Thalassia Salentina
Thalassia Sal. 38 (2016), 65-79
ISSN 0563-3745, e-ISSN 1591-0725

DOI 10.1285/i15910725v38p65
http: siba-ese.unisalento.it - © 2016 Università del Salento

LOUIS PAUL TAVERNE[1], LUIGI CAPASSO[2]

[1] Royal Institute of Natural Sciences of Belgium, Directorate Earth and History of Life, Vautierstreet, 29, B-1000 Brussels, Belgium. e-mail: louis.taverne@gmail.com
[2] Museo Universitario dell'Universitá "G. d'Annunzio" di Chieti-Pescara, Piazza Trento e Trieste, 1, I-661000 Chieti, Italy. e-mail: lcapasso@unich.it

REVISION OF *IONOSCOPUS PETRAROJAE* (IONOSCOPIFORMES, OSTEICHTHYES) FROM THE ALBIAN OF PIETRAROJA (CAMPANIA, SOUTHERN ITALY)

SUMMARY

The skeleton of *Ionoscopus petrarojae*, an ionoscopiform fish (Halecomorphi) from the marine Albian of Pietraroja (Campania, southern Italy), is studied in details. The fish exhibits all the anatomical features that characterize the family Ionoscopidae, a maxillary sensory canal, a dermosphenotic fused to the skull roof and bearing an innerorbital flange, a dermopterotic longer than the parietal, pitted infraorbitals, monospondylous vertebrae, fossae on the lateral faces of the vertebrae, more than 15 supraneurals and amioid-like scales. *Ionoscopus petrarojae* differs from the well known *Ionoscopus cyprinoides* by numerous osteological characters. The erection of a new genus for *I. cyprinoides* is suggested. Comparisons are done between *I. petrarojae* and the ionoscopid species *Oshunia brevis* and *Quetzalichthys perrilliatae*. Comments are given on the systematic position of *I. petrarojae* within Ionoscopidae. *I. petrarojae* is the plesiomorphic member of the family. It still has a large dermosphenotic that covers the autosphenitic, as in Ophiopsidae. *"Ionoscopus" cyprinoides*, *O. brevis* and *Q. perrilliatae* share a new derived character. The dermosphenotic is reduced. The autosphenotic is no more hidden and becomes a visible part of the skull roof.

INTRODUCTION

The marine Albian strata (Early Cretaceous) of Pietraroja, a small village in the Benevento Province (Campania), yield the most famous Early Cretaceous ichthyofauna discovered in Italy. These fossiliferous geologic layers of Pietraroja are known since the 18^{th} century but the first scientific excavations

Fig. 1. *Ionoscopus petrarojae* Costa, 1853. Holotype MPUN N° M 507 (photo courtesy of Dr. Maria Carmela Del Re, Museum of Paleontology, Università degli Studi di Napoli Federico II). Total length: 61 cm.

on the site were performed by Oronzo G. Costa, the father of the Italian paleoichthyology, and date back to the second half of 19th century. The fossil fishes of Pietraroja have been principally studied by D'Erasmo (1914-1915) in an exhaustive monograph published in two volumes. The historical account of all those geological and paleontological investigations is related by Capasso (2007) in a beautifully illustrated book.

The aim of our present paper is to re-describe one of the largest fishes of the Pietraroja ichthyofauna, the ionoscopid species *Ionoscopus petrarojae* Costa, 1853 and to discuss its relationships with the other Ionoscopiformes.

Ionoscopus petrarojae is the type species of the genus *Ionoscopus* Costa, 1853. Other species exist in the genus, *I. striatissimus* (Münster, 1842), *I. münsteri* (Giebel, 1848), *I. cyprinoides* (Wagner, 1863), *I. analibrevis* Stuetzer, 1972, all four from the Tithonian of Germany, and *I. desori* (Thiollière, 1858) from the Kimmeridgian of France.

Costa has described twice the holotype of the Italian species, firstly under the name *Ionoscopus petrarojae* (Costa, 1853-1860: 2-5, pl. 1) and later as *Oeonoscopus petraroiae* (Costa, 1864: 58-63, pl. 18). New studies of the Pietraroja specimen were performed by D'Erasmo (1915: 5-12, pl. 2[9], fig. 1, 2) in the second part of his monograph and by Stuetzer (1972: 72-77, pl. 7, fig. 1) in his unpublished doctoral thesis. Unfortunately, in all these publications, the description of the skull is always very schematic, not at all detailed. The cranial reconstruction proposed by D'Erasmo (1915: fig. 18) is for instance almost totally erroneous.

Ionoscopiformes are an order of Mesozoic halecomorph fishes ranging

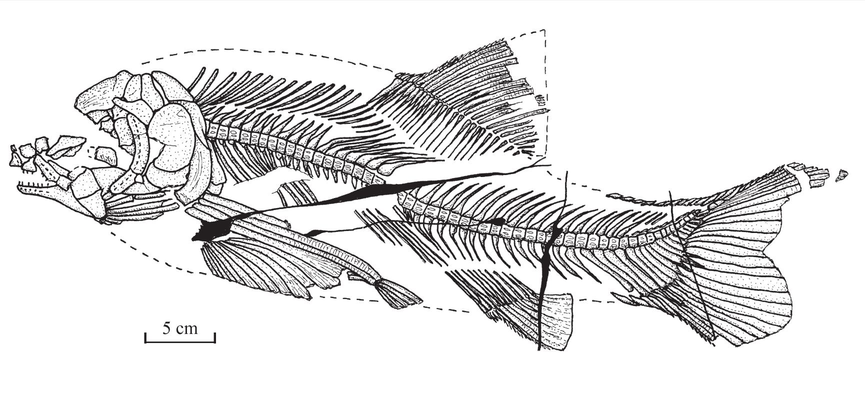

Fig. 2. *Ionoscopus petrarojae* Costa, 1853. Reconstruction of holotype MPUN N° M 507.

in time from the Middle Triassic to the Early Cretaceous. Their oldest occurrence is located in the Anisian strata of China (Xu *et al.*, 2014; Xu and Shen, 2015) and in the Ladinian deposits of Europe (López-Arbarello *et al.*, 2014). They are essentially found in marine deposits. Only one freshwater species has been recorded until now in the Democratic Republic of Congo (Taverne, 2015). The order contains about a dozen of genera. A few other genera have been cited as possible ionoscopiform candidates but they need all to be re-studied before their eventual inclusion in the order. Ionoscopiformes have a worldwide geographic distribution, including eastern Asia, Europe, North, Central and South America, Africa and Australia.

Ionoscopiform fishes are principally characterized by three features. A maxillary sensory canal lies on the maxilla. The dermosphenotic is sutured to the skull roof and bears an innerorbital flange linking the bone to the upper posterior infraorbital. The order is divided in two families, Ionoscopidae and Ophiopsidae. Ionoscopidae have the parietal shorter than the dermopterotic, pitted infraorbitals, monospondylous vertebrae ornamented with lateral fossae, 15 or more supraneurals and amioid-like scales, while Ophiopsidae exhibit a parietal as long as the dermopterotic, smooth infraorbitals, vertebrae devoid of lateral fossae, diplospondyly in the caudal region, less than 15 supraneurals and ganoid scales.

MATERIAL AND METHODS

The specimens hereafter studied belong to the collections of the Museum of Paleontology of the Università degli Studi di Napoli Federico II (MPUN) and to the Luigi Capasso registered collection (CLC) in Chieti. The material has been studied with two stereomicroscopes, a Nikon SMZ 1500 with a *camera lucida* and a Leica Wild M 8. The first author has made the drawings for the figures. The photo of Fig. 1 was provided by the Museum of Paleontology of the Universita degli Studi di Napoli Federico II.

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii Klein, 1885
Series Neopterygii Regan, 1923
Division Holostei Müller, 1845
Subdivision Halecomorphi Cope, 1871
Order Ionoscopiformes Grande & Bemis, 1998
Family Ionoscopidae Lehman, 1966
Genre ***Ionoscopus*** Costa, 1853
Species ***Ionoscopus petrarojae*** Costa, 1853

Emended diagnosis

Large ionoscopid fish. Dermethmoid (= rostral) triangle-shaped and crossed by the rostral sensory commissure. Nasals broad and in contact on the midline. Parietal wide. Dermopterotic longer than parietal. Dermosphenotic triangular, fused to the skull roof, covering the autosphenotic and bearing a short innerorbital flange. Orbitosphenoid and pleurosphenoid present, not forming an interorbital bony septum. Toothed jaws. Premaxilla with a long nasal process. Maxilla bearing a maxillary sensory canal. One large supramaxilla. Lower jaw short, with a deep coronoid region and articulated with the quadrate and the symplectic at the level of the orbital posterior margin. Third infraorbital ornamented with pits and groves. Two postorbitals (= suborbitals), the dorsal one deep. Preopercle crescent-like. Gular plate small. Hyoid bar thin. Pectoral fins very long, reaching the pelvic girdle and with 17 rays. Ventral fins small, with 5 rays. No fringing fulcra on the pectoral and the ventral fins. 56 (24 + 32) monospondylous vertebrae, including 11 centra in the ural series. Lateral faces of the vertebrae ornamented with two fossae, except in the ural region. Dorsal fin with 7 basal fulcra, 21 rays and 24 pterygiophores. Dorsal fin origin before the ventral fins origin. Anal fin with 4 basal fulcra, 10 rays and 11 pterygiophores. Last complete neural spine on the preural vertebra 3. 12 hypurals. 3 epurals. About 10 uroneural-like neural arches. 2 urodermals. Caudal fin with 25 principal rays, 15 dorsal and 5 ventral basal fulcra. Dorsal, anal and caudal fins with fringing fulcra. Amioid-like scales.

Holotype

MPUN N° M 507. A complete specimen, with the left side exposed (Fig. 1, 2). Total length: 61 cm.

Other material

CLC A-7. An incomplete specimen, with a badly preserved skull roof, a partial body, some fin rays and scales. Length of the piece: 30 cm.

An incomplete and badly preserved specimen figured by D'Erasmo (1915: pl. 2, fig. 2) has been destroyed or lost during World War II.

Formation and locality

Limestones of Pietraroja, marine Albian (Early Cretaceous), around the village of Pietraroja, province of Benevento, Campania, southern Italy.

Morphometric data

The morphometric data are given in percentage (%) of the standard length (49 cm) of the holotype.

Head length (opercle included)	26.5 %
Head depth	22.9 %
Maximum body depth (between the head and the dorsal fin	36.7 %
Length of the pectoral fin	31.6 %
Prepelvic length	54.1 %
Length of the ventral fin	8.2 %
Predorsal length	55.1 %
Length of the dorsal fin basis	22.9 %
Preanal length	72.4 %
Length of the anal fin basis	10.4 %
Caudal peduncle depth	15.3 %

Osteology

The skull (Fig. 3)

The skull of the holotype is seen from its left side. The cranial bones are rather thick and those of the skull roof are covered by a thin layer of ganoin that is ornamented with feebly marked ridges.

The dermethmoid (= rostral) is triangle-shaped, with a pointed anterior extremity. It bears the rostral sensory commissure. The two nasals are present. They are large bones that meet on the midline, separating the frontals from the dermethmoid. Only the left frontal is preserved on the holotype but the middle region of the bone is lost, due to the fossilisation. The parietal is broader than long and the skull is medio-parietal. The dermopterotic is

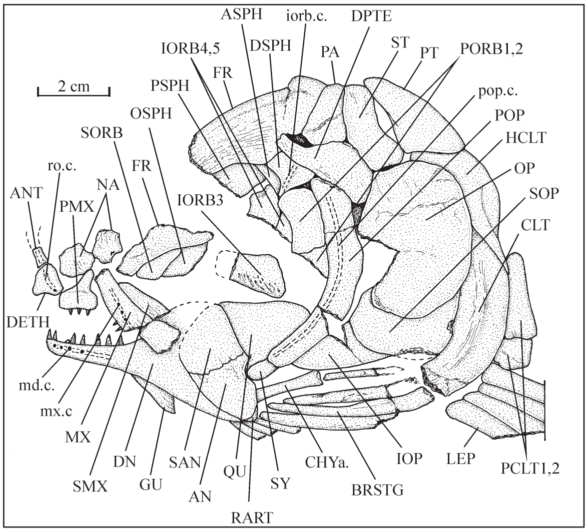

Fig. 3. *Ionoscopus petrarojae* Costa, 1853. Skull of holotype MPUN N° M 507.

elongated, with a rather narrow anterior region and a deeper posterior one. It extends anteriorly before the parietal level. The triangular dermosphenotic is sutured to the frontal and the dermopterotic and it covers a great part of the autosphenotic. The top of the infraorbital sensory canal runs through the dermosphenotic and forms a short pointed ventral flange that joins the fifth infraorbital. The posterior margin of the skull roof is covered by a large supratemporal (= extrascapular) that reaches the midline. The supraorbital and the otic sensory canals are not visible.

Well developed orbitosphenoid and pleurosphenoid are articulated to the ventral face of the frontal. They are not extended ventrally and they do not form a bony interorbital septum. Anteriorly, the orbitosphenoid reaches the ethmoid region.

A large triangular quadrate is the only preserved element of the palatine arch. The pterygoid bones and the palatine are lost. There is no bony quadratic process on the quadrate. Both the quadrate and the symplectic are articulated with the lower jaw. This articulation is located at the level of the orbital posterior margin. A great part of the symplectic is hidden by the preopercle.

The premaxilla, the maxilla and the dentary are toothed. The teeth are rather large, conical and acuminate. Those of the lower jaw are a little larger than those of the upper jaw and the periphery of their base is ornamented with numerous very thin grooves (Costa, 1853-1860, pl. 1, fig. 2 e, E). The premaxilla extends dorsally, forming a long but narrow ascending (nasal) process. The maxilla is long and broad but its posterior extremity is missing. It bears a maxillary sensory canal that is open by a series of pores. There is only one elongate supramaxilla, of which the posterior extremity also is lost. The symphyseal margin of the dentary and its anterior toothed region are narrow but the bone deepens abruptly in its posterior half to form a broad coronoid process with the very wide suprangular. The articular fossa for the quadrate and the symplectic is located near the upper margin of the angular. The inner face of the mandible is not visible but it is probable that an articular was fused to the angular. There is a small retroarticular sutured at the posterior ventral corner of the angular. The mandibular sensory canal is open by large pores in the anterior part of the dentary.

The orbital bony ring is incompletely preserved. The anterior narrow tubular region of right antorbital is visible just above the dermethmoid. The other part of the bone is missing. We do not know if the antorbital was reaching the orbit or not. The other orbital bones belong to the left side of the skull. The rather small first supraorbital is sutured to the lateral margin of the frontal, just behind the nasal level. Large fragments of the third, fourth and fifth infraorbitals are present. They are wide bones. The third infraorbital is pitted and ornamented with some weakly developed grooves in its lower region. There are two postorbitals (= suborbitals) located against the anterior border of the preopercle. The dorsal postorbital is deeper than broad. A large part of the ventral postorbital is lost, due to a break in the substratum. As already written, the dermosphenotic is included in the skull roof.

The preopercle is elongated, crescent-like and it reaches dorsally the margin of the skull roof. The preopercular sensory canal is well visible. The opercle, subopercle and interopercle are articulated together. The opercle is large, more or less ovoid, a little deeper than broad and with a rather smooth surface. The wide subopercle has a concave upper margin and a convex lower margin. It bears a well developed process on the anterior dorsal corner. The triangle-shaped interopercle is the smaller of the three bones. Seven branchiostegal rays are attached to the anterior ceratohyal. The first three are short and the four following long. A small gular plate is partly visible under the dentary.

The girdles (Fig. 2, 3)

The posttemporal is a large triangular bone that reaches anteriorly the supratemporal and remains ventrally on the upper margin of the opercle. The hypercleithrum (= supracleithrum) has a broad upper region but becomes very narrow in its lower portion that articulates with the broad crescent-like cleithrum. The most ventral part of the cleithrum is missing. There are two postcleithra, a deep dorsal one and a small ventral one. Each pectoral fin contains 17 segmented rays. Their distal extremities are lost. At least, the last ones are also branched. The fin is devoid of fringing fulcra. The pectoral fins are extremely elongate and they reach the pelvic fins.

The pelvic bones and the ventral fins are short. The origin of the ventral fins is located at the level of the twenty-fourth vertebra. Each ventral fin contains 5 rays. Their distal extremities are lost. Fringing fulcra are absent.

The axial skeleton (Fig. 2)

The axial skeleton contains 56 monospondylous vertebrae, of which 24 are abdominal and 32 caudal, including the 12 *centra* of the ural series. The first three vertebrae are hidden by the opercle and the pectoral girdle but a trace of the first neural arch and of the outlines of the second and third vertebrae remain visible. The lateral face of the *centra* is ornamented with two fossae separated by a horizontal crest. However, this ornamentation progressively disappears on the *centra* of the ural series. There are 19 supraneurals. The last four supraneurals are located under the first pterygiophores of the dorsal fin. The neural and haemal arches are articulated on their respective *centra* and not fused with them. The neural spines of the first fifteen vertebrae are rather short. Those located below the dorsal fin are much longer. The neural spines of the sixteenth and the seventeenth vertebrae are especially elongated. They are positioned just behind the nineteenth supraneural. It seems that their elongation is the result of the capture of posterior supernumerary supraneurals. From the level of the thirtieth vertebra, there is a slight posterior sliding of the neural arches that overlap the border between two *centra*. The haemal arch is represented by small paired haemapophyses (= parapophyses) in the abdominal region. The haemal spines are rather short and slightly curved. There are twenty pairs of long ribs, the first ones being slightly curved and the last ones very long and rectilinear, except the last pair of ribs, those of the twenty-fourth vertebra, that are extremely short. The first pair of ribs is articulated with the haemapophyses of the fifth vertebra.

The dorsal and anal fin (Fig. 4, 5)

The dorsal fin is composed of 28 elements, 7 basal fulcra, 1 short, segmented and pointed ray, 20 segmented and branched rays. There are 24 pterygiophores. Those of the middle region are longer than the first elements of the series. The basal fulcra are supported by the first three pterygiophores. The other pterygiophores bear one ray, except the last one that supports two rays. There are fringing fulcra all along the anterior margin of the first short pointed ray and of the first long segmented and branched ray. The origin of the fin is located at the level of the 20th vertebra.

The anal fin contains 14 elements, 4 basal fulcra, 1 short, segmented and pointed ray and 9 segmented and branched rays. There are 11 long and thin pterygiophores. The first two pterygiophores support the basal fulcra. Each

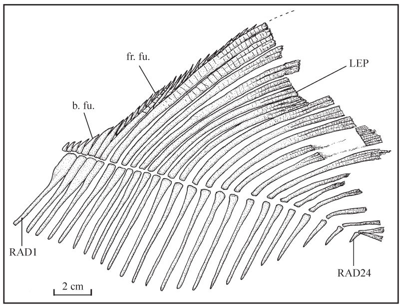

Fig. 4. *Ionoscopus petrarojae* Costa, 1853. Dorsal fin of holotype MPUN N° M 507.

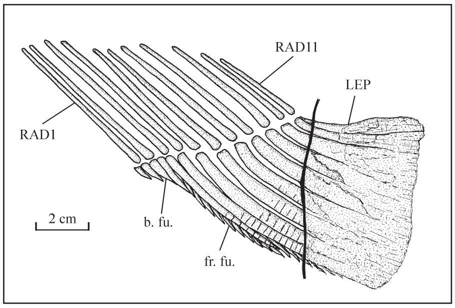

Fig. 5. *Ionoscopus petrarojae* Costa, 1853. Anal fin of holotype MPUN N° M 507.

following pterygiophore supports one ray, except the last one that bears two rays. Fringing *fulcra* are present along the first short unbranched ray and the first long branched ray. The origin of the fin is positioned at the level of the 33rd vertebra.

The caudal endoskeleton and fin (Fig. 6)

The terminal portion of the vertebral axis is upturned and the last *centra* become more and more small. The 41st vertebra (= preural vertebra 3, PU 3) bears the last complete neural spine. Posteriorly, there are about 10 elongated free uroneural-like elements that are not articulated to the *centra*. The caudal fin is supported by 19 hypochordal elements, 6 haemal spines, the parhypural and 12 hypurals. The first haemal spine involved in the caudal fin support belongs to the 38th vertebra (= preural vertebra 6, PU 6). There are 12 ural *centra* and the 44th vertebra (= ural vertebra 1, U 1) is the first of the ural

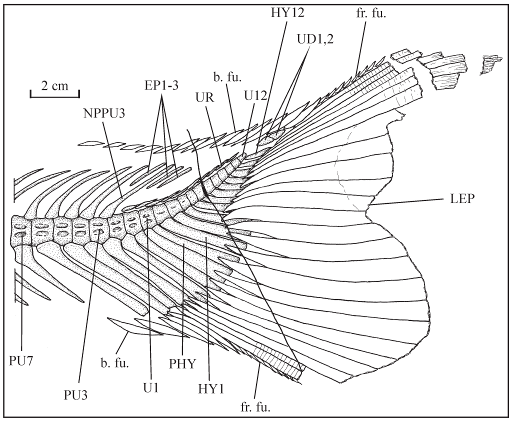

Fig. 6. *Ionoscopus petrarojae* Costa, 1853. Caudal endoskeleton and fin of holotype MPUN N° M 507.

series. Between the 38th and the 43rd *centra*, there is a slight backward sliding of the neural and haemal arches that articulate on two successive vertebrae. The first ural *centrum* is not broader than the preceding ones but it bears both the parhypural and the first hypural. There are 3 short and thin epurals. The first one is located just before the neural spine of the 41st vertebra and the two other behind this neural spine. Two urodermals are present.

The caudal fin is large, forked and contains 25 principal rays, about 15 basal *fulcra* in the dorsal lobe and 5 basal *fulcra* in the ventral lobe. The dorsal basal *fulcra* extend forward till the level of the 39th vertebra. The most external dorsal and ventral principal rays are narrow but the central rays are very broad. There are fringing *fulcra* all along the margin of the most external dorsal and ventral principal rays.

The squamation

The scales are large, ovoid, longer than deep and amioid-like (Schultze, 1966).

DISCUSSION

Ionoscopus petrarojae and the Ionoscopidae

Today, three genera are referred to Ionoscopidae, the European *Ionoscopus*, the type-genus of the family, *Oshunia* Wenz & Kellner, 1986 from the Aptian of Brazil and *Quetzalichthys* Alvarado-Ortega & Espinosa-Arrubarrena, 2008 from the Albian of Mexico. *Oshunia* and *Quetzalichthys* contain only a single species, *Oshunia brevis* Wenz & Kellner, 1986 and *Quetzalichthys perrilliatae* Alvarado-Ortega, Espinosa-Arrubarrena, 2008.

Ionoscopus petrarojae exhibits all the features that characterize the family Ionoscopidae. The dermopterotic is longer than the parietal. The basal region of the third infraorbital is ornamented with a few pits and ridges. The vertebrae are monospondylous, even in the caudal region, and their lateral faces are ornamented with fossae. There are more than 15 supraneurals. The scales are amioid-like. The placement of *I. petrarojae* in Ionoscopidae is thus totally justified.

Ionoscopus petrarojae, *Ionoscopus cyprinoides* and the genus *Ionoscopus*

Today, *Ionoscopus cyprinoides* is the only species of the genus of which the cranium is really well known (Stuetzer, 1972: fig. 3-6; Grande and Bemis, 1998: fig. 410B, 411B; Maisey, 1999: fig. 1A, 8A, B, 9A, B, 10A, B). Osteological characters referring to *Ionoscopus* in the modern paleontological literature are always based on this species and not on the type-species *I. petrarojae*. But some specialists have expressed a doubt concerning the placement of *I. cyprinoides* and *I. petraroiae* in the same genus (Maisey, 1999: 7; Alvarado and Ortega, Espinosa and Arrubarrena, 2008: 168). A detailed comparison of the two species is thus needed.

(1) The dermethmoid is a well developed triangular bone bearing the rostral sensory commissure in *I. petrarojae* but is reduced to a bony tube only carrying the rostral commissure in *I. cyprinoides*.

(2) The parietal is a large bone in *I. petrarojae* but is strongly reduced in *I. cyprinoides*.

(3) In *I. petrarojae*, the dermosphenotic is wide, covering almost entirely the autosphenotic, and has a short innerorbital process. In *I. cyprinoides*, the dermosphenotic is much smaller and does not cover the autosphenotic that becomes visible on the skull roof. *I. cyprinoides* also exhibits a long innerorbital process.

(4) The dermosphenotic meets the dorsal postorbital in *I. petrarojae*. The two bones are largely separated in *I. cyprinoides*.

(5) The coronoid region of the mandible is proportionally much deeper in *I. petrarojae* than in *I. cyprinoides*.

(6) The articulation between the quadrate and the lower jaw is located at the level of the orbit posterior margin in *I. petrarojae* but largely posterior to this level in *I. cyprinoides*. The lengthening of the mandible in *I. cyprinoides* induces a shortening of the preopercle and modifies the shape and size of the opercular series in regard to same elements in *I. petrarojae*.

(7) The upper postorbital is deep in *I. petrarojae*. In *I. cyprinoides*, the upper postorbital is much smaller than the lower postorbital.

(8) The hyoid bar is thin in *I. petrarojae* but much more robust in *I. cyprinoides*.

(9) The very long pectoral fins reach the pelvic girdle in *I. petrarojae* but are much shorter in *I. cyprinoides* and remain largely separated from the ventral fins.

(10) The vertebral axis contains 56 *centra* in *I. petrarojae* and 62 or 63 in *I. cyprinoides*.

(11) There are 19 supraneurals in *I. petrarojae* and 22 in *I. cyprinoides*.

(12) The dorsal fin origin is located in front of the level of the ventral fin origin in *I. petrarojae* and slightly posterior to this level in *I. cyprinoides*.

(13) The dorsal basal *fulcra* of the caudal fin extend much more anteriorly in *I. petrarojae* than in *I. cyprinoides* but are also much smaller.

(14) In *I. petrarojae*, the last complete neural spine is articulated on PU 3 but there are still complete neural spines on the first ural vertebrae in *I. cyprinoides*.

(15) There are 3 epurals in *I. petrarojae* and 5 to 8 epurals in *I. cyprinoides*.
(16) There are 2 urodermals in *I. petrarojae* and 7 or 8 urodermals in *I. cyprinoides*.

Such an amount of differences effectively suggests that the two species do not belong to the same genus and that a new generic name should be erected for *Ionoscopus cyprinoides*.

The skeleton of the three other German species ranged in the genus *Ionoscopus* is to poorly known to allow a useful comparison with *I. petraroiae* and *I. cyprinoides*. Thus, these three remaining species must be re-studied before taking any decision about their generic appurtenance.

In *Ionoscopus desori*, the dermosphenotic completely covers the autosphenotic that does not appear on the skull roof and the innerorbital process is short (De Saint-Seine, 1949: fig. 78, 79). *I. desori* also has the dorsal postorbital deeper than the ventral one (ibid., 1949: fig. 79). For these two characters, *I. desori* resembles *I. petrarojae* but differs from *I. cyprinoides*. *I. desori* probably is a good candidate to be included in the genus *Ionoscopus sensu stricto*.

Ionoscopus petrarojae, Oshunia brevis and *Quetzalichthys perrilliatae*

The data on *Oshunia brevis* hereafter mentioned come from Wenz, Kellner (1986) and Maisey (1991, 1999) and those on *Quetzalichthys perrilliatae* from Alvarado - Ortega and Espinosa - Arrubarrena (2008).

O. brevis differs from *I. petrarojae* by many characters. The supraorbitals and the supramaxilla are lost. The orbitosphenoid is hypertrophied and forms a bony interorbital septum. The dermosphenotic is small and does not cover the autosphenotic. The ventral region of the preopercle is enlarged. There are only 46 or 47 vertebrae. Not only the preural but also the ural *centra* are ornamented with fossae. The origin of the dorsal fin is posterior to that of the ventral fins. The fins are devoid of fringing fulcra. There are complete neural spines on the first ural *centra*.

All these differences clearly show that *O. brevis* and *I. petrarojae* do not belong to the same genus.

Q. perrilliatae also greatly differs from *I. petrarojae*. The triangular dermethmoid reaches the frontals. The nasal is partly tubular. The parietal is divided in two sections. The dermopterotic bears a posterior brush-like process. The posterior margin of the supratemporal is denticulated. The dermosphenotic is small and does not cover the autosphenotic. The anterior part of the maxilla is extremely narrow. The ventral postorbital is deeper than the dorsal element. The gular plate is enlarged. The hypercleithrum is very elongated. There are 63 vertebrae. The preural and the ural centra are ornamented with fossae. The first ural *centra* bear complete neural spines.

It is clear that these two species belong to two different genera.

The systematic position of *Ionoscopus petrarojae* within Ionoscopidae

Ionoscopus petrarojae seems to be the most plesiomorphic member of the family Ionoscopidae. It still possesses a large triangular dermosphenotic sutured with the other bones of the skull roof and that covers almost entirely the autosphenotic. The innerorbital flange is short because there is a close contact between the dermosphenotic and the most dorsal infraorbital. The masked autosphenotic does not appear on the skull roof. The Ophiopsidae also exhibit this primitive morphology, with the dermosphenotic covering totally or almost totally the autosphenotic (Lane and Ebert, 2012: fig. 4B, 2015: fig. 6A, B; López-Arbarello *et al.*, 2014; fig. 6; Taverne, 2015: fig. 5, 10; among others).

"Ionoscopus" cyprinoides, *Oshunia brevis* and *Quetzalichthys perrilliatae* share a new apomorphy. Their dermosphenotic is reduced and located above the uncovered autosphenotic that becomes a visible component of the skull roof (Maisey, 1991: fig. p. 159, 1999: fig. 1A, B; Grande and Bemis, 1998: fig. 410A, B; Alvarado-Ortega and Espinosa-Arrubarrena, 2008: fig. 5).

Oshunia brevis and *Quetzalichthys perrilliatae* differs from *Ionoscopus petrarojae* and from *"Ionoscopus" cyprinoides* by another apomorphy. Even the small vertebrae of the ural series are ornamented with well marked lateral fossae (Wenz and Kellner, 1986: fig. 4; Alvarado-Ortega and Espinosa-Arrubarrena, 2008: fig. 7).

Oshunia brevis is the more specialized member of the family, with a few advanced characters, such as the loss of the supraorbital and of the supramaxilla or the hypertrophy of the orbitosphenoid that forms an ossified interorbital septum (Maisey, 1991: fig. p. 159, 1999: fig. 1B).

ACKNOWLEDGMENTS

We greatly thank Prof. Dr. Maria Rosaria Ghiara, head of the museums of the Universita degli Studi di Napoli Federico II, and Dr. Maria Carmela Del Re, head of the Museum of Paleontology of the same university, for allowing us the access to the material studied in the present paper. We are also grateful to the anonymous reviewers who have read and commented our text.

List of abbreviations used in the text-figures

AN: angular; ANT: antorbital; ASPH: autosphenotic; BRSTG: branchiostegal ray; CHY a.: anterior ceratohyal; CLT: cleithrum; DETH: dermethmoid (= rostral); DE: dentary; DPTE: dermopterotic; DSPH: dermosphenotic; EP 1-3: epurals 1 to 3; FR: frontal; GU: gular plate; HCLT: hypercleithrum (= supracleithrum); HY 1-12: hypurals 1 to 12; IOP: interopercle; IORB 3-5: infraorbitals 3 to 5; LEP: fin ray (= lepidotrichia); MX: maxilla; NA: nasal; NP PU3: neural spine of preural vertebra 3; OP: opercle; OSPH: orbitosphenoid; PA: parietal; PCLT 1, 2: postcleithra 1 and 2; PHY: parhypural; PMX: premaxilla; POP: preopercle; PORB 1, 2: postorbitals (= suborbitals) 1 and 2; PSPH: pleurosphenoid; PT: posttemporal; PU 3, 7: preural vertebrae 3 and 7; QU: quadrate; RAD 1-24: pterygiophores (= radials) 1 to 24; RART: retroarticular; SAN: surangular; SMX: supramaxilla; SOP: subopercle; SORB 1: supraorbital 1; ST: supratemporal (= extrascapular); SY: symplectic; U 1, 12: ural vertebrae 1 and 12; UD 1, 2: urodermals 1 and 2; UR: uraneural-like neural arches; b. fu.: basal fulcra; fr. fu.: fringing fulcra; iorb. c.: infraorbital sensory canal; md. c.: mandibular sensory canal; mx. c.: maxillary sensory canal; pop. c.: preopercular sensory canal; ro. c.: rostral sensory commissure.

REFERENCES

Alvarado-Ortega J., Espinosa-Arrubarrena L., 2008 - A new genus of ionoscopiform fish (Halecomorphi) from the Lower Cretaceous (Albian) lithographic limestones of the Tlayúa Quarry, Puebla, Mexico. *Journal of Paleontology*, 82(1): 163-175.

Capasso L., 2007 - Pietraroja pietre e memorie. Ed. Paper's World, Teramo: 1-181.

Costa O. G., 1853-1860 - Ittiologia fossile italiana. Opera da servire di supplemento alle ricerche su i pesci fossili di L. Agassiz. Napoli: I-VIII + 1-67.

Costa O. G., 1864 - Paleontologia del regno di Napoli. Parte 3. *Atti dell'Academia Pontaniana*, 8: 1-196.

D'Erasmo G. 1914 - La fauna e l'età dei calcari a ittioliti di Pietraroia. Parte I. *Palaeontographica Italica*, *Memorie di Paleontologia*, Pisa, 20: 1-58.

D'Erasmo G., 1915 - La fauna e l'età dei calcari a ittioliti di Pietraroia. Parte II. *Palaeontographica Italica*, *Memorie di Paleontologia*, Pisa, 21: 59-111.

De Saint-Seine P., 1949 - Les poissons des calcaires lithographiques de Cerin (Ain). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 2: 1-357.

Grande L., Bemis W. E. 1998 - A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Journal of Vertebrate Paleontology*, 18 (Suppl. 1, Memoir 4): 1-690.

Lane J. A., Ebert M., 2012 - Revision of *Furo muensteri* (Halecomorphi, Ophiopsidae) from the Upper Jurassic of Western Europe, with comments on the genus. *Journal of Vertebrate Paleontology*, 32(4): 799-819.

Lane J. A., Ebert M., 2015 - A taxonomic reassessment of *Ophiopsis* (Halecomorphi, Ionoscopiformes), with a revision of Upper Jurassic species from the Solnhofen archipelago, an a new genus of Ophiopsidae. *Journal of Vertebrate Paleontology*, 35(1), e883238: 1-23.

López-Arbarello A., Stockar R., Burgin T., 2014 - Phylogenetic relationships of the Triassic *Archeosemionotus* Deecke (Halecomorphi, Ionoscopiformes) from the "Perledo fauna". *Plos/One*, 9(10): 1-12.

Maisey J. G., 1991 - *Oshunia* Wenz and Kellner, 1986. *In:* MAISEY, J. G. (ed.), *Santana fossils. An illustrated atlas*: 157-168. T.F.H. Publications, Inc., Neptune City.

Maisey J. G., 1999 - The supraotic bone in neopterygian fishes (Osteichthyes, Actinopterygii). *American Museum Novitates*, 3267: 1-52.

Schultze H.-P., 1966 - Morphologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). *Neues Jahrbuch der Geologie und Paläontologie Abhandlungen*, 126: 232-314.

Stuetzer P. H., 1972 - Morphologie, Taxonomie und Phylogenie der Ionoscopidae (Actinopterygii, Pisces). [unpublished Ph. D. thesis, University of München], Dissertations und Fotodruck Frank, 1-141.

Taverne L., 2015 - Osteology and phylogenetic relationships of *Congophiopsis lepersonnei* gen. nov. (Halecomorphi, Ionoscopiformes) from the Songa Limestones (Middle Jurassic, Stanleyville Formation), Democratic Republic of Congo. *Geo-Eco-Trop*, 38(2) [2014]: 223-240.

Wenz S., Kellner W. A., 1986 - Découverte du premier Ionoscopidae (Pisces, Halecomorphi) sud-américain, *Oshunia brevis* n. g., n. sp., dans le Crétacé inférieur de la Chapada do Araripe (nord-est du Brésil). *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4[e] série, 8, section C, 1: 77-88.

Xu G.-H., Shen C.-C., 2015 - *Panxianichthys imparilis* gen. et sp. nov., a new ionoscopiform (Halecomorphi) from the Middle Triassic of Guizhou, China. *Vertebrata PalAsiatica*, 53(1): 1-15.

Xu G.-H., Zhao L.-J., Coates M. I., 2014 - The oldest ionoscopiform from China sheds new light on the early evolution of halecomorph fishes. *Biology Letters*, 10: 1-5.