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A new Cenomanian ichthyofauna from southeastern Morocco and its relationships with other early Late Cretaceous Moroccan faunas

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Abstract

A new ichthyofauna from southeastern Morocco, comprising five forms, is briefly discussed. The faunal composition differs from the Early Cenomanian Kem Kem and Early Turonian Goulmima assemblages, but is close to that from Jebel Tselfat. We propose a Late Cenomanian age for the new fauna and that from Jebel Tselfat. The evolution of these fish assemblages shows the Moroccan fish faunas to have been related to those from South America until at least the Early Turonian. Central Tethyan influence on faunas seems to have been restricted to a short period of time during the beginning of the Late Cenomanian transgressive phase.

Introduction

In 1997, the Musée d'Histoire Naturelle of Boulogne-sur-Mer (Pas de Calais, northern France) and the Muséum national d'Histoire naturelle (Paris) obtained about seventy specimens of small fish preserved as negatives on slabs of fine-grained sandstone. The fossils were found about 100 km south of Erfoud (Morocco), probably on the escarpment of the Kem Kem plateau near the Oued (wadi) Daoura, although precise data on stratigraphical and geographical provenance are lacking. Anatomical details are barely distinguishable on the original individuals. The present faunal list and descriptions are based on black silicone rubber positive casts. Specimens are small, measuring 50 mm or less in length. Since there is no sign of incomplete ossification of bones in most of the skeletons, we assume the majority of specimens to represent adults of small size rather than juveniles.

Intensive collecting during the last few years in various parts of Morocco has yielded several rich fish assemblages. A comparison between these and the present fauna in time and space has resulted in a comprehensive picture of faunal succession in this area (Figure 1).

Geological setting and faunal characteristics

Kem Kem beds

The non-marine Kem Kem red beds (Sereno et al. 1996) of 'Infracénomanien' age (Clariond 1933) are exposed over 250 km north and south of Erfoud, in the Tafilalet and Kem Kem in southeastern Morocco (Lavocat 1954). They rest unconformably on Palaeozoic strata and are overlain a marine Cenomanian-Turonian platform. The fauna of the Kem Kem beds comprises turtles, snakes, varanoid lizards, dinosaurs, crocodiles, and pterosaurs (Lavocat 1948, Buffetaut 1994, Russell 1996, Sereno et al. 1996, Tong & Buffetaut 1996, Kellner & Mader 1997). The fish fauna is represented by elasmobranchs, coelacanths, lungfishes, polypterids, gars, amiids, semionotids, osteoglossids, ostariophids, clupeomorphs, and acantomorphs (Tabaste 1963, Wenz 1980, Dutheil 1997, in press a, b, Forey 1997, Forey & Grande 1998). Elasmobranch biostratigraphy suggests a Cenomanian age (Dutheil 1996, Sereno et al. 1996).

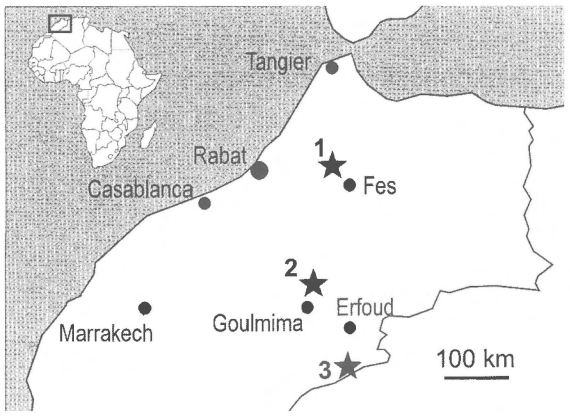

Figure 1. Map of Morocco showing location of the main early Late Cretaceous fish assemblages: 1 – Jebel Tselfat, Late Cenomanian; 2 – Goulmima, Early Turonian; 3 – Kem Kem beds, Early Cenomanian; and the new locality (Daoura), Late Cenomanian.

Goulmima

The Cenomanian-Turonian transgression follows conformably on top of the Kem Kem beds. At Akerboûss, north of Erfoud, the section reaches a thickness of 51 m (Ferrandini et al. 1985), with the ammonite *Neolobites vibrayeanus* (d'Orbigny) dating the base of the succession (i.e., unit 1 of Ferrandini et al. 1985) as early Late Cenomanian (Thomel 1972). This carbonate succession is well exposed at the top of a cliff, extending about 5 km parallel to the north of the road leading from Errachidia to Goulmima. Several localities east of the villages of Tadirhoust and Asfla, 15 and 20 km north of Goulmima, respectively, have yielded a diverse vertebrate fauna. Fishes occur in ovoid, early diagenetic calcareous nodules at the top of the succession, in association with the Early Turonian ammonite genus *Mammites*. The vertebrate fauna comprises several forms of marine reptiles and fishes, particularly sclerorhynchids, pycnodontids, ichthyodectids, araripichthyids, osmeroidids, pachyrhizodontids and enchodontids (Cavin 1995, 1997a, b, 1999).

Jebel Tselfat

Another important early Late Cretaceous Moroccan fish fauna occurs at the Jebel Tselfat, northwest of Fès, near the town of Sidi-Kacem. Two localities (Aïn el Kerma and Sigda) have yielded rich assemblages, comprising 21 actinopterygian taxa (pycnodonts, aspidorynchids, ichthyodectids, elopids, pachyrhizodontids, tselfatiids, clupavids, clupeids, photichthyids, ichthyotringids, dercetids, enchodontids, polymixiids, and berycids), described by Arambourg (1954) and reviewed in a series of subsequent papers. The fossil fishes are preserved on bituminous-shale slabs; bone material is often crushed or absent. Skeletons are thus preserved as negatives.

There are no absolute (radiometric or magnetic) age assignments, nor has any microfauna been recorded. Based on vertebrate assemblages, Arambourg (1954) dated these beds as Early Cenomanian.

Systematic palaeontology

The present faunal analysis is preliminary; specimens available were not collected by us personally. Despite this drawback, the proportional abundance of each form in our sample is indicated. It should be borne in mind, however, that this need not represent true abundance at the sampling locality.

Pycnodontidae (sensu Nursall 1996) indet.

Order Pycnodontiformes
Suborder Pycnodontoidei
Family Pycnodontidae (sensu Nursall 1996)
Pycnodontidae (sensu Nursall 1996) indet.

Material – A single specimen (Plate I, Figure A), a small juvenile of approx. 16 mm standard length, without temporal fossae and a peltate pattern of squamation (Wenz, pers. comm.). Following Nursall (1996), these two features characterise the Pycnodontidae, but exclude the present form from the derived Pycnodontidae (e.g. *Pycnodus*, *Coelodus*, *Tepexichthys*, and *Stemmatodus*).

Otocephala indet.

Subclass Teleostei
Cohort Clupeocephala
Subcohort Otocephala
Otocephala indet.

Material – This represents the second-most abundant species (approx. 31%; Plate I, Figure D), which, in common with the clupavids, *Lusitanichthys characiformis* (Cenomanian of Portugal; Gayet 1981) and *Clupavus maroccanus* (Cenomanian of Jebel Tselfat; Arambourg 1950, Taverne 1995), shows modifications of elements associated with the first vertebrae. This taxon shares possible synapomorphies of Otocephala (Clupeomorpha and Ostariophysi; Johnson & Patterson 1996) such as a pleurostyle and the fusion

of hypural two and the compound terminal vertebral centrum (Lecointre & Nelson 1996). A detailed description of the present form will be published elsewhere (Cavin, in prep.).

Aff. *Spratticeps*

Superorder Clupeomorpha
Order incertae sedis
aff. *Spratticeps*

Material – This is the commonest form in the sample (approx 61%; Plate I, Figure B). On the basis of Taverne's (1997) work on fossil primitive clupeomorphs, and of Grande's (1982, 1985) revisions of clupeomorph fishes, the present form can be shown to be a clupeomorph in that it has several abdominal scutes. It shares with the ellimmichthyiforms, plus the more derived clupeomorphs, a complete series of dorsal scutes between the skull and dorsal fin (character 11 of Taverne 1997), and shares with *Eoknightia* and the more derived clupeomorphs a reduced first ural centrum in comparison with the first preural centrum (character 18 of Taverne 1997). It does not show, however, a synapomorphy of *Santanaclupea* plus the clupeiforms, i.e. the presence of a recessus lateralis, nor an apomorphy of clupeiforms, i.e., loss of the beryciform foramen. Thus, the new material may be placed near *Spratticeps gaultinus* in the cladogram proposed by Taverne (1997). It shares with that species a similar ornament of the posterior part of the skull roof (Patterson 1970). Although preservational styles of *S. gaultinus* and the present form differ significantly (the former being known only from four isolated braincases, which makes a comparison difficult), the new material is provisionally referred to as aff. *Spratticeps*.

Paraclupeidae indet.

Order Ellimmichthyiformes
Family Paraclupeidae
Paraclupeidae indet.

Material – Two specimens of Clupeomorpha are clearly different from aff. *Spratticeps*; one of these (M. Dechamps collection) is well preserved (Plate I, Figure C). It is a deep-bodied fish with a very convex abdominal region, with ventral and dorsal scutes, the latter having 'wings', which give them a subrectangular shape as in Paraclupeidae (= 'Ellimmichthyidae', Chang & Grande 1997). The present form is currently being studied by Zaragüeta (MNHN, Paris) and is here regarded as an indeterminate paraclupeid.

Rhynchodercetis sp.

Division Neognathi
Section Eurypterygii
Order Alepisauriformes
Suborder Ichthyotringoidei
Family Dercetidae
Rhynchodercetis sp.

Material – This longirostrine dercetid is rare (approx. 6%) and not well preserved (Plate I, Figure E). Available specimens show an elongate rostrum, edentulous jaws and small dorsal fins allowing a preliminary placement in *Rhynchodercetis*. These features are unique to the genus and are not shared with closely related species such as *Dercetoides venator* (see Chalifa 1989), *Hastichthys gracilis* (see Chalifa 1989) and *Cyranichthys ornatissimus* (see Casier 1965). Additional material is needed to determine its systematic affinities more precisely.

Relationships

The fish assemblage of the Daoura locality differs significantly from that of the nonmarine, Early Cenomanian Kem Kem beds and of the marine Early Turonian of Goulmima. The forms listed above have phylogenetic relatives in the Jebel Tselfat assemblage, however, for instance the presence of a primitive clupeomorph, a possible clupavid, and *Rhynchodercetis*. Although the Daoura assemblage is still poorly known, the similar faunal composition with that of the Jebel Tselfat suggests these faunas to be of comparable age.

Arambourg (1954) pointed out that most species of the Jebel Tselfat were known only from this locality, but that most had close relatives at several other early Late Cretaceous 'Mesogean' localities, such as Komen or 'Karst Triestain' (Slovenia), Hvar Island (Croatia), and Haquil and Hgula (Lebanon). Subsequent authors, and Gaudant (1978) in particular, confirmed this view, noting the close affinities between acanthopterygians of the Jebel Tselfat and of the Lebanese Cenomanian. On the basis of comparisons of faunal assemblages, Arambourg (1954) dated the Jebel Tselfat as Early Cenomanian, an assignment relying in part on close similarities between the faunas from this locality and from Hvar Island (Lesina). The age of the fish-bearing

shales at the latter locality was originally thought to be Cenomanian. Radovcic (1975) dated it as Turonian, based on the presence of the bivalve genus *Chondrodonta*. This would imply that the Jebel Tselfat assemblage might actually be younger than previously thought.

In view of the geological setting in the probable source area of the present Daoura assemblage, we propose a Late Cenomanian age for this and for the Jebel Tselfat faunas.

Evolution of fish assemblages

The relatively limited geographical distribution and stratigraphical range which characterises the Kem Kem, Daoura, Jebel Tselfat and Goulmima assemblages, allows the general evolutionary pattern of fish faunas in northwest Africa during the early Late Cretaceous to be reconstructed.

The Early Cenomanian assemblages of the Kem Kem beds contain at least two genera that show sister-species pairings with South America, viz. *Mawsonia* and *Calamopleurus* (Wenz 1980, Forey & Grande 1998). The presence of sister-group pairings between Africa and South America has been established for older fish taxa (e.g., *Dastilbe/Parachanos*, *Ellimmichthys longicostatus/E. goodi*), and for terrestrial vertebrates (Buffetaut & Rage 1993), such as *Irritator/Spinosaurus* (Sereno et al. 1998).

The Late Cenomanian is marked by the beginning of an important transgressive phase. The opening of the Erfoud-Errachidia carbonate platform is oriented to the east or northeast. This connection enabled the arrival of Tethyan (Mesogean) invertebrate faunas, with some endemic species of rudistid bivalves and ostracods (Ferrandini et al. 1985). The new fish fauna described in the present contribution probably relates to this stage in the evolution of the basin. Its relationships with the Jebel Tselfat assemblage, then situated near the northern margin of the south Tethyan carbonate platform (Dercourt et al. 1993), are probably ascribed to the same northeasterly marine channel. Three units, corresponding to three different palaeoenvironments, have been defined in the Late Cenomanian part of the Erfoud-Errachidia carbonate platform. The lowermost corresponds to sediments deposited in a quiet, shallow-marine environment, the middle one to an enclosed proximal reef platform, and the uppermost to an infra- or mediolittoral setting (Ferrandini et al. 1985). It is impossible at present to determine from which of these units the Daoura fish fauna originated. The Lower Turonian is marked by the highest sea level of the transgressive phase and by the disappearance of facies zonation (Ferrandini et al. 1985). The opening of the Atlas Gulf allowed new faunas to reach the area, as demonstrated by the Goulmima fish assemblage, which contains forms with South American affinities, such as *Araripichthys* and *Goulmimichthys* (Cavin 1997a), and others with wider geographical ranges, and which is very different from the Daoura fauna presented here. The evolution of faunal composition in fish assemblages is due to modifications in palaeoenvironmental conditions (i.e., deeper-marine environment) and in palaeogeographical influences (i.e., connection with South American faunas).

Conclusion

During the 5 Ma Cenomanian/Early Turonian transition interval, a restricted geographical area in southeastern Morocco was characterised by important changes in fish assemblages. The first change – between the Early Cenomanian Kem Kem fish fauna, with South America affinities, and the probably Late Cenomanian Daoura fauna (with central Tethyan affinities) – may be ascribed to a modification of the palaeoenvironment: the former being terrestrial, the latter shallow marine. The next change between the Daoura and the Early Turonian Goulmima faunas (both marine) was probably due to modifications in the palaeogeography: connections with the central Tethys first, and with South America later. Thus, the southeastern Moroccan fish faunas were related to South America faunas until at least the Early Turonian. A central Tethyan influence appears to be restricted to a short interval during the beginning of the Late Cenomanian transgressive phase. Although the faunal list presented here is preliminary, our results confirm that transgression occurred from the east or northeast.

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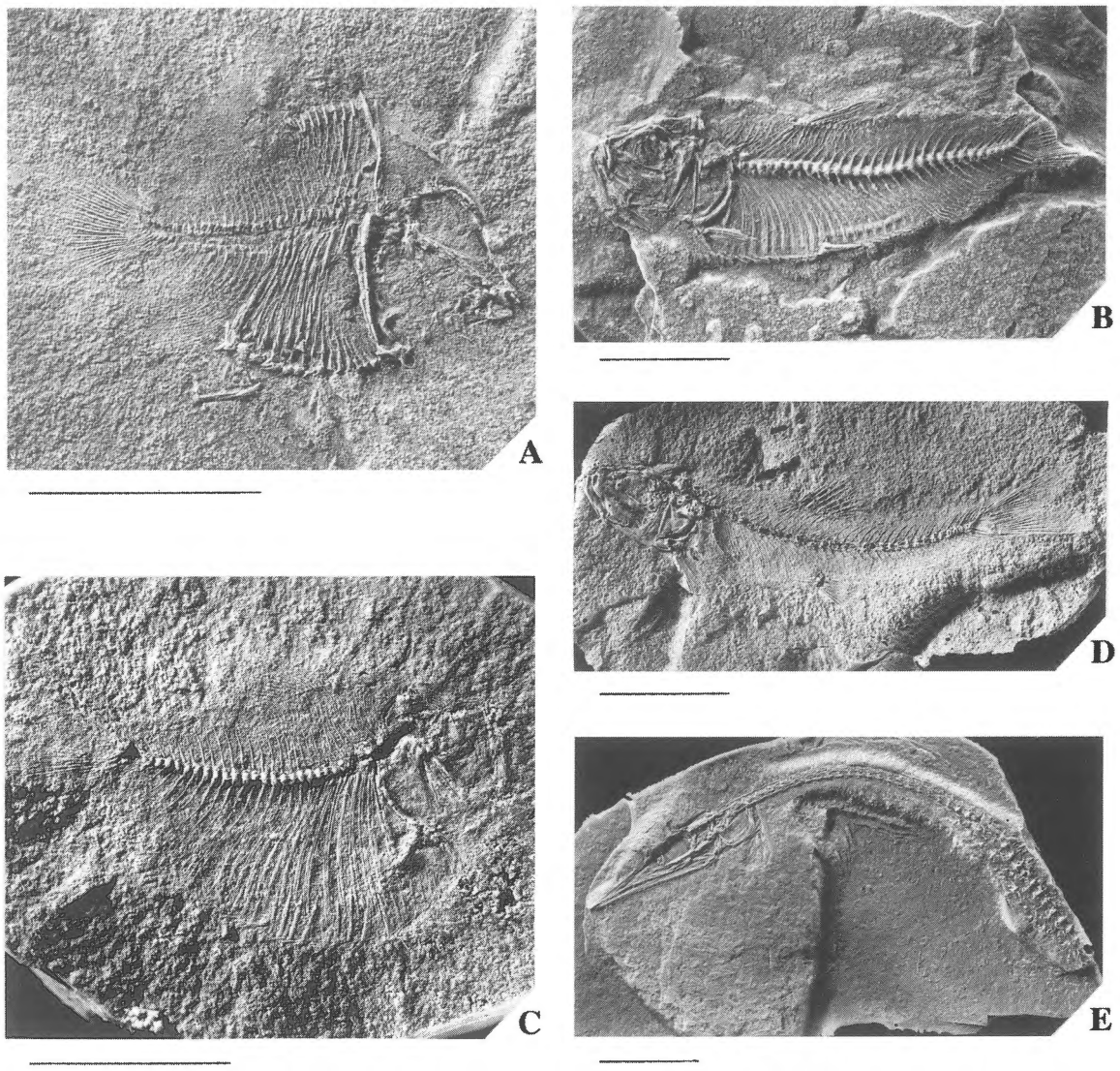

Plate I. Late Cenomanian fishes from Daoura (southeastern Morocco); black silicone rubber positive casts. Scale bar equals 10 mm. Figure A: Pycnodontidae indet. Figure B: aff. *Spratticeps*. Figure C: Paraclupeidae indet. Figure D: Otocephala indet. Figure E: *Rhynchodercetis* sp.