



INSTITUT DE FRANCE
Académie des sciences

Comptes Rendus

Géoscience

Sciences de la Planète

Bouziane Khalloufi and Nour-Eddine Jalil

Overview of the Late Triassic (Carnian) actinopterygian fauna from the Argana Basin (Morocco)

Volume 352, issue 6-7 (2020), p. 495-513

Published online: 15 January 2021

Issue date: 15 January 2021

<https://doi.org/10.5802/crgeos.34>

Part of Special Issue: Some aspects of current State of Knowledge on Triassic series on both sides of the Central Atlantic Margin

 This article is licensed under the
CREATIVE COMMONS ATTRIBUTION 4.0 INTERNATIONAL LICENSE.
<http://creativecommons.org/licenses/by/4.0/>



*Les Comptes Rendus. Géoscience — Sciences de la Planète sont membres du
Centre Mersenne pour l'édition scientifique ouverte*

www.centre-mersenne.org

e-ISSN : 1778-7025



Some aspects of current State of Knowledge on Triassic series on both sides of the Central Atlantic Margin / *Quelques aspects de l'état des connaissances des séries triasiques de part et d'autre de la Marge Atlantique*

Overview of the Late Triassic (Carnian) actinopterygian fauna from the Argana Basin (Morocco)

Bouziane Khalloufi^{*, a, b} and Nour-Eddine Jalil^{c, d}

^a Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng, Kantarawichai district, Maha Sarakham 44150, Thailand

^b Laboratoire Informatique et Systématique UMR 7205, Université Pierre et Marie Curie (UPMC-Paris 6), Muséum national d'Histoire naturelle, Paris, France

^c Centre de Recherche en Paléontologie – Paris (MNHN, CNRS, Sorbonne Université), CP 38, 57 rue Cuvier, CP 38, 75231 Paris CEDEX 5, France

^d Muséum d'Histoire naturelle de Marrakech, Dept. de Géologie (FSSM), Université Cadi Ayyad, Maroc

E-mails: khalloufi.bouziane@hotmail.fr (B. Khalloufi), nour-eddine.jalil@mnhn.fr (N.-E. Jalil)

Abstract. The continental outcrops of the Argana Basin (High Atlas of Morocco) have provided the richest tetrapod assemblage and the only known actinopterygian fauna of the Triassic of North Africa. Unlike the tetrapod remains, widely distributed throughout the basin, the actinopterygians are rare and come from a single locality. They are dated as the Late Triassic (Carnian) and have been attributed to six forms. Here, this ichthyofauna is reviewed for the first time since its original description. Two forms, endemic to the basin, are recognized as valid species and their generic attributions confirmed: the redfieldiiform *Mauritanichthys rugosus*, related to the genus *Lasalichthys* from the Late Triassic of North America, and the “perleidiform” *Dipteronotus gibbosus*, congeneric with Middle Triassic species of Europe. The other actinopterygian taxa are known by insufficiently preserved remains and need a complete material to be confidently identified. Two specimens previously referred to the redfieldiiform *Ischnolepis* are considered as Redfieldiiformes indet. and probably correspond to a new taxon. The three last forms, previously referred to the “perleidiforms” *Procheirichthys* and *Perleidus*, and to the redfieldiiform *Atopocephala*, are considered as Actinopterygii indet.

Keywords. Actinopterygii, Redfieldiiformes, “Perleidiforms”, High Atlas, Argana Corridor.

Available online 8th January 2021

* Corresponding author.

1. Introduction

In North Africa, the Argana Basin, or Argana Corridor, provides exceptional exposures of Permian to Upper Triassic continental fluvial-dominated sediments deposited in a rift basin. These sediments crop out in the western High Atlas of Morocco between the cities of Imi n'Tanout in the north and Amskrout in the south and extend over a length of 80 km for a maximum width of approximately 25 km (Figure 1A,B). Exposures consist of red-beds mainly formed by conglomerates, sandstones and siltstones, and have been divided into eight lithostratigraphical units or members (named T1 to T8, Figure 1C) belonging to three formations: the Permian Ikakern Fm (T1 and T2), and the Triassic Timezgadiouine (T3 to T5) and Bigoudine Fms (T6 to T8, Brown, 1980, Khaldoune et al., 2017, Tixeront, 1973, Tourani et al., 2000). Fossil remains have been reported from the lithostratigraphical units T2, T3, T4, T5 and T6 and dozens of localities have been identified by Dutuit [1976] and successive researchers. Fossils consist of charophytes, ostracods and abundant and diversified vertebrates represented both by isolated or articulated bone remains and ichnofossils [Dutuit, 1976, Jalil, 1999, Jalil and Janvier, 2005, Jalil and Peyer, 2007, Khaldoune et al., 2017, Klein et al., 2010, Lagnaoui et al., 2012, Medina et al., 2001, Tourani et al., 2010, Zouheir et al., 2020]. They offer the most important Permian-Triassic vertebrate fauna of North Africa. Tetrapods are represented by more than 15 species belonging to amphibians (nec-trideans, metoposaurids, almasaurids), sauropsids (pareiasaurs, captorhinids, azendohsaurids, phytosaurs, aetosaurs, and rauisuchians), and dicynodont synapsids (see Khaldoune et al. [2017] for a taxonomic list). Other sarcopterygian remains are identified as a ceratodontid lungfish and possibly a coelacanth [Martin, 1979a,b, 1981]. Actinopterygians are Late Triassic (Carnian) in age and, except isolated scales, are all from the so-called locality XI of Dutuit [1976], at the base of the unit T5 [Dutuit, 1976, Khaldoune et al., 2017, Khalloufi et al., 2017, Martin, 1979a, 1980b,a, 1982].

The locality XI (Figure 1B) consists of three fossiliferous layers with different faunal associations. The basal most layer yielded postcranial remains of a dicynodont, the intermediate provided dicynodonts, rauisuchian reptiles and metoposaurid tem-

nospondyls, and the upper most level, formed by a reddish to brownish sandstone, delivered temnospondyls, lungfishes and the actinopterygian remains [Dutuit, 1976]. The actinopterygian material has been studied by Martin [1979a, 1980b,a, 1982], who identified two main groups, Redfieldiiformes (represented by *Mauritanichthys rugosus* Martin, 1980b and by fragments attributed to the genera *Atopocephala* and *Ischnolepis*) and “perleidiforms” (represented by *Dipteronotus gibbosus* Martin, 1980a and the genera *Perleides* and *Procheirichthys*). This is the only occurrence of these groups in North Africa. No review of the Argana Basin actinopterygians has been realized since their original description. The aim of this paper is to provide an updated overview of this fauna with comments on anatomy and phylogenetical affinities.

2. Materials and methods

The actinopterygian material from the Argana Basin consists of about 30 specimens, housed in the palaeontological collection of the Muséum national d'Histoire naturelle, Paris, France. They are in anatomical connection but incomplete for most of them. Apart few exceptions, the specimens are badly preserved, as they are often fragmented and crushed with sometimes displaced or missing bones. In order to highlight the contrast between bones and sediment, the specimens were observed under UV light, in addition to white light. Observations were made with a stereomicroscope and photographs were taken with a Nikon D800 camera. UV light observations were realized thanks to two Fluotest Forte UV quartz lamps emitting at 180 W (λ excitation centered around 365 nm). The close-up view of the scale (Figure 3G) was captured using a digital microscope Hirox RH2000. Silicone molds have been made for a few specimens preserved as natural casts (negative bone imprint). Photographs of the holotype of *Dipteronotus cyphus* (GSM18188 and GSM18189), housed at the British Geological Survey, were obtained from GB3D Type Fossils (<http://www.3d-fossils.ac.uk>). Photographs of specimens of *Dipteronotus aculeatus* (Triassic, France) from the Grauvogel collection were obtained from the Staatliches Museum für Naturkunde Stuttgart. Bone nomenclature follows the terminology of Schultze [2008] and Wiley [2008], based on homologies between sarcopterygian

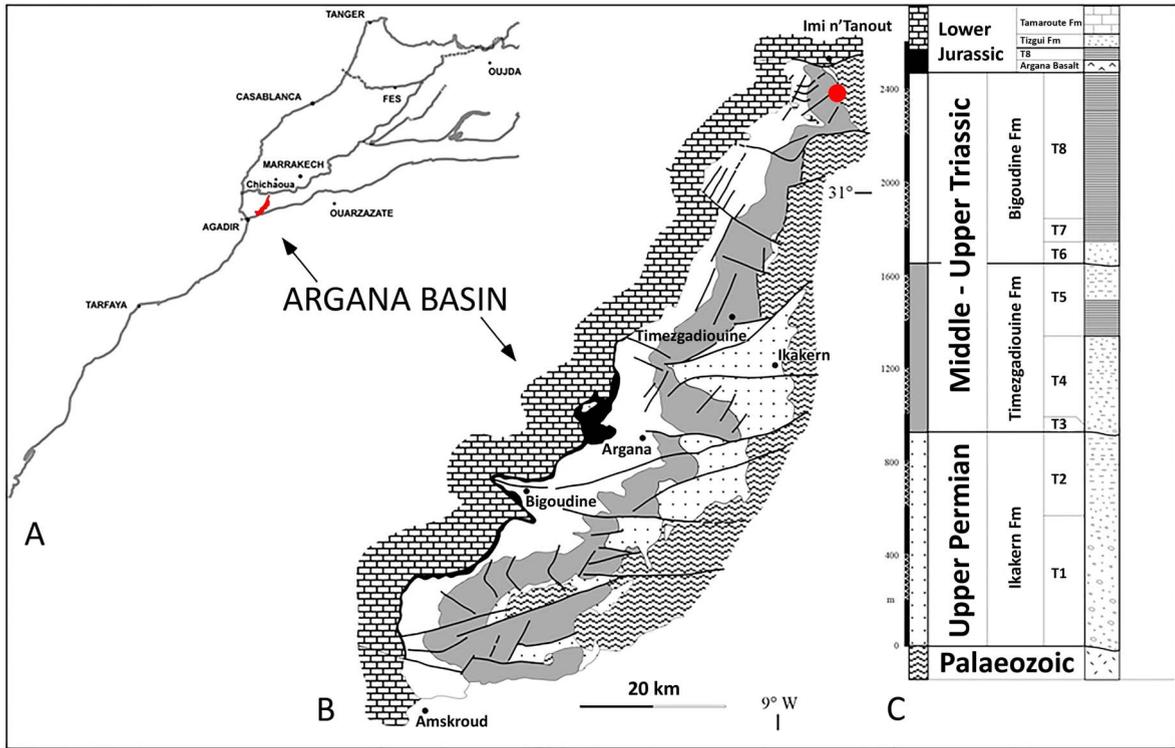


Figure 1. Location and stratigraphy of the Argana Basin. (A) Geographical map of Morocco, showing the location of the Argana Basin, in red. (B) Simplified geological map of the Argana Basin (modified from Tixeront, 1973, 1974). The locality XI is indicated by a red dot. (C) Stratigraphical section of the Argana Basin (modified from Tourani et al., 2000).

and actinopterygian skull bones, and that of Mickle [2015] for snout bones, which mainly corresponds herein to the use of “parietal” and “postparietal” instead of “frontal” and “parietal”, respectively.

Institutional abbreviation. MNHN.F, Muséum national d’Histoire naturelle, Paris, France, Palaeontological collection.

3. Palaeontological systematics

Actinopterygii Cope, 1887 Redfieldiiformes Berg, 1940

Redfieldiiformes are a clade of actinopterygians formed by at least 17 genera, known from the Lopin-gian to Early Jurassic, mostly in non-marine environments of Australia, Africa (Morocco, South Africa, Zambia and possibly Madagascar), Asia (South Korea), South America (Argentina), North America (USA) and putatively Europe (England, Germany,

Ireland, Poland and Switzerland, see Gibson, 2018, Gouiric-Cavalli et al., 2017, Hutchinson, 1973a, Kim et al., 2020, Lombardo, 2013, Schaeffer, 1984, Schaeffer and Mc Donald, 1978, Sytchevskaya et al., 2009). Their general features include an elongated body covered with ganoid scales, the dorsal and anal fins located posteriorly, and a hemi-heterocercal caudal fin. The prominent snout, which can be ornamented with ridges and/or tubercles, is formed by nasals, premaxillo-antorbital, a rostral and usually a postrostral. The nasal is usually excluded from the orbital rim by the supraorbital, and the single pair of nostrils are surrounded by the nasal, supraorbital, premaxillo-antorbital and rostral. Other features of the skull concern the presence of a large and rectangular dermosphenotic, a rectangular or crescent-shaped dermosphenotic, a hatchet-shaped preopercle, and a single (rarely two) plate-like branchiostegal ray [Gibson, 2018, Hutchinson, 1973a, Schaeffer, 1984]. Extensive studies and cladistic analyses

have been performed by Hutchinson [1973a, 1978], Schaeffer [1967, 1984] and Schaeffer and Mc Donald [1978], and the monophyly of the group is currently not questioned. Its phylogenetical position among actinopterygians remains unclear and Xu [2020] suggested to consider it as stem-Neopterygii related to Pholidopleuriformes. In Africa, redfieldiiforms have been reported in the Lopingian Madumabisa shales in Zambia (*Ischnolepis*, Haughton, 1934, Hutchinson, 1973a), but they are mostly known from the Anisian of the Upper Beaufort series in South Africa (*Atopocephala*, *Daedalichthys*, *Denwoodichthys* and *Helichthys*, Brough, 1931, 1934, Hutchinson, 1973a, Sytchevskaya et al., 2009) and from the Carnian of the Argana Basin in Morocco (*Mauritanichthys*, cf. *Ischnolepis* and cf. *Atopocephala*, Martin [1979a, 1980b, 1982], see Discussions below for the last two).

Mauritanichthys rugosus Martin [1980b] (Figure 2A–D)

Holotype. MNHN.FALM 312, specimen with missing posterior part and incomplete skull.

Referred material. MNHN.FALM 313, 314, 315, incomplete bodies.

Description. The specimens ALM 312 and ALM 313, the most complete, reach 11–12 cm in length, corresponding to an estimated standard length of 15 cm. The body is fusiform, covered with ganoid scales, and was apparently five to six times longer than deep. The pectoral fin is in ventral position. The pelvic fin is located midway between the pectoral and anal fins. The dorsal and anal fins are incompletely known and, although no specimen shows the posterior extremity of the body, they were probably located very posteriorly, owing to the dorsal and ventral outlines of the body. The caudal skeleton is unknown.

The skull is incompletely preserved in all specimens and then can only be partly reconstructed. The snout region, very damaged, is ornamented with tubercles. The postrostral separates the nasals, at least in their posterior portion. More anteriorly, tubercle marks on the sediment correspond to the position of the rostral. The skull roof, mainly observed on the holotype, is ornamented with tubercles and ridges. It is formed by a large pair of parietals (“frontals” sensu Martin, 1979a, 1980b, 1982) and a pair of wider than long trapezoidal postparietals (“parietals” sensu

Martin, 1979a, 1980b, 1982). The dermopterotic is rectangular, lying ventrally along the postparietal and the posterior part of the parietal. The dermosphenotic is also rectangular, longer than deep, and forms a large part of the dorsal edge of the orbit. The reconstruction proposed by Martin (1979a, 1980b, 1982) for the other bones of the skull roof and the orbital region cannot be confirmed herein.

The morphology of the opercular series and jaws are mostly known from the specimen ALM 314 (Figure 2C,D). The subopercle (Sop, Figure 2D) and the opercle (Op., Figure 2D) are both deeper than long, anteriorly inclined and almost comparable in size. Their surface is slightly ornamented with horizontal to radial ridges. The anterodorsal part of the opercle is damaged and the presence of an antopercle cannot be assessed. The preopercle (Pop, Figure 2D) is hatchet-shaped, with two limbs forming a right angle. Its dorsal limb, incompletely preserved, is massive and anteriorly in contact with the jugal (i.e., the infraorbital edging posteroventrally the orbit). It is surrounded ventrally by the maxilla and dorsally by the dermohyal and the dermopterotic (this last contact is visible on the specimen ALM 313).

The dermohyal (Dh, Figure 2D) is only known by its triangular ventral tip, alongside the anterior border of the opercle and the posterodorsal margin of the preopercle. A large circular branchiostegal ray (B.r, Figure 2D) lies close to the subopercle and the mandible.

The maxilla (Mx, Figure 2D) is anteriorly tapered and posteriorly expanded, without any posteroventral process. It is ornamented with longitudinal ridges. Its anterior part extends to the snout and bears small and sharp teeth. The posterior part bears a dorsal expansion, in close contact with the anteroventral margin of the preopercle and the jugal. The lower jaw is formed by a deep angular (Ang, Figure 2D), with faint ornamentation, and by an elongated dentary (De, Figure 2D) marked by strong longitudinal ridges. The oral border of the dentary is not apparent and no teeth can be observed.

The infraorbital series is incompletely preserved. The jugal (Ju, Figure 2D) is tear-shaped, with a large and rounded posterior part. Its surface is ornamented with radial ridges.

The cleithrum is only known by incomplete remains. The supracleithrum (Scl, Figure 2D) is very deep and it extends along the opercle and a large

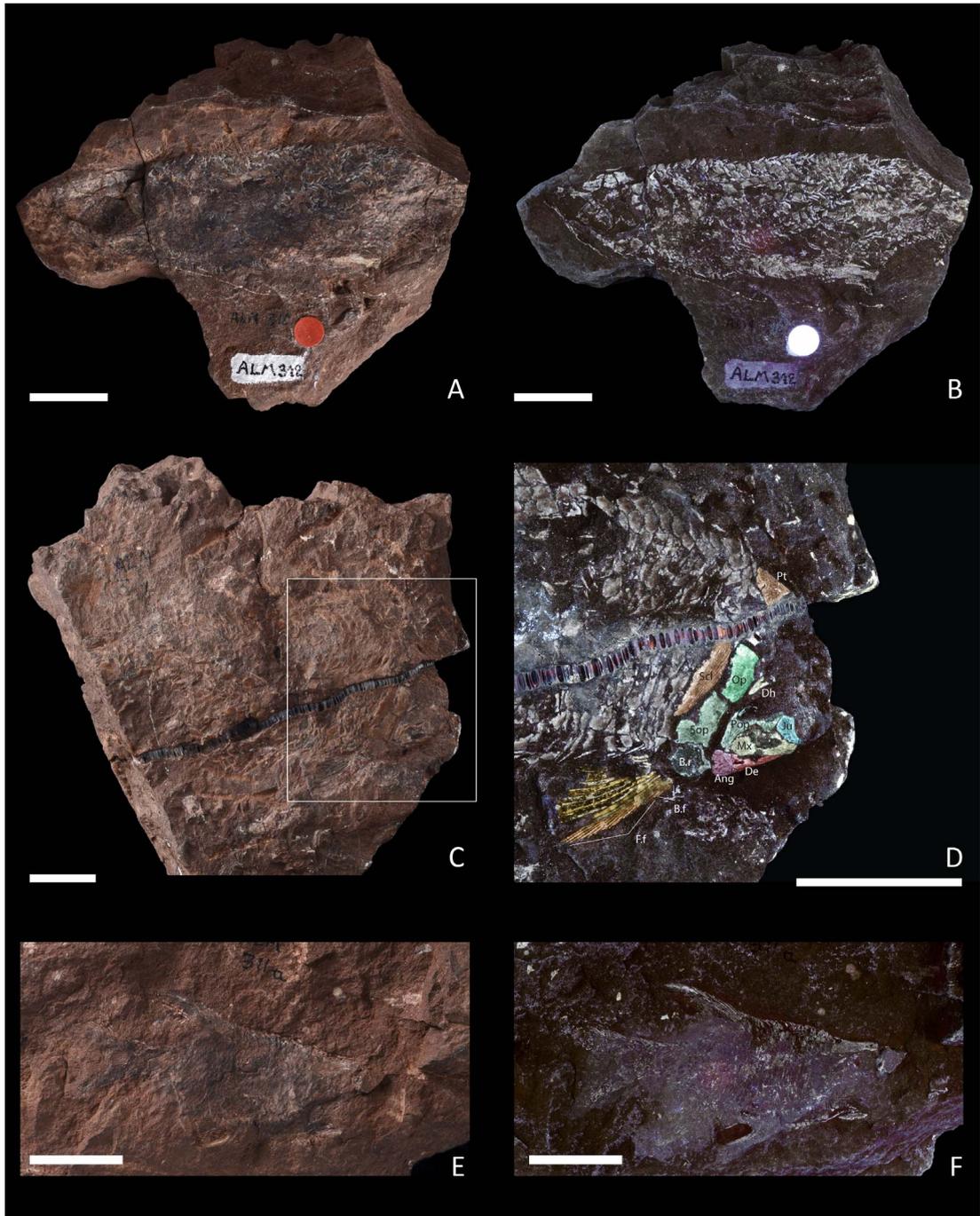


Figure 2. (A–D). *Mauritanichthys rugosus* Martin [1980b]. (A,B) MNHN.FALM 312, holotype, under white (A) and UV (B) lights. (C) MNHN.FALM 314, under white light, (D) MNHN.FALM 314, close up of the skull, with labeled and colored bones, under UV light. (E,F) Redfieldiiformes indet., formerly referred to cf. *Ischnolepis* [Martin, 1979a, 1982]. MNHN.FALM 311a, under white (E) and UV (F) lights. Abbreviations: Ang, angular; B.f, basal fulcrum; B.r, branchiostegal ray; De, dentary; Dh, dermohyal; F.f, fringing fulcrum; Ju, jugal; Mx, maxilla; Op, opercle; Pop, preopercle; Pt, post-temporal; Scl, supracleithrum; Sop, subopercle. Scale bars: 20 mm.

part of the subopercle. It is ornamented with well-marked longitudinal ridges. The post-temporal (Pt, Figure 2D) is triangular, longer than deep although its anterior part is not entirely preserved. It is ornamented with rugae. The pectoral fin comprises at least 10–12 rays, which are unsegmented proximally, their distal part being not well preserved. The fin is preceded by two basal fulcra (B.f, Figure 2D) and the first two rays support a dozen of fringing fulcra (Ff, Figure 2D). The pelvic fin is represented by remains corresponding to 7 to 8 rays, preceded by scutes.

Only a few rays of the dorsal fin are preserved. The anal fin comprises at least 20 rays, including segmented and distally branched ones.

The body is covered with ganoid scales arranged in at least 35 rows from the pectoral girdle region to middle of the anal fin. As suggested by Martin [1979a, 1980b, 1982]), more than 40 rows should be present. The most anterior flank scales are deeper than long, while they are rhomboid in the rest of the body. All scales have a unornamented surface and a smooth posterior border.

Discussion. *Mauritanichthys rugosus* can be referred to Redfieldiiformes based on the presence of a single plate-like branchiostegal ray, hatchet-shaped preopercle, large and rectangular dermopterotic, rectangular dermosphenotic, skull bones and snout ornamented with tubercles and ridges. Redfieldiiformes usually possess a well-developed dermosphenotic, which can be narrow and crescent-shaped (as in *Atopocephala*, *Schizurichthys*, *Ischnolepis*, *Brookvalia*, *Phlyctaenichthys*, *Calaichthys* and *Denwoodichthys*, most of them formerly included in the Brookvaliidae and Schizurichthyidae, sensu Hutchinson, 1973a) or as developed as the dermopterotic. This latter condition, considered as derived according to Schaeffer [1984], is present in *Mauritanichthys* and in the South African genera *Daedalichthys* and *Helichthys*, the Australian *Geitonichthys* and *Molybdichthys*, and the North American *Cionichthys*, *Lasalichthys*, *Dictyopyge* and *Redfieldius* [Gibson, 2018, Hutchinson, 1973a, 1978, Schaeffer, 1967, 1984, Schaeffer and Mc Donald, 1978]). Among these, *Molybdichthys*, *Cionichthys* and *Lasalichthys* share with *Mauritanichthys* a pectoral girdle ornamented with parallel ridges, and unornamented scales with smooth posterior border (except *Cionichthys greeni*

which possesses posteriorly denticulated scales, see Schaeffer, 1967). *Mauritanichthys* differs from all these genera by the exclusive combination of the following features: the opercle and subopercle deeper than long, the marked anterior contact of the preopercle with the jugal, the anteriormost flank scales significantly deeper than long, and the contact between the preopercle and the dermopterotic.

Martin [1980b] closely linked *Mauritanichthys* to *Lasalichthys*, noting that the latter differs by the postrostral less reduced in size, the triangular shape of postparietal and the absence of preopercle/dermopterotic contact. He insisted to maintain the validity of *Mauritanichthys* and *Lasalichthys* by considering the postrostral size variability as a generic diagnostic feature. As a result, he avoided putting also in synonymy *Lasalichthys* and *Synorichthys*, which also mainly differ by the postrostral condition, reduced in *Lasalichthys* and absent in *Synorichthys*. On the contrary, Gibson [2018] considered the absence or presence of a reduced postrostral as intrageneric variability and placed *Synorichthys* into synonymy with *Lasalichthys*. From the three features used by Martin [1980b] to distinguish *Mauritanichthys* from *Lasalichthys*, the postrostral dimension cannot be herein confidently described in *Mauritanichthys* (see above) and the contact between the preopercle and the dermopterotic is possibly present in specimens referred to *Lasalichthys* (see Gibson [2018]: Figure 6). Thus, the differences between *Mauritanichthys* and *Lasalichthys* seem to be restricted to the shape of the postparietal (trapezoidal in the former and triangular in the latter) together with the aforementioned combination of features which includes the opercle and subopercle deeper than long, the marked anterior contact of the preopercle with the jugal and the anteriormost flank scales significantly deeper than long. These elements are considered sufficient to maintain the validity of the genus *Mauritanichthys*.

Redfieldiiformes indet. (Figure 2E, F)
1979a, 1982 cf. *Ischnolepis*, Martin

Referred material. MNHN.EALM 310, 311, subcomplete specimens.

Discussion. Martin [1979a, 1982] doubtfully related two specimens from the Argana Basin to *Ischnolepis*,

mainly on the basis of the cranial bones. The only described species of the genus is *Ischnolepis bancrofti* Haughton [1934], known by a few specimens originating from an imprecise locality in Lunsemfwa Valley, Madumabisa shales, in Zambia. The age of the locality was debated but it is most likely to be Lopingian (see Discussion in Barbolini et al. 2016a,b, Haughton 1934, Hutchinson 1973a, Jubb and Gardiner 1975, Murray 2000), which makes *Ischnolepis* the only known Palaeozoic redfieldiiform.

Although subcomplete, both Argana specimens are poorly preserved and only the general body proportions, fin morphology, and the shape and ornamentation patterns of a few bones can be confidently reconstructed. Based on the descriptions, reconstructions and photographs in Haughton [1934] and Hutchinson [1973a], *I. bancrofti* shares with the two Argana specimens a well-developed pelvic fin, long-based anal fin, oblique opercular series with a small opercle, cleithrum ornamented with ridges, and anteriorly placed orbit. However, none of these features is exclusive to these two taxa, which significantly differ on the general proportions of the body and fins. The body of *I. bancrofti* is 3.5–4 times longer than deep, and the head is about one fifth of the body length, while the Moroccan specimens have a body less elongated, only 2.5 times longer than deep, and their head length is about one quarter to one third the body length. Another difference concerns the relative position of the unpaired fins. In *I. bancrofti*, the dorsal fin front is nearly opposite to the anal fin front, which is considered by Xu [2020] as a derived feature supporting the clade formed by the Pholidopleuriformes and Redfieldiiformes. On the contrary, the Argana specimens show a dorsal fin front located well anteriorly to the anal fin front, almost reaching the level of the pelvic fin front, a conformation also encountered in the redfieldiiforms *Brookvallia spinosa* and *Phlyctaenichthys* [Hutchinson, 1973a, Wade, 1935]. The anal fin of the Argana specimens clearly shows fringing fulcra while the presence of these latter cannot be confirmed in *I. bancrofti*. A small portion of the cleithrum of ALM 311 (Figure 2E,F) shows an ornamentation with longitudinal grooves, which corresponds to the description of *Ischnolepis* by Haughton [1934], while Hutchinson [1973a] described the cleithrum of *Ischnolepis* as covered by fine grooves with rows of tiny tubercles.

The skull morphology of the two Argana specimens fits well with the Redfieldiiformes diagnosis, with a hatchet-shaped preopercle and a probable crescent-shaped dermosphenotic. Nevertheless, the body and fin proportions are different from those of all known redfieldiiforms, including *Mauritanichys* from the Argana Basin, and *Ischnolepis*. These two specimens, which probably correspond to the same species, are considered as Reldfieldiiformes indet.

4. “Perleidiforms”

“Perleidiforms” are a paraphyletic assemblage constituted by Triassic to Early Jurassic stem-neopterygian families. They are known in marine and continental environments, in an almost cosmopolitan distribution, with occurrences in Africa, North and South America, Europe (including Greenland), China and Australia [Bürgin, 1992, Hutchinson, 1973a, López-Arbarello and Zavattieri, 2008, Sun et al., 2009]. Together with the Peltopleuriformes, they were previously referred to the grade “subholosteans”, mainly characterized by a hemiheterocercal caudal fin with epaxial rays, flank scales deeper than long, vertical or almost vertical preopercle (usually still in contact with the maxilla), and an equal ratio between radials and lepidotrichia. “Perleidiforms” differ from peltopleuriforms by a larger and wedge-shaped preopercle, a supraorbital sensory canal entering in the postparietals, different squamation pattern (with thick and subrectangular to rhomboid scales, deeper than long only in the anterior trunk region), and tooth morphology, with peg-like marginal teeth and crushing inner ones [Lombardo and Brambillasca, 2005, Schaeffer, 1956, Sun et al., 2012, 2013, Tintori and Lombardo, 1996]. They show a great morphological diversity, with elongated to deep-bodied forms (e.g., Bürgin, 1992, Lombardo and Tintori, 2004). In the Argana Basin, Martin [1979a, 1980a, 1982] described a new species of *Dipteronotus*, *D. gibbosus*, and referred with caution five specimens to the genera *Perleides* and *Procheirichthys*. Recently, Xu [2020] investigated the phylogenetical relationships of several neopterygian taxa and proposed to use the clades Platysiagiiformes (Platygiasidae), Polzbergiiformes (Polzbergiidae and Cleithrolepididae) and Louwoichthyiformes (Pseudobeaconiidae, including *Dipteronotus*, and Louwoichthyidae) to include

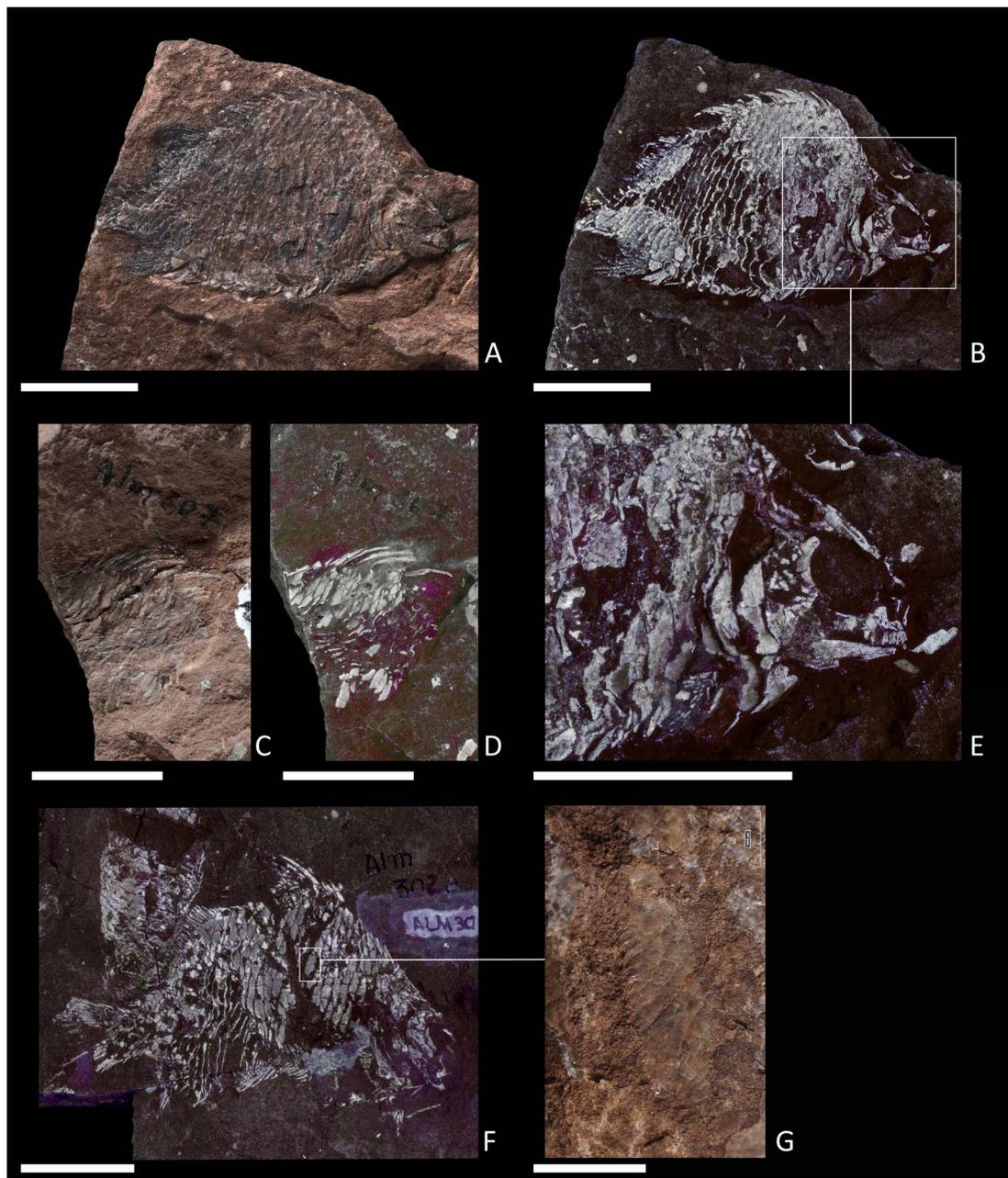


Figure 3. *Dipteronotus gibbosus* Martin, 1980a. (A,B) MNHN.FALM 301b, holotype, under white (A) and UV (B) lights. (C,D) MNHN.FALM 307, under white (C) and UV (D) lights. (E) Close-up of the skull of MNHN.FALM 301b, under UV light. (F) MNHN.FALM 302a, under UV light. (G) MNHN.FALM 302a, close-up view of one scale, under white light. Scale bars: 20 mm (A–F), 2 mm (G).

several “perleidiform” genera. Although based on a cladistic analysis, this nomenclature is not followed herein because of doubts on the position of *Dipteronotus* (see Discussion).

Dipteronotus gibbosus Martin [1980a] (Figure 3)

Holotype. MNHN.FALM 301a,b, subcomplete specimen, part and counterpart.

Referred material. MNHN.FALM 302a,b, subcomplete specimen, part and counterpart; MNHN.FALM 303 (not seen), 307, 308, 309 (with doubt), incomplete bodies. The specimens ALM 306 and 322, doubtfully referred by Martin [1979a, 1982] to the species, are not retained herein.

Description. The body is deep, ca. 1.7 times longer than deep on the holotype ALM301a,b, which measures 6 cm in standard length for a total depth of 3.6 cm (3.4 cm excluding the elongated dorsal spine-like ridge scales). The head is slightly deeper than long and its length is little less than a quarter of the standard length. The dorsal and anal fins are posteriorly located, the dorsal fin being longer with a front located more anteriorly than the anal. The body is covered by ganoid scales and its dorsal outline shows a marked hump located immediately behind the skull. This hump is extended on the anterior half of the body and is curved or with a marked angle, depending on specimens (Figure 3A–D,E, see Discussion). It is covered by elongated spine-like ridge scales (“first dorsal fin” sensu Gall et al., 1974, Martin, 1979a, 1980a, 1982, see Discussion in Tintori, 1990).

The skull roof is incompletely preserved. The parietal (“frontal” sensu Martin, 1979a, 1980a, 1982) covers most of the orbit. It is visible in section and is ornamented with tubercles. Imprints of the postparietal (“parietal” sensu Martin, 1979a, 1980a, 1982), dermopterotic and extrascapular are present, but without any accurate delimitations between bones. As noted by Martin [1979a, 1982], the rostral region of the skull is markedly anteroventrally curved. The orbit is large. The preopercle is only known by its ventral part, the dorsal part being either not preserved or fragmented in the available material. It is almost vertical, according to the position of the orbit and the opercle, and to the course of the slightly curved preopercle sensory canal (visible on ALM 302a, Figure 3F). Its ventral part is posteriorly bordered by the subopercle and anteroventrally by the maxilla. The opercle is ovoid. The subopercle is deeper than long, roughly twice deeper than the opercle; its anterior margin is concave.

The maxilla has a well-developed posterior part, with dorsal and ventral expansions, and a straight and thinner anterior part. As reported by Martin [1982], a premaxilla could be present, but with no clear evidence. Teeth are limited to the anteriormost

half of the upper jaw. They are peg-like, long, slender and tightly packed. The mandible is massive with well-marked posterior part and symphysis. It does not bear teeth on the holotype but the specimen ALM 309, putatively attributed to *D. gibbosus*, shows dentary teeth which are acute and tightly packed.

The cleithrum and supracleithrum are unornamented. The cleithrum shape can be described from its imprint on ALM 301a. It is arched, with a slightly posterior protrusion between the dorsal and ventral branches. The supracleithrum and post-temporal are damaged. The pectoral fin contains at least 8–10 rays, with fringing fulcra on the leading rays (as observed on ALM 302a, Figure 3F). The pelvic fin possesses at least 5 rays.

Scales are arranged in 32 or 33 anteriorly inclined rows. No ornamentation can be observed on their surface, but the posterior margin, when preserved, shows a dentate edge (Figure 3G). Scales of the flank are deeper than long, and those located around the dorsal and anal fins are smaller and more irregularly distributed. Scales at the level of the caudal peduncle are almost rhomboid. The dorsal and ventral body midlines are covered by a series of spine-like ridge scales, which are elongated along the dorsal hump. On the holotype, the dorsal hump is curved and covered by ten moderately elongated spine-like ridge scales, posteriorly oriented (Figure 3A,B). On the specimens ALM 302a,b, 307 and 308 the hump outline shows a more marked angle and the spine-like ridge scales are slenderer (Figure 3C,D,F). These variations in size and shape could be related to ontogeny or sexual dimorphism (see Discussion). Ventrally, the spine-like ridge scales located in front of the anal fin are also well developed, without reaching the size of the dorsal ones. No distinction is made herein between ridge scales and scutes.

The dorsal fin is extended from the 23rd to the 29–30th rows of scales, and reaches the level of the caudal peduncle. Three fulcra of increasing size and at least 17–18 rays are present. However, the distinction between basal fulcra, ridge scales and even first rays is uneasy, especially when the rays are unsegmented or when only the proximal segment is preserved. No fringing fulcra can be observed, possibly because of a lack of preservation of the distal part of the first rays.

The anal fin contains at least 15 rays, formed by an unsegmented proximal part, shorter than those of

the dorsal fin rays and by a segmented and branched distal part. However, the branching pattern cannot be accurately described. The posterior part of the fin is not preserved. As for the dorsal fin, no fringing fulcra is observed, possibly due to the poor preservation of the distal portion of the leading rays.

The caudal fin is deeply forked and hemiheterocercal in configuration, with a short axial body lobe. The fin contains about 24 rays, including 4 or 5 in epaxial position. The rays are segmented but no pattern of branching can be described since their distal extremity is not preserved. The upper lobe of the fin is preceded by one or two scutes and two to three basal fulcra, whereas the lower lobe is preceded by three or four scutes and two basal fulcra, but the distinction between first rays and basal fulcra is unclear. No fringing fulcra is observed.

Discussion. The genus *Dipteronotus* comprises three Middle Triassic (Anisian–Ladinian) European species, *D. cyphus*, *D. aculeatus* and *D. olgiatii* [Egerton, 1854, Gall et al., 1974, Jörg, 1969, Milner et al., 1990, Tintori, 1990, Tintori et al., 2016]. The main generic feature is the presence of a dorsal hump covered with elongated spine-like ridge scales, with a well-marked angle immediately posteriorly to the last elongated ridge scale. A fourth European species, “*Dipteronotus*” *ornatus* Bürgin, 1992, was described from the Middle Triassic of Monte San Giorgio, but shows a hump with reduced ridge scales. This species was removed from *Dipteronotus* by Lombardo and Tintori [2004] and included in the genus *Stoppania* by Lombardo et al. [2008].

Based on the presence of a dorsal hump covered by elongated spine-like ridge scales, Martin [1979a, 1980a, 1982] attributed the Argana specimens to the genus *Dipteronotus*, and erected the species *D. gibbosus*. However, noting that the Moroccan species differs by its curved dorsal hump and the head proportions, he emended the diagnosis of *Dipteronotus* of Gall et al. [1974] by replacing “dorsal outline of the body showing a marked angle” by “showing a curve or a marked angle” and “head height comprised at least 3 times in the body height” by “at least 2.5 times”. Tintori [1990] rejected this emendation, and consequently the attribution of the Moroccan form to *Dipteronotus*, considering the sharp angle of the hump behind the last elongated spine-like ridge scale as “the most striking character of *Dipteronotus*

itself”. He suggested close relationship of the Moroccan form with *Pseudobeaconia*.

As in *Dipteronotus aculeatus*, the body shape of *D. gibbosus* shows a significant intraspecific variability, possibly related to ontogeny (Jörg, 1969: Figures 1–2; Gall et al., 1974: 138–139, pl. IIIc; Martin 1979a, 1982). Gall et al. [1974] discussed these variations and pointed out the presence of a marked angle on the hump of *D. aculeatus* in deeper specimens, when the hump outline is more curved in a slenderer specimen, presumably juvenile. In *D. gibbosus*, Martin (1979a: 98–99; 1982: 359) described one or two possible young specimens (ALM 306 and 322) but their identifications are doubtful and they are not considered herein. However, two specimens (ALM 302a,b and 307) show a dorsal hump with a more marked angle than in the holotype. ALM 302a,b (Figure 3F) is deformed and ALM 307 (Figure 3C,D) is very incomplete, but they clearly show a marked angle immediately posteriorly to the last elongated spine-like ridge scale. When compared to the holotype, these two specimens also show more elongated spine-like ridge scales, closer in shape to those of the European *Dipteronotus* species. Another specimen from the Argana Basin, ALM 308, possesses comparable spine-like ridge scales but the dorsal hump outline cannot be retraced. In these respects, the dorsal ridge scales and the dorsal hump of *D. gibbosus* do not significantly differ from those of the other species of the genus; *D. gibbosus* is thus maintained in *Dipteronotus*. The holotype ALM 301a,b, with a smooth curved hump, probably corresponds to a subadult specimen or shows sexual dimorphism.

D. gibbosus differs from *D. cyphus*, *D. aculeatus* and *D. olgiatii* by meristic features, body proportions, and by the subopercle significantly deeper than the opercle (instead of being of about same size in *D. olgiatii*, the situation is confused in the other species, see Gall et al., 1974, Lombardo and Tintori, 2004, Tintori, 1990, Woodward, 1910). In all *Dipteronotus* species, the scale surface is smooth, and the posterior border is serrate in *D. cyphus*, *D. gibbosus* and *D. aculeatus* (Figure 3G; Gall et al., 1974:133, Woodward, 1910) while it shows a single spine-like process in *D. olgiatii* [Tintori, 1990]. The head height to body height ratio is variable among species, but also among individuals. Gall et al. [1974] diagnosed *Dipteronotus* (*D. aculeatus* and *D. cyphus*) with a body height at least 3 times the head height, and

they noticed intraspecific variability in *D. aculeatus*. The holotype of *D. gibbosus* shows a body height about 2.5 times the head height, which led Martin [1979a, 1980a, 1982]) to modify the generic diagnosis (see above). This ratio slightly differs in ALM 302a,b (Figure 3F). In *D. olgiatii*, the body height is less than 2.2 times the head height, but the original description is based on a single specimen. This ratio is too variable to be reliably used as diagnostic for the genus.

The genus *Dipteronotus* was usually considered as a Perleididae or a Cleithrolepididae (see Bürgin, 1992, López-Arbarello and Zavattieri, 2008, Milner et al., 1990, Sun et al., 2012, Tintori, 1990, Tintori et al., 2016, Wade, 1935). Recently, Xu [2020] related it to Pseudobeaconiidae, a family erected by López-Arbarello and Zavattieri (2008, see also López-Arbarello et al., 2010) to include *Pseudobeaconia* and *Mendocinichthys*, both from the Late Triassic of Argentina. A similar view was proposed by Hutchinson (1973b: 18–19), who suggested to link “*Praesemionotus*” (= *Dipteronotus*) *aculeatus*, *Pseudobeaconia* and “*Mendocinia*” (= *Mendocinichthys*). All these taxa share the presence of a series of dorsal spine-like ridge scales between the skull and the dorsal fin. However, *Pseudobeaconia* and *Mendocinichthys* only show reduced dorsal spine-like ridge scales and possess no dorsal hump. Moreover, among the diagnosis of the family [López-Arbarello and Zavattieri, 2008], the elongated body is 2–3.5 times longer than deep, the dorsal and anal fins are equal or almost equal in size, and the scales are ornamented with marginal concentric ridges of ganoine and possess a smooth border. *Dipteronotus* differs by the deeper shape of its body, the dorsal fin longer than the anal fin, and the absence of scale ornamentation, except for the posterior border, which is not smooth. The inclusion of *Dipteronotus* into Pseudobeaconiidae, which would require deep changes on the diagnosis of the family, is not followed herein.

Dipteronotus gibbosus shows superficial resemblances with the deep-bodied “perleidiforms” *Stoppiania*, *Felberia*, *Cleithrolepidina*, *Cleithrolepis* and *Hydropessum*. It differs from these taxa by the dorsal elongated spine-like ridge scales. It also differs from *Stoppiania* and *Felberia* by the absence of ornamented scales, from *Cleithrolepidina* and *Cleithrolepis* by its deeper dentary and the tooth

morphology and from *Hydropessum* by the lack of ornamentation of the opercular series and pectoral girdle [Hutchinson, 1973a, Lombardo and Tintori, 2004]. *D. gibbosus* shares with *Stoppiania ornata* and *Felberia* the reduced scales at the basis of the dorsal and anal fins. This feature is unknown (absent or undescribed) in the European species of *Dipteronotus*.

From this comparison, the Moroccan form strongly differs and cannot be related to pseudobeaconiids and to the deep-bodied “perleidiforms” *Stoppiania*, *Felberia*, *Cleithrolepidina*, *Cleithrolepis* and *Hydropessum*. It shares the synapomorphies of *Dipteronotus*, including a hump showing a marked angle and covered by elongated spine-like ridge scales; consequently, it constitutes a valid species of this genus.

Actinopterygii indet. The three following taxa cannot be confidently referred or related to any actinopterygian clade.

Actinopterygii indet. sp. 1 (Figure 4A,B)
1979a, 1982 cf. *Procheirichthys*, Martin

Referred material. ALM 317, 318, 320, articulated post-cranial bodies; ALM 319a,b, post-cranial body with incomplete skull and pectoral girdle, part and counterpart (missing from MNHN.F collection).

Discussion. Martin [1979a, 1982] included these four specimens in *Procheirichthys*, a monotypic genus known by a single specimen of *P. ferox* from the Anisian of Hawkesbury Sandstone, Brookvale, Australia [Hutchinson, 1973a, Wade, 1935]. The Argana specimens share with *Procheirichthys* the dorsal and anal fins of limited extent, located in the last third part of the body and preceded by basal and fringing fulcra, and the caudal skeleton with epaxial rays. Based on the descriptions of Wade [1935], Hutchinson [1973a], Martin [1979a, 1982]) and Frickhinger [1995], they also share a somewhat similar squamation, with smooth scales of moderate size, and an anal fin with the most proximal ray segment longer than the following ones. Except the size, the Argana specimens being considerably smaller (7 cm) than *P. ferox* (16.3 cm), the differences between these two forms are weak. The anal fin of the Argana specimens possesses more rays and is more posteriorly extended. Due to the almost total absence of skull,

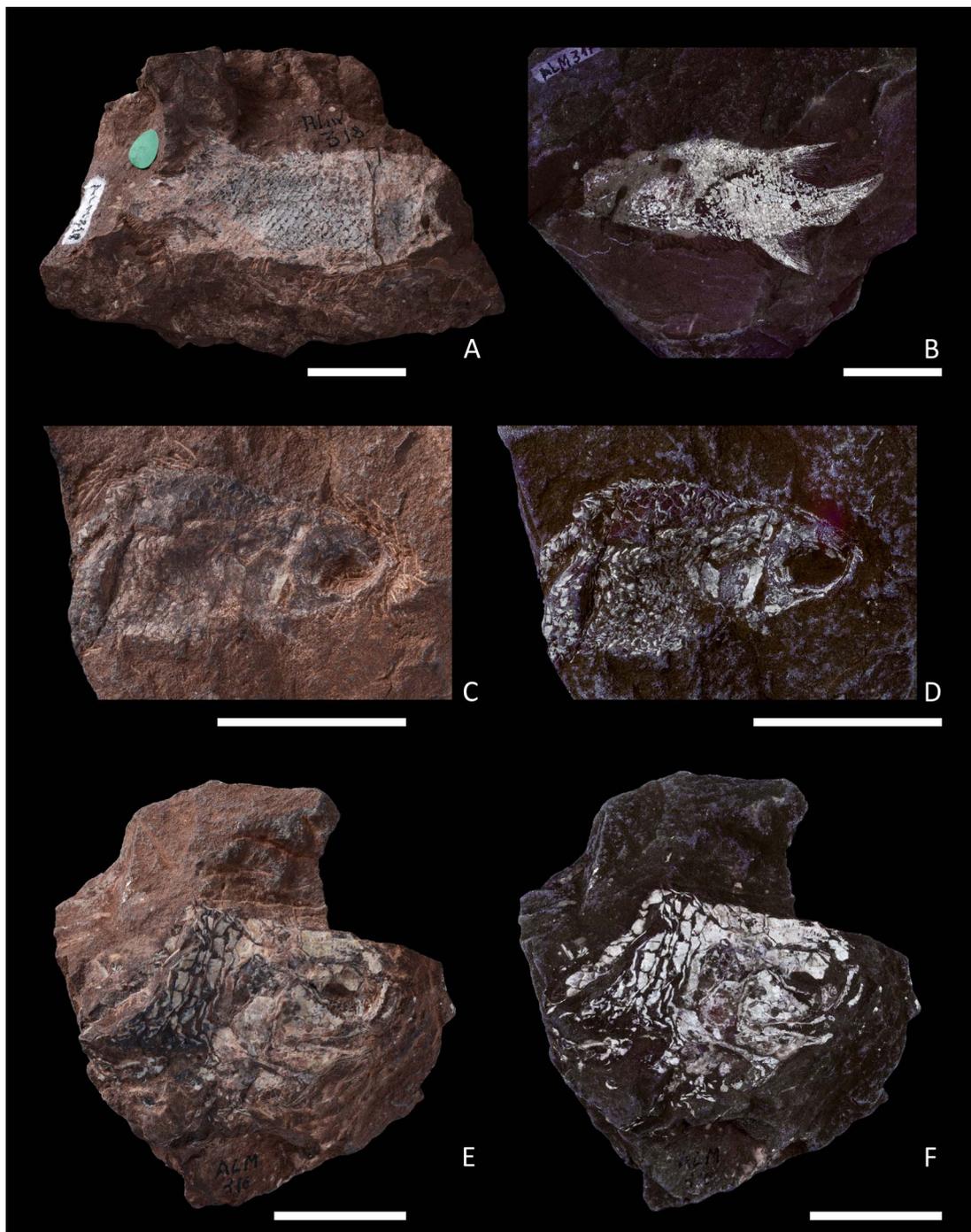


Figure 4. (A,B) Actinopterygii indet. sp. 1, formerly referred to cf. *Procheirichthys* [Martin, 1979a, 1982]. (A) MNHN.FALM 318, under white light. (B) MNHN.FALM 317, under UV light. (C,D) Actinopterygii indet. sp. 2, formerly referred to cf. *Atopocephala* [Martin, 1979a, 1982], MNHN.FALM 321, under white (C) and UV (D) lights. (E,F) Actinopterygii indet. sp. 3, formerly referred to cf. *Perleidus* [Martin, 1979a, 1982], MNHN.FALM 316, under white (E) and UV (F) lights. Scale bars: 20 mm.

the precise proportions of the Argana specimens are unknown but they seem slightly less deep than *Procheirichthys*, and the unpaired fins are located slightly more posteriorly.

The only known cranial features were described by Martin [1979a, 1982] from a specimen not studied herein (ALM 319a,b, missing from the MNHN.F collection) in which the skull material is limited to the opercular series, a small portion of the maxilla and the branchiostegal rays. Post-cranial features like the moderately elongated body and the dorsal and anal fins posteriorly located and in almost opposite position are also encountered, to some degree, in different Triassic actinopterygians, such as the pseudobeaconiid *Mendocinichthys*, the “perleidiforms” *Fuyuanperleidus* and *Manlietta*, and various redfieldiiforms. These taxa differ from the Argana specimens by meristic features of the fins and scale rows. *Mendocinichthys* also differ by the presence of small spine-like ridge scales between the skull and dorsal fin and *Fuyuanperleidus* by the very deep series of flank scales [López-Arbarello and Zavattieri, 2008, Sun et al., 2012]. According to the skull description of ALM 319a,b by Martin [1979a, 1982], *Manlietta* also differs by the opercular series proportions [Hutchinson, 1973a] and redfieldiiforms by the presence of one or two plate-like branchiostegal rays. These Argana specimens are herein considered as Actinopterygii indet.

Actinopterygii indet. sp. 2 (Figure 4C, D)
1979a, 1982 cf. *Atopocephala*, Martin

Referred material. MNHN.FALM 321, subcomplete specimen.

Discussion. This single small specimen was referred with caution to the redfieldiiform *Atopocephala* by Martin [1979a, 1982]. It is subcomplete but preserved folded up on itself. Except squamation and part of the pectoral girdle, few post-cranial features can be observed. The skull is incomplete and well exposed.

The genus *Atopocephala* comprises the single species *A. watsoni* Brough, 1934, described on the basis of a unique specimen from the Anisian of Karoo Series, at Bekkerskraal, South Africa [Hutchinson, 1973a, López-Arbarello, 2004]. As noticed by Martin [1979a, 1982], the skull of ALM 321 shows several

similarities with *Atopocephala*, the most important of which are the well-developed parietal (“frontal” sensu Martin [1979a, 1982]) and the strong opercle (in Martin [1982], “strong preopercle” in Martin [1979a]). To these can be added the curved upper jaws, large and anteriorly placed orbit, ornamentation of cranial dermal bones with tubercles, maxilla close to the ventral border of the orbit, and presence of longitudinal ridges on the pectoral girdle. However, none of these features or their combination is specific to *Atopocephala*. Differences between ALM 321 and *Atopocephala* concern the subopercle, significantly larger than the opercle in the former while the opercle is the largest in the latter. As highlighted by Martin [1979a, 1982], *Atopocephala* differs also by the less developed opercular series and pectoral girdle. The backwardly directed spines on the opercle and subopercle, distinctive of *Atopocephala*, cannot be confidently confirmed on ALM 321, in which the posterior part of the opercular series is damaged. Martin [1979a, 1982] interpreted tenuous imprints on the pectoral girdle as possible subopercle spines but this view is not shared herein.

One of the most striking features of ALM 321 is the upwardly curved upper jaw, a morphology reminiscent of the condition observed in *Atopocephala* and, to a certain extent, in various short snouted redfieldiiforms such as *Dictyopyge*, *Helichthys*, *Geitonichthys*, and *Molybdichthys* [Hutchinson, 1973a, Schaeffer, 1984]. In ALM 321, the presence of a premaxilla is unclear, but the anterior part of the upper jaw is flanked or extended by a bone ornamented with denticles. Identified as the antorbital by Martin [1979a, 1982], it constitutes an important part of the snout and possibly a portion of the anterior edge of orbit. It is evocative in shape and position of the “antorbital”, “premaxilla” or “premaxillo-antorbital” of various redfieldiiforms, in which teeth-bearing bone and bone ornamented with denticles can be confused. However, the preservation of ALM 321 is not sufficient to confidently relate it to Redfieldiiformes; this specimen is herein considered as Actinopterygii indet.

Actinopterygii indet. sp. 3 (Figure 4E, F)
1979a, 1982 cf. *Perleidus*, Martin

Referred material. ALM 316, skull with partial pectoral girdle and squamation.

Discussion. This single specimen consists of a skull with several missing areas, associated to an incomplete pectoral girdle and the very first scale rows. Martin [1979a, 1982] related it to *Perleidus* on the basis of the proportion of the skull and the deepness of the cleithral scales. He emphasized features shared with “*Perleidus*” *madagascariensis* and “*Perleidus piveteaui*”, from the Early Triassic of Madagascar, such as the infraorbital inserting between the suborbital (“preopercle” in Martin, 1979a) and the maxilla, the square postparietal, and the proportion of the mandible. Lombardo [1995] questioned this identification owing to the limited preservation of the Moroccan specimen. The two Malagasy “*Perleidus*” species were recently reviewed, synonymized, included in the genus *Teffichthys* and excluded from Perleididae by Marramà et al. [2017]. ALM 316 differs from *Teffichthys* and perleidids in particular by the shape of the preopercle, hatchet-shaped and in contact with the anterodorsal edge of the maxilla in the Moroccan specimen while it is deeper and usually in contact only with the posterodorsal edge of the maxilla in the two other taxa (note that the preopercle shape shows a sizeable intraspecific variability in *Teffichthys*, see Marramà et al., 2017: Figure 4). The first scales beyond the two or three first rows are moderately deeper than long in ALM 316 instead of being several times deeper than long as it is in perleidids and several specimens of *Teffichthys*. Another important difference is the shape of the jaw, which is curved upward anteriorly in ALM 316; oral margins of the maxilla and dentary are straight in *Teffichthys* and perleidids.

Such curved jaws are reminiscent of the Argana specimen ALM 321, related with caution to the redfieldiiform *Atopocephala* by Martin ([1979a, 1982] but considered herein as an indeterminate actinopterygian), and also of various redfieldiiforms. The “nasal” (sensu Martin, 1979a, 1982) of ALM 316 is also evocative of the “antorbital” of ALM 321 (sensu Martin, 1979a, 1982) by its position, edging anteriorly the orbit, and its ornamentation, with strong denticles. However, in ALM 316, a small bone edging anteroventrally the orbit and bearing what appears to be the tripartite canal should correspond to the antorbital. Portions of sensory canals present on the parietal and the preopercle of ALM 316 show a double row of pores, which is an uncommon feature among actinopterygians, but known in the redfieldi-

iform *Lasalichthys* [Gibson, 2018, Schaeffer, 1984]. Other features of Redfieldiiformes, like the single branchiostegal ray and the skull roof ornamented with ridge and/or tubercles, are not directly observed in ALM 316. Martin [1979a] identified numerous branchiostegal rays but they are too poorly preserved to be confirmed as such. Except the “nasal” ornamented with denticles, the skull roof bones of ALM 316 are apparently smooth but minute imprints on the sediment suggest that the hidden face is possibly ornamented with tubercles.

The morphology of the preopercle and the flank scales tends to exclude ALM 316 from Perleididae but also from “perleidiforms” and *Teffichthys*, while features shared with ALM 321 are reminiscent of redfieldiiforms. This specimen is treated as Actinopterygii indet.

5. Conclusion

In North Africa, extended Permian and Triassic fossiliferous continental exposures have been reported in Algeria (Permian, Triassic, Tiguentourine and Zarzaitine Series, see Attar et al., 1981, Dahoumane et al., 2016, Jalil, 1999), Niger (Permian, Moradi Formation, see Steyer et al., 2006) and Morocco (Permian, Triassic, Argana Basin, see Jalil, 1999, Khaldoune et al., 2017), but only the Argana Basin has yielded a significant actinopterygian fauna. Except ichnofossils, a few occurrences of microfossils (charophytes and ostracods) in the T4 member [Medina et al., 2001], and unpublished plant remains in the Ikakern Formation (Dutuit, 1976, Feys and Greber, 1963, Jalil, 1999, Koning, 1957; N.J. pers. obs.), most of the body fossils from the Argana Basin are macrovertebrate bone remains. The age of the different units, with the exception of the T4 member, was estimated from vertebrates and throughout comparison with closely related faunal assemblages. The tetrapod fauna from the T5 member (aetosaurs, metoposaurids, almasaurids, stahleckeriid dicynodonts, rauisuchians and phytosaurs, see Buffa et al., 2019, Butler et al., 2019, Jalil and Peyer, 2007, Khaldoune et al., 2017, Olivier et al., 2019) strongly suggests a Late Triassic (Carnian) age. In particular, this fauna is very close to the Late Triassic assemblages of the North American Chinle Formation and Newark Supergroup, and from Krasiejów and Woźniki, in Poland [Khaldoune et al., 2017]. The contribution of the actinopterygians in

dating and biogeography purposes is limited. From the six forms previously described in the basin, only two taxa are reliably identified, *Mauritanichthys rugosus* Martin [1980b] and *Dipteronotus gibbosus* Martin [1980a]. *Mauritanichthys*, endemic to the Argana Basin, shows affinities with the sub-contemporaneous *Lasalichthys* from the Chinle Formation and the Newark Supergroup. *Dipteronotus gibbosus* is the youngest representative of a genus otherwise known by several European species ranging from Anisian to Ladinian, in marine, brackish or deltaic environments [Bürgin, 1992, Gall and Grauvogel-Stamm, 2005, Tintori, 1990, Tintori et al., 2016]. Other actinopterygian taxa from the Argana Basin probably correspond to new forms, but are represented by poorly preserved material and their phylogenetical affinities remain unclear, except saying that they are neither Holostei nor Teleosteomorpha. The absence of these two clades in the Argana Basin agrees with their relative abundance during the Triassic, low in continental localities comparatively to marine environments [Cavin, 2017, Romano et al., 2016]. Further study on this ichthyofauna requires more detailed investigation for specimens preserved in volume (e.g., by the use of micro-computed tomography scanning), or the collect of new material.

The actinopterygian remains are rare in the Argana Basin, in comparison to tetrapods. All the actinopterygian material was collected from a hard sandstone level of the locality XI, using dynamite, during a single fieldwork in 1966 [Dutuit, 1976]. Recent fieldworks and prospecting throughout the Permian-Triassic outcrops of the Argana Basin led to the discovery of new localities and several tetrapod bones (e.g., pareiasaurs, rhynchosaurians, moradisaurin captorhinids, metoposaurids, phytosaurs; see Khaldoune et al., 2017), but no new actinopterygian remains have been found. This peculiar distribution pattern can partly be explained by the deposition conditions along the basin. Isolated remains are common but the localities providing well preserved material are rare, and most tetrapod localities are related to in-situ massive mortality or post-mortem accumulation [Dutuit, 1976]. Taphonomic and detailed sedimentological studies for the locality XI and for the basin, like those performed for the metoposaurid locality XIII [Tourani and Benaouiss, 2009] will better guide future prospecting for actinopterygian remains.

Acknowledgments

Authors are grateful to Rachid Essamoud (Geology Department, Faculty of Sciences Ben M'sik, Hassan II University of Casablanca) and Sylvie Bourquin (UMR 6118, Rennes University) for their invitation to contribute to this special volume, to Gaël Clément and Alan Pradel (UMR 7207, MNHN, Paris) for access to the collections under their care, to Erin Maxwell (Staatliches Museum für Naturkunde, Stuttgart) and Léa Grauvogel-Stamm for photographs of *Dipteronotus aculeatus*, to Dario de Franceschi and Didier Merle (UMR 7207, MNHN, Paris) for technical support, to Philippe Loubry (UMR 7207, MNHN, Paris) for the photographs and to Fatima Khaldoune (OCP Group, Khouribga) for useful discussions. This manuscript was improved thanks to the comments of Sebastian Voigt and an anonymous reviewer. BK was partly funded by the Fondation Ars Cuttoli, Paul Appell.

References

- Attar, A., Fabre, J., Janvier, P., and Lehman, J. P. (1981). Les Vertébrés de la formation de Tiguentourine (Permo-Carbonifère, bassin d'Illizi, Algérie). *Bull. M.N.H.N., Paris, 4e sér.*, 3(section C, no. 4), 301–309.
- Barbolini, N., Bamford, N. K., and Tolan, S. (2016a). Permo-Triassic palynology and palaeobotany of Zambia: a review. *Palaeontol. Afr.*, 50, 18–30.
- Barbolini, N., Smith, R. M. H., Tabor, N. J., Sidor, C. A., and Angielczyk, K. D. (2016b). Resolving the age of Madumabisa fossil vertebrates: palynological evidence from the mid-Zambezi Basin of Zambia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 457, 117–128.
- Berg, L. S. (1940). Classification of fishes, both recent and fossil. *Trav. Inst. Zool., Académie des Sciences de l'URSS*, 5, 1–517.
- Brough, J. (1931). On the fossil fishes from the Karroo System, and some general considerations on the bony fishes of the Triassic period. *Proc. Zool. Soc. Lond.*, 101(1), 235–296.
- Brough, J. (1934). On the structure of certain catopterygid fishes. *Proc. Zool. Soc. Lond.*, pages 559–571.
- Brown, R. H. (1980). Triassic rocks of Argana valley, southern Morocco, and their regional structural implications. *Bull. Am. Assoc. Pet. Geol.*, 64, 988–1003.

- Buffa, V., Jalil, N.-E., and Steyer, J.-S. (2019). Re-description of *Arganasaurus (Metoposaurus) aze-rouali* (Dutuit) comb. nov. from the Upper Triassic of the Argana Basin (Morocco), and the first phylogenetic analysis of the Metoposauridae (Amphibia, Temnospondyli). *Pap. Palaeontol.*, 5, 699–717.
- Bürgin, T. (1992). Basal Ray-finned Fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland) – Systematic Palaeontology with Notes on Functional Morphology and Palaeoecology. *Schweizerische Palaontologische Abhandlungen (Mémoires suisses de Paléontologie, Memorie svizzere di Paleontologia)*, 114, 1–164.
- Butler, R. J., Jones, A. S., Buffetaut, E., Mandl, G. W., Scheyer, T. M., and Schultz, O. (2019). Description and phylogenetic placement of a new marine species of phytosaur (Archosauriformes: Phytosauria) from the Late Triassic of Austria. *Zool. J. Linnean Soc.*, 187, 198–228.
- Cavin, L. (2017). *Freshwater Fishes - 250 Million Years of Evolutionary History*. ISTE Press, Elsevier, London, Oxford, UK.
- Cope, E. D. (1887). Geology and palaeontology - Zittel's manuel of palaeontology. *Am. Naturalist*, 21, 1014–1019.
- Dahoumane, A., Nedjari, A., Aït-Ouali, R., Taquet, P., Vacant, R., and Steyer, J.-S. (2016). A new Mastodonsauroid Temnospondyl from the Triassic of Algeria: implications for the biostratigraphy and palaeoenvironments of the Zarzaïtine Series, Northern Sahara. *C. R. Palevol.*, 15, 918–926.
- Dutuit, J.-M. (1976). Introduction à l'étude paléontologique du Trias continental marocain. *Mem. M.N.H.N., nouvelle série (C), Sciences de la Terre*, 36, 1–253.
- Egerton, P. M. d. G. (1854). On a fossil fish from the Upper Beds of the New Red Sandstone at Bromsgrove, Palichthyologic notes, No. 6. *Quart. J. Geol. Soc. Lond.*, 10, 367–371.
- Feys, R. and Greber, C. (1963). Le Stéphanien et l'Autunien du Souss dans les Ida ou Zal (Haut-Atlas occidental – Maroc). *Notes et Mem. Serv. Geol. Maroc*, 22, 19–35.
- Frickhinger, K. A. (1995). *Fossil Atlas Fishes*. Mergus, Melle, Germany.
- Gall, J. C., Grauvogel, L., and Lehman, J. P. (1974). Faune du Buntsandstein. V. - Les poissons fossiles de la collection Grauvogel-Gall. *Ann. Paléontol. (Vertébrés)*, 60, 129–147.
- Gall, J.-C. and Grauvogel-Stamm, L. (2005). The early Middle Triassic 'Grès à Voltzia' Formation of eastern France: a model of environmental refugium. *C. R. Palevol.*, 4, 637–652.
- Gibson, S. Z. (2018). A new species of *Lasalichthys* (Actinopterygii, Redfieldiiformes) from the Upper Triassic Dockum Group of Howard County, Texas, with revisions to the genera *Lasalichthys* and *Synorichthys*. *J. Vert. Paleontol.*, 38, article no. e1513009.
- Gouiric-Cavalli, S., Zavattieri, A. M., Gutierrez, P. R., Cariglino, B., and Balarino, L. (2017). Increasing the fish diversity of the Triassic faunas of Gondwana: a new redfieldiiform (Actinopterygii) from the Middle Triassic of Argentina and its palaeobiogeographical implications. *Pap. Palaeontol.*, 3, 559–581.
- Haughton, S. H. (1934). 3. On some Karroo fishes from Central Africa. *Ann. South Afr. Mus.*, 31, 97–104.
- Hutchinson, P. (1973a). A revision of the redfieldiiform and perleidiiform from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). *Bull. Br. Mus. (Nat. Hist.), Geol.*, 22, 233–354.
- Hutchinson, P. (1973b). *Pseudobeaconia*, a perleidiiform fish from the Triassic Santa Clara Formation, Argentina. *Breviora*, 398, 1–24.
- Hutchinson, P. (1978). The anatomy and phylogenetic position of *Helichthys*, a redfieldiiform fish from the Triassic of South Africa. *Paleontology*, 21(4), 881–891.
- Jalil, N.-E. (1999). Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. *J. Afr. Earth Sci.*, 29, 219–226.
- Jalil, N.-E. and Janvier, P. (2005). Les pareiasaures (Amniota, Parareptilia) du Permien supérieur du Bassin d'Argana, Maroc. *Geodiversitas*, 27, 35–132.
- Jalil, N.-E. and Peyer, K. (2007). A new rauisuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco. *Palaeontology*, 50, 417–430.
- Jörg, E. (1969). Eine Fischfauna aus dem Oberen Buntsandstein (Unter-Trias) von Karlsruhe-Durlach (Nordbaden). *Beiträge zur naturkundlichen Forschung in Südwestdeutsch-*

- land*, 28, 87–102.
- Jubb, R. A. and Gardiner, B. G. (1975). A preliminary catalogue of identifiable fossil fish material from Southern Africa. *Ann. South Afr. Mus.*, 67, 381–440.
- Khaldoune, F., Germain, D., Jalil, N.-E., and Steyer, J.-S. (2017). Les vertébrés du Permien et du Trias du Maroc (Bassin d'Argana, Haut Atlas occidental) : fenêtre ouverte sur l'évolution autour de la grande crise fini-paléozoïque. In Zouhri, S., editor, *Paléontologie des vertébrés du Maroc : état des connaissances*, Mem. Soc. geol. France, nouvelle série, 180, pages 103–166. La Société Géologique de France, Paris.
- Khalloufi, B., Brito, P. M. M., Cavin, L., and Dutheil, D. B. (2017). Revue des ichthyofaunes mésozoïques et cénozoïques marocaines. In Zouhri, S., editor, *Paléontologie des vertébrés du Maroc : état des connaissances*, Mem. Soc. geol. France, nouvelle série, 180, pages 167–248. La Société Géologique de France, Paris.
- Kim, S.-H., Lee, Y.-N., Park, J.-Y., Lee, S., and Lee, H.-J. (2020). The first record of redfieldiiform fish (Actinopterygii) from the Upper Triassic of Korea: implications for paleobiology and paleobiogeography of Redfieldiiformes. *Gondwana Res.*, 80, 275–284.
- Klein, H., Voigt, S., Hminna, A., Saber, H., Schneider, J., and Hmich, D. (2010). Early triassic archosaur-dominated footprint assemblage from the Argana basin (Western High Atlas, Morocco). *Ichnos*, 17, 215–227.
- Koning, G. d. (1957). *Géologie des Ida-ou-Zal (Maroc). Stratigraphie, pétrographie et tectonique de la partie SW du bloc occidental du Massif ancien du Haut Atlas*. PhD thesis, Leide University, Leide. 209 p.
- Lagnaoui, A., Klein, H., Voigt, S., Hminna, A., Saber, H., Schneider, J. W., and Werneburg, R. (2012). Late Triassic Tetrapod-Dominated Ichnoassemblages from the Argana Basin (Western High Atlas, Morocco). *Ichnos*, 19, 238–253.
- Lombardo, C. (1995). *Perleidus altolepis* (Actinopterygii, Perleidiformes) from the Kalkschieferzone of Ca' Del Frate (N. Italy). *Geobios M.S.*, 19, 211–213.
- Lombardo, C. (2013). A new basal actinopterygian fish from the Late Ladinian of Monte San Giorgio (Canton Ticino, Switzerland). *Swiss J. Geosci.*, 106, 219–230.
- Lombardo, C. and Brambillasca, F. (2005). A new perleidiform (Actinopterygii, Osteichthyes) from the Late Triassic of Northern Italy. *Bollettino della Società Paleontologica Italiana*, 44, 25–34.
- Lombardo, C., Rusconi, M., and Tintori, A. (2008). New perleidiform from the Lower Ladinian (Middle Triassic) of the northern Grigna (Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 114, 263–272.
- Lombardo, C. and Tintori, A. (2004). New perleidiforms from the Triassic of the Southern Alps and the revision of *Serrolepis* from the Triassic of Württemberg (Germany). In Arratia, G. and Tintori, A., editors, *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*, pages 179–196. Verlag Dr. Friedrich Pfeil, München, Germany.
- López-Arbarello, A. (2004). The record of Mesozoic fishes from Gondwana (excluding India and Madagascar). In Arratia, G. and Tintori, A., editors, *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*, pages 597–624. Verlag Dr. Friedrich Pfeil, München, Germany.
- López-Arbarello, A., Rauhut, O., and Cerdeño, E. (2010). The Triassic fish faunas of the Cuyana Basin, Western Argentina. *Palaeontology*, 53, 249–276.
- López-Arbarello, A. and Zavattieri, A. M. (2008). Systematic revision of *Pseudobeaconia* Bordas, 1944, and *Mendocinichthys* Whitley, 1953 (Actinopterygii: 'Perleidiformes') from the Triassic of Argentina. *Palaeontology*, 51, 1025–1052.
- Marramà, G., Lombardo, C., Tintori, A., and Carnevale, G. (2017). Redescription of 'Perleidus' (Osteichthyes, Actinopterygii) from the Early Triassic of northwestern Madagascar. *Rivista Italiana di Paleontologia e Stratigrafia*, 123, 219–242.
- Martin, M. (1979a). Actinoptérygiens, Dipneustes et Crossoptérygiens du Trias Continental supérieur marocain. Thèse de 3e cycle, Université Paris VII, Paris. 121 p.
- Martin, M. (1979b). *Arganodus atlantis* et *Ceratodus arganensis*, deux nouveaux Dipneustes du Trias supérieur continental marocain. *C. R. Acad. Sci. Paris D*, 289, 89–92.
- Martin, M. (1980a). *Dipteronotus gibbosus* (Actinopterygii, Chondrostei), nouveau colobodontidé du Trias supérieur continental maro-

- cain. *Geobios*, 13, 445–449.
- Martin, M. (1980b). *Mauritanichthys rugosus* n. gen. et n. sp., Redfieldiidae (Actinopterygi, Chondrostei) du Trias supérieur continental marocain. *Geobios*, 13, 437–440.
- Martin, M. (1981). Les Dipneustes et Actinistiens du Trias supérieur continental marocain. *Stuttgarter Beiträge zur Naturkunde, B (Geologie und Paläontologie)*, 69, 1–29.
- Martin, M. (1982). Les actinoptérygiens (Perleidiformes et Redfieldiiformes) du Trias supérieur continental du couloir d'Argana (Atlas occidental, Maroc). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 162, 352–372.
- Medina, F., Vachard, D., Colin, J.-P., Ouarhache, D., and Ahmamou, M. F. (2001). Charophytes et ostracodes du niveau carbonaté de Taourirt Imzilen (Membre d'Aglegal, Trias d'Argana); implications stratigraphiques. *Bulletin de l'Institut Scientifique, Rabat, section Sciences de la Terre*, 23, 21–26.
- Mickle, K. E. (2015). Identification of the Bones of the Snout in Fossil Lower Actinopterygians -A New Nomenclature Scheme Based on Characters. *Copeia*, 103, 838–857.
- Milner, A. R., Gardiner, B. G., Fraser, N. C., and Taylor, M. A. (1990). Vertebrates from the Middle Triassic Otter Sandstone Formation of Devon. *Palaeontology*, 33, 873–892.
- Murray, A. M. (2000). The Palaeozoic, Mesozoic and Early Cenozoic fishes of Africa. *Fishes Fisheries*, 1, 111–145.
- Olivier, C., Battail, B., Bourquin, S., Rossignol, C., Steyer, J. S., and Jalil, N.-E. (2019). New dicynodonts (Therapsida, Anomodontia) from near the Permo-Triassic boundary of Laos: implications for dicynodont survivorship across the Permo-Triassic mass extinction and the paleobiogeography of Southeast Asian blocks. *J. Vert. Paleontol.*, 39, e1584745.
- Romano, C., Koot, M. B., Kogan, I., Brayard, A., Minikh, A. V., Brinkmann, W., Bucher, H., and Kriwet, J. (2016). Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biol. Rev.*, 91, 106–147.
- Schaeffer, B. (1956). Evolution of the Subholostean fishes. *Evolution*, 10, 201–212.
- Schaeffer, B. (1967). Late Triassic fishes from the Western United States. *Bull. Amer. Museum Natural History, New York*, 135, 285–342.
- Schaeffer, B. (1984). On the relationships of the Triassic-Liassic redfieldiiform fishes. *Am. Mus. Novitates*, 2795, 1–18.
- Schaeffer, B. and Mc Donald, N. (1978). Redfieldiid fishes from the Triassic-Liassic Newark Supergroup of eastern North America. *Bull. Am. Mus. Nat. Hist., New York*, 159, 129–174.
- Schultze, H. P. (2008). Nomenclature and homologization of cranial bones in actinopterygians. In Arratia, G., Schultze, H. P., and Wilson, M. V. H., editors, *Mesozoic Fishes 4 – Homology and Phylogeny*, pages 23–48. Verlag Dr. Friedrich Pfeil, München, Germany.
- Steyer, J. S., Damiani, R., Sidor, C. A., O'Keefe, F. R., Larsson, H. C. E., Maga, A., and Ide, O. (2006). The vertebrate fauna of the Upper Permian of Niger. IV. *Nigerpeton ricqlesi* (Temnospondyli: Cochleosauridae), and the Edopoid Colonization of Gondwana. *J. Vert. Paleontol.*, 26, 18–28.
- Sun, Z., Lombardo, C., Tintori, A., Jiang, D., Hao, W., Sun, Y., and Lin, H. (2012). *Fuyuanperleidus dengi* Geng et al., 2012 (Osteichthyes, Actinopterygii) from the Middle Triassic of Yunnan Province, South China. *Rivista Italiana di Paleontologia e Stratigrafia*, 118, 359–373.
- Sun, Z., Tintori, A., Jiang, D., Lombardo, C., Rusconi, M., Hao, W., and Sun, Y. (2009). A New Perleidiform (Actinopterygii, Osteichthyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geol. Sin.*, 8, 460–470.
- Sun, Z., Tintori, A., Jiang, D., and Motani, R. (2013). A new perleidid from the Spathian (Olenekian, Early Triassic) of Chaohu, Anhui Province, China. *Rivista Italiana di Paleontologia e Stratigrafia*, 119, 275–285.
- Sytchevskaya, E. K., Anderson, H. M., and Anderson, J. M. (2009). Late Triassic fishes of South Africa. In Shishkin, M. A. and Tverdokhlebov, V. P., editors, *Researches on paleontology and biostratigraphy of ancient continental deposits (Memories of Professor Vitalii G. Ochev)*, pages 197–215. Nauchnaya Kniga, Saratov.
- Tintori, A. (1990). *Dipteronotus olgiatii* n. sp. (Actinopterygii, Perleidiformes) from the Kalkschieferzone of Ca' Del Frate (N. Italy) (Preliminary note). *Atti Ticinensi di Scienze della Terra*, 33, 191–197.
- Tintori, A. and Lombardo, C. (1996). *Gabanellia agilis* gen. n. sp. n., (Actinopterygii, Perleidiformes) from

- the Calcare di Zorzino of Lombardy (North Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 102, 227–236.
- Tintori, A., Lombardo, C., and Kustatscher, E. (2016). The Pelsonian (Anisian, Middle Triassic) fish assemblage from Monte Prà della Vacca/Kühwiesenkopf (Braies Dolomites, Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 282, 181–200.
- Tixeront, M. (1973). Lithostratigraphie et minéralisations cuprifères et uranifères stratiformes, syn-génétiques et familières des formations détritiques permotriassiques du couloir d'Argana, Haut-Atlas occidental (Maroc). *Notes et Mem. Serv. Geol. Maroc*, 249, 147–177.
- Tixeront, M. (1974). Carte géologique et minéralisations du Couloir d'Argana. *Notes et Mem. Serv. Geol. Maroc*, 205.
- Tourani, A. and Benaouiss, N. (2009). Depositional and climatic settings of the Upper Triassic temnospondyl-bearing strata of the Irohalene mudstone in Argana Basin (Western High Atlas, Morocco). In *1er Congrès International sur la Paléontologie des Vertébrés du Nord de l'Afrique, Marrakesh, Morocco*. Abstract book, 34.
- Tourani, A., Benaouiss, N., Gand, G., Bourquin, S., Jalil, N.-E., Broutin, J., Battail, B., Germain, D., Khaldoune, F., Sebban, S., Steyer, J.-S., and Vancant, R. (2010). Evidence of an Early Triassic age (Olenekian) in Argana Basin (High Atlas, Morocco) based on new chirotherioid traces. *C. R. Palevol.*, 9, 201–208.
- Tourani, A., Lund, J. J., Benaouiss, N., and Gaupp, R. (2000). Stratigraphy of Triassic syn-rift deposition in Western Morocco. In Bachmann, G. H. and Lerche, I., editors, *Epicontinental Triassic, Volume 2 - International Symposium Halle, 21.-23, September 1998*, pages 1193–1215. Schweizerbart Science Publishers, Stuttgart, Germany.
- Wade, T. T. (1935). *The Triassic fishes of Brookvale, New South Wales*. British Museum (Natural History), London, England.
- Wiley, E. O. (2008). Homology, identity and transformation. In Arratia, G., Schultze, H. P., and Wilson, M., editors, *Mesozoic Fishes 4 - Homology and phylogeny*, pages 9–21. Verlag Dr. Friedrich Pfeil, München, Germany.
- Woodward, A. S. (1910). On *Dipteronotus cyphus*, Egerton. A ganoid fish from the Lower Keuper of Bromsgrove, Worcestershire. *Proc. Geol. Assoc.*, 21, 322–323.
- Xu, G.-H. (2020). A new stem-neopterygian fish from the Middle Triassic (Anisian) of Yunnan, China, with a reassessment of the relationships of early neopterygian clades. *Zool. J. Linnean Soc.*, zlaa053, 1–20.
- Zouheir, T., Hminna, A., Klein, H., Lagnaoui, A., Saber, H., and Schneider, J. W. (2020). Unusual archosaur trackway and associated tetrapod ichnofauna from Irohalene member (Timezgadiouine formation, Late Triassic, Carnian) of the Argana Basin, Western High Atlas, Morocco. *Hist. Biol.*, 32, 589–601.