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Additions to the Late Cretaceous (Cenomanian/Turonian) actinopterygian fauna from the Agoult locality, Akrabou Formation, Morocco, and comments on the palaeoenvironment

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Abstract

Actinopterygian fishes recovered from southeastern Morocco in 2006–2009 indicate the presence in the area of a number of forms not previously documented for northern Africa. The fauna is generally similar at the familial level to that of marine Cenomanian and Turonian sites long known from Lebanon and from the Jebel Tselfat locality in northern Africa, but includes elements (e.g., Macrosemiidae) that had not previously been reported from deposits of this age in the Tethys basin. Some taxa previously reported from this site are here reidentified or identified more precisely. The fauna represented includes a macrosemiid *(Agoultichthys chattertoni)* and two other holosteans, at least three different ellimmichthyiforms (two paraclupeids and the sorbinichthyid *Sorbinichthys africanus*), two dercetids, one Teleostei incertae sedis, the clupavid *Lusitanichthys*, at least two pycnodontiforms, and three or more species of acanthomorph. Some of these taxa are essentially circum-Tethyan, such as the Dercetidae; however, others, such as the Paraclupeidae, are known from Cretaceous deposits worldwide, including Mexico, Europe, Canada, and China. Increased collecting and documentation of the area indicates that the small ichthyofauna reported from Oued Daoura, is likely from the same locality or one very close (in area or stratum), but we retain the name "Agoult locality". The specimens reported here were collected, or purchased at the locality, by the authors, and are thus from a known outcrop.

Introduction

Cretaceous marine fishes of Morocco and North Africa have been known for many decades, but new localities and faunas have also been discovered more recently (e.g., Goulmima, CAVIN 1995; Oued Daoura, CAVIN & DUTHEIL 1999). The addition of these new localities increases our knowledge of the fish faunas and palaeoenvironment of this time period, and provides more information on the faunas and biogeographic provinces that were present.

Most fossils coming from Morocco have been found by commercial collectors and sold to institutions worldwide. While these collections provide much new material for study, it removes the fossils from their original context and thus deprives us of important data. The specimens reported here come from a locality that was visited by all of us. This allowed us to collect some of the fossils in situ and also recover associated geological data.

The geology of southeastern Morocco has been studied by a number of authors (e.g., FERRANDINI et al. 1985, ETTACHFINI & ANDREU 2004, and references therein) and is currently under study by two of us (GIBB & CHATTERTON). The Moroccan Cretaceous North Saharan Platform has been divided into several formations, which record the incursion of the Tethys Sea from the east or northeast into this area of Africa. The lowest of these formations are continental deposits, the Ifezouane and Aoufous formations.

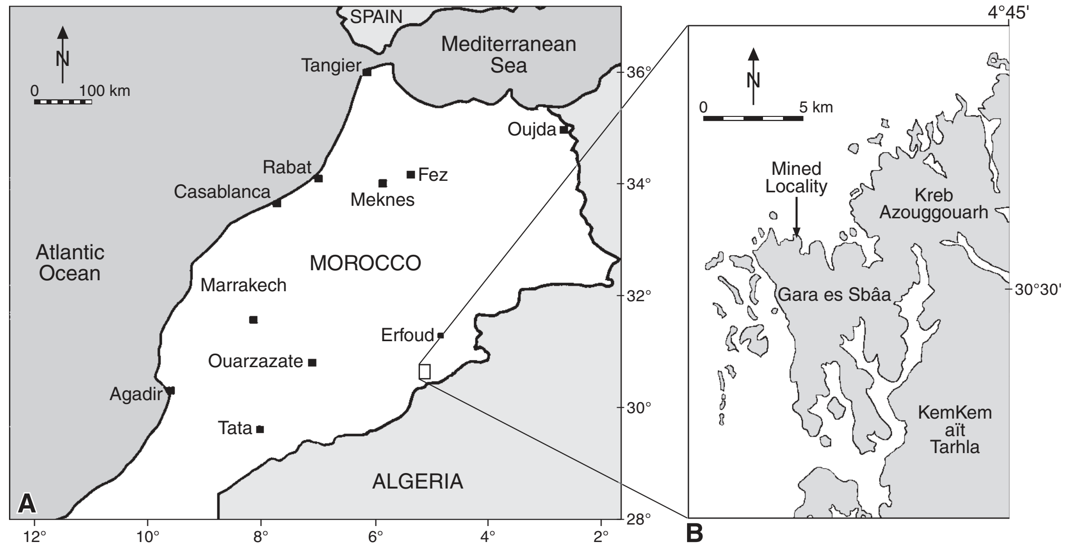

Fig. 1.
Locality map. **A,** map showing the location of the fossil site in southeastern Morocco. **B,** Cretaceous strata (shaded grey) in the area of the Agoult fossil site. Arrow indicates the quarry from which came the fossils reported here. Modified from SAADI et al. (1982) and ENGEL et al. (2012).

These were previously referred to as part of the Continental Intercalaire, a term used to contain all the continental sediments between the marine Upper Carboniferous and marine Lower Cretaceous in the central area of the Sahara (see review in LEFRANC & GUIRAUD 1990). Some of the Continental Intercalaire deposits are now called the Kem Kem Beds (e. g., SERENO et al. 1996). Overlying the freshwater Kem Kem Beds are the marine deposits of the Akrabou Formation (ETTACHFINI & ANDREU 2004) from which came the fossils reported here.

The Cenomanian-Turonian Akrabou Formation has been subdivided in a number of ways. FERRANDINI et al. (1985) studied this marine series of carbonates (= Akerboüss), which they considered to be a subhorizontal calcareous bar, termed the second Hamada, which is a major geomorphological feature of the region. Their studies in the Erfoud-Errachidia area, close to where the fossil fishes of this study were found, indicated the presence of four successive members, defined by the palaeoenvironments and biostratigraphy as (from bottom to top): 1) calm, shallow infralittoral; 2) calm, shallow proximal platform; 3) infralittoral to mediolittoral; 4) rising eustatic level. The first three environments were attributed to the Upper Cenomanian, with only the fourth representing the Turonian, based on ammonites, rudists and foraminifers (FERRANDINI et al. 1985). They noted that palaeobiogeographically, the Cenomanian in the Erfoud-Errachidia area is of a Tethyan nature, albeit with some endemic elements in the fauna.

In contrast, ETTACHFINI & ANDREU (2004) considered the whole Akrabou Formation to have been deposited on an open marine platform. They also divided the Formation into four units (C1, C2, T1 and T2), based on lithostratigraphy, and organized by transgressive-regressive sequences. However, unlike FERRANDINI et al. (1985), ETTACHFINI & ANDREU (2004) ascribed their two upper units to the Turonian, with the caution that the boundary between the Cenomanian and Turonian was not clearly marked. They also noted that *Goulmimichthys arambourgi*, a pachyrhizondontid fish described by CAVIN (1995) from the lower Turonian of the Goulmima locality in Morocco, is from the T2 layer. The four units of ETTACHFINI & ANDREU (2004) represent: C1) sublittoral carbonates deposited in a calm, shallow proximal platform; C2) lithologically similar to C1 but with the depositional centre shifted to the west and a stepwise progression of the facies from littoral to supralittoral from the southeast to the west; based on the invertebrate fauna, this unit has a Tethyan influence indicating the platform was open to the north and northeast; T1) deepening of the water with an inundation of the platform under an open sublittoral environment; T2) a regression of the sea towards the north and northeast under a limited or restricted sublittoral environment. ETTACHFINI & ANDREU (2004) indicated that although this platform was connected to the Tethys in the Late Cenomanian and much of the Turonian, it also had a minor connection with the Atlantic Ocean.

A number of different holostean and teleostean fishes has been recovered, showing a good diversity, mostly by commercial collectors as well as by a number of palaeontologists (including all of us). They come from the Akrabou Formation, in the region of the Moroccan/Algerian border, on a hill called variously Gara es Sbaa, Gara Sba, Gara Sebaa or Gara Sbâa (Fig. 1). Most recently, MARTILL et al. (2011) named the restricted Plattenkalk laminites bearing the fossil fishes as the Gara Sbaa Member of the Akrabou Formation. This is the only member of the formation to be named. MARTILL et al. (2011) indicated that the laminites representing their new member are not laterally extensive, and the top of the member cannot be determined as the laminites form the top of the hill on which the fossil localities crop out. We feel it is premature to name this member until it has been properly mapped and its extent is documented. We also follow MURRAY & WILSON (2009) and CAVIN et al. (2010) in referring to the marine deposits at the top of the Gara Sbaa hill, from which come the fish fossils discussed here, as the Agoult locality to distinguish it from the underlying freshwater sediments of the Kem Kem beds on the same hill, which have produced dinosaurs and other vertebrates including a dinosaur named for the hill, and for which the locality name Gara Sbaa was used in earlier literature (LAVOCAT 1954, SERENO et al. 1996). A detailed stratigraphic column of the upper limestones of the Akrabou Formation and the position of the fish-bearing sediments is shown in Figure 2.

History of collecting at the Agoult locality

Commercial collectors have been recovering fossils from sediments in the Erfoud-Errachidia area for many years, but it is more recently that fish palaeontologists have visited the locality. One of us (CHATTERTON) has been working in the area for well over a decade, in deposits ranging from the Devonian through to the Cenomanian. CHATTERTON became aware of the material from the Agoult locality between 2000 and 2002, and in 2004 acquired some specimens, which he showed to the second author (WILSON). In May 2006, CHATTERTON and the third author (GIBB) visited the deposits and collected more material themselves. At that time, they conducted extensive measuring, description, and sampling of strata at 10 cm intervals in order to analyse the stable isotope geochemistry. Finally, in May 2009, all four authors spent time collecting at the Agoult locality and measuring below the section (Fig. 3A–C), and purchased additional material from the commercial collectors who had arranged to meet us at the site.

Lionel CAVIN and colleagues visited the Agoult locality in May 2008 (CAVIN et al. 2010). They also excavated at a number of other fossiliferous sites in the area, visited at various times over more than a decade, and correlated the strata in those locations. Their stratigraphic columns (CAVIN et al. 2010: fig. 3) indicate the restricted nature of the fossiliferous laminites of the Agoult locality. Later on, some time in November and December of 2008, David MARTILL and colleagues visited the Agoult locality while working on the Kem Kem beds in the area (MARTILL et al. 2011). Other colleagues may also have since visited the locality. With the increased numbers of palaeontologists having collected at the site and having purchased material from the commercial collectors, we now know there is a much greater diversity of species than previously realized. As MARTILL et al. (2011) recognized, the Agoult locality truly is a Lagerstätte and we

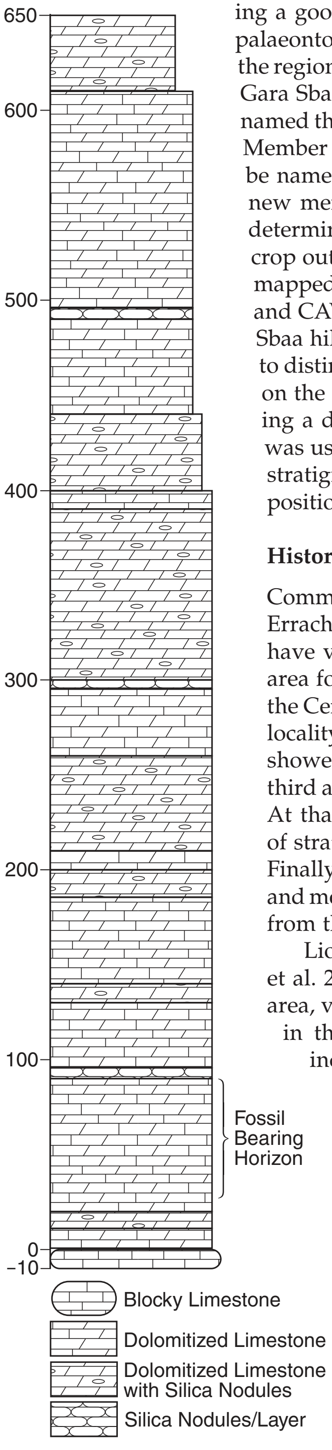

Fig. 2.
Stratigraphic column for the Agoult locality, from slightly below the base of the fossil-bearing strata to the top of Gara es Sbâa. Modified from ENGEL et al. (2012).

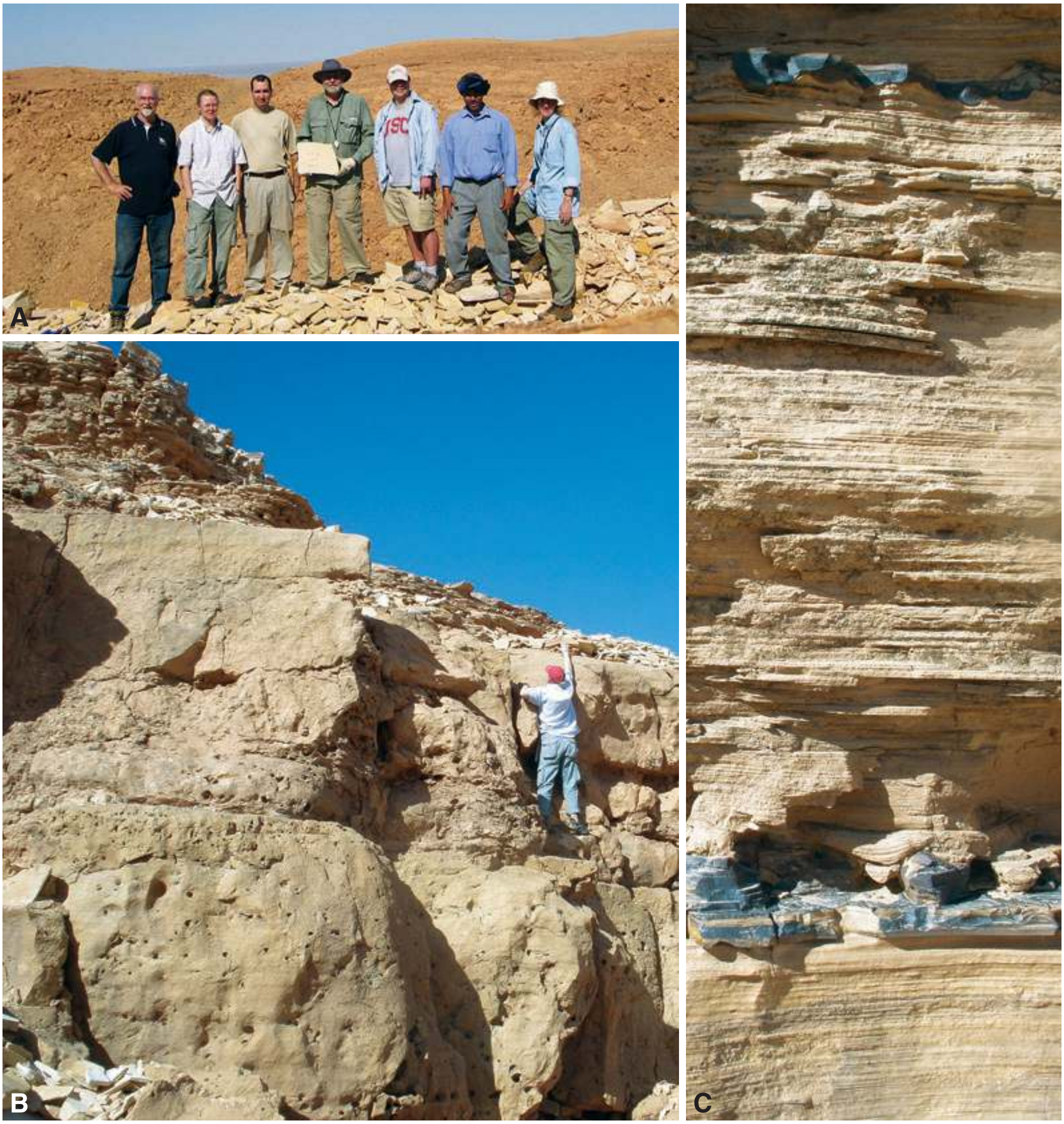

Fig. 3.
A, the authors and field party standing in the fossil quarry on Gara es Sbâa, Morocco, May 2009. From left to right: Brian CHATTERTON, Stacey GIBB, Darrin MOLINARO, Mark WILSON, Todd COOK, Hammi AIT H'SSAINE, Alison MURRAY. **B,** Stacey GIBB measuring the section; note the blocky limestone at the bottom of the photograph, which marks the base of the section in Figure 2. **C,** Photograph of the sediments showing the laminated nature of the limestones and the silica nodules.

will greatly increase our knowledge of the Early Cretaceous ichthyofauna of the Tethyan area as more of this material is described and published.

During our field trip in May 2009, we also collected more rock samples for isotopic analyses, to quantify the marine signature of the laminites that was already apparent from the 2006 samples collected for stable isotope geochemistry. In 2006, the lithology of the section, just above the "blocky limestone" (Fig. 2), was measured and documented. Once the stable isotope geochemistry was completed for all the 2006 rock samples as well as all of the specimens in our collections, the locality was revisited in 2008 and the exact horizon in which the fossils occur was confirmed. Further sampling of the horizon was carried out on 5–30 centimetre distance intervals. The fossil-bearing horizon is approximately 43 to 90 centimetres above the 'blocky limestone' unit, and slightly below the first, distinct, silica layer. The geochemistry confirmed a normal marine palaeoenvironmental setting. Here we document the diversity of fishes and reconstruct the palaeoenvironment of the Akrabou Formation in this locality.

Materials and methods

Some of the fossil fish specimens are preserved as poorly defined natural moulds, whereas others preserve the bone, allowing more detailed examination of the features. Some fossils were split in the field revealing part and counterpart. Others were prepared by hand from one side. The fossil fishes were collected and exported from Morocco under permits from the Ministère de l'Énergie, des Mines, de l'Eau et de l'Environnement, and are catalogued in the collections of the University of Alberta Laboratory for Vertebrate Palaeontology (UALVP). Samples for isotopic analyses were obtained from the outcrop at ~10 cm intervals as well as from the fish-bearing slabs, as far as possible on the same bedding plane as the fish.

Systematic palaeontology

Infraclass Neopterygii REGAN, 1923
Order Pycnodontiformes BERG, 1937

Family Pycnodontidae sensu NURSALL, 1996b
(Fig. 4)

Material: Five specimens: UALVP 43595, 51608, 51667, and 51713, each preserved separately on a single slab, and UALVP 51669 preserved in part and counterpart.

Description. UALVP 43595 can be attributed to the family Pycnodontidae based on the presence of an apomorphy of that family, the parietal peniculus, a bony strut that projects posteriorly from the parietal bone (NURSALL 1996b). The remaining specimens are very similar in visible features, although the parietal peniculus is not visible, and all specimens in our collections likely are conspecific or very closely related.

Remarks. CAVIN et al. (2010) and MARTILL et al. (2011) also reported pycnodontiform material from the Agoult locality. CAVIN et al. (2010: fig. 8A) listed their specimen as pycnodontiform indet., but the photograph provided is too small for us to make out any details other than general body shape. However, based on the roundness of the body profile, that specimen may represent the same form as the one reported here. The specimen figured by MARTILL et al. (2011: fig. 8C) was identified by them as a pycnodontid and provisionally a new species of *Pycnodus*, but no justification for either is provided. Based on the general body shape of this fish, in particular the body that is not as round as the others and the head that is significantly pointed in lateral view, the pycnodontiform presented in MARTILL et al. (2011) is not the same species as the one we report here. Therefore, there are at least two pycnodontiforms present in the Agoult locality, at least one of which is definitely a pycnodontid.

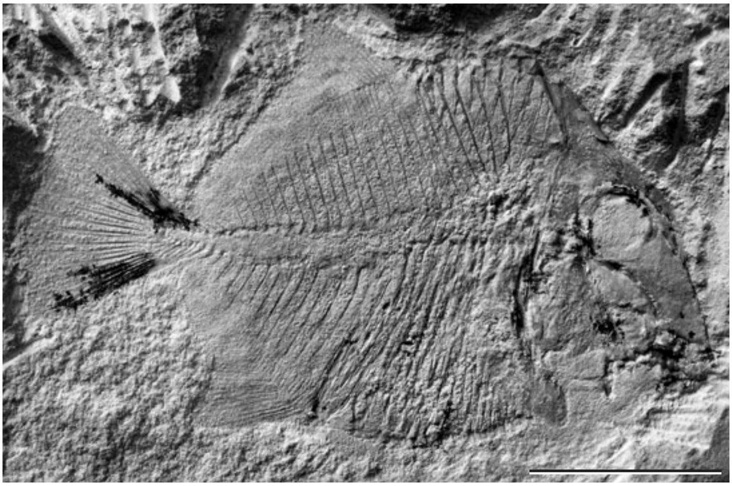

Fig. 4.
Pycnodontidae sensu NURSALL (1996b), UALVP 43595. Scale bar = 1 cm.

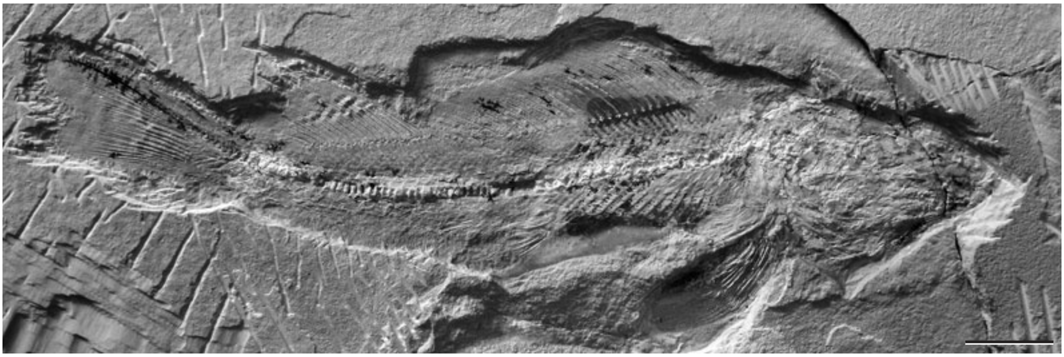

Fig. 5.
Agoultichthys chattertoni MURRAY & WILSON 2008, holotype UALVP 43599. Scale bar = 1 cm.

Division Holostei MÜLLER, 1845
Subdivision Halecomorphi Cope, 1872
Order Macrosemiiformes sensu GRANDE & BEMIS, 1998
Family Macrosemiidae THIOLLIÈRE, 1858

Agoultichthys chattertoni MURRAY & WILSON, 2009
(Fig. 5)

Material: UALVP 47133 holotype, new referred material UALVP 43597, 43599, 51618, 51619, 51620, 51714.

A single specimen collected in 2007 was described as a new species of Macrosemiidae. Six addition specimens were collected in 2008 and 2009. Another specimen is reported and figured by MARTILL et al. (2011: fig. 8A).

Description. *Agoultichthys chattertoni* differs from other members of the Macrosemiidae by having a higher number of scales in a lateral row (68, compared to 50 or fewer in other genera), and more numerous dorsal fin rays (about 47 compared to fewer than 40 in other genera). The dorsal fin is separated into two lobes, as in some macrosemiid taxa, rather than the single continuous fin of other macrosemiid taxa. A complete description is given by MURRAY & WILSON (2009) and here we note only new information provided by the new specimens, not visible on the holotype. These additional specimens confirm that the anal fin is not absent, but is very small and placed in an anterior position close behind the pelvic fins.

Remarks. MURRAY & WILSON (2009) placed the new species in a basal position within the family, as sister group to all the other genera except *Notagogus*. The addition of the information from the new specimens does not change any of the data used in the analysis of MURRAY & WILSON (2009), but in the reconstruction (MURRAY & WILSON 2009: text-fig. 3) the anal fin should be much closer to the pelvic fins.

Order Amiiformes HAY, 1929
Superfamily Amioidea BONAPARTE, 1838

Unnamed genus and species A
(Fig. 6A)

Material: UALVP 43600, a complete fish.

Description. This small amioid has about 60 ossified monospondylous vertebral centra, most of them with two lateral fossae per centrum, including about 11 ural centra. It has a long, bow-shaped dorsal fin of about 37 rays and a rounded caudal fin that retains a series of fringing fulcra, more prominent in the dorsal lobe than the ventral lobe. A series of about 17 supraneurals interdigitates with the proximal pterygiophores of the dorsal fin. In the caudal skeleton there is a reduced number of ural neural arches with only two present, and more than one caudal fin ray contacts each upper hypural, although the more anterior hypurals maintain a one to one ratio with the caudal fin rays. Scales are not detectable and must have been very thin.

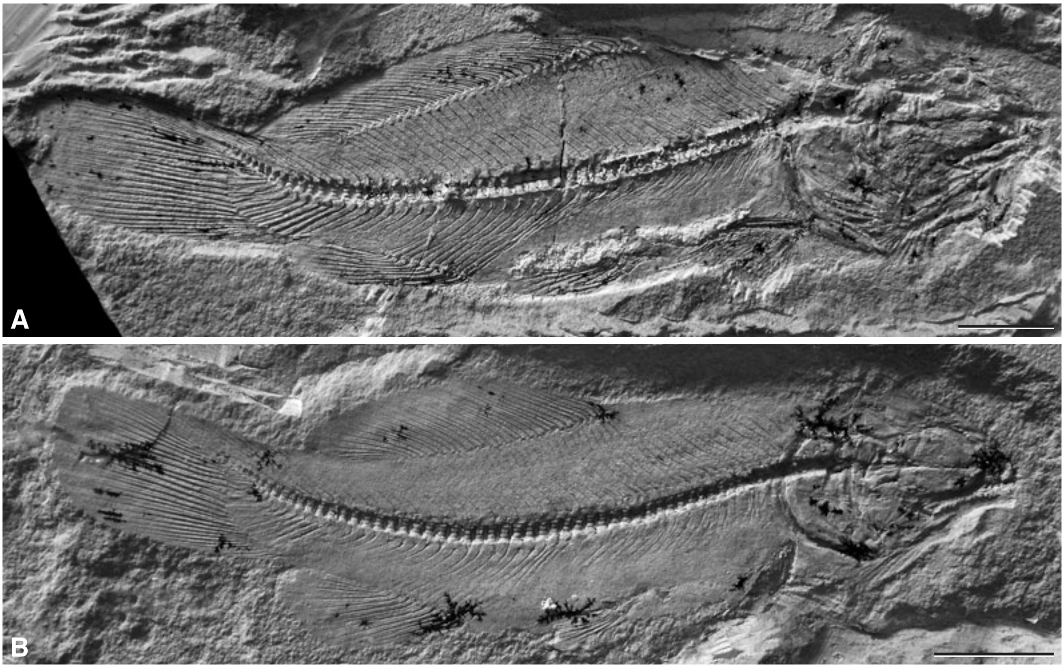

Fig. 6.
Amiioidei, **A**, unnamed genus and species A, UALVP 43600. **B,** unnamed genus and species B, UALVP 43601. Scale bar = 1 cm.

Remarks. Based on the extensive review by GRANDE & BEMIS (1998), this fish can be classified in the Amiiformes as opposed to the Ionoscopiformes, and it is more closely related to Amioidea than to Caturoidea on the basis of its rounded caudal fin, elongate and bow-shaped dorsal fin, and number of ural neural arches reduced to two or less. However, it lacks some synapomorphies of derived amioids (the "Amiida", "Amiista", and Amiidae sensu GRANDE & BEMIS 1998), such as loss of fringing fulcra in the caudal fin, number of caudal fin rays contacting each hypural reduced to a one to one ratio for all hypurals, diplospondyly in the caudal vertebrae, and strong and coarse ornamentation on skull bones. Therefore, it does not belong to any of these more derived clades. We conclude that it represents an undescribed genus and species of amioid closely related to the Amiidae and/or Sinamiidae.

Unnamed genus and species B
(Fig. 6B)

Material: UALVP 43601, a complete fish.

Description. This little amioid differs at the specific and probably at the generic level from the one discussed above, yet is similar in many ways. It has only about 7 ural centra and including those, about 58 ossified monospondylous vertebral centra, most of them with two lateral fossae per centrum. It has a somewhat long, bow-shaped dorsal fin of about 31 rays, significantly shorter and more posteriorly placed than the dorsal fin of Species A. The margin of the caudal fin is rounded and, unlike that of Species A, lacks fringing fulcra. There are a few more supraneurals (20) than in Species A and the posterior eight of these also interdigitate with the proximal pterygiophores of the dorsal fin. In the caudal skeleton the number of ural neural arches is reduced to two, and more than one caudal fin ray contacts each upper hypural.

Remarks. Like Species A discussed above, and also based on GRANDE & BEMIS (1998), this fish can also be classified in the Amiiformes within or very close to Amioidea, on the basis of its rounded caudal fin, somewhat elongate and bow-shaped dorsal fin, and number of ural neural arches being two or fewer, but it also lacks some synapomorphies of more derived amioids ("Amiida", "Amiista", and Amiidae), including number of caudal fin rays reduced to a one to one ratio with the hypurals, diplospondyly in the caudal vertebrae, and strong and coarse ornamentation on skull bones. We conclude that, like Species A, it also represents an undescribed genus and species of amioid closely related to the Amiidae and/or Sinamiidae. Between the two species there are differences in shapes of skull bones, differences in fin size and placement, and differences in caudal fringing fulcra (present in species A but absent in species B), suggesting that although similar, the species will likely be found to be generically distinct when a full description and analysis are performed.

Subdivision Teleostei MÜLLER, 1845
Incertae sedis

Unnamed species

(Fig. 7)

Material: UALVP 51599, a complete fish in part and counterpart.

Description. The specimen has a standard length (SL) of 102 mm, the head length is one quarter of SL, and the narrow body has a depth of only 15 % SL. The head is poorly preserved, with the opercular and circumorbital series missing or unidentifiable. The jaws are short, with robust, slightly recurved teeth present on the premaxilla and dentary. The pectoral girdle is ventral and the pelvic girdle is positioned under the posterior part of the dorsal fin, which itself is half-way between the head and tail.

There are 45 vertebrae, with a compound caudal centrum (presumed fused first ural and first preural centra) and one ural centrum (ural 2 in diural terminology). The arch of the parhypural and the second hypural appear fused with the fused centrum, although this may be an artefact of preservation. Eight long, thin supraneurals are present. The caudal fin has probably five hypurals, but the upper part of the caudal skeleton is covered by the elongate proximal ends of the fin rays, which obscure any hypurals. There are two long uroneurals and three epurals.

Remarks. This single specimen cannot yet be assigned to a particular taxon within the Teleostei. Although it may have modified anterior neural arches, indicating relationship with the Ostariophysi, it lacks a sufficiently well-preserved head and anterior vertebral region to definitively place it in that group. At present, we leave it incertae sedis within the Teleostei, until more, better-preserved, material is recovered.

Cohort Clupeocephala PATTERSON & ROSEN, 1977
Superorder or Subcohort Clupeomorpha GREENWOOD et al., 1966

Order Ellimmichthyiformes GRANDE, 1982

The Paraclupeidae were once the only family in the extinct order Ellimmichthyiformes, which is placed as the sister group of the Clupeiformes within the Clupeomorpha (GRANDE 1985). More recent analyses (e. g., ALVARADO-ORTEGA et al. 2008) have since supported the recognition of a second family, Sorbinichthyidae, first erected by BANNIKOV & BACCHIA (2000). MURRAY & WILSON (this volume) erect a third family in the order for the basal genus *Armigatus* and its apparent sister group *Diplomystus*. Of the three previously recognized species of ellimmichthyiform represented in our Moroccan material, two are paraclupeids and one is a sorbinichthyid. We also reevaluated the taxon referred to as "aff. *Spratticeps*" by CAVIN & DUTHEIL (1999); we believe it is actually an ellimmichthyiform, probably best placed in the Paraclupeidae.

Family Sorbinichthyidae BANNIKOV & BACCHIA, 2000

Sorbinichthys africanus MURRAY & WILSON, 2011

(Fig. 8)

Material: UALVP 51640 holotype, a complete fish; UALVP 47186 and UALVP 51641 (paratypes), both preserved as part and counterpart of a complete fish; UALVP 53733.

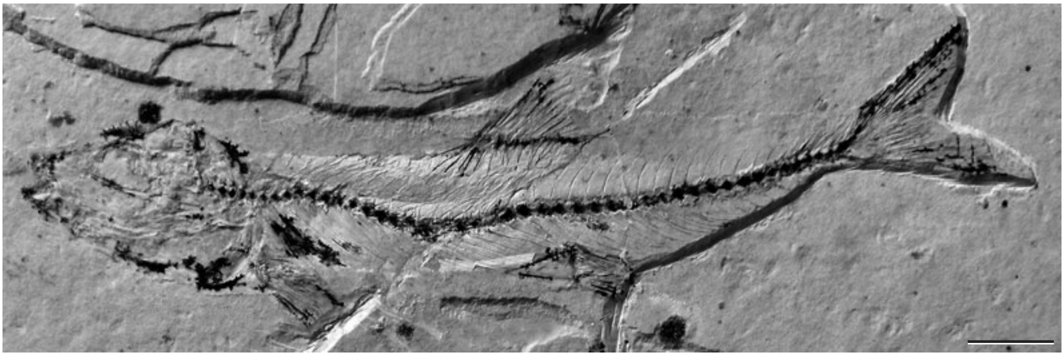

Fig. 7.
Teleostei incertae sedis, UALVP 51599. Scale bar = 1 cm.

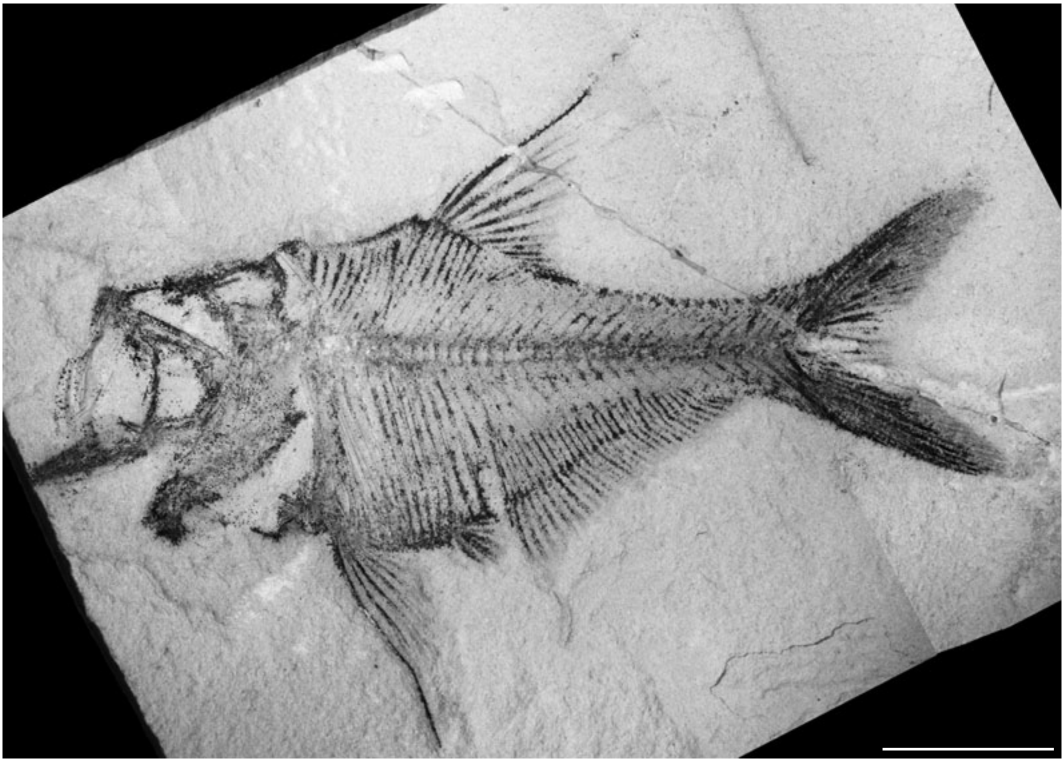

Fig. 8.
Sorbinichthys africanus MURRAY & WILSON, 2011, UALVP 53733. Scale bar = 1 cm.

Description. This species shares with the type species, *Sorbinichthys elusivo*, a greatly expanded dorsal limb of the posttemporal, a distinctive caudal fin with a wide, deep notch between hypurals 3 and 4 and anterior procurrent rays extending deeply between the neural and haemal spines, and a greatly elongated second principal dorsal fin ray. *Sorbinichthys africanus* differs from *S. elusivo* by having fewer ribs (12 or 13 pairs compared to 15 or 16 in *S. elusivo*), a jaw articulation more posteriorly placed and a corresponding more elongate lower jaw than in *S. elusivo*, and the elongated second principal dorsal ray relatively shorter than in *S. elusivo*.

Remarks. MARTILL et al. (2011: fig. 9B) identified one of their specimens in their figure caption as *Ellimmichthys* sp., and referred to it in the text as "*Ellimmichthys*-like form". Based on their photograph, we believe their specimen is referable to *Sorbinichthys africanus*. The Moroccan species of *Sorbinichthys* greatly extends the known range of the genus in the Tethys Sea. Previously, the genus was only known from marine Cenomanian deposits of Lebanon. The small size of the specimens suggests that this species was unlikely to be strongly pelagic; it probably inhabited near-shore waters and if the ancestral form was also small, it likely dispersed in the Tethys following the shallower waters near shore.

Family Paraclupeidae CHANG & CHOU, 1977

(Fig. 9)

Material: A new genus and two new species of paraclupeid are described elsewhere (MURRAY & WILSON, this volume). One species is represented by many specimens, including the holotype UALVP 47178 preserved in part and counterpart, and paratypes UALVP 47134, 51647, 51649, 51648, 51659 and 51657, all complete fish, the first three in part and counterpart and the last three with no counterpart.

The second species of the new genus is represented by only three specimens in our collections, the holotype UALVP 51653, a complete fish, and paratypes UALVP 51664, also a complete fish but overlying a decapod crustacean, and UALVP 51715, a complete fish, smallest of the three.

Description. The type species of the new genus is represented by the majority of the paraclupeid specimens, which are deeper in body than the second species. The second species is clearly less deep-bodied. Both species are included in the Paraclupeidae based on synapomorphies of the order and family, such as presence of both an abdominal and predorsal series of scutes, and anterior ribs articulating in pits on the centra but posterior ribs articulating on parapophyses off the centra.

Remarks. MARTILL et al. (2011: fig. 9A) figured a specimen that almost certainly belongs to the type species of the new genus, but in the figure caption they incorrectly identified it as "clupeid *Diplomystus* sp." *Diplomystus* is an ellimmichthyiform, not a clupeid; the Clupeidae are a derived family of the order Clupeiformes, which is the sister-order to the Ellimmichthyiformes.

Family ?Paraclupeidae

Unnamed species

(Fig. 10)

Material: There are numerous specimens of a small clupeomorph in our collections, with some of the best preserved being catalogued under numbers UALVP 47155, 51622, 51618, 51604, 51621, 51680 and 51679, all complete fish. These represent the same taxon that was referred to as "aff. *Spratticeps*" by CAVIN & DUTHEIL (1999).

Description. This clupeomorph is small, with the largest in our collections being about 32 mm SL, with others ranging from 23–30 mm. The head is about 30 % of SL, and the body is shallow, only 27–31 % of SL. There are eight long, thin predorsal bones with perhaps ten small dorsal scutes above them. There are about 23 abdominal scutes of which 10 are postpelvic. Total vertebrae number 37 to 38 with 23 or 24 abdominal and 13 or 14 caudal. These counts differentiate this species from the other Ellimmichthyiformes already known from the site.

Remarks. CAVIN & DUTHEIL (1999) first noted the presence of a small clupeomorph in the Moroccan sediments and attributed it to "aff. *Spratticeps*". CAVIN et al. (2010) further suggested that MURRAY et al. (2007) and WILSON et al. (2009) might be referring to the same taxon of clupeomorphs when they reported the presence of two paraclupeids; however, we were in fact referring to the paraclupeid and the sorbinichthyid fishes noted above. CAVIN & DUTHEIL (1999) noted that their Moroccan form lacked a recessus lateralis but that it had a beryciform foramen in the anterior ceratohyal, indicating similarity to the Ellimmichthyiformes, but also had a reduced first ural centrum, a character of the Clupeiformes according to CHANG & MAISEY (2003). CAVIN & DUTHEIL (1999) suggested it could be placed near *Spratticeps* in the cladogram of TAVERNE (1997), which genus was placed as intermediate between Ellimmichthyiformes and Clupeiformes. PATTERSON (1970) named the genus *Spratticeps* based on four

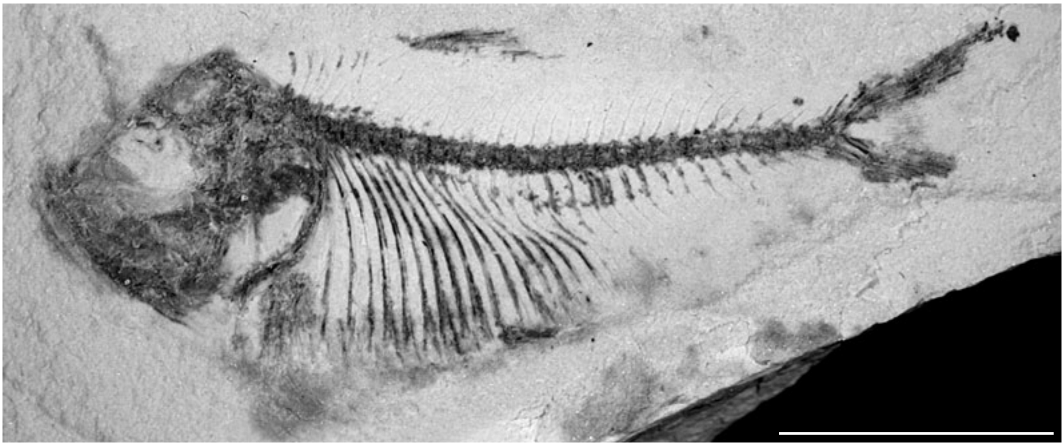

Fig. 9.
The third specimen of the second species of Paraclupeidae MURRAY & WILSON, this volume, UALVP 51715. Scale bar = 1 cm.

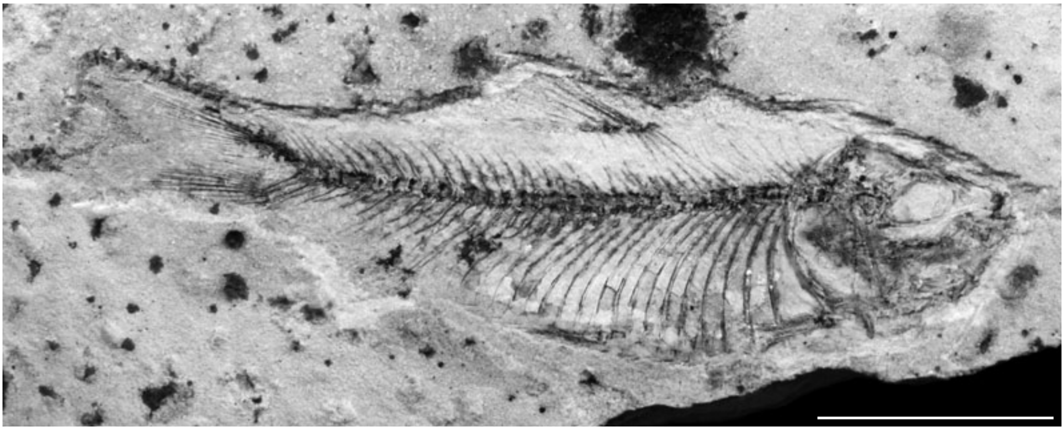

Fig. 10.
The fourth ellimmichthyiform, ?Paraclupeidae, from the Agoult locality, previously identified as "aff. *Spratticeps*" by CAVIN & DUTHEIL (1999), UALVP 51679. Scale bar = 1 cm.

specimens preserving isolated braincases – no postcranial material is known; he left them as Clupeiformes incertae sedis. Based on preserved size, PATTERSON (1970) suggested that these fishes would have had neurocrania about 30 mm in length. If proportions of *Spratticeps* were similar to those of *Denticeps*, or ellimmichthyiforms, many of which have a neurocranium length (anterior end of frontals to posterior end of supraoccipital bone) of one quarter to one sixth of the standard length, then *Spratticeps* could have been about 120–150 mm standard length. This is much larger than any of our specimens recovered from the Agoult locality, and much larger than the one figured by CAVIN & DUTHEIL (1999).

CAVIN & DUTHEIL (1999) noted that their Moroccan material also shared with *Spratticeps gaultinus* a similar pattern of ornamentation on the posterior portion of the skull roof. Ornamentation of the skull roof is also found in a number of ellimmichthyiform species but the presence and form of ornamentation has not been found to be a good indicator of relationships (see MURRAY & WILSON, this volume).

Although we have not yet studied our specimens in detail, we here refer them to the Ellimmichthyiformes. The character of the first ural centrum being reduced in size compared to the first preural centrum, the only character causing CAVIN & DUTHEIL (1999) to place the Moroccan specimens outside of the

Ellimmichthyiformes, is problematic. The original character was that of CHANG & MAISEY (2003), and, as noted by MURRAY & WILSON (this volume), they indicated that the first ural centrum (diural terminology) was significantly smaller than the first preural centrum. Examination of our "aff. *Spratticeps*" specimens shows this is not the case; the ural centrum is only slightly smaller than the first preural centrum, and the two are similar to the respective sizes of these elements in other ellimmichthyiforms. It is likely that this taxon can be included in the Paraclupeidae as redefined by MURRAY & WILSON (this volume) based on numbers and form of dorsal and abdominal scutes and the articulation of the ribs, but the left and right halves of the anterior neural spines are separate, indicating it would be placed in a basal position in the family, or even more basally in the order.

Superorder Ostariophysi GREENWOOD et al., 1966
Order incertae sedis
Family Clupavidae TAVERNE, 1977

Lusitanichthys africanus CAVIN, 1999

(Fig. 11)

Material: Many specimens in our collection can be assigned to this species, including UALVP 47176, 47179, 51600, 51601, 51602, 51603, 51605, 51606, 51607, 51623, 51632, and 51692. Only two of these (UALVP 51632 and 51692) are preserved as part and counterpart.

Description. This species has the two median prinicipal caudal fin rays expanded proximally and a full neural spine on the second preural centrum, indicating its membership in the Clupavidae (GAYET 1981). The neural arches of the anterior vertebrae are modified, as noted by GAYET (1981) and CAVIN (1999). The vertebral counts given by CAVIN (1999) were 39–41 total with 23–25 being abdominal and 16 caudal. We find a larger range, with 37–42 total vertebrae. The posterior 15–17 are caudal in that they have no associated pleural ribs; however, we cannot determine if the anterior-most of these vertebrae actually have a haemal spine or whether the left and right parapophyses are just very close together. The first anal pterygiophore inserts between the neural spines of the 11th and 12th, or 12th and 13th, centra anterior to the caudal skeleton (i.e., anterior to the first ural centrum of diural terminology).

Remarks. This fish was first reported by CAVIN & DUTHEIL (1999, as Otocephala indet.) and described by CAVIN (1999, in the family Clupavidae). MARTILL et al. (2011: fig. 9C) figured a specimen they identified as "ostaryophysian [sic] close to *Lusitanichthys*". Although it is difficult to be sure based only on the photograph, the specimen they have figured seems to have a longer head length compared to body length than *Lusitanichthys*, and possibly a lower vertebral count.

The vast majority of our specimens of this taxon are less than 45 mm standard length (SL), and CAVIN (1999) reported his specimens as being 33 mm or less in SL. However, one of our specimens (UALVP 51632) is much larger, attaining 72 mm SL. There are no skeletal differences between the larger and smaller *Lusitanichthys africanus* specimens.

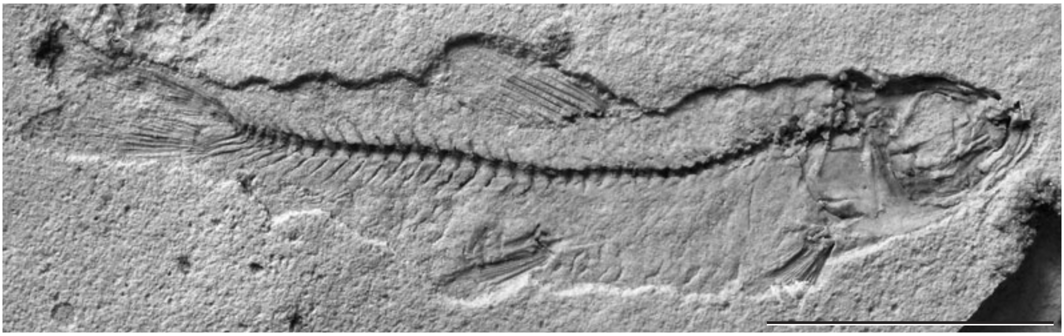

Fig. 11.
Lusitanichthys africanus CAVIN, 1999, UALVP 47176. Scale bar = 1 cm.

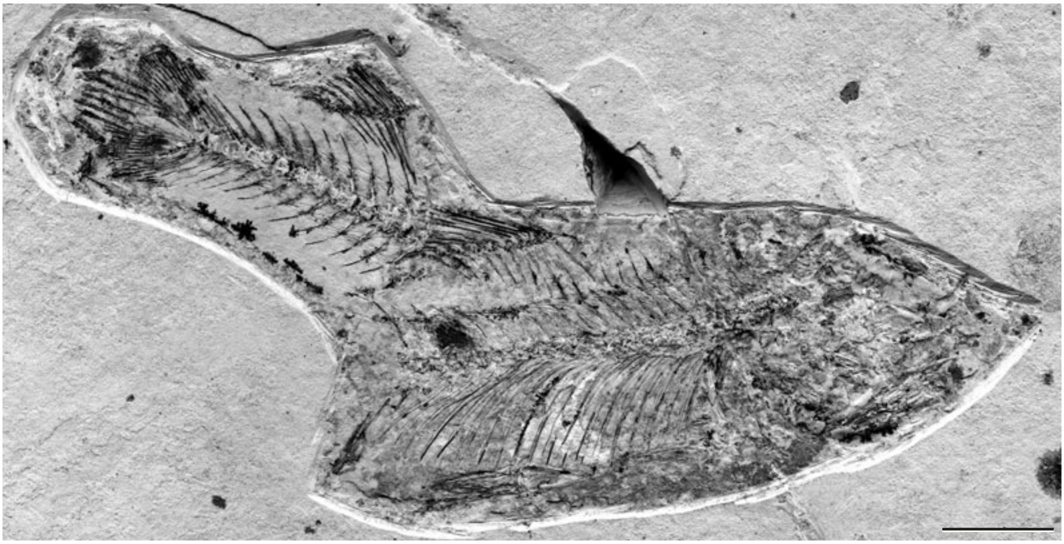

Fig. 12.
Cf. Chanoidei, UALVP 51625. Scale bar = 1 cm.

Cf. Suborder Chanoidei GRANDE & POYATO-ARIZA, 1999
(Fig. 12)

Material: UALVP 51625 is an almost complete fish that partially dissociated during fossilization such that the posterior half of the fish, including the anal fin, is flipped dorsoventrally and slightly rotated so that the anal fin lies near the dorsal fin and the tail and caudal fin are upside-down relative to the trunk and head.

Description. The head region is not well preserved, with the jaws almost completely missing, and the distal parts of the caudal fin rays are not preserved, making a count of the principal rays impossible. The specimen measures 81 mm in SL, has a head length of 29 mm (36 % SL), and a body depth anterior to the dorsal fin of about 23 mm (28 % SL). It is a fairly deep-bodied fish, with robust pleural ribs reaching to the ventral body wall.

There are 38 vertebrae, not including the compound centrum (fused first preural and first ural centra using the diural terminology) and any more posterior ural centra. The anterior few vertebral centra have modified, expanded and fenestrated neural arches. Nineteen pairs of pleural ribs are present. Numerous intermuscular bones are found in the trunk, and in the tail both dorsal and ventral to the vertebral column. The pectoral fin has at least ten rays. The pelvic fin is positioned at a point below the middle of the dorsal fin, and has eight or nine rays. The dorsal fin has two procurrent and 11 principal rays borne on 11 pterygiophores. The anal fin is made up of one procurrent ray and ten branched rays supported by nine pterygiophores. Seven of these pterygiophores are preserved in place under the anal fin, but the two anterior-most anal pterygiophores remained with the front half of the fish and are located posterior to the pelvic fins.

The caudal skeleton has a compound centrum (the fused first preural and first ural centrum, in diural terminology). The uroneural also appears to be fused with this unit. There are two epurals and possibly two uroneurals. At least six hypurals are present, but a broken bone may represent the remains of a seventh. Flanges are present on the neural and haemal spines of the second preural centrum. The total number of caudal-fin principal rays cannot be determined, but a distinctive feature is that the median principal ray of the fin articulates, via an expanded, triangular base, with both the second and third hypurals, which are separated by a V-shaped gap.

Remarks. The median principal ray of the caudal fin articulating on both the second and third hypurals is somewhat similar to the condition found in *Chanos chanos* (FUJITA 1990: fig. 30) and also similar to that seen in the Aptian-Albian *Dastilbe* (MAISEY 1991: figures on p. 281). The presence of two epurals, rather than one as in most gonorhynchiforms (e. g., GRANDE & ARRATIA 2010), is another similarity to *Dastilbe* (e. g., BRITO & AMARAL 2008). The modified neural arches of the anterior vertebral centra are similar to those seen in *Tharrhias araripis*, as illustrated by POYATO-ARIZA (1996: fig. 14) and POYATO-ARIZA et al. (2010: fig. 7.4). Both *Dastilbe* and *Tharrhias* are usually classified in the Chanoidei (GRANDE & POYATO-ARIZA 1999), and, although many key synapomorphies of that group cannot be seen in the fossil, the available evidence leads us to suggest a tentative relationship of the Moroccan fish with the Chanoidei.

Order Aulopiformes ROSEN, 1973
Suborder Enchodontoidei BERG, 1937 [according to SILVA & GALLO 2011]
Superfamily Ichthyotringoidea GOODY, 1969 [following SILVA & GALLO 2011]
Family Dercetidae WOODWARD, 1901 [according to SILVA & GALLO 2011]
Rhynchodercetis ARAMBOURG, 1943

***Rhynchodercetis* sp.**
(Fig. 13)

Material: Numerous specimens are in the collections, including UALVP 43594.

Description. These specimens show a very elongate dercetid fish, ranging in size from about 5 cm to 12 cm standard length (SL). The head length is about 28 % of SL, with the jaws extending far forward from the orbit. It appears the lower jaw is only slightly shorter than the upper jaw, although the precise relative lengths are often difficult to determine. There are about 60–63 vertebrae in total, with the anterior ones being much longer than deep, but the posterior ones being almost as deep as long. The dorsal fin is placed posteriorly on the body, and the pelvic fins are positioned below the insertion of the dorsal fin. The anal fin is closer to the caudal fin than it is to the pelvic fins. There are triradiate scutes preserved in many of the specimens, apparently in a single row on each flank. At least one specimen is preserved with still-articulated remains of a small fish in the region of its stomach, and another with the digested remains of fish in its posterior abdomen.

Remarks. The Moroccan specimens belong with the family Dercetidae, based on the elongate rostrum, the shallow, elongate body (CHALIFA 1989), and lateral rows of distinctive, tri-radiate scutes (BLANCO et al. 2008). CHALIFA (1989: tab. 2) distinguished four dercetid genera based on several characters. From her comparisons, the Moroccan species is tentatively placed

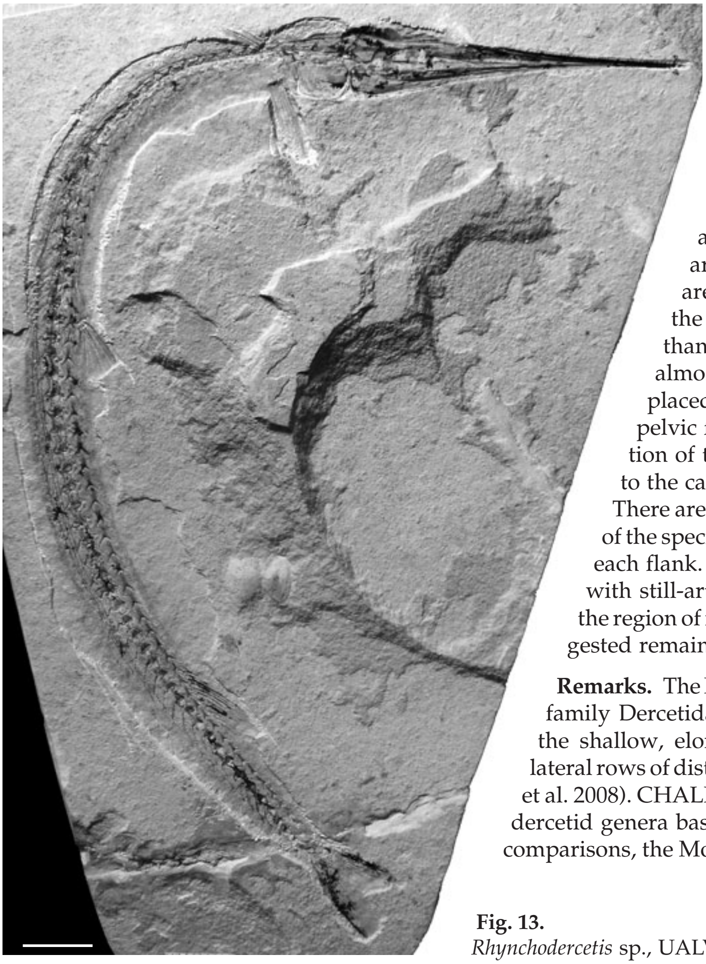

Fig. 13.
Rhynchodercetis sp., UALVP 43594. Scale bar = 1 cm.

Fig. 14.
Cf. *Dercetis* sp., UALVP 51617. Scale bar = 1 cm.

in the genus *Rhynchodercetis*, based on the elongate rostrum with lower jaw somewhat shorter than the upper jaw, and the two rows of tri-radiate scutes. MARTILL et al. (2011: fig. 10C) reported *Rhynchodercetis* from the Agoult locality, and our material appears to be very similar. CAVIN & DUTHEIL (1999) also reported *Rhychodercetis* sp. from Daoura. *Rhynchodercetis yovanovitchi* is known from Jbel Tselfat Morocco; based on the description and poor photos, there is nothing to distinguish *R. yovanovitchi* from the Agoult specimens. *Rhynchodercetis yovanovitchi* is abundant in the Moroccan Lower Cenomanian of Jbel Tselfat (ARAMBOURG 1943, CHALIFA 1989). The Lower Cenomanian Ein-Yabrud beds contain two other related species (CHALIFA 1989), *Rhynchodercetis gracilis* and *Dercetoides venator*.

Cf. *Dercetis* AGASSIZ, 1834

(Fig. 14)

Material: UALVP 51617, 51668, both complete skeletons.

Description. These two specimens represent an undescribed species in the diverse family Dercetidae (for a list of recognized species, see SILVA & GALLO 2011). The overall proportions, with moderately elongated body and with a skull that is not greatly elongated but nevertheless has a tapered rostrum like other members of the family (GOODY 1969), are similar to those seen in *Dercetis* AGASSIZ, 1834, and in *Dercetoides venator* CHALIFA, 1989. In addition, as in *Dercetis*, *Dercetoides* and *Rhynchodercetis*, there is a single row of tri-radiate scutes along each flank. However, as in *Dercetis* (CHALIFA, 1989) there is also a row of scutes along the dorsal midline anterior to the dorsal fin. The anal fin is short, but the dorsal fin is greatly elongated, unlike that of most dercetids, with a base that is about 40 % of the total length of the fish. In most other dercetids the dorsal fin is very short (GOODY 1969, TAVERNE 2006a,b). An exception is *Ophidercetis italiensis* TAVERNE, 2005a, which has an even more elongate dorsal fin, but unlike in the two specimens from Agoult, in *Ophidercetis* the skull is more elongate and the body and anal fin are also greatly elongate.

Remarks. These two specimens represent an undescribed species of dercetid close to *Dercetis*. UALVP 51617 is preserved with an even smaller fish, possibly of the same species, in the region of its stomach. TAVERNE (2005a) noted that many dercetid fossils contain the remains of prey fishes that are smaller or almost as large as the fish that consumed them. Alternatively, viviparity has been suggested for some actinopterygians in which a smaller individual is preserved inside a larger one (e. g., RENESTO & STOCKAR 2009). In our dercetid specimen, the individual preserved inside the other is well ossified and about one third of the standard length of the fish encompassing it. This may indicate it is more likely a food item than an embryo, but whether it is prey or young cannot be clearly determined.

Sept Acanthomorpha sensu JOHNSON & PATTERSON, 1993

The following specimens, representing three different species, are all included in the Acanthomorpha based on the form of the first anal pterygiophore being a type III hemaxanal complex (see BLOCH 1969; the form in which the first anal fin pterygiophore is elongated to the point at which it reaches, or almost nearly so, the vertebral centrum), and on presence of spines in the dorsal and anal fins.

Order incertae sedis
Superfamily Aipichthyoidea OTERO & GAYET, 1996

Family incertae sedis

Two of the taxa, with two specimens each, are further classified in the Aipichthyoidea based on the thoracic position of the pelvic fins, and each having a caudal fin with 19 principal rays, a condition found only in Aipichthyoidea and Pharmacichthyidae among acanthomorphs (TAVERNE 2004). The specimens cannot be attributed to the Pharmacichthyidae, as that family is characterized by having only a single spine in the dorsal and anal fin, and the dorsal spine and pelvic spine uniquely bear hooks on their anterior edges. Aipichthyoids are characterized by having three supraneurals positioned in advance of the first dorsal pterygiophore and a single neural spine between the first and second dorsal pterygiophore. The relationships of the supraneural bones, neural spines and dorsal fin pterygiophores can be expressed as a formula, which was termed "Johnson's formula" (attributed to JOHNSON 1994) by OTERO & GAYET (1996) and TAVERNE (2004), but the relationship of these bones was previously discussed by AHLSTROM et al. (1976) and the formula is better attributed to them. According to OTERO & GAYET (1996), the predorsal formula for Aipichthyoidei is 0+0+0/x/, where "0" indicates a supraneural bone, "/" indicates a neural spine, and "x" indicates a dorsal pterygiophore bearing an unspecified number of fin spines. In the original formula of AHLSTROM et al. (1976), the "x" was a number indicating the number of spines that were associated with the pterygiophore.

The aipichthyoid predorsal formula is found in UALVP 51611 (species A below). In species B (below) one of the specimens has the regular aipichthyoid formula and the other has the second pterygiophore inserting between the first and second neural spines alongside the first pterygiophore, giving a predorsal formula of 0+0+0/x+x/. This somewhat aberrant predorsal formulae is not considered sufficient reason to exclude the specimen from the Aipichthyoidei, although further study is needed.

Unnamed species A

(Fig. 15)

Material: UALVP 51611, complete fish.

Description. This is a deep-bodied fish, with a standard length (SL) of about 50 mm, and greatest body depth, of 33 mm, below the centre of the dorsal fin. The head length is about one third of SL. There are five spines and 22 rays in the dorsal fin, and three spines with 12 rays in the anal fin.

Remarks. UALVP 51611 cannot be included in the two named aipichthyoid families, as it differs from Aipichthyidae PATTERSON, 1964, in numbers of fin spines (five dorsal and three anal in the Moroccan form compared to two or four dorsal spines and four to five anal spines in Aipichthyidae; OTERO & GAYET 1996), and it has three epurals in the caudal skeleton unlike the two epurals of Aipichthyoididae GAYET, 1980. It is not congeneric with the incertae sedis *Friegichthys* OTERO, 1997, either, as it also has more numerous dorsal fin spines (three in *Freigichthys*; OTERO 1997) than that genus. It is left incertae sedis in the suborder.

Unnamed species B

(Fig. 16)

Material: UALVP 51665, a complete fish, and UALVP 47142, missing the head and tail.

Description. This species is relatively longer compared to its body depth than species A. UALVP 51665 has an SL of 50 mm, head length about 40 % of SL and greatest body depth of 25 mm at the midpoint of

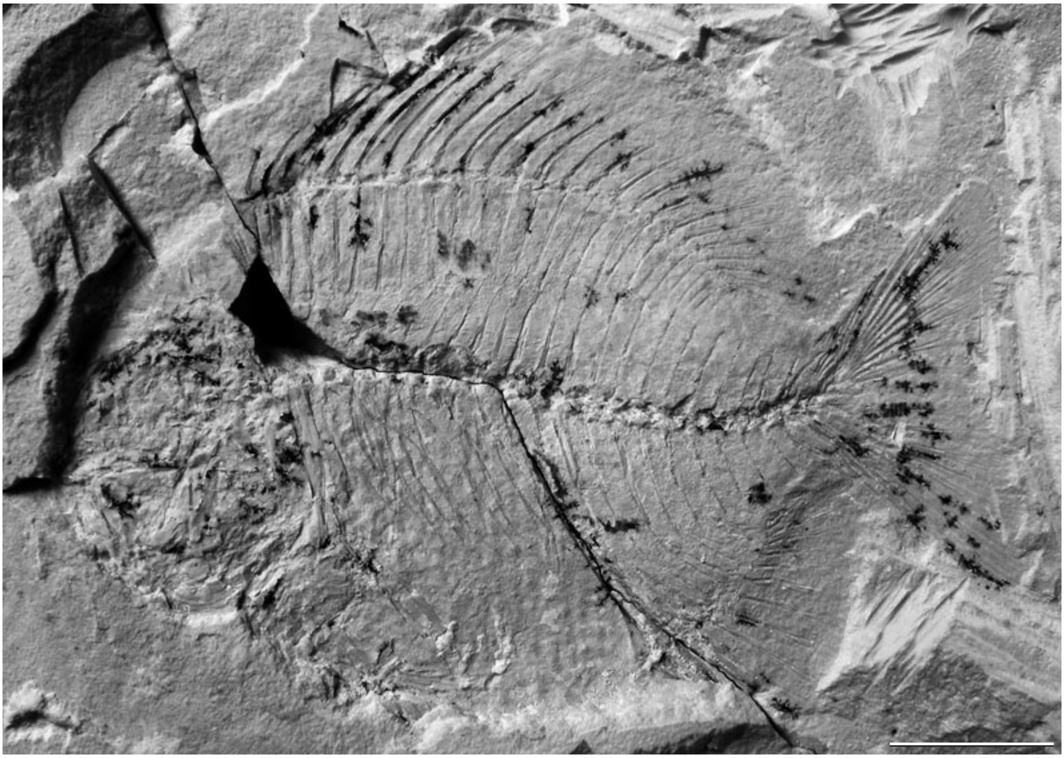

Fig. 15.
Acanthomorpha species A (Aipichthyoidea), UALVP 51611. Scale bar = 1 cm.

Fig. 16.
Acanthomorpha species B (Aipichthyoidea), UALVP 51665. Scale bar = 1 cm.

the dorsal fin. It also has a typical aipichthyoid predorsal formula (0+0+0/x/x/), but UALVP 47142 has the formula: 0+0+0/x+x/x/; however, we consider this to be individual variation until further study. The dorsal fin has 11–12 spines and 10 rays. The anal fin of UALVP 51665 has five spines and 10 rays; that of UALVP 47142 is incompletely preserved. UALVP 51665 has a total of 26 vertebrae, of which 11 are abdominal. There are three epurals in the caudal skeleton.

Remarks. UALVP 47142, from the 2007 collections, is a partial fish, missing both the caudal region and the anterodorsal skull. The lack of crucial elements in this fossil prevented us from determining its identity other than as an acanthopterygian fish (MURRAY et al. 2007). Although UALVP 47142 is too incompletely preserved to compare well with UALVP 51665, there is no obvious reason to consider it a separate taxon. We also tentatively attribute the specimen figured by MARTILL et al. (2011: fig. 11 A,B) to this same taxon, based on their photograph, in which the fish appears to have eleven or twelve dorsal fin spines with nine rays and the anal fin with four spines and ten rays; this specimen appears to have a less deep body (about 37 % of SL) than our specimens. Species B cannot be attributed to any other aipichthyoid genus based on its possession of a much greater number of dorsal fin rays than found in all others (see OTERO & GAYET 1996, OTERO 1997, TAVERNE 2004).

Order incertae sedis

Unnamed species C

(Fig. 17)

Material: UALVP 51610 and UALVP 51667, both complete fish, and UALVP 51666, a complete fish in part and counter part.

Description. These three specimens are the smallest acanthomorphs in our collection, with UALVP 51610 being about 24 mm SL, and UALVP 51666 about 18 mm and UALVP 51667 having an SL of only 17 mm. The body depth varies from 47–58 % SL (the largest specimen being the deepest bodied) and head length is roughly one third of SL. The three specimens differ slightly in counts, although both UALVP 51610 and 51666 have an anal fin with four spines and 12 rays (the rays are difficult to discern in UALVP 51667, but there appear to be ten). UALVP 51610 has a dorsal fin with eight spines and 14 rays, and there are 26 total vertebrae of which 9 are abdominal. UALVP 51666 has seven spines and 15 rays in the dorsal fin, and there are 27 total vertebrae of which 11 are abdominal. UALVP 51667 has seven spines and perhaps 13 rays, and 25 vertebrae of which 10 are abdominal. All three specimens have two supraneurals in advance of the first neural spine, and a third supraneural and the first dorsal pterygiophore insert between the first and second neural spines, giving a predorsal formula in this species of 0+0/0+x/x/. There are 18 principal rays in the caudal fin.

Remarks. The slight differences in number of dorsal fin rays and spines, and numbers of abdominal vertebrae among the three specimens are not considered indicative of separate species although this may change with future study. The number of caudal-fin principal rays indicates the affinity of this species with Polymixiidae, Dinopterygidae and Pycnosteroididae; however, all three of these families have teeth on the entopterygoid (PATTERSON 1964); the Moroccan specimens have no sign of teeth on any of the palatal bones. A late Cretaceous fish from Italy, *Johnsonperca annavaccarii* TAVERNE, 2010, has the same predorsal formula as the Moroccan specimens. It was placed in the Perciformes (TAVERNE 2010); however, we do not include the Moroccan species in that order because of the 18 principal rays in the caudal fin. Somewhat similar dorsal formulae, in which three supraneurals are present and fill the space between the occiput and first dorsal fin pterygiophore, are found in some beryciforms, such as *Diretmus* (JOHNSON & PATTERSON 1993: fig. 20K). Two other acanthomorphs from the Cretaceous of Morocco, *Omosoma* and *Omosomopsis* from the Jbel Tselfat (GAYET 1978), are distinguished from the Agoult specimens by having only four spines in the dorsal fin.

Associated fauna and flora and palaeoenvironment

There is a diverse fauna associated with the fish remains from the Agoult locality, some of which have been reported by MARTILL et al. (2011). Based on our own collections, the invertebrate fauna includes:

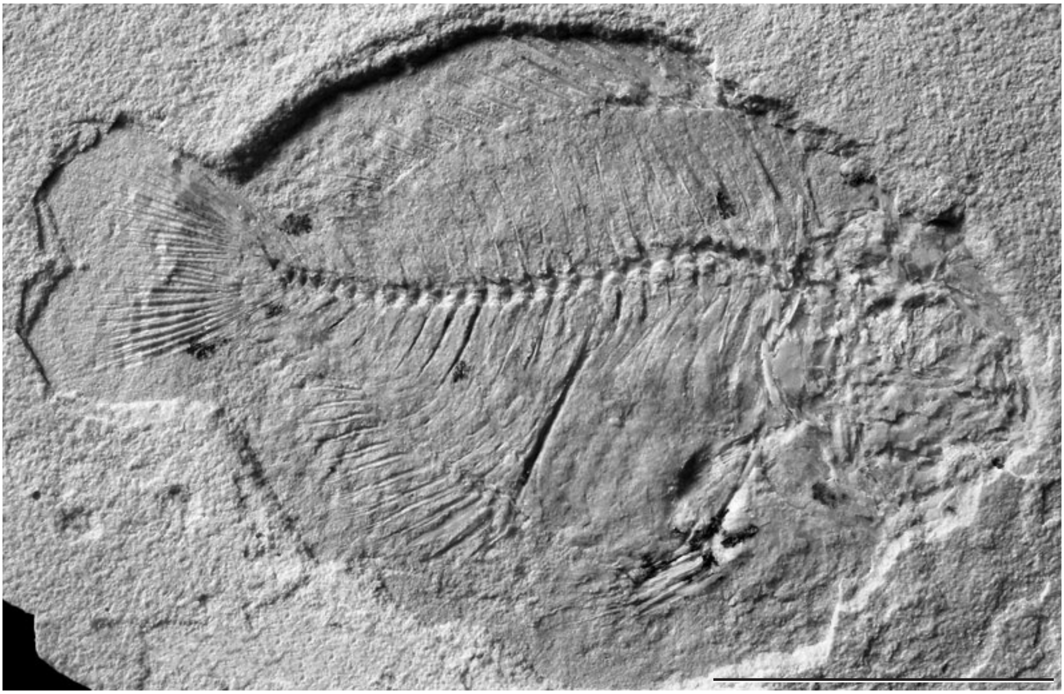

Fig. 17.
Acanthomorpha species C (Order incertae sedis), UALVP 51610. Scale bar = 1 cm.

Mollusca – bivalves, gastropods; Arthropoda – horseshoe crabs, crabs, shrimps, lobsters, isopods, rare beetles (ENGEL et al. 2012); and Echinodermata – pelagic crinoids. These animals would have lived in the same environment as the fishes (with the exception of the insects). MARTILL et al. (2011) additionally reported an insect identified as a hymenopteran, which presumably fell into the water and was later fossilized. Those authors also reported and figured the only non-fish vertebrate known from the site, a small lizard of unknown size. Unfortunately, the specimen itself is at present unaccounted for (MARTILL et al. 2011), and it is not known if the lizard was a marine form or a terrestrial form that was washed into the marine environment.

Plant fossils from Agoult are also known, with a number in our collections. These include horsetails, ferns, dicotyledons, and monocotyledons. A few ichnofossils are also present, with traces of insect damage on some of the leaf edges (ENGEL et al. 2012). The fairly common occurrence in the deposits of terrestrial plants and of some insects capable of flying indicates a near-shore environment.

The environment during deposition of the sediments at the Agoult locality has been presented as being an open marine platform (ETTACHFINI & ANDREU 2004). In addition, our (GIBB) isotope data indicates waters of normal marine salinity at the levels where the fish are found (but not for some of the beds above and below those levels). A marine setting for the slightly dolomitized lithographic limestone was established (by GIBB) from stable isotope geochemistry acquired from the rock samples collected every 5–30 cm (typically every 10 cm) throughout the six metre section and from the matrix on the bedding planes of every fossil in our collections from 2006−2008. The silica nodules and their layers were also analyzed and provided equivalent ratios to the surrounding strata. The isotopic data confirmed a normal marine palaeoenvironment: $\delta^{18}O_{carb(VPDB)}$ of −0.892 ‰. The resultant palaeotemperature is approximately 24.8 °C. These data thus support the hypothesis that the Tethys Sea in this region was an open marine carbonate platform, with a connection to the east with the Atlantic Ocean (FERRANDINI et al. 1985, MURRAY 2000, CAVIN et al. 2001, ETTACHFINI & ANDREU 2004, MURRAY & WILSON 2009).

The fishes themselves also indicate that the platform waters were likely very shallow, and near shore. Paraclupeids have been recovered from both marine and freshwater, as well as estuarine sediments, but all those from marine waters were interpreted as likely coming from nearshore areas (HAY et al. 2007). Macrosemiids have been reported from both freshwater and reef environments in Spain, and the Mexican specimens are likely marine reef or brackish water inhabitants (GONZALEZ-RODRIGUEZ & REYNOSO 2004). Dercetids have been found in marine deposits of the Tethys (e. g., *Apuliadercetis* TAVERNE 2006a; *Nardodercetis* TAVERNE 2005b; *Ophidercetis* TAVERNE 2005a; *Caudadercetis* TAVERNE 2006b) as well as marine deposits from elsewhere (Western Interior Seaway, WILSON & CHALIFA 1989; South America, FIGUEIREDO & GALLO 2006), and some at least of these are from deposits interpreted as outer shelf (FIGUEIREDO & GALLO 2006). Pycnodonts are also possibly reef-dwellers found predominantly in shallow epicontinental seas (NURSALL 1996a). These various lines of evidence indicate that the Agoult locality samples a depositional environment of nearshore waters in a shallow open platform, with no evidence of brackish or freshwater influence.

Faunal comparisons

Both CAVIN & DUTHEIL (1999) and BANNIKOV et al. (2010) noted the faunal similarity of the Moroccan locality ("Daoura" in the former paper and "Oued Sebaa" in the latter, but probably both synonymous with, or at least close to, the Agoult locality of this paper) and the lower Cenomanian locality Jbel Tselfat. Recently, work has recommenced at Jbel Tselfat, with new outcrops discovered and well over 100 specimens collected (KHALLOUFI et al. 2010). Both the Agoult and Jbel Tselfat faunas contain pycnodonts, paraclupeids, clupavids, dercetids and acanthomorphs. However, this similarity is not limited to the Moroccan faunas. Clupavids alone seem to have had a restricted distribution in the Tethys; although *Clupavus brasiliensis* SILVA SANTOS, 1985 was placed in the type genus of this family, that species does not appear to have the diagnostic enlarged bases of the two median caudal fin rays and differs from the type species in having three epurals and four uroneurals compared to two epurals and three uroneurals in *C. maroccanus*. Paraclupeids are known from sites worldwide, including many other Tethyan areas. Similarly, dercetid fishes were successful Late Cretaceous marine fishes (BLANCO & ALVARADO-ORTEGA, 2006). Members of this family have been reported from many areas around the Tethys Sea, including the Cenomanian of Israel and Lebanon as well as the Cenomanian-Campanian of England, Trieste, Sicily, Italy, and Slovenia. Dercetids are also present in Turonian deposits of Brazil, Mexico, and Canada (WILSON & CHALIFA 1989, FIGUEIREDO & GALLO 2006). It seems that these fishes were part of a widespread ichthyofauna that was not limited to the Moroccan or Tethyan area.

In the Cenomanian and Turonian, the Tethys Sea extended over many parts of northern Africa. It reached into southern Morocco as well as into Tunisia, Algeria, Libya, and Egypt, and as far as Mali and Niger (SMITH et al. 1994, CAVIN & DUTHEIL 1999, MURRAY 2000, ETTACHFINI & ANDREU 2004). This shallow expansion of the Tethys during this time allowed many fishes to extend their distributions throughout the area (LOPEZ-ARBARELLO 2004). An additional connection from the Tethyan transgression through to the Atlantic Ocean also occurred (ETTACHFINI & ANDREU 2004) and is reflected in the similarities among the fish faunas from the Late Cretaceous in northern Africa and areas on the western side of the Atlantic (CAVIN & DUTHEIL 1999, MURRAY & WILSON 2009).

A number of fish faunas are known from the Cenomanian/Turonian, and the similarities of their fish assemblages have been noted by several authors (e. g., CAVIN & DUTHEIL 1999, FOREY et al. 2003, EKRT 2005, CUMBAA & MURRAY 2008). CUMBAA & MURRAY (2008) emphasised that the various Tethyan localities they compared all represent different environments, varying from shallow lagoonal-reef (Dalmatian Coast) to pelagic external platform (Goulmima, Morocco). The environment during deposition at the Agoult locality is similar to that of Goulmima, being an open marine platform. However, the faunas from these two Moroccan localities are not similar. The two localities share the presence of pycnodonts, but there the similarity ends. The Goulmima fauna has in general more basal teleosts, such as crossognathiforms, elopomorphs and enchodontoids, which are as yet unknown from Agoult. By contrast, more derived teleosts such as acanthomorphs are relatively diverse in Agoult, with at least three species, whereas none are reported from Goulmima. This difference may suggest a different age for the two sites, with Goulmima being Turonian, and Agoult possibly Cenomanian. However, acanthomorphs are known from the Turonian Dalmatian coast and Bohemian Basin localities (CUMBAA & MURRAY 2008). With more collecting at the Agoult locality, a greater diversity of fauna is expected, making the Tethyan faunal connections more clear.

As more fossil deposits are found around the world, the similarities among the faunas from distant areas become apparent. Many of these fishes seem to represent geographically wide-ranging families; however, at the species level they are apparently much more restricted in their range. Whether this reflects their true distributions, or merely a bias caused by lack of fossils or even a lack of systematic revisions, may become clear with increased interest driving new finds and more excavations in Cretaceous deposits throughout the world.

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