



Supposed and direct evidence of trophic relationships within the marine fish community from the Lower Turonian of Goulmima, Morocco

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Introduction

The diet of fishes is determined by analysis of gut contents. Sometimes, these observations can be made on well preserved fossil material. Microremains are considered as gut contents if they form concentrations in the body cavity or if they are linked with supposed fossilized soft tissues of the alimentary canal.

The morphology of teeth, fin insertion and the general shape of the body can provide informations about the way of life and the diet of fishes. These characteristics are taken into account to establish trophic relationships.

The fossil fishes concerned by this work come from the marine Lower Turonian of a locality situated near Goulmima, a town on the southern slope of the Moroccan Atlas (Cavin 1995). This locality yields ammonites (*Mammites* sp.), marine reptiles and several actinopterygians. The fishes, generally well preserved, are contained in calcareous nodules. They are prepared in acid baths and by mechanical ways. The microremains of the matrix are kept.

Results

The components of the ichthyofauna represented by articulated specimens are listed. Every taxon is followed by the supposed and direct evidence concerning its diet.

Actinopterygii

Ichthyodectidae

n. sp. This species, under description, has typical ichthyodectid features: the standard length can reach about 80 centimeters, the body is elongated and laterally compressed. The mouth is large with high and pointed teeth. This morphology is typical for a fast swimming predator.

The nodule of one small specimen (about 20 centimeters from the snout to the pelvic fins) contains numerous microremains of actinopterygians, in particular small vertebrae (0.7 mm in diameter) small mandibles and small teeth of indeterminate teleosts. Some of these small teeth (about 1.7 mm in length) are compressed laterally and have a sinuous shape, looking like enchodontid teeth. Some others (less than 1 mm in length) are also laterally compressed but have a hook-like shape reminiscent of the pharyngeal teeth of the eotrigonodontid *Stephanodus* or of an indeterminate pycnodont (Estes & Sanchiz 1982). These three groups were common in North Africa during the Upper Cretaceous (Arambourg 1952; Cappetta 1972). These microremains are contained in the matrix of the nodule and are not necessarily connected with the gut contents of the articulated fish. However, some other microremains are concentrated in the pelvic region of the ichthyodectid and are more surely gut contents. Among them is a small bone (5 mm in maximal length), detached during preparation, that I consider as a vomer of a small pycnodont c. f. *Palaeobalistum* (fig. 1a). In occlusal view, this bone is triangular. It bears three rows of crushing teeth. The two lateral ones are composed of teeth with two small lateral cusps, the medial one is composed of teeth with a poorly developed median crest. Dorsally, this bone bears a high ridge. This structure is similar to those observed in *Palaeobalistum gutturosus* from the Lower Cenomanian of Jebel Tselfat (Arambourg 1954, fig. 7 A) except that in this latter species, two irregular rows of small teeth are present between the main rows. This feature perhaps appeared during ontogeny. Vertebrae of small teleosts are equally present in this concentration.

Araripichthyidae

Araripichthys n. sp. This species is the first occurrence of an Araripichthyidae outside of the Santana Formation in Brazil. It is at present known by a single specimen. This enigmatical teleost has a deep, laterally compressed body without pelvic girdle and fins. The jaws are edentulous and the premaxilla protrusible. The dorsal and anal fins are unknown but were probably very high as in the Brazilian species. This morphology indicates a slow-swimming fish with a high manoeuvrability living probably near the bottom.

No direct evidence of its diet is known at present. The structure of the edentulous mouth indicates a microphagous and probably detritus-feeding fish (not durophagous as the superficially alike pycnodonts).

Pachyrhizodontidae

Goulimimichthys arambourgi Cavin, 1995. It is apparently the most common species in the locality of Goulmima. This spindle-shaped fish, with a standard length generally under 300 millimeters, has a widely split mouth and numerous small spiny and slightly internally curved teeth.

Several specimens show an elongate structure along the long axis of the body, below the vertebral column, that can be interpreted as preservation of soft tissues of the alimentary canal. The holotype (BHN 2 P 2) shows such a structure. The alimentary canal forms a compressed tube split at the level of the pelvic girdle. Several vertebrae and other bones of teleosts are present in this opening and clearly belong to gut contents. Some of these vertebrae (fig. 1d), about 2 mm in length, have a neural arch occupying the entire dorsal surface of the centrum as in *Enchodus* sp. or *Eurypholis* sp. (Goody 1969). A preopercular is present too, and is rather similar to the preopercular of enchodontids. The presence of small Enchodontoidei is confirmed by the discovery in the matrix of other nodules of teeth and dentaries. These latter bones, not related to alimentary canals, are very small (2 mm in length) and bear slightly curved pointed teeth, the anterior-most being approximately twice as long as any other teeth in the row (fig. 1c). This structure is very similar to that of the Enchodontoidei and in particular with *Enchodus venator* from the Lower Cenomanian of the Jebel Tselfat (personal observation).

At present, no articulated skeleton of Enchodontoidei, whether juvenile or adult, is known in this locality.

Osmeroididae

Osmeroides n. sp. This new species of albuloidei is the first discovery of the genus *Osmeroides* outside Europe. The skull and the body are dorso-ventrally compressed. The mouth is wide and the palatine bones bear numerous small viliform teeth. This morphology is typical of a sea-bottom fish, feeding on invertebrates and small fishes. Small invertebrates, especially indeterminate gastropods and brachiopods, are present in the matrix of nodules but none of them are concentrated in the body cavity of an osmeroidid. A coprolite with microremains of actinopterygians is present in the body cavity of one individual (fig. 1b): this is a small ovoid pellet, less than one centimeter in length, situated between the pelvic fins of the specimen. The pellet bears at its surface five vertebrae in anatomical connection of an indeterminate small teleost.

Discussion

A simplified network of trophic relationships between the fishes of the community of Goulmima can be drawn (fig. 2). Predators are the most abundant in numbers of species and of individuals. The ichthyodectid species and *G. arambourgi* have a typical predator and pelagic-fish morphology. On the other hand, the osmeroidid species seems to have been benthic with perhaps a more varied diet in relation with its crushing teeth.

Three levels of trophic relationships can be separated within the ichthyovorous forms. The topmost one consists of large individuals of ichthyodectid (a). There is no direct evidence of their diet but the diet of the smaller individuals of this species is known. The middle one consists of the latter individuals (a') plus *Goulimimichthys arambourgi* (b) and *Osmeroides* n. sp. (c). Direct evidence of the diet of these three forms is known by the presence of microremains in the body cavity. The last level consists of juveniles of three taxa (d, e, f). *Araripichthys* n. sp. (g) is a non-ichthyovorous fish and *Osmeroides* n. sp. (c) probably belongs partially to this category.

Three taxa are known only by microremains: the pycnodont c. f. *Palaeobalistum*, the indeterminate enchodontoidei and the indeterminate teleost, three forms represented only by very small bones certainly from juveniles. These data could mean that the environment of deposition was favourable as nursery ground for some species, like the existing mangrove swamps (Lowe-McConnell 1987). The existence of a favorable environment for the presence of young fishes from Mesozoic localities were recognized in the fresh-water fish fauna from the Kimmeridgian of Songa in Zaire (De Saint-Sein & Casier 1962) and from the Lower Cretaceous fresh water fish faunas of Montsech and Las Hoyas in Spain (Wenz & Poyato-Ariza 1994).

A trophic level reconstruction was established on the basis of stomach contents for the well-known ichthyofauna from the Santana Formation in Brazil (Maisey 1994). The Upper part (Romualdo Member), commonly considered as Albian in age, contains an ichthyofauna which at the family level is rather close to the Moroccan one (in particular Ichthyodectidae, Araripichthyidae, Albuloidei and Pachyrhizodontidae). Moreover, the kind of preservation of fossil fishes is superficially similar (calcareous nodules) at both localities and could imply a more or less similar environment of deposition. The trophic relationships are more completely known than at Goulmima but share some similarities. The numerous pachyrhizodontids (*Rhacolepis buccalis* in the Romualdo Member and in the Goulmima fauna) occur at an intermediate level in the trophic hierarchy. Ichthyodectids are present in both localities at a high level of the trophic hierarchy. However, in Brazil an aminoid, *Enneles* ("Calamopleurus"), represents the highest level whereas this group is still unknown in the Goulmima locality. The Araripichthyidae and Albuloidei are not considered in the network of trophic relationships of the Romualdo fauna because no direct evidence of their diet is known. Moreover a Brazilian species, *Vinctifer comptoni*, possesses a well developed basket of gill rakers suggesting a filtering mode of feeding. This kind of nutrition is unknown in the Goulmima fauna at present.

A difference between the two trophic networks is the composition of some stomach contents: in the Romualdo fauna, all but one species found in the alimentary canals of fishes are known to be represented in other nodules by articulated specimens and the majority of them are adult individuals. In the Goulmima fauna, two species at least are known only by juvenile specimens present only in stomach contents. This difference between the two faunas could be due to the smaller number of nodules from Goulmima hitherto prepared (about 40) or to a difference in the paleoenvironment (favorable to the presence of young individuals of some species only at Goulmima).

Conclusion

This preliminary work suggests that the network of trophic relationships between the fish is simpler in the community of Goulmima than in the community of the Romualdo Member. This is probably due to the smaller number of available prepared specimens. In particular, no invertebrates appear in the trophic hierarchy (some ammonites, brachiopods and gastropods are present in the matrix of nodules but never linked with the alimentary canals of fishes). This is in contrast with the Romualdo fauna and the majority of present ichthyofaunas where invertebrates participate in large numbers to the lowest level of the trophic hierarchy.

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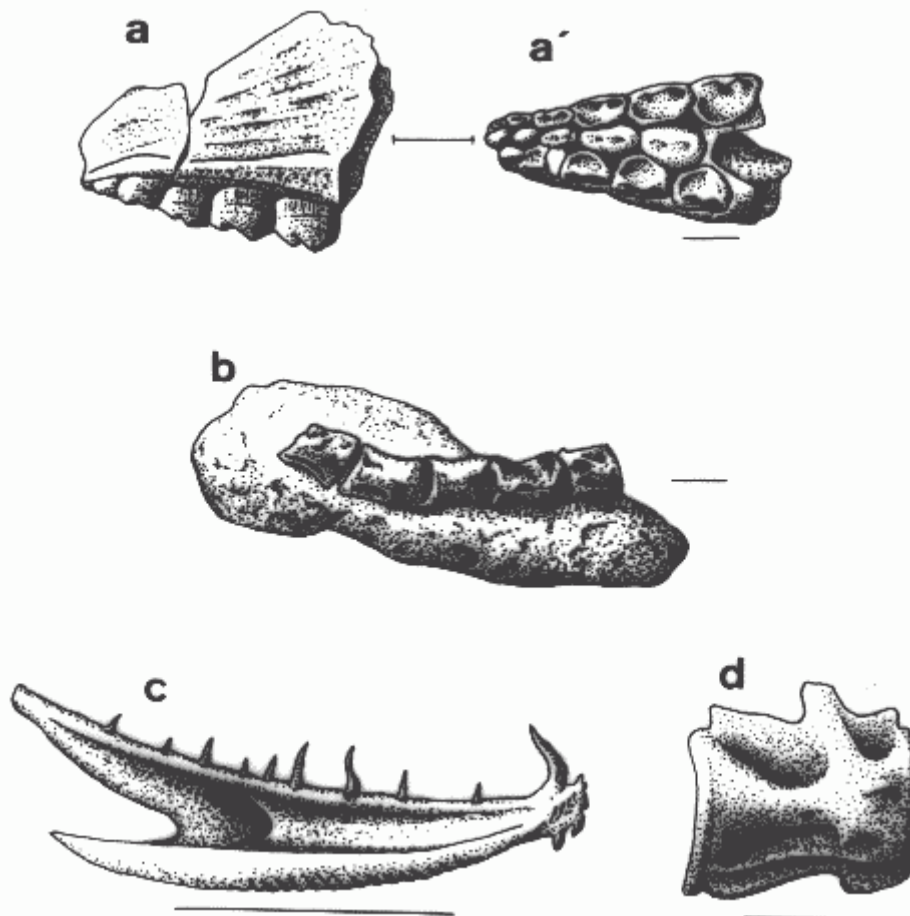


Figure 1
a: vomer of a pycnodont c. f. *Palaeobalistum*. Scale bar: 1mm.
a: lateral view.
a': occlusal view.

b: coprolite of *Osmeroides n. sp.* with vertebrae of an indeterminate teleost. Scale bar: 1mm.
 c, d: *Enchodus c. f. venator*. Scale bar: 1mm.
 c: dentary in medial view.
 d: vertebra in lateral view.

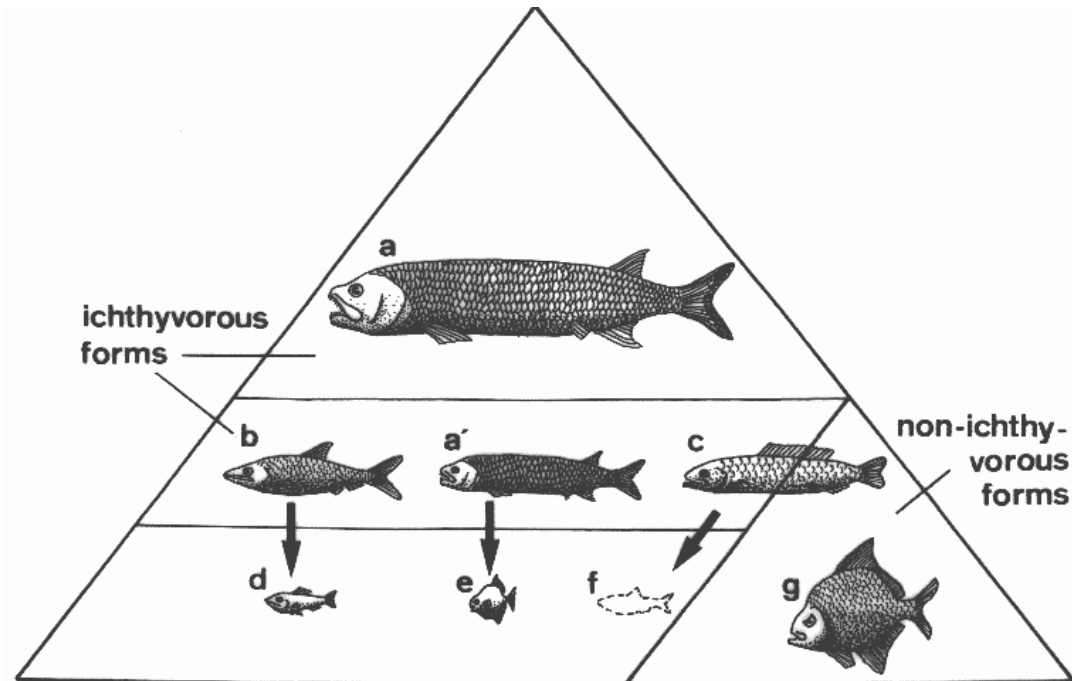


Figure 2
 Trophic relationships within the ichthyofauna of Goulmima.
 The triangles and the three levels represent supposed trophic relationships based upon size, shape and set of teeth of fishes.
 Arrows represent direct evidence of trophic relationships based upon microremains.
 a, a': Ichthyodectidae *n. sp.*
 a: individuals of large size.
 a': individuals of middle size.
 b: *Goulmimichthys arambourgi*.
 c: *Osmeroides n. sp.*
 d: *Enchodus c. f. venator*. Juvenile.
 e: Pycnodont *c. f. Palaeobalistum*. Juvenile.
 f: indeterminate teleost. Juvenile.
 g: *Araripichthys n. sp.*

