Article

A New Enigmatic Teleost Fish from the Mid-Cretaceous of Lebanon

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Abstract: Teleosts form the largest clade among the extant actinopterygians, some extinct forms of which are still poorly positioned in the phylogeny. The Tselfatiiformes and Araripichthyidae are such examples. A newly discovered genus and species from the Cenomanian of Haqel, Lebanon, is described, and its systematic affinities are discussed. It shares several characteristics (deep and compressed body with elongated and high dorsal and anal fins, edentulous maxilla, and sinusoidal vertebral column) with both the Tselfatiiformes and *Araripichthys*, making it difficult to place within the teleosts. It shares with *Abisaadichthys*, among the tselfatiiforms' family Protobramidae, an autogenous retroarticular, and with *Araripichthys* premaxillae with a long ascending process, well-developed maxillary articular condyle and two supramaxillae. Moreover, it shows some unique characteristics (a thin maxilla with two large supramaxillae, fused articular and angular bones, mandibular sensory canal opening on the external side of the anguloarticular, first dorsal pterygiophore having the same enlarged semi-circular plate as the first anal pterygiophore) justifying its generic status. Comments on some of the protobramids are presented, and the necessity for phylogenetic analysis to place the Tselfatiiformes, *Araripichthys* and *Ypsiloichthys* within the teleosts is outlined.

Keywords: Teleostei; Tselfatiiformes; *Araripichthys*; Lebanon; mid-Cretaceous; *Ypsiloichthys sibelleae*

1. Introduction

Despite the progress in paleoichthyology, either through new findings or the development of techniques used in the study of the material, some groups remain poorly known compared to others, either anatomically or taxonomically. The poor knowledge can result from several factors, notably the scarcity of the fossil record. Among these groups are two enigmatic contemporaneous ones: the Tselfatiiformes and the Araripichthyidae. These two groups have been difficult to classify amongst teleosts for many years.

The Tselfatiiformes, a peculiar, extinct order grouping several morphologically diversified taxa, spans a relatively short stratigraphical range from the Albian to Campanian [1]. The paleogeographical distribution of this order is extensive, as fossil remains were found throughout the world, in Europe, Africa, America (North, Central, and South), and Asia. In the last twenty to forty years, the order has been extensively studied by Taverne [2–14] and in part by Taverne and Gayet [1,15], among other authors who have also attempted to place the tselfatiiforms or now included members of this group within the teleosts: Le Danois and Le Danois [16] placed *Tselfatia formosa* and *Protobrama avus* into two distinct suborders within the order Scombriformes; Patterson [17] and Bardack [18] placed the family Plethodidae within the Osteoglossomorpha; Taverne [19] placed the Plethodidae and the Tselfatiidae (a family that is no longer valid) in the Elopiformes; the same author [2] then placed the family Tselfatiidae, which is no longer valid, within the Clupeocephala; Nelson [20] created the order Tselfatiiformes to group some of the taxa mentioned above. Since then, several taxa were discarded and others placed in the Tselfatiiformes, but their

position within the teleosts remains controversial. Only one point is agreed upon by most authors: the Tselfatiiformes is a basal clupeocephalan group [1,4,15,21].

Moreover, not only their phylogenetic position is discussed, but also the intrarelationships within the group. The currently accepted phylogeny is that proposed by Taverne and Gayet [1] without a computer-based analysis, only a discussion of characters, indicating that the Tselfatiiformes includes around 20 genera divided into three families: Eoplethodidae, monogeneric and monotypic *Eoplethodus chaneti* known only by a caudal skeleton re-described by Taverne [7]; Plethodidae to include most of the genera of the order whose members are large scombriform-like fishes [1]; and Protobramidae, the Lebanese endemic family with three genera and four species which are small and deep-bodied with long dorsal and anal fins. Cavin [21], on the other hand, argues that the Tselfatiiformes is not monophyletic and suggests including the members of the Lebanese endemic family in the new suborder with *Araripichthys* and *Acanthichthys*, other small deep-bodied fish with long dorsal and anal fins, called Protobramoidei.

As for *Araripichthys*, a Cretaceous genus known from Brazil, Venezuela, and Morocco, with only a few specimens in each locality, it has also had a complicated taxonomical history. When first described, *Araripichthys castilhoi*, the then single species of the genus, was assigned to the Beryciformes, an acanthomorph order, within its suborder and family, the Araripichthyoidei and Araripichthyidae respectively, by Santos [22]. Later, Maisey [23] and Maisey and Blum [24] placed it as *incertae sedis* within the Elopocephala. Patterson [25] suggested close relationships with the Elopomorpha or its placement within the Pachyrhizodontoidei. Arratia and Chorn [26] noted a similarity in general morphology between *Araripichthys castilhoi* and a primitive acanthomorph, *Acanthichthys major*, and their differences. Cavin [21], as mentioned previously, included it in a phylogenetic analysis that resulted in its placement with *Acanthichthys* and the protobramids in the Protobramoidei within the Clupeocephala. Maisey and Moody [27] discussed all these earlier phylogenetic placements of *Araripichthys* while describing a new species of the genus from Venezuela, *A. axelrodi*, and discussing another species described by Cavin [28] from Morocco, *A. corythophorus*. Alvarado-Ortega and Brito [29] described another new species, *A. weberi*, and proposed placing the genus *Araripichthys* as *incertae sedis* within the Elopocephala. This taxonomic history of *Araripichthys* has been recently discussed by Mayrinck et al. [30] and Maisey and Moody [27], to whom it is referred for more details and discussion of the characters used for these placements. It should be noted that Mayrinck et al. [30] also conclude an *incertae sedis* placement as a basal teleost for *Araripichthys* based on the previously known anatomical data for the genus and their paleohistological study.

All these mentioned Cretaceous taxa are *incertae sedis* within the teleosts. Among the tselfatiiforms, the family Protobramidae was primarily associated and compared to *Araripichthys*, sharing that general body shape, small and deep with long dorsal and anal fins. New material from the Cretaceous of Lebanon sharing a similar morphotype to these two taxa, deep and compressed body with a mixture of pleisiomorphic and specialized characters, is described here. The systematic affinities of the identified taxa are discussed, and the importance of including it and the previously mentioned taxa in phylogenetic analysis is stressed.

2. Geological Setting

Lebanon has been famous for its fossil-rich deposits for centuries, mainly for their fish fossil content and excellent preservation quality, hence its Lagerstätten qualification. Hückel [31] called such deposits the "Fish Shales" localities, with one of them being Haqel, from where 93 species of cartilaginous and ray-finned fish species have been described [32]. It comprises limestones described as hard, laminated, well-bedded, and rich in fossils [31,33]. The limestones are described as sometimes silicified [34], with the presence of chert [35] or flint nodules [36]. Haqel belongs to the Sannine Formation [37].

Despite the numerous excavations and studies on this site, the exact age of the deposits is still controversial. Botta [35] first attributed to Haqel an early Cretaceous age.

Fraas [38] gave a more precise age suggesting a Turonian one for these fish fossil layers in the "radiolite zone". Later, several authors suggested an older age, Cenomanian, whether based on micro or macrofossils and in some cases, other authors followed their dating of the site without many investigations. Some examples of authors suggesting or confirming a Cenomanian age are Pictet and Humbert [39], Douvillé [40], Zumoffen [41], and Dubertret [34]. Patterson [42] gave a more precise age of mid-Cenomanian based on fish fossils correlation. Hückel [31] stated that Haqel deposits are of the "later part of the early Cenomanian"; Saint-Marc [43,44] followed the Cenomanian age proposition of Zumoffen [41] and Hückel [31], who mentioned the presence of the ammonite *Acanthoceras mantelli* (Sowerby, 1814) [45] (nowadays, *Mantelliceras mantelli* (Sowerby, 1817) [45]). Hemleben [46] stated that Haqel outcrops are of the late Cenomanian age based on the planktonic foraminifera. More recently, Wippich and Lehmann [47], doubting the presence of *Mantelliceras mantelli*, suggested a Late Cenomanian age of Haqel based on the presence of another ammonite *Allocrioceras* cf. *annulatum* (Shumard, 1860) [48]; this age being confirmed as well by Fuchs et al. [36].

As stated above, the exact age is still not agreed upon, whether because authors have not been using the same index fossils or not sampling at the same levels. An extensive biostratigraphical study is currently being conducted to give an exact age, among other precisions such as for the paleoenvironment, to the Lagerstätte deposits of Haqel and other famous fossil-bearing localities in Lebanon, such as Hjoula, which has always been thought to be of the same age as Haqel [32].

3. Materials and Methods

3.1. Described Material

The studied specimen MHNG GEPI V5786 (Figure 1) originated from Haqel quarry in Lebanon and housed at Muséum d'histoire naturelle de Genève in Switzerland. It was collected by the Abi Saad family, who have been collecting fossils in the Haqel and Hjoula quarries in Lebanon for several years and collaborating with scientists and institutions worldwide. The exact date of collection is unknown. The Muséum d'histoire naturelle de Genève acquired it in 2022 by purchasing it from the Abi Saad family in accordance with Lebanese legislation for fossil transactions, making the museum its legal owner. The specimen was initially prepared by the quarry's owners. However, additional preparation was required to remove some overlying matrix using an entomological pin. The specimen was observed using a Leica DM2500 stereomicroscope. The specimen was scanned using a micro-computed laminographic system at the RX Solutions company in Annecy, France (Figures 2C and 3C; Videos S1 and S2). The scanned slices were processed using Adobe Photoshop 2023 and Dragonfly softwares. The interpretive drawings were made using Adobe Illustrator 2023.

3.2. Comparative Material

The following fossils were examined to compare them with the new taxon, and their photographs are provided in Supplementary Materials unless stated otherwise:
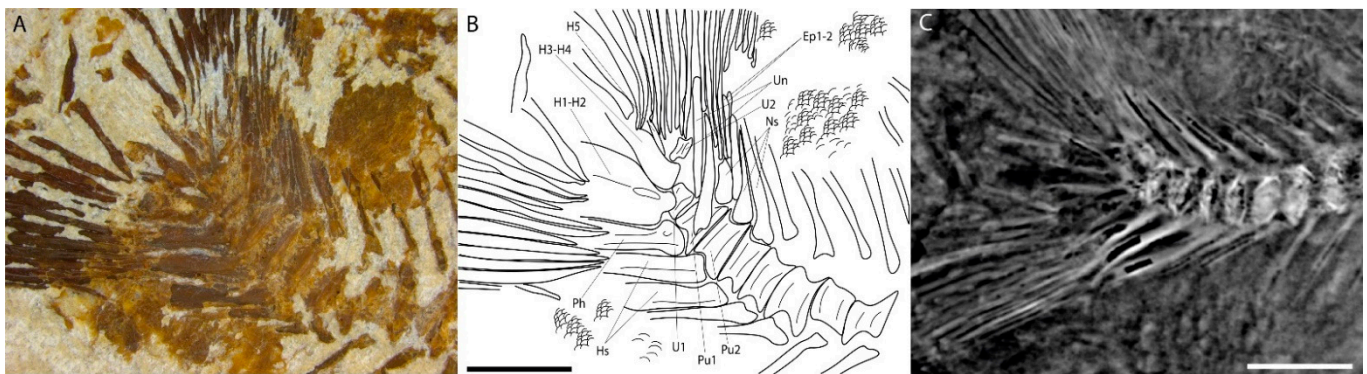
Abisaadichthys libanicus: FSL-573086, holotype, originating from Hjoula, Lebanon (Figures 4, S1 and S2).
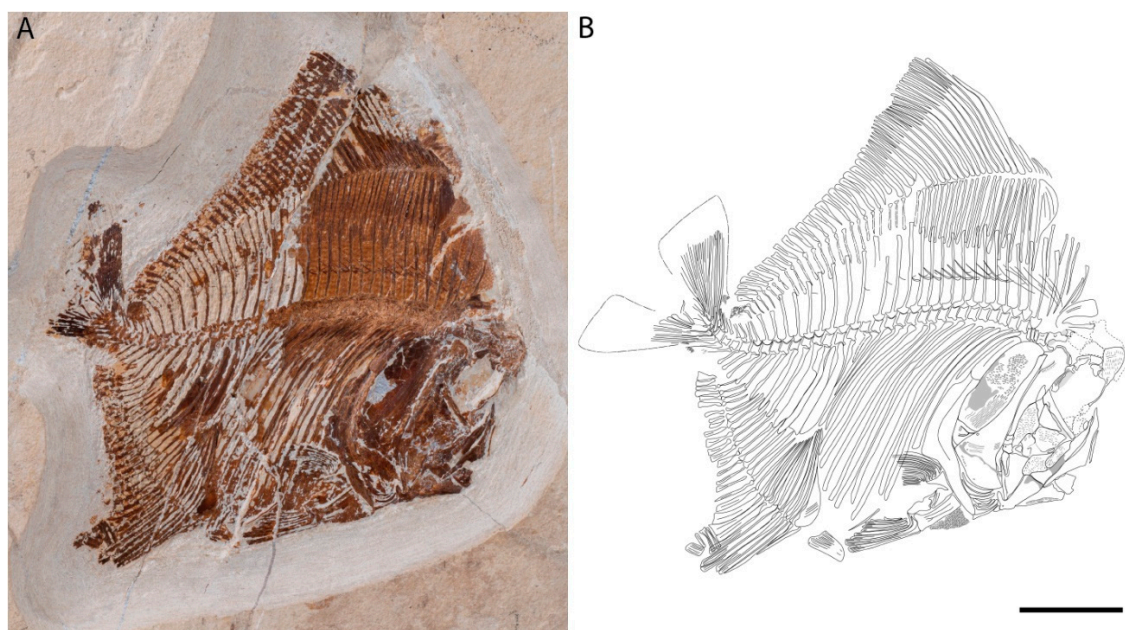
Figure 1. *Ypsiloichthys sibelleae* gen. et sp. nov., holotype MHNG GEPI V5786, (**A**) original specimen; (**B**) interpretive line drawing of (**A**). Scale bar: 2 cm.
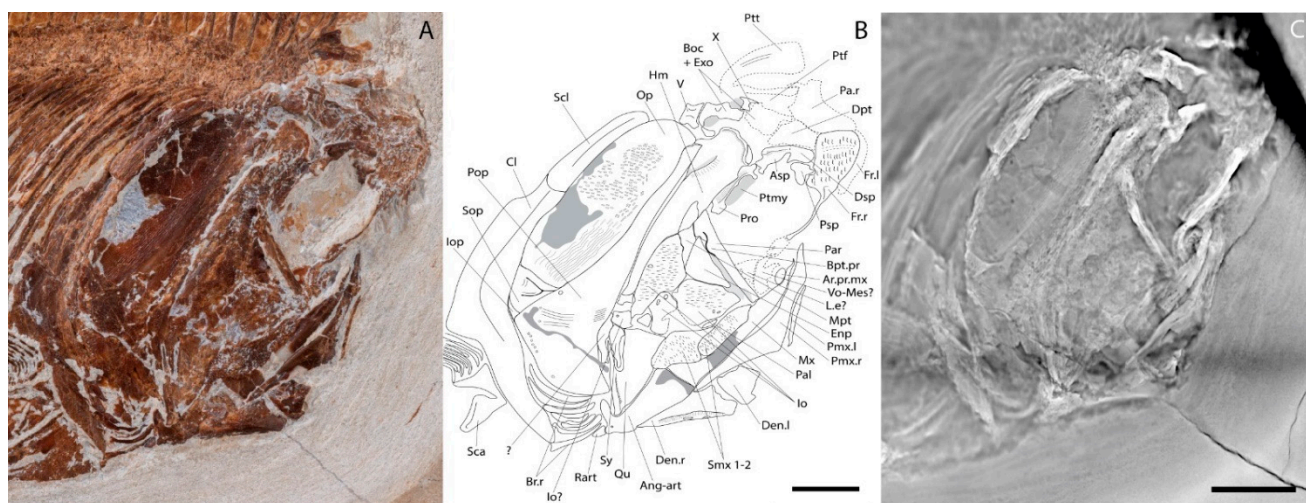
Figure 2. Skull of *Ypsiloichthys sibelleae* gen. et sp. nov., (**A**) photograph of the skull region; (**B**) interpretive line drawing of (**A**); (**C**) micro-computed scanning slice of the skull and pectoral region. Scale bars: 1 cm.

Figure 3. Caudal region of *Ypsiloichthys sibelleae* gen. et sp. nov., (**A**) closed-up photograph of the caudal region; (**B**) interpretive line drawing of (**A**); (**C**) micro-computed scanning slice of the caudal region. Scale bars: 0.5 cm.
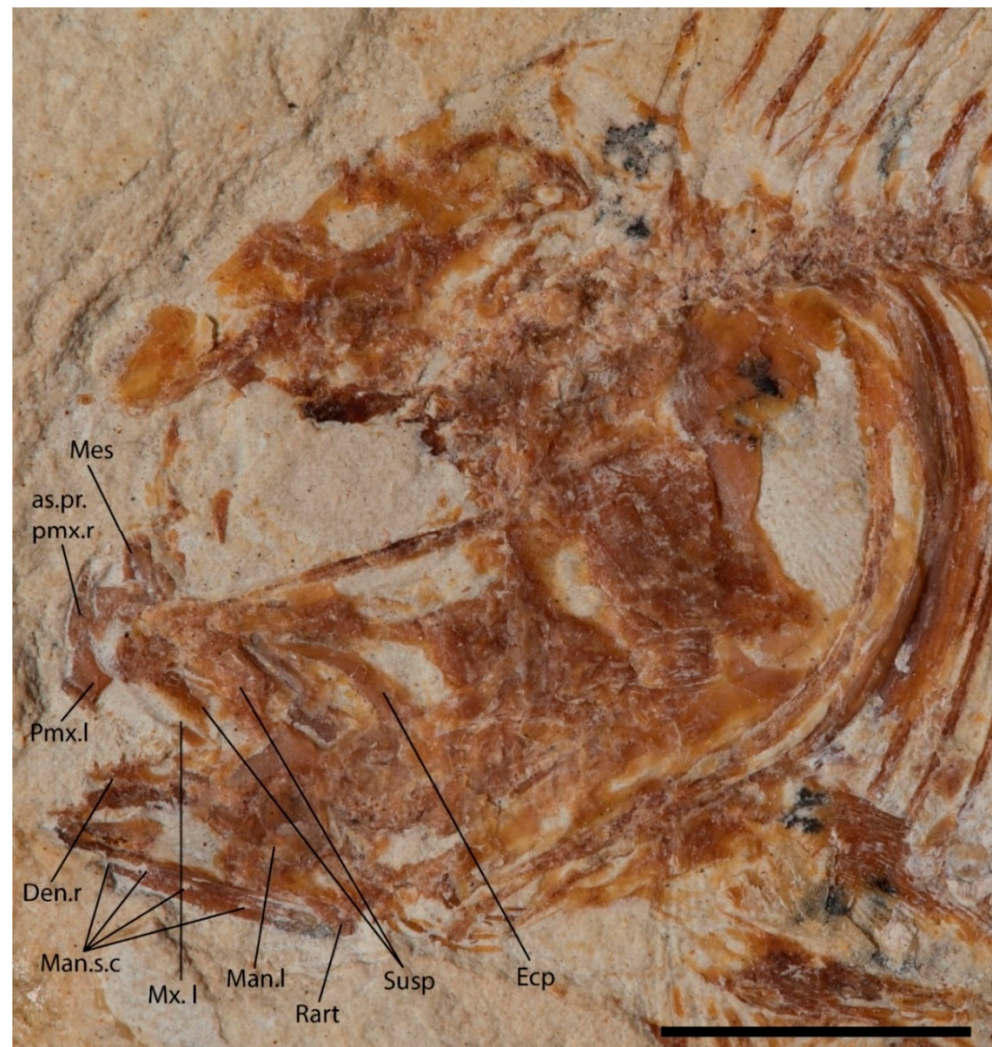
Figure 4. Skull region of *Abisaadichthys libanicus* Taverne and Gayet (2004) [15], holotype FSL-573086. A close-up of the skull region indicates our interpretations of some cranial elements. Scale bar: 0.5 cm.

Protobama avus: FSL-573081 and FSL-573082 a, b, additional material, originating from Hjoula, Lebanon b (Figures S3 and S4A,B respectively).

Protobrama woodwardi: FSL-573084, holotype, and FSL-573085, paratype, originating from Hjoula Lebanon (Figure S5A,B respectively).

Eusebichthys byblosi: MNHN-HAK-306, holotype, originating from Haqel, Lebanon (Figures S6 and S7).

3.3. Abbreviations

Anatomical—The anatomical abbreviations mostly follow Forey (1973) [49]: Ang-art, anguloarticular; Ar.pr.mx, articular process of maxilla; Ar.pr.mx.r, articular process of right maxilla; Asp, autosphenotic; Boc, basioccipital; Bpt.pr, basipterygoid process of parasphenoid; Br.r, branchiostegal rays; Cl, cleithrum; Den.l, left dentary; Den.r, right dentary; Dpt, dermopterotic; Dsp, dermosphenotic; Ecp, ectopterygoid; Enp, endopterygoid; Ep, epural (numbered 1–2); Exo, exoccipital; Fr.l, left frontal; Fr.r, right frontal; H, Hypurals (numbered 1–5); Hm, hyomandibula; Hs, Haemal spine; Io, infraorbitals; Iop, interopercle; L.e, lateral ethmoid; Man.l, left mandible; Man.s.c, mandibular sensory canal; Mes, mesethmoid; Mpt, metapterygoid; Mx, maxilla; Mx.l, left maxilla; Ns, neural spines; Op, opercule; Pa.r, right parietal; Pal, palatine; Par, parasphenoid; Ph, Parhypural; Pmx.l, left premaxilla; Pmx.r, right premaxilla; Pop, preoperculum; Pro, prootic; Psp, pterosphenoid; Ptf, post-temporal fossa; Ptmy, posterior myodome; Ptt, post-temporal; Pu, Preural centrum (numbered 1–2); Qu, quadrate; Rart, retroarticular; Sca, scapula; Scl, supracleithrum; Smx 1–2, supramaxillae 1–2; Sop, subopercle; Susp, suspensorium; Sy, symplectic; U, ural centrum (numbered 1–2); Un, uroneural; V, vertebrae; Vo, vomer; X, foramen for vagus.

Institutional—FSL: Université de Lyon, Faculté des Sciences, Lyon, France;
MHNG: Muséum d'histoire naturelle de Genève, Suisse;
MNHN: Muséum National d'histoire naturelle, Paris, France.

4. Results

4.1. Systematic Paleontology

Teleostei Müller, 1845 [50]
Incertae sedis
Ypsiloichthys gen. nov.
ZooBank LSID: urn:lsid:zoobank.org:pub:19D94A46-A9BB-4DCA-8FB1-513F869BC9FE
Type species. *Ypsiloichthys sibelleae* gen. et sp. nov.

Etymology. The generic name is derived from the Greek "ypsilos" for deep and "ichthys" for fish, with respect to its high and deep dorsal and anal fins. The species epithet "sibelleae" is named after Sibelle Maksoud, who is currently working on a detailed study of the site from where this fish originates.

Holotype. MHNG GEPI V5786 (Figures 1–3) is a single and almost complete specimen preserved in a lateral view, lacking some skull roof and caudal elements.

Diagnosis. moderate-sized deep bodied teleost fish characterized by: high dorsal and anal fins; forked caudal fin; cycloid scales covering the entire body and the bases of the dorsal, anal and caudal fins; supraorbitals absent; edentulous jaws; well-developed ascending process of premaxilla; thin maxilla with a well-developed articular condyle; two large supramaxillae, the posterior one with a process extending along the dorsal margin of the anterior one; entry of the mandibular sensory canal on the external side of angular; fused articular and angular; retroarticular excluded from joint facet of the quadrate; hyomandibula with long opercular process; subopercle with a triradiate ridge pattern on its posteroventral corner; pectoral girdle and fins inserted low on the flank; presence of pelvic girdle and fins in connection with the pectoral girdle in thoracic position; wing-like anterior extensions of the few first haemal spines; large semi-circular first dorsal and anal pterygiophores; neural and haemal arches articulated with the centra; presence of supraneurals and epineurals; two ural centra; two uroneurals; five hypurals; 'Z' or step-like segmented caudal fin rays.

Locality and Horizon. The material studied here consists of a single specimen (Figure 1) preserved in the right lateral view, originating from the limestones of Haqel, Lebanon, which belong to the lowermost horizon of the upper Cenomanian of the Sannine Formation.

Species diagnosis. Same as genus, for monotypy.

Counts, measurements, and proportions. All the measurements and counts of different elements were made following Taverne and Gayet [15] (Figure 1) and are shown in Tables 1 and 2.

Table 1. Table showing the counts of different elements of *Ypsiloichthys sibelleae*.

Counts	*Ypsiloichthys sibelleae*
Vertebrae (Total)	39–40
Abdominal centra	18
Caudal centra	21–22
Hypurals	5
Dorsal pterygiophores	48–49
Anal pterygiophores	26–27
Pectoral fin rays	20–21
Pelvic fin rays	8
Dorsal fin rays	49–51
Anal fin rays	31–33
Caudal fin rays (Total)	34
Branchiostegal rays	6–7
Ribs (in pairs)	15–16

Table 2. Table showing the measurements in mm or as a percentage of the standard length of *Ypsiloichthys sibelleae*.

Measurements (as % of SL)	*Ypsiloichthys sibelleae*
Total length (mm)	102
Standard length (mm)	85
Maximum body depth	84
Head length	40
Head depth	49
Predorsal length	21
Peanal length	79
Dorsal fin base length	77
Anal fin base length	50

4.2. Description

This deep-bodied fish is preserved at the surface of a limestone bed. All the elements described below are in the right lateral view. Some elements from the left side are partially seen. However, it does not provide much information. The specimen exhibits some fractures. Its total length is about 102 mm, and its standard length is about 85 mm. Its maximum body depth is around 67 mm (Table 2). Some mechanical preparation was made to reveal more elements, mainly in the skull region.

4.2.1. Cranium

Skull roof. A piece of the left frontal is barely visible as an elongated oval bone contacting the right frontal, but the type of suture between the two bones is unclear. The right frontal is almost entirely visible. It is longer than wide (length to width ratio = 2.59) and strongly constricted at the orbit (minimal interorbital width = ca. 3 mm, maximal temporal width = 4.2 mm). The right frontal is almost rectangular and strongly ornamented. It is crossed laterally, near its posterior border, by a ridge that could be a supraorbital canal, but we are uncertain of its nature due to its transversal orientation. On its lateral margin, from the posterior border to the orbital region, the frontal is sutured to the dermopterotic and the dermosphenotic, respectively. In the orbital region, the ventral side of the frontal is sutured with the pterosphenoid. Anteriorly, the frontal tapers into a rod-like projection contacting, towards its anterior tip, a bone from the ethmoidal region pierced by a foramen. The nature of this bone is unknown as this entire vomero-etmoidal region is not well preserved, covered in part in the matrix, and could not be prepared because of the fragility

of these bones and the surrounding ones. We delimited three bones, with the largest one a possible vomero-mesethmoid bone and another wedged between it and the parasphenoid, which could be the lateral ethmoid.

Posterior to the frontals, the region is poorly preserved, where different elements and the limits between them are difficult to discern. These elements include the right parietal. The exact shape is uncertain, but it seems rectangular, longer than wide. It is in contact with the frontal anteriorly and with the dermopterotic laterally. The latter's limit and shape cannot be precisely identified, either. Yet, it is clear that the dermopterotic is slightly ornamented.

The circumorbital series. The series is formed by two large infraorbital and a few smaller ones that could be broken fragments from a larger one. One large infraorbital overlaps the ventro-anterior part of the hyomandibular shaft on its posterior border. It is ornamented by densely arranged low irregular tubercles. It covers the underlying metapterygoid dorsally. Another large infraorbital is located at the same level as the first large one and is slightly less ornamented than it. Two smaller bones are wedged ventrally between the large infraorbitals and could also be infraorbitals; however, they have little to no ornamentation on their surfaces. All these bones are pierced by small foramina for the infraorbital canal. The uncertainty of the number, shape, and limits of the infraorbitals is due to the poor preservation and the presence of a matrix in this region.

The dermosphenotic is wedged between the autosphenotic posteriorly, the dermopterotic dorsally and the frontal anteriorly. Its exact shape is uncertain as we could not decipher its limits with the autosphenotic. Nevertheless, it has a smooth surface. There is an opening between the dermosphenotic/autosphenotic bones and the pterosphenoid towards their ventral margins. No supraorbital was observed on this specimen.

The braincase. The right autosphenotic is well developed with a prominent lateral process. It forms a stout inclined ridge on the upper dorsolateral margin of the orbit. It is pierced by a foramen posterodorsally with an unknown function. The ventral process of the autosphenotic forms a bridge with the anterodorsal tip of the prootic. Its lateral margin forms the anterior part of the hyomandibular facet.

The visible part of the prootic is a thin rectangular bone. Posteriorly, it extends below the anterior margin of the hyomandibula, and on its straight anterior margin, it forms the lateral wall of the posterior myodome. No foramen or grooves are observed on the prootic.

The supraoccipital is not visible on this specimen. A posttemporal bone belonging to the pectoral girdle is located just above the posttemporal fossa, which in turn is located above an almost rectangular complex formed by the basioccipital and the exoccipital bones, whose line of suture is not visible. It has a foramen for the vagus nerve X. Posterior to the basioccipital condyle is the first vertebral centrum separate from the basioccipital.

The orbital portion of the parasphenoid is an elongated straight bone with almost the same width over its entire length. The presence or absence of teeth cannot be determined because of the overlying matrix. It bears a large ventrolaterally directed basipterygoid process that contacts the endopterygoid.

Near the posterodorsal corner of the orbit, a bone identified as the pterosphenoid is located in contact with the frontal and close to the sphenotic bones. It is almost triangular and small.

There is no evidence of a sclerotic ring.

The upper and lower jaws. The maxilla is edentulous, like the rest of the jaws. It is greatly elongated and thin and tapers anteriorly, bearing on its dorsal margin two large supramaxillae. Its ventral margin is straight, and its surface is smooth. Its anterior extremity is bent inwards, forming a strongly developed articular condyle for articulation with the vomero-ethmoidal region. Both supramaxillae are strongly ornamented and large, with the anterior one longer than deep, whereas the posterior one's main body is almost as deep as long. The posterior supramaxilla has an elongated and thin anterior process extending over the posterodorsal border of the anterior supramaxilla. A small part of the palatine can be seen beyond the dorsal border of the two supramaxillae that probably cover the rest of

it. The premaxillae form the oral margin of the jaw. Only the right premaxilla is entirely visible and well-preserved. It has a long ascending process, as long as the oral margin. As the maxilla, it has a smooth surface. The posterior end of the premaxilla ends at the level of the posterior border of the right dentary. Thus the premaxilla probably covered part of the mandible when the mouth was closed.

The lower jaw is deep. The retroarticular is separate and visible as a small triangular bone not contributing to the joint surface for the quadrate. The angular and articular are fused. The anguloarticular forms a deep articular facet for the quadrate. There is an opening on the lateral side of the bone for the emergence of the mandibular sensory canal. Both dentaries can be seen, but only the right one is visible. The latter is longer than deep (length to depth ratio = 2.56), contacting, over its entire posterodorsal margin, the ventral margin of the anguloarticular. The coronoid process is very deep and slopes anteriorly towards a moderately deep symphysis. Two openings of the sensory canal are visible on the horizontal plateau of the ventral margin of the dentary. The mandible is edentulous.

Hyopalatine and gill arches. The right hyomandibula is an elongated bone with a shaft approximately as broad as its articular head dorsally and narrowing ventrally. A strong descending ridge runs obliquely from the articular head. A well-developed opercular process extends along the upper posterior margin of the bone. The hyomandibular articular facet on the braincase is located in the dermopterotic, autosphenotic, and maybe the intercalar.

The right quadrate is a deeper-than-long fan-shaped bone with the symplectic inserted in the deep notch between its upper posterior margin and the quadratic process. The quadratic process is short, not reaching the level of the dorsal margin of the bone. The articular condyle is single-headed. The symplectic is triangular with a broader dorsal extremity that tapers ventrally.

The endopterygoid is a large, thick triangular bone articulating dorsally with the parasphenoid. It contacts the metapterygoid posteriorly. No other bones of the pterygoid series are visible, and those identified show no evidence of teeth.

Of the rest of the hyoid arch, only six to seven slightly arched branchiostegal rays are visible and located posterior to the mandible and below the preopercle. They vary somewhat in width and length and are arranged in a fan fashion.

The opercular series. The right opercle is a large oval-shaped bone, much deeper than long (with a length-to-depth ratio = 0.39). It shows strong ornamentation over its entire surface. The dorsal half displays well-defined tubercles and a pattern of low vertical ridges in the lower half. A deep L-shaped preopercle lies on the anterior border of the opercle. It has a thin, long dorsal arm that reaches the opercular process for the hyomandibula. The much shorter and broad ventral arm tapers anteriorly around eight small foramina open along the ventral margin of the ventral arm. A thin fracture crosses this part of the preopercle close to these foramina. Posterior to the preopercle and ventral to the opercle, there is a triangular-shaped subopercle that displays a triradiate ridge pattern. These ridges are located behind a large foramen for the preopercular sensory canal. A small interopercle is wedged between the subopercle, preopercle, and cleithrum.

4.2.2. Post-Cranium

Pectoral girdles and fins. A large posttemporal bone is located above the basioccipital and exoccipital complex. It almost reaches the parietal. It has a long and thin ventral arm (or process). But because of the poor preservation of this region, we cannot provide further information.

A long and posteriorly curved cleithrum is present along the posterior margin of the opercular bones, starting at around half of the length of the opercle. Its dorsal limb is longer and broader than the ventral one. The dorsal limb forms an edged corner, which corresponds to the point of maximal curvature. Below this point, the pectoral fins are visible. The supracleithrum is an elongated and thin bone having the same depth over its entire length and slightly overlapping the cleithrum on its dorsal part. The postcleithrum and the extrascapular bones are not visible.

The scapula is located along the ventral limb of the cleithrum. It has a complex shape with an upper triangular part and a lower knob-like part, next to which there is the coracoid. The latter bone's shape cannot be easily discerned.

The pectoral fin is inserted low on the flank, including 20–21 rays not segmented nor bifurcated.

Pelvic fin and girdle. The pelvic fin inserts approximately at the same level as the pectoral fin in the thoracic position, and both insert posteriorly to the origin of the dorsal fin. The basipterygium is almost trapezoidal. There are about eight to nine fin rays, unsegmented but bifurcated at their distal ends, with some displaced fins almost reaching the anal fin. The first ray has a long-curved base laying against the pelvic bone. It is slightly broader at its base than the other rays and rapidly bifurcating.

Medial fins. The dorsal fin is large, originating at the fourth or fifth vertebral centrum level, anteriorly to the origin of both the pelvic and pectoral fins and posteriorly up to the caudal peduncle. It contains around 49 to 51 fin rays (including the first one or two procurrent fin rays) that are not segmented and only branched at their distal ends. These rays are supported by around 49 pterygiophores, thus having a one-to-one arrangement with the fin rays, except for the first proximal dorsal pterygiophore articulating with the procurrent and first principal rays. This first dorsal pterygiophore forms a large plate with a curved anterior margin that extends into a long and thin ventral branch. The following six pterygiophores are each composed of an elongated thin proximal radial with a medial ridge along its length, whereas all the rest lack this ridge. Every two pterygiophores insert in the gap between two successive neural spines, except for the first enlarged pterygiophore inserting alone between the fourth and fifth neural spines. The first dorsal fin rays are considerably longer than the last ones near the caudal fin insertion; they decrease progressively in length, giving the dorsal fin a sickle-shaped margin.

The anal fin is large but smaller than the dorsal fin. It originates at the level of the 27th vertebral centrum and extends posteriorly up to the caudal peduncle. It includes around 31 to 33 fin rays that are unsegmented and branched at their distal ends. They are supported by around 27 anal pterygiophores, having a similar one-to-one arrangement of the radials with the fin rays to that of the dorsal fin. The first anal pterygiophore forms, as the dorsal one, a large posteriorly curved plate that extends dorsally into a thin and long branch forming a crest running along its posterior border. It is articulating with the procurrent and principal anal fin rays.

On the other hand, the arrangement between the anal pterygiophores and haemal spines is not as regular as in the dorsal fin. In the posterior part of the fin, one to three pterygiophores insert between two successive haemal spines. The last few pterygiophores are slightly inclined posteriorly rather than vertically, like the first ones. Similarly, to the dorsal fin shape and dorsal fin rays, the first anal fin rays are longer than the last ones reaching the caudal fin giving the anal fin a sickle-shaped margin.

Vertebral column. For detailed counts and measurements, check Tables 1 and 2.

The vertebral axis of this specimen has a slight sinusoidal curvature. It comprises around 39 to 40 vertebral centra, with 18 abdominal ones and 21 to 22 caudal ones, including three preurals and two or three ural ones. The first few centra are higher than long, but the rest, mainly in the caudal region, are as long as high. Due to the poor preservation of the centra, it is difficult to determine the ornamentation and the presence of lateral fossae on them. Each neural and haemal arch is articulated or sutured to its corresponding centrum but not fused.

We counted 15 to 16 ribs, having the same width over their entire length, slightly curved from the back of the skull to the mid of the body at the level of the 17th or 18th vertebral centrum.

The neural spines are thin and rod-like, oriented vertically except for the first two at the back of the skull and the last near the caudal region that becomes posteriorly inclined. The neural arches are in contact with each other.

The first haemal spines bear anterior wing-like expansions on their proximal parts. We are uncertain of the presence of these expansions on the last haemal spines because they are covered by the matrix. Like the neural spines, the previous haemal spines near the caudal peduncle change orientation from straight to posteriorly inclined.

We note the presence of rod-like supraneurals from the back of the skull to the dorsal fin origin, inserted on the anterior margin of the first neural spines. The epineural are present from the back of the skull posteriorly to the posttemporal bone till at least the middle of the caudal region, where only fragments can be seen as most of this region is still covered by matrix. These epineural are thin and curved, especially in the abdominal region, and some seem to be bifurcated. Ossified epipleurals and epicentral are absent.

Caudal skeleton and fin. This region is not well preserved. The caudal fin seems forked, having equal dorsal and ventral lobes. It comprises 29 principal and five procurrent fin rays only seen on the dorsal lobe. In this lobe, the segmentation of most of the principal rays is 'Z' or step-like (Figure 3A), and the distal ends of all the principal fin rays are bifurcated. The caudal region comprises 17 to 19 vertebrae with two or three ural centra supporting the hypurals. There are five hypurals: two ventral ones, H1 and H2, fused, at least at their proximal ends where they display a small fenestra between them and are articulated to U1; two dorsal ones H3 and H4, also fused, at least at their proximal ends, and separated from the complex H1–H2 by a diastema; the fifth hypural H5 is smaller than the others and completely separate from H3–H4 complex. A small centrum is associated with the hypurals H3–H4 and H5, which is probably U2. The parhypural is rod-like with the same width over its entire length and a large articular head with the preural centrum Pu1. There are two long and rod-like uroneurals attached to Pu1. We counted two epurals lying over a reduced neural spine of the Pu1. The neural spine of Pu2 is longer than the latter but shorter than the one preceding it (neural spine of Pu3).

Scales. The body is covered by smooth cycloidal scales, more or less oval-shaped and arranged in an overlapping pattern. Even the bases of the dorsal, anal, and caudal fins are covered with scales. There are no pits on the surface of these scales. It is impossible to ascertain the number of scales covering the body of this specimen, and the lateral line scales are not visible.

5. Systematic Affinities

The specimen under study displays two typical clupeocephalan characters, which are the exclusion of retroarticular from the joint surface for the quadrate and the co-ossification of the angular and the articular, that are considered as shared derived characters for the Clupeocephala by Nelson [51] and Patterson and Rosen [52]. In her revision of characters supporting the clupeocephalan clade, Arratia [53] retained these two characters, although she noticed they are present in other groups of teleosts by convergence. She added another homoplastic synapomorphy of clupeocephalans, the presence of six or fewer hypurals, which is also present in *Ypsiloichthys sibelleae*. The three uniquely derived novelties Arratia [53] identified for the clade (early ossification of autopalatine, hyoidean artery piercing ventral hypohyal, toothplate of last pharyngobranchial or pharyngobranchial cartilage four corresponding to growth of only one toothplate) are rarely observed in fossils, and in particular, are not visible in *Y. sibelleae*.

Specific general body features of *Y. sibelleae*, such as a laterally compressed body, elongated dorsal and anal fins, arrangement of pectoral and pelvic fins, the structure of the jaws, and the opercular series, are reminiscent of the paenecontemporaneous tselfatiiforms and/or the genus *Araripichthys*.

5.1. The Tselfatiiformes and the Protobramidae

From the list of Tselfatiiformes apomorphies suggested by Taverne and Gayet [15], this specimen has six out of the eight characters. These features are as follows: neural and haemal arches articulated but not fused to the corresponding centra; body more or less deep and compressed; postcleithra lost; dorsal and anal fins very long and reaching the caudal

peduncle; dorsal and anal rays not segmented; absence of ossified epipleurals. *Ypsiloichthys sibelleae* lacks the following two apomorphies: absence of anterior supramaxilla and fusion of hypurals 3 and 4 into a hypural plate. This taxon has two supramaxillae, anterior and posterior; within the Tselfatiiformes, the protobramids have no supramaxilla, whereas the plethodids only have one [1]. As for the hypurals, this specimen has four separate hypurals (H1–H2 fused only at their tips and wholly separated from H3–H4 that are also only fused at their tips), hence lacking a hypural plate.

One crucial feature that differs between *Y. sibelleae* and all the plethodids is its paired premaxillae, conversely to the fused ones in this group. The protobramids, on the other hand, possess paired premaxillae as in *Ypsiloichthys*; however, the ascending process differs as it is absent in *Protobrama avus* and poorly developed in *P. woodwardi* and present and curved in *Eusebichthys*. Taverne and Gayet [15] noted a poorly developed ascending process in the holotype of *Abisaadichthys*; however, based on another specimen (CLC S-290), Taverne and Capasso [54] reported the presence of an elongated narrow symphyseal ascending process indicating a preservation bias. Moreover, based on our observation of the holotype (FSL-573086) (Figure 4), we noticed that what was interpreted by the authors as the mesethmoid's long branch is a well-developed ascending process of both premaxillae with the right premaxilla not observed entirely. Similarly, the interpreted mesethemoid in CLC S-290 [54] (Figure 3) can also be a part of the right premaxilla, not entirely visible. But in the three protobramids, the oral arm of the premaxilla is not as developed as in *Ypsiloichthys*, where the arm extends well beyond the maxilla (Figure 2).

Thus, *Ypsiloichthys* exhibits more affinities to the protobramids among the Tselfatiiformes. First, the specimen under study fits the overall discoidal body shape of the Protobramidae, with a head that is short and high, having, in particular, a similar ratio of head length overhead depth (HL/HD = 0.82) close to that of *Abisaadichthys libanicus* (holotype, HL/HD = 0.88). The dermal bones of the skull roof in *Ypsiloichthys sibelleae* are not well preserved, therefore, cannot be compared in detail to the protobramids' skull roofs. However, other elements are identified in this new taxon and shared with all the protobramid genera, such as the absence of interorbital septum, absence of supraorbital bone(s), and absence of epipleurals and epicentral; the presence of supraneurals and epineurals, and scales covering the basis of unpaired fins. The presence of first anal pterygiophores that are elongated, obliquely and posteriorly oriented, forming a large plate, is also shared between the three protobramids and *Ypsiloichthys*; however, in the latter, the first dorsal pterygiophore forms an even larger plate whereas in the protobramids these plates are much smaller compared to the anal ones.

Moreover, Taverne and Gayet [1,15] described the protobramids as having edentulous parasphenoid and palato-quadratic bones except for the endopterygoid, with the dentary and premaxilla teethed to weakly teethed in *Protobrama* and *Abisaadichthys*, and completely toothless in *Eusebichthys*, as in *Ypsiloichthys*. The maxilla being always toothless, is one of the several synapomorphies of the Protobramidae, also seen as *Ypsiloichthys*. As for the parasphenoid and the palate-quadratic bones, teeth are either absent or undetectable because of the orientation of the bones. The latter authors also described large infraorbitals in *Eusebichthys* and *Abisaadichthys* and numerous small and fragmented ones in both species of *Protobrama*. Later, Taverne and Capasso [54] noted the presence of five large visible infraorbitals and about seven large visible ones in *Abisaadichthys* and *Eusebichthys*, respectively, based on the new material. They also stated that both species must have had more infraorbitals than those preserved. However, *Ypsiloichthys* shows two large infraorbitals and some fragments of other infraorbitals, with a different arrangement and shape than what was described for *Eusebichthys* and *Abisaadichthys* and certainly less numerous.

Furthermore, our observations of the holotype of *Abisaadichthys* (Figure 4) allowed us to doubt the infraorbitals interpretation by Taverne and Gayet [15] of the bones located between the parasphenoid and the jaws, which are probably bones of the suspensorium and

not from the circumorbital series. Moreover, the latter region is not well enough preserved to precisely discern the nature and limits of these bones.

Ypsiloichthys shares one important character with *Abisaadichthys* and *Eusebichthys*, that is the short ventral branch of the cleithrum and the insertion of the pectoral fins low on the flanks, unlike in *Protobrama* and the members of the family Plethodidae. Moreover, it shares only with *Abisaadichthys* the presence of an autogenous retroarticular excluded from the joint facet of the quadrate, pelvic girdle and fins, and wing-like anterior extensions on some of the haemal spines. However, Taverne and Capasso [54] stated the presence of "a small autogenous retroarticular in which the condyle of the quadrate is fitted" in a new specimen CLC S-290 assigned to *Abisaadichthys* by the latter authors, in addition to the presence of an autogenous retroarticular and pelvic girdle and fins in a new specimen CLC S-460 assigned to *Eusebichthys* by the same authors.

Ypsiloichthys differs from *Eusebichthys* and *Protobrama* by having epurals, whereas, as stated by Taverne and Gayet [1,15], they lack free epurals. *Abisaadichthys* was also considered to lack epurals, but later, Taverne and Capasso [54] stated that it has two short epurals seen on CLC S-290 and not the holotype. If true, the new taxon shares an additional character with the most primitive protobramid.

As for the other caudal elements, Taverne and Gayet [1,15] stated that *Abisaadichthys* has a separate ural centrum 2, three uroneurals, and 19 principal caudal rays. In contrast, *Protobrama* and *Eusebichthys* have a fused ural centrum 2 to the hypural plate, a single uroneural, and increased principal caudal rays. *Ypsiloichthys* exhibits two ural centra, two uroneurals, and 29 principal caudal fin rays. *Protobrama* and *Eusebichthys* have little to no segmentation of the principal caudal fin rays. In contrast, Abisaadichthys and *Ypsiloichthys* have segmented rays but with a different pattern, 'Z' or step-like in *Ypsiloichthys* (Figure 3A) and straight in *Abisaadichthys* (Figure S2).

In conclusion, *Ypsiloichthys* seems to share most of the characters with the protobramids among the Tselfatiiformes and, more specifically, with *Abisaadichthys*. However, several important characters have been re-described or discovered in the new material of *Abisaadichthys* and *Eusebichthys* in Taverne and Capasso [54]. We noted some misinterpretation in the original material of *Abisaadichthys* (FSL-573086) and significant differences between the interpretations of the *Eusebichthys* and *Abisaadichthys* material in the two publications (Taverne and Gayet [15] vs. Taverne and Capasso [54]), which make us question if the new material truly belongs to the latter genera (e.g., absence/presence of retroarticular and pelvic girdle and fins; retroarticular included/excluded from joint facet for the quadrate; differences in the shape of ascending process of premaxilla and preopercle; number, shape, and arrangement of infraorbitals (Figure 10 in Taverne and Capasso [54] and Figure 17 in Taverne and Gayet [15]). It is also important to mention that the absence of supramaxilla as a synapomorphy for the protobramids can be challenged as the interpreted ectopterygoid by Taverne and Gayet [15] in *Eusebichthys* can be a potential supramaxilla (Figure S7). This can be confirmed following an extensive revision of the family. However, this revision and/or commenting on the differences in the descriptions of the specimens of *Eusebichthys* and *Abisaadichthys* in the two previously mentioned publications are out of the scope of the present paper, and only the characters relevant to the comparison with *Ypsiloichthys* were discussed. A revision of the family Protobramidae is currently in progress.

5.2. Araripichthys

When comparing *Ypsiloichthys sibelleae* to other deep-bodied fishes from the mid-Cretaceous, we found a striking resemblance between its jaw and that of *Araripichthys castilhoi*. The premaxillae are quite distinguished from all the tselfatiiforms, with an elongated ascending process similar to that of *Araripichthys*. In addition to that, a well-developed maxillary articular condyle is present in both taxa. Maisey and Blum [24] questioned if *Araripichthys* mouth was protrusible but then stated that considering this well-developed condyle between the vomer and the maxilla, the protrusibility of the latter

seemed unlikely. In *Ypsiloichthys*, we are unsure of the element to which the maxilla is articulated with its condyle, as the vomero-ethmoid region is not well preserved, and the shape of the bones in this region is unclear.

The smaller *Ypsiloichthys* shares with *Araripichthys* several other characteristics such as (Maisey and Blum [24] and Maisey and Moody [27]): the same deep and compressed general body shape, as previously stated; high and long dorsal and anal fins extending to caudal peduncle; a narrow caudal peduncle; a short and high head; absence of supraorbital; sinusoidal vertebral column (more prominent in *Araripichthys* than in *Ypsiloichthys*); the first anal pterygiophore forming a large, posteriorly curved plate, having ridges and expanded distally, but in *Ypsiloichthys* more semi-circular. Note that all these characters are also shared with the three protobramid genera. Additionally, *Araripichthys* and *Ypsiloichthys* share these characters: the level of the longest dorsal fin ray located above the insertion of the anal fin, and the absence of teeth on the maxilla and dentary, also shared with *Eusebichthys*.

As for the characters only shared between *Ypsiloichthys* and *Araripichthys*: the presence of two supramaxillae covering more than half of the length on the maxilla's dorsal border, premaxilla with an elongated ascending process having almost half of the length of the premaxilla; well-developed articular condyle of the maxilla; a large round opening present between the pterosphenoid and the sphenotic seen in *Araripichthys*, probably present in *Ypsiloichthys*, however slightly covered by matrix; neural arches in contact with each other (Figure 11 in Maisey and Moody [27]); body covered by numerous circular cycloid scales arranged in an overlapping pattern with even the bases of the unpaired fins covered with scales.

Other elements worth mentioning, such as the opening between the autosphenotic and prootic in *Ypsiloichthys* very similar to an opening in *Araripichthys* illustrated but not discussed by Maisey and Blum [24] (p. 210, bottom figure); the prootic with a long crest in both taxa, however, the bone itself in longer and thinner in *Ypsiloichthys*; the presence of large infraorbital with a close arrangement between the two taxa, but they are more numerous in *Araripichthys*; the presence of two uroneurals and hypurals 1 and 2 fused only at the proximal ends with a fenestra at the anterior parts.

On the other hand, *Ypsiloichthys* differs from *Araripichthys* by having: presence of pelvic girdle and fins; neural and haemal arches articulated with their corresponding centra rather than fused to them as in *Araripichthys*; a thin maxilla almost all over its length with a long articular condyle, conversely to the maxilla with a posteriorly and ventrally convex border and a thin rodlike anterior part bearing a strong articular condyle as in *Araripichthys*; two large supramaxillae with one longer than wide and another shorter and wider unlike the two large supramaxillae of almost equal size in *Araripichthys*; a separate retroarticular not contributing to the joint surface for the quadrate; a fused angular and articular; the mandibular sensory canal entry on the external side of the anguloarticular rather than from behind the angular in *Araripchthys*; a first dorsal pterygiophore having the same enlarged and curved plate as the anal one which is not the case for *Araripichthys*; presence of seven hypurals in *Araripichthys* with H3 and H4 separate, whereas in *Ypsiloichthys*, presence of five hypurals with H3 and H4 fused.

Several other characters cannot be compared between the two as they are unknown in *Ypsiloichthys*, and they are as follows in *Araripichthys* as described by Maisey and Blum [24]: the supraoccipital with a prominent crest; parietals extending dorsally over the endochondral part of the supraoccipital; V-shaped epioccipital with a dorsal portion attached below the parietal and a mesially extended ventral portion meeting the supraoccipital; edentulous vomer with a visible connection to the maxilla.

6. Discussion and Conclusions

Within the teleosts, many groups are properly classified and considered monophyletic based on morphological synapomorphies. However, several groups are still not supported as monophyletic, and several others have an unknown placement within the teleosts.

One group with the two latter issues is the Tselfatiiformes. This peculiar Cretaceous group includes many morphologically diversified taxa and is considered monophyletic by Taverne and Gayet [1] based on eight apomorphies. The latter authors also proposed lists of synapomorphies for each of the three families of the order and autapomorphic characters for many of the species. Nevertheless, they did not provide a phylogenetic analysis, and the order was never included in one except for including some of its members in the cladistic analysis of Cavin [21]. The latter recovered members of the Plethodidae (*Tselfatia*, *Bananogmius,* and *Bachea*) in a monophyletic group as the Tselfatiiformes, a basal clupeocephalan and the members of the Lebanese endemic family Protobramidae with *Araripichthys* and *Acanthichthys* grouped in his new suborder Protobramoidei. Several other taxa have been described and placed within the Tselfatiiformes solely based on character discussion and mainly within the family Plethodidae. Taverne and Gayet [1] agree with Cavin [21] that the Tselfatiiformes are basal clupeocephalan.

Another mid-Cretaceous taxon with uncertain relationships within the teleosts is *Araripichthys*. This genus has been referred variously to Beryciformes, Lampridiformes, Elopocephala *incertae sedis*, Elopomorpha, Pachyrhizodontoidei, Protobramoidei (see Maisey and Moody [27] and Mayrinck et al. [30] for reviews). Even in a recent analysis combining anatomical and paleohistological data, *Araripichthys* was still recovered in an *incertae sedis* position as a basal teleost [30].

The newly described taxon here was found to be closely related to the protobramids, mainly among the Tselfatiiformes and *Araripichthys,* as it shares the same general morphology of a small deep and compressed body with elongated and high dorsal and anal fins, forked caudal fins among other characters such as an edentulous maxilla and a sinusoidal vertebral column. Based on the comparisons in the systematic affinities section above, we found it to be closer to *Abisaadichthys*, the least specialized genus among the Protobramidae, mainly based on the two following characters: autogenous retroarticular and the presence of pelvic girdles and fins. As previously noted, separate retroarticular and pelvic girdles and fins were found in the new material of *Eusebichthys* [54]. However, we made no further conclusions as we did not observe this new material.

A critical aspect in which *Ypsiloichthys* is similar to only *Araripichthys* is the composition and shape of the upper jaw, as both have premaxillae with an elongated ascending process, possess two supramaxillae and a well-developed maxillary articular condyle.

On the other hand, *Ypsiloichthys* differs from both *Araripichthys* and *Abisaadichthys* by having two clupeocephalan characters lacking in both groups: a retroarticular excluded from the joint surface of the quadrate (its exclusion/inclusion is doubted in *Abisaadichthys* because of the two different interpretations of Taverne and Gayet [15] and Taverne and Capasso [54] respectively) and fused articular and angular bones. It also exhibits a unique combination of characters, whether some are shared with one of the two groups or only present in it (the long premaxillary ascending process, a thin maxilla with two large supramaxillae, mandibular sensory canal opening on the external side of the anguloarticular complex, first dorsal pterygiophore having the same enlarged semi-circular plate as the first anal pterygiophore). Hence, *Ypsiloichthys sibelleae* merits its generic status. Its reconstruction is provided in Figure 5.

Moreover, the already complex situation in the teleostean lineages (Elopocephala vs. Osteoglossocephala) is made even more complicated but interesting with the recent recovery of a new clade Eloposteoglossocephala (Elopomorpha + Osteoglossomorpha) as a sister group to the Clupeocephala by Parey et al. [55] based on genetic data. In this study, no morphological characters are provided for their monophyletic clade. However, only one is discussed and proposed as a possible synapomorphy: the fusion of the retroarticular with the angular and/or articular.

Figure 5. Reconstruction of *Ypsiloichthys sibelleae* gen. et sp. nov. Artwork by Alain Bénéteau.

Because of the previous hypotheses of the phylogenetic relationships of these fishes, Tselfatiiformes and *Araripichthys*, and within the teleosts, in addition to *Ypsiloichthys sibelleae* with its combination of characters that precludes assignment to a particular clade, a cladistic analysis based on a compilation of a new set of all relevant characters to these groups is necessary. Such characters are discussed here and can be used for this analysis. This will allow us to test the monophyly of the Tselfatiiformes and their placement, as well as that of *Araripichthys* and *Ypsiloichthys* within the Teleostei. However, it is beyond the scope of this paper.

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