

BIOMECHANICAL FRAGMENTATION IN SHELL-BEDS FROM THE LATE TRIASSIC OF THE LOMBARDIAN BASIN (NORTHERN ITALY). PRELIMINARY REPORT

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Riassunto. Frammenti di conchiglie sono molto diffusi nelle coquine presenti sia al tetto del Calcare di Zorzino che nelle soprastanti unità bacinali Norico-Retiche, benchè depostesi in ambienti a bassa energia. L'aspetto spigoloso dei frammenti, in associazione alla presenza di evidenti tracce di predazione del tutto simili a quelle dovute ai moderni pesci, fa ritenere che la bioframmentazione ad opera dei numerosi pesci durofagi fosse molto importante già nel Triassico Superiore.

Abstract. Shell-beds rich in shell fragments are very common in the Lombardia basal facies in the Late Triassic. Biofragmentation by durophagous fishes, which were very common, must be regarded as the main taphonomic process on the basis of the shape of fragments and the presence of predatory traces, such as semicircular notches on the fragment edges or punctures on whole valves. Scattered patches of shell-fragments are also common and are considered as ejecta and/or coprolites from durophagous fishes. Furthermore, shell material fragmented by living fish (*Pogonias cromis* and *Diplodus sargus* among others) is comparable in shape with the Triassic material presented here. The shell-beds here described were deposited in a low energy environment, which precludes waves or currents mechanical damages. *Paralepidotus ornatus*, the most common Triassic durophagous fish, pycnodonts, other semionotids and the placodont reptile *Psephoderma alpinum*, are the most important shell-predators in the Late Triassic. *Modiolus*, *Laternula* and *Protocardia* were the more commonly preyed molluscs.

Introduction.

The Late Triassic of Lombardy yields several fossiliferous levels, the most important of which are those rich in nicely preserved vertebrates (Fig. 1).

During the initial stage of a new research program intended to compare the dentition and the diet of modern durophagous teleosts with those of Late Triassic neopterygians found in those sites, I observed fragmented lamellibranch shells, together with rare whole valves, from the gut content of the white bream *Diplodus sargus* (Fig. 2). Such biomechanical fragmentation provides a

possible origin for the shell fragments found in the shell-bed in the Zogno2 vertebrate locality, of the uppermost Calcare di Zorzino (Zorzino Limestone) (Tintori, 1993b). In addition, several shell-beds in the younger upper Argillite di Riva di Solto (Riva di Solto Shale, ARS2 of Jadoul et al., 1994) show complete individuals or single valves together with sharp shell fragments of the same kind of those from the Zogno2 shell-bed. The few complete fishes that have been found in the upper Riva di Solto Shale belong to durophagous species (Tintori, 1983 and pers.obs.). Scattered remains, which are quite common in the shell-beds themselves, have also been identified as belonging to durophagous species.

Ejecta and coprolites found, together with complete and well articulated vertebrate specimens, above and below the shell-bed in Zogno2, contain similar shell fragments (Fig. 3).

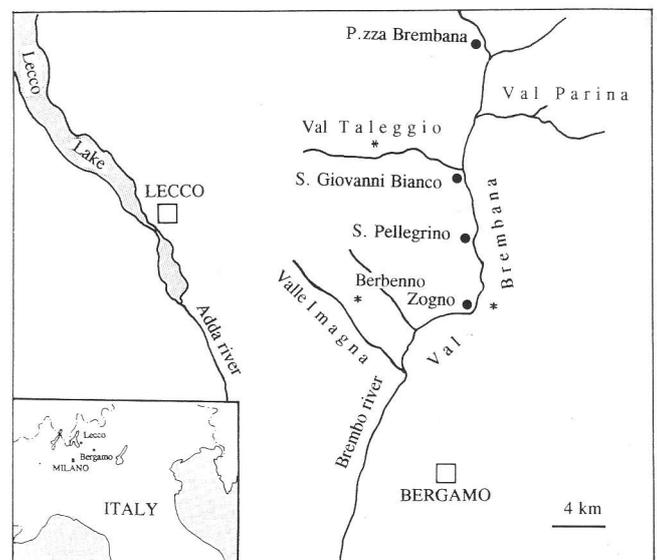


Fig. 1 - Map of the Bergamo area. Asterisks mark the cited fossil sites.

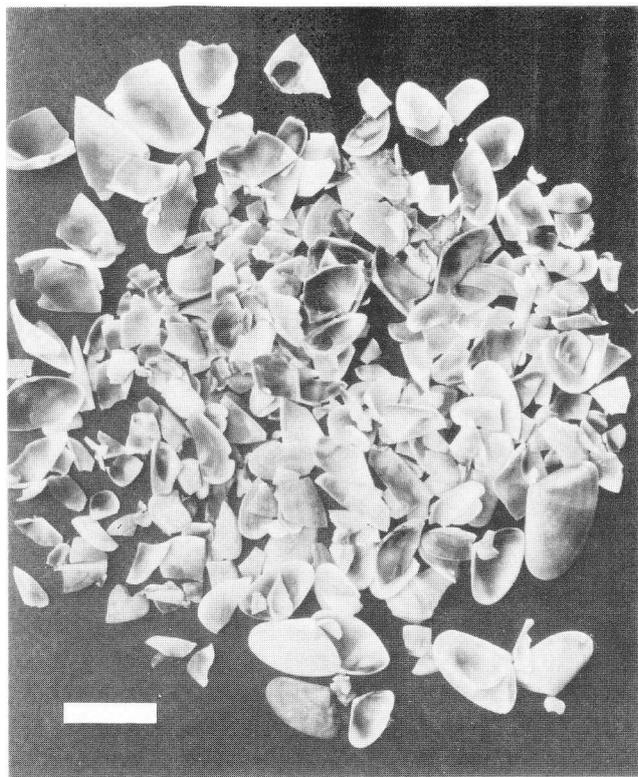


Fig. 2 - *Donax* shell material from the gut of a recent *Diplodus sargus*. Note the presence of rare whole valves. Scale-bar: 10 mm.

Biological shell fragmentation.

The importance of biomechanical fragmentation of shells has been reported for recent environments (Trewin & Welsh, 1976; Boucot, 1981; Vermeij, 1993; Cadée, 1994; Cate & Evans, 1994) but has received less emphasis in paleoenvironmental studies. Several authors deal with evidence of fossil-shell predation (see for instance Boucot, 1981, 1990; Robba & Ostinelli, 1975), but usually only for paleobiological purposes. Furthermore, in most cases they refer to repaired shells of molluscs which could survive the attack (repaired shell) or were left almost complete even if predation was successful. Carter (1968), Boyd & Newell (1972) and Robba & Ostinelli (1975) recorded shells showing sequences of holes, possibly from teeth of fish, which are represented in the assemblage only by isolated teeth or otoliths. Zangerl and Richardson (1963, pp. 135-138, pl. 44, fig. D) figured ejecta (gastric residue pellet) similar in shape and size to those from the Zorzino Limestone and recorded large amounts of shell fragments. Though they "have no record of possible predators on molluscs", in my opinion their ejecta can be confidently ascribed to fishes, as the much more common ejecta made of fish remains.

However, in general, only identifiable fossils are described in palaeoenvironmental studies. Fragmented material is generally not described. Dealing with fossil

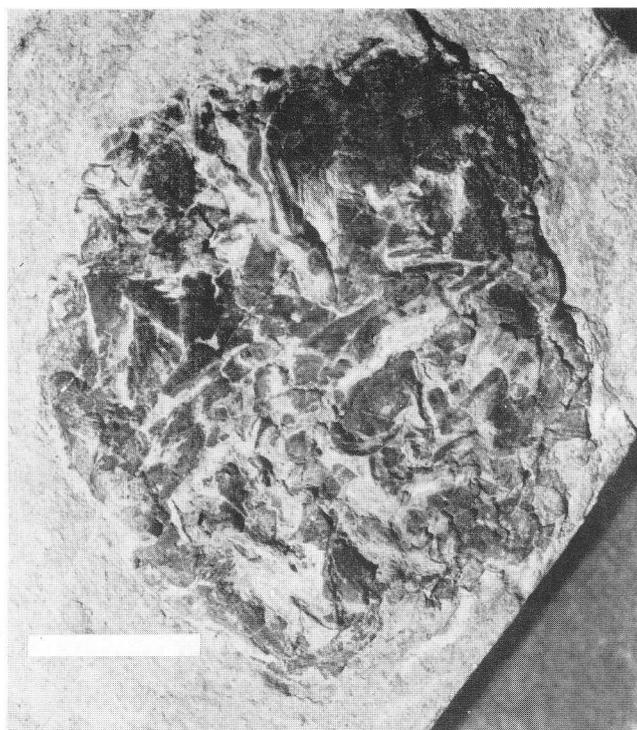


Fig. 3 - Ejecta made of fragmented *Modiolus*-like shells. Zorzino Limestone, Norian, Late Triassic, B2 locality near Brembilla (Bergamo-Italy). Scale-bar: 10 mm.

assemblages, it may be difficult to establish if fragments were generated by sediment compaction crushing whole valves or during collection and preparation of the sample, or if fragments were originally present in the rock. Only a careful survey in the field and time-consuming preparation will allow identification of 'in-place' crushed shells versus isolate fragments. Furthermore, fragments produced by predators, could be reworked in a high energy environment or weakened by bioerosion, so that the original fragment characters will disappear (Trewin & Welsh, 1976; Cadée, 1994). Thus, rapid burial is required to 'freeze' in a shell-bed the original structure of shelly material (see for instance Trewin & Welsh, 1972) so that reliable identification of the origin of shell fragments would be possible. Following Kidwell (1991) classification of shell-beds, our coquinas are confidently assigned to single event-concentration type, thus caused by a rapid and simple process, mostly consisting in turbidity currents or storm concentrations. These coquinas are much harder than the surrounding shaly or marly layers and can be easily collected in large slabs.

Material and methods.

Late Triassic shell-beds from Lombardy, though tightly cemented, offer the opportunity of sound observations if well prepared. Zogno2 shell-bed shows a thin marly film covering the lower surface, which is the

more interesting because contains the largest fragments. Slabs which remained exposed for at least a couple of years show a natural preparation because atmospherical agents leave shell-fragments in good evidence. In this case, it is sufficient to remove the remaining shale in between the fragments. Freshly collected slabs underwent a repeated treatment with hot (boiling) dilute hydrogen peroxide for few minutes followed by drying in a stove. After each cycle the softened matrix was removed by thin needles.

The Riva di Solto Shale shell-beds must be mechanically prepared. Shell material is very thin and fragile and the shaly matrix, soaked with ethyl alcohol, can be easily removed by needles from both the lower and upper surfaces.

Careful investigations of prepared surfaces allow to discriminate whole valve crushed in place by sediment compaction (Fig. 5; Pl. 1, fig. A), from original isolated fragments. So far only qualitative analysis has been carried on, mainly in the search of predatory traces.

The Late Triassic shell-beds.

The Zogno2 shell-bed.

The thin shell-bed at the Zogno2 locality lies at the top of level 10, a 30 cm thick fossiliferous unit (Tintori, 1993b), just below the barren, unlaminated bed 9. The shell-bed has an irregular thickness, varying between two and three centimeters and usually splits in two sub-units. The lowermost sub-unit yields the largest fragments and the rare whole valves. Almost all the fragments are from *Modiolus* shells (Pl. 1, fig. B), mostly of small size. In addition, very rare *Isognomon* and 'Macro-dus' are present. All shell fragments show sharp edges and corners and, in a few cases, small semicircular notches are visible along the otherwise straight edges (Pl. 1, fig. C, D). These notches can be confidently considered as predatory traces as similar ones have been detected on shell fragments found in the gut of *Diplodus sargus* (Fig. 4). Minute remains of bone, teeth and scales are scattered among shell material.

In thin section, bioclasts appear densely packed, with some intraclast and scarce micritic matrix. A size gradation is present, so that a deposition by a turbidity current may be assumed. Turbidites have been already recorded in the Zorzino Limestone basins and in areas more proximal than the fossiliferous sites they are much more common (Jadoul, 1986). The paleotopography of the area (Jadoul et al., 1992) and lack of an erosional base of the shell-bed, implies that the original slope was not steep and the source area was nearby. Furthermore, slope instability is proved by slumped laminated beds in the same vertebrate level at Zogno2 (Tintori, 1993b).

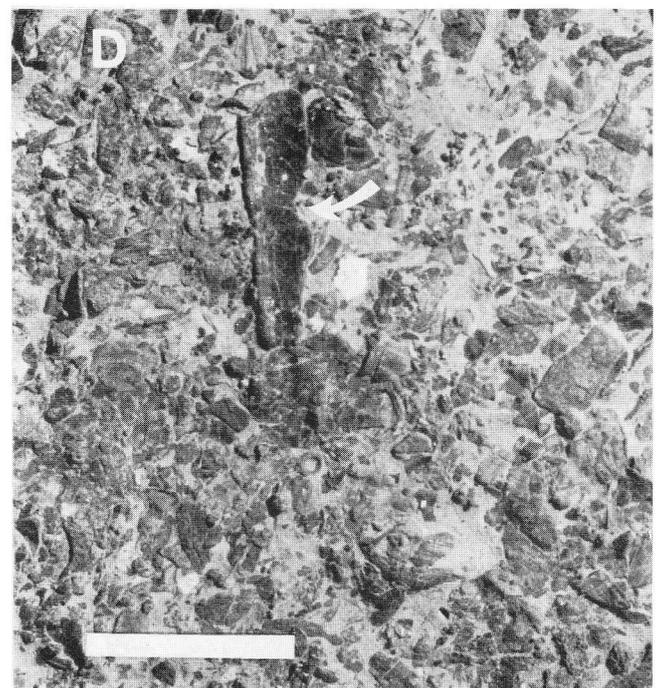
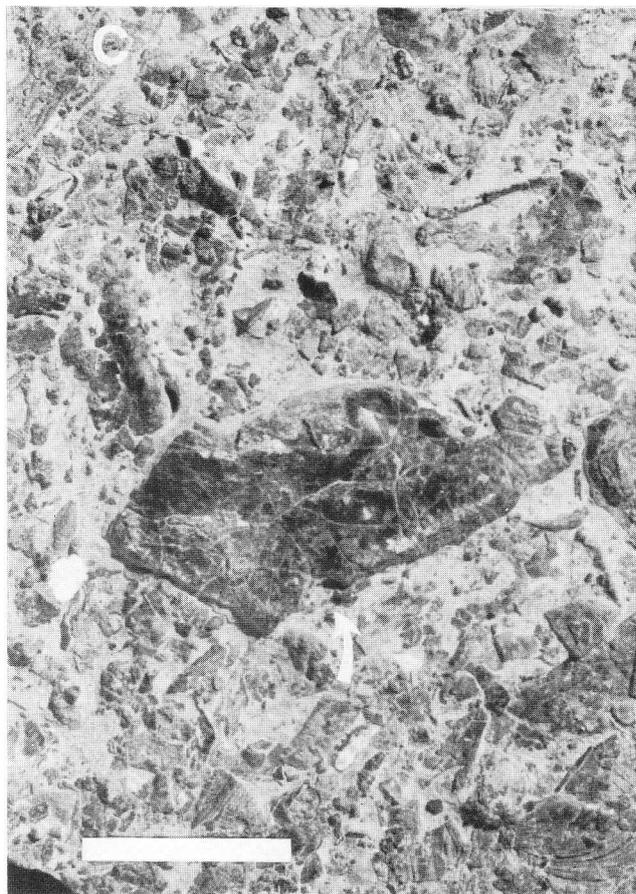
The possibility that a graded-bed is produced by in-place bioturbation (Cadée, 1976; Trewin & Welsh, 1976) is here not considered because, generally the sea bottom was anoxic as the preservation of hundreds of totally articulate fishes and other organisms undoubtedly indicate (Tintori, 1992).

Shell material found in ejecta and coprolites, from this and other similar localities (Fig. 2), shows the same shape and size of that from the shell-bed. It must be pointed out that ejecta and coprolites have been preserved only because of anoxic bottom conditions and lack of reworking.

The Riva di Solto Shale shell-beds.

Shell-beds are also common in the units overlying the Zorzino Limestone, namely the Riva di Solto Shale and the Calcare di Zu (Zu Limestone), reaching 2-3% of the whole thickness in some members (Boccaletti, 1983; Jadoul et al., 1994). They are currently interpreted as storm layers (Boccaletti, 1983; Masetti et al., 1989). Depositional environment had to be rather quiet, apart for storm-waves, judging from shales and marls surrounding shell-beds (Jadoul et al., 1994). Higher environmental energy is also represented by thick oolitic or bioclastic beds that show totally different characters (Boccaletti, 1983; Lakew, 1990) and are common in the upper part of the sequence. In this preliminary report, only a few coquinas from the upper Riva di Solto Shale (ARS2 of Jadoul et al., 1994) have been investigated.

The dominant bivalves in these latter coquinas are small endobiotic pelecypods such as *Protocardia*, *Nuculana*, *Laternula*. Bissate epifauna was still present, though very rare in most cases. Again scattered remains of vertebrates are relatively common and most can be ascribed to durophagous organisms (*Brembodius*, *Sargodon*, *Paralepidotus* and *Psephoderma*) for which teeth have been found and identified by the author. The preservation of vertebrate isolated elements can be related to absent, or very short, sediment reworking. The upper surface of these storm-layers, consists in a pavement of whole valves or articulated specimens, while sharp shell fragments are very common in the lower part of each layer (Pl. 1, fig. A). Shell convexity is mainly upward directed. Rare subcircular holes are present on upper complete specimens (Fig. 5A), as well as notches along the shell edge (Fig. 5B). These boreholes can confidently identified as tooth marks, though it cannot be checked whether the inner side was chipped, which usually is the case for tooth punctures in shells preyed by *Diplodus sargus* (Fig. 4). This morphology, for impact-holes, is probably independent from the mechanism causing it. Pether (1995) ascribes similar holes on Holocene *Tellina* shells to the new ichnogenus *Beli-*



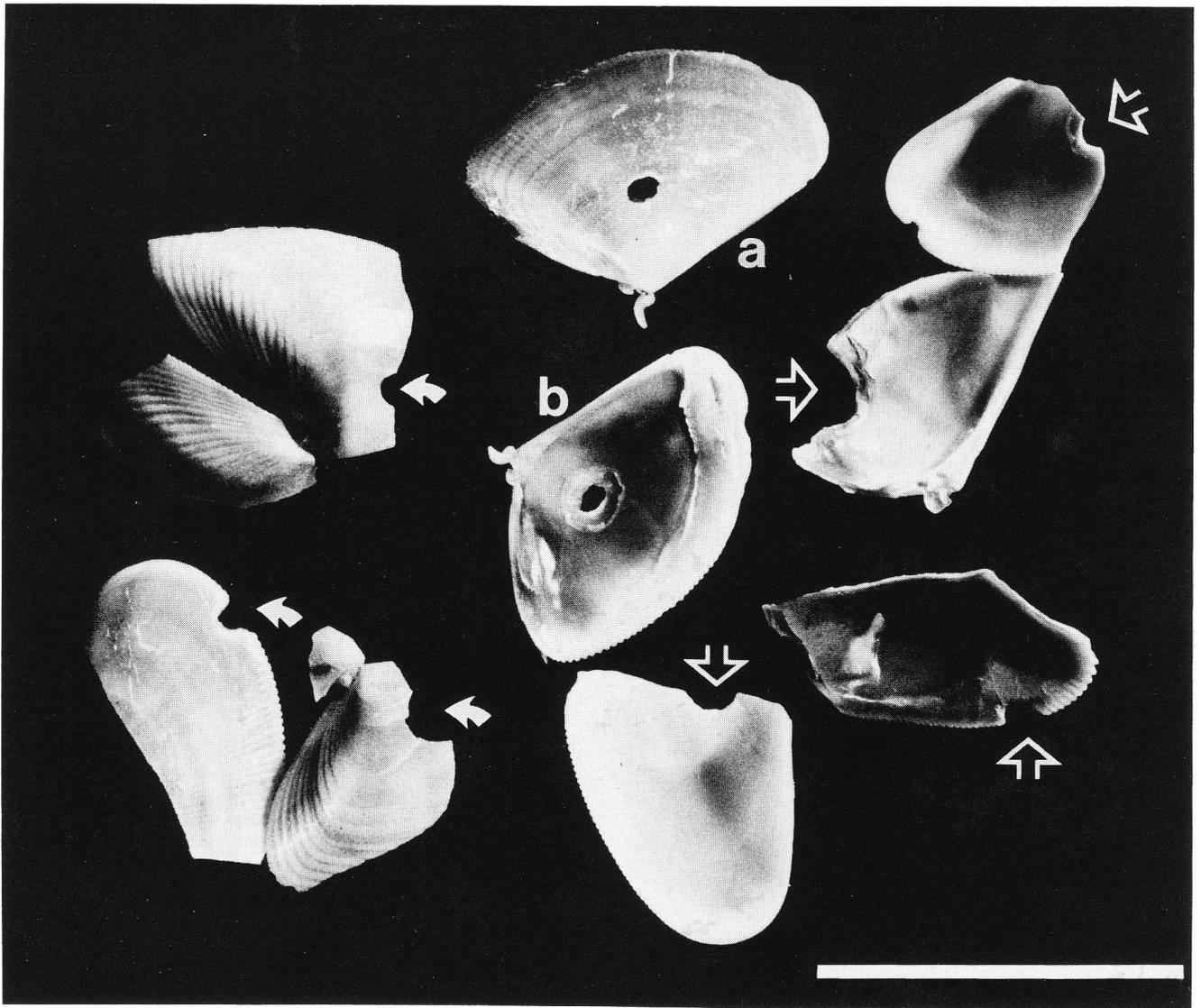


Fig. 4 - Selected *Donax* shell material from the gut of a recent *Diplodus sargus*, showing different kind of tooth-marks. a, exterior and b, interior view of same punctured whole valve; full arrow, exterior, and open arrow, interior view of tooth-notches along the valve edge or a fracture line. Note the flared inner edge of tooth traces. Scale bar: 10 mm.

chnus, interpreting them as due to stomatopod crustaceans. Actually, those *Tellina* specimens have been described after a mining process which involves separation of coarse sediments by energetic sieving. Furthermore, there is no notice of similar behaviour by living stomatopod (Pether, 1995). Shells with mechanical impact-hole, showing one-side flaring, can be found in high energy environment such as beaches made of coarse sand and small pebbles (pers.obs.). Thus, depositional environment is very important in interpreting the origin of similar boreholes: higher is the environment energy, lower is the confidence on their origin.

Boreholes by gastropods and cephalopods show a more regular shape and have a more restricted stratigraphic range: the first are known only since late Early Cretaceous for gastropods and Pliocene for octopus cephalopod (Sohl, 1969; Robba & Ostinelli, 1975; Boucot, 1990). A single find of possible naticid gastropod boreholes from the Carnian Cassian Formation of Northern Italy is recorded, but it is usually considered as an isolated experiment (Fürsich & Wendt, 1977).

Diagenetic features, such as pseudo-borings by pressure-dissolution (Lescinsky & Benninger, 1994) can also be excluded for our Norian samples, because of the

PLATE 1

Fig. A - Lower surface of a shell-bed from Riva di Solto Shale - Member 2, Berbenno (Bergamo, Italy). Fragments and isolated complete valves (mainly showing downward directed concavity) are irregularly mixed. Scale-bar: 10 mm.

Fig. B-D- Lower surface of the Zogno2 shell-bed (Zorzino Limestone, Zogno, Bergamo, Italy), showing the largest fragments due to size-gradation. Arrows point to tooth-marks. Scale-bars: 10 mm.

bored shells were covered only by the shaly matrix. Furthermore, the subcircular shape of the holes do not fit for the flat shell fragments making the coquina bed.

Dominance of infaunal bivalves does not preclude predation from fishes, especially from those with prehensil chisel-like anterior teeth (*Brembodus*, *Sargodon*). In fact, the recent *Diplodus sargus* can exclusively prey on infauna (see the *Donax* remains of Fig. 2 which made the only gut content of a couple of specimens). The matrix of these shell-beds is fine-grained, indicating a quiet environment, well below normal wave base where mechanical shell breakage is unlikely. Storm-beds are

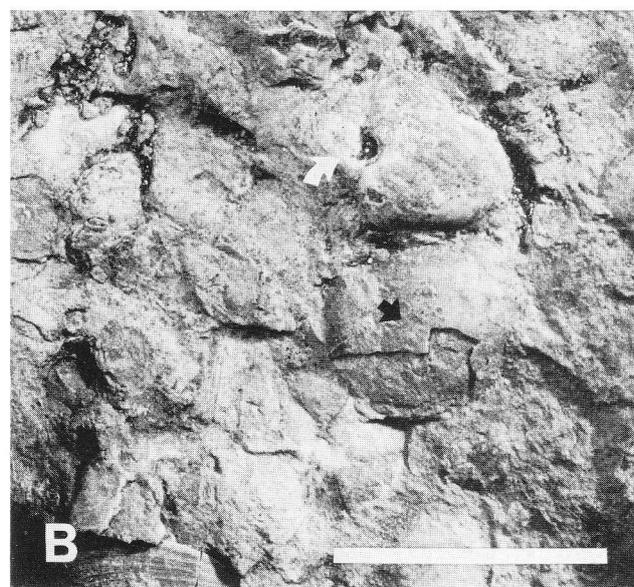
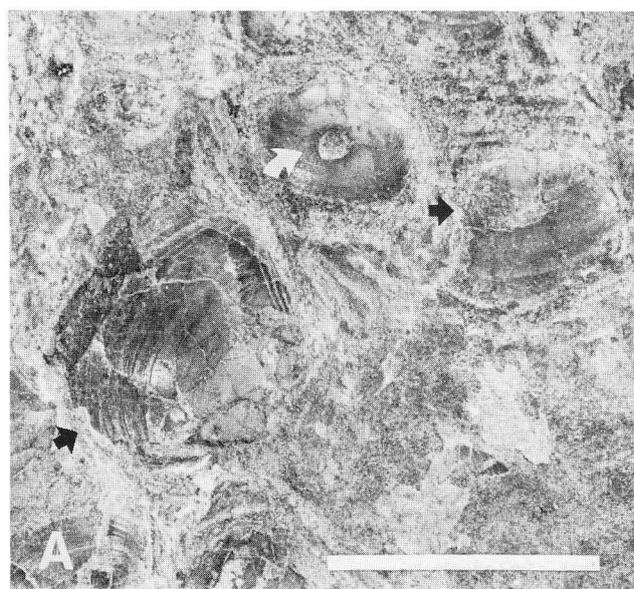


Fig. 5 - A and B, *Protocardia* whole valve from the upper surface of a Argillite di Riva di Solto (Member 2) shell-bed from Berbenno (Bergamo, Italy), Norian, Late Triassic. White arrow, possible tooth mark; black arrow, whole valve showing in place fragmentation due to sediment compactation. Scale bar: 10 mm.

separated by shaly or marly layers which often yield scattered bivalves, commonly articulated, but rarely in life position.

The vertebrate durophagous fauna.

Durophagous vertebrate fauna of the Zorzino Limestone include the most common marine reptile species, the placodont *Psephoderma alpinum* (Pinna & Nosotti, 1989; Renesto & Tintori, 1995), and at least eight out of the 40-50 fish species, the pycnodonts *Brembodus*, *Gibbodon* and *Eomesodon* (Tintori, 1981), *Legnonotus* and an undescribed Macrosemiidae (Tintori & Renesto, 1983) and the semionotids *Sargodon tomicus*, *Dapedium noricum* and *Paralepidotus ornatus* (Tintori, 1983; in press). The presence of teeth of these species in the shell-beds of the Riva di Solto Shale and the Zu Limestone, is evidence of their survival until the end of the Triassic. Each of these organisms has a peculiar feeding activity, that can be inferred from the type of dentition and body shape and size. Pycnodonts, for instance, possibly fed on encrusting organisms, which were detached by their nibbling anterior teeth and then crushed by the molariforms, as well as on free-living shelled benthos. Gut content of a few pycnodonts (Lehman, 1966; Viohl, 1990) proved they predated on echinoids, corals and bivalves. At Norian time pycnodonts were small and relatively uncommon. Therefore, prey species would include only small organisms. Similarly, the macrosemiid *Legnonotus* was only a few centimetres long and its teeth were not very powerful. On the other hand, both *Psephoderma* and *Sargodon* were large, reaching respectively 2m and 1m in length, but they were also rare. *Paralepidotus ornatus* was, by far, the most common fish feeding on shelled molluscs. So far, about one hundred specimens of *Paralepidotus ornatus* have been prepared, ranging from seven up to 50 cm in standard length (Tintori, in press). Crushing teeth are borne by the vomers and the dermopalatines as well as by the dentalosplenic and the coronoid in the lower jaw. When *Paralepidotus* reached a standard length of 25-30 cm its teeth became hemispherical, which are well adapted to crush shelled mollusc (Tintori, 1992). In addition there are some indications of schooling, since rare mass mortality events affected several specimens of *Paralepidotus ornatus*, mainly of similar size (Tintori, 1993a). Thus, it is probable that *Paralepidotus* is the main shell fragment producer in these Norian basins and most of the shell-bearing ejecta can be confidently ascribed to it. Crustaceans too could prey on molluscs: however only a few undescribed, very large specimens seem to be adapted to this trophic niche (see also Pinna, 1974; Garassino & Teruzzi, 1993), so that their importance had to be limited.

Discussion.

The feeding activity of modern durophagous fish such as *Pogonias cromis* (the Black drum, see Cate & Evans, 1994) or *Diplodus sargus* (the white bream, Bini, 1970), suggests that biomechanical fragmentation by Triassic durophagous may have been an important source of shell fragments. Late Triassic shell-beds are often rich in shell fragments, ejecta and coprolites contain similar shell fragments. This cannot be considered as a 'frozen behavior', category 1 of reliability sensu Boucot (1990), thus a direct prove for fishes eating shell, especially if we want to ascribe these traces to a single fish species. Actually, shell fragments have never been recorded in the coelomatic cavity of our Triassic fishes. This may be due to the fact that most hard material is often rejected after being crushed in the mouth (Cave, 1978; Buxton & Clarke, 1991). In addition, heavy scale covering of most of the Norian fishes precludes observations of the interior. However, I feel confident in assigning these shell fragments to reliability category 2A ('close association of a behavioral nature, but not actually in position', Boucot 1990), considering them to be remains of bivalve predation by fishes and reptiles. In the Late Triassic, neopterygians undergo their first important radiation gi-

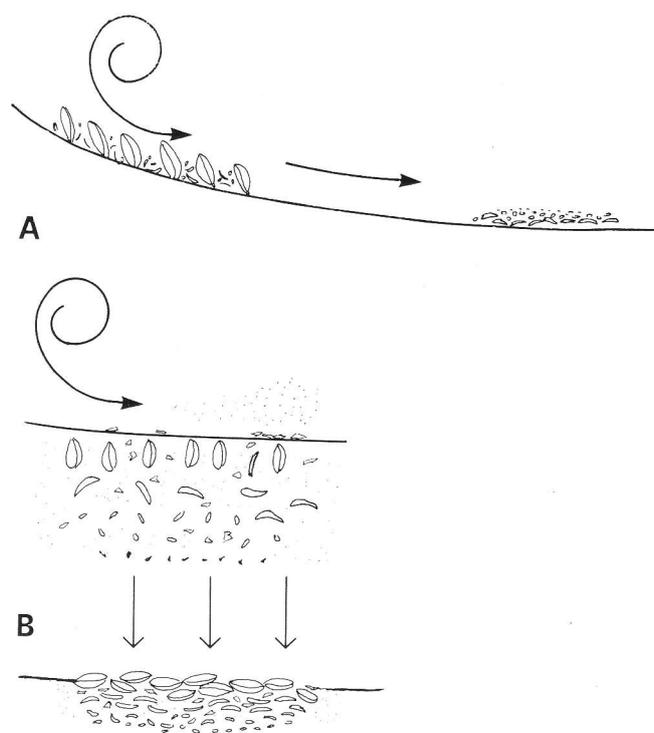


Fig. 6 - The origin of shell-beds. A) Zogno2: storm-waves reworked loose fragments, mainly from fish-predation, leaving byssate live specimens in place. A turbidite current transported the fragments down to the anoxic part of the basin. Only fragmented shells are present. B) Riva di Solto Shale (Member 2): storm-waves winnowed fine-grained sediment, concentrating shells in place. Live, dead and fragmented shells are represented.

ving rise to many marine durophagous species. The presence of numerous durophagous predators suggests the possibility of high rates of biomechanical shell fragmentation.

Possibly, shell fragments now found in the Zogno2 shell-bed remained close to the mollusc (mainly *Modiolus* and *Isognomon*) banks were *Paralepidotus* fed. Accumulation of large amounts of these bioclasts along the upper part of the basin flanks, led to local instability and, perhaps during a storm, to turbidity currents or to mass flows (see also Jadoul et al., 1992) that ran along the gentle slope for a rather short distance in the same way as other coarse-grained shallow sediments (Jadoul, 1986). The live attached bivalves were not removed by storm waves (Fig. 6A). The result was that only shell fragments were redeposited in a thin layer along the lower part of the basin flank, in anoxic waters. This storm event could also mix the oxic and anoxic waters, leading to a temporary oxygenation of the bottom. The barren, non-laminated level 9, which overlies the shell-bed, may represent the record of this oxic or disaerobic stage, when a few benthic organisms could colonize the usually anoxic bottom.

The round, flat ejecta and, more rarely, cylindrical coprolites made of shell fragments which are present in the laminated beds yielding vertebrates above and below the shell-bed, can be explained as fish moving a few hundreds of meters from their feeding environment and egesting or defecating, in this case, above the anoxic part of the basin. Though this behaviour is uncommon, demersal fishes having usually a rather restricted living area (Boucot, 1981), it has been proved in modern fishes, whose gut-content is very rarely made of exotic shell material (Cave, 1978; Cate & Evans, 1994).

Sharpness of the fragments in the shell-bed, ejecta and coprolites, comparable with that from living fishes gut content (Cate & Evans, 1994; pers.obs.), implies that they were neither submitted to a high energy environment, such as beaches or tidal channels, where bioclasts are abraded and rounded, nor to long post-mortem exposure that leads to encrustation or boring by algae and other organisms (Cadée, 1968). Thus, it is assumed that the fish mouthed and crushed live molluscs, and not previously fragmented shells, during their search for food on the bottom.

Also, monotypy of preys is characteristic of bottom-feeding fishes, which prefer to predate mainly on a single locally abundant species, changing only under unfavourable condition (Dugas, 1986). Bivalves living around the anoxic part of the basins were mainly byssate and poorly differentiated, with local dominance of a single or few species. For instance, in the same stratigraphic position of the Zogno2 shell-bed, in an adjacent area of Val Taleggio (Gaetani & Tintori, 1979), there is a

similar one made of whole valves of *Modiolus*, *Isognomon*, *Gervillia* and 'Macroodus', more or less in the same proportions. Presence of fragments of a single species in the Zogno2 shell-bed can be related either to the presence of monotypic banks in the source area or to selective feeding on *Modiolus*. Whole valves of *Modiolus* and *Isognomon*, are common in the vertebrate levels, together with other benthic invertebrates (pers. obs.). However, *Modiolus* has a thinner shell and a more elongate shape than *Isognomon*. These characters may explain the small mouthed *Paralepidotus* preference in handling *Modiolus* rather than *Isognomon*.

In the Riva di Solto Shale most of the shell-beds can be interpreted as in place storm reworking of a living community of endobiotic molluscs in a muddy bottom. In this case, live, naturally dead and preyed shells were concentrated as the storm waves reworked the superficial sediments, moving away most of the mud (Fig. 6B). Later on in the sequence, shallower bottoms (Boccaletti, 1983; Jadoul et al., 1994) provided higher energy environments, so that biomechanical fragmentation characters were canceled by physical and other biological events.

Conclusions.

It is highly probable, reliability category 2A of Boucot (1990), that shell fragments making the Zogno2 shell-bed were produced by feeding activity of bottom dwelling fish (mostly *Paralepidotus*) in a shallow, quiet environment along the basin margins. Similar origin can be proposed for at least part of the fragments of the other described shell-beds from the Riva di Solto Shale member 2, though in a different environment and with different depositional mechanism.

The possibility that shell-fragments in other Mesozoic and post-Mesozoic single-event shell-beds are biomechanical in origin rather than produced by mechanical fragmentation must be considered. Presence of scattered fish remains in shell-beds, can be considered as particularly important in order of this identification since they are not usually preserved in high-energy environments.

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