ORIGINAL ARTICLE

Thick brachiopod shell concentrations from prodelta and siliciclastic ramp in a Tortonian Atlantic–Mediterranean strait (Miocene, Guadix Basin, southern Spain)

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Abstract Carbonate production by brachiopods in shallow-water habitats is generally expected to be not sufficiently high and temporally persistent to allow them to form very thick and densely packed shell concentrations. The formation of thick brachiopod concentrations requires long-term persistence of populations with high density of individuals, and such circumstances are assumed to be rare especially during the Cenozoic. However, here we show that the large-sized brachiopod *Terebratula terebratula,* the most common species in benthic assemblages with epifaunal bivalves and irregular echinoids, formed several decameter- to meter-thick, densely packed concentrations in shallow siliciclastic, high-energy environments, in a seaway connecting the Atlantic Ocean with the Mediterranean Sea during the Latest Tortonian (Late Miocene, Guadix Basin, southern Spain). This brachiopod formed (1) meter-scale, thick, parautochthonous concentrations in a prodelta setting and (2) thin, mainly allochthonous, tide- and storm-reworked concentrations in megaripples and dunes. The abundance of brachiopods at the spatial scale of the Guadix Basin seems to be mainly related to intermediate levels of sedimentation rate and current velocity because abundance and thickness of shell concentrations decline both (1) in onshore direction towards delta foresets with high sedimentation rate generated by debris flows and (2) in offshore direction with increasing levels of tide- and storm-induced substrate instability. Although brachiopods in dune and megaripple deposits are more fragmented, disarticulated, and sorted, and have a higher pedicle/brachial valve ratio than in prodelta deposits, taphonomic damage is still relatively high in prodelta deposits. *Terebratula terebratula* thus formed thick concentrations in spite of that disintegration processes were relatively intense along the whole depositional gradient. Therefore, population dynamic of this species was probably characterized by production maxima that were comparable to some Cenozoic molluscs in terms of their productivity potential to form thick shell concentrations in shallow subtidal environments. We suggest that temporal changes in brachiopod carbonate production have a significant spatial and phylogenetic component because multiple large-sized species of the family Terebratulidae, which underwent radiation during the Cenozoic, attained high abundances and formed shell concentrations in temperate regions.

Keywords Taphonomy · Paleoecology · Shell beds · Gilbert-type delta · Tidal setting · Brachiopoda · Miocene

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Introduction

Analyses of temporal changes in abundance and preservation of skeletal carbonate producers allow us to evaluate whether the dynamics of skeletal carbonate production, loss, and recycling change through time, and to infer consequences of such changes for the ecology and functioning of benthic ecosystems (Kidwell and Bosence 1991;

Kidwell and Brenchley 1994; Harper et al. 1997; Martin 2003; Nebelsick et al. 2005; Payne and Finnegan 2006; Westphal et al. 2010). For example, a hypothesized increase in the biomass (and carbonate) production over the course of the Late Mesozoic and Cenozoic can be related to evolutionary innovations triggered by an increase in the supply of nutrients and energy that can minimize or eliminate trade-offs between energetic investments into individual growth and reproduction (Bambach 1993; Finnegan et al. 2011). Such changes are likely to be coupled with increased carbonate production as well (Vermeij 1995), although skeletal carbonate production can be temporarily decreased at times of major extinction events (Hautmann et al. 2008; Kiessling et al. 2008).

Skeletal concentrations (i.e., densely packed bioclastic deposits) represent one end-member of possible outcomes of carbonate preservation dynamics where net skeletal preservation is maximized owing to high production rates, low disintegration rates, and/or low sedimentation rates (Kidwell 1986, 1991; Davies et al. 1989; Fürsich and Oschmann 1993; Tomašových et al. 2006a). Therefore, tracing variations in spatial and temporal distribution of skeletal concentrations can be useful in assessing the changes in the functional role of key skeletal carbonate producers in benthic ecosystems through time. For example, brachiopods formed thin, centimeter-scale simple concentrations in the Paleozoic, whereas molluscs formed thick, meter-scale and complex concentrations in the Cenozoic (Kidwell and Brenchley 1994, e.g., Norris 1986; Kidwell 1989; Kondo et al. 1998; Aguirre and Farinati 1999; Cantalamessa et al. 2005; Navarro et al. 2008; Carnevale et al. 2011), although the timing of this shift in the thickness of concentrations remains poorly explored and some Late Paleozoic and Early Mesozoic shell beds can be thick and internally complex (Garcia and Dromart 1997; Simões et al. 2000; Tomašových 2004; Tomašových et al. 2006b; Clapham and Bottjer 2007; Courville et al. 2007; Álvaro et al. 2007; Sterren 2008). The causes of such shifts in the thickness and composition of concentrations can be related to an increase in skeletal productivity rates because (1) present-day brachiopods seem to have, on average, smaller resource acquisition and growth rates than molluscs (Curry et al. 1989; Rhodes and Thompson 1993; Peck 1996, 2001), (2) an increase in the abundance and activity of skeletal destroyers and burrowers and the depth of bioturbation (Sepkoski et al. 1991; Droser and Bottjer 1993) can be expected to increase rates of skeletal disintegration (thus acting in the opposite direction, reducing thickness of concentrations, Kidwell and Brenchley 1996), and (3) skeletal durability of brachiopods seems to be comparable to durability of molluscs in tropical environments either because they can produce very thick shells (as in bouchardiids, Carroll et al.

Fig. 1 a, b Geographic location of the Guadix Basin in the Betic ▶ Cordillera (southern Spain). c Detailed map of the study area in the northern part of the Guadix Basin. The outcrops of the depositional systems with brachiopods are indicated: Gilbert-type delta and shelf. d Schematic cross section revealing both the angular unconformity limiting Units II and III and the eastward post-depositional tilting

2003; Simões et al. 2007; Krause et al. 2010; Rodríguez and Simões 2010) or they occur in sediments with carbonate cement precipitation (Tomašových and Zuschin 2009).

The relatively small per-individual carbonate productivity and the small contribution to overall ecosystem productivity by brachiopods can result from limiting processes operating at multiple spatial scales. Brachiopods are expected to be less efficient than molluscs when dealing with predation (Harper and Wharton 2000; Kowalewski et al. 2005; Aberhan et al. 2006) and grazing (Vermeij 1977; Asgaard and Stentoft 1984; Tomašových 2008; Zuschin and Mayrhofer 2009; Radley 2010), soft-bottom disturbance (Thayer 1983), and competitive interactions (Thayer 1985), effectively reducing their population growth rates and survivorship at small spatial scales. At broad spatial scales, differences in range-size and evolutionary dynamics related to lower dispersal ability and smaller net diversification rates can indirectly scale down to differences in productivity observed at the scales of ecosystems (Valentine and Jablonski 1983; Peck 2008). However, all these scenarios predict that brachiopods did not keep up with ecosystem-level increase in productivity and should be not able to generate very thick shell concentrations in shallow-water environments during the Cenozoic owing to ecological limits imposed on their population dynamics at multiple spatial scales.

Here, we show that some large-sized brachiopods of the family Terebratulidae formed very thick shell concentrations (i.e., densely packed deposits consisting of skeletal particles larger than 2 mm; Kidwell 1991; Fürsich 1995) in shallow-water temperate environments during the Cenozoic, implying that some brachiopod lineages that evolved during the Cenozoic achieved relatively high levels of carbonate productivity over significant temporal duration in shallow-water environments. We evaluate depositional and taphonomic conditions that led to the origin of conspicuous, meter-scale shell concentrations formed by the large-sized brachiopod species *Terebratula terebratula* in a well-documented Upper Tortonian (Upper Miocene) paleogeographic seaway connecting the Atlantic Ocean and the Mediterranean Sea (Lee et al. 2001; García-Ramos 2006; Toscano-Grande et al. 2010). This species was very widespread and common in the Mediterranean region in the Miocene and Pliocene (Bitner and Moisette 2003), and many other species of the genus *Terebratula* occupied diverse environments and frequently formed a dominant

Figure a–e
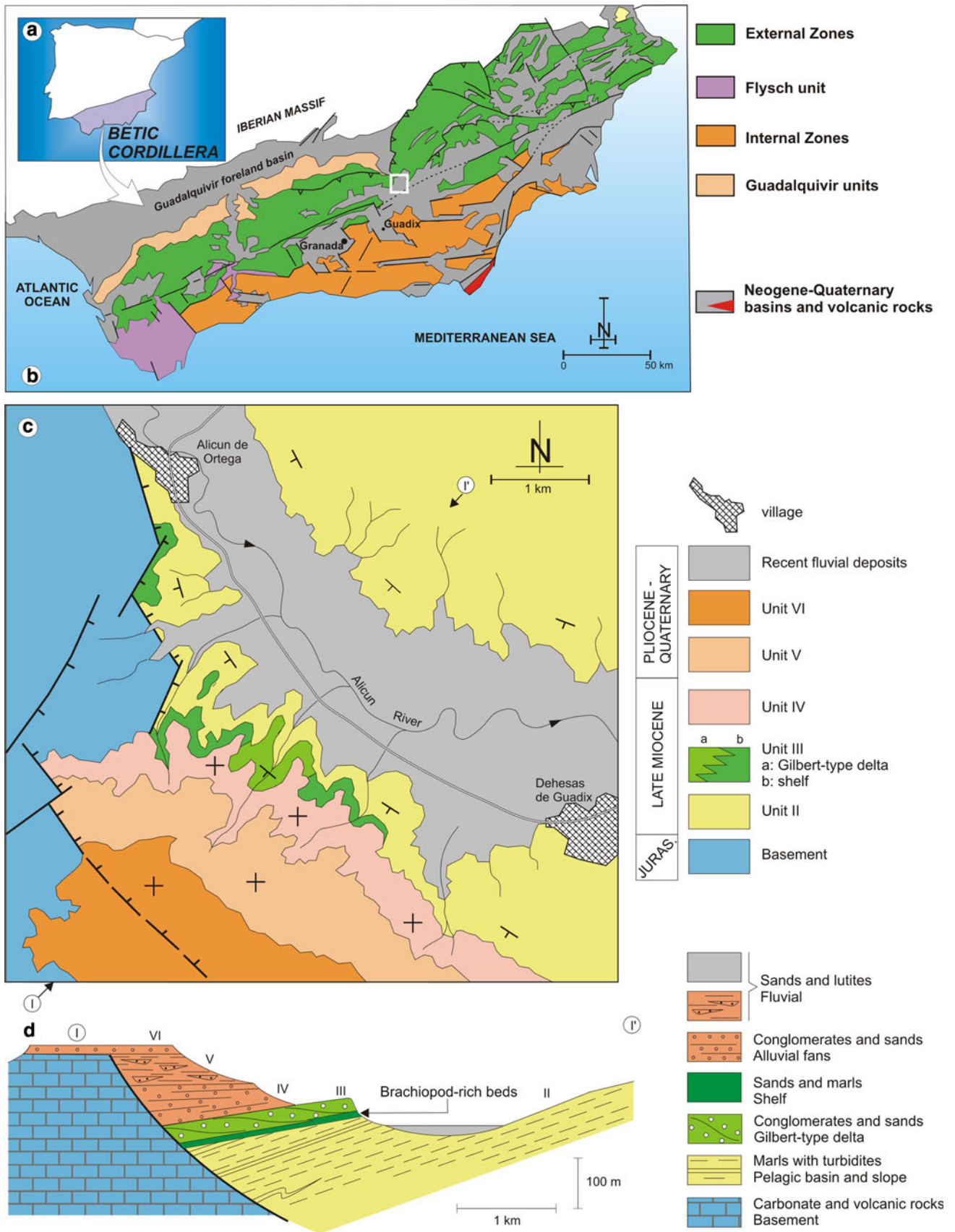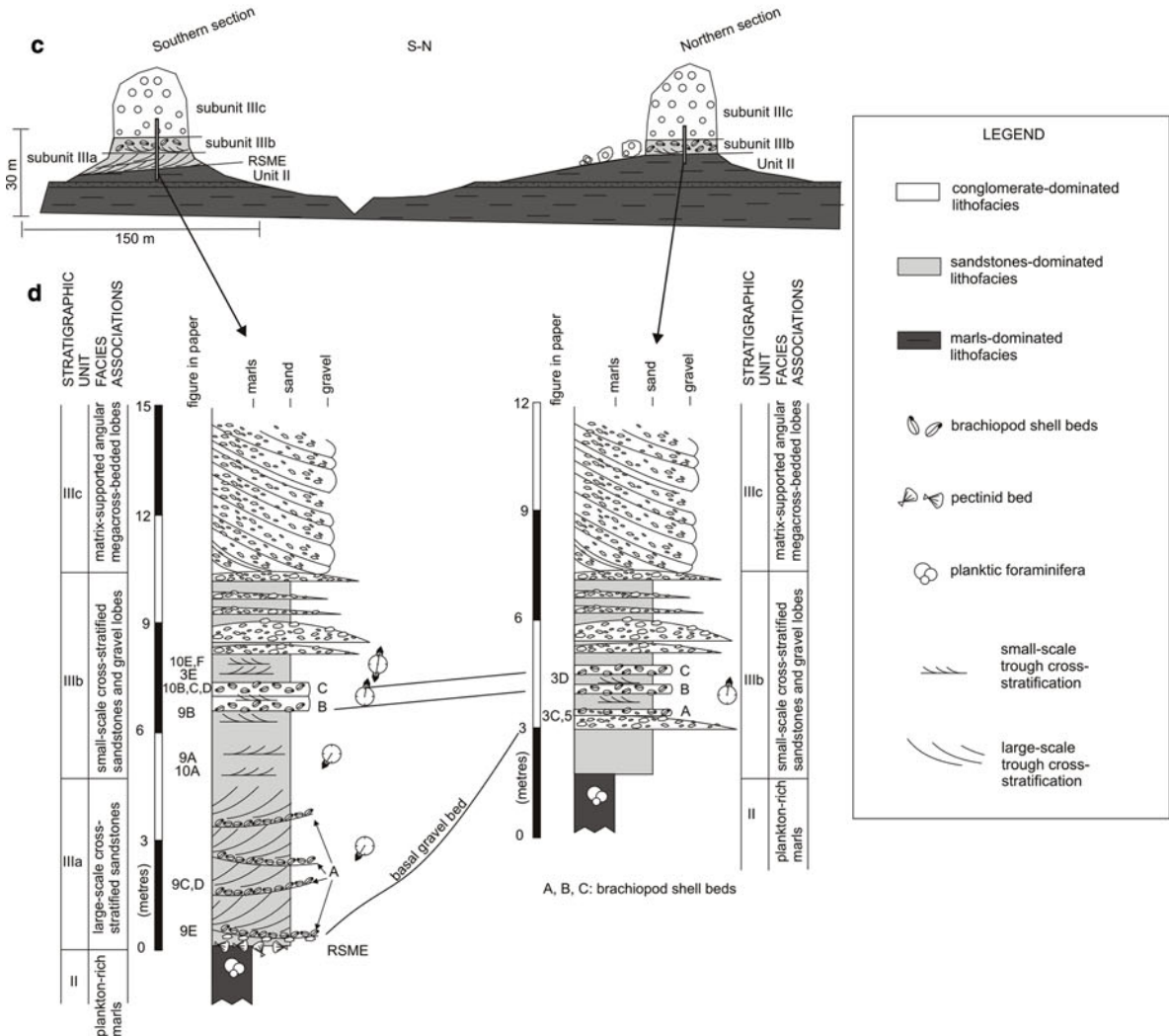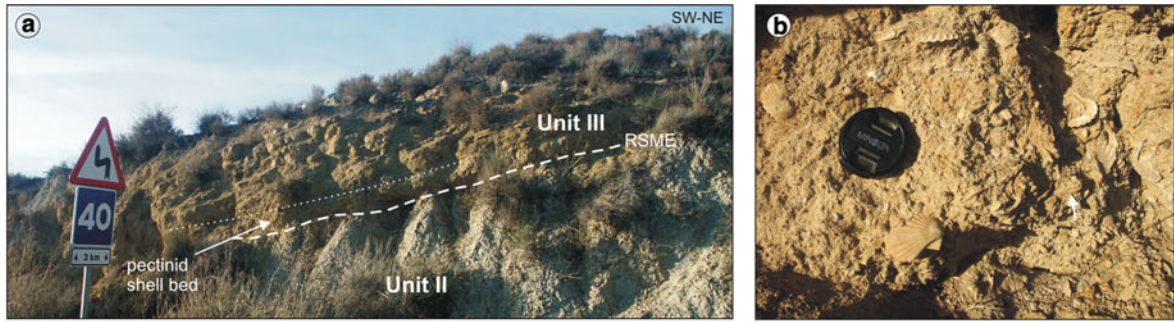
(e)	Stratigraphic Units	Facies associations	Sedimentary processes	Sedimentary subenvironment	brachiopods
Unit III	Subunit IIIc	matrix-supported angular gravels	cohesionless-debris flow	Gilbert-type foreset	lack of shells
	Subunit IIIb	matrix-supported angular gravels and small-scale trough bidirectional cross-bedded sandstones	cohesionless-debris flow and flood- and ebb-tidal-currents	Gilbert-type bottomset and upper shoreface	tidal- and debris flow-reworking thick shell-mass accumulations
	Subunit IIIa	large-scale trough cross-bedded sandstones	storm-wave and ebb-tidal-currents	lower shoreface to inner ramp	storm-reworking fine shell-mass accumulations at foreset and basal lag of the dunes
Unit II		planktic-rich marls alternating with Ta-c Bouma sequence sandstones	suspension settling and turbidity flow	outer ramp	lack of shells

◄ **Fig. 2 a** Section showing the regressive surface of marine erosion (RSME) limiting the underlying marl-dominated Unit II, and the overlying sandstone-dominated Unit III, here represented by a pectinid shell bed and a southwestward migrating dune (subunit IIIa). **b** Detail of the pectinid shell bed at the base of the Unit II (*cover cap* for scale). A brachiopod shell can be identified (*arrow*). **c** Schematic cross section revealing the lateral and vertical relation between subunits IIIa, IIIb, and IIIc of Soria et al. (2003). **d** Synthetic stratigraphic log showing the coarsening-upward vertical stacking of the subunits IIIa–c. **e** Summary table with simplified sedimentary features and environmental interpretation of the stratigraphic subunits

component of benthic assemblages, both in terms of abundance and carbonate production in the Mediterranean region during the Miocene–Pleistocene. This genus went extinct in the Pleistocene and thus does not contribute to the present-day productivity of brachiopods in the Mediterranean and in the Eastern Atlantic.

Geological setting

The outcrops with shell concentrations formed by the brachiopod *Terebratula terebratula* are located along the northern margin of the Guadix Basin, which is one of the Neogene-Quaternary intramountain basins situated in the central sector of the Betic Cordillera in southern Spain (Fig. 1a, b). Basin-fill sediments have been separated into six stratigraphic genetic units bounded by basinwide discontinuities (Fernández et al. 1996; Soria et al. 1999). They range in age from the Late Miocene to the Quaternary (Fig. 1c). According to Fernández et al. (1996), the first three units (I, II, and III) were deposited in a marine setting and are Late Tortonian in age. They correspond to the *Discoaster quinqueramus* biozone or biozone NN11 according to the biozonation of Martini (1971).

Brachiopod concentrations occur in the marine unit III (Fernández et al. 1996) (Fig. 1c, d). They are located in the lower part of this unit, very close to the basal surface, which is interpreted as a tectonically controlled forced regression surface separating plankton-rich basin marls (Unit II) from shallow-marine siliciclastic depositional systems (Unit III) (Soria et al. 2003) (Fig. 2a). The regressive surface of marine erosion (RSME) is overlain by a 50-cm-thick, normal-graded bed consisting of densely packed pectinids, isolated brachiopods and granule-sized gravels to sands (Fig. 2b). This bed is abruptly replaced by the deposits of the Unit III that start with deposits originating on a siliciclastic ramp, and develop vertically into a coarse-grained (mainly gravelly and sandy) Gilbert-type delta on the basin margin, containing five progradational phases (Soria et al. 2003). The first progradational phase is formed by large-scale cross-stratified sandstones in the lower part (IIIa), by small-scale cross-stratified sandstones and gravel lobes in the middle part (IIIb), and by matrix-

supported angular gravels in the upper part (IIIc) (Fig. 2c, d). Brachiopod concentrations were traced along a 500-m-long N–S transect that is perpendicular relative to the eastward direction of delta progradation. They correspond to the prodelta of the first sigmoidal lithosome (i.e., the first progradational phase) in the northern part and to ramp deposits in the southern part of the transect.

Materials and methods

The data collected in this study derive from field observations of natural cliffs, including quantitative taphonomic scoring of bioclast preservation and quantitative counting of bioclasts in the field, supplemented by paleocurrent measurements from cross-stratified deposit types. We analyzed two outcrops 300 m apart a N–S-oriented transect that were correlated by tracing their bedding planes along the outcrops. The northern section is situated in a proximal position relative to the shoreline. The southern section is situated in a more distal, offshore position with increasing marine influence (Figs. 2, 3).

First, we computed absolute abundances of bioclasts, pebbles and matrix by point-counting using a two-dimensional grid with a 1 cm-mesh and 30 cm^2 surface area. Second, we quantified preservation of 240 macroinvertebrate specimens, focusing on (1) size, (2) orientation, (3) disarticulation, (4) fragmentation, and (5) encrustation, similarly as in a protocol used by Olóriz et al. (2002, 2004). The orientation was quantified as azimuthal orientation assigned to four categories (0–10°, 10–45°, 45–80°, 80–90°) and as the proportion of convex-up valves. The proportion of disarticulated valves corresponds to the number of disarticulated valves relative to the total number of valves (i.e., articulated shells contribute with two valves). The fragmentation was scored as follows: the complete valves (fragmentation absent), valve with approximately less than 10% of surface removed (low fragmentation degree), valves with between 10 and 50% of surface removed (moderate fragmentation degree) and valves with more than 50% of surface removed (high fragmentation degree). A similar protocol applies to encrustation: no encrustation (with no epibionts), low encrustation degree with less than 10% of the surface encrusted, high encrustation degree with more than 60% of the surface encrusted, and moderate encrustation degree representing an intermediate state between low and high encrustation.

We quantified abundances and preservation of macroinvertebrates in four samples of fossil assemblages. One sample corresponds to the dune deposits from the ramp (southern section), and three samples correspond to shell beds from the prodelta (northern section). The taphonomic indices of Olóriz et al. (2002) were computed in analyses of preservation of whole-fauna assemblages (fragmentation
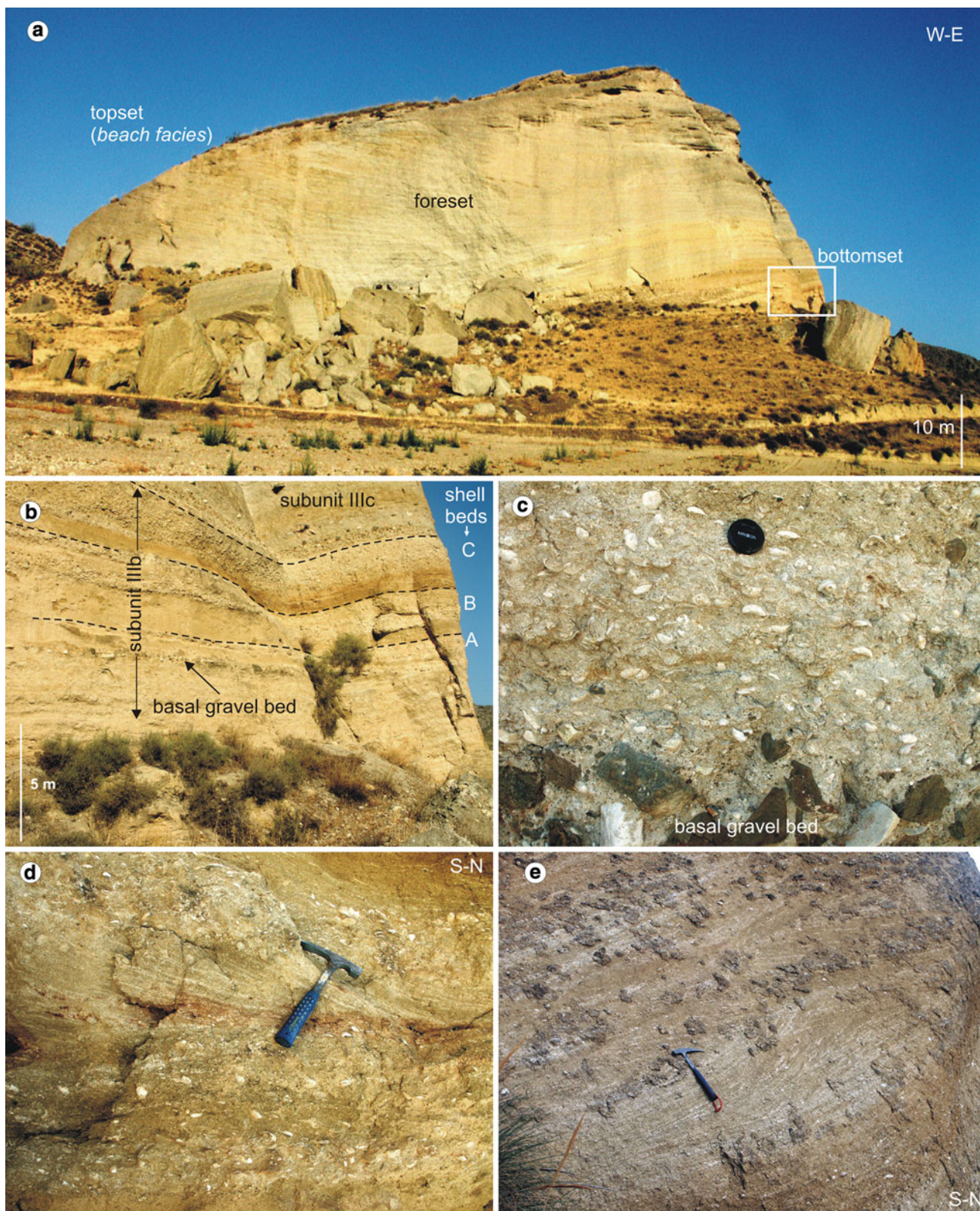
index and encrustation index). To minimize the effects of intrinsic factors and to focus solely on the preservation of the main skeletal producers (brachiopods), we computed per-sample proportions of brachiopod specimens affected by a particular type of taphonomic damage (e.g., the number of species with low, moderate and high

◄ **Fig. 3** Brachiopod shell concentrations in the northern and southern outcrop. **a** Location of brachiopod concentrations in the prodelta—bottomset of a Gilbert-type delta—(northern section) showing westward-dipping clinoforms (delta deposits show 10° post-depositional tectonic tilt toward the west). **b** A detail showing the three brachiopod shell beds (A, B, C) alternating with cross-bedded sand and gravel lobes (northern section). The bed with basal gravels representing the first coarse-grained sediment input from the delta is used as a marker to correlate northern and southern sections. **c** Brachiopod shells in the shell bed A supported by very coarse grained to granule matrix. This bed overlies a bed with angular volcanic and limestone pebbles to cobble-sized clasts (basal gravels bed) (*cover cap* for scale) (northern section). **d** Brachiopod concentration overlying trough cross-stratified sand that records the migration to the north of 3D-megaripples (northern section). **e** Isolated brachiopod shells (*white grains*) in cross-stratified sands representing bidirectional northward and southward migration of 3D-megaripples in the southern section (*hammer* for scale)

fragmentation relative to all brachiopod specimens). In analyses of brachiopod preservation, we evaluated (1) similarities in size-frequency distributions among the four samples, (2) size-specificity of taphonomic damage across all samples in boxplots, and (3) among-sample similarities in proportions of taphonomic damage for brachiopod assemblages.

Results

Three laterally and vertically changing facies associations in the stratigraphic unit III were identified in the northern and southern section (Fig. 2d, e), including (1) subunit IIIa represented by large-scale trough cross-bedded sandstones (dunes), (2) subunit IIIb represented by matrix-supported angular gravel and small-scale trough cross-bedded sandstones (megaripples), and (3) subunit IIIc showing mega-cross-bedding consisting of matrix-supported angular gravels. Subunit IIIa is exposed at the base of the southern section only, whereas subunits IIIb and IIIc are exposed in both sections. Below, we describe the geometry, fabric, preservation, and composition of whole-fauna assemblages present in brachiopod concentrations in the subunits IIIa and IIIb, followed by the description of brachiopod preservation.

Northern section: shell concentrations in the prodelta

Here, brachiopod concentrations correspond to a 3-m-thick coarsening-upward interval composed of gravel-rich layers and cross-stratified sandy layers (Fig. 3a–c). They belong to the subunit IIIb and overlie plankton-rich marls of the Unit II. Three shell beds A, B and C can be distinguished in this coarsening-upward interval, which is characterized by an increase in the proportion of gravel and high-energy sedimentary structures. The middle one, B, has the lowest

abundance of brachiopods. The thickness of lower and upper shell beds (A and C) decreases distally to the south, while the shell-poor bed B thickens in the same direction. The interval with brachiopod concentrations is overlain by matrix-supported and inversely graded, gravelly, lens-shaped bodies with a bed thickness ranging from 1 to 3 m and a lateral extent of 50–150 m. Here, brachiopod shells are preferentially located in coarser-grained intervals, and typically appear at the top or form small-scale trough cross-stratified sets (3D-megaripples, following the subaequous bedforms classification of Ashley 1990) migrating to the north.

The lower shell bed A, has a maximum thickness of 1.5 m and consists of very coarse to coarse-grained sand with abundant pebbles and bioclasts (Fig. 4). The matrix constitutes 57% of the rock, whereas the bioclasts form 35% and mainly consist of brachiopods (Fig. 4). The pebbles (8%) are sedimentary and volcanic in origin (Figs. 3c, 4b).

The middle shell bed B (Fig. 5), is 20 cm thick in the proximal part and 4 m thick in the distal part. It is characterized by well-developed cross-bedding with a lower shell content, and consists of a very coarse to coarse-grained sandy matrix (56% of the rock), 1 cm-sized pebbles (29%), and bioclasts (15%). The proportion of pebbles and bioclasts diminishes towards the basin.

The shell bed C (Fig. 6) attains 2 m in its thickest part and is formed by a coarse-grained sandy matrix (54% of the rock), with a high proportion of bioclasts (39%) and low content in pebbles (7%) that attain 10–15 mm in size. The packing and sorting of brachiopod specimens is relatively uniform throughout the whole bed thickness (Fig. 6).

The fossil assemblages of the shell beds A and C are dominated by *Terebratula terebratula* (Fig. 7) that forms 65–76% of the macroinvertebrate fossil assemblage (Fig. 8). Bivalves (16–28%) of the family Pectinidae, Cardiidae, and Ostreidae, and encrusting and ramose bryozoans (1–8%) are less common (Fig. 4d). Regular and irregular echinoids, delicate ramose bryozoans, and ahermatypic corals occur in the shell bed A only (Fig. 4d). In general, the diversity decreases upwards from shell bed A to C.

The mean size of all bioclasts is 3.2 cm. Specimens smaller than 20 mm are almost absent (5.2%). The fragmentation index of the whole assemblage is moderately high at all stratigraphic levels (24–53%), with the highest values at the base and at the top of the shell bed C (Fig. 8). Fragmentation in brachiopods mainly affected the commissure and the foramen. The fragmentation index was higher in the brachial valve (43%) than in the pedicle valve (32%). Disarticulation is extensive, affecting 100% of bivalves and 98% of brachiopods. Pedicle valves predominate (76% of valves). The disarticulated valves are mainly oriented convex-up in the shell bed A and in the lower part of the shell bed C (54%), and mostly concave-up in the upper part of the shell bed C
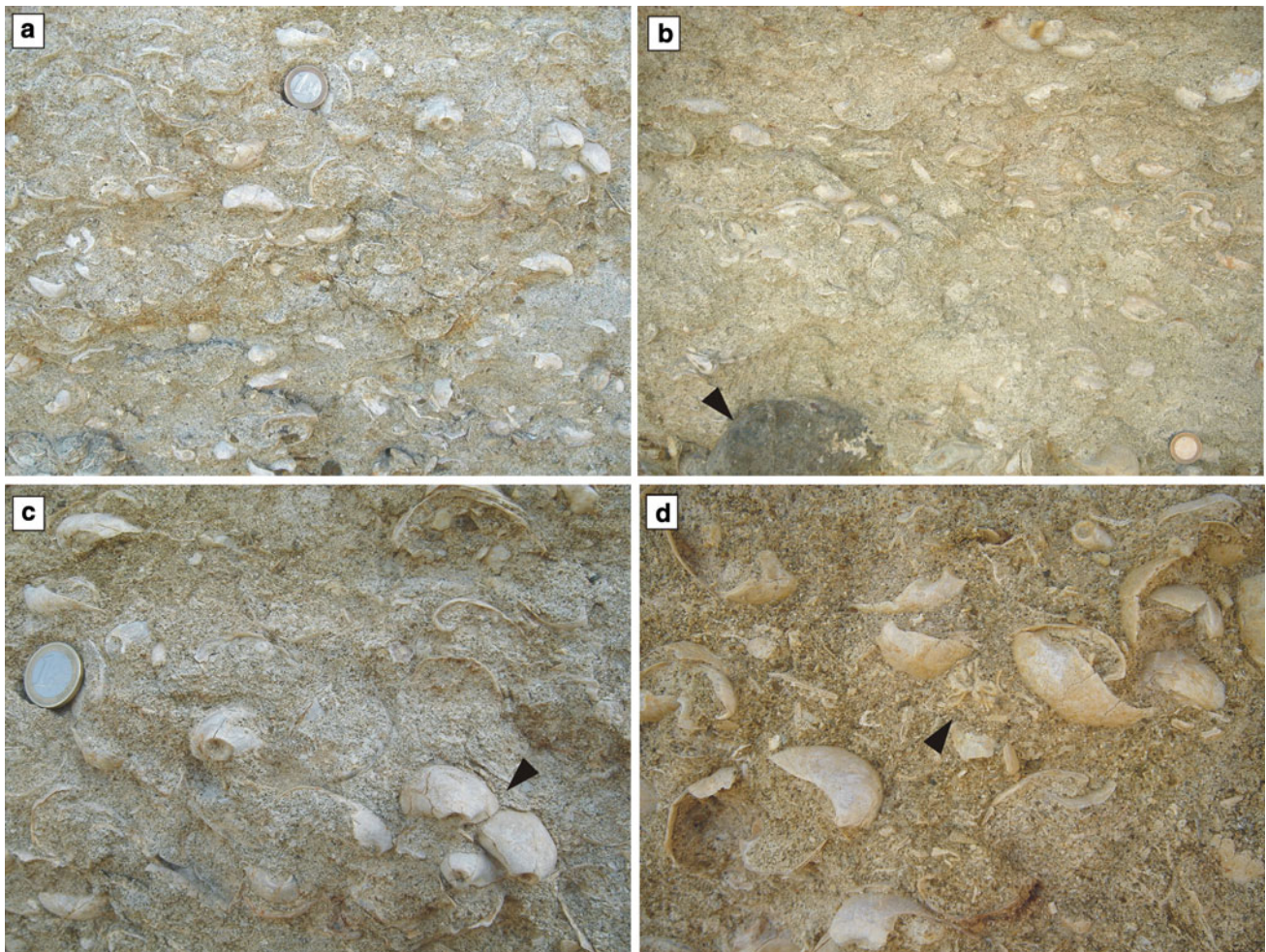
Fig. 4 Side-views of the shell bed A. **a** Densely packed shell concentrations. **b** Base of the shell bed A with a cobble-sized volcanic clast (*arrow*). **c** Detail of imbricate convex-up-oriented pedicle valves (*arrow*). **d** Presence of delicate ramose bryozoans (*arrow*)


Fig. 5 Shell bed B with uncommon, mostly disarticulated and strongly fragmented brachiopod valves and very abundant volcanic pebbles

(67%). The orientation of specimens is mainly subhorizontal (∼50% of the shells), and some specimens are nested or imbricated (Figs. 4c, 6c, d). The encrustation index attains the highest values in the shell bed A (17%) and the lowest values in the shell bed C (9%). It is higher in brachial valves (25%) than in pedicle valves (16%), and the encrusters occur on both the external and internal sides of the valves. The diversity of the encrusters and borers is higher in the shell bed A where encrusting bryozoans, serpulids, sessile foraminifera, and *Entobia* were found. Bryozoans dominate (54%) in the epizoan assemblage.

Southern section: shell concentrations in tidal- and storm-dominated offshore settings

These deposits overlie plankton-dominated basin marls of the Unit II with a sharp and erosional base, and laterally replace
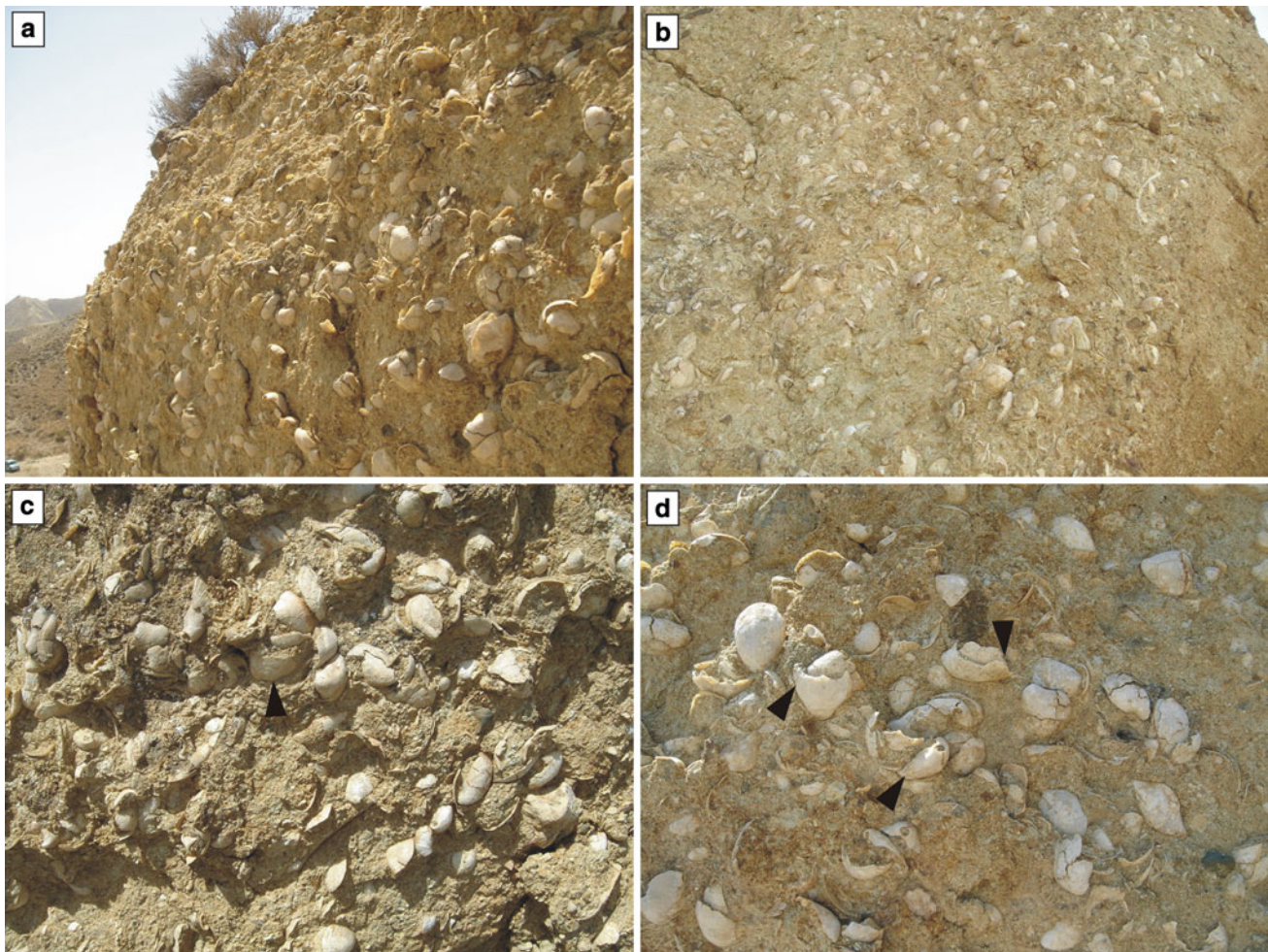
Fig. 6 Side views of the shell bed C from the prodelta. **a** Typical spectacular side view of the brachiopod accumulations. **b** A detail with disarticulated valves being commonly oriented concordantly with stratification. **c** Densely packed concentrations with nests of disarticulated valves (*arrow*). **d** Nested disarticulated valves of brachiopods (*arrows*)

coarser deltaic deposits described in the northern section. They are represented by 1.5-m-thick trough cross-stratified sands (3D-dunes) in the lower part of the unit and by 0.5-m-thick trough cross-stratified sands (3D-megaripples) in the upper part of the unit (Figs. 9a–c). Isolated brachiopods occur in the leeward-side of the dunes. At some places, normally graded shell beds dominated by brachiopod valves drape erosional reactivation surfaces within the dune foreset (Fig. 9d) and form lags with subangular gravels at the base of dunes (Figs. 9e). Paleocurrent indices are consistent with unidirectional flow that is oriented SSW for dunes, whereas bidirectional flow is oriented N–S for megaripples, which record herringbone structures. Moreover, the contact between the large- and small-scale cross-stratified sandstones is characterized by dense concentrations of shells where brachiopods and other benthic macroinvertebrate bioclasts form laminae of trough cross-stratified structures (Figs. 9c, 10a–d). Up-section, shell packing decreases upwards in the small-scale cross-stratified interval (Fig. 10e, f).

The brachiopod concentrations in the large-scale cross-stratified interval (3D-dunes interval) are dominated by *Terebratula terebratula*, forming 83% of the macroinvertebrate fossil assemblage. The rest of the specimens correspond to pectinids (17%). Diversity is thus very low. The mean size of all bioclasts is 2.7 cm, lower than the mean size of bioclasts in shell concentrations in the northern section (Fig. 11). The size of complete specimens of *Terebratula* ranges between 2.1 and 3.9 cm. The fragmentation index (45%) is also mostly higher than in the northern section (Fig. 11), with the exception of the lower index at the top of the shell bed C. Fragmentation is more intense in brachial valves. All specimens are disarticulated, and pedicle valves predominate. The valves are mainly oriented convex-up (69%). In contrast to the northern section, encrustations and borings are nearly absent (Ei = 0.06%), represented only by two specimens with bryozoans.

The lenticular concentrations (Fig. 10a–d) at the base of the small-scale cross-stratified interval (3D-megaripples
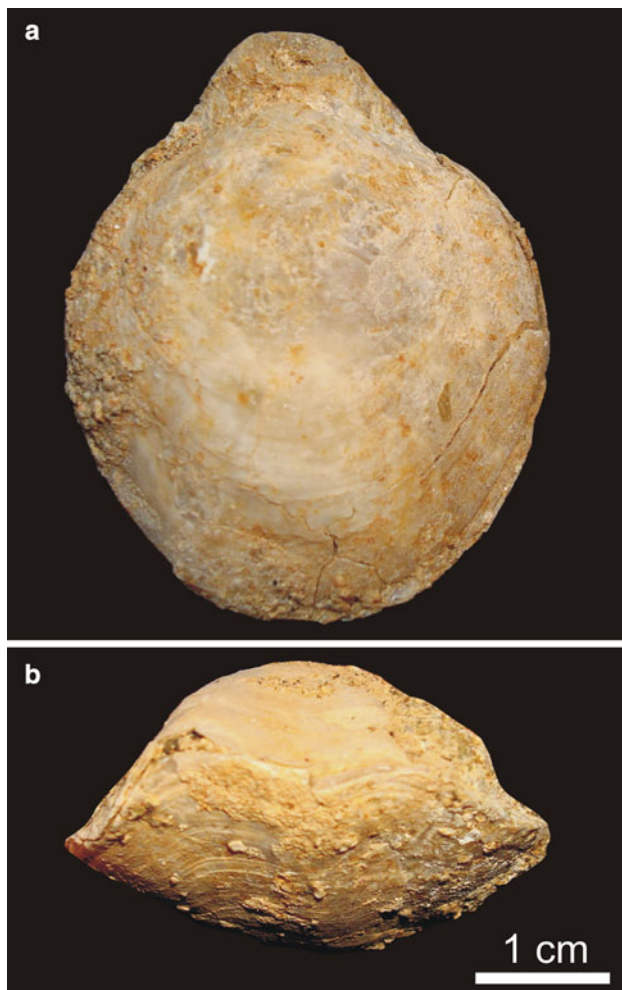
Fig. 7 *Terebratula terebratula*. **a** Dorsal view. **b** Anterior view

interval) are characterized by relatively well-preserved brachiopods, locally forming clusters with disarticulated valves. Other benthic macroinvertebrates are very scarce, limited to pectinid fragments (8% of the assemblage). Valves are commonly disarticulated (90%), nested or imbricated, with a high abundance of pedicle valves (70%). The position within the bed is variable, although many valves are in vertical position (50%). Among the valves registered in horizontal position dominate those oriented concave-up (70%). Fragmentation index is moderately high (68%). The abundance of brachiopods in the megaripples decreases towards the top. In the uppermost parts, the valves are represented by very small fragments (<2 cm), and complete valves of brachiopods and bivalves are rare. They are concordant with the stratification and mostly oriented convex-up.

Brachiopod preservation

Three samples from the shell beds A and C (bottom and top) from the northern section have all significantly larger

median size (median = 3.3–3.8 cm) than the dune assemblage from the southern section (median = 2.95 cm) (Fig. 12, Wilcoxon rank sum test, p[shell bed A vs. dune] < 0.0001, p[shell bed C base vs. dune] = 0.002, p[shell bed C top vs. dune] = 0.022). The three samples from the shell beds in the northern section have similar medians, although the shell bed A has still a significantly higher median size than the top of the shell bed C (Wilcoxon rank sum test, $p = 0.0244$). In addition, pooled across all samples, brachiopods show size-specific preservation because larger specimens are more encrusted (and such specimens are, on average, less fragmented and disarticulated, Fig. 13). The dune assemblage has significantly more convex-up than concave-up-oriented valves. In contrast, the assemblage from the base of the shell bed C has significantly more concave-up-oriented valves than would be expected under the equal probability of preservation of valves in concave-up or convex-up orientation (Fig. 14a). The shell bed A has approximately equal number of convex-up and concave-up-oriented valves.

One of the conspicuous features of preservation of the brachiopod *Terebratula terebratula* is that pedicle/brachial valve ratio significantly deviates from the expected 0.5 ratio in all sampling units, in both prodelta and ramp conditions (Fig. 14b). However, pedicle/brachial valve ratio is less biased in all three samples from the prodelta than in the sample from the dune deposits. Brachial valves are generally more fragmented and encrusted than pedicle valves across all samples, although not significantly (Fig. 14c). The dune assemblage has the highest proportions of fragmented and disarticulated valves. The shell bed A and C have comparably moderate proportion of fragmented and disarticulated specimens, although the upper part of the shell bed C has a very high number of fragmented specimens. The fragmentation mainly affected the valve margins close to the commissure and the pedicle foramen. The proportion of encrusted specimens is significantly higher in the shell bed A than in other beds (Fig. 14d–f).

Discussion

Ability of brachiopods to form thick shell concentrations in shallow habitats

The fossil assemblages in the shell concentrations described here are characterized by the dominance of epifaunal suspension-feeders and by the absence or rarity of infaunal forms (e.g., irregular echinoids forming 4% in shell bed A of the northern section).

Although the biogenic components forming deposits with common bryozoans and molluscan remains are typical

Table 1 Occurrences with high abundance of brachiopods belonging to the family Terebratulidae in Miocene–Pleistocene deposits (see discussion of the systematics of the genus *Terebratula* in Lee et al. 2001; García-Ramos 2006; Toscano-Grande et al. 2010)

Region	Species	Sediment	Stage	Habitat	References
Paratethys (S Germany)	*Gurlarnella waltli*	15-cm-thick bryozoan marl with sand	Lower Miocene (Burdigalian)	Shallow subtidal	Bitner and Schneider (2009)
Paratethys (Poland)	*Terebratula styriaca*	Marls with algae, bryozoans, serpulids, molluscs	Middle Miocene (Langhian)	Shallow subtidal	Bitner and Pisera (2000)
Mediterranean (Menorca)	*Terebratula maugerii*	100–200-cm-thick bioturbated calcarenites	Upper Miocene (Messinian)	Deep subtidal	Llompart and Calzada (1982)
Mediterranean (Cessaniti)	*Terebratula sinuosa*	10-m-thick succession of sands	Upper Miocene (Tortonian)	Deep subtidal	Gaetani and Saccà (1983)
Mediterranean (Malta)	*Terebratula terebratula*	20–300-cm-thick marls and biomicrites with coralline algae	Upper Miocene (Tortonian)	Shallow subtidal	Pedley (1976)
Mediterranean (S Spain)	*Maltaia pajaudi*	10-m-thick succession of molluscan shell beds and bioturbated sands	Lower Pliocene	Shallow subtidal	Toscano-Grande et al. (2010)
Mediterranean (Apulia)	*Terebratula calabra*	50–300-cm-thick bioturbated spiculitic calcilutites	Upper Pliocene	Deep subtidal	Taddei Ruggiero (1994)
Mediterranean (Apulia)	*Terebratula siracusana*	50–300-cm-thick bioturbated spiculitic calcilutites	Upper Pliocene	Deep subtidal	Taddei Ruggiero (1994)
Mediterranean (Calabria)	*Gryphus minor*	20-cm-thick bryozoan-brachiopod sands and fine conglomerates	Lower Pleistocene	Deep subtidal	Gaetani and Saccà (1983)
Mediterranean (Calabria)	*Terebratula scillae*	20-cm-thick fine sands	Lower Pleistocene	Deep subtidal	Gaetani and Saccà (1983)
Mediterranean (Messina)	*Terebratula scillae*	Bryozoan-brachiopod coarse-grained cross-bedded sands	Lower Pleistocene	Deep subtidal	Gaetani and Saccà (1983)
Mediterranean (Apulia)	*Terebratula scillae*	10–30-cm-thick calcarenite and bioclastic sand	Lower Pleistocene	Deep subtidal	Taddei Ruggiero (1994)

of present-day temperate marine environments (sensu Lees and Buller 1972), the extremely high abundance and volumetric contribution of brachiopods is generally not a typical attribute of Cenozoic deposits originating in high-energy shallow-water environments. We stress that Cenozoic deposits contain brachiopod concentrations but these typically formed in deep-shelf environments (e.g., Harper and Pickerill 2008; Hendy and Kamp 2004) where the intensity of predation can be expected to be lower. In addition, brachiopods also form high-density populations on the present-day sea-floor in shallow-water habitats (e.g., Lee 1978; Richardson 1981; Försterra et al. 2008; Tomašových 2008), but such occurrences do not invariably result in the formation of thick concentrations because (1) high population density will be not necessarily sustained over long temporal duration and (2) production rates can be counteracted by high disintegration rates. For example, in spite of high abundance of terebratulid brachiopods in living communities in cool-temperate habitats in the northern hemisphere, they disintegrate rapidly in many

cases (Noble et al. 1975; Emig 1990; Tomašových and Rothfus 2005), significantly reducing their potential to form brachiopod-dominated death assemblages.

During the Miocene–Pleistocene, the terebratulid genus *Terebratula* attained a broad geographic range in the Mediterranean and Paratethys. Species of this genus formed shell concentrations or were numerically common not only in the Guadix Basin but also in many other shallow-water and relatively high-energy environments during the Late Miocene and Pliocene (Table 1; Pajaud 1976, 1977; Pedley 1976; Calzada 1978; Llompart and Calzada 1982; Gaetani and Saccà 1983, 1984; Taddei Ruggiero 1985, 1994; Gaetani 1986; Bitner and Pisera 2000; Bitner and Martinell 2001; Toscano-Grande et al. 2010). Other genera belonging to the family Terebratulidae were also very common in shallow-water environments in the Mediterranean and Paratethys during the Cenozoic (Bitner and Schneider 2009). Although non-micromorphic brachiopods producing substantial amount of calcium carbonate are almost lacking in Holocene times in the eastern Atlantic and Mediterranean in
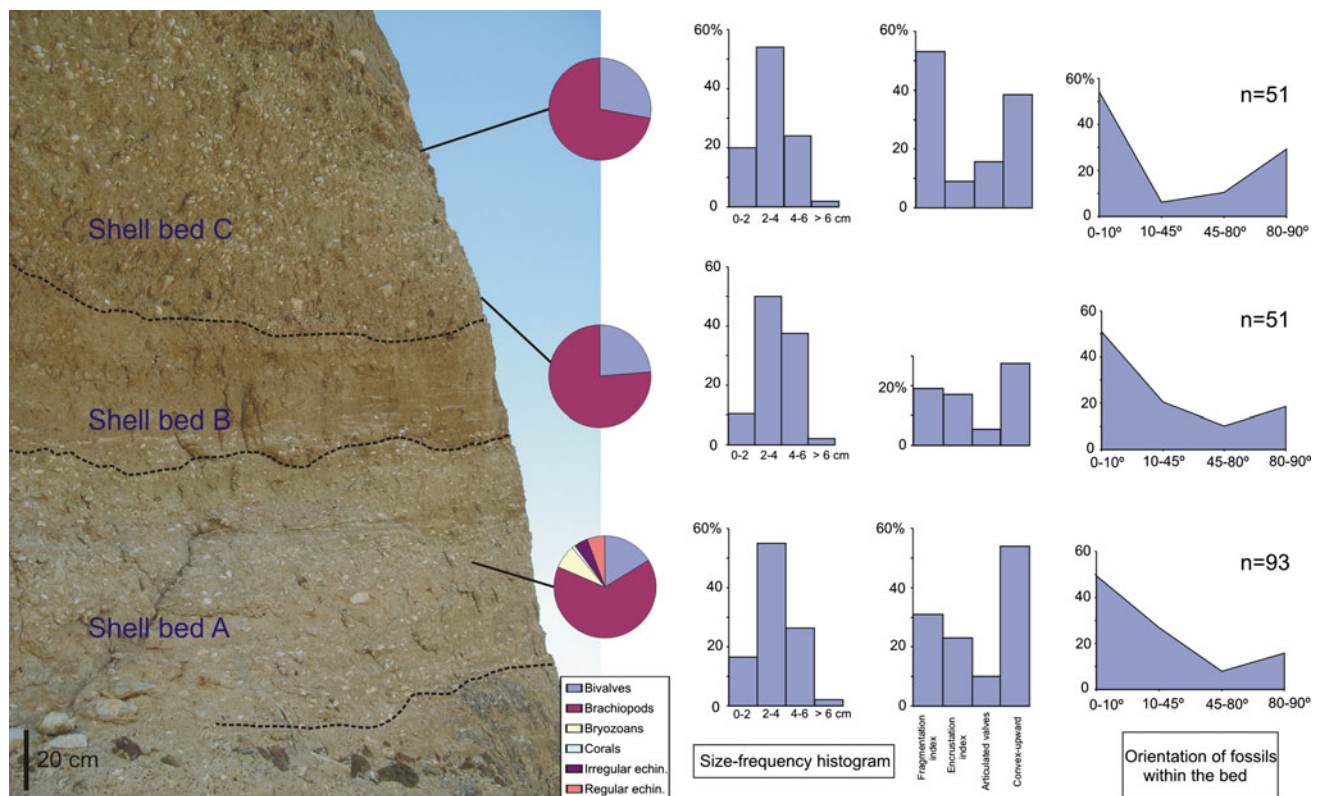
Fig. 8 Composition of macroinvertebrate assemblages (pie diagrams), size structure, taphonomic indices, and orientation of valves in the shell bed A, and lower and upper parts of shell bed C in the northern section, computed on the basis of both brachiopods and bivalves

the shallowest environments, *Gryphus vitreus* that also belongs to the family Terebratulidae still occurs frequently in dense populations in high-energy deep-shelf and slope environments where it specifically exploits mixed-bottom substrates with constant high-energy bottom currents and weak sedimentation rates (Boullier et al. 1986; Emig 1987, 1989). This implies that the ability to achieve high population density and to have the potential to form shell concentrations were partly shared among the members of the family Terebratulidae and thus is phylogenetically conserved (i.e., species in some clades are characterized by consistently higher population growth rates than in other clades). In addition, the Cretaceous-Cenozoic radiation of long-looped terebratulid brachiopods in temperate zones of the southwestern Pacific also led to the evolution of relatively diverse brachiopod clades that presently occupy a wide range of shallow environments in cool-temperate zones, can be relatively abundant in shallow environments (Richardson and Watson 1975; Richardson 1981), and formed marked shell concentrations in the Cenozoic of the southern hemisphere (Allan 1937; MacKinnon et al. 1993; Hendy and Kamp 2004).

It is possible that, rather than representing unusually high carbonate production rates, the origin of brachiopod concentrations dominated by *Terebratula terebratula* is related to very low disintegration rates. However, the assemblages with brachiopods are certainly affected by substantial preservational bias because pedicle valves are significantly more common than brachial valves in both proximal and distal settings. The predominance of pedicle valves can be related to a higher vulnerability of brachial valves to mechanic breakage (Velbel and Brandt 1989) and/or higher susceptibility to out-of-habitat winnowing and differential transport (Simões and Kowalewski 2003; Simões et al. 2005) because pedicle valves of *Terebratula terebratula* are not only larger and more convex than brachial valves but also slightly thicker, especially in the posterior umbonal parts and thus are likely less susceptible to transport or in situ disintegration (Holland 1988; Velbel

Fig. 9 Sedimentary structures in the southern section. **a** Stacking of ▶ sets of cross-stratified sandstones representing the migration of 3D-dunes with a brachiopod concentration at the top. **b** Detail of the brachiopod bed consisting of trough cross-bedded brachiopod shells representing the migration of a 3D-dune. **c** 1.5 m-high sets of cross-stratified sands representing 3D-dunes migrating to the south and limited by erosional reactivation surfaces (marked by *arrows*) draped by brachiopods and bivalve shell accumulations. **d** Detail of the internal unconformity surface between cross-stratified sandstone sets and lags with broken shells (*cover cap* for scale). **e** Lag of clasts (basal gravel bed, see Fig. 3b, c of the northern section) and bioclasts underlying the cross-stratified sandstone set shown in c (*cover cap* for scale)
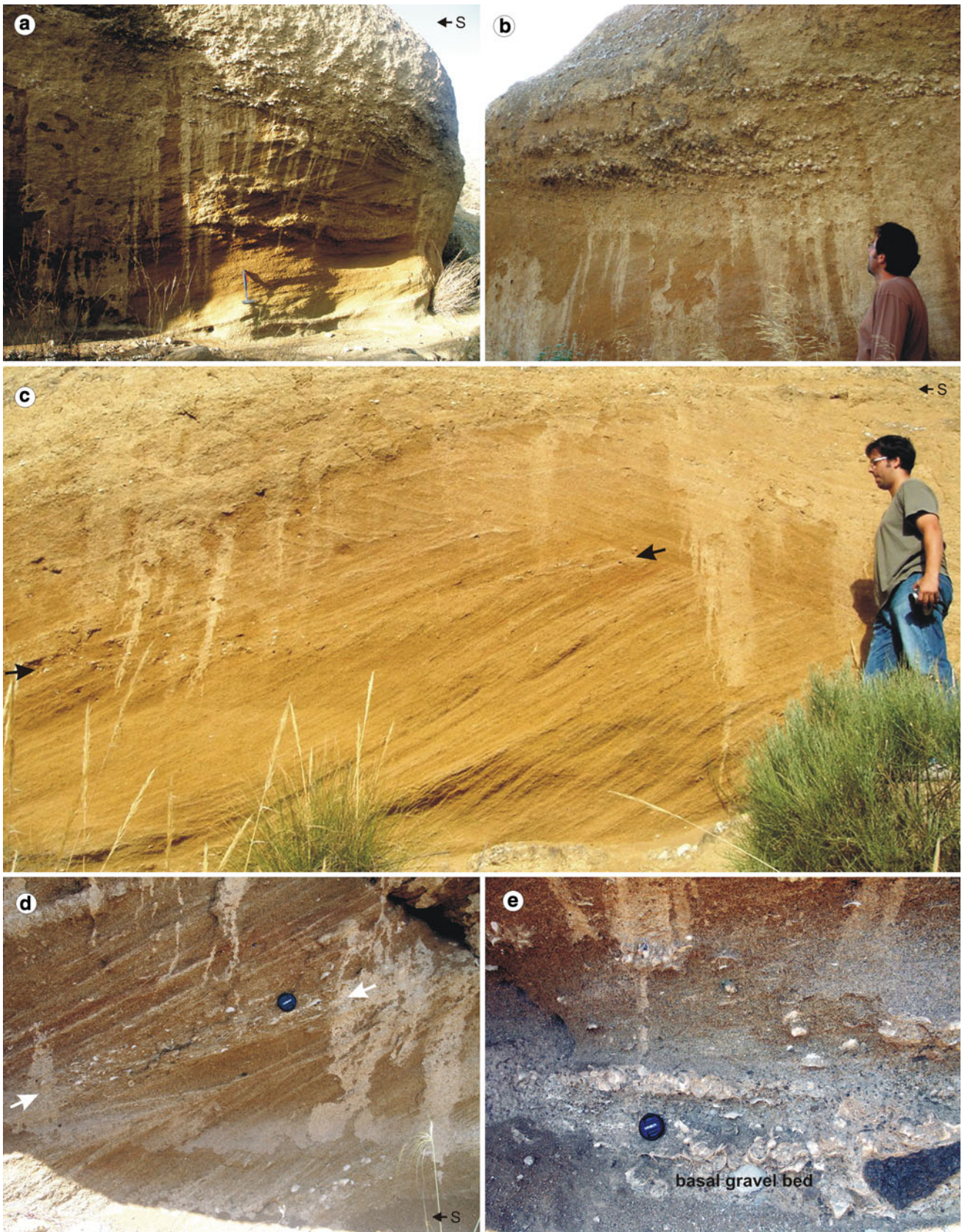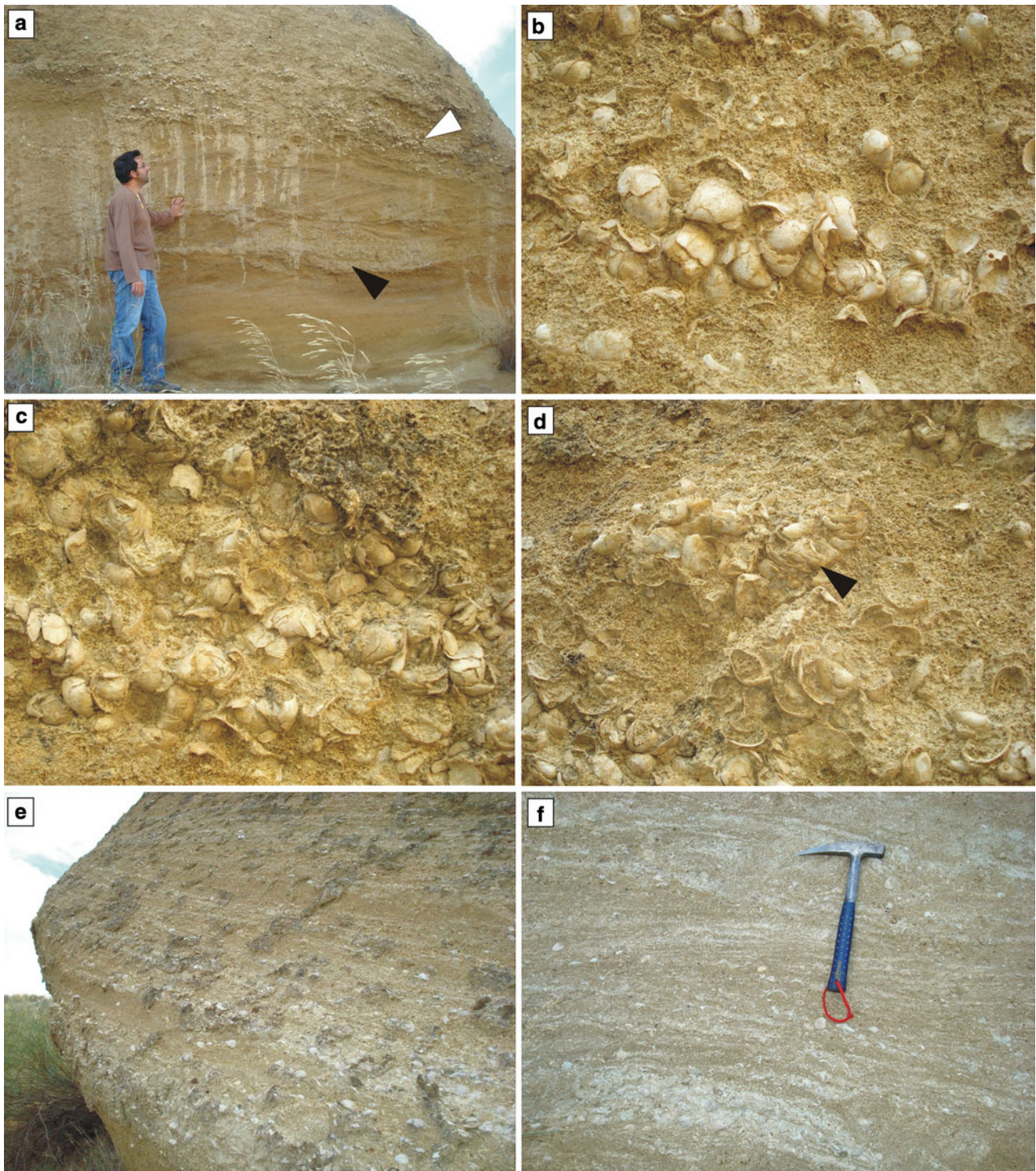
Fig. 10 Brachiopod concentrations in the southern section. **a** 3D-megaripples with lenticular concentrations (*white arrow*) and local bioturbated interval (*black arrow*). **b** Detail of a lens with densely packed disarticulated valves in the lower part of the 3D-megaripples interval. **c** Densely packed disarticulated valves of *Terebratula terebratula*. **d** Densely packed disarticulated valves in lenticular concentrations showing imbrication (*arrow*). **e**, **f** Upper part of the 3D-megaripple interval with undifferentiated very small bioclasts (*white horizons*) and dispersed brachiopod valves

Fig. 11 Taphonomic indices of shell concentrations in the prodelta (shell bed A and C) and tidal- and storm-dominated ramp (shell concentrations at the base of the 3D-dunes and lenticular shell concentrations in the lower part of the 3D-megaripples)
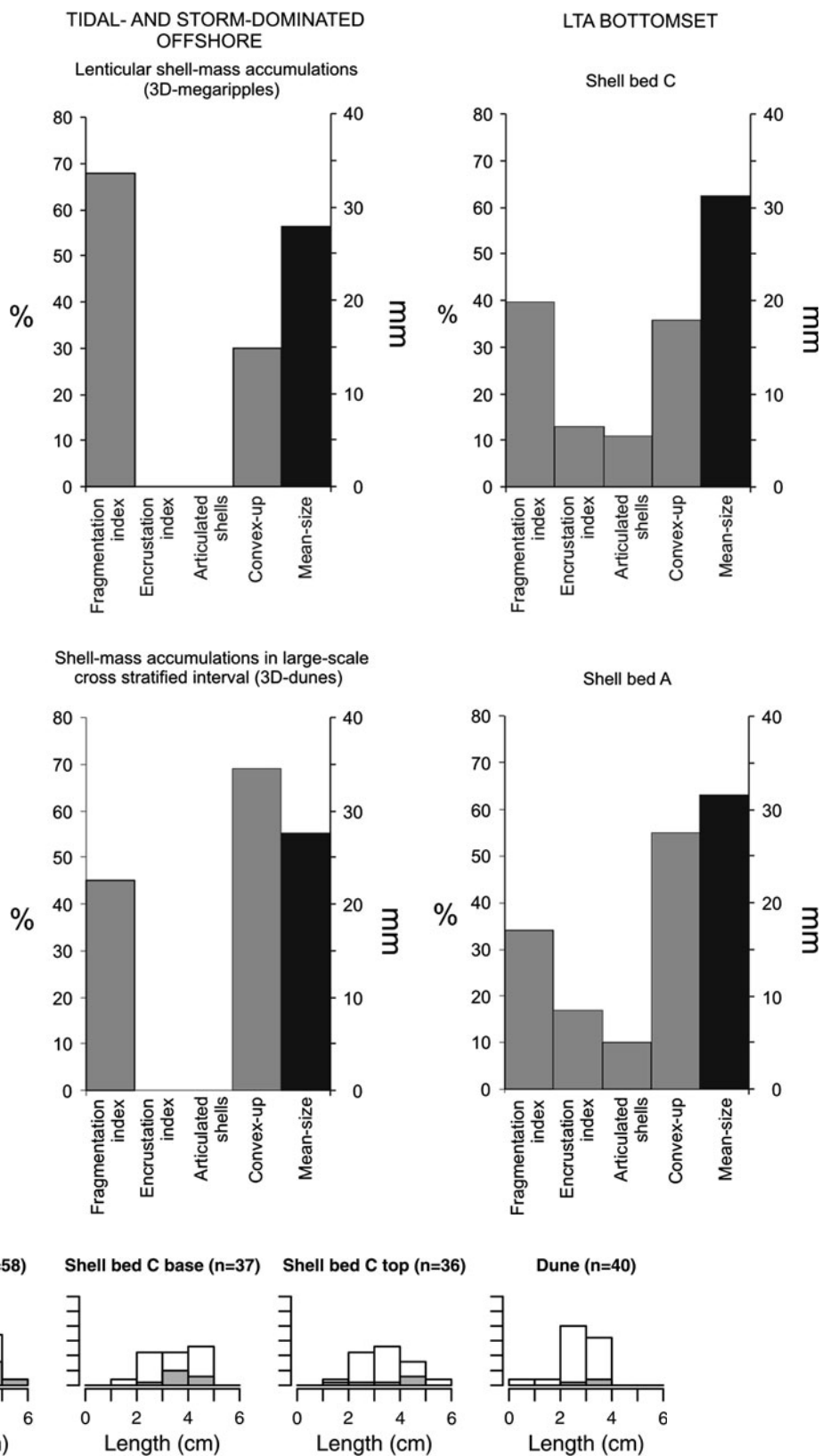
Fig. 12 Size-frequency distributions of brachiopods in one assemblage from dune deposits in the southern section (ramp) and in three assemblages from shell beds A and C in the northern section (prodelta). Note: *white* for pedicle valve and *grey* for brachial valve
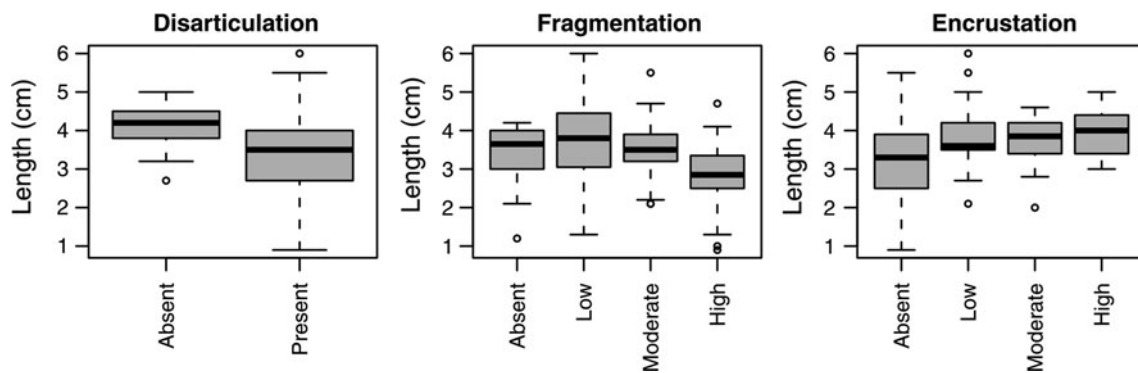
Fig. 13 Size-specific preservation of brachiopod specimens in box-plots, pooling all four sampled assemblages. Brachiopod specimens more affected by encrustation are larger than disarticulated and fragmented specimens. Boxplots show medians and the 25 and 75 quartiles, whiskers denote values 1.5 times the interquartile range, and *white circles* mark extreme values
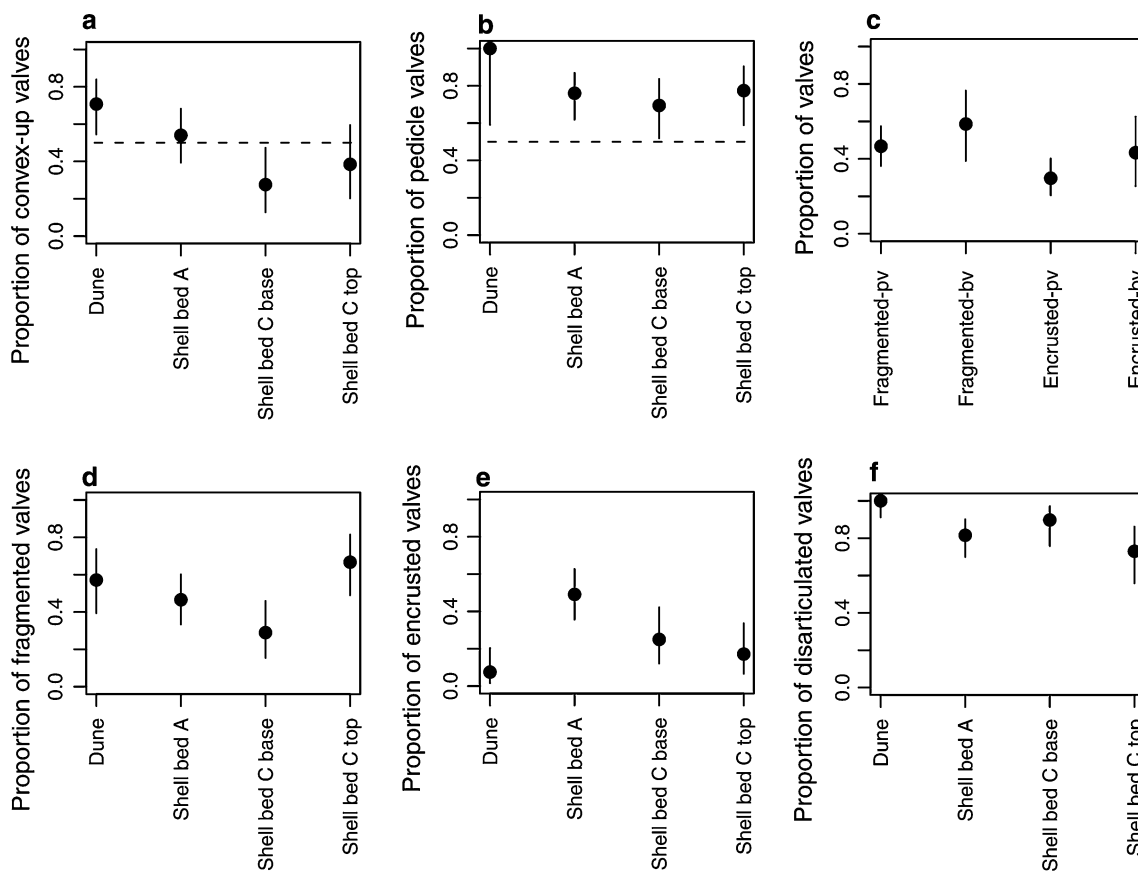
Fig. 14 a Convex-up-oriented valves are more common in the dune assemblage than in shell beds. **b** In all assemblages the proportion of pedicle valves significantly differs from the expected value of 0.5 if preservation probability of both valves would be equal. This bias is stronger in dunes than in shell beds. **c** Brachial valves (bv) are generally more fragmented and encrusted than pedicle valves (pv), although the differences are relatively small (pooling all four sampled assemblages). **d–f** Proportions of fragmented (grades 2–4), encrusted (grades 2–4), and disarticulated valves in four assemblages

and Brandt 1989; Alexander 1990). The proportion of brachial and pedicle valves in brachiopod fossil concentrations (Brett and Baird 1986) and Recent environments (Noble and Logan 1981; Simões and Kowalewski 2003; Simões et al. 2005) has been used to infer shell transport,

environmental energy and residence time on the sea-bottom. Simões and Kowalewski (2003) found the pedicle/brachial ratio to be a result of differential valve transport in tidal flat and beach environments, whereas Noble and Logan (1981) found differential preservation of valves of

Terebratulina septentrionalis in brachiopod death assemblages from rocky subtidal environments to occur without significant transport.

In addition, in spite of spatial differences in brachiopod preservation between proximal and distal settings, disarticulation and fragmentation of individual brachiopod specimens is moderate to relatively high in both types of environments. Therefore, the origin of these thick concentrations was not conditioned by unusually low rates of disintegration. Rather, they originated under conditions of relatively high disintegration rates but those were not sufficiently high to counteract the high rate of brachiopod production and thus the ability of brachiopods to dominate the sediment volumetrically. Finally, although concentrations of *Terebratula terebratula* in dunes and megaripples are clearly associated with conditions of winnowing, erosion and resedimentation, the thickest concentrations in proximal settings correspond to higher net sedimentation rates, implying that the effects of sedimentation rates were less critical in the origin of concentrations than conditions allowing high production rates.

Brachiopod concentrations from prodelta

Matrix-supported angular gravel in lobe bodies are interpreted as cohesionless debris-flow lobes frozen at the prodelta (sedimentary subenvironment corresponding to the bottomset of the Gilbert-type delta). The prodelta deposits of this delta are coarser than common prodelta deposits due to the redeposition of foreset conglomerates downward by slope instability. This type of delta is termed 'modified Gilbert-type delta' (Postma and Roep 1985). The vertical aggradation pattern of the prodelta with the shell beds A, B, and C, which is fed by siliciclastic sediment supply directly from the delta feeder-mouth and also from failures of sediments from delta foresets, is indicative of a relatively high sedimentation rate in the prodelta. Depth of the brachiopod accumulation can be deduced from the deltaic clinoform geometry. It is calculated approximately as the vertical distance (delta height) between topset facies (where the coastline position is marked by beach deposits as was reported by Soria et al. 2001) and prodelta facies of the deltaic clinoform (bottomset setting). This distance corresponds to 30 m (see Fig. 3a). *Terebratula terebratula* was also documented from similar depths (20–50 m) from the Middle Miocene of Malta (Pedley 1976).

Bidirectional 3D-megaripples present in the depositional subunit IIIb reveal a shallow-marine setting (prodelta/shoreface) dominated by tidal ebb and flood currents. However, the source habitat of the shells, i.e., the original environment in which the brachiopod lived, was probably close to the prodelta because the bottomset deposits with densely packed brachiopods are poorly sorted and mostly lack indicators of high-energy conditions. In this sense, the assemblage registered in the prodelta is probably parautochthonous. With the exception of encrustation levels that are lower in the dune deposits, taphonomic damage is generally lower in the prodelta deposits where brachiopods are more common. Therefore, the gradient in the thickness of concentrations between the prodelta and high-energy ramp deposits is caused by a combination of higher productivity rates and lower disintegration rates in the prodelta environment (Tomašových et al. 2006b).

In the prodelta shell-beds (northern section), the diversity decreases upwards and might indicate (1) conditions of increased sediment disturbance, (2) environmental changes that affected the composition of regional species pools, or (3) changes that favored species adapted to low resource availability or firm and temporally stable substrate, excluding infaunal species or those with high metabolic rates. The almost monospecific shell bed C, containing *T. terebratula*, most likely represents the diversity minimum and probably an increase in stress conditions. Modern dense populations of large-sized brachiopods occur in low-productivity polar habitats and in deep-shelf and slope habitats (e.g., Emig 1989; Pennington et al. 1999; Peck et al. 2005; Gili et al. 2006).

The diversity of the fossil assemblages also decreases from the lower shell bed A of the prodelta to the shell mass-accumulations from 3D-dunes and 3D-megaripples southward (distal parts). Taphonomic features and sedimentary structures of shell beds point to increased hydrodynamics conditions to the south (Fig. 11). In contrast, a comparatively low water energy is evidenced by lower values of shell fragmentation and of convex-up orientations within shell bed C in proximal parts of the delta (Fig. 11).

Traction-dominated flow during the deposition of the shell bed A can be inferred from a dominant convex-up orientation of valves (e.g., Futterer 1982; Kidwell and Bosence 1991; Messina and Labarbera 2004). The presence of encrusters on internal sides of valves indicates that the dead individuals were not immediately buried and high proportions of disarticulated specimens also indicate that the time of exposure on the sediment–water interface was not minor. However, the low fragmentation index of shell beds A and C shows that exposure did not last long after death of the brachiopod. The decreasing values of encrustation in shell bed B and at the top of C suggest a more rapid burial, a less stable substrate, and/or greater turbidity related to higher sedimentation rate and water energy. The increase in concave-up-oriented valves and the decreasing proportions of encrustation in the shell bed C, together with the decrease in diversity, suggest a more intense bioturbation and a less stable substrate, and/or greater turbidity related to higher sedimentation rate. Delta progradation finally resulted in proximal and shallower delta deposits (foreset beds with lack
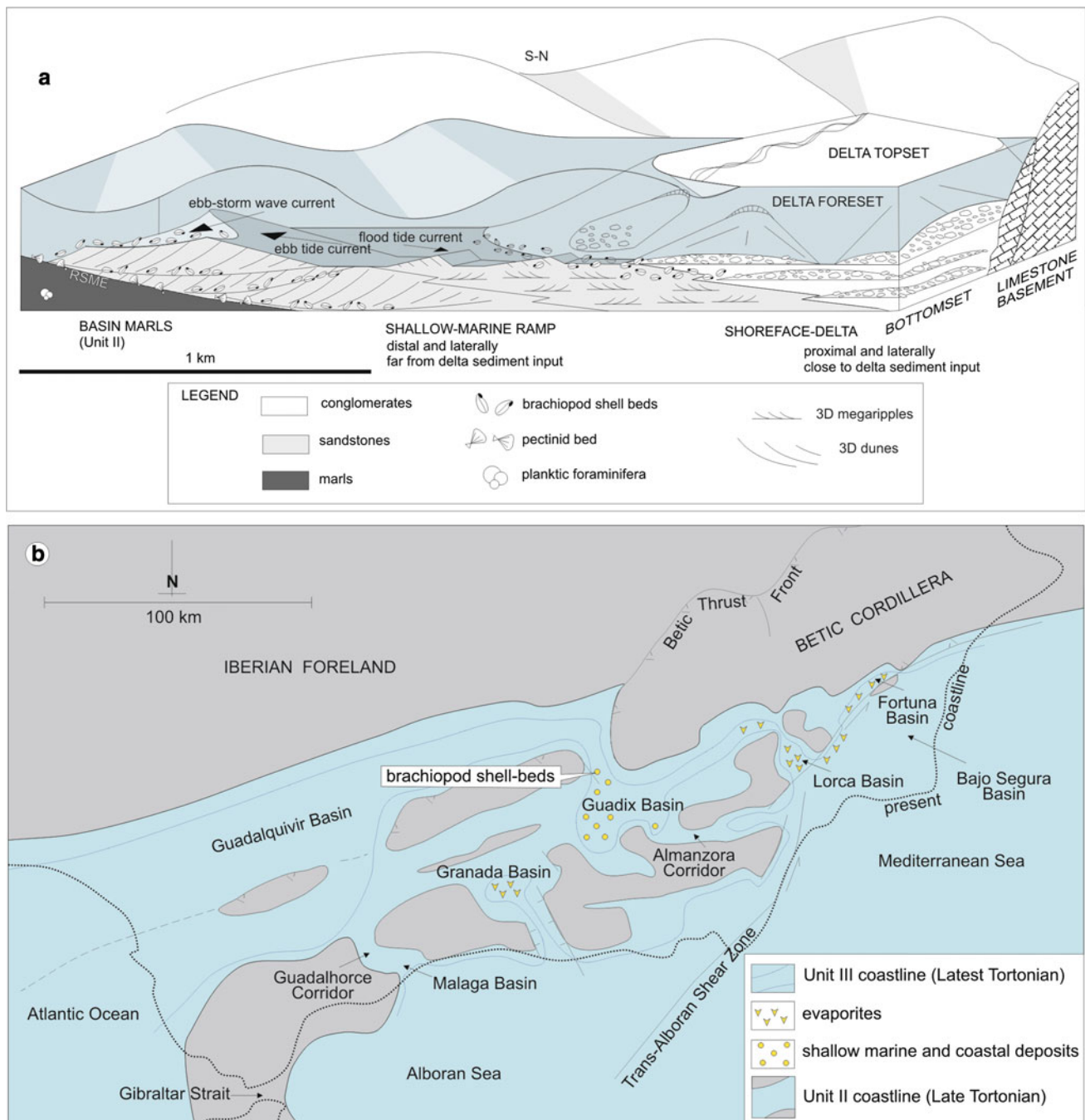
Fig. 15 a Scheme illustrating the hydrodynamics and distribution of depositional systems (delta and ramp settings) where the brachiopod concentrations occur (approximate scale). **b** Simplified paleogeography of the Betic seaways connecting the Atlantic Ocean and Mediterranean Sea during the latest Tortonian, when brachiopods developed in the northern Guadix seaway (modified from Soria et al. 1999)

of brachiopods shells) overlying the prodelta deposits with the shell beds. Brachiopods linked to prodelta deposits suggest their retreat to offshore habitats (bottomset areas coeval to prograding foreset) in the context of delta shallowing. Pedley (1976) also observed that individuals of *T. terebratula* attain larger size in habitats with low net sedimentation rates and turbidity.

Brachiopod concentrations from tidal- and storm-dominated siliciclastic ramp

The presence of bedforms resembling large-scale 3D-dunes and small-scale (2D and 3D) megaripples suggests the activity of strong currents capable of transporting sand grains and brachiopod shells. The decrease in the bedform

height from the bottom to the top of the interval can be interpreted as a result of decreasing current velocity. The concentrations with brachiopods (and bivalves) that drape reactivation surfaces of 3D-dune foresets can be interpreted as storm beds. Storms eroded the dune on its leeward-side and deposited a normally graded bed of shells, reflecting the loss of energy of the storm-wave. Shells were probably mainly reworked from the brachiopod factory, which was located in more proximal areas. The location of the storm beds in more distal areas relative to the brachiopod factory on southward-dipping dune foresets indicates that the formation of storm beds took place through southward-flowing storm ebb currents. Therefore, dune migration to the south is related to high-energy ebb currents that were presumably more constant in time than the sporadic storm ebb-currents. Basinward unidirectional dune migration and bidirectional migration of the overlying megaripples recording herringbone structures can be interpreted as signs of deposition in a tidal setting. Dunes are interpreted as migrating across a tidal-dominated offshore setting that was episodically affected by storms. The prevalence of a given tidal current (ebb-tidal current, in this example) is very common and depends on the morphology of the coastal setting or its relative distance from the amphidromic points of each tidal area (Kvale 2006). The absence of mud-drapes or tidal bundles could be related to a lack of mud (the delta supplied very coarse-grained sediment) and to the high-energy nature of the currents. Tidal dunes developed parallel to the dominant tidal constituent (Darlymple and Rhodes 1995). Large- and small-scale cross-stratified sands forming composed dunes in shallow marine analogue settings can be related to tidal cycles of different duration (Longhitano et al. 2010, 2011). Small-scale structures such as megaripples and large-scale structures such as dunes reflect short-term and long-term processes, respectively (Longhitano and Nemec 2005).

In the southern section, shell concentrations at the base of the dunes are characterized by very high values of fragmentation and disarticulation, highly biased pedicle/brachial valve ratios, the smallest mean size of shells, and by the highest proportion of convex-up orientations. The size of specimens also decreases from the lower parts of the prodelta towards 3D-dunes and 3D-megaripples. All indicate the presence of long-term high-energy conditions as well as transport of the shells from more proximal settings (prodelta represented by the northern section) by bottom currents. Predominantly convex-up-oriented valves indicate the activity of long-term high-energy currents (e.g., Futterer 1982; Kidwell and Bosence 1991; Messina and Labarbera 2004) during the deposition of the large-scale cross-stratified interval (3D-dunes interval). However, the lenticular and densely packed shell concentrations at the base of the small-scale cross-stratified interval (3D-megaripples interval) are characterized by well-preserved disarticulated valves, oriented mainly concave-up, and can also record temporarily restricted colonization events in high-energy ramp habitats that were quickly smothered by sediment. Dominance of concave-up orientation of valves indicates the presence of turbulent/vortical flow and suspension settling (Futterer 1982).

The brachiopod and bivalve remains from the upper part of the megaripples are predominantly oriented convex-up and lack encrusters, implying an increase in the current velocity and a decrease in substrate stability. To conclude, taphonomy and geometry of the shell concentrations in distal parts dominated by tidal dunes and storms indicate an increase in the degree of transport and reworking of the fossil assemblage to the south (allochthonous assemblage). Thus, the brachiopod habitat was distally limited by tidal- and storm-dominated siliciclastic offshore dynamics and proximally limited by prograding foreset facies. The higher energy currents were directed southward during storm-wave-ebb stages, reworking the brachiopods from prodelta to more distal areas in an inner ramp setting. However, *Terebratula terebratula* probably also temporarily colonized megaripples as indicated by preservation of spatially restricted clusters in the southern section. The capacity to inhabit high-energy environments is also evidenced by another member of the family Terebratulidae, *Gryphus vitreus*, which is presently commonly attached to small rocks in troughs of megaripples under strong bottom currents (Emig 1987).

The diversity of the fossil assemblages also decreases laterally from the lower shell bed A of the prodelta to the shell concentrations in 3D-dunes and 3D-megaripples. Taphonomic features and sedimentary structures preserved in the shell concentrations point to an increase in the hydrodynamic activity to the south (Fig. 11).

Paleoenvironmental and paleogeographic control

Taphonomy and geometry of the shell concentrations in distal parts dominated by tidal dunes and storms indicate an increase in the allochthony of the fossil assemblage to the south, but probably also a decrease in population density of brachiopods in the same direction (Fig. 11). Thus, the brachiopod habitat was distally limited by tidal- and storm-dominated siliciclastic offshore dynamics and proximally limited by prograding foreset facies. Reductions and expansions of the onshore-offshore habitats of brachiopods at the short time scale have been reportedly caused by variations in sediment (water turbidity) and nutrient supply (Tomašových 2006b). Pedley (1976) proposed that *T. terebratula* had a low tolerance to turbidity and wave action. Foreset subenvironments represent nutrient-richer and higher siliciclastic supply than prodelta sub-environments.

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