

# BILATERAL ASYMMETRY AND BILATERAL VARIATION IN FISHES \*

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## INTRODUCTION

ONE ordinarily sees in bilaterally symmetrical animals creatures composed of identical halves, each a mirror image of the other. Closer scrutiny, however, discloses some degree of asymmetry in many of the paired structures. The differences between the two sides usually involve the internal organs, but also affect certain superficial structures, as well as reactions and movements. Bilateral unlikenesses may be rare, common, unusual, or invariable. When the sides are different, the better development may occur on the left side or on the right side, or sometimes on the left and sometimes on the right, in any conceivable ratio. The differences between the sides may involve the presence or the absence of a structure, the size or the shape of paired elements, or the number of meristic parts. Asymmetries are known to characterize all stages of development, from the unfertilized egg to the dying adult.

Fishes, like all other vertebrates, exhibit such differences between the corresponding structures of the left and right sides. Many bilateral dissimilarities have been treated. The numerous scattered contributions are most adequately summarized in a book, *Das Rechts-Links-Problem im Tierreich und beim Menschen*, by Wilhelm Ludwig (1932). Most of the recorded asymmetries, however, have been inadequately described or unsatisfactorily explained.

The objects of this study are to present new data on the bilateral differences between the left and the right elements of paired structures of fishes; to integrate these findings with previously recorded information; to analyze new and old data by modern statistical methods; to contribute suggestions that may help to explain the observed differences; to give a general picture of the asymmetries; to discuss the bearing of these findings and interpretations on the question of right-handedness in man, and on problems in such fields of biology as general systematics and evolution; and

to offer suggestions for further researches on the bilateral asymmetries of fishes.

Particular attention is paid to the flatfishes (order Heterosomata), the most extremely asymmetrical of all vertebrates. Bilateral differences in external characters are emphasized. The major asymmetries in the digestive and circulatory systems are in general neglected, as they are well known and were extensively summarized, for vertebrates in general and for fishes, by Ludwig (1932: 224-237, figs. 109-110). Similarly, only incidental consideration is given to asymmetries in the egg and in the embryo, and to bilateral differences in growth and movements. Numerical differences are the most thoroughly analyzed, according to methods that call for some explanation.

STATISTICAL METHODS

The chief attempt to develop a statistical method for the analysis of quantitative bilateral asymmetries appears to have been made by the German zoologist and biometrician Georg Duncker (1904), in a treatise entitled "Symmetrie und Asymmetrie bei bilateren Thieren." Duncker's statistical methods were reviewed and accepted by Ludwig (1932 : 4-8).

Duncker (1904: 555) proposed an index of asymmetry, designated *a*, with the following formula:

$$a = \frac{0n \cdot (D') - (L)}{n[\sum(D') + (D)]}$$

in which the differences are all expressed in terms of right count minus left count, and

*f'* = frequencies of positive differences, without regard to amount of difference;

*D'* = positive differences (*f' × Δ*); for example, when the counts of parts are 13 on the right and 10 on the left, *f'* = 1 and *D'* = 3;

*f*, = frequencies of negative differences;

*D*, = negative differences; for example, counts of 10 on the right and 13 on the left give *f*, = 1 and *D*, = 3;

*n* = number of specimens. Symmetrical counts (as 10 left and 10 right) are included in *n*, but are otherwise disregarded in the formula.

It can be shown that the index of asymmetry has one of the

desirable features of the coefficient of correlation in that complete asymmetry is represented by an index of + 1 when the stronger development is on the right, and of — 1 when the left side is the better developed. Complete symmetry is indicated by 0.

The formula for  $a$  was derived by empirical trial. How sound it may be as a joint measure of the amount and direction of asymmetry we do not know. We have avoided the use of the formula because we see no way of estimating the standard error of the index and, more particularly, because it does not fit our purposes. It is true that Ludwig fixed an  $a$  value of about 0.05 as the threshold of significance, but apparently by unwarranted, arbitrary choice.

Our main objection to the use of Duncker's index is that it confuses two functions of asymmetry — amount and direction. When the proportion of asymmetry is low, the value of  $a$  will be low even though among the few asymmetrical individuals the rights may strongly predominate over the lefts, or vice versa. Thus, for a sample in which every one of the 100 variants out of 10,000 specimens has a higher count on the right side,  $a = 0.01$ , though the significance of the direction of asymmetry — among the asymmetrical individuals, of course — is unquestionable. In a second series in which, out of a total of 100 specimens, 50 have the count greater on the right side and 40 have a higher number on the left,  $a = 0.1$  — a value far above Ludwig's limit of significance. For the first sample the value of  $a$  is one tenth as great as in the second series, yet the direction of asymmetry is much more definite and almost infinitely more significant.

We have separated the two functions of asymmetry. The *amount* of overall asymmetry is expressed as a percentage figure,

$$\frac{100(L - R)}{N}$$

in which  $L$  and  $R$  represent counts that are higher or development that is otherwise better (on some indicated basis) on the left and right sides, respectively, and  $N$  is the total number of specimens, symmetrical plus asymmetrical, in the sample. The values for  $N$ ,  $L$ , and  $R$  are tabulated. Since we are only incidentally interested in the amount of asymmetry, we have not tried to determine the standard error of the percentage of asymmetry.

The *direction* of asymmetry in the portion of the sample having

different values on the two sides is expressed in the tables by the percentage of dextrality,

$$\frac{100 R}{L + R'}$$

in which  $L$  and  $R$  have values as indicated above. The reliability of observed differences between the sides is determined from the values for  $L$  and  $R$  by the now widely used  $\chi^2$  test, and the Yates correction is applied when the expected number (the median between the  $L$  and  $R$  values) is less than 25. The method is described in most textbooks of statistics, for instance, in Snedecor (1940: 168-171) and Simpson and Roe (1939: 296-300).

The probability ( $P$ ) that the ratio of lefts and rights differs from one of equality, in other words, that the result could have been obtained by chance alone, is generally given. In the tables a percentage figure ( $100 P$ ) is entered, indicating the probabilities in 100 that the results are due to chance. The  $100 P$  values are expressed as whole numbers (chances in 100), or to tenths (1 to 9 chances in 1,000), or to hundredths, from 0.01 to 0.09 (1 to 9 chances in 10,000). The  $100 P$  values of 0.00 indicate values of less than 0.005; that is, probabilities of less than 1 in 20,000 that the results are due to chance. Too strict reliance on these  $P$  values is unwarranted, for several statistical reasons, but, relatively speaking, they are valuable as an index of the reliability of the observed differences. The naïve faith of biologists in a definite threshold of reliability, at  $P = 0.01$  or  $P = 0.05$ , is to be condemned and avoided. Much higher values afford some evidence of significance, to the degree of reliability indicated by the value of  $P$ .

The tables in textbooks give only a few corresponding values of  $\chi^2$  and  $P$ , but, since in the simple comparison of two figures or in "2 X 2 tables"  $\chi^2$  has one degree of freedom, and since  $\chi$  at one degree of freedom equals  $t$  with an infinite degree of freedom, one needs merely to read off the  $P$  value corresponding to  $\chi = t$ , at 0 skewness, in the newer tables (Salvosa, 1930: tables, pp. 1-60; Carver, 1940: 1-61; Lowan, 1942). It needs be noticed that Salvosa's table, repeated by Carver, gives half of the area of the Type III curve, whereas the "W. P. A. table" (edited by Lowan) gives the whole area. To arrive at the  $P$  value the figures in either table are to be subtracted from 1, but the differences obtained from the use of Salvosa's table are to be multiplied by 2.

## DEXTRALITY AND SINISTRALITY IN FLATFISHES

When one thinks of left-handedness and right-handedness in fishes, his thoughts are apt to turn first to the fishes of the order Heterosomata, in which, during the metamorphosis, one eye shifts to the top of the head, or, more commonly, to the opposite side, so that either the left or the right side comes to bear both of the eyes, leaving the other half of the body blind. During the transformation many asymmetries develop: to a greater or a lesser degree, depending on the genus and species, the anterior part of the skull becomes twisted; the muscular development is more or less weakened on the blind side; the teeth in many species become reduced in number or even totally lost on the eyed side; the color disappears from the blind side; and other inequalities appear. The general morphological nature of the asymmetry is well known (for discussion and references see Norman, 1934: 10-22) and the adaptational advantage is obvious, but the reasons why some species lie on the left side, others on the right side, and still others on either side remain unexplained. The problem warrants new study.

The two species of the genus *Psettodes*, constituting the very primitive family Psettodidae, are the only flatfishes which are indiscriminately sinistral (with both eyes on the left side) or dextral (eyes right), on a basis which can be interpreted plausibly as primordial (Regan, 1910: 488). The optic chiasma in this genus is dimorphic (with either left or right nerve the upper one), as it is in fishes in general (p. 285), and left-eyed and right-eyed individuals are said to occur with about equal frequency. We know of no adequate published data on the laterality of this genus. Some authors have described *P. erumei* as dextral, others as sinistral, and there has even been some discussion as to whether the right-eyed and left-eyed individuals represent a single species. Oshima (1927: 178) listed five sinistral specimens and one dextral from Formosa. The five collected by Carl L. Hubbs at Batavia, Java, in 1929, include two that are sinistral; three, dextral. Twelve specimens from the Philippine Islands and from Batavia, Java, and Hong Kong, China, kindly loaned us by Dr. Leonard P. Schultz of the United States National Museum, comprise three sinistral and nine dextral. The total tally for *P. erumei* (entered in Table I) is therefore ten sinistral and thirteen dextral.

A small group of flounders related to *Citharus* comprises three sinistral genera hitherto placed in the Bothidae and two dextral genera previously classed in the Pleuronectidae (Hubbs, *In press*). In the left-eyed species the nerve of the right eye is dorsal in the chiasma; in the right-eyed forms, the left nerve is superior. There seems to be some obligatory relation between laterality and type of chiasma in this group, for the one known reversed specimen, the dextral individual of *Citharoides macrolepidotus*, referred to below, has the nerve of the left eye dorsal, as it is in the species that are normally dextral. It is suspected that the flounders of the sinistral family Scophthalmidae may show the same relation between the side bearing the eyes and the mode of crossing of the optic nerves.

All flatfishes comprising the four major families are interpreted as normally either dextral or sinistral, whether they be soles (*Cynoglossidae* and *Soleidae*), which, though highly specialized in other respects, retain the primitive dimorphic type of chiasma, or flounders and their allies (*Bothidae* and *Pleuronectidae*), which have developed a monomorphic chiasma. In all bothids in which the character has been studied the right nerve has always been found to cross dorsally to the left nerve, and the eyes are almost invariably on the left side, whereas in all pleuronectids examined, with the exception of one specimen (pp. 245-246), the left optic nerve has been determined to be dorsal in the decussation, and the eyes and color are normally on the right side. These significant relations between the side bearing the eyes and the type of optic chiasma were discovered by Williams (1902: 34), and were then thoroughly demonstrated in a classical study by Parker (1903). Parker's conclusions have been widely quoted, as by Jordan (1905, 2: 482-483) and Ludwig (1932: 234-237). His results have been extended and confirmed by other workers, including Regan (1910: 487-488), Mayhoff (1912), Wu (1932: 46-47), Norman (1934: 28-29, fig. 19), and Hubbs and Marini (1939: 159-160). The data have been summarized by Gudger (1935: 26-35, fig. 5) and Hubbs (*In press*).

Since the location of the eyes is almost invariable in the respective families, the tongue soles (*Cynoglossidae*) are regarded as normally sinistral; the true soles (*Soleidae*), as normally dextral. Because of the almost constant position of the eyes in most species, and because of the correlation between the location of the eyes and the

special type of monomorphic chiasma, the turbot (Bothidae) are regarded as normally sinistral; the flounders proper (Pleuronectidae), as characteristically dextral. Specimens with the eyes on the side that is normally blind are said to be reversed. This condition is regarded as abnormal, even for those species or races which often have the eyes on the "wrong" side, including the invariably reversed Asiatic races of one species.

#### REVERSAL OF SIDES IN FLOUNDERS

Extensive reviews of the problem of reversal in flounders (Ludwig, 1932: 234-237; Norman, 1934: 27-29, *et passim*; Gudger, 1935; Hubbs and Kuronuma, 1943 : 298-301) have shown: (1) that sinistral Soleidae are exceedingly rare and that dextral Cynoglossidae are still unknown; (2) that dextrality occurs with extreme rarity in all bothids, except in a very few Pacific species which are said to be indifferently sinistral or dextral; and (3) that sinistrality is so rare as to appear teratological in all Pleuronectidae, except the two species now referred to *Platichthys* and possibly also the North Pacific species *Hippoglossoides elassodon* and the New Zealand genus *Rhombosolea*. Our study proves that *Hippoglossoides elassodon* is now to be removed from the list (pp. 237-238). Adequate data on the proportion of rights and lefts in *Rhombosolea* are not available.

In the European flounder, now known as *Platichthys flesus*, the percentage of reversal varies widely, but usually remains below 50 per cent, as demonstrated by Duncker (1895: 82-83; 1900 : 339-340), Berg (1932: 3-7), Ludwig (1932: 235), Norman (1934: 28), and Gudger (1935: 20, 29-30). Geographical variation in laterality that is even more remarkable is exhibited by the Pacific species *P. stellatus*, in which the percentage of reversal is 49 to 60 in western North America, 68 about Kodiak Island and the Alaska Peninsula, and 100 in Japan (Hubbs and Kuronuma, 1942: 298-301). Since the data for *Platichthys stellatus* are now very extensive, the differences in percentage of reversal between the species of *Platichthys* are certainly not related, as Gudger (1935: 21) thought that they might be, to the size of the commercial catch.

The reversal of sides in the Japanese population of *Platichthys stellatus* seems to be invariable or at least nearly constant, for all the 476 Japanese specimens examined were sinistral. Hybrids between this sinistral *Platichthys* and the dextral species *Kareius bi-*



*coloratus* were both sinistral (14) and dextral (13). These data furnish some of the strongest evidence that reversal is genetically determined.

As the foregoing account shows, reversal is a common phenomenon only in Pacific species and in *Platichthys flesus* of Europe. Jordan and Goss (1889: 230-233, 242-245), Jordan and Evermann (1898: 2602-2712), Parker (1903: 231), Jordan (1905, 2: 481-483, 492), and Regan (1910: 487) were impressed by the indiscriminate laterality of several flounders along the west coast of the United States. The high frequency of reversal in the flounders of the northeastern Pacific can be explained in part only by the greater development in that region of the groups concerned, namely, the Paralichthyinae and the Pleuronectidae (see zoogeographic analysis by Norman, 1934: 48-50). It may, of course, be only a series of coincidences (1) that the Pacific species of *Platichthys* is reversed more often than the Atlantic form; (2) that the only species of *Paralichthys* reported to have both eyes commonly on the right side is *P. californicus*; and (3) that among the genera related to *Paralichthys* only eastern Pacific representatives, *Hippoglossina* and *Xystreurus*, are reported to be indiscriminately sinistral or dextral. The almost complete restriction to the Pacific Ocean of the species with aberrant laterality still poses a problem.

Except for *Platichthys stellatus* no statistical data of consequence have been reported on the percentage of reversal among the Pacific species which are claimed to be more or less indiscriminately right-sided or left-sided. Parker's (1903: 231-232) figures of 11 sinistral (normal) and 15 dextral (reversed) examples of *Paralichthys californicus*, as well as those of 50 dextral (normal) and 50 sinistral (reversed) specimens of *Platichthys stellatus*, though repeated by Ludwig (1932: 235-236) and by Gudger (1935: 19-21), probably represented selected samples. Extensive series of counts are called for to determine how "indiscriminate" the sidedness is in the variable Pacific species. A small number of counts are contributed toward this need in Table I. The data for *Psettodes erumei* are discussed on page 234. The data for *Tephrinectes sinensis* are those of Oshima (1927: 193), who reported 4 sinistral and 3 dextral specimens from Formosa, and of Wu (1932: 47, fig. 17) who recorded 2 sinistral and 4 dextral examples from China; plus one dextral specimen from Canton, China. *Paralichthys californicus* is almost surely nor-

TABLE I

DATA ON SIDE BEARING EYES IN PACIFIC FLATFISHES REPORTED TO BE MORE OR LESS INDISCRIMINATELY SINISTRAL OR DEXTRAL

Based on material in the Museum of Zoology of the University of Michigan (except as noted in the text). The limited data on *Platichthys stellatus* are a slight supplement to the more than 18,000 counts for this species published by Hubbs and Kuronuma (1942: 299-300). None of the material was selected for sidedness.

Family (and normal condition)	Species and locality	Number of specimens	
		Sinistral	Dextral
Psettodidae (indiscriminate)	<i>Psettodes erumei</i> , Philippines, Java, and China	10	13
Bothidae (normally sinistral)	<i>Tephrinectes sinensis</i> , Formosa and China .....	6	8
	<i>Hippoglossina stomata</i> , southern California .....	3	0
	<i>Paralichthys californicus</i> , southern California .....	93	57
	<i>Xystreurus liolepis</i> , southern California .....	9	18
Pleuronectidae (normally dextral)	<i>Hippoglossoides elassodon</i> , Frederick Sound, Alaska (shrimp trawls, Sept. 1, 1939) .....	0	312
	Other localities, Alaska and Puget Sound .....	0	16
	<i>Platichthys stellatus</i> , California	13	13

mal oftener than reversed; our counts, yielding a *P* value of 0.003, are 93 sinistral and 57 dextral (part of the material is in the California Academy of Sciences). It is possible that *Xystreurus liolepis*, by contrast, may be more commonly reversed than normal, for the ratio in the material at hand is 9 sinistral to 18 dextral. The allocation of *Xystreurus* in the Bothidae is not to be questioned, for the right optic nerve is the more dorsal (Hubbs and Marini, 1939: 159). Frequent variation in the side bearing the eyes is thus confirmed for all species just mentioned. We find no basis and no confirmation, however, for the statements that *Hippoglossoides ekssodon* is "sometimes" or "frequently" sinistral (Jordan and Gilbert, 1883: 826, 827; Jordan and Goss, 1889: 230; Jordan and

Evermann, 1898: 2605, 2615). If reversal does occur in this species, it must be with rare frequency. The three specimens of *Hippoglossina stomata* listed are all sinistral, as was a specimen recorded previously (Hubbs, 1916: 168). More data on this genus are greatly needed, since the statements in the literature (Jordan and Goss, 1889: 230, 242; Jordan and Evermann, 1898: 2620; Norman, 1934: 28, 65) are based on very limited material and are somewhat conflicting.

Variability in the location of the eyes is, for some unknown reason, much less common in the northwestern than in the north-eastern Pacific. In his elaborate doctoral study of Japanese flounders and soles, based on the extensive collections which Carl L. Hubbs made in 1929, Katsuzo Kuronuma determined, among the hundred species occurring in Japan: (1) that supposedly indiscriminate laterality characterizes only *Psettodes erumei* and *Tephrinectes sinensis*, which barely reach the waters of Japan proper and are unrepresented in the collections made there in 1929; (2) that *Platichthys stellatus* (as already stated) is invariably reversed in Japan; (3) that out of nearly 2,400 specimens, representing the other Japanese species, only two are reversed. The ratio of 1: 1,200 for reversed : normal individuals of these ninety-seven species may be too high, for the Japanese collectors from whom the specimens were received in 1929 may have preserved both of these reversed flatfish because of their abnormality. One is a dextral example of *Citharoides macrolepidotus*, one of the two Japanese examples at hand of this citharid (Hubbs, *In press*). The other one is the unique sinistral representative (Pl. I, Fig. 2) found among the 201 specimens of the pleuronectid species *Tanakius kitahame* collected in 1929. The only other known cases of reversal among the flounders of eastern Asia are: (1) a dextral specimen of *Paralichthys olivaceus*, with the right optic nerve dorsal (Wu, 1932: 47), (2) a dextral example of the bothid species *Pseudorhombus pentophthalmus* (Kamohara, 1935: 682, fig. 6), and (3) a sinistral *Limandella yokohamae*, with the left optic nerve superior (Wu, 1932: 47). The reversed specimens recorded by Wu were found in an extensive study of Chinese flatfishes.

The discovery of occasional reversal in five additional species, just mentioned, strengthens the opinion that all species of flounders may occasionally have the eyes and color on the side which is

normally blind and white. Why the phenomenon of reversal is frequent in only a few species remains a total enigma.

DECREASED VIABILITY OF REVERSED FLOUNDERS

There is some evidence that sinistral individuals of normally dextral flounders (*Platichthys*) are less viable than the right-handed ones. Published statements to this effect are based on the following data for *Platichthys flesus* of Europe (Duncker, 1900: 339-340):

. . . Apstein fand unter 154 jungen (3,5-8,4 cm langen) Tieren aus der **Eckernförder** Bucht 56 (= 36,4 %), ich<sup>2</sup> unter 90 gleichfalls jungen (1,9-6,6 cm langen) aus der Neustadter Bucht 31 (= 34,4 %) linksaugige; unter 225 markt-reifen **Stücken** aus der westlichen Ostsee und von der Nahe der **Elbmündung** erhielt ich dagegen nur 53 (= 23,6 %) **linksäugige**, sodass der Prozentsatz der letzteren bei den jungen Tieren **höher** war. Dementsprechend finde ich auch bei dem Plymouth-Material in den drei kleineren der sechs unterschiedenen Grossen-gruppen linksaugige Exemplare etwas häufiger, als in den drei **grösseren** (ge-schlechtsreifen) und zwar bei beiden Geschlechtern in dem nahezu gleichen **Verhältnis** 1 : 0,85 ( $\sigma^3 = 7,14 : 6,12$  %,  $\text{♀} = 4,20 : 3,52$  %). Unter 192 **meta-morphosierenden** Larven von Megavissey-Harbor waren nur 11 (= 5,73 %) linksaugige, also nicht **mehr**, als unter dem noch nicht geschlechtsreifen Teil des Materials.

Da eine nachtragliche Veränderung der Augenstellung bei den Plattfischen ausgeschlossen ist, so lässt sich nur auf eine **höhere** Sterblichkeit der linksaugigen Exemplare gegen die Geschlechtsreife hin schliessen.<sup>4</sup> Ob der von mir gefundene Unterschied der Geschlechter in der Augenstellung — nahezu 1 mal soviel **links-äugige Männchen**, wie Weibchen — **ein** durchgreifender ist, muss einstweilen **dahingestellt** bleiben.

Duncker's conclusion that the percentage of sinistrality decreases with age in the flounder of the Baltic Sea seems to be statistically valid, provided the results were not greatly affected by local or temporal variation. The ratio of lefts to rights in the young was 87: 157; in the adults, 53: 172. The  $\chi^2$  value for the difference between these ratios is 8.18, corresponding to a *P* value of 0.004; that is, there are only 4 chances in 1,000 that the differences in the ratios would have been caused by chance.

Duncker's evidence was confusingly presented by Gudger (1935:

<sup>1</sup> *Mitth. deutsch. Seefischereiver.*, 1894, No. 5.

<sup>2</sup> *Ibid.*, 1897, No. 1.

<sup>3</sup> Ich verstehe unter „markt-reif“ Tiere von ca. 20 cm Länge und **darüber**.

<sup>4</sup> Vielleicht ist eine Erfahrung **erwähnenswert**, die ich **kürzlich** (Ende Mai 99) mit 67 jungen (1,5-3 cm langen) Elbbutt machte. Für das Aquarium gefangen, erlitten diese 67 Tiere einen längeren Transport in demselben **Gefäss** unter gleichen Bedingungen; es kamen lebend an 14 links- und 31 rechtsaugige; es gingen **unterwegs ein** 11 links- und 11 **rechtsäugige**.

22-23, 29). Apparently misled by the title of Apstein's paper, Gudger attributed to the plaice (*Pleuronectes platessa*) Apstein's figures (1894: 106) on the percentage of sinistrality in young flounders (*P. flesus*). These were the data utilized by Duncker in the passage just quoted, and they apply without doubt to the flounder. Assuming that they refer to the plaice, Gudger was confronted by a seemingly enormous decrease with age in the number of reversed individuals in that species. To explain the change he postulated an almost complete mortality of the young plaice, but, of course, no amount of nonselective mortality would affect the proportion of reversed to normal individuals. There is no reason to think that young plaice are reversed except with the extreme rarity that characterizes this phenomenon in most flatfishes. Similarly, confirming the statements by Williams (1902: 34) and Parker (1903: 230), we find no reversed individuals among more than one hundred transformed young of the related species, the winter flounder, *Pseudopleuronectes americanus americanus* (these specimens, from Massachusetts, grade down to 11 mm. in standard length).

Confirmatory though not fully conclusive evidence on the decreased viability of reversed flounders was kindly furnished us by the late Dr. E. Victor Smith, of the University of Washington (Table II). His extensive data appear to show that the Puget Sound form of the starry flounder, a race of *Platichthys stellatus rugosus*, is slightly oftener sinistral (reversed) when young than when adult. Unfortunately the most acceptable comparison, between the 1928 and 1929 adults and the 1930 and 1931 fish, largely young, both from Boundary Bay, does not yield a statistically reliable result: the ratios of sinistral to dextral fish are 444: 475 and 254: 234, respectively; the  $\chi^2$  value for the difference in ratios is 1.78, corresponding to a  $P$  value of 0.18. A rather highly trustworthy difference exists between the ratios for the Boundary Bay adults (445: 475) and for the fish, very largely young, taken in the same year about the San Juan Islands (3,436: 3,151):  $\chi^2 = 4.79$  and  $P = 0.03$ . One cannot exclude with full confidence, however, the possibility that racial, annual, or seasonal variations were responsible for the observed differences. The data in Table II are a breakdown of figures summarized by Hubbs and Kuronuma (1942: 300). Other counts of normal and reversed individuals of *Platichthys stellatus* published by these authors are too diverse for locality, or too uniform or too

TABLE II

RELATION BETWEEN AGE AND SINISTRALITY IN *PLATICHTHYS STELLATUS*  
FROM PUGET SOUND

The data were kindly furnished by the late Dr. E. Victor Smith, of the University of Washington. Localities are as follows: (1) San Juan Islands; (2) Boundary Bay; (3) Seattle. More specific data on age are not at hand.

Age	Locality	Year	Number of specimens examined	Percentage reversed (sinistral)	Median
Very large majority in first year	1	1928	1,687	52.22	52.18
	1	1929	4,900	52.14	
Largely in first year, with a few scattered through older years	2	1930	277	52.71	51.95
	2	1931	211	51.18	
Mostly small, but more large fish than in preceding series	3	1929	422	50.47	50.47
	3	1930			
All large, none less than two years old	2	1928	318	49.69	8.64
	2	1929	601	47.59	

indefinite as to age, to bear significantly on the problem of present concern.

The dextral individuals of *Platichthys*, normal in the sense that dextrality is almost universal in the Pleuronectidae, seem to have a slightly better chance than the sinistral ones to reach maturity. It is difficult, but not impossible, to reconcile this interpretation with the evidence (Hubbs and Kuronuma, 1942: 298-301) that laterality is inherited in *Platichthys stellatus*, that reversal has remained close to 50 per cent on the American west coast for decades, and that reversal is invariable in Japan. Further and more detailed data on the proportion of left-eyed to right-eyed individuals in the young of the starry flounder, particularly in recently transformed young, are still a great desideratum, as Gudger (1935: 21-22) wrote. So far as possible, in such studies efforts should be made to eliminate the factors of racial, annual, and seasonal variation, which were not completely excluded in the accumulation of the data discussed above.

The supposedly decreased viability of reversed flounders has been cited by Parker (1903 : 229-238), Mayhoff (1912: 84-85), Norman

(1934: 28), and others as evidence that the monomorphic chiasma arose as a product of selection. The extreme twisting of the optic nerves in reversed bothids and pleuronectids has been stressed by Parker and subsequent workers as a mechanical disadvantage; the monomorphic chiasma of the Bothidae and the Pleuronectidae is interpreted as allowing a simple and direct ontogeny. The dorsal location of the nerve of the migrating eye in both groups leads in the normal (unreversed) individuals to a partial uncrossing rather than a double crossing of the optic nerves. Such adaptations toward direct development are frequent — whatever the evolutionary mechanism may be. But if sinistrality in the Bothidae and dextrality in the Pleuronectidae arose because these conditions have a selectional advantage, why has reversal of sides become common in several species of Bothidae and in both species of *Platichthys*? In particular, we may well ask, Why *has Platichthys stellatus* become invariably reversed in eastern Asia?

Whatever may be its evolutionary basis, reversal of sides in the flounder families with a monomorphic chiasma is surely to be regarded as a secondary development (Parker, 1903: 234; Norman, 1934: 28). Ambilaterality is obviously both primitive and common only in the Psettodidae, and presumably remains primitive, though it has become rare in the Soleidae and also in the Citharidae and probably in the Scopthalmidae (Hubbs, *In press*).

#### INCOMPLETE MIRROR IMAGING IN REVERSED FLOUNDERS

One of the most remarkable features of variation in the side of flounders bearing the eyes is the lack of complete mirror imaging (the one completely reversed specimen described on pp. 245-246 provides an exception to this statement and to each of the following generalizations in this section). On superficial examination dextral and sinistral examples of the same species do appear to be mirror images, and indeed they were commonly so regarded prior to 1903, but closer inspection has shown that certain structures exhibit no reversal. Thus, as already pointed out (p. 235), it has been demonstrated adequately that the right optic nerve is invariably dorsal in all Bothidae and that the left nerve is dorsal in all Pleuronectidae, without respect to the side bearing the eyes. The monomorphic asymmetry is established prior to metamorphosis (Williams, 1902: 34; Parker, 1903: 230; Jordan, 1905, 1: 174).

That the viscera in the flatfishes constantly maintain the bilaterally asymmetrical arrangement that is characteristic of fishes in general, with the liver on the left side and the intestinal coils against the right body wall, has already been determined (Cunningham and MacMunn, 1894: 801; Cunningham, 1907: 176; Norman, 1934: 29). I have verified this conclusion by an examination of numerous flounders, including both dextral and sinistral specimens of: (1) *Psettodes erumei*, a species of the Psettodidae, in which neither side can be said to be normal, neither reversed; (2) *Citharoides macrolepidotus*, one of the ordinarily sinistral species of the Citharidae; (3) *Paralichthys californicus* and *Xystreureys liolepis*, members of the normally sinistral family Bothidae; and (4) *Platichthys stellatus*, representing the normally dextral Pleuronectidae. The typical pattern of asymmetry holds for both dextral and sinistral individuals of *P. stellatus* on the American west coast and for the exclusively sinistral Japanese race; also for the dextral and sinistral hybrids between *Kareius bicoloratus* and *Platichthys stellatus*. Hubbs and Kuronuma (1942: 295-298) obviously drew up their description of the visceral anatomy of these species and the hybrids from sinistral specimens and wrongly indicated that this pattern holds also for the dextral hybrids and *Kareius*; for those forms the term "blind side" in the published account should have read "right side" or "eyed side." It is obvious that the more fundamental features of visceral asymmetry are fixed prior to metamorphosis, in the pattern that is characteristic of fishes in general.

There is at least one other bilateral asymmetry in certain flatfishes that maintains a constant pattern unrelated to the general twisting of the head and body. In representative specimens of the few flatfishes in which these folds remain separate, instead of being symmetrically conjoined (Schmidt, 1915: 442-443; Hubbs, *In press*), we find that the right branchiostegal membrane embraces the urohyal and is covered by the more deeply pigmented left membrane. This is true of *Psettodes erumei* and of *Citharoides macrolepidotus*, whether the specimen be dextral or sinistral in respect to eyes and color. The left membrane also overlaps the right in another sinistral citharid, *Citharus macrolepidotus*, as well as in the dextral citharid *Brachypleura novae-zeelandiae*. The left membrane is also constantly the outer one in *Lophopsetta aquosa* and other Scopthalmidae, of which only sinistral specimens are known. We



conclude that this asymmetry in the folding of the gill membranes must be established very early in the life of these flatfishes, prior to metamorphosis. In fact, the pattern was established very early in the evolution of modern fishes: the left membrane overlaps the right in *Amia calva*, and this condition is more or less definitely retained throughout the teleost series (Hubbs, 1920: 62, see also pp. 278-280 of the present paper).

#### A COMPLETELY REVERSED FLATFISH

An exception to the rule that there is no complete reversal of bilateral parts in flounders is furnished by the one known sinistral example (Pl. I, Fig. 2) of *Tanakius kitaharae* (Jordan and Starks), a Japanese species of the normally dextral Pleuronectidae (Pl. I, Fig. 1). This specimen, already referred to (pp. 235, 239), is an adult 220 mm. in standard length. It was collected in the Pacific Ocean off Onahama, Japan, by the Fukushima-ken Fishery Experiment Station, and was presented to Carl L. Hubbs in Japan in 1929.

In all essential respects this sinistral example seems to be the mirror image of a normal *Tanakius*. The intestine projects into the backward extension of the coelome on the left side, rather than on the right side, as it normally does in this and several other genera, without any hitherto known exception. The liver is on the right side, rather than on the left, as it is in all other flatfishes so far as previously determined, whether they be dextral or sinistral. The intestinal coils are on the left side, rather than the right, as in all other known specimens. This is the general rule for fishes. *Situs inversus viscerum* is presumably rare among the Pisces, although Lynn (1943) recorded an incidence of 4.7 per cent among 510 single embryos of trout and a higher percentage among conjoined twins. Ludwig (1932: 379) quoted data on *situs inversus* in amphibians, but not in fishes.

Suspecting that this fish might represent a complete reversal, we examined the crossing of the optic nerves. The right nerve was found to pass dorsally to the left nerve, a position never recorded in a pleuronectid, either normal or reversed. The optic nerves cross but once, instead of twice, as they do in all other known reversed flounders, with one exception, whether they be referable to the Pleuronectidae or to the Bothidae (Hubbs, In press). In this

respect the reversed *Tanakius* agrees with the reversed (dextral) *Citharoides*, but that fish (p. 235) retains the normal asymmetry of viscera and of branchiostegal membranes. The appearance is that of a sinistral specimen of the typically sinistral Bothidae, as represented by Parker's often reproduced figure 5 (1903) or by Mayhoff's figure 3 (1912), rather than that of a reversed example of the normally dextral Pleuronectidae. It seems certain, however, that this specimen is not a bothid, for it is obviously a reversed individual, and all its characters stamp it as an aberrant member of the pleuronectid species *Tanakius kitaharae*.

This specimen provides the first known exception to the rule that the optic chiasma is invariably **monomorphic** in the Bothidae and Pleuronectidae. It furnishes the first known case, for either family, of the mirror imaging of the chiasma. That the left optic nerve is normally the more dorsal in *Tanakius kitaharae* was demonstrated by the dissection of ten dextral specimens.

In the more usually observed asymmetrical characters this specimen is also reversed. The blind side is nearly colorless and is less muscular than the ocular side. The urinary papilla is on the eyed surface. The head parts are just the reverse of normal.

In two other respects the completely reversed *Tanakius* specimen is slightly teratological. The posterior end of the dorsal fin is somewhat deflected onto the blind side, instead of retaining, as usual, a position along the median dorsal line. On the eyed side of the abdomen, an isolated segment of the lateral line, with well-developed pored scales, extends upward for some distance from between the pelvic fin and the anus.

It seems obvious that reversal is more fundamental in this specimen than in any other known flatfish.

#### INTERPRETATION OF REVERSAL IN FLATFISHES

A reversed symmetry of the early embryo or egg — involving some embryonic structure or position, the direction of cell cleavage, or the constitution of the egg itself — probably accounts for the complete change-over of right and left elements in the specimen just described, but seems not to be involved in the ordinary reversal of sides in the Heterosomata. No other specimen of flatfish is known to have all its organs reversed. Usually in two and sometimes in three characters reversed flatfishes are not perfect mirror images

of normal specimens. The asymmetries of the optic chiasma in the Bothidae and the Pleuronectidae, of the viscera in all flatfishes, and of the gill membranes in several genera (pp. 243-245), obviously become established in a pattern which is unrelated to the later twisting of the head. These almost invariable asymmetries must be fixed very early in development, for certain flatfishes metamorphose at a small size (data on the size at transformation were summarized by Norman, 1934: 30-33). The types and degree of asymmetry seem to bear little relation to the size at which one eye migrates to the opposite side of the head. Some flatfishes, particularly the tropical Bothidae, transform at a surprisingly large size. The record case is that of *Laeops parviceps*, of which there has been described a postlarva 70.5 mm. in standard length, with one eye still on each side of the head (Hubbs and Chu, 1934: 3-6, pl. 2).

The one completely transformed specimen of *Tanakius* is, therefore, the only reversed flatfish that is fundamentally comparable to sinistrally coiled snails. Reversal in the Gastropoda has been traced to a 180° change in the direction of cell cleavage. The literature on reversal of coiling in gastropods was reviewed at length by Ludwig (1932: 159-191, figs. 103-105).

Sinistrality in normally dextral flounders and dextrality in those that belong to the sinistral groups are no more related to situs in the viscera in flatfishes than left-handedness is associated with situs inversus in man.

A number of authors, including Cunningham (1907: 175-176), Gudger (1935: 35), and Hubbs and Kuronuma (1942: 301), have concluded that laterality, whether normal, reversed, or variable, is genetic. The facts of the case (p. 237) lead very strongly to this conclusion. The production of rights and lefts in approximately equal numbers, in the hybrids derived from the natural crossing of the dextral species *Kareius bicoloratus* and the invariably sinistral Japanese races of *Platichthys stellatus* (Hubbs and Kuronuma, 1942: 300), suggests strongly that simple genetic factors are involved in determining whether a flounder be left-eyed or right-eyed. There is no evidence that cytoplasmic inheritance is operative in the development of flatfish asymmetry.

From the viewpoints both of bionomics and of developmental mechanics many theories have been advanced to explain why some

flatfishes lie on the left side, others on the right. Involved theories have been published, by Ludwig (1942: 237), for example, to explain how unilaterality became established and how reversal has taken place. **Lamarckian** factors have been stressed by many of the theorists. None of the hypotheses proposed has met with any general acceptance (Norman, 1934: 13, 31). Most of the attempted explanations have some unacceptable or unprovable basis. As a whole, these proposals have transcended factual information and have merely added confusion to a difficult puzzle.

The one interpretation that has been generally agreed upon, since Parker's work was published in 1903, is that reversal is a secondary and not a primary feature, except in *Psettodes*. This conclusion seems to be warranted both for the soles, which retain the primitive dimorphic chiasma, and for the Bothidae and Pleuronectidae, which have a monomorphic decussation of the optic nerves. It may be questioned for the members of the small families Citharidae and Scophthalmidae (Hubbs, *In press*).

Whether or not reversed flounders are to be regarded as teratological depends in part on the point of view (Gudger, 1935). It has been noted, however, that reversal of the sides often occurs in flounders that have other abnormalities, such as ambicoloration and partial albinism. Gudger (1935) referred to a number of such specimens, including the exceedingly abnormal turbot reported by Cunningham (1907), and has since described three specimens combining reversal with ambicoloration (Gudger, 1936a; Gudger and Firth, 1937). The completely reversed specimen of *Tanakius kitaharae* recorded above shows other anomalies (p. 246). In the New Zealand genus *Rhombosolea* reversal is usually accompanied by the reappearance of the normally lacking pelvic fin of the blind side, according to Norman (1926: 278-280; 1934: 28-29). In species which are rarely reversed there is apparently some association between reversal of sides and other abnormalities, particularly **ambicoloration**. Since the coloring of both sides is interpreted as a return toward symmetry (see following section), it may be that this return is often carried beyond the mid-point, so as to lead to a change in the side bearing both eyes. In view of the data given in the next paragraph this is a more plausible idea than that the reversal of the sides leads to ambicoloration.

It seems to be significant, in this connection, that such anomalies

as ambicoloration are apparently no more common in the several North Pacific flounders which are notable for their indiscriminate laterality than they are in species which always or almost always have the eyes and color on one of the sides. None of the reversed specimens listed in Table I showed any sign of ambicoloration or other abnormality. We have heard of only three cases of ambicoloration in *Platichthys stellatus*, the flatfish with the record proportion of reversals, and only one of these reports rests on a specimen, a dextral individual from southeastern Alaska that was described by Gudger (1941). One hearsay record was mentioned by Gudger, and we can now add a third report. Silva, the long-time fisherman of Morro Bay, California, described to us personally what was certainly another ambicolorate *Platichthys*, "the same on both sides." These three teratological individuals are the only ones which have been noticed by men who have handled many thousands of starry flounders. Among the 476 specimens examined of the invariably sinistral Japanese race not one presented any obvious anomaly. There is no reason to think that ambicoloration and other terata are any commoner in *Platichthys stellatus*, which varies geographically from a condition of indiscriminate laterality to one of complete reversal, than they are in flatfish species that are never or virtually never reversed.

#### TERATOLOGICAL RETURN TOWARD SYMMETRY

The teratological condition of flatfishes known as ambicoloration, with related modifications, has been interpreted as a return toward the symmetrical structure of ordinary fishes. Not only the color but also other characters of the eyed side, for example, ctenoid scales, may appear on the eyeless side. The migrating eye may not have rotated the usual distance, and the forward extension of the dorsal fin, which ordinarily follows the transit of the eye, may not have been completed. As a result, a dorsal hook is commonly developed in extreme examples of ambicoloration. The subject was treated at some length, with a review of the literature, by Norman (1934: 22-27, figs. 18-19), and more recently has been extensively investigated by Gudger (1935, 1936a, 1936b, 1941; Gudger and Firth, 1935, 1936, 1937).

Although numerous ambicolorate flatfish have been described, the condition must be extremely rare. The aberration is so striking

that it has often come to the attention of zoologists. Numerical data on the relative frequency of ambicoloration have not been published. It may be of interest, therefore, to note that among the 2,412 specimens of Japanese flounders handled by Katsuzo Kuronuma (doctoral thesis, University of Michigan, probably still unpublished), only three were colored on both sides, and these may have been preserved because of their abnormality. Two of the specimens are of *Verasper variegatus*, a species that usually has scattered dark spots on the lower surface. One of the two has the hooked dorsal fin commonly associated with ambicoloration. The other *Verasper* and the one ambicolorate specimen of the abundant species *Limandella yokohamae* have a normal dorsal fin.

#### SECONDARY ASYMMETRIES IN FLATFISHES

Although there are a few basic asymmetries that maintain a left—right gradient unaltered by the reversal of the sides, the majority of the head and body characters develop bilateral dissimilarities along with or following the migration of the eye. Profound differences, for example, arise between the corresponding left and right elements in the skeleton and the musculature. Many of these secondary asymmetries have been described, and efforts have been made to interpret the findings (Norman, 1934: 1-55, figs. 1-28). Some have argued that the migration of the eye directly causes the excessive twisting of the anterior part of the skull; others have regarded the flexure of the skull as the primary movement, which carries the eye along with it. Objections have been raised, however, to any such simple cause-and-result relationship. In modern view it seems much more plausible to assume that a multitude of factors is involved, and that the whole genetic and developmental mechanism is keyed to the production of an organism that is asymmetrical in almost every element of internal and external anatomy.

Next to the unilateral position of the eyes, the bilateral difference in color is the most conspicuous feature in the asymmetry of the Heterosomata. In most flatfishes whichever side is blind is white, and almost entirely devoid of melanophores, whereas the upper side is thoroughly equipped with chromatophores. These color cells expand and contract as the exposed side marvelously simulates the color and the color pattern of the bottom on which the fish lies (references in Norman, 1934: 21).

Not all flatfishes, however, are unpigmented on the lower surface. In the primitive, relatively not greatly asymmetrical species *Psettodes erumei* we note a slight darkening of the under side. Similarly, a gray shade covers this side in the secondarily subsymmetrical flounders, such as *Atheresthes*. One such form first loses, then regains pigment on the under surface (Norman, 1934: 21). Oddly, some of the more or less extremely asymmetrical flounders, such as certain species of *Glyptocephalus*, *Taeniopsetta*, *Engyophrys*, and *Verasper*, develop dark pigment on the blind side, either as a shade or as a pattern of bars or spots. The adult male of *Crossorhombus kobensis*, a Japanese bothid, has a large violet wedge on the lower surface (Hubbs, 1915: 459). The dark spots on the lower surface of the "hogchoker," an American sole, are almost wholly confined to *Trinectes maculatus maculatus*, the northern subspecies (Hubbs and Allen, 1944: 128). Such variations in the pigmentation of the side on which the flatfishes lie are not readily explainable.

Since it was shown by Cunningham (1891, 1893, 1895; Cunningham and MacMunn, 1894) that flatfishes illuminated from below develop pigment on the normally white skin, some have thought that the lack of color is the direct result of the absence of light. Cunningham found, however, that heredity is involved, for in early development the pigment of the illuminated blind side first disappeared, "and it was only later after long exposure to light that pigment developed on the lower side."

In many flounders the lateral line is developed only on the eyed side, or is better developed there. Basic data are a part of the systematic literature (reviewed by Norman, 1934). In the best statistical analysis of this asymmetry Duncker (1900: 374-375, 392; 1904: 576-578, 646-647, 653) demonstrated that the accessory branch of the lateral line of *Platichthys flesus* averages longer on the ocular side than on the blind side. Quantifying the length of the line by listing the number of the dorsal ray opposite which the line ended, Duncker determined for 1,024 dextral specimens that the length was alike on the two sides in 590 fish, greater on the eyed (right) side in 279, and greater on the blind (left) side in only 155. In sinistral (reversed) flounders the degree of asymmetry was approximately the same, but the direction was altered: the accessory lateral line was usually longer on the left surface. In both cases the greater development was on the side that bears the eyes.

The perfection of scale development on the two sides of flounders is another character that is associated in some way with the direction taken by the migrating eye in metamorphosis. Commonly the scales of the upper side are ctenoid, whereas those of the opposite surface are cycloid (see systematic literature, especially Norman, 1934). Again it is not a problem of which side is right or which is left, but, rather, a question of which half of the body bears both eyes and which half has none. That definite hereditary factors are involved is clearly indicated by the manner in which the tubercular scales are developed on the blind side — whether left or right — in *Kareius X Platichthys* hybrids (Hubbs and Kuronuma, 1942: 278-287, pl. 4).

An asymmetrical location of either the anus or the urinary papilla, and usually of both these structures, is also correlated with the general somatic asymmetry established at metamorphosis. Schmidt (1915: 444), as quoted by Norman (1934: 19), "has drawn attention to the asymmetrical position of the anal papilla, which in all flatfishes, including those in which the vent is placed on the blind side, is situated on the ocular side of the median line." We have confirmed this finding for numerous species. The only species that we have found to furnish an exception to Schmidt's rule are the primitive flounder *Psettodes erumei*, in which a urogenital papilla lies close to the anus, in the same fossa, slightly on the blind side and in line between the anus and the front of the anal fin, and the members of three American bothid genera (*Citharichthys*, *Etopus*, and *Syacium*), in which both the papilla and the anus are deflected onto the blind side (Hubbs, *In press*). In dealing with *Platichthys flesus* Duncker (1895: 81) pointed out that the papilla is the urogenital opening in the males but only the urinary opening in ripe females, and we observe the same situation in *Tanakius kitabarae*. Duncker found the papilla on the blind side in only one specimen of *P. flesus*, among very many studied, and mentioned that Gottsche made a similar observation on one plaice that was white on both sides. Hubbs (1915) noted that the anus of flatfishes in general either lies on the mid-ventral line or is more or less transposed to the blind side, except in *Citharoides* and *Citharus*. In a thorough survey of this character throughout the pleuronectoid flatfishes Norman (1934) determined, in confirmation, that the anus is usually more or less displaced onto the blind side, and lies definitely on the eyed



side only in the two genera just mentioned. In *Citharoides*, as in its close relative *Citharus*, the urinary papilla arises on the edge of the anal opening on the eyed side of the body (in the reversed fish as well as in the normal specimens at hand); in another citharid, *Brachypleura*, the two organs are also on the eyed side, but are slightly separated (Hubbs, *In press*). In all bothids and in all pleuronectids examined the anus and the urinary papilla are separated from each other by a considerable expanse of body surface.

A test was made of the conclusion that the location of the urinary papilla is consistently correlated with the eyedness or blindness rather than with the sinistrality or dextrality of the sides. In more than two hundred specimens of *Platichthys stellatus*, nearly equally divided between rights and lefts, the papilla was on the eyed side without exception. In all the specimens the anus was on the blind side. Similar findings were obtained on normal and reversed specimens, though in smaller numbers, of *Paralichthys californicus* and of *Xystreureys liolepis*.

Unlike the major features of visceral topography, which early develop a gradient of asymmetry unrelated to that taken by the eyes, the posterior openings of the kidney and the intestine have, therefore, an asymmetry that is quite consistent with that of the eyes and color. Apparently the positions of the urinary papilla and of the anus are among the numerous characters that are fixed subsequent to metamorphosis.

Likewise, in some flatfishes marked asymmetries correlated with the position of the eyes appear in the area of the gill covers; this region may be larger or more posterior or otherwise different on one side than on the other. These differences between the two surfaces are reversed when there is a change-over in the position of the eyes. In this respect the superficial gill-cover structures do not follow the monomorphic asymmetry of the branchiostegal membranes and rays (p. 244), which is obviously established earlier in development.

An interesting asymmetry involving the presence of a bone on one side and its absence on the other is exhibited by *Citharoides macrolepidotus*. In this species the supplementary maxillary bone is developed consistently on the blind side but is lacking on the ocular surface.

In the three genera of the Citharidae examined, namely, *Citharus*, *Citharoides*, and *Brachypleura*, a peculiar asymmetry is evident in

the structure of the pectoral fin rays. In the fin of the eyed side the articulations of the rays are much longer than broad, whereas in the blind-side fin the joints of the rays are much broader than long (Hubbs, *In press*). An approach toward this condition is shown by some other flatfishes, including *Psettodes erumei*.

In almost all flatfishes the paired fins are larger and otherwise better developed on the eyed side than on the blind side — whether the eyed side be left or right, and whether the specimen be normal or reversed in respect to the position of the eyes. The supporting data fill the systematic literature on the Heterosomata (ably reviewed by Norman, 1934). It was concluded by this ichthyologist (p. 20) that the pectorals in some flounders are subequal, and, as an exception to the general rule, we find that *Psettodes* usually has the pectoral fin of the blind side the larger (p. 257). In a number of genera of both flounders and soles the pectoral or pelvic fin of the ocular side may be well developed when its mate of the blind side is rudimentary or totally lacking. In these genera, of course, there is a constant difference in the number of pectoral or pelvic rays on the two sides. Bilateral variation in the number of rays in the paired fins, in species of flatfishes having these fins well developed on both sides, calls for special treatment.

BILATERAL VARIATION IN NUMBER OF RAYS IN PAIRED FINS  
ON THE TWO SIDES OF FLATFISHES

When, as usual, the paired fins of flatfishes are developed on both sides, the fin of the eyed surface as a general rule has on the average a higher number of rays than does the corresponding fin of the blind side — whether the eyes face to the left or to the right. The first and still the most thorough statistical demonstration of this secondary asymmetry was made by Duncker (1897: 819-820; 1900: 356-357, 362; 1904: 630-633; data reviewed by Ludwig, 1932: 6-8). In *Platichthys flesus* Duncker found that in the normal or dextral individuals the right pectoral nearly always contains more rays than the left fin; that the number of pelvic rays when different on the two sides is higher on the right side in the ratio of about 2: 1; and that the differences are accentuated, when only the branched rays are enumerated (data reanalyzed in Tables III-IV). In sinistral or reversed individuals the left fin (now on the eyed side) has the higher number of rays; the asymmetry is almost the

TABLE III

AVERAGE NUMBER OF PECTORAL AND PELVIC RAYS ON THE LEFT AND RIGHT SIDES OF DEXTRAL AND SINISTRAL FLOUNDERS (*PLATICHTHYS FLESUS*)

Based on 1,060 dextral and 60 sinistral specimens, from Plymouth, England; data from Duncker (1900: 356). The averages for the right fin are in bold-faced type.

	Eyed side, average	Blind side, average
Total pectoral rays		
Dextral specimens .....	<b>10.804</b>	10.143
Sinistral specimens .....	10.800	<b>10.217</b>
Branched pectoral rays		
Dextral specimens .....	<b>6.215</b>	2.529
Sinistral specimens .....	6.373	2.746
Total pelvic rays		
Dextral specimens .....	<b>5.983</b>	5.960
Sinistral specimens .....	6.033	<b>5.950</b>
Branched pelvic rays		
Dextral specimens .....	0.778	0.276
Sinistral specimens .....	0.800	<b>0.350</b>

same in degree, but reversed in direction. Obviously the correlation is not with the rightness or the leftness of the side but, rather, with eyedness or blindness.

Confirmatory results (Tables IV—V) were obtained in an analysis of the number of pectoral and pelvic rays on the eyed and blind sides of normal and reversed starry flounders, *Platichthys stellatus rugosus*. The counts were all made on specimens collected in the Columbia River mouth, Oregon and Washington, on July 20-21, 1926. The series of 225 specimens comprises 89 normal (dextral) and 136 reversed (sinistral) individuals. Since none of the fish were adult and most were small, the counts were made under a microscope and, when necessary, the skin was cut to make sure that the smallest rudiments were included. The counts of branched rays are valid for the bilateral comparison for specimens of this size, but do not equal the counts that would be obtained from adult fish, since additional rays dichotomize with increasing size. Perhaps in larger fish a significant difference between the eyed and the blind sides might be demonstrated in the number of branched pelvic rays, to conform with Duncker's results on *P. flesus*. There

TABLE IV

ASYMMETRY IN NUMBER OF RAYS, TOTAL AND BRANCHED, IN FLOUNDERS OF THE GENUS *PLATICHTHYS***L** signifies that the count is higher on the left side; **R**, that the count is higher on the right side.

	N	L	R	100 (L + R)	100R	100 P
				N	L + R	
<i>Platichthys flesus</i> *						
Dextral specimens						
Pectoral rays						
Total .....	1,059	17	661	64	97	0.00 †
Branched .....	1,014	2	992	98	100	0.00
Pelvic						
Total .....	1,056	20	41	6	67	1
Branched .....	1,054	31	425	43	93	0.00
<i>Platichthys stellatus</i>						
rugosus †						
Dextral specimens						
Pectoral rays						
Total .....	89	3	40	48	93	0.00
Branched .....	89	0	89	100	100	0.00
Pelvic rays						
Total .....	89	2	3	6	60	...
Branched .....	89	1	1	2	50	...
Sinistral specimens						
Pectoral rays						
Total .....	136	57	5	46	8	0.00
Branched .....	136	135	0	99	0	0.00
Pelvic rays						
Total .....	136	10	3	10	23	10
Branched .....	136	5	0	4	0	7

\* Data from Duncker (1904: 647-648), for specimens from Plymouth, England.

† A 100 P value of 0.00 indicates that the odds are less than 1 in 20,000 that the result obtained is due to chance.

Original data, for young specimens from the mouth of the Columbia River, Oregon and Washington, collected July 20-21, 1926.

is a greater difference between the pelvic rays of the two fins than the figures indicate, because in a number of specimens with the same count in the right and the left pelvic the fin of the blind side only has the last ray rudimentary. As in *P. flesus*, the differences in the pectoral ray counts are much greater for the number of branched

TABLE V

DIFFERENCES BETWEEN PECTORAL RAY COUNTS OF THE TWO SIDES IN DEXTRAL AND SINISTRAL SPECIMENS OF *PLATICHTHYS STELLATUS RUGOSUS*

Based on 89 dextral and 136 sinistral specimens collected July 20-21, 1926, in Columbia River mouth.

	Excess of count of eyed side over that of blind side										
	-1		1	2	3	4	5	6	7	8	
Total rays											
<i>D</i> *		46	36	4		.					0.46
<i>S</i> † .....		74	52	3		1					0.44
Branched rays											
<i>D</i> *				4	11	18	17	24	14	1	5.03
<i>S</i> †.....				9	16	25	33	34	11	7	4.91

\* Dextral (normal) specimens, with the right count (that of eyed side) typically higher than the left count.

† Sinistral (reversed) specimens, with the left count (that of eyed side) typically higher than the right count.

rays than for the total number of rays (Table V). This differential seems to hold for flounders in general, with at least one outstanding exception: in *Xystreureys liolepis* the rays are branched in the pectoral fin of the blind side (either right or left), but remain unbranched in the long straplike pectoral of the ocular side (Hubbs and Marini, 1939: 162). The mean difference between the counts of dichotomized rays on the two sides is nearly the same in the dextral and sinistral specimens, showing again that the number of rays is correlated with eyedness or blindness rather than with rightness or leftness.

The conclusion that eyedness of the side is correlated with the differential development of the paired fins among flatfishes in general is verified by systematic descriptions and, more particularly, by a statistical study of the Japanese species (Table VI). The outstanding exception to the rule appears, from this tabulation, to be provided by the most primitive of all the flounders, *Psettodes*, which has a dimorphic optic chiasma and one eye on the top of the head. In *Psettodes erumei* the fin of the blind side seems to have the higher average ray count, almost surely not a lower average. The blind-side fin also averages the larger and the stronger (this is true in four-

TABLE VI

FREQUENCY DISTRIBUTIONS OF RAY COUNTS OF THE TWO PECTORAL FINS IN JAPANESE  
PSETTODID, CITHARID, BOTHID, AND PLEURONECTID FLATFISHES

The counts were made by Research Assistant Katsuzo Kuronuma on material which Carl L. Hubbs collected in Japan in 1929. Supplementary counts for *Psettodes erumei* and *Citharoides macrolepidotus* are added. All the counts for the *Psettodes* are of specimens from Java, the Philippines, and China. Of the nine specimens of the *Citharoides* counted two only are from Japan; the others, from the Philippines. Counts of eleven other Japanese species, omitted because of inadequate series, stand in agreement with those included. The *t* values are the differences between the means (mean for ocular side minus mean for blind side) divided by the standard error of the difference.

	Number of pectoral rays									<i>M</i> ± <i>SE</i>	<i>t</i>	100 <i>P</i>
	7	8	9	10	11	12	13	14	15			
<b>PSETTODIDAE</b> (indiscriminate laterality)												
<i>Psettodes erumei</i>												
Ocular side .....					..	..	1	10	6	14.29 ± .14	1.45	15
Blind side .....					..	..	1	5	11	14.59 ± .15		
<b>CITHARIDAE</b>												
<i>Citharoides macrolepidotus</i>												
Ocular side .....				9	..	..	..	..	..	10.00 ..	•	
Blind side .....				8	1	..	..	..	..	10.11 ..		
<b>BOTHIDAE</b> (sinistral)												
<i>Paralichthys olivaceus</i>												
Ocular side .....				6	33	41	13	..	..	11.66 ± .08	3.08	0.2
Blind side .....				14	43	26	7	..	..	11.29 ± .09		
<i>Pseudorhombus arsius</i>												
Ocular side .....					2	10	..	..	..	11.83 ± .11	2.81	1
Blind side .....					6	4	..	..	..	11.17 ± .21		

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TABLE VI (Concluded)

	Number of pectoral rays									M ± SE	t	100 P
	7	8	9	10	11	12	13	14	15			
<b>PLEURONECTIDAE (dextral, Cont.)</b>												
<i>Xystrias grigorjewi</i>												
Ocular side .....				30	125	17	..	..	..	10.92 ± .04	0.19	85
Blind side .....			1	24	136	11	..	..	..	10.91 ± .04		
<i>Verasper variegatus</i>												
Ocular side .....				2	17	7	1	..	..	11.26 ± .13	-0.37	71
Blind side .....				3	13	10	1	..	..	11.33 ± .14		
<i>Verasper moseri</i>												
Ocular side .....			1	..	1	9	1	2	..	12.07 ± .32	0.21	83
Blind side .....				..	1	12	1	..	..	12.00 ± .10		
<i>Clidoderma asperrimum</i>												
Ocular side .....	-			..	..	5	7	5	..	13.00 ± .19	2.54	1
Blind side .....				..	2	7	8	..	..	12.35 ± .17		
<i>Pleuronichthys cornutus</i>												
Ocular side .....				13	59	69	7	..	..	10.47 ± .06	1.29	20
Blind side .....				16	70	55	7	..	..	10.36 ± .06		
<i>Lepidopsetta mochigarei</i>												
Ocular side .....			1	3	11	18	2	..	..	11.49 ± .14	1.85	6
Blind side .....			2	7	13	12	1	..	..	11.09 ± .16		
<i>Limanda punctatissima</i>												
Ocular side .....			5	9	3	..	..	..	..	9.25 ± .13	3.38	21
Blind side .....				7	..	..	..	..	..	8.58 ± .15		
<i>Limandella herzensteini</i>												
Ocular side .....			1	11	55	38	4	..	..	10.32 ± .07	4.74	0.00
Blind side .....				29	63	13	2	..	..	9.87 ± .07		

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<i>Limandella yokohamae</i>														
Ocular side .....			5	89	127	23	..	•	..	10.69 ± .04	} 3.28			
Blind side .....	2	11	118	95	18	..	..	..	10.48 ± .05					
<i>Deristes rikuzenius</i>														
Ocular side .....	1	8	52	9	..	..	..	..	9.99 ± .07	} 1.65				
Blind side .....		16	49	5	..	..	..	..	9.84 ± .06					
<i>Microstomus achne</i>														
Ocular side .....	1	1	17	4	..	..	..	..	10.04 ± .13	} 2.60	0.9			
Blind side .....	1	8	14	..	..	..	..	..	9.57 ± .12					
<i>Tanakius kitaharae</i>														
Ocular side .....			11	98	63	11	1	..	..	10.42 ± .05	} 1.39	16		
Blind side .....			14	104	60	6	..	..	..	10.32 ± .05				
<i>Glyptocephalus stelleri</i>														
Ocular side .....				13	14	11	2	..	..	11.05 ± .14	} 0.56	58		
Blind side .....				9	25	5	1	..	..	10.95 ± .11				
<i>Platichthys stellatus</i>														
Ocular side .....			1	12	36	16	..	..	..	11.03 ± .09	} 3.83	0.01		
Blind side .....			5	25	30	5	..	..	..	10.54 ± .09				
<i>Kareius X Platichthys hybrids</i>														
Ocular side .....			1	3	7	10	2	..	..	11.39 ± .21	} 2.06	4		
Blind side .....	..	..	..	7	12	4	..	..	..	10.87 ± .14				
<i>Kareius bicoloratus</i>														
Ocular side .....			1	..	33	44	4	..	..	11.61 ± .07	} 2.80	0.5		
Blind side .....	2	..	8	38	33	33	2	..	..	11.28 ± .09				

Bilateral Asymmetry in Fishes

teen of the seventeen specimens at hand; in the other three the fin is slightly longer on the eyed side). In *Citharoides macrolepidotus*, another very primitive species (Hubbs, *In press*), the number of rays seems to average as high on the blind as on the eyed side, if, indeed, it is not higher. In this species the fin of the lower surface, though shorter, is broader and has heavier rays than the fin of the upper side.

*Atheresthes*, a pleuronectid genus with the left eye on the dorsal margin, and the only member of the subfamily Pleuronectinae with the primitive type of olfactory lamellae, gives a very slightly but not reliably higher average for the blind (left) side. In *Atheresthes*, which contrasts with *Psettodes* in this respect, the fin of the ocular side is much larger than that of the eyeless side. The number of rays is probably about equal on the two sides in both species of *Verasper* (the average is slightly higher on the eyed side in one species and on the blind side in the other). It is perhaps significant that all the species just mentioned are more or less pigmented on the blind side, which in most flounders is white. A few other species have the averages very close, but the great majority have more rays in the eyed-side pectoral than in the blind-side fin. In the Bothidae the dimorphism in ray number is roughly proportionate to the degree of bodily asymmetry: slight in the most symmetrical genus, *Paralichthys*; somewhat more marked in *Pseudorhombus*; striking in the more asymmetrical genera, such as *Arnoglossus* and *Laeops* (Table VI) and *Chascanopsetta* (Kuronuma, 1940 : 48). Among the Pleuronectidae the dimorphism in numbers is less markedly increased in the most asymmetrical representatives. In the sinistral flounders (Bothidae) the difference between the upper pectoral fin (in this family the left one) and the right pectoral is greater as a rule than that between the right — normally uppermost — and left fins in the dextral group (Pleuronectidae). This asymmetry may be correlated with the probably greater number of rays in the left pectoral fin of the ambidextrous *Psettodes*. In six of the nine bothids tabulated (and also in *Chascanopsetta lugubris*) the ray counts of the two pectoral fins are found to differ on the average by more than 1.00 ray; the greatest difference for any of the pleuronectids is 0.67 ray.

As would be expected from the detailed analyses on *Platichthys stellatus*, the invariably sinistral (reversed) Japanese races of this

species have on the average more rays in the left (upper) pectoral than in the fin of the right side. The difference (0.49) is a little greater than the average for the Japanese pleuronectids. About the same difference (0.52) exists between the ray counts of the eyed-side and blind-side pectorals in the *Kareius X Platichthys* hybrids, which are dextral and sinistral in approximately equal numbers (Hubbs and Kuronuma, 1942: 298-301). The only other reversed specimens treated in Table VI are one each of *Citharoides macrolepidotus* and *Tanakius kitabarae*.

In the cases which have just been cited the number of rays in the pectoral fin, the characteristic which corresponds in the fish most literally to handedness in man, is associated with the general asymmetry of the body. In a somewhat converse relation various bodily asymmetries in the fiddler crabs appear to be correlated with the right or left location of the larger cheliped (Duncker, 1903; 1904: 632-633; Ludwig, 1932: 6-8, 202-210). Such relations give credence to the theories that dominant handedness in man may be related to some other major asymmetry, at some phase of development. There are, however, facts that argue against the validity of various causal relations that have been propounded.

#### ASYMMETRIES AND BILATERAL VARIATIONS IN ESSENTIALLY SYMMETRICAL FISHES

Like vertebrates in general, fishes other than the flounders and the soles appear on superficial examination to be completely symmetrical about the sagittal axis, but closer scrutiny indicates that in many respects the two sides are not perfect mirror images of each other. Dissection discloses that there are many fundamental and almost invariably monomorphic asymmetries in the digestive and circulatory systems. With very rare reversals, either right or left directions are taken or flexures assumed by various embryonic processes. Such asymmetries in the adult and embryo are well known and have been treated at length by Ludwig (1932), who gives a plethora of references. They are considered here only incidentally, and only so far as they are related to more superficial asymmetries. Particular stress is laid on the differences between corresponding structures of the two sides in degree of development, as measured by the number of parts making up these organs. The numerical treatment simplifies the statistical analysis of the data.

BILATERAL VARIATION IN NUMBER OF RAYS IN THE LEFT  
AND RIGHT PECTORAL FINS OF *LEPTOCOTTUS ARMATUS*

Particular emphasis has been placed in the present study on the differences between the two pectoral fins in respect to the number of rays. Among the bilateral asymmetries of fishes this is the one that corresponds most closely to right-handedness and left-handedness in man.

Our attention was directed to this problem during an analysis of meristic variation in *Leptocottus armatus*, a marine cottid fish of western North America. We noted that, when the number of pec-

TABLE VII

ANALYSIS OF ASYMMETRY IN PECTORAL RAY COUNTS OF  
*LEPTOCOTTUS ARMATUS*

*L* indicates that the count is higher on the left side; *R*, that the right fin has the higher number of rays.

Analyses	N	L	R	$100(L + R)$	$100 R$	100 <i>P</i>
				N	L + R	
Analysis by localities						
1. Sitkalidak Island, Alaska .....	174	10	19	17	66	14
2. Admiralty Island, Alaska . . .	104	7	16	22	70	9
3. Puget Sound, Washington .....	245	13	37	20	74	0.1
4. Grays Harbor, Washington ....	103	3	13	16	81	2
5. Nestucca Bay, Oregon .....	136	6	18	18	75	3
6. Humboldt Bay, California .....	221	13	31	20	70	1
7. San Francisco Bay region .....	223	17	32	22	65	3
8. Elkhorn Slough, California* ..	145	8	25	23	76	0.5
9. Morro Bay, California .....	218	14	30	20	68	2
10. Near Santa Barbara, California	397	33	49	21	60	10
11. Anaheim Bay, California .....	109	7	25	29	78	0.3
12. Mission Bay, California .....	119	10	19	24	66	14
Analysis by subspecies						
1-7. <i>L. a. armatus</i> .....	1,214	69	167	19	71	0.00
8. <i>Intergrades</i> * .....	145	8	25	23	76	0.5
9-12. <i>L. a. australis</i> † .....	847	65	124	22	66	0.00
Grand total .....	2,206	142	316	21	69	0.00

\* Including nineteen specimens from Monterey Bay at Monterey and three from Old Creek near Cayucos, California.

† Including eight specimens from Santa Cruz, California.  
Including four specimens from Lower California.

total rays differs on the two sides, the count for the right fin is usually the higher (Table VII). This relation holds for all twelve localities, from each of which a large sample was studied. In about one specimen in four or five the counts are asymmetrical (the percentage of asymmetry varies from 16 to 29, and usually runs from 20 to 25). Among the asymmetrical specimens from 60 to 81 per cent are right-handed, in the sense that the right pectoral fin (corresponding to the hand) has more rays than the left fin. The differences are of probable to almost certain reliability; the odds of significance are at least 7: 1, usually much higher. When the asymmetrical counts are summed up for the two subspecies, the probability that the indicated excess of right-handedness was caused by chance is seen by the  $\chi^2$  test to be less than 1 in 20,000.

As a question of methodology it should be noted that much more decisive results were obtained by applying the  $\chi^2$  test to the fifth part of the counts (those that are asymmetrical) than by following the customary method of using all the counts to analyze the difference between the means for the two sides. When the latter course is followed, the bilateral differences are obscured by the mass of symmetrical counts, and the  $P$  values are much higher, that is, less indicative of significance (Table VIII).

TABLE VIII

COMPARISON OF AVERAGE NUMBER OF PECTORAL RAYS IN  
*LEPTOCOTTUS ARMATUS*

	Specimens	Mean $\pm$ SE		Difference (R - L)		100 P
		Left fin (L)	Right fin (R)			
<i>L. a. armatus</i>						
Sitkalidak Island, Alaska .....	174	19.42 $\pm$ .04	19.47 $\pm$ .04	0.05	0.8	42
Admiralty Island, Alaska .....	104	19.20 $\pm$ .05	19.29 $\pm$ .05	0.09	1.3	19
Puget Sound, Washington .....	245	18.98 $\pm$ .03	19.08 $\pm$ .03	0.10	2.5	1
Grays Harbor, Washington .....	103	18.86 $\pm$ .05	18.96 $\pm$ .05	0.10	1.4	16
Nestucca Bay, Oregon .....	136	18.93 $\pm$ .04	19.01 $\pm$ .04	0.08	1.3	19
Humboldt Bay, California .....	221	18.91 $\pm$ .03	19.00 $\pm$ .03	0.09	2.2	3
San Pablo Bay, California .....	157	18.45 $\pm$ .05	18.54 $\pm$ .05	0.09	1.3	19
Intergrades						
Elkhorn Slough, California ..	125	18.35 $\pm$ .05	18.44 $\pm$ .05	0.09	1.3	19
<i>L. a. australis</i>						
Morro Bay, California .....	218	18.28 $\pm$ .03	18.35 $\pm$ .03	0.07	1.8	7
Near Santa Barbara, California.	397	18.37 $\pm$ .03	18.40 $\pm$ .03	0.03	0.7	48
Anaheim Bay, California .....	109	18.42 $\pm$ .06	18.59 $\pm$ .06	0.17	2.0	5
Totals and weighted means ...	1,864	18.72	18.80	0.08		

Throughout its long coastal range *Leptocottus armatus* is clearly right-handed in the sense that the right fin usually has the larger number of rays when the number in the two fins is different. The significance of this relationship becomes clearer on further analysis.

The independent variation of the two pectorals in number of rays, leading to a higher number in one fin than the other, is partly counteracted by the tendency for the two fins to vary together in number of rays. The coefficients of correlation for the twelve localities vary from 0.56 to 0.73, with standard errors ranging from 0.03 to 0.06; for *Leptocottus armatus armatus*,  $r = 0.61 \pm 0.05$ ; for *L. a. australis*,  $r = 0.67 \pm 0.04$ ; for the species as a whole,  $r = 0.63 \pm 0.05$ . For all the coefficients the significance is below the 1 per cent ( $P = 0.01$ ) level, indicating a highly reliable correlation.

When the number of pectoral rays is higher in one fin than in the opposite fin, the count in the first fin is usually higher than the mean value for both fins. In other words, in respect to the number of rays the two pectoral fins show a positive correlation between deviation from partner and deviation from mean. The pertinent coefficients of correlation range for the twelve localities from 0.37 to 0.60, with only one value above 0.48. The corresponding standard errors range from 0.03 to 0.06, and  $P$  is consistently below 0.01. For the northern and southern subspecies, respectively,  $r = 0.44 \pm 0.05$  and  $0.43 \pm 0.04$ .

In counting the rays in hundreds of pectoral fins of *Leptocottus* it became evident that the lowermost ray in a given fin was usually short when the ray count was high, and that this ray was ordinarily long when the count was low. Consequently, to test this observation and to analyze the relationship the lowermost ray of each pectoral was measured in numerous specimens from five localities. The measurements were made to the nearest 0.1 mm. and converted into thousandths of the standard length of the fish. For each locality the inverse relationship between number of rays and length of lowest ray was reliably established (Table IX).

It would seem that the small ventralmost ray usually present in pectoral fins having a high number of rays might be given a lower numerical value (some fractional value) than is assigned to the larger corresponding ray usually occurring in fins with fewer rays. On this basis there would be less than 1.0 ray difference between

TABLE IX

RELATION BETWEEN NUMBER OF PECTORAL RAYS AND AVERAGE LENGTH OF LOWERMOST RAY IN FIVE SERIES OF *LEPTOCOTTUS ARMATUS*

TU . . . . .  
 . TU . . . . .  
 . . . . .  
 . . . . .

	15	16	17	18	19	20	21
NO . . . . . Cali- . . . . . (168 . . . . . ; M = 18.38)	69.0? (± ?; ?)	.. *	72.0 (±1.1; 22)	63.9 (±.6; 183)	54.2 (±.7; 128)	46.5? (± ?; 2)	.. ..
M . . . . . B . . . . . (137 . . . . . ; M = 18.79)	.. ..	.. ..	72.7? (± ?; 3)	64.1 (±1.0; 66)	53.0 (±.6; 190)	46.9 (±2.0; 15)	.. ..
G . . . . . H . . . . . W . . . . . (101 . . . . . ; M = 18.91)	.. ..	.. ..	69.5? ( ?; 2)	67.6 (±1.2; 33)	58.0 (±.7; 148)	45.0 (±1.0; 19)	.. ..
Nestucca B . . . . . O . . . . . (136 . . . . . ; M = 18.97)	.. ..	.. ..	.. ..	64.8 (±1.1; 39)	56.0 (±.5; 202)	48.0 (±.9; 31)	.. ..
S . . . . . . . . . . A . . . . . (91 . . . . . ; M = 19.40)	.. ..	.. ..	.. ..	67.6? (± ?; 5)	67.7 (±.8; 103)	55.4 ( .9; 77)	47.7? (± ?; 3)

the two fins when, for example, the counts are 18 left and 19 right, for the eighteenth ray of the left fin is more of a ray than is the nineteenth element of the right fin. Convention and convenience demand that the rays be enumerated as whole numbers, but it is important to keep in mind that the classes of ray counts could be indefinitely divided, according to the degree of development of the last ray. Not only for the pectoral fins but also for many other meristic series we are finding that there are many gradations between the successive counts; that is, that there is no real distinction between continuous and discontinuous (or discrete) variations. We expect to deal with this problem in a separate paper. For the present it may suffice to state that the lowermost pectoral ray in *L . . . . .* varies from the merest rudiment to a large ray, providing all transitional conditions between successive counts (of 18 and 19, for example).

The degree of development of pectoral fins with any given ray count is best measured by the size of the lowermost ray. This ray

varies much more in length than any other one and is the only one that grades into a rudiment. It is presumably the last to be formed in ontogeny. It may be assumed that, when an embryonic fin is larger than usual, it will develop an extra ray at the lower edge. If the fin in the embryo is smaller than usual, the lowermost ray will presumably be the one that fails to form. A slight increase in fin size at the critical time of ray formation would leave room for only a minute ray; a larger increase would permit a larger ray to be developed at the lower fin margin. This reasoning is in line with the idea that meristic elements such as vertebrae, scales, and fin rays are laid down at a relatively constant distance apart, in absolute terms, and that the number of elements developed depends on the space available, up to the time when development stops. It is immaterial whether the elements are formed simultaneously in a given space or whether the formation of parts continues as the space for development increases. In either case the potentiality for segment formation eventually ceases, and thus fixes a limit to the space over which the segments may form, either on one occasion or over a period of time. The number of parts laid down will then be proportional to the available space. Such an explanation seems to hold for the number of scales that are formed over the body (Hubbs, 1941a; Neave, 1943: 81-82) and is applicable to the determination of the number of elements in various meristic series (Hubbs, 1926b).

Although the discussion may be oversimplified, one may continue with the same line of reasoning, using a diagram (Fig. 1) to help visualize the relations which the size of the pectoral fin at the time when the formation of new rays at the ventral edge ceases bears to the number of pectoral rays and to the size of the lowest ray in each fin. Let 5 be the usual condition, representing a pectoral fin with 18 rays of which the eighteenth is of moderate size, but longer on the right than on the left side. Fins 4, 3, 2, and 1 on the right side represent successively smaller fins, in which room is left at the lower end first for a short ray 18, then for a very long ray 17 (since there is now no room for ray 18 to form), next for a rather long ray 17, and finally for a ray 17 of moderate length. Further steps in the same direction would yield a fin with only 16 rays. On the left side similar changes take place, but ray 18 drops out sooner. Fins 6, 7, 8, and 9 on the right side are progressively larger, and



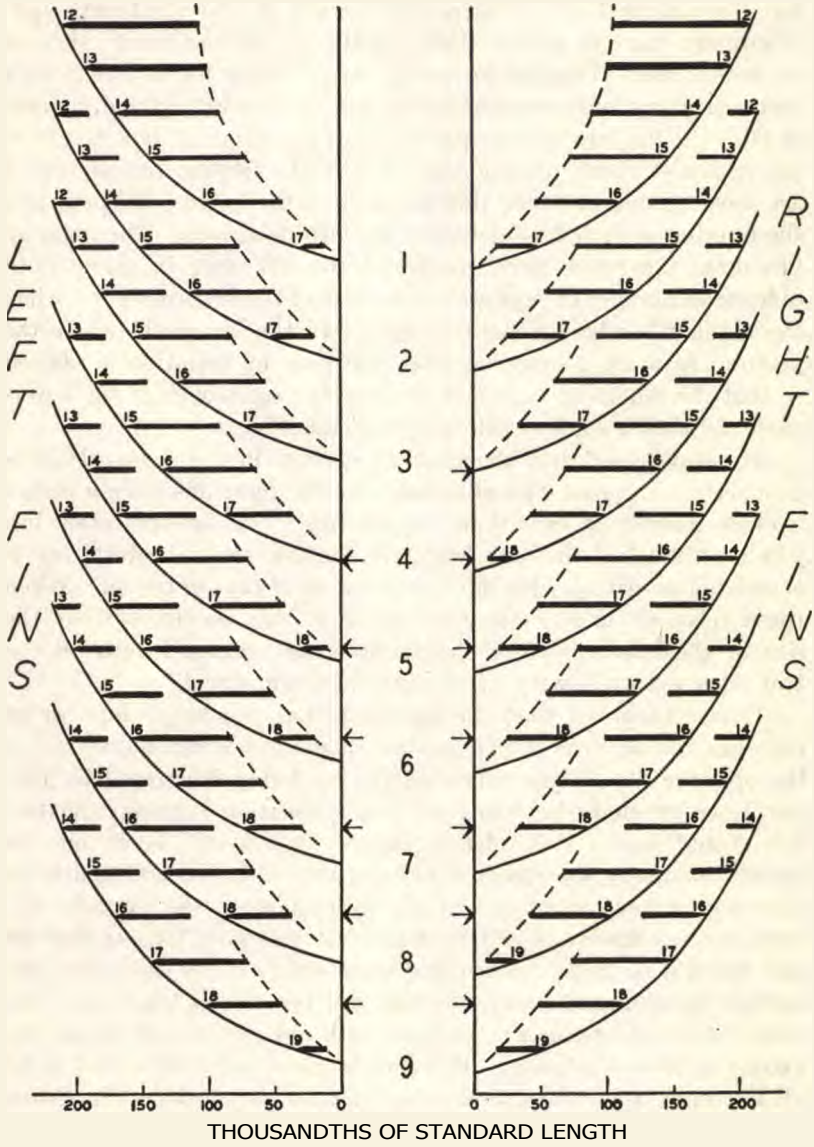


FIG. 1. Diagrams of lower portion of left and right pectoral fins of *Leptocottus armatus*, to illustrate the theory that the number of rays and the length of the lowermost ray are correlated with the size of the fin. The arrows point to the position of ray 18.

are characterized by an increasing length of the eighteenth ray; eventually there is added a nineteenth ray, at first small, then of moderate size. Further increases would allow for a still longer nineteenth ray and occasionally for yet another ray, giving a count of 20. On the left side similar changes again occur, but ray 19 is not added so soon. By the rule of normal variation fins of type 5 are most abundant, since this is taken as the mean condition, and the number of each type decreases in both directions. The diagram visualizes the lesser development of the left side, in terms both of average number of rays and of the size of the lowermost ray when the number is alike on the two sides. In the far north, where the pectoral rays are more numerous, the base of variation is shifted so that the nineteenth ray now replaces the eighteenth as the lowermost ray that is of moderate length (Table IX).

It seems clear that the number of rays in the pectoral fin is positively associated with sidedness, for the right fins have a higher average number of rays than the left fins. The interpretation has just been reached that the length of the lowermost pectoral ray is correlated positively with the total number of rays in the fin. When these relations were both determined, it was concluded that the size of the lowermost ray should differ in average length on the two sides, even when the ray counts are symmetrical.

It was observed that the fin which has the larger number of rays has the lowermost ray smaller than the corresponding ray of the opposite fin. Again following the reasoning illustrated by Figure 1 we conclude that the positive correlation between the two fins should render this relation almost invariable. When one fin (more commonly the right) is differentially enlarged sufficiently to introduce a new, short ray at the lower border, the opposite fin, with one ray fewer, should be somewhat enlarged, too, so that its last ray will be large. When one fin is differentially decreased just enough to eliminate a ray, the last ray becomes a large one; the other fin should be nearly as much reduced and should retain the extra ray, of a small size. The correlation was indeed found to be all but invariable in *Leptocottus* and almost as consistent in *Cottus bairdii* (p. 274). It was checked in 421 of the 458 specimens of *Leptocottus* that have asymmetrical pectoral ray counts. Of the 421 all but one had the lowermost ray the smaller in the fin having the higher count. In the one exception the last ray of the fin with

TABLE X

RELATIVE LENGTHS OF THE LOWERMOST RAY IN THE TWO PECTORAL FINS OF *LEPTOCOTTUS ARMATUS*

The consistent data for the five localities mentioned in Table IX have been combined. Specimens with no measured difference between the lengths of the lowermost ray of the two sides are equally apportioned among those having the ray longer on the left side and those having the ray longer on the right.

	Difference between lengths of lowermost pectoral rays of the two sides, in thousandths of the standard length									
	0	4	5-8	9-12	13-16	17-20	21-24	25-28	29-32	33-36
Ray counts equal										
Ray longer in left fin ...	33.5	86	43	15	8	1			1	
Ray longer in right fin ..	33.5	119	90	51	16	4	2			1
Left fin with more rays										
Ray longer in right fin ..		1		3	8	10	11	5	4	1
Right fin with more rays										
Ray longer in left fin ...		2	4	11	16	23	14	8	7	
Ray longer in right fin ..			1							
	Statistical calculations									
	Mean*		No. of specimens							100 P
			Δ = 0-4			Δ = 5-36				
Ray counts equal			119.5			168				0.07 †
Ray longer in left fin ...	4.18									
Ray longer in right fin ..	5.58		152.5							
Left fin with more rays										11 §
Ray longer in right fin ..	20.23		1			42				
Right fin with more rays .	18.01		2			84				
Ray longer in left fin ...	18.31		2			83				
Ray longer in right fin ..	7.0?					1				

\* Means were derived from uncombined data.

This 100 P value, derived from the  $\chi^2$  test, estimates the reliability of the distribution of the data according to whether the difference is none to slight (0-4) or moderate to large (5-36).

In computing this mean the value of 7 (for the specimen with the longer owermost ray in a right pectoral with the higher ray count) is included as a minus figure.

§ This 100 P value estimates the reliability of the difference between the means, and is computed from the uncombined frequencies. In determining  $\lambda$  and hence P the correction for diverse size of samples was used.

more rays (the right fin) was only 0.007 of the standard length longer than the corresponding ray of the left fin. The last pectoral ray averaged 0.019 of the standard length shorter in the fin with the higher number of rays, and was found to be more than 0.008 shorter in 118 out of 126 specimens (Table X). The difference in the length of the ray appears to be somewhat greater when the left fin has more rays than the right, presumably because the lowermost ray of the left fin has two reasons for being small: because it is in the fin with the higher ray count and because it is on the left side. The lowest ray of the right fin correspondingly has a double reason for being especially large: it is in the fin with the fewer rays and it is on the favored right side. The difference, however, is not of assured statistical reliability.

The most significant result obtained from measuring the length of the lowermost pectoral ray — the most sensitive criterion of the degree of development of the fin at the time the rays are formed — is the indication that on the average the right fin is the better developed even when the ray count is the same on the two fins. The evidence for right-handedness is, therefore, not limited to the fins with different ray counts, and the proportion of rights to lefts is greater than is indicated by the ray counts alone. The better development of the right fin is measured by the greater difference between the length of the last ray of this fin and that of the left fin, when the number of rays in the two fins is the same and when the lowermost ray of the right fin is the longer. The contrast is often striking. The moderate to large differences, of 5 to 36 thousandths of the standard length — those large enough to be observable and to be well beyond the error of measurement — are much more frequent when the right ray is the longer. When the left ray is the longer the difference is more often none to slight (0 to 4 thousandths of the standard length). The  $\chi^2$  test indicates that a very reliable distinction exists in the distribution of the data according to whether the difference in ray length for the two fins is none to slight, 0 to 4, or moderate to large, 5 to 36:  $\chi^2 = 11.41$ ;  $P = 0.0007$ .

#### BILATERAL VARIATION IN NUMBER OF RAYS IN THE TWO PECTORAL FINS OF OTHER FISHES

After having found that the number of pectoral rays is higher on the right oftener than on the left side of *Leptocottus armatus*,

we turned our attention to published and original data on other fishes (Table XI), to learn whether what might be called right-handedness is of universal occurrence in fishes. The most pertinent published data were presented by the distinguished German student of variation Georg Duncker.

In a European percid, *Acerina cernua*, Duncker (1897 : 819, 830; 1900: 359; 1904: 560-562, 647, 651) found the asymmetrical counts to be divided nearly equally between lefts and rights. The ratios were 92:93 for 1,000 females and 65 : 49 for 650 males. He seemed to have some reliance on the indicated tendency toward sinistrality in the males, but Ludwig (1932: 4-7), in reviewing the same data, regarded the counts as symmetrical. The  $\chi^2$  test indicates the difference to be wholly untrustworthy.

In one moderately adequate sample of another cottid, the European fresh-water *Cottus gobio*, results very much like those here given for *Leptocottus* were secured by Duncker (1897: 830; 1904: 567-568, 647, 652), who stated that dextrality was also evident in a smaller series (150 specimens) of the marine cottid *Myoxocephalus scorpius*. Duncker regarded the preponderance of higher ray counts in the right pectorals as significant, but Ludwig (1932: 6), who arbitrarily fixed a limit of reliability at about 0.05 in Duncker's coefficient of asymmetry (see p. 232), regarded the fins of *Cottus gobio* as probably symmetrical. On the  $\chi^2$  test the difference (20 L: 42 R) appears trustworthy.

Duncker (1908: 55, 103) discovered that at three localities the European pipefish *Syngnathus typhle* also has a higher count of rays in the right pectoral oftener than in the left fin.

Duncker's results, except for the neutral case of *Acerina*, thus stand in line with our findings on *Leptocottus*. To test this indication that fishes are predominantly right-handed in respect to the number of pectoral rays, new counts were taken on large series of two other species of the Cottidae, and pectoral ray counts of several species of cyprinodont and cyprinid fishes, previously made during other studies in our laboratory, were analyzed to see whether they, too, showed any significant bilateral asymmetry (Table XI).

The results for *Cottus bairdii bairdii* stand nicely in line with the data we secured on *Leptocottus armatus* and with those given by Duncker for *Cottus gobio*. The 1,372 specimens counted constituted a definite unit, for they were all taken in one poisoning of a

TABLE XI

BILATERAL VARIATION IN NUMBER OF RAYS IN THE  
Two PECTORAL FINS OF VARIOUS FISHES

This table supplements Table VII. For source of data and other details refer to the accompanying text.

	N	L	R	100 (L + R)	100R	100 P
				N	L + R	
Cottidae						
<i>Cottus bairdii bairdii</i> .....	1,372	73	223	22	75	0.00*
<i>Cottus gobio</i> .....	354	20	42	18	68	0.5
<i>Clinocottus analis australis</i> .	976	58	45	11	44	20
Syngnathidae						
<i>Syngnathus typhle</i> † .....	1,290	103	155	20	60	0.1
Percidae						
<i>Acerina cernua</i> .....	1,650	157	142	18	47	38
Cyprinodontidae						
<i>Cyprinodon nevadensis</i> .....	1,725	261	178	25	41	0.00
<i>Oryzias latipes</i> .....	368	74	44	32	37	0.6
Poeciliidae						
<i>Mollienisia sphenops</i> .....	743	74	63	18	46	35
Cyprinidae						
<i>Siphateles</i> , several forms .....	365	55	50	29	48	62

\* A 100 P value of 0.00 indicates odds less than 1 in 20,000 that the result obtained is due to chance.

† The data are consistent for three localities.

spring pool on the grounds of the Wolf Lake Hatchery, Michigan. There were found 296 fish with the pectoral ray count different on the two sides, and of these the right count was the higher in 223; the left count, in only 73. The odds are much more than 1,000,000 to 1 against obtaining this difference by chance. The detailed statistical relations between the ray counts of the left and right fins of *Coitus bairdii* also agree beautifully with those for *Leptocottus armatus*. Thus the coefficient of correlation between the two counts is  $0.64 \pm 0.02$ . There is also a strong positive correlation between the deviation of each count from the mean and the deviation of the same enumeration from the count of the partner fin. The lowermost ray of the fin with the higher ray count is shorter than the corresponding element of the opposite fin in 288, or 97 per cent,

of the 296 specimens with asymmetrical counts (it was the longer in the eight other specimens). The mean for the left fin is 14.586, with standard error 0.0170; for the right fin,  $14.696 \pm 0.0166$ . The *t* value is 4.62 and the probability that the difference is due to chance is only 4 in 1,000,000. Thus, with sufficiently large samples (decreasing the standard errors), reliable indications of left—right asymmetry can be obtained by statistically comparing the means for the counts for the two sides.

The indication that the cottoid fishes are uniformly right-handed received a setback when the pectoral ray counts were made on 976 specimens of *Clinocottus analis australis*, collected on various dates in the tide pools of the adjacent headlands of Point Fermin and Whites Point, San Pedro, California. The ratio of lefts to rights in the 11 per cent of the specimens with asymmetrical counts proved to be 58 : 45. The chances are five to one that the left fin *has* on the average more rays than the right when the number differs on the two sides. The odds against *Clinocottus* being as strongly right-handed as *Leptocottus australis* or *Cottus bairdii* are almost infinitely large. How unsafe it is to generalize!

Slight to certain indications of sinistrality in the pectoral fins, as indicated by the number of rays, come also from counts of three cyprinodont fishes, and a bare suggestion of left-handedness is furnished by 105 counts for several forms of *Siphateles*, a genus of Cyprinidae from the American deserts (Table XI). The counts for *Cyprinodon nevadensis*, which were kindly made available by Robert R. Miller, pertain to various isolated subspecies living in the springs of the Death Valley region, California and Nevada. Virtually all the populations of the species are included in the data, and no indication was obtained that the races differ greatly in their tendency to be left-handed. The counts on *Oryzias latipes*, the *medaka* of the Japanese rice fields, were taken on series from many parts of Kyūshyū and Honshyū. Those for *Mollienisia sphenops* were made by Research Assistant W. Robert Martin on various subspecies from Guatemala and Mexico.

#### BILATERAL VARIATION IN NUMBER OF RAYS IN THE TWO PELVIC FINS

Moderately trustworthy figures indicate that the pelvic fin of *Leptocottus armatus* agrees with the pectoral fin in being better

developed on the right than on the left side (Table XII). The asymmetrical counts are so few, however, that separate analysis by localities is unwarranted. Out of a total of 3,208 specimens from all places only 58 had the count different on the two sides —24 on

TABLE XII

BILATERAL VARIATION IN NUMBER OF RAYS IN THE  
TWO PELVIC FINS OF FISHES

For source of data and other details see text.

	N	L	R	100 (L + R)	100R	100 P
				N	L + R	
<i>Leptocottus armatus</i>						
All counts (a) .....	3,208	24	34	2	59	19
Inner ray rudimentary in op- posite fin (b) .....	3,208	20	38	2	66	2
Sum, a + b .....	3,208	44	72	4	62	0.9
<i>Cyprinodon nevadensis</i>	1,821	313	280	33	47	18
<i>Siphateles obesus pectinifer</i>	409	43	15	14	26	0.02
<i>Siphateles</i> , several forms .....	1,884	182	112	16	38	0.00
<i>Rhinichthys osculus</i>	727	47	42	12	47	78

the left and 34 on the right. The greater weakness of the left side was better shown by the occasional **rudimentation** of the last ray. If we count this condition as R and the opposite situation as  $\bar{L}$ , the ratio of variants is 20 L: 38 R. Combining the two sets, we find 44 sinistral to 72 dextral fish, in regard to the development of the pelvic fin. On this basis the distinction is rather trustworthy (see table). Usually there was no question whether or not the last ray was to be counted as rudimentary, for such a ray as a rule was very slender and was much less than half the length of the other rays. Often this ray could be detected only with good light and high magnification. A conscious effort was made to avoid the personal error of treating a ray as rudimentary in the left fin when a ray equally reduced was not so listed for the right fin. The recorded difference is thought attributable neither to chance nor to personal error. Somewhat figuratively we might speak of *Leptocottus armatus* as moderately right-footed.

Other fishes, however, are found to have the higher count oftener in the left pelvic than in the right fin (Table XII). This is almost



certainly true of the cyprinid fish *Siphateles*, as is indicated not only by the sum of counts of many series from different waters in the Great Basin, but also by the asymmetrical counts (43 lefts to 15 rights) among 409 additional enumerations for a single collection of *Siphateles obesus pectinifer* seined at one time along a beach of Walker Lake, Nevada. The results for the *Cyprinodon nevadensis* material (the same as that used for the pectoral counts) are by no means conclusive, but suggest that this species also may have the left pelvic fins slightly better developed than their right mates. No significant difference is indicated for *Rhinichthys osculus* (several subspecies).

The suckers (Catostomidae) show an unusually high percentage of bilateral asymmetry in the number of pelvic rays, and would therefore furnish excellent material to determine which fin, if either, more commonly has the higher count. Of 1,772 specimens counted 338, or 19 per cent, had the pelvic fins asymmetrical in the number of rays. Most of the counts, however, were made in other researches, and too few have been tabulated according to the side having the higher ray count to provide more than a hint that these fishes may also be slightly sinistral in respect to the pelvic fins.

In *Cyprinodon nevadensis*, which often lacks the pelvic fin on one or both sides (Miller, 1943 : 9-11), there is an indication of sinistral-frailty, in the sense that the right fin seems to atrophy oftener than the left. Of 1,822 fish counted by Miller 112 (6 per cent) have one pelvic missing, and of these the fin is lacking on the left side in 47 specimens and on the right side in 65 ( $x^2 = 2.91$ ;  $P = 0.09$ ). In a race of wild carp (*Cyprinus carpio*) often lacking one or both pelvic fins Thompson and Adams (1936) found that the fin might be missing on either the left or the right side or on both sides, but they did not give the ratios.

#### ASSOCIATION BETWEEN ASYMMETRICAL DEVELOPMENT OF PECTORAL AND PELVIC FINS

Very little evidence is available to test the query, Is there an association between the better development, as measured by ray counts, of the pectoral and the pelvic fins? That is, to speak semi-figuratively, are right-handedness and right-footedness and left-handedness and left-footedness associated in the individual fish? The data for *Leptocottus armatus* and *Cyprinodon nevadensis* (Table

XIII) show no significant association, as measured by the  $\chi^2$  test. Fish with more right than left pectoral rays often have more left than right pelvic rays. As yet there is no reason to assume that any definite association or correlation exists between the differential bilateral development of the pectoral and the pelvic fins.

TABLE XIII

ASSOCIATION BETWEEN RIGHT-LEFT VARIATIONS IN NUMBER OF  
PECTORAL AND PELVIC RAYS

The counts were made by Carl L. Hubbs on 1,670 specimens of *Leptocottus armatus*, representing localities from Lower California to southwestern Alaska, and by Robert R. Miller on 1,724 specimens of *Cyprinodon nevadensis*, representing virtually all populations of this desert fish of the Death Valley region. For the counts of the *Cyprinodon* that are asymmetrical in both fins,  $\chi = 0.75$ ; the corresponding *P* value is 0.39.

	Count higher in		
	Left pectoral	Neither pectoral	Right pectoral
<i>Leptocottus armatus</i>			
Count higher in left pelvic .....	3	19	4
Count higher in neither pelvic .....	98	1,295	215
Count higher in right pelvic .....	1	30	5
<i>Cyprinodon nevadensis</i>			
Count higher in left pelvic .....	45	210	33
Count higher in neither pelvic .....	177	875	124
Count higher in right pelvic .....	39	200	21

BILATERAL ASYMMETRY AND VARIATION IN BRANCHIOSTEGAL  
CHARACTERS

Some of the most significant yet least noticed of the bilateral asymmetries of fishes relate to the **branchiostegal** membranes which enclose the branchial chamber ventrally on each side. In species having the two membranes separate that of one side **overlaps** the other. The overlapping member is the more ventral in position when the membranes are folded together. In some fishes the bony branchiostegal rays which support the soft tissues differ in number on the two sides.

*Overlap of branchiostegal membranes.* — It has already been noted (p. 244) that the few flounders with separate gill membranes follow

the general rule for fishes that the left membrane overlaps the right. This basic asymmetry has generally been overlooked, we believe, except in one paper (Hubbs, 1920). Observations made in connection with other researches, particularly a comparative study by Hubbs and Lagler (MS) on the gill structures of the clupeoid fishes, led us to conclude that the left branchiostegal membrane invariably folds over the right one in all fishes in which the membranes have not become united with each other or with the isthmus. This conclusion is now confirmed by a determination of the overlap relations of these tissues in ten specimens of the ladyfish, *Albula vulpes*, from various localities; in 476 young herring, *Clupea harengus*, from one series taken near Woods Hole; and in 183 fingerling king salmon, *Oncorhynchus tshawytscha*, from streams in Oregon, Washington, and Idaho (Table XIV).

As is true of almost all generalizations in biology, we now find,

TABLE XIV

**BILATERAL ASYMMETRY AND VARIATION IN BRANCHIOSTEGAL CHARACTERS OF ESSENTIALLY SYMMETRICAL FISHES**

For source of data and other details see text.

	N	L	R	100 (L + R)	100R	100 P
				N	L + R	
Overlap of branchiostegal membranes						
<i>Albula vulpes</i> .....	10	10	0	100	0	0.4
<i>Clupea harengus</i> .....	476	476	0	100	0	0.00
<i>Oncorhynchus tshawytscha</i> .....	183	183	0	100	0	0.00
<i>Esox vermiculatus</i> .....	442	410	32	100	7	0.00
Number of branchiostegal rays						
Left membrane overlapping right						
<i>Albula vulpes</i> .....	10	9	0	90	0	0.8
<i>Oncorhynchus tshawytscha</i> .....	46	37	0	80	0	0.00
<i>Esox vermiculatus</i>						
Posterior rays .....	410	28	58	21	67	0.1
Anterior rays .....	410	110	51	40	32	0.00
Total rays .....	410	88	52	34	37	0.2
Right membrane overlapping left						
<i>Esox vermiculatus</i>						
Posterior rays .....	32	1	1	6	50?	..
Anterior rays .....	32	3	9	37	75	15
Total rays .....	32	2.	8	31	80	11

however, that in at least one species some exceptions to this rule occur. Among 442 specimens of *Esox vermiculatus* from southern Michigan, examined to determine the bilateral variation in the number of branchiostegal rays, 32 (7 per cent) have the right membrane external. It was a real surprise to note this variation in a character which has remained invariable, in regard to the typical condition, throughout the Holostei and the Teleostei. These data on the folding of the branchiostegal membranes emphasize both the fundamental nature of the left-right relationships in general and their susceptibility to reversal.

Because of the sharp compression of the head the membranes in the herring overlap throughout most of their length. Posteriorly the first three branchiostegals on the right side form a prominent shelf, the recess of which receives the adjacent edge of the left membrane. In this region, therefore, the left membrane overlaps the right one, but is in turn overlapped by a process from the right side.

*Number of branchiostegal rays.* — The rule that the left branchiostegal membrane overlaps the right led us to wonder whether this asymmetry might not be correlated with a bilateral difference in the number of branchiostegal rays. We had noticed for years that the number of these bony stays is often different on the two sides in certain fishes, particularly the Salmonidae (salmons and trouts) and the Esocidae (pikes), but we had made no tabulations to determine whether the counts average the higher on the left or on the right side.

Jordan and Evermann (1896 : 479) described the branchiostegals of the king salmon, *Oncorhynchus tshawytscha*, as "B. 15 or 16 to 18 or 19, the number on the two sides always unlike," but we know of no correlation of counts with the sides. Examining forty-six fingerlings of this species from Oregon and Washington, we find that the counts are alike on the two sides in 20 per cent of the fish, and that in the other 80 per cent the count is one or two higher on the left side than it is on the right (Table XIV). When the counts are symmetrical the last (anteriormost) ray is often reduced in size or even rudimentary on the right side. *Oncorhynchus tshawytscha* may therefore be classed as strongly sinistral in respect to the number of branchiostegal rays. In this species the left branchiostegal membrane consistently overlaps the right, but only for a short distance

anteriorly, since the two membranes diverge widely backward. In the region of overlap the anteriormost rays are the more deeply covered by tissue on the left side.

An even closer correlation between the character of the two branchiostegal membranes and the number of rays in these membranes seems to hold in the ladyfish, *Albula vulpes* (Table XIV). In this primitive clupeoid the left membrane not only overlaps the right membrane but is also much more expansive. In association with the greater available space the left rays outnumber the right by one or two in nine out of the ten specimens examined; in only one is the number equal on the two sides.

In *Esox vermiculatus* the membranes are subequal in size and the difference in number of rays on the two sides requires long statistical analysis for reliable demonstration (Table XIV). When, as is usual, the left membrane overlaps the right, the left branchiostegals on the average outnumber the right. This is not true, however, of the posterior rays, which are attached to the outer surface of the hyoid arch, behind the posterior insertion of the geniohyoid muscle. These outer, posterior, rays on the average are more numerous on the right side. The anterior rays, which are attached to the inner surface of the arch because they are overlain by the large m. *geniohyoideus*, have the average count definitely higher on the left side. In respect to the number of rays the posterior group of branchiostegals is dextral; the anterior group is strongly enough sinistral to render the total number slightly but significantly higher on the left side. This seeming contradiction finds a plausible explanation in the better average development of the geniohyoid muscle on the left side when the left membrane overlaps the right. The extent of this muscle is no doubt correlated with the number of anterior rays.

When the right branchiostegal membrane overlaps the left, as it does in 32 of the 442 specimens of *Esox vermiculatus* studied, the numerical relations of the branchiostegal rays seem also to be reversed (Table XIV). Now the anterior rays and the total rays on the right side appear to outnumber those on the left. Because of the small number of specimens the difference between the sides, though probable, is by no means certain. For the anterior rays and the total rays, however, the relative numbers of rights and lefts can be regarded as reliably different in the two lots (those with

the left membrane overlapping and those with the right membrane the more external); the probability of obtaining ratios of 110: 51 and of 3: 9 from two parts of a homogeneous series is about 2 in 1,000; the probability of getting counts of 88: 52 and of 2: 8 from two samples of a homogeneous whole is about 8 in 1,000. The direction of overlap of the membranes and the different muscular development along the hyoid arches of the two sides seem to be more significant than leftness or rightness as such, as a correlative of ray number.

Such bilateral differences in the number of branchiostegal rays will probably be found to occur in relatively few fishes. The acanthopterygian fishes and their relatives have a low number of branchiostegals (4 posterior + 0 to 4 anterior), and the number is often constant for species and even families (Hubbs, 1920). In many soft-rayed fishes also the number is constant within families (for example, three throughout the Cyprinidae and Catostomidae). Differences between the sides are to be looked for among those malacopterygian fishes which, like *Albula*, *Esox*, and the Salmonidae, have a high and variable number of branchiostegals.

It will be interesting to determine whether average differences exist between the numbers of gill rakers on the arches of the left and right sides. No pertinent counts seem to be available.

#### BILATERAL ASYMMETRY AND VARIATION IN OTHER CHARACTERS

The paired fins and the branchiostegal membranes and rays are by no means the only bilateral structures of fishes that may be differentially developed on the two sides. Several additional characters have been tested, and an indefinite number remain to be studied. The few analyses that have been made support the impression gained from systematic studies that the various bilateral organs are generally about equally developed on the two sides. The left and right elements of a few structures, however, differ markedly in average number or in other indices of relative development.

*Scales and plates.* — The only extensive comparison of the right and left scale counts on individual fishes which we have found is that by Voris (1899: 236-237), whose data for the minnow *Hyborhynchus notatus* were reanalyzed by Duncker (1904: 578, 647, 653) and Ludwig (1932: 6). The difference between counts higher on the right

TABLE XV

## BILATERAL VARIATION IN SCALE, GILL, AND TOOTH CHARACTERS AND IN MEASUREMENTS OF FISHES

For source of data and other details see text.

	N	L	R	100 (L ± R)	100 R	100 P
				N	L + R	
Lateral-fine scales						
Hyborhynchus <i>notatus</i> .....	500	144	169	62	54	16
Plates along fin bases, <i>Zeus faber</i>						
Along dorsal base .....	250	68	76	58	53	50
Along anal base .....	250	65	61	50	48	72
Dorsal plus anal plates .....	250	79	79	63	50	100
Gill slits in hagfish						
<i>Bdellostoma stouti</i> .....	550	62	33	17	35	0.3
Teeth on rostrum, sawfishes						
<i>Pristis</i> , three or more species....	84	20	28	57	58	31
Measurements, <i>Acerina cernua</i>						
Head length .....	692	76	60	20	44	16
Mandible length .....	692	86	103	27	54	21

side and those greater on the left is small and hardly of trustworthy significance (Table XV). For 600 specimens of *Percina caprodes* from Turkey Lake, Indiana, Moenkhaus (1895: 282-283) gave an average of 89.46 for the left lateral-line count and of 89.74 for that of the right side, which, considering the number of specimens, would seem to be a significant difference, again favoring the right side. However, for 300 specimens for Tippecanoe Lake, Indiana, he gave a higher average for the left side (87.69 as compared with 87.45).

The modified scales that form the large plates along the dorsal and anal bases of *Zeus faber* differ in number somewhat oftener than not on the two sides (Table XV), but the counts are higher on the one side almost exactly as often as on the other. The data, from Byrne (1902), were also treated by Duncker (1904: 564-567, 647, 652) and Ludwig (1932: 6).

A nearly constant asymmetry in an epidermal plate in the desert tortoise, *Gopherus agassizii*, was mentioned by Grant (1936: 225). He stated that the left gular plate is the better developed in 331 out of 366 specimens. This relation holds true in several specimens examined by Norman Hartweg and us.

*Gill slits in hagfish.* — One of the most noteworthy bilateral differences in countable characters, that of the number of external gill openings in *Polistotrema stouti*, escaped the notice of Ludwig (1932). The count is asymmetrical in about one sixth of the specimens, and in these the openings are more numerous on the left side nearly twice as often as on the right (Worthington, 1905: 628-633; counts summarized and analyzed in our Table XV). The bilateral difference in number of gills was found to be somewhat less extreme, for the last or supernumerary opening in eleven fish was accompanied by a remarkably reduced gill or by no gill.

*Rostral teeth of sawfishes.* — *Bilateral* variation occurs with very high frequency in the number of teeth along the two edges of the rostral blade of the sawfishes (genus *Pristis*). Out of 84 specimens of at least three species from various localities 48, or 57 per cent, had 1 to 3 teeth more on one side than the other (Table XV). The count was higher on the left in 20 and on the right in 28. The difference in laterality is not reliable ( $P = 0.31$ ), and the data are vitiated by their diversity. Large series of counts for single species at one locality are needed. Some of our data were kindly furnished by Leonard P. Schultz and by J. L. Baughman.

*Pharyngeal teeth of Cyprinidae.* — In many minnows the pharyngeal teeth of the main row on the two arches slide together to form a cutting mechanism. In several European species the teeth mesh in such a way that the number is higher on one side, usually the left, than on the other (von Siebold, 1863: 172, 189, 214, 223, 227, 232, 236). The preponderance of higher counts on the left varies considerably (Table XVI), and most species have the same number on both sides. *Tinca tinca* is said to have commonly four or five on either side (von Siebold, 1863: 107). Subsequent discussions of bilateral asymmetry in cyprinid dentition, for example, those of von Martens (1896: 10) and Ludwig (1932: 230), are obviously based on von Siebold's account. The later authors compared the asymmetrical dentition of cyprinids with the similar arrangement of hinge teeth which occurs, with very uncommon reversals, in the shells of bivalve molluscs (for references and for data on the asymmetries in freshwater mussels see van der Schalie, 1936).

Like asymmetry has been found to characterize most, and probably all, American Cyprinidae (chiefly western) in which the pharyngeal teeth of the main row commonly vary from four to five.



TABLE XVI

BILATERAL ASYMMETRY IN NUMBER OF PHARYNGEAL TEETH IN  
CYPRINID FISHES

For source of data see text.

	N	L	R	100 (L + R)	100 R	100 P
				N	L + R	
<b>European species</b>						
Hybrid, " <i>Abramidopsis</i> Leuckartii" .....	45	24	0	53	0	0.00
<i>Leucaspis delineatus</i> .....	36	31	0	86	0	0.00
<i>Rutilus rutilus</i> (4 races) .....	104	79	0	76	0	0.00
<i>Telestes agassizii</i> .....	72	33	2	49	6	0.00
<i>Phoxinus phoxinus</i> .....	51	45	2	92	4	0.00
<i>Chondrostoma</i> (3 species) .....	95	10	1	12	9	2
<b>Western United States species</b>						
<i>Gila orcuttii</i> (a) .....	40	38	0	95	0	0.00
Hybrids (a X b) .....	40	31	1	80	3	0.00
<i>Siphateles mohavensis</i> (b) .....	40	10	0	25	0	0.4
<i>Siphateles obesus obesus</i> .....	47	33	0	70	0	0.00

As a general rule, to which individuals but not species form exceptions, the higher number is on the left side when the count is asymmetrical. Supporting statistical data are not available for most species, but have been given by Snyder (1917 : 62) for *Siphateles obesus obesus* and by Hubbs and Miller (1943 : 356) for *Gila orcuttii*, *Siphateles mohavensis*, and hybrids between these species. These data are also analyzed in Table XVI.

Crossing of optic nerves. — The left-right relations in the decussation of the optic nerves of flatfishes have already been referred to (pp. 234-236). Some families of flatfishes and all fishes of other orders have a dimorphic chiasma, for either the left or the right nerve may be the more dorsal in the chiasma (in the Pisces there is no intermingling of the fibers where the nerves cross). Parker's counts (1903 : 222-224) of one hundred specimens of each of ten species led him to conclude that there is no significant difference in the number of individuals with the left nerve or the right nerve the more dorsal. Larrabee's more intensive research (1906), however, proved that the right nerve of the brook trout (*Salvelinus fontinalis*) and the cod (*Gadus morhua*) is on top somewhat oftener than is the

left nerve. The differences, though proportionately small, are quite reliable statistically (Table XVII). The mathematical significance of the difference seems not to have been appreciated by Ludwig (1932: 232-234). Whether the other species studied have the nerve of one side dorsal the more frequently cannot be stated with assurance, for one hundred counts of each are insufficient for the

TABLE XVII

**BILATERAL VARIATION IN LOCATION OF OPTIC NERVES IN CHIAMA OF  
ESSENTIALLY SYMMETRICAL FISHES**

All data for *Salvelinus* and most of those for *Gadus* are from Larrabee (1906); all other material is from Parker (1903). Specimens with the left or the right nerve thjnore dorsal are listed under *L* or *R*, respectively.

	<i>N</i>	<i>L</i>	<i>R</i>	100 ( <i>L</i> + <i>R</i> )	100 <i>R</i>	100 <i>P</i>
				<i>N</i>	<i>L</i> + <i>R</i>	
<i>Salvelinus fontinalis</i> .....	4,642	2,057	2,585	100	56	0.00
<i>Fundulus majalis</i> .....	100	51	49	100	49	84
<i>Menidia menidia notata</i> .....	100	61	39	100	39	3
<i>Poronotus triacanthus</i> .....	100	53	47	100	47	55
<i>Pomatomus saltatrix</i> .....	100	43	57	100	57	16
<i>Stenotomus chrysops</i> .....	100	49	51	100	51	84
<i>Tautoglabrus adspersus</i> . . .	100	43	57	100	57	16
<i>Tautoga onitis</i> .....	100	45	55	100	55	32
<i>Prionotus carolinus</i> .....	100	53	47	100	47	55
<i>Gadus morhua</i> .....	1,152	471	681	100	59	0.00
<i>Melanogrammus aeglefinus</i> . .	100	48	52	100	52	69

determination of this point. Larrabee demonstrated that no significant differences in the offspring resulted when specimens of brook trout and cod with the left and the right nerve the more dorsal were mated in different combinations. For this reason we have tabulated as a unit all of his data for each species.

*Proportional measurements.* —Little effort has been made to determine whether bilateral differences exist in the body dimensions of the essentially symmetrical fishes (constituting all groups other than the Heterosomata or flatfishes). The only thorough test of this sort relating to parts not known to be asymmetrical was made by Duncker (1900: 562-564, 647, 651). His data, referring to the length of the head and of the mandible on the two sides of *Acerina cernua*, were reviewed by Ludwig (1932: 6-7), who regarded these

parts as symmetrical. The measurements were probably not expressed very precisely, for the indicated percentage of asymmetry is only 20 and 27, respectively, for the head and the mandible. When the measurements were bilaterally asymmetrical the head was more frequently the longer on the left side, the mandible more frequently the longer on the right. The differences, however, prove on the  $\chi^2$  test to be of very low reliability (Table XV).

Significant differences between the relative lengths of the lowermost pectoral ray on the two sides have been demonstrated for cottoid fishes (pp. 266-272 and 274).

*Coloration in a larval eel.* — One interesting case of bilateral asymmetry in coloration has been recorded for a fish in which the body and eyes are symmetrical. <sup>3</sup> The postlarvae of an eel, known as *Leptocephalus diptychus*, are marked on each side by a row of conspicuous spots, which alternate in position, though all are clearly seen from both sides of the transparent ribbon-like body. In both specimens the spots number three on the left side and four on the right (Eigenmann and Kennedy, 1901).

#### ASSOCIATION OF SEX WITH BILATERAL ASYMMETRIES IN FISHES

The question has arisen whether the left-and-right asymmetries of fishes are correlated in any way with sex. There is considerable evidence that the proportion of left-handedness differs in males and females of the human species (Ludwig, 1932; Wile, 1934). The published data are **conflicting**, and some workers claim that the apparently greater incidence of left-handedness in human males is the result of social factors. Ludwig, however, concluded (p. 311) that 4 to 5 per cent of human adult males are left-handed, and that the percentage is only about half as large in adult females.

The original data for pectoral rays in *Leptocottus armatus* and for pectoral and pelvic rays in *Cyprinodon nevadensis*, and Duncker's data for pectoral rays in *Acerina* and *Syngnathus* and for pectoral rays and three other characters in *Platichthys flesus*, all referred to previously, are available for a test of the association of sex with bilateral asymmetry in fishes (Table XVIII). The frequencies for the two sexes are not certainly different for any character, but give some evidence of being different, especially for the pectoral rays. In some species the males are indicated as possibly the more sinistral, in others the more dextral, in respect to number of pectoral rays.

TABLE XVIII

## ASSOCIATION OF SEX WITH BILATERAL ASYMMETRIES IN FISHES

Counts higher on the left or the right side are listed under L or R, respectively. Significance of association is determined by the  $\chi^2$  test ( $x = t$ ).

	N	L	R	t	100 P	Males *
<b>Pectoral rays</b>						
<i>Leptocottus armatus</i>						
Males ■■■■■■	839	62	120 }	1.30	19	L
Females ■■■■■■	814	40	106 }			
<i>Acerina cernua</i>						
Males ■■■■■■	650	65	49 }	1.23	22	L
Females ■■■■■■	1,000	92	93 }			
<i>Syngnathus typhle</i>						
Males ■■■■■■	202	19	46 }	1.43	15	R
Females ■■■■■■	362	31	45 }			
<i>Cyprinodon nevadensis</i>						
Males ■■■■■■	857	132	102 }	1.48	14	R
Females ■■■■■■	853	128	74 }			
<i>Platichthys flesus</i> (dextral)						
Total rays						
Males ■■■■■■	562	5	351 }	1.93	5	R
Females ■■■■■■	497	12	310 }			
Branched rays						
Males ■■■■■■	528	2	516 }	1.36	17	L
Females ■■■■■■	486	0	476 }			
<b>Pelvic rays</b>						
<i>Cyprinodon nevadensis</i>						
Males ■■■■■■	888	146	130 }	0.42	67	L
Females ■■■■■■	911	155	148 }			
<i>Platichthys flesus</i> (dextral)						
Total rays						
Males ■■■■■■	559	6	19 }	1.22	22	R
Females ■■■■■■	497	14	22 }			
Branched rays						
Males ■■■■■■	558	17	222 }	0.28	78	L
Females ■■■■■■	496	14	203 }			
<b>Extent of lateral line</b>						
<i>Platichthys flesus</i> (dextral)						
Males ■■■■■■	480	71	141 }	0.94	35	R
Females ■■■■■■	544	84	138 }			
<b>Side bearing eyes</b>						
<i>Platichthys flesus</i>						
Males ■■■■■■	602	40	562 }	0.21	83	L
Females ■■■■■■	518	20	498 }			

\* In this column L indicates that the males appear to be more **sinistral** and R that they may be more **dextral** than the females in the given character.

This association of sinistrality and dextrality with sex, if it actually exists, is not related to the differential development of the fins in the species as a whole.

#### SEXUAL RIGHTS AND LEFTS

In the literature on bilateral asymmetry reference has frequently been made to the "sexual rights and lefts" of *Anableps*. This is a genus of surface-swimming viviparous cyprinodont fishes still more famous for the division of the eye into two parts, one adapted for aerial vision and one for subaqueous vision.

These statements regarding sexual rights and lefts in *Anableps* rest on the accounts by Garman (1895a: 73-74, pl. 7; 1895b: 1012-1013, figs. 1-4). In monographing the Cyprinodontes this author discovered that the structure of the gonopodium (a highly modified anal fin) of *Anableps* adapts it more for sidewise than for vertical motion, and that this intromittent organ appears to be functionally effective toward the left in some males, toward the right in others. He also observed that the oviducal opening of the female is covered either by an enlarged scale (the "foricula"), which opens along either its left or right edge, or, in one species, by several scales which open on one side of a groove. Garman assumed that mating can occur only between dextral males and sinistral females and vice versa. This was a logical deduction but remains to be proved. The theory that the males always mate from one side only is hardly consistent with the equal development on the two sides of the spiny contact organs on the scales.

Garman stated that nearly three fifths of the males are dextral, and two fifths sinistral, whereas the females exhibit the reversed ratio (about three fifths sinistral and two fifths dextral). He thought that these ratios confirmed his theory that only rights can mate with lefts, and lefts with rights. Garman's data, however, were scarcely adequate. His ratio of counts of lefts to rights for the males was 6: 11 for *Anableps anableps* and 8: 14 for all three species; for the females, 34: 21 for *A. anableps* and 36: 23 for all species. In specimens at hand the left—right ratios are as follows: for *A. anableps* males, 0: 1; for *A. dowei* males, 2: 3; for *A. dowei* females, 3: 1. These counts added to Garman's are analyzed for the three species combined (Table XIX). The deviation of the ratios from equality may be rated as probable but not dependable.

TABLE XIX

## ANALYSIS OF SEXUAL LEFTS AND RIGHTS AMONG FISHES

External structures only are considered. For source of data see text.

				100 (L R)	100 R	100 P
					L -- R	
Genital opening on left (L) or right (R) side in <i>Anableps</i>						
Males .....	28	10	18	100	64	19
Females .....	63	39	24	100	38	9
Concavity on left (L) or right (R) side of gonopodium of males						
<i>Poeciliopsis</i> and <i>Poecilistes</i> (various species, Mexico and Guatemala) .....	400+	400+	0	100	0	0.00*
<i>Alloballus kidderi</i> .....	164	0	164	100	100	0.00
Unnamed genus, Guatemala .....	277	0	277	100	100	0.00
Xiphophorini (7 species) .	365	182	183	100	50	100
<i>Gambusia affinis affinis</i> . .	353	179	174	100	49	84
<i>Dermogenys pusillus</i> .....	80	36	44	100	55	37
Location, left (L) or right (R), of aproctal side of males of Phallostethidae						
<i>Phenacostethus smithi</i> . . .	334	155	179	100	54	19
Asymmetries in females of <i>Horaichthys</i>						
Location of genital pore, on midline or to left (L) or right (R) † .....	210	126	42	80	25	0.00
Presence of pelvic fins on both sides or only on left (L) or right (R) .....	210	205	0	98	0	0.00

\* A 100 P value of 0.00 indicates that the odds are less than 1 in 20,000 that the result obtained is due to chance.

† Approximate figures, obtained from Kulkarni's statement that in about 210 females the genital pore was on the left side in about 60 per cent, on the right side in 20 per cent, and on the median line in the rest.

Naturally little significance can now be attributed to Garman's theory about the role of selection in the origin and in the possible future changes of these left-right relations in the sexes of *Anableps*.

Nor can much credence be placed in his theory (1896: 232) that the sexual rights and lefts of *Anableps* were evolved to prevent close inbreeding between fish that swim habitually in pairs, side by side. In the first place, according to our observations, the various surface-swimming cyprinodonts commonly move in small groups, and there is no reason to believe that they pair off at any time other than when they are actually spawning. The idea that the pairs continually swim together seems to have stemmed from a fancy which Agassiz expressed when he applied the name *Zygonectes*, meaning "yoke swimmer," to the surface-swimming forms of *Fundulus*. In the second place, it is not to be expected that sibs would be any more uniformly rights or lefts than are more distant relatives. A more plausible theory is that the one-sided structure of the sex organs makes possible the completion of the copulatory act while the pair maintains the surface-swimming position for which *Anableps* is marvelously adapted. On the basis of recent work on sex recognition and breeding habits in fishes it seems probable that a male *Anableps* will attempt to mate with any other individual of the species, but will complete the act only with females and perhaps only with females having the opposite turn to the sex organs.

Garman's treatment of **sexual** rights and lefts in *Anableps* has been reviewed and discussed by numerous authors, including von Martens (1896: 8-9), Meisenheimer (1921: 166-167), and Ludwig (1932: 230-231). Von Martens compared the two types of *Anableps* adults with the sexual rights and lefts of gastropods. Ludwig wrongly included *Zygonectes* among the South American genera in which the sperm duct penetrates the anal fin.

Garman wrote of "an allied genus of the family" in which the males only are modified into rights and lefts. He referred to *Jenynsia*, now classed in a separate family. Langer (1913: 208-210) also discussed the question of rights and lefts in *Anableps* and *Jenynsia*, and stated that a male of *Jenynsia lineata*, which he observed, consistently mated to the right.

Sexual rights and lefts may also be distinguished among the **Poeciliidae**, the most speciose family of cyprinodont fishes. In some species we have noted that the fleshy structures connected with the oviducal openings are consistently directed toward one **side**. More definite bilateral asymmetries, in certain genera, characterize the gonopodium of the males (this is the **intromittent** organ, a modified

anal fin). In the Poeciliopsinae this structure is folded to form a tube along one side: on the left side in most genera; on the right side in *Allophallus* (and in another, unnamed genus from Guatemala); and on either side in *Xenophallus* (Hubbs, 1936: 232-235). Statistical data have now been gathered to fortify these observations (Table XIX). Unfortunately, no adequate material is at hand by which to determine the ratio of rights to lefts for *Xenophallus*.

Sexual rights and lefts may also be distinguished among the poeciliid fishes in which the gonopodium is not folded to form a rigid tube. In the tribe Xiphophorini, for example, rays 3 and 5 of the anal fin in the adult male are more or less pulled toward each other to form a broad groove. As a result the deep trough of ray 5, along the fundamentally posterior edge of the gonopodium, is twisted toward the same side. The last anal rays are directed toward the opposite side. In this group as many males have the gonopodium concave on the left side as on the right. This was found to hold true for all seven species in the tribe, namely *Platypoecilus couchianus*, *P. xiphidium*, *P. variatus*, *P. maculatus*, *Xiphophorus montezumae*, *X. pygmaeus*, and *X. helleri*. The consistent data for all the species were consolidated for presentation in Table XIX.

*Gambusia*, taken as an example of the many poeciliids which have the gonopodium proper rather rigidly fixed in one plane, is also indiscriminate in the laterality of the intromittent organ (Table XIX). In this genus only a trace of concavity is appreciable on either side of the gonopodium, but the short posterior rays are fluted, with the major concavity on either the left side or the right. In perhaps 10 per cent of the specimens examined the allocation into rights and lefts was more or less arbitrary, either because the concavity was very shallow or because of a doubly sigmoid curvature of the posterior rays.

Apparently the fixation of the concavity on one side of the gonopodium in the Poeciliidae was correlated with the elaboration of the trough into a definite tube.

There is some evidence to indicate that the poeciliids customarily copulate from one side. Philippi (1908: 17) stated that among dozens of males of "*Glaridichthys januarius*" (= *Phalloceros caudimaculatus*) which he had observed all except four, which were reversed in this respect, swung the gonopodium to the left. Out of about twenty-five males of "*Glaridichthys decem-maculatus*" (= *Cnesterodon decem-*



*maculatus*) all copulated to the right, except three which moved the gonopodium to the left. Langer (1913: 214) indicated that the morphology of the gonopodium made movement to the one side easier in these two poeciliids. Ludwig (1932: 230-231), quoting Meisenheimer (1921: 167) as a secondary authority, also stated that copulating usually to the left or to the right in these two cyprinodonts is correlated with the asymmetrical structure of the **gonopodia**. These organs in *Phallogeros* and *Cnesterodon* are nearly symmetrical and form no definite tube, but the posterior rays are curved to one side and movement of the sexual organ appears, at least in preserved specimens, to be easier toward one side (toward the right in the single male of each genus at hand). The indicated correlation between bilateral asymmetries in reproductive habits and in secondary sexual structures, in these and other viviparous cyprinodonts, calls for further inquiry.

Sexual rights and lefts also occur among the viviparous half-beaks, Indo-Pacific fishes hitherto placed in the Hemiramphidae but more satisfactorily classed in a separate family, Dermogenyidae. In certain species of *Zenarchopterus* an enormously enlarged anal ray lies on either the left or the right side of the fin. In *Z. brevirostris* this ray lies to the left in three specimens, to the right in six (Mohr, 1926: 253, fig. 15). In *Z. xiphoborus* it is on the left side of the fin in one fish, on the right in three (Mohr, 1934: 11-12, fig. 2). We find that the rather elaborate gonopodium of *Dermogenys*, described in detail by Mohr (1936), is likewise either sinistral or dextral. On either the left or the right side the first three rays of the four-rayed gonopodium are folded to form a groove, which is partly enclosed by a fleshy process arising from the membrane between the third and the fourth rays. In eighty males of *Dermogenys pusillus* from various parts of Java, collected in 1929, the tube thus formed lies on the left side in thirty-six specimens and on the right in forty-four (Table XIX). The slight preponderance of dextral males in these data is not dependable statistically.

The males of the family Phallostethidae comprise individuals that are known to be rights and lefts in respect to mating behavior as well as structure. The complex clasping organ or priapium of these remarkable Asiatic fishes is asymmetrical in that, for example, the anus opens on the "proctal" side and the ctenactinia arise on the opposite or "aproctal" side. That the proctal and aproctal

sides are either right or left has been observed in all the main treatises on the phallostethids (Regan, 1916: 5, 23; Myers, 1928: 5; Villadolid and Manacop, 1934: 200; Bailey, 1936: 453; Aurich, 1937: 264, 266, 275, 282; Herre, 1942: 139). Villadolid and Manacop observed that a given male always clasps a female from the same side. Aurich showed for certain species that the asymmetry involves the rudimentary pelvics of the males, before these fins lose their obvious identity in the organization of the priapium. Since no statistical data have been published to itemize how "indiscriminate" the laterality of the priapium is, we have made counts of the side that is aproctal in 334 males of *Phenacostethus smithi* Myers, all collected by Hugh M. Smith at Bangkok, Siam (Thailand). This side was found to be left in 155 fish and right in 179 (Table XIX). The deviation from equality is not very reliably significant ( $\chi^2 = 1.72$ ;  $P = 0.2$ ).

In another bizarrely specialized Asiatic fish, *Horaichthys setnai*, bilateral asymmetries (Table XIX) are associated with clasping (Kulkarni, 1940). In this cyprinodont the females are usually lefts, in the sense that the oviduct opens to the left of the median ventral line in about 60 per cent of the individuals and to the right side in only 20 per cent (Kulkarni, 1940: 401). A much more remarkable asymmetry in this fish is the almost invariable lack of the right pelvic fin in the female. Ordinarily, no trace could be found of either the right pelvic or its basal bone, at any stage of development. An adaptation seems to be involved (Hubbs, 1941b: 447), for the lack of the one fin provides the integumentary surface, opposite the oviduct, that is needed for the attachment of the spiny-headed spermatophore of this weird little fish.

Another very striking bilateral asymmetry associated with reproduction has been discovered recently in an unnamed cyprinodont genus from Guatemala. One of the several unique characteristics of this fish is the development on one side only of a structural complex to which a clasping function is obviously to be ascribed. The upper edge of the pectoral fin is transformed into an elaborate system of hooks and spines, and the scales on the base of the fin are enlarged and hardened to form a stiff plate with a free edge. In the single mature male collected it is the right fin that is so modified. The left pectoral is essentially normal, for it shows scarcely a trace of the bizarre specialization of the opposite member. Incidentally,

since Garman brought up the comparison, we might remark that in one respect this fish corresponds much more closely than *Anableps* with the fanciful *jaftak* of Persian literature, "a sort of bird that is said to have but one wing, on the opposite side to which the male has a hook, and the female a ring, so that when they fly they are fastened together." The female of the Guatemala poeciliid, however, shows no apparent modification which could be correlated with the clasping device of the male.

#### BILATERAL ASYMMETRY OF RAYS

To some extent in many fishes, most notably in breeding males which have fins that are modified for clasping or copulation, the two halves of certain soft rays lose their complete bilateral symmetry. This is spectacularly true of cyprinid fishes, in which the pectoral fin of the breeding male is enlarged and thickened and bears nuptial *tubercles* on the inner surface. In *Rhinichthys atratulus*, for example, the basal part of the main pectoral rays is very different on the two sides. The upper hemitrichia (phyletically the left halves of the rays on the left fin and the right halves on the right fin), as compared with the lower hemitrichia, are ribbon-like instead of cylindrical, lack the posterior keel that is developed on the other side, have the segments fused farther outward, and have their origins much farther back along the base of the fin.

In adult males of *Gambusia* the "dorsal components" of rays three to five of the pectoral fin remain slender, while the "ventral components" of the same rays become greatly dilated (Turner, 1942: 394). These components are the left and the right halves of the rays, but the bilateral relations have become reversed during the evolution of the fin. What is now the right, dorsal, inner face of the left fin was the left, outer, surface when the fin held its primordial fin-fold position. What is now the right half of each fin of the more advanced teleosts was originally the left side; what is now inner was then outer.

In the adult males of the *Poeciliopsinae* the detailed structure of the left and right elements of certain rays of the gonopodium are strikingly different (Hubbs, 1924: 26, pl. 2; 1926a: 63, 68; 1936: 233-235). In *Pamphorichthys minor* an even more remarkable bilateral asymmetry of a soft ray is manifested: on the left side the second pelvic ray retains the usual rodlike form, but on the right

side three subterminal segments are expanded into strong bispinous processes. This discovery was made by Luis Howell Rivero, whose unpublished drawing we reproduce, with thanks, as Figure 2.

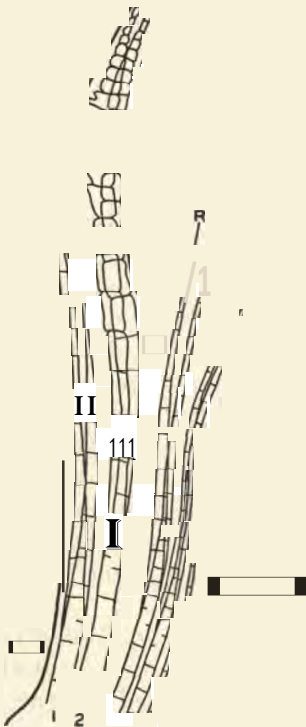


FIG. 2. Right pelvic fin of *Pamphorichthys minor*, showing the bilateral asymmetry of ray 2. Drawing by Luis Howell Rivero

The pectoral fins usually show some asymmetry between the left and right elements of each ray, particularly in the basal region of attachment, in correlation with the shift of the pectoral base from a longitudinal axis and ventral location to a vertical axis and lateral position. The outer and inner halves of the pectoral rays bear very different structural relations to the body. In the dorsal and anal fins the right and left sides of the spines (which, unlike the soft rays, are median unpaired structures) are somewhat dissimilar when the spines are heteracanthous, that is, when alternate spines are directed to right and to left. These asymmetries are not confined to breeding males.

Thus small parts of the body which have a bilaterally paired structure, or which merely have right and left sides, may develop bilateral asymmetry comparable to the dissimilarities between halves of the organism. When the bilaterally paired pectoral fins show such asymmetry within the ray structures, the direction of asymmetry is reversed on the two sides of the body, and each fin as a whole becomes the mirror image of the other. The spatial sequence of asymmetry is correlated with the general asymmetry of the fin, for the outer half of each ray differs from the inner half in the same way, whether either half be (fundamentally) left or right. This relation recalls the secondary asymmetries of the flatfish, in which the direction of asymmetry is correlated with the general asymmetry of the body, not with rightness or leftness as such.

## GENERAL INTERPRETATIONS AND CONCLUSIONS

On the foregoing pages we have presented a considerable body of new evidence indicating that the right and the left sides of fishes are not exact mirror images of each other. Previous findings that point to the same conclusion are reviewed. Both the new and the old data have been subjected to statistical test, to appraise the trustworthiness of the information. Some suggestions have been made toward an explanation of certain of the observed differences between the sides. In the following sections the observations are further integrated, and the interpretations are brought to bear on certain problems of general biology.

## EXTENT OF BILATERAL ASYMMETRIES

Some degree of difference between the left and right elements of bilaterally paired structures may now be said to be of frequent occurrence among fishes. Particularly notable asymmetries, involving locomotion as well as structure, characterize the *Cephalochordata* — the highly modified derivatives of the ancestors of the fishes (Ludwig, 1932: 222-224). Marked differences between the sides occur in the gill region of the *Marsipobranchii*, which are at once the most primitive and among the most specialized of the fishes (p. 284 and Ludwig, 1932: 230). Among the more typical fishes many bilateral asymmetries occur, some of which are common to all the vertebrates (Ludwig, 1932: 224-228, figs. 109-110), whereas others are peculiar to fishes as a whole or to particular groups of fishes. The special asymmetries recorded through this treatise characterize many of the *Pisces*, both primitive and specialized.

The differences between the sides are best known and most strikingly displayed in the flatfish order (*Heterosomata*), but are by no means confined to that group. Some of the bilateral dissimilarities of the flatfishes are unrelated to the major asymmetry of the eyes and color, but numerous other differences between the sides are definitely correlated with the position of the eyes. Reversal of the sides involves only the latter set of asymmetries. Among the bilateral differences that are correlated with eyedness or blindness rather than with leftness or rightness as such are those that involve the number of rays in the paired fins. As a general rule, the fin of the blind side is the less developed.

Not only in the flatfish order but also among fishes in general bilateral asymmetries appear in all parts of the body, superficial as well as internal. Average differences between the paired fins, particularly as measured by the number of rays, seem to be frequent. Other asymmetries are exhibited in the folding of the branchiostegal membranes; in the number of branchiostegal rays; in the number of gill slits in a hagfish; in the teeth; in the crossing of the optic nerves; and in many other characters. Asymmetries in sexual structures produce sexual rights and lefts. Even fin rays may show differences between the left and the right rows of segments.

Bilateral differences thus characterize all groups of fishes and appear in many structures.

#### FACTORS DETERMINING BILATERAL ASYMMETRIES

Why the two sides of fishes differ from each other is a question which has never been adequately answered, and it seems doubtful that any simple, general explanation will be forthcoming. Some students of the problem have theorized that the asymmetries in the adult may be traced to a reversal of the flexure or the structure in the embryo or egg. The data on the flatfishes go far to negate this idea, for reversal of the eyes is correlated with only certain of the other bilateral differences — except in the single specimen which we interpret as completely reversed.

This lack of correlation between different asymmetries in the flatfishes and the independent manifestation of different asymmetries in teratological flatfishes which show a partial return toward symmetry are among the facts which lead us to conclude that a multitude of factors is involved in the asymmetry of the Heterosomata, and that the whole genetic and developmental mechanism has been keyed together to produce animals with sides as unlike as are those of the flounders. We think that this conclusion applies also to fishes other than the exceedingly asymmetrical Heterosomata.

The large degree of independence that seems to exist between the factors responsible for asymmetries in fishes may be regarded as an example of a general phenomenon. Simple cause-and-effect relations, particularly those that call for many consequences of some one developmental factor, are often easier to assume than to prove or confirm, and often fail to meet critical tests. Thus it has been proved by researches on dogs that the different symptoms of achon-

droplasia, though ordinarily associated with one another and related to the same endocrines, are caused in large part by independent genetic factors which are capable of being separated by appropriate genetic tests (Stockard, 1941).

That there is no consistent favoring of either the left or the right side is indicated by the facts: (1) that many structures show in different groups the same bilateral asymmetry, except for a 180° change in direction; (2) that many of the known asymmetries are subject to such reversal by individual variation; and (3) that individuals may be sinistral in some characters, dextral in others. Among individuals with a different ray count in the two pectoral fins the right count may be the higher more frequently in some species, the left count the higher more frequently in others. This contrast may even be shown by different species within one group. One family of flatfishes has the eyes and color on the left side, another is eyed and colored on the right side; and in each group individual reversals occur, rarely in most species but very commonly in others. There is little evidence of correlation between the sidedness of the pectoral and the pelvic fins.

In general, it appears to be of little concern to an animal whether the right side or the left side is better developed. As Sumner and Huestis (1921 : 445) have pointed out, structural changes in the anterior—posterior and the dorsal—ventral axes would seriously modify the environmental relations and welfare of an organism, but reversal in bilateral asymmetries has no such fundamental significance. It would appear that sinistrality and dextrality as such have little or no effect on an animal's chance for survival and reproduction. It is therefore easy to understand why, in respect to certain characters, some species are sinistral and others dextral, still others, either sinistral or dextral, in a 50: 50 proportion or in any other ratio.

Asymmetry in itself, without reference to which side is favored, can often be interpreted with high plausibility as of adaptive value. Thus asymmetries in internal organs make for a division of labor between the sides. A flounder lying flat on one side is in a favorable position to simulate the bottom and thus to escape recognition and possible destruction.

Environmental factors related to the earth's rotation may have some effect on asymmetrical form and growth in plants, but they seem wholly unrelatable to bilateral asymmetries in free-swimming

animals. Little credence can be placed in the theories (for instance, those discussed, some with favor, by Wile, 1934) that sinistrality or dextrality in animals is due to such factors.

#### BEARING OF BILATERAL DIFFERENCES ON SYSTEMATICS

Since many superficial as well as internal characters are often more or less different on the two sides, it is obviously a wise policy in systematic studies to count or measure given characters consistently on one side, or to study both sides. The danger of inconsistent attention to the sides is perhaps greatest in racial studies. Thus, if in a research on the races of king salmon one investigator were to count the branchiostegal rays on the left side for certain localities and another (or the same) worker were to enumerate the rays of the right side for other localities, the sharp bilateral differences (p. 280) would likely be misinterpreted as characters of geographical races.

It remains to be determined whether direction and amount of asymmetry are consistent enough through series of species or groups to be usually indicative of phyletic relationship. Examples can be cited of such consistency, for instance, in the general pattern of visceral asymmetry of large groups. Whether the right or the left optic nerve is uppermost in the chiasma is a prime distinction between two families of flatfishes (p. 235). But whether in general the type of bilateral asymmetry of given structures is of systematic significance is an unanswered problem.

#### RELATION TO PROBLEM OF HANDEDNESS IN MAN

Many of the theories of handedness, reviewed at great length in such books as those by Parson (1924), Ludwig (1932), and Wile (1934), presuppose that this phenomenon is peculiar to man, or that handedness in man is unrelated to the observed bilateral asymmetries of other animals. The immense scattered literature on the subject is turgid with religion, mysticism, antique folklore, vaporous philosophy, Lamarckism, a plethora of mere argumentation, and an endless series of semiscientific ideas based on totally inadequate data. Most authors, even those with biological background, stress the ambidexterity of lower animals and apes and the imperfect development of right-handedness in primitive and degenerate men, and look on the elaboration of dextrality as an accompaniment of



progressive human evolution. Geneticists are flirting with the odd theory that left-handed humans are the survivors of identical twins, of which the dextral partner has failed to develop.

A consideration of bilateral asymmetries in the lower vertebrates, particularly the asymmetrical development of the forelimbs, helps to remove human handedness from its isolated position, and to integrate this phase of human biology with general biology. Some fishes which show bilateral asymmetry in the forelimb can be said to be right-handed, but even in these species many individuals have the left limb better developed than the right. Other species, however, may be said to be left-handed as a rule. Much of the discussion of factors determining bilateral asymmetries (pp. 298-300) applies to the problem of right-handedness.

In some flatfishes, as in man, handedness is correlated with modifications of the central nervous system, and handedness in fishes as well as in *Homo sapiens* is undoubtedly inherited. Whether or not man's ancestors were ambidextrous (a debated question), there is no good reason to assume that right-handedness in our species is a peculiar or an isolated phenomenon. No reliable evidence was obtained to indicate that sinistrality or dextrality in fishes is associated with sex.

An appreciation of the biological naturalness of handedness in man should help to dispel remaining traces of the primitive folklore which associates right-handedness with righteousness and left-handedness with the sinister. It should also help to exclude from the realm of serious consideration the not infrequently held misconception of handedness as a purely cultural expression.

The prevalence of right-handed and left-handed conditions among the fishes removes the necessity for explaining human handedness on a specifically human basis, but does not preclude the possibility that right-handedness in man arose as an adaptation connected with the handling of tools or the wielding of weapons. There is particular plausibility in the frequently proposed idea that holding the shield on the vital left side and wielding the spear by the strong right arm were basically correlated with the sharp differentiation between the arms of man. It seems unlikely that these customs initiated right-handedness; it is more probable that through natural selection the differentiation of the arms may have been intensified and rendered more nearly universal.

## SUGGESTIONS FOR FURTHER RESEARCH

Several new lines of inquiry into the problem of laterality in fishes present themselves. An extensive statistical inquiry into the extent of the phenomenon is needed to understand the various correlations involved and to bring the data on asymmetry to bear on systematic problems. By focusing attention on the number of rays in the pectoral and pelvic fins, for example, we may learn whether dextrality and sinistrality are related to taxonomy, to shape or position of fin, to habitat, or to mode of life; whether symmetry or asymmetry is the usual condition; whether dextrality is more frequent than sinistrality in individuals and in species. Other lines of research are needed to determine whether locomotor or other functional asymmetries are involved.

By modern methods of physiological research it may be possible to determine whether there is a difference in the metabolic level of the two pectoral fins during the stage at which the number of fin rays and the relative length of the lowest ray are established. The oxidation-reduction pattern may be determinable by the vital stain method which has recently been used by Rulon (1935) and by Child (1942, 1943) in demonstrating the axial gradients in developing animals, including the fish *Oryzias*. In this way one might be able to test and analyze the correlations between differential metabolism and distinctive segment numbers, which have been suggested (as by Hubbs, 1926b) on largely theoretical grounds. The idea that available space is a main factor in determining the number of meristic elements (p. 268) can be put to test. In using paired structures of individual embryos or larvae one would largely eliminate many variables — such as the age, previous history, stage of development, and genetic constitution of the subject.

Perhaps sometime we shall learn by such studies why, for example, the pectoral fin in one race or species ordinarily forms fifteen rays, whereas this fin in a related kind of fish produces sixteen rays. An answer to this problem would materially advance our appreciation of the physiological fundamentals of speciation.

## SUMMARY

The left and the right halves of fishes are not perfect mirror images, for many of the organs are more or less unlike on the two

sides. Bilateral asymmetries affect all groups of fishes and appear in various organs, superficial as well as internal.

Duncker's index of asymmetry ( $a$ ) confuses the amount and the direction of asymmetry. It seems better to express these factors separately, as the percentages of asymmetry and dextrality. The significance of the ratios of lefts and rights among the asymmetrical individuals is appraised by the  $\chi^2$  test, which leads to a probability estimate ( $P$ ).

The outstandingly asymmetrical vertebrates are the flatfishes (Heterosomata). *Psettodes* is the only genus that is indiscriminately dextral or sinistral, on a primordial basis. Some families are normally dextral, others sinistral; one family has both dextral and sinistral genera. Reversal of sides is generally very rare, but is common in a few species, chiefly of the North Pacific. There is some evidence that reversal is accompanied by a decrease in viability. Reversed flounders are not true mirror images of normal individuals, for asymmetries of the optic nerves, viscera, and branchiostegal membranes remain unaltered. Only one specimen, newly discovered, seems to represent a complete change-over of the sides, presumably because of some basic reversal in the embryo or egg. Ambicoloration is regarded as a teratological return toward symmetry, in which various asymmetries are differently combined and therefore appear to be due to independent genetic factors. Most asymmetries in flatfishes are associated with the location of the eyes and color on one side. As a general rule, the pectoral fin of the eyed side, whether right or left, has on the average more rays than does the fin of the blind side.

Many bilateral asymmetries also characterize the essentially symmetrical fishes. Thus the pectoral and pelvic rays may be more numerous on the right side oftener than on the left. In other species the left fin is more frequently better developed when the two are unlike. The number of rays appears to be determined by the size of the fin when the formation of rays is completed. In general, the number of meristic parts in a structure probably depends on the space that is available at the time when the formation of the countable parts is completed. The length of the lowermost pectoral ray measures the degree of development of the fin. As yet there is no reason to assume that there is any positive correlation between the pectoral and the pelvic fin in regard to the direction of bilateral asymmetry.

With some reversals in *Esox*, the left branchiostegal membrane overlaps the right in fishes having these membranes separate. In *Albula*, *Oncorhynchus*, and *Esox* the branchiostegal rays in the left membrane more or less consistently outnumber those of the right. The trustworthiness of bilateral differences in the scale counts of fishes remains to be proved. In a hagfish the gill openings on the left side are more numerous oftener than are those on the right. In cyprinid fishes with asymmetrical dentition the larger number of pharyngeal teeth usually occurs on the left arch. In *Salvelinus* and *Gadus* the right optic nerve is the more dorsal in the chiasma slightly oftener than is the left nerve.

There is no clear-cut evidence that bilateral asymmetries in fishes are associated with sex. Sexual rights and lefts involving bilateral differences in reproductive structures and habits characterize several genera of fishes. Differences also occur between the two sides of certain soft rays.

A multitude of independent but usually associated factors appears to be responsible for bilateral asymmetries — an example of a general biological principle. Because of the average differences between the sides it is desirable in systematic and racial studies to make the counts consistently on one side or to study both sides. Some patterns of asymmetry are consistent enough to be of taxonomic value, but how generally the amount and direction of bilateral asymmetries can be used as systematic characters is not now apparent.

The frequent occurrence of bilateral differences between the forelimbs and between the left and right elements of many other structures of fishes counters the widespread idea that handedness is a peculiarly human trait, or the result of training.

It may be possible, particularly through physiological studies, to correlate the degree of development and the metabolic characteristics of the embryonic pectoral fin with the number of rays that are formed. Such investigations may materially advance our understanding of the physiological fundamentals of speciation.

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Head region of normal and totally reversed specimens of  
*Tanakius kitaharae*

FIG. 1. Normal (dextral) specimen, 210 mm. in standard length,  
from Sea of Japan

FIG. 2. Reversed (sinistral) specimen, 220 mm. long, from off  
Onahama, Japan 

