

## REDESCRIPTION AND PHYLOGENETIC RELATIONSHIPS OF *ARGYROPELECUS LOGEARTI* (TELEOSTEI: STOMIIFORMES: STERNOPTYCHIDAE), WITH A BRIEF REVIEW OF FOSSIL *ARGYROPELECUS*

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**Key-words:** Stomiiformes, Sternoptychidae, *Argyropelecus logearti*, redescription, phylogenetic relationships, Miocene, Mediterranean.

**Abstract.** *Argyropelecus logearti* Arambourg, 1929 is redescribed in detail based on new material. The material consists of many previously unreported specimens from type and other localities. Based on new information presented here *Argyropelecus logearti* is interpreted to be most closely related to the extant species *Argyropelecus hemigymnus*. *Argyropelecus logearti* provides an early fossil that can be placed in the phylogenetic context of living *Argyropelecus* species.

*Argyropelecus* has a fossil record ranging from Oligocene to Pleistocene. Fossil representatives of this genus are listed here for future reference.

**Riassunto.** Viene ridescritto in dettaglio, sulla base di nuovi reperti, *Argyropelecus logearti* Arambourg, 1929. I nuovi reperti provengono dalla località tipo Sidi-Brahim (Algeria) e da due nuove località: Renault (Algeria) e Torricella Peligna (Italia centrale). Alla luce delle nuove osservazioni morfologiche qui presentate, *Argyropelecus logearti* viene considerato il sister taxon della specie *Argyropelecus hemigymnus*. *Argyropelecus logearti* rappresenta la prima specie fossile ad essere integrata in uno studio filogenetico effettuato sui congenerici viventi.

La documentazione fossile del genere *Argyropelecus*, che si estende dall'Oligocene al Pleistocene, viene inoltre analizzata criticamente.

### Introduction

*Argyropelecus logearti* was described by Arambourg (1929) based on two well preserved, but incomplete, specimens collected from the Miocene sediments of northern Algeria. Several specimens were successively collected from northern Algeria and, more recently, another specimen from central Italy has been found by the Italian fossil collector Erminio Di Carlo, and donated to the Museo Geo-Paleontologico dell'Alto Aventino. Recently, during a visit to the paleontological institute of the Muséum National d'Histoire Naturelle in Paris, the Arambourg's type specimens were re-examined, together with the still undescribed *Argyropelecus*

*logearti* material. Based on these newly reported fossils, some previously unreported information on this species was uncovered.

The objective of this study is to redescribe *Argyropelecus logearti* in more detail than previously known. The fossil described below was compared to other fossil and living congeners and placed within the phylogenetic interpretation of Harold (1993).

*Argyropelecus* species represent a group of oceanic fishes, inhabiting the mesopelagic zone, with a fossil record ranging from Oligocene to Pleistocene. The genus *Argyropelecus* was described by Cocco (1829) from a sample of "mare sporco" from the Strait of Messina which included the type species, *A. hemigymnus* Cocco, 1829. Since that time, six other valid living species have been described and many fossils have been found. The extant species include the following: *Argyropelecus aculeatus* Valenciennes, in Cuvier and Valenciennes, 1850, *Argyropelecus affinis* Garman, 1899, *Argyropelecus gigas* Norman, 1930, *Argyropelecus lychnus* Garman, 1899, *Argyropelecus olfersi* (Cuvier, 1829), and *Argyropelecus sladeni* Regan, 1908.

Many authors (e. g. Baird 1971, Weitzman 1974) have been surveyed the anatomy and systematics of *Argyropelecus* species. Harold (1993) was the first to provide a cladistic study of interrelationships among *Argyropelecus* species.

According to Baird (1971), *A. aculeatus*, *A. affinis*, *A. gigas*, *A. hemigymnus*, and *A. sladeni* occur in the Atlantic, Pacific and Indian Oceans, while *A. olfersi* occurs in the Atlantic and Pacific Oceans, and *A. lychnus* is geographically restricted to the eastern Pacific Ocean. *Argyropelecus hemigymnus* is the only species that occurs in the Mediterranean Sea.

Several aspects of population biology (Baird et al. 1990; Jumper & Baird 1991) and trophodynamics (Hopkins & Baird 1973, 1985) of these fishes have been inves-

tigated. Following the trophic classification of Gartner et al. (1997), these fishes could be included in the hard-bodied zooplanktivore guild. The diet of *Argyropelecus* species mainly comprises copepods, ostracods, amphipods, euphysiids, and planktonic molluscs. Although some of the extant species show a sympatric distribution, the competitive interactions may be reduced by the occurrence of different feeding strategies (Hopkins & Baird 1985).

### Materials and methods.

**Materials examined.** *Argyropelecus aculeatus* Valenciennes. One whole specimen preserved in alcohol (MPP, uncatolgued) from the Atlantic coasts of Morocco.

*Argyropelecus hemigymnus* Cocco. One whole dried and one skeletonized specimen (MPP, uncatolgued) from the Messina Strait. Also, one articulated skeleton (MPP 2.10.(2)) from the Pleistocene of Vrica, Calabria, Southern Italy.

*Argyropelecus logearti* Arambourg. Seventeen articulated skeletons from the late Miocene of two localities near Oran, Algeria (MNHN ORA268 d+g, Sidi-Brahim, holotype; MNHN ORA269, Sidi-Brahim, paratype; MNHN ORA270, Sidi-Brahim, paratype; MNHN ORA271, Sidi-Brahim; MNHN ORA769 d+g, Renault, paratype; MNHN ORA770 d+g, Renault; MNHN ORA771, Renault, paratype; MNHN ORA772 d+g, Renault, paratype; MNHN ORA773 d+g, Renault; MNHN ORA774 d+g, Renault; MNHN ORA1074 d+g, Renault, paratype; MNHN ORA1284; MNHN ORA1289, Renault; MNHN ORA1290, Renault; MNHN ORA1292, Renault; MNHN ORA1293 d+g, Renault; MNHN ORA1294, Renault). Also, one articulated skeleton (MGPA TOR001, paratype) from the middle Miocene of Torricella Peligna, Abruzzo, Central Italy.

**Methods.** Counts and measurements were made following Landini & Menesini (1978). SL=Standard length.

**Institutional abbreviations.** MGPA, Museo Geopaleontologico dell'Alto Aventino, Palena, Italy; MNHN, Muséum National d'Histoire Naturelle (Institut de Paléontologie), Paris, France; MPP, Dipartimento di Scienze della Terra and Museo di Storia Naturale e del Territorio, Università di Pisa, Pisa, Italy.

**Anatomical abbreviations.** Osteological terms mostly follow Weitzman (1974) and Fink & Weitzman (1982). Choice of abbreviations mostly follows Grande & Bemis (1998). ang, angular; appg, anterior process of pelvic girdle; br, branchiostegal rays; cha, anterior ceratohyal (=ceratohyal, see Nelson 1969); chp, posterior ceratohyal (=epihyal, Nelson 1969); cl, cleithrum; cor, coracoid; d, dentary; dsf, dorsal fin rays; ep, epural; ept, ectopterygoid; fr, frontal; hs, haemal spines; iop, interopercle; ip, ischial process of pelvic girdle; is, iliac spine (=postabdominal spine); h, hyomandibula; hyp, hypural; mpt, metapterygoid; msp, mesopterygoid; mx, maxilla; ns, neural spines; op, opercle; pa, parietal; pal, palatine; pas, parasphenoid; pcf, pectoral fin rays; phy, parhypural; pmx, premaxilla; pop, preopercle; pr, dorsal fin pterygiophores; pro, prootic; psmx, posterior supramaxilla; pto, pterotic; pts, pterosphenoid; pup, pubic

process of pelvic girdle; q, quadrate; ra, radials; sca, scapula; se, supraethmoid; smx, supramaxilla; sn, supra-neurals; sop, subopercle; spo, sphenotic; ssa, modified scale; sym, symplectic; un, uroneural; vo, vomer.

### Systematic paleontology

Subdivision **Teleostei** (sensu Patterson & Rosen, 1977)

Order Stomiiformes (sensu Harold & Weitzman, 1996)

Infraorder Gonostomata (sensu Harold, 1998)

Family Sternoptychidae (sensu Weitzman, 1974)

Genus *Argyropelecus* Cocco, 1829

***Argyropelecus logearti* Arambourg, 1929**

(Figs. 1 to 9A)

1929 *Argyropelecus logearti* Arambourg, pp. 11-15, pls. 1-3, figs. 1-2.

**Holotype.** MNHN ORA268 d+g, impression of nearly complete skeleton (d, right side counterpart; g, left side counterpart).

**Referred Specimens.** See above in materials examined section.

**Etymology.** The specific epithet "logearti" honours Mr. M. Logeart who donated the holotype to Camille Arambourg.

**Locality and Horizon.** *Argyropelecus logearti* is an oceanic species restricted to the Middle-Upper Miocene of the Mediterranean area.

The type locality is the Upper Miocene biosiliceous sediments of Sidi-Brahim, near Oran, northern Algeria (Arambourg 1929). Furthermore, several specimens were collected in analogous Upper Miocene sediments near Renault, Algeria. The ichthyoliferous sediments consist of laminated diatomites of Messinian age (see e.g., Cornée et al. 1994) that were deposited in response to coastal upwelling. The associated fauna comprises other sternoptychids, myctophids, clupeids, bregmacerotids, and paralepidids (Arambourg 1927).

An additional specimen has been recently collected in the sapropelitic laminites of the Tuffillo structural unit (sensu Patacca et al. 1992), near the town of Torricella Peligna (Carnevale, in prep.), Abruzzo, central Italy. Based on planktonic foraminifera and calcareous nannofossil content, the sediments date back to the Middle Miocene, Serravallian (Carnevale et al. 2001). The associated fauna consists primarily of gonostomatids, paralepidids, myctophids, stomiids, and gadiforms, representing a mesopelagic assemblage.

**Emended diagnosis.** *Argyropelecus logearti* differs from other *Argyropelecus* species by the following combination of characters: (1) it has a single postabdominal spine and a narrow body trunk, as in *A. hemigymnus*; (2) it differs from *A. hemigymnus* in having a heavily developed dorsal blade, strong deepening of the cephalic-abdominal portion of the body, well developed parietal, maximum body size attained more than 40 mm SL, and only the posteriormost proximal radial of the dorsal fin cartilaginous in adults.

**Description.** Counts and measurements for *Argyropelecus logearti* are summarized in Tab. 1 and 2. Although the specimens are about 5 cm or less in standard length, they appear to be adults based on the strong ossification of most skeletal elements. Unfortunately, all the specimens examined are incomplete, but, because of the conspicuous number of specimens, it was still possible to infer the outline of the body. The outline of the body

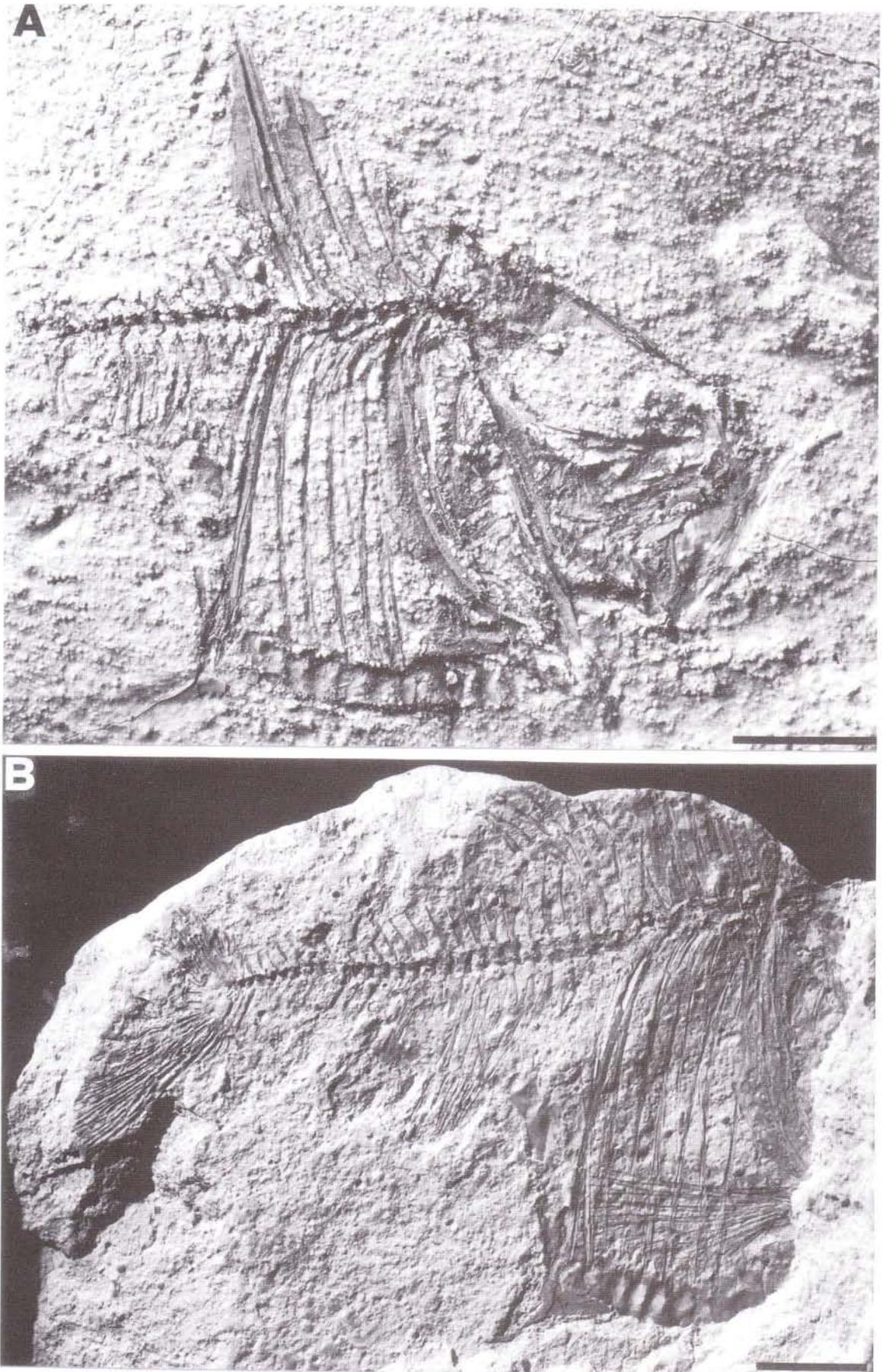


Fig. 1 - *Argyropelecus logearti* Arambourg, from the Miocene of the Mediterranean area. A, holotype, MNHN ORA268g, right side, lateral view. B, paratype MNHN ORA772g, right side, lateral view. Scale bar 5 mm.

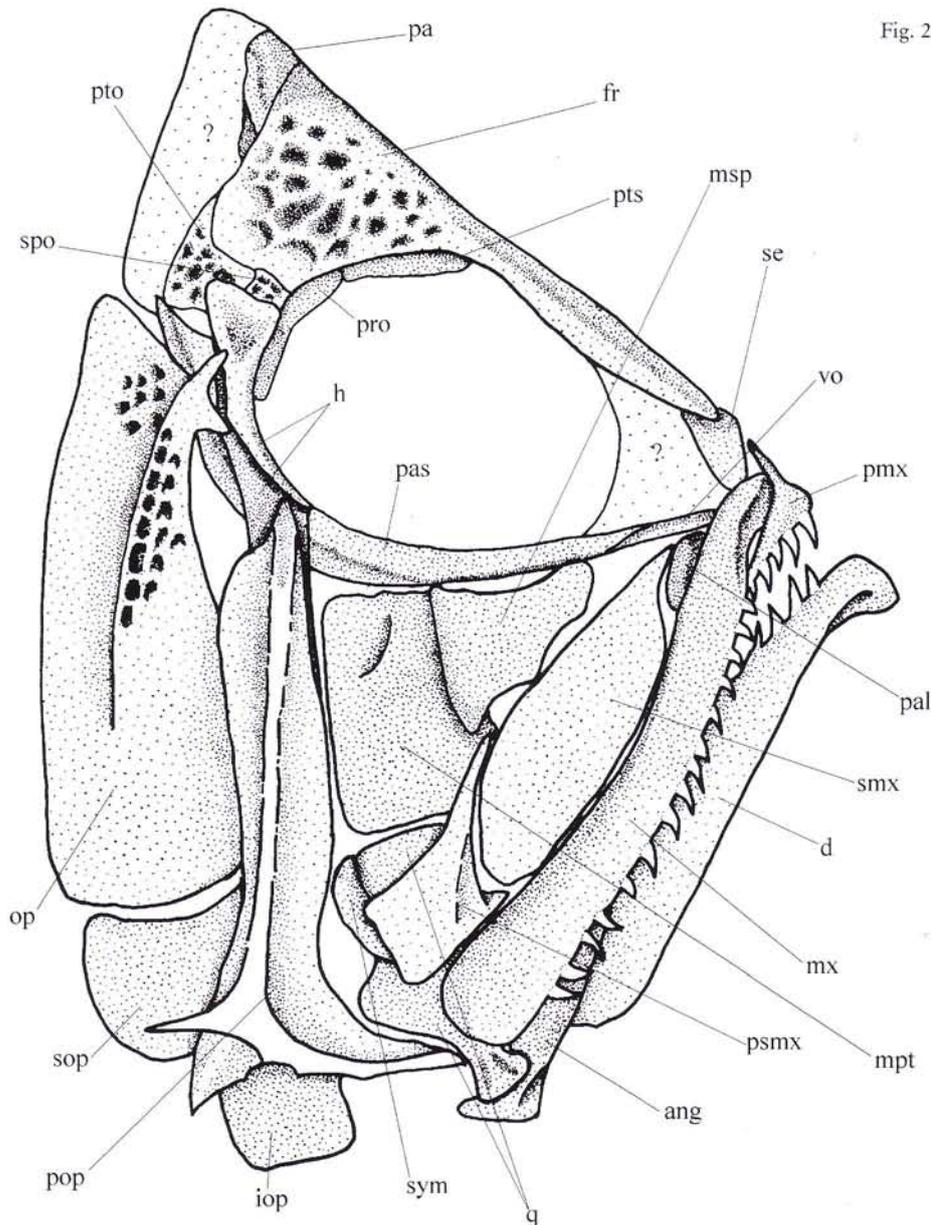


Fig. 2 - *Argyropelecus logearti* Arambourg, restoration of the skull, right side, lateral view.

(Fig. 1) is very similar to that of some other members of the genus *Argyropelecus*, such as *A. aculeatus*, *A. olfersi* and *A. lychnus*. The body trunk, that is, the region posterior to the anal fin origin, is narrow, similar to that of *A. hemigymnus*. The cephalic-abdominal portion of the body is hypertrophied, discoid in outline, with a heavily developed dorsal blade. The head is well developed in length and depth with respect to the whole cephalic-abdominal portion of the body.

The general outline of the neurocranium (Fig. 2) is clearly recognizable in the holotype MNHN ORA268. The braincase is very small. Some bones in the otic and ethmoid regions of the skull are crushed and difficult to interpret. The frontal bones are the largest bones of the skull roof. These bones are heavily pitted and have a developed, vertically oriented, median longitudinal ridge with a smooth dorsal profile. Located anterior to the frontals is a small subrectangular supraethmoid. Posterior to and sutured to the frontals are the parietals. These bones have a dorsal longitudinal crest

that is continuous with the posterior part of the longitudinal frontal crest. This crest continues laterally on the surface of the parietals. The lateral border of the parietal does not contact the sphenotic, but approaches the antero-dorsal portion of the pterotic. This feature is also observed by Baird (1971) in *A. hemigymnus* and by Weitzman (1974) in *A. aculeatus* but not in *A. affinis* and *A. gigas*. Just ventral to the posterior part of the frontals are the pterotic and the sphenotic. These bones are extensively pitted on the surface. The parasphenoid is strongly arched, similar to that described by Weitzman (1974) on *A. aculeatus*. According to Weitzman (1974) this shape may be correlated with the large dimensions of the eyes, the depth of the head and the absence of the otic bullae. The parasphenoid bears a ventral keel extending posteriorly beyond the point of dorsal inflection. This feature is recognized as a synapomorphy of the genus *Argyropelecus*. As for many other species of the genus *Argyropelecus* (*A. aculeatus*, *A. hemigymnus*, *A. lychnus*, *A. olfersi* and *A. sladeni*), the dorsal limb of the

parasphenoid is nearly as long as the ventroanterior limb. Toward the anterior end of the parasphenoid the vomer is visible.

The orbital bones are not preserved in any of the examined specimens.

The mouth is strongly oblique and heavily toothed. The premaxilla is a small bone with a relatively well-developed ascending process. An elongated ascending process is characteristic of *Argyropelecus* and is also present in *Polyipnus* (Harold 1994). The maxillae constitute most of the biting surface of the upper jaw. Like the other bones of the jaw, the maxilla bears small pointed teeth that are round in cross section. Above the dorsal limb of the maxilla there are two supramaxillary bones. The anterior supramaxilla is very large, ovoid in outline, whereas the posterior is nearly square with a long antero-dorsal process. The lower jaw of *A. logearti* is composed of the dentary and anguloarticular. The lower jaw dentition is similar to that of the maxilla and premaxilla. The dentary has a small symphyseal process.

The suspensorium of *A. logearti* consists of the hyomandibula, quadrate, symplectic, metapterygoid, mesopterygoid and palatine. A long and slender ectopterygoid is visible on MGPA TOR001. The outline of the hyomandibula is partially obscured by other bones, but its dorsal portion is clearly visible. The hyomandibula bears an anteriorly directed spine. Many recent *Argyropelecus* species show an association between hyomandibular spine and metapterygoid (Weitzman 1974). The metapterygoid of *A. logearti* lacks the posterior-dorsal spine associated with the hyomandibular spine. The quadrate is subtriangular and elongate. The symplectic is nearly clavate in outline.

The opercular bones are vertically elongate, similar to those of other *Argyropelecus* species. The opercle is subrectangular in outline, whereas the subopercle is subtriangular. The interopercle is nearly of the same size of the subopercle. The preopercle consists of an elongate dorsal arm at right angle to a short ventral, anterior arm. A lamella of bone, covering the laterosensory canal, courses the entire length of the preopercle. The preopercle bears a robust posteriorly-directed spine ventrally. Just above the posteriorly-directed spine is a small outward hooked spine that originates on the lamella of bone covering the laterosensory canal. This spine, likewise in *A. hemigymnus*, extends beyond the posterior edge of the preopercle. This feature makes *A. logearti* different from *A. aculeatus*, *A. affinis*, *A. gigas* and *A. olfersi*, whose upper spine not extends beyond the posterior edge of the preopercle.

The anterior portion of a posterior ceratohyal and the posterior part of an anterior ceratohyal bearing three branchiostegal rays are preserved on MGPA TOR001 (Fig. 3). Some branchiospines are preserved on the holotype.

The number of vertebrae in *A. logearti* is 38. A

similar vertebral number is also observed in *A. affinis*, *A. bullockii*, *A. gigas*, *A. hemigymnus*, and *A. olfersi*. The two anteriormost vertebrae bear no ribs, whereas the third bears a slender rib. There are 7 pairs of autogenous ribs articulating with the transverse processes of the 4<sup>th</sup> through 10<sup>th</sup> vertebrae. The ribs are deep and compressed as in *A. aculeatus*, *A. cosmovicii*, *A. hemigymnus*, *A. lychnus*, *A. olfersi*, *A. sladeni* and possibly *A. bullockii*. The seventh rib bears a dorsally directed spine-like process on the dorsal surface; this feature is visible only in MGPA TOR001. Two slender autogenous ribs are articulated with the 11<sup>th</sup> and 12<sup>th</sup> vertebrae. The nine anterior neural spines are separate in vertebrae. The neural spines beyond the 9<sup>th</sup> vertebra and the haemal spines beyond the 12<sup>th</sup> vertebra are expanded in the median plane and strongly spatulate. This degree of expansion is similar to that of *A. aculeatus*, *A. cosmovicii*, *A. hemigymnus*, *A. lychnus*, *A. olfersi* and *A. sladeni*. There are traces of poorly preserved epineural intermuscular bones fused at the base of the anterior neural spines.

The caudal fin is forked, with subequal lobes. The number of caudal fin rays is 32. *A. logearti* exhibits the typical *Argyropelecus* caudal skeleton (see e.g., Weitzman 1974) (Fig. 4). The first preural centrum and the ural centra are fused. The six hypurals and the parhypural are autogenous. The first and the second hypurals are fused to each other. Co-ossification of first and second hypurals is also observed in *A. aculeatus*, *A. hemigymnus*, *A. lychnus*, *A. olfersi* and *A. sladeni*. There is one flat and expanded epural. The parhypural bears a spine on its dorso-lateral surface.

The dorsal fin in *A. logearti* consists of eight soft rays supported by seven pterygiophores. As in other *Argyropelecus* species, the posterior pterygiophore (8<sup>th</sup>) was probably cartilaginous. *A. logearti* has eight supraneurals (Fig. 5). The anterior supraneural is unmodified, showing the plesiomorphic condition of more primitive sternoptychids. The remainder are of the advanced type (Weitzman 1974) and constitute the so-called dorsal blade. The supraneural morphology of *A. logearti* is very similar to that of *A. aculeatus*. As in other *Argyropelecus* species, the seventh and the eighth supraneurals are fused to each other from their distal extremity to the distal tip of their shared neural spine. The modified supraneurals (dorsal blade) of *A. logearti*, and in particular the posterior two, are strongly expanded and compressed as in *A. aculeatus* and *A. hemigymnus*. Fused supraneurals 7 and 8 have an external posterior process that bear paired wing-like processes. The situation in *A. aculeatus* and *A. hemigymnus* is similar to that of *A. logearti*. The triangular posterior process of the dorsal blade is short and leaves a gap between the posterior margin of the supraneurals and the dorsal fin. A similar condition is observed in *A. affinis*, *A. gigas*, *A. hemigymnus*, *A. aculeatus*, and possibly *A. cosmovicii*.

The anal fin of *A. logearti* consists of eleven (6+5)

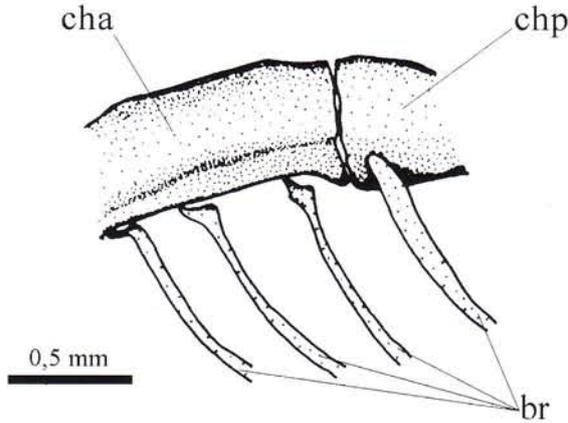


Fig. 3 - *Argyropelecus logearti* Arambourg, part of the hyoid apparatus, left side, lateral view, MGPA TOR001.

soft rays. The fin is supported by ten pterygiophores (Fig. 6). A similar anal fin pattern is reported for *A. hemigymnus* (Schultz 1964; Weitzman 1974). The two pterygiophores (6<sup>th</sup> and 7<sup>th</sup>) bordering the anal fin hiatus exhibit medial flattened processes that contact one another (synapomorphy of *A. aculeatus*, *A. hemigymnus*, *A. lychnus*, *A. olfersi* and *A. sladeni*; Harold 1993). These two pterygiophores bear small spinous processes in their distal ends.

The pectoral fin of *A. logearti* has nine soft rays that articulate with four radials. The pectoral girdle of *A. logearti* is similar to that of other *Argyropelecus* species (Fig. 7). The posttemporal + supracleithrum is clearly visible on MNHN ORA1293. As in other *Argyropelecus* species, the ossification of this bone is restricted to its distal half. The cleithrum is elongate and extensively pitted. The anterior part of the cleithrum is strongly arched. Coracoid and scapula were preserved in many specimens.

The pelvic fin of *A. logearti* consists of six soft rays. The occurrence of six soft pelvic rays is widespread in the genus *Argyropelecus*. The radials were not preserved in any of the examined specimens. The basipterygia of *A. logearti* are vertically oriented showing the typical condition of *Argyropelecus* species. The ischial and pubic processes are separated by a narrow, highly acute angle (Fig. 8). *A. logearti* has a single iliac spine (postabdominal spine) with serrate edges that bear a small dorso-posterior spine. As in *A. cosmovicii* and *A. hemigymnus*, in *A. logearti* the iliac spines are fused into a single median structure. Nevertheless, the two fossil species differ from *A. hemigymnus* in their different orientation of the iliac spine; the iliac spine is more or less obliquely directed in *A. logearti* and *A. cosmovicii* whereas that of *A. hemigymnus* is horizontally oriented (Fig. 9). As suggested by Jerzmanska (1968) the iliac spine of *A. cosmovicii* differs from that of *A. logearti* and *A. hemigymnus* because of the absence of serration. As in *A.*

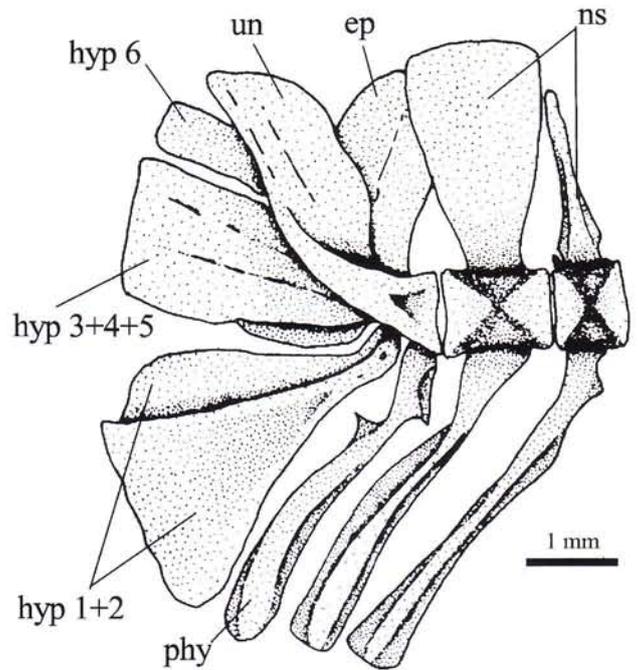


Fig. 4 - *Argyropelecus logearti* Arambourg, caudal skeleton, right side, lateral view, MNHN ORA772.

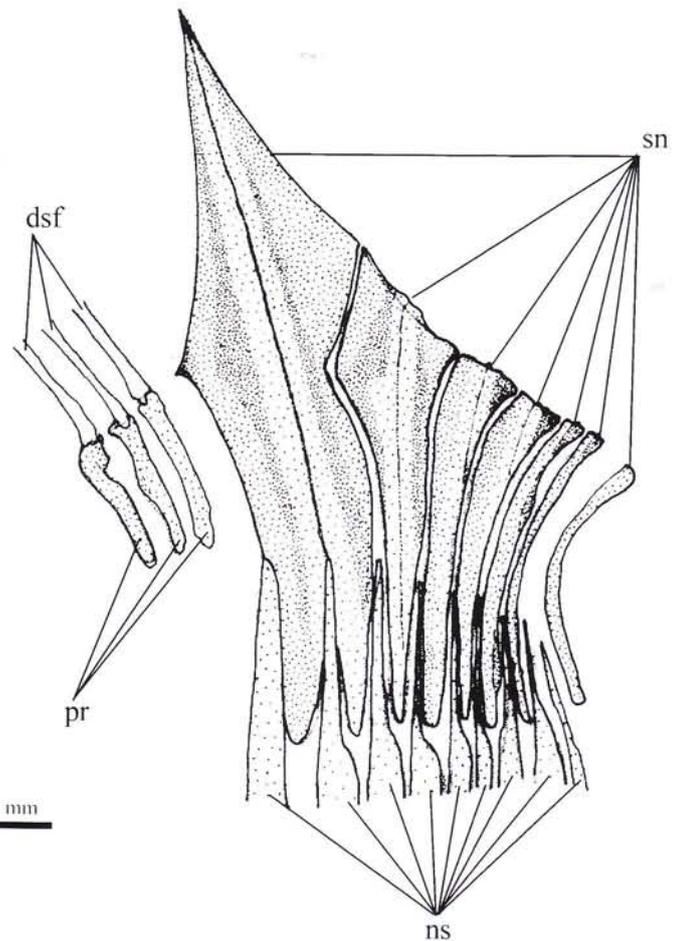


Fig. 5 - *Argyropelecus logearti* Arambourg, supraneurals and associated structures, right side, lateral view, MNHN ORA771g.

*aculeatus*, *A. bullockii*, *A. cosmovicii*, *A. hemigygnus*, *A. lychnus*, *A. olfersi*, and *A. sladeni*, anteriorly to the iliac spine of *A. logearti* there is a triangular process closely associated with the abdominal modified scales. Arambourg (1929) erroneously misidentified this structure as the right iliac spine.

The original squamation of *A. logearti* is poorly preserved. There are several, stiff, modified scales along the ventral edge of the body. Ten of these are located along the abdominal keel (PV photophore scales, see Harold, 1994), 4 between the pelvic and anal fins (VAV photophore scales, see Harold, 1994) (Fig. 8) and 4 posterior to the anal fin (AC photophore scales, see Harold, 1994). These bony scales are found in representatives of the hatchetfish genera *Argyropelecus* and *Polyipnus*.

### The relationships of *Argyropelecus logearti*

*Argyropelecus logearti* shows several diagnostic characters of the Sternoptychini (deep-bodied hatchetfishes: *Polyipnus* and *Sternoptyx*, other than *Argyropelecus*), including (see Weitzman 1974): deep and highly compressed body; vertically oriented pelvic girdle, with consequent absence of the extensor proprius pelvic muscle (see Winterbottom 1974); abdominal keel-like structure; presence of preopercular spines; presence of postabdominal spines; a bony crest on the parietal continuous with that of the frontal bone. The species clearly belongs to the clade constituted by *Argyropelecus* and *Sternoptyx* based upon the following characters (see Weitzman 1974, and Harold 1993): heavily pitted bones of the skull; mesopterygoid and ectopterygoid shape; absence of a coronoid process of the dentary; elongation of preopercle and hyomandibular.

As discussed above, a cladistic study of *Argyropelecus* interrelationships was recently produced by Harold (1993). Because the object of this paper is not to revise the interrelationships of *Argyropelecus* species, I will accept the phylogeny proposed by Harold (1993) and place *A. logearti* within that framework.

Unfortunately, many of the characters listed by Harold (1993) correspond to soft anatomy or delicate structures, such as infrapharyngobranchials, hypobranchials, ligaments and photophores that have little chance to fossilize and thus, there is no way to examine the fossils for these characters. Nevertheless, I consider many other characters observed on the fossils enough to placing *A. logearti* within the phylogeny of Harold (1993). The characters of *Argyropelecus logearti* relevant to placing it within Harold's cladogram are here summarized (Fig. 10).

Characters (1) and (2), according to Harold (1993, p. 125), are derived for the genus *Argyropelecus*. These characters are: (1) Incomplete ossification of the ventral limb of the posttemporal and (2) Parasphenoid with a ventral, median keel-like structure extending pos-

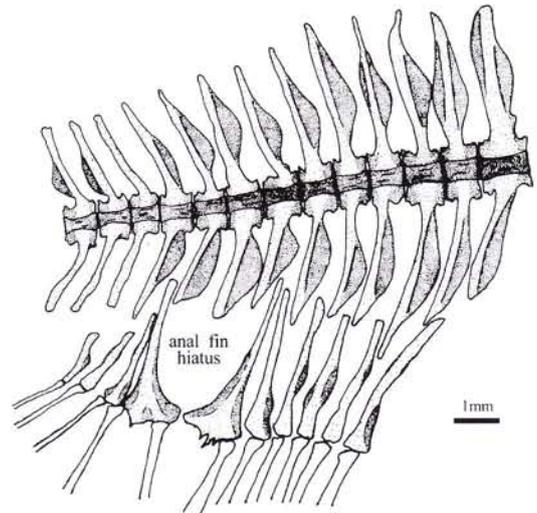


Fig. 6 - *Argyropelecus logearti* Arambourg, axial skeleton and anal fin, right side, lateral view, MNHN ORA772g.

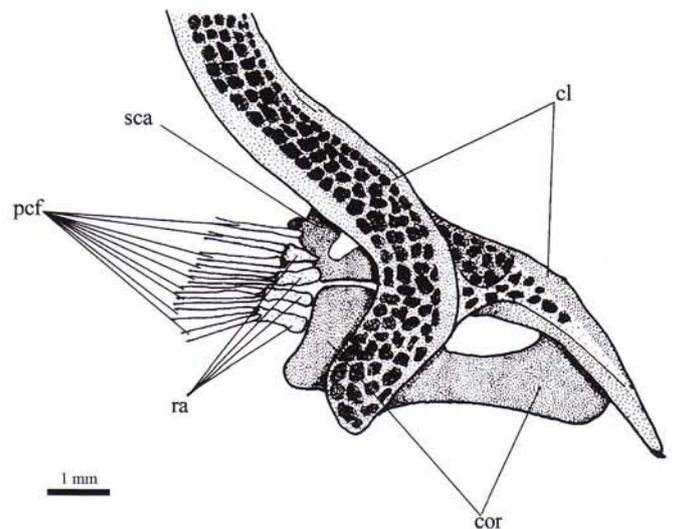


Fig. 7 - *Argyropelecus logearti* Arambourg, pectoral girdle, right side, lateral view, MNHN ORA268d.

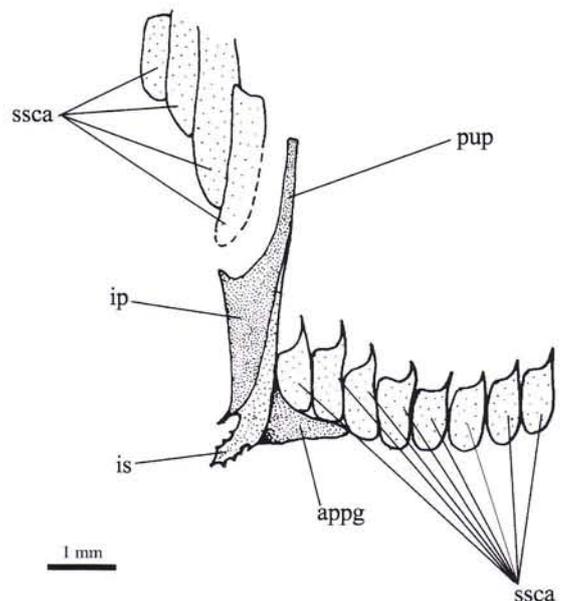


Fig. 8 - *Argyropelecus logearti* Arambourg, pelvic girdle and associated structures, right side, lateral view, MNHN ORA772g.

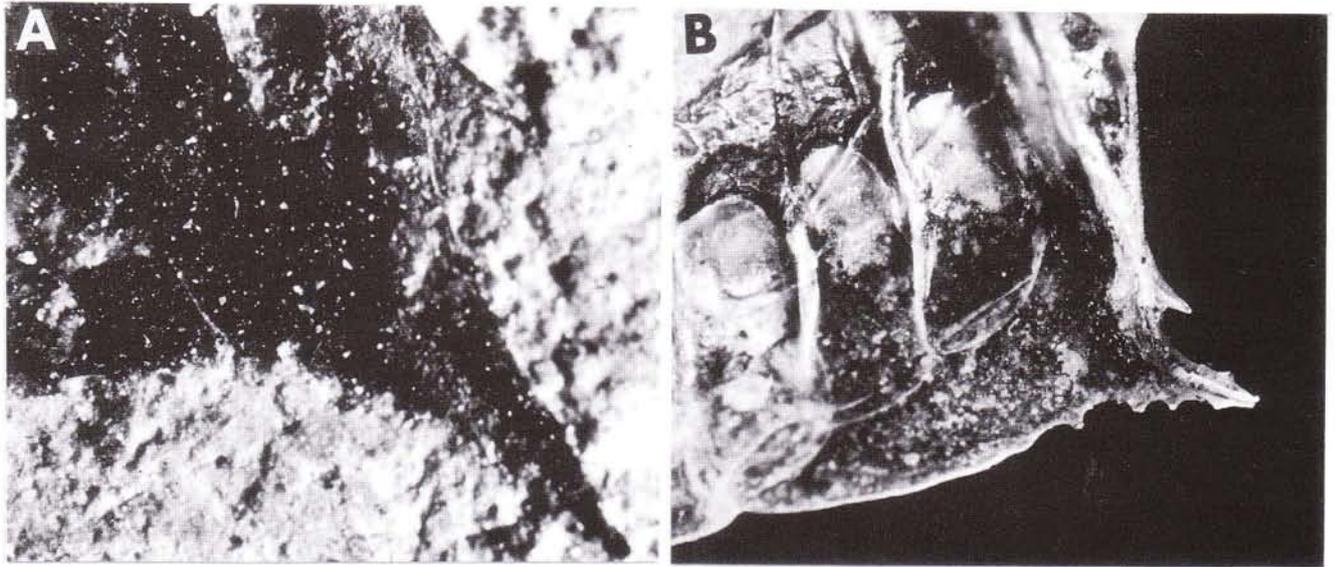


Fig. 9 - Comparison of the postabdominal spine (=iliac spine) in *Argyropelecus logearti* Arambourg (MGPA TOR001, left side, lateral view) (A) with that of *Argyropelecus hemigymnus* Cocco (MPP, uncatalogued, left side, lateral view) (B).

teriorly beyond the point of dorsal inflection. *A. logearti* has these two characters.

Characters (3), (4), (5), (6), (7), (8) and (9), according to Harold (1993, pp. 125-126), are derived for the *lychnus-sladeni-olfersi* plus *aculeatus-hemigymnus* clade. These characters are: (3) A dorsally directed spine is present on the dorsolateral surface of the parhypural. *A. logearti* clearly has this (Fig. 4). (4) Neural and haemal spines are greatly expanded and spatulate in the median plate. Neural and haemal spines of *A. logearti* are expanded and spatulate in the median plate (Fig. 6). (5) The articular heads of the sixth and the seventh anal fin pterygiophores have extensive medial blade-like processes on their proximal surface. *A. logearti* has this character (Fig. 6). (6) A dorsally directed spine-like process is present on the dorsal surface of the seventh, well developed pleural rib. This character is preserved only in MGPA TOR001. (7) Pleural ribs deep and compressed with respect to their longitudinal axes. *A. logearti* has pleural ribs deep and greatly compressed. (8) A triangular blade-like process extending anteriorly located at the base of the anteriormost iliac spine. This character is clearly visible in many of the observed specimens (Fig. 8); as discussed above, Arambourg (1929) erroneously described it as the right iliac spine. (9) Dorsal and ventroanterior limbs of the parasphenoid are similar in length. *A. logearti* has this character (see description).

Characters (10), (11) and (12), according to Harold (1993, p. 126), are derived for the *aculeatus-hemigymnus* clade. These characters are: (10) Seventh and eighth supraneurals expanded and compressed. The fused seventh and eighth supraneurals of *A. logearti* are expanded and laterally compressed (Fig. 5). (11) Shafts of the seventh and eighth supraneurals fused from their distal tips to a point slightly ventral to the distal tip of

their shared neural spine. *A. logearti* clearly has this. (12) An external posterior process of the posterior element of the dorsal blade has paired wing-like processes. As discussed above *A. logearti* has this character.

Within the *aculeatus-hemigymnus* clade, Harold (1993, p. 128) listed seven autapomorphies for *A. hemigymnus* and one for *A. aculeatus*. *A. aculeatus* is characterized by the presence of prominent scalloping or serration on the dorsal margin of the longitudinal crest of the parietal. This feature was not observed in *A. logearti*. Of the seven autapomorphies of *A. hemigymnus* recognized by Harold (1993, pp. 128-129), two of them, (13) presence of a single postabdominal spine and, (14) narrow and subcylindrical body trunk, were also observed in *A. logearti*. Thus, these characters can be now considered as synapomorphies of the two species. As discussed above, a single postabdominal spine (Figs 1A, 1B, 8, 9) and the narrow body trunk (Fig. 1B) were clearly visible in many of the examined specimens. In agree with Harold (1993) in considering these characters as the result of developmental heterochronies. Heterochrony refers to phylogenetic differences in timing and rate of development (De Beer 1940; Gould 1977; Alberch et al. 1979; Fink 1982; Hall 1992).

In *A. hemigymnus* (and possibly in *A. logearti*), development of the basiptyrgia proceeds from separate pelvic plates in postlarvae to a fused postabdominal spine in adults (Harold 1993, pp. 129, 131). Therefore, the fusion of the right and left iliac structures in adults is achieved with a terminal addition in the ontogenetic trajectory, representing the result of peramorphosis (recapitulation, in the sense of Haeckel 1866, and Cope 1887). Alternatively, the presence of a single postabdominal spine could be interpreted as the result of differential divergence of adults to the ancestral ontogeny

Specimen	Total length	Standard length	Head length	Head depth	Body depth	Caudal peduncle depth	Orbit diameter	Pre-pectoral length	Pre-dorsal length	Pre-pelvic length	Pre-anal length
ORA268	?	?	12	15	25	?	5	13	22	21	20
ORA772	50	42	14	?	?	5,5	?	18	24	29	30
ORA269	?	?	8	9	14	?	3	9	9,5	13	11,5
ORA270	?	?	8	13	19	?	3,5	8,5	17	15	16
ORA271	?	?	?	?	?	?	?	?	?	?	?
ORA771	?	?	10,5	14	22,5	?	4,5	11,5	17	19	?
ORA1293	?	?	15	19	?	?	6	17	?	?	?
ORA774	?	?	?	?	30	?	?	?	?	?	?
ORA1074	?	?	16	26	36	?	?	19	30	32	35
ORA769	?	41	17	22	35	6	6	20	27	?	33
ORA773	?	?	?	?	35	?	?	?	?	?	?
ORA1290	?	?	?	?	?	?	?	?	?	?	?
ORA1289	?	?	8,2	?	?	?	4	?	17	?	?
ORA1294	?	?	?	?	?	?	5	?	?	?	?
ORA1291	?	?	?	?	?	?	?	?	?	?	?
ORA770	?	?	12	17	?	?	5	14	?	23	?
ORA1284	?	?	4,2	8	?	?	1,8	?	?	?	?
ORA1292	?	?	?	?	22	?	?	?	?	?	?
TOR001	?	32	12	?	?	3,2	5,3	12	14	19	22

Tab. 1 - Measurements of *Argyropelecus logearti* Arambourg.

(recapitulation, in the sense of Von Baer 1828, and Garstang 1922).

As discussed above, *A. cosmovicii* also has a single postabdominal spine. The validity of this character appears to be dubious without a revision of these fossil species. Nevertheless, in this study we consider this character as a synapomorphy of *A. logearti* and *A. hemigymnus*, until the relationships of *A. cosmovicii* will be better understood.

On the contrary, the presence of a narrow body trunk may result through paedomorphic alteration of developmental programs. Paedomorphosis refers to retention of ancestral juvenile characters in the descendant adult phase (McNamara 1986). Paedomorphosis has been noted in several assemblages of fishes (e.g., Nielsen 1969; Fink 1981; Bemis 1984; Weitzman & Vari 1988; Winterbottom 1990; Grande & Bemis 1991; Johnson & Brothers 1993; Bemis et al. 1997), including sternoptychids (Weitzman 1974; Harold 1990a, b). A narrow body trunk in fact, is typical of the postlarval stage of development of congeners (see e.g., Jespersen 1915; Sanzo 1931; Ahlstrom et al. 1984).

*Argyropelecus logearti* could be interpreted as the result of a mosaic of paedomorphic, peramorphic and unmodified anatomical parts, a case explained with the emergence of dissociated heterochrony, a common phenomenon recognized by numerous authors (Edgecombe & Chatterton 1987; McNamara 1988; Raff 1996;

Wagner 1996).

None of the other derived characters listed in Harold (1993) for *A. hemigymnus* were found in *A. logearti*. For *A. hemigymnus* Harold (1993, pp. 128-129) lists: (A) an uncinat process of the second infrapharyngobranchial, which articulates with the epibranchial of the first gill arch, describes a shallow arc away from the main axis of the bone; (B) parietal very small, appearing a wedge-shaped ossification posterior to the frontal; (C) maximum body size attained is less than 40 mm SL; (D) photophores develop rapidly, and clusters attain their

Species	Pectoral fin rays	Dorsal fin rays	Anal fin rays	Total vertebrae
<i>A. logearti</i>	9	8	11	38
<i>A. hemigymnus</i>	9-11	8	11	36-39
<i>A. aculeatus</i>	9-11	9	12	34-36
<i>A. lychnus</i>	10-11	9	11-13	35-37
<i>A. sladeni</i>	10-11	9	12	35-37
<i>A. offersi</i>	10-11(12)	9	12	36-38
<i>A. affinis</i>	(10)11-12	9	12-13	38-40
<i>A. gigas</i>	(10)11	9-10	12-13	38-39
<i>A. bullocki</i>	11	9	12	37-38
<i>A. cosmovicii</i>	?	?	?	35-36

Tab. 2 - Comparison of some meristic features between *Argyropelecus logearti* Arambourg, and other living and fossil *Argyropelecus* species. Data from Badcock (1984), Baird (1986), David (1943), Jerzemska (1968), Schultz (1964).

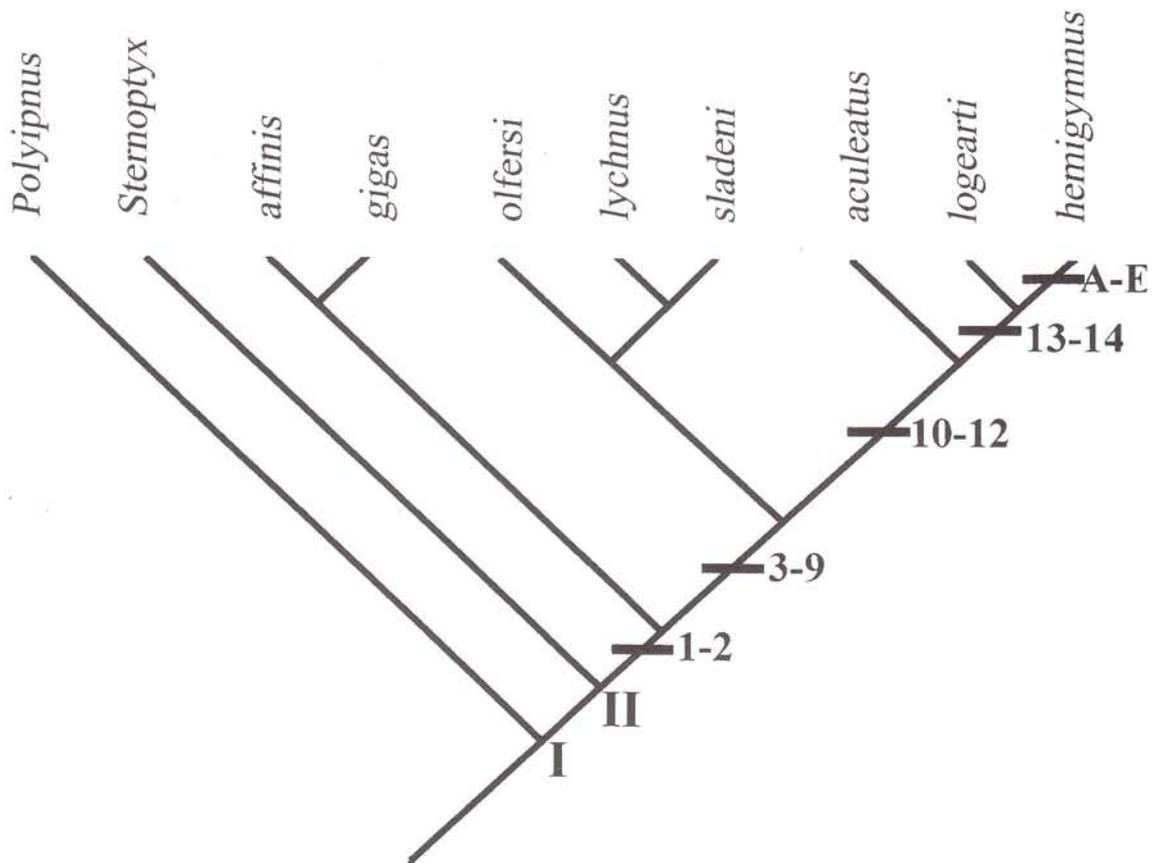


Fig. 10 - Cladogram showing the proposed placement of *Argyropelecus logearti* Arambourg, within the phylogeny of Harold (1993). Numbers and letters refers to characters discussed in text. Synapomorphies supporting nodes I and II are discussed in Weitzman (1974) and Harold (1993). Synapomorphies supporting *affinis-gigas* and *olfersi-lychnus-sladeni* clades are discussed in Harold (1993).

full complement at a relatively small body size; (E) posterior three proximal radials of the dorsal fin are cartilaginous in adults. Of these characters for *A. hemigymnus*, *A. logearti* clearly lacks (B), (C) and (E), whereas (A) and (D) could not be verified because were not preserved in the fossils. In summary, using Harold's (1993) cladogram, we find that *A. logearti* represents the putative sister taxon of *A. hemigymnus*, occupying a derived position in *Argyropelecus* phylogeny (Fig. 10). At this time no autapomorphies for *Argyropelecus logearti* have been found, and thus, this species can be diagnosed only by combinations of characters.

However, although the examined specimens provide many useful characters to understand the phylogenetic position of *Argyropelecus logearti*, further findings could improve the robustness of our phylogenetic interpretation.

#### Brief review of fossil *Argyropelecus*

Living species of the genus *Argyropelecus* are discussed above, and the fossil record of the genus is briefly presented below as an aid for future studies of biogeography and interrelationships within the genus. The fossil taxa are given in chronological order.

#### Oligocene

(1) *Argyropelecus cosmovicii* Cosmovici et Pauca, 1943. The type locality is in the Oligocene menilite beds of the Pietra Neamt, Romania (Ciobanu 1977; Cosmovici & Pauca 1943). The preservation of material is good. This species was also reported by Jerzmańska (1968) from two Oligocene localities of the Polish Carpathians (menilite beds of Przysietnica, and black shales of the Skole Unit) and by Gregorová (1993) from the Oligocene menilite beds of Moravia.

(2) *Argyropelecus* sp. from early Oligocene deposits of Khadum, in northern Caucasus (Bannikov & Parin 1997; Danil'chenko 1960). Following Jerzmańska (1968), I consider the specimens described by Danil'chenko (1960) and referred to *A. cosmovicii*, as members of another species. A different systematic placement is justified because of different morphologies of anal fin pterygiophores and preopercular spines in *Argyropelecus cosmovicii* and the Caucasian material.

(3) *Argyropelecus* sp. from Oligocene deposits of Romanian Carpathians. In agreement with Gregorová (1993), I consider belonging to the genus *Argyropelecus* these specimens originally described as *Sternoptyx prisca* Pauca, 1933 (Ciobanu 1977; Pauca 1933).

#### Miocene

(4) *Argyropelecus logearti* Arambourg, 1929. The

type locality is in the Upper Miocene deposits of Sidi-Brahim and Renault, near Oran, Algeria. This species is also reported from the Middle Miocene deposits of Torricella Peligna, Abruzzo, Central Italy. See above for description and discussion.

(5) *Argyropelecus bullockii* David, 1943. The type locality is from Upper Miocene siliceous sandstone of Modelo Formation, in the Santa Monica Mountains, California. The material consists of two well preserved articulated skeletons described and figured in David (pp. 11-13, fig. 4; p. 60, fig. 11). An additional specimen assigned to this species is reported by David (1943) from the diatomaceous deposits of the Monterey Formation of Lompoc, in the Santa Maria Basin, Southern California. The specimen was briefly described (p. 123) but not figured. The diatomaceous deposits near Lompoc dates back to the Late Miocene (see Chang et al. 1998).

(6) *Argyropelecus affinis* from California (Baird 1971). The reported locality is within the Miocene deposits of Cabrillo Beach, Palos Verdes, California. The material consists of two specimens in a good state of preservation, originally described by Baird (1971) as Fossils A and B.

(7) *Argyropelecus* sp. from the Middle Miocene deposits of Bluss Cove, near Malaga; Palos Verdes, California. The material consists of one specimen deposited at the Los Angeles County Museum. This specimen was described as Fossil C by Baird (1971). Baird (1971) describes few differences between this fossil and the extant *A. lychnus*.

#### Pliocene

(8) *Argyropelecus hemigymnus* Cocco, 1829 from the Pliocene of Southern Italy (Landini & Menesini 1986). The reported locality is in Middle Pliocene deposits of Stuni, near the city of Crotona, Calabria, Southern Italy. The material consists of 9 specimens, most of them showing a good state of preservation.

(9) *Argyropelecus* sp. from the late Pliocene of central Italy (Sorbini 1988). The reported locality is in the Pliocene deposits of the Metauro River, in the Marche region, central Italy.

#### Pleistocene

(10) *Argyropelecus hemigymnus* Cocco, 1829 from the Pleistocene of central Italy (Landini & Sorbini 1993). The reported locality is within Lower Pleistocene deposits of the Samoggia River, near Bologna, central Italy.

(11) *Argyropelecus hemigymnus* Cocco, 1829 southern Italy (Landini & Menesini 1978). This material is from Lower Pleistocene deposits of Vrica, near the city of Crotona, Calabria, southern Italy, and it consists of 17 well preserved specimens.

(12) *Argyropelecus hemigymnus* Cocco, 1829 from the early Pleistocene of the Bradano Trough, southern Italy (Girone 2000). The material consists of otoliths collected from the Monty section, near Montalbano Jonico.

#### Species removed from *Argyropelecus*

*Argyropelecus dentatus* (Liebus, 1927) from middle Eocene of Austria. This material is based only on otoliths, originally described as a ganoid, and successively referred by Nolf (1985) to the genus *Argyropelecus*. This material has been recently revised by Nolf (pers. comm.) and included in the beryciform species ?"Diretmidarum" *dentatus*.

*Argyropelecus weinfurteri* Brzobohaty et Schultz, 1978 from the Miocene of Paratethys. The type locality is in the Middle Miocene (Badenian) sediments of northern Carpathians (Brzobohaty & Schultz, 1978). This species is also reported by Rado (1981) and Pana & Rado (1985) from the Middle Miocene of Romania. The material consists of otoliths assigned by Brzobohaty (1982, 1983) to *Valenciennellus weinfurteri* and more recently considered by Brzobohaty & Nolf (in press) belonging to *Valenciennellus tripunctulatus*.

The genus *Argyropelecus* has few fossil species, ranging throughout the mid to late Cenozoic. Moreover, two living species, *A. affinis* and *A. hemigymnus* (and possibly *A. lychnus*), are also known in the fossil record. Several fossil taxa, such as *Argyropelecus cosmovicii* and the Miocene specimens from California, are known by well preserved articulated skeletons and could contribute to a phylogenetic study based on osteology of living and fossil species. Thus, further investigations on morphology and phylogeny of fossil *Argyropelecus* are needed to the understanding of biogeography and evolutionary history of this taxon.

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## REFERENCES

- Ahlstrom E.H., Richards W.J. & Weitzman S.H. (1984) - Families Gonostomatidae, Sternoptychidae, and associated stomiiform groups: development and relationships. In Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, Jr. A.W. & Richardson, S.L. (Eds.) - Ontogeny and systematics of fishes. *Am. Soc. Ichthyol. Herpetol. Spec. Publ.*, 1: 464-498, Lawrence.
- Alberch P., Gould S.J., Oster G.F. & Wake D.B. (1979) - Size and shape in ontogeny and phylogeny. *Paleobiology*, 5: 296-317, Chicago.
- Arambourg C. (1927) - Les Poissons Fossiles d'Oran. *Mat. Cart. géol. Algérie*, 1er Sér.-Paléont., 6: 1-218, Algier.
- Arambourg C. (1929) - *Argyropelecus logeari*, un nouveau Poisson bathypélagique du Sahélien. *Bull. Soc. Géol. France*, 29: 11-15, Paris.
- Badcock J. (1984) - Sternoptychidae. 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, pp. 302-317, Unesco, Paris.
- Baird R.C. (1971) - The systematics, distribution, and zoogeography of the marine hatchetfishes (family Sternoptychidae). *Bull. Mus. Comp. Zool.*, 142: 1-128, Cambridge.
- Baird R.C. (1986) - Tribe Sternoptychini. In Smith, M.M. & Heemstra, P.C. (Eds.) - *Smiths' Sea Fishes*, pp. 255-259. Springer-Verlag, Berlin.
- Baird R.C., Jumper G.Y. & Gallaher E.E. (1990) - Sexual dimorphism and demography in two species of oceanic midwater fishes (Stomiiformes: Sternoptychidae) from the eastern Gulf of Mexico. *Bull. Mar. Sci.*, 47: 561-566, Miami.
- Bannikov A.F. & Parin N.N. (1997) - The List of Marine Fishes from Cenozoic (Upper Paleocene-Middle Miocene) Localities in Southern European Russia and adjacent Countries. *J. Ichthyol.*, 37: 149-161, Moscow.
- Bemis W. (1984) - Paedomorphosis and the evolution of the Dipnoi. *Paleobiology*, 10: 293-307, Chicago.
- Bemis W., Findeis E.K. & Grande L. (1997) - An overview of Acipenseriformes. *Environ. Biol. Fishes*, 48: 25-71, Dordrecht.
- Brzobohaty R. (1982) - Rybi fauna spodnobadenských vapni-tych jilu v Brne-Kralove Poli a její paleogeografický vyzman. *Acta Mus. Moraviae, Sci. Nat.*, 57: 57-64, Brno.
- Brzobohaty R. (1983) - Fish otoliths from the West Carpathians Tertiary and their biostratigraphical significance. *Knihovn. Zem. pl. naf.*, 4: 247-266, Brno.
- Brzobohaty R. & Nolf D. (In press) - Stomiiformes (Teleostei, Otolithen) aus dem Miozän der Karpatischen Vortiefe (Westkarpaten, Mähren) und der Zentral Paratethys. *Cour. Forsch. Senckenberg*, Frankfurt am Main.
- Brzobohaty R. & Schultz O. (1978) - Die Fischfauna des Badenian. *Chronostrat. Neostrat.*, 6: 441-465, Wien.
- Carnevale G., Cascella A., Danese E., Landini W. & Merola D. (2001) - A new fish bed locality from the Middle Miocene of Torricella Peligna, Abruzzo. *Geoitalia 2001* abstr. book, p. 234.
- Chang A.S., Grimm K.A. & White L.D. (1998) - Diatomaceous Sediments from the Miocene Monterey Formation, California: A lamina-scale investigation of biological, ecological, and sedimentary processes. *Palaios*, 13: 439-458, Lawrence.
- Ciobanu M. (1977) - Fauna Fosila din Oligocenul de la Piatra Neamt. Editura Academiei Republicii Socialiste Romania, Bucuresti.
- Cocco A. (1829) - Su di alcuni nuovi pesci del mare di Messina. *Giorn. Sci. Lett. Art. Sicilia*, 26: 46-50, Palermo.
- Cope E.D. (1887) - The origin of the fittest. Macmillan, New York.
- Cornée J.J., Saint Martin J.P., Conesa G. & Muller J. (1994) - Geometry, paleoenvironment and relative sea-level (accommodation space) changes in the Messinian Murdjadjo carbonate platform (Oran, western Algeria): consequences. *Sediment. Geol.*, 89: 143-158, Amsterdam.
- Cosmovici N.L. & Pauca M. (1943) - Ein neuer fossiler Fisch mit erhaltenen Leuchtorganen: *Argyropelecus cosmovicii* sowie Erwägungen der Ablagerung der Menilitschiefer. *Bull. Sect. Sci. Acad. Roum.*, 26: 271-280, Bucuresti.
- Danil'chenko P.G. (1960) - Kost'istye ryby maikopskikh otlojeniy Kavkaza. *Dokl. Acad. Nauk SSSR*, 78: 28-32, Moscow. [in Russian].
- David L.R. (1943) - Miocene fishes of southern California. *Geol. Soc. Am., Spec. Pap.*, 43: 1-181, Baltimore.
- De Beer G.R. (1940) - Embryos and ancestors. Clarendon Press, Oxford.
- Edgecombe G.D. & Chatterton B. (1987) - Heterochrony in the Silurian radiation of encrinurine trilobites. *Lethaia*, 20: 337-351, Oslo.
- Fink W.L. (1981) - Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. *J. Morphol.*, 167: 167-184, New York.
- Fink W.L. (1982) - The conceptual relationship between ontogeny and phylogeny. *Paleobiology*, 8: 254-264, Chicago.
- Fink W.L. & Weitzman S.H. (1982) - Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. *Bull. Mus. Comp. Zool.*, 150: 31-93, Cambridge.
- Garstang W. (1922) - The theory of recapitulation: A critical restatement of the biogenetic law. *J. Linn. Soc., Zool.*, 35: 81-101, London.
- Gartner Jr. J.V., Crabtree R.E. & Sulak K.J. (1997) - Feeding at depth. In Randall, D.J. & Farrell, A.P. (Eds.) - *Deep-Sea Fishes*, pp. 115-193, Academic Press, San Diego.
- Girone A. (2000) - The use of fish otoliths for paleobathymetric evaluation of the Lower to Middle Pleistocene

- deposits in Southern Italy. *Boll. Soc. Paleont. Ital.*, 39: 235-242, Modena.
- Gould S.J. (1977) - Ontogeny and phylogeny. Harvard University Press, Cambridge.
- Grande L. & Bemis W. (1991) - Osteology and phylogenetic relationships of fossil and Recent paddlefishes (Polyodontidae), with comments on the interrelationships of Acipenseriformes. *Soc. Vert. Paleont. Mem.*, 1: 1-121, Lawrence.
- Grande L. & Bemis W. (1998) - A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Soc. Vert. Paleont. Mem.*, 4: 1-690, Lawrence.
- Gregorová R. (1993) - Sur la presence d'*Argyropelecus cosmovicii* Cosmovici et Pauca, 1943 (Poisson Téléostéen, Sternoptychidae) dans l'Oligocène des Couches à Ménilite. *Acta Mus. Moraviae, Sci. Nat.*, 78: 39-46, Brno.
- Haeckel E. (1866) - Generelle Morphologie der Organismen: Allgemeine Grundzüge der Organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descenz-Theorie. Reimer, Berlin.
- Hall B.K. (1992) - Evolutionary developmental biology. Chapman and Hall, New York.
- Harold A.S. (1990a) - *Polyipnus danae* n. sp. (Stomiiformes: Sternoptychidae): a new hatchetfish species from the South China Sea. *Can. J. Zool.*, 68: 1112-1114, Ottawa.
- Harold A.S. (1990b) - Redescription of *Polyipnus fraseri* Fowler, 1934 (Stomiiformes: Sternoptychidae), with remarks on paedomorphosis. *Proc. Biol. Soc. Wash.*, 103: 509-515, Washington.
- Harold A.S. (1993) - Phylogenetic relationships of the sternoptychid *Argyropelecus* (Teleostei: Stomiiformes). *Copeia*, 1993: 123-133, Lawrence.
- Harold A.S. (1994) - A taxonomic revision of the sternoptychid genus *Polyipnus* (Teleostei: Stomiiformes), with an analysis of phylogenetic relationships. *Bull. Mar. Sci.*, 54: 428-534, Miami.
- Harold A.S. (1998) - Phylogenetic relationships of the Gonostomatidae (Teleostei: Stomiiformes). *Bull. Mar. Sci.*, 62: 715-741, Miami.
- Harold A.S. & Weitzman S.H. (1996) - Interrelationships of Stomiiform Fishes. In Stiassny, M.L.J., Parenti, L.R. & Johnson, G.D. (Eds.) - Interrelationships of Fishes, pp. 333-353, Academic Press, San Diego.
- Hopkins T.L. & Baird R.C. (1973) - Diet of the hatchetfish *Sternoptyx diaphana*. *Mar. Biol.*, 21: 34-46, Heidelberg.
- Hopkins T.L. & Baird R.C. (1985) - Feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. *Bull. Mar. Sci.*, 36: 260-277, Miami.
- Jerzmanska A. (1968) - Ichthyofaune des couches à ménilite. *Acta Pal. Pol.*, 13: 379-488, Warszawa.
- Jespersen P. (1915) - Sternoptychidae (*Argyropelecus* and *Sternoptyx*). Report of the Danish Oceanographic Expedition to the Mediterranean. II. Biology A2, pp. 1-41, København.
- Johnson G.D. & Brothers E.B. (1993) - *Schindleria*: A paedomorphic goby (Teleostei: Gobioidae). *Bull. Mar. Sci.*, 51: 441-471, Miami.
- Jumper G.Y. & Baird R.C. (1991) - Location by olfaction: a model and application to the mating problem in deep-sea hatchetfish *Argyropelecus hemigymnus*. *Am. Nat.*, 138: 1431-1458, Chicago.
- Landini W. & Menesini E. (1978) - L'ittiofauna plio-pleistocenica della sezione della Vrica (Crotone - Calabria). *Boll. Soc. Paleont. Ital.*, 17: 143-175, Modena.
- Landini W. & Menesini E. (1986) - L'ittiofauna della sez. di Stuni e i suoi rapporti con l'ittiofauna plio-pleistocenica della Vrica (Crotone, Calabria). *Boll. Soc. Paleont. Ital.*, 25: 41-63, Modena.
- Landini W. & Sorbini L. (1993) - Biogeographic and paleoclimatic relationships of the Middle Pliocene ichthyofauna of the Samoggia Torrent (Bologna, Italy). *Cienc. Terra*, 12: 83-89, Lisboa.
- Liebus A. (1927) - Neue Beiträge zur Kenntnis der Eozänfauna des Krappfeldes in Kärnten. *Jb. geol. Bundesanst.*, 77: 333-393, Wien.
- McNamara K.J. (1986) - A guide to the nomenclature of heterochrony. *J. Paleont.*, 60: 4-13, Lawrence.
- McNamara K.J. (1988) - The abundance of heterochrony in the fossil record. In McKinney, M.L. (ed.) - Heterochrony in evolution: a multidisciplinary approach, pp. 287-325, Plenum Press, New York.
- Nelson G.J. (1969) - Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. Nat. Hist.*, 141: 475-552, New York.
- Nielsen J.G. (1969) - Systematics and biology of the Aphyonidae (Pisces, Ophidioidea). *Galathea Rep.*, 10: 7-90, København.
- Nolf D. (1985) - Otoliti Piscium. Handbook of Paleoichthyology, v. 10, pp. 1-146. Gustav Fisher Verlag, Stuttgart.
- Pana I. & Rado G. (1985) - Otolithes badeniens de la zone périrécifale de Bahna. *Anal. Univ. Bucuresti*, 34: 3-13, Bucuresti.
- Patacca E., Scandone P., Bellatalla M., Perilli N. & Santini U. (1992) - La zona di giunzione tra l'arco appenninico meridionale nell'Abruzzo e nel Molise. In Tozzi, M., Cavinato, G.P. & Parotto, M. (Eds.) - Studi preliminari all'acquisizione dati del profilo CROP 11 Civitavecchia-Vasto. *St. Geol. Cam., spec. publ.* 1991/2, pp. 417-441, Camerino.
- Patterson C. & Rosen D.E. (1977) - Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull. Am. Mus. Nat. Hist.*, 158: 81-172, New York.
- Pauca M. (1933) - De nouveaux Poissons fossiles dans l'Oligocène de Piatra Neamt. *C. R. Séan. Inst. Géol. Roum.*, 19: 4-12, Bucuresti.
- Rado G. (1981) - Otolite din depozitele langhiene (Badenien inferior) de la Lapugiul de Sus. *Anal. Univ. Bucuresti*, 30: 29-49, Bucuresti.
- Raff R.A. (1996) - The Shape of Life: Genes, development, and the evolution of animal form. University of Chicago Press, Chicago.

- Sanzo L. (1931) - Sottordine: Stomiatoidei. In Uova, larve e stadi giovanili di Teleostei, Fauna e Flora del Golfo di Napoli, 38: 42-92, Napoli.
- Schultz L.P. (1964) - Family Sternoptychidae. In Fishes of the Western North Atlantic, pp. 241-273. Sears Foundation for Marine Research, Yale University, New Haven.
- Sorbini L. (1988) - Biogeography and climatology of Pliocene and Messinian fossil fish of Eastern-Central Italy. *Boll. Mus. Civ. St. Nat. Verona*, 14: 1-85, Verona.
- Von Baer K.E. (1828) - Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion. Bornträger, Königsberg.
- Wagner G.P. (1996) - Homologues, natural kinds and the evolution of modularity. *Am. Zool.*, 36: 36-43, Lawrence.
- Weitzman S.H. (1974) - Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatooid Families. *Bull. Am. Mus. Nat. Hist.*, 153: 328-478, New York.
- Weitzman S.H. & Vari R.P. (1988) - Miniaturization in South American freshwater fishes: an overview and discussion. *Proc. Biol. Soc. Wash.*, 101: 444-465, Washington.
- Winterbottom R. (1974) - A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Phila.*, 125: 255-317, Philadelphia.
- Winterbottom R. (1990) - The *Trimmatom nanus* species complex (Actinopterygii, Gobiidae). *Syst. Zool.*, 39: 253-265, London.