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An unexplored anatomic region for phylogenetics: Architecture of the epicranial portion of the dorsal fin of the Bothidae (Teleostei: Pleuronectiformes)

by

Bruno CHANET (1)

Résumé. – Une région anatomique ignorée en phylogénie : architecture de la partie épïcrañienne de la nageoire dorsale des Bothidae (Teleostei : Pleuronectiformes)

L'architecture de la partie épïcrañienne de la nageoire dorsale des Bothidae est ici étudiée pour la première fois. Ce travail montre que les espèces de Bothidae présentent une variabilité importante dans les relations entre le neurocrañe et les ptérygiophores de la nageoire dorsale. Cinq caractères sont identifiés et leurs informations phylogénétiques potentielles sont discutées. Plusieurs clades possibles au sein des Bothidae sont proposés sur la base de ces observations. L'intérêt potentiel de ces caractères pour la phylogénie est souligné et les hypothèses sont comparées à celles fournies par les travaux anatomiques et moléculaires.

Key words. – Dorsal fin, Anatomy, Phylogeny, Bothidae, Pleuronectiformes

Our understanding of the phylogeny of at least several groups of flatfishes, order Pleuronectiformes, has been greatly improved by the study of the architecture of the epicranial portion of the dorsal fin. Besides their unique ocular asymmetry (Chapleau, 1993; Friedman, 2008), flatfishes are known to have a dorsal fin extending onto the dorsal part of the neurocranium (Chapleau, 1993), region commonly called the epicranial portion of the dorsal fin. Within Soleidae, a high and important diversity has been recognised, from a phylogenetic perspective, in the structure of the relationships of the supracranial pterygiophores (Chapleau, 1989). Several synapomorphies have been identified in this region for Soleoidei (Chapleau and Keast, 1988), Cynoglossidae (Chapleau and Keast, 1988) and Citharidae (Hoshino, 2001). However, for several families, such as Pleuronectidae (Cooper and Chapleau, 1998) or Scophthalmidae (Chanet, 2003), the epicranial portion of the dorsal fin does not fundamentally differ among genera. Nevertheless, the anatomy of this region was not been studied for other flatfish families, as Paralichthyidae, Samaridae and Bothidae. Here we present a study of the complex supracranial morphology among the following bothid genera: *Arnoglossus* Bleeker, 1862, *Asterorhombus* Tanaka, 1915, *Bothus* Rafinesque, 1810, *Chascanopsetta* Alcock, 1894, *Crossorhombus* Regan, 1920, *Engyophrys* Jordan & Bollman, 1890, *Engyprosoon* Günther, 1862, *Grammatobothus* Norman, 1926, *Japanolaeops* Amaoka, 1969, *Kamoharaia* Kuronuma, 1940, *Laeps* Günther, 1880, *Lophonectes* Günther, 1880, *Monolene* Goode, 1880, *Parabothus* Norman, 1931, *Perissias* Jordan & Evermann,

1898, *Taeniopsetta* Gilbert, 1905, *Psettina* Hubbs, 1915 and *Trichopsetta* Gill, 1889.

The Bothidae comprise a diverse and globally distributed family of the Pleuronectiformes order with 349 nominal species (Nelson *et al.*, 2016). These flatfishes present several particular features (ossification of neoneural ligaments (Patterson and Johnson, 1995) into brush-like intermuscular bones (Fig. 1), called myorhabdoids (Hensley, 1977; Chapleau, 1993; Fukui, 1997; Chanet *et al.*, 2004), absence of the neural spine on the first precaudal vertebra (Fig. 1) (Amaoka, 1969), asymmetry in pelvic fin morphology (Fig. 1) (Amaoka, 1969; Hensley and Ahlstrom, 1984; Chapleau, 1993; Fukui, 1997). Several authors (Chabanaud, 1949; Amaoka, 1969; Hensley, 1977; Hensley and Ahlstrom, 1984; Chapleau, 1993; Munroe, 2005, 2015) regarded Bothidae as a monophyletic group. However, the relationships within this family are still very uncertain and its systematics still require investigations due to the high diversity and confusion in the alpha-systematics of the family (Munroe, 2015). The anatomy of many bothid species has been described (Amaoka, 1969) but the epicranial portion of the dorsal fin was not investigated so far. Amaoka (1969) proposed an evolutionary tree for bothids (p. 326, fig. 131). His investigation, however, was based solely on Japanese species and used an eclectic approach, mixing unidentified character-states and making it difficult to reconstruct the group's evolutionary history. Fukui (1997) tried to resolve the interrelationships of 21 bothid taxa based on adult and larval morphology. However, this analysis is weakly supported with only 16 characters, 4 of them uninformative. Thus, a comprehensive phylogenetic tree of bothid species is actually wanting and remains one of the main goals regarding the systematics of flatfishes. Molecular works dedicated to bothid species are still scarce (see discussion) and morphological studies did not take into consideration the anatomy of the epicranial portion of the dorsal fin of the Bothidae. Here, original observations are presented that contribute to resolve the phylogeny of bothid species.

MATERIAL AND METHODS

The specimens of Bothidae examined are listed below. Institutional abbreviations followed Eschmeyer (1998). Lengths in mm are expressed as standard lengths (SL).

Arnoglossus sp. ANSP 145256, 108, 110, 124 mm; *Arnoglossus blachei* BMNH 1930.5.6.36, 73.7 mm; *Arnoglossus* (?*fisoni*) Ogilby, 1898, I. 33372003, 80, 89, 96, 97, 98, 99 mm; *Arnoglossus conspersus*, USNM 282243, 52, 68 mm; *Arnoglossus fisoni*?, AMS I. 33661001, 96 mm; *Arnoglossus imperialis* (Rafinesque, 1810),

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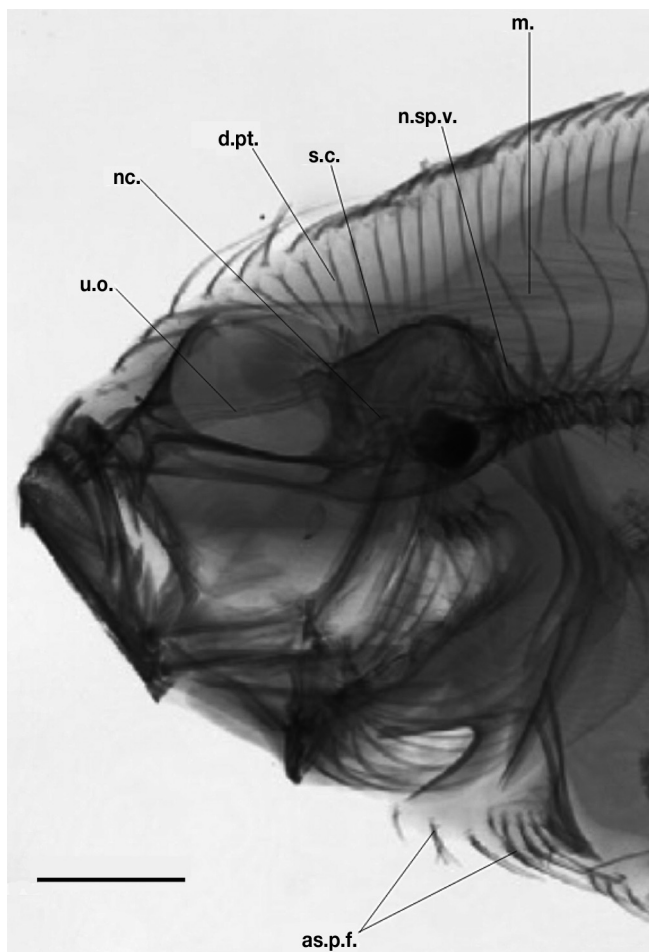


Figure 1. – Anteriormost part of an x-rayed *Arnoglossus blachei* BMNH 1930.5.6.36. (SL: 73.7 mm). as.p.f.: asymmetrical pelvic fins; d.pt.: dorsal-fin pterygiophore; m.: myorhabdoi; n.sp.v.: absence of neural spine on the first precaudal vertebra; nc.: neurocranium; s.c.: supraoccipital crest; u.o.: upper orbit. Scale bar = 0.5 cm.

NMC 60-0322, 130 mm; USNM 282257, 115, 125, 130, 135 mm; *Arnoglossus tapeinosoma* (Bleeker, 1865), USNM 38709, 59, 91 mm; *Arnoglossus thori* Kyle, 1913, USNM, 28277, 61, 63 mm; *Arnoglossus laterna* (Wallbaum, 1792), MNHN 1995-608, 61, 79, 83, 84 mm; *Arnoglossus thori* Kyle, 1913, MNHN 1962-62, 84, 91, 97, 100, 104 mm; *Asterorhombus intermedius*, MNHN 1999-1992, 80, 100, 103 mm; *Bothus lunatus*, NMC 68-2101, 142 mm; *Bothus podas*, MNHN 1977-126, MNHN 1975-422, MNHN 1958-154, 69, 94, 100 mm; *Bothus maculiferus*, NMC 68-0275, 74, 115 mm; *Bothus obliquiocularis*, USNM 93078, 45, 70 mm; *Chascanopsetta porigera* (Gilbert, 1905), USNM 282756, 227, 230, 390 mm; *Chascanopsetta crumenalis*, USNM 25509, 168, 178, 196, 202, 236 mm; *Chascanopsetta lugubris*, USNM 236129, 142, 144, 147, 162, 164 mm; *Crossorhombus azureus*, I.22806-020, 95, 97, 107 mm; *Crossorhombus azurea*, I.31484009, 85, 90, 93 mm; *C. valderostratus* (Alcock, 1890), USNM 37931, 36, 38, 40, 84 mm; *Engyophrys sanctilaurentii*, MNHN 2002-824, 89 mm; *Engypropon bleekeri*, I. 33663001, 70, 74, 77, 78 mm; *Engypropon grandisquamma*, I. 20771-044, 70, 77, 78 mm; *Grammatobothus polyophthalmus*, USNM 260480, ?? mm. USNM 260449, 100 mm, NMC 77-0034, 98 mm; *Japanolaeops dentatus*, MNHN 2000-4376,

75, 82 mm; *Kamoharaia megastoma*, MNHN 1986-1047, 105 mm; *Laeops guntheri*, USNM 37394, 55-60-62-64 mm; *Laeops clarus*, USNM 93558, 112-117 mm; *Lophonectes gallus*, MNHN 1890-132, 106 mm; *Monolene sessilicauda*, USNM 26002, 78-81-86-88-90-90-92-108 mm; *Monolene atrimana*, USNM 59555, 79, 80, 85, 85, 90, 99, 100, 113, 116 mm; *Parabothus* sp., ANSP 145297, cleared and stained, 74 mm; *Perissias taenipterus*, USNM 28645, 65, 80 mm; *Psettina variegata*, USNM 93091, 92 mm; *Taeniopsetta* sp., ANSP 145354, cleared and stained, 78 mm; *Taeniopsetta radula*, USNM 51639, 114 mm; *Tosarhombus neocaledonicus*, MNHN 1994-320, MNHN 1994-321, MNHN 1994-323, MNHN 1994-324, MNHN 1994-325, MNHN 1994-326, 118, 128, 130, 134, 142, 143, 158 mm; *Trichopsetta carribae*, USNM 214582, cleared and stained, 83 mm; USNM 208574, 54, 82, 83, 87, 88, 97, 105 mm.

RESULTS

Examination of 130 radiographed and cleared and stained specimens belonging to 19 genera and 38 species of bothids allows the identification of 5 anatomical characters. These are listed below and in Table I. Figures 1 to 4 show the character-states for these

Table I. – Number of epicranial dorsal-fin pterygiophores among the species studied.

Taxon	Number of epicranial dorsal-fin pterygiophores
<i>Arnoglossus blachei</i> (1)	15
<i>Arnoglossus</i> (?) <i>fison</i> (1)	14
<i>Arnoglossus conspersus</i> (1)	12
<i>Arnoglossus fisoni</i> ? (4)	14
<i>Arnoglossus imperialis</i> (1)	14
<i>Arnoglossus tapeinosoma</i> (1)	12
<i>Arnoglossus thori</i> (4)	14
<i>Arnoglossus laterna</i> (4)	16
<i>Asterorhombus intermedius</i> (1)	11
<i>Bothus podas</i> (3)	13
<i>Bothus maculiferus</i> (2)	16
<i>Chascanopsetta porigera</i> (3)	15
<i>Chascanopsetta crumenalis</i> (4)	14
<i>Chascanopsetta lugubris</i> (5)	15
<i>Crossorhombus azureus</i> (3)	15
<i>Engyophrys sanctilaurentii</i> (1)	8
<i>Engypropon bleekeri</i> (4)	16
<i>Grammatobothus polyophthalmus</i> (3)	12
<i>Japanolaeops dentatus</i> (2)	14
<i>Kamoharaia megastoma</i> (1)	15
<i>Laeops guntheri</i> (4)	12
<i>Laeops clarus</i> (2)	14
<i>Lophonectes gallus</i> (1)	12
<i>Monolene sessilicauda</i> (8)	11
<i>Monolene atrimana</i> (9)	11
<i>Parabothus</i> sp. (1)	14
<i>Perissias taenipterus</i> (2)	13
<i>Taeniopsetta</i> sp. (1)	11
<i>Taeniopsetta radula</i> (1)	10
<i>Tosarhombus neocaledonicus</i> (7)	14
<i>Trichopsetta carribae</i> (1)	13

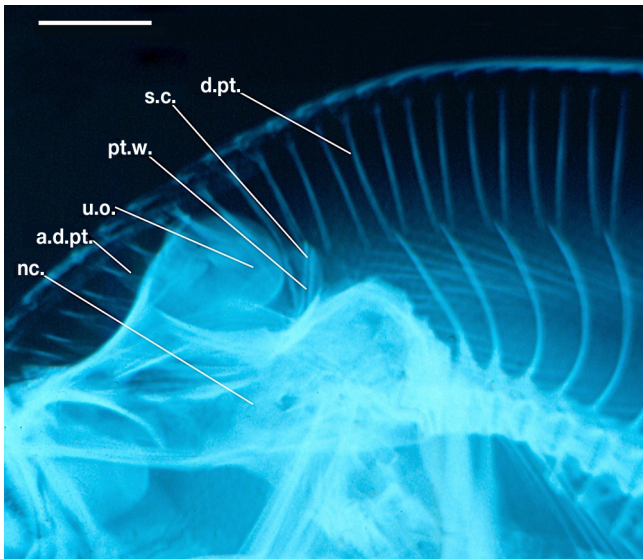


Figure 2. – Anterior part of an X-ray *Bothus maculiferus* NMC 680275 (115 mm). a.d.pt.: anterior dorsal hourglass-shaped pterygiophore; d.pt.: dorsal-fin pterygiophore; nc.: neurocranium; pt.w.: pterygiophore well; s.c.: supraoccipital crest; u.o.: upper orbit. Scale bar = 0.5 cm.

characters. These characters are:

Supraoccipital crest

The supraoccipital crest is reduced, with no dorsal expansion in *Arnoglossus blachei* (Fig. 1), *A. imperialis*, *A. laterna*, *A. thori*, *Asterorhombus*, *Chascanopsetta*, *Engyprophrys*, *Japanolaeops*, *Kamoharaia*, *Laeops*, *Monolene*, *Perissias*, *Psettina* and *Taeniopsetta*. In contrast, in *Arnoglossus macrolophus*, *A. fisoni*, *A. tapeinosoma*, *Bothus* (Fig. 2), *Crossorhombus*, *Engyprosoyon*, *Grammatobothus*, *Lophonectes*, *Parabothus* (Fig. 4), *Tosarhombus* and *Trichopsetta*, the supraoccipital crest is developed with a flattened dorsally orientated expansion.

Pattern on the dorsal margin of the supraoccipital crest

The dorsal margin of the supraoccipital crest is smooth or slightly crenulated in the studied specimens belonging to the taxa: *Arnoglossus* (Fig. 1), *Asterorhombus*, *Chascanopsetta*, *Engyprophrys*, *Grammatobothus*, *Japanolaeops*, *Kamoharaia*, *Laeops*, *Lophonectes*, *Monolene*, *Perissias*, *Psettina*, *Taeniopsetta* and *Trichopsetta*. The proximal tips of the anteriormost dorsal-fin pterygiophores in the taxa mentioned above are in contact with this margin or can be inserted into the small notches of the crenulate dorsal margin (Fig. 1). Conversely, in *Bothus* (Fig. 2), *Crossorhombus*, *Engyprosoyon* (Fig. 3), *Parabothus* (Fig. 4) and *Tosarhombus*, the supraoccipital crest presents deep wells (Fig. 2) where the proximal parts of the dorsal-fin pterygiophores are inserted. The latter pattern of insertion is illustrated but not mentioned by Chabanaud (1933: 62, fig. 43) for *Platophrys mancus* (now valid as *Bothus mancus* (Broussonet, 1782)) and by Amaoka (1969: 229-241, fig. 97, 98, 103) for *Bothus mancus*, *B. myriaster*, *Crossorhombus kobensis*, *Engyprosoyon grandisquama*, *E. multisquama*, *Parabothus kienensis* and *Tosarhombus octoculatus* (Amaoka (1969: 229-241, fig. 97, 98, 103) The traces of these wells are figured by small circles on the supraoccipital crest in dorsal view of the neurocranium in figure 103 of Amaoka (1969).

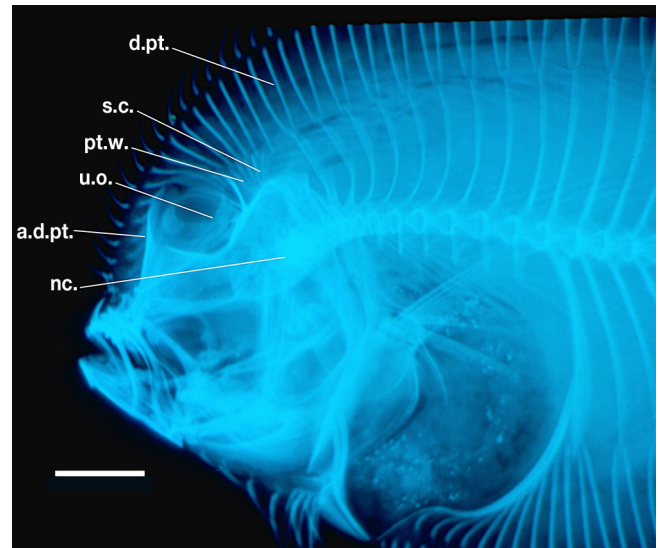


Figure 3. – Anterior part of a X-rayed *Engyprosoyon bleekeri* I 33663001 (L.S: 78 mm). a.d.pt.: anterior dorsal hourglass shaped pterygiophore; d.pt.: dorsal-fin pterygiophore; nc.: neurocranium; pt.w.: pterygiophore well; s.c.: supraoccipital crest; u.o.: upper orbit. Scale bar = 0.5 cm.

Shape of the anteriormost dorsal-fin pterygiophores

Dorsal-fin pterygiophores are usually enlarged distally in flatfishes (Cole and Johnstone, 1902; Chapleau and Keast, 1988; Chapleau, 1989) (Fig. 1). But, in *Bothus* (Sasaki and Yamashita, 2003: 330, fig. 4, for *Bothus myriaster*) and (Fig. 2), *Crossorhombus*, *Engyprosoyon* (Fig. 3), *Parabothus* (Fig. 4) and *Tosarhombus*, the anteriormost dorsal-fin pterygiophores are enlarged proximally and distally, each of these bones is hourglass-shaped (Figs 3, 4).

Epicranial pterygiophores inserted in the ethmoid region

Most of bothid species do not present pterygiophores inserted in ethmoid region, like *Arnoglossus* (Fig. 1). However, in *Grammatobothus*, *Bothus* (Fig. 2), *Crossorhombus*, *Engyprosoyon* (Fig. 3), *Parabothus* (Fig. 4) and *Tosarhombus*, some dorsal-fin pterygiophores are inserted in the ethmoid region.



Figure 4. – Anterior part of a cleared and stained *Parabothus* sp ANSP 142297 74 mm. a.d.pt.: anterior dorsal hourglass-shaped pterygiophore; d.pt.: dorsal-fin pterygiophore; nc.: neurocranium; pt.w.: pterygiophore well; s.c.: supraoccipital crest; u.o.: upper orbit. Scale bar = 0.5 cm.

Number of epicranial dorsal-fin pterygiophores

In the bothid species studied (Table I), 11 to 16 dorsal-fin pterygiophores are present above the neurocranium.

DISCUSSION

The anatomy of the epicranial region of the dorsal fin of Bothidae appears to provide a diversity of patterns, which may be useful to better understand the phylogeny of this family. The interrelationships between the bothid genera solely on the basis of these characters are surely premature and cannot be done only with this study. Nevertheless, several anatomical characters are really peculiar and it can be thought that there is a close relationship between several genera. Even if these hypotheses are confirmed by a phylogenetic analysis of a greater number of anatomical characters, different groups could be identified within Bothidae.

Within *Arnoglossus*, high variability is observed for the epicranial region, especially for characters 1, 2 and 5. Regarding this matter Norman (1934: 175) stated: “the genus *Arnoglossus* still remains a somewhat heterogeneous group, but I am unable to find any valid reason for its further subdivision”. Fukui (1997) pointed out that the genus *Arnoglossus* needs to be reviewed and accurately defined. Even if only two species (*A. tenuis* and *A. polyspilus*) are included in the molecular analysis performed by Li *et al.* (2015), the probable polyphyly of the genus seems to be confirmed by the limited data presented in that molecular study.

The supraoccipital crest (character 1) is generally small in flatfishes (Amaoka, 1969). The presence of a dorsally developed crest may be an evolved character shared by *Bothus*, *Crossorhombus*, *Engyprosopon*, *Grammatobothus*, *Lophonectes*, *Parabothus*, *Tosarhombus* and *Trichopsetta*. *Bothus*, *Crossorhombus*, *Engyprosopon*, *Parabothus* and *Tosarhombus* show a unique state of character (character 2): the proximal part of the posteriormost epicranial pterygiophores inserts into wells in the supraoccipital crest. This character is a probable synapomorphy of these genera. Furthermore, proximally and distally enlarged, hourglass-shaped pterygiophores (character 3) and epicranial pterygiophores inserted into the ethmoid region (character 4), are only present in *Bothus*, *Crossorhombus*, *Engyprosopon*, *Grammatobothus*, *Parabothus* and *Tosarhombus*. These latter genera probably belong to the same clade within the Bothidae. These hypotheses are depicted in the phylogeny showed in Fig. 5.

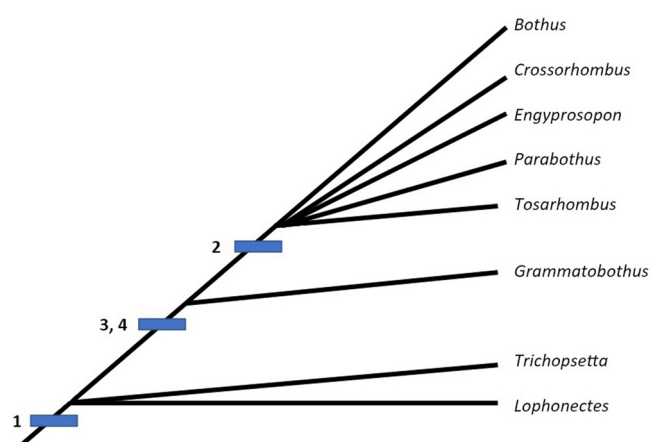


Figure 5. – Hypothetical relationships between some bothid genera based on the anatomy of the epicranial region of the dorsal fin. Numbers indicate the characters (see text).

The number of epicranial dorsal-fin pterygiophores (character 5) is remarkably constant within some genera (Table I), but no character-state can be identified for this structure. This meristic value could be a useful tool in an alpha-taxonomic perspective or to determine specific interrelationships. It still does not seem to provide data to resolve relationships between genera however.

Therefore, it is possible here to test the hypothesis that *Bothus*, *Crossorhombus*, *Engyprosopon*, *Grammatobothus*, *Parabothus* and *Tosarhombus* form a monophyletic group and that *Lophonectes* and *Trichopsetta* are likely sister groups for this putative clade. Furthermore, *Chascanopsetta*, *Monolene* and *Taeniopsetta* may constitute another clade within the Bothidae. In previous works on the interrelationships of the Bothidae based on morphology, Fukui (1997) did not find the groups mentioned above, while Amaoka (1969) proposed the existence of an *Engyprosopon* subsystem (he called it Q, p. 265) gathering the genera *Crossorhombus*, *Engyprosopon*, *Parabothus* and *Tosarhombus* in a single group. However, approaches and methods of both Amaoka (1969) and Fukui (1997) are different: Amaoka (1969) used an eclectic approach and examined only Japanese species, while in Fukui's analysis the number of taxa exceeds the number of informative characters. Therefore the results can hardly be compared. In molecular works, these putative genera groupings were never present either. The genera *Bothus*, *Engyprosopon* and *Crossorhombus* do not form a clade based on a study of nucleotide sequences of the 12S and 16S mitochondrial ribosomal genes (Berendzen and Dimmick, 2002). However, only five species belonging to four genera were examined for the Bothidae. Azevedo *et al.* (2008) found that 3 European *Arnoglossus* species form a monophyletic group close to *Crossorhombus* while *Bothus* and *Laeops* genera were closely related based on sequences of the mitochondrial 12S and 16S ribosomal genes. On the other hand, Espiñeira *et al.* (2008) studied the COI sequences of two species of *Bothus* and 5 species of *Arnoglossus*, the here proposed groupings are absent. Li *et al.* (2015), Campbell *et al.* (2019), Chen *et al.* (2019), Atta *et al.* (2022) and Duarte Ribeiro (2024) did not recover neither similar relationship.

The aim of this study is not to face morphological work with molecular results. Both provide clues and data for species identification and explaining the systematics of Bothidae.

The present morphological analysis is surely too weak to support the phylogeny of the Family and incomplete to attempt to resolve the still uncertain interrelationships of bothid genera. Consequently, any change in the systematics of the family is proposed. However, the study of the anatomy of the epicranial portion of the dorsal fin of the Bothidae could be promising and worthy of interest in a phylogenetic perspective. In addition, it could provide data for resolving intrafamilial relationships and should be taken into account in research on the phylogeny of Bothidae. At least, we hope it will help to detect homoplasies, to define subgroups and samplings of taxa for further and future works focused on the search of bothid species intrarelationshi

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