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## First Record of Reversed Symmetry in *Etropus cyclosquamus* and Second Record in *Citharichthys spilopterus* (Bothidae, Pisces) in the Gulf of Mexico, with a Plausible Genetic Explanation for Reversal

RAMON RUIZ-CARUS AND STEVE J. RIDER

The discovery of the first instance of reversed eye symmetry in the shelf flounder, *Etropus cyclosquamus*, and the second instance in the bay whiff, *Citharichthys spilopterus*, are reported. Two reversed bay whiffs and three reversed shelf flounders were collected in the Gulf of Mexico. Four of these specimens were taken from the vicinity of Fort Walton Beach, Okaloosa County, in northern Florida, and one was taken from Higgs Beach in Key West, Monroe County, FL. The collection of these fish is reported because of the infrequent occurrence of reversed eye symmetry in flatfishes in the Gulf of Mexico. The fish serve as the first record of eye symmetry reversal in *E. cyclosquamus* and the second record for *C. spilopterus* in the Gulf of Mexico. This is the second record of reversal for the genus *Etropus* and the third record for *Citharichthys* in the western Atlantic Ocean. The putative causes of symmetry reversal in pleuronectiform fish are briefly examined. A plausible genetic explanation for reversal is proposed. The explanation attempts to reconcile the environmental causality of eye symmetry with the accepted genetic model of Brown and Wolpert.

Pleuronectiform fish have a peculiar ontogenetic metamorphosis (Lauder and Liem, 1983; Brewster, 1987). This process of larval metamorphosis results in demersal juveniles with sinistral or dextral eye symmetry. In sinistral species, the right eye migrates to the left side of the head, and vice versa in dextral species. The pleuronectiform family Bothidae includes species of *Etropus* and *Citharichthys* with sinistral eye symmetry (Ahlstrom et al., 1984). Symmetry reversal is the change in the directionality of eye migration (Policansky, 1982b), and it is relatively common for some flatfishes in temperate waters (Gudger, 1935; Dawson, 1964, 1966, 1971; Dawson and Heal, 1976; Cameron et al., 1992). However, symmetry reversal has rarely been observed in the 54 pleuronectiform species existing in the Gulf of Mexico (Springer and Woodburn, 1960; Guthertz, 1967; Topp and Hoff, 1972; Flores-Coto et al., 1991; Fournie et al., 1996).

Pleuronectiform fish constitute an important portion of the ichthyofauna in estuarine habitats of the Gulf of Mexico, and the genera *Etropus* and *Citharichthys* accounted for 0.1%–5.0% of the total catch of this ichthyofauna (Moe and Martin, 1965; Yañez-Arancibia et al., 1986; Florida Marine Research Institute, 1993, 1994, 1995). Nevertheless, there is only one record of symmetry reversal in the Gulf of Mexico for either of these two genera. Dawson (1969) described the first dextral fish in the genus *Citharichthys*, a 15.9-mm standard length (SL) *C. abbotti* from Boca del Rio, Veracruz,

Mexico. The second record for the genus was a 40.5-mm total length *C. spilopterus* taken in the White Oak River, NC, by Wilkins and Lewis (1971). The only record of symmetry reversal in the genus *Etropus* was reported by Taylor et al. (1973), who captured a 45.0-mm SL *E. crosotus* in Ossabaw Sound, GA.

Dawson (1969), Wilkins and Lewis (1971), and Taylor et al. (1973) did not report the frequency of occurrence of symmetry reversal, but accounts of other pleuronectiforms in western Atlantic localities north of the Gulf reported a frequency of 1 in 2,000 (0.05%) in *Trinectes maculatus* (Acharidae) (Moore and Posey, 1972; Koski, 1974) and a frequency of up to 57 in 1,295 (4.4%) in laboratory-reared *Paralichthys dentatus* (Paralichthyidae) (Bisbal and Bengston, 1993).

We report here the discovery of the first case of symmetry reversal in a new species of pleuronectiform and the second instance of dextrality in another species. Two dextral specimens of *Etropus cyclosquamus* Leslie et Stewart, 1986, and three dextral specimens of *Citharichthys spilopterus* Günther, 1862, were collected in the Gulf of Mexico. These specimens are reported because of the infrequent occurrence of this event. The dextral bothids found in Florida serve as the first record of symmetry reversal in *E. cyclosquamus* and the second record in *C. spilopterus* in the Gulf of Mexico. These specimens also represent the second record for the genus *Etropus* and the third record for *Citharichthys* in the western Atlantic Ocean.

TABLE 1. Meristic counts and morphometric measurements of dextral Bothidae. SL = standard length, HL = head length, B = blind side, O = ocular side, gill rakers = upper + lower, vertebrae = precaudal + caudal.

	Specimen				
	FSBC 18358	FSBC 18359	FSBC 18718	FSBC 18409	FSBC 18408
Dorsal fin rays	78	77	77	77	75
Anal fin rays	57	56	57	57	56
Caudal fin rays	4, 5, 4, 4	4, 5, 4, 4	4, 5, 4, 4	4, 5, 4, 4	4, 5, 4, 5
Pectoral fin rays B	10	10	10	10	10
Gill rakers	19 = 5 + 13	17 = 4 + 13	15 = 4 + 11	10 = 5 + 5	11 = 6 + 5
Lateral line scales	45	45	45	40	41
Vertebrae	33 = 10 + 23	33 = 10 + 23	33 = 10 + 23	34 = 10 + 24	33 = 10 + 23
Total length	128.1	108.2	86.2	72.0	41.6
Standard length	103.6	87.2	71.0	60.2	33.8
Body depth	52.1 (50% SL)	43.1 (49% SL)	31.5 (44% SL)	31.0 (52% SL)	14.3 (42% SL)
Head length	32.2 (31% SL)	25.9 (30% SL)	19.8 (28% SL)	14.8 (25% SL)	8.7 (26% SL)
Eye diameter	4.7 (15% HL)	4.4 (17% HL)	3.4 (17% HL)	3.8 (26% HL)	2.3 (26% HL)
Upper jaw length	11.8 (37% HL)	9.2 (36% HL)	7.9 (40% HL)	4.2 (28% HL)	2.5 (29% HL)
Caudal fin length	24.5 (76% HL)	21.0 (81% HL)	16.1 (81% HL)	11.8 (80% HL)	7.2 (83% HL)
Pectoral fin length O	15.3 (15% SL)	12.6 (14% SL)	9.8 (14% SL)	11.1 (18% SL)	5.7 (17% SL)
Pectoral fin length B	12.4 (12% SL)	10.8 (12% SL)	8.1 (11% SL)	8.2 (14% SL)	4.6 (14% SL)
Anus opens in	B	B	B	B	B
Scale type B	Cycloid	Cycloid	Cycloid	Cycloid	Cycloid
Head profile	Concave	Concave	Concave	—	—

Here, we briefly examine the putative causes of eye symmetry reversal in pleuronectiform fish and propose a plausible genetic explanation for the reversal. The explanation attempts to reconcile the environmental causality of eye symmetry (Munroe, 1996) with the accepted genetic model of Brown and Wolpert (1990).

#### MATERIALS AND METHODS

Five specimens showing reversed symmetry were captured from 1993 to 1996 by the Fisheries-Independent Monitoring Program of the Florida Marine Research Institute (FMRI), Florida Department of Environmental Protection. The fish were collected with either an otter trawl or a beach seine. Both nets had 3.1-mm mesh. The specimens were fixed in 10% buffered formalin and preserved in 50% aqueous isopropanol. Morphometric data were obtained to the nearest 0.1 mm with Vernier calipers. Morphometric measurements of less than 5 mm were made to the nearest 0.1 mm with an ocular micrometer. Meristic data were acquired by direct count and also from x-radiographs. Morphometrics and meristics data were gathered according to Dawson's (1969) method. The specimens were accessioned in the Florida Marine Research Institute's collections (FSBC). The following catalog numbers were assigned: *E. cyclosquamus*—FSBC 18408

and 18409; *C. spilopterus*—FSBC 18358, 18359, and 18718.

#### RESULTS

The five specimens with reversed symmetry represent 0.5% of the 956 *Citharichthys* and *Etropus* captured in 1993–96 (Florida Marine Research Institute, 1993, 1994, 1995).

*Etropus cyclosquamus* Leslie et Stewart, 1986—shelf flounder

**FSBC 18409** (1) 59.0 mm SL; 2 May 1995; 08:55 Central Daylight Time (CDT); 6-m otter trawl, 3.1-mm mesh; 3.1–3.1 m water depth; 15.4–14.7 ppt salinity; 24.1–23.8 C water temperature; 30°24.09'N, 86°36.41'W, Fort Walton vicinity, Okaloosa County, Florida. **FSBC 18408** (1) 32.9 mm SL; 17 May 1993; 23:50 CDT; 6-m center bag seine, 3.1-mm mesh; 3.4–0 m water depth; 16.8–16.7 ppt salinity; 25.8–25.7 C water temperature; 30°23.75'N, 86°31.80'W, Fort Walton vicinity, Okaloosa County, Florida.

The two dextral *E. cyclosquamus* have meristic features and morphometric measurements that fall within the ranges reported for this species (Leslie and Stewart, 1986). Meristic and morphometric data are displayed in Table 1. Eye symmetry reversal is the only unusual external characteristic evident in these specimens

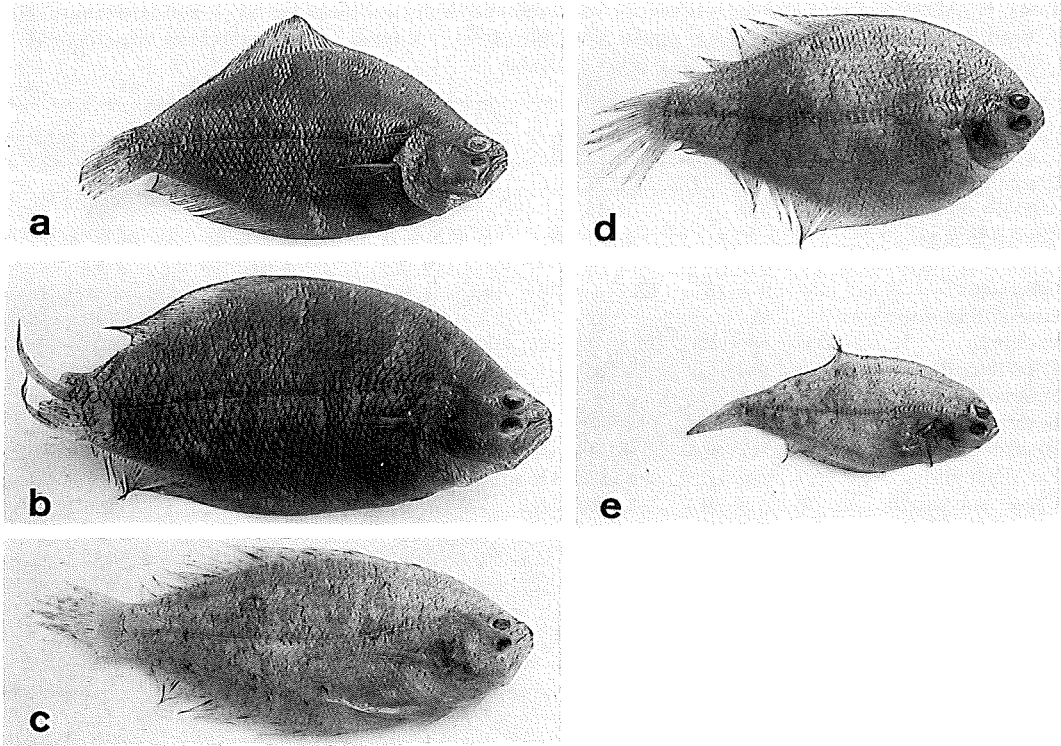


Fig. 1. External morphology. Eye symmetry reversal is the only unusual external characteristic that is evident in dextral specimens. (a) *Citharichthys spilopterus*, FSBC 18358. (b) *Citharichthys spilopterus*, FSBC 18359. (c) *Citharichthys spilopterus*, FSBC 18718. (d) *Etropus cyclosquamus*, FSBC 18408. (e) *Etropus cyclosquamus*, FSBC 18409.

(Fig. 1). The dextral shelf flounders show no osteological abnormalities, and the position and coiling of the viscera are similar to those in sinistral specimens. The locality of collection is within the known geographical distribution of this species (Leslie and Stewart, 1986; Florida Marine Research Institute, 1993, 1994, 1995).

*Citharichthys spilopterus* Günther, 1862—bay whiff

**FSBC 18358** (1) 104.3 mm SL; 2 Oct. 1995; 08:27 CDT; 6-m otter trawl, 3.1-mm mesh; 5.6–5.3 m water depth; 28–26 ppt salinity; 25.4 C water temperature; 30°21.37'N, 87°08.22'W, Fort Walton Beach vicinity, Okaloosa County, Florida. **FSBC 18359** (1), 85.0 mm SL; 11 Oct., 1993; 21:16 CDT; 6-m otter trawl, 3.1-mm mesh; 3.0–2.7-m water depth; 27.5 ppt salinity; 24.2 C water temperature; 30°20.70'N, 87°07.77'W, Fort Walton Beach vicinity, Okaloosa County, Florida. **FSBC 18718** (1) 71.8 mm SL; 13 March 1996; 12:55 Eastern Standard Time; 21.3-m beach seine, 3.1-mm mesh;

0.7–0 m water depth; 33.8 ppt salinity; 21.5 C water temperature; 24°32.48'N, 81°47.14'W, Higgs Beach, Key West, Monroe County, Florida.

The three symmetry-reversed *C. spilopterus* show meristic features and morphometric measurements that are within the ranges reported for this species (Gutherz, 1967; Dawson, 1969). Meristic and morphometric data are displayed in Table 1. Eye symmetry reversal is the only unusual external characteristic evident in these specimens (Fig. 1). Two of the three reversed bay whiffs do exhibit some osteological abnormalities. In FSBC 18358, the 5th to 10th abdominal vertebrae are abnormal, with the 6th to 8th being partially fused. The 11th, 15th, and 16th caudal vertebrae are abnormal, and the 15th and 16th caudal vertebrae are fused. The 49th anal pterygophore is incomplete. In FSBC 18359, the 7th and 8th caudal vertebrae are fused. FSBC 18718 has normal osteology. The osteological characteristics are shown in Figure 2. The three dextral *C. spilopterus* show position and coiling of the viscera similar to sinistral specimens. The localities of collection

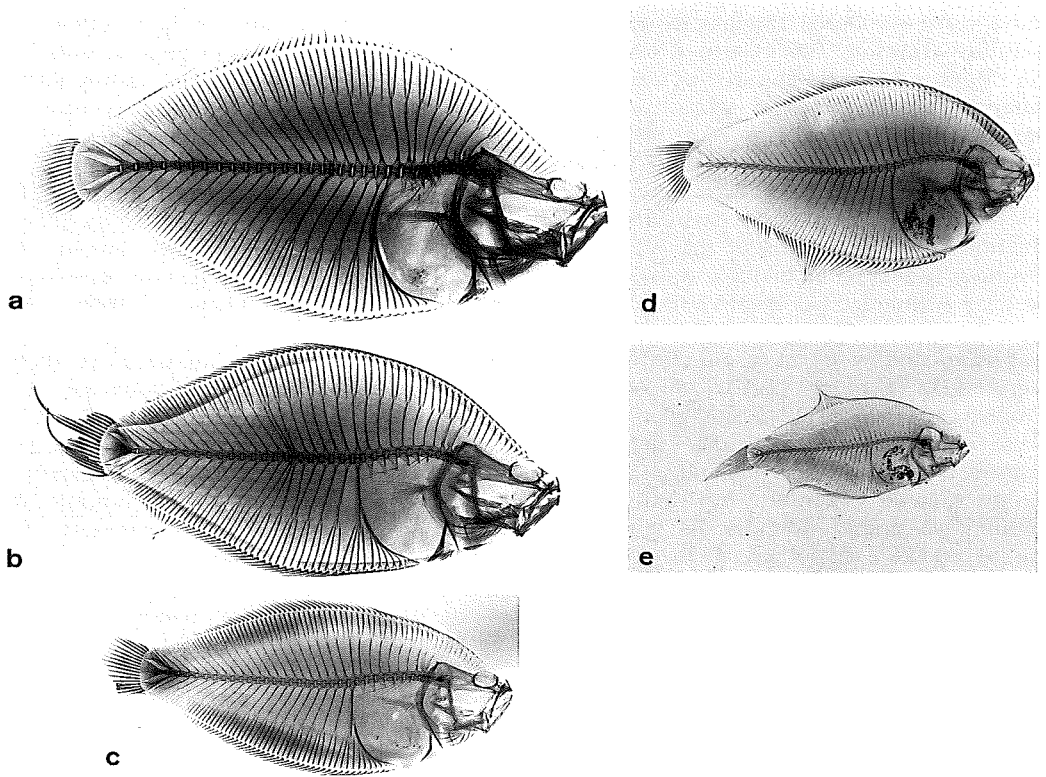


Fig. 2. Internal morphology; osteology. (a) *Citharichthys spilopterus*, FSBC 18358. Abdominal vertebrae: 5th to 10th abnormal; 6th to 8th partially fused. Caudal vertebrae: 11th, 15th, and 16th abnormal; 15th and 16th fused. Anal pterygophore: 49th incomplete. (b) *Citharichthys spilopterus*, FSBC 18359. Caudal vertebrae abnormal; 7th and 8th fused. (c) *Citharichthys spilopterus*, FSBC 18718. Normal. (d) *Etropus cyclosquamus*, FSBC 18408. Normal. (e) *Etropus cyclosquamus*, FSBC 18409. Normal.

are within the known geographical distribution of this species (Gutherz, 1967). The localities in the vicinity of Fort Walton Beach and Higgs Beach in the Florida Keys were recently characterized (Florida Marine Research Institute, 1993, 1994, 1995).

#### DISCUSSION

Pleuronectiform fish with reversed eye symmetry have been known since 1777 (Duhamel du Monceau, 1777), but our understanding of the causality of symmetry is still far from complete. It has been observed that abnormalities or anomalies such as symmetry reversal, ambicoloration, incomplete eye rotation, and hooked dorsal fin occur more frequently in flatfishes in northern latitudes (Munroe, 1996). Dawson (1962), Gartner (1986), and Munroe (1996) suggested that environmental fluctuations during larval development are the cause of these abnormalities or anomalies. The environmental factors included seasonal

changes in water temperature, seasonal changes in light, and depth in shallow-water habitats. This proposition was alluded to by Munroe (1996) as the ecological hypothesis.

Other ecological factors, such as population density and food levels, were also suggested when unanticipated reversed specimens occurred under experimental aquaculture conditions (Houde, 1971; Bisbal and Bengtson, 1993). Recently, environmental quality determinants such as pollution and other human impacts have been correlated with changes in the fish reproductive system (Savvaitova et al., 1995; Shatunovskii et al., 1996) and have been implicated as the possible cause of diverse fish teratologies. However, these teratologies did not include symmetry reversal (Cameron et al., 1992; Fournie et al., 1996).

Because there is no experimental evidence to support an environmental induction of eye symmetry, it is not possible to evaluate the validity of the ecological hypothesis. Even the physical factor that has been viewed as the pu-

tative cause—seasonal changes in water temperature (Dawson, 1962; Gartner, 1986; Munroe, 1996)—could be disputed by available incidental data (Policansky, 1982c; Cameron et al., 1992), and it is inconsistent with an accepted genetic model, Brown and Wolpert's (1990) model of right-left asymmetry.

The studies suggesting an environmental induction of symmetry indicate that inheritance, the most fundamental biological property controlling symmetry, has been overlooked. The genetic origin of pleuronectiform symmetry was postulated by Cunningham (1907) and reiterated by Gudger (1935). Subsequently, Hubbs and Hubbs (1945) analyzed fisheries data, museum specimens, and experimental hybridization data and concluded that "... simple genetic factors are involved in determining whether a flounder be left-eyed or right-eyed." The hypothesis of the genetic origin of eye symmetry was confirmed with genetic crosses by Policansky (1982a, 1982b, 1984), and his data still remain as the only evidence to substantiate genetic determination of eye symmetry in pleuronectiforms. It is obvious from Policansky's experimental crosses that eye symmetry is inherited. Eye symmetry under the Mendelian model of inheritance segregated in Mendelian ratios and excluded as a causal factor the underlying hypothesis of maternal inheritance of symmetry sensu Sturtevant (1923). Boklage (1984) critically analyzed Policansky's data, and he actually broadened their scope by suggesting a one- or two-locus mechanism to explain eye symmetry inheritance. Boklage also concurred with Policansky's conclusion that eye symmetry variation in the starry flounders is genetic in origin.

Brown and Wolpert (1990) proposed a genetic model to explain the mechanism by which molecular asymmetry determines symmetry at a higher structural level. The model is based on the simple premise that the causality of symmetry should be found at the molecular level because asymmetry is built into the DNA, protein, and carbohydrate molecules of every organism. Brown and Wolpert (1990) substantiated their model with Layton's (1976), as well as other experimental evidence. Layton (1976) elucidated the inheritance of symmetry of situs inversus viscerum (SIV) in conjoined twins, showing it to be inherited as a single-gene autosomal recessive trait. A normal gene at the *iv* locus showed complete dominance and control of normal asymmetry. The absence of this control was observed in *iv* homozygotes in which asymmetry was randomly

determined. Brown and Wolpert (1990) observed that asymmetries in general were mutually correlated but were not tightly linked. This observation is applicable to pleuronectiform fish in which eye symmetry reversal and color pattern shifts were simultaneously reported (Dawson, 1962, 1964, 1966, 1971; Taylor et al., 1973; Gartner, 1986). Consequently, if eye symmetry and SIV are linked, they should follow the same genetic model proposed by Brown and Wolpert (1990), and a plausible explanation of the causality of eye symmetry could be hypothesized. In higher vertebrates, the autosomal recessive gene *iv* in homozygote condition showed a ratio of 1:1 for SIV symmetry. The presence of the *iv* gene specified normal symmetry, and its absence in homozygotic condition induced random allocation of normal and reversed symmetry (Layton, 1976). Random allocation of symmetry was suspected to reside in a morphogenic gradient present in the early stages of larval development (Driever and Nüsslein-Volhard, 1988a, 1988b; Nüsslein-Volhard, 1991). The morphogenic exponential concentration gradient was created by a morphogen—a protein—that diffused randomly from the antero-posterior axis, and it was the inducer of bilateral differentiation of the embryo. The morphogen's molecular structure and its rate of synthesis are genetically controlled. Symmetry is determined with respect to the morphogen structural orientation and responds to the random morphogenic gradient in early ontogeny. The SIV gene controlling organogenesis symmetry was mapped to chromosome 12 in murine vertebrates, and it is closely linked to the immunoglobulin *Igh-C* locus (Hanzlik et al., 1990). The gene controlling organogenesis symmetry—the *iv* gene—showed a 1:1 ratio in genetic crosses of *Xiphophorus maculatus* (Poeciliidae) (Barker-Cohen, 1961). This ratio is identical to the one observed for higher vertebrates (Layton, 1976) and suggests that Brown and Wolpert's (1990) model is applicable to fish.

Under Brown and Wolpert's (1990) model, the explanation for the rarity of reversed eye symmetry in pleuronectiform fish in the Gulf of Mexico is evident. Eye symmetry should be coded by an autosomal recessive gene with reduced penetrance. In order to produce a fish with reversed eye symmetry, the alleles must be homozygous, and their presence must be coupled with the correct random morphogenic gradient. This model, assuming variable penetrance, explains a cline such as the one observed for the starry flounder in temperate wa-

ters (Policansky, 1982a). But according to Policansky (pers. comm.), it cannot explain the occurrence of those fish showing two independent symmetric characters with opposing directionality—for example, a bothid that has an optic chiasma in which the right optic nerve crossing is dorsal to the left optic nerve but also has dextral eye symmetry. Policansky's objection could be settled by assuming independence between the anterodorsal axis and the dorsoventral axis. The independence of the dorsoventral axis and anteroposterior axis has been demonstrated for *Drosophila* by Nüsslein-Volhard (1991). This process follows the universal mechanisms controlling body shape (De Robertis et al., 1990; McGinnis and Kuziora, 1994).

The model of Brown and Wolpert (1990) explains the genetic factor controlling eye symmetry. However, to account for the low frequency of reversed Bothidae in the Gulf of Mexico, additional biological factors (e.g., the mechanics of mating and courtship between fish with opposing symmetry) must be evaluated in conjunction with the genetic factor. If courtship behavior and the mechanics of mating reduce the fitness of dextral morphs, then the resulting reduction in the number of fertilized eggs will further diminish the occurrence of dextral symmetry. Biological factors like these conceivably play an important role in controlling the frequency of dextral bothids.

The scarcity of sinistral morphs in the family Pleuronectidae was suggested by Gudger (1935) to be the result of almost 100% mortality of reversed *Pleuronectes platessa*. However, in the family Bothidae, the discovery of few dextral specimens in the Gulf of Mexico suggests that sinistral eye symmetry is not a fixed character in this group and that perhaps currently unidentified biological factors keep the frequency of dextral morphs low.

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