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First record of blister pearls in the oyster *Hyotissa hyotis* (Linné, 1758) from Pliocene deposits at Sidi Brahim, Lower Chelif Basin (north-west Algeria)

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Abstract

Fossil pearls are rare but important palaeoecological indicators in proving the former presence of parasites. A single right valve of *Hyotissa hyotis* from the Pliocene of Sidi Brahim shows numerous blister pearls inside the adductor muscle imprint. At the same locality, numerous shells with smooth adductor scars and without any blisters, have been collected. The structures in the studied valve can be assigned to blister pearls with high confidence due to their similarity to other Cenozoic pearls from Austria. The blister pearls likely formed as a reaction to parasite infestation. It is possible that some parasites especially targeted areas associated with the adductor muscles in the oyster genus *Hyotissa*, because similar blister pearls have previously been described in a congeneric species, *H. squarrosa*, from the Miocene of Austria.

Key words: Fossil pearls, blisters, parasites, oysters, Mediterranean Sea, Miocene

1. Introduction

Most bivalves, including oysters, have the ability to produce pearls, or organic gemstones that can form naturally, as a result of a defensive reaction of the host organism to a foreign body such as parasite (De Baets et al., 2011b; Binder, 2015; Li et al., 2016). When worms or other parasites infest living molluscs they will be encapsulated in a $CaCO_3$ concretion formed by the nacreous layer of the host shell in order to incapacitate and neutralise the parasite. Modern pearls are often cultivated and used as decorative elements in jewelry (Li et al., 2016). As such, the pearl formation process can be studied experimentally in pearl cultures. In such experiments, living oysters will undergo a surgical operation in order to implant the nucleus inside the shell. Subsequently, the oyster recognises this as an irritant and starts secreting aragonite to encapsulate the implanted nucleus. Naturally formed pearls are generally more irregular in shape (Haws et al., 2006) in comparison to regularly shaped artificial ones. In contrast to modern pearls, fossil specimens are less common. The environmental controls on the shape of fossil pearls are not well known. Such often occur in the form of blisters in the shell interior and are referred to as blister pearls. The oldest blister pearls have been recorded from the bivalve genus *Nuculodonta* from the Silurian of Sweden (Lilljedahl, 1994) and from an unidentified cardiolid bivalve from the Silurian of Bohemia, Czech Republic (Kříž, 1979). Among the earliest pearls are also pearl pits recorded from Early Devonian ammonoids from North Africa, Germany and the Czech Republic (De Baets et al., 2011a). Blister pearl-like galls have also been documented in Miocene sea urchins of the species *Clypeaster melitensis* from Morocco (Roman, 1952). Similarly, a pearl-like structure has been observed in the land snail *Canistrum ovoideum* (family Bradybaenidae); this could be of pathological origin (Bachmayer & Uetz, 1975). Finds of fossil pearls are common in the Cretaceous of North America, where *Inoceramus* was a major producer (Newton, 1908; Jackson, 1909; Russell, 1929; Brown, 1940). Fossil pearls are also relatively common in the Cenozoic of Europe, Asia and America (Marwick & Hamilton, 1922; Jackson, 1926; Berry, 1936; Zilch, 1936; Vokes, 1955; Wagner, 1957; Bachmayer & Binder, 1967; Isaji & Kato, 2011; Binder, 2015; Li et al., 2016). The abundance of pearls in Cenozoic strata could either be due to a collecting bias or to the late evolutionary success of this type of defence mechanism in molluscs. Fossil blister pearls have often been used as a proxy in studying parasitic associations (De Baets et al., 2011b). However, such structures may be the result of a variety of other irritants, such as grains of minerals (De Baets et al., 2011b). Fossil pearls are largely restricted to epifaunal molluscs, which could be due to their greater accessibility by parasites in comparison to infaunal taxa (De Baets et al., 2011b).

The Pliocene of Algeria is rich in shelly fossils (Khalili et al., 2022), but fossils pearls have been previously overlooked by researchers. Here we record blister pearls from the upper oyster bed at the Sidi Brahim outcrop for the first time. The aims of the present paper are threefold; to describe blister pearl-like structures in *Hyotissa hyotis*, to discuss pearl formation and, lastly, to discuss the palaeoecological and palaeobiogeographical importance of this specimen.

2. Geological background and locality

The Sidi Brahim outcrop is located in the Dahra Mountains (Figs. 1, 2) which surround the north-eastern side of Lower Chelif Basin, about 1.5 km south of the city of Sidi Ali. This outcrop has been studied by many authors during many decades (Anderson, 1936; Atif et al., 2008; Satour, 2012; Satour et al., 2013; Bendella et al., 2021; Benyoucef et al., 2021). The Neogene series is complete in the Lower Chelif Basin and ranges from the Burdigalian to the Pliocene (Benyoucef et al., 2021). The Neogene sediments rest with diastrophic unconformity on an allochthonous bedrock of Cretaceous to Oligocene

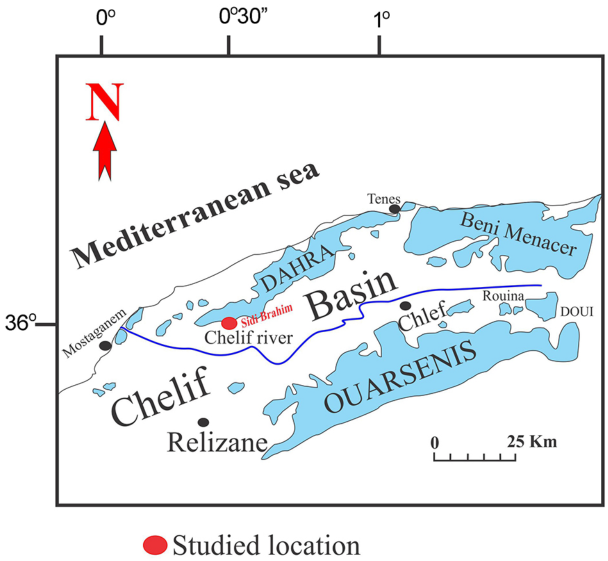

Fig. 1. Location of the Sidi Brahim outcrop (after Benyoucef et al., 2021).

age (Benyoucef et al., 2021). The Neogene series is divided into Miocene and Pliocene sedimentary cycles (Benyoucef et al., 2021). The Miocene began with a Burdigalian transgressive phase over the Cretaceous substratum, and is represented by conglomerates, sandstones and dark marls commonly called "marnes bleues" ('blue marls') (Benyoucef et al., 2021). Another transgressive phase took place during the Late Miocene, followed by regression (Messinian salinity crisis) (Benyoucef et al., 2021). An abrupt marine transgression has been noted at the start of the Pliocene, and this is terminated by the Astian regression (Benyoucef et al., 2021). The marine part of the Pliocene consists of sandstones with intercalated grey sandy marls rich in benthic macro- and microfauna (Slama Formation of Anderson, 1936) (Benyoucef et al., 2021). The Pliocene is represented by grey and whitish marls of the upper part of the "Tahria" Formation in the area of the Sidi Brahim outcrop. The latter deposits contain dispersed oyster shells. In general, an increase in sands and sandstones from the base to the top of the section is noted, and shell beds containing oysters and other bivalves, gastropods and scaphopods (Satour, 2012) can be recognised. These beds correspond to the "Slama" Formation.

3. Material

Oyster shells were studied at outcrop for the presence of pearls. The specimen described and illustrated here is a right valve of the oyster *Hyotissa hyotis*, with a length of 104 mm, a width of 89 mm

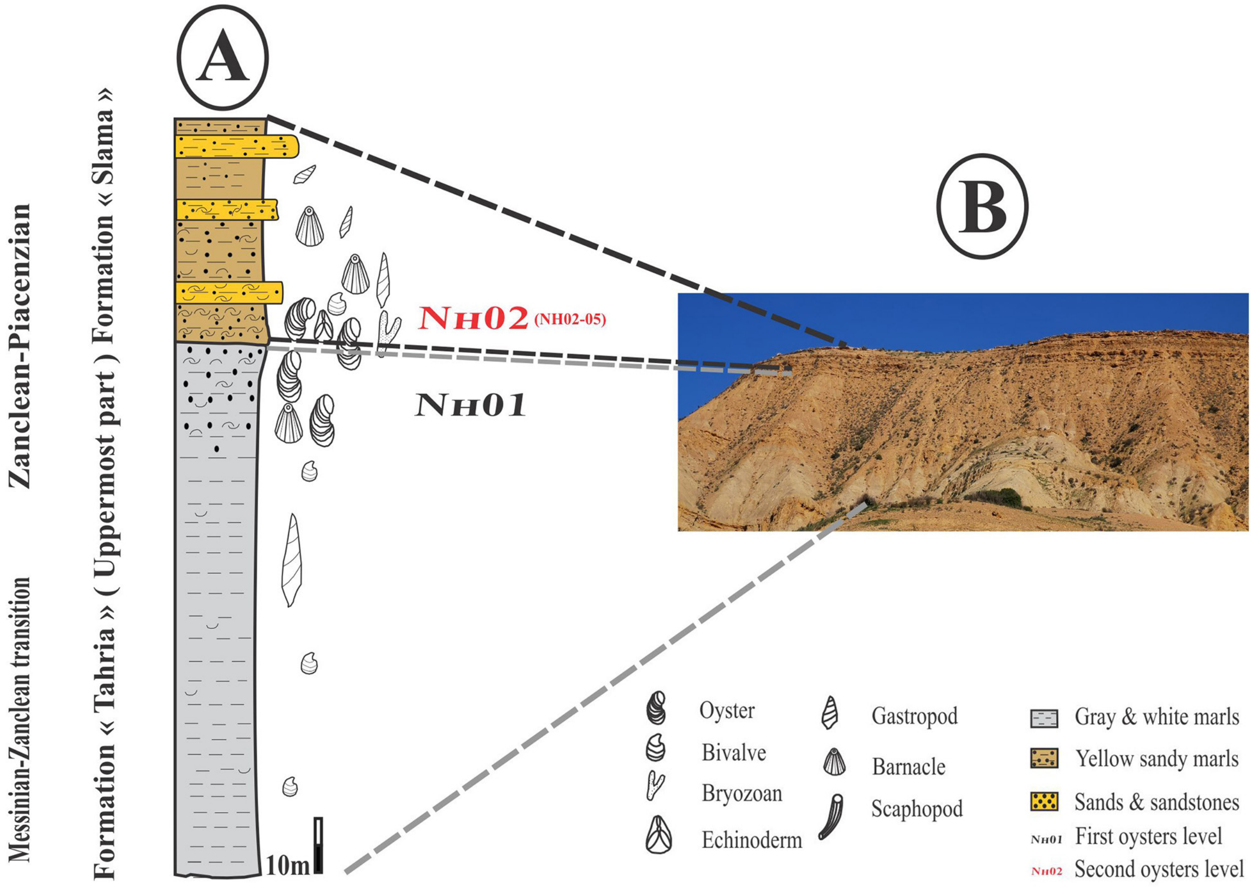

Fig. 2. Stratigraphy of the Sidi Brahim outcrop.

and a thickness of 18 mm. This valve was recovered from sandstones in the second oyster level at Sidi Brahim, and is of Pliocene age (Figs. 1A, B, 2). Unstable environmental conditions likely caused the disarticulation of oyster shells here (Khalili et al., 2022). However, oyster shells are well preserved and either moderately abraded or not at all here. The studied valve is now housed in the collections of the Laboratory of Paleontology, Stratigraphy and Paleoenvironments at the University of Oran 2 (NH02-05).

4. Results

The single right valve of *Hyotissa hyotis* shows numerous (i.e., about ten) blister pearls inside the adductor muscle imprint (Fig. 3). The development of blisters is variable; some are elevated and well developed, whereas others are low and barely identifiable. Blisters have circular to semi-circular outlines and measure between 1 and 3 mm in diameter and about 0.5 to 2 mm in height. The surface of the adductor muscle scar as well as blisters is smooth. The blisters are located in the frontal half of the adductor muscle imprint, but their distribution is random. The shell interior beyond the adductor muscle scar is devoid of any blisters. The valve is dark brown in colour and has a slightly abraded external surface. The shell structure is well preserved and characteristic to Pycnodonteinae. Shells of various oyster taxa may be closely similar, but the well-preserved exterior and interior of the present valve allows identification without doubt.

5. Discussion

5.1. Interpretation of structures

The general morphology of blisters inside the valve of *Hyotissa hyotis* is similar to that of blister pearls in other Cenozoic bivalves from Austria, the United Kingdom, Canada, the United States, China, Japan and New Zeeland (Marwick & Hamilton, 1922; Jackson, 1926; Berry, 1936; Zilch, 1936; Vokes, 1955; Wagner, 1957; Bachmayer & Binder, 1967; Isaji & Kato, 2011; Binder, 2015; Li et al., 2016). The surface of the adductor scar in a healthy individual of *Hyo-*

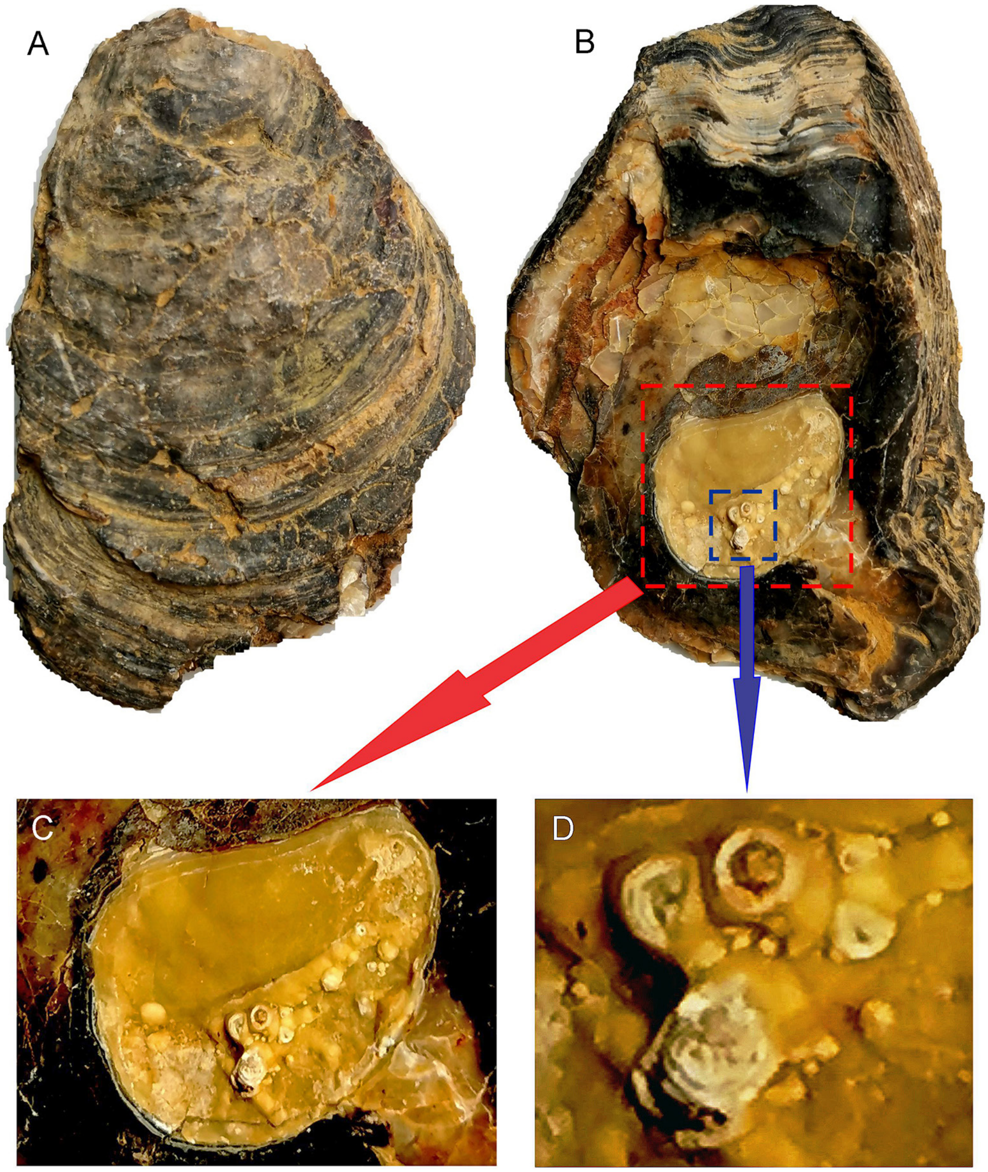

Fig. 3. A – External view of *Hyotissa hyotis* (Linné, 1758); B – Internal view; C – Internal surface of right valve, showing a cluster of blister pearls; D – Closeup view of broken blister pearls, showing multiple nacreous layers of $CaCO_3$.

tissa hyotis is smooth and lacks blisters. Numerous fossil shells with smooth adductor scar imprints occur at the same locality. Thus, the structures in the studied valve can be assigned to blister pearls with high confidence as they have the characteristic shape and concentric-lamellar structure.

5.2. Formation of blister pearls

Oysters are filter-feeding animals; they slightly open their valves to allow water-carrying nutrients to circulate through their shell interior. During feeding, there is an increased possibility for parasites enter the mantle cavity. The blister pearls likely formed as a reaction to parasite infestation (De Baets et al., 2011a, b). This is supported by the occurrence of blister pearls in the muscle attachment scar. It is difficult to imagine how non-parasitic foreign bodies could have reached the shell surface below the muscle. On the other hand, one could easily imagine how a parasite could have bored into the muscle of the host oyster. During formation of blister pearls, the foreign body ("nucleus") was enveloped by calcium carbonate in the form of aragonite as a result of an immunological defensive reaction of the oyster (Li et al., 2016). The blister pearls are composed of multiple nacreous layers of CaCO3 deposited on top of each other, which can be seen in broken blisters in the studied valve (Fig. 3D).

The production of cultured pearls requires specific conditions such as clean water or with a little turbidity, to maintain the oysters stable at the bottom; thus, areas exposed to tidal currents are not suitable. Temperature must be relatively constant without extreme variations (Haws et al., 2006). Size and quality of the cultured pearls are related to the size of the host oyster and the number of nuclei (Nur et al., 2020). The size of the fossil blister pearls studied here is rather small compared to similar records from the Cenozoic of Austria (Binder, 2015). The studied valve is of normal size in comparison with other valves of the species found at the same locality. Thus, the infestation of this shell of *Hyotissa hyotis* did not cause changes in its size. This could mean that the possible parasites were not too virulent.

Fossil blister pearls have not been described previously from *Hyotissa hyotis* but they do occur in *H. squarrosa* (de Serres, 1843) from the Miocene of Austria, in which a node-like blister has been observed near the scar of the adductor muscle (Binder, 2015). Thus, it is possible that some parasites especially targeted areas associated with the adductor muscles in this oyster genus. In future studies these pearls can be used as proxies in estimating the health of oyster populations among the Sidi Brahim shell concentrations.

6. Conclusions

Structures in the studied valve of *Hyotissa hyotis* can be assigned to blister pearls with high confidence, because of their characteristic shape and concentric-lamellar structure.

The blister pearls in *Hyotissa hyotis* likely formed as a reaction to parasite infestation. After infestation by a parasitic organism, the oyster recognised it as an irritant and started secreting aragonite in order to encapsulate it.

Some parasites may have especially targeted areas associated with the adductor muscles in the genus *Hyotissa*, because similar blister pearls have been previously described in the adductor scars of a congeneric species, *H. squarrosa*, from the Miocene of Austria.

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