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PALAEONTOLOGICAL EVIDENCE OF PISCIVOROUS HABITS OF SOME PYCNODONTS FROM THE MIDDLE CENOMANIAN OF LEBANON

RIASSUNTO

L'autore presenta due casi di resti di pasto di picnodonti ritrovati nel calcare Cenomaniano Medio di En Nammoura, Libano; essi consistono in un coprolite ed un rigurgito. Entrambi sono icno-fossili conseguenti alla nutrizione del picnodonte *Acrorhinichthys poyatoi*. Il coprolite ha una struttura spiralata, indicando che l'ultimo tratto dell'intestino dei picnodonti era, probabilmente, rappresentato da una valvola a spirale, similmente a quanto accade nei selaci e negli actinopterigi primitivi (storioni). Il coprolite contiene alcune scaglie, parzialmente digerite, di un actinopterigio di piccola taglia. La massa di rigurgito è costituita dai resti scheletrici di un piccolo actinopterigio, forse un clupeiforme; tutte le ossa sono frammentate e sono presenti anche elementi scheletrici larghi e piatti che sono forse riconducibili a ossa craniche; sono ugualmente presenti anche alcune piccole scaglie. I due nuovi reperti paleontologici rafforzano le recenti prove che dimostrano come alcune linee evolutive di picnodonti, a partire da abitudini predatorie su animali invertebrati bentonici (livello trofico III), dotati di parti dure (molluschi, echinodermi, coralli), siano andate specializzandosi, almeno con alcune specie, verso abitudini francamente predatorie su altri pesci (livello trofico IV). Anche alla luce di queste nuove scoperte, l'autore propone una riconsiderazione dei picnodonti quali super-predatori all'interno dell'habitat delle scogliere coralline mesozoiche.

SUMMARY

This study presents two cases of the remains of pycnodont meals found in the Middle Cenomanian limestone of En Nammoura, Lebanon. These comprise a regurgitation and a coprolite. Both are icno-fossils that have resulted from the feeding habits of the pycnodont *Acrorhinichthys poyatoi*. The regurgitated mass consists of the skeletal remains of a small actinopterygian, which might have been a clupeiform. All of the bones are fragmented, and there are also broad, flat skeletal elements that appear to be cranial bones; some small flakes are also present. The coprolite has a spiral structure, which indicates that the last section of the pycnodont intestine would have been a spiral valve, similar to sharks and the primitive actinopterygians (sturgeons). The coprolite contains some apparently partially digested flakes of a small actinopterygian. These two new palaeontological findings reinforce the recent studies that have shown how some evolutionary lines of pycnodonts that started from predatory habits on benthic invertebrate animals (trophic level III) that had hard parts (molluscs, echinoderms, corals), at last with some species, became specialised towards habits that were predatory on other fish (trophic level IV). Also, in light of these new discoveries, the author proposes a reconsideration of these pycnodonts also as super-predators within the habitat of the Mesozoic coral reefs.

INTRODUCTION

The pycnodonts are actinopterygian fish that lived about 160 million years ago, from the Noricum (upper Triassic) to the Eocene. Today they are completely extinct. They had a laterally compressed body that had relatively large unequal fins, which helped them to move easily through their reef environment. One of their most salient features was their dentition. In the classical form, this included the association of scalpelliform anterior (incisive) teeth that had a free cutting edge and were highly mobile (as they were connected to the separate and articulated premaxilla and dentary bones) with the molar (back) teeth that had a rounded masticatory surface. These latter were arranged in longitudinal side-by-side sets, and their use was based on a few very powerful movements. This limited movements of the posterior dentition was because they were connected to the massive vomer and prearticular bones that had loose joints.

The prearticulars of both sides form a strong and angular 'mortar' in cross-section, into which the 'pestle' of the (unpaired) vomerine dentition fit (Kriwet, 2003). Thurmond (1974) indicated that the two prearticulars were not tightly fixed in pycnodonts, and they proposed a lateral adductive/abductive mandibular action. However, Nursall (1999) rejected this interpretation and suggested that the prearticulars were tightly fixed. At a functional level, this posterior dentition has generally been defined as 'durophagous dentition', which is particularly suitable for mastication of molluscs with hard shells, or of calcareous shell echinoderms (echinids). Indeed, these invertebrates were, in turn, typical inhabitants of the Mesozoic cliffs. Thus, Nursall (1996) proposed that pycnodonts inhabited the shallow marginal seas, often with reefs, and were restricted to durophagous habits. In addition, some recent studies have noted that although the food available for pycnodonts might have been very varied, the molariform posterior teeth indicate this predominantly durophagous feeding strategy (Poyato-Arizza, 2005). Kriwet (2001) presented data on the kinematics of this feeding apparatus, and discussed the feeding habits of these extinct pycnodont fish that have been interpreted as a monophyletic group, related to all other neopterygians, and characterised by potential omnivorous feeding habits.

More recently Vullo *et al.* (2019) discovered and described a new pycnodont collected in the Palaeocene phosphates deposits of Morocco: *Pycnodus multicuspidatus*, known just only through a single incisiform tooth. This pycnodont is characterized by a dental morphology that shows a broad, fan-shaped multicuspid crown. This morphology was interpreted as well adapted for benthic macro-algal scraping (Vullo *et al,* 2019).

Notwithstanding this, two recent discoveries have shown that within the vast and heterogeneous group of pycnodonts there were certainly predatory carnivorous species. Indeed, Vullo *et al.* (2017) described three new genera of pycnodonts (all of which belong to the new Serrasalmimidae family) of the Upper Cretaceous/ Palaeocene of Morocco. These had sharp posterior teeth, and their feeding behaviour would have been close to that of the current piranhas.

Furthermore, Kölbl-Ebert *et al.* (2018) identified and described a new pycnodont from the famous Jurassic field of Solnhofen area, in Germany, which was also characterised by posterior teeth with cutting masticatory margins. Also in this case, they indicated the structural analogies with the dentition of the current piranhas, as the generic name attributed to this new fossil clearly indicates: *Piranhamesodon pinnatomus*. Kölbl-Ebert *et al.* (2018) identified and described ray-finned teleost fish from the same fossiliferous field that showed particular damage to their unpaired fins that appeared to be caused by bites inflicted by predators. Thus, the simultaneous presence of both predator and prey within the same field was demonstrated. In summary here, it can be said that the Jurassic pycnodont *Piranhamesodon pinnatomus* represents an example of a flesh-finned fish eater that was under a form of predatory ‘fish farming’. Even today, fish that habitually prey on other fish – or occasionally on other animals – can mainly practice predation of the fins, which will leave their victims alive. Indeed, direct observations of the dietary habits of the piranhas of today have emphasised the importance of feeding on the fins of other fish, which thus represent a widely available and renewable food resource (Sazima and Machado, 1990).

Other direct palaeontological evidence of the feeding behaviours of pycnodonts has come from studies of the remains of meals found within their visceral cavity, as preserved in correspondence with what would have been the intestine of these fish. Contrary to what might logically be expected for durophagous fish, such remains have only been described exceptionally. From Table 1, which is reproduced from the important study of KRIWET (2001), it can be seen that the remains of the last meals consumed have only been identified in the following eight genera of pycnodonts: *Arduafrons*, *Gyrodus*, *Iemanja*, *Nursallia*, *Proscinetes*, *Tepexichthys*, *Pycnodus* and *Neoproscinetes* (LEHMAN, 1966; BLOT, 1987; NURSALL, 1999; MAISEY, 1996). As indicated by KRIWET (2001), all of the gut contents reported in Table 1 are extremely stereotypic, and they always consist of monospecific invertebrate remains. KRIWET (2001) also noted that: "*monotypy prey is very characteristic for recent bottom-feeding Actinopterygians, which prefer to feed mainly on a single and locally abundant species.*" As is clearly shown in Table 1, the prey that have been found in correspondence of the visceral area of these genera of pycnodonts are basically three: (i) in five specimens of fossil fish, there were fragments of the echinoderm (a single specimen of *Arduafrons*, two specimens of *Gyrodus*, two specimens of *Nursallia*); (ii) in about 10 further specimens, there were fragments of a bivalve mollusc shell (a single specimen of *Proscinetes*, some specimens of *Tepexichthys*, two specimens of *Pycnodus*); and finally (iii) in a single case, there were fragments of the coral exoskeleton (*Neoproscinetes*) (MEISEY, 1996). A further, final case of the remains of a meal identified in correspondence to the digestive tract of a pycnodont represents at the present state of our knowledge the only example of possible predation occurring on another fish. This is the example of *Iemanja* from the Cretaceous field of Cearà, in Brazil, which is preserved in the American Museum of Natural History in New York (item no. 13963). This specimen includes at the level of the visceral area small actinopterygian vertebrae, indicative of small actinopterygian prey (KRIWET, 2001).

Table 1: The gut contents previously reported for pycnodonts (modified from KRIWET, 2001).

Genus	N° specimens	Gut contents
Arduafrons	One	Spines of monospecific echinoderms
Gyrodus	Two	Spines of monospecific echinoderms
Nursallia	Two	Spines of monospecific echinoderms
Proscinetes	One	Fragments of shells of monospecific bivalves
Tepexichthys	Several	Fragments of shells of monospecific bivalves
Pycnodus	Two	Fragments of shells of monospecific bivalves
Neoproscinetes	One	Coral fragments (?)
Iemanja	One	Small actinopterygian vertebrae

Considering the extraordinary number of specimens of fossil pycnodonts identified to date (which must by now amount to tens of thousands of specimens), the presence of only about 20 specimens with traces of the remains of a meal at the level of the visceral area means that these are a particular rarity. This must have some structural and/or general explanation, which would not appear to simply be connected to the difficulties of conservation through the fossilisation processes. Indeed, the extreme rarity of the remains of calcareous shells of marine invertebrates (i.e., molluscs, echinoderms) in correspondence with the visceral area appears to totally contradict the hypothesis that the pycnodonts were actually mainly durophagous fish. To explain this obvious inconsistency, Kriwet (2001) made the following comment: "*the rareness of shell and other prey fragments in the visceral area in may be due to the fact that most of the hard material was rejected after being crushed, similar to the condition found in many recent durophagous Actinopterygians*".

Precisely in the context of this minimal knowledge, and in particular consideration of the relevance that regurgitation might have had in the interpretation of the diet of the pycnodonts, two fossil findings are described in the present study. These consist of specifically of a regurgitation and a coprolite in pycnodonts from one of the most conserved *Fossil-Lagerstätt* known today; namely, the fossiliferous deposit of En Nammoura, in Lebanon, dated to the Middle Cenomanian (Cretaceous) (Capasso, 2017).

MATERIALS AND METHODS

The subjects of this study are two specimens of *Acrorhinichthys poyatoi* Taverne & Capasso 2015 from the Middle-Cenomanian (Cretaceous) settlement of En Nammoura, in Lebanon, that have been exceptionally well preserved. The two specimens are the following:

(1) The holotype of the species, as sample CLC S-630 a, b, part and counterpart of a perfectly preserved complete specimen from En Nammoura, Lebanon. Total length, 87 mm; standard length, 72 mm.

(2) The paratype A of the same species, as sample CLC S-461, a perfectly preserved complete specimen from En Nammoura, Lebanon. Total length, 114 mm; standard length, 98 mm.

Both of these specimens were described in detail by Capasso and Taverne (2015), from the osteological, comparative and systematic point of view. They belong to the "Luigi Capasso public collection" (CLC) that is kept in Chieti (Italy). This is a legally registered public collection, and has been declared part of the Italian Cultural Heritage by a Decree of the Ministry of Cultural Heritage and Activities, dated 11 October, 1999, following the disposition of the Italian law for the protection of the cultural heritage (N° 1089/1939).

The specimens of this collection were also subject to a prescription order for their conservation and availability for study, on the basis of Article 30 of Italian Law N° 42/2004.

The specimens were examined under a stereomicroscope (Wild M 8; Leica). The macro-photographs were taken by Luciano Lullo, from the ‘G. d’Annunzio’ University of Chieti–Pescara, and the micro-photographs were taken by Dr. Joan Viciano Badal, from the same University. The scanning electron microscope used to determine the micro-elemental composition of some of these specimens was a Gemini SEM 450 (Zeiss) of the Electronic Microscopy Centre of the University of L’Aquila, Italy, under the direction of Prof. Luca Lozzi. All of the scanning electron microscopy analyses of these fossil fish samples were performed by Dr. Maria Giammatteo and Dr. Lorenzo Arrizza.

OBSERVATIONS

These two specimens of *Acrorhinichthys poyatoi* Taverne & Capasso 2015 in this study both show fossil traces (icno-fossil) that appear to be linked to their last meal. Indeed, specimen CLC S-630 shows a mass of skeletal and dermal remains of an actinopterygian right by its mouth, without any anatomical connection. This can be assumed to be interpretable as vomiting or regurgitation. On the contrary, specimen CLC S-461 has a brown mass near to the anus that can be assumed to represent a coprolite.

Both of these icno-fossils have been documented in detail, as they appear to represent two important traces of pycnodont food. The first part of this study was to find evidence that these traces of meals under question actually belong to the specimens of fossil fish with which they were found in topographic association. As En Nammoura is one of the most conserved palaeontological deposits in the world, this idea is certainly supported. The detail and perfection with which the fossilisation of the finest anatomical structures occurred, which is well documented for these vertebrates, invertebrates and plants that have been described to date in the literature, are undoubtedly connected to both the sedimentation rate and the extreme fineness of the sediment (Capasso, 2017).

Regurgitation versus *rejection*

Specimen CLC S-630 shows a mass of skeletal and dermal remains of another fish positioned exactly in front of its mouth (Figure 1A). Both the pycnodont and the mass lie on the same sedimentary plane, although, near the mouth, the mass has a relatively high stratigraphic thickness. The mass has a roughly circular profile, with a maximum diameter of ~20 mm. The relations between this mass and the pycnodont mouth are very important. As can be seen in Figure 1B, the mouth of the pycnodont is slightly open; indeed, the premaxilla and vomer were open with respect to the dentary and the prearticular. In the opening space between the bones that make up the upper part of the mouth and those that make up its lower part, some skeletal elements that are also seen in the regurgitated mass are clearly visible.

Analysis of the mass under stereomicroscopy shows that it consists of a tangle of bones and scales. These are small bones, and it is possible to identify among them what seem to be mainly vertebral apophyses, axonostats and ribs of a small-sized actinopterygian, probably a clupeid (Figure 2). All of the bones that make up this mass have lost their anatomical relationships, and most of them are broken, which prevents precise anatomical identification (Figure 2). In the farthest part from the mouth of the pycnodont there are also two thin but extended bones; these might correspond to the cranial bones of the small clupeid (e.g., the opercula); also, the structure of the scales is characteristic of that of an actinopterygian.

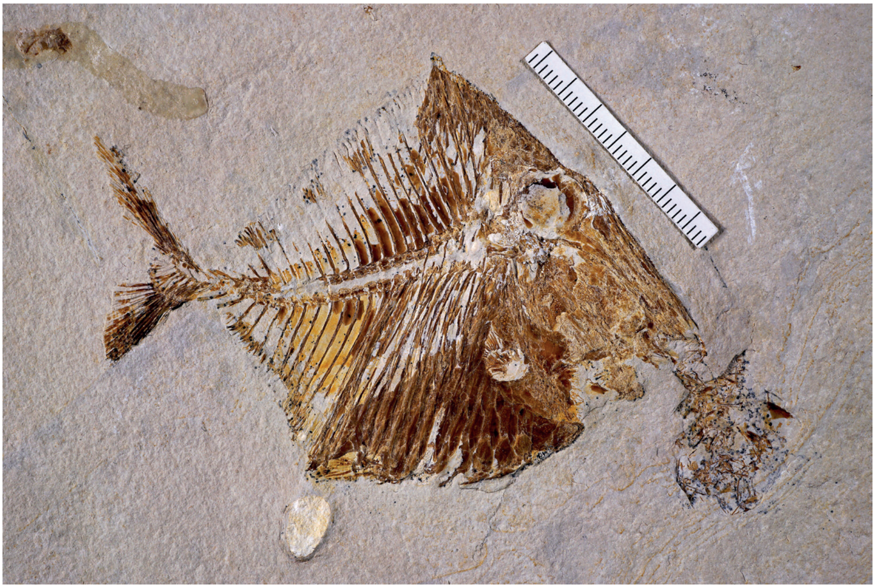

Figure 1. (A) Holotype of the species *Acrorhinichthys poyatoi* Taverne & Capasso 2015 as an exceptionally well-preserved specimen from the mid-Cretaceous settlement of En Nammoura, in Lebanon (CLC S-630).

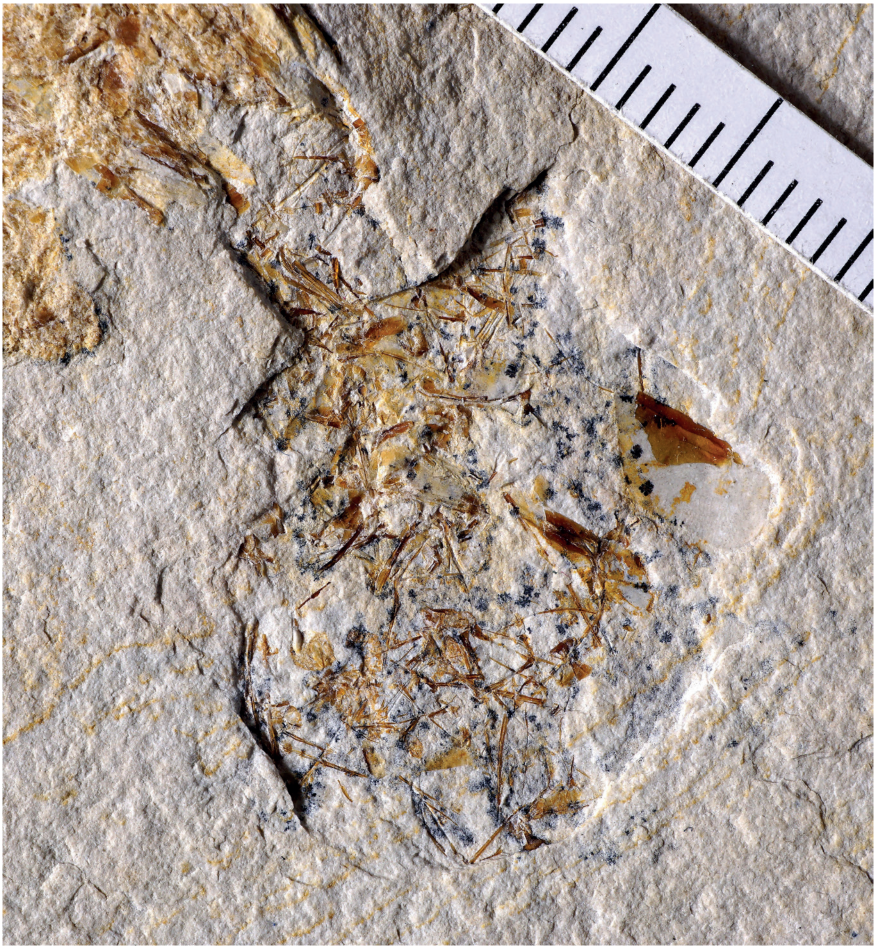

Figure 1. (B) Detail of the mass of skeletal remains and scales that shows a subcircular profile and is positioned just in front of the mouth.

Coprolite

Specimen CLC S-461 shows a brown mass in the vicinity of the anus (Figure 3A), which is elongated, at ~10.5 mm long, and of variable width, from about 1 mm to 2 mm. This has the appearance of a spiral (Figure 3B). The mass is located a few millimetres lower than the anal opening, and is shifted forward slightly with respect to it.

This mass, as indicated, has a brownish colour and an ‘earthy’ appearance. In the stereomicroscopy examination, inside this mass there are clearly visible and numerous scales that appear lighter in colour, and diaphanous in

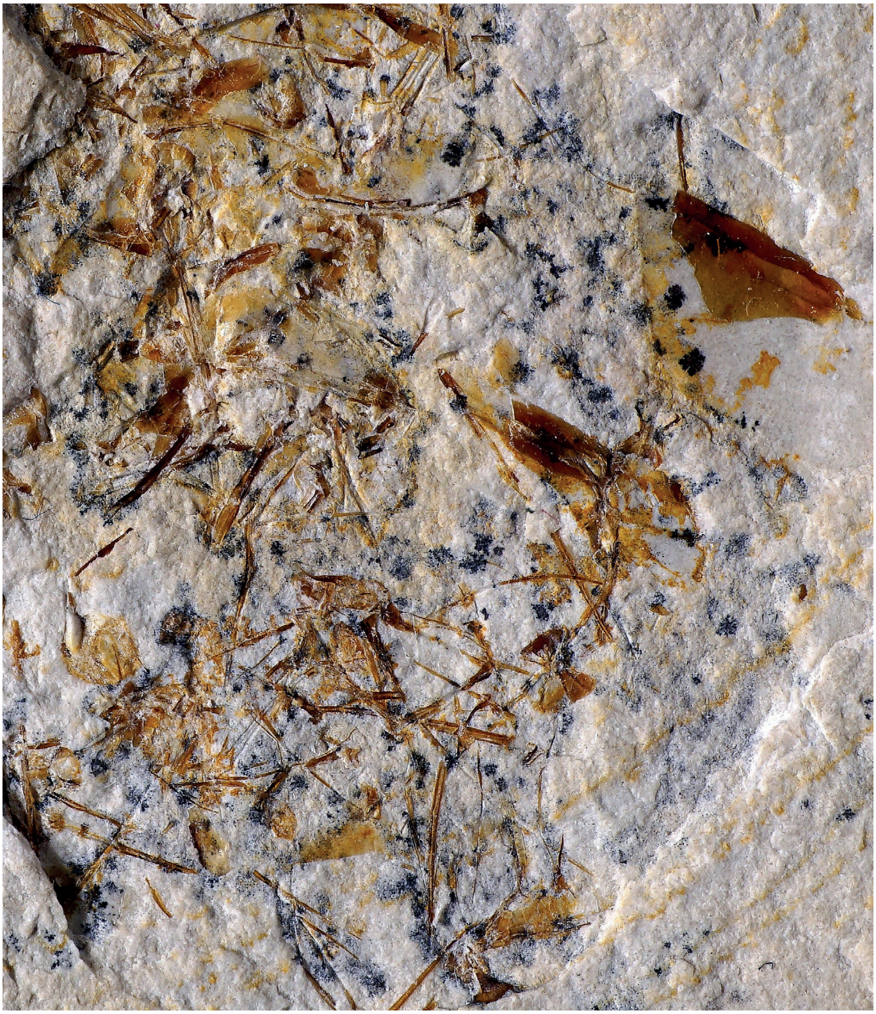

Figure 2. Stereomicroscopy examination of the scales and skeletal elements that constitute the regurgitated mass positioned just in front of the mouth of the holotype of *Acrorhinichthys poyatoi* Taverne & Capasso 2015 (CLC n. S-630). Note how the individual skeletal elements are broken, completely disjointed, and randomly mixed together. Two large fragmentary bones that can be seen located in the most anterior part of the regurgitated mass appear to represent remains of opercula.

appearance. These are partially broken up, although the broken parts have remained near to the main body of each scale (Figure 4A). These appear to be small-sized actinopterygian flakes, and the high-magnification analysis also showed the presence of the characteristic growth capillary lines (Figure 4B).

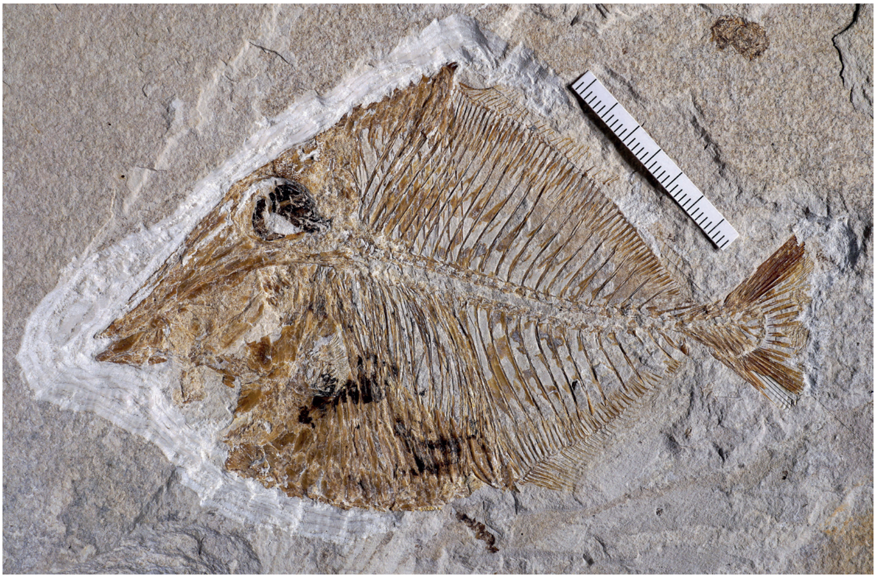

Figure 3. (A) Paratype A of *Acrorhinichthys poyatoi* Taverne & Capasso 2015, as an exceptionally well-preserved specimen from the mid-Cretaceous settlement of En Nammoura, in Lebanon (CLC S-461).

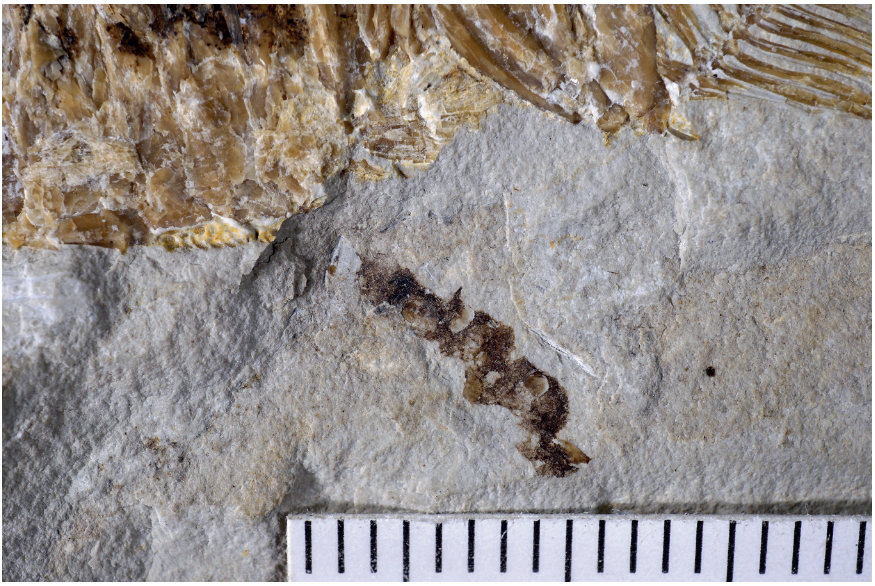

Figure 3. (B) Detail of the coprolite located at the anus.

These scales are almost uniformly distributed in the coprolite mass (Figure 5A), and they are easily distinguishable with respect to the coprolite mass, even when examined under UV light (Figure 5B).

Pycnodont specimen CLC S-461 shows some traces of brownish and earthy looking material also in correspondence with its visceral area. This material is clearly visible below the bones, right in the central part of the visceral area itself (Figure 3A). All of this material has also been examined under the microscope. However, this has not allowed the identification of areas that are sufficiently large enough to document the possible presence of skeletal remains or flakes of any prey. It is possible that the removal of the bones in this region of the left side would have exposed further details of this mass occupying a part of the visceral area, but this would have caused serious and irreversible damage to the find. Intuitively, this mass might represent the contents of the digestive tract of the pycnodont; i.e., the intestine.

Figure 4. (A) The coprolite associated with specimen CLC S-461 has a helical structure and contains a series of flakes of a small actinopterigian, which is partially broken up.

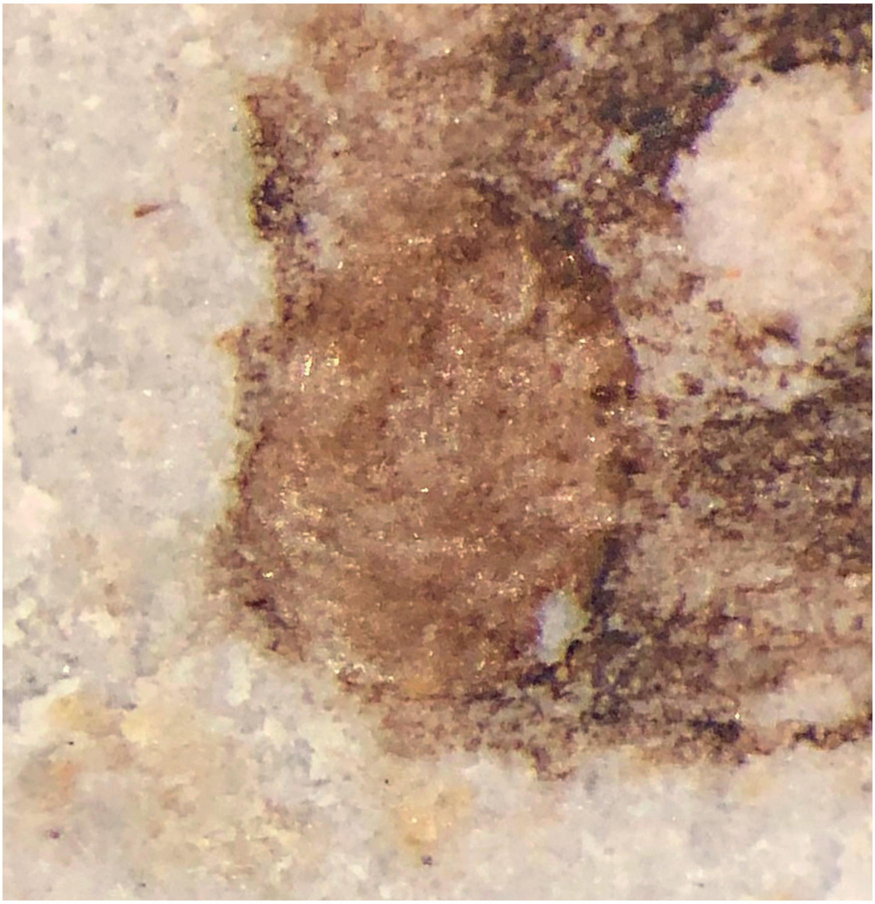

Figure 4. (B) At higher magnification, the capillary growth lines of the scales are very evident.

It appeared useful to perform chemical analysis of this material, using a tiny powder sample and subjecting it to element microanalysis with a probe applied to scanning electron microscope. The result of this analysis showed that the mass occupying a part of the visceral area is mainly composed of Calcium carbonate (Figure 6A), which will be related to the calcareous matrix. However, there were also Iron salts and traces of Phosphorus, which would be connected to the composition of the neighbouring bones. There were also traces of Sulphur, which would appear to be related to the remains of sulphate-containing proteins, along with a few traces of Aluminium, Magnesium, Sodium and Manganese. Extending from the exact interpretation of

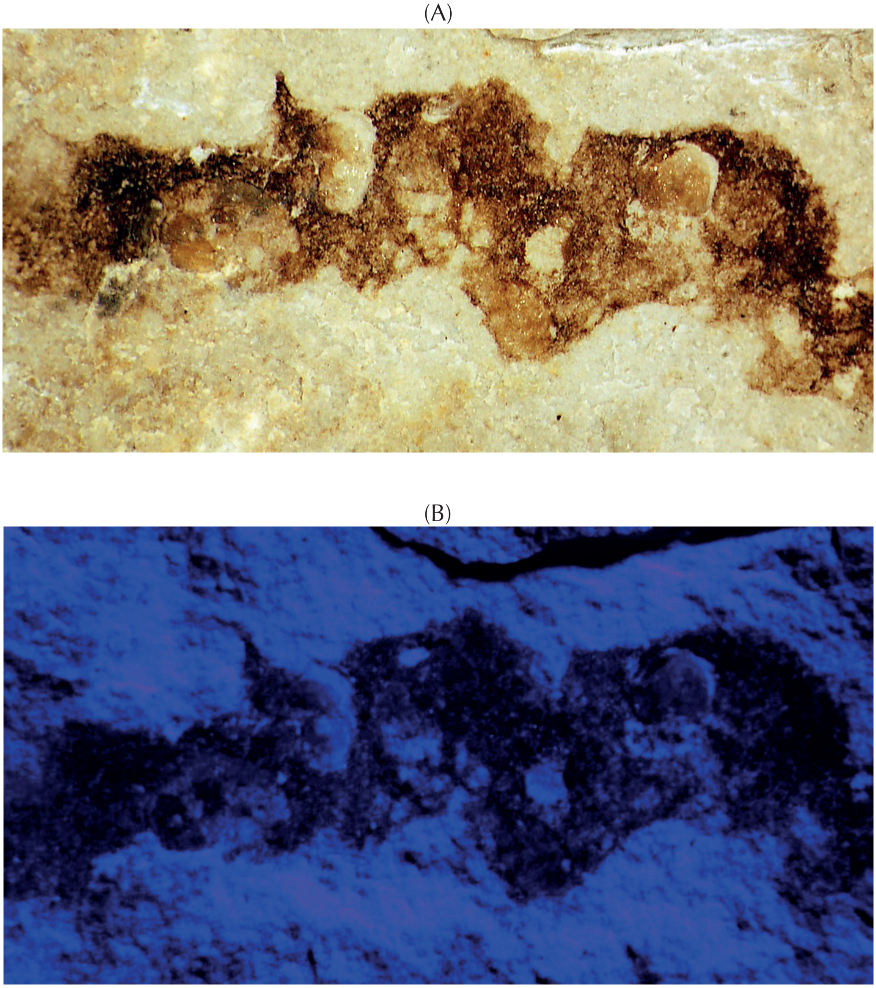

Figure 5. Observations under the stereomicroscope with normal (A) and ultraviolet (B) light show that the scales are more luminescent than the matrix.

the chemical nature of these materials, what mattered in particular here is that microanalysis was performed on a sample of the coprolite taken from the counter-mould of this specimen, and this showed exactly the same composition, with identification also of these trace elements (Figure 6B). These data strengthen the topographic evidence (i.e., that the coprolite examined was fossilised in the vicinity of the anus), and show that the coprolite in question has the same chemical element composition as the mass of the organic remains that were still contained in the visceral area of the same fish.

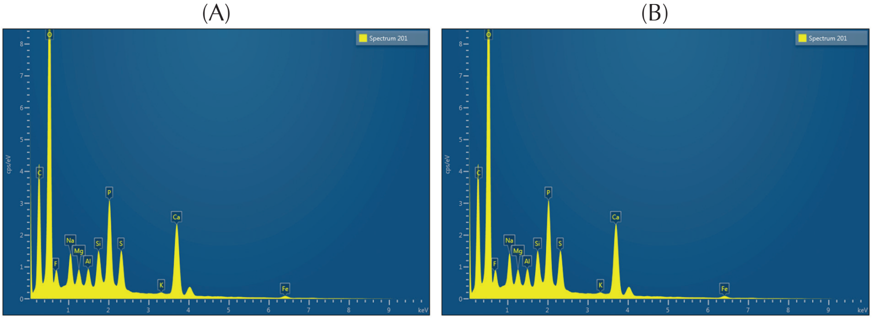

Figure 6. The element composition of the earthy brown material contained in correspondence of the visceral area (A) coincides perfectly with the composition of the coprolite matrix (B). The spectra of the elemental composition were obtained using a microanalytic probe connected to a scanning electron microscope.

DISCUSSION

Many new palaeontological studies have been carried out recently or reinterpreted regarding the feeding behaviour of the pycnodonts, and more generally, regarding their actual ecological position within the reef environment of the Mesozoic seas. These studies essentially relate to four aspects: (i) the possible presence of fish remains within the gut (Kriwet, 2001); (ii) the discovery of species with teeth that are clearly specialised for a piscivore diet (Vullo *et al.*, 2017); (iii) the secondary injuries due to aggression on fish that were probably under predation (Kölbl-Ebert *et al.*, 2018); and finally, (iv) the possible presence of poison-associated structures that might also be used for hunting (Capasso, 2018). Therefore, the findings described in the present study represent a significant addition to this list, and provide information that although not exactly direct, is certainly significant with respect to the possibility of the reconstruction of the actual eating habits of the pycnodonts.

The idea that the pycnodonts were species that strictly specialised in a durivorous diet, which remains typical of many predatory fish that still inhabit reef environments, has long been supported by many studies and was well summarised, for example, by Nursall (1996). This idea is certainly strongly supported at least by the following three observations: (i) the anatomy of the dental apparatus, which is typical of most pycnodonts; (ii) the presence of some traces of invertebrates with hard shells (e.g., molluscs, echinoderms, corals) preserved in the fossil state within the visceral area of numerous pycnodonts from various locations and dating back to different geological periods; and (iii) the presence of the fossilised remains of mollusc shells and echinoderms with indications of predation, or in any case, with evidence of damage, in association with pycnodont fossils.

This last aspect undoubtedly represents indirect evidence, and therefore must be considered as an assumption. However, many studies have pointed to pycnodonts as the possible durophagous animals that contributed to the depositions of masses of calcareous shells of molluscs that have been found in various palaeontological deposits. For example, in the locality of Pasquia Hills (Saskatchewan, Canada) actual accumulations dated to the upper Cretaceous have been found that contained the hard parts of invertebrates (mixed with other remains of hard parts of vertebrates) that represent the remains of shells that were crushed to provide food. Among the animals responsible for these predations, the pycnodonts have also been indicated (CUMBAA *et al.,* 2013). Even more clearly, ZATOŃ and SALOMON (2008) described an enormous accumulation of shellfish shells that had been fragmented by durophagous animals (with the characteristic rupture angles) from the Middle Jurassic for various locations of the Polish Jura. These have demonstrated less use of digestive acids, and a mode of fragmentation that was compatible also with that attributable to pycnodonts. Finally, MARTILL (1990) described some examples of ammonite shells of the genus *Kosmoceras* from the Middle Jurassic Lower Oxford Clay of England that showed characteristic traces of predation in the form of bites. This morphology is again compatible with the morphology of the anterior dentition of some semionotiform fish (*Lepidotes*) and of some pycnodonts (*Mesturus*). However, in some other palaeontological contexts (e.g., Toarcian, in Japan), similar lesions have been indicated as due to predation by other types of ammonites (TAKEDA and TANABE, 2015). Also ANDREW *et al.* (2010) interpreted the abundant specimens of fatally bitten ammonite shells from Lower Jurassic of Lyme Regis, Dorset (U.K.).

This type of durophagous diet certainly places the pycnodonts within an ecological niche of predators of the Mesozoic cliffs, although only when invertebrates were their prey. Moreover, this ability to prey on other fish represents a crucial step in the evolution of pycnodont feeding, which has until now been very little documented.

As is well known, the theoretical concepts of the trophic levels as developed by LINDEMAN (1942) need to be applied in a specially modified way when it comes to studies of fish ecology, such as was seen for the coding by GERKING (1994). In this case, indeed, excluding trophic level I, which includes photosynthetic organisms (not including fish), trophic level II is represented by herbivorous fish, or those that feed heavily on algae and higher plants. Planktivores (i.e., plankton feeders) and benthivores (i.e., benthos feeders) are important representatives of trophic level III. Finally, the predatory fish, as piscivores, that feed on other fish, are part of trophic level IV. In this scheme, therefore, the predatory fish comprise at least two types: those that prey on other animal invertebrates near the bottom (i.e., in the benthic environment), and those that feed on other fish in the open water (i.e., in the pelagic environment). The former occupies a lower trophic position (as level III) than the latter (as level IV), and these latter can be described as super-predator of the marine environment (and of aquatic environments in general). Therefore, the pycnodonts that fed on the benthic organisms, such as shellfish, molluscs, echinoderms and corals, were level III predators.

The ability to prey on other fish represents a huge leap forward in the trophic scale of the reef ecosystem. Therefore, when the pycnodonts, or at least some of them, acquired the ability to prey on other fish, they clearly changed their position within the food chain, passing from trophic level III to trophic level IV. This hypothesis that pycnodonts can be considered as super-predators was also considered and discussed by Ebert *et al.* (2015). However, having studied the associations for perfectly preserved fossil fish of Ettling (Bavaria), they abandoned this hypothesis because they could not find any direct evidence of such predatory abilities of pycnodonts towards other fish.

It is possible that this transition took place gradually, and indeed, only today do we have the first palaeontological evidence that in the upper Jurassic there were pinnivorous pycnodonts; i.e., those that fed on parts of the fins of other fish. This defines a predatory piscivorous behaviour, although it leaves the prey alive, although mutilated (Kölbl-Ebert *et al.,* 2018). It has also by no means been excluded that there might also have been species of pycnodonts that were scale-eaters, as some fish are currently (e.g., *Lamprologus*, *Callochromis*), or even that there were pycnodont mucous feeders, as are other living fish today (e.g., *Aspidontus*, *Holocentrus*) (Gerking, 1994). Indeed, the structure of the coprolite described in the present study could also be interpreted in this sense of a scale-eater, as the presence of only scales of an Actinopterygian was demonstrated, without any traces of skeletal elements.

In this sense, the real function of the incisor teeth that were particularly mobile and sharp, which characterised all of the pycnodonts, and considering also those that had a particularly ‘durophagous’ rear dentition, might indicate the need for re-evaluation. It might have been precisely these teeth that allowed the trophic ‘leap’ of some pycnodonts, and possibly for those also equipped with poison glands for hunting.

Indeed, I believe that the establishing of fish-eating habits might have been concurrent with the development of both the tendency towards the specialisation of the teeth towards predatory abilities – or at least some of them, as the anterior dentition – and the tendency for specialisation of part of the scaly coating, in the sense of serving as the poison-delivering apparatus.

CONCLUSION

The icno-fossils described in the present study represent two further pieces of evidence of the predatory fish-eating behaviour of some pycnodonts. Indeed, although this evidence is associated only with the species *Acrorhinichthys poyatoi*, it clearly indicates that the last meal consumed by these animals was a small Actinopterygian, or part of one. This new palaeontological evidence adds to the relatively scarce information that is already available and has been identified in recent years indicating that at least some pycnodonts were fish-eaters. This transition from predators of the inert benthic animals that defined their feeding as trophic level III to fish predators of trophic level IV might have occurred concurrently with the different evolutionary lines that were typical of the pycnodonts. Some species would have evolved towards fish-eating habits, even with later specialisation of their teeth (Serrasalmimidae), while other species, instead, appear to have used only their incisor teeth for predation of fish, as in the documented case of *Acrorhinichthys poyatoi*. In either case, these tendencies to fish-eating habits appear not to have been so rare, as also shown by the cases of mutilation of the actinopterygian fins recently described for the Solnhofen Jurassic field, and the possible presence of skeletal remains of small actinopterygians in correspondence of the visceral area from the Cretaceous in Brazil.

The new observations presented here broaden the range of palaeontological evidence for the fish-eating habits of the pycnodonts, and will help to rethink the ecological setting of these extinct fish. The pycnodonts evidently also represented super-predators of the Mesozoic reef environment, equipped as they were with their special instruments of attack that made their hunting more effective, in terms of their sharp teeth and their poison-delivering apparatus. Furthermore, it must be emphasised that the regurgitation *versus* vomiting described here represents the first direct evidence for the hypothesis formulated by KRIWET (2001). According to this hypothesis, the remains of hard parts of prey during digestion in the digestive tract of pycnodonts has been very rare as these fish regurgitated these parts after having chewed their prey, and only ingested the softer parts. This behaviour is similar to that which many durophagous fish species follow even today (Figure 7).

Finally, the structure of the coprolite in specimen CLC S-461 that demonstrates a decidedly helical morphology appears to indicate that the last section of the pycnodonts intestine might have had a convoluted, helical structure. This would thus be similar to that of the spiral valve typical of the selaceans and of the primitive actinopterygians (sturgeons).

Figure 7. A puffer-fish regurgitating the fragments of a calcareous shell of a predated and shredded gastropod. Photograph taken in an aquarium (from the internet site: https://youtu.be/R8t1lJgGNA4).

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