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Feeding specializations in Late Triassic fishes

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Abstract

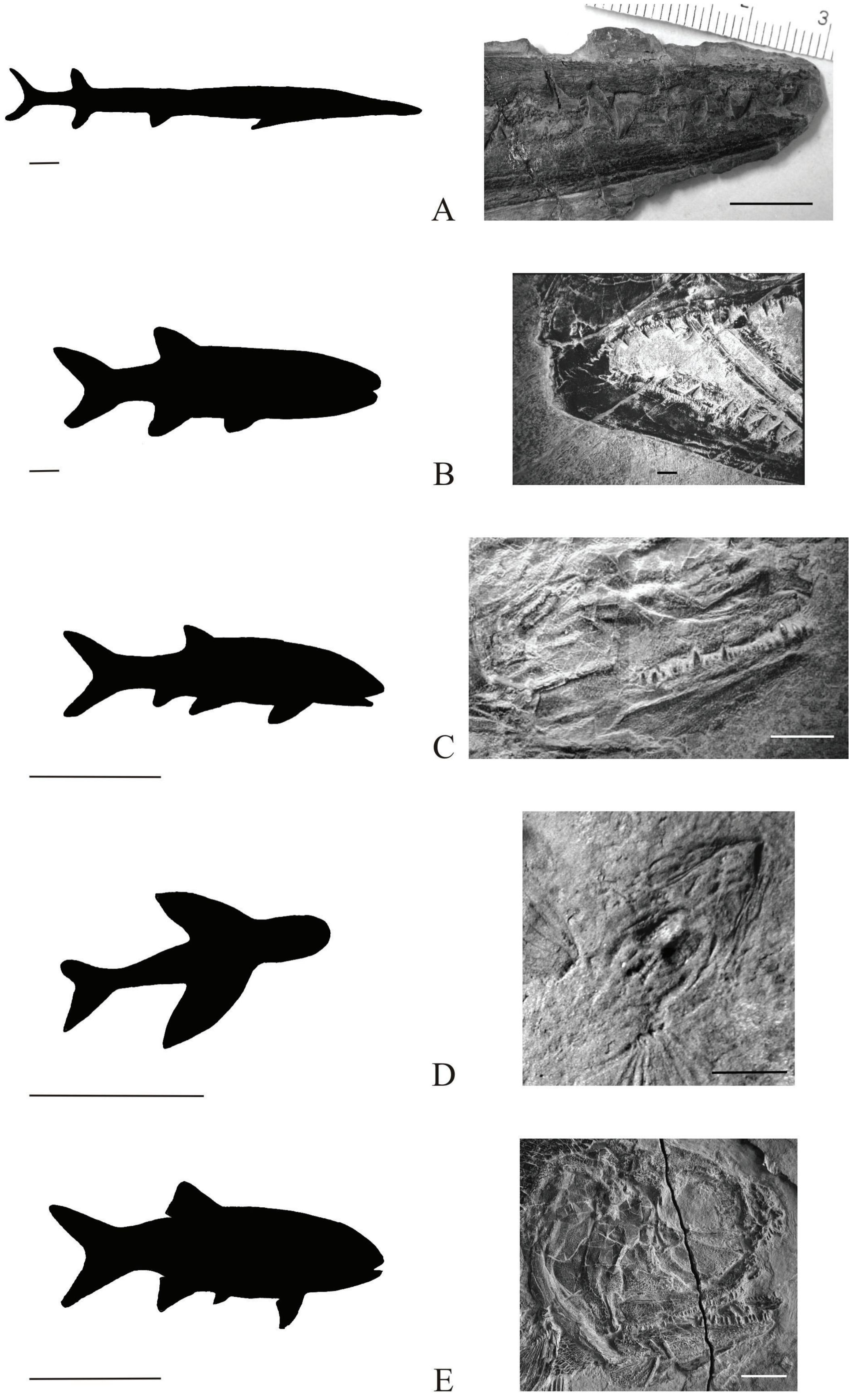
The ichthyofauna of the Zorzino Limestone represents an important proof of the richness and variety reached by bony fishes during the Norian and, at the same time, it testifies the beginning of the faunal transition which will be realized during the Jurassic. The thousands of specimens and the extraordinary quality of preservation found in the fossiliferous levels of this unit allowed, in the last years, not only to follow such a crucial moment in the evolution of vertebrates, but also to reconstruct the mode of life and the trophic adaptations reached by the different groups, living in the depositional basins. As evidence of this peculiar evolutionary period, the large predators at the highest trophic levels are still represented by 'primitive' basal actinopterygians; on the contrary, the most derived neopterygians specialized in durophagy, a trophic niche previously almost unexploited by actinopterygians. Within the main trophic categories, anyway, we can find different morphological specializations, which probably allowed the fishes to exploit most of the available trophic resources.

Keywords: Actinopterygians, Late Triassic, Zorzino Limestone, functional morphology, trophic niches, biodiversity.

Introduction and geological setting

In the last thirty years the Calcare di Zorzino (Zorzino Limestone, middle Norian, Late Triassic) has yielded an extraordinary rich ichthyofauna: at least 25 genera have been already described or are under study, but probably more than 50 genera are represented (Tintori 1981, 1983, 1995a, 1995b, 1996a, 1996b; Tintori and Renesto 1983; Tintori and Sassi 1992; Tintori and Lombardo 1996; Lom-bardo and Brambillasca 2005). A few species are represented by hundreds or thousands of specimens, like pholidophorids (Zambelli 1986), others by dozens and many others by few or single specimen. This fauna is important because it records the first major radiation of neopterygians (among these, pycnodonts, semionotids, macrosemiids and pholi-dophorids), when paleopterygians were still important, especially at the top of the trophic hierarchy, with the genera *Saurichthys, Birgeria, Thoracopterus* and *Gabanellia* (Tintori 1990a; Tintori and Sassi 1992; Tintori and Lombardo 1996; Tintori 1998).

The Zorzino Limestone is inferred to have been deposited in a marine basin associated with early Mesozoic rifting (Jadoul et al. 1994). The basin opened within a wide and thick carbonate platform, the Dolomia Principale Formation, that extended overall of the western margin of the Tethys. Because of the widespread shallow-water environment, connections between the basin and the open sea were probably only through very long tidal channels (Renesto and Tintori 1995). On the other hand, the restricted environment allowed differentiation of anapparently largely endemic vertebrate fauna including both marine and terrestrial species on small temporary islands. Superficial waters were well oxygenated, allowing nekton to thrive, and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also at the margins of the basin conditions at bottom were favourable to life. The fossils found allow reconstruction of life assemblages of both superficial waters and benthic settings at the margins of the basin, as well as those of nearby islands, where also several terrestrial reptiles could live (Blake et al. 2000).

Trophic adaptations: fish predation

The fauna coming from the Zorzino Limestone is fundamental to understand and to follow the extraordinary diversification reached by the bony fishes during Middle-Late Triassic. In fact, this time span records the passage from a 'primitive' fauna (dominated by paleopterygians) to a more advanced one, with the first important radiation of neopterygians which overtook the paleopterygians in both number of species and specimens (Tintori 1998). In spite of this, the large predators at the highest trophic levels are still represented by 'primitive' basal actinopterygians, such as *Saurichthys* and *Birgeria* that could both reach and exceed 1 meter in length and were present almost everywhere throughout the Triassic, as evidence of their successful adaptation. These two genera, lacking the scale covering in order to lightening the body weight, are very different in body morphology (the former being long and narrow, with an elongated snout, and the latter large and massive, with a powerful skull), according to their mode of preying upon other fishes. *Saurichthys* was probably able to catch its preys with quick and sudden darts, owing to the strong forward push given by the median and caudal fins; on the contrary, in *Birgeria*, a slow chaser living near the bottom, the large and mobile mouth allowed this fish to expand quickly the oral cavity engulfing water and preys, just as happens in extant grouper. In both taxa the dentition consists of large and striated conical teeth alternating with much smaller ones, typically adapted to hold and shear preys. Similar teeth are very common also as isolated finds, especially in the so called 'Rhaetian bone beds' of England and central Europe: they have been usually referred to as '*Saurichthys*-type' and '*Birgeria*-type'. However, a comparative study by Gozzi (2004) shows that it is impossible to distinguish *Birgeria* and *Saurichthys* teeth. On the other hand, it must be pointed out that *Saurichthys* is always much more common than *Birgeria* in all the well known fossil fish assemblages from the Triassic (Stensio 1921 and pers. obs.) and also today the Barracudas are mostly gregarious and live in large schools.

Among predators, two middle size subholosteans (advanced paleopterygians, *sensu* Schaeffer 1973): *Gabanellia* and *Thoracopterus* (Tintori and Sassi 1992; Tintori and Lombardo 1996). The predator habits of these genera are inferred by the strong powerful dentition made of sharp, radially striated, uneven teeth in *Gabanellia* and by the three rows of conical acuminate ones in *Thoracopterus. Gabanellia* was most likely a good swimmer, owing to its streamline section, the light scale covering and the large, falcate tail: we can imagine it was able to keep high speed for rather long distance (Tintori and Lombardo 1996). *Thoracopterus* shows specialized features in body and fins morphology comparable to those of the extant flying fishes, with long pectoral and pelvic fins and ventral lobe of the caudal fin longer than the dorsal one; the tooth-row pattern on both jaws of *Thoracopterus* suggests that this fish used to catch preys while swimming upward, since this direction allowed the widest possible gape (Tintori and Sassi 1992). Both genera may be considered as able to reach high speed in open waters and their maximum size is 25-30 cm. Probably they chased the small (average length 5-7 cm) pholidophorids which lived in schools and/or smaller larval or juvenile stages of the many fishes that thrived there. It must be point out that also the large *Saurichthys* preyed on similar small fishes as can be seen in some Norian specimens (pers. obs.);

Plate 1
Body outline (average size; scale bar = 100 mm) and dentition (scale bar = 10 mm) of predator fishes of the Zorzino Limestone.

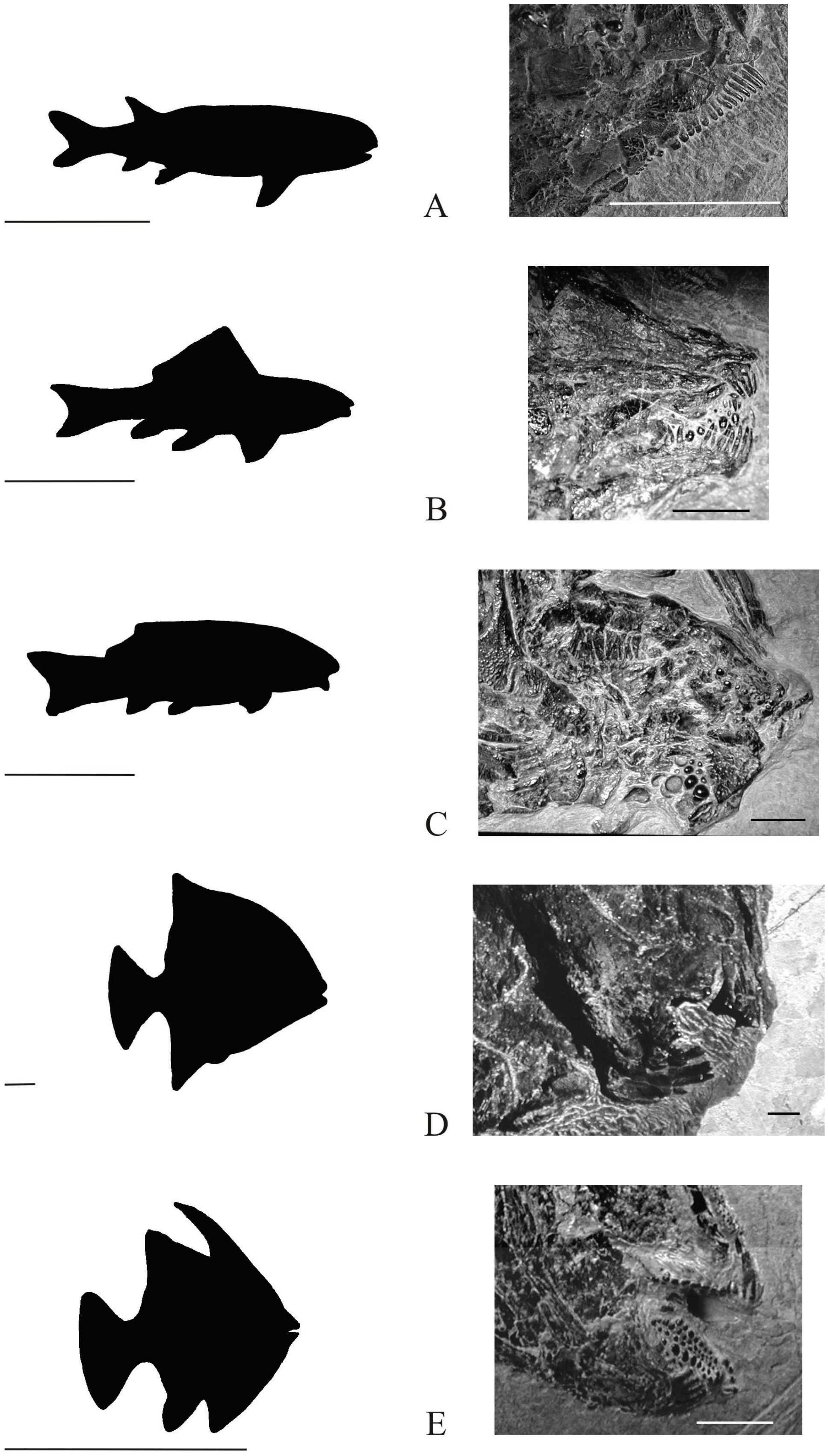
A) *Saurichthys*; dentition of specimen MCSNBG 3319 (Museo Civico di Storia Naturale "E: Caffi", Bergamo).

B) *Birgeria*; dentition of specimen MPUM 9334 (Museo di Paleontologia dell'Università degli Studi di Milano).

C) *Gabanellia*; dentition of specimen MPUM 7755;

D) *Thoracopterus*; dentition of specimen MCSNBG 7815.

E) Amiiformes gen. n.; dentition of specimen MPUM 9335.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nothing sure is known about prey size of *Birgeria*, even if the powerful mouth seems to make it able to size very large ones (see also Beltan 1980, where the supposed embryos are actually preys).

Conical teeth, arranged in several rows, are also visible in a underscribed neopterygian genus, belonging to the Amiiformes. This fish represents quite an exception, among the Norian advanced actinopterygians, as it shows 3 series of conical and striated marginal teeth, regularly arranged on both upper and lower jaws, and minute palatal ones, surely not suited for crushing hard exoskeletons. However, the real shape of these teeth is quite different from that of those of the cited paleopterygians, being more blunt, so probably less efficient in piercing the body of the preys. Actually, this kind of teeth could well belong to some generalized perleidiform, thus, in some way, an 'advanced' neopterygian simply was 'copying' more primitive (phylogenetically) subholosteans, probably without reaching their high specialization degree. If compared with the other piscivorous predators previously seen, it's worth stressing how this neopterygian actually appears less specialized, not only in the teeth shape: teeth borne by maxillary and dentary are not much differentiated in size; the massive body, covered with heavy ganoid scales and the hemiheterocercal caudal fin, owing to its asymmetry, were not particularly efficient for fast swimming or quick movements. Therefore, we can consider this fish as a small generalist predator, which could use its teeth to catch preys such as small, slow swimming fishes or crustaceans.

Other peculiar predators in this fish-fauna, as well as in all the other Triassic ones, are the coelacanths. The Zorzino Limestone yields at least two different coelacanths, presently under study (Lops, PhD project): size of these Norian fishes can reach about 1 m. We suppose that they swam slowly near the rough bottom as the modern *Latimeria* does. Coelacanths lack maxilla bone, so the largest teeth are a few fangs on the palatal bones: this peculiar position is related to the cranian kinesis present in this fish group, allowing the ethmoidal region of the skull to be lowered powerfully when the mouth quickly closes grasping/engolfing the prey. Furthermore, even if the coelacanths may well be considered a relict already in the Triassic, they were still quite common (for instance, in the Zorzino Limestone fauna we have more coelacanths than *Birgeria* specimens). Finally, it is worthy noting that true large pelagic predators adapted to fast swimming became common only in the Early Jurassic, with genera as *Caturus*, *Hypsocormus* and *Pachycormus*, all neopterygians fishes (Webb 1982). Actually, this could be related to the preservation of depositional environment, rather than to faunal composition: actinopterygians could have began to occupy this trophic niche from Late Triassic onwards, even if, in spite of the huge number of specimens found, very rare are the taxa related to this kind of predators. Anyway, we observe an important change in the marine fish trophic web just above the boundary between Triassic and Jurassic, possibly between Sinemurian (Lyme Regis and Osteno Fauna) and Early Toarcian (Holzmaden fauna): if this could be related to the appearance of the first primitive teleosteans (the Leptolepiformes) is to be considered. Anyway we must notice again that the large predators were phylogenetically more primitive than most of their preys, the small basal teleosteans.

Plate 2
Body outline (average size; scale bar = 100 mm) and dentition (scale bar = 10 mm) of durophagous fishes of the Zorzino Limestone.

A) *Endennia*; dentition of specimen MPUM 8434.

B) Macrosemiidae gen. n.; dentition of specimen MPUM 9341.

C) *Paralepidotus*; dentition of specimen GP 1673, (Museo di Scienze Naturali di S. Pellegrino T. (BG)).

D) *Sargodon*; dentition of specimen GP 1874; (Museo di Scienze Naturali di S. Pellegrino T., (BG)).

E) *Brembodus*; dentition of specimen MCSNBG 4899.

Trophic adaptations: durophagy

On the contrary, during the upper Triassic the most derived neopterygians specialized in durophagy, owing to the new arrangement of the skull bones, first of all the posteriorly free maxilla, which allowed the development of a more powerful muscular system and, consequently, the capability of exerting a strong pressure on a small area with the development of large, strong and flattened inner teeth (Schaeffer and Rosen 1961). As a con-sequence, neopterygians were able to exploit a new trophic niche: hard shelled organisms such as echinoids, crustaceans or molluscs constituted a source of food that was till then substantially precluded to most actinopterygians, owing to anatomical constrains. This can be considered the starting point for the extraordinary radiation of neopterygians at the end of the Triassic.

Most of neopterygians of the Zorzino Limestone were in fact more or less specialized to feed upon invertebrates grasped with the prehensil anterior teeth and crushed with the grinding inner ones, with the exception of small microphagous forms like the pholidophorids. Among the more specialized duro-phagous were the semionotiformes and the pycnodontiformes: in these fishes, the body morphology is related to an higher degree of manovrability as they had to pick fixed or slowly moving organisms such as bissate bivalves or possibly echinoderms. Size of the different species is also quite different, varying from a few centimeters up to 1 m. Thus, through a combination of different dentitions, body shapes and sizes, a number of durophagous could live together, just as it happens today in many temperate and tropical near-shore environments.

Pycnodonts have been one of the most successful order of fishes, lasting for more than 150 My from the Late Triassic to the Eocene, all over the world especially during Cretaceous (Nursall 1999). They are considered the best durophagous among osteichthyans, paralleled only by the most derived teleosts: they were usually very deep bodied, laterally compressed and their dorsal and anal fins show a very long inserction. Anterior, prehensil teeth are chisel-like in all know Triassic genera (*Brembodus*, *Gibbodon*, *Eomesodon* as well as other undescribed genera), but they may also be blunt conical in few later genera. Regarding size, Triassic pycnodonts are quite small, reaching the maximum length of about 12 cm with *Brembodus* (Tintori 1981). In the Jurassic and especially in the Cretaceous they growed up to 1 m.

A similar diference in prehensil teeth is shown by the Norian semionotiformes, where *Sargodon* has chisel-like anterior teeth while *Paralepidotus*, *Semionotus*, *Dapedium*, *Dandya* and an yet un-described genus, have more or less pointed antero-lateral teeth. Apart from *Semionotus* and *Paralepidotus*, the other genera are very deep bodied fishes (Tintori 1983, 1996). Again, also size is well differentiated, from a few centimeters of *Dandya* and *Dapediun*, to 50 cm for *Paralepidotus* and up to 1 m for *Sargodon*. We must note that the first two are the less specialized for durophagy, but they are of the same size of the coeval pycnodonts: thus, probably they did not compete directly, leaving to the pycnodonts the hardest preys.

Somewhat less specialized are the Macrosemiids (Bartram 1977). The most common is *Legnonotus krambergeri* up to 6-7 cm, while other larger taxa are still underscribed. Triassic Macrosemiids are quite fusiform in shape and crushing teeth are not actually very stout. Possibly they chased mostly swimming crustaceans, very common in the Zorzino Limestone fauna (Pinna 1974). Again, a different nich has been exploited, furthermore with species of different size.

Within the more advanced durophagous groups, we must report an atypical subholostean genus (Lombardo and Brambillasca 2005): *Endennia*, with its peculiar kind of dentition, made of long and cilindrical marginal teeth with flattened apex, and differentiated palatal crushing ones, was in fact probably able to reach full durophagy like neopterygians, even if in a different way. In spite of the restricted possibility of protruding the ethmoidal region, the projecting marginal teeth and the differentiated crushing ones probably allowed *Endennia* to improve its feeding capability. Moreover, even if its quite fusiform body was completely covered by thick ganoine scales, the seemingly loose articulation between them could have improved the mobility of this fish, making it able to pursue moving preys. It might be therefore hypothesized that the anterior teeth were used for seizing small swimming organisms such as crustaceans, which were crushed with the triturial teeth. Anyway, we do not exclude other possible food among the invertebrates provided with harder mineralized parts, as molluscs or echinoderms, common in the Zorzino Limestone.

Invertebrates are in fact well represented in the Zorzino Limestone, with several crustaceans genera (Pinna 1974; Garassino and Teruzzi 1993; Basso and Tintori 1994) echinoderms (echinoids, ophiuroids, crinoids and asteroids) (Blake et al. 2000), jelly-fish and scleractinia. Rare gastropods and common bivalves contributed to constitute a benthic fauna rich in individuals, even if poor in species. However, usually only coproliths made of broken bivalves shells are quite common in the fishes bearing levels, proving the predation by durophagous fishes.

Conclusions

The fossil assemblage of the Zorzino Limestone represents one of the highest point of ichthyofaunal biodiversity during the whole Mesozoic and the kind of distribution of primitive and advanced taxa within the different trophic specializations is a meaningful proof of the Middle-Upper Triassic faunal transition. As seen before, we record the presence, among specialized paleopterygian predators, of a single exception represented by a more generalist neopterygian taxon; on the contrary, durophagy is exclusive of the advanced forms, but a single specialized paleopterygian genus. At the Upper Triassic-Lower Jurassic boundary we will assist to a drastic change in the ichthyofaunal composition, with the predominance of neo-pterygians, which will be able to occupy all the available trophic niches.

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Riassunto

[Specializzazioni trofiche nei pesci del Triassico Superiore]

L'ittiofauna del Calcare di Zorzino rappresenta un'importante testimonianza della ricchezza e diversità raggiunta dai pesci ossei durante il Norico (Triassico superiore); allo stesso tempo essa rappresenta la fase iniziale del grande cambiamento faunistico che si realizzerà nel corso del Giurassico Inferiore con la comparsa dei primi veri teleostei.

Come prova di questo particolare momento evolutivo i grandi predatori ai livelli trofici più alti sono ancora rappresentati dagli attinotterigi basali; viceversa, i più evoluti neotterigi si sono specializzati nella durofagia, una nicchia trofica precedentemente preclusa agli attinotterigi.

All'interno di ciascuna categoria trofica, comunque, si possono riconoscere differenti specializzazioni morfologiche che hanno permesso ai pesci di sfruttare le risorse alimentari disponibili. Così tra i predatori s.s. troviamo i grandi (superiori al metro) *Saurichthys* e *Birgeria*, il primo molto comune e simile al Barracuda sia come morfologia che come tecnica di caccia, il secondo più raro e confrontabile con le cernie. Entrambi i generi sono diffusi in tutto il Triassico a testimonianza del loro adattamento ottimale. Più piccoli e con nicchie diverse sono *Gabanellia*, veloce nuotatore da crociera, e *Thoracopterus*, un agile pesce volante. Tra le forme più avanzate (neotterigi) l'unico predatore di medie dimensioni è rappresentato da un genere non ancora descritto che mostra tuttavia denti più tozzi, corpo coperto da scaglie ganodi e coda asimmetrica, come se non avesse raggiunto l'elevata specializzazione dei sopraccitati paleotterigi.

Per contro, i neoterigi mostrano una spettacolare radiazione legata alla durofagia: picnodonti (*Brembodus, Gibbodon, Eomesodon*, etc.), semionotiformi (*Paralepidotus, Sargodon, Semionotus, Dandya, Dapedium,* etc.), macrosemidi (*Legnonotus*, etc.) sono molto diffusi e rappresentano gruppi che poi domineranno il resto del Mesozoico. Diversità nelle dentature e nelle dimensioni permettono loro di occupare molte nicchie trofiche fino ad allora inesplorate. Anche qui c'è tuttavia una eccezione, il paleotterigio *Endennia*: questo genere presenta una dentatura triturante accoppiata a denti a piolo laterali.

Il gran numero e la straordinaria conservazione degli esemplari del Calcare di Zorzino hanno permesso non solo di seguire un momento così importante nell'evoluzione dei vertebrati, ma anche di ricostruire il modo di vita e gli adattamenti trofici raggiunti dai differenti gruppi di pesci che vivevano nei bacini di deposizione.

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