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The distribution of the *recessus orbitalis* across flatfishes (order: Pleuronectiformes)

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Abstract

The *recessus orbitalis* is an accessory organ of flatfishes functioning in the protrusion of the eyes. This character along with cranial asymmetry and a forward insertion of the dorsal fin have been considered synapomorphies for the Pleuronectiformes. New dissections and examination of images taken in the wild show that the *recessus orbitalis* is present in all representatives of Pleuronectoidei examined, but is absent in the single species of Psettoidei dissected. Psettoidei, the most primitive pleuronectiform taxon, contains three recognized species; thus the absence of the *recessus orbitalis* in this lineage is unclear without further dissections. Ancestral character estimation at the family-level for the *recessus orbitalis* indicates that the *recessus orbitalis* was likely absent in the common ancestor of Pleuronectiformes, but was most likely present in the common ancestor of the Pleuronectoidei. Given that so few species of flatfishes have been assessed for the *recessus orbitalis* to date, additional characterization of the distribution of the *recessus orbitalis* across flatfishes will further inform what states this character may have and if it is a synapomorphy of Pleuronectiformes or simply a derived character-state of Pleuronectoidei.

Key Words: Pleuronectoidei; Phylogenetics; Psettoidei; *Psettodes*

Significance Statement

Flatfish monophyly has been supported anatomically by three synapomorphies. One of these is the *recessus orbitalis*, an accessory organ that aids in the protrusion of the eyes. It has been considered to present across all flatfishes (Pleuronectiformes) but previously only assessed in three families. Here we present the first description of this accessory organ from flatfishes in over 100 years demonstrating its broad occurrence in Pleuronectoidei and conspicuous absence in Psettoidei. Our results from Psettoidei are based on a single species, requiring further dissections to conclude on the presence of the *recessus orbitalis* in Psettoidei and consequently on *recessus orbitalis* as a pleuronectiform synapomorphy.

Flatfishes, by possessing cranial asymmetry, are atypical among vertebrates and are classically considered to belong to a single order, Pleuronectiformes (Norman, 1934; Chapleau, 1993; Munroe, 2005). Cranial asymmetry associated with ocular migration is one of three synapomorphies proposed by Chapleau (1993) in support of monophyly of the Pleuronectiformes along with an advanced position of the dorsal fin over the cranium and the presence of a *recessus orbitalis*.

The *recessus orbitalis* is a muscular sac-like evagination localized in the posterior side of the orbit in some flatfishes. This organ has been demonstrated to be involved in the protrusion of the eyes above the body surface (Fig. 1A) (Holt, 1894). This ability is essential to flatfish species when buried in the substrate as it allows the fish to project its eyes above the material camouflaging the body, thus maintaining sight e.g. (Cole and Johnstone, 1902; Norman, 1934). Consequently, the *recessus orbitalis* is considered an accessory organ helping vision by Holt (1894). This author described this structure in several pleuronectid species, one scophthalmid and one soleid (Fig. 1B, Table 1). Several years later, Cole and Johnstone (1902) described the *recessus orbitalis* in detail in the plaice, *Pleuronectes platessa* L. 1758 (Pleuronectidae). Since Holt (1894) and Cole and Johnstone (1902) no direct observations of the *recessus orbitalis* have been described in the literature.

The seminal work of Chapleau (1993) conducted a thorough cladistic analysis of flatfishes and recognized the need for additional study of the *recessus orbitalis* given the very limited documentation to date (Table 1). Nevertheless, Chapleau (1993) considered the presence of this organ as a synapomorphy supporting the monophyly of the Pleuronectiformes. However, Chabanaud (1937) remarked that the most primitive flatfish family, Psettodidae, constituting one of the two flatfish suborders and consisting of a single genus *Psettodes* e.g. (Norman, 1934; Chapleau, 1993; Munroe, 2005), are not capable of protruding their eyes. This observation of Chabanaud (1937) based on two of the three recognized species of *Psettodes* suggests that the *recessus orbitalis* is absent in the species of this family. Since Chapleau (1993), authors have pointed out that the distribution of the *recessus orbitalis* has not been determined wholly across pleuronectiform fishes and may not be present in *Psettodes* (Chanet *et al.*, 2020; Campbell *et al.*, 2013). Chanet *et al.* (2020) concluded that the presence of this organ cannot be used to define the pleuronectiform order as a clade and that further work should be dedicated to the anatomy and the distribution of the *recessus orbitalis* conducted on fresh specimens. The present study shows the results of dissections of the orbital region in

various flatfish species, Psettodidae included, reaffirming the existence of and describing the taxonomic distribution of the *recessus orbitalis*.

All fish specimens examined by the authors were obtained from fish markets and were not collected as part of faunal surveys. The care and use of experimental animals complied with Taiwanese animal welfare laws, guidelines and policies as approved by the National Taiwan University. This project did not involve experiments on live fishes nor the handling of any live fishes. The orbital region of fish specimens was dissected following the protocol described by Holt (1894) with examined taxa described in Supplemental Document S1: Psettodidae, *Psettodes erumei* (Bloch & Schneider 1801); Bothidae, *Arnoglossus yamanakai* Fukui, Yamada, & Ozawa 1988, *Chascanopsetta lugubris* Alcock 1894; Citharidae, *Brachypleura novaezeelandiae* Günther 1862 ; Cynoglossidae, *Cynoglossus ochiaii* Yokogawa, Endo, & Sakaji 2008; Paralichthyidae, *Pseudorhombus levisquamis* (Oshima 1927); Poecilopsettidae, *Poecilopsetta plinthus* (Jordan & Starks 1904); Samaridae, *Samariscus latus* Matsubara & Takamuki 1951; Soleidae *Aseraggodes kobensis* (Steindachner 1896); and *Pegusa lascaris* (Risso 1810) (N. Schnell, personal communication). To further evaluate the distribution of the *recessus orbitalis* across pleuronectiforms, we examined photos of flatfishes in their natural environments (Supplemental Document S2).

The *recessus orbitalis* is absent in both left-eyed and right-eyed *Psettodes erumei* (Fig. 1C & 1D), but was present in all pleuronectoids examined (Fig. 1E & 1F, Table 1, Supplemental Document S2, and Data Supplement). In *Psettodes*, the skinning of the orbital region shows only the *adductor mandibulae* muscle and no other structure (Burgin, 1989). While in each examined pleuronectoid taxon, a sac-like structure is present, i.e. the *recessus orbitalis*, immediately behind the bulb (Fig. 1E & 1F). Anatomical observations from seven pleuronectoid families in this study have been complemented by the examination of photographs taken in the wild for various species (Supplemental Document S2). In these species, extruded eyes can be observed and we interpret this ability as revealing the existence the *recessus orbitalis*. The presence of the *recessus orbitalis* has now been indirectly or directly observed in 12 pleuronectoid families: the single family of Citharoidea, all five families in the Pleuronectoidea, and six families in the Soleioidea (Figure 2).

The *recessus orbitalis* has been directly observed, see Table 1, in Bothidae, two species (this study), Citharidae, one species (this study, Fig. 1F), Cynoglossidae, one species (this study),

in Paralichthyidae, one species, (this study, Fig. 1E), in Pleuronectidae, six species (Holt, 1894; Cole and Johnstone, 1902), in Poecilopsettidae, one species (this study), in Samaridae, one species (this study), in Scopthalmidae, one species (Holt, 1894) and in Soleidae, three species (this study; Holt (1894)). Moreover, the presence of this organ has been deduced in 27 species and three additional families: the Achiridae, the Cyclopsettidae, and the Rhombosoleidae (Supplemental Document S2). But, this organ is absent in *Psettodes erumei* (this study, Fig. 1C & 1D). The latter observation is confirmed by the study of myology of the cephalic region of *Psettodes erumei* (Burgin, 1989).

Is the recessus orbitalis a synapomorphy of the Pleuronectiformes? Given the available data, we conducted ancestral character estimation of the *recessus orbitalis* with the package *ape* version 5.3 in R version 3.6.1 (Paradis and Schliep, 2018). To do so, we created a family-level phylogeny of Pleuronectiformes by pruning the maximum likelihood phylogeny from Campbell et al. (2019) to a single representative of each flatfish family as well as the outgroup family Centropomidae. The *recessus orbitalis* for a family was considered present if a single species in that family either through dissection or photographs was indicated to have the *recessus orbitalis* (Figure 2). Of all flatfish examined, only *Psettodes erumei* has direct evidence for the absence of the *recessus orbitalis*. Absence of this character in *Psettodes belcheri* Bennet 1831 is supported by indirect observation (Chabanaud, 1937); therefore, Psettodidae and the outgroup family (Centropomidae) were considered to not have the *recessus orbitalis*. We then conducted squared-change parsimony ancestral character estimation. The probability of the *recessus orbitalis* being present in the common ancestor of all pleuronectiforms was 0.07 and for the common ancestor of pleuronectoids was 0.96 (Figure 2).

The ancestral character estimation conducted at the family-level highlights the need for future examinations of pleuronectoids as so few species out of the total pleuronectiform diversity have been directly assessed for the presence or absence of the *recessus orbitalis* (17 / >800). In addition to characterizing the known distribution of this character, the examination of more pleuronectiform species can answer if secondary loss of the *recessus orbitalis* has occurred and if there is variation in the physical form of the *recessus orbitalis* itself. Our efforts were widespread and examined representatives from all three pleuronectoid superfamilies including the earliest-branching superfamily of pleuronectoids, Citharoidea. The six species within

Citharoidea have been more recently accepted into a single family, Citharidae. Citharids possess unique anatomical features for pleuronectoids often considered primitive, such as a spine in the pelvic fin, separated gill membranes and vomerine teeth (Hoshino, 2001). Although the Citharoidea has several primitive flatfish characteristics, it does appear to possess the *recessus orbitalis* based on direct evidence from a single species. The evidence gathered for both Citharoidea and Psettoidei for the presence or absence of the *recessus orbitalis* is based on a single species from each group, and limits conclusions that can be drawn regarding the *recessus orbitalis* in these taxa. Establishment of the presence or absence of this trait more broadly across the Citharoidea in addition to all three species of Psettoidei with further dissections would substantially contribute towards determining if the *recessus orbitalis* is synapomorphic for the Pleuronectiformes.

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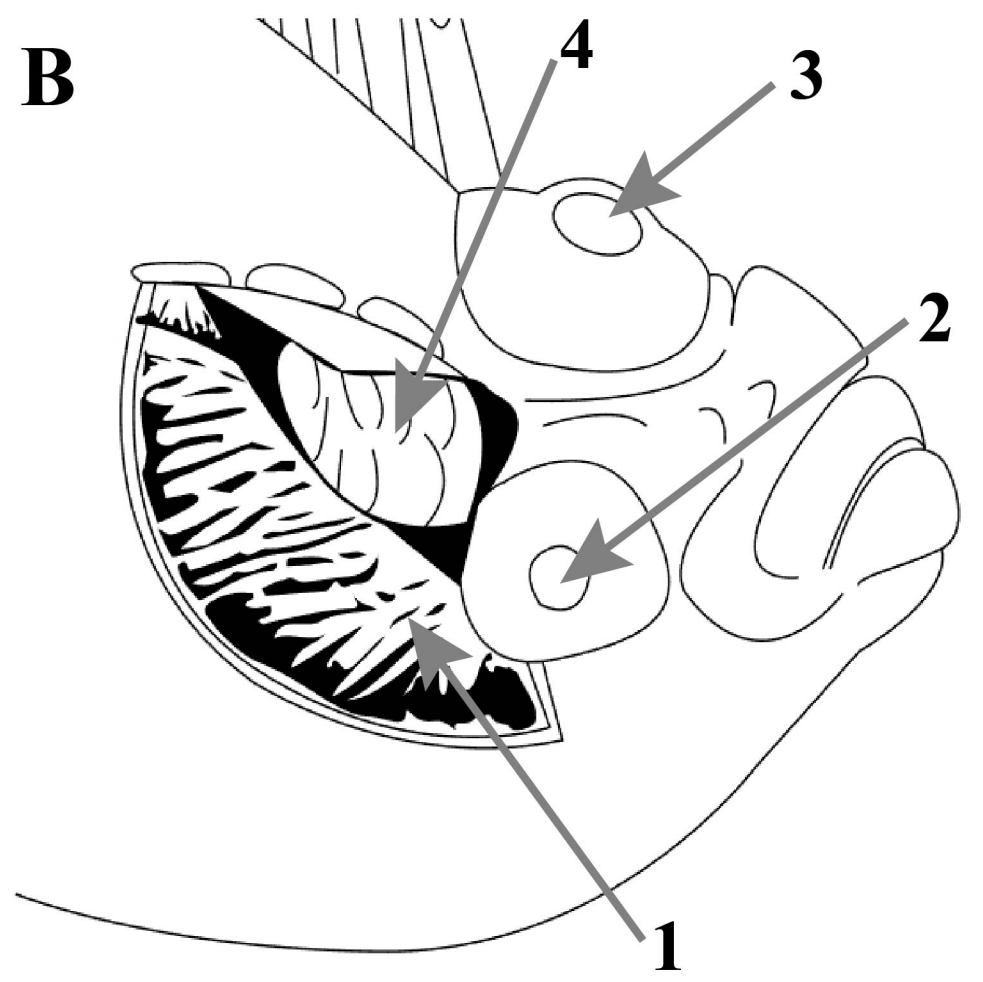
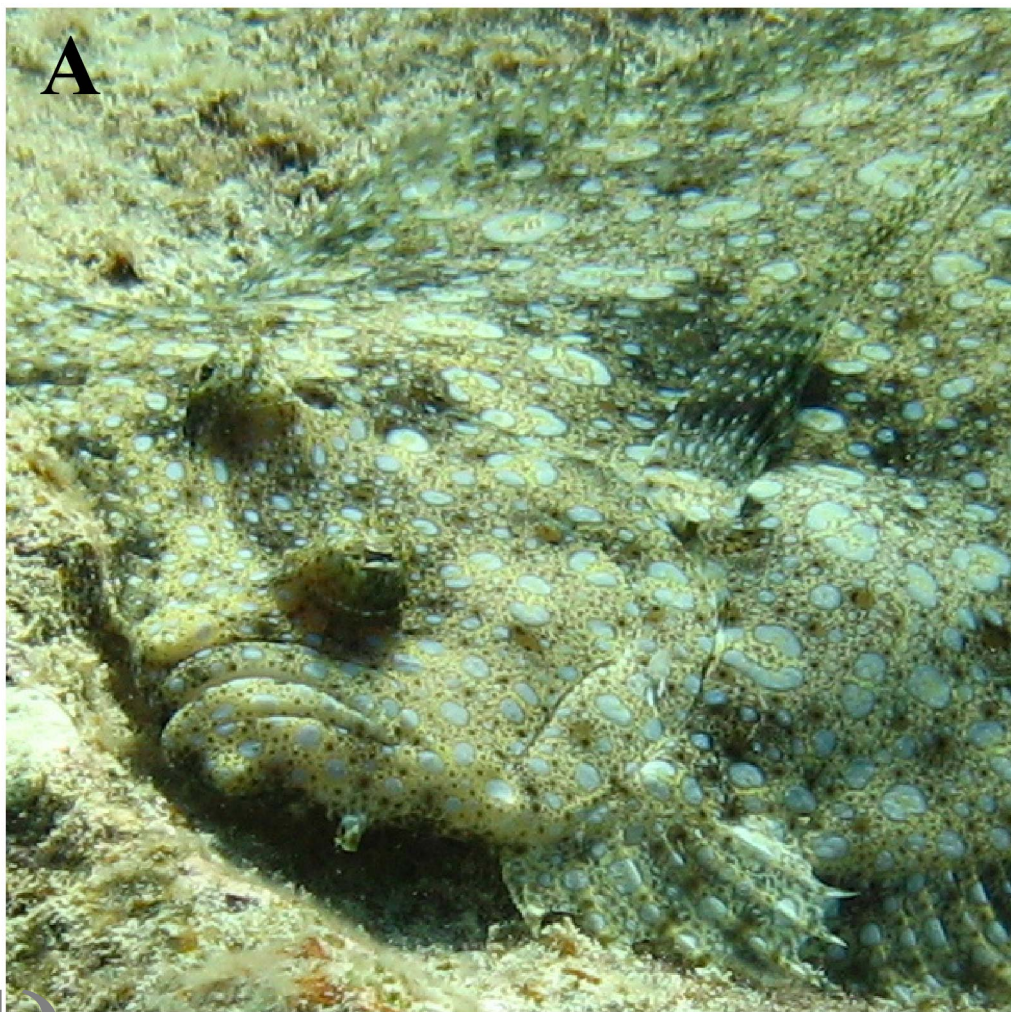
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Table 1 Pleuronectiform taxa for which the presence of the *recessus orbitalis* has been evaluated through dissection. The presence is indicated as well as the reference. Classification follows Campbell et al. (2019).

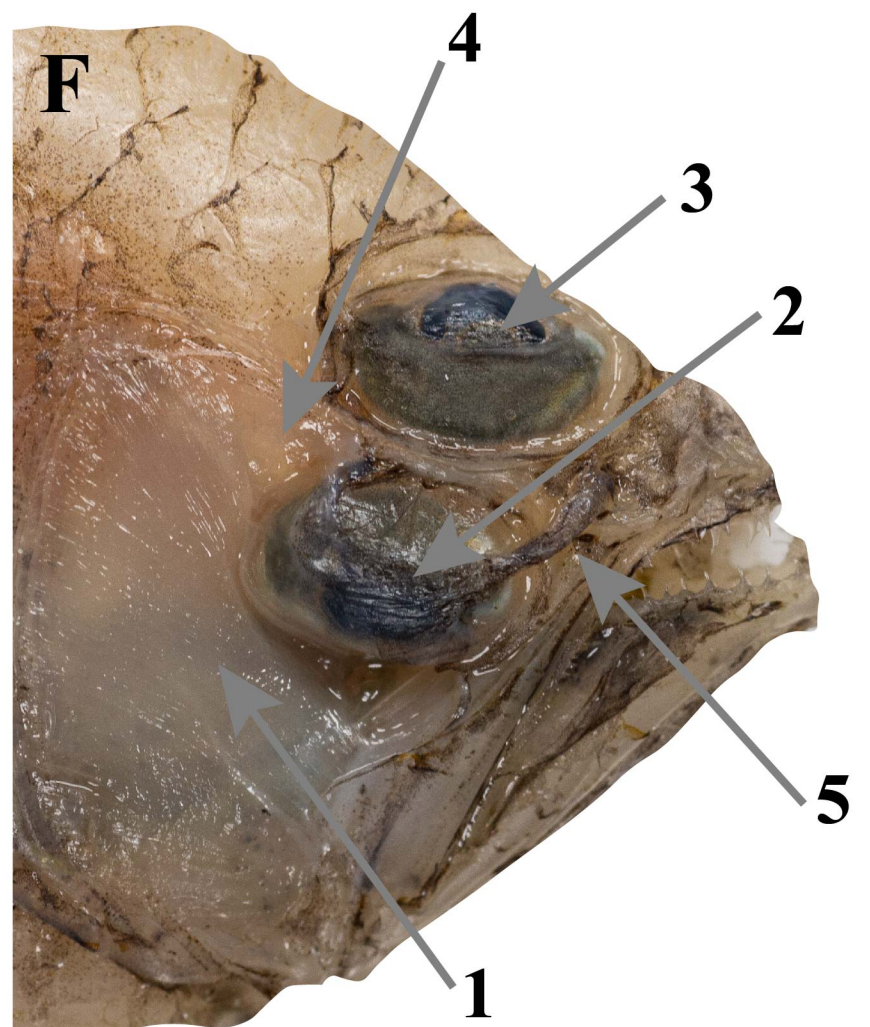
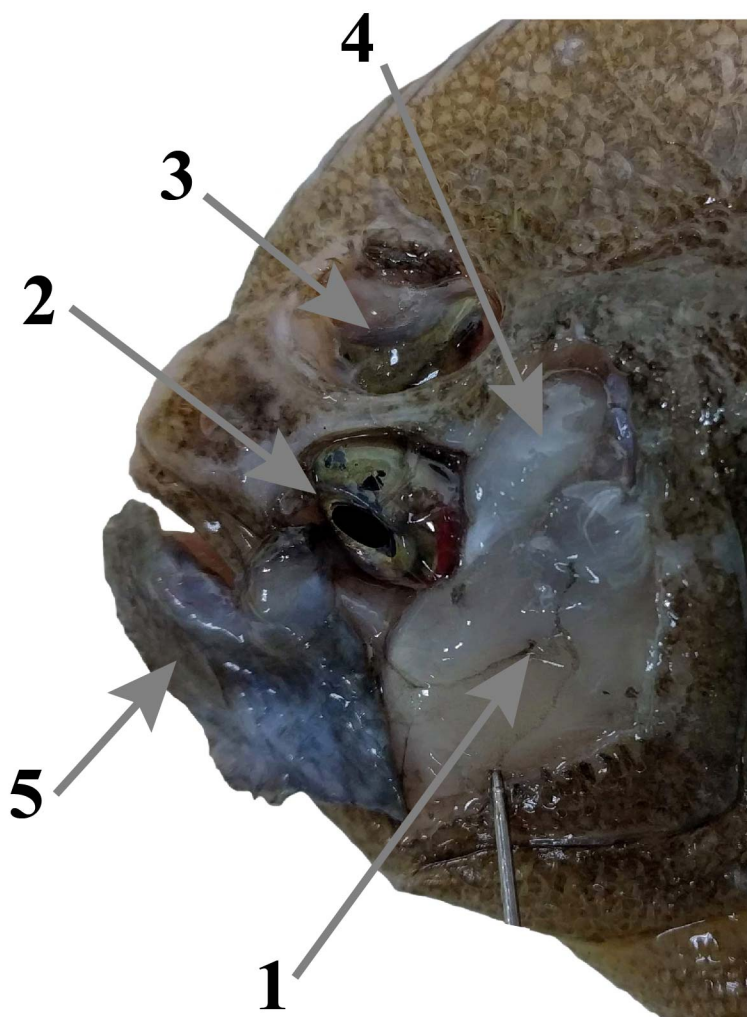
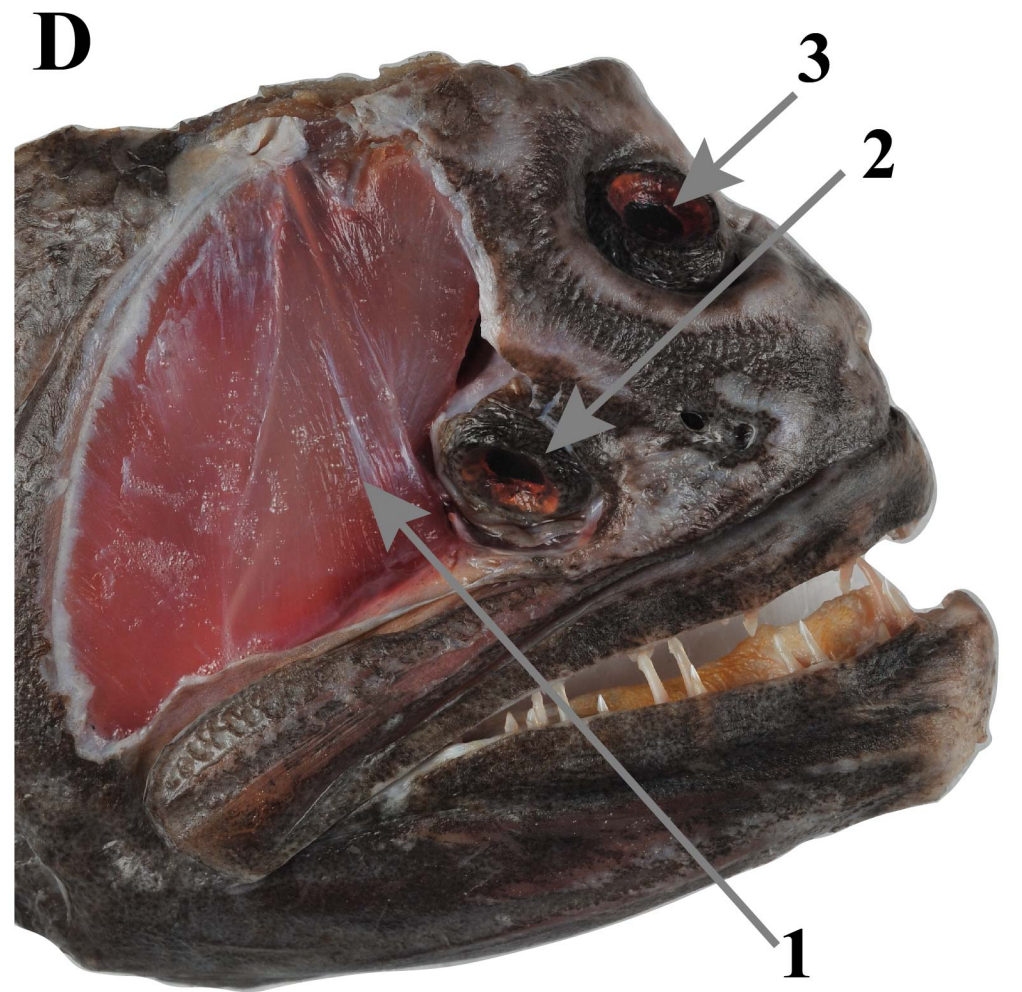
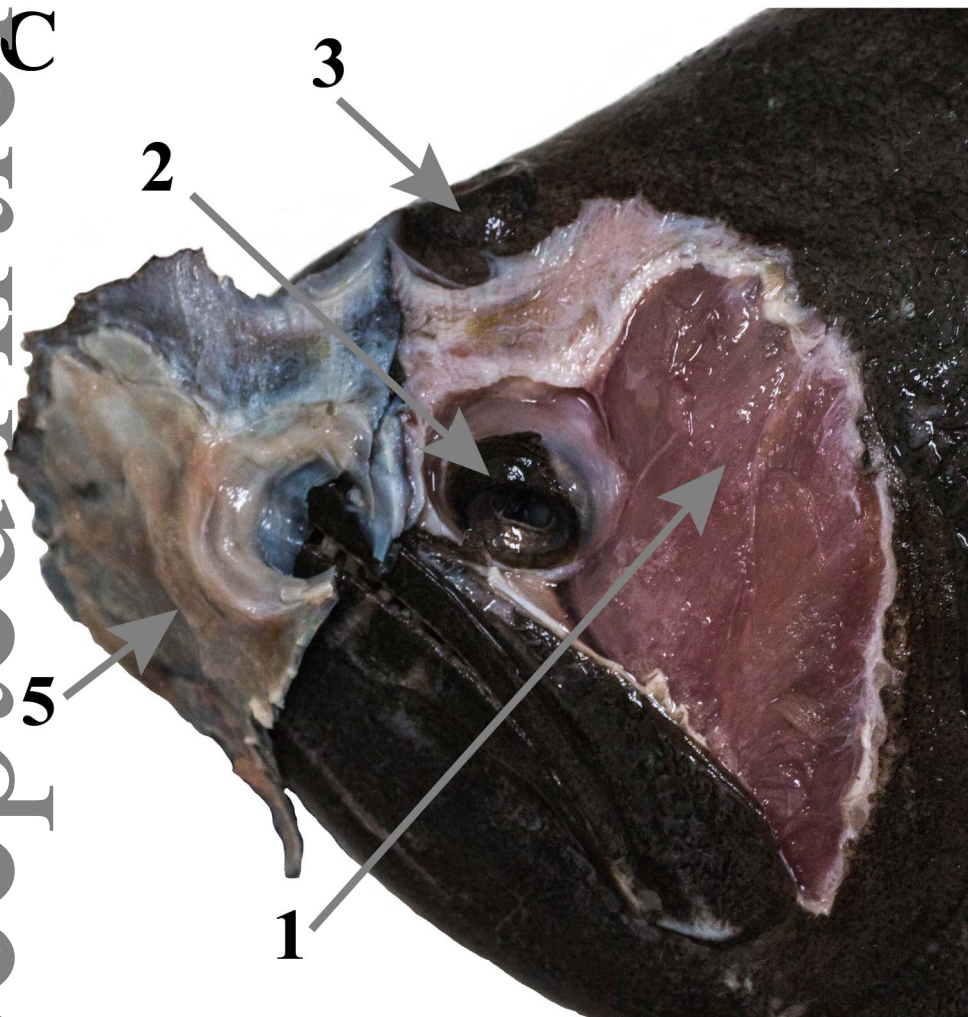
Suborder	Superfamily	Family	Species	<i>Recessus Orbitalis</i> Present?	Sources
Psettoidei		Psettodidae	<i>Psettodes erumei</i> (Bloch & Schneider 1801)	No	Burgin (1986), This Study
Pleuronectoidei	Citharoidea	Citharidae	<i>Brachypleura novaezeelandiae</i> Günther 1862	Yes	This Study
	Pleuronectoidea	Scophthalmidae	<i>Scophthalmus rhombus</i> (L. 1758)	Yes	Holt (1894)
		Pleuronectidae	<i>Hippoglossus hippoglossus</i> (L. 1758)	Yes	Holt (1894)
			<i>Hippoglossoides platessoides</i> (Fabricius 1780)	Yes	Holt (1894)
			<i>Platichthys flesus</i> (L. 1758)	Yes	Holt (1894)
			<i>Pleuronectes platessa</i> L. 1758	Yes	Cole and Johnstone (1902)
			<i>Limanda limanda</i> (L. 1758)	Yes	Holt (1894)
			<i>Microstomus kitt</i> (Walbaum 1792)	Yes	Holt (1894)
		Paralichthyidae	<i>Pseudorhombus</i> cf. <i>levisquamis</i> (Oshima 1927)	Yes	This Study
		Bothidae	<i>Arnoglossus yamanakai</i> Fukui, Yamada, & Ozawa 1988	Yes	This Study
			<i>Chascanopsetta lugubris</i> Alcock 1894	Yes	This Study
	Soleoidea	Poecilopsettidae	<i>Poecilopsetta plinthus</i> (Jordan & Starks 1904)	Yes	This Study
		Samaridae	<i>Samariscus latus</i> Matsubara & Takamuki 1951	Yes	This Study
		Cynoglossidae	<i>Cynoglossus ochiaii</i> Yokogawa, Endo, & Sakaji 2008	Yes	This Study
		Soleidae	<i>Aseraggodes kobensis</i> (Steindachner 1896)	Yes	This Study
			<i>Pegusa lascaris</i> (Risso 1810)	Yes	This Study
			<i>Solea solea</i> (L. 1758)	Yes	Holt (1894)

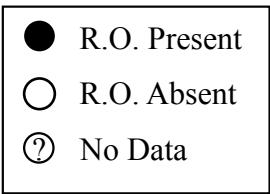
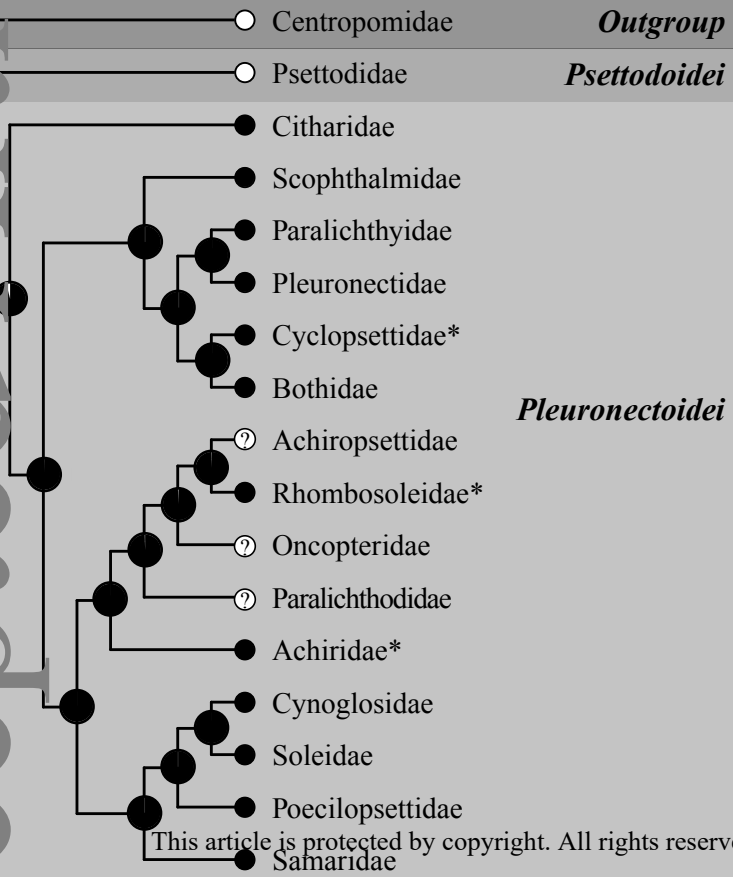
Figure 1 (A) Example of a flatfish (Bothidae, left-eyed species) utilizing the *recessus orbitalis* to protrude its eyes while stationary on the substrate. Photo by M. Campbell. (B) The *recessus orbitalis* in a plaice, *Pleuronectes platessa*, (right-eyed species, modified from Holt 1894, pl. XXX, fig. 5). (C) Ocular side of a dissected left-eyed *Psettodes erumei* (NTUM 16050, 40.0 cm SL). (D) Ocular side of a dissected right-eyed *Psettodes erumei* (NTUM NTUM17077, 39.5 cm SL). (E) Ocular side of a dissected *Pseudorhombus cf. levisquamis* (left-eyed species, NTUM 16051, 23.0 cm SL). (F) Ocular side of a dissected *Brachypleura novaezeelandiae* (right-eyed species, NTUM17076, 7.6 cm SL). Legend: 1. *Adductor mandibulae* muscle; 2. Non-migrating eye; 3. Migrating eye; 4. *Recessus orbitalis*; 5. Removed skin.

Figure 2 Distribution of the *recessus orbitalis* across families of flatfishes (Pleuronectiformes) accompanied by ancestral character estimation of this character conducted at the family-level. Pleuronectoid family relationships follow Campbell et al. (2019). Confirmed absence of the *recessus orbitalis* is indicated by white circle at a tip, confirmed presence by a black filled circle, and unknown by a question mark (?) in a circle. If the presence of the *recessus orbitalis* was deduced from photographs, it is indicated by an asterisk "*" following the family name. The probability of the *recessus orbitalis* in nodes of the tree is proportional to the amount of black area within each circle.



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