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FISH TAPHONOMY AND TRIASSIC ANOXIC BASINS FROM THE ALPS: A CASE HISTORY

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Riassunto. Nelle Alpi Calcaree, sia Meridionali che Settentrionali, il Triassico Medio-Superiore presenta spesso rocce depostesi in bacini anossici e ricche in Vertebrati fossili. Alcune località fossilifere erano già conosciute e sfruttate attorno alla metà del secolo scorso e hanno fornito notevolissime collezioni paleontologiche (ad esempio la Formazione di Besano e i Seefelder Schichten); in altri casi la scoperta e la raccolta di fossili è avvenuta in tempi recenti (Calcare di Zorzino). Soprattutto nel passato le raccolte paleontologiche costituivano il risultato secondario dello sfruttamento minerario: infatti i livelli bituminosi presenti erano cavati per scopi farmaceutici, quali la produzione dell'unguento "Ittiolo". Terminato negli ultimi decenni tale sfruttamento, queste unità hanno destato l'interesse dell'industria petrolifera come potenziali rocce madri di petrolio, potendo raggiungere e superare il 40% di contenuto totale in materia organica (TOC).

Queste unità sono state comunemente interpretate come depostesi in bacini con condizioni anossiche al fondo, anche e soprattutto per la presenza delle ricche faune a Vertebrati. Tuttavia lo studio tafonomico di questi fossili, qui effettuato per la prima volta, non sempre fornisce indicazioni a sostegno di questa ipotesi. In alcuni casi, principalmente riguardo alla Formazione di Besano, la tafonomia dei Vertebrati permette la formazione di un differente modello deposizionale. In realtà in questa unità, molti fossili giacciono isoorientati sulle superfici di strato e con molti elementi scheletrici dispersi unimodalmente attorno alla parte principale del corpo. Questo tipo di conservazione implica una leggera bioturbazione in presenza di correnti di fondo in grado di orientare la distribuzione di ossa e scaglie disarticolate. L'autore ipotizza quindi un ambiente disaerobico al fondo, o comunque non permanentemente anossico, con alternanze di periodi anossici con altri nei quali era ancora presente una piccola quantità di ossigeno anche all'interfaccia acqua/sedimento. Per quanto riguarda altre unità, ad esempio il Calcare di Zorzino e la Kalkschieferzone, la conservazione di Vertebrati sempre perfettamente articolati, è in pieno accordo con l'anossia al fondo, benché il TOC sia nettamente inferiore a quello della Formazione di Besano.

Abstract. Anoxic basins, rich in fossil vertebrates, are frequently represented in the Middle and Upper Triassic rocks of both Southern and Northern Calcareous Alps. Some of the localities have been known since the second half of the XIX century and have yielded a great deal of specimens (Formazione di Besano, Seefelder Schichten), some others have been only recently found (Calcare di Zorzino). In the past times, these sites have generally been the object of economical rather than paleontological interests: their bituminous levels, in fact, were mainly exploited for pharmaceutical purposes.

Their present economical interest resides in that they may have been oil sourse-rocks. The formations in question have a medium/high total organic matter content (TOC, up to 40%). This, together with the

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presence of abundant, well preserved fossil vertebrates, have always led the previous Authors to think the basins bottom was anoxic; they assumed, in fact, that marine vertebrates fossilizate mainly under anoxia. Nonetheless, the taphonomic study of these vertebrate remains, here carried on for the first time, only in some cases supports this idea; in the others, most of all as concerns the Formazione di Besano, it has allowed the proposition of a different model. Fossils, in fact, often lie isooriented and disarticulate, with unimodal dispersal of the single elements. This implies the presence of light bioturbation and currents at the bottom and thus a disaerobic, rather than anoxic environment. Regarding other units, such as the Calcare di Zorzino and the Kalkschieferzone, the anoxic bottom conditions are well supported by the preservation of very small sized, completely articulated specimens, though the TOC shows remarkably lower rates than in the Formazione di Besano.

Introduction.

Already at the middle of the last century fossil vertebrates were known from Triassic dark, well-bedded rocks of different sites in the Alps (Costa, 1853-1860; Bellotti, 1857; Bronn, 1858; Kner, 1866a, b; Deecke, 1888; De Zigno, 1891; Bassani, 1892). This fauna was sporadically studied in following years (Gorjanovic-Kramberger, 1905; De Alessandri, 1910; Boni, 1937; Brough, 1939) to be only recently the object of new researches (Griffith, 1959; Tintori et al., 1985; Rieppel, 1985; Sander, 1989; Pinna & Nosotti, 1989; Tintori, 1990 a, b; Tintori & Renesto, 1990). Because of the high organic matter content, some of the rock units were exploited for drugs production. This latter having practically ceased after the Second World War, the same rocks have been since then assuming new importance as potential oil source-rocks.

The fossil localities are quite regularly distributed in the time span between the Anisian/Ladinian boundary (Formazione di Besano) and the Norian (Dolomie di Forni, Seefelder Schichten, Calcare di Zorzino), passing through the Late Ladinian (Formazione di Perledo-Varenna, Kalkschieferzone Member of the Calcare di Meride) and the Carnian (Calcare del Predil, Reingrabener Schiefer). The fact that vertebrate remains are associated with laminated rocks whose total organic matter content is higher than usual (up to 40%, see Tintori et al., 1985; Bechstadt et al., 1991; Bernasconi, 1991) has induced to interpret their depositional environment as strictly anoxic. But this axiom "Organic-Carbon-rich rock=anoxic bottom environment" has been lately questioned, in the light of new sedimentologic (Pedersen & Calvert, 1990; Gall, 1990) as well as paleontological data (Tintori, 1991). The taphonomic study of vertebrates seems to be a fundamental means in the reconstruction of the depositional environments and, in particular, of the water-column conditions near the basin bottom. Though several experiments and applications of fish taphonomy are related to fresh-waters (Elder & Smith, 1988), I am convinced that several conclusions can be nevertheless applied to marine environments.

Anoxic environments.

Wide and deep lakes can developed anoxic conditions at their bottom in tropical climates, where there is no input of cold, oxygenated water reaching the bottom

(Demaison & Moore, 1980). Smaller basins can have anoxic bottom also in temperate climates, but it is often a seasonal phenomenon (Wilson, 1980, 1988; Elder & Smith, 1988). Concerning marine environments, upwelling areas seem to play an important role (Demaison & Moore, 1980; Savrda et al., 1984; Suess, von Huene et al., 1990), but they usually create disaerobic, rather than anoxic, conditions; nonetheless, great quantities of organic matter accumulate, as a consequence of a very high productivity in the surface water. Semienclosed, silled basins like the Black Sea and the Baltic Sea can also develop anoxic bottoms (Grasshoff, 1975; Demaison & Moore, 1980; Calvert, 1991). Yet, in these cases, silling alone is not enough to cause anoxia, but peculiar patterns of water circulation are needed (Grasshoff, 1975); in particular, the freshwater input must be very high, to induce water stratification.

A comparison between modern environments and the restricted Triassic basins is fairly problematic. These latter were in fact remarkably smaller and, rather than by wide land extensions, were often surrounded by carbonate platforms (Tintori et al., 1985; Gaetani et al., 1992) which, forming very high sills, almost completely isolated the single basins. Possibly, water stratification was due to the sinking of waters which had become more saline (3.8-4%) and thus densier because of evaporation. They could flow down the same canyons where debris and turbidites flow (Jadoul, 1985, fig. 13) or seep through the carbonatic rocks and fault surfaces. These waters accumulated in the deepest areas of the basins; they had no way out, except for deep tidal canals which crossed the whole platform and, therefore, became progressively oxygen depleted. This fact probably induced a partial mixing in somewhat shallower waters, which thus represented a disaerobic layer, transitional to the anoxic bottom. It is worth remarking that salinity at the surface and margins of the basins was normal: this is witnessed by the invertebrate fauna (among others echinoderms, corals and brachiopods have been found), and by the absence of evidences of salt deposition (i.e. gypsum) at the bottom.

A similarity with the case of the Baltic Sea can be only recognized in the Kalkschieferzone (see Tintori, 1990 a, b); in other units (Formazione di Besano) the reconstruction of a model seems to be even more difficult, because outcrops are so sporadic as to prevent a proper knowledge of the basin.

At any rate, to propose a model for the Triassic anoxic basins is beyond the aim of the present paper, while it is the object of a research which is being carried out by the author himself together with his collegues of the University of Milano. This paper will only deal with the taphonomy contribution to the interpretation of bottom environment.

Fish taphonomy.

Because different authors give the word taphonomy different definitions and meanings (see Wilson, 1989 for a deeper discussion), it is worth specifying which use will be made of it in this paper. We will consider the time before the organism's

primary burial, which, in this case, is also the ultimate one. This part of taphonomy is called biostratinomy, here comprising the necrolysis, that corresponds to the organism's death and decomposition (Müller, 1979). It should be remembered that biostratinomical processes are affected by the characteristics of water or, at most, of the sediment/water interface. On the contrary, the conditions inside the sediment influence the diagenetic history of fossil specimens. This is a fundamental criterion for the recognition of depositional environments.

Fish (as well as other vertebrates) taphonomy is particularly effective because their skeleton is made up of a great number of elements, resulting to be very sensible to the different depositional conditions. Thus, fossilization certainly implies a loss of information (taphonomic loss sensu Wilson, 1989) which mostly concerns the physiology and anatomy of the organisms, as well as their relationship with the environment; but, on the other hand, it also provides valuable information about the depositional environment of the rocks including the organisms themselves (taphonomic gain).

Schäfer (1972) wrote "Fish carcasses are more vulnerable to decay than other vertebrates". First of all we must consider the possibility of floating in an oxic environment, not necessarily at the surface. "Carcasses that float never reach the sea floor intact" (Schäfer, 1972) because their skeleton can lose some parts or even disintegrate. This case rarely applies to Triassic fishes owing to their heavy ganoid scale covering: the developed gas is never enough to allow the carcasses to rise. As far as I know, only a few *Paralepidotus ornatus* (Agassiz, 1833-1843) from the Lombardian Norian show incomplete skeletons, and among them only specimens of 12-15 cm in standard length. Smaller and larger (up to 50 cm) specimens are usually found complete and wholly articulate (Tintori, in prep.). It is important to recognize that these incomplete specimens had reached the bottom already devoid of some bones and scales: in fact, we do not find these elements around the fossil as we do in the case of bottom bioturbation.

Therefore, the first condition for the preservation of a complete, undisturbed skeleton is that it must quickly reach the bottom, and rest there during the whole decay period. "However, buoyancy is not the only factor: there are scavengers, wave action and bottom currents, all of which may affect the decaying carcass and disintegrate it completely" (Schäfer, 1972). The kind of preservation of fossil fishes will then reflect the presence or absence of these factors. In particular, a unimodal dispersal, with correlated position of simular elements, indicates current transport, while multidirectional dispersal reveals scavengers action (Elder & Smith, 1988).

The characters above discussed will then be taken into consideration when dealing with specimens from the different Triassic localities.

After Schäfer (1972), whose work is considered as a "classic", other authors have used fossil fishes in the environmental interpretation (see among other Wilson, 1980; Elder & Smith, 1988), though limitedly to limnology and paleolimnology. Lacustrine environment, especially those of small to medium size, seem to offer an easier inter-

pretation than others; conditions, in fact, vary regularly, often even seasonally. Furthermore, the small area involved usually allows a complete knowledge of the sediments and a detailed study. As regards marine environments, they are much more complex, and authors have general dealt only with anatomy and taxonomy of fossil vertebrates (Brough, 1939; Griffith, 1977).

The fossiliferous units.

Formazione di Besano.

The Formazione di Besano (in the past also called Scisti Ittiolitici di Besano or Grenzbitumenzone) crops out in a narrow area across the boundary between Italy and Canton Ticino (Switzerland) near Varese: it is the most famous among these fossiliferous units and also the one which has yielded the greatest amount of specimens. Several nice fossils were found in the Italian outcrops, in the last century, during paleontological researches as well as during the industrial exploitation of bituminous schists (up to 40% total organic carbon, TOC; Bernasconi, 1991). Unfortunately, all this material was completely destroyed when the Museo Civico di Storia Naturale di Milano was bombed during the Second World War. At the beginning of this century, digging was started also in Switzerland, near Serpiano. The aim was the industrial exploitation of bitumen, at first as a source of energy, then for the production of "Saurol", an oily compound used for skin deseases (De Alessandri, 1910). The activity ceased soon after the end of the Second World War, but paleontological researches, started in the 1920s on the Swiss side, continued until the 1970s, to be then started again on the Italian side by the Museo Civico di Storia Naturale di Milano. All authors have always considered the depositional environment as strictly anoxic; but no one of them has ever considered vertebrate taphonomy. Sander (1989) recognized a certain alteration in the bones distribution, but he drew no conclusions from this observation.

The main fossiliferous level consists of laminated, grey/hazel-brown dolomites, quite regularly alternated to black oil-shales, which are the reachest in organic carbon. Other three similar, but thinner, levels are present in the Calcare di Meride (Sander, 1989). Fossils are found in both the lithotypes, and the kind of preservation is also very similar (Kuhn-Schnyder, 1974; pers. obs.). From a taphonomic point of view, it implies that during deposition the bottom environment must have been almost constant.

Thousands of specimens have been collected by Swiss team from Zürich (Burgin et al., 1989): more than 30 fish and 15 reptile genera are represented. Though many of them are found wholly articulate, several show unimodal dispersal of skull bones and distal fin elements. Dispersal is mostly antero-posterior in small fishes: skull bones lie along or around the body, while distal segments of lepidotrichia are scattered behind the fins themselves (Brough, 1939, pl. 4, fig. 6 or pl. 7, fig. 3 for istance; Schwarz, 1970; pers. obs.). Multidirectional dispersal is fairly rare in fishes (Brough, 1939, pl. 3,

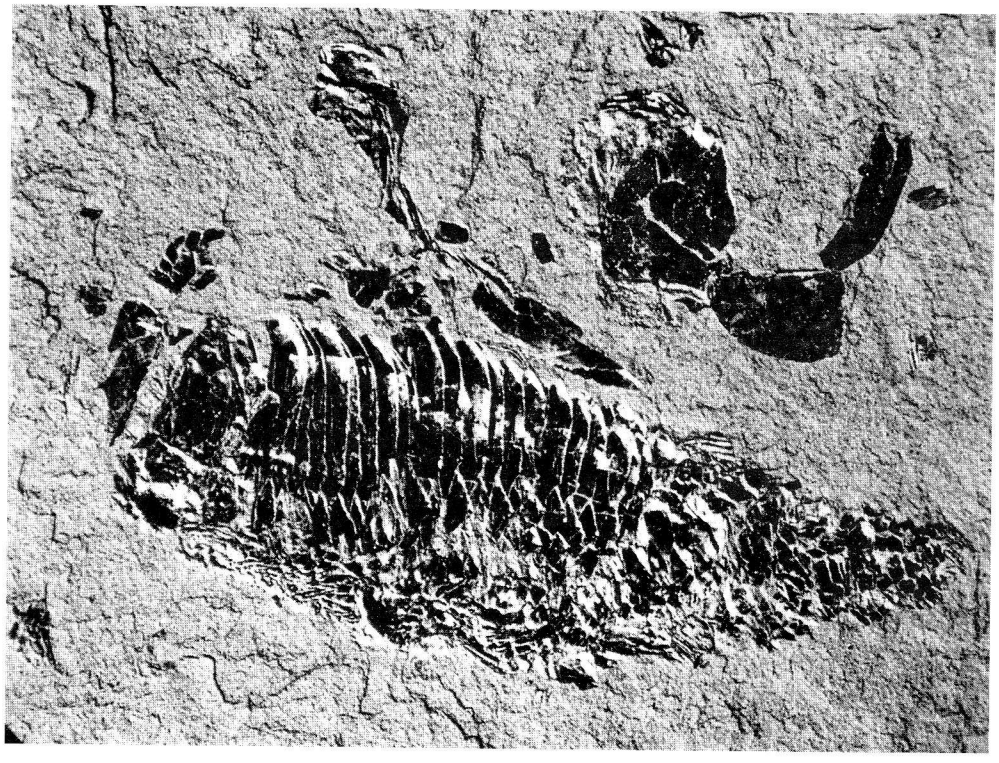

Fig. 1 - *Peltopleurus lissocephalus* from the Formazione di Besano (after Brough, 1939, pl. 4, fig. 6). Disarticulate specimen: skull bones are backward scattered, implying a slight bioturbation activity and the presence of bottom currents directed from the left to the right side of the picture. Length of the specimen: 34 mm.

fig. 4). As regards reptiles, these are usually larger than fishes and the eventual bones scattering, though still unimodal, is transversal to the body (i.e. the *Mixosaurus* picture in Burgin et al., 1989). The examination of fossils distribution on a layer surface (Kuhn-Schnyder, 1974, fig. 8), though not really corresponding to the field situation (H. Furrer, Zürich, pers. comm.) reveals that small fishes are parallely arranged, with most skulls in the same direction. This is an evidence of bottom currents, further proved by the antero-posterior dispersal of bones. The same figure shows the position of two *Mixosaurus*: their bodies form an angle of about 60° with the small fishes. Bones dispersal of the specimen figured in Burgin et al. (1989) precisely reflects the current direction. The considerable dimensions (and thus weight) of the displaced vertebral centra point to a relatively swift current.

Currents at the bottom of a shallow basin imply a partial and/or temporary mixing of waters, bringing oxygen to the bottom itself. Therefore, at least a disaerobic environment can take place, allowing a faster decomposition of vertebrate soft parts

and then a mainly unimodal dispersal of bones by the current. Because these conditions probably had a seasonal character (probable monsoonic climate), after the currents ceased all the oxygen on the bottom was consumed, and a new anoxic environment established.

Thin, pyritic patinas on reptiles and fish bones suggest a rapid burial in organic-rich, sulfidic muds (Brett & Baird, 1986); the micro-environment around the organism is strongly different from the adjacent sediment, poorer in organic matter. Brett & Baird (1986) assert that fossils pyritization mainly occurs in "minimally aerobic environment", and not in an anaerobic one. Since this process apparently takes place at or just below the sediment/water interface, it would support the idea that bottom waters were not totally anaerobic.

We can conclude that vertebrate biostratinomy certainly points to the presence (though in minimal amounts) of oxygen at the bottom (disaerobic environment). These conditions, depending on currents action, possibly had seasonal character, alternating to a strictly anaerobic environment. It follows that the very high TOC of the unit is not only the result of the bottom environment; to explain it, we must also hypothesize a very high organic input, provided by the sea as well as the surrounding lands.

Seefelder Schichten.

The Seefelder Schichten, in the Innsbruck area (Austria), contain some of the richest bituminous levels of the alpine Triassic, reaching a 40-50% in TOC (Brandner, Innsbruck, pers. comm.). From these rocks the "Ychthyol", a pharmaceutical oily compound, was obtained through distillation; the already mentioned "Saurol" was a later competing copy, with a different name because of trade mark. Unfortunately, the Seefeld fish fauna was studied only around the middle of the last century (Kner, 1866a, 1867) and very little is now known about it. A nice collection lies at the Innsbruck University: fishes are generally well preserved, with articulate bones and scales. Though most specimens are medium sized (*Paralepidotus ornatus*), they are not disturbed, not even at the fin edges.

The depositional basin of this formation has been recently interpreted (Bechstadt et al., 1991) as large, persistent and rather deep, induced by tensional tectonics. It was surrounded by the Dolomia Principale carbonate platform, but was probably in communication with the open sea, which provided a greater amount of nutrients. This is supported by the finding of conodonts and ammonite nuclei (Donofrio, Innsbruck, pers. comm.).

The characteristics of this basin can be then summarized in a totally anoxic bottom and a high productivity of the surface water as well as of the surrounding areas.

Calcare di Zorzino.

Various fossiliferous localities have been exploited in the Calcare di Zorzino (and, subordinately, in the basal part of the Argilliti di Riva di Solto) in the Bergamo area and they have yielded several thousands of vertebrates: mostly fishes, but also

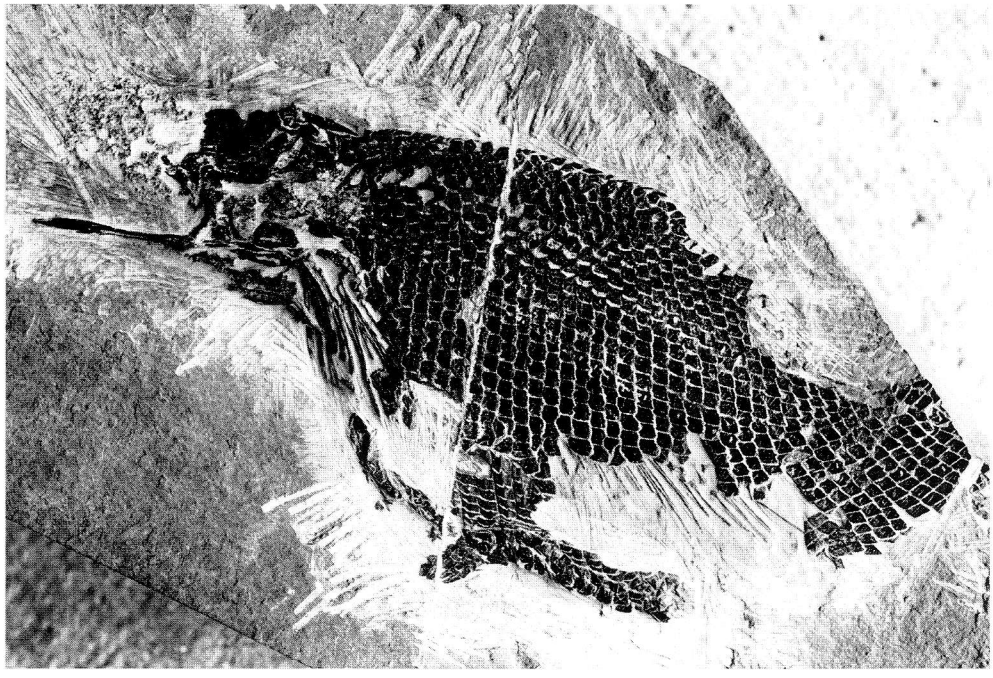

Fig. 2 - *Paralepidotus ornatus* from the Calcare di Zorzino (locality Zogno II, bed 11). Head with only endocranium, parietal and dermosphenotic bones; body lacking most of the postero-dorsal and ventral scales, allowing ribs and haemal spines to be seen. Fin dermal rays absent. No detached elements are observed around the specimen, implying a post-mortem transport in oxic environment and successive deposition in a totally anoxic one, which has not allowed further bone and scale disarticulation. Length of the specimen: 120 mm.

reptiles. Associated with vertebrates are also invertebrates: crustaceans, molluscs, brachiopods, echinoderms, scleractinia. The research is still in course by the Dipartimento di Scienze della Terra dell'Università di Milano under the author's guidance, but fossiliferous levels are so wide and rich that work could go on for decades. All fossils are to be considered as allochthonous.

The main fossiliferous level usually consists of closely laminated, 3 meters thick, more or less marly limestones, with TOC around 1% (Tintori et al., 1985). Some layers show no lamination and are barren. Fossils distribution, both horizontally and vertically, is random; no particular orientation has been observed. At Zogno 2, where field work is in progress, a peculiar layer, 3-5 cm thick, is very rich in fossil though it shows only a faint lamination. Exclusively here the above mentioned incomplete specimens of *Paralepidotus ornatus* are found, together with complete specimens of the same and other species.

The kind of preservation is identical in all the fossiliferous levels, thus resulting to be independent of mineralogical composition and TOC. Lamination might have

seasonal character, but there is no evidence to support it. The deposition of micritic mud, provided by the surrounding carbonate platform, occurred by decantation of single particles.

Vertebrate taphonomy in the Calcare di Zorzino is homogeneous and of easy interpretation: specimens are always articulate, both when their size is small (*Pholidophoridae*, *Macrosemiidae*, *Thoracopteridae*, etc.) and large (*Semionotidae*, *Saurichthys*, large reptiles such as *Psephoderma* and *Endennasaurus* etc.).

In particular, reptile taphonomy seems to confirm the bottom anoxia of the basin. Marine specimens, in fact, are generally complete and articulate (Renesto, 1984; Pinna & Nosotti, 1989); terrestrial specimens, on the contrary, are mostly incomplete, suggesting a previous transportation within oxygenated waters (basin surface) where they had partially decomposed (Wild, 1978, 1991; Pinna, 1980). Only a few flying reptiles (Wild, 1978) are found still complete and articulate: perhaps they fell directly into the sea and then rapidly sank to the anaerobic zone, where their decomposition was prevented.

Invertebrates also provide precious information. Echinoderms (echinoids, ofiuroids, crinoids are found) are perfectly preserved: all their elements are still in the

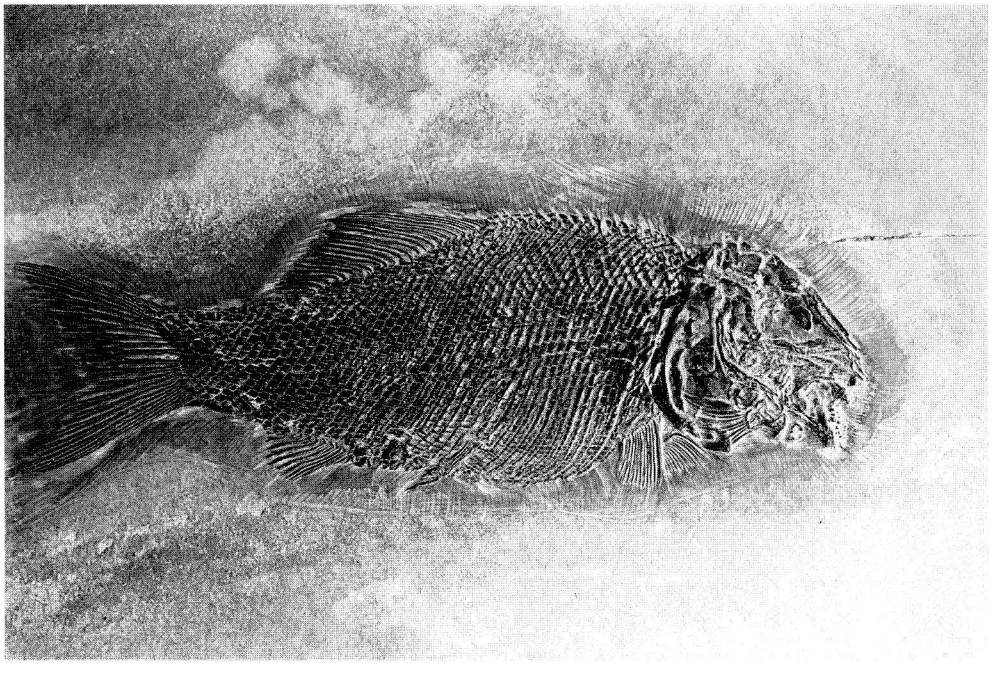

Fig. 3 - *Paralepidotus ornatus* from the Calcare di Zorzino (locality Zogno II, bed 12). Complete specimen: no or very short vertical post-mortem transport within oxic waters. Fully anoxic bottom. S.l. of the specimen: 128 mm.

original position. In echinoids, for example, spines are still articulated to their test. All systems are intact and tests are flattened, which means the internal cavity was never filled by sediment. Schäfer (1972) affirms these systems take only a few days to be disarticulated in the North Sea, oxygenated and cold. In the case of the Calcare di Zorzino, waters were certainly warmer, so that the process should have been even faster. It follows that these echinoids have moved to the anoxic bottom as still alive, and that burial has occurred before the destruction of peristomatic and periproctal systems. Though sedimentation rate can be considered as high, certainly it was not high enough to bury any organisms in a few hours or days.

No evidence of pyritization of/on fossils has been detected, while abundant framboidal pyrite is disseminated in the sediment. This is typical of anaerobic environments, as pointed out by Brett & Baird (1986).

In conclusion, the absence of bioturbation and current evidence, together with the framboidal pyrite observed in the sediment, support the information provided by vertebrate and invertebrate taphonomy, all pointing to a totally anoxic bottom environment. The relatively low organic matter content of the sediment is due to low productivity at the basin surface and on the surrounding carbonate platform.

These same conclusions can be applied to the depositional environment of the Dolomia di Forni in the Tolmezzo (Udine) area (Tintori et al., 1985; Della Vecchia et al., 1990) as well as of other small basins inside the carbonate platform on the Prealps near Brescia (Tintori et al., 1985).

Kalkschieferzone (Calcare di Meride).

The locality of Ca' del Frate, near Besano (Varese), has been known since the beginning of this century (De Alessandri, 1910) but only recently it has yielded a considerable amount of specimens (Tintori et al., 1985; Tintori, 1990 a, b; Tintori & Renesto, 1990). Its fauna consists of about 10 fish genera, one reptile and a couple of crustacean genera (Tintori, 1990 d); it is very little differentiated, suggesting a hostile environment. The succession is apparently characterized by intervals with alternatively normal and very low salinity. Fossiliferous levels consist of very finely laminated, more or less marly limestones, with a varvate aspect. Light, thick, carbonatic laminae alternate to dark, thin ones, richer in clay and organic matter. The seasonal character of deposition has been proposed by Tintori (1990 a) on the basis of the different average size of *Prohalecites* found in the two lithologies. The TOC is altogether low: not even the levels with the highest clay and organic matter content can be considered as bituminous.

Vertebrate taphonomy is well represented in *Prohalecites* (Tintori, 1990 a): this small fish (max 45 mm) is always found perfectly articulate and randomly oriented. The same can be said of the other vertebrate specimens as well as of crustaceans (Tintori, 1990 d); these latter are often found with soft body and eggs preserved. Sometimes great amounts of these organisms lie on a layer surface, testifying the possibility of mass mortality.

The environmental interpretation of this unit has been recently discussed by Tintori (1990 a, b, c; 1991), who hypothesizes a shallow basin with a totally anoxic bottom. The anoxia would be due to water stratification, originated by high freshwater input after abundant rains, which could also explain mass-mortality events.

An alternative hypothesis could be the formation, in extreme conditions, of microbic films, isolating the dead organism on the bottom (Gall, 1990). The preservation of vertebrates in this unit is thus very good, in spite of a low TOC. Thus, the organic matter was preserved only because of peculiar bottom conditions and not of overproduction. On the other hand, the shallow basin, with its low productivity and wide salinity oscillations, was not favourable to large biomasses.

Calcare del Predil.

The lowermost Carnian Calcare del Predil (cropping out around Cave del Predil, Carnia, Udine) yields fishes together with invertebrates and plant remains. Fossils were studied during the last century (Bronn, 1858; Kner, 1866 b) when the locality was named Raibl, being under Austrian sovereignity (Tintori & al., 1985); only recently field work has been resumed and a preliminary revision of the fauna has been done (Tintori, 1990 e). The fish fauna is little differentiated (about 10 genera), but comprises species with a peculiar behaviour, such as the gliding fish *Thoracopterus*.

Vertebrate specimens are found scattered in more or less laminated, marly limestones, alternated to massive limestones yielding benthic invertebrates (molluscs and corals). These massive levels are related to debris flow events at the oxygenated margins of the basin, and their deposition took place by decantation of particles in quiet waters (Jadoul & Nicora, 1986). The size of fishes contained in the Calcare del Predil is small, rarely exceeding 10 cm. Only *Birgeria*, *Polzbergia* and *Saurichthys* can be larger. Very small specimens (<2 cm) possibly represent larval stages. The preservation of such small, wholly articulate specimens (Tintori 1990 e, p. 45), besides a very high sedimentation rate, requires also a totally anoxic bottom environment. This is further proved by some specimens (in particular belonging to *Peltopleurus*) which are strongly arched, sometimes so much that the vertebrate column is broken and the head lies upside-down on the back. In some other genera the scale covering was too rigid to allow the vertebrate column to arch.

Nonetheless, a few other specimens suggest that the bottom was not really anoxic; they are, in fact, partially disarticulate, with bones and scales multidirectionally arranged. This fact would testify a slight biological activity at the bottom, with no currents. Unfortunately, we do not precisely know the relative position of articulate and disarticulate specimens, so that we cannot go into further details. Yet, the number of partially disarticulate specimens seems to be remarkably smaller than that of articulate ones, inducing us to hypothesize that, in terms of time, the anoxic environments was predominant. As no current indications can be found, the slight, sporadic oxygen input was possibly related to debris flow events, causing a certain mixing of waters.

We can then conclude that the depositional environment of the Calcare del Predil, as inferred from fish taphonomy, was subject to oxygen oscillations. The prevailing anaerobic conditions allowed the preservation of organic matter, whose small quantity in the sediment is the result of dilution caused by a high sedimentation rate (Brett & Baird, 1986).

Conclusions.

Fossil taphonomy in the various localities of the Triassic fish-yielding units of the Alps is remarkably different. There are two main modes of preservation. In the first the specimens, complete or not, are always wholly articulated, thus with bones and scales in their original position. This is the case of the vertebrates from the Calcare di Zorzino, the Seefelder Schichten and the Kalkschieferzone implying a quiet, anoxic bottom environment.

In the second preservation mode, besides complete specimens, there are also a variable number of partially disarticulated specimens. This mode of preservation has been studied by several authors (Schäfer, 1972; Elder & Smith, 1988; Wilson 1989), all of which agree in ascribing it to little quantities of oxygen at the water/sediment interface. Further information is provided by bones dispersal, which can be unimodal or multidirectional. In the former case (Formazione di Besano) oxygen was possibly brought by relatively slow currents, also confirmed by specimens isoorientation. In the latter case (Calcare del Predil), lacking any current evidence, we may think that oxygen was due to a mixing of bottom waters, induced by debris flow and turbiditic events. Therefore, the basins of the Formazione di Besano and Calcare del Predil are not to be considered as strictly anoxic, at least for a certain period of their depositional histories.

In conclusion, looking at the TOC of the different units, we can observe that there is not direct relationship between the TOC itself and the anoxic environment. In fact, among the high TOC units, the basin of the Formazione di Besano is here considered as at least sometimes disaerobic and the Seefelder Schichten one as totally anoxic. Equally, the low TOC units are either deposited under anoxic (Calcare di Zorzino, Kalkschieferzone) or disaerobic (Calcare del Predil) conditions. Thus, primary productivity must be much more important than the depositional environment in accumulating organic matter in sediments.

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