Rivista Italiana di Paleontologia e Stratigrafia | volume 110 | no. 3 | pp. 725-731 | December 2004

SHORT NOTE - NOTA BREVE

PALAEOBIOLOGICAL OBSERVATIONS ON THE "COCOONED" MYTILID *AMYGDALUM* (BIVALVIA, UPPER PLIOCENE)

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Received September 16, 2003; accepted April 30, 2004

Key-words: *Amygdalum*, Pliocene, Mediterranean, byssal nesting, taphonomy, palaeoecology.

Abstract. Fossil specimens referred to the extant Atlantic-Mediterranean species *Amygdalum politum* (Verrill & Smith, 1880), occur in Upper Pliocene mudstones cropping out in northern Puglia (Southern Italy). *Amygdalum* is an infaunal mytilid living within a cocoon made of byssal threads, sediment and mucus. The examined material occurs in grey clayey silt, mainly massive, and in stratified yellowish clayey silt. The specimens from the grey mudstones are closed, strongly compressed, deformed and obliquely oriented. Also in the yellowish mudstones the shells are closed, compressed and intensely fractured but are concordant to the bedding plane and concentrated in a single pavement. On a whole, the associated macrofauna is indicative of upper slope tending to outer shelf environments. Taphonomic and palaeoecologic observations, together with the few available literature data, suggest that this bivalve lived in a particularly fluid substrate, keeping its vertical life position thanks to the stabilizing effect of the byssal cocoon. Since this species was able to cope with high turbidity waters, as suggested by taphonomic observation, it can be argued that the byssal cocoon acted also as a filter for the inhalant current.

Riassunto. In sedimenti pelitici del Pliocene terminale, affioranti nella parte settentrionale della Puglia, sono presenti fossili riferibili alla specie attuale atlantico-mediterranea *Amygdalum politum* (Verrill & Smith, 1880). *Amygdalum* è un mitilide infaunale che produce un bozzolo costituito da bisso, sedimento e muco, all'interno del quale vive annidato. Il materiale proviene da silts argillosi grigi, tendenzialmente massivi e da silts argillosi giallastri, stratificati. Nella prima litologia i gusci sono chiusi, fortemente compressi, deformati ed in posizione obliqua; anche nei silts giallastri i gusci sono a valve chiuse, compressi e fratturati ma sono concordi alla stratificazione e concentrati in un *pavement*. Nel complesso, la macrofauna associata indica una tendenza alla superficializzazione, dalla scarpata superiore alla piattaforma esterna. Le osservazioni tafonomiche e paleoecologiche, assieme ai pochi dati di letteratura, suggeriscono che il bivalve vivesse in un sedimento particolarmente fluido, mantenendo l'assetto verticale tramite l'azione stabilizzante del bozzolo. I dati tafonomici suggeriscono che la specie vivesse in condizioni di elevata torbidità ma, poiché esso non sembra possedere adattamenti morfologici utili per affrontare tali condizioni, si può ipotizzare che il bozzolo sia un elemento di utile per far fronte a questa condizione, agendo a mo' di filtro per proteggere il sifone inalante.

Introduction

A detailed documentation of the functional morphology of the shell-byssus system in the bivalve family Mytilidae was given by Stanley (1970, 1972). Most mytilids (e.g. *Mytilus*) live byssally attached on hard substrates. In this case the shell has a trapezoidal or triangular outline and a broad ventral side to improve adherence and stability. Also, the wedge-shaped shell allows a nestling habit within rock crevices. Other species are adapted to live infaunally or semi-infaunally in soft substrates, with endobyssate attachment (e.g. *Modiolus*). Their shell tends to be ovate to somewhat cylindrical, with a sub-terminal umbo and, in life position, they are vertically to obliquely oriented, depending on the degree to which they are able to burrow. However, not all infaunal mytilids match the "*Modiolus* model" of life habit. In some mytilids, among them the genus *Amygdalum* Megerle, 1811, the byssus is used to form a "cocoon", within which the bivalve is nested.

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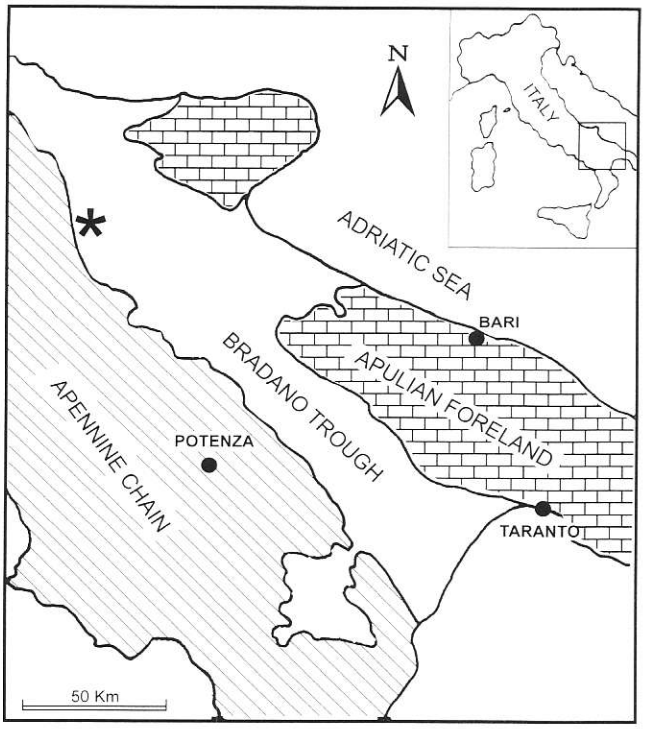


Fig. 1 - Structural map of part of Southern Italy and location of the section (star).

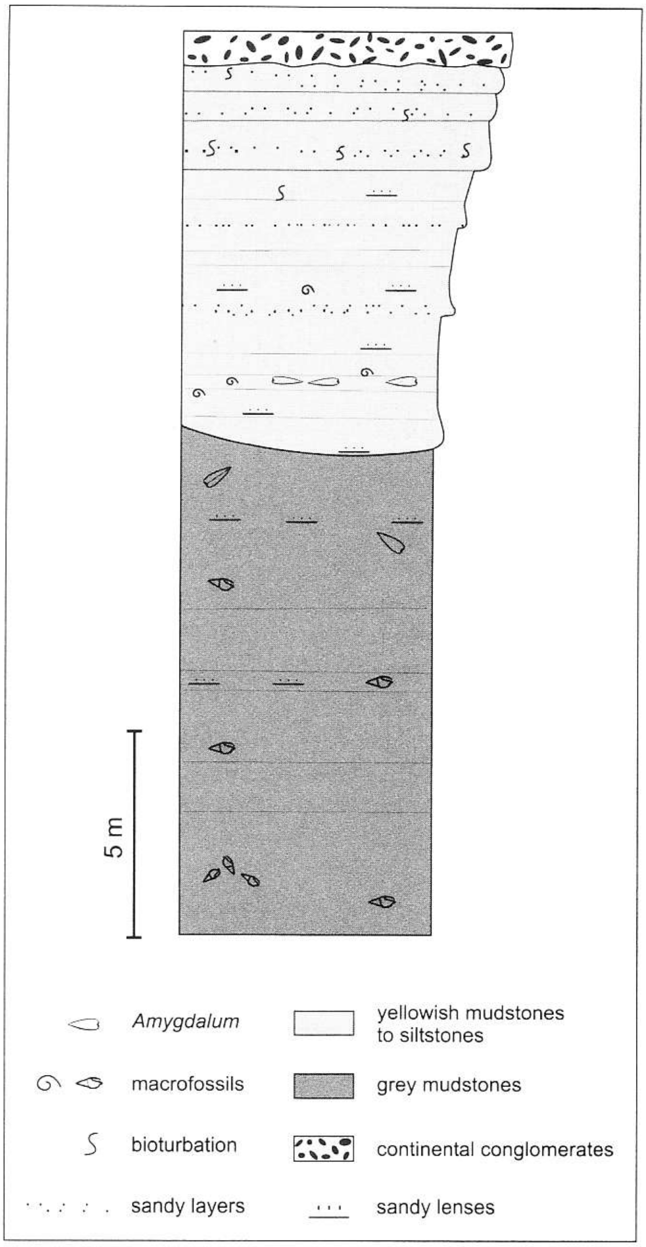


Fig. 2 - Sketch of the Upper Pliocene section.

As far as we are aware, there is no palaeontological study on *Amygdalum* and the find of fossil specimens in Upper Pliocene deposits of Puglia (Southern Italy) prompted us to investigate the palaeoecology and taphonomy of this unusual bivalve.

Geological setting and material

The examined material is from Upper Pliocene mudstones cropping out near Lucera, in the northern part of Puglia, Southern Italy (Fig. 1). They belong to the Plio-Pleistocene sequence of the Bradano Trough, mostly encompassing depositional environments ranging from the slope to the inner shelf (D'Alessandro et al. 2003). The specimens come from a short section, about 20 m long, consisting of two slightly different silty-clayey units (Fig. 2). In the lower part, grey, somewhat massive or poorly stratified mudstones are exposed. They contain a dispersed macrofauna, mainly consisting of molluscs among which *Nassarius* gr. *semistriatus* (Brocchi, 1814), *Aporrhais uttingeriana* (Risso, 1826), mostly articulated *Corbula gibba* (Olivi, 1792), *Nucula sulcata* Bronn, 1831, *Abra longicallus* (Scacchi, 1834) and *Entalina tetragona* (Brocchi, 1814) are the most common taxa. Rare and highly dispersed specimens of *Amygdalum* mainly occur in the upper part. The grey mudstones are cut by yellowish mudstones, rather well stratified and with thin lenses of very fine sand. The basal contact is a sharp concave surface thought to represent a slump scar. The macrofauna in the yellowish mudstones is even rarer and less diverse, but similar in preservation to that from the lower mudstones. Articulated full grown shells of *Corbula gibba* are locally common in a 30-40 cm thick bed, whereas the relatively numerous specimens of *Amygdalum* form a pavement in the upper part of the same bed. The echinoid *Brissopsis lyrifera* (Forbes, 1841) is represented by rare specimens, mostly with disarticulated spines.

On a whole, macrofauna and sedimentological features point to an upward shallowing, from the upper slope to the outer shelf.

Like most mytilids, the representatives of *Amygdalum* have smooth, featureless shells and the main differences among congeners are provided by shell shape and size, and also by the colour pattern. Moreover, the present material is rather poorly preserved. Based on shell outline and size, the fossil species does not seem different from *Amygdalum politum* (Verrill & Smith, 1880) [= *A. luteum* (P. Fischer, 1883)], a deep-sea species living in the Mediterranean Sea and in the Atlantic Ocean. Good illustrations of this species were given by Giannuzzi-Savelli et al. (2001).

The "cocooned" mytilids

An early mention about the nestling habit of *Amygdalum* was reported by Soot-Ryen (1955). Recently, Oliver (2001) reported detailed observations on the ecology and the soft-part anatomy of *Amygdalum anoxiculum*, a new deep-sea species from the Arabian Sea. In undisturbed box-corers this species was found entirely burrowed into muddy sediment, with the posterior margin at the mud-water interface and "cocooned" within its byssal nest. Other specimens, previously collected by dredging, showed the byssal nest as a large bundle attached to the ventral side. This observation accounts for the misinterpreted records of *Amygdalum* from the Mediterranean. Bombace (1968) reported two dredged specimens with a byssal nest covering the posterior third of shell, whereas Giudice & Gaglini (1984) and Smriglio et al. (1988) reported dredged specimens with a mud-rich byssus bundle attached ventrally (Fig. 3). Clearly, in the dredged specimens the byssal nest is often altered in shape, ripped, or completely destroyed.

Oliver (2001) remarked that the wrapping nest would help to avoid unwanted sediment entering the long pedal aperture, and to limit and shelter the inhalant aperture. Indeed, the small and poorly ridged labial palps would not be able to deal with and evacuate great amounts of sediment and the gills could be easily clogged. This type of labial palps is thought to be more related to food sorting rather than to mantle cavity cleansing.

However, not all the species of *Amygdalum* seem to share the cocooned habit, since Allen (1955) reported *A. papyrium* (Conrad, 1846) as infaunally attached to the roots of sea-grasses, a mode of life similar to that of *Modiolus*.

Morton (1980a) reported a cocooned habit also in *Arcuatula elegans* (Gray, 1828), an infaunal mytilid whose shell is similar to that of *Amygdalum* (Fig. 4). The nest formed by *Arcuatala* is "a soft gelatinous blob" containing very thin byssal threads and its adaptive meaning must be different from that of *Amygdalum*, as suggested by the same author, probably serving mainly to protect this thin-shelled bivalve from predation.

A byssal nest was also reported for *Musculista senhousia* (Benson in Cantor, 1842) by Morton (1974). In this case, the posterior margin of the shell is not wrapped and some byssal threads are attached to sand grains forming an anchor. This nest is believed to protect and anchor the bivalve, and also to prevent the entry of sediment into the mantle cavity.

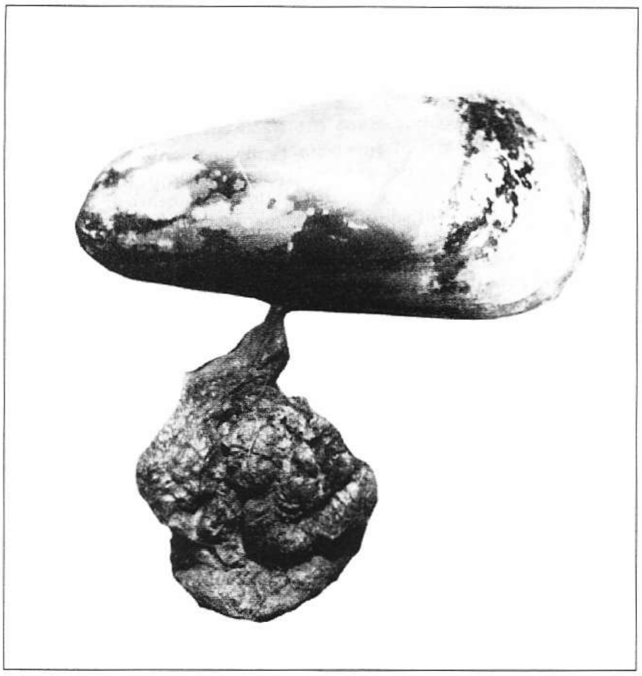


Fig. 3 - A dredged specimen of *Amygdalum politum* with remains of the byssal cocoon as a mud-rich byssus bundle (modified after Giudice & Gaglini 1984).

Also the epifaunal mytilid *Musculus discors* (Linné, 1767) is known to weave a byssal nest (Merrill & Turner 1963), which is believed to be mostly related to reproduction and protection of juveniles, as a brooding chamber, as more recently reported by Ockelmann (1983) for another species of *Musculus*.

Small, neoteneous, epifaunal species of *Dacrydium* are also known to spin a nest (Ockelmann 1983), by which they probably attach to the substrate.

A still different byssal cocoon is built by *Gregariella coralliophaga* (Gmelin, 1791), which was observed by Morton (1980b) as nestling in *Lithophaga* boreholes left in dead coral skeletons and with a byssal cocoon around the posterior region of the shell. In this case, the functional meaning of the nest is presumed to be mainly related to protect the borehole entrance.

The meaning of the coarse byssal nest produced by the Mediterranean species "*Amygdalum*" *agglutinans* (Cantraine, 1835) may be similar to that of *Gregariella*. However, this species is notably different from *Amygdalum* and should be assigned to a distinct genus.

Further, many mytilids use to attach byssal secretions on the shells, such as hairs and bristles, whose primary importance must be a kind of protection. Also this aspect, like the byssal nest, "raises a number of question awaiting further studies" (Ockelmann 1983).

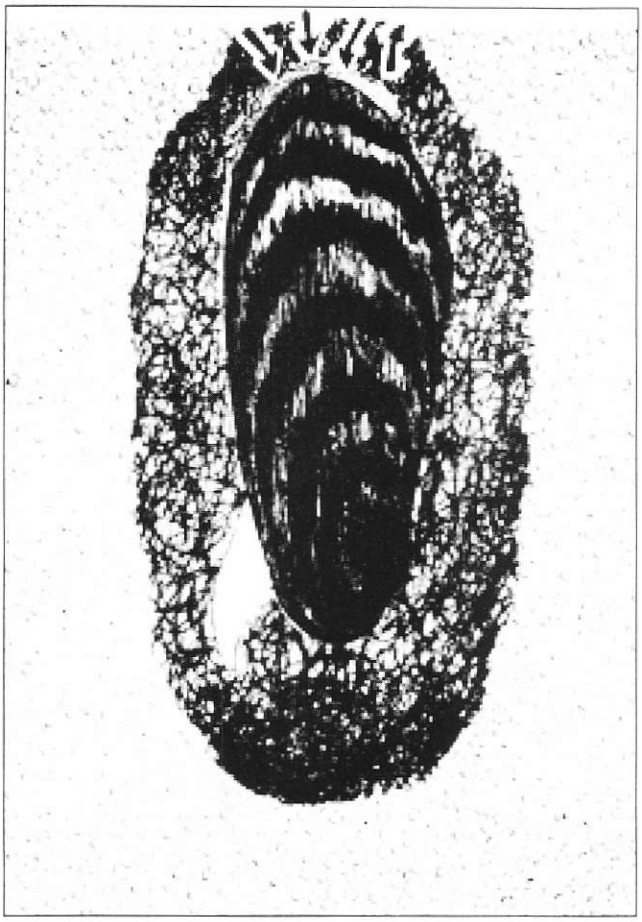


Fig. 4 - *Arcuatula elegans* in life position (modified after Morton 1980a). Although the byssal cocoon of *Arcuatula* is mostly gelatinous, with very thin byssal threads, this illustration provides also a good schematic view of the cocoon of *Amygdalum*.

Taphonomic and palaeoecological observations

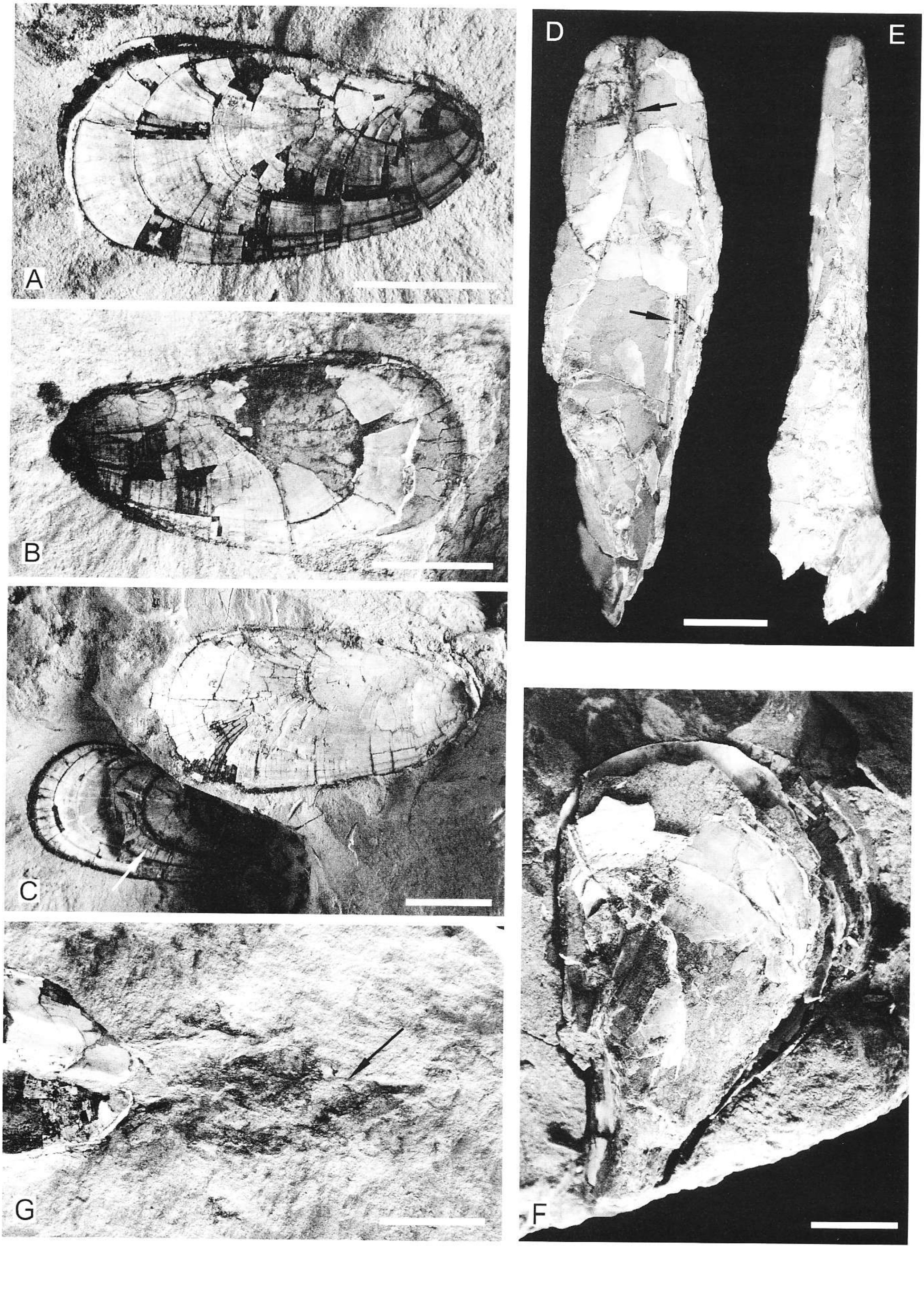
Most specimens are from a 30-40 cm thick bed in the lower part of the yellowish mudstones, where they form a loosely-to-densely packed thin concentration. These specimens (Figs 5A-C), are preserved as perfectly closed shells, filled with sediment, mostly concordant to the bedding plane and more or less compressed, i.e. flattened along the commissure plane. The fragile shell-wall is intensely fractured along radial and concentric lines, giving a "mosaic" appearance. In the grey mudstones the *Amygdalum* shells are highly dispersed and obliquely oriented. Also in this case, the shells are closed and filled with sediment but, in the few available specimens, they appear to be compressed in a dorso-ventral direction and strongly deformed (Figs 5D-F). They are also intensely fractured, but without a regular pattern. In a single case, a specimen whose valves are concordant to bedding plane and opened ("butterfly position"), exhibits a dark elongated spot with a "frayed" appearance, extending for about 30 mm from the umbonal area (Fig. 5G).

Differences in shell orientation and deformation of the *Amygdalum* shells indicate that they underwent different taphonomic processes (Fig. 6). The shells from the grey mudstones were mostly buried in life position and reoriented obliquely by compaction. Due to their orientation, these shells underwent a more severe deformation than the others, as testified by a shell (Fig. 5D, E) which is strongly compressed and the original dorsoventral dimension (probably about 40 mm) is less than 10 mm. The specimens in the yellowish mudstone clearly have been excavated and reoriented possibly by episodic weak bottom currents, as supported by the occurrence of silty-sandy laminae. Furthermore, these articulated shells, with no signs of exposure on the sea floor, provide evidence for a rapid burial. The byssal nest probably prevented the valves to open after death but, since such a structure quickly decays, rapid burial must have occurred. Because of its concordant orientation, these shells, although compressed, were less heavily deformed than those in the grey mudstones.

In terms of "episodic" and "background" taphonomic processes (Speyer & Brett 1991), the shells from the grey mudstones point to a background process, controlled by a persistent accumulation of sediment, whereas those from the yellowish mudstones are indicative of an event-related process (winnowing and disinterment of bivalves). In both cases, an high sedimentation rate (>10 cm/10^3 years: Brett & Allison 1998) may be inferred. Such an high rate of muddy sedimentation must have affected the bottom consistency, which can be argued to have been soupy (sensu Bromley 1996), as testified by deformation and fragmentation of shells, due to the strong compaction of a water-rich sediment.

The single shell in butterfly position from the grey mudstones testifies a short period of exposure on the bottom, probably due to an episodic rise of water energy. The dark spot may represent a remain of the byssal cocoon, partly disintegrated after death. It is worth noting the close resemblance of this feature with the byssus bundle found on the dredged specimens of *Amygdalum* (Fig. 3). This may represent the first case of byssus fossilization.

Fig. 5 - *Amygdalum politum* (Verrill & Smith, 1880). **A-C**: Material from the yellowish mudstones. A: inner view of a left valve (internal mould removed). B: Inner view of a right valve (internal mould removed). C: Inner view of a left valve (internal mould removed) and of a complete shell with its internal mould (arrowed). **G-F**: Material from the grey mudstones. G: Shell in butterfly position with a dark spot (arrowed) thought to be remains of the byssal cocoon. D: Dorsal view of a strongly compressed and deformed shell (arrowed: dorsal commissure line). E: Lateral (right valve) view of the same shell. F: Deformed shell resembling *Mytilus*. Scale bars = 10 mm.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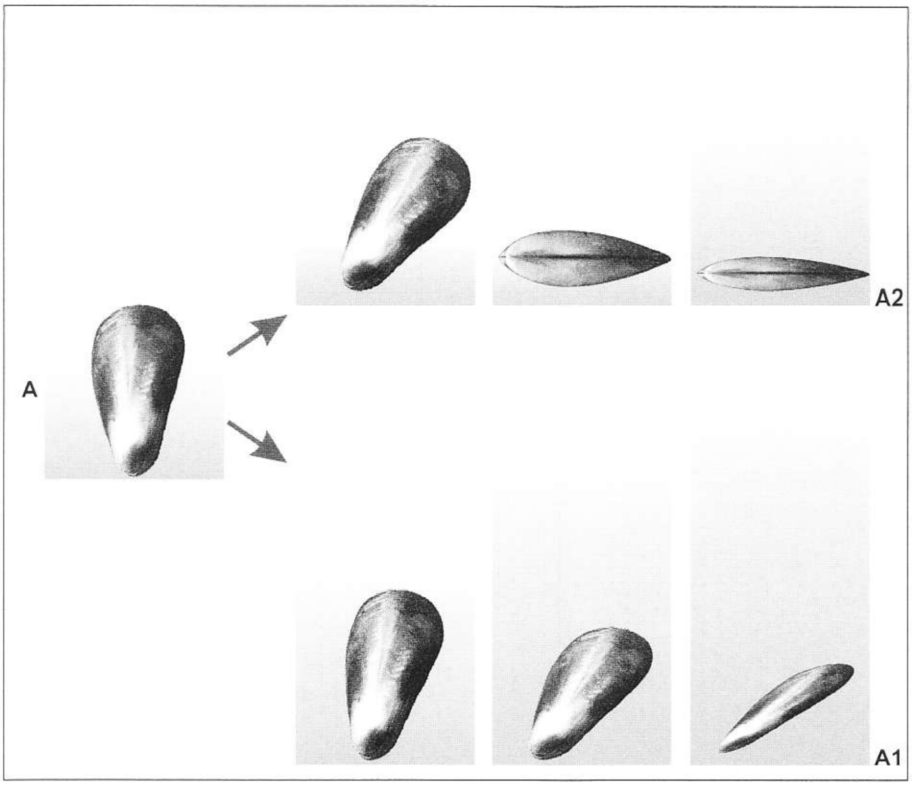

Fig. 6 - Taphonomic model explaining the different preservational conditions of *Amygdalum* in the study case. A: *Amygdalum* in life position. A1 (grey mudstones): Burial in life position under persistent accumulation of sediment and strong compactional deformation. A2 (yellowish mudstones): Episodic disinterment and reorientation by winnowing, burial, and moderate compactional deformation.

The macrofauna associated with *Amygdalum* points to relatively deep environments, which can be referred to upper slope/outer shelf, probably not exceeding 200-300 m. This is in rather good accordance with the Mediterranean and Atlantic records of *Amygdalum politum*, all from depths exceeding 400 m. Probably, the past bathymetric distribution of *A. politum* was a little shallower than at present-day.

There is no evidence of oxygen depletion in the bottom waters. This supports the hypothesis by Oliver (2001) that there is no general relation between oxygen depletion and life conditions of *Amygdalum*, although the species he studied lives in strongly dysaerobic conditions.

As remarked above, taphonomic data indicate a particularly fluid substrate, related to a high rate of mud sedimentation. Further evidence for such a sedimentary setting is provided by the occurrence of *Corbula gibba*, a bivalve thriving under conditions of high rates of sedimentation and water turbidity (Di Geronimo & Robba 1989).

Discussion

There is accumulating evidence that taphonomy is potentially useful in reconstructing environments and life habits, especially if combined with palaeoecology. Further, a feed-back approach, taking into account neontologic and paleontological data, is important to acquire knowledge on both living and extinct organisms. In the present study, this integrated approach led to a better knowledge of a poorly known bivalve and of its unusual life habit.

Amygdalum can be considered as a virtually immobile shallow burrower, seemingly with no reburrowing ability. There are contrasting aspects in its adaptive strategy, since the lack of reburrowing ability would require a deeply buried life position ("sheltered" strategy, according to Kondo 1998), whereas a shallow life position would require a quick burrowing ability ("exposed" strategy), except in uncompacted physically stable substrates. In order to colonize such substrates, adaptations to cope with rapid sedimentation and soupy consistency of substrate are needed. Based on the present observations and on the scant available literature data (Oliver 2001), the byssal cocoon probably enables *Amygdalum* to keep a vertical life position, allowing it to "float" in a particularly fluid muddy sediment. *Amygdalum* does not seem to have anatomic adaptations to cope with high turbidity conditions, although taphonomic evidence suggests such conditions. It may be argued (Oliver 2001) that the cocoon also protects the bivalve from sediment entering the mantle cavity, not only from the pedal aperture, but also through the inhalant current, thus working also as a filter and enabling the bivalve to live in turbid environments.

Acknowledgements. Authors are grateful to Franz T. Fürsich (Universität Würzburg) for reviewing the early drafts of this paper, to Elio Robba (Università di Milano) and to an anonymous referee, who provided useful comments and suggestions. Work supported by Fondi d'Ateneo 2002, resp. D'Alessandro.

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