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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 63

PHYLOGENETIC POSITION OF  
THE CITHARIDAE, A FAMILY  
OF FLATFISHES

BY  
CARL L. HUBBS

ANN ARBOR  
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FREDERICK M. GAIGE

*Director of the Museum of Zoology*

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# PHYLOGENETIC POSITION OF THE CITHARIDAE, A FAMILY OF FLATFISHES

## INTRODUCTION

DURING a study of the bilateral asymmetry of fishes it was recently discovered that two genera which had previously been referred to the flatfish family Bothidae have characters that call for their classification in a new family, Citharidae (Hubbs and Hubbs, 1945: 235, 248, 252-54, 258, 262-63). These genera are *Citharus* Röse of the Mediterranean and the adjacent Atlantic coast of Africa and *Citharoides* Hubbs of Japan and the Philippines, with which *Paracitharus* Regan of southeastern Africa has been confused. The very close relationship between these genera had been recognized (Hubbs, 1915: 452-53; Regan, 1920: 209; Norman, 1934: 44, 62, 168-70), but the isolated and primitive position of the group thus composed had not been duly appreciated.

In working on the taxonomy of these flounders it was also learned that the Indo-Pacific genus *Brachypleura* Günther agrees not only in superficial features but also in more fundamental characters with the *Citharus* group. Despite the fact that *Brachypleura* and the similar genus *Lepidoblepharon* Weber have the eyes and color on the right side, whereas *Citharus* and its more immediate allies are eyed and colored on the left side, the two groups of genera are classified in the same family, Citharidae. The division into sinistral and dextral groups has been used as a family character in separating the two main groups of flounders (Bothidae and Pleuronectidae), as well as the two generally recognized families of soles (Cynoglossidae and Soleidae). In the new case the character is used for only subfamily separation, because of the small size and compactness of the Citharidae and because of the lack of other conspicuous and consistent differences between the sinistral Citharinae and the dextral Brachypleurinae.

In the retention of the pelvic spine and in certain other characters the Citharidae resemble the most primitive flatfish genus *Psettodes*, for which a separate family and by some a still larger group has lately been recognized (Regan, 1910: 486-91; Kyle, 1921: 118-20; Jordan, 1923: 167; Regan, 1929: 324; Chabanaud, 1933c: 1064; 1934a: 1876; 1934b: 127; 1934c: 279; 1936a: 226; 1936c: 29-30; 1936d: 498-504; 1937a: 3-7; 1937b: 368-69; Norman, 1934: 1-22, 41-43, 56-57; Berg, 1940: 492). The Citharidae may be regarded as somewhat transitional between the Psettodidae and the main group (Bothidae plus Pleuronectidae) of the pleuronectoid flatfishes.

Kyle (1900: 342, 354-56) made *Citharus* the type of a new subfamily. He failed, however, to recognize the true relationships of *Citharus*. His group, to which he gave the unacceptable name Hippoglosso-rhombinae, was equivalent to the Paralichthyinae of more recent workers.

## FAMILY CITHARIDAE

DIAGNOSIS AND COMPARISONS.—The Citharidae are heterosomate fishes agreeing only with the Psettodidae (*Psettodes* and *Joleaudichthys*) in the structure of the pelvic fin, which has one spine and five soft rays. They differ from the Psettodidae and resemble all other Heterosomata in lacking spines in the dorsal and anal fins. They contrast with the Psettodidae and also with all soles (Soleoidea) in having the nerve of the migrating eye consistently dorsal in the chiasma. The following are characters by which the Citharidae are distinguished from the Psettodidae but agree with all other Heterosomata so far as known: the eyes are normally on one side; the dorsal fin extends far forward over the cranium; the anteriormost interhemal is enlarged to form a bony boundary to the coelom; the palatines and the glossohyal are toothless; the urohyal is sharply angulated; the gill-rakers are not reduced to clumps of spines; the urinary papilla is removed from the mid-ventral line; the vertebrae number more than 25 (the vertebrae are as few as 24 or 27 in a few achirine soles, according to Chabanaud, 1937a: 43–44). Other features of external and internal anatomy could be added to this list. The Citharidae do not share with the Psettodidae the relatively limited departure from bilateral symmetry which characterizes that group.

In at least two other respects there appears to be a significant agreement with *Psettodes*. Although it is not large, as it is in *Psettodes*, the supplementary maxillary may be either present or absent, instead of being consistently lacking as it is in all other flatfishes so far as known. The urinary papilla arises from the rim of the anus, so that these structures are not separated by a greater or lesser expanse of body surface as they are in other flounders. In these characters the Brachypleurinae (*Brachypleura* at least) do not conform well with the Citharinae. Most citharids agree with *Psettodes* in having 15 branched caudal rays, but this character is of limited value in the Heterosomata.

The gill-membranes are more widely separated in the Citharidae than in any other flatfish group except the Psettodidae. The membranes are also separate in the Scophthalmidae (pp. 18, 23–23), but are united in all of the genera of Bothidae (as herein restricted) and in all Pleuronectidae. Unlike the soles these flounder groups with connected membranes have the seventh branchiostegal ray of each side united posteriorly with its mate to form a V, which, of course, is not true of the Citharidae.

The development of vomerine teeth in *Citharus* and *Brachypleura*, representing the two subfamilies of Citharidae, and in certain Scophthalmidae, is a primitive feature that links both families with the Psettodidae. No vomerine teeth have been reported (Norman, 1934) in any of the genera which I here refer to any of the other major families of Heterosomata.

Another feature in which the Citharinae resemble both the Psettodidae

and the Scophthalmidae is the branching, at least at the tip, of all or almost all of the soft rays in each fin. The Citharidae, particularly the Citharinae, contrast with the Scophthalmidae in having the pelvic fins short-based. In neither of these characters are the Brachypleurinae fully consistent with the Citharinae.

A characteristic of all Citharidae not shared with any other family of flatfishes is the location of the anus on the eyed side, rather than on the mid-ventral edge or on the blind side. This feature is not described for *Lepidoblepharon*.

In numerous other characters *Citharus*, *Citharoides*, and *Paracitharus* agree with one another so fully that their kinship can hardly be questioned, and there are many features which point to the less intimate but still relatively close phyletic relationship between the Brachypleurinae and the Citharinae.

#### COMPARATIVE DATA

Since the pelvic spine and some other important characters of the Citharidae have been overlooked, a cross section of the whole series of pleuronectoid flatfishes was examined to make certain of the consistency of the observed differences between the Citharidae and the other groups. In all there were thus studied 99 species, referred to 58 genera, and representing all of the families and all but the 2 subantarctic subfamilies. Except for a few specimens kindly loaned for this study by Dr. Leonard P. Schultz of the United States National Museum, all of the material is preserved in the Museum of Zoology of the University of Michigan. Information on *Paracitharus macrolepis* has kindly been furnished by Dr. Ethelwynn Trewavas of the British Museum. Her co-operation, during the vandalous robot bombing of London, is deeply appreciated. Detailed data on United States National Museum specimens of Citharinae have been supplied by Dr. Robert R. Miller.

#### CLASSIFIED LIST OF PSETTODOID AND PLEURONECTOID FLATFISHES EXAMINED IN THE PRESENT STUDY

The classification, sequence, and nomenclature are taken from Norman (1934), with modifications due to certain new phylogenetic concepts (p. 23). The nomenclature of certain subfamilies and families reflects agreement with Norman (1931, 1934) rather than with Chabanaud (1930, 1931*a*) in regard to the application of certain old generic names (*Rhombus*, *Bothus*, and *Scophthalmus*). Later, Chabanaud (1937*a*: 15-16) returned to Norman's views.

Except by Hubbs and Hubbs (1945: 244, 248), the small North Atlantic group here delimited as the family Scophthalmidae has previously been given only subfamily rank (as Scophthalminae). The name Scoph-

thalmidae, however, was used by Chabanaud (1933b: 5; 1937a: 13; and some intervening papers) as a substitute for Bothidae. There was no warrant for that action. The name Brachypleurinae was proposed by Chabanaud, but he did not recognize the primitive relationships of the group (see p. 34).

An outline of the classification of the Heterosomata is given in the phylogenetic diagram (Fig. 1, p. 24).

Family Psettodidae

*Psettodes erumei* Schneider

Family Citharidae

Subfamily Citharinae

*Citharus macrolepidotus* (Bloch)

*Citharoides macrolepidotus* Hubbs

*Paracitharus macrolepis* (Gilchrist)<sup>1</sup>

Subfamily Brachypleurinae

*Brachypleura novae-zelandiae* Günther

Family Scopthalmidae

*Psetta maxima* (Linnaeus)

*Scopthalmus rhombus* (Linnaeus)

*Lophopsetta aquosa* (Mitchill)

*Lepidorhombus whiff-iagonis* (Walbaum)

Family Bothidae

Subfamily Paralichthyinae

*Tephrinectes sinensis* (Lacépède)

*Hippoglossina stomata* Eigenmann and Eigenmann

*Paralichthys dentatus* (Linnaeus)

*Paralichthys lethostigma* Jordan and Gilbert

*Paralichthys albigutta* Jordan and Gilbert

*Paralichthys californicus* (Ayres)

*Paralichthys olivaceus* (Temminck and Schlegel)

*Pseudorhombus malayanus* Bleeker

*Pseudorhombus oligodon* (Bleeker)

*Pseudorhombus arsuis* (Hamilton)

*Pseudorhombus pentopthalmus* Günther

*Pseudorhombus cinnamomeus* (Temminck and Schlegel)

*Tarphops oligolepis* (Bleeker)

*Xystreuryx liolepis* Jordan and Gilbert

*Verecundum rasile* Jordan

*Taeniopsetta* sp. (Japan)

*Ancylopsetta quadrocellata* Gill

*Syacium gunteri* Ginsburg

*Syacium* sp. (Haiti)

*Citharichthys sordidus* (Girard)

*Citharichthys xanthostigma* Gilbert

*Citharichthys stigmaeus* Jordan and Gilbert

*Citharichthys macrops* Dresel

*Citharichthys spilopterus* Günther

*Citharichthys gilberti* Jenkins and Evermann

*Etropus microstomus* (Gill)

*Etropus crossotus atlanticus* (Parr)

Subfamily Bothinae

*Arnoglossus thori* Kyle

*Arnoglossus aspilos* (Bleeker)

*Arnoglossus tenuis* Günther

*Arnoglossus* sp. (Japan)

*Asterorhombus intermedius* (Bleeker)

*Psettina ijimae* (Jordan and Starks)

*Engyproson grandisquama* (Temminck and Schlegel)

*Crossorhombus kobensis* (Jordan and Starks)

*Crossorhombus* sp. (Japan)

*Bothus ocellatus* (Agassiz)

*Bothus leopardinus* (Günther)

*Bothus pantherinus* (Rüppell)

*Bothus myriaster* (Temminck and Schlegel)

*Parabothus kiensis* (Tanaka)

*Chascanopsetta lugubris* Alcock

*Laeps kitaharae* Smith and Pope

Family Pleuronectidae

Subfamily Pleuronectinae

*Atheresthes stomias* (Jordan and Gilbert)

<sup>1</sup> Examined in the British Museum by Dr. Trewavas.

- Atheresthes evermanni* Jordan and Starks  
*Hippoglossus hippoglossus* (Linnaeus)  
*Hippoglossus stenolepis* Schmidt  
*Hippoglossoides platessoides platessoides* (Fabricius)  
*Hippoglossoides platessoides limandoides* (Bloch)  
*Hippoglossoides classodon* Jordan and Gilbert  
*Hippoglossoides dubius* Schmidt  
*Acanthopsetta nadeshnyi* Schmidt  
*Cleisthenes pinetorum herzensteini* (Schmidt)  
*Lyopsetta exilis* (Jordan and Gilbert)  
*Eopsetta jordani* (Lockington)  
*Xystrias grigorjewi* (Herzenstein)  
*Psettichthys melanostictus* Girard  
*Verasper variegatus* (Temminck and Schlegel)  
*Verasper moseri* Jordan and Gilbert  
*Clidoderma asperrimum* (Temminck and Schlegel)  
*Hypsopsetta guttulata guttulata* (Girard)  
*Pleuronichthys decurrens* Jordan and Gilbert  
*Pleuronichthys cornutus* (Temminck and Schlegel)  
*Pleuronichthys verticalis* Jordan and Gilbert  
*Pleuronichthys coenosus* Girard  
*Pleuronichthys ritteri* Starks and Morris  
*Isopsetta isolepis* (Lockington)  
*Parophrys vetulus* Girard  
*Lepidopsetta bilineata* (Ayres)
- Lepidopsetta mochigarei* Snyder  
*Limanda limanda* (Linnaeus)  
*Limanda aspera* (Pallas)  
*Limanda punctatissima* (Steindachner)  
*Limandella herzensteini* (Jordan and Snyder)  
*Limandella yokohamae* (Günther)  
*Pseudopleuronectes americanus americanus* (Walbaum)  
*Devistes rikuzenius* Jordan and Starks  
*Tanakius kitaharae* (Jordan and Starks)  
*Pleuronectes quadrituberculatus* Pallas  
*Pleuronectes platessa* Linnaeus  
*Microstomus kitt* (Walbaum)  
*Microstomus achne* (Jordan and Starks)  
*Microstomus pacificus* (Lockington)  
*Glyptocephalus cynoglossus* (Linnaeus)  
*Glyptocephalus stelleri* (Schmidt)  
*Glyptocephalus zachirus* Lockington  
*Liopsetta putnami* (Gill)  
*Platichthys flesus flesus* (Linnaeus)  
*Platichthys stellatus rugosus* Girard  
*Kareius bicoloratus* (Basilevsky)
- Subfamily Poecilopsettinæ  
*Poecilopsetta plinthus* (Jordan and Starks)
- Subfamily Paralichthodinae (unrepresented)
- Subfamily Samarinae  
*Samariseus* sp. (Japan)
- Subfamily Rhombosoleinae (unrepresented)

The characteristics of the Citharidae are discussed in greater detail under eight headings.

#### FIN STRUCTURE

The discovery that *Citharus*, *Citharoides*, *Paracitharus*, and *Brachypleura* possess a spine in the pelvic fin ran counter to accepted views concerning the fin structure and classification of the flatfishes. The entire order Heterosomata had been regarded as lacking spines in all the fins until Regan (1910: 486) found that the primitive genus *Psettodes* has a pelvic spine and

about 10 dorsal spines. Most subsequent authors, as Norman (1934: 56-57), have rested the case on Regan's evidence, but Chabanaud (1934b: 126; 1937a: 3-4) has indicated that the anal fin of *Psettodes* also has spines, or, in his terminology, "rayons acanthoides." Chabanaud stated that the dorsal spines number 8 to 10 and the anal spines 3 in this genus. The count of 3 may be an error, unless it was based on *P. belcheri*. In 17 specimens of *P. erumei* I find 2 with 1 and 15 with 2 anal spines. All fin spines in *Psettodes* are slender and flexible, but possess the technical characters of spines (Hubbs, 1944: 71-73): they are single, median, solid structures, not composed of a pair of articulated hemitrichia, and have an internal structure, indicated by optical properties, different from that of soft rays.

Until now spines have not been reported to occur in any other flatfish, except in the fossil genus *Joleaudichthys*. In describing this genus Chabanaud (1937a: 51-73, Pl. 1, Fig. 9; Figs. 4-6) indicated its obvious relationships by referring it to the order Psettodoidea, but he appears to have transgressed necessity by erecting the new family Joleaudichthyidae. The pelvic rays in the fossil were given as I, 5, and several anterior rays of the dorsal and 4 in the anal fin were regarded as possibly, but probably not, "acanthoides." They are figured, however, as short and unbranched, and I think it probable that they were spines.

The pelvic fin formula was found to be I, 5 in *Citharus macrolepidotus* (3 specimens), *Citharoides macrolepidotus* (7), and *Brachypleura novaezeelandiae* (2), just as it is in the Psettodidae. According to the examination of British Museum specimens by Trewavas "the simple ray" is distally flexible and tapering and has no cross sutures. It is presumed that a pelvic spine is also developed in *Lepidoblepharon ophthalmolepis*, the other flatfish referred to the Citharidae. In *Citharoides*, *Paracitharus*, and *Brachypleura* the pelvic spine is flexible, but possesses all the attributes of a spine. The spine in *Citharus* is heavier and is rather pungent at its tip. In this one respect *Citharus* is even more primitive than *Psettodes*. The 5 other pelvic rays in all citharids examined are composed of articulated hemitrichia. In *Citharus*, *Citharoides*, and *Paracitharus* all 5 pelvic soft rays are branched—another indication of relationship with *Psettodes*. In *Brachypleura* 4 of the soft rays are branched; the outermost is simple.

Since the highly significant character of the presence of a pelvic spine has hitherto been overlooked in the Citharidae it was wondered whether this spine might not occur in other pleuronectoids. An examination of a long series of species brings no confirmation of this suspicion. Among the species of the preceding list, which provides a good coverage of the whole group, the first pelvic ray was found to be articulated in all except those referred to the Psettodidae and the Citharidae. The presence of a pelvic spine may therefore be regarded as diagnostic of these families.

The fact that the pelvic rays number I, 5 in the Psettodidae and 6 in many pleuronectoids led Regan (1910: 486) to apparently erroneous interpretations which have remained unchallenged. In the first place he regarded the typical pleuronectoid pelvic of 6 soft rays as having been directly derived from the psettodoid fin of 1 spine and 5 soft rays. "It is clear to me," he wrote, "that the anterior pelvic ray of this [*Hippoglossus*] and other genera with 6-rayed pelvic fins corresponds to the spine of *Psettodes*, and that the formation of joints in response to mechanical requirements has reconverted spines into articulated rays in the dorsal and pelvic fins of the Heterosomata." This idea runs counter to the generally accepted and well-substantiated view (Goodrich, 1904) that the articulations of the lepidotrichia were derived from rows of scales along either side of the primitive fin rays. Regan's suggestion lacks plausibility for this and other reasons.

In the second place Regan regarded the 6-rayed pelvic of most pleuronectoids as evidence that the flatfishes were derived—through a *Psettodes*-like form—from the typical percoid fishes which have I, 5 pelvic rays. It seems much more plausible to assume that the pelvic spine of the Psettodidae and the Citharidae, as well as the dorsal and anal spines of the Psettodidae, became reduced and lost, and that the ancestor of the Heterosomata had more than 5 soft rays in addition to the spine in the pelvic fin. A large amount of evidence indicates that the number of pelvic rays has not been increased after the count became reduced to 5 in the lower Acanthopterygii. In the Pleuronectidae the number of pelvic rays varies from 3 to 13 (Norman, 1934: 282), and it is probably only a coincidence, or some simple mechanical response, which accounts for the radial formula of 6 for most pleuronectoids and of I, 5 for the few known species of Psettodidae and Citharidae. It may be recalled that the soft-rayed Cyprinodontes also usually have 6 pelvic rays, though the number varies from 0 to 9.

The citharids agree in having the base of the pelvic fin of the ocular side somewhat the longer and the more anteriorly inserted. It lies on the mid-ventral edge. In *Brachypleura* I find that the blind-side pelvic is connected by membranes with the anal fin. *Brachypleura* is apparently unique among all flatfishes in this respect, although in several groups the pelvic of the ocular side joins the anal.

In *Citharus*, *Citharoides*, and *Brachypleura*, as in all other genera of pleuronectoids listed (pp. 8–9), the first dorsal ray and the first anal ray were seen to be articulated soft rays, not spines, as they are in *Psettodes*. Dorsal and anal spines are therefore diagnostic only of the Psettodidae.

The epicranial extension of the dorsal fin of the Citharidae, described and figured in detail for *Citharus* by Chabanaud (1933b: 25–26, Figs. 8–9, 17), and the enlargement of the first interhemal are characters that trenchantly separate this family from the Psettodidae and align it with the

Scophthalmidae, Bothidae, and Pleuronectidae. In the branching of almost all rays in all the fins the Citharinae, as already noted, agree with the Psettodidae and the Scophthalmidae (in the scophthalmids some of the dorsal and anal rays seem unbranched at first glance but on magnification are seen to be dichotomized at the tip). In the brachypleurine citharids many of the rays remain simple.

In the number of caudal rays (17 principal, 15 branched) *Citharus* and *Citharoides* agree with *Psettodes* and with the percoid fishes in general. This formula holds for the 3 specimens of *Citharus* and the 9 of *Citharoides* examined, and Norman (1934: 402) counted 15 branched rays in *Lepidoblepharon*. Regan (1910: 486) stressed this character as evidence that "*Psettodes* is simply an asymmetrical Percoid." The number of caudal rays is reduced in the vast majority of pleuronectoid fishes, as Norman (1934) showed in figures and text, though he failed to distinguish clearly between the principal and total ray counts. The number, however, is not very significant in this group. Several of the Pleuronectinae are described by Norman as having 15 branched rays in the caudal, and 1, *Microstomus achne*, is listed as having 16 forked rays in this fin. In 4 specimens of this species I count 17 or 18 branched and, therefore, 19 or 20 principal caudal rays. This is an anomalously high number for a percoid, since increases beyond the basic number of 17 principal and 15 branched rays have apparently been extremely rare, perhaps limited to individual variants. The high number in *Microstomus achne* may represent a secondary increase, or may be a primitive feature indicating the origin of the flatfishes from a prepercoid stock. Norman figured all members of the family Bothidae (as that group was delimited by him), with the exception of 2 species of *Arnoglossus*, as having fewer than 15 branched caudal rays. In *Lophopsetta aquosa* of the Scophthalmidae I find that the divided caudal rays vary from 12 to 15. *Brachypleura* is atypical for a citharid in that it has only 13 or 14 branched caudal rays (in the 2 specimens at hand, 13 according to Norman, 1934: 401). The caudal ray formula of the Citharidae thus shows some indication of primitiveness and of relationship between this family and the Psettodidae, but the evidence is not very reliable.

A distinctive feature of the Citharidae is the very strongly marked bilateral asymmetry in the structure of the pectoral rays of the two sides. On the eyed side the rays are slender, and the articulations are much longer than broad, whereas in the fin of the blind surface the rays are thicker and the articulations are much broader than long. This character holds for *Citharus*, *Citharoides*, and *Brachypleura* and presumably for the two other genera of the family. In no other flounders have I observed so strong a bilateral asymmetry of these articulations, although in some other genera, including *Psettodes*, the articulations are definitely the longer in the fin of the ocular side.



This comparison of the fins of the Citharidae with those of other heterosomate fishes confirms the opinion recently expressed (Hubbs, 1944) that the detailed fin structure is of prime importance in the classification of fishes.

#### POSITION OF EYES AND CROSSING OF OPTIC NERVES

Which side bears the two eyes and which optic nerve is the more dorsal in the chiasma have become questions of leading importance in modern interpretations of the taxonomy of the flatfishes (Parker, 1903; Regan, 1910, 1929; Norman, 1934; Chabanaud, 1937*a*). Parker proved that the soles (Soleidae in the broadest sense) agree with fishes in general in having a dimorphic chiasma, with the nerve of either the left or the right eye the more dorsal in the optic chiasma, whereas in some species of flounders the left nerve, in others the right, is consistently the higher at the point of crossing. These fishes were therefore said to have a monomorphic chiasma. In the genera of flounders which are normally dextral (with eyes and color on the right side) the left nerve was found to cross over the right in all individuals examined, even in reversed specimens. Similarly in the normally sinistral groups the right nerve was seen to be superior, even though the individual be variant in having the eyes on the right side. As a result the chiasma was characterized as partly uncrossed in the normal individuals but as doubly crossed in the reversed specimens. Parker regarded the normal condition as having a mechanical advantage. It is significant that he had no information on the chiasma of either the Psettodidae or the Citharidae, and no data on reversed individuals of Scophthalmidae.

Regan (1910: 487-88) applied Parker's findings in a detailed taxonomic revision of the groups of flounders and soles, separating the normally sinistral types, with the right optic nerve the more dorsal, into the Bothidae and the ordinarily dextral genera, with the left nerve superior, into the Pleuronectidae. He extended Parker's data by discovering that in *Psettodes* either the left or the right optic nerve may lie on top of the other one in the chiasma, and he pressed this observation as one reason for regarding *Psettodes* as close to the ancestral type of the flatfishes. Much has been made of the dimorphism of the chiasma in *Psettodes*, but the published evidence is restricted to 2 sinistral individuals dissected by Regan, one with the left nerve dorsal, the other with the right. I now confirm the conclusion that the chiasma is dimorphic in both sinistral and dextral specimens of *Psettodes erumei* (Table I).

Because of their bearing on the allocation of the Citharidae I bring together the available frequency data on the way the optic nerves cross in flatfishes, and add a number of new counts (Table I). Each family as recognized has its own type of asymmetry, in respect to the location of the eyes and the mode of crossing of the optic nerves. The data follow:

TABLE I

RECORDED FREQUENCIES OF THE TWO TYPES OF OPTIC CHIASMA IN FLATFISHES  
The classification, sequence, and nomenclature are modified from Norman (1934).

	Eyes Sinistral		Eyes Dextral		Authority*
	Left Nerve Dorsal	Right Nerve Dorsal	Left Nerve Dorsal	Right Nerve Dorsal	
Psettodidae: indiscriminately sinistral or dextral; nerve of migrating eye either dorsal or ventral					
<i>Psettodes</i> sp. ....	1	1	.....	.....	R
<i>Psettodes erumei</i> .....	1	4	6	5	O
Citharidae: normally sinistral, rarely dextral, in Citharinae; dextral in Brachypleurinae; nerve of migrating eye dorsal in either normal or reversed fish					
Citharinae					
<i>Citharus macrolepidotus</i> .....	.....	3	.....	.....	O
<i>Citharoides macrolepidotus</i> .....	.....	5	1	.....	O
Brachypleurinae					
<i>Brachypleura novae-zeelandiae</i> ....	.....	.....	2	.....	O
Scophthalmidae: normally sinistral; nerve of migrating eye dorsal in normal fish, of unknown position but hypothesized to be dorsal in reversed fish					
<i>Lophopsetta maculata</i> .....	.....	68	.....	.....	P
<i>Lepidorhombus whiff-iaonis</i> .....	.....	2	.....	.....	M
<i>Phrynorhombus norvegicus</i> .....	.....	2	.....	.....	M
Bothidae: normally sinistral (indifferent in a few species); nerve of migrating eye dorsal only in nonreversed fish					
Paralichthyinae					
<i>Tephrinectes sinensis</i> .....	.....	1	.....	1	W
<i>Tephrinectes sinensis</i> .....	.....	.....	.....	1	O
<i>Hippoglossina stomata</i> .....	.....	3	.....	.....	H & M; O
<i>Paralichthys dentatus</i> .....	.....	17	.....	.....	P
<i>Paralichthys albigutta</i> .....	.....	11	.....	.....	P
<i>Paralichthys "brasiliensis"†</i> .....	.....	1	.....	.....	P
<i>Paralichthys californicus</i> .....	.....	19	.....	17	O; P
<i>Paralichthys olivaceus</i> .....	.....	.....	.....	1	W
<i>Pseudorhombus pentophthalmus</i> ..	.....	.....	.....	1	W
<i>Xystreurus liolepis</i> .....	.....	.....	.....	2	H & M; O
<i>Azevia panamensis</i> .....	.....	1	.....	.....	P
<i>Syacium papillosum</i> .....	.....	34	.....	.....	P
<i>Syacium micrurum</i> .....	.....	1	.....	.....	P
<i>Citharichthys sordidus</i> .....	.....	11	.....	.....	P
<i>Citharichthys spilopterus</i> .....	.....	1	.....	.....	P
<i>Etropus rimosus</i> .....	.....	10	.....	.....	P
Bothinae					
<i>Arnoglossus laterna</i> .....	.....	2	.....	.....	M
<i>Bothus ocellatus</i> .....	.....	5	.....	.....	P
<i>Bothus mancus</i> .....	.....	1	.....	.....	P

TABLE I (Cont.)

	Eyes Sinistral		Eyes Dextral		Authority*
	Left Nerve Dorsal	Right Nerve Dorsal	Left Nerve Dorsal	Right Nerve Dorsal	
Pleuronectidae: normally dextral (a few species variable); nerve of migrating eye dorsal only in nonreversed fish					
Pleuronectinae					
<i>Atheresthes stomias</i> .....	.....	.....	1	.....	P
<i>Atheresthes stomias</i> .....	.....	.....	1	.....	H & M
<i>Atheresthes evermanni</i> .....	.....	.....	1	.....	H & M
<i>Hippoglossus hippoglossus</i> .....	1	.....	12	.....	P
<i>Hippoglossoides p. platessoides</i> .....	.....	.....	2	.....	M
<i>Hippoglossoides p. limandoides</i> .....	.....	.....	1	.....	P
<i>Eopsetta jordani</i> .....	.....	.....	31	.....	O; P
<i>Psetticichthys melanostictus</i> .....	.....	.....	23	.....	P
<i>Hypsopsetta g. guttulata</i> .....	.....	.....	1	.....	P
<i>Isopsetta isolepis</i> .....	.....	.....	1	.....	P
<i>Parophrys vetulus</i> .....	.....	.....	11	.....	P
<i>Limanda limanda</i> .....	.....	.....	16	.....	M
<i>Limanda ferruginea</i> .....	.....	.....	51	.....	P
<i>Limandella yokohamae</i> .....	1	.....	.....	.....	W
<i>Pseudopleuronectes a. americanus</i> .....	.....	.....	100	.....	P
<i>Pleuronectes platessa</i> .....	.....	.....	30	.....	M
<i>Pleuronectes "platessa"†</i> .....	.....	.....	1	.....	P
<i>Tanakius kitaharae</i> .....	.....	1‡	10	.....	O
<i>Microstomus kitt</i> .....	.....	.....	2	.....	M
<i>Glyptocephalus zachirus</i> .....	.....	.....	6	.....	P
<i>Liopsetta putnami</i> .....	.....	.....	1	.....	P
<i>Platichthys f. flesus</i> .....	38	.....	13	.....	M
<i>Platichthys stellatus rugosus</i> .....	50	.....	50	.....	P
Poecilopsettinae					
<i>Poecilopsetta hawaiiensis</i> .....	.....	.....	1	.....	H & M
Rhombosoleinae					
<i>Oncopterus darwini</i> .....	.....	.....	1	.....	P
Soleidae: almost invariably dextral; nerve of migrating eye either dorsal or ventral					
Soleinae					
<i>Solea solea</i> .....	.....	.....	15	14	P
<i>Buglossidium luteum</i> .....	.....	.....	2	.....	M
Achirinae					
<i>Achirus lineatus</i> .....	.....	.....	6	8	P
<i>Trinectes m. maculatus</i> .....	.....	.....	3	3	P
Cynoglossidae: invariably sinistral so far as recorded; nerve of migrating eye either dorsal or ventral					
<i>Symphurus plagusia</i> .....	.....	1	.....	.....	P
<i>Symphurus plagiusa</i> .....	13	4	.....	.....	P
<i>Symphurus plagiusa</i> .....	22	23	.....	.....	O

\* The counts are taken from the following sources: H & M = Hubbs and Marini, 1939: 159-60; M = Mayhoff, 1912: 83; O = original determinations made for this paper and for Hubbs and Hubbs, 1945; P = Parker, 1903: 225-31 (the basic reference); R = Regan, 1910: 488; W = Wu, 1932: 47.

† Identification probably wrong, for locality is outside known range.

‡ Completely reversed specimen, with situs inversus of viscera.

PSETTODIDAE.—Indiscriminately sinistral or dextral; chiasma dimorphic; nerve of either eye dorsal in both sinistral and dextral specimens.

CITHARIDAE.—Normally sinistral, rarely dextral, in the Citharinae; dextral in the Brachypleurinae; right nerve dorsal in sinistral specimens; left nerve dorsal in dextral fish, whether they are reversed specimens of sinistral species or representatives of the normally dextral species; chiasma therefore basically dimorphic, but normally of the one type or the other in each species; nerve of migrating eye consistently dorsal in chiasma. In all 3 available specimens of *Citharus macrolepidotus*, all sinistral (normal), the right nerve crosses over the left. This is true also of the 5 normal specimens of *Citharoides macrolepidotus* dissected. In a reversed or dextral specimen, however, the left nerve (again that of the migrating eye) is on top, as it normally is in the dextral genus *Brachypleura*. No reversal of sides has been established for the Mediterranean species (as noted on p. 31, Chabanaud, 1931b: 17–18, erred in assuming that the Linnaean description of *Pleuronectes linguatula* was based on a reversed specimen of *Citharus linguatula* = *C. macrolepidotus*). Both specimens at hand of the dextral species *Brachypleura novae-zeelandiae* have the left nerve superior. The conclusions, that the chiasma in the citharids is fundamentally dimorphic though usually monomorphic, and that the type of chiasma in these fishes is definitely correlated with the side bearing the eyes, admittedly rest on very limited data. I think the evidence rather secure, however, in view of the lack of variation throughout the Bothidae and Pleuronectidae in respect to the position of the nerves. Only one exception has been published to the rule that the chiasma is monomorphic in these two large families, which comprise nearly all flounders. The one exception, noted in Table I, that of a reversed (sinistral) pleuronectid, *Tanakius kitaharae*, presents a very special case, which has been described in another paper (Hubbs and Hubbs, 1945: 245–46). This individual seems to be the only completely reversed flatfish known, for among all specimens examined it alone also exhibits *situs inversus viscerum*. The reversed *Citharoides* retains the normal asymmetries of viscera and of gill-membranes, which are determined prior to metamorphosis and which therefore bear no relation to the side that carries the two eyes. The reversal of the optic nerves in the reversed *Citharoides* is not regarded as teratological, as it is in the reversed *Tanakius*. These points were also brought out in the paper by Hubbs and Hubbs.

SCOPHTHALMIDAE.—Almost invariably sinistral, with no species of indeterminate laterality; chiasma seemingly monomorphic, because the right nerve—that of the migrating eye—is dorsal in all specimens dissected and described. The type of chiasma has not been reported, however, for any of the few reversed specimens known in this group (Gudger, 1935: 13–14). None has been observed in *Lophopsetta aquosa* among several thousand

specimens examined, largely by Daniel Merriman and staff of the Bingham Oceanographic Laboratory (thanks are due Dr. Merriman for this information). Considering the probable derivation of the Scopthalmidae from the Citharidae I venture to predict that in reversed (dextral) individuals of the Scopthalmidae the left nerve (that of the migrating eye) will be found to lie dorsal to the right nerve. If so the chiasma of the scopthalmids, like that of the citharids, may be regarded as potentially dimorphic though almost invariably monomorphic.

**BOTHIDAE.**—Normally sinistral, but indiscriminately sinistral or dextral in a few species (data reviewed by Hubbs and Hubbs, 1945); chiasma strictly monomorphic, with nerve of right (migrating) eye dorsal, whether the individual be normal or reversed in regard to the position of the eyes.

**PLEURONECTIDAE.**—Normally dextral, but indiscriminately dextral or sinistral in one and possibly several species, and uniformly sinistral in Asiatic races of *Platichthys stellatus* (date reviewed by Hubbs and Hubbs, 1945); optic chiasma strictly monomorphic (so far as known, except in the one completely reversed specimen of *Tanakius kitaharae* mentioned above), with nerve of left eye dorsal.

**SOLEIDAE.**—Dextral, with extremely rare exceptions; chiasma dimorphic; either left or right nerve the more dorsal, without regard to location of eyes, and in approximately equal frequency (Table I).

**CYNOGLOSSIDAE.**—Sinistral, without any recorded exception; chiasma dimorphic; either left or right nerve superior, without regard to location of eyes, and in about equal frequency. Parker's limited data on this group suggested that the left nerve might be the more dorsal oftener than the right nerve, but original data, comprising the last entry in Table I, indicate an approximately equal number of rights and lefts in regard to the nerve that is the uppermore in the chiasma.

The correlation of the type of optic chiasma with the position of the eyes in the flounders has been interpreted as adaptive (Parker, 1903; further discussion and references in Hubbs and Hubbs, 1945), for when the nerve of the migrating eye (or of the eye which normally migrates in the given family) is the more dorsal, the chiasma is partly uncrossed rather than doubly crossed, as it is when the nerve of the migrating eye is ventral in the chiasma. Why then has the chiasma remained regularly dimorphic in both dextral and sinistral soles? The explanation may lie in the relative development of the optic nerves. In the flounders the optic lobes and nerves are larger than in the soles (Evans, 1937: 309-10), are much more conspicuous than the olfactory nerves, and occupy a large part of the cavity in which they lie. A complicated arrangement (double crossing) of the nerves may therefore involve a mechanical or developmental disadvantage.

In the soles, on the other hand, the optic nerves are tiny strands lying loose in an extensive space under the large olfactory nerves. In these fishes the olfactory and tactile senses obviously dominate the visual and probably have done so throughout the phylogeny of the group. The double twist of the optic nerves in half the individuals of each species of sole has apparently not been of sufficient selectional significance to lead in the soles, as it has in the flounders, to a fixation of the optic chiasma type in correlation with the usual position of the eye.

#### DEGREE OF ASYMMETRY

None of the Citharidae shares with *Psettodes* the relatively limited asymmetry which has been emphasized in placing *Psettodes* near the root of the flatfishes, as was done by Regan (1910: 486-91), Norman (1934: 2-22, 56-57), and Chabanaud (1933a; 1934c; 1936a; 1937a). The citharids, it is true, are among the less asymmetrical of the pleuronectoids, but other flounders, such as those of the pleuronectid genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, and *Cleisthenes*, deviate less than the citharids do from the symmetrical body plan of the presumed ancestor of the flatfishes. That this is true is readily appreciated from the treatment given these genera by Norman (1934).

#### STRUCTURES OF THE GILL REGION

One of the outstanding features by which the Citharidae diverge from the Psettoidoidea and resemble the other pleuronectoids is the shape of the urohyal. In *Citharus* (Chabanaud, 1933b: 16-17, Fig. 7) and *Citharoides* this bone, as is usual in the Pleuronectoidea, comprises two arms, the lesser of which is hooked forward ventrally. *Psettodes* has, as one of its primitive characters, a nearly straight-edged urohyal (Chabanaud, 1933a: 147, Fig. 5), as have also the cynoglossid soles (Kyle, 1921: 88). An intermediate condition is displayed by *Brachypleura*, for in this citharid genus the edge of the urohyal forms a right angle.

A second point of divergence between the Citharidae and the Psettodidae involves a specialization by which *Psettodes* stands apart from all other Pleuronectoidea. The gill-rakers of the Citharidae are normally developed, not reduced to clumps of teeth as they are in *Psettodes* (Chabanaud, 1933a: 148, Fig. 6).

In the wide separation of the gill-membranes the citharids are the flatfishes that most closely approach *Psettodes*. The Scopthalmidae also have the membranes separate, but the incision is somewhat less deep than in the Citharidae and the Psettodidae. In all other flatfishes so far as indicated the gill-membranes are connected, and in the Bothidae and Paralichthyidae the seventh rays of the two sides are united posteriorly to form a V.

These very significant differences were discovered by Schmidt (1915), whose findings, although summarized by Norman (1934: 18, Fig. 19), were not fully utilized by that author in his reclassification of the Heterosomata. Schmidt (pp. 442-43) concluded that the branchiostegal structures of flatfishes fall into three categories. In the first type, represented by various species now referred to the Pleuronectinae and in one member each of the Paralichthyinae and the Bothinae, he found the membranes to be widely united, the posteriormost or seventh rays of each side [not the seventh and eighth rays] to be united distally, and sliding valves to be well developed. This is obviously a very highly specialized condition, which is quite consistent throughout the Bothidae (excluding as I now do the Citharinae and Scophthalmidae) and the Pleuronectidae (exclusive of the Brachypleurinae). I have verified the structure for all species of these two families, as listed on pages 8-9. The V-shaped union of the two last branchiostegal rays varies somewhat in regard to the length of the union, for the combined structure may be a Y rather than a V, and in regard to the firmness of the connection (in some species, as *Tarphops oligolepis* of the Paralichthyinae, the approximated terminal portions of the rays are not very tightly bound together). The structural pattern is very distinctive, however, and I regard it as indicative of the common origin and the close relationship of the Bothidae and the Pleuronectidae, as these groups are here circumscribed.

Schmidt's second type of branchiostegal structure, obviously the primitive one, is exemplified in extreme condition by *Psettodes erumei* (Schmidt, 1915: 434, Fig. 11; figure reproduced by Norman, 1934: Fig. 15). Such branchiostegal membranes are separate and overlapping and the sliding valves are usually developed. Schmidt (pp. 442-43) found this type to hold for *Psettodes erumei*, for *Citharus macrolepidotus*, and for four species which I refer to the Scophthalmidae, namely *Psetta maxima*, *Psetta maotica*, *Scophthalmus rhombus*, and *Lepidorhombus boscii*. I have verified Schmidt's findings for *P. maxima* and *S. rhombus*. Norman (1934: 18) was of the opinion that overlapping membranes characterize all of the Scophthalminae (Scophthalmidae), and I think this must be true, for the same type of branchiostegal structure is also seen in *Lophopsetta aquosa* and *Lepidorhombus whiff-iajonis*. All of the citharids examined have the membranes fully separate. This is true not only of *Citharus*, *Citharoides*, and *Paracitharus*, but also of *Brachypleura*, for which Norman (1934: 400) wrongly described the membranes as "more or less united." In all specimens examined by me and by Trewavas, having this primitive type of branchiostegals, the left membrane overlaps the right, as it generally does in fishes (Hubbs and Hubbs, 1945: 244-45, 278-80).

The third type of branchiostegal structure is characteristic of the Soleoidea (Schmidt, 1915: 443; Norman, 1934: 18). In the soles the membranes

are described as fused, the last branchiostegals as not connected distally, and the sliding valves as lacking.

From these facts it is clear: (1) that the Citharidae and the Scopthalmidae agree with the Psettodidae in having the branchiostegal membranes separate; (2) that the great majority of the pleuronectoids (all Bothidae and all Pleuronectidae) have in common a highly specialized type of branchiostegal structure, in which the membranes are connected and the last ray of each side is united distally with its mate; and (3) that the soles have the membranes united but the rays all separate.

#### JAWS AND DENTITION

The primitive position of the Citharidae is also indicated by the retention of the supplementary maxillary (supramaxilla) in some genera of the family. Hitherto the presence of this jaw bone has been held to be diagnostic of the Psettodidae. It has been described as lacking in all other heterosomate fishes. I find it to be developed, however, in some citharids—though never to the large size that it attains in *Psettodes*. All 9 specimens of *Citharoides macrolepidotus* at hand have a small to medium-sized supplementary maxillary attached movably by suture to the upper posterior edge of the maxillary, on the blind side only. In *Paracitharus macrolepis* (4 specimens) Trewavas finds, on the blind side, a vestigial threadlike supplementary maxillary, with or without a posterior cartilaginous expansion (all specimens were smaller than the one adult available of *Citharoides macrolepidotus*). In 1 of the 3 examples of *Citharus macrolepidotus* examined the supplementary maxillary is discernible, again on the blind side only, as a splint suturally united with the maxillary. No trace of the bone appears in the 2 available specimens of *Brachypleura novae-zeelandiae*, nor in any scophthalmid, bothid, or pleuronectid examined (pp. 8–9).

The Citharidae agree further with the Scopthalmidae and approach the Psettodidae in having the jaws and teeth about equally developed on the 2 sides. This point is of limited importance, however, for many of the Bothidae and Pleuronectidae also exhibit little bilateral asymmetry in these characters.

The presence or absence of vomerine teeth provides strong evidence on the phyletic position of the Citharidae. These teeth are developed in *Citharus*, but not in *Citharoides* or *Paracitharus*, and are strong in *Brachypleura*, though lacking or nearly so in *Lepidoblepharon*. They are, therefore, either present or absent (or obsolescent) in each subfamily of the Citharidae. There is similar variation in the Scopthalmidae. The vomerine teeth are developed in *Psettodes*, but are lacking in all soles and in all the Bothidae and in all the Pleuronectidae (Norman, 1934), as these families are here restricted. The presence of vomerine teeth is obviously a primi-



tive character, which confirms the view that the small families Psettodidae, Citharidae, and Scopthalmidae are primitive. The fact that some citharids and some scopthalmids lack these teeth does not negate this conclusion. Obviously the vomerine teeth have become lost independently on several lines of flatfish evolution (p. 28).

The palatine and glossohyal teeth are lacking in the Citharidae as in all Heterosomata other than the Psettodidae. The teeth on the jaws of *Citharus* slightly approach those of *Psettodes* in strength, but this resemblance has little meaning, for the jaw teeth of *Citharoides* are small and various bothids and pleuronectids also have canines.

#### NUMBER OF VERTEBRAE

In the number of vertebrae the Citharidae contrast with the Psettodidae and fall within the range of variation for the other pleuronectoids. The formula for *Citharus macrolepidotus* is  $10 + 24 = 34$  (Chabanaud, 1933b: 6) or  $10 + 25 = 35$  (Norman, 1934: 168). The number of vertebrae is unrecorded for other genera of Citharidae, but is probably similar to that of *Citharus*. Much has been made of the fact that *Psettodes erumei* has  $10 + 14 = 24$  vertebrae, the formula which seems to be basic and ancestral among the percoid fishes (Boulenger, 1902: 301-2; 1905: 421-22; Regan, 1910: 491; 1929: 324; Chabanaud, 1933a: 143; Norman, 1934: 8). All other Heterosomata were said in these papers to have 28 or more vertebrae. There still seems to be significance in the  $10 + 14 = 24$  formula for *Psettodes erumei*, though it has been shown that *Psettodes belcheri* has  $10 + 15 = 25$  vertebrae (Chabanaud, 1937a: 7); that 1 bothid, *Tephrinectes sinensis*, has only  $10 + 17 = 27$  (Norman, 1934: 63); and that some achirine soles have as few as  $7 + 17 = 24$  and  $9 + 18 = 27$  (Chabanaud, 1937a: 43-44). Without doubt the vertebrae have increased in number along each of the main phyletic lines of the Heterosomata (p. 28). The fossil psettodid *Joleaudichthys sadeki* agrees with *Psettodes erumei* in having  $10 + 14 = 24$  vertebrae (Chabanaud, 1937a: 51).

#### POSITION OF ANUS AND OF URINARY PAPILLA

In describing *Citharoides* I (1915: 453) pointed out that it agrees with *Citharus* in having the vent on the eyed side, whereas "in all other flounders examined the anus is on the preanal ridge or on the blind side." The location of the anus on the eyed side was confirmed for *Citharus* by Chabanaud (1933b: 10), who found the vent to be on the blind side in the "Arnoglossinae" (= Bothinae). Norman (1934), who observed the location of the anus in all genera of pleuronectoids, stated that this opening was on the eyed side only in *Citharus* and *Citharoides* (*Citharoides* plus *Paracitharus*). In all other genera he described the vent as being either on the blind side or approximately on the mid-ventral line. I have further confirmed these

finding by examining the series of genera listed on pages 8-9. In the *Psettodidae* the anus lies very slightly on the blind side, in a rather large fossa; in the Citharidae, including *Brachypleura*, on the eyed side; in the Scopthalmidae, Bothidae, and Pleuronectidae, on the blind side or median line. In the Bothidae the opening is nearly always far on the blind side. It is more commonly on or near the mid-line in the Pleuronectidae, even in some genera that are highly asymmetrical in other respects. When it is located on the ventral ridge the actual opening may be turned slightly toward either side. Apparently, the deflection of the anus onto the blind side has occurred on several independent lines (p. 28). The Citharidae stand well apart, in the location of the anus definitely on the eyed side.

The urinary papilla in *Citharus*, *Citharoides*, and *Brachypleura* is located as in nearly all flatfishes on the eyed side of the body. Schmidt (1915: 444), whose conclusion was repeated by Norman (1934: 19), claimed that this structure is situated on the ocular side in all flatfishes. There are exceptions to this rule, however, and one of these exceptions involves another character in which the Citharidae diverge from the Psettodidae and correspond with most other pleuronectoids. In *Psettodes* the papilla, perhaps urogenital in this genus, lies on the mid-ventral edge, in line between the anus and the origin of the anal fin, as shown by Chabanaud (1934b: 125) for *P. belcheri* and by original observation on *P. erumei*. A second exception is furnished by all species studied (see p. 8) of 3 related American genera, namely *Syacium*, *Citharichthys*, and *Etropus*. In these species, but in none of the other flounders examined, I find that the genital papilla is on the blind rather than on the eyed side and that it lies very close to the anus, toward the mid-ventral line. Its position on that side of the body seems to be related to the twisting of the membrane behind the last pelvic ray of the ocular side onto the blind side. The whole anal region of the body seems to have rotated toward the uncolored side.

*Citharus* and *Citharoides* approach *Psettodes* in the close juxtaposition of the anus and the papilla. In these citharids the papilla arises just within the rim of the anus; in *Psettodes*, within the same scaleless fossa. In *Brachypleura* the papilla lies just above the edge of the anus. In nearly all other pleuronectoids the anus and papilla are separated by a narrow to broad band of the general body integument, and in the majority of the species these openings lie on the opposite sides of the body. The separation is not wide in *Hippoglossus*, in which, presumably as a primitive relict character, the deflection of the papilla to the eyed side is less than in any other flounder genus examined except *Psettodes*. Nor, as mentioned above, are the anus and papilla widely set apart in the 3 genera having the papilla secondarily displaced to the blind side.

## OTHER COMMON CHARACTERS OF THE CITHARIDAE

The known species of Citharidae are strikingly alike in several features, in addition to the characteristics brought out in the preceding discussions. Among the common characters listed by me in 1915 (pp. 452-53) the one which by itself seems most distinctive, excepting the location of the anus, is the fact that the dorsal and anal fins remain high to their very end, whereas in nearly all flounders, as can be seen from the figures in Norman's monograph, the posterior rays become more or less markedly reduced in length. This is a character that is common to all citharids, including the brachypleurine genera *Brachypleura* and *Lepidoblepharon*.

Among the additional common characters of *Citharus* and *Citharoides* (*Citharoides* plus *Paracitharus*), which were pointed out by Norman (1934: 44, 168-71), and which appear also to characterize *Brachypleura*, the considerably enlarged posterior nostril is noteworthy.

In all citharids the mouth is large; the mandible is more or less arched downward anteriorly and hooked at the symphysis; the vomer is trenchant and projects conspicuously into the mouth cavity; the origin of the dorsal lies somewhat on the blind side, and the posterior ends of the dorsal and anal are slightly deflected to that side; the scales are very large; the lateral line has a long and flat-topped curve; the upper orbit is larger and markedly in advance of the lower (*Lepidoblepharon* excepted). None of these characters by itself is completely diagnostic of the Citharidae, but the consistent combination is highly distinctive and indicative of the phyletic integrity of the group.

The Citharinae (*Citharus*, *Citharoides*, and *Paracitharus*) have in common a peculiar feature of coloration, not shared with the Brachypleurinae. This is the development of a conspicuous dark spot in the posterior axil of the dorsal and of the anal fin.

## PHYLETIC POSITION OF THE CITHARIDAE

The characters which the Citharidae share with the Psettodidae (p. 6), outstanding among which are the pelvic spine, the supplementary maxillary, the overlapping branchiostegal membranes, and the vomerine teeth, locate the citharids well down toward the psettodid base of the flatfish line of evolution (Fig. 1). From several points of view the Citharidae may now be regarded as transitional between the Psettodidae and the more typical members of the pleuronectoid series.

The Scopthalmidae share many characters with the Citharidae and are thought probably to have been derived from that group. The particularly close resemblance between *Citharus* and *Lepidorhombus*, which is seemingly the most primitive scopthalmid, further indicates, as Norman (1934: 44) suggested, the probable derivation of the scopthalmid series from the

*Citharus* group. This lineage, however, was presumably not within the bothid phyletic series, as Norman assumed, but rather on a lower branch of the flatfish line of phylogeny.

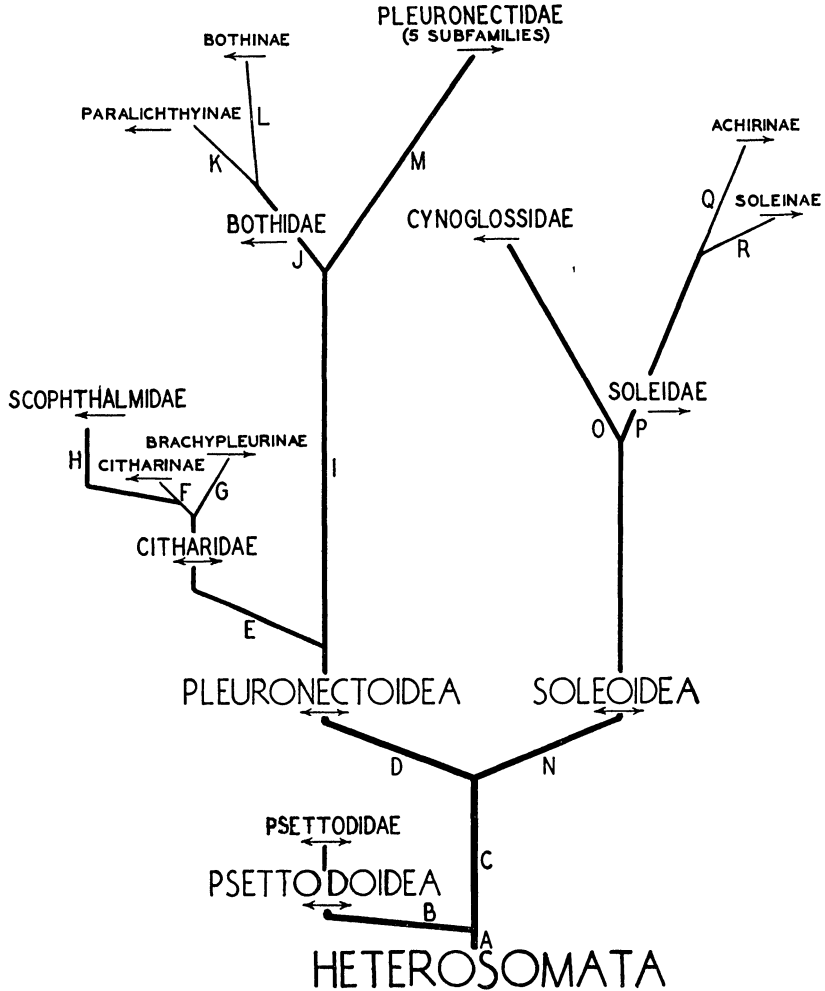


FIG. 1. Phylogeny of the Heterosomata. Arrows indicate whether the members of a group are all sinistral or all dextral, or either sinistral or dextral. Letters designate the phyletic lines, which are discussed in the text. According to Chabanaud the Achirinae and Soleinae should each be elevated to family rank and should be divided into sub-families.

The main ascending branch of the Pleuronectoidea apparently rose from the base of the citharid stock. The integrity of this main evolutionary line is attested by the consistent association of the monomorphic type of optic

chiasma with the usual position of the eyes and by the specialization of the branchiostegal structures. The branching of this line into the Bothidae and the Pleuronectidae seems to have been a relatively recent event in terms of the evolution of the whole group of flatfishes. These interpretations are diagrammed in Figure 1.

It seems rather clear that the Citharidae branched off from near the base of the pleuronectoid line, after the main trunk divided into the Pleuronectoidea and the Soleoidea. That the soles did diverge very early is indicated by their retention of certain very primitive features (Parker, 1903; Regan, 1910; Kyle, 1921; Norman, 1934; and numerous papers by Chabanaud). They retain the dimorphic type of chiasma, unrelated to the position normally taken by the eyes. They have the nostrils more nearly symmetrical than in most pleuronectoids (a somewhat complicated point, as indicated by Norman, 1934: 257-58). The urohyal retains its primitively straight shape only in the cynoglossid soles and in *Psettodes*. In these and in other respects the citharids definitely line up with the pleuronectoids rather than with the soleoids.

These views on the phylogeny of the Citharidae contrast sharply with current opinion. In the phyletic lines as lettered on Figure 1, summarizing the new interpretations, it may be noted the citharid base stem *E* is set apart from the main line *I* of pleuronectoid evolution, and this side line *E* is located not far above the point where the main trunk (*A-C*) divided into the pleuronectoid (*D*) and soleoid (*N*) stocks. An approach is therefore made toward the psettodid line (*B*).

The Citharidae are made up of two divisions. The Citharinae (*F*) are withdrawn from the subfamily Paralichthyinae (*K*) of the family Bothidae. The Brachypleurinae (*G*) are abstracted from the Samarinae, one of the five subfamilies into which the Pleuronectidae (*M*) are generally divided. The citharine line *F* is now regarded as the base from which the Scopthalmidae (*H*) sprang.

#### GENERAL REMARKS ON THE PHYLOGENY OF THE FLATFISHES

In other respects the phylogenetic scheme illustrated in Figure 1 differs from that of Regan (1910: 490) and the somewhat modified plan of Norman (1934: 43). (1) The Psettodidae are placed on a side branch (*B*) of the ancestral stem line (*A-C*) rather than on a direct line ascending from a typical percoid to the common ancestor of the pleuronectoid and soleoid stocks (*D* and *N*). This change is demanded by the features of high specialization which in *Psettodes* (as in most living relicts of generalized groups) are combined with characters of extreme primitiveness. I refer particularly to the arrow-shaped teeth and to the modification of the gillrakers into clumps of teeth. (2) The Scopthalmidae (*H*) are removed

from the Bothidae (*J*). (3) The bothids are supposed to have branched into two subfamilies (*K* and *L*) rather than to have formed a direct line of three subfamilies (*K + E*)  $\rightarrow$  *L*  $\rightarrow$  *H*. (4) The Bothidae, as restricted, are assumed to have had, not very remotely in terms of affinity, a common origin with the Pleuronectidae (*M*).

In agreement with Regan and other authorities (references on p. 5) I divide the Heterosomata primarily into the Psettodidae on the one side and all other families on the other. I do not see the need, however, for following Kyle (1921: 119-21) and Chabanaud (1934*a-c*; 1936*a-d*; 1937*a-b*) in the view that the Psettodoidea and the Heterosomata (thus restricted) form separate evolutionary lines. The discovery that the Citharidae have a pelvic spine and other characters in common with the Psettodidae goes far toward breaking down the isolated allocation of *Psettodes*.

Much less do I see the need for believing that the flounders and the soles, and even divisions of each of these groups, have had separate origins from symmetrical fishes. In this belief Kyle (1921: 119-21) appears to have stood alone, on ground that was far from firm.

The discovery that sinistral and dextral genera are both included in the small, compact family Citharidae, obviously a monophyletic group, dispels the suspicion that the Bothidae and the Pleuronectidae may have had a separate origin, and that the Cynoglossidae and the Soleidae may likewise have arisen independently. Left-eyed and right-eyed species might represent separate developments from symmetrical fishes, but they may also represent modifications of an ancestor, like *Psettodes*, that was indifferently sinistral or dextral.

Although it seems inherently probable that the origin of the unique asymmetry of the flatfishes was a single evolutionary event, it must be admitted that the Heterosomata as a whole are held together by little more than the single character of the two eyes being on one side of the head. Many features in which the several families agree now appear to represent convergent adaptations, as outlined in the following section. Some members of each main line possess primitive features that call for an origin before the time when the specialized characters may be supposed to have evolved. Stripped of such convergences the various groups of flatfishes show little more than the characteristics of the Acanthopterygii in general. The polyphyly of the Heterosomata remains a possibility.

On similar grounds the warrant for dividing the Heterosomata other than the Psettodoidea into the flounders (Pleuronectoidea) and soles (Soleoidea) has been questioned. Regan (1929: 324) and Norman (1934) indeed abandoned these superfamily groupings, and Norman brought the lines of the sinistral and dextral flounders (Bothidae and Pleuronectidae) and those of the sinistral and dextral soles (Cynoglossidae and Soleidae) all close to

the basic family Psettodidae. Chabanaud (1933*a, c*; 1934*c*; 1936*a, c*; 1937*a*) gave much consideration to the possible multiple origin of the Soleoidea from other flatfishes. The problem was also treated by Norman (1934: 2-4, 15-16, 37-38). The capacity of the pleuronectoids to evolve most characteristics of the soleoids is strikingly shown by the subantarctic Rhombosoleinae, a subfamily of Pleuronectidae (Norman, 1926, 1934).

The soles, however, do have a few characters in common, including a distinctive branchiostegal structure (pp. 19-20), and they agree in having the primitive, dimorphic type of chiasma. It seems wisest to regard the Soleoidea as a natural group, which split off from other Heterosomata very early.

The early cleavage of the Heterosomata into Pleuronectoidea and Soleoidea is confirmed by the structure of the anterior parts of the brain and the anterior cranial nerves. In the flounders the olfactory lobe and nerve of the eyed side are differentially enlarged (Norman, 1934: 13-14), and the optic nerves are large and conspicuous. In the soles, of both the dextral and the sinistral family, the olfactory lobes and nerves are subsymmetrical, and the large olfactory nerves conceal the threadlike optic nerves.

The primary division of the Heterosomata (other than the Psettodoidea) into the Pleuronectoidea and the Soleoidea certainly has the support of precedent, for these groups correspond to the families Pleuronectidae and Soleidae into which the flatfishes were divided by leading taxonomists of the past (Bonaparte, 1846: 47-51; Gill, 1893: 197; Jordan and Evermann, 1898: 2602; Kyle, 1900: 351-52).

It seems most in line with the available evidence to regard the Heterosomata as a natural group, with three primary divisions, Psettodoidea, Pleuronectoidea, and Soleoidea. For those who insist on group ranking I would suggest that the Heterosomata (name dating from Bonaparte, 1846, rather than from Cope as commonly stated) be treated as an order; the three divisions, as suborders or superfamilies.

#### CONVERGENT EVOLUTION IN FLATFISHES

The phylogeny of the flatfishes as treated above and as portrayed in Figure 1 does not represent the only possible course of evolution. Different phyletic diagrams and classifications would result from a shift in primary emphasis to other characters. These other characters, however, are mostly highly adaptive ones, which appear to have been subject repeatedly to independent development within the group. If the picture as given is essentially correct, there must have been involved a great amount of convergent evolution, of an obviously Darwinian nature. Such convergence in the two main lines of flatfish phylogeny—the pleuronectoid and the soleoid—has already been emphasized by writers, including Norman (1934: 37).

Examples of what may be regarded as convergent adaptation, along the lettered phyletic lines represented in Figure 1, may now be cited:

Extension of dorsal fin forward onto the head: lines *D* (to a variable extent along several lines) and *N*; forming a hook in front of the mouth in some rhombosoleines (*M*, part) and in soles (*N*).

Loss of dorsal and anal spines: line *C*, or lines *D* and *N*.

Loss of pelvic spine: lines *H*, *I*, and *N*.

Loss of supplementary maxillary: lines *F* (partial loss), *G*, *H*, *I*, and *N*.

Loss of palatine teeth: line *C*, or lines *D* and *N*.

Loss of vomerine teeth: lines *F* (partial), *G* (partial), *H* (partial), *I*, and *N*.

Hooklike modification of urohyal: *F*, *G* (partial modification), *H*, *I*, and *P* (not *O*).

More or less invariable location of eyes on left side: lines *F* and *H*, *J*, and *O*.

More or less invariable fixation of eyes on right side: lines *G*, *M*, and *P*.

Union of gill-membranes: lines *I* (with distal fusion of last pair of branchiostegals) and *N*.

Loss of rachis and parallel disposition of lamellae in olfactory organ: lines *G* (slightly), *H* (partly), *L* (few), and *M* (most; at least 2 independent lines) (Norman, 1934: 41-43, Figs. 26-27).

Increased compression of body: lines *E* and branches (slight to moderate), *K*, *L*, *M* (probably on several lines), and *N*.

Increase in number of vertebrae and fin rays: lines *B* (from 24 to 25 in one species), *E* (moderate), *K* (from 27 to moderate number), *L* (to high number), *M* (to high number), and *N* (from 24 to 52—Chabanaud, 1937a: 43-47).

Increased basal length of pelvic fin of eyed side: lines *F* (slight), *G* (moderate), *H* (great; both fins), *K* (slight to moderate), *L* (great), *M* (slight to moderate), and *N* (slight to great).

Pelvic fin of eyed side united with anal: *G* (not quite, but in one genus pelvic of blind side connected with anal), *H* (in part), *L* (almost in some), *M* (almost in several; fully in a few rhombosoleines), and *N* (in part).

Pelvic fin of blind side lacking: lines *M* (in a few), *O*, and *P*.

Pectoral fin obsolete on blind side: lines *K* (in a few), *L* (both fins, in a few), and *N* (both fins in *O*).

Anus deflected to blind side: lines *B* (very slightly), *E*, *K*, *L*, *M*, and *N*.

Mouth much reduced in size and markedly twisted, and teeth more or less obsolete on eyed side: lines *K* (in part), *L* (in part), *M* (in part), and *N*.

Many similar convergences could be pointed out. Thus, the lateral line has frequently become obsolescent or obsolete on the blind side, and has



repeatedly developed, or lost, its anterior arch, or its supratemporal branch. The scales of the blind side have lost their ctenii in many genera throughout the group. Isolated genera have the scales modified into bony tubercles. Pectoral or pelvic fins are greatly produced in unrelated genera; and the anterior dorsal rays in unconnected species may be similarly prolonged, or freed of membranes, or greatly branched. Body form varies from excessively deep to greatly elongate, with rounded or angular contours, all without regard to basic affinity.

Convergence does run riot in the Heterosomata. Superficial resemblances in adaptive characters are so numerous as to obscure relationships. The flatfish provide some of the most striking examples of convergent modification: witness the extremely close resemblance between the Soleidae and certain Rhombosoleinae, a subfamily of the Pleuronectidae (Norman, 1926: 257-86, Figs. 8-11; 1934: 20, 38, 413-35, Figs. 302-17). The parallel adaptations appear at all phyletic levels. Groups which seem most primitive in several characteristics are (in agreement with a general rule) highly specialized in other respects. In the Heterosomata it is more than usually necessary to seek the underlying threads of characters which can be relied upon to indicate relationships. It is thought that some such characters have been found and that the phyletic scheme discussed above and portrayed in Figure 1 approximates the true lines of heterosomate evolution. Further evidence, of course, may be expected to modify the scheme.

### SUBFAMILIES, GENERA, AND SPECIES OF CITHARIDAE

So far as discovered only 5 species of the primitive family Citharidae persist. Each one represents a monotypic genus, and the 5 genera comprise 2 subfamilies. The characters of these groups are outlined in the following key.

#### KEY TO THE CITHARIDAE

- 1a.—Eyes and color normally on left side; nerve of right eye dorsal in chiasma (except on reversed specimens). All dorsal and anal rays and all pelvic soft rays branched. A conspicuous spot in posterior axil of dorsal and of anal fin .....Citharinae
- 2a.—Vomer strongly toothed; teeth on sides of premaxillary rather large, uniserial; teeth in front of mandible biserial, those of inner row fixed. Gape strongly arched downward anteriorly. Supplementary maxillary on blind side weak or lacking. Origin of dorsal beside middle of slit of posterior nostril of blind side.
- 3a.—Tubules of lateral line T- or Y-shaped, with each fork usually further branched ..... *Citharus macrolepidotus*
- 2b.—Vomer toothless; teeth on sides of premaxillary very small, in bands; teeth in front of mandible in a large band or clump, those of inner row depressible. Gape weakly arched downward anteriorly. Supplementary maxillary (of blind side only) consistently developed. Origin of dorsal just above and behind slit of posterior nostril of blind side.

- 3b.—Tubules of lateral line typically with a single terminal branch, either dorsal or ventral. Supplementary maxillary small to moderate .....  
*Citharoides macrolepidotus*
- 3c.—Tubules of lateral line almost invariably T- or Y-shaped. Supplementary maxillary vestigial ..... *Paracitharus macrolepis*
- 1b.—Eyes and color on right side; nerve of left eye dorsal in chiasma. Only the posterior dorsal and anal rays branched; at least the anteriormost pelvic soft ray simple. No spots in axils of vertical fins ..... *Brachypleurinae*
- 4a.—Vomer strongly toothed. Scales deciduous, fewer than 35 in lateral line. Eyeball, interorbital, snout, and jaws scaleless. Upper eye well in advance of lower (as in *Citharinae*). Posterior nostril of blind side above first dorsal ray. Anterior dorsal rays greatly produced in males. Branched caudal rays 13 or 14.  
*Brachypleura novae-zeelandiae*
- 4b.—Vomer "toothless, or perhaps with a few teeth at its posterior border." Scales firm, more than 50 in lateral line. Eyeball (on upper exposed part), interorbital, snout, and jaws scaled. Eyes on same vertical. Posterior nostril of blind side below first dorsal ray. Anterior dorsal rays not known to be produced in either sex. Branched caudal rays 15 ..... *Lepidoblepharon ophthalmolepis*

## CITHARINAE

Three of the 5 citharid genera make up the typical subfamily Citharinae. These 3 genera are *Citharus* of the Mediterranean Sea and the adjacent Atlantic coast of Africa, *Citharoides* of Japan and the Philippines, and *Paracitharus* of southeastern Africa. The differences between *Citharoides* and *Citharus* were pointed out by me (1915: 542-43) and *Paracitharus* was differentiated from *Citharus* by Regan (1920: 209). *Paracitharus* was synonymized with *Citharoides* and the combined group was further compared with *Citharus* by Norman (1934: 168-70).

Genus *Citharus* Röse

Nomenclatorial problems arise in regard to the proper name for this genus and of the subfamily and the family of which it is the type. The problems were presented, with synonymy and literature references, by Norman (1934: 168), who chose the name *Eucitharus* for the genus. Röse's name *Citharus* seems acceptable, however, because it complies with Article 2 of the International Rules of Zoological Nomenclature in being uninominal, and this post-Linnaean author qualifies under Article 25 in that he used a binary (though not binominal) system. In Opinions 20 and 24 the International Commission has validated uninominal generic names proposed by binary authors. It is true that Röse gave no description, but he did give instead "an indication," in the form of citations of names which were accompanied by descriptions. In this way he fulfilled the first stipulation of Article 25, as interpreted in Opinion 1.

*Citharus macrolepidotus* (Bloch)

The one species of *Citharus*, inhabiting the Mediterranean Sea and the adjacent African shores of the Atlantic Ocean, likewise has a complicated synonymy (cited at length by Chabanaud, 1931*b*: 17 and by Norman, 1934: 169). It has ordinarily been called *Citharus* or *Eucitharus linguatula*, but it seems certain that the Linnaean name was not based on this species. *Pleuronectes linguatula* was put by Linnaeus in the section, "*Oculis a latere dextro*," and was defined as "P. oculis dextris, ano sinistro, dentibus acutis," on the basis of the following description by Artedi, "*Pleuronectes oculis a dextra, ano ad latus sinistrum, dentibus acutis*." It would seem definite that Artedi examined a specimen of some flatfish with the eyes dextral and the anus on the blind side, as is usual in flatfishes. The Citharidae do not accord with this description, for they are the only flatfishes which have the anus on the ocular side. Chabanaud's assumption (1931*b*: 18) that Artedi described a reversed specimen is quite unacceptable, for two reasons. First, no one has since recorded a reversed specimen of this species. Second, a reversed *Citharus*, like the reversed *Citharoides* described by Hubbs and Hubbs (1945), would surely have had the anus as well as the eyes on the right side. Considering the number of fin rays and some of the pre-Linnaean references cited by Artedi, I think that *Pleuronectes linguatula* Linnaeus was based on a sole, likely *Solea solea* (Linnaeus). The next name, *Pleuronectes macrolepidotus* Bloch, 1787, seems available and valid, despite the contrary opinion of Moreau and Chabanaud, and despite the probably erroneous locality of Brazil. Bloch's plate certainly represents this species. Bloch's name takes clear precedence over *Pleuronectes citharus* Spinola, 1807. (For references see Chabanaud, 1931*b*: 17 or Norman, 1934: 169.)

The 3 specimens of this species examined were kindly loaned by Dr. Leonard P. Schultz, United States National Museum. They were collected in the Bay of Naples, Italy, by S. E. Meek. For a detailed study of multiple branched lateral line tubes in this flounder I am indebted to Dr. Ethelwynn Trewavas, of the British Museum, and to Dr. Robert R. Miller, of the United States National Museum.

Genus *Citharoides* Hubbs

*Citharoides*.—Hubbs, 1915: 452–53 (original description; comparison; type, *C. macrolepidotus* Hubbs). Norman, 1934: 44, 62, 120 (in part; description; comparisons). Chabanaud, 1937*a*: 15 (listed). Okada and Matsubara, 1938: 417 (comparisons). *Brachypleurops*.—Fowler, 1934: 341 (original description; comparison; type, *B. axillaris* Fowler).

Since the nominal type species seem to be identical, this generic synonymy does not appear to be questionable. As explained below Norman (1934: 170) probably erred in synonymizing *Paracitharus* with *Citharoides*.

*Citharoides macrolepidotus* Hubbs

*Citharoides macrolepidotus*.—Hubbs, 1915: 453–54, Pl. 25, Fig. 1 (original description; comparison; Albatross station 4874, Korean Strait, Japan).

*Citharoides macrolepis* (misidentification).—Norman, 1934: 170–71 (synonymy in part; Korean Strait; Japan). Okada, 1938: 263 (“Honsyu, Sikoku, Kyusyu, Tyosen (Korea),” but not “S. Africa”). Okada and Matsubara, 1938: 419, Pl. 103, Fig. 2 (records, presumably the same, in Japan).

*Brachypleurops axillaris*.—Fowler, 1934: 341–43, Fig. 95 (original description; Philippine Islands).

Of this species I have at hand 2 half-grown, 1 normal (sinistral) and 1 reversed (dextral), both from Nagasaki, collected by Dr. Ichirô Kaneko, who with great generosity presented me with his large and valuable private collection in 1929; also 7 adult paratypes of *Brachypleurops axillaris* Fowler from the Philippine Islands, kindly loaned by Dr. Leonard P. Schultz of the National Museum. These paratypes came from the following Albatross stations:

Sta. 5273, 13° 58' 45" N., 120° 21' 35" E., July 14, 1908 (4).

Sta. 5278, 14° 00' 10" N., 120° 17' 15" E., July 17, 1908 (2).

Sta. 5353, 7° 50' 45" N., 116° 43' 15" E., January 1, 1909 (1).

Comparison of the adult paratypes of *Brachypleurops axillaris* with the two half-grown specimens from Nagasaki, Japan, discloses no differences that seem to be of specific significance. I therefore synonymize that nominal species with *Citharoides macrolepidotus*.

Norman apparently erred in synonymizing this species with *Arnoglossus* or *Paracitharus macrolepis* of southeastern Africa. That species, as described by him, has Y- or T-shaped lateral line tubules, whereas the Asiatic form ordinarily has tubules with a single branch. Of 142 lateral line scales on 7 paratypes of *Brachypleurops axillaris*, as kindly observed and recorded by Dr. Robert R. Miller, of the United States National Museum, the tubule is single and unbranched in only 7, has 1 branch extending upward and backward from the end of the straight part in 87, has 1 branch angled downward and backward in 45, is bifurcate in only 3, and in 1 bears a Y-shaped subterminal dorsal branch.

This character of the branching of the lateral line tubules is difficult to determine without good magnification and illumination and has been erroneously interpreted. Under cursory examination only the straight part of the tube is visible. Gilchrist's artist drew the tubules as simple in the type figure of *Arnoglossus macrolepis*. Norman distinguished *Citharus* (his *Eucitharus*) from *Citharoides* (really *Paracitharus*, for his one specimen of *Citharoides* was almost devoid of scales) on the basis of the simple lateral line tubes. But Trewavas has ascertained and has kindly informed me that the specimen of the European genus figured by Norman (Fig. 121, p. 169)

has the tubules branched, with each fork subdivided. Robert R. Miller has determined that all 7 specimens of *Citharus macrolepidotus* in the United States National Museum have T- or Y-shaped tubules, often with each branch subdivided, in various patterns. The lateral line scales of this species were described and figured by Chabanaud (1933b: 11-12, Figs. 1-2) as having an unbranched tube with a large external pore in the posterior field, but Miller was unable to find any unbranched tubules in the National Museum specimens. The main horizontal part of each tubule bears at the posterior end a large pore, from which the branches arise. In *Citharoides macrolepidotus* this median pore is usually small or lacking.

Another difference between *Citharoides macrolepidotus* and *Paracitharus macrolepis* seems to lie in the extent of development of the supplementary maxillary, as is indicated on p. 20.

### Genus *Paracitharus* Regan

*Paracitharus*.—Regan, 1920: 207, 209 (original description; comparison; type, *Arnoglossus macrolepis* Gilchrist). Barnard, 1925: 384, 389 (comparisons; description).

*Citharoides* (misidentification).—Norman, 1934: 44, 62, 120 (description and comparisons based primarily on *Paracitharus*).

Although the specific distinction of *Paracitharus macrolepis* and *Citharoides macrolepidotus* seems rather certain, on the evidence presented under the heading of the last species, the generic separation is questionable. A more thorough comparison of the 2 types is needed.

### *Paracitharus macrolepis* (Gilchrist)

*Arnoglossus macrolepis*.—Gilchrist, 1904: 1, 12-13, Pl. 31 (original description; off Tugela River, Natal). Gilchrist and Thompson, 1917: 398 (reference).

*Paracitharus macrolepis*.—Regan, 1920: 210, Fig. 2 (description). Von Bonde, 1922: 6 (listed); 1925: 286, 288 (records, Portuguese East Africa). Barnard, 1925: 389 (synonymy; description). Fowler, 1925: 203 (description; Natal).

*Citharoides macrolepis*.—Norman, 1934: 170-71, Fig. 122 (synonymy in part; description; Natal). Okada, 1938: 263, and Okada and Matsubara, 1938: 419 (South Africa record only).

Regarding the scale structure in the species Ethelwynn Trewavas writes: "I have examined again a specimen from Natal and 3 specimens from the Zanzibar region. The first has several lateral line scales left, all with branched tubules. Several lateral line scales of both sides are preserved in the Zanzibar fishes, all with branched tubules except one scale of the blind side in one (having an upper branch only) and two of the blind side in another (tubule opening by one pore in the median posterior notch of the scale)."

The similarity of the names of the 3 citharines (*Citharus macrolepidotus*, *Citharoides macrolepidotus*, and *Paracitharus macrolepis*) involves no

nomenclatorial difficulties, illustrates the very close relationship between the species, and emphasizes the common characteristic of large scales.

#### BRACHYPLEURINAE

The subfamily Brachypleurinae was erected by Chabanaud (1937a: 22-24) with the same limits as here assigned, namely for *Brachypleura* and *Lepidoblepharon*. He regarded the subfamily, however, as a division of the Samaridae rather than of the Citharidae.

The relationships of *Brachypleura* particularly bothered Kyle (1900: 361), who noted its peculiar characters and suggested that it might be advisable to refer it to a distinct subfamily. As a provisional designation for the group, however, he suggested the unacceptable name "Solei-Hippoglossinae."

The pertinence of the Brachypleurinae to the Citharidae has already been attested (pp. 5 and 7). The relationship between these groups was obscurely appreciated by Fowler (1934: 341-42, Fig. 95), when he regarded his *Brachypleurops axillaris* (a synonym of *Citharoides macrolepidotus*) as a member of the Samarinae, greatly like *Brachypleura*.

#### Genus *Brachypleura* Günther

The synonymy and characters of this genus and of its 1 species, and of the following genus and species, are well treated by Weber and De Beaufort (1929: 134, 142-46, Figs. 36-37) and by Norman (1934: 399-402, Figs. 289-90).

#### *Brachypleura novae-zeelandiae* Günther

The material of this species examined, loaned by the United States National Museum through the co-operation of Dr. Leonard P. Schultz, comprises a male and a female specimen from off the Ganjam coast of India, in 25-35 fathoms. These were originally from the Indian Museum, and presumably are paratypes of *Brachypleura xanthosticta* Alcock.

#### Genus *Lepidoblepharon* Weber

This genus is referred to the Brachypleurinae and to the Citharidae because it and *Brachypleura* have been intimately associated and exhibit a very close correspondence in superficial characters. It remains to be determined with certainty, however, whether *Lepidoblepharon* possesses a pelvic spine, free branchiostegal membranes, and other fundamental citharid characters.

#### *Lepidoblepharon ophthalmolepis* Weber

Apparently only the type specimen of this species has been collected. It was deposited in the Amsterdam Museum, and we can only pray that it may have been saved from the ravages of war.

## SUMMARY AND CONCLUSIONS

Five monotypic genera, *Citharus*, *Citharoides*, *Paracitharus*, *Brachypleura*, and *Lepidoblepharon*, heretofore classed in the sinistral Bothidae and the dextral Pleuronectidae, possess characters which justify their reclassification in a distinct primitive family, Citharidae. These characters include a pelvic spine and free gill-membranes in all genera and vomerine teeth and a supplementary maxillary in some. Various other characters are consistent with this interpretation. The Citharidae are regarded as transitional between the Psettodidae and the ordinary flounders. They are thought to have been ancestral to the Scopthalmidae, which group is removed from the Bothidae and is accepted as of family rank.

The Citharidae are divided into the Citharinae, with eyes on the left side, and the Brachypleurinae, with eyes on the right. Thus, sinistrality and dextrality appear to have arisen three times instead of only twice from ancestral flatfishes which, like *Psettodes*, are indiscriminately sinistral or dextral. In the citharids the nerve of the migrating eye lies dorsal in the chiasma: the right nerve is superior in sinistral specimens, and the left nerve is dorsal in dextral examples, whether they be reversed or normally dextral.

The characters of the Citharidae strengthen the view that the asymmetrical fishes (Heterosomata) comprise a monophyletic group derived from primitive Acanthopterygii.

Convergent evolution in adaptive characters has been very extensive in the Citharidae, as in other flatfish families. Characters indicative of true relationship are hidden, but some appear to have been discovered.

Like other primitive groups of flounders—in fact, like archaic groups in general—the citharids are represented in the Recent fauna by few genera and species. They comprise 5 monotypic genera referable to 2 subfamilies, and these relicts are all fishes of moderately deep water. The living Psettodidae are limited to 2 species of 1 genus. The Scopthalmidae may be referred to 6 genera and 10 species, all confined to the North Atlantic.

Following are changes suggested in the nomenclature and status of the three known Citharinae:

*Eucitharus linguatula* (Linnaeus) → *Citharus macrolepidotus* (Bloch).

*Citharoides macrolepis* (Gilchrist), in part → *Citharoides macrolepidotus* Hubbs.

*Brachypleurops axillaris* Fowler → *Citharoides macrolepidotus* Hubbs.

*Citharoides macrolepis* (Gilchrist), in part → *Paracitharus macrolepis* (Gilchrist).

The status of the two Brachypleurinae, *Brachypleura novae-zeelandiae* Günther and *Lepidoblepharon ophthalmolepis* Weber, remains unchanged. The pertinence of *Lepidoblepharon* to the Citharidae seems highly probable but requires confirmation.

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