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Osteology of *Arnoglossus sauvagei* (Capellini, 1878) (Pleuronectiformes, Bothidae), a fossil flatfish from the Mediterranean Miocene

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ABSTRACT - Two fossil flatfish specimens discovered in laminated diatomites of the Mediterranean Basin are herein re-examined and described. They belong to the single species Arnoglossus sauvagei *(Capellini, 1878) (Bothidae, Pleuronectiformes). The latter's affinities with extinct and extant species of the genus* Arnoglossus *living in the Mediterranean Sea are discussed.*

INTRODUCTION

The Messinian pre-evaporitic marine deposits of the Mediterranean Basin mostly consist of laminated diatomites (Pellegrino et al., 2018; Carnevale et al., 2022). These strata are rich in articulated skeletal remains of bony fishes, which have been studied by many authors (Sauvage, 1870, 1873, 1880; Arambourg, 1925, 1927; Leonardi, 1959; Sturani & Sampò, 1973; Gaudant, 1978; Landini, 1981; Bradley & Landini, 1984; Bedini et al., 1986; Chanet, 1996; Gaudant, 2002, 2008; Carnevale, 2004, 2006, 2007; Carnevale et al., 2022). The aforementioned works have investigated the sedimentology, paleoecology and paleodiversity of these deposits. Among various teleostean species, the small (ca. 50 mm in length) fossil flatfish species *Arnoglossus sauvagei* (Capellini, 1878) is known from Messinian laminated diatomites of both Gabbro (Italy) and Oran-Raz-el-Aïn (Algeria) (Arambourg, 1925, 1927; Chanet, 1997). Several authors (Arambourg, 1927; Landini, 1981; Chanet & Schultz, 1994; Chanet, 1996, 1997) have mentioned this species, but without providing a complete description of its skeleton. Specimens of *A. sauvagei* from the Italian Messinian have been reported as *Rhombus sauvagei* Capellini, 1878 or *Rhombus sauvageus* by De Bosniaski (1878) and Sauvage (1880). Woodward (1901: p. 608) considered these names as invalid due to poor definition. This species has been considered as a member of the family Soleidae in the order Pleuronectiformes (De Bosniaski, 1880; D'Erasmo, 1930; Sturani & Sampò, 1973; Landini et al., 1978). Landini (1981) studied the whole set of fossils assigned to this species that were discovered in Italy; based on meristic data, he concluded that all of them can be gathered into a single species in the family Bothidae, namely, *Arnoglossus sauvagei*. Some fossil juvenile flatfish specimens from the Messinian of Spain have also been identified as *Arnoglossus* sp. and *A. sauvagei* by De La Chapelle & Gaudant (1987) and Gaudant et al. (1994). *Arnoglossus sauvagei* was mentioned by Chanet & Schultz (1994) and Chanet (1996, 1997) in their studies of fossil pleuronectiforms, and by Gaudant (2008) in his work dedicated to the teleostean paleodiversity of the Messinian of Algeria. Chanet (1997) noted that another fossil species from the Messinian of Oran-Raz-el-Aïn (Algeria), *Citharichthys oranensis* Arambourg, 1927, is identical to *A. sauvagei* from Gabbro. Thus, the former species became a junior synonym of the latter, which appears to be present along both shores of the Western Mediterranean Sea in the Messinian laminated diatomites. The aim of the present work is to provide a detailed description of the osteology of the species in order to clarify its systematic position.

MATERIALS AND METHODS

The present study is based on two well-preserved fossils of *Arnoglossus sauvagei*, namely: the holotype of *Rhombus sauvagei* from the Messinian of Gabbro (Italy), specimen stored in the Muséum National d'Histoire Naturelle (= MNHN; Paris, France); and a second specimen described as *Citharichthys oranensis* by Arambourg (1927), Arambourg collection number 265, Messinian of Oran (Algeria), outcrop of Raz-el-Aïn, specimen stored in the MNHN. Due to poor preservation of the Oran specimen, the present redescription is based on the holotype except where specified otherwise. The following recent material was examined for comparison: *Arnoglossus thori* Kyle, 1913 (MNHN-IC-1962-62; Banyuls, France) (five specimens) and *Arnoglossus laterna* (Walbaum, 1792) (MNHN-IC-1975-0608; Mediterranean Sea) (four specimens).

Anatomical abbreviations

an.pt: anal-fin pterygiophore; ang-art: angulo-articular; as.pr: ascending process; cl: cleithrum; co: coracoid; d: dentary; d.pt: dorsal-fin pterygiophore; ect: ectopterygoid; ent: entopterygoid; e: epipleural; ep: epural; ey.tr: eye

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traces; fr: frontal; h.a: haemal arch; hmd: hyomandibula; h.sp: haemal spine; hyp: hypural; m: myorhabdoi; mx: maxilla; n: neurocranium; n.a: neural arch; n.sp: neural spine; p.b: pelvic bone; p.f: pectoral fin; php: parhypural; pmx: premaxilla; pcl: postcleithrum; pop: preopercle; ph: parhypural; ps: parasphenoid; PU: preural centrum; q: quadrate; r: rib; sop: subopercle.

SYSTEMATIC PALEONTOLOGY

Order Pleuronectiformes Bleeker, 1859
Family Bothidae Smitt, 1892

Genus *Arnoglossus* Bleeker, 1862

Arnoglossus sauvagei (Capellini, 1878)
(Figs 1-6)

Description - Arnoglossus sauvagei is a small flatfish; the total length (TL) of the holotype is 49 mm, whereas its standard length (SL) is 42 mm. Specimen nº 265 of the Arambourg collection (MNHN) is more fragile and smaller (TL = 43 mm) than the holotype; therefore, it might be a juvenile.

Cephalic skeleton - Only the overall shape of the neurocranium is preserved: the limits between the different bones cannot be detected. The ethmoid region is poorly preserved, only the imprint of the distal end of the parasphenoid being visible. In the orbital region, the frontals develop a high, shell-like vertical blade supporting the upper orbit, which preserves the imprint of the right eye (Fig. 2). The dorsal border of this region is rounded and supports the anteriormost proximal pteriogophores of the dorsal fin. The neurocranium does not seem to feature a developed occipital crest. A straight parasphenoid forms the ventral border of the neurocranium. The imprint of the other left eye can be detected more ventral to the parasphenoid on the left entopterygoid. With such an organisation, *Arnoglossus sauvagei* has an asymmetrical skull with its two eyes located on the left side.

In the splanchnocranium, the left hyomandibula is well preserved. It is an elongated bone with two articular processes; the main part of the bone is hidden by the preopercle. The quadrates are also present; they have a long posterodorsal spine. The articulation facet with the angulo-articular is not well developed. The eyed-side quadrate is larger than its homologue from the blind side. A large rhomboid entopterygoid and a broad ectopterygoid are present.

The left maxilla is the sole preserved bone of the eyed-side upper jaw. This bone has its proximal end broken, while the rest of the bone consists of a distally-widened blade with an anteriorly rounded dorsal edge. The left-side lower jaw is elongated, with a poorly developed coronoid process. The limit between the dentary and the angulo-articular bone is sigmoid. The dentary bears a dozen sharp teeth on its oral edge. The posterior region of the angulo-articular joint has an acetabulum which articulates with the quadrate. No supramaxilla is present on the left side.

The blind-side premaxilla is a robust bone with fine teeth (Fig. 3). Anteriorly, this bone presents two dorsally directed processes. The first such process is thin, needle-like and slightly curved posterodorsally. The second is shorter, thicker and forms a globular mass. The blind-side maxilla is partially hidden by the premaxilla. This bone presents a distally enlarged extremity. No supramaxilla is present on the blind side. Only the outline of the blind-side mandible can be observed. This mandible is more elongated and thinner anteriorly than the eyed-side mandible. Fine teeth are present on this mandible. Few bones of the opercular series are clearly visible (Fig. 2). The shape of the two preopercles is discernible. They are angled bones, the two branches of which form an angle of approximately 115°. The anterior edge of each branch is straight, while the posterior edge is rounded. The blind-side preopercle is slightly wider than its eyed-side homologue. No trace of a preopercular sensory canal can be detected. A fragment of the eyed-side subopercle is visible ventrally.

Fig. 1 - (color online) Holotype of *Arnoglossus sauvagei* (Capellini, 1878), photograph. Scale bar = 0.5 mm.

The urohyal of *Arnoglossus sauvagei* is hidden by the other bones, but its shape can be outlined on specimen n° 265 of the Arambourg collection (Fig. 4). It is a hook-shaped bone with a robust, straight dorsal branch and a curved, anteroventrally directed ventral branch. A posterior lamina is present on this branch. The anterior tip of the dorsal part is missing (Fig. 4).

Postcranial axial skeleton - Thirty-seven vertebrae form the axial skeleton of *Arnoglossus sauvagei*, including ten precaudal vertebrae and 27 caudal vertebrae. Each precaudal vertebra has a pair of ventrally oriented haemal arches. Their length increases progressively from the fourth to the last precaudal vertebra. Each of the haemal arches bears a pair of fine pleural ribs. Except for the first one, each precaudal vertebra displays a long and fine neural spine, which is anteriorly curved in the anterior precaudals to become straight further posteriorly. In the caudal region, the first spines are straight, whereas the following spines are shorter and project posterodorsally. Each caudal vertebra has a long haemal spine. The first such spine is vertical and robust. It supports the first anal fin pterygiophore on its anterior edge. Further posteriorly, the haemal spines become progressively more posteroventrally oriented. Numerous intermuscular bones are present throughout the axial skeleton. At the base of the neural spines there are fine, rod-shaped epimerals. Similarly, at the base of the haemal spines, hypomerals are visible, being similar to the epimerals. Along the haemal and neural spines, myorhabdoi are present. These are rod-shaped bones with pointed, "brush-like" branches at both extremities (Fig. 5).

Median fins - Spines are absent on the median fins (Fig. 1). Each median fin extends along the entire length of the body, up to the caudal fin. The dorsal fin has 74 rays. It is present above the skull with 13 epicranial rays. Each dorsal ray is supported by a thin pterygiophore. In the supracranial region, these are inserted perpendicular to the neurocranium. Posteriorly, the pterygiophores of each median fin are in contact, in pairs, with the distal end of a neural spine or a haemal spine. The anal fin is comprised of 60 rays. The two anteriormost anal rays are supported by the first anal fin pterygiophore. The latter is a long, sigmoid bone that supports anteriorly two anal rays and the next nine pterygiophores on its ventral edge (Fig. 2). Its posterior end is attached to the anterior face of the first haemal spine. The following pterygiophores are supported by the haemal spines.

Paired fins - The skeleton of each pectoral fin is formed by a large, curved cleithrum supporting a coracoid and a needle-like postcleithrum on its dorsal edge (Fig. 2). The whole bone complex supports six or seven pectoral rays. The pelvic fin rays are poorly preserved. A few traces allow to estimate their number at five on each pelvic fin. The pelvic fins are supported by pelvic bones. These are long and thin, and join the distal end of the cleithra.

Caudal fin and endoskeleton - Only 11 caudal rays are preserved. They are supported by a set of hypural plates (Fig. 6). In the hypocercal lobe, the endoskeleton consists of the parhypural and a hypural plate formed by the fusion of hypurals 1 and 2. This lower hypural plate is not fused to the centrum of PU1. In the epicercal lobe, two hypural plates support the rays of the caudal fin: one such plate is formed by the fusion of the epural and hypural 5, while another, larger and more ventral one, results from the fusion of hypurals 3 and 4. The latter hypural plate is fused with centrum PU1. The exact shape of the upper hypural

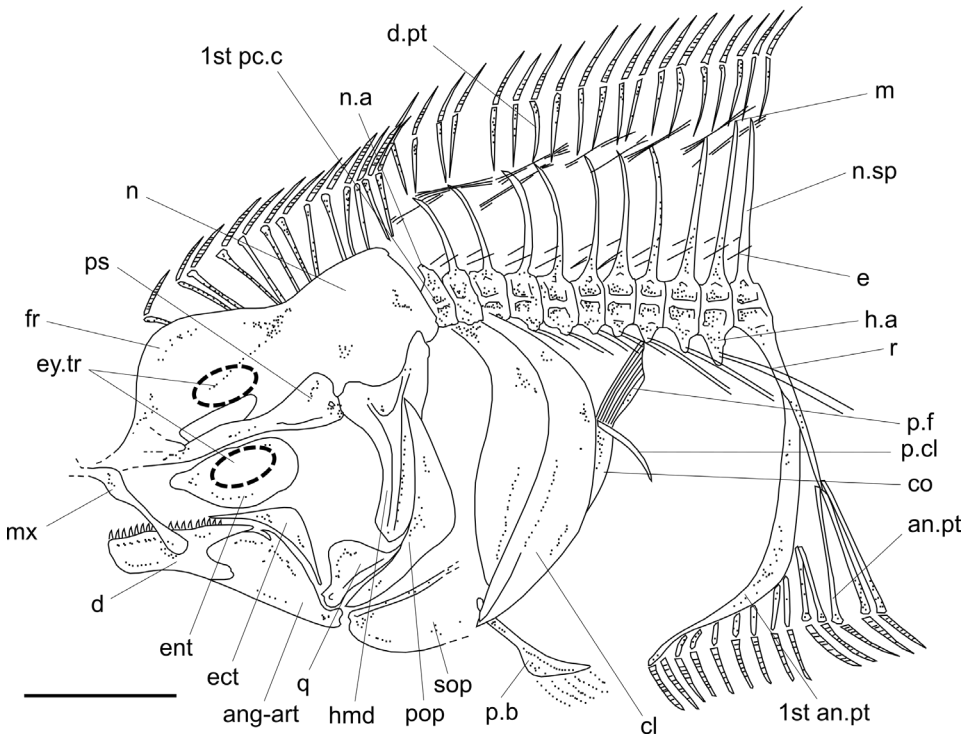

Fig. 2 - Anterior part of the eyed side of the *Arnoglossus sauvagei* (Capellini, 1878) holotype, line drawing. Scale bar = 0.3 mm.

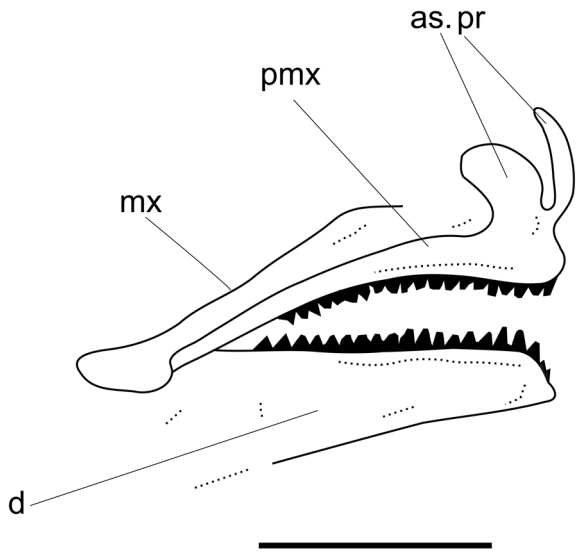

Fig. 3 - Anterior part of the blind-side skeleton of the mouth of the *Arnoglossus sauvagei* (Capellini, 1878) holotype, line drawing. Scale bar = 0.1 mm.

plate (= epural + hypural 5) is uncertain. The haemal and neural spines of centrum PU2 also support the caudal rays. The haemal arch of PU2 is fused to the centrum. There is no trace of uroneural 1.

Landini (1981: p. 10, fig. 2) described the caudal endoskeleton of this species as having a peculiar ventral hypural plate (= fused hypurals 1 and 2) fused with PU1. This architecture is uncommon in pleuronectiform species (Amaoka, 1969; Hensley, 1977; Hensley & Ahlstrom, 1984) and has not been observed in the specimens examined herein.

DISCUSSION

Arnoglossus sauvagei displays the following characters: 1) asymmetrical skull; 2) epicranial extension of the dorsal fin up to the orbital region; 3) no supramaxilla; 4) elongated and sigmoid first anal pterygiophore supporting the anteriormost anal fin rays; 5) free parhypural; 6) no uroneural 1; 7) no spines on median fins; 8) urohyal bearing an anteroventrally directed ventral branch; 9) haemal arch of PU2 fused to the centrum; 10) first dorsal fin pterygiophores perpendicular to the skull roof; 11) eyed-side mesopterygoid present; 12) hypurals 3 and 4 fused together and to the centrum of PU1; 13) hypurals 1 and 2 fused together; 14) no neural spine on first precaudal centrum; and 15) myorhabdoi present.

According to Chapleau (1993), Cooper & Chapleau (1998), Hoshino (2001) and Chanet et al. (2020), character 1 is an apomorphic state for flatfishes, while characters 2-8 are synapomorphies of Pleuronectoidei. Character 9 is a synapomorphy of Pleuronectoidei (absent in citharid and achirid species). Character 10 is a plesiomorphic state for Pleuronectoidei, but indicates that *Arnoglossus sauvagei* is not a samarid, nor a member of the Achiridae-(Soleidae-Cynoglossidae) clade. Character 11 is also a plesiomorphic state for Pleuronectoidei, further showing that the fossil species studied herein does not belong to Soleidae or Cynoglossidae. Within Pleuronectoidei, characters 12 and 13 are only present in flounders of the scophthalmid, paralichtyid, pleuronectid and bothid families. Character 14 only exists in bothids and paralichthyids of the *Cyclopsetta* group (= Cyclopsettidae sensu Campbell et al., 2019). Character 15 is an apomorphy of Bothidae (Hensley, 1977; Chapleau, 1993; Chanet et al., 2004). Therefore, *Arnoglossus sauvagei* can be regarded as a member of the family Bothidae.

With 270 nominal Recent species (Eschmeyer & Fricke, 2023), Bothidae is among the most speciose families of Pleuronectiformes (Munroe, 2005), though

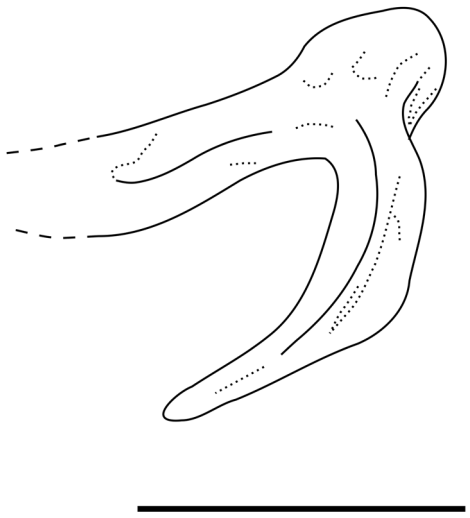

Fig. 4 - Urohyal of the *Arnoglossus sauvagei* (Capellini, 1878) holotype in left lateral view, line drawing. Scale bar = 0.1 mm.

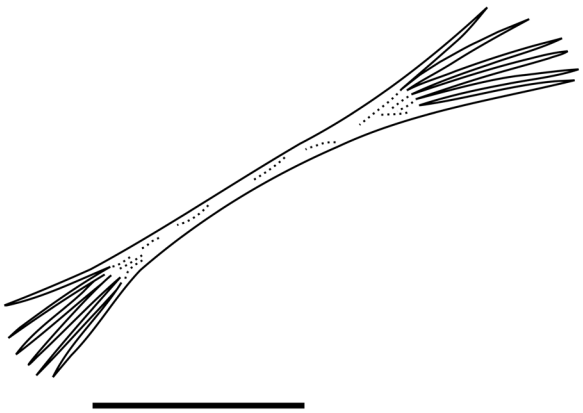

Fig. 5 - Myorhabdoi of the *Arnoglossus sauvagei* (Capellini, 1878) holotype, line drawing. Scale bar = 0.05 mm.

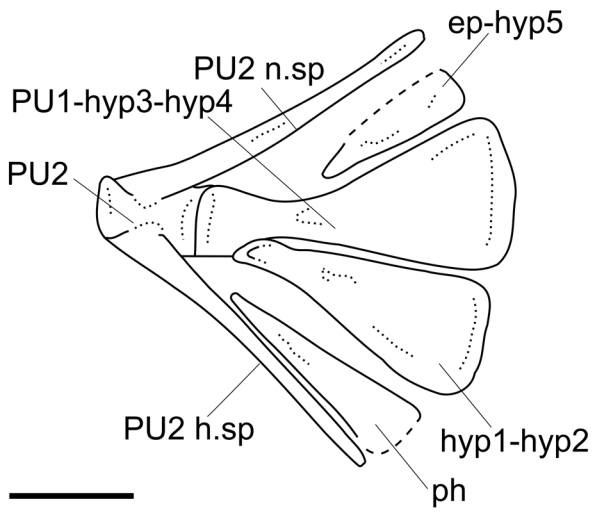

Fig. 6 - Caudal endoskeleton of the *Arnoglossus sauvagei* (Capellini, 1878) holotype in left lateral view, line drawing. Scale bar = 0.2 mm.

one whose systematics are still in need of revision due to the high diversity and confusions in the alpha-taxonomy (Munroe, 2015). Within this clade, the species reappraised herein has been placed in the Recent genus *Arnoglossus* by Landini (1981). This genus encompasses 67 extant species (WoRMS - World Register of Marine Species - *Arnoglossus* Bleeker, 1862) that are known vernacularly as scaldfishes. It was defined by Bleeker (1862: p. 427) based on characters that cannot be detected on the fossils, including the shape of the lateral line. Norman (1934: p. 175) noted that "[t]he genus *Arnoglossus* still remains a somewhat heterogeneous group, but I am unable to find any valid reasons for its further subdivision". Nevertheless, the same author, and later Amaoka (1969), redefined the genus, once again on the basis of characters that are not apomorphies. Several authors, using morphological or molecular data, have subsequently examined the systematics of bothid taxa (Fukui, 1997; Li et al., 2015; Chanet, 2024). Overall, their analyses tend to show that the genus *Arnoglossus* is not monophyletic. That said, in the absence of new results on the systematics of the family Bothidae, the studied specimens are provisionally assigned to the genus *Arnoglossus*.

Gaudant (2002) remarked on the similarity, existing at least in terms of genera, between the Messinian and Recent Mediterranean ichthyofaunas. It is therefore of interest to compare *A. sauvagei* with Recent species of the genus *Arnoglossus* occurring in the Eastern Atlantic and nearby seas, including the Mediterranean cul-de-sac. Five Recent *Arnoglossus* species are present in this broad area (Fischer & Hureau, 1987; Béarez et al., 2017), namely: *A. ruepelli* (Cocco, 1844), *A. laterna* (Walbaum, 1792), *A. imperialis* (Rafinesque, 1810), *A. thori* Kyle, 1913 and *A. grohmanni* (Bonaparte, 1837) (= *A. kessleri* Schmidt, 1915). The osteology of these species has only been partially described by Chabanaud (1933) for *A. laterna* and *A.* (= *Kyleia*) *thori*, with only meristic data being known for the remaining species (Tab. 1). These data tend to show that *A. sauvagei* slightly differs from the Recent Mediterranean species of *Arnoglossus* in terms of postcephalic anatomy, and especially in the number of rays that comprise the median fins (Tab. 1). These differences could be viewed as minor, and *A. sauvagei* might thus be considered as a member of some Recent species. However, pending the results of further systematic analyses of the bothid species as well as a comprehensive re-examination of the genus *Arnoglossus*, the attribution of the fossils dealt with herein to *A. sauvagei* is maintained. Consequently, even if the evolutionary history of the Bothidae still needs clarification, the available data suggest that, with *Arnoglossus sauvagei* and *Oranobothus arambourgi*, the diversity of bothid fishes was lower than today in the Late Miocene as far as the Mediterranean Sea is concerned. This may be the result of the peculiar biogeochemical and oceanographic dynamics which the Mediterranean region was subjected to during the Late Miocene (Agiadi et al., 2024); these included widespread deoxygenation events (with sapropel formation) and conspicuous salt deposition as proposed by Mancini et al. (2024).

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Arnoglossus sauvagei	10 precaudal vertebrae, 27 caudal vertebrae, 74 dorsal rays (with 13 epicranial rays), 60 anal rays
Arnoglossus thori	10 precaudal vertebrae, 27 caudal vertebrae, 78-83 dorsal rays (with 14 epicranial rays and sometimes an elongated second ray), 60-68 anal rays
Arnoglossus laterna	10 precaudal vertebrae, 27-30 caudal vertebrae, 85-95 dorsal rays (with 16 epicranial rays), 65-72 anal rays
Arnoglossus imperialis	10 precaudal vertebrae, 28 caudal vertebrae, 78-106 dorsal rays with four to five elongated anterior rays forming a large crest, 74-82 anal rays
Arnoglossus ruepelli	10 precaudal vertebrae, 35 caudal vertebrae, 110-118 dorsal rays, 86-94 anal rays
Arnoglossus grossmani (= *A. kessleri*)	10 precaudal vertebrae, 32 caudal vertebrae, 80 dorsal rays, 51-57 anal rays

Tab. 1 - Meristic values in *Arnoglossus sauvagei* (Capellini, 1878) and Recent *Arnoglossus* species from the Eastern Atlantic and related seas (including the Mediterranean cul-de-sac). Data on Recent species come from Chabanaud (1933) and Nielsen (1986).

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