adapted from Koho et al. (2008) by incorporating the main benthic foraminiferal species found in our samples.

Productivity and Water Temperature

The ecological and environmental distribution of extant species of planktic foraminifera is associated with levels of primary productivity and temperature (roughly warm-oligotrophic vs. cold-eutrophic species) (Hemleben et al. 1989; Sierro et al. 2003). The taxonomy generally follows the concepts of Kennett and Srinivasan (1983) with consideration of other sources (e.g., Poore and Berggren 1975; Malgrem and Kennett 1977; Darling et al. 2006; Schiebel and Hemleben 2017). Productivity based on planktic foraminiferal assemblages was assessed by comparing samples containing *Terebratula* with those where it was absent. The attribution of the planktic species to a category (warm-oligotrophic vs. cold-eutrophic) was based on information provided by Spezzaferri et al. (2002), Sierro et al. (2003), and Incarbona et al. (2013). We performed a modern analogue technique (MAT) with the packages analogue and analogueExtra (Simpson 2007) to estimate sea-surface temperature (SST) from the Águilas Zanclean samples. As a training data set, we used the modern North Atlantic planktic foraminiferal data set from Kucera et al. (2005), available at the Pangaea repository. The fossil species were standardized with the closest extant

relatives using the morphogroups proposed by Serrano et al. (2007). The exception was that we included *Globorotalia hirsuta* as a proxy for *G. margaritae* (e.g., *Globoturborotalita rubescens* was taken as a proxy for *Globoturborotalita gr. apertura*; *Globorotalia inflata* for *G. puncticulata*; *Globigerinoides ruber* [lumping pink and white types] for *Globigerinoides obliquus* and *Globigerinoides extremus*). We computed an NMDS ordination of the modern data set and the Águilas samples, and we superimposed the calculated SST isotherms on the ordination plot using the function *ordisurf* from *vegan*. The variance of the Kucera et al. (2005) data set explained by SST was calculated with canonical correspondence analysis (CCA).

To evaluate bottom-water temperatures, we selected 12 specimens of *Terebratula calabra* collected from different stratigraphic intervals and shell beds from the Águilas Basin for oxygen isotope analysis. The specimens were embedded in resin and cut along a longitudinal axis to produce thin sections, which were subsequently screened for diagenetic alteration with the cathodoluminescence microscope Technosyn 8200 MK II at the GeoZentrum Nordbayern, University Erlangen–Nuremberg. Selected samples of nonluminescent *Terebratula* shells were polished, etched in 5% HCl solution for 15 seconds (Crippa et al. 2016), sputtered with gold, and photographed under a scanning electron microscope (Jeol JSM 6400) at the University of Vienna. Carbonate powders extracted with a microdrill from the secondary layer somewhat posterior to the middle part of the shell were reacted with 100% phosphoric acid at 70°C using a Gasbench II connected to a Thermo Fisher Delta V Plus mass spectrometer at the GeoZentrum Nordbayern, University Erlangen–Nuremberg. All values are reported in per mil relative to VPDB. Reproducibility and accuracy were monitored by replicate analysis of laboratory standards calibrated by assigning $\delta^{13}\text{C}$ values of +1.95‰ to NBS19 and -47.3‰ to IAEA-CO9 and $\delta^{18}\text{O}$ values of -2.20‰ to NBS19 and -23.2‰ to NBS18. Reproducibility for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was ± 0.09 and ± 0.08 (1 SD), respectively. To estimate temperatures from oxygen isotopes, we used the equation from O’Neil et al. (1969). We assumed a seawater $\delta^{18}\text{O}_{\text{sw}} = +1.5‰$ VSMOW for the

western Mediterranean in the late Zanclean, based on Recent seawater composition in the eastern Mediterranean (Schmidt 1999; Rohling 2013). Sample S104 was identified as an outlier and was excluded from analysis.

Results

Benthic Foraminiferal Assemblages and Bathymetry of the *Terebratula* Samples

The Q-mode NMDS ordination plot (Fig. 5A) shows that the samples with *Terebratula* occupy a transitional position between *Terebratula*-barren bottomset and foreset samples, as was already observed from lateral facies variations in the field (Fig. 2B). The exceptions are CA10 (a bottomset sample with rare *Terebratula*) and TB (*Terebratula* biostrome), which shows affinity with the samples at the base of the CA section. PERMANOVA finds a significant difference among bottomset, foreset, and *Terebratula* samples, but only ~19% of the total variance is explained by these groups. Permutation

tests applied on PERMDISP find a significant although moderate compositional variation between the bottomset and foreset samples (permutest: $F = 4.77$, $df = 2$, $p = 0.022$), whereas a post hoc Tukey's honest significant difference test for multiple comparisons among groups indicates a significant compositional difference only between bottomset and foreset samples ($p = 0.013$). The benthic foraminiferal composition of the samples containing *Terebratula* is characterized, in general, by the dominance of *Bolivina* gr. *dilatata* and *Cassidulina carinata*, followed by cibicidids and asterigerinids (Fig. 6). The TB sample is dominated by cibicidids. The equation of Báldi and Hohenegger (2008) yielded depth estimates of ~50 to 90 m for the *Terebratula* samples when including non-overlapping shallow-water species and the vertical distribution range of planktic foraminifera (Fig. 5B). These values are consistent with estimates based on sedimentological models. Removing non-overlapping shallow-water species yielded bathymetric estimates of ~90

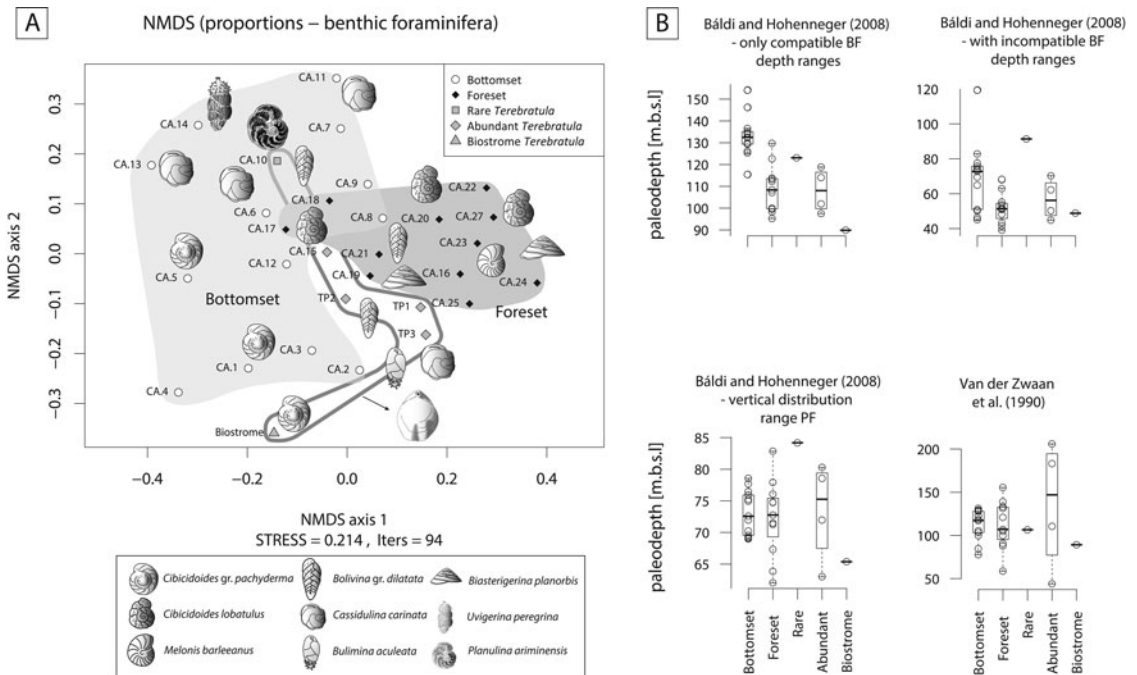


FIGURE 5. A, Q-mode nonmetrical multidimensional scaling (NMDS) ordination. Samples containing *Terebratula* mostly occur at the transition from foreset to bottomset. B, Box plots of depth estimates using the transfer function from Báldi and Hohenegger (2008) and the regression equation for planktic/benthic ratio from van der Zwaan et al. (1990). BF, benthic foraminifera; PF, planktic foraminifera.

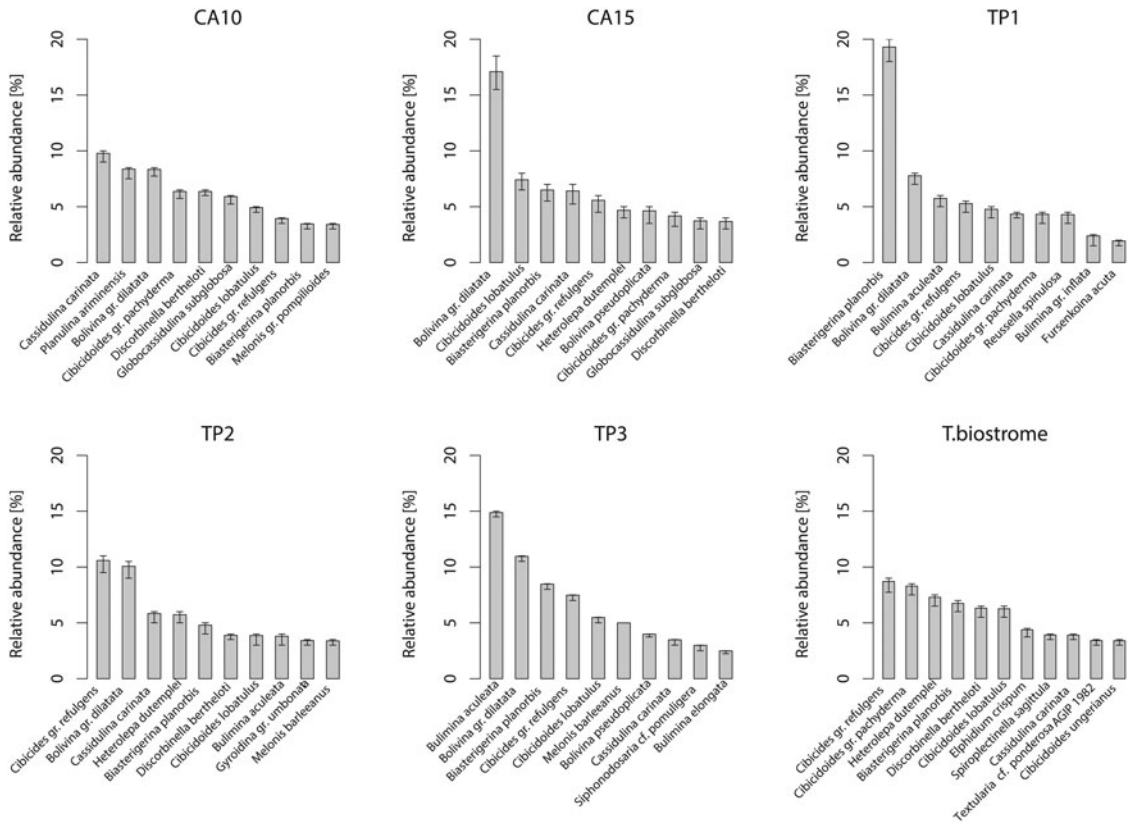


FIGURE 6. Relative abundance of benthic foraminiferal species in the *Terebratula* samples with 95% confidence intervals (percentile method). Only species with relative abundance higher than ~3% are shown. CA, Cabezo Alto; TP, *Terebratula* pavement.

to 125 m. The regression function by van der Zwaan et al. (1990) returned unrealistic depth estimates for the *Terebratula* samples (50–200 m), most probably because of onshore transportation of planktic foraminifera by currents (Murray 1976).

Organic Carbon Enrichment and Oxygenation

The box plots show that samples with *Terebratula* contain a slightly higher proportion of benthic foraminifera belonging to the EG of “sensitive species” (AEG1) compared with samples where *Terebratula* is absent (Fig. 7). The *Terebratula*-containing samples vary between ~35% to ~60% of AEG1 (in the TB sample), the latter being the maximum value in the data set. All these samples fall within the range shown by samples devoid of *Terebratula* with regard to the proportion of benthic species belonging to the EGs of “indifferent species”

(AEG2), “tolerant” (AEG3), and “second-order opportunists” (EG4). Most *Terebratula* samples, however, display low proportions (~10%) of benthic species of EG4 (Fig. 7). The exception is sample CA10, a bottomset sample, which contains ~20% of EG4 species and rare *Terebratula*. In the whole data set, “first-order opportunists” (EG5) were absent.

Productivity

The *Terebratula* samples fall within the ranges of cold-eutrophic and warm-oligotrophic species contained in the *Terebratula*-barren samples (Fig. 8A). Sample CA10 displays the maximum proportion of cold-eutrophic species (~60%), whereas TB yields a relatively low proportion (~30%) (Fig. 8A). Overall, the *Terebratula* samples are dominated by warm-oligotrophic species, except for sample CA10 (Fig. 8A). The NMDS ordination of the nannoplankton

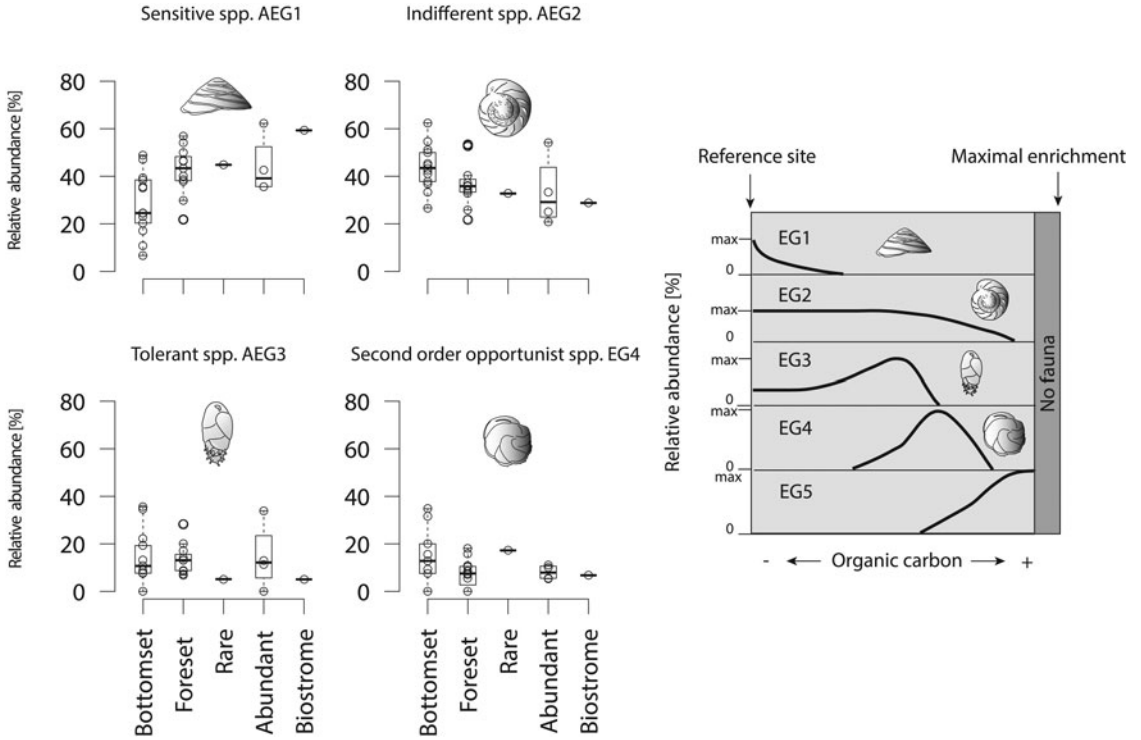


FIGURE 7. Relative abundance of aggregate ecological groups (AEG) of benthic foraminifera, partitioned into *Terebratula*-barren bottomset and foreset samples and those samples with rare, abundant, or biostrome-forming *Terebratula*. The conceptual scheme regarding the faunal response of benthic foraminiferal ecological groups (EG) to organic enrichment is based on Alve et al. (2016) and Jorissen et al. (2018).

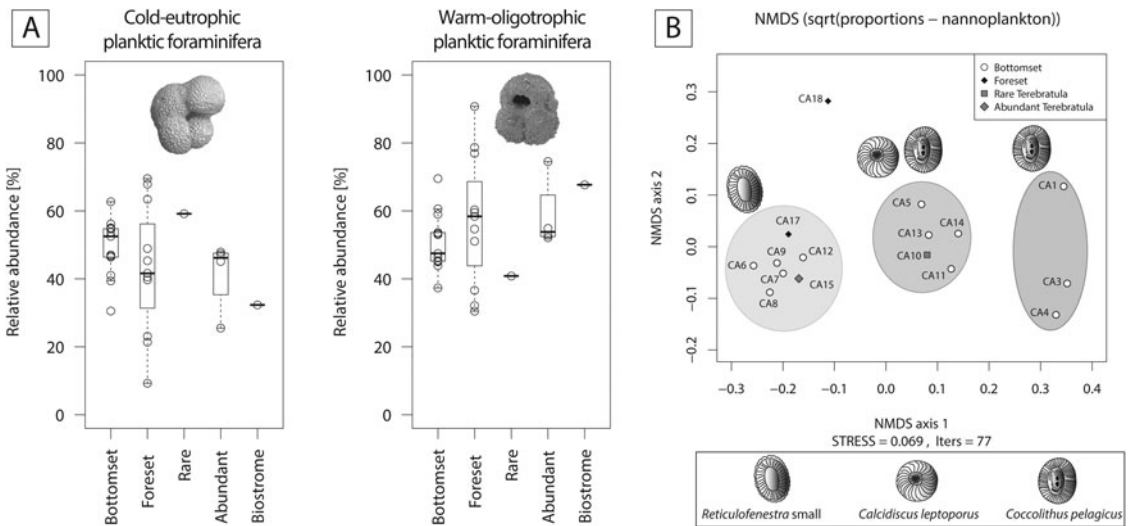


FIGURE 8. A, Relative abundance of cold-eutrophic and warm-oligotrophic species of planktonic foraminifera, partitioned into *Terebratula*-barren bottomset and foreset samples and those samples with rare, abundant, or biostrome-forming *Terebratula*. B, Q-mode nonmetric multidimensional scaling (NMDS) of the Cabezo Alto (CA) section nannoplankton samples.

(Fig. 8B) shows that the sample with rare *Terebratula* is associated with a *Calcidiscus leptoporus*–*Coccolithus pelagicus* assemblage, whereas the sample with abundant *Terebratula* is included in the *Reticulofenestra* small assemblage. In six additional *Terebratula* outcrops, nanoplankton were rare in four samples and absent in the other two. The samples with rare nanoplankton, however, contain the *Calcidiscus leptoporus*–*Coccolithus pelagicus* assemblage.

Seawater Temperature

The MAT analysis using data from Kucera et al. (2005) shows that SST ranges from $\sim 16^{\circ}\text{C}$ (for sample CA10) to $\sim 22^{\circ}\text{C}$ (samples TP1, TP3, and *Terebratula* biostrome) (Fig. 9). The *Terebratula* samples CA15 and TP2 fall within the range of 17°C to 19°C . CCA estimates that SST explains 39% of the variance (permutation test: $F = 540.46$, $df = 1$, $p = 0.001$) in the Kucera et al. (2005) data set.

Regarding the oxygen isotopes, the *Terebratula* samples displayed a good preservation of the secondary layer fibers (Fig. 10A–C). The exception is sample S86, which shows cracks in the fibers. All analyzed *Terebratula* samples were nonluminescent, except for the punctae in some specimens (Fig. 10D–F). The volume of nonluminescent shell material is far greater than that of the sediment infilling the punctae. We therefore assume that the oxygen isotopic signal represents primary, diagenetically unaltered values. The $\delta^{18}\text{O}_{\text{calc}}$ of the 12 *Terebratula* samples varies between -0.32 and 1.16 , with a mean value of 0.71 (Table 1). Assuming that the seawater $\delta^{18}\text{O}$ in the Águilas Basin during the late Zanclean was $+1.5\text{‰}$ by analogy with the warmer Recent eastern Mediterranean (Schmidt 1999; Rohling 2013), then the $\delta^{18}\text{O}_{\text{calc}}$ values translate into temperatures between 17.1°C and 23.8°C (mean: 19.1°C). Three measurements, done along the posterior–anterior axis of an isolated *Terebratula* shell from the

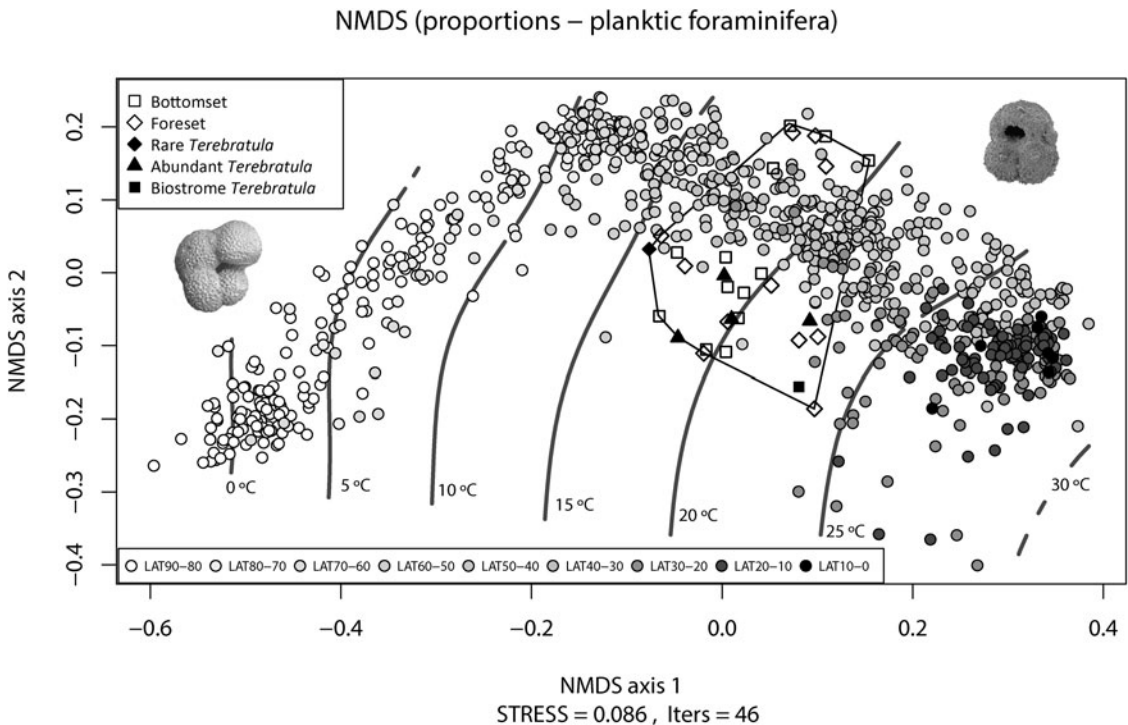


FIGURE 9. Nonmetric multidimensional scaling (NMDS) of planktic foraminifera performed on the standardized Pliocene samples from the Águilas Basin (squares, diamonds, and triangles) and the Kucera et al. (2005) extant data set (circles). The calculated sea-surface temperature (SST) for the Pliocene samples is based on the modern analogue technique. SST isotherms are superimposed on the NMDS plot with the *ordisurf* function in R. Black line: the range of SST covered by the Pliocene samples.

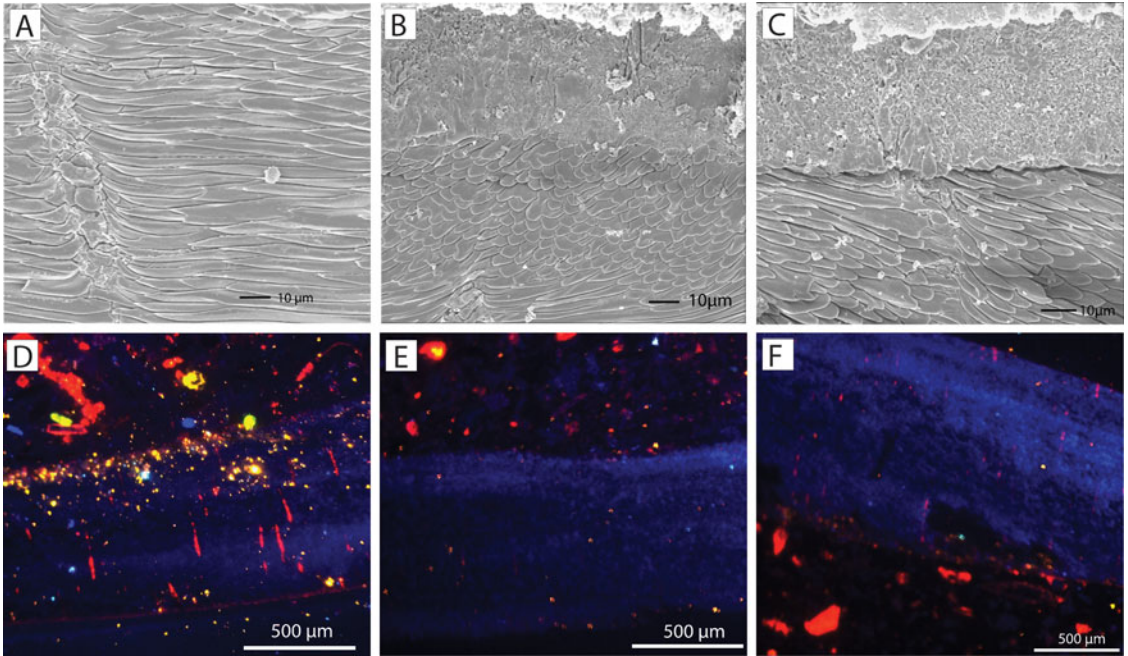


FIGURE 10. A–C, Scanning electron microscope (SEM) images of ultrastructural details of *Terebratula* from the study area. The shells display good preservation of the fibers in the secondary layer. D–F, Nonluminescent shells of *Terebratula*, although some of the punctae are luminescent.

foreset facies (sample CA28) (measurements S81, S102, S103), yield $\delta^{18}\text{O}_{\text{calc}}$ values of 0.71, 0.91, and 0.57 VPDB. The calculated temperatures are 19.1°C, 18.2°C, and 19.7°C, respectively. A fourth measurement from the anterior part of the shell (S104) is considered to be an outlier (Table 1).

Discussion

Bathymetric Distribution

Terebratula calabra in the studied sequence of the Águilas Basin is very rare or absent in the rhodalgal facies (lower shoreface; ~25–30 m depth) (Figs. 2A and 4D,E) and in the deepest

TABLE 1. Oxygen isotope values from the secondary layer of *Terebratula* specimens from the study area, with estimation of the temperature. S104 is an outlier and not considered for the interpretation.

Sample	Outcrop	$\delta^{18}\text{O}_{\text{calc}}$ (‰ VPDB)	$\delta^{18}\text{O}_{\text{w}}$ (‰ VSMOW) (Rohling 2013)	T_{calc} °C (O'Neil et al. 1969)	$\delta^{18}\text{O}_{\text{w}}$ (‰ VSMOW)	T_{calc} °C (O'Neil et al. 1969)
S74	CBl.Tereb.Biost.	1.16	1.5	17.1	0	10.7
S75	CBl.Tereb.Biost.	0.83	1.5	18.6	0	12.1
S77	TP2	0.97	1.5	17.9	0	11.5
S78	CBrE1.Tere.Biost.	0.43	1.5	20.4	0	13.8
S79	Tere.pav.Balsa	1.16	1.5	17.1	0	10.7
S80	TP1	0.92	1.5	18.2	0	11.7
S81	CA.28	0.71	1.5	19.1	0	12.6
S83	Ter.pav.Balsa	0.91	1.5	18.2	0	11.7
S85	TP3	0.53	1.5	19.9	0	13.3
S86	TP2	0.36	1.5	20.7	0	14.1
S87	CA.15	0.84	1.5	18.5	0	12
S88	CBl.Tereb.Biost	-0.32	1.5	23.8	0	17
S102	CA.28	0.91	1.5	18.2	0	11.7
S103	CA.28	0.57	1.5	19.7	0	13.2
S104	CA.28	-1.91	1.5	31.6	0	24.3

fine-grained sandy facies (offshore) (Figs. 2A, 4C, and 5). The maximum population density occurs close to (but notably below) the shoreface–offshore transition in fine-grained sands at estimated paleodepths of about 60 to 90 m (Figs. 2A,B, 4B, and 5B). The benthic foraminiferal assemblage of the *Terebratula* samples (Fig. 6) characterizes an offshore environment (e.g., Sgarrella and Moncharmont Zei 1993; Rasmussen 2005; Milker et al. 2009; Frezza et al. 2010; Mojtahid et al. 2010).

Substrate

Modern Terebratulida bathymetrically equivalent to *Terebratula* mostly occur in shallow rocky habitats in bays and fjords (Supplementary Table 1). *Terebratula* species, instead, were abundant in soft sediments: coarse to muddy sands (e.g., Gaetani 1986; Barrier et al. 1987; Dominici 2001; Gramigna et al. 2008). *Terebratula*, like certain other brachiopods (Rudwick 1961; Richardson 1981; Llopart and Calzada 1982), was potentially attached to ascidians, whose spicules are pervasive in section CA. We did not quantify the percentage of *Terebratula* shells affected by pedicle attachment traces (*P. obliquus*), but this trace is rare. This matches previous reports on several species of *Terebratula*, in which 1% or less were affected by *P. obliquus* (Taddei Ruggiero and Bitner 2008). Other members of Terebratulinae are known to facultatively form clusters, such as *Pliothyryna* (Bell and Bell 1872; Rudwick 1961) and *Liothyrella* (Foster 1974; Richardson 1981; Peck et al. 1997). A cluster of *Terebratula calabra* from the Águilas Basin was illustrated by García-Ramos and Zuschin (2019).

Oxygenation, Organic Enrichment, and Productivity

Among the dominant benthic foraminifera in the *Terebratula* samples, a first group of species (*B. gr. dilatata*, *Bulimina aculeata*, *C. carinata*) suggests that *Terebratula* in this basin was subject to seasonal inputs of labile organic matter, possibly associated with episodes of dysoxia at the seafloor (Barmawidjaja et al. 1992; Fontanier et al. 2003; Langezaal et al. 2006; Abu-Zied et al. 2008; Mendes et al. 2012). This interpretation is reinforced by the presence of the *Calcidiscus leptoporus*–*Coccolithus pelagicus* nannoplankton

assemblage in several *Terebratula* samples, suggesting productivity pulses triggered by coastal upwelling (Silva et al. 2009; Auer et al. 2014). In contrast, the “*Reticulofenestra* small” nannoplankton assemblage in sample CA15 points to an opportunistic response to increased eutrophic levels, environmental disturbance, or water stratification related to continental runoff or riverine input (Wade and Bown 2006; Ćorić and Hohenegger 2008; Auer et al. 2014). This latter assemblage correlates with warmer-water SST indicated by planktic foraminiferal assemblages (Supplementary Fig. 2). A second group of benthic foraminifera (*Heterolepa dutemplei*, *P. ariminensis*, *Cibicides* gr. *refulgens*, *Discorbina* *bertheloti*, *Cibicoides* gr. *pachyderma*, *Biasterigerina planorbis*, and *Cibicoides lobatulus*) suggests oligotrophic, well-oxygenated background conditions under the influence of strong bottom currents (Donnici and Barbero 2002; Schönfeld 2002; Szarek et al. 2006; Fontanier et al. 2008; Koho et al. 2008; Schweizer et al. 2009; Frezza et al. 2010; Buosi et al. 2012). Background oligotrophism and high oxygen levels are suggested by the proportional dominance of the “sensitive” and “indifferent” EGs of benthic foraminifera (Fig. 7) and warm-oligotrophic planktic foraminifera (Fig. 8A). Note here that the sample from the *Terebratula* biostrome (TB), however, is mostly characterized by oxiphylic species such as *C. gr. pachyderma* and *C. gr. refulgens*, which are suspension-feeding epizoans (Koho et al. 2008; Schweizer et al. 2009). Our data from the Águilas Basin suggest, overall, that *Terebratula* preferred oligotrophic and well-oxygenated habitats, under moderate to strong currents, but tolerated mesotrophic conditions and fluctuating concentrations of oxygen levels at the seafloor (Fig. 11).

Seawater Temperature

Modern (1981–2010) water temperatures off Águilas (SE Spain) range from 13.5°C to 28°C (range = 14.5°C). The monthly averages are between 17°C and 22°C, and the annual mean is 19.4°C (Guijarro et al. 2015) (Fig. 12A). The temperatures calculated from the oxygen isotope ratios (min = 17.1°C; max = 23.8°C; mean = 19.1°C; Table 1), as well as MAT (min = 16.3°C; max = 21.9°C; mean = 19.7°C), are consistent with the modern average temperatures. The

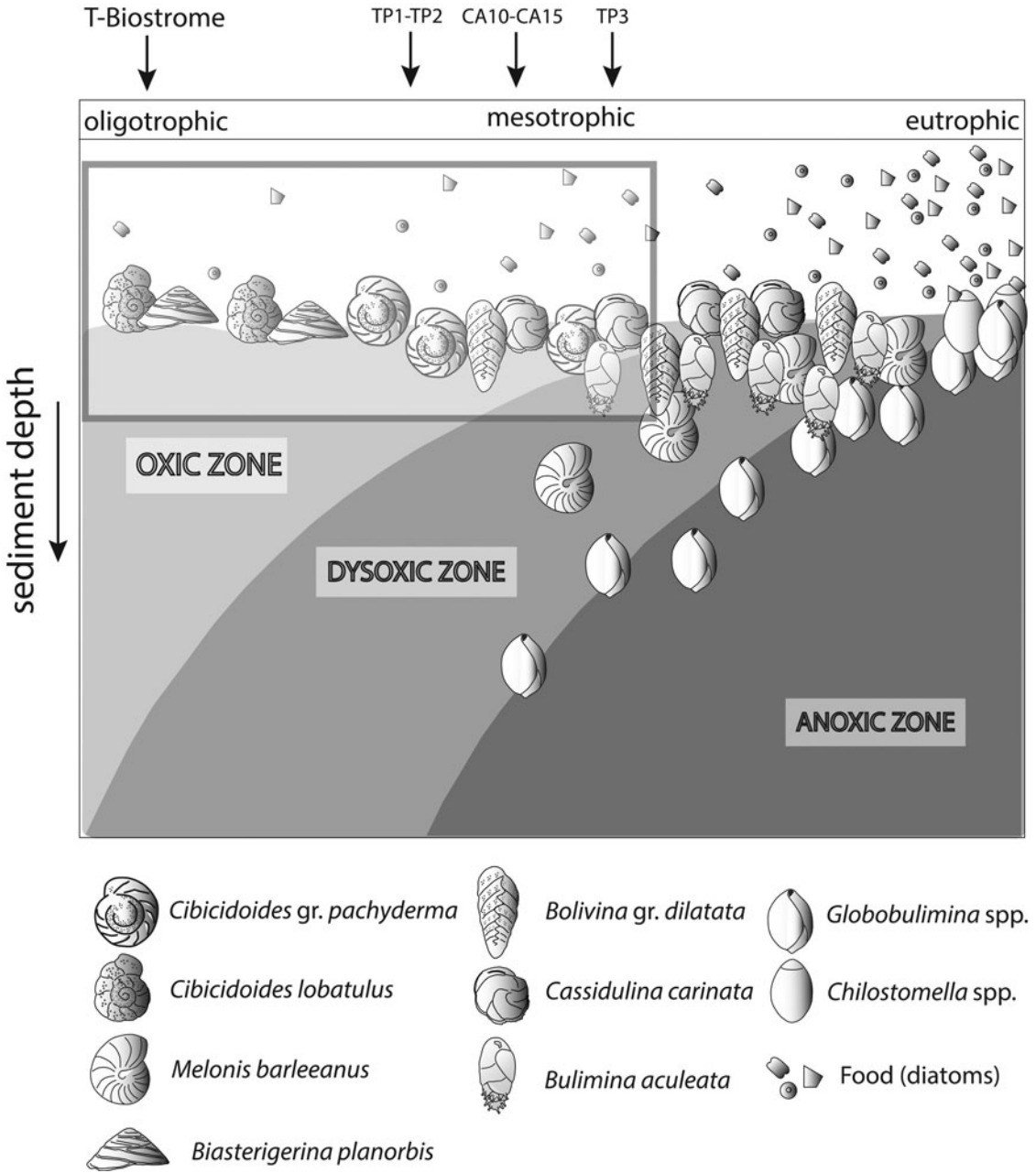


FIGURE 11. TROX model (adapted from Koho et al. 2008) conceptually representing the range of conditions interpreted for the *Terebratula* samples, marked by an inset. CA, Cabezo Alto; TP, *Terebratula* pavement.

MAT results are similar for the *Terebratula*-barren and *Terebratula*-bearing samples (Fig. 12B). This suggests that temperature alone does not explain the presence/absence distribution patterns of *Terebratula* during the Zanclean. Given that *Terebratula* lived in offshore environments, the

temperatures derived from oxygen isotope ratios would not be representative of sea-surface conditions. The assumption is that, for the Zanclean, Mediterranean SST was higher than today (Templado 2014; Tindall and Haywood 2015). In the Águilas Basin, during the late Zanclean,

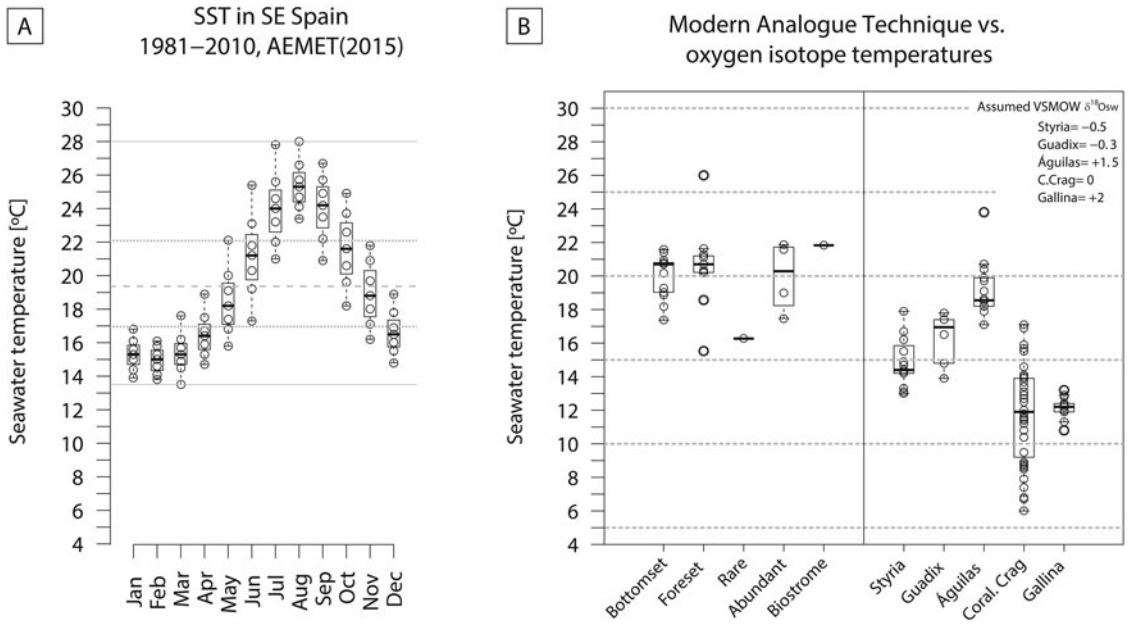


FIGURE 12. A, Monthly sea-surface temperatures (SST) off Águilas for the period 1981–2010 (data from Guijarro et al. 2015). B, Comparison between SST estimated from modern analogue technique using the Kucera et al. (2005) data set of planktonic foraminifera and bottom temperatures from oxygen isotopes of *Terebratula* shells from the Águilas Basin. *Terebratula* oxygen isotopes from Styria, Guadix, and Gallina and *Pliothyryna* from the Coralline Crag are included for comparison. The data were taken from Bojar et al. (2004), Clark et al. (2016), Rollion-Bard et al. (2016), and Vignols et al. (2018). All temperatures were calculated using the equation given by O’Neil et al. (1969). $\delta^{18}\text{O}_{\text{sw}}$ was assumed based on the values proposed by Lear et al. (2000) for the Styria and Guadix samples. For the *Pliothyryna* samples, $\delta^{18}\text{O}_{\text{sw}}$ was assumed as 0‰ VSMOW.

other paleoclimatic proxies are the species *Clypeaster* cf. *aegyptiacus*, *Echinolampas* spp., *Hyothisa* sp., *Talochlamys ercolaniana*, *Hinnites crispus*, *Spondylus crassicosta*, and *Gigantopecten latissimus* (García-Ramos and Zuschin 2019). These species are considered to be warm-temperate to subtropical taxa (Brébion et al. 1978; Ávila et al. 2015). For these species, Monegatti and Raffi (2001) proposed monthly average SST of 24°C–25°C for at least five to six months. The relatively narrow range of temperatures obtained from oxygen isotopes (6.7°C; 3.6 °C without the 23.8 outlier; Fig. 12B) suggests that *Terebratula* either preferentially lived below the thermocline (cf. Houpert et al. [2015] for the seasonal thermoclines in the modern Mediterranean) or grew during particular seasons of the year. “*Terebratula*” sp. from Styria (Langhian, Austria), *T.* cf. *calabra* from Guadix (Tortonian, Spain), and *T. scillae* from Gallina (Calabrian, Italy) (Bojar et al. 2004; Clark et al. 2016; Rollion-Bard et al. 2016) also display relatively narrow temperature ranges: 4.9°C, 3.9°C, and 2.4°C, respectively.

An exception is *Pliothyryna maxima*, another member of *Terebratulinae*, from the Coralline Crag (Zanclean, UK), showing a large range of 11.1°C (Vignols et al. 2018). Importantly, however, the data in those studies are derived from a sclerochronological approach on one or two specimens, sometimes mixing signals from the primary and secondary brachiopod shell layers. Oxygen isotope ratios measured on the primary shell layer and posterior and anterior parts of the shell should be interpreted with caution, because they are likely affected by nonequilibrium isotope fractionation (e.g., Romanin et al. 2018). The similar brachiopod species *Liothyrella uva* from Antarctic waters is subject to temperature ranges of only 2°C–3°C, not surviving above 4.5 °C (Peck 2005). In contrast, the cool-temperate *Liothyrella neozelanica* experiences values between 8°C and 18°C (Lee 1991). The relatively narrow temperature ranges of different *Terebratula* species should be further investigated as a possible cause for their extinction during the dramatic climate changes of the

late Pleistocene, which would have left them insufficient time to adapt (Peck 2007). Note also that *Terebratula* not surviving beyond the Jaramillo Subchron coincides with the onset of the strongest glacial–interglacial shifts during the Pleistocene (e.g., Rohling et al. 2014).

Environmental Factors Limiting the Distribution of *Terebratula* in the Águilas Basin

Terebratula had an optimum close to the OTZ, but why was the genus rare or absent in the shoreface and basinward beyond the OTZ? Our data suggest that oxygenation levels, food availability, or temperature—which have been invoked to explain the distribution of some brachiopod species (e.g., Tunnicliffe and Wilson 1988; Kowalewski et al. 2002; Tomašových et al. 2006; Peck 2007)—might not have acted as limiting factors in the Águilas Basin. This is because *Terebratula* appeared to be fairly tolerant to local variations in these parameters.

Preferred Habitat of Terebratula: Upper Offshore.—The consistent pattern in the Águilas Basin is the peak abundance of *Terebratula* in sediments devoid of coralline algae. Accordingly, light penetration might have exerted an important influence on the distribution of *Terebratula* in relation to grazing pressure (Noble et al. 1976; Witman and Cooper 1983; Asgaard and Stenthof 1984; Asgaard and Bromley 1991; Tomašových 2008; Zuschin and Mayrhofer 2009; Radley 2010). The bioerosion assemblages in the *Terebratula* biostrome are interesting because they display affinity with the *Gnathichnus* ichnofacies (Bromley and Asgaard 1993; De Gibert et al. 2007). Bromley and Asgaard (1993) proposed the *Entobia* ichnofacies for deep tier–dwelling borings in littoral rocky substrates subject to long exposure. The *Gnathichnus* ichnofacies, instead, characterizes shallow-tier structures on briefly exposed substrates (i.e., shells) in deeper water (De Gibert et al. 2007). The outcrop from the Pliocene Roussillon Basin (De Gibert et al. 2007), for example, was a shoreface environment whose shell beds are mostly composed of ostreids and pectinids. There, the dominant traces are *G. pentax* (rasping traces produced by regular echinoids feeding on algae) and *Radulichnus inopinatus* (produced by the radular grazing activity of gastropods or polyplacophorans)

(De Gibert et al. 2007). In contrast, the dominant macrobioerosion trace in the *Terebratula* biostrome is *Entobia* isp., whereas other traces such as *G. pentax* (Fig. 4L) are rare (Molinu et al. 2013). García-Ramos and Zuschin (2019) argued that the rare occurrence of the bioerosion trace *Gnathichnus* on *Terebratula* shells, coupled with the absence of *Radulichnus*, may indicate dim light or aphotic conditions, in line with interpretations elsewhere (Bromley 2005). This interpretation is consistent with the microendolith assemblages reported by Molinu et al. (2013) from the *Terebratula* biostrome. That assemblage is dominated by fungal traces (*Saccomorpha clava*, *Orthogonum lineare*, *Flagrichnus* isp.), whose producers are more common in relatively deep aphotic environments (e.g., Glaub 2004; Wisshak 2012). The microendolith trace *R. clavigera* is also present in the *Terebratula* biostrome. The producer of this trace characterizes the euphotic zone (Golubić and Radtke 2008), but can also be common in deep euphotic habitats (Wisshak 2012). Overall, the microendolith assemblages suggest irradiances around 0.01% or less (Wisshak 2012), which classifies the habitat from the *Terebratula* biostrome as a transition from upper to lower circalittoral (Cameron and Askew 2011). Such microendolith ichnoassemblages pointing to dim light are consistent with the absence of coralline algae in the *Terebratula* samples. The dysphotic zone (1–0.01% irradiance) can occur at depths between 40 and 120 m in some Mediterranean localities (Ballesteros 2006). Recent shells of the brachiopod *Gryphus vitreus* are affected by the endolithic green alga *Ostreobium queketti* (which is adapted to extremely low light conditions) to a depth of 130–135 m off Corsica (Emig 2018). Similar benthic foraminiferal assemblages as in the *Terebratula* biostrome (Fig. 6) occur at 70–80 m depth in the Strait of Bonifaccio (Buosi et al. 2012), which supports the above interpretation based on microendolith ichnoassemblages.

Exclusion of Terebratula Offshore: The Upper Foreset.—The rarity or absence of *Terebratula* in shoreface environments was discussed earlier, but in the Águilas Basin the distribution of this brachiopod in upper offshore (circalittoral) environments is not homogeneous (Fig. 2A). The peak density occurs in the foreset–

bottomset transition (i.e., the lower rollover of the clinofolds). Why was *Terebratulula* rare or absent in the upper foreset? The rhodalgal facies disappears basinward beyond the OTZ (coincident with the topset–foreset transition; i.e., upper rollover zone) (Fig. 2A). This suggests that the upper foreset was already under poorly lit conditions or other excluding environmental factors for coralline algae were present. *Terebratulula* could have potentially colonized this habitat, which was safe from high grazing pressure, but it was absent. This pattern can be explained by peak sedimentation rates at the upper foreset (upper offshore, circalittoral) due to its proximity to the upper rollover, which is a threshold between high and low hydrodynamic conditions (from sediment advection and bypass at the topset to sedimentation at the foreset) (Driscoll and Karner 1999; Cattaneo et al. 2007; Mitchell 2012). Thus, the environmental conditions at the upper foreset likely surpassed the physiological capacity of *Terebratulula* to cope with sedimentation (Williams et al. 2018). Sedimentation rates decrease gradually down the foreset (Mitchell 2012). Accordingly, the facies belt at the foreset–bottomset transition marks the threshold of sedimentation rates tolerated by *Terebratulula*.

Exclusion of Terebratulula Offshore: Beyond the Lower Rollover.—*Terebratulula* density rapidly decreases beyond the lower rollover basinward (Figs. 2A and 3C). This is coincident with Gaetani (1986) and Barrier et al. (1987), who report *T. calabra* as being restricted to proximal circalittoral environments, whereas other Terebratulidina such as *T. scillae*, *G. vitreus*, and *Stenosarina sphenoides* display a deeper optimum in the lower circalittoral and bathyal (Gaetani and Saccà 1985). A common pattern of subaqueous delta-scale clinofold systems is the association with offshore currents running parallel to the shoreline along the foreset–bottomset transition (e.g., Pomar et al. 2002; Cattaneo et al. 2007; Patruno and Helland-Hansen 2018). The occurrence of aggrading sandwave fields migrating basinward at the localities of Terros and La Carolina (García-Ramos and Zuschin 2019) demonstrates the sustained development of cyclonic current systems during the late Zanclean in the Águilas Basin (Fig. 1C). This interpretation is supported by

the dominance in the benthic foraminiferal assemblages of suspension-feeding species that favor vigorous currents and by the abundance in the *Terebratulula* biostrome of clionoid sponges, which cannot cope with high levels of turbidity (Carballo et al. 1994; Taylor et al. 2003). This pattern does not seem unique to the Águilas Basin, because records of *Terebratulula* at the lower rollover and adjacent bottomset of delta-scale clinofolds are described elsewhere (e.g., Llompart and Calzada 1982; Pomar and Tropeano 2001; Soria et al. 2003; Videt 2003; Gramigna et al. 2012; Massari and D’Alessandro 2012; Reolid et al. 2012). As brachiopods are facultatively active suspension feeders (La Barbera 1977; Wildish and Kristmanson 1997), the attenuation or disappearance of the along-slope currents basinward possibly affected the *Terebratulula* paleocommunity; this reflects the physiological cost of shifting from passive to permanently active suspension feeding (La Barbera 1977; James et al. 1992). An analogous case of offshore and onshore decrease in population density as a function of bottom current velocity has been described for extant communities of the terebratulid *G. vitreus* (Emig 1989; Emig and García-Carrascosa 1991).

Environmental Distribution of Terebratulinae in Other Studies

Cenozoic to Quaternary Terebratulinae have often been found in relatively shallow-water environments, from boulders at the toe of beach cliffs (Aigner 1983; Dixon 2011; Betancort et al. 2014) to intertidal and very shallow subtidal gravelly bottoms (Diedrich 2012). They often occur adjacent to sandwave fields where tidal or other types of currents are present but attenuated (Barrier et al. 1987; Roetzel et al. 1999; Pomar and Tropeano 2001; Courville and Crônier 2003; Kroh et al. 2003; Bosselaers et al. 2004; Calvo et al. 2012; Reolid et al. 2012). Such conditions prevent burial of the brachiopod paleocommunity by migrating subaqueous sandwaves. These brachiopods have also been found close to submarine hard-bottom structures that they possibly colonized, including shallow-water submarine cliffs (Kroh et al. 2003; Pervesler et al. 2011). Smaller species, such as *Maltaia maltensis* and “*Terebratulula*”

styriaca, were able to inhabit crevices and sheltered microenvironments in coralline algal buildups (e.g., Bianucci et al. 2011; M. Harzhauser personal communication 2019), cavities in coral reefs (Barbera et al. 1995), or in parareefal environments (Conesa et al. 2007). In the Pleistocene, some species colonized dykes in seamounts and walls on paleoclimbs at bathyal depths (Ietto and Bernasconi 2005; Titschack et al. 2005). Other species have also been reported from muddy bottoms at bathyal depths (Thomsen et al. 2005; Rögl et al. 2008), but it remains to be determined whether these assemblages were transported. Most occurrences, however, are associated with environments close to the lower shoreface–offshore transition and upper offshore settings, often co-occurring with bryozoans and/or acorn barnacles (De Porta et al. 1979; D’Alessandro and Iannone 1982; Gaetani 1986; Studencki 1988; Taddei Ruggiero 1996; Bitner and Pisera 2000; Montenat et al. 2000; Gramigna et al. 2008; Pavia and Zunino 2008; Puga-Bernabéu et al. 2008; Di Stefano and Longhitano 2009; Messina et al. 2009; Long and Zalasiewicz 2011; Giannetti et al. 2018, 2019; Crippa et al. 2019). Terebratulid colonization of the photic zone and their co-occurrence with coralline algae have sometimes been explained by the onset of eutrophic conditions triggered by upwelling, which can be deleterious for phototrophic and mixotrophic organisms (Brandano et al. 2016). Other authors interpreted that *Terebratula*, which is often typical of monospecific to paucispecific assemblages, was an opportunist able to colonize environments subject to disturbance associated with mesotrophic conditions (Masari and D’Alessandro 2012). Overall, the available evidence points to *Terebratula* preferring habitats where grazing disturbance was reduced because of poorly lit environments (e.g., Pedley and Grasso 2002; Brandano et al. 2015).

Conclusions

The late Zanclean deposits of the Águilas Basin record cycles of *Terebratula* paleocommunities that developed offshore (circalittoral) on fine-grained sediments deposited at the foreset–bottomset transition of subaqueous delta-scale clinoforms. These deposits therefore

provide a good scenario to understand the paleoenvironmental distribution of this taxon in space and time. The analysis of benthic and planktic foraminiferal and nannoplankton assemblages suggests that, overall, *Terebratula* thrived in relatively warm, oligotrophic to mesotrophic, well-oxygenated environments influenced by strong bottom currents. The oxygen isotopes showed that *Terebratula* in this basin lived in a relatively narrow range of temperatures (6.7°C). Such narrow ranges have also been reported for other species, potentially helping explain their extinction during the abrupt climate changes of the late Pleistocene: these brachiopods may have been unable to adapt quickly enough to such high-amplitude seawater temperature fluctuations after the Jaramillo Subchron. The consistent occurrence of terebratulids in sediments devoid of coralline red algae, combined with the bioerosion assemblages in the *Terebratula* biostrome, suggest that the limiting factor affecting the onshore distribution of *Terebratula* was light penetration and the associated high grazing pressure. This would explain the virtual absence of *Terebratula* in shoreface environments. Higher sedimentation rates at the shoreface–offshore transition also excluded the *Terebratula* paleocommunity in the upper foreset. In contrast, further offshore beyond the foreset–bottomset transition, we conclude that the attenuation or disappearance of along-slope currents was responsible for the lack of *Terebratula* populations.

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