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THE LATE TRIASSIC-HETTANGIAN BIVALVES TURNOVER IN LOMBARDY (SOUTHERN ALPS)

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Riassunto. Una delle più grandi estinzioni in massa del Fanerozoico è avvenuta al limite Retico-Hettangiano. Secondo alcuni studiosi, essa sarebbe stata preceduta da un'estinzione di minore entità alla fine del Carnico.

In questo studio vengono analizzate le associazioni faunistiche presenti nelle formazioni del Trias superiore lombardo e le loro variazioni nel tempo in concomitanza con i cambiamenti delle litofacies. Nella Formazione di Gorno e nell'Arenaria di Val Sabbia del Cordevolico-Julico sono state distinte 5 associazioni a Bivalvi. Dall'analisi paleoecologica di questi Molluschi si osserva una prevalenza di specie sospensivore dell'infauna nella prima e nella seconda associazione, sostituite gradualmente nelle successive da specie epifaunistiche bissate, in stretto rapporto con il modificarsi delle litofacies. Nella soprastante Dolomia Principale norica la maggior parte dei Bivalvi precedenti scompaiono, sostituiti da specie di *Neomegalodon*, *Isognomon* e Gasteropodi. Viene evidenziato come tale scomparsa non sia dovuta ad estinzione in massa, ma all'instaurarsi di condizioni bacinali diverse più adatte alle nuove associazioni di Bivalvi eurialini. Nelle sovrastanti Argillite di Riva di Solto, Calcare di Zu e Dolomia a *Conchodon* sono state distinte 4 zone di associazione di Bivalvi. La comparsa di nuovi generi e l'aumento del numero di specie sono in stretta concomitanza con la sostituzione dei sedimenti carbonatici di piattaforma peritidale da parte di sedimenti argillo-marnosi di bacini interni. Nel Calcare di Sedrina dell'Hettangiano inf. viene considerata la fauna della Cenozona 1 di Gaetani (1970) con abbondanti *Chlamys* e vengono evidenziati l'affinità e i rapporti filetici con le specie delle sottostanti zone d'associazione retiche. Vengono inoltre calcolati l'indice di diversità, i rapporti di comparsa e scomparsa delle specie di Bivalvi del Trias superiore lombardo, oltre a quelli dei *Megalodontidae* e *Dicerocardiidae* revisionati da Végh-Neubrandt (1982) e molto diffusi nella Dolomia Principale e nel Dachsteinkalk, formazioni eteropiche con quelle lombarde. Viene infine evidenziato come nelle linee filetiche di *Megalodontidae*, alcuni caratteri morfologici variino con gradualità e continuità sia nella successione di specie triassiche che in quelle liassiche.

In conclusione le associazioni di Bivalvi nel Trias superiore della Lombardia, e più in generale nelle Alpi meridionali, non registrano particolari momenti di estinzioni di massa, ma dei cambiamenti, anche improvvisi e drastici, in stretta concomitanza con il variare delle condizioni ambientali. L'affinità tra i Bivalvi del Retico superiore e dell'Hettangiano dimostra che la grande crisi faunistica al limite Retico-Liassico è riconducibile ad un rapido ricambio faunistico, conseguenza della frammentazione e dell'annegamento della piattaforma carbonatica, in seguito a movimenti tettonici attivatisi alla fine del Retico.

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Abstract. One of the major mass extinctions of the Phanerozoic took place at the Rhaetian-Hettangian boundary. According to some researchers, it might have been preceded by a minor event at the end of the Carnian. The faunal association present in the Late Triassic formations of Lombardy and their changes related with the lithofacies changes are analysed here.

In the Carnian Gorno Formation and Val Sabbia Sandstone, five bivalve assemblages have been distinguished. From the trophic analysis of these molluscs, we observe the infaunal suspension feeders predominance in the 1st and 2nd assemblage. They are gradually replaced by epibyssate species in the following associations, closely related with the lithofacies changes. In the overlying Norian Dolomia Principale, most bivalves disappear. They are replaced by species of *Neomegalodon*, *Isognomon* and gastropods. It is pointed out that this decline is not due to mass extinction, but to the settlement of different conditions in the basin which fitted better the euryhaline bivalve assemblages. In the overlying Riva di Solto Argillite, Zu Limestone and *Conchodon* Dolomite, 4 bivalve assemblage zones have been distinguished. Both, the new genera appearance and the number of species increase are closely linked to the substitution of calcareous facies of peritidal platform with argillaceous and arenaceous sequences of inner basin. In the Hettangian Sedrina Limestone, the fauna treated by Gaetani (1970), rich in bivalves, is examined. The diversity and the phyletic relationship of this species with those of the Rhaetian zones are pointed out. The diversity, the origination and extinction rate are calculated for the bivalve species of Lombardy and for the *Megalodontidae* and *Dicerocardiidae* revised by Végh-Neubrandt (1982). Eventually, some morphologic changes in the phyletic lineage of megalodontids have been pointed out too.

Concluding, faunal crisis like mass extinction is not recorded by the bivalve assemblages of the Late Triassic of Lombardy and Southern Alps in general. They reflect pseudoextinctions, sudden and severe turnover, certainly depending on the changing environmental conditions. The affinity among the late Rhaetic bivalves and those of the Hettangian demostrates that the big faunal crisis at the Rhaetian-Hettangian boundary in Lombardy is traceable back to a rapid faunal turnover consequent to the rifting and sinking of the carbonate platform.

Introduction.

Five principal mass extinctions were recognised during the Phanerozoic (Raup & Sepkoski, 1982), respectively at the end of the Ordovician, Frasnian-Famennian boundary, end of Permian, Late Triassic, end of Cretaceous; further minor events must be considered. These dramatic periods of crisis in the biosphere were marked by the death of whole systematic groups. Global environmental perturbations might have provoked them, interfering on the delicate balance between the biosphere and the environment.

Scientists have tried to explain these great biological crises with different theories and hypotheses. For some, the extinction process is nothing more than the end of a life cycle, having each species its own specific and predetermined period of life, in close analogy with the life of the individual and regardless of fatal accidents or disease. This theory was proposed by Brocchi (1814), and was then developed by Beurlen (1933), Zunini (1933), and particularly by Schindewolf (1950) with the typostrophic theory. According to Lyell (1832), Darwin (1859), Neumayr (1889), Andrusov (1891), Davitashvili (1969) interpreted the extinction of species as the consequence of competitions among them, and of the gradual or sudden physical or chemical changes outside local or regional environmental conditions. Also, it is due to the inability of the individuals to adapt themselves to the new living conditions, while mass extinction phenomena are wildly exaggerated by the notorius imperfection of the fossil record. Cuvier (1825) and d'Orbigny (1852), consider the periodic disappearing of whole systematic groups as the consequence of catastrophic local or world-wide events, which entirely destroyed the life within an area. Particularly, d'Orbigny established a whole time series of world-wide global holocausts as providing the main reference points for stratigraphy.

Modern evolutionary biology refutes the hypothesis of the specific life cycles, while the theories concerning the extinction due to adaptive incapability, which is not enough documented because of the lack of fossiles, as well as that claiming for sudden extinctions for natural cataclysm, are the matter of debate nowadays. The debate started after the theory of Alvarez et al. (1980) claiming for the impact of a huge extraterrestrial object which, at the end of the Cretaceous, might have caused sudden changes in the world climatic conditions, with the consequent mass extinction of whole systematic groups, dinosaurs among them. Numerous are the hypotheses formulated to explain the mass extinction phenomena: periodic waves of cosmic radiations, intense volcanic activity, increase in radioactivity, terrible floods due to bolide impacts in the oceans, geomagnetic field reversals, instantaneous changes in seawater chemistry, sea level fluctuations. A wide survey of these theories can be found in Donovan (1989). At present, most researchers consider the mass extinction phenomena over a period of 2-4 million years, as being due more to a series of different accidents almost casually concentrated in time than to one catastrophic accident (Hoffman, 1989).

The Late Triassic extinction.

The extinction events which occurred at the end of the Triassic is one of the five major mass extinctions of the Earth's biota, comparable in importance to that of the Late Cretaceous. According to Hallam (1981), a cumulative loss of genera of about 42% occurred in Europe concomitant with this event, with a specific regional loss of bivalves of 92%. This faunal crisis is regarded by some scientists as the consequence of large-body impacts considering that the huge Manicouagan structure (about 70 km across) in Quebec has about the same age (about 210 MA). For Hallam (1981) the Late Triassic extinction is the effect of world-wide regression and an anoxic event associated with the Liassic transgression. Laws (1982) described the faunal assemblages at the Triassic-Liassic boundary in the Gabbs Formation; considering that at least 50% of Triassic bivalve genera continue into the Jurassic, he concludes that the physical factors which governed the Late Triassic event are not registered in Nevada. Hoffman (1985) and Benton (1986) debate on the possibility of a dual peak, in the Carnian and Rhaetian. Newton et al. (1987) criticise the idea of multiphase Late Triassic extinctions, and Johnson & Simms (1989) show "that a high proportion of extinctions are explicable in terms of directly observable facies changes".

For the supporters of the theories of catastrophes, a world-wide mass extinction must be documented in regional and local areas as well. In the Italian region of Lombardy, the Late Triassic and Liassic formations are well developed and rich in fossils. They were studied by the researchers of the Dipartimento di Scienze della Terra dell'Università di Milano. The researches, carried out under the guidance of C. Rossi Ronchetti, provided important data to be considered for the debated question of the Rhaetic-Liassic extinction.

Stratigraphy.

The lithofacies of the Late Triassic and earliest Hettangian formations in Lombardy are briefly described. For more complete and detailed information concerning the Triassic stratigraphy of Southern Alps reference can be made to the stratigraphic table of Pisa (1974), Gaetani (1975), Gaetani & Jadoul (1979), Gnaccolini (1983), Jadoul (1986).

The sequence and relationships between the formations in Lombardy compared those of Julian Alps (Raibl) are reported in Fig. 1.

Carnian.

Lombardy.

- *Metalliferous Bergamasc Limestone* (MBL). This formation has been described by Assereto & Casati (1965), Vaché (1966), Assereto, Jadoul & Omenetto (1977), Gnaccolini (1983), Garzanti & Jadoul (1985). It is characterized by lagoonal and peritidal carbonates having a total thickness of 50 to 120 metres. Dark-grey limestones predominate; siltstones associated with carbonate mudstones, marls and micritic bivalve-bearing limestones, oolitic grainstones are relatively frequent, whereas subtidal limestone with dasycladaceans are subordinate. Facies analysis testifies a typical lagoonal environment with carbonate deposits, and with terrigenous, oolitic and bioclastic intercalations transitional to carbonate tidal flats.

- *Val Sabbia Sandstone* (VVS). Described by Assereto & Casati (1965), Gnaccolini (1983, 1987), Gnaccolini & Jadoul (1988) it reflects a deltaic-lagoonal depositional system and has a maximum thickness of 500 metres gradually decreasing down to 0 metres. The lithofacies are represented by reddish-greenish sandstones and siltstones alternating with grey limestones, marls, microcrystalline dolomites, grey hybrid arenites, siltites and volcanic litharenites. This unit was deposited within an open lagoon with mixed calcareous-terrigenous sedimentation, borded seaward by tidal carbonate flats. The fauna present is mainly of euryaline bivalves such as *Pachycardia*, *Trigonodus* and *Heminajas*.

- *Gorno Formation* (GF). Gnaccolini (1986) published a thorough sedimentological study of the formation previously described by Assereto & Casati (1965) and Allasinaz (1966). The formation consists of siliciclastic and carbonate lagoonal deposits. The main lithofacies are composed by carbonate deposits (packstones, wackestones, grainstones), and by terrigenous mudstones (litharenites, siltstones). A total thickness of about 400 metres was measured; the fossil contents is usually abundant. A reference section for the Julian substage was suggested by Allasinaz (1966) within this formation.

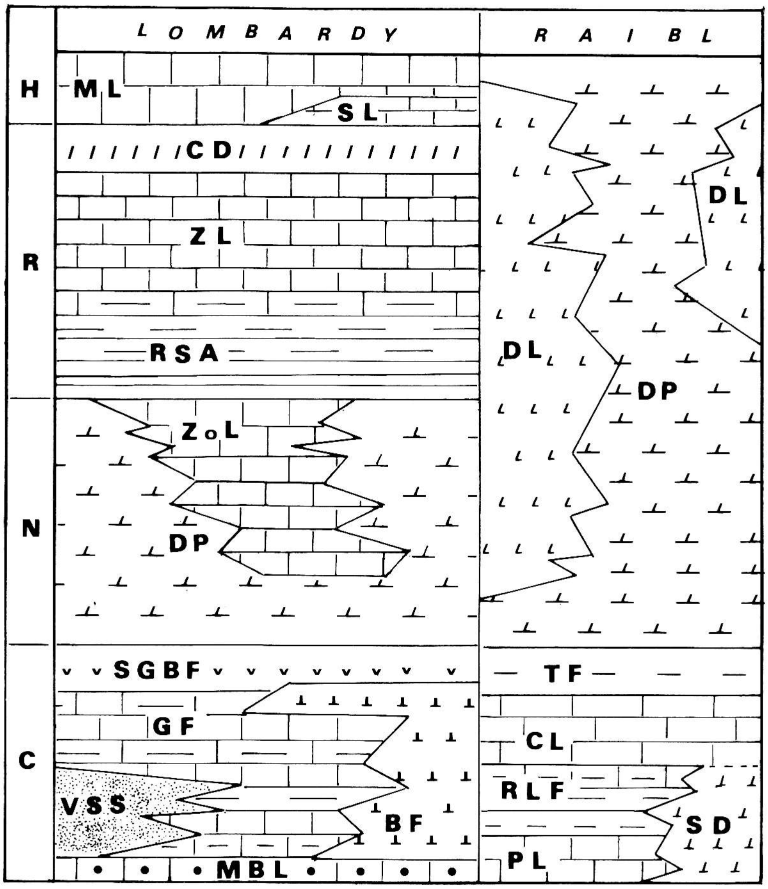

Fig. 1 - Schematic representation of Late Triassic to Hettangian stratigraphy in Lombardy and Raibl area. Lombardy: MBL) Metalliferous Bergamasco Limestone; VSS) Val Sabbia Sandstone; GF) Gorno Formation; BF) Breno Formation; SGBF) S. Giovanni Bianco Formation; DP) Dolomia Principale; ZoL) Zorzino Limestone; RSA) Riva di Solto Argillite; ZL) Zu Limestone; CD) *Conchodon* Dolomite; ML) Moltrasio Limestone; SL) Sedrina Limestone. Raibl area: PL) Predil Limestone; RLF) Rio del Lago Formation; CL) Conzen Limestone; TF) Tor Formation; SD) Schlern Dolomite; DP) Dolomia Principale; DL) Dachstein Limestone.

- *Breno Formation* (BF). Described by Assereto & Casati (1965) in Val Camonica and Assereto et al. (1977) in Val Brembana, is reported to reach a thickness of about 400 metres. The lower member is made of limestones, often oolitic or pisolitic, which were deposited in different carbonate environments from back reef (Val Camonica) to carbonate tidal flat (Val Brembana) with rather shallow and quiet waters; the upper member consists of a thick peritidal sequence of limestone beds, dolostones, algal mats with tabular fenestras, oncoids and, sometimes, grainstone beds with bird's-eyes, testifying tidal flats and coastal sabhkas. Fossils are rare, difficult to extract, but remarkable for the presence of *Neomegalodon* and *Trachyceras aonoides*.

- *S. Giovanni Bianco Formation* (SGBF). Described by Assereto & Casati (1965). It includes a sequence of green polychrome clays, alternating with marls and yellow dolostones, associated with evaporitic sediments such as "carniole" and gypsum. This formation 120 to 150 metres thick, without fossiles, witnesses a Late Carnian regressive phase.

Julian Alps.

I consider useful to describe briefly the Carnian formations of the Julian Alps and to compare the formations and faunas of Lombardy with those of Raibl, where instead the stratotype of Moisisovic's Julian substage has been established. The formations of the Raibl Group (Auctorum), overlying the light-grey dolostones of the Schlern Dolomite and described by Allasinaz (1966), succeed each other as follows.

- *Predil Limestone* (PL) (Raibl Ichthyolitic Schichten). Black limestones in layers 3 to 5 cm thick, with marl inclusion, very rich in fish and plant remains, organic material and ammonites (*Trachyceras aon*). The total thickness is 200 metres.

- *Rio del Lago Formation* (RLF). The formation consists of marls, degradable and anoxic argillites (Taube Schiefer Auctorum) at the bottom; limestones, mudstones with abundant bivalves in the middle part; massive limestone beds containing bivalve debris in the upper part. Thickness about 485 metres.

- *Conzen Limestone* (CL). Limestone and dolostone beds, sometimes siliceous or bearing large megalodontids, in a sequence which is about 210 metres in thickness.

- *Tor Formation* (TF). Calcareous dark-reddish siltstones alternating with mudstones and argillites. Whole bivalve shells are concentrated in calcarenite layers 5 to 10 cm thick. These lithofacies suggest quiet water and soft muddy bottom. The thickness exceeds 150 metres.

Faunal associations.

The bivalve assemblages from the Gorno Formation (Lombardy) and the Rio del Lago Formation (Raibl) formerly described by Allasinaz (1966) are to be considered. The two formations exhibit similar lithologies and are likely to have deposited under same environmental conditions. Among the considered bivalves, 52% are from Lombardy and 16% from Raibl. Out of 85 species listed by Allasinaz for the Julian stratotype and whose stratigraphic range has been checked, 24 are also present in the Cordevolian (28%), 5 in the Tuvalian (5%), while the species which are exclusively of Julian are 42 (49%). The low affinity with the Tuvalian is quite possibly the consequence of the scarce records of bivalves in this substage that is represented at Raibl by the Tor Formation, poorly fossiliferous and not yet studied in detail. It is also represented in Lombardy by evaporitic unfossiliferous sediments of the S. Giovanni Bianco Formation. The Cordevolian fauna in the two areas is distinctly less rich if compared with the fauna of S. Cassiano, recently studied by Zardini (1981), Urlichs (1974), Fürsich & Wendt (1977). Five faunal assemblages of paleoecologic significance can be distinguished in Lombardy and Raibl area (Tab. 1):

Genera	Life habits	Assemblages				
		1	2	3	4	5
Neomegalodon	E,R,s					+
Newaagia	E,C,s					+
Pinna	S,B,s					+
Pteria	E,B,s					+
Curionia	S,B,s				+	+
Entolium	E,Sw,s				+	+
Praechlamys	E,B,s				+	
Entolioides	E,Sw,s				+	
Neobakevellia	S,B,s				+	+
Mysidioptera	E,B,s			+		
Filopecten	E,B,s			+	+	
Myophoricardium	I,F,s			+	+	
Myophoriopis	I,F,s			+	+	
Pseudomyoconcha	S,B,s			+	+	
Plagiostoma	E,Sw,s			+		
Schafhaeutlia	I,F,s		+	+		+
Costatoria	I,F,s		+	+		
Modiolus	S,B,s		+	+		
Cercomya	I,F,s		+			
Pleuromya	I,F,s		+			
Septihoernesia	S,R,s		+	+	+	+
Mytilus	E,B,s		+	+		
Septiola	E,B,s		+	+		
Gervillia	E,B,s			+		
Parallelodon	E,B,s		+			
Neoschizodus	I,F,s		+			
Myophoria	I,F,s		+	+	+	+
Solenomorpha	I,F,s		+			
Heminajas	I,F,s	+	+			
Pachycardia	I,F,s	+				
Trigonodus	I,F,s	+	+			

Tab. 1 - Life habits of Carnian bivalve assemblages of Lombardy and Raibl area. B) Byssally attached; C) cemented; E) epifaunal; F) free; I) infaunal; R) reclining; S) semi-infaunal; Sw) swimming; d) deposit feeder; s) suspension feeder.

) *Trigonodus, Pachycardia, Heminajas* Assemblage with species from the terrigenous sandy siltstones of V. Sabbia Sandstone. These bivalves are infaunal free suspension-feeders, euryaline; they are large and thick-shelled bivalve, which indicate a high energy environment of the littoral zone close to the shore-line.

2) *Septiola, Neoschizodus, Parallelodon, Modiolus, Myophoria, Septihoernesia* Assemblage. This assemblage is the richest in genera, species and number of individuals both in Lombardy and in Raibl area. Bivalves were recovered from an alternation of limestone and mudstone layers deposited in quiet, shallow waters of the inner sublitoral zone with soft muddy uncompacted bottom. This assemblage mainly includes infaunal

and subordinate semi-infaunal suspension feeders (Tab. 1).

3) *Costatoria, Modiolus, Schafhaeutlia, Plagiostoma, Pseudomyoconcha, Myophoriopis, Filopecten, Mysidioptera* Assemblage. Rich in genera and species, it differs from the above mentioned assemblage for the presence of scallops. The species occur in alternating thin limestones and marls deposited as shallow substrates of soft mud in the inner sublitoral zone, and influenced by weak currents. Free-lying and attached epifaunal suspension-feeders dominate the assemblage, but some shallow-burrowing infaunal suspension-feeders are common as well; several members of the assemblage are characterized by a high number of individuals.

4) *Neobakevellia, Curionia, Pinna, Pteria, Newaagia, Entolioides, Entolium, Praechlamys* Assemblage. The species occur in limestones, marls, dolostones sedimented in shallow rough water, however, not strong enough to prevent the settlement of living epifaunal taxa. This assemblage is characterized mainly by epifaunal, free swimming and semi-infaunal suspension-feeders.

5) *Schafhaeutlia, Neomegalodon* Assemblage. The bivalves typically occur in limestone and dolostone beds. Most species come from the Breno Formation (Lombardy) and the Conzen Limestone of Raibl. The megalodontids were epifaunal reclining suspension-feeders inhabiting shallow and calm marine basins, commonly close to coral reefs.

Norian.

All over the Southern Alps the main Norian formations are represented by the Dolomia Principale (DP) and the Dachstein Limestone (DL). The lithofacies, the depositional cycles, the evolution and the geodynamic meaning of these formations have been treated by Bosellini (1967, 1989), Bosellini & Hardie (1985); Casati (1964) and Jadoul (1986) described the Lombardy's lithofacies. In Lombardy the Dolomia Principale (DP) is up to 1200-1500 metres thick; it is overlain by the 120-1100 m thick the Zorzino Limestone (ZoL) which occurs discontinuously and partially replaces the former unit (Fig. 1).

The Dolomia Principale (DP) is composed of shallow-water carbonate facies representing a thick peritidal sequence of dolostones and limestones. This carbonatic lithofacies was set up within a thick and wide shelf of tidal flats and lagoons, with internal basins where organic-rich anoxic carbonates, graded calcarenites, rudites and shales accumulated.

Faunal assemblage.

The best known Norian fauna of Lombardy, coming from Songavazzo and described by Terranini (1958), it includes 32 species grouped into 18 genera belonging to Porifera, Hydrozoa, Bivalvia, Gastropoda. The bivalves make up 62% of the whole fauna, the gastropods 25%. Among bivalves, 9 species belong to *Neomegalodon* (40%), the others are assigned to *Parallelodon*, *Modiolus*, *Gervillia*, *Isognomon*, *Neoschizodus*

(15%), *Dicerocardium*, *Gonodon*. *Worthenia* is the dominant genus among the gastropods making up 50% of the whole gastropod fauna. As regards the age-range of species, 21 are restricted to the Norian (62%), 7 occur in the Carnian as well and 5 extend into the Rhaetian. The dominance of slow-burrowing shallow infaunal and reclining epifaunal bivalves points toward a moderately stable substrate in an inner-shelf environment.

Rhaetian (1).

Lombardy.

The Rhaetian stratigraphic sequence in Lombardy is represented by the following formations: Riva di Solto Argillite, Zu Limestone and *Conchodon* Dolomite, whose relationships are shown in Fig. 1. The lithologic sequence described by Desio (1929), Vecchia (1950), Pollini (1955), Belloni (1960, 1963), Allasinaz (1962), Gnaccolini (1964, 1965) covers the whole region of Lombardy and allows us to draw a complete picture of the Rhaetian environment.

- *Riva di Solto Argillite* (RSA) (Swabian facies Auctorum). This formation is composed of fissile black shales intermittently laminated and thin bedded dark grey limestones. The limestone intercalations become more frequent towards the upper part. Both lithofacies and faunas which are low-diversity with a great number of individuals, indicate shallow, calm oxygen-deficient waters. The fossils, essentially bivalves, occur abundantly in finely laminated shales. This formation reaches 1500 metres in thickness.

- *Zu Limestone* (ZL) (Carpathian facies Auctorum). It includes dark-grey micritic and bioclastic limestones in medium to massive beds, and thin interbeds of marl. The thickness ranges from 300 to 1040 metres. The fauna is mainly composed of bivalves; brachiopods and corals may occasionally concur. The faunal association and lithofacies indicate shallow well oxygenated waters, sometimes clear and warm (scleractinian corals), influenced by wave and tidal action.

- *Conchodon Dolomite* (CD) (Koessen facies Auctorum). This calcareous sequence is represented by micritic limestones, massive dolostone beds, that sometimes bear large *Conchodon*, *Neomegalodon* and rare *Chlamys* specimens. Thickness ranges from 80 to 100 metres.

Faunal associations.

The stratigraphic ranges of taxa and 4 faunal assemblage zones were proposed by Allasinaz (1962) in Lombardy. These assemblage zones, recognized in Umbria as well (Sirna, 1968), were based on the numeric frequence pertaining to species, the preva-

(1) The Subcommission on Triassic Stratigraphy of IUGS in the Lausanne's meeting of 20-23 October 1991 has decided to adopt the Rhaetian as the uppermost stage of the Triassic (personal communication of M. Gaetani, Vice-Chairman of STS).

Genera	Life habits	Assemblages				
		Rhaetian				Hettangian
		1	2	3	4	5
Plicatula	E,C,s					+
Gryphaea	E,R,s					+
Tutcheria	I,F,s					+
Praeconia	I,F,s					+
Astarte	I,F,s					+
Cardinia	I,F,s					+
Conchodon	E,R,s			+	+	
Neomegalodon	E,R,s			+	+	
Liostrea	E,C,s			+	+	+
Entolium	E,Sw,s			+	+	+
Chlamys	E,B,s			+	+	+
Pteria	E,B,s		+	+		+
Camptonectes	E,B,s		+			
Parallelodon	E,B,s			+		+
Homomya	I,F,s		+			
Pholadomya	I,F,s		+			+
Protocardia	I,F,s		+	+		
Atreta	E,C,s		+	+	+	
Praechlamys	E,B,s		+			
Rhaetavicula	E,B,s	+	+			
Pteromya	I,F,s	+	+			
Palaeocardita	I,B,s	+	+			
Placunopsis	E,C,s	+	+			
Plagiostoma	E,Sw,s	+				+
Pseudocorbula	I,F,s	+				
Myophoriopis	I,F,s	+				
Myophoria	I,F,s	+				
Neoschizodus	I,F,s	+				
Gervillia	E,B,s	+				
Pinna	S,B,s	+				+
Mytilus	E,B,s	+				
Modiolus	S,B,s	+				
Nuculana	I,F,d	+				
Palaeonucula	I,F,d	+				

Tab. 2 - Life habits of Rhaetian and Hettangian bivalve assemblages of Lombardy. See Tab. 1 for explanation of symbols.

lence of specific genera and the appearance of new genera. As a matter of fact, they are ecozones which reflect the changes of the environmental conditions over the time, and the transition from zone to zone occurs through the gradual replacement of genera and species with newly appeared ones. Let's now examine the 4 assemblage zones focussing on the life habits of bivalves (Tab. 2).

1) *Bactryllium*, *Modiolus*, *Laternula*, *Neoschizodus* Assemblage, including other genera as *Palaeonucula*, *Nuculana*, *Mytilus*, *Pinna*, *Gervillia*, *Myophoria*, *Myophoriopis*,

Pseudocorbula, *Plagiostoma*. Free burrowing infaunal suspension-feeders are predominant, except for *Palaeonucula* and *Nuculana* which are deposit-feeders. The species belonging to these genera prefer shallow-water soft muddy substrates containing a large mixture of coarse debris in sheltered subtidal conditions. *Modiolus* and *Mytilus* apparently *gregarius* live in groups inhabiting intertidal and subtidal zone conditions.

2) *Homomya*, *Palaeocardita*, *Promathildia* Assemblage, including also *Placunopsis*, *Pteromya*, *Rhaetavicula*, *Praechlamys*, *Atreta* (= *Dimyodon*), *Protocardia*, *Pholadomya*. The specific assemblages are rather various, with the prevalence of epibyssate suspension-feeders adapted to less protected hard-substrates. Usually infaunal suspension-feeders like *Protocardia*, *Palaeocardita*, *Homomya*, *Pholadomya*, *Pteromya* are associated; they prefer muddy carbonate sands of protected or moderately exposed intertidal and shallow subtidal environments. However, they also show tolerance for a variety of sediments. Some of these bivalves are large pectinacean scallops which prefer sandy substrata; the presence of cemented forms such as *Placunopsis* and *Atreta* is of note.

3) *Rhaetina*, *Chlamys*, *Retiophyllia* (= *Thecosmilia*) Assemblage, including also *Pteria*, *Liostrea*, *Entolium*. This assemblage mainly include epibyssate suspension-feeders which inhabited both carbonate and clastic substrates in a high energy environment of the sublittoral zone. The presence of brachiopods (*Rhaetina*) and corals (*Retiophyllia*) suggests that the assemblage should have lived more offshore and under higher energy than the previous assemblage.

4) *Conchodon*, *Neomegalodon*, corals Assemblage. The life habit of these bivalves was described by Zapfe (1964), Tichy (1974, 1980), Allasinaz & Zardini (1977), Végh-Neubrandt (1982). Bosellini (1967) regarded the megalodontid bearing beds as deposited in the subtidal zone below the lowest tide mark a down to maximum depth of 10 m, in clear rough water. Reclining suspension-feeders bivalves, medium to large-sized are found in life position or as chaotically accumulated loose valves.

Julian Alps.

In the Julian Alps the argillaceous, arenaceous and calcareous facies of Lombardy's formations are completely replaced by the dolomite and carbonate sequences of Dolomia Principale and Dachstein Limestone which represent the whole Late Triassic-Early Liassic span of time. The change from the Dolomia Principale to the Dachstein Limestone is usually interpreted as a transition from inner to outer platform. In fact, the Dachstein Limestone contains facies referred to outer lagoon or platform margins, and preludes to the appearance of basinal pelagic facies. The faunal association of these sequences, mainly megalodontids and dicerocardiids, has been studied by Zapfe (1964), Tichy (1974, 1980), Allasinaz (1965, 1977), and in detail by Végh-Neubrandt (1982) who reviewed all the species of *Megalodontidae* and *Dicerocardiidae* known for the Triassic. Table 6 lists the genera and respective number of species according to the distribution tables Végh-Neubrandt; all uncertain records have been disregarded.

Genera	Ladinian	Carnian	Norian	Rhaetian	Hettangian
NUCULOIDA					
Palaeonucula				2	
Nuculana		1		2	
ARCOIDA					
Parallelodon	1	3	2	1	1
MYTILOIDA					
Mytilus	2	3			
Modiolus	1	3	1	6	
Septiola		1			
Pinna	1	2		2	1
PTERIOIDA					
Pteria	1	3		2	2
Rhaetavicula				1	
Neobakevellia	1	5			
Gervillia	2	3	1	1	
Cassianella	1				
Septihoernesia		2			
Isognomon			1		
Leptochondria	3				
Ornithopecten	4				
Entolium	6	5		1	2
Entolioides		4			
Filopecten		1			
Camptonectes	3	2	1		
Pleuronectites	2				
Praechlamys	3	3			
Chlamys				4	7
Granulochlamys	1	2			
Plicatula					2
Newaagia		1			
Placunopsis				1	
Atreta				1	
Plagiostoma	1	2		1	2
Mysidioptera	9	3			
Liostrea				1	3
Gryphaea					1
UNIONOIDA					
Pachycardia		2			
Trigonodus		4			
Unionites	1	1			
TRIGONIOIDA					
Myophoria		1	1		
Costatoria		6			
Heminajas		3			
Neoschizodus	1	1	3	1	

Genera	Ladinian	Carnian	Norian	Rhaetian	Hettangian
VENEROIDA					
Schafhaeutlia	8	5	1		
Curionia		1			
Pseudomyochonca	2	1			
Tutcheria					1
Palaeocardita				3	
Praeconia					1
Astarte					1
Cardinia					1
Myophoricardium		1			
Myophoriopis		2		1	
Pseudocorbula				2	
Protocardia				1	
Dicerocardium			1		
HIPPURITOIDA					
Neomegalodon		5	9	1	
Conchodon				1	
PHOLADOMYOIDA					
Pholadomya				1	1
Homomya				1	
Solenomorpha	1	1			
Pteromya				4	
Pleuromya		3			
Cercomya		1			
Total	55	87	21	42	26

Tab. 3 - List of bivalve genera with respective number of species on Ladinian to Hettangian in Lombardy.

Hettangian.

A detailed summary of the Jurassic stratigraphy of Southern Alps has been given by Gaetani (1975). In Lombardy, two formations overlie the *Conchodon* Dolomite: the 2000 to 3000 m thick Moltrasio Limestone, and the Sedrina Limestone that has thickness of 120 to 150 m. At the beginning of the Liassic the Lombardy Basin, like most of the Southern Alps, was a wide peritidal carbonate platform characterized by high sedimentation rate. These conditions lasted until the beginning of the Hettangian, which was followed by a general deepening of the basin to bathyal conditions. Gnaccolini (1965 a) pointed out at M. Crocione the transitional boundary from dark grey massive limestones and dolostones of *Conchodon* Dolomite to grey cherty limestone of the Moltrasio Formation. A discontinuous bed, 50 cm in thickness, with abundant *Chlamys* shells lies in the lower part of the Moltrasio and Sedrina Limestones. It corre-

Order	Number of species	Number extinct by end of Trias	Percentage extinct by end of Trias
Nuculoida	5	5	100
Arcoida	8	7	88
Mytiloida	23	22	96
Pterioida	108	89	82
Unionoida	8	8	100
Trigonioida	17	17	100
Veneroida	33	29	88
Hippuritoida	16	16	100
Pholadomyoida	13	12	92
Total	231	205	88

Tab. 4 - Relationship of extinction to bivalve orders at the end of the Triassic.

sponds to the "Grenzbivalvenbank" of Kronecker (1910). Bistram (1903), Rossi Ronchetti & Brena (1953), Cuzzi (1957), Berini (1957), Bertuletti (1962), Gaetani (1970) described the Hettangian fauna which includes bivalves, gastropods, brachiopods, and a lower number of ammonites. In particular, Bistram (1903), Berini (1957), Bertuletti (1962) and Gaetani (1970) give a complete list of species recovered from the *Chlamys*-bed (Grenzbivalvenbank) which, on the basis of the Bistram's ammonites, was assigned to the Early Hettangian. In faunal assemblage 5 of Tab. 2 we list the bivalve genera only, with their life habit. Among the bivalves of this level *Chlamys* prevails in number of both species (6 have been described by Bertuletti) and individuals. Of these *C. (C.) dispar*, *C. (C.) falgeri*, *C. (C.) valoniensis* and *C. (C.) thiollierei* (66% of *Chlamys*) are present in the Rhaetian too. No doubt, the faunal association of the Hettangian is remarkably different from that of the Rhaetian, but this is due to the change of the environmental conditions consequent to the shallow water shelf submersion and pelagic realm settlement.

Stage	Diversity	First appearances	Last appearances	Origination rate (%)	Extinction rate (%)
Hettangian	26	6	-	23	-
Rhaetian	42	26	28	62	66
Norian	21	2	4	9	19
Carnian	87	39	46	45	56
Ladinian	55	-	9	-	16

Tab. 5 - Faunal turnover data on Late Triassic to Hettangian bivalve species in Lombardy. Data are plotted in Fig. 2.

Faunal comparison among Late Triassic bivalves.

To the above mentioned studies provide the basis for Table 3 which serves as a necessary data base for the preparation of Tables 4 and 5. Table 4 shows the extinction rate within orders at the end of the Triassic. Table 5 displays the diversity, first and last appearances and relative percentage ratio to diversity for each stage. Based on this data, the graphical plots of Fig. 2 A have been obtained; they show a Carnian increase in diversity (87) followed by a rapid reduction during the Norian (21); another increase occurred during the Rhaetian (42), followed by a rapid Hettangian (26) decline. Naturally, the Carnian and Rhaetian peaks reflect a high origination and extinction rate.

If we simply consider the numerical data shown in the plots of Fig. 2 A, we might accept the existance of two extinction peaks in the Late Triassic, in accordance with the hypothesis of Benton (1986). On the contrary, if we consider the same parameters shown in Tables 6, 7 concerning the turnover of the megalodontids and dicerocardiids, a rapid increase of the rate of species diversity is to be noted from Carnian to Norian with a Norian peak (79), followed by a reduction during the Rhaetian (26). Moreover, the number of Carnian and Norian genera is basically similar, while it decreases in the Rhaetian.

These data contradict the previous ones only apparently. In fact, a maximum frequence of genera and species in the Dolomia Principale and Dachstein Limestone sequence corresponds, to the crisis of the Norian bivalves registered in Lombardy. Actually, the number of *Neomegalodon*'s species is high in Lombardy too (Allasinaz, 1965), as well as the number of gastropods, and corals species that are not considered in this research. The apparent contradiction is exclusively due to environmental changes which caused rapid fluctuations in the faunal associations. In effect, from the comparison of the Carnian assemblages of the Gorno Formation with the Rhaetian ones contained in the Riva di Solto Argillite, a high faunal affinity at the genus level (70% in common) is to be stressed, while species change, but are phyletically linked each other (paleospecies or chronospecies). In the Carnian Gorno Formation, the different assemblages alternate until one gradually prevails. Interfingerings of *Neomegalodon* bearing limestone beds of the Breno Formation have been also described (Jadoul, 1986).

The same depositional mechanism occurred again about 10 MA later in the Rhaetian Riva di Solto Argillite. This latter passes up without an evident break into calcareous mudstones of the Zu Limestone with *Chlamys*, *Neomegalodon* and scleractinian corals in its upper part. The rapid change of environmental conditions implies the vertical alternation of different faunal assemblages with consequent variation of the diversity, appearance and extinction rates.

The environmental conditions were relatively uniform through time during the Dolomia Principale deposition allowing the megalodontids and dicerocardiids to find adeguate habitats; therefore, groups having a high evolutionary rate quickly appeared.

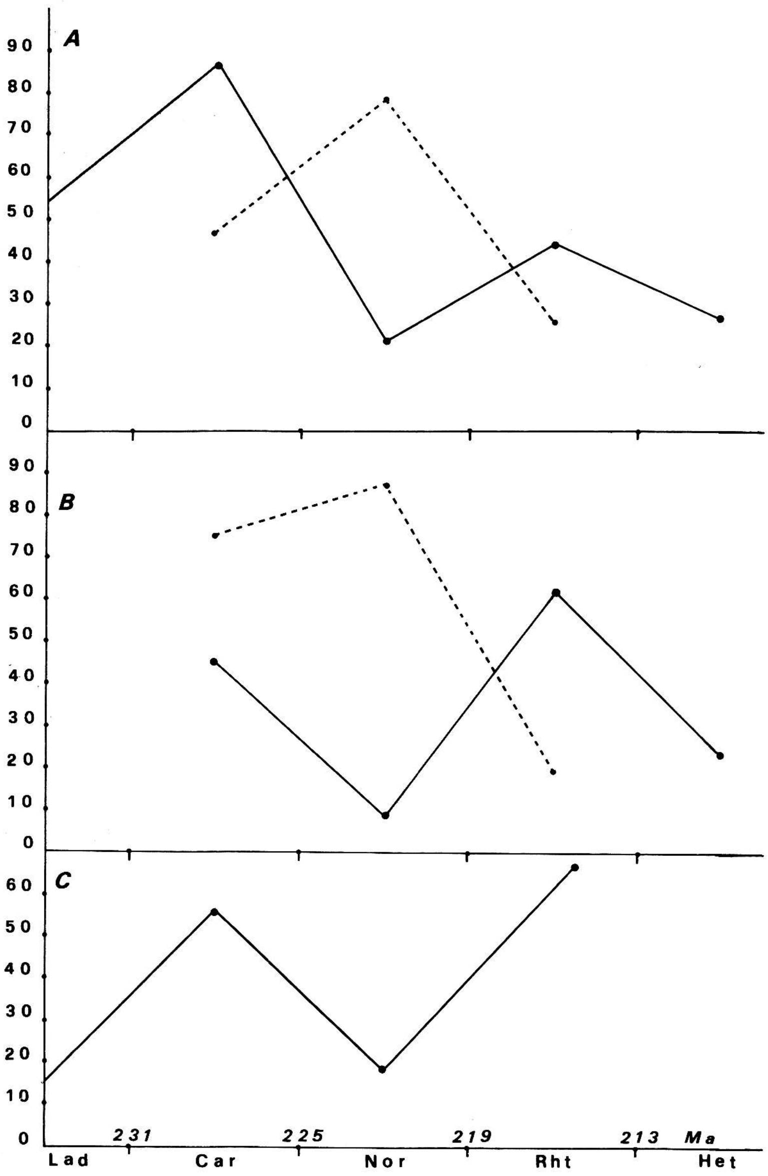

Fig. 2 - A) Graphical plots of specific diversity; B) origination rate and C) extinction rate for Late Triassic and Early Jurassic bivalves (v. Tab. 5). Continuous line) bivalves species in Lombardy; dotted line) *Megalodontidae* and *Dicerocardiidae* species in Southern Alps (v. Tab. 7). Origination and extinction rates are plotted as a percentage.

Genera	Carnian	Norian	Rhaetian
MEGALODONTIDAE			
Neomegalodon	17	34	1
Triadomegalodon	3	8	7
Gemmellarodus	2	8	
Rossiodus	14	3	
Paramegalodus		3	
Rhaetomegalodon		2	11
Conchodon			6
Ampezzania		2	
DICEROCARDIIDAE			
Dicerocardium		19	1
Cornucardia	5		
Physocardia	6		
Laubeia	1		
Total	48	79	26

Tab. 6 - *Megalodontidae* and *Dicerocardiidae* genera recorded in the Late Triassic of the Southern Alps with respective number of species per stage.

Stage	Diversity	First appearances	Last appearances	Origination rate (%)	Extinction rate (%)
Rhaetian	26	5	26	19	100
Norian	79	69	75	87	95
Carnian	48	36	46	75	96

Tab. 7 - Faunal turnover data on Late Triassic *Megalodontidae* and *Dicerocardiidae* species in Southern Alps. Data are plotted in Fig. 2.

In this respect, the continuous and rapid increase in dimensions of the *Megalodontidae* described by all researchers and carefully examined by Végh-Neubrandt (1982) is relevant; starting from a size of 10-15 cm of the Carnian species a maximum height of 50-60 cm is observed in the Norian-Rhaetian species with intermediate phenotypes. Furthermore, considering that several gastropod species (*Worthenia*, *Purpurina*) and other systematic groups are associated with *Neomegalodon* in the Dolomia Principale, the hypothesis of a Late Carnian - Norian extinction or faunal crisis seems not to have occurred in Lombardy. Actually, the marked variations of faunal assemblages are closely related with the fluctuation of the environmental conditions.

Faunal turnover at the Rhaetian-Hettangian boundary.

Severe changes in the faunal associations occurred at the Rhaetian-Hettangian boundary in Lombardy. The cumulative species loss of approximately 88%, slightly inferior to 92% reported by Hallam (1981), as well as the percentage ratio of first and last appearance to diversity make evident these changes (Tab. 5). If these numerical values only are considered, it would be logic to suppose a mass extinction at the Rhaetian-Hettangian boundary. However, if we compare the bivalve species included in assemblage 5 with those of assemblages 3 and 4 (Tab. 2) of the Zu Limestone and *Conchodon* Dolomite which are older, we can see that out of 6 *Chlamys* species present in the Early Hettangian (Bistram, 1903; Gaetani 1970, 1975) 4 are also present in the just mentioned Rhaetian assemblages (60% of the scallops). Of the 50 Rhaetian species described by Allasinaz (1962) 9 extend to the Lias. Of the 6 *Chlamys* species described by Bertuletti (1962) in the Early Hettangian *Ch. (Ch.) dispar, Ch. (Ch.) falgeri, Ch. (Ch.) valoniensis* and *Ch. (Ch.) thiollierei* (66%) were present in the Rhaetian assemblages (Zones 3 and 4).

As pointed out by Johnson (1984), the increase in maximum height from the Rhaetian (63.5 mm) to the Hettangian (77 mm) of the *Ch. (Ch.) valoniensis* is remarkable, as well as the phyletic descent of Jurassic *Ch. (Ch.) pollux* from *Ch. (Ch.) valoniensis*. It is to be noted that the affinity rate is higher among the species of the Early Hettangian and those of the Rhaetian *Chlamys* and *Conchodon* assemblage zones, than between the latters and the slightly older *Palaeocardita* assemblage zone of the Riva di Solto Argillite.

Obviously, new faunal associations including brachiopods, gastropods, ammonites appear in the Hettangian which were absent in the Rhaetian. However, these new taxa are closely related to the drastic environmental changes; in fact, a quick transition from the shallow-water calcareous facies of the *Conchodon* Dolomite to the deeper water facies of the Moltrasio and Sedrina Limestones is observed. According to Gaetani (1975, p. 383): "In the Sebino area the Upper Carnian-Norian is some 5000 meters thick, totally shallow water sediments, with a sedimentation rate of about 0.5 meters per 1000 years." In some areas (Varesotto), emersion and erosion conditions occurred. However, sedimentation took place in shallow water peritidal conditions and these conditions continued lasted until earliest Liassic, a rapid general deepening of the basin to bathyal conditions occurred later on. This rapid change of the sedimentary conditions resulted in drastic faunal changes which resemble a mass extinction at the Rhaetian-Hettangian boundary.

Actually, the *Megalodontidae* considered extinct at the end of the Triassic, lasted in the calcareous Liassic facies of the Dolomia Principale and the Dachstein Limestone. The Triassic megalodontids have a thinner cardinal apparatus than the Devonian species, and are grouped under the genus *Neomegalodon* which suddenly appeared at the end of the Ladinian as phyletic descendant from the Paleozoic *Megalodon*. The ranges and species diversity of *Megalodontidae* and *Dicerocardiidae* are reported in Table 6. The *Neomegalodon* species rapidly increase in number from Carnian (17) to Norian (34), then decrease to only one species in the Rhaetian. The *Rossiodus* species spread in the Carnian (14) and are represented by only 3 species in the Norian. *Triadomegalodon* after a rapid initial increase (3 to 8 species in the Norian), remained numerically constant in the Rhaetian. *Paramegalodus* and *Rhaetomegalodon* appeared in the Norian; the former with few species (3) restricted to the Norian, the latter developed in the Late Rhaetian being represented by 11 species, and probably survived until the Hettangian. All these genera and respective species are phyletically related and make up a homogeneous phylogenetic lineage.

Several morphologic characters such as the development and twisting of the umbones, the different development of the anterior and posterior areas, the modification of the myophores laminas, the presence of 1 or 2 postero-dorsal carinae and, above all, the continuous and rapid increase in dimensions from Carnian to Rhaetian, gradually changes within different lineages.

In some phyletic lineages described by Végh-Neubrandt (1982) the species of Triassic genera grade into species of Liassic genera. Example are the *Laubeia* ->*Physocardia* -> *Cornucardia* -> *Dicerocardium* -> *Protodiceras* -> *Diceras* phyletic lineage; the sequence made of *Rossiodus rimosus* -> *R. buchi* -> *R. columbella* -> *R. haueri* -> *R. stoppani* -> *Conchodon* which became extint in the Rhaetian; the main lineage including *Triadomegalodon compressus* -> *T. tofanae* -> *T. damesi* -> *Rhaetomegalodon* -> *Pachymegalodon* -> *Pachyrisma* -> *Juramegalodon*. This last phyletic lineage seems directly linked to the Paleozoic *Megalodon* through the species *T. cassianus* that has a massive and primitive hinge plate.

The sudden reduction in the species number which took place from Norian to Rhaetian (75 Norian species became extinct) is certainly greater than that occurred at the end of Rhaetian when the survived 26 species became extinct. The drastic extinction of Noric megalodontids is due to the reduction of the habitat of these bivalves closely related with changes of sedimentary condition in the basin. In the carbonatic platform of the Dolomia Principale, wide basins with deltaic-clastic sedimentation developed, where the Riva di Solto Argillite, Zu Limestone and other units were deposited. Unfavourable conditions for megalodontids settled which, instead, were favourable for other bivalve genera. On the other hand, the megalodontids continued to develop and evolve where carbonatic platform conditions permaned (Dachstein Limestone).

As previously said, a complete change of the environmental conditions took place at the Rhaetian-Liassic boundary, with the pseudoextinction of the Triassic megalodontids, as suggested by numerical data. Actually the Triassic megalodontids did not reach a mass extinction; they underwent modifications with that evolutionary potentiality which is typical of the group and evolved into the Jurassic genera *Pachyrisma, Durga, Pachymegalodon, Pachyrismella, Protodiceras* and *Juramegalodon*.

Then, we can conclude that in Lombardy, and probably all over the Southern Alps, mass extinctions of bivalves likely to call extraterrestrial or catastrophic causes are not documented neither in the Late Triassic nor at the Rhaetian-Hettangian boundary. The faunal turnover is more likely to be attributed to a rapid change in the sedimentary conditions consequent to the flooding of the Late Triassic pericratonic margins connected to rifting process, which affected the entire western Tethys, according to what has been explained by Bosellini (1989). We cannot exclude the contemporary action of climatic changes involving an increased rainfalls. This is now being studied by some researchers.

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