

# First identification of the genus *Argyrosomus* (Teleostei, Sciaenidae) in Neogene African outcrops

**Olga OTERO**

Muséum national d'histoire naturelle, UMR 7207, Département Géologie,  
57 rue Cuvier, F-75231 Paris cedex 05 (France)  
and UMR 8606 UFR SFA, Université de Poitiers,  
40, av. du Recteur Pineau, F-86000 Poitiers (France)  
[otero@mnhn.fr](mailto:otero@mnhn.fr)

**Philippe BÉAREZ**

Muséum national d'Histoire naturelle,  
UMR 7209, Département Écologie et gestion de la biodiversité,  
57 rue Cuvier, 75231 Paris cedex 05 (France)  
[bearez@mnhn.fr](mailto:bearez@mnhn.fr)

**Thodoris ARGYRIOU**

University of Alberta, Department of Biological Sciences,  
Edmonton, Alberta T6G 2E9 (Canada)  
and Museum of Palaeontology and Geology, National and Kapodistrian,  
University of Athens, Panepistimiopolis, Athens (Greece)  
[argyriou@ualberta.ca](mailto:argyriou@ualberta.ca)

---

Otero O., Béarez P. & Argyriou T. 2013. — First identification of the genus *Argyrosomus* (Teleostei, Sciaenidae) in Neogene African outcrops. *Geodiversitas* 35 (1): 49-65.  
<http://dx.doi.org/10.5252/g2013n1a4>

## ABSTRACT

Disarticulated fossil remains of a same indeterminate perciform have been described in Neogene deposits from Africa, in Libya (Upper Miocene of Sahabi) and in Namibia (Middle Miocene of Arrisdrift), and then from Germany (Lower Miocene of Langenau). Found in association with strictly or dominantly freshwater faunas, they were supposed to be freshwater fish. However, their distribution was rather difficult to interpret and their comparison with freshwater ichthyotaxa did not permit to attribute them neither to a known genus even nor to a known family. By comparison with marine perciforms, the review of the African fossils allowed us to attribute them to the genus *Argyrosomus* (Teleostei, Sciaenidae) or “Meagre”. Only new fossil material and an acute study of the osteology of extant species might allow specific attribution of this bony material. These African fossils and those from Langenau constitute the whole bony fossil record of the genus *Argyrosomus* De La Pylaie, 1835 that

**KEY WORDS**

Sciaenidae,  
*Argyrosomus*,  
 fossil bones,  
 Miocene,  
 Africa,  
 freshwater.

is also known by otoliths from European Miocene deposits (Mediterranean and Paratethyan seas). These marine fish, today present along European and African (and also Asian and West Pacific) coasts, have certain members that frequently enter estuaries and coastal freshwater streams. So, our identification of disarticulated bony remains completes the fossil record of *Argyrosomus*. It allows us to date their presence along the African West coast since at least the Middle Miocene and it indicates that their affinity with fresh water existed yet in the Lower Miocene.

**RÉSUMÉ**

*Première identification du genre Argyrosomus (Teleostei, Sciaenidae) dans des sites néogènes africains.*

Des restes fossiles désarticulés d'un même perciforme indéterminé ont été décrits dans des dépôts néogènes d'Afrique en Libye (Miocène supérieur de Sahabi) et en Namibie (Miocène moyen d'Arrisdrift), puis d'Allemagne (Miocène inférieur de Langenau). Associés à des faunes à dominante ou strictement dulçaquicoles, ils étaient supposés d'eau douce. Cependant, leur distribution était difficile à expliquer et leur comparaison avec les ichtyo-taxons d'eau douce ne permettait de les attribuer ni à un genre, ni même à une famille connus. Par comparaison à des perciformes marins, la révision des fossiles africains a permis de les attribuer au genre *Argyrosomus* De La Pylaie, 1835 (Teleostei, Sciaenidae) ou « Maigre ». Seuls l'obtention de matériel fossile supplémentaire et une étude poussée de l'ostéologie des espèces actuelles permettraient éventuellement une attribution au niveau spécifique de ce matériel osseux. Ces fossiles africains et ceux de Langenau constituent la totalité du registre fossile osseux du genre *Argyrosomus*, qui était par ailleurs déjà connu par des otolithes dans des niveaux miocènes d'Europe (Méditerranée et Paratéthys). Ces poissons marins, aujourd'hui présents le long des côtes européennes et africaines (et aussi asiatiques et ouest-pacifiques), voient certains de leurs représentants envahir régulièrement les estuaires et les cours d'eau côtiers. Notre identification de restes osseux désarticulés complète le registre fossile d'*Argyrosomus*. Elle nous permet de dater leur présence le long des côtes ouest africaines depuis au moins le Miocène moyen et nous indique que leur affinité à l'eau douce existe déjà au Miocène inférieur.

**MOTS CLÉS**

Sciaenidae,  
*Argyrosomus*,  
 Os fossiles,  
 Miocène,  
 Afrique,  
 eau douce.

**INTRODUCTION**

In 1987, Gaudant described the fossil fish remains of the diverse freshwater dominant assemblage from Sahabi (Late Miocene, Libya). Among rather common Nilotic taxa, he signaled the presence of premaxillae that clearly belong to a perciform fish but does not correspond to any of the extinct or extant taxa known so far in the African inland waters. He cautiously ascribed the fossil to an inde-

terminate perciform fish. In 2003, Otero signaled resembling premaxillae and associated bones from Middle Miocene deposits of the Orange River at Arrisdrift (Namibia). These Namibian fossils were collected from terrace deposits in a lateral channel of the river in association with a typically continental vertebrate fauna (Pickford & Senut 2003). On that basis, Otero (2003) compared the fish remains with freshwater extinct and modern African fish. She concluded that the fossils belong

to perciform fishes unknown so far from modern and ancient fresh waters, with the exception of the Late Miocene from Sahabi. She suggested that these enigmatic fossils may belong to a perciform taxon that entered sporadically the African freshwaters during the Tertiary but failed to conquer further inland waters. Finally, Gaudant (2006) signaled and figured two premaxillae that belong to the same enigmatic perciform taxa from a Lower Miocene freshwater fish assemblage in Langenau (Germany), and on that record he suggested that the ichthyofauna may have an African component, including the channids, a perciform family distributed in Asia and Africa today.

Indeed, two hypotheses may explain the occurrence of a same fish in fossiliferous outcrops *c.* 7 Ma in Libya and *c.* 17 Ma in Namibia (Fig. 1). First, it is an African freshwater fish that temporarily invade European freshwaters in Germany during the Lower Miocene. But in that case, we miss 10 Ma of its history in the inland waters across the continent, which is hard to accept when considering the Miocene fossil record of African freshwater fish (Otero 2010; Fig. 1). Second hypothesis, the taxon is not a freshwater fish but an Atlantic marine animal that tolerates freshwaters and enters estuaries and coastal rivers. This explains this geographically disjoint distribution and the absence of this taxon further inland in Africa.

In the frame of using freshwater fish to redraw the paleo-hydrography of continental Africa (Otero *et al.* 2009; Argryriou *et al.* 2012; Pinton *et al.* 2013), we had to review this poorly determined material. The collect of new material at Sahabi, by the East Libya Neogene Research Project (ENLRP), offered the good opportunity for this review. To identify the fish and state about the marine origin of the fossil, we focused on the perciform fish that inhabit the African coastal waters, notably those frequently entering estuaries and coastal fresh water streams. The results are presented here. In the paper, we demonstrate that the fossils belong to sciaenid fishes of the genus *Argyrosomus* De La Pylaie, 1835, and we discuss their fossil record and notably their presence in the two freshwater dominant fossil assemblages from Sahabi at 7 Ma (Libya; Boaz *et al.* 2008) and from Arrisdrift at 17 Ma (Namibia; Pickford & Senut 2000).



FIG. 1. — Location of the main Miocene freshwater fish outcrops of Africa. Those that yielded *Argyrosomus* De La Pylaie, 1835 are in grey and their names are given in bold and italics. The white line delimitate the modern limits of ichthyoregions (Roberts 1975).

## MATERIAL AND METHODS

### OUTCROPS AND PALEOENVIRONMENTS

The teleost fish bones and bone fragments recovered from the Middle Miocene deposits at Arrisdrift (Namibia) belong to at least two fish taxa that do not exist in any other freshwater fish assemblage in Africa with the exception of the perciform fish in common with Sahabi (Otero 2003). In Arrisdrift locality, the terraces of the paleo-river Orange also yielded an assemblage of mammals, squamates, turtles and birds inhabiting a subtropical climate with summer rains; the fossil assemblage is dated around 17 Ma (Pickford & Senut 2003). The Late Miocene to Early Pliocene deposits at Sahabi (Libya) yielded a mixed ichthyofauna that was first studied by Gaudant (1987). The dominant Nilo-Sudan freshwater component is characterised by *Polypterus* Lacepède, 1803, *Clarias* Scopoli, 1777, or *Heterobranchus* Saint-Hilaire, 1809, *Clarotes* Kner, 1855, *Synodontis* Cuvier, 1816, and *Lates* Cuvier, 1828, and recently reported (Argryriou *et al.* 2012) *Semlikiichthys* Otero & Gayet, 1999, whereas a marine component includes sharks and

TABLE 1. — *Argyrosomus* De La Pylaie, 1835 fossil material included in the study.

Attribution	Bone	Locality	sample n°
<i>Argyrosomus</i> sp.	1 maxilla	Sahabi	8P96B
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	6P17A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	33P109A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	20P109A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	89P17A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	55P62A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	42P63A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	10P96B
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	11P96B
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	19P96B
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	21P207A
<i>Argyrosomus</i> sp.	1 premaxilla	Sahabi	2P209A
<i>Argyrosomus</i> sp.	1 dentary	Sahabi	86P17A
<i>Argyrosomus</i> sp.	1 dentary	Sahabi	101P60A
<i>Argyrosomus</i> sp.	1 dentary	Sahabi	12P96B
<i>Argyrosomus</i> sp.	1 dentary	Sahabi	13P96B
<i>Argyrosomus</i> sp.	1 dentary	Sahabi	99P99A
<i>Argyrosomus</i> sp.	1 first vertebra	Sahabi	52P62A
<i>Argyrosomus</i> sp.	1 premaxilla	Arrisdrift	AD 260'97
<i>Argyrosomus</i> sp.	1 dentary	Arrisdrift	PQ-AD 20'82
<i>Argyrosomus</i> sp.	1 dentary	Arrisdrift	AD 483'00
<i>Argyrosomus</i> sp.	1 dentary	Arrisdrift	AD 557'99
<i>Argyrosomus</i> sp.	1 angulo-articular	Arrisdrift	AD 83'00
<i>Argyrosomus</i> sp.	1 angulo-articular	Arrisdrift	AD 172'95
<i>Argyrosomus</i> sp.	1 angulo+ retro-articular	Arrisdrift	AD 5'95
<i>Argyrosomus</i> sp.	1 angulo-articular	Arrisdrift	AD 14'95
<i>Argyrosomus</i> sp.	1 quadrate	Arrisdrift	AD 102'95
<i>Argyrosomus</i> sp.	1 first vertebra	Arrisdrift	AD 110'98
cf. <i>Argyrosomus</i> sp.	1 post-abdominal vertebra	Arrisdrift	AD 375'96
? <i>Argyrosomus</i> sp.	1 abdominal vertebra	Arrisdrift	AD 103'00
? <i>Argyrosomus</i> sp.	1 abdominal vertebra	Arrisdrift	AD 637'00

sparids. More recently, the ENLRP realised excavations in the area and collected fossils in a renewed constraint stratigraphical context (Boaz *et al.* 2008). The *Argyrosomus* remains all belong to member U1 of the Sahabi Formation, aged *c.* 7 Ma, where the deposits correspond to continental estuarine environment with alternative dominance of marine water and of the fresh waters of the Eo-Sahabi stream (Boaz *et al.* 2008)

#### ARGYROSOMUS FOSSIL MATERIAL AND ITS PRESERVATION

The list of the *Argyrosomus* fossils studied is presented (Table 1). It includes all the African material, recovered from Arrisdrift and from Sahabi. The material from Arrisdrift is hosted at the Geological survey of Namibia. The Libyan fossils are actually in loan at

the University of Poitiers (OO, material collected in the 1980's, originally studied by Gaudant [1987]), and at the Department of Biological Sciences of the University of Alberta, Canada (TA, material collected in the last years). All the Libyan material will be permanently housed in the Museum of Vertebrate Paleontology, Benghazi (ex-Garyounis) University.

Both sites yielded premaxillae, dentaries and vertebrae including first centra of *Argyrosomus*. In addition, in Sahabi, one maxilla was recovered, whereas in Arrisdrift one quadrate and several angulo-articulars of *Argyrosomus* were also collected (one with the retro-articular in connection; Table 1). The bones are rather weathered and broken. The best preserved fossil is probably the quadrate from Arrisdrift. Due to its dorsal laminar flange, this bone is relatively more fragile than the other *Argyrosomus* remains fossilized. Moreover,

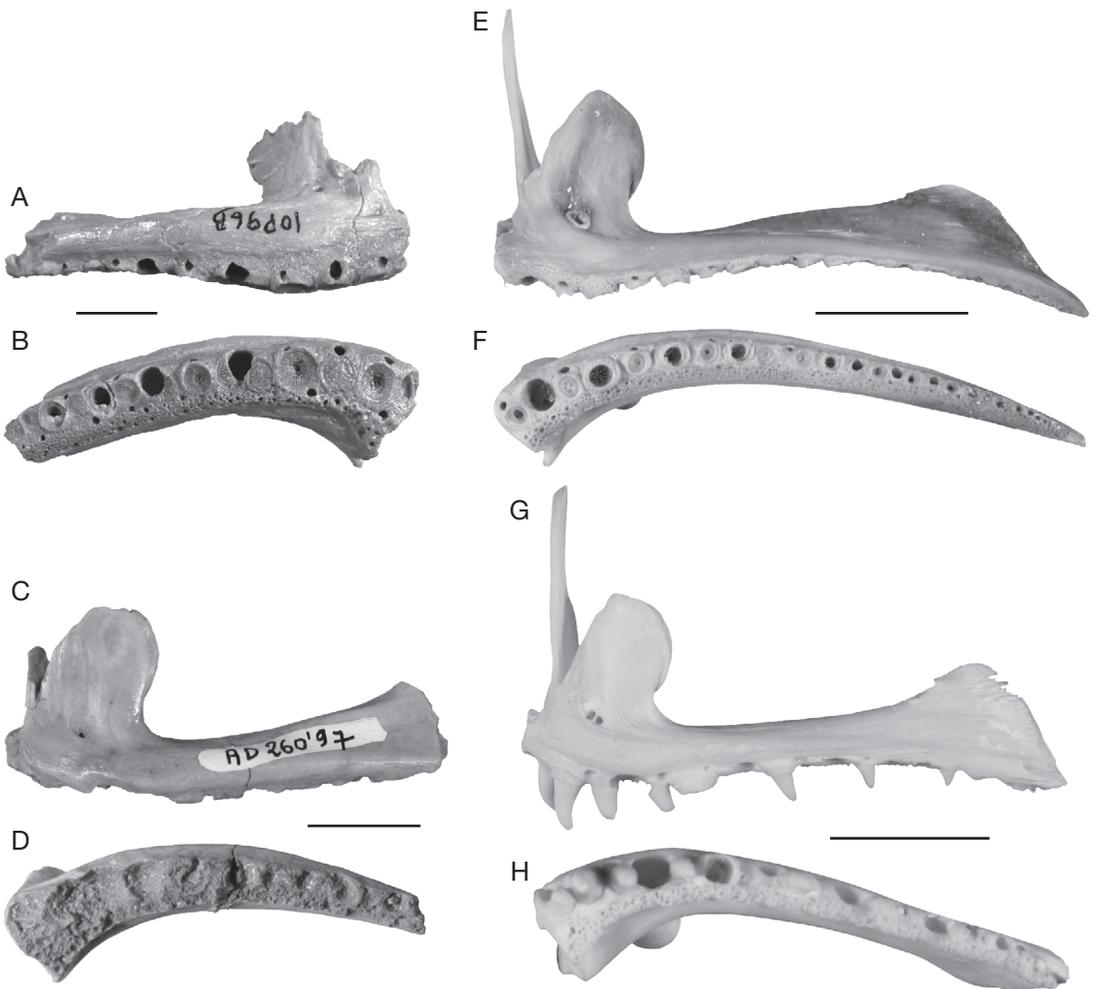


FIG. 2. — Premaxillae of fossil and modern *Argyrosomus* De La Pylaie, 1835 fish: **A, B**, *Argyrosomus* sp. from Sahabi (10P96B); **C, D**, *Argyrosomus* sp. from Arristrift (AD 260'97); **E, F**, *A. japonicus* (Temminck & Schlegel, 1843) (MNHN ICOS-00290); **G, H**, *A. regius* (Asso, 1801) (MNHN ICOS-00554); **A, C, E, G**, lateral views; **B, D, F, H**, occlusal views. Scale bars: 10 mm.

it is preserved complete whereas other *Argyrosomus* fossil remains are found fragmentary and some show evidence of sub-aquatic transport and rolling.

Finally, following a remark of Gaudant in his review of this paper, we add here some details on a premaxilla collected in Lower Miocene deposits at Langenau (Upper Freshwater Molasse, Germany), and on this locality environment. We attribute this fossil described by Gaudant (2006) to *Argyrosomus*. The fossil assemblage at Langenau includes terrestrial

vertebrate disarticulated bones. Moreover, besides an *Argyrosomus* fossil bone, the outcrop yielded sciaenid otoliths (Martini 1983), and also bony remains of mugilids and moronids from the same *Argyrosomus*-bearing “yellow layer” (Gaudant 2006), featuring typically a marine proximal/estuarine environment.

#### METHODS

The fossils were identified through the comparison with their homologues of two modern

TABLE 2. — Scaenid species present in the Eastern Atlantic and in the Mediterranean waters. For size range and water depth habitat, common values are given together with maximum values observed. \* Data collected in fishbase: information taken from Chao & Trevavas (1990) except: <sup>1</sup>, Bauchot (1987); <sup>2</sup>, Bianchi et al. (1993); <sup>3</sup>, Bianchi et al. (1999); <sup>4</sup>, Chao (1986b); <sup>5</sup>, Chao & Trevavas (1990); <sup>6</sup>, Chauvet (1991); <sup>7</sup>, Griffith & Heemstra (1995); <sup>8</sup>, Heemstra (1986); <sup>9</sup>, IGFA (2001); <sup>10</sup>, Lal Mohan (1984); <sup>11</sup>, Longhurst (1964); <sup>12</sup>, Maigret & Ly (1986); <sup>13</sup>, Riede (2004); <sup>14</sup>, Sanches (1991); <sup>15</sup>, Sasaki (2001); <sup>16</sup>, Schneider (1990); <sup>17</sup>, Sommer et al. (1996).

species	Atlantic		Atlantic South-East	maximum size (cm)	environment	waterdepth habitat (m)	ecology	about the other species in the genus
	North-East	Central-East						
<i>Argyrosomus coronus</i>			Angola to South Africa	(200) <sup>3</sup>	marine & brackish <sup>13</sup>	(?)20 to 40(100) <sup>13</sup>	benthopelagic <sup>13</sup>	6 sp. 3 in the Indo-West Pacific including African east coast + 1 in Arabian sea,
<i>A. inodorus</i>			Namibia and South Africa (Southeast Atlantic (Namibia southwards around the Cape of Good Hope and northwards at least as far as the Kei River in South Africa))	115(145) <sup>7,5</sup>	marine & brackish <sup>13</sup>	0 to 100 <sup>7</sup>	benthopelagic <sup>13</sup>	1 around Madagascar, 1 along western coast of South Africa
<i>A. regius</i>	Norway to Gibraltar and Congo, and Mediterranean Sea			150(230) <sup>5,12</sup>	marine & brackish <sup>13</sup>	15 to 300 <sup>16</sup>	benthopelagic <sup>13</sup>	
<i>Atractoscion aequidens</i>			Mauritania to South Africa	90 (130) <sup>8,15</sup>	marine & brackish	(15)100 to 200	benthopelagic	1 sp, NE Pacific
<i>Miracorvina angolensis</i>			Gulf of Guinea to southern Angola	60 (128)	marine	(50)150 to 300	demersal	monospecific genus
<i>Pantheroscion mbizi</i>			Guinea to southern Angola	25 (56)	marine <sup>16</sup>	(50)80 to 200(350)	demersal	monospecific genus
<i>Pseudotolithus elongatus</i>			Senegal to southern Angola	30 (47) <sup>5,11</sup>	marine & brackish	(0)50 to 100 <sup>5,14</sup>	demersal	all valid species of the genus are found in the Atainic Central and South
<i>P. epibercus</i>			Guinea-Bissau to southern Angola <sup>5,13</sup>	35 (60)	marine & brackish	0 to 160	demersal	Easty waters
<i>P. moorii</i>			Gambia to southern Angola	25 (50)	marine & brackish <sup>14</sup>	15 to 100 <sup>14</sup>	demersal	
<i>P. senegalensis</i>			Morocco to Namibia	50 (114) <sup>5,9</sup>	marine & brackish	0 to 70	demersal	
<i>P. senegalus</i>			Mauritania <sup>12</sup> to Angola	85 (230) <sup>5,9</sup>	marine & brackish	0 to 150	demersal	
<i>P. typus</i>			Mauritania <sup>12</sup> to Angola, becoming scarce north of Cape Verde	50 (140) <sup>9</sup>	marine, brackish & freshwater <sup>16</sup>	0 to 150 <sup>16</sup>	demersal	
<i>Pteroscion peli</i>			Senegal to Namibia	20 (32)	marine & brackish	0 to 50(200)	benthopelagic	monospecific genus
<i>Sciaena umbra</i>	English Channel to Mauritania, Mediterranean and Black seas			28 (70) <sup>1</sup>	marine & brackish <sup>6</sup>	?? To 200 <sup>6</sup>	demersal <sup>6</sup>	3 sp: 2 in Peru, 1 South American,
<i>Umbрина canariensis</i>	Eastern Atlantic; Bay of Biscay to Mediterranean; Western Indian Ocean; probably also in the Arabian Sea		South Africa <sup>8</sup> , western coast of Africa <sup>10</sup> ;	40 (80) <sup>5,17</sup>	marine	(50)150 to 200(300) <sup>14,4</sup>	demersal	13 other species are found in Eastern Pacific waters (9) and Western Atlantic (4), two of the latter being also brackish
<i>U. ciroso</i>	Bay of Biscay and Gibraltar to southern Morocco, the Mediterranean and Black seas and Sea of Azov		Eastern Atlantic and Western Indian Ocean; Mediterranean & Gibraltar <sup>5</sup> to the coast of Africa to the Persian Gulf. May eventually be found in Namibia <sup>2</sup>	40 (73)	marine & brackish <sup>9,5</sup>	0 to 100	demersal	
<i>U. ronchus</i>	Eastern Atlantic and Western Indian Ocean; Mediterranean & Gibraltar <sup>5</sup> to the coast of Africa to the Persian Gulf. May eventually be found in Namibia <sup>2</sup>		Guinea to Angola	50 (100) <sup>10</sup>	marine to freshwater <sup>16</sup>	0 to 200 <sup>16</sup>	demersal <sup>16</sup>	
<i>U. steindachneri</i>			Guinea to Angola	47	marine	15 to 100	benthopelagic	

TABLE 3. — Modern material for comparison.

Genus	Species	Type of material	Collection number	Total length (mm)	Weight (g)	Provenance
<i>Argyrosomus</i>	<i>regius</i>	dry skeleton	Otero_MAR25	270		North Atlantic (Poitiers fish market)
		dry skeleton	Otero_MAR34	450		North Atlantic (Poitiers fish market)
		dry skeleton	MNHN ICOS-00554		3800 (guttled)	Noirmoutier, France
<i>Argyrosomus</i>	<i>japonicus</i>	dry skeleton	MNHN ICOS-00290	643	3352	Ja'alan Bani Bu Ali (fish market), Oman
<i>Sciaena</i>	<i>wieneri</i>	dry skeleton	Béarez_5057	995	12400	Lima (fish market), Peru

species present along African coasts, i.e. *A. japonicus* (Temminck & Schlegel, 1843) and *A. regius* (Asso, 1801). The former is notably present in the marine waters along the African East coast (and also along Asian and Australian coasts), and the latter along the Mediterranean Northern African border (Table 2). We also discuss that the fossils cannot belong to another sciaenid fish having members along the Atlantic and the Mediterranean coast of Africa, i.e. genera *Atractoscion* Gill, 1862, *Miracorvina* Trewavas, 1962, *Pentheroscion* Trewavas, 1962, *Pseudotolithus* Bleeker, 1863, *Pteroscion* Fowler, 1925, *Sciaena* Oken, 1817, and *Umbrina* Cuvier, 1816 (Table 2).

#### MATERIAL FOR COMPARISON CHECKED FOR THE STUDY

Dry skeletons of *Argyrosomus regius*, *A. japonicus* and *Sciaena wieneri* (Table 3).

#### SYSTEMATICS

Class TELEOSTEI Müller, 1844  
sensu Patterson & Rosen, 1977  
Order PERCIFORMES  
sensu Johnson & Patterson, 1993  
Family SCIAENIDAE Cuvier, 1829

Genus *Argyrosomus* De La Pylaie, 1835

TYPE SPECIES. — *Argyrosomus procerus* De La Pylaie, 1835 (valid name *Argyrosomus regius* (Asso, 1801)).

#### DESCRIPTION OF ARGYROSOMUS FOSSIL REMAINS

All the fossils have been ascribed to the sciaenid genus *Argyrosomus*.

Like in many perciforms, the premaxilla of *Argyrosomus* has a stout articular head and an elongated alveolar process that bears the teeth ventrally (Fig. 2). When preserved, the ascending process is much higher than the leaf-shaped articular process and reaches twice its height in *A. regius*. The ascending process and the leaf-shaped articular process separate from each other close to the base, and form a sharp angle. The ascending process is broken in the fossils but its base and the shape of the articular process are similar than in extant specimens, notably by their relative position, by the opening for venous vessels and for the maxillary nerve branch that opens laterally on the articular process, and also by the rounded dorsal edge of the articular process. The alveolar process of *Argyrosomus* has an anterior edge which is squarish in lateral view and projects frontwards the ascending process. Moreover, at the back of the bone, a low posterior process grows gradually from the dorsal edge of the alveolar process and along all (*A. regius*) or most of its posterior quarter (*A. japonicus*). In our fossils, only the anteriormost part of the posterior process is preserved as all the premaxillae lack their posterior tip. Ventrally on the alveolar process, a row of enlarged caniniform teeth extends along the lateral margin, the second tooth being the largest, and two to three rows of villiform teeth

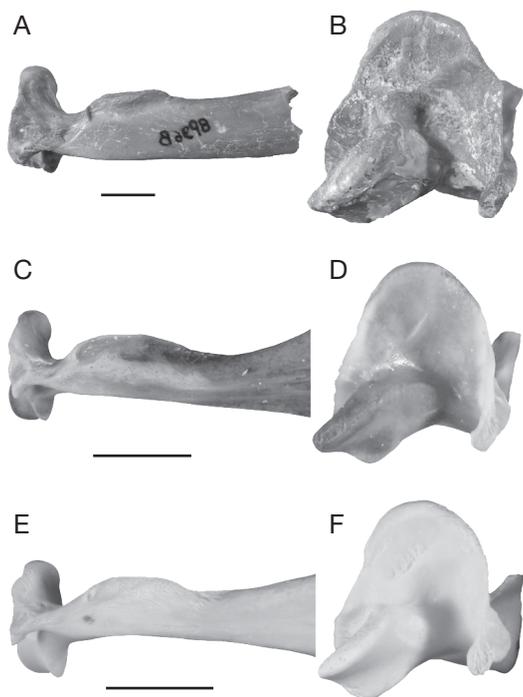


FIG. 3. — Maxillae of fossil and modern *Argyrosomus* De La Pylaie, 1835 fish: **A, B**, *Argyrosomus* sp. from Sahabi (8P96B); **C, D**, *A. japonicus* (Temminck & Schlegel, 1843) (MNHN ICOS-00290); **E, F**, *A. regius* (Asso, 1801) (MNHN ICOS-00554); **A, C, E**, lateral views of the bone; **B, D, F**, median views of the articular head. Scale bars: 10 mm.

develop medially, except at the symphysis where the alveolar process is covered by small teeth. The teeth are not preserved in the fossils but the size and distribution of the tooth sockets correspond in all the features to the *Argyrosomus* pattern.

A single fossil *Argyrosomus* maxilla has been recovered, at Sahabi. It is preserved in its anterior half only so that the enlarged posterior dorsal plate, rather common in perciforms, cannot be observed (Fig. 3). As shown between the three specimens figured in front views, the articular head varies in height, direction and extension of the dorsal process where the palatine articulates. Generally, the articular head of the fossil is the most massive element. However, this feature may vary within a same species and especially in relation with the size of the specimen, as observed in other perciform fish (e.g., *Lates*; Otero 2004). The maxillary internal process is medio-ventrally

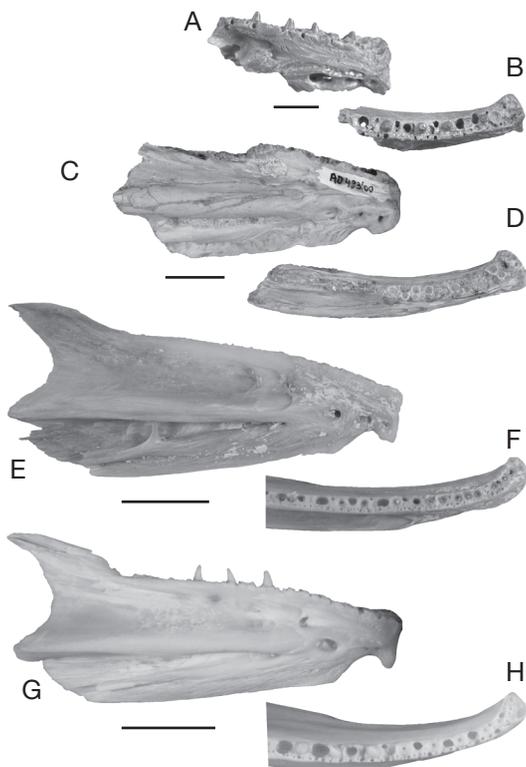


FIG. 4. — Dentaries of fossil and modern *Argyrosomus* De La Pylaie, 1835 fish: **A, B**, *Argyrosomus* sp. from Sahabi (101 P60A); **C, D**, *Argyrosomus* sp. from Arristrift (AD 486-00); **E, F**, *A. japonicus* (Temminck & Schlegel, 1843) (MNHN ICOS-00290); **G, H**, *A. regius* (Asso, 1801) (MNHN ICOS-00554); **A, C, E, G**, lateral views; **B, D, F, H**, occlusal views. Scale bars: 10 mm.

directed and surrounded by a groove. In lateral view, a stout dorsal crest allows the attachment of the *adductor mandibulae* I on a length which is about the same size as the head height.

In *Argyrosomus*, the ventral plate that develops below the sensory canal of the *dentary* is vertical so that the bone is narrow in dorsal view (Fig. 4). There is a strong ventral notch between the symphysis and the ventral plate of the bone so that a prominent chin hangs at the symphysis. It is even noticeable in the fossils where it might have been somewhat weathered during transport, at least in certain specimens. Another peculiar feature is the dorsally projecting “spoiler” at the dorsal posterior branch of the bone but it is observed in modern specimens only as the pos-

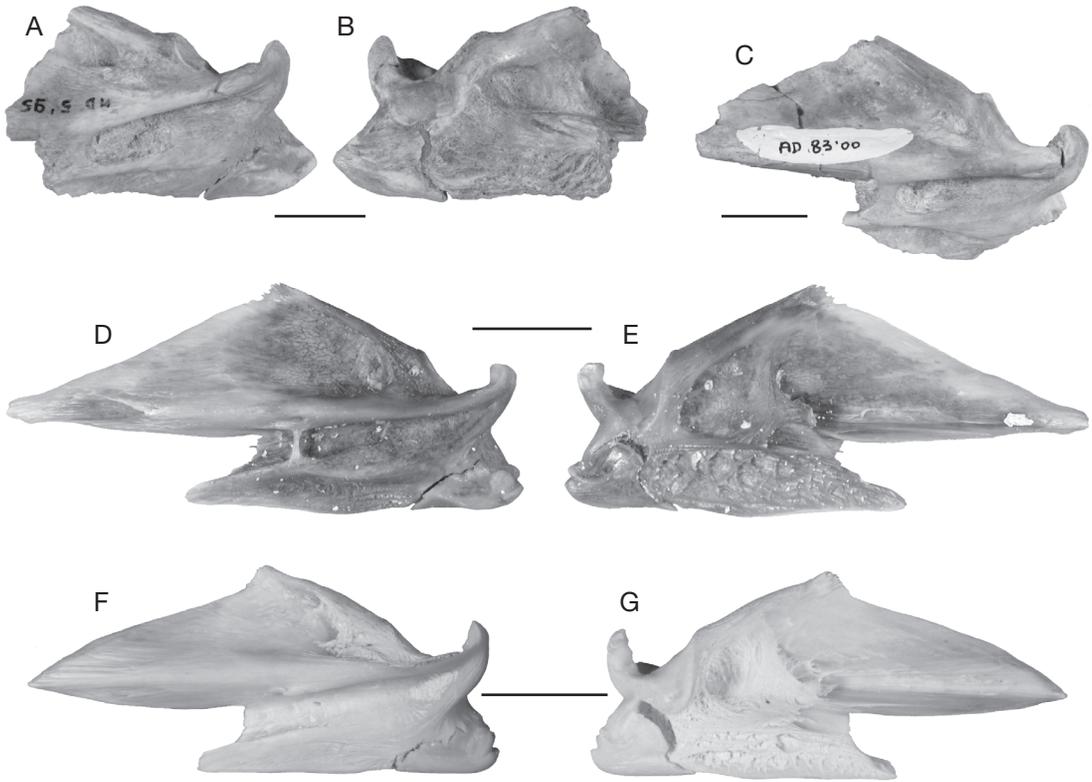


FIG. 5. — Angulo-articulars of fossil and modern *Argyrosomus* De La Pylaie, 1835 fish: **A-C**, *Argyrosomus* sp. from Arristrift (AD 83'00); **D, E**, *A. japonicus* (Temminck & Schlegel, 1843) (MNHN ICOS-00290); **F, G**, *A. regius* (Asso, 1801) (MNHN ICOS-00554); **A, C, D, F**, lateral views; **B, E, G**, median views. Scale bars: 10 mm.

terior part of fossil dentaries is always broken. The opening of the various foramina is similar in both fossil and modern specimens, notably between the fossils and *A. japonicus*. The upper foramen of the dentary opens in front of a large and deep lateral groove for the lip ligaments and the mandibular sensory canal runs in a bony tube with three openings in front of the upper foramen level. The fourth elongated opening of the mandibular sensory canal does not reach the posterior border of the bone. Finally, the dentary tooth patch in *Argyrosomus* develops as a mirror of the premaxilla dentition, with one inner row of enlarged teeth and one outer row of smaller ones. In dorsal view, the symphysis seems slightly enlarge in the fossil.

Like the bones formerly described, fossil angulo-articular (Fig. 5) are fragmentary. They lack the

anterior extremity that inserts in the dentary. The glenoid cavity is deep so that the articulation with the quadrate must be tight. The whole bone is also rather deep, with an angle ranging between 30° and 40° between the postero-dorsal pad that projects upward and forward and the horizontal pad that develops above the sensory canal from the glenoid cavity. The angulo-articular sensory canal runs in an open deep groove usually covered by a thin bridge at the mid-length of the bone (lacking in the *A. regius* specimen figured). One of the most characteristic features of *Argyrosomus* is the shape of the posterior edge of the angulo-articular and the position of the retro-articular. This bone is only preserved in one fossil, at Arristrift, but its position is known by the shape of its suture line with the angulo-articular in some other specimens. In lateral view, the posterior edge of the bone shows a

notch below the caudal tip of the glenoid cavity. The retro-articular articulates with the angulo-articular below this notch and projects posteriorly, behind the posterior tip of the angulo-articular (Fig. 5). In lateral view, the retro-articular is at least twice as long as high and it extends anteriorly until the front level of the glenoid cavity.

The single *Argyrosomus* fossil quadrate is known from Arrisdrift. It was found connected with a posterior fragment of the ectopterygoid. In lateral view it resembles modern quadrates notably by the high outline and the posterior bumped edge (Fig. 6). The articular condyle and the base of the posterior border of the bone are particularly wide, notably when observed in anterior view because the anterior edge is much thinner than the posterior one. There is a median expansion of the condyle in the fossil. It exists in a reduced version in *A. japonicus* but not in the specimen of *A. regius*.

The abdominal vertebrae show a delicate striated ornamentation of the bone. Only first vertebrae have been identified in both Arrisdrift and Sahabi (Fig. 7). Their bean-shaped articulation facets for the exoccipital are medially connected. In lateral views the centra exhibit parallel edges. The anterior face of the centrum is less wide, almost rounded, and either more or less pointed dorsally (Arrisdrift) or somewhat dorso-ventrally flattened (Sahabi). The posterior face of the centrum is bigger than the anterior one and somewhat dorso-ventrally flattened.

No other fossil bony remain from Arrisdrift and Sahabi can be confidently attributed to *Argyrosomus*.

## DISCUSSION ON THE SYSTEMATIC ATTRIBUTION OF THE FOSSILS

The attribution of fossil disarticulated bones to a single taxon is always questionable even when found in the same outcrop. However, several arguments support this hypothesis for the bones described from Sahabi on one hand and from Arrisdrift on the other. In both cases, 1) the bones belong to fishes of similar size range and they represent almost all the fossil fish of the deposit that cannot be attributed to other taxa; 2) they all show

a similar ossification pattern (bulky bone with similar aspect of the bony tissue); 3) the articulation of some bones is observed (retro and angulo-articular), or their shapes fit for their articulation or connection (dentary and angulo-articular; angulo-articular and quadrate), or their shapes fit in anatomical position (the singular dentition pattern of the premaxilla and of the dentary are mirror images of each other); and most confident 4) we can unambiguously attribute the described remains to the genus *Argyrosomus*.

Effectively, the morphology of the fossil remains fits in any detail with what is observed in *Argyrosomus*. We might add that they, conversely, differ from any other African perciform whenever it is marine (PB pers. obs.) or freshwater (OO pers. obs). Finally, after checking accurately the other sciaenid fish present along the western African and Mediterranean coasts, it appears that only *Argyrosomus*, *Umbrina* and *Sciaena* to a lesser extent have brackish and freshwater members present along both coasts (but only the two formers have members in the South East Atlantic; Table 2). Moreover, the fossils from Arrisdrift do not present the distinctive features present in other sciaenid genera apart from *Argyrosomus*. For instance, like in *Argyrosomus* only, the premaxillary alveolar process projects forwards the ascending process, and the retroarticular projects backwards the posterior level of the angulo-articular, which is not seen in *Sciaena*. These features appear to be generally stable among perciforms, and particularly among sciaenids (e.g. Otero 2004; Taniguchi 1970). In the case of *Umbrina*, the global shape of the bones is significantly different because these fishes have short and deep jaws, as shown on the premaxilla and maxilla figured by Schultz (2004) and observed in the reference collection. According to Gaudant's (2006) comments and figures, a premaxilla collected in a German Lower Miocene freshwater assemblage, at Langenau, fits in all the details that are preserved in *Argyrosomus*; it is hereby confidently attributed to this genus.

Finally, we chose not to attribute the *Argyrosomus* fossil remains to any nominal species. As demonstrated by Griffiths & Heemstra (1995), *Argyrosomus* species are rather hard to distin-

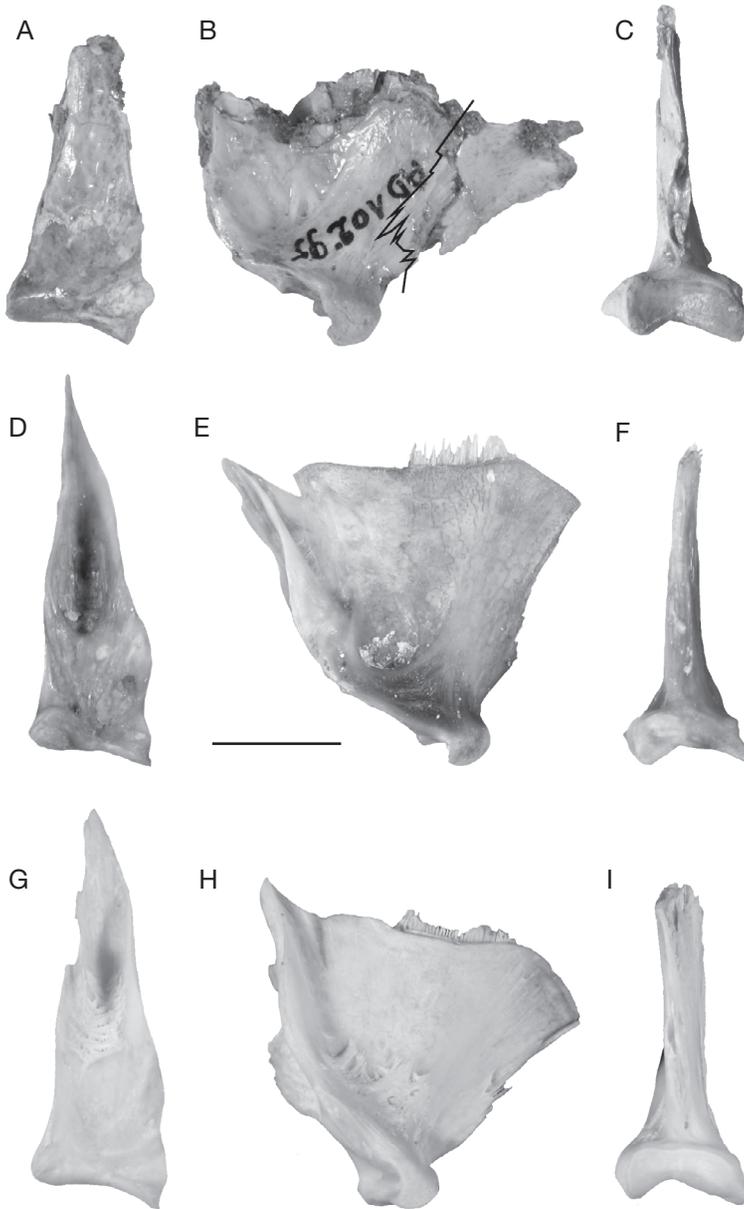


FIG. 6. — Quadrates of fossil and modern *Argyrosomus* De La Pylaie, 1835 fish: **A-C**, *Argyrosomus* sp. from Arrisdrift (AD 102'95); **D-F**, *A. japonicus* (Temminck & Schlegel, 1843) (MNHN ICOS-00290); **G-I**, *A. regius* (Asso, 1801) (MNHN ICOS-00554); **A, D, G**, lateral views; **B, E, H**, anterior views; **C, F, I**, posterior views. Scale bar: 4 mm.

guish. Indeed, the differences that we observed between the modern specimens of the reference collection are light and may correspond to individual or specific variation. The fossil remains are

far too scarce to intent any specific attribution. We can only suggest that the Arrisdrift and Sahabi *Argyrosomus* may belong to extinct species but more fossil material is necessary to attempt

a more confident attribution. Hopefully, future field missions will provide more, well preserved, diagnostic material, which, combined with an accurate review of the extant species anatomy, may lead to a confident specific attribution.

## DISCUSSION ON THE IMPLICATIONS OF THE PRESENCE OF *ARGYROSOMUS* IN MIOCENE FOSSIL DEPOSITS AT SAHABI AND ARRISDRIFT

### PALEO-ENVIRONMENTAL IMPLICATIONS

The Sciaenidae (croakers and drums) is one of the largest perciform families in number of species and distribution with about 70 genera and 270 species worldwide (Nelson 2006). Sciaenids are primary marine fish and they inhabit coastal and brackish waters of temperate and tropical areas (Trewavas 1977; Chao 1986a). Some of these marine freshwater-tolerant taxa are sometimes found in estuarine assemblages in association with freshwater fish, notably in Africa (Simier *et al.* 2004). Moreover, sciaenids are also known to have secondarily invaded continental waters in both North and South America (Chao 1978) where six genera and 28 species are freshwater (Chao 1986a; Casatti 2003), and Southeast Asia (Baird *et al.* 2001) as well.

The genus *Argyrosomus* itself counts nine valid extant species. They inhabit the coastal waters of temperate and tropical areas along the Atlantic and Mediterranean coasts (Table 2) and also Indian and Pacific coasts (Trewavas 1977; Chao 1986a; Griffiths & Heemstra 1995). Moreover, some *Argyrosomus* species inhabiting coastal waters also invade estuarine freshwaters, although no species is restricted to freshwater. This is notably the case of the three species that are present along the Mediterranean and Atlantic African coasts (Table 2). As examples, Simier *et al.* (2004) place *Argyrosomus regius* in the category of “marine species occasional in estuaries”, whereas Lobry *et al.* (2003) define the species as “marine adventitious species” in their study of the fish fauna of the Gironde Estuary. Concerning *Argyrosomus japonicus*, a species present along the African East coast including South

Africa, Farmer (2008) observed that wherever it occurs, this fish exploits a diverse range of coastal habitats, which includes the lower reaches of rivers, estuaries, protected embayments, exposed ocean beaches, and areas around reef structures in both nearshore and offshore waters. In addition, he noted that the highly migratory adults move between all of these habitats whereas the juveniles are found exclusively in nearshore waters. Similarly, James *et al.* (2008) place *Argyrosomus japonicus* from South Africa in the category of euryhaline marine species which usually breed at sea with the juveniles dependant on estuaries as nursery areas. The temporary increase in the count of adult specimens during several successive years in the estuarine freshwaters might be linked to the invertebrate food resources modified by the loss of the macrophyte beds during the concerned years (James *et al.* 2008). This biological factor appears to be more important to *Argyrosomus* than other non biotic factors such as salinity and temperature (e.g., Davies 1982; Whitfield 1984; James *et al.* 2008).

The size of the fossil specimens was estimated to range between 60 and 100 cm, which clearly represent adult specimens. Finding *Argyrosomus* in the Miocene freshwater dominant assemblage at Arrisdrift (Namibia), Sahabi (Lybia) and also Laugenau (Germany) indicates probable similar ecology to that of modern African species, notably with adult specimens that invade rivers and estuaries. Moreover, we can confidently confirm that the genus was yet present in the South Atlantic (at least its eastern coast) during the Middle Miocene.

### THE FOSSIL RECORD

The sciaenid fossil record starts in the Lower Eocene with otoliths reported by Nolf (1995a) from the Ypresian Bashi Marls, Mississippi. Then most of the fossil record concentrates in the Oligocene and the Neogene terrigenous marine deposits from Europe and America. While articulated skeletal remains are rather rare as fossils, the otolith record is extremely rich, particularly during the Neogene (Schwarzhan 1993). Further details on the sciaenid fossil record are to be found in Nolf

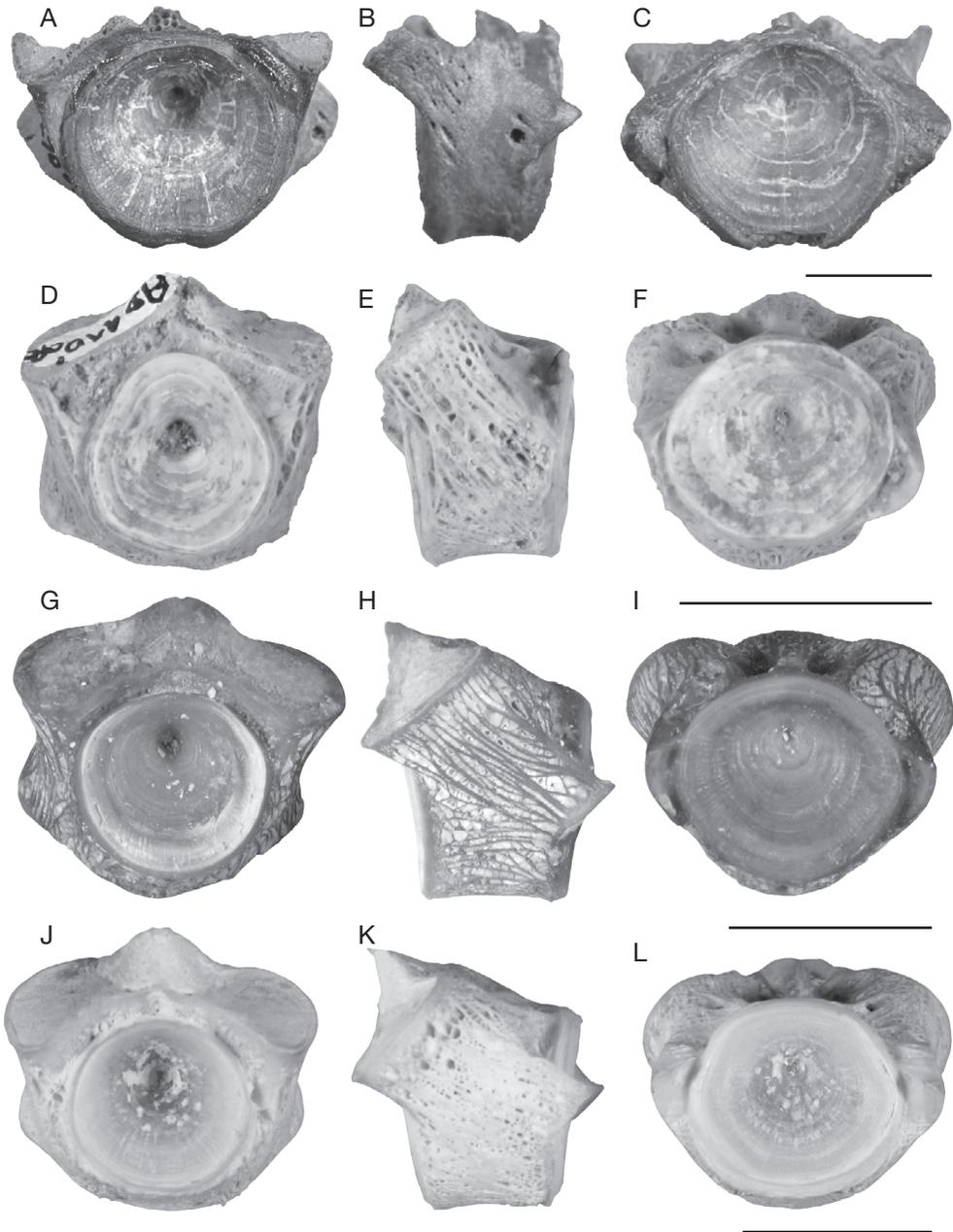


FIG. 7. — First vertebrae of fossil and modern *Argyrosomus* De La Pylaie, 1835 fish: **A-C**, *Argyrosomus* sp. from Sahabi (52P62A); **D-F**, *Argyrosomus* sp. from Arristrift (AD 110'98); **G-I**, *A. japonicus* (Temminck & Schlegel, 1843) (MNHN ICOS-00290); **J-L**, *A. regius* (Asso, 1801) (MNHN ICOS-00554); **A, D, G, J**, anterior views; **B, E, H, K**, lateral views; **C, F, I, L**, dorsal views. Scale bars: 10 mm.

(1995a, b), Schwarzhans (1993) and Girone & Nolf (2009) for otoliths and in Schultz (2004) and Bannikov *et al.* (2009) for bony material. So

far, the genus *Argyrosomus* has only been identified from its otoliths, in the fossil record, and it is known to have been present in the Mediter-

anean Sea and Paratethys since the Early and Middle Miocene (e.g., Nolf & Cappetta 1989; Reichenbacher & Cappetta 1999; Brzobohatý *et al.* 2007). The *Argyrosomus* remains identified here at Langenau, Arrisdrift and Sahabi constitute the bony fossil record of the genus, and include also its first records from the African Neogene.

The relative abundance of otoliths and the scarcity of articulated skeletons of sciaenids in the fossil record have been interpreted by Bannikov *et al.* (2009) as primarily related to the life habits of these fishes. These bottom-dwelling carnivores are common in nearshore marine and brackish environments with oxygenated coarse-grained, sandy or soft grounds. According to Bannikov *et al.* (2009) “[...] *these fishes are therefore absent or extremely rare in the depositional environments characterized by ecological or sedimentary features that allow the preservation of articulated skeletal remains (anoxic bottoms, microbial mats, etc.), whereas their preferred clastic depositional environments evidently favor the preservation of their large and massive otoliths [...]*”. With a bony fossil record in Arrisdrift and Sahabi, the situation is different for *Argyrosomus* in these African outcrops when compared to the generalized situation for the family: i.e. in that case, the clastic depositional environments favor the preservation of bony remains. Another peculiarity is the paleoenvironmental signature of the whole fossil assemblages which is freshwater dominant, rather than marine as in other already known cases. Indeed, as shown in river stream and estuarine deposits at Arrisdrift, Sahabi (and Landenau), clastic depositional environment may concentrate sciaenid bones (see also Otero 2010, for other examples). So, we invoke here combined diagenetical context (notably early diagenesis) to explain the frequent scarcity of bony remains of sciaenids in marine and brackish environments and their presence in freshwater dominant environments, rather than the clastic feature of the depositional environment alone. The identification of sciaenid bony remains attributed to *Umbrina* and *Trewasciaena* Schwarzhans, 1993, in Late Miocene mixed assemblage from Austria (Schultz 2004), supports this interpretation.

## CONCLUSION

The ichthyofaunal assemblages and more generally the faunas yielded from Sahabi (Libya) and Arrisdrift (Namibia) differ one from the other. We can reasonably await differences between the freshwater assemblages sampled in these two fossil outcrops, due to their age and biogeography. Effectively, the fossil assemblages are respectively 7 Ma (Sahabi) and 17 Ma (Arrisdrift) and these 10 Ma are far enough to see change in the diversity at least at a specific level (OO pers. obs.; Pinton *et al.* 2013). But the probably most impacting data are geographical as these localities are over 6000 km far across the African continent, and they belong to ichthyoregions that are separated for long by the Central African shear zone. This geological structure may have operated as a main biogeographical barrier notably for inland fish faunas and explain differences at generic level (*ibidii*). Moreover, the fact that the water systems, fossilized in each locality, differ in both their size and deposit dynamic supports again the predictable difference between Arrisdrift and Sahabi ichthyofauna.

The distribution of *Argyrosomus* bony fossils does not illustrate unsuspected continental biogeographical links between Miocene ichthyofaunas. Their identification in dominantly or strictly freshwater assemblages from Langenau (Early Miocene, Germany), Arrisdrift (Middle Miocene, Namibia) and Sahabi (Upper Miocene, Libya), in both European and African continents, is due to their wide marine distribution notably along the African and Paratethyan coasts and to the ability of their adults to invade distal segment of freshwater streams. These findings constitute both the only bony records of the genus and they include the first continental fossil records for the family in Africa.

## Acknowledgements

We greatly thank B. Senut (MNHN, Paris) and M. Pickford (Collège de France, Paris) for lending the fish material from Arrisdrift; M. Gayet (CNRS, Lyon) who transmitted these fossils, and also G. Carnevale and J. Gaudant who accepted to review the paper. We extend our gratitude towards

the ELNRP (directors: N. Boaz, A. Muftah and M. Shawahidi) and the Benghazi University, Libya, for collecting and lending the fish material from Sahabi. The ELNRP excavations that produced the fossils described here were funded by the NSF-RHOI (BNS-0515591 and BCS-0321893), Shell Exploration and Production Libya and the Special Account for Research Grants of the National and Kapodistrian University of Athens. Figures by OO.

## REFERENCES

- ARGYRIOU T., OTERO O., PAVLAKIS P. & BOAZ N. 2012. — Description and paleobiogeographical implications of new *Semlikiichthys* (Teleostei, Perciformes) fish material from the Late Miocene deposits of Sahabi, Libya. *Geobios* 45: 429-436.
- BAIRD I. G., PHYLAVANH B., VONGSENEOUK B. & XAIY-AMANIVON K. 2001. — The ecology and conservation of the smallscale croaker *Boesemania microlepis* (Bleeker, 1858-59) in the mainstream Mekong River, Southern Laos. *Natural History Bulletin of the Siam Society* 49: 161-176.
- BANNIKOV A. F., CARNEVALE G. & LANDINI W. 2009. — A new Early Miocene genus of the family Sciaenidae (Teleostei, Perciformes) from the eastern Paratethys. *Comptes-Rendus Palevol* 8 (2009): 535-544.
- BAUCHOT M.-L. 1987. — Poissons osseux, in FISCHER W., BAUCHOT M. L. & SCHNEIDER M. (eds), *Fiches FAO d'identification pour les besoins de la pêche. Méditerranée et mer Noire. Zone de pêche 37. Vol. II*. Commission des communautés européennes and FAO, Rome: 891-1421.
- BIANCHI G., CARPENTER K. E., ROUX J.-P., MOLLOY F. J., BOYER D. & BOYER H. J. 1993. — *FAO Species Identification Field Guide for Fishery Purposes*. The living marine resources of Namibia, FAO, Rome. 250 p.
- BIANCHI G., CARPENTER K. E., ROUX J.-P., MOLLOY F. J., BOYER D. & BOYER H. J. 1999. — *Field Guide to the Living Marine Resources of Namibia*. FAO species identification guide for fishery purposes. FAO, Rome, 265 p.
- BOAZ N. T., EL-ARNAUTI A., AGUSTÍ J., BERNOR R. L., PAVLAKIS P. & ROOK L., 2008. — Temporal, Lithostratigraphic, and Biochronologic Setting of the Sahabi Formation, North-Central Libya, in SALEM M. J., EL-ARNAUTI A. & EL-SOGER SAHLEH A. (eds), *Geology of East Libya* 3: 959-972.
- BRZOBHATÝ R., NOLF D. & KROUPA O. 2007. — Fish Otoliths from the Middle Miocene of Kienberg at Mikulov, Czech Republic, Vienna Basin: their paleoenvironmental and paleogeographic significance. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 77: 167-196.
- CASATTI L. 2003. — Family Sciaenidae (drums or croakers), in REIS R. E., KULLANDER S. O. & FERRARIS JR C. J. (eds), *Check List of the Freshwater Fishes of South and Central America*. Edipurcs, Porto Alegre: 599-602.
- CHAO L. N. 1978. — A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). *NOAA Technical Report NMFS Circular* 415: 1-65.
- CHAO L. N. 1986a. — A synopsis on zoogeography of the Sciaenidae, in UYENO T., ARAI R., TANIUCHI T. & MATSUURA K. (eds), *Indo-Pacific fish biology*, Proceedings of the Second International Conference of Indo-Pacific Fishes, Ichthyological Society of Japan, Tokyo: 570-589.
- CHAO L. N. 1986b. — Sciaenidae, in WHITEHEAD P. J. P., BAUCHOT M.-L., HUREAU J.-C., NIELSEN J. & TORTONESE E. (eds), *Fishes of the North-Eastern Atlantic and the Mediterranean*, Volume 2. Unesco, Paris: 865-874.
- CHAO L. N. & TREWAVAS E. 1990. — Sciaenidae, in QUERO J.-C., HUREAU J.-C., KARRER C., POST A. & SALDANHA L. (eds), *Check-list of the fishes the eastern tropical Atlantic (CLOFETA)*. Vol. 2. JNICT, Lisbon, SEI, Paris, UNESCO, Paris: 813-826.
- CHAUVET C. 1991. — Le corb ou brown meagre (*Sciaena umbra*-Linnaeus, 1758) quelques éléments de sa biologie, in BODOURESQUE C. F., AVON M. & GRAVEZ V. (eds), *Les espèces marines à protéger en Méditerranée*, GIS Posidonie, France: 229-235.
- DAVIES B. R. 1982. — Studies on the zoobenthos of some southern Cape coastal lakes: Spatial and temporal changes in the benthos of Swartvlei, South Africa, in relation to changes in the submerged littoral macrophyte community. *Journal of the Limnological Society of Southern Africa* 8, 33-45.
- FARMER B. M. 2008. — *Comparison of the Biological and Genetic Characteristics of the Mulloway Argyrosomus japonicus (Sciaenidae) in Different Regions of Western Australia*. Ph.D. thesis. Murdoch University, Western Australia, 217 p.
- GAUDANT J. 1987. — A preliminary report on the osteichthyan-fish fauna from the Upper Neogene of Sahabi, Libya, in BOAZ N. T., EL-ARNAUTI A., GAZIRY A. W., DE HEINZELIN J. & BOAZ D. D. (eds), *Neogene Paleontology and Geology of Sahabi, Libya*. Alan R. Liss Inc.: 91-99.
- GAUDANT J. 2006. — Occurrence of skeletal remains of Channids (Teleostean Fishes) in the Otnangian (Lower Miocene), Langenau near Ulm (Württemberg, Germany). *Stuttgarter Beiträge zur Naturkunde, serie B*, 361: 1-15.
- GIRONE A. & NOLF D. 2009. — Fish otoliths from the Priabonian (Late Eocene) of North Italy and South-East France – Their paleobiogeographical significance. *Revue de micropaléontologie* 52 (2009): 195-218.
- GRIFFIN D. L. 2011. — The late Neogene Sahabi rivers of the Sahara and the hamadas of the eastern Libya-Chad

- border area. *Palaeogeography, Palaeoclimatology, Palaeoecology* 309: 176-185.
- GRIFFITHS M. H. & HEEMSTRA P. C. 1995. — A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from southern Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* 65: 1-40.
- HEEMSTRA P. C. 1986. — Sciaenidae, in SMITH M. M. & HEEMSTRA P. C. (eds.), *Smiths' Sea Fishes*, Springer-Verlag, Berlin: 616-619.
- IGFA 2001. — *Database of IGFA Angling Records until 2001*. IGFA, Fort Lauderdale, USA.
- JAMES N. C., WHITFIELD A. K. & COWLEY P. D. 2008. — Long-term stability of the fish assemblages in a warm-temperate South African estuary. *Estuarine, Coastal and Shelf Science* 76: 723-738.
- LAL MOHAN R. S. 1984. — Sciaenidae, in FISCHER W. & BIANCHI G. (eds) *FAO species identification sheets for fishery purposes, Western Indian Ocean (Fishing Area 51)*. Vol. 4. FAO, Rome, 9 p.
- LOBRY J., MOURAND L., ROCHARD E. & ELIE P. 2003. — Structure of the Gironde estuarine fish assemblages: a comparison of European estuaries perspective. *Aquatic Living Resources* 16 (2): 47-58.
- LONGHURST A. R. 1964. — Bionomics of the Sciaenidae of tropical West Africa. *Journal du Conseil international pour l'exploration de la mer* 29 (1): 93-114.
- MAIGRET J. & LY B. 1986. — *Les poissons de mer de Mauritanie*. Sciences Naturelles, Compiègne, 213 p.
- MARTINI E. 1983. — Die Fischfauna von Langenau bei Ulm (Unter-Miozän, Ottang-Stufe). *Stuttgarter Beiträge zur Naturkunde* (B) 91: 1-25.
- NELSON J. S. 2006. — *Fishes of the World* (4th edition), John Wiley, New Jersey, 601 p.
- NOLF D. 1995a. — Studies on fossil otoliths - the state of the art, in SECOR D. H., DEAN J. M. & CAMPANA S. E. (eds), *Recent Developments in Fish Otolith Research*. The Belle W. Baruch Library in Marine Science, University of South Carolina Press, 19: 513-544.
- NOLF D. 1995b. — Les otolithes : une source d'informations exceptionnelles sur les poissons actuels et fossiles. *Nouvelles de la Science et des Technologies* 13 (2-4): 251-253.
- NOLF D. & CAPPETTA H. 1989. — Otolithes de poissons pliocènes du Sud-Est de la France. *Bulletin de l'Institut royal de Belgique, Sciences de la Terre* 58: 209-271.
- OTERO O. 2003. — Fossil fish from Arrisdrift (Middle Miocene, Namibia). *Memoirs of the Geological Survey of Namibia* 19: 35-42.
- OTERO O. 2004. — Anatomy, systematics and phylogeny of both Recent and fossil latid fish (Teleostei, Perciformes, Latidae). *Zoological Journal of the Linnean Society* 141: 81-133.
- OTERO O. 2010. — What controls the freshwater fish fossil record? A focus on the Late Cretaceous and Tertiary of Afro-Arabia. *Cybiurn* 34 (1): 93-113.
- OTERO O., PINTON A., MACKAYE H. T., LIKIUS A., VIGNAUD P. & BRUNET M. 2009. — Fishes and palaeogeography of the African drainage basins: relationships between Chad and neighbouring basins throughout the Mio-Pliocene. *Palaeobiogeography, Palaeoclimatology, Palaeoecology* 274: 134-139.
- PICKFORD M. & SENUT B. 2000. — Geology and Palaeobiology of the Namib Desert, South-western Africa. *Memoirs of the Geological Survey of Namibia* 18: 1-155.
- PICKFORD M. & SENUT B. 2003. — Miocene Palaeobiology of the Orange River Valley, Namibia. *Memoirs of the Geological Survey of Namibia* 19: 1-22.
- PINTON A., AGNÈSE J.F., PAUGY D. & OTERO O. 2013. — A large-scale phylogeny of Synodontis (Mochokidae, Siluriformes) reveals the influence of geological events on continental diversity during the Cenozoic. *Molecular Phylogenetics and Evolution* 66 (2013): 1027-1040.
- REICHENBACHER B. & CAPPETTA H. 1999. — First evidence of an early Miocene marine teleostean fish fauna (otoliths) from La Piollade (Montpellier, France). *Paleovertebrata* 28, 1-46.
- RIEDE K. 2004. — *Global register of migratory species – from global to regional scales*. Final Report of the R&D-Projekt 808 05 081. Federal Agency for Nature Conservation, Bonn, 329 p.
- ROBERTS T. R. 1975. — Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society* 57 : 249-319.
- SANCHES J. G. 1991. — *Catálogo dos principais peixes marinhos da República de Guiné-Bissau*. Publicações avulsas do I.N.I.P., no. 16, 429 p.
- SASAKI K. 2001. — Sciaenidae. Croakers (drums), in CARPENTER K. E. & NIEM V. H. (eds.), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 5. Bony fishes part 3 (Menidae to Pomacentridae)*. FAO, Rome: 3117-3174.
- SCHNEIDER W. 1990. — *FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea*. Prepared and published with the support of the FAO Regional Office for Africa. FAO, Rome, 268 p.
- SCHULTZ O. 2004. — Die Fischreste aus dem Unter-Pannonium (Ober-Miozän) von Mataschen, Steiermark (Österreich). *Joannea – Geologie und Paläontologie* 5: 231-256.
- SCHWARZHANS W. 1993. — *A comparative morphological treatise of recent and fossil otoliths of the family Sciaenidae (Perciformes)*. Verlag Dr. Friedrich Pfeil, Piscium Catalogus: Part Otolithi piscium 1 (1993), München, 245 p.
- SIMIER M., BLANC L., ALIAUME C., DIOUF P. S. & ALBARET J. J. 2004. — Spatial and temporal structure of fish assemblages in an “inverse estuary”, the Sine Saloum system (Senegal). *Estuarine, Coastal and Shelf Science* 59: 69-86.

- SOMMER C., SCHNEIDER W. & POUTIERS J.-M. 1996. — *FAO species identification field guide for fishery purposes: The living marine resources of Somalia*. FAO, Rome, 376 p.
- TANIGUCHI N. 1970. — Comparative Osteology of the Sciaenid Fishes from Japan and its Adjacent Waters – III. Premaxillary and Dentary. *Japanese Journal of Ichthyology* 17 (4):135-140.
- TREWAVAS E. 1977. — The sciaenoid fishes (croakers or drums) of the Indo-West-Pacific. *Transactions of the Zoological Society London* 33 (4): 235-541.
- WHITFIELD A. K. 1984. — The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. *Estuarine, Coastal and Shelf Science* 18: 315-329.

*Submitted on 2<sup>nd</sup> December 2011;  
accepted on 8 March 2012;  
published on 29 March 2013.*