

Two new paraclupeid fishes (Clupeomorpha: Ellimmichthyiformes) from the Upper Cretaceous of Morocco

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Abstract

A collection of fossil fishes from the Akrabou Formation of Morocco has provided a number of new species, including three members of the Ellimmichthyiformes. Two of these are here described in one genus and placed in the family Paraclupeidae. One, named here *Thorectichthys marocensis* gen. et sp. nov., is represented by numerous fairly well preserved specimens, but the second species, *T. rhadinus* sp. nov., is represented by only three specimens, which are not well preserved. The third ellimmichthyiform from the Akrabou Formation, also represented by three specimens, is a member of the family Sorbinichthyidae. The Ellimmichthyiformes include species that have been found in a diversity of freshwater as well as estuarine or marginal marine habitats, from South and North America, the Mediterranean region and Asia. The Ellimmichthyiformes range from Neocomian (early Early Cretaceous) through Eocene in age, with the Moroccan material being probably early Turonian or possibly late Cenomanian in age, and from normal-salinity marine waters. The new paraclupeids, as well as a number of other recently described ellimmichthyiforms, are included in a new analysis of relationships based on previously documented osteological characters. The analysis indicates that the new genus *Thorectichthys* is sister to a clade containing *Ellimma*, *Ellimmichthys*, *Rhombichthys*, *Paraclupea*, *Tycherichthys*, and *Triplomystus*.

Introduction

Fishes of the extinct order Ellimmichthyiformes GRANDE, 1982, have a broad geographic, environmental, and temporal distribution, with members known from freshwater and marine environments throughout the world, including China, North and South America, Africa, Europe, and the Levant. The oldest known are from early Early Cretaceous (Neocomian; SILVA SANTOS & SILVA CORRÉA 1985) deposits, and the youngest are found in the Eocene. Most are from marine waters, but freshwater forms of separate lineages are known in the latest Cretaceous and in the Eocene.

The Ellimmichthyiformes are regarded as the sister group of the Clupeiformes within the Clupeomorpha (GRANDE 1982, 1985). The order as originally conceived was considered to have only a single family, Paraclupeidae (e.g., CHANG & MAISEY 2003), but BANNIKOV & BACCHIA (2000) erected a second family, Sorbinichthyidae. Many new genera and species have been added to the order over the last decade, and interest in this widely distributed group of fossil fishes has increased.

The genus *Armigatus*, with three species (*A. alticarpus*, *A. namourensis*, and *A. brevissimus*) found in the Cenomanian of Lebanon, and *A. brevissimus* from the Cenomanian of Portugal, has sometimes been included in the order Ellimmichthyiformes (e.g., CHANG & MAISEY 2003, FOREY 2004, HAY et al. 2007), but it or a clade composed of *Armigatus* plus *Diplomystus* has also been placed outside the order as the sister group to the Ellimmichthyiformes (e.g., GRANDE 1982, 1985; ZARAGÜETA-BAGILS 2004; ALVARADO-ORTEGA et al. 2008).

Based on the results of their phylogenetic analysis, ALVARADO-ORTEGA et al. (2008) divided the ellimmichthyiforms (excluding *Armigatus*) into two monophyletic families, Sorbinichthyidae and Paraclupeidae. Sorbinichthyidae included *Sorbinichthys elusivo*, *Diplomystus dubertreti* and *D. birdi*, all from the Cenomanian of Lebanon, two Eocene species, *Diplomystus dentatus* from North America and *D. shengliensis*

from China, and an unnamed species of *Diplomystus* from the Cenomanian of Britain (ALVARADO-ORTEGA et al. 2008). A recently discovered genus from freshwater Maastrichtian deposits in Canada has also been assigned to this family (NEWBREY et al. 2010), along with a second species of *Sorbinichthys* from Late Cretaceous deposits of Morocco (MURRAY & WILSON 2011). *Kwangoclupea dartevellei* (CASIER 1965) was originally described as a species of *Diplomystus* (but assigned to the Clupeidae). TAVERNE (1997), in his redescription, gave it a new genus and placed it in an intermediate phylogenetic position between Ellimmichthyiformes and Clupeiformes.

The Paraclupeidae, according to ALVARADO-ORTEGA et al. (2008), comprise *Scutatospinosus itapagipensis* from the Early Cretaceous of Brazil, *Ezcutuberezi carmenae* from the Valanginian to Barremian of Spain, *Ellimma branneri* from the Aptian-Albian of Brazil, *Ellimmichthys goodi* from the Aptian-Albian of Equatorial Guinea, *Ellimmichthys longicostatus* from the Hauterivian-Barremian of Brazil, '*Diplomystus*' *solignaci*, from the Senonian of Tunisia, three species of *Triplomystus*, two from the Cenomanian of Lebanon (*T. noorae* and *T. oligocostatus*) and one from the Albian of Mexico (*T. applegatei*), an unnamed genus ("Paraclupea-like") from the Aptian-Albian of Mexico, and *Paraclupea chetungensis* from Early Cretaceous of China. The family Paraclupeidae also contains *Tychoichthys dunveganensis* from the Cenomanian of Canada (HAY et al. 2007), and two other species that were not included in the analysis of ALVARADO-ORTEGA et al. (2008): *Ellimmichthys maceioensis* MALABARBA et al., 2004, from the Aptian-Albian of Brazil, and *Ellimma cruzi* SILVA SANTOS, 1990 from the Aptian of Brazil. *Rhombichthys intocabilis* KHALLOURI et al., 2010 was assigned to the Paraclupeidae in the original description.

We report here the recovery of two new ellimmichthyiforms from a single, marine, Turonian-Cenomanian locality in southeastern Morocco that previously yielded the macrosemiid *Agoultichthys chattertoni* MURRAY & WILSON, 2009, and the sorbinichthyid ellimmichthyiform *Sorbinichthys africanus* MURRAY & WILSON, 2011. The two new species are considered to be congeneric. Their relationships are investigated by means of a phylogenetic analysis that includes data from fossil taxa not previously included in such an analysis.

Geology

The ellimmichthyiform material reported here was recovered from the northwestern margin of the Kem-Kem Plateau, in southeastern Morocco. The area is near the Algerian border, southeast of the town of Alnif. Most of the material was collected by commercial collectors, but the authors and their colleagues also visited the site and made collections in 2007, 2008 and 2009. Isotope analysis of the sediments indicates that, although the deposits vary in salinity, the layers from which the fish come are all normal marine salinity (S. GIBB, pers. comm., 2011); none of the fishes come from brackish or hypersaline environments.

The locality is part of the Moroccan Cretaceous North Saharan Platform. This platform, documenting the incursion of the Tethys Sea, has been separated into several formations, with the ellimmichthyiform material coming from the marine deposits of the Akrabou Formation (ETTACHFINI & ANDREU 2004), which overlie the freshwater Kem Kem Beds (e.g., SERENO et al. 1996). The age of the Akrabou Formation is Cenomanian-Turonian. Where the actual boundary between the two lies within the formation has not been conclusively demonstrated, but the fish fauna, from higher in the sequence, may well be early Turonian in age, rather than late Cenomanian.

The deposits were laid down when the area was broadly connected to the Tethys Sea, but also likely influenced by the Atlantic Ocean through minor connections (ETTACHFINI & ANDREU 2004). The major Tethys and minor Atlantic connections are reflected in the fish faunas of these regions.

Material and methods

The fossil material is catalogued and housed in the collections of the University of Alberta Laboratory for Vertebrate Palaeontology (UALVP). A few specimens are preserved as part and counterpart, but most are preserved on a single slab, either with the bone intact or as natural moulds. Specimens were revealed when split in the field and some were further prepared by hand. Latex peels were made of several specimens that were preserved as natural moulds. Comparative materials are from the UALVP, Canadian Museum of Nature (CMN) and Royal Tyrrell Museum of Palaeontology (TMP).

Taxonomic Note

POYATO-ARIZA et al. (2000: 575) named *Ezcutuberezi carmeni* in honour of Carmen Horgue, “whose love for palaeontology led her to assist in the finding of the Arratia Valley ichthyofauna.” It appears therefore, that the ending of the specific epithet is an incorrect original spelling based on an inadvertent error (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999: Article 32.5.1), and should be corrected to the feminine *E. carmenae*, which we use in this paper.

Systematic Palaeontology

Subdivision Teleostei MÜLLER, 1845
Cohort Clupeocephala PATTERSON & ROSEN, 1977
Superorder Clupeomorpha GREENWOOD et al., 1966
Order Ellimmichthyiformes GRANDE, 1982

Family Paraclupeidae CHANG & CHOU, 1977 (sensu ALVARADO-ORTEGA et al. 2008)

Included species: ‘*Diplomystus*’ *solignaci* GAUDANT & GAUDANT, 1971, *Ellimma branneri* (JORDAN, 1910), [*Ellimma guineensis* GAYET, 1989 is a subjective junior synonym of *Ellimmichthys goodi*, see MURRAY et al. 2005], *E. cruzi* SILVA SANTOS, 1990; *Ellimmichthys goodi* (EASTMAN, 1912), *E. longicostatus* (COPE, 1886), *E. maceioensis* MALABARBA et al., 2004, *Ezcutuberezi carmenae* POYATO-ARIZA et al., 2000, *Paraclupea chetungensis* SUN, 1956, *Rhombichthys intoccabilis* KHALLOUFI et al., 2010, *Scutatuspinosus itapagipensis* SILVA SANTOS & SILVA CORRÉA, 1985, *Triplomystus noorae* FOREY et al., 2003, *T. oligoscutatus* FOREY et al., 2003, *T. applegatei* ALVARADO-ORTEGA & OVALLES-DAMIÁN, 2008, *Tychoichthys dunveganensis* HAY et al., 2007. This family also includes a *Paraclupea*-like specimen from Mexico (ALVARADO-ORTEGA et al. 2008); however, we cannot distinguish this taxon here as a description is not yet available.

Thorectichthys, gen. nov.

Diagnosis. A paraclupeid fish, based on the presence of dorsal and ventral series of scutes and anterior ribs articulating in pits on centra whereas posterior ribs articulate on parapophyses, differing from all other members of the family by the following combination of characters: anal fin long with 22–25 rays compared to 17 or fewer rays in *Ellimmichthys* (10–14), *Ellimma* (12–15), ‘*Diplomystus*’ *solignaci* (14), *Scutatuspinosus* (9), *Triplomystus noorae* (17) and probably *T. applegatei* (16 anal pterygiophores) and *Rhombichthys* (12 or 13 anal pterygiophores) [but 23 rays in *Tychoichthys*, 24 in *Ezcutuberezi* and more than 18 in *Paraclupea*]; 5 or 6 predorsal bones compared to 7 or more in *Paraclupea* (8–9), *Ellimmichthys* (8–9), *Ellimma branneri* (8), *Tychoichthys* (7), *Ezcutuberezi* (12), “*D*”. *solignaci* (7), *Rhombichthys* (7–8) and *Scutatuspinosus* (10) [but 5 or 6 in *Ellimma cruzi* and *Triplomystus*]; 24–26 scutes in abdominal series compared to less than 20 in *Ellimmichthys maceioensis* and 27 or more in *Triplomystus noorae* (32–33), *T. applegatei* (33), *Tychoichthys* (36), *Ezcutuberezi* (30), *Paraclupea* (38–43), *Ellimmichthys longicostatus* (32), *Ellimma branneri* (27–30), and *Rhombichthys* (35–46) [*Triplomystus oligoscutatus* has 23–25 and *Scutatuspinosus* has 25, and *Ellimma cruzi* is unknown]; further differs from *Triplomystus* in having no post-dorsal series of scutes.

Etymology. Generic name from the Greek “thorektes”, masculine, meaning a warrior armed with a breast plate, in reference to the abdominal scutes of the fish, and “ichthys” meaning fish.

Type species: *Thorectichthys marocensis*, sp. nov.

Thorectichthys marocensis, sp. nov. (Figs. 1A,B,E, 2–5)

Diagnosis. A deep-bodied fish with body depth being between 57 and 65 % of standard length, having a deeper body in relation to standard length than *Ellimmichthys*, *Ellimma*, ‘*Diplomystus*’ *solignaci*, *Scutatuspinosus* and *Paraclupea*, and having a less-deep body than *Ezcutuberezi* and *Tychoichthys*. *Rhombichthys* as described varies in body depth with size. Eight scutes in predorsal series [compared to 7 in ‘*D*’. *solignaci*, or

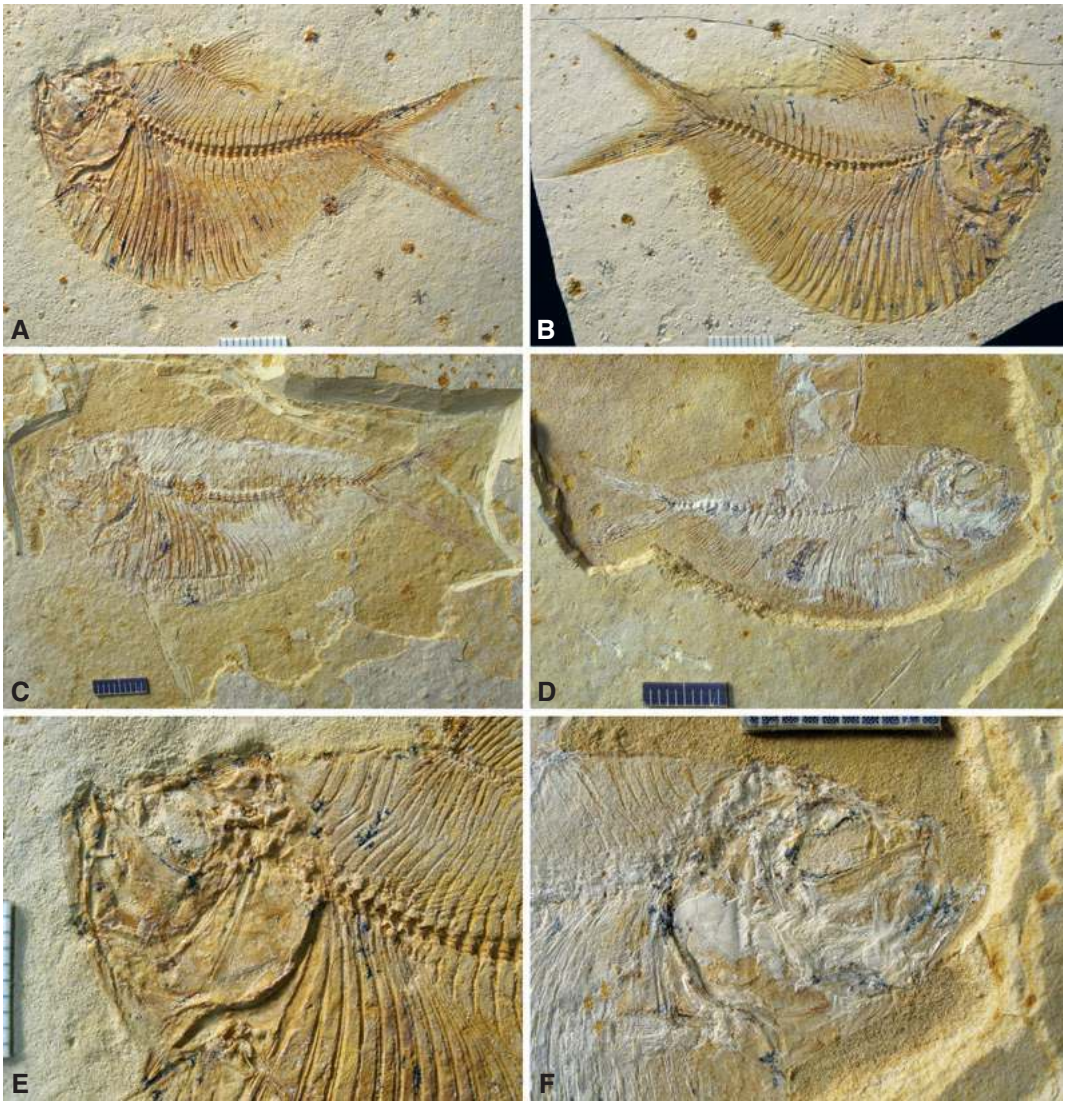


Fig. 1.

Thoretichthys gen. nov. **A,B**, *T. marocensis* sp. nov., photograph of the part and counterpart of the holotype, UALVP 47178 **C,D**, *T. rhadinus*, sp. nov. **C**, photograph of the holotype, UALVP 51653, and **D**, the paratype UALVP 51664. **E**, anterior portion of the holotype of *T. marocensis* sp. nov. shown in **A**. **F**, anterior portion of the paratype of *T. rhadinus* sp. nov. shown in **D**. Scale bars = 1 cm.

more than 9 in *Paraclupea* (18), *Ellimmichthys* (12–14), *Ellimma branneri* (12–13), *Rhombichthys* (12 or more), *Scutatuspinosus* (10–11), *Tycheroichthys* (16), and *Triplomystus* (12–13) [but 8 present in *Ellimma cruzi*, more than five in *Ezcutuberezi*]. The number of scutes and depth of body also distinguish it from the second new species in this genus (see below).

Holotype. UALVP 47178, part and counterpart of a complete fish.

Paratypes. UALVP 47134, 51647 and UALVP 51649 all complete fish preserved in part and counterpart, and UALVP 51648, 51659 and 51657 both complete fish with no counterpart.

Etymology: The specific epithet is named for the country of origin.

Type locality: Near Agoult, Morocco, Akrabou Formation, on the northwestern margin of the Kem-Kem Plateau.

Age: Probably early Turonian, possibly late Cenomanian.

Description

The description that follows is predominantly based on the holotype UALVP 47178, as it is the best preserved specimen, except for the description of the caudal skeleton, which is better preserved in the paratype UALVP 47134. Information from other specimens is noted throughout.

General body form. This is a deep-bodied fish with a distinct angle in the body outline at the dorsal fin origin (Fig. 1A,B), although the angle is not as abrupt as in *Triplomystus* or *Tycheoichthys*. It has a broadly rounded ventral aspect in lateral view. Preservation of all specimens is in lateral view, indicating that the body of this species was much deeper than wide, as is typical of other ellimmichthyiforms. The mouth is sharply upturned, so that the jaws are almost vertical in orientation and the mouth opens dorsally (Figs. 1E, 2). Counts and measurements for several individuals of varying sizes are given in Table 1.

The greatest body depth is 57 % to 65 % of standard length (SL), with the holotype being 64 %. The head length from the tip of the dentary to the posterior edge of the opercle is 31 % to 37 % of SL. The caudal fin is strongly forked, with the fin being roughly one third of standard length, or forming about one quarter of the total length of the fish.

Table 1.

Counts and measurements of seven specimens of the paracupeid *Thorectichthys marocensis* gen. et sp. nov. Measurements are given in millimetres; proportions are given as percentages.

UALVP	47178	47134	51612	51647	51648	51651	51659
standard length (SL)	53.7	29.5	21.0	41.1	56.1	25.6	44.4
total length	71.9	37.9	27.4	50.2	73.6	30.1	55.3
head length	17.0	10.9	6.5	12.9	17.3	9.5	14.1
head/SL	31	36	31	31	31	37	32
head depth	19.6	12.4	7.3	12.2	17.6	10.2	15.7
head depth/SL	36	38	35	30	31	40	35
greatest body depth	34.9	21.2	12.0	24.1	35.1	16.2	26.5
body depth/SL	64	65	57	59	63	63	60
predorsal length	10.1	4.8	8.9	14.9	21.7	11.3	19.2
predorsal/SL	41	40	42	36	39	44	43
prepelvic length	28.5	17.7	12.5	24.8	29.5	13.6	~24
prepelvic/SL	64	54	60	60	53	53	54
preanal length	40.0	22.7	14.1	30.1	38.8	20.3	30.1
preanal/SL	74	74	67	73	69	79	68
dorsal fin rays	16	17	15	ii 15	ii 15	? 15	i 14
anal fin rays	24	? 24	?	? 24	25	24	24
pectoral fin rays	6+	? 14	9+	13	?	12	10+
pelvic fin rays	3+	? 6	?	?	? 5	?	?
caudal fin rays	19	19	17+	?	19	?	?
abdominal vertebrae	16	16	16	17	17	18	16
caudal vertebrae (incl u1+u2)	17	18	17	18	17	18	18
total vertebrae	33	34	33	35	34	36	34
predorsal bones	5	5	5	5	5	5	5
abdominal scutes	24	24	? 25	23	24	22	24
pre-pelvic scutes	17	17	18	17	18	16	18
post-pelvic scutes	7	7	6	6	6	6	? 6
pre-dorsal scutes	? 8	8	5+	8	8	?	? 8
pairs of ribs	15	15	15	15	15	15	14
epurals	3	?	?	? 2	? 2	?	?
uroneurals	2	2	?	?	?	?	?

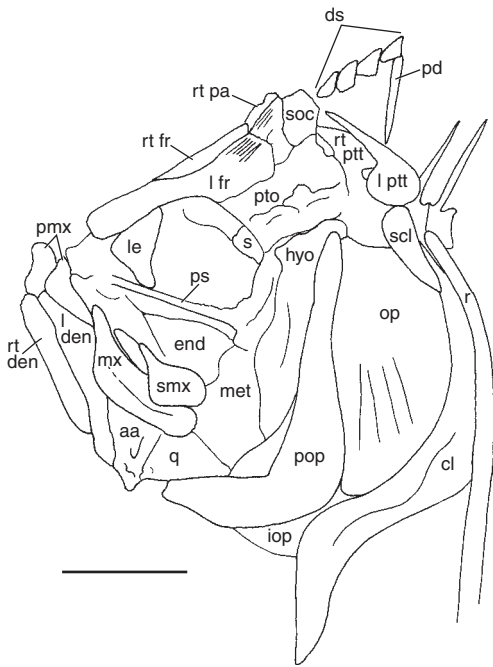


Fig. 2. *Thorectichthys marocensis* gen. et sp. nov., camera lucida drawing of the head based on the peel of the holotype, UALVP 47178. Scale bar = 5 mm. Abbreviations: **aa**, anguloarticular; **cl**, cleithrum; **den**, dentary; **ds**, dorsal scutes; **fr**, frontal bone; **hyo**, hyomandibula; **iop**, interopercula; **l**, left; **le**, lateral ethmoid; **met**, metapterygoid; **mx**, maxilla; **op**, opercle; **pa**, parietal bone; **pd**, predorsal bone; **pmx**, premaxilla; **pop**, preopercula; **ps**, parasphenoid; **ptt**, posttemporal; **q**, quadrate; **rt**, right; **s**, sphenoid; **scl**, supraclathrum; **soc**, supraoccipital bone; **smx**, supramaxilla.

Triplomystus (FOREY et al., 2003). *Tychoichthys*, from the Western Interior Seaway of Canada, has a head that is equally as long as deep (HAY et al., 2007).

There is no frontal fontanel, and no recessus lateralis; neither of these is expected to be present in an ellimmichthyiform. The skull roof is ornamented with strong, deep ridges extending roughly antero-posteriorly (Fig. 1E). There are about nine ridges on the posterior portion of the frontal bone (of traditional terminology) and about six ridges continue onto the parietal bone (of traditional terminology), although they angle posterodorsally on this bone. The ornamentation does not continue onto the supraoccipital or pterotic. Ornamentation on the skull roof is also found in *Ellimma*, *Ellimmichthys* and *Paraclupea*.

The frontal bone is narrow anteriorly, but expands laterally to join the sphenoid and pterotic. The dorsal aspect of the head in lateral view is sharply angled (Fig. 2) because of the angle in the frontal bone, but it is straight posteriorly where it joins the parietal bone.

The parietal bone appears to bear a canal on its posterior edge, which would be the supratemporal commissure; the commissure apparently crossed the midline to the other parietal. The left and right parietal bones meet in the midline anterior to the supraoccipital. The visible part of this latter bone is smaller than the parietal bone, and confined to a crest at the posterior end of the skull.

The pterotic bears a dorsal flange, and traces of the sensory canals can be distinguished, extending anteroposteriorly through the ventral portion of the bone. The anterior edge meets the triangular sphenotic ven-

In at least two ellimmichthyiforms, allometric growth results in larger individuals having a proportionally deeper body than smaller individuals (e.g., *Triplomystus noorae* FOREY et al., 2003 and *Ezkutuberezi carmenae* POYATO-ARIZA et al., 2000). *Rhombichthys intocabilis* apparently has an even more extreme variation in body depth. KHALLOUFI et al. (2010) included a presumed juvenile specimen in this species that has a rounded ventral aspect, quite unlike the greatly developed ventral aspect of the holotype, with the body depth changing from 67% to 110% of standard length. In *Thorectichthys marocensis*, the greater body and head length compared to standard length is found in the intermediate-sized specimens, and therefore the differences are more likely caused by preservation and individual variation, rather than differential growth of individuals.

The dorsal fin origin is positioned anteriorly, close behind the head, with the predorsal length (from the dorsal fin insertion to the tip of the snout) being 36–42% of SL. The pelvic fin origin is positioned posteriorly, just behind the midpoint of SL, giving a prepelvic length of 53–64% of SL. The anal fin origin is positioned posteriorly, under a point half way between the dorsal fin insertion and the caudal fin, with the preanal length being about three quarters (67–79%) of SL. In these features, the new species is more similar to the deep-bodied ellimmichthyiforms such as *Triplomystus* and *Tychoichthys*, rather than the more stream-lined forms such as *Diplomystus* and *Paraclupea*. There are no scales preserved in any specimens.

Skull roof. The morphology of elements in the skull area is not easy to make out on most specimens. Some bones and features are clear, but other bones are preserved only as impressions, and many bones are crushed, obscuring details. The head is slightly deeper than long (except one specimen, Table 1). Most paraclupeids have a head longer than deep, except for

trally and the edge of the frontal dorsally. Dorsal to the pterotic and superficial to the other bones of the skull is a large, irregularly shaped extrascapular bone (not visible on the holotype). It bears the crushed remains of the triradiate sensory canals. The extrascapula is relatively larger compared to those of *Armigatus brevissimus* and *Denticeps clupeioides* (GRANDE 1985:fig. 4). Anterior to the sphenotic and ventral to the frontal bone there is a thin bone preserved in the posterodorsal part of the orbit. We identify this as the median orbitosphenoid.

Orbital region. No infraorbital bones are preserved or identifiable in any specimen. The parasphenoid is edentulous. The posterior part still visible in the orbit is expanded, indicating a basiptyergoid process was likely present, as in other ellimmichthyiforms (CHANG & MAISEY 2003), although it has been crushed. The lateral ethmoid reaches the parasphenoid, but it is poorly preserved in the holotype. The anterior part of the head is not clearly preserved in any specimen, so presence and details of the mesethmoid, vomer and nasals cannot be determined.

Jaws. The upper jaw is most clearly seen in the latex peel of the holotype (UALVP 47178), although details of the lower jaw are not clear. The jaws in most specimens are preserved in the closed position; however in UALVP 51647 and 51659 the jaws are open and tall, fine, conical teeth are visible on the dentary and possibly on the premaxilla.

The jaws are positioned almost vertically, and the gape would have opened dorsally in the living fish. The articulation of the quadrate and anguloarticular is positioned below the anterior part of the orbit. The lower jaw, measured from the anterior tip of the dentary to the anguloarticular facet for the quadrate, is slightly more than half of the head length (measured horizontally from the ventral surface of the dentary to the posterior edge of the opercle). The anguloarticular is predominantly obscured, with only the facet visible. Whether or not a retroarticular is present and contributing to the facet for the quadrate cannot be determined.

The premaxilla is gently curved ventrally and the anterior end is swollen. The maxilla has a narrow anterodorsal end that fits over the premaxilla. The posteroventral portion of the maxilla is much deeper, as is normal in ellimmichthyiforms. The maxilla, excluding the anterodorsal projection, is about twice the length of the premaxilla. There are two supramaxillae (Fig. 2). The slightly larger posterior one bears an anterior projection that lies dorsal to the posterior portion of the anterior supramaxilla, as common in ellimmichthyiforms.

Hypopalatine bones and gill arches. The hyomandibula is preserved along the anterior edge of the preopercle, and extends dorsally farther than that bone. It has a single head articulating on the pterotic, and the shaft is as wide as the head. The posterior process for articulation with the opercle is partly visible. The metapterygoid, having a roughly square shape, is between the quadrate, entopterygoid and ventral tip of the hyomandibula. It is larger than the quadrate. A trace of the entopterygoid is visible between the quadrate and parasphenoid. There are no teeth on the parasphenoid, but UALVP 51657 preserves small, fine teeth on the entopterygoid. The curved ectopterygoid is preserved abutting the anterodorsal edge of the quadrate in the holotype, close to its articulation with the anguloarticular. The triangular part of the quadrate is visible, but its articulation with the symplectic is hidden beneath the preopercle in the holotype. In UALVP 47134, the slender wedge-shaped symplectic is visible, positioned near the bend in the preopercle where the dorsal and ventral limbs meet.

Elements of the gill arches are almost completely obscured by the overlying bones in most specimens. On the holotype there are remains of five branchiostegal rays preserved. Two specimens, UALVP 51649 and 51650 (Fig. 3), preserve the anterior and posterior ceratohyals in lateral view. There is a large beryciform foramen in the anterior ceratohyal, similar in placement and shape to that of *Diplomystus* sp. from the Cenomanian of England (FOREY 2004: fig. 9). The preserved branchiostegal rays are thin, not spathiform as found in a number of other clupeomorphs (MCALLISTER 1968). Ventral to the ceratohyal in UALVP 51649 is a long ridge of bone interpreted as belonging to the urohyal. It is slightly longer than the anterior ceratohyal, and probably was much longer than deep.

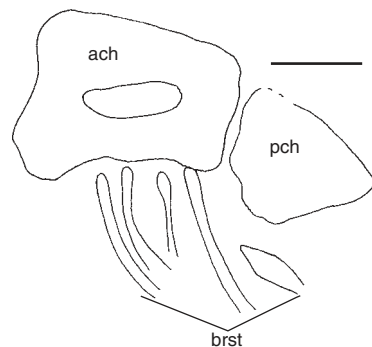


Fig. 3. *Thorectichthys marocensis* gen. et sp. nov., outline drawing of the ceratohyal and associated bones of specimen UALVP 51650b. Scale bar = 2 mm. Abbreviations: **ach**, anterior ceratohyal; **brst**, branchiostegal rays; **pch**, posterior ceratohyal.

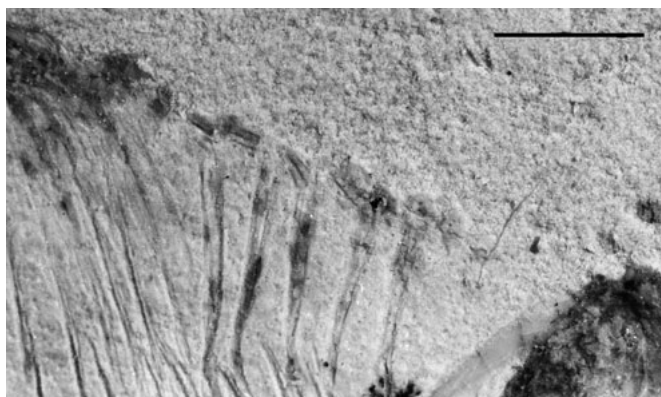


Fig. 4. *Thorectichthys marocensis* gen. et sp. nov., photograph of the predorsal scute series and predorsal bones, UALVP 51647a. Scale bar = 2 mm.

Opercular series. The opercular bone is much taller than wide. The dorsal portion is poorly preserved, but appears to have been flat and angled, sloping posteroventrally to anterodorsally. There is no dorsal projection as found in *Triplomystus* (FOREY et al. 2003: fig. 42) and *Diplomystus dentatus* (GRANDE 1982: fig. 4; pers. obs.), and no ornamentation as found in *Tychoichthys* (HAY et al., 2007; pers. obs.) or *Ellimma branneri* (CHANG & MAISEY 2003: fig. 4).

The preopercle is distinctly angled, forming dorsal and ventral limbs, with the dorsal limb longer than the ventral. The bone is crushed in the holotype, so whether the sensory canal was completely open, or opened via

pores, cannot be determined; most ellimmichthyiforms have the preopercular canal opening via pores, and this seems to be the case in UALVP 51649, which has the canal bone enclosed, but no pores can be clearly distinguished. The canal appears to be enclosed in UALVP 51649, but the number of pores cannot be determined. A portion of the subopercle is visible between the preopercle and opercle at their ventral edges. Below this is the interopercle. Details of these bones are not visible.

Paired fins and girdles. The bones of the pectoral girdle can be identified, with the posttemporal, supraclithrum, cleithrum, scapula and coracoid all preserved (Fig. 2). A long thin bone lying below and posterior to the pectoral fin in the holotype is tentatively identified as a displaced postcleithrum. The number of postcleithra in ellimmichthyiforms varies, with a single one present in *Tychoichthys* (HAY et al. 2007) and *Armigatus namourensis* (FOREY et al. 2003), two in *Triplomystus* (FOREY et al. 2003) and apparently one in *Diplomystus dentatus* (pers. obs. CMN 8881, CMN 52057). Other ellimmichthyiforms may have no postcleithra (GRANDE 1985).

The posttemporal rests on the dorsal surface of the epiotic. The anteroventral portion is broad and preserves part of the sensory canal. The dorsal arm of the posttemporal in the holotype appears fairly short, but in UALVP 51647 (Fig. 4) and 51649 this dorsal arm is long, reaching close to the supraoccipital crest. The narrow, long supraclithrum reaches the posteroventral edge of the posttemporal. The dorsal tip of the cleithrum is obscured under the supraclithrum and opercle in all specimens, but it appears to be the narrowest part of the bone. The rest of the cleithrum is broad, and has a sigmoidal shape hugging the posteroventral part of the opercle but extending significantly below the bones of the opercular region. The ventral tip is pointed. The coracoid shadows the posterior part of the ventral portion of the cleithrum below the opercular region, and a small scapula is preserved articulating with a few fin rays. Details of the suture between scapula and coracoid cannot be determined. There are only six pectoral fin rays preserved in the holotype, but other specimens preserve 12 to 14 rays. The rays are not clearly visible in any specimen, so the size of the fin cannot be estimated.

The pelvic girdle is not visible beneath the abdominal scutes in any specimen, although all preserve one or a few rays to indicate the position of the fin. There may have been five or six pelvic rays.

Vertebral column. There are 33–34 total vertebrae including the last two ural centra (of the diurnal terminology). Of these, 16 to 18 are abdominal, and 15 or 16 are caudal centra, not including any ural centra. The centra become relatively taller in the posterior portion of the column compared to the anterior centra. There are 15 pairs of pleural ribs (a single specimen has only 14 pairs), associated with all the abdominal vertebrae. The anterior seven pairs articulate on the centra, and appear to be inserted into pits on the lateral surface of these centra. The more posterior ribs articulate with the parapophyses, and become distally displaced posteriorly in the column associated with the greater length of the parapophyses. Intermuscular bones are preserved in two series, the epineural and epipleural. Epineural bones (we cannot determine if these are fused to the neural arches, which would then allow us to call them epineural processes following ARRATIA 1997) are associated with vertebral centra six through 26 or 27 (preural centrum 4). The anterior

eight are positioned proximally on the neural spines and the posterior ones are positioned more distally. The epipleural series is associated with at least vertebrae 10 through 16, although more may be present, and they become positioned more distally towards the posterior end. The epipleurals are associated with the parapophyses. Each epineural is the length of 2.5 centra, and the epipleurals are slightly shorter, about the length of 2.0 centra. In UALVP 51659, the epipleural series clearly continues to the 28th or 29th centrum (the third anterior to the first preural centrum) and are associated with the haemal spines. No epicentrals are evident.

Predorsal bones, dorsal and ventral

scutes. Five predorsal bones are preserved in front of the dorsal fin. These are long and narrow, tapering toward the proximal ends. Two series of scutes are present, the abdominal series and the predorsal series. *Triplomystus* is unique in having a third, postdorsal, series of scutes. The predorsal scutes are not well preserved; most specimens, including the holotype, have eight. Details of these scutes are best preserved in UALVP 51647 (Fig. 4), in which there appear to be nine scutes. The anterior seven are small, and about as deep as long, and roughly circular, with a horizontal ridge on each. The other two (posteriormost) scutes are slightly larger but also bear the ridge. The posterior edges of the scutes show no signs of spines nor is the posterior edge produced into a median spine.

Abdominal scutes are robust and fairly well preserved (Figs. 1A,B). They extend from the ventral edge of the body about one third of the way up to the vertebral column. In *Tychoerichthys* and *Triplomystus* (HAY et al. 2007, FOREY et al. 2003), the abdominal scutes are longer, extending half way to the vertebral column, but in other ellimmichthyiforms (e.g., *Armigatus*: FOREY et al. 2003; *Scutatuspinosus*: SILVA SANTOS & SILVA CORRÉA 1985) the abdominal scutes are less extensive with only short lateral wings. The scutes narrow significantly dorsally, meeting one another anteriorly and posteriorly only at their ventralmost portions, unlike the extensive contact seen in *Tychoerichthys* (HAY et al. 2007, pers. obs.). There are 23–25 scutes in the abdominal series, 16–18 anterior to the pelvic origin, and 6 or 7 between the pelvic and anal fin origin. The scutes in the middle of the series are longer than the anteriormost and posteriormost scutes. The scute in front of the pelvic fin is not significantly smaller than the others.

Median fins. The dorsal fin is positioned closer to the head than the tail, at the deepest part of the body. It is triangular in shape, and contains 14–15 long principal rays preceded by two much shorter procurrent rays. The shape of the anal fin cannot be determined, as in all specimens only the most proximal ends of the rays are preserved. There are 23 or 24 anal rays in this species.

Caudal fin. The caudal fin is deeply forked, and is about one third of SL, or in other words, it represents about a quarter of the total length of the fish. It is best preserved in UALVP 47134, to which the following description applies with exceptions noted.

We count 19 principal rays in the caudal fin, as common in ellimmichthyiforms, although in most

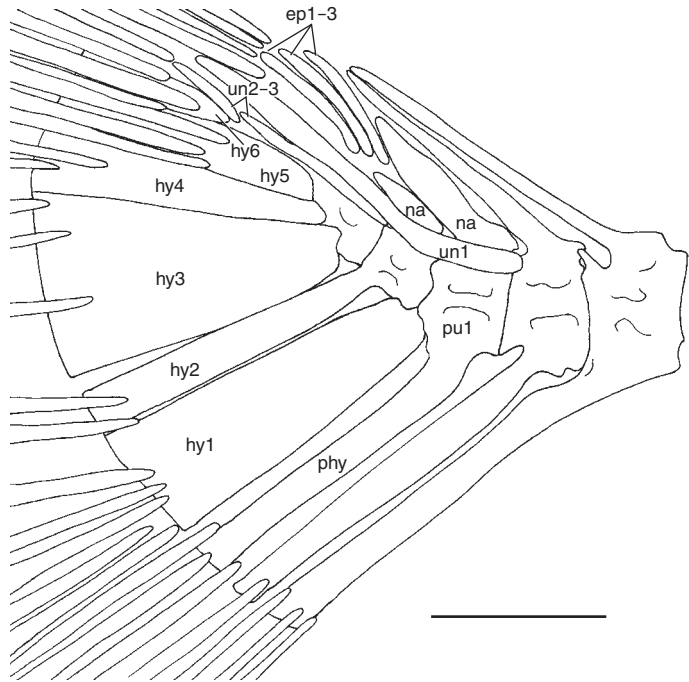


Fig. 5. *Thorectichthys marocensis* gen. et sp. nov., caudal skeleton based on specimen UALVP 47134 and peel of specimen UALVP 51648. Scale bar = 2 mm. Abbreviations: **ep 1-3**, epurals 1-3; **hy 1-6**, hypurals 1-6; **na**, neural arch; **phy**, parhypural; **pu1**, first preural centrum; **un 1-3** (based on relative position only).

specimens a count is difficult because of preservation. There are four ventral and four dorsal procurent rays in UALVP 47134. A dorsal caudal scute is visible in UALVP 51648.

The neural spine on the first preural centrum is shorter than the preceding neural spines (Fig. 5). There is a small neural arch on the first ural centrum; whether or not the second ural centrum (diural terminology) also has a neural arch cannot be determined. As noted by ARRATIA (2010), uroneurals may be associated with different ural centra and so “uroneural one” of different fishes may not be homologous bones. It is not possible for us to determine with which centrum each uroneural was developmentally associated, and we here simply number them in sequence from anterior to posterior. There are three uroneurals. The first one extends anteriorly to reach the posteriormost edge of the second preural centrum, and the second uroneural underlies the first but does not extend to the posterodorsal tip of the first. Three epurals are most clearly preserved in UALVP 51648; they fill the space between the neural spine of the second preural centrum and the first uroneural. The first ural centrum (diural terminology) is only slightly smaller than the first preural centrum, and the second ural centrum is somewhat smaller than the preceding one.

The rays of the dorsal lobe of the caudal fin greatly overlap the hypural plates, but details can still be determined. There are six hypurals. The first reaches but was likely not fused with the first ural centrum; it has a broad hooked proximal base. The second hypural is narrower, and also reaches the first ural centrum with which it appears fused. The other four hypurals are triangular, and close together. Although the majority of the hypurals in all specimens are preserved only as impressions, it appears that the third hypural is expanded posteriorly, leaving no diastema between the second and third hypural plates, similar to the condition found in *Triplomystus*. The base (haemal arch) of the long, slender parhypural is fused with the first preural centrum.

Thorectichthys rhadinus, sp. nov.

(Figs. 1C,D,F)

Diagnosis. Differs from the type species *Thorectichthys marocensis* by having six predorsal bones (instead of five), having more total (24–26 compared to 22–25) and postpelvic (8–9 compared to 6–7) abdominal scutes and more pairs of ribs (17–18 compared to 14–15). In addition, there are 10–11 scutes in the predorsal series (8 in *T. marocensis*), and the body depth is 40–48 % of standard length (compared to 57–65 % in *T. marocensis*).

Holotype: UALVP 51653, a complete fish.

Paratypes: UALVP 51664, a complete fish overlying a decapod crustacean and UALVP 51715, a complete fish.

Etymology: From the Greek “rhadinós” meaning slender, tapering or lithe, in reference to the body depth of this species being much less than in *T. marocensis*.

Type locality: Agoult fossil locality, near Agoult, Morocco, Akrabou Formation, on the northwestern margin of the Kem-Kem Plateau.

Age: Possibly late Cenomanian, but more probably early Turonian.

Description

General body form. This second species is similar to *Thorectichthys marocensis* in the short dorsal and long anal fin, deeply forked tail, and placement of the paired fins. It differs from *T. marocensis* in general form by having a shallower body depth. The smallest specimen, UALVP 51715, has somewhat different body proportions, with a relatively shorter but deeper head and shorter pre-pelvic length, than the other two, probably indicating allometric growth. Counts and measurements for the three specimens are given in Table 2.

Skull roof. Little can be seen in terms of details of the skull bones. There is no recessus lateralis present. The head does not angle sharply in lateral view; it slopes in a straight line from the anterior part of the frontal bones through to the posterior end of the supraoccipital. There is no ornamentation visible on any of the skull bones. The parietal bones appear to meet in the midline, and the supraoccipital is confined to a small area at the back of the skull.

Orbital region. No infraorbital bones are preserved in any of the specimens. The parasphenoid is a narrow bone in lateral view, but it is expanded at the posterior end indicating it likely had a basipterygoid projection. The lateral ethmoid reaches the level of the parasphenoid. There is no sign of teeth on the parasphenoid or ectopterygoid, but very fine, small teeth seem to be present on the entopterygoid in the paratype (UALVP 51664).

Jaws. The articulation of the lower jaw (angular/quadrato) is positioned under the anterior part of the orbit, with the jaws being oriented antero-dorsally. The premaxilla is short and does not fully exclude the maxilla from the gape (visible in paratype, UALVP 51664). The maxilla is angled in the middle and about twice as long as the premaxilla. The large posterior supramaxilla is visible, but if there is an anterior supramaxilla it is obscured in all specimens. No teeth are visible in either the holotype or paratypes on any upper jaw bones, but dentary teeth are present although not well developed.

Hypopalatine bones and gill arches. The anterior ceratohyal is visible in lateral view; it is similar to that of *T. marocensis* in size and shape and bears a beryciform foramen, albeit one that is slightly smaller than that of *T. marocensis*. Four fine, thin branchiostegal rays are also preserved. Other bones of the arches are not clear.

Opercular series. The opercle in the holotype bears traces of ornamentation similar to that seen in *Tychoerichthys*, consisting of fine ridges or grooves radiating posteroventrally from the point of articulation with the hyomandibula. The preopercle is L-shaped and broadest at the angle of the dorsal and ventral limbs. The preopercular canal is enclosed in bone but the number of pores opening to the exterior cannot be determined.

Paired fins and girdles. The pectoral fin is poorly preserved and a ray count is not possible; there are at least 10 pectoral rays in the paratype. The cleithrum is a robust sigmoidal bone, as in other paraclupeids. The pelvic fin contains at least five fin rays in the paratype. The pelvic girdle is not visible in either specimen.

The cleithrum is S-shaped, with the thin, laminar coracoid being broad, deep and reaching to the ventral tip of the cleithrum. The supracleithrum of the paratype (UALVP 51664) is long and narrow and appears to have a canal running throughout its length. Posterior to the coracoid and medial to the pectoral fin rays in the holotype (UALVP 51653) is a partial robust bone that is interpreted as a postcleithrum. The posttemporal in all specimens has a long narrow dorsal process.

Vertebral column. The holotype (UALVP 51653) has 36 vertebrae: two ural centra (diurnal terminology), preceded by 15 caudal centra and 19 abdominal centra. The paratype (UALVP 51664) has two extra abdominal centra for a total of 38

Table 2.

Counts and measurements for the only two known specimens of the paraclupeid *Thorectichthys rhadinus* gen. et sp. nov. Measurements are given in millimetres; proportions are given as percentages.

	UALVP 51653	UALVP 51664	UALVP 51715
standard length (SL)	66.3	44.9	30.9
total length	84.9	56.2	37.1
head length	18.1	13.6	10.8
head/SL	27	30	35
head depth	17.5	9.7	9.7
head depth/SL	26	22	31
greatest body depth	32.0	20.8	12.3
body depth/SL	48	46	40
predorsal length	25.0	17.7	13
predorsal/SL	38	39	42
prepelvic length	31.7	24.0	17.5
prepelvic/SL	48	53	57
preanal length	47.1	32.3	23.7
preanal/SL	71	72	77
dorsal fin rays	ii15	(17 pterygio- phores)	ii16
anal fin rays	(25 pterygio- phores)	22	?
pectoral fin rays	?	10+	14
pelvic fin rays	?	?5	?
caudal fin rays	19	?	?
abdominal vertebrae	19	21	20
caudal vertebrae (incl u1+u2)	17	17	16
total vertebrae	36	38	37
predorsal bones	6	6	6
abdominal scutes	25 or 26	26	24
pre-pelvic scutes	17	18	16
post-pelvic scutes	8 or 9	8	8
pre-dorsal scutes	?	10 or 11	?10
pairs of ribs	18	17	18
epurals	?3	?	?
uroneurals	?2	?	2

vertebrae. There are 17 or 18 pairs of ribs. The seven or eight anterior ribs articulate in pits on the centra and the posterior 10 or 11 articulate on parapophyses. Epineural and epipleural bones are present in series that extend to the fourth preural centrum. Whether or not the epineural bones are actually fused to the neural arches (and hence could be called epineural processes; see ARRATIA 1997) cannot be determined. The epipleural bones are Y-shaped at least in the caudal region. There is no indication that epicentral bones were present.

Predorsal bones, dorsal and ventral scutes. There are six predorsal bones in all specimens. They are long and narrow, similar in shape to those of *T. marocensis*. There are 10 or 11 scutes in the dorsal series preserved in the paratype, but the number in the holotype cannot be determined. They are small and sub-rectangular, similar to those of *T. marocensis*, with no spines or ornamentation. The abdominal series contains 25–26 scutes, eight or nine of which are postpelvic.

Median fins. The dorsal fin is clearly preserved in the holotype; there are 15 full rays preceded by two much shorter rays. The anal fin in both specimens is long, but details cannot be determined as neither clearly preserves the fin rays. There are 25 anal fin pterygiophores in the holotype and 22 fin rays and pterygiophores in paratype UALVP 51664.

Caudal fin. The caudal fin is best preserved in the paratype (UALVP 51664). There are 19 principal rays, and the fin is deeply forked. As in *T. marocensis*, the rays of the dorsal lobe deeply overlap the upper hypurals. The neural spine on the second preural centrum is shorter than the other neural spines, as in other paraclupeids. There are three epural and three uroneural bones, and the epurals fill the space posterior to the first preural neural spine. The first ural centrum (diural terminology) appears to bear a neural arch, but whether or not the following ural centrum also bears a neural arch cannot be determined. The first uroneural (numbered based on position only) extends to the anterior end of the first preural centrum. There are six hypural plates. The hypural diastema appears to be absent, although most of the hypurals are preserved only as impressions lacking bone. The second hypural is sub-rectangular, reaching and probably fused with, the first ural centrum, and the first hypural has an enlarged, hooked proximal base. The arch of the parhypural is fused with the first preural centrum. There is a possible caudal scute dorsal to the first preural centrum, in front of the caudal fin.

Phylogenetic analysis

Phylogenetic methods. The most recent set of phylogenetic data for the Ellimmichthyiformes was published by ALVARADO-ORTEGA et al. (2008), and was based in part on the earlier work by ZARAGÜETA-BAGILS (2004) and morphological studies by GRANDE (1982, 1985) and others.

Using the data of ALVARADO-ORTEGA et al. (2008) as a starting point, we added taxa that were omitted by earlier authors and/or were described in recent years. These include *Kwangoclupea dartevellei* (was '*Diplomystus dartevellei*'; CASIER, 1965; data used here are based on TAVERNE 1997), *Ellimmichthys maceioensis* MALABARBA et al., 2004, and *Ellimma cruzi* SILVA SANTOS, 1990, from Brazil, *Rhombichthys intocabilis* KHALLOUFI et al., 2010, from the Palestinian Territory, *Tychoichthys dunveganensis* HAY et al., 2007, from Canada, *Horseshoeichthys armigserratus* NEWBREY et al., 2010, from Canada, the two new species of *Thorectichthys* from Agoult, Morocco, described here, and *Sorbinichthys africanus*, MURRAY & WILSON, 2011, for a total of 28 taxa including the five outgroup genera *Chanos*, *Ornatogulum*, *Denticeps*, *Chirocentrus*, and *Odaxothrissa*. Additional data were taken from WOODWARD (1895), SIGNEUX (1951), and CHANG & GRANDE (1997).

We also critically evaluated all characters and states, modifying some and deleting a few, and adding several new characters to take into account morphologies seen in the new species (Appendix 1). The resulting data matrix contains 62 characters (Appendix 2). Initial analyses were done using PAUP version 4 (SWOFFORD 2002), employing heuristic searches with default options except for 1000 random-addition-sequence replicates. We used MacClade v. 4 (MADDISON & MADDISON 2005) to create constraint trees subsequently used in PAUP analyses as discussed below. The relationships of “wild-card” taxa (see below) were investigated by adding each wild-card taxon separately to the analysis, with outgroup constraint as described above, to assess to what clade on the preferred tree those wild-card forms could be most reliably assigned.

Phylogenetic results. Unfortunately the inclusion of a number of taxa for which much of the data was coded as missing resulted in a nearly completely unresolved polytomy for the initial analysis involving

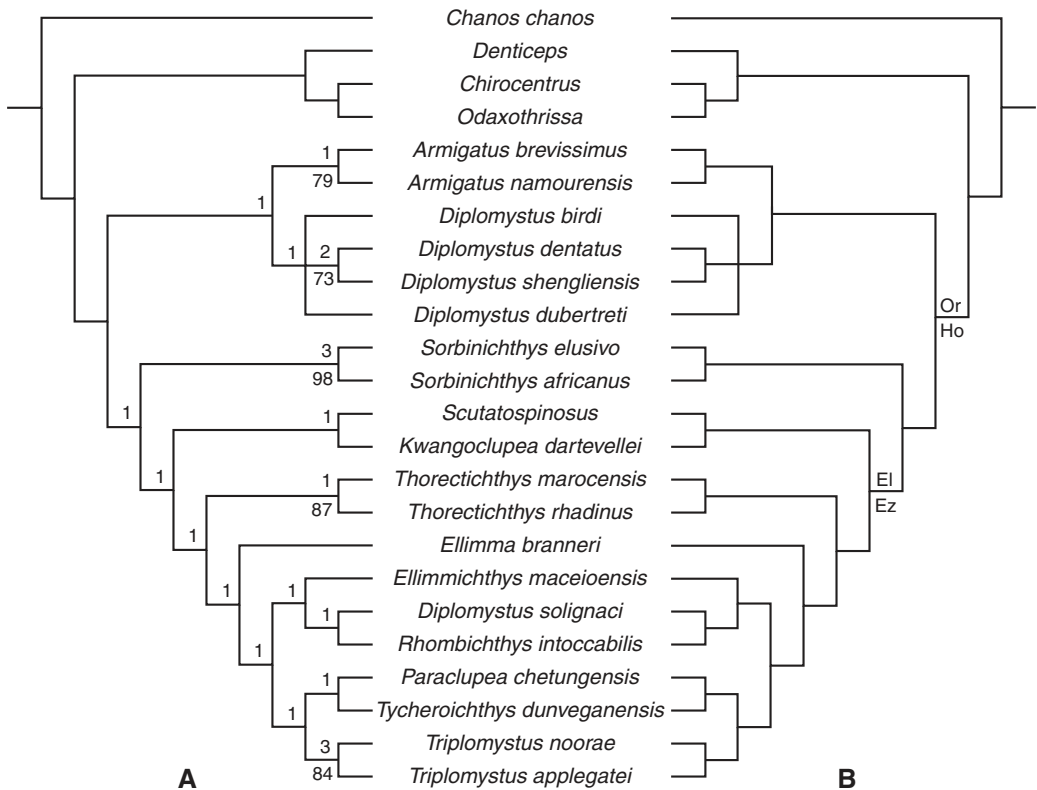


Fig. 6.

Results of the present phylogenetic analysis based on 62 characters and 24 taxa including the new genus *Thorectichthys* with two species, and employing constrained outgroup relationships (see text). **A**, strict consensus of three most-parsimonious trees at 176 steps, C.I.=0.44, R.I.=0.57, R.C.=0.25. Decay (Bremer support) values are indicated above each node. Bootstrap percentages are indicated below nodes where the percentages are greater than or equal to 50%. **B**, majority-rule consensus tree with arbitrary resolution of the polytomy among species of *Diplomystus*. The most conservative position of each of four wild-card taxa is indicated by the following codes: **El**, *Ellimmichthys longicostatus*; **Ez**, *Ezcutuberezi carmenae*; **Ho**, *Horseshoeichthys*; **Or**, *Ornategulum*.

28 taxa. We identified four taxa as especially problematic, acting as ‘wild-cards’, inclusion of any one of which in the analysis created a basal or near-basal polytomy: *Ornategulum*, *Ellimmichthys longicostatus*, *Ezcutuberezi carmenae*, and *Horseshoeichthys armigserratus*.

We then excluded all four of these taxa from the analysis. In the resulting trees, the outgroup clade Clupeiformes persistently was resolved as paraphyletic. We therefore created a constraint tree with outgroup topology as follows: (*Chanos* ((*Denticeps* (*Odaxothrissa*, *Chirocentrus*)) (all ingroup taxa))), i.e., *Chanos* as the most remote outgroup, and the Clupeiformes as the sister group of the ingroup. The constrained analysis generated trees that had identical in-group structure to those of the unconstrained analysis, and we concluded that the result was robust with respect to monophyly or paraphyly of the clupeiform outgroup. The outgroup-constrained analysis produced three shortest trees of length 176 steps. The strict consensus tree and the majority-rule consensus tree are identical (Fig. 6) and contain a polytomy among species of *Diplomystus*, the same polytomy that also appears in one of the three shortest trees. The other two shortest trees differ only in whether *D. birdi* or *D. dubertreti* is sister to the other three species of *Diplomystus* (*D. solignaci* is recovered as not being a member of the genus *Diplomystus*).

We further investigated the decay (Bremer support) of this result, and conducted a bootstrap analysis with 100 replicates. Neither decay nor bootstrap analyses indicated strong support for any clade except for five species pairs. Support values are shown in Figure 6A.

Unambiguous synapomorphies were mapped onto each node using MacClade version 4 (MADDISON & MADDISON 2005), using an arbitrary resolution of the polytomy among species of *Diplomystus*.

Phylogenetic discussion. The recovered phylogeny divides Ellimmichthyiformes into two clades. One clade contains the two studied species of *Armigatus* as each other's sister species, sister in turn to a clade of the four species of *Diplomystus* (Figs. 6, 7). Some authors have excluded *Armigatus* from the order Ellimmichthyiformes, but we prefer to include it. If the proposed sister-group relationship between *Armigatus* and *Diplomystus* is corroborated, exclusion of *Armigatus* would also require exclusion of *Diplomystus*. This clade of *Armigatus* + *Diplomystus* is united by two synapomorphies: third hypural expanded posteriorly, leaving no gap between second and third (31:1), and distal end of uroneural 2 reaching distal end of first uroneural (38:0). However, the clade does not appear to have a name. Based on our study and supported by general agreement on the basal position of *Armigatus* within double-armoured herrings (GRANDE 1982, CHANG & MAISEY 2003, ZARAGÜETA-BAGILS 2004, and ALVARADO-ORTEGA et al. 2008), we propose the family Armigatidae, nov., for the family with type genus *Armigatus* (the family name Diplomystidae cannot be used because it is preoccupied by a family of catfishes with type genus *Diplomystes*), and suborder Armigatoidei, nov., for the suborder containing both *Armigatus* and *Diplomystus*.

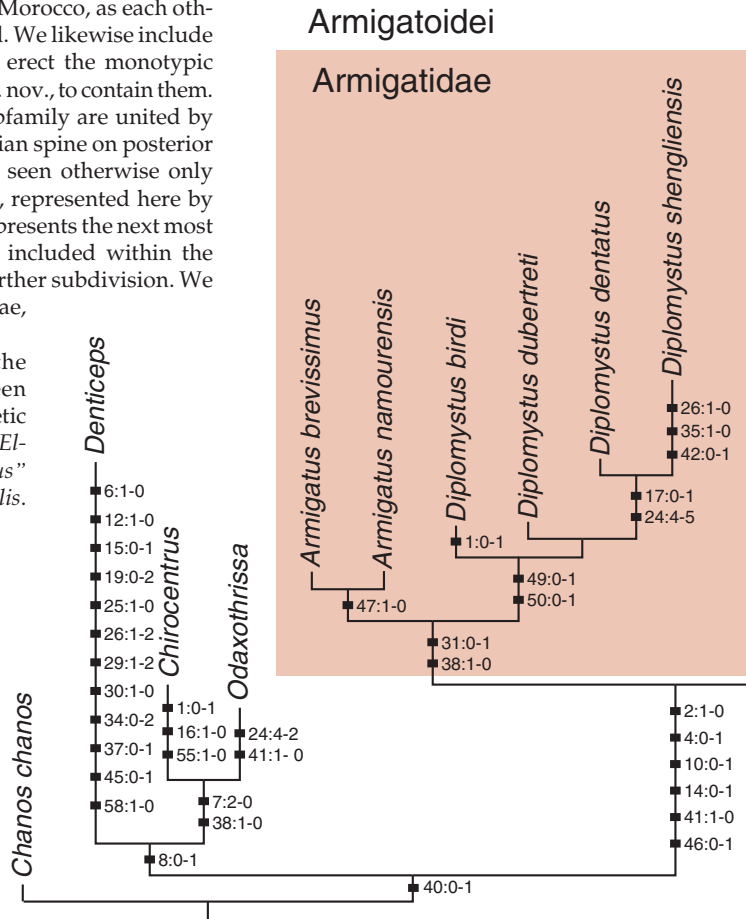
The second clade within Ellimmichthyiformes is herein called the suborder Ellimmichthyoidei GRANDE, 1982, new rank. It contains as its most basal clade the monotypic family Sorbinichthyidae, with two species. The sister group to Sorbinichthyidae is the family Paraclupeidae CHANG & CHOU, 1977. Next most basal is a clade consisting of *Scutatuspinosus* and *Kwangoclupea*. *Scutatuspinosus* is the type genus of the subfamily Scutatuspinosinae SILVA SANTOS & SILVA CORRÉA, 1985, which we retain within the family Paraclupeidae as its most basal clade.

The two new paraclupeids from Morocco, as each others' sister species, are next most basal. We likewise include them within the Paraclupeidae but erect the monotypic subfamily Thorectichthyinae, subfam. nov., to contain them. *Thorectichthys* and its monotypic subfamily are united by possession of a strong posterior median spine on posterior pedorsal scutes (51:0), a condition seen otherwise only in *Kwangoclupea*. The genus *Ellimma*, represented here by *Ellimma branneri* (JORDAN, 1910), represents the next most basal clade. It has previously been included within the family Paraclupeidae but without further subdivision. We hereby name the subfamily Ellimminae, subfam. nov., to contain it.

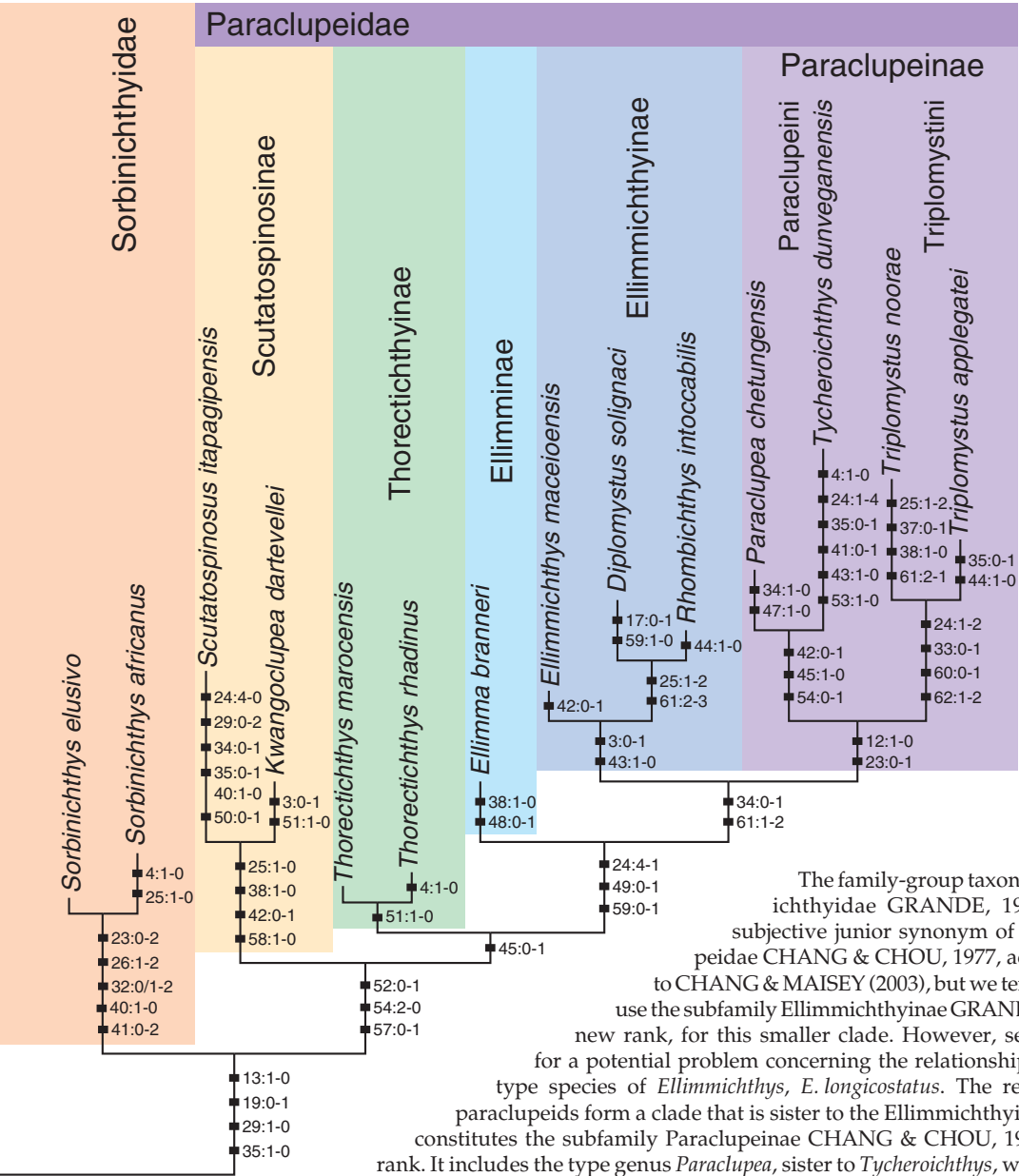
The remaining members of the Paraclupeinae are divided between two sister clades in our phylogenetic tree (Figs. 6, 7). One clade contains *Ellimmichthys maceioensis*, "*Diplomystus*" *solignaci*, and *Rhombichthys intoccabilis*.

Fig. 7.

The most-parsimonious tree resulting from the present study based on 24 taxa and 62 characters, including constrained outgroup relationships (see text), with unambiguous character changes for each node based on AccTran optimisation and an arbitrary resolution of the polytomy among species of *Diplomystus* (compare with Fig. 6A). The new genus *Thorectichthys* with its two new species *T. marocensis* and *T. rhadinus* are shown as Paraclupeidae, subfamily Thorectichthyinae.



Ellimmichthyoidei



The family-group taxon Ellimmichthyidae GRANDE, 1982, is a subjective junior synonym of Paraclupeidae CHANG & CHOU, 1977, according to CHANG & MAISEY (2003), but we tentatively use the subfamily Ellimmichthyinae GRANDE, 1982, new rank, for this smaller clade. However, see below for a potential problem concerning the relationships of the type species of *Ellimmichthys*, *E. longicostatus*. The remaining paraclupeids form a clade that is sister to the Ellimmichthyinae, and constitutes the subfamily Paraclupeinae CHANG & CHOU, 1977, new rank. It includes the type genus *Paraclupea*, sister to *Tychoeroichthys*, with those collectively sister to two species of *Triplomystus*. The two small clades within the Paraclupeinae can be called the Tribe Paraclupeini CHANG & CHOU, 1977, new rank, containing *Paraclupea* and *Tychoeroichthys*, and the tribe Triplomystini, new, with type and only genus *Triplomystus*. Synapomorphies for the various clades can be seen in Figure 7.

Synapomorphies uniting the Paraclupeidae are: predorsal scutes increasing in size posteriorly (52:1), number of predorsal scutes six to fourteen (54:0) (except Paraclupeini), and postpelvic abdominal scutes bearing prominent and strong ventral spine (57:1)

Thorectichthys is united with other Paraclupeidae except for Scutatospinosinae by possession of a neural arch on the first preural centrum (character 45:1). *Thorectichthys* is resolved as more basal than remaining

paraclupeids because it has many more anal rays (23–24) than the fourteen or fifteen of most paraclupeids (24:1), it lacks subrectangular scutes (49:1), and it lacks wide, spatulate abdominal scutes (59:1).

The four wild-card taxa were each evaluated by adding each of them separately to the 24 taxa and running the same kind of analysis as used to obtain the preferred tree (Fig. 6A). Each of these taxa, when added to the analysis, produced a large number of shortest trees and a largely unresolved phylogeny, a result typical of wild-card taxa. The explanation is that significant numbers of missing and/or inapplicable character states cause the lack of resolution.

Ornategulum has previously been hypothesized to be the most basal known clupeomorph (GRANDE 1982) or in a basal polytomy with clupeiforms and ellimmichthyiforms (ALVARADO-ORTEGA et al. 2008). A previous candidate (e. g., GRANDE 1985) for most basal clupeomorph, the Albian *Erichalcis arcta* FOREY, 1975, has been shown to be a composite taxon of which the holotype is a basal euteleost (ARRATIA 1999), while some paratypes are clupeomorphs (HERMUS et al. 2004). In this study, *Ornategulum* is one of many lineages in a basal ellimmichthyiform polytomy that is caused in the strict consensus when it alone is added to the analysis. Similarly, the second wild-card taxon, *Horseshoeichthys*, also participates in a basal ellimmichthyiform polytomy when it alone is added to the analysis.

The third wild-card taxon, *Ellimmichthys longicostatus*, is the type species of *Ellimmichthys*. When added by itself to the analysis, it is resolved in the strict consensus as an incertae sedis member (in a polytomy) of the Ellimmichthyoidei but less basal than Sorbinichthyidae. This raises a potential issue because the type genus of the family Ellimmichthyidae and subfamily Ellimmichthyinae has as its type species *E. longicostatus*, for which the relationships are not certain to lie within the clades named after it, although that clade is among its possible close relatives. However, in our matrix there are still many missing character-state codings for *Ellimmichthys longicostatus*, and we hope that future study of the specimens or discovery of better specimens of this important species will resolve this issue.

The third wild-card taxon is *Ezkutuberezi carmenae*. When added alone to the analysis, it also is resolved, in the resulting strict consensus, in a polytomy as an incertae sedis member of the Ellimmichthyoidei less basal than Sorbinichthyidae.

A formal classification based on these results is as follows:

Superorder Clupeomorpha

Order Clupeiformes

Order Ellimmichthyiformes GRANDE, 1985

Suborder Armigatoidei, new

Family Armigatidae, new

Genus *Armigatus*

Genus *Diplomystus*

Suborder Ellimmichthyoidei GRANDE, 1985, new rank

Family Sorbinichthyidae BANNIKOV & BACCHIA, 2000

Genus *Sorbinichthys*

Family Paraclupeidae CHANG & CHOU, 1977

Subfamily Scutatuspinosinae SILVA SANTOS & SILVA CORRÉA, 1985, new rank

Genus *Scutatuspinosus*

Genus *Kwangoclupea*

Subfamily Thorectichthyinae, new

Genus *Thorectichthys*, new

Subfamily Ellimminae, new

Genus *Ellimma*

Subfamily Ellimmichthyinae GRANDE, 1982, new rank

Genus *Ellimmichthys*

'*Diplomystus*' *solignaci*

Genus *Rhombichthys*

Subfamily Paraclupeinae CHANG & CHOU, 1977, new rank

Tribe Paraclupeini CHANG & CHOU, 1977, new rank

Genus *Paraclupea*

Genus *Tychoichthys*

Tribe Triplomystini, new

Genus *Triplomystus*

Discussion

Members of the Ellimmichthyiformes occur in a wide variety of habitats, ranging from fresh waters through estuarine and marginal marine environments. They have been recovered from South and North America, the Mediterranean region, Africa and Asia, in deposits ranging in age from Neocomian (early Early Cretaceous) through Eocene. This diversity of environments, locations and ages confounds our understanding of the biogeography of the group. However, if our phylogeny is correct, there are a few conclusions that can be drawn. The Armagatoidei probably arose in the eastern Tethys, with the oldest fossils of both genera recorded being Cenomanian fossils from Lebanon (Fig. 8; note that the Portuguese record of *Armigatus brevisimus* is not plotted). From this origin in the eastern Tethys, members of *Diplomystus* had reached North America and Asia by the Eocene, and entered fresh waters. All members of the suborder are found in northern hemisphere localities. Another species, *Horseshoeichthys armigserratus* from the Maastrichtian of Canada, also follows this northern pattern, but remains of uncertain relationship.

The Ellimmichthyoidei have a more global distribution. The basal Sorbinichthyidae are restricted to the Tethys, suggesting an origin of the suborder in that region, but the Paraclupeidae spread from there in all directions, both east and west to modern day Mexico and Asia, as well as north to Canada and south to West Africa and Brazil. The Scutatospinosinae, with *Scutatospinosus* in Brazil and *Kwangoclupea* on the Atlantic coast of Democratic Republic of the Congo (formerly Zaire), may have reached these southern Atlantic localities from the Tethys region through an intermittent marine connection. Such a connection, separating West Africa from the rest of the continent, has been suggested as occurring during later time periods (e.g., SMITH et al. 1994) and might also have been present in the mid Cretaceous. This passageway being open during the mid Cretaceous would also have allowed the Ellimmichthyinae to spread between Tethyan localities in Tunisia (*'Diplomystus' solignaci*) and the Levant (*Rhombichthys intoccabilis*), and Brazil (*Ellimmichthys maceioensis*), as well as allowing the dispersal of Ellimminae (*Ellimna branneri* in Brazil), and *Ellimmichthys goodi* and *E. longicostatus*, which are plotted as incertae sedis in Figure 8. The Thorectichthyinae, as currently known, remained restricted in the Tethys region.

Paraclupeinae are the most widely distributed of the subfamilies. Paraclupeine species also appear restricted to the Northern Hemisphere, but this is because some are not plotted on the map; ALVARADO-ORTEGA et al. (2008) reported a "Paraclupea-like" form from Mexico, but it has yet to be described and is not included in Figure 8. A sister-group relationship between *Triplomystus noorae* and *T. applegatei* shows this genus was in both the eastern Tethys (Lebanon) and south of the Western Interior Seaway (Mexico). Paraclupeines also reached the farthest north of the order, with *Tycheroichthys dunveganensis* in the northern portion of the Western Interior Seaway during the Cenomanian. The sister-group relationship between *Tycheroichthys* and *Paraclupea chetungensis* found in China suggests the Paraclupeini at least were capable of long-distance dispersals.

The biogeography of the group becomes even less clear when relative ages of the fossil localities are taken into consideration. The most derived ones (Ellimmichthyinae and Paraclupeinae) are middle Cretaceous forms, but within each sister-group pair in Paraclupeinae (Fig. 7), one taxon is Early Cretaceous (*Triplomystus applegatei*, Albian, ALVARADO-ORTEGA & OVALLES-DAMIÁN 2008, and *Paraclupea chetungensis*, with no more precise age, CHANG & GRANDE 1997); and the sister taxon is Late Cretaceous (both Cenomanian; *Triplomystus noorae*, FOREY et al. 2003; and *Tycheroichthys dunveganensis* HAY et al. 2007). Additionally, *Paraclupea chetungensis* is from freshwater deposits (CHANG & GRANDE 1997). Other ellimmichthyiforms described in *Diplomystus* (not included in this paper) from similarly aged Early Cretaceous freshwater deposits of Japan, may well belong in *Paraclupea* (CHANG & MIAO 2004). The Ellimmichthyinae species are all different ages, with *Ellimmichthys maceioensis* being Aptian-Albian (MALABARBA et al. 2004), *Rhombichthys intoccabilis* Cenomanian (KHALLOUFI et al. 2010), and *'Diplomystus' solignaci* Senonian (GAUDANT & GAUDANT 1971; post-Turonian Cretaceous). Therefore, within the more derived Paraclupeidae are some of the oldest ellimmichthyiforms, and there are taxa ranging over perhaps 25 or more million years. The discrepancy of ages becomes greater within the family as a whole, which includes taxa from the Neocomian (*Scutatospinosus*) as well as the Eocene (*Diplomystus*), a gap of at least 65 million years.

It remains evident that much more study of the fossil clupeomorphs is needed. With more fossil finds and more study of the relationships of the ellimmichthyiforms, we will eventually form a better understanding of the biogeography of these double-armoured clupeomorphs.

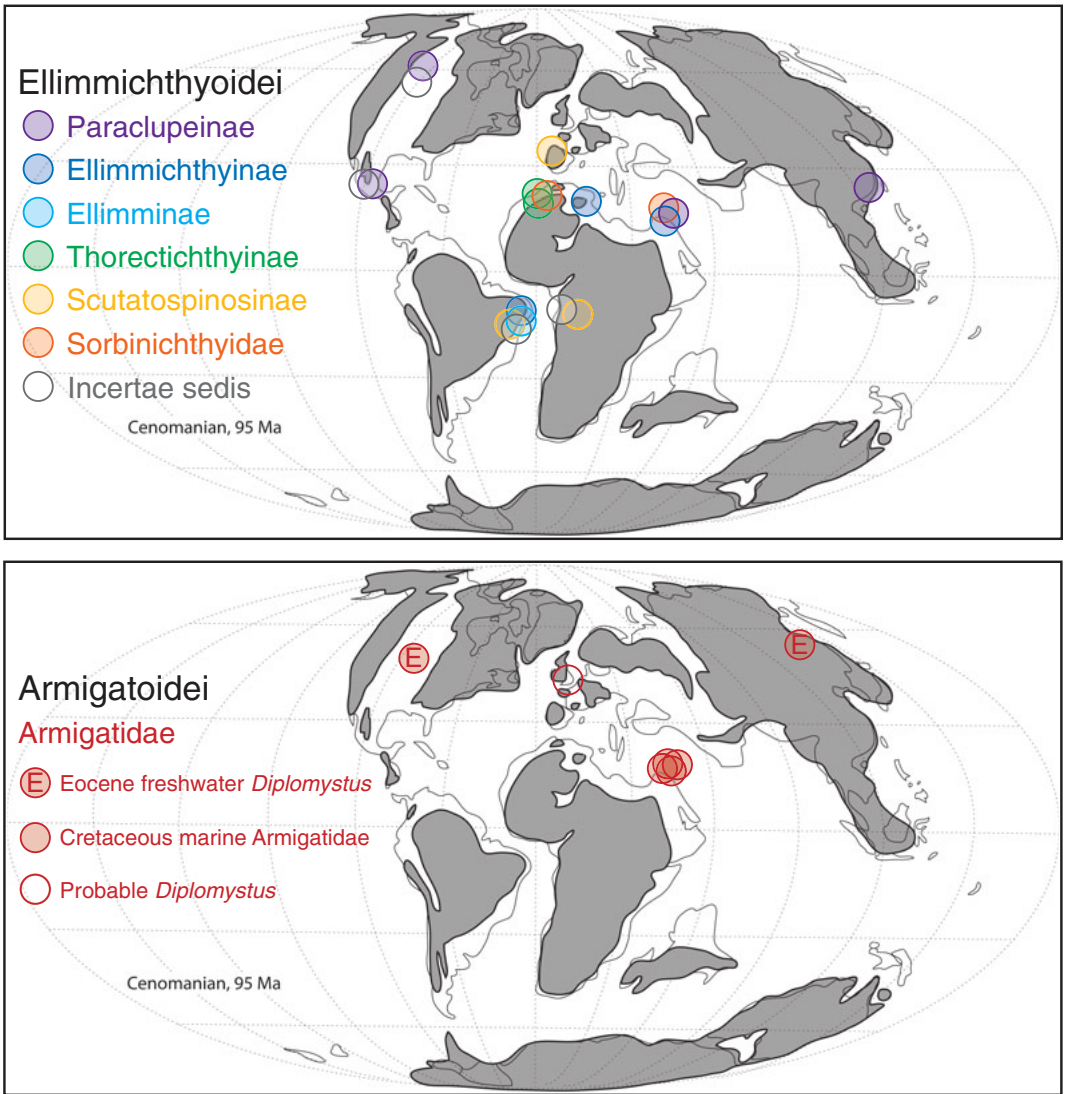


Fig. 8. Distribution of many of the known Ellimmichthyiformes. Both maps are plotted on a palaeo-projection of the continents during the Cenomanian based on SMITH et al. (1994), although some fossils are of younger age. Upper map shows the location of the Ellimmichthyoidei and lower map shows the Armigatoidei. See text for details.

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Appendix 1

List of characters and states used in the analysis

Elimmichthyiform characters and states unless otherwise indicated are from ALVARADO-ORTEGA et al. (2008) who used some characters described by ZARAGÜETA-BAGILS (2004), who in turn used a number of characters from CHANG & MAISEY (2003). Explanation of the characters can be found in these publications. Our modifications to these characters are noted below. The number preceded by “Z” indicates the number the character was given in ZARAGÜETA-BAGILS (2004).

- 1/Z56 Anterior dorsal margin of body: rounded and convex [0]; almost straight, forming a marked angle at the dorsal fin insertion [1]. This character may be affected by growth and size of an individual (see KHALLOUFI et al. 2010).
- 2/Z1 Skull roof: parietal bones contacting each other in the midline [0]; supraoccipital separates parietal bones [1].
- 3/Z2 Lateral profile of skull roof: a straight line from anterior tip of frontal to back of skull, with no distinct angle apparent [0]; with distinct angle between anterior and posterior parts, normally in the region of the parietal [1]. The character and two states were originally: depth of supraoccipital crest low [0]; high [1]. These states have been interpreted differently by different researchers (see ALVARADO-ORTEGA et al., 2008). We modified them here to follow the descriptions in ALVARADO-ORTEGA et al. (2008), so as to base the comparison on more objective criteria.
- 4/Z3 Ornamentation of skull roof: absent [0]; present [1]. The original character 4 was: ornamentation of dermal bones of skull roof: absent [0]; present on middle part of frontals [1]; present on posterior part of frontals and parietals [2]; present on posterior part of frontal, parietal and pterotic bones [3]; present on frontal, parietal and supraoccipital bones [4]. In *Rhombichthys* ornamentation is only present on the parietal bones, and in *E. branmeri*, the ornamentation only develops in larger specimens. We have simplified this character to a simple absence or presence of ornamentation.
- 5/Z4 Ornamentation of skull roof bones: fine, more or less parallel grooves [0]; strong grooves with numerous fine, radiating ridges [1].
- 6/Z6 Posttemporal fossa: absent [0]; present [1].
- 7/Z7 Cavity in the temporal region of the skull: pre-epioccipital fossa (between parietal, epioccipital and pterotic bones) [0]; pre-epioccipital fenestra (between the parietal, epioccipital and supraoccipital bones) [1]; absence of cavity or fenestra [2].
- 8/Z8 Recessus lateralis: absent [0]; present [1].
- 9/Z10 Supramaxillary bones: two [0]; one or none [1].
- 10/Z11 ‘Basipterygoid’ process of parasphenoid: absent [0]; present [1].
- 11/Z12 ‘Osteoglossid’ tooth patch on the parasphenoid: absent [0]; present [1].
- 12/Z13 Supraorbital bone: absent [0]; present [1].
- 13/Z16 Antorbital bone: absent [0]; present [1].
- 14/Z14 Beryciform foramen within the anterior ceratohyal: absent [0]; present [1].
- 15/Z15 Foramen in posterior ceratohyal: absent [0]; present [1].
- 16 Teeth on entopterygoid: absent [0]; present [1]. The states for this character were originally: fine or absent [0]; strong [1]. They have been modified here to present or absent, because the teeth may vary on the entopterygoid of an individual, and additionally, the robustness is difficult to determine objectively.
- 17 Total number of vertebrae excluding ural centra: 30–40 [0]; 41–43 [1]; more than 50 [2]. The character of ALVARADO-ORTEGA et al. (2008) referred to caudal, rather than total non-ural centra, but based on the numbers they gave, we believe this to have been in error. The states have been modified here to accommodate the new information from the Moroccan fossils. Two of the original states were “31–32” and “33–39” non-ural vertebrae; these two states were combined and the range increased to “30–40”. The original state 4 was 73 non-ural vertebrae, but we changed this to “more than 50” to include the 51 vertebrae of *Ornategulum* which previously fit none of the states.
- 18/Z17 Halves of the neural arches of most abdominal vertebrae: separate medially [0]; fused medially [1].
- 19/Z18 Pleural ribs: all ribs articulate with parapophyses along the abdominal region [0]; anteriormost ribs articulate with deep pits on the lateral side of all abdominal centra and those located posteriorly articulate with well-developed parapophyses [1]; all ribs articulate with deep pits on the lateral side of all abdominal centra [2].
- 20/Z19 Epineurals and epipleurals in the caudal region: 0, absent; 1, present.
- 21/Z20 Epicentrals: 0, absent; 1, present.
- 22 Shape of cleithrum: L-like (having a single angle in the bone) [0]; S-like (having two angles) [1].

- 23/Z22 Dorsal process of posttemporal: slender and sharp [0]; sub-rectangular [1]; broad, wider at distal tip than at midpoint of bone [2]. We have added state 2, a diagnostic character of *Sorbinichthys*, to unite the two species of that genus.
- 24 Number of anal fin rays: eight to eleven [0]; fourteen or fifteen [1]; seventeen or eighteen [2]; twenty [3]; twenty-two to thirty-two [4]; thirty-six to forty-one [5]. The original states as written did not match the ranges shown in the figure (ALVARADO-ORTEGA et al., 2008) and did not fit with the numbers in the new species. Therefore, we modified the states to allow inclusion of the new species that had overlapped the previous character state ranges, and have also combined state 4 (23 rays) with state 5 (24–30 rays) [and broadened the range to accommodate the new species], which had the least difference between the two, to reduce the number of states. [In descriptions where only pterygiophore numbers are noted or visible in figures, we have used the number of pterygiophores plus one to be the number of anal fin rays].
- 25 Number of dorsal fin rays: eight to thirteen [0]; fourteen to nineteen [1]; twenty-one to twenty-five [2]. We modified the character states by altering the ranges to include the additional species.
- 26/Z23 Number of hypurals: seven [0]; six [1]; five [2].
- 27/Z24 Hypural 2: 0, autogenous; 1, fused to first ural centrum (diural terminology).
- 28/Z25 Length of hypural 1: long, reaching ural centrum 1 [0]; short, not reaching ural centrum 1 [1]. (Diural terminology).
- 29/Z26 Proximal end of hypural 1 (was originally termed “articulation of hypural 1): massive and forming an upward process [0]; sharp [1]; massive but no upward process [2]. We have added an extra state to accommodate *Denticeps* and others that are more massive, but do not have a distinct upward process.
- 30/Z27 Shape of hypural 2: distal end distinctly broader than proximal end [0]; very thin and stick-like [1]. State 0 of this character was given as “symmetrical to hypural 4” by ALVARADO-ORTEGA et al. (2008). We have modified the states to make the shape of hypural 2 explicit.
- 31/Z28 Diastema between second and third hypural: third hypural not expanded posteriorly leaving a gap or notch between the second and third hypural [0]; third hypural expanded posteriorly, leaving no gap or notch between second and third hypural [1]. The character and states given by both ZARAGÜETA-BAGILS (2004) and ALVARADO-ORTEGA et al. (2008) were hypural diastema present (state 0) or absent (state 1) which have been variously interpreted by different researchers. Here we revert to the original state descriptions of CHANG & MAISEY (2003), which seem more clear to us, and we interpret the diastema as present even if it is only a distal notch between the two hypurals. We additionally created a new character 32 to express the distinct large diastema found in *Sorbinichthys*:
- 32 Shape of diastema between hypurals 2 and 3: small triangular notch [0]; deep triangular cavity [1]; large concavity formed by hypural 3 having a concave ventral edge [2]. We have added an extra state to distinguish the distinctive condition of *Sorbinichthys* from the much less extensive diastema of others.
- 33/Z30 Size of first ural centrum (diural terminology): roughly the same size (length and depth) as the preural centra [0]; much smaller than the preural centra [1]. We have slightly modified these states to more closely follow CHANG & MAISEY (2003). We consider state 0 to be present unless the first ural centrum is distinctly smaller than the first preural centrum.
- 34/Z29 Number of uroneurals: three [0]; two [1]; one [2]. *Odaxythrissa* and *Chirocentris* have two free uroneurals and the pleurostyle, so we coded them as state “0”; state “2” does not apply to any of our taxa, but we leave it here anyway.
- 35/Z31 First uroneural: extends anteriorly to reach second preural centrum [0]; does not reach second preural centrum [1]. ZARAGÜETA-BAGILS (2004) used the character: proximal extremity of the first uroneural: contacting preural centrum 2 [0]; contacting preural centrum 1 [1]. We have changed the wording for these states to more closely follow CHANG & MAISEY (2003) and express more clearly the two characters. We coded those taxa that have a pleurostyle as “not applicable” for this character.
- 36/Z32 Fusion of first uroneural and first ural centrum: absent [0]; present [1]. *Chanos* is coded as having character state 1, following the coding for *Odaxythrissa* and *Chirocentrus* by ZARAGÜETA-BAGILS (2004) and ALVARADO-ORTEGA et al. (2008), although the precise composition of the terminal complex has not been clarified developmentally.
- 37/Z33 First uroneural bearing a dorsal expansion of laminar bone: absent [0]; present [1].
- 38/Z34 Distal end of second uroneural: reaching the distal end of the first uroneural [0]; not reaching the distal end of the first uroneural [1].
- 39/Z35 Parhypural: base/arch of bone fused with preural centrum 1 [0]; autogenous [1].
- 40/Z24 Fusion of hypural two and first ural centrum: absent [0]; present [1]. In the character list of ALVARADO-ORTEGA et al. (2008), character 39 (fusion between hypural 2 and first ural centrum: absent [0]; present [1]) was equivalent to character 27 (hypural 2: autogenous [0]; fused to first ural centrum [1]), but the two were coded differently for some taxa. We here follow their character 27.

- 41/Z37 Number of epurals: three [0]; two [1]; none, or those present are weakly ossified, perhaps cartilaginous [2]. We have added state 2 to encompass both species of *Sorbinichthys*, which appear to lack epurals, but may in fact have cartilaginous epurals (P. FOREY pers. comm. 2010).
- 42/Z38 Position of epurals: epurals fill the space between the neural spines of pu1 and pu2 [0]; epurals are located far from the spine of pu2, leaving an open space between them [1].
- 43/Z39 Caudal scutes: absent [0]; present [1].
- 44/Z40 Neural spine of first preural centrum: large or lanceolate [0]; short or sub-rectangular [1].
- 45/Z42 Neural arch of first ural centrum: absent [0]; present [1].
- 46/Z45 Predorsal scutes: absent [0]; present [1]. ALVARADO-ORTEGA et al. (2008) listed this as: predorsal scute series: absent [0]; present, incomplete (absent in anterior part) [1]; present, complete [2]. We have split this character in two, in order to include species in which predorsal scutes are present, but we cannot determine if the series is complete. The second part of this character is as follows:
- 47/Z45 Predorsal scute series: incomplete (absent in anterior part) [0]; complete [1].
- 48/Z47 Subrectangular scutes (i. e., scutes significantly broader than long) in anterior part of predorsal series: absent [0]; present [1]. We have interpreted these to be present when the scutes are significantly broader (the lateral wing deeper dorsoventrally) than they are long (anteroposteriorly).
- 49/Z47 Subrectangular scutes in posterior part of predorsal series: absent [0]; present [1].
- 50/Z48 Series of spines on the posterior margin of the lateral wings of the predorsal scutes: absent [0]; present [1]. We have modified the wording, combining the character description from both ALVARADO-ORTEGA et al. (2008) and ZARAGÜETA-BAGILS (2004), to exclude scutes with single median spines which are accounted for in the next character.
- 51/Z49 Prominent median strong spine on posteriormost predorsal scutes: absent [0]; present [1].
- 52/Z50 Size of scutes of predorsal series: all scutes of same size [0]; irregular in size, size of scutes increasing posteriorly [1]. We have considered state 1 to apply even if there is only a single irregularly shaped scute.
- 53/Z51 Surface of predorsal scutes: smooth [0]; ornamented with radiating grooves [1].
- 54/Z52 Number of predorsal scutes: six to fourteen [0]; sixteen to nineteen [1]; twenty to forty-one [2]. The ranges of the states for this character given by ALVARADO-ORTEGA et al. (2008) have been modified to include the number found in the newly included species and decrease the number of states.
- 55/Z52 Abdominal scute series: absent [0]; present [1].
- 56/Z53 Complete abdominal scute series between isthmus and anus (i. e., postpelvic scutes are present): absent [0]; present [1]. This character is invariant in our data matrix but we have retained it for use with different terminal taxa or better specimens of poorly known taxa.
- 57/Z54 Postpelvic abdominal scutes bearing very prominent and strong ventral spine: absent [0]; present [1].
- 58/Z55 Size of lateral wings of abdominal scutes: small [0]; large, extended upward and covering the abdominal cavity laterally for at least one quarter of the distance from ventral body edge to vertebral column [1]. We added the quantitative part of state one to make this more objective.
- 59/Z55 Shape of lateral wing of abdominal series scutes: spine-like, with large spaces between wings of scutes [0]; wide or spatula-like, with wings of adjacent scutes touching for most of their length [1]. We have added the descriptive phrases to clarify our meaning.
- 60 Postdorsal scute series: absent [0]; present [1].

We added two more characters based on meristics:

- 61 Number of abdominal scutes (in some taxa they will not be equivalent to vertebral counts): fewer than 20 [0]; 22–30 [1]; more than 32 [2].
- 62 Number of predorsal bones: 10 or more [0]; 7–9 [1]; 6 or fewer [2].

Appendix 2

Data matrix

Taxon / Character number	0-10	11-20	21-30	31-40	41-50	51-60	61-62
<i>Chanos chanos</i>	0100-?20?0	01?0001031	1200110111	00-1-10110	100100----	----0----0	-0
<i>Chirocentrus</i>	110??10100	011??02?01	0014110111	0100-10011	100100----	----0----0	-?
<i>Denticeps</i>	0100-02110	0010110021	1014021020	0102101101	100110----	----110000	0?
<i>Odaxothrissa</i>	0100-10110	0110011??1	?002111111	0000-10011	0001-0----	----110100	00
<i>Ornategulum</i>	0001100001	0111?12001	?0?0101121	??00001001	000100----	----0----0	-0
<i>Armigatus brevissimus</i>	?00??12001	1?11??????	?????11011	1-00100001	00?10?0???	??????????	??
<i>Armigatus namourensis</i>	000111?001	11?1010001	0104111011	1-00100001	0011010000	1011110100	12
<i>Diplomystus birdi</i>	1?????????	?????0?0??	??41?1???	???????????	?????11011	1??21???	11
<i>Diplomystus dentatus</i>	001????001	1??1011???	01?5011011	1-00100001	00?1011011	100211?100	21
<i>Diplomystus dubertreti</i>	0?11????0?	??1?1?0???	??42?1???	???????????	?????11011	??21?????	?1
<i>Diplomystus shengliensis</i>	0010-???	0????11???	?050010??	1-00000?01	010??11011	10021??100	?1
<i>Diplomystus solignaci</i>	1?1???????	?????11???	??121?0?1	100???????	00?1?1??1?	????111100	31
<i>Ellimma branneri</i>	A0011???	0??1?10?1?	?10111?0??	0100000001	0011?11110	1110111110	11
<i>Ellimmichthys longicostatus</i>	1?0???????	?????001?	???????????	???????????	???????????	????111?10	??
<i>Ellimmichthys maceioensis</i>	1?110???	?????0???	?1?11?102?	1-01000101	0101111010	11101111?0	21
<i>Ezkutuberezi carmenae</i>	100?????0?	?????0?1?	?1?42?1021	??0?0000?1	100101?000	111?111100	20
<i>Horseshoeichthys armigserratus</i>	0000-?000?	?00????0??	001???????	???????????	?????1????	0?0???????	??
<i>Kwangoclupea dartevellei</i>	00111?0001	0?????0???	??40?1001	0100000001	0101011000	010?1110-0	11
<i>Paraclupea chetungensis</i>	10011???	0??1?10???	?1?1111011	0100000101	0111010-10	1111111110	21
<i>Rhombichthys intocabilis</i>	1011????01	0101?10110	01012?1021	0001000001	0000?11010	1110111110	31
<i>Scutatuspinosus itapagipensis</i>	000?????0?	01????0???	?100010021	??01100000	0111011001	11101110-0	10
<i>Sorbinchthys africanus</i>	1?00-???	010??10011	0024020001	0200000100	2-00011000	10?2110100	00
<i>Sorbinchthys elusivo</i>	1?01????0?	0????10011	?024120001	0200000100	2-0?011000	10?2110100	00
<i>Thorectichthys marocensis</i>	10010?001	0?01010111	0104110001	0000000101	0011111000	0100111100	12
<i>Thorectichthys rhadinus</i>	1000-??0?1	0??1010111	0104110001	0000000101	0011111000	0100111100	12
<i>Triplomystus applegatei</i>	10011?????	00????011?	?1121?1011	0011100101	0010111010	1110111111	22
<i>Triplomystus noorae</i>	1001110001	000??10111	1112211011	??11001001	0011?11010	1110111111	12
<i>Tycheroichthys dunveganensis</i>	1000-???	000??0111	011411????	0101100101	1101011110	1101111110	21

A=0/1

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