



Borers and epizoans on oyster shells from the upper Tortonian, Lower Chelif Basin, NW Algeria

Vrtalci in epizoji na zgornjetortonjskih ostreidnih lupinah iz Spodnjega Chelif bazena, SZ Alžirija

Rachid KHALILI, Linda SATOUR & Saci MENNAD

University of Oran 2 - Mohamed Ben Ahmed, Algeria, Laboratory of Palaeontology, Stratigraphy and Palaeoenvironments, El M'Naouer, BP 1015, ex IAP, Es Senia 31000 Oran, Algeria;
e-mail: rachido1990@gmail.com, satourlind@gmail.com, sassiy2@gmail.com

Prejeto / Received 18. 4. 2022; Sprejeto / Accepted 27. 3. 2023; Objavljeno na spletu / Published online 4. 8. 2023

Key words: Miocene, borings, encrustation, *Entobia*, *Gastrochaenolites*, *Caulostrepsis*, *Trypanites*, *Maeandropolydora*, foreshore, shoreface

Cljučne besede: miocen, vrtnanje, inkrustacija pas bibavice, *Entobia*, *Gastrochaenolites*, *Caulostrepsis*, *Trypanites*, *Maeandropolydora*, plitvi podplimski pas

Abstract

The three oyster lenses of the upper Tortonian of Djebel Touaka site which are described herein contain three species, *Crassostrea gryphoides* (Schlotheim), *Ostrea lamellosa* (Brocchi) and *Hytissa squarrosa* (De Serre). The density of shell packing between the lenses is dissimilar. Most of the specimens are disarticulated and poorly fragmented; they exhibit a random distribution and orientation, without any distinct sorting. Bioerosion and encrustation are featured on both surfaces of left and right valves.

The identified ichnogenera are *Entobia* (Bronn), *Gastrochaenolites* (Leymarie, 1842), *Caulostrepsis* (Clarke, 1908), *Trypanites* (Mägdefrau, 1932) and *Maeandropolydora* (Voigt, 1965). Encrusters are scarce, represented by juvenile oysters/other bivalves, bryozoans and barnacles. The coexistence of borings on both sides of valves means that they probably occur not only while alive, but they keep happening after death. The oyster beds were deposited in a foreshore to shoreface environment, from the combined action of wave currents and sedimentation rate.

Izveček

Opisane so tri ostreidne akumulacije iz zgornjega tortonija Djebel Touka v Alžiriji. Ostreidne plasti vsebujejo vrste *Crassostrea gryphoides* (Schlotheim), *Ostrea lamellosa* (Brocchi) in *Hytissa squarrosa* (De Serre). Gostota ostreidnih lupin variira. Večina primerkov je disartikuliranih in nekoliko fragmentiranih. Razporejeni so naključno in brez preferenčne orientacije. Prav tako niso sortirane. Sledovi bioerozije in preraščanja so prisotni na obeh straneh levih in desnih loput. Prepoznani so bili *Entobia* (Bronn), *Gastrochaenolites* (Leymarie), *Caulostrepsis* (Clarke), *Trypanites* (Mägdefrau) in *Maeandropolydora* (Voigt). Preraščanja se stojijo iz juvenilnih primerkov ostrig in drugih školjk, mahovnjakov in ciripednih rakov. Hkratna prisotnost izvrtin na obeh straneh lupin pomeni, da je do preraščanj prišlo tudi po smrti ostreidnih školjk. Ostreidne akumulacije so nastale v širšem območju plimovanja in v plitvem podplimskem pasu pod skupnim vplivom valovanja in hitrostjo odlaganja sedimenta.

Introduction

Many papers have debated the fossil oyster's paleoecological and biostratigraphic properties (e.g., El-Hedeny, 2005, 2007; El-Sabbagh, 2008; Lopes, 2011; Domènech et al., 2014; El-Sabbagh et al., 2015; El-Sabbagh & El-Hedeny, 2016; Breton et al., 2017). The stratigraphic studies of Miocene

deposits of the Lower Chelif Basin had been the purpose of several anterior authors (Mansour, B, 2004; Belekebir et al., 2008; Belhadji et al., 2008; Atif et al., 2008; Saint-Martin, 2008; Satour et al., 2011, 2013, 2020). According to Neurdin-Trescartes, (1995), the paleogeography of Lower Chelif Basin during the Miocene changed through the

time and the space, dependant on different supplies of sediment, coming into the basin either from the north (uplifted coastal block) from the east (shore currents bringing detrital materials from the Krouminie), and from the south from the area of Medea and Bou Hanifa.

The upper Tortonian outcrop of Sig Valley reveals three main oyster lenses with different repartition and orientation. The oyster shells are among the most favourable substrates for attachment and settlement of organisms. The effect of this latter may be simulated as encrustation or boring traces, which are very common in all the geological time epochs, and they are considered as the result of trace makers behavior, engraved on organic or rocky substrates (Gibert et al., 2004).

The purpose of this paper is to bring out and record the main traces produced by endoskeletozoa

and episkeletozoa, in hopes of better understanding the environmental conditions during life and after death of oysters.

Geographic and geologic context

The stratigraphic studies of Miocene deposits of the Lower Chelif Basin had been the purpose of several earlier authors (Neurdin-Trescarte, 1992; Mansour, 2004; Belekebir et al., 2008; Belhadji et al., 2008; Atif et al., 2008; Saint-Martin, 2008; Satour et al., 2011, 2013, 2020; Satour, 2021). The upper Miocene deposits are more distinguished in the center of the basin and contain many discontinuities, allowing a large variety of facies (Perrodon, 1957).

The studied outcrop belongs to the anticline of Djebel Touaka. It is located at approximately 1.5 km, south of the Sig City (Fig. 1). It is exposed

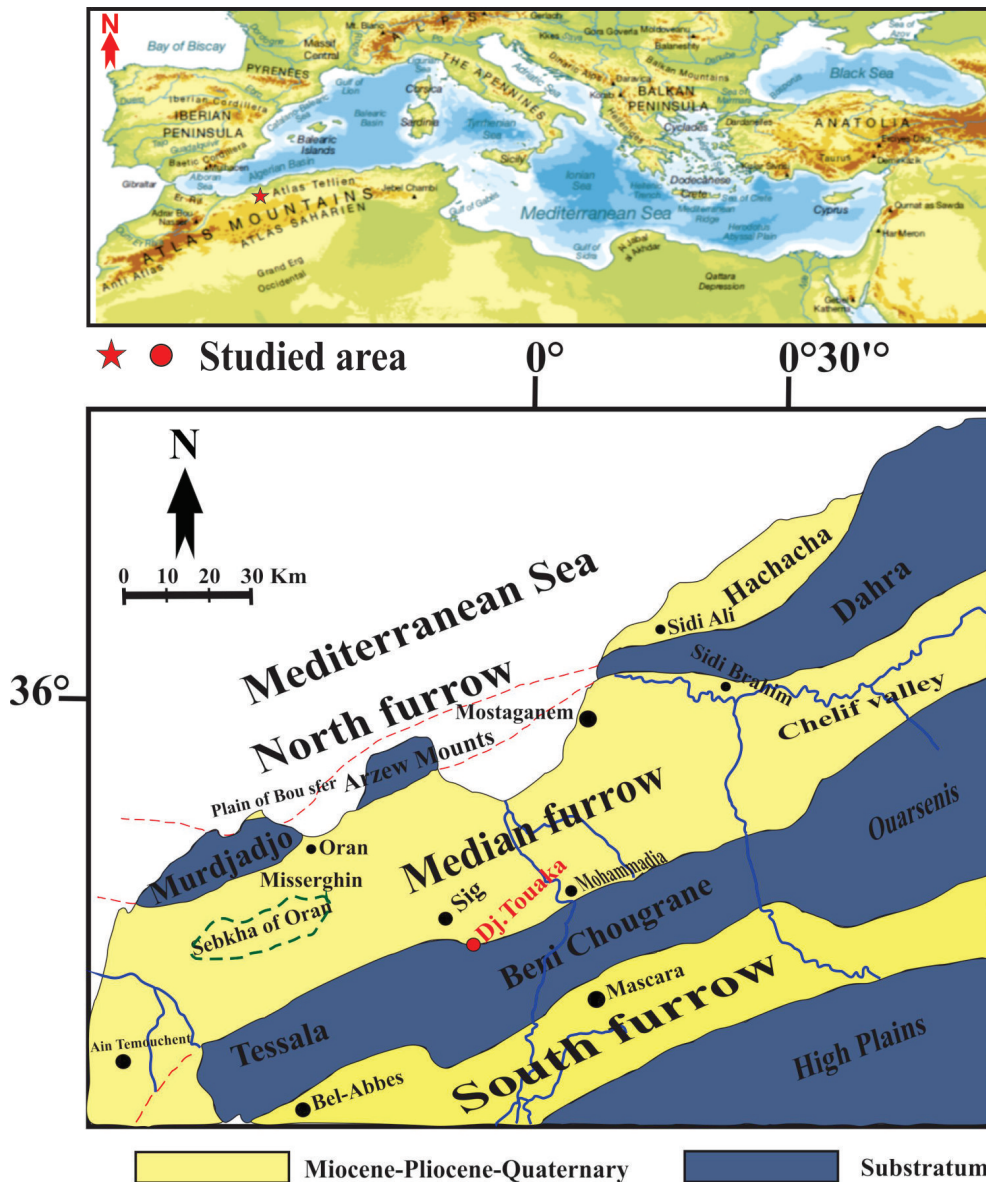


Fig. 1. Geographic and geologic localization of the studied area.

on the eastern side of the Sig Valley and belongs to the Beni Chougrane mounts. The upper Tortonian section is unconformably overlies the red sandstones of the second post-nappe cycle (Saint Martin, 1990). From bottom to top, it comprises numerous sandstones layers at the base showing horizontal, oblique and cross bedding, sandy yellowish marls contain three larger oyster's beds, blue marl, and alternation of fossiliferous limestone and marls, followed by the Messinian diatomites and El Bordj sands (Bessedik et al., 1997; Mansour, 2004) (Fig. 2).

Methodology

After washing and cleaning, 186 specimens were identified and analysed from the three oyster beds: 30 specimens were recovered from the first bed, 127 from the second bed, and 29 specimens from the third bed. The oyster shell beds were collected directly from the surface or by digging about 30 cm in sediments. The shells have different sizes (less than 70 mm for small shells and more than 70 mm for medium and large shells). They were described in the field by measuring the lateral extension, thickness; packing density and

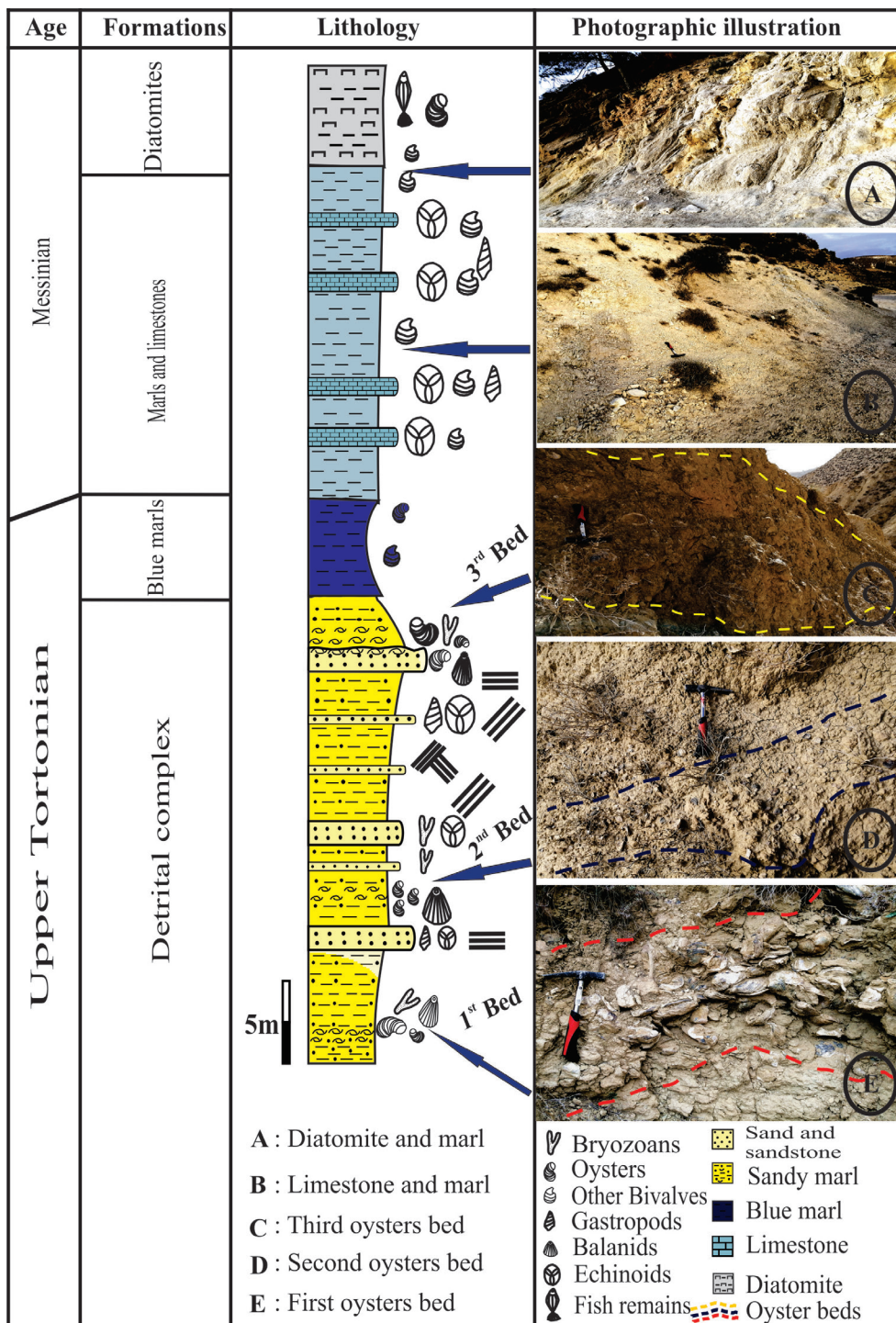


Fig. 2. Lithostratigraphic section of the upper Tortonian beds of Djebel Touaka (Sig).

shell orientation, taphonomic properties (disarticulation, borings and encrustation) were analysed in the laboratory.

The oyster specimens are stored at the Laboratory of paleontology, stratigraphy and paleoenvironments of the University of Oran 2.

Results

Description of oyster's beds

The collected oysters are almost disarticulated. However, two specimens from the third lens are preserved with valves still connected and showing vertical aggregates in the first and second beds (in french: Crassat d'huitres). They are adult forms, belonging to two families, Ostreidae and Gryphaeidae (Fig. 3).

The first lens takes place at the base of the marls, sometimes yellowish and sandy, with a lateral extension of about 40 m and variable thickness (30 to 70 cm), represented essentially by *Ostrea lamellosa* (16 left valves; LV), *C. gryphoides* (6 left valves, 3 right valves; RV) and *H. squarrosa* (5 LV). The distribution of the specimens shows

a strong concentration in the center (more than 60 percent) and becomes less dense (rarely seen) when we move toward the northeast and the southwest directions (less than 15 percent). They have a random distribution and slightly slanted with a predominance of concave-down valves compared to convex-up ones.

The second lens appears toward the middle of the detrital complex, in the yellowish sandy marls with a metric extension (about 70 m). The assemblage of oysters belongs to *O. lamellosa* (112 LV) and *H. squarrosa* (15 LV), characterized by small size and homogenous repartition (without any defined orientation of shells).

The third lens sets down at the surface of the last indurated sandstones bar (hard ground), appears like a tabular bed, with a lateral extension of 30 m. The collected shells were assigned to *O. lamellosa* (24 LV, 3 RV), *H. squarrosa* (2 articulated shells) and *Spondylus crassicosta* (one articulated shell). The specimens distributed at the surface of the sandstone bar (the last sandstone layer), show significant dominance of convex-up valves and without any observed direction.

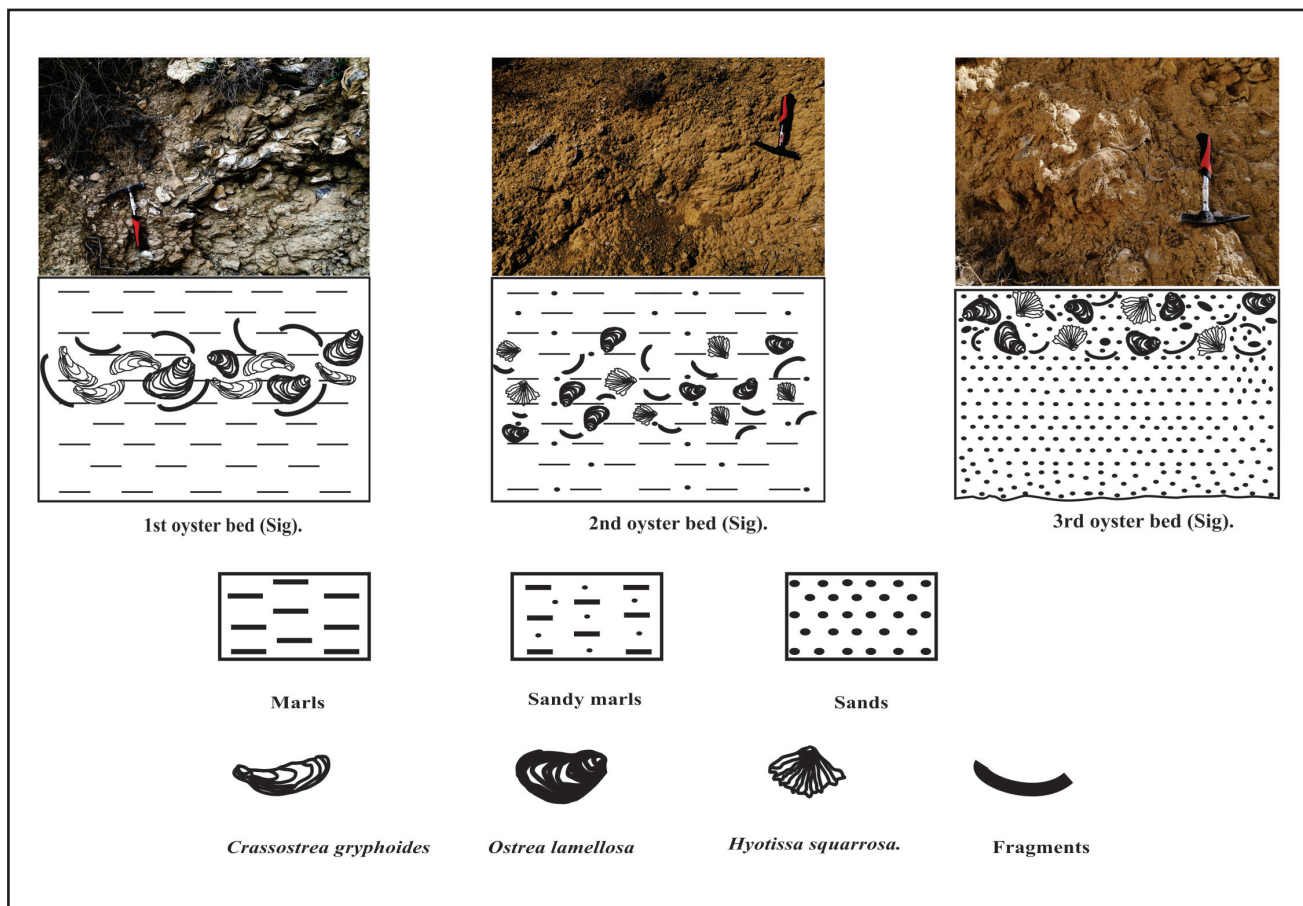


Fig. 3. The three beds identified from the upper Tortonian of Djebel Touaka (Sig).

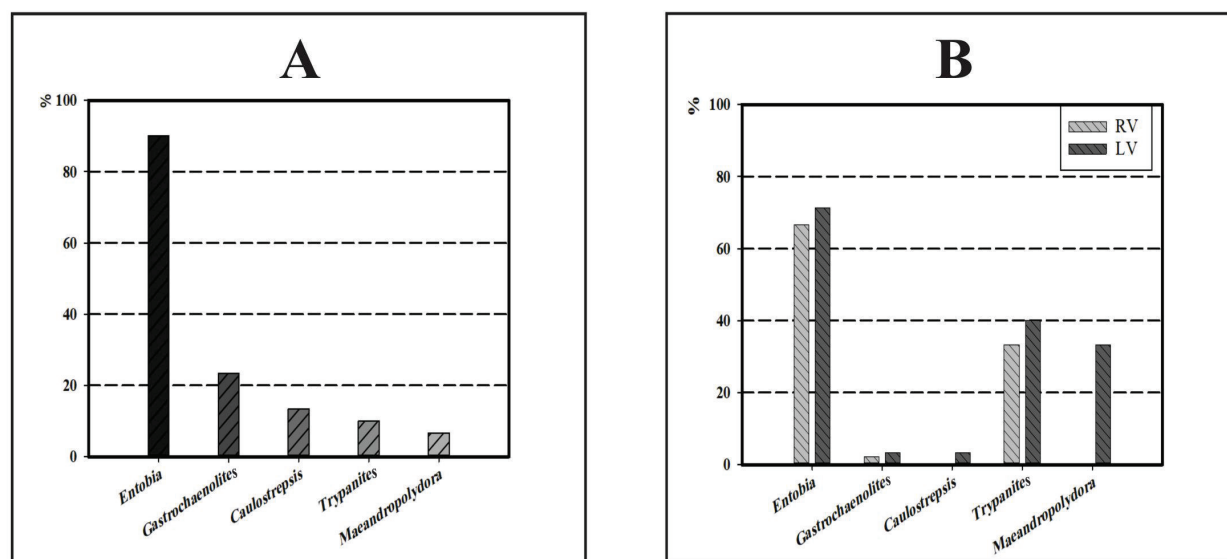


Fig. 4. Relative proportion of determined ichnogenus. **A:** All ichnogenera present in the three beds. **B:** All ichnogenera present in the three beds depending on valves (RV: right valves, LV: left valves).

Bioerosion

Both, the left and right valves are generally bioeroded (Fig. 4). Most of the bioerosion occurs on the external side, with fewer occurrences on the interior of the shells. The traces produced by endoskeletozoans are present on 60 % of the analyzed valves, recorded often on *C. gryphoides* and *O. lamellosa*; this may be due to the limited occurrence of *H. squarrosa*.

The most prominent trace marks produced by predators in the different valves from the three lenses are *Entobia* (90 %), *Gastrochaenolites* (23.33 %), *Caulostrepsis* (13.33 %), *Trypanites* (10 %) and *Maeandropolydora* (6.66 %).

Systematic ichnology

Ichnogenus *Entobia* (Bronn, 1837-38)

Ichnospecies type: *Entobia retiformis* (Stephenson, 1952)

Entobia cretacea (Portlock, 1843)

Material: Left and right valves of *C. gryphoides*, *O. lamellosa* and *H. squarrosa*.

Localities: Djebel Touaka at Sig, on the South-West border of the Lower Chelif Basin (Mascara province, North-West Algeria).

Description: According to Bromley and D'Alessandro (1984), these traces correspond to round apertures connected between each other

with cylindrical galleries on subsurface drilled by the siliceous sponges (oftenly *Cliona*). The diameter of these apertures measures between 0.1 and 1.5 mm, and sometimes with different diameters on the same shell (Lopes, 2011).

Two ichnospecies had been identified.

Entobia retiformis (Stephenson, 1952): This ichnospecies corresponds to perforations with millimetric diameter, organized following a right, oblique or sinuous lines (Fig. 5d).

Entobia cf. cretacea (Portlock, 1843): It differs from the precedent by apertures and chambers less wide and extension without wall, also by one canal interconnecting the chambers. This ichnospecies forms a network of long and right tunnels, connected with the surface by several aligned apertures (Figs. 6g, 6i).

Remarks: The ichnogenus *Entobia* is the most frequent in the recorded material. The opening chambers are distributed over both the right and the left valves of *C. gryphoides*, *O. lamellosa* and *H. squarrosa*, in about 90 % of specimens from the three beds, but are significantly more distinct at the external surface of the left valves (71.43 %) of all the determined species compared with the right valves (66.66 %). The intense exposure to *Entobia* contributes to the destruction of most of the right valves, due to their smaller thickness.

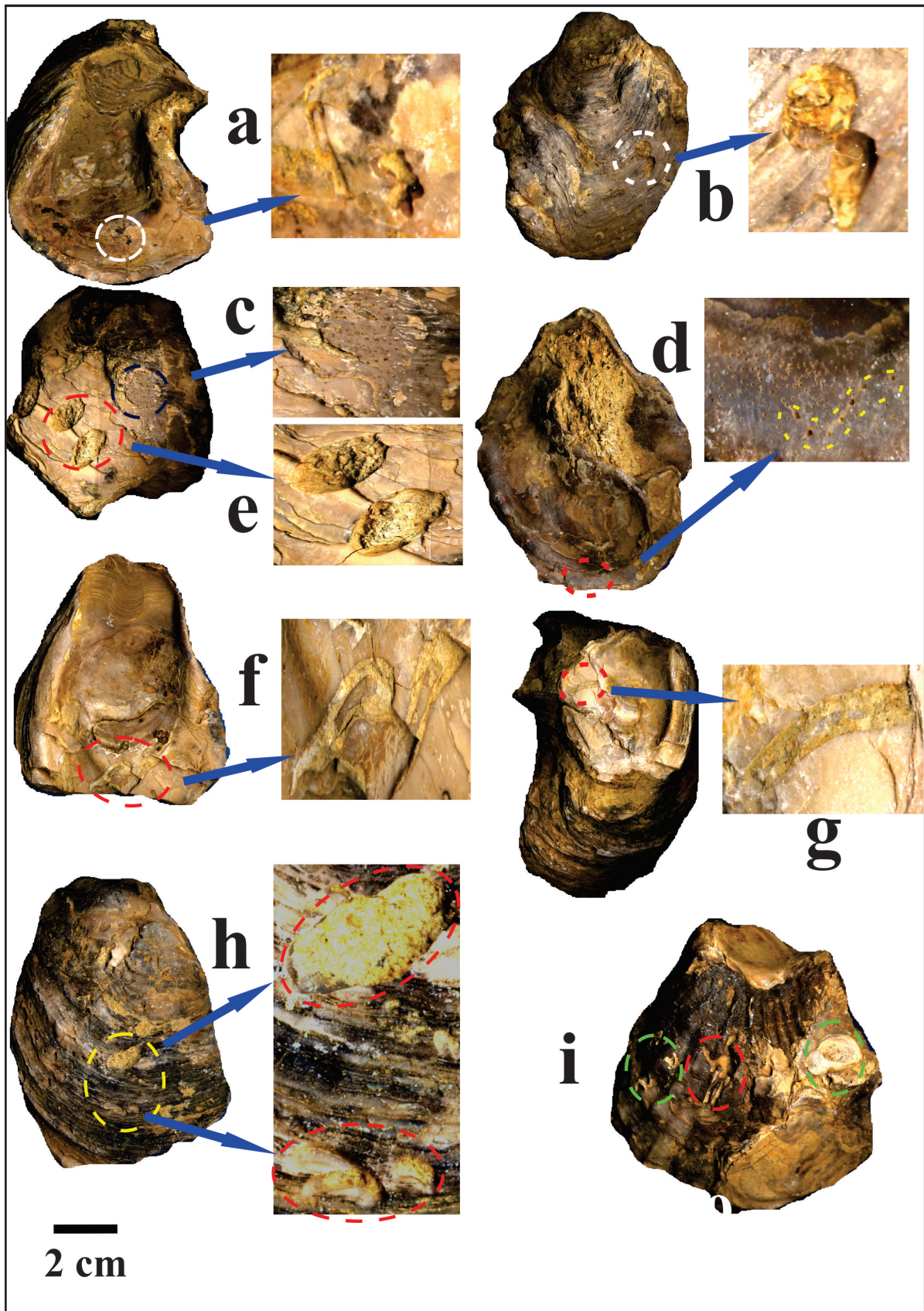


Fig. 5. Ichnofossils: **a** - *C. taeniola* on the internal surface of left valve of *C. gryphoides*; **b, d** - *Gastrochaenolithes* cf. *dijugus* on the external side and *E. retiformis* on the internal side of right valve of *C. gryphoides*; **c, e** - *Entobia* ichnosp. and *Gastrochaenolithes* cf. *dijugus* on the external face of left valve of *C. gryphoides*; **f** - *M. sulcans* on the inner side of left valve of *C. gryphoides*; **g** - *Gastrochaenolithes* cf. *dijugus* and cluster of *G. torpedo* on the outer side of *C. gryphoides*; **h** - *C. taeniola* over encrusted bivalve on the of left valve of *C. gryphoides*; **i** - *Caulostrepsis* ichnosp. on the outer surface of left valve of *H. squarrosa*, and encrustation by juvenile / adult oysters and balanids (eroded).

Ichnogenus *Gastrochaenolites* (Leymerie, 1842)

Ichnospecies type: *Gastrochaenolites torpedo*
(Kelly & Bromley, 1984)

Gastrochaenolites cf. *dijugus* (Kelly & Bromley, 1984)

Material: Left and right valves of *C. gryphoides*, *O. lamellosa* and *H. squarrosa*.

Localities: Djebel Touaka at Sig, on the South-West border of the Lower Chelif basin (Mascara province, North-West Algeria).

Description: This ichnogenus is typically produced by bivalves and attributed to multiple taxons, *Lithophaga* (Rios, 1994; Mauna et al., 2005), *Hiatella* and mytilids (Kelly & Bromley, 1984), also suspensivorous gastrochenids and pholadids (Tapanila & Hutchings, 2012). The openings are large and elongated, tilted toward the host substrate. They are simple and not aligned, solitary or in cluster, rarely with a striped parabolic base. The diameter is between 7 and 43 mm with 19 mm in average (Santos et al., 2011). In the case where these apertures are round and the neck unobservable, these characters are typical for the species.

Remarks: This ichnogenus was found frequently on the outer side of the left valves, except for some specimens of *C. gryphoides*, where it was produced on the right valves (Fig. 5.b). It is present on 23.33 % of the specimens, with 2.12 % on the right valves and 3.25 % on the left valves. The ichnospecies that were determined are: *Gastrochaenolites* cf. *dijugus* (Figs. 5b, 5e, 5h, 6.f) and *G. torpedo* (Figs. 5h, 6c, 6h).

Ichnogenus *Caulostrepsis* (Clarke, 1908).

Ichnospecies type: *Caulostrepsis taeniola*
(Clarke, 1908).

Caulostrepsis taeniola (Clarke, 1908)
(Figs. 5a, 5g, 6f)

Material: Left and right valves of *C. gryphoides*, *O. lamellosa* and *H. squarrosa*.

Localities: Djebel Touaka at Sig, on the South-West border of the Lower Chelif basin (Mascara province, North-West Algeria).

Description: *Caulostrepsis* is the product of different families of marine polychaetes (Bromley, 1978, 1994) or spionids (Barrier & D'Alessandro, 1985). It can be elongated, U-shaped, sinuous or straight. Occasionally, it appears in a figure 8-form.

Remarks: This ichnogenus appears only in the inner face of thicker left valves, in 13.33 % of the specimens, frequently parallel to the growth

lamellae of oyster valves. It is represented here by one species: *C. taeniola* (Clarke, 1908). It is absent from the second bed.

Ichnogenus *Trypanites* (Mägdefrau, 1932)

Material: Left and right valves of *C. gryphoides*, *O. lamellosa* and *H. squarrosa*.

Localities: Djebel Touaka at Sig, on the South-West border of the Lower Chelif basin (Mascara province, North-West Algeria).

Description: Generated by polychaetes and sipunculids (Bromley, 1994; Wilson, 2007). It has a shape of a complicated network of thin shallow tubes with a cylindrical to sub-cylindrical form, straight or sinuous, characterized by a single entry.

Remarks: The ichnogenus featured here occurs on the outer side of left valve of 10 % of the specimens from the first and the second bed (Fig. 6d).

Ichnogenus *Maeandropolydora* (Voigt, 1965)

Ichnospecies type: *Maeandropolydora sulcans*
(Voigt, 1965)

Maeandropolydora sulcans (Voigt, 1965)

Material: Left and right valves of *C. gryphoides*, *O. lamellosa* and *H. squarrosa*.

Localities: Djebel Touaka at Sig, on the South-West border of the Lower Chelif basin (Mascara province, North-West Algeria).

Description: Generally long and meandering tubes excavated by several forms of polychaetes, mostly Spionidae (Bromley & D'Alessandro, 1983). It was also interpreted as traces of suspensivorous annelids from different families (Bromley, 1994). These tubes have a diameter between 0.5 and 3 mm. They are frequently found parallel to the structure of growth layers of oyster valves.

Remarks: It is the less prominent ichnogenus, occurring on the inner face of left valve from the first and the second bed, present in 6.66 % of the specimens. One ichnospecies has been named and has the morphology of *M. sulcans* (Voigt, 1965) (Figs. 5f, 6b, 6d).

Encrustation

The total of encrusters in the three beds is very scarce: 5.95 % by barnacles, 6.48 % by bryozoans and 21.62 % by juvenile oysters and other bivalves (Fig. 7). Most of the analyzed specimens were found encrusted on the outer side of the left valves, and few of them exhibit encrusters on the inner side.

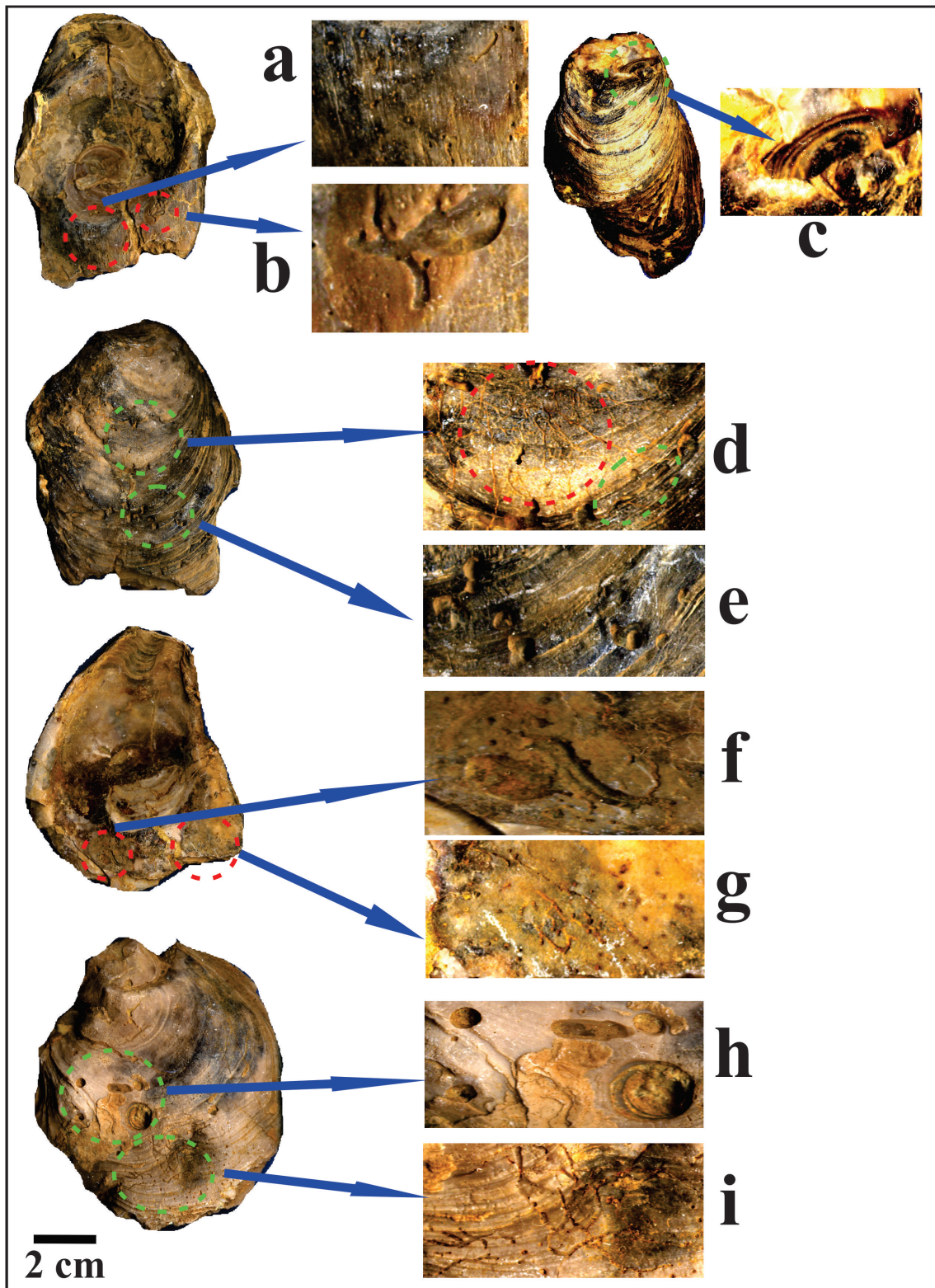


Fig. 6. **Ichnofossils:** *O. lamellosa*: **a** - *Entobia* ichnosp., *Caulostrepsis* ichnosp.; **b** - *M. sulcans*, on the internal surface of left valve; **c** - *G. torpedo* on the external side of *O. lamellosa* left valve, *O. lamellosa*; **d** - *Trypanites* ichnosp., *M. sulcans*; **e** - *Gastrochaenolithes* ichnosp., on the external face of left valve; *O. lamellosa*: **f** - *C. taeniola*, *Gastrochaenolithes* cf. *dijugus* and *Entobia* ichnosp.; **g** - *Entobia cretacea*, on the inner side of left valve of *O. lamellosa*; *O. lamellosa*: **h** - Cluster of different sizes of *G. torpedo*, *Entobia* ichnosp.; **i** - *E. cretacea* on the outer face of right valve.

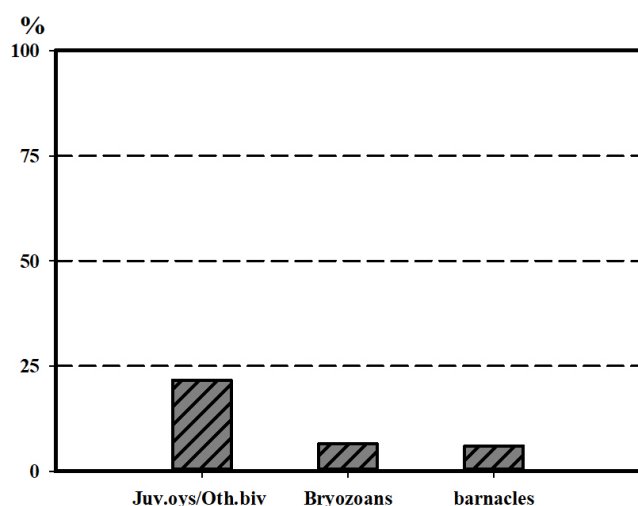


Fig. 7. Relative proportion of identified encrusters in the three beds.

The packed and dense bryozoans colonizing the internal surface of left valve; belong to the cheilostoma type (Figs. 8d–h). These thin carbonate network colonies were found only on oysters from the first and the third bed. Barnacles are recorded in several individuals of *O. lamellosa* from the second bed and one specimen of *C. gryphoides* from the first bed (Fig. 8e). They grow on the outer face of left valves, frequently forming clusters with few solitary specimens. Encrustation by juvenile oysters and other bivalves was observed from the first bed and more clearly from the second bed (Fig. 5i).

Discussion

The immense quantity of marls series interrupted by sands is the result of the upper Tortonian transgression (Belhadji et al., 2008). The intense ratio of disarticulation on oyster shells, combined with moderate fragmentation, signifies an extended time-averaging during deposit (Kidwell & Bosence, 1991; Brett & Baird, 1993). However, in the opinion of Allen (1992), disarticulated valves may serve as a sign of rapid burial episodes. These conditions may indicate that oyster shells were remobilized at a limited distance.

The scarcity of right valves suggests that they suffered from multiple sorting and reworking, because of their thinner nature, small size and low resistance to fragmentation (Lescinsky et al., 2002; El-Sabbagh et al., 2015) which led to easy decomposition after death. However, the abundance of left valves reflects the mode of life among oysters, by attaching themselves to hard substrate by means of left valves (Stenzel, 1971), which renders their remobilizing by wave currents more difficult.

The second bed is distinguished by oysters having smaller size and thinner left valves, in comparison with the two other beds. The specimen's assemblage shows a mixture of adult and younger individuals, with predominance of adults. This might indicate that they deposited during a period of deepening in a lower energy environment, affecting the shell growth.

In this area, borings were generated by predators such as sponges, polychaetes, bivalves and gastropods, they are assigned to *Domichnia* and *Fodinichnia* ethological groups, while that encrustation belongs to juvenile oysters (and other bivalves), bryozoans and balanids (cirripedes).

The abundant occurrence of *Entobia* in oyster shells from the different beds, especially on the second bed, could indicate lower energy conditions within the subtidal environment, such as low sedimentation rate and limited duration exposure on the seafloor; preferred by clinoid sponges, producer of this ichnogenus (Calcinai et al., 2005). Alternatively, it could be due to the relative absence of other organisms remains or to the occurrence of large submarine assemblage of shells (Lopes, 2011); which represent the favorable substrate available for settlement.

The rare occurrence of *Gastrochaenolites* may be due to the fact that mytilids and lithophages, which are responsible for this kind of boring, prefer to colonize lithified, hard rocky structure and large size shells (Lopes, 2011). Their record is more observable on the outer surface of left and right valves compared to the inner surface, signifying that they were produced probably during the lifetime and after the death of oysters.

On the other hand, the ichnogenera *Caulostrepsis*, *Trypanites*, and *Maeandropolydora* are found on the left valves from the first and the third beds, both on external and internal sides of large size shells. This may indicate that the larger size polychaetes created these borings and they favor large oyster shells for their settlement. As stated by Lopes and Buchmann (2008), the ichnogenus *Caulostrepsis* is infrequent amid small size bivalves.

The activity of encrusters was generally rare. Bryozoans were found only in the first bed, but barnacles are present in all beds mostly. This is probably due to the unstable environmental conditions causing sea level variations, which ranged from high to low wave currents. Oyster shells buildings forming vertical aggregates (in French, "Crassat d'huitres") are numerous, especially on *C. gryphoides*, of the first bed, which was reported

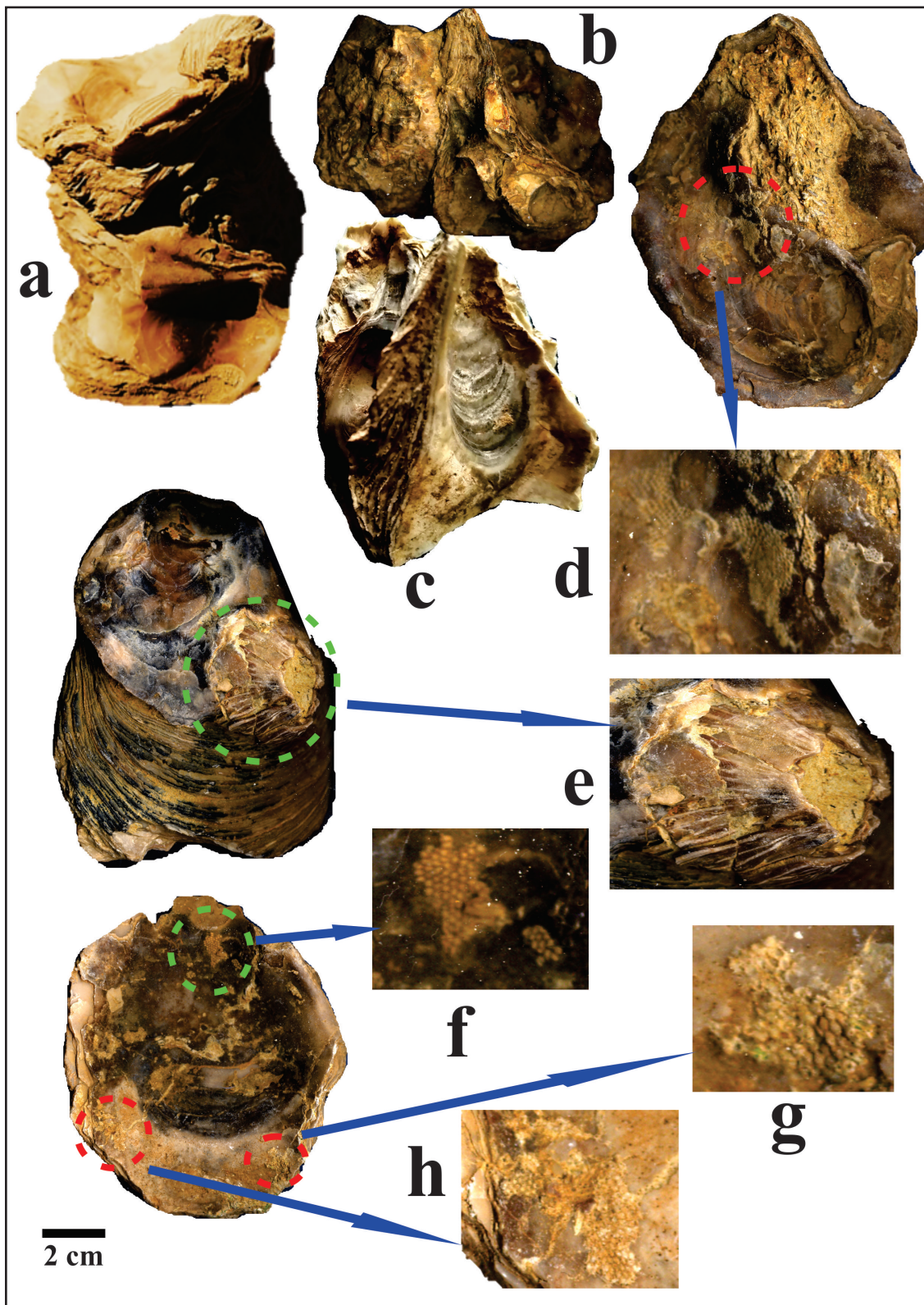


Fig. 8. **Encrustation:** Oysters aggregate: **a** - *C. gryphoides*, **b**, **c** - *H. squarrosa*; **d** - Bryozoans colonies on the internal side of right valve of *C. gryphoides*; **e** - the external surface of left valve of *O. lamellosa*, encrusted by solitary barnacle and other oyster bivalve; **f**, **g**, **h** - Bryozoans colonies distributed over the inner face of right valve of *O. lamellosa*.

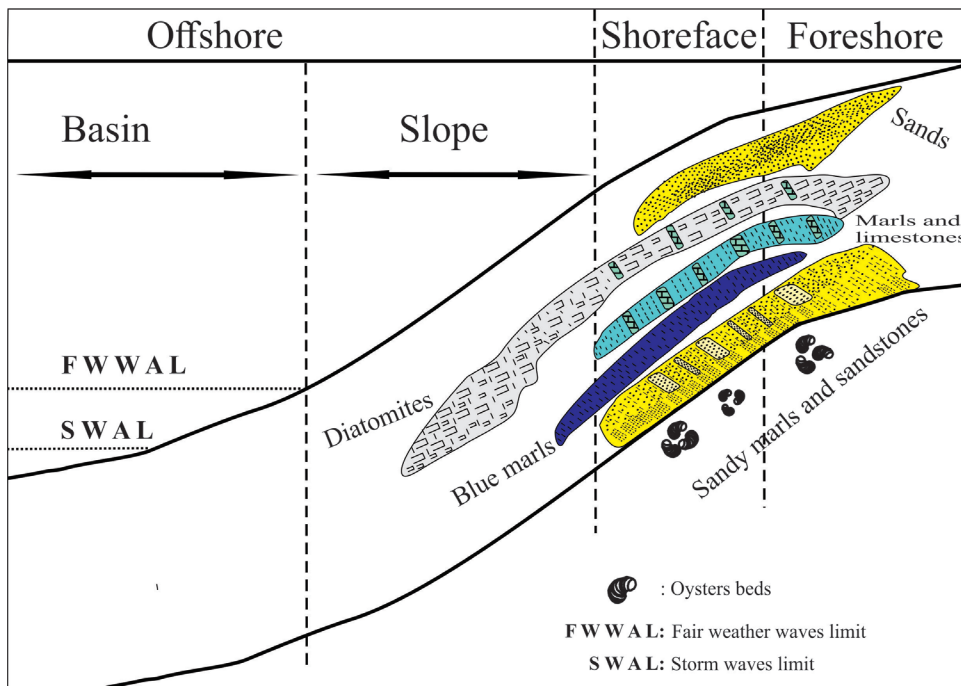


Fig. 9. Bathymetric and spatial distribution of the upper Tortonian of Djebel Touaka (Sig), marine deposits environments.

previously on oyster shells by Hocquet (1995 in Videt, 2004), El-Hedeny, 2005) and El-Sabbagh & El-Hedeny (2016). They are also observed on the species *O. lamellosa*, *H. squarrosa* of the second bed. Their occurrence is limited to the first bed, probably due to sediment input that obstructs their forming. However, they are quite recurring on the second bed, possibly in reference to the lightweight and the small size of oyster's species, which may prevent their shells from sinking rapidly after death into the substrate. These build-ups are absent on the third bed. According to Hocquet (1995) the size and surface occupied by this construction are controlled by three main factors: environment hydrodynamics (must be calm and low energy), sea level (low marine level periods) and sedimentation supply (low sedimentation rate).

The features of the upper Tortonian deposits reflect paleoecological conditions coincides an environment which range from foreshore to shoreface, emphasized by turbulent, high energy and quiet periods (Fig. 9).

Conclusion

Three species of oysters were determined in the studied area, distributed over three beds, *Ostrea lamellosa*, *Hyotissa squarrosa*, and *Crassostrea gryphoides*. The first two are present in all beds, whereas the last species is limited to the lowest one. Shells show varied orientations and distribution in the space. The shells are mostly disarticulated and affected by moderate fragmentation and abrasion.

The epizoans activities are numerous, but their frequency ranges from weak to moderate. The most dominant activity is bioerosion traces, reflecting multiple shapes, round, sub-round elongated and meandering. Five ichnogenera were defined: *Entobia*, *Gastrochaenolites*, *Caulostrepsis*, *Trypanites* and *Maeandropolydora*. These boring processes are registered commonly on the external side of valves, with fewer occurrences on the internal side. This later may confirm that they are produced while oysters were alive and after death and disarticulation.

The higher percentage of *Entobia* among identified ichnogenera is perhaps due to the abundance of oyster specimens, which represent the available favored substrate for installation.

The existence and the diversity of encrusters are proportionally limited; they include juvenile oysters/other bivalves, bryozoans and barnacles, recorded on both outer and inner surfaces of left and right valves.

The complicated modality of borings and bioincrustations indicate that oysters underwent many phases of burial and uncovering resulted from the fluctuation of sea level, causing probably shells displacement at a short distance. From a paleoecological point of view, a foreshore to a shoreface environment reigned during the upper Tortonian of Djebel Touaka at Sig and it was characterized by low energy currents, interrupted by agitated and high energy intervals. This latter maybe confirmed by the recurring installments of sands layers showing sedimentary structures and the presence of the species *Spondylus crassicosta*, which indicates a nearest reef activity.

Acknowledgment

This work is done under the framework of the doctoral training of 3rd cycle, entitled: Geology of Marine and Continental Environments, Integrated Stratigraphy, Chronology and Dynamics of Paleoenvironments. This study is carried out with the support of the DGRSDT (Ministry of Higher Education and Scientific Research). We also thank the observers for their constructive criticism.

References

- Allen, J.R.I. 1992: Transport hydrodynamics. In: Briggs, D.E.G. & P.R. Crowther (eds.): *Palaeobiology: A synthesis*. Backwell Scientific Publications, 237–230.
- Atif, K., Bessedik, M., Belkebir, L. & Mansour, B. 2008: Le passage Mio-Pliocène dans le bassin du bas Chéelif (Algérie). *Biostratigraphie et Paléoenvironnement*. *Geodiversitas*, 30/1: 97–116.
- Belkebir, L., Labdi, A., Bessedik, M., Mansour, B. & Saint Martin, J.P. 2008: Biostratigraphie et lithologie des séries serravallo-tortoniennes du massif du Dahra et du bassin du Chéelif (Algérie). Implication sur la position de la limite serravallo-tortonienne. *Geodiversitas*, 30/1: 9–19.
- Belhadji, A., Belkebir, L., Saint Martin, J.P., Mansour, B., Bessedik, M. & Conesa, G. 2008: Apports des foraminifères planctoniques à la biostratigraphie du Miocène supérieur et du Pliocène de Djebel Diss (bassin du Chéelif, Algérie). *Geodiversitas*, 30/1: 79–96.
- Bessedik, M., Benammi, M., Jaeger, J.J., Ameer-Chehbeur, R., Belkebir, L. & Mansour, B. 1997: Gisement à rongeurs d'âge tortonien dans des dépôts lagunaires et marins de transition en oranie: corrélation marin continental. *Actes du congrès BiochroM'97*, Aguilar J P, Legendre S, Michaux J (eds.): *Mém Trav E P H E*, Inst. Montpellier, 21: 293–300.
- Breton, G., Wisshak, M., Néraudeau, D. & Morel, N. 2017: Parasitic gastropod bioerosion trace fossil on Cenomanian oysters from Le Mans, France and its ichnologic and taphonomic context. *Acta Palaeontologica Polonica*, 62/1: 45–57. <https://doi.org/10.4202/app.00304.2016>
- Brett, C.E. & Baird, G.C. 1993: Taphonomic approaches to temporal resolution in stratigraphy. In: Kidwell, S.M. & Behrensmeier, A.K. (eds.): *Taphonomic approaches to time resolution in fossil assemblages*. *Paleontological Society, Short Course*, 6: 250–274.
- Brocchi, G. 1814: *Conchiologia fossili subapennina con osservazioni geologiche sugli Apennini e sul adiacente*. Stamp. Reale, Milano, 1–2: 712 p.
- Bromley, R.G. & D'Alessandro, A. 1983: Bioerosion in the Pleistocene of southern Italy: ichnogenera *Caulostrepsis* and *Maeandropolydora*. *Rivista Italiana di Paleontologia e Stratigrafia*, 89: 283–309.
- Bromley, R.G. & D'Alessandro, A. 1984: The ichnogenus *Entobia* from the Miocene, Pliocene and Pleistocene of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 90/2: 227–296.
- Bromley, R.G. 1994: The palaeoecology of bioerosion. In: Donovan, S.K. (ed.): *The Palaeobiology of trace fossils*. John Wiley and Sons, Chichester: 134–154.
- Bronn, H. G. 1837–1838: *Lethaia Geognostica oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen*. Schweizerbart, Stuttgart: 1350 p.
- Calcinai, B., Bavestrello, G. & Cerrano, C. 2005: Excavating sponge species from the Indo-Pacific Ocean. *Zool. Stud.*, 44/1: 5–18.
- Clarke, J.M. 1908: The beginnings of dependent life. *New York State Museum, Bulletin*, 121: 146–196.
- De Serres M. 1843: Observations sur les grandes huîtres fossiles des terrains tertiaires des bords de la Méditerranée. *Annls Sci. Nat. Zool.*, 2e sér., 19: 143–168, pl. 2–3.
- Domènech, R., Farinati, E.A. & Martinell, J. 2014: *Crassostrea patagonica* (d'Orbigny, 1842) shell concentrations from the late Miocene of Río Negro province, NE Patagonia, Argentina. *Span. J. Palaeontol.*, 29/2: 165–182.
- El-Hedeny, M. 2005: Taphonomy and paleoecology of the Middle Miocene oysters from Wadi Sudr, Gulf of Suez, Egypt. *Revue de Paléobiologie*, 24: 719–733.
- El-Hedeny, M. 2007: Encrustation and bioerosion on Middle Miocene bivalve shells and echinoid skeletons: Paleoenvironmental implications.
- El-Hedeny, M. & El-Sabbagh, A.M. 2007: Macro-borings on late Cretaceous oysters of Egypt. *N. Jb. Geol. Paleontol. Abh.*, 244/3: 273–286.
- El-Sabbagh, A.M., Mansour, H. & El-Hedeny, M. 2015: Taphonomy and paleoecology of Cenomanian oysters from the Musabaa Salama area, southwestern Sinai, Egypt. *Geosciences Journal*, 19/4: 655–679. <https://doi.org/10.1007/s12303-015-0014-5>
- El-Sabbagh, A.M. & El-Hedeny, M. 2016: A shell concentration of the Middle Miocene *Crassos-*

- trema gryphoides (Schlotheim, 1813) from Siwa Oasis, Western Desert, Egypt. *Journal of African Earth Sciences*, 120: 1–11. <https://doi.org/10.1016/j.jafrearsci.2016.04.007>
- El-Sabbagh, A.M., El Hedeny, M., Rashwan, M.A. & Aal, A. 2016: The bivalve *Placuna* (Indoplacuna) miocenica from the Middle Miocene of Siwa Oasis, Western Desert of Egypt: Systematic paleontology, paleoecology, and taphonomic implications. *Journal of African Earth Sciences*, 116: 68–80. <https://doi.org/10.1016/j.jafrearsci.2015.12.022>
- Gibert, J.M., Domènech, R. & Martinell, J. 2004: An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class, *Fixichnia*. *Lethaia*, 37: 429–437. <http://dx.doi.org/10.1080/00241160410002144>
- Hocquet, S. 1995: Enregistrement morphologique et chimique des paramètres du milieu dans la coquille de *Crassostrea gigas* Thunberg. Modèle actuel en milieu naturel et expérimental. DEA «Paleontologie, Dynamique Sédimentaire et Chronologie», Université de Dijon. 50 p. (inédit).
- Kelly, S.R.A. & Bromley, R.G. 1984: Ichnological nomenclature of clavate borings. *Palaeontology*, 27/4: 793–807.
- Kidwell, S.M. 1986: Models for fossil concentrations: paleobiologic implications. *Paleobiology*, 12/1: 6–24.
- Kidwell, S. M. & Bosence, D.W.J. 1991: Taphonomy and time-averaging of marine shelly faunas. In: Allison, P.A. & Briggs, D.E.G. (eds.): *Taphonomy: releasing the data locked in the fossil record*. *Topics in Geobiology*, 9: 115–209.
- Lescinsky, H.L., Ledesma-Vazquez, J. & Johnson, M.E. 1991: Dynamics of Late Cretaceous Rocky Shores (Rosario Formation) from Baja California, Mexico. *Palaios*, 6: 126–41. <https://doi.org/10.2307/3514878>
- Lescinsky, H.L., Edinger, E. & Risk, M.J. 2002: Mollusc shell encrustation and bioerosion rates in a modern peiric sea: taphonomy experiments in the Java Sea, Indonesia. *Palaios*, 17/2: 171–191. <https://doi.org/10.1669/0883-1351%282002%29017%3C0171%3AMSEA-BR%3E2.0.CO%3B2>
- Leymarie, A. 1842: Suite du mémoire sur le terrain Crétacé du Département de l'Aube. *Mémoires de la Société Géologique de France*, 5: 1–34.
- Lopes, R.P. 2011: Ichnology of fossil oysters (Bivalvia, Ostreidae) from the southern Brazilian coast. *Gaea*, 7/2: 94–103. <https://doi.org/10.4013/gaea.2011.72.02>
- Lopes, R.P. & Buchmann, F.S.C. 2008: Comparação tafonômica entre duas concentrações fossilíferas (shell beds) da Planície Costeira do Rio Grande do Sul, Brasil. *Gaea*, 4/2: 65–77. <https://doi.org/10.4013/gaea.20082.03>
- Mansour, B. 2004: Les diatomées messiniennes du bassin du Bas Chélif (Algérie nord occidentale). Thèse de doctorat d'Etat. Université d'Oran., 286 p. 106 fig., 2 tabl., pl. IX.
- Neurdin-Trescartes, J. 1995: Paléogéographie du Bassin du Chélif (Algérie) au Miocène. Causes et conséquences. *Géologie Méditerranéenne*, 22/2: 61–71. <https://doi.org/10.3406/geolm.1995.1569>
- Portlock, J.E. 1843: Report on the geology of the county of Londonderry and of parts of Tyrone and Fermanagh. Dublin & London (Milliken): 784 p.
- Saint Martin, J.P. 1990: Les formations récifales coralliennes du Miocène supérieur d'Algérie et du Maroc. *Mémoires du Muséum National d'Histoire Naturelle, Sér. C, Sciences de la Terre*, 56: 351 p.
- Saint Martin, J.-P. 2008: Biodiversité dans les calcaires micritiques blancs des plates-formes messiniennes d'Algérie. *Geodiversitas*, 30/1: 165–179.
- Satur, L., Lauriat Rage, A., Belkebir, L., Mansour, B., Saint Martin, J.P. & Bessedik, M. 2011: Les bivalves ptériomorphes du Tortonien supérieur du Dahra: systématique et paléoécologie. *Bulletin du service géologique national, Algérie*, 22: 119–139.
- Satur, L., Lauriat-Rage, A., Belkebir, L. & Bessedik, M. 2013: Biodiversity and taphonomy of bivalves assemblages of the Pliocene of Algeria (Bas Chelif basin). *Arabian journal of Geosciences*, 7: 5295–5308. <https://doi.org/10.1007/s12517-013-1154-4>
- Satur, L., Saint Martin, J.P., Belkebir, L. & Bessedik, M. 2020: Evolution de la diversité des bivalves messiniens de la bordure méridionale du bassin du Bas Chélif (Algérie nord occidentale).
- Schlotheim, E.F. 1813: Beitrag zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *Leonhard's Jahrbuch für Mineralogie*, t. 7.
- Stenzel, H.B. 1971: Oysters. In: Moore R.C. (ed.): *Treatise on Invertebrate Paleontology*. Part N., Mollusca 6, Bivalvia. Geological Society of America & University of Kansas Press, 3: i-iv, N953-N1224.
- Stephenson, L.W. 1952: Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of

- Texas. United States Geological Survey, Professional Papers, 242: iv + 226 pp.
- Videt, B. 2004: Dynamique des paléoenvironnements à huîtres du Crétacé Supérieur nord aquitain (SO France) et du Mio-Pliocène andalou (SE Espagne): biodiversité, analyse séquentielle, biogéochimie. Mémoire Géosciences, Rennes, 108: 1–261
- Voigt, E. 1965: Über parasitische Polychaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. Paläontologische Zeitschrift, 39: 193–211.