Pleuronectiformes: Relationships

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B ASICS of the current working model for evolution of pleu-ronectiforms were proposed by Regan (1910, 1929) and Norman (1934). In his monograph, Norman treated the floun-ders (Psettodidae, Bothidae, Pleuronectidae), and though he did not publish a revision of the remaining pleuronectiforms, his key and classification of the soleoids were published posthu-mously (1966). Norman's model and classification with the modifications of Hubbs (1945), Amaoka (1969), Futch (1977), and Hensley (1977) represent the most recent, detailed hypoth-esis for pleuronectiform evolution. We will refer to this as the Regan-Norman model (Fig. 358) and classification (preceding article, this volume) and consider it the working hypothesis to be reexamined using adult, larval, and egg characters.

Formation of the Regan-Norman model involved an eclectic approach, i.e., a combination of phyletic and phenetic methods. Although some of the groups currently recognized appear to be based on synapomorphies, many are clearly based on symple-siomorphies and were recognized as such by the authors. This search for horizontal relationships among pleuronectiforms us-ing eclectic methods, with one exception, has been the only approach used in this group. The exception is the recent work of Lauder and Liem (1983) in which a cladogram for flatfishes
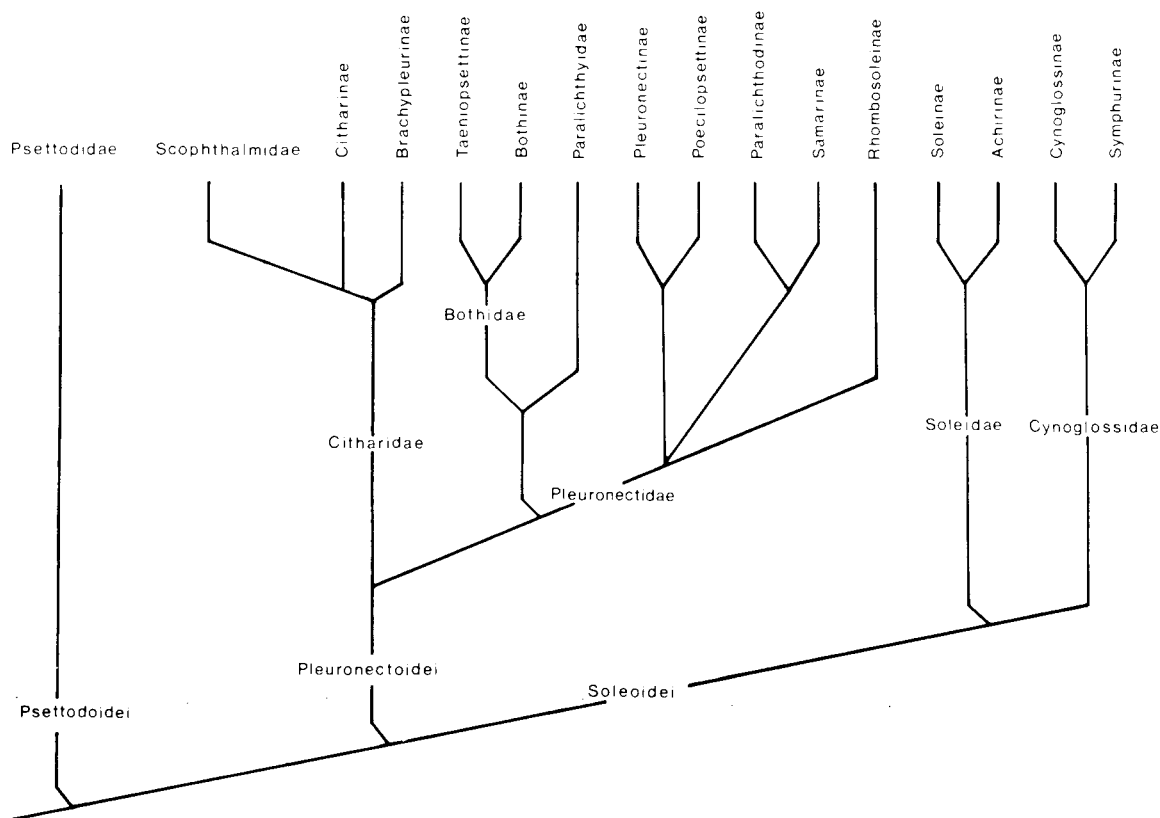
Psettodidae   Scophthalmidae   Citharinae   Brachypleurinae   Taeniopsettinae   Bothinae   Paralichthyidae   Pleuronectinae   Poecilopsettinae   Paralichthodinae   Samarinae   Rhombosoleinae   Soleinae   Achirinae   Cynoglossinae   Symphurinae

Bothidae

Citharidae

Soleidae   Cynoglossidae

Pleuronectidae

Pleuronectoidei

Soleoidei

Psettodoidei

Fig. 358. Current hypothesis for interrelationships of pleuronectiform fishes. Based on Norman (1934, 1966), Hubbs (1945), and Amaoka (1969).

is presented. However, these authors present this as a tentative hypothesis and admit that the interrelationships expressed are still problematic. Most of the character states they use are reductive, few characters were analyzed, and the authors were understandably unaware of recent character surveys, since much of this information is unpublished.

We have made the assumption that the order Pleuronectiformes is monophyletic and the sister group is the remaining percomorph fishes (sensu Rosen and Patterson, 1969 and Rosen, 1973). Although the monophyly and origin of the group is still open to question and hypotheses of multiple origins have been proposed (e.g., Kyle, 1921; Chabanaud, 1949; Amaoka, 1969), a monophyletic model with a percomorph sister group still appears to be the most parsimonious. In other words, with the information available, there appears to be no need to hypothesize multiple origins for flatfishes; to do so demands the inclusion of a great deal of convergence.

RELATIONSHIPS

The following discussion of relationships within the pleuronectiforms is cursory and preliminary. In fact, it asks more questions than it answers and illustrates that more work (particularly osteological) is needed in certain groups before the

order can be subjected to an in-depth cladistic analysis. Until this work is completed, it is premature to offer a new hypothesis of interrelationships for the entire order.

Adult characters

Several criteria were used for selecting characters for discussion: (1) amount of information available on the distribution of character states; (2) characters commonly used in the past to define groups of pleuronectiforms; (3) those for which our knowledge of distributions of states is limited, but appear to indicate groupings different from those hypothesized in the working classification and which need additional study; and (4) characters which are well known in certain groups and are potentially useful for elucidating relationships within these groups. Characters and character complexes used in this study are discussed below. Characters and states are presented in Table 179.

Optic chiasma.—The relationship between the optic chiasma and ocular asymmetry of pleuronectiforms has been investigated by several workers beginning mainly with the work of Parker (1903). Hubbs (1945) examined this relationship further and presented all data from previous studies. Parker found that most fishes have a dimorphic optic chiasma, i.e., the nerve of the left

or right eye is dorsal with about equal frequency (state referred to here as truly dimorphic). Exceptions to this are species of paralichthyids (sinistral) and pleuronectines (dextral) where the right or left optic nerve, respectively, is always dorsal, even in reversed individuals, i.e., the optic chiasma is monomorphic. The Soleidae and Cynoglossidae, however, retain a truly dimorphic optic chiasma. Subsequent work by Regan (1910) and Hubbs (1945) showed that in the indiscriminately dextral or sinistral *Psettodes* the optic chiasma is also truly dimorphic. In addition, Hubbs presented evidence of a third state, at least in *Citharoides* (sinistral), where the nerve of the migrating eye is dorsal even in reversed individuals. He thus interpreted the Citharidae as having a basically dimorphic optic chiasma and predicted the same for scophthalmids, although apparently no one has examined a reversed scopthalmid to test this prediction. A truly dimorphic optic chiasma as found in *Psettodes* and the soleoids has been interpreted as plesiomorphic for pleuronectiforms. The type of optic chiasma found in *Citharoides* and predicted for scophthalmids (i.e., nerve of the migrating eye always dorsal) was interpreted as an intermediate state between the truly dimorphic and the monomorphic chiasmata as found in pleuronectoids. We agree with this interpretation of polarity. However, some plesiomorphic states have been used to define groups: Psettodidae, truly dimorphic; Citharidae, basically dimorphic; Scophthalmidae, predicted to be basically dimorphic; and Soleoidei, truly dimorphic.

Major problems exist with the use of the optic chiasma for phylogenetic inference. One of these concerns the feasibility of actually determining which state exists in a group. Demonstrating the occurrence of truly dimorphic chiasmata is relatively simple. All that is needed is to show that either optic nerve is dorsal regardless of which eye has migrated; reversed individuals are not necessary. To demonstrate occurrence of the basically dimorphic state, reversals are needed and the nerve of the migrating eye must always be dorsal. Likewise, reversed individuals must be examined to show a monomorphic chiasma. Here the nerve to the right eye must be dorsal in all individuals (including reversals) of normally sinistral species and the nerve of the left eye must be dorsal in all individuals of normally dextral species. When one actually examines the data for this character (see Hubbs, 1945), states have been determined for very few pleuronectiform groups. The occurrence of the basically dimorphic state in the Citharidae was demonstrated in only one species. Of greater significance, however, is the fact that a monomorphic state has been shown for very few pleuronectoid species. Within the pleuronectoids it has been widely assumed that all paralichthyids, bothids, and pleuronectids have monomorphic optic chiasmata, and that because of this they are monophyletic and not closely related to the soleoids (truly dimorphic). It is worthy of note here that a monomorphic optic chiasma has never been demonstrated for four pleuronectid subfamilies (Poecilopsettinae, Rhombosoleinae, Samarinae, Paralichthodinae), the Bothidae, or the paralichthyid genus *Thysanopsetta*.

Ocular asymmetry.—This character (sinistral, dextral, indiscriminate) is obviously interrelated with the optic chiasma in certain groups, i.e., those with basically dimorphic and monomorphic chiasmata. The evolution of ocular asymmetry and its relationship to the optic chiasma is not well understood, although there is one major hypothesis (Norman, 1934; Hubbs, 1945) which states that primitively, pleuronectiforms were indiscriminate in ocular asymmetry and the optic chiasma was

truly dimorphic. Soleoids became discriminate (soleids dextral and cynoglossids sinistral), but retained a truly dimorphic chiasma. Psettodids remained indiscriminate and truly dimorphic. Citharids and presumably scophthalmids became discriminate (scophthalmids and citharines sinistral and brachypleurines dextral) but retained some ontogenetic plasticity in regard to the optic chiasma, since reversed individuals still have the nerve of the migrating eye dorsal (basically dimorphic). The remaining pleuronectoids became discriminate (Paralichthyidae and Bothidae sinistral and Plueronectidae dextral) and evolved a monomorphic chiasma. The only exceptions with regard to ocular asymmetry are certain indiscriminate paralichthyids and pleuronectines. However, most of these indiscriminate pleuronectoids have been shown to have a monomorphic optic chiasma (a possible exception is *Tephrinectes*). It would thus appear that indiscriminate ocular asymmetry in pleuronectoids developed secondarily from discriminate ancestors (Hubbs and Hubbs, 1945).

Making phylogenetic interpretations from two states of ocular asymmetry is difficult or impossible without corroborative evidence. Thus, a statement to the effect that two or more dextral (or sinistral) pleuronectoid groups are most closely related to each other because they are dextral (or sinistral) without additional evidence of synapomorphies is circular, and may lead to the recognition of polyphyletic groups. This reasoning was the basis for the proposed close relationship in the Regan-Norman model between the Pleuronectinae and the remaining pleuronectid subfamilies (Poecilopsettinae, Rhombosoleinae, Samarinae, Paralichthodinae) and for treating the genera *Mancopsetta* and *Thysanopsetta* as members of the Bothidae and Paralichthyidae, respectively.

Ribs and intermuscular bones.—In pleuronectiforms that possess ribs, these appear to be homologous with the pleural and epipleural ribs of other teleosts, and the presence of these bones should be considered plesiomorphic for the order. Two groups lack both series of ribs, the Achirinae and apparently the Cynoglossidae. Chabanaud (1940) reports epipleural ribs in some cynoglossids but mentions no genera or species. We have not seen them in cleared-and-stained *Symphurus* species or in radiographs of several *Cynoglossus* species. Although it is still commonly believed that all soleoids lack both series of ribs (e.g., Nelson, 1976; Lauder and Liem, 1983), Chabanaud (1940, 1941) found short epipleural ribs in *Solea, Microchirus,* and *Aesopia,* and we have seen them in *Aseraggodes.*

Chabanaud (1940, 1950, 1969) found additional rib-like bones ("metaxymyostes") in certain pleuronectiforms. Some of his statements about these were in error, and it is now clear he was referring to *Bothus podas* and *Samaris cristatus* (Hensley, 1977). Amaoka (1969) found these ("intermuscular") bones in all species of his Bothidae and presented very detailed descriptions of their morphology. One of his primary justifications for elevating Norman's (1934) Bothinae to the family level was the presence of these bones in the group and their absence in Norman's Paralichthyinae. Norman considered *Engyophrys, Trichopsetta, Monolene, Taeniopsetta,* and *Perissias* to be paralichthyines. All of these genera have intermuscular bones (Amaoka, 1969; Futch, 1977; Hensley, 1977; pers. observ.) and are considered here to be bothids.

Bothid intermuscular bones are in five series. Amaoka (1969) called these series epimerals, epicentrals, hypomerals, and myorhabdoi (two series). He interpreted three of these (epi-

merals, epicentrals, hypomerals) as homologous with those of lower teleosts (see Phillips, 1942). The presence of these bones was the main reason both Chabanaud (1949a) and Amaoka (1969) hypothesized that pleuronectiforms were polyphyletic and that at least the Bothidae, and in the case of Chabanaud also the Samarinae, were derived from some lower teleostean group. Hensley (1977) presented arguments for interpreting the pleuronectiforms as monophyletic and the presence of intermuscular bones in at least the Bothidae as being apomorphic.

Chabanaud (1969) described intermuscular bones in *Samaris* as being in two series. However, we recently examined a cleared-and-stained specimen and found differences with Chabanaud's description. In the abdominal region, rib-like or intermuscular bones are in three series. Bones of the middle series are unbranched and in the horizontal skeletogenous septum. Most bones of the dorsal and ventral series are branched. In the region of the caudal vertebrae, there are only the dorsal and ventral series. There are none of the dorsal and ventral myorhabdoi as found in the Bothidae. Although the three series of bones found in *Samaris* resemble the epimerals, epicentrals, and hypomerals of bothids, a more detailed comparison is required before a statement about homologies can be made.

Amaoka (1969) interpreted bothids as lacking pleural and epipleural ribs, but possessing the five series of intermuscular bones. However, there is another interpretation. It is possible that Amaoka's epicentrals (limited to the horizontal skeletogenous septum of the abdominal region) and abdominal hypomerals are homologous to epipleural and pleural ribs, respectively, of other pleuronectiforms, and that the presence of myorhabdoi, epimerals, and caudal hypomerals are apomorphic states.

Postcleithra. — The absence of postcleithra was a character state, apparently apomorphic, used by Norman (1934) and subsequent authors to distinguish the Soleoidei from the Psettodoidei and Pleuronectoidei. However, an adequate survey of this character has never been made among the pleuronectoids. In a preliminary survey, we found postcleithra absent in certain pleuronectoids, i.e., the Samarinae and the bothid genera *Mancopsetta* and *Pelecanichthys*. Postcleithra are definitely present in the rhombosoleines *Oncopterus, Azygopus, Ammotretis,* and *Colistium,* but they may be absent in *Pelotretis, Peltorhamphus,* and *Rhombosolea* (Norman, 1934: fig. 25c; Chabanaud, 1949). Although lack of postcleithra in pleuronectiforms is reductive, their absence in certain pleuronectoids may indicate a closer relationship between some of these groups and soleoids than hypothesized in the Regan-Norman model. The occurrence of this specialization in *Pelecanichthys* is almost certainly an independent reduction, since this genus shows several synapomorphies with other bothids.

Vomerine teeth. — Hubbs (1945, 1946) interpreted the presence of vomerine teeth as a primitive state for the order, and we concur. However, Hubbs presented this interpretation as evidence that citharids and scophthalmids were closely related and represented an intermediate grade in pleuronectoid evolution. The presence of vomerine teeth cannot be used to infer phylogenetic relationships among pleuronectiforms.

Fin spines. — Hubbs (1945, 1946) presented the distributions for dorsal, anal, and ventral-fin spines in pleuronectiforms. *Psettodes* is the only genus with dorsal and anal spines. This genus and the Citharidae are the only flatfishes with ventral-fin spines.

Hubbs properly interpreted their presence in these groups as plesiomorphic for the order. However, again, he used a horizontal or eclectic approach and inferred a close relationship between the citharid genera and interpreted the group as an intermediate grade in pleuronectoid evolution. The presence of these spines does not indicate phylogenetic (vertical) relationships.

Supramaxillae. — Supramaxillae occur in *Psettodes* and the citharids *Eucitharus* and *Citharoides* (Hubbs, 1945). In *Psettodes,* the bones are well developed and apparently present on both sides. The two citharid genera have them reduced in size, confined to the blind side, or sometimes missing. The presence of these bones is plesiomorphic for the order and should not be used to infer phylogenetic relationships.

Ventral-fin placements and base lengths. — Evolution of ventral-fin asymmetry in pleuronectiforms is not well understood. Most of our knowledge concerning the relationship between ocular and ventral-fin asymmetry has come from some rare examples of reversals in forms with asymmetrical ventral-fin morphology (see Norman, 1934). For comparative purposes, i.e., attempting to determine homologous states, it would appear to be more correct to compare ocular and blind-side ventral fins between groups rather than those of the right and left sides (see Hubbs and Hubbs, 1945). At present, there are several problems in using ventral-fin morphology to elucidate phylogenetic relationships. Most work here has dealt only with external morphology and much of this has not been sufficiently detailed or accurate. What is needed are thorough comparisons of basipterygia as well as fins. Due to the paucity of accurate and detailed studies of these structures in flatfishes, it is not possible to adequately define character states for an in-depth comparison throughout the order. Thus, ventral-fin characters were not included in Table 179. What follows is a discussion of general patterns of ventral-fin morphology.

Ventral fins with short bases and symmetrical placements have been correctly considered plesiomorphic states in pleuronectiforms, and any type of asymmetry in placement, size, shape, or meristics as having been derived from symmetrical states (e.g., Norman, 1934; Hubbs, 1945; Amaoka, 1969). Most ventral-fin characters used have involved positions of the fins relative to the midventral line and relative lengths of the fin bases. Unfortunately, symmetry (plesiomorphic states) in both of these characters has been used to define groups. Short-based fins and symmetry or near symmetry in placement and base lengths occur in *Psettodes,* the Paralichthyidae (except the *Cyclopsetta* group), the Citharidae, most soleines, most or all Pleuronectinae, and the Poecilopsettinae. States where the ocular ventral fin is on the midventral line and has a base extending farther anteriorly than that of the blind side form a continuum. Thus, groups with the base of the ocular ventral fin only slightly extended anterior to that of the blind side (origin of blind fin at transverse level of about the second or third ray of the ocular fin) are the Samarinae, possibly some Soleinae, *Paralichthodes,* the Taeniopsettinae, and *Monolene*; groups where the origin of the ocular fin is farther anterior relative to that of the blind fin are the Rhombosoleinae, all Bothinae (except *Monolene*), and possibly some Soleinae. Two groups, the Scophthalmidae and Achirinae, have both ventral-fin bases close to or virtually on the midventral line and the anterior basipterygial processes extended. The *Cyclopsetta* group has the ocular fin on the mid-

TABLE 179. CHARACTERS AND STATES FOR PLEURONECTIFORM GROUPS. Where appropriate states are indicated by underlined letters. See text and Figs. 359–364 for hypural fusion patterns.

Taxon	Optic chiasma (Truly Dimorphic, Basically Dimorphic, Mono-morphic)	Ocular asymmetry (Dextral, Sinis-tral, Indis-criminate)	Ribs (Present, Absent)		Intermuscular Bones (Present, Absent)				Post-cleithra (Present, Absent; Present only in Larvae)	Vomerine teeth (Present, Absent)	Ventral-fin formula (ocular side/blind side)	Supra-maxilla (Present, Absent)
			Epi-pleural	Pleural	Epi-centrals	Hypo-merals	Epi-merals	Myo-rhabdoi				
Psettodidae	TD	I	P	P	A	A	A	A	P	P	I, 5/I, 5	P
Citharidae												
Brachypleurinae												
Brachypleura	?	D	P	P	A	A	A	A	P	P	I, 5/I, 5	A
Lepidoblepharon	?	D	P	P	A	A	A	A	P	P	I, 5/I, 5	?
Citharinae												
Citharoides	BD	S	P	P	A	A	A	A	P	A	I, 5/I, 5	P
Eucitharus	?	S	P	P	A	A	A	A	P	P	I, 5/I, 5	P
Scophthalmidae	?	S	P	P	A	A	A	A	P	P, A	6/6	A
Paralichthyidae												
*Cyclopsetta group	?	S	P	P	A	A	A	A	P	A	5–6/6	A
**Pseudorhombus group	?	S	P	P	A	A	A	A	P	A	6/6	A
***Paralichthys group	M	S, I	P	P	A	A	A	A	P	A	6/6	A
Tephrinectes	M?	I	P	P	A	A	A	A	P	A	6/6	A
Thysanopsetta	?	S	P	P	A	A	A	A	P	A	6/6	A
Bothidae												
Taeniopsettinae	?	S	P?	P?	P	P	P	P	P	A	6/6	A
Bothinae	?	S	P?	P?	P	P	P	P	P, A	A	6/6	A
****Mancopsetta	?	S	P	P	A	A	A	A	A	A	7/5–7	A
Pleuronectidae												
Pleuronectinae	M	D, I	P	P	A	A	A	A	P	A	4–7/4–7	A
Poecilopsettinae	?	D	P	P	A	A	A	A	P	A	6/6	A
Paralichthodinae	?	D	?	?	?	?	?	?	?	A	6/6	A
Samarinae	?	D	P?	P?	P	P	P	A	A	A	5/5	A
Rhombosoleinae	?	D	P	P	A	A	A	A	P, A?	A	6–13/0–6	A
Soleidae												
Soleinae	TD	D	P	A	A	A	A	A	A	A	5/5	A
Achirinae	TD	D	A	A	A	A	A	A	PL	A	3–5/2–4	A
Cynoglossidae	TD	S	A	A	A	A	A	A	A	A	0–2/4	A

* Citharichthys, Cyclopsetta, Etropus, Syacium.
** Cephalopsetta, Pseudorhombus, Tarphops.
*** Ancylopsetta, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Verecundum, Xystreurys.
**** Achiropsetta and Neoachiropsetta are considered synonyms.

ventral line, but the basipterygium of the blind fin is placed in a more anterior position than that of the ocular side. Another unique state is the loss of the blind ventral fin in some genera of the Rhombosoleinae, although the basipterygium of the blind side is probably still present. The Cynoglossidae are the only pleuronectiforms in which the blind ventral-fin base is oriented along the midventral line and the ocular fin is in a more dorsal position or absent. In cynoglossids missing the ocular fin, at least the dorsal process of the left basipterygium is still present.

Vertebral transverse apophyses.—Regan (1910) used the presence of transverse apophyses on caudal vertebrae as a state to distinguish his bothid subfamilies Platophrinae and Bothinae from the Paralichthyinae (=Paralichthyidae with modifications). Norman (1934) combined the Platophrinae and Bothinae into his Bothinae and Scophthalminae and again used transverse apophyses on caudal vertebrae to distinguish the bothines and scophthalmines from the paralichthyines. Amaoka (1969) used the presence of these structures to define his Bothidae and distinguish them from the other sinistral flounders he treated (Paralichthyidae, Citharidae, Psettodidae). Hensley (1977) and Futch

(1977) found transverse apophyses in *Engyophrys, Trichopsetta,* and *Monolene* and suggested this as a character state indicating these genera were more closely related to the Bothidae than the Paralichthyidae. We have since found them in *Perissias.* As previously stated, Norman (1934) had placed these four genera in the Paralichthyinae. Amaoka (1969) presented the most detailed descriptions of these structures. Basically, there are two pairs of transverse apophyses on the vertebrae, an anterior and a posterior pair. They are found on many abdominal and most caudal vertebrae. Subsequently, we have found that the transverse apophyses seen by Regan (1910) and Kyle (1921: fig. 32) in the scophthalmids are very similar to those present in the Bothidae. They are similar in shape and occur in two pairs.

Amaoka (1969) interpreted the occurrence of these structures in the Bothidae as indicative of a relationship to some fish group other than the Percomorpha and used this as evidence that the Bothidae arose independently from the remaining pleuronectiforms. To support this, he cites the occurrence of similar structures in anguilliforms (Trewavas, 1932; Asano, 1962).

Recently in a preliminary survey of this character or complex in other flatfishes, we found transverse apophyses on some vertebrae in the Samarinae, Cynoglossidae, and Soleinae. However,

TABLE 179. EXTENDED.

Vertebral transverse apophyses (Present, Absent) Anterior	Posterior	First neural spine (Present, Absent, Absent or Reduced)	Position of urinary papilla (Midventral, Ocular side, Blind side)	Position of vent (Midventral, Ocular side, Blind side)	Haemal arch on parhypural (Present, Absent, Rudimentary)	Articulation of parhypural with terminal half centrum (Present, Absent)	Hypural fusion pattern (1-6)	Number of autogenous epurals	Haemal spine on PU2 (Autogenous, Fused)	Total caudal-fin rays	Branched caudal-fin rays	Infraorbital lateral line canal on ocular side (Present, Absent)
A	A	P	M	M	P	P	1	1	A	24–25	15	P
A	A	P	O	O	R?	A	6	1	F	21	13	A
A	A	P	O	O	P?	P	1	2, 3?	A	23	15	P
A	A	P	O	O	R?	A	2	2, 3?	A	22–23 (usually 23)	15	P
A	A	P	O	O	A	A	4	1	F	21	14–15	P
P	P	P	O	M, B	A	A	6	1, 2?	F	16–17	13–15	P
P	P	A	B	B	A	A	6	0	F	17	11	A
A	A	P	O	B	R?	A	6	0	F	17–18 (usually 17)	10–13	P
A	A	P	O	M, B	A	A	6	0, 1, 2?	F	18	13	P
?	?	P	O	M	R?	A	1	2	F	20	14	P?
?	?	P	O	B	R?	A	1	1	F	15–16	0	A?
P	P	A	O	B	A	A	6	0	F	16–18 (usually 17)	10–13	A
P	P	A	O	B	A	A	6	0	F	15–18 (usually 17)	9–13	A
A	A	AR	O	M	R?	A	1	1	F	14–19 (usually 16–18)	13–14	A
A	A	P	O	M, B	A	A	6	1, 2?	F	17–24	10–16	P
A?	A?	AR	O	M	R	A	1	1	F	20	14–15	?
?	?	P	?	B	?	?	1	?	?	16	12	?
P	A	A	O	M	A	A	5	1?	F	16	0–12	A
A	A	AR	O	M, B	A	A	1, 4	1	F	17–20	8–15	A
P	A	A	O	M	A	A	4	1	F	16–20 (usually 18)	0–18	?
A	A	AR	O	B	A	A	1, 2?, 3	1, 2?	A	15–18 (usually 16)	11–17	P
P	A	AR	M	B	A	A	4	0, 1	F	8–14	0	A

in these groups, they occur only as one pair on the anterior end of the vertebra. In addition, the *Cyclopsetta* group has two pairs of very small lateral protuberances on most vertebrae. How to interpret the presence of vertebral transverse apophyses in pleuronectiforms is still open to question.

First neural spine.—Amaoka (1969) found that the neural spine of the first vertebra is missing in the Bothidae and interpreted this as a synapomorphy for the group, since absence of this spine is apparently rare or unknown in other teleosts. We have made a preliminary survey for this in other pleuronectiforms not treated by Amaoka. Some of this survey was based on radiographs, and due to the close proximity of the first vertebra and neurocranium, in some groups we are not sure if the first neural spine is present, absent, or greatly reduced. The states in other groups are more certain, since some cleared-and-stained material was available. A greatly reduced or missing first neural spine is not limited to the Bothidae (Table 179).

Position of the urinary papilla.—All flatfishes have a papilla on the posteroventral area of the abdomen near the anal-fin origin. Schmidt (1915, cited by Norman, 1934) commented on its position in flatfishes, claiming it was located on the ocular side in all species. However, Chabanaud (1934), Hubbs (1945), and Hubbs and Hubbs (1945) found it to be on the midventral line

in *Psettodes.* In addition, Hubbs (1945) and Hubbs and Hubbs (1945) found the papilla on the blind side in the paralichthyid genera *Syacium, Citharichthys,* and *Etropus.* We have found it in the same position in *Cyclopsetta.* Another exception here may be certain cynoglossids. Menon (1977: fig. 45) shows the urinary papilla on the blind side in a species of *Cynoglossus,* but claims it is attached to the first anal-fin ray in all species of the family. A midventral position for the papilla is generalized for teleosts and plesiomorphic for pleuronectiforms.

Position of vent.—Position of the anus in flatfishes has been reviewed by Norman (1934), Hubbs (1945), and Hubbs and Hubbs (1945). A midventral position is plesiomorphic for the order. In flatfishes where the vent is on or near the midventral line, it is often very difficult to determine what state is represented. It is on the blind side in several groups, but apparently on the ocular side only in the Citharidae. Hubbs (1945) interpreted the distribution of these states as indicating that deflection of the vent to the blind side has occurred several times within the order.

Caudal-fin complex.—The caudal fin and skeleton of many species of pleuronectiforms have been illustrated and discussed (e.g., Monod, 1968; Amaoka, 1969). The caudal skeleton of *Psettodes* is reported to be the most primitive among living
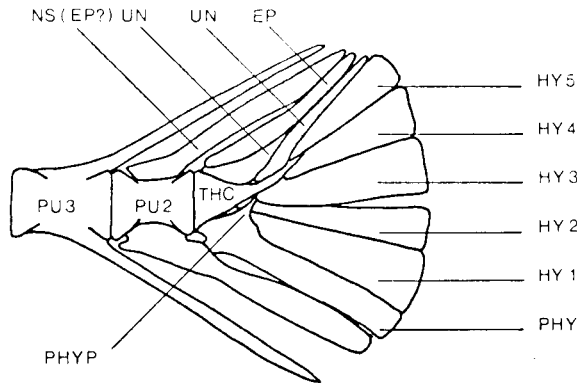
Fig. 359. Caudal skeleton of *Psettodes bennetti*. Hypural pattern 1. EP = epural, HY 1–5 = hypurals 1–5, NS = neural spine, PHY = parhypural, PHYP = parhypurapophysis, PU 2, 3 = preural centrum 2, 3, THC = terminal half centrum, UN = uroneural. Redrawn from Monod (1968).

flatfishes. It can be characterized as follows (Fig. 359): a parhypural with a haemal arch and parhypurapophysis; five autogenous hypurals; two pairs of uroneurals, i.e., pairs of stegurals and splinter bones; two epurals, the first between the neural-arch remnants of the second preural centrum; terminal half centrum, i.e., fusion of two ural centra and the first preural centrum; haemal spine of the second preural centrum autogenous; haemal spine of the third preural centrum fused; and 24–25 caudal rays, 17 principal, 15 branched. The caudal skeleton of *Psettodes* has been labelled as basically percoid (e.g., Wu, 1932; Monod, 1968; Amaoka, 1969). It should be noted here that the neural spine of the second preural centrum is interpreted as probably a captured epural, and that apparently only one free epural remains. This is one of the more important differences between *Psettodes* and all other pleuronectiforms, which have a neural spine on the second preural centrum and apparently a basal number of two epurals. There are at least two hypotheses which may explain this difference: (1) The earliest pleuronectiforms may have had three free epurals, the anteriormost becoming wedged in the neural-arch remnant on the second preural centrum (i.e., captured) and, thus forming a secondary neural spine. In *Psettodes* the remaining epurals were fused (Amaoka, 1969) or one was lost, while both were retained in the remaining flatfishes, at least primitively. (2) The earliest pleuronectiforms had two epurals, the anteriormost being captured in *Psettodes*, leaving one free epural. In the remaining flatfishes a neural spine on the second preural centrum was acquired by fusion of this vertebra with an anterior one bearing a spine. Rosen (1973) has discussed the second hypothesis to account for secondary acquisition of a neural spine on the second preural centrum and offered as evidence the frequent occurrence of double spines on the second preural centrum. Such anomalies are frequent in

pleuronectiforms (see Cole and Johnstone, 1902; Barrington, 1937; Chabanaud, 1937; Amaoka, 1969; Okiyama, 1974; Futch, 1977; Fig. 360H). However, although a detailed survey for these doubled spines has never been done, it appears that doubled neural spines on this vertebra are just as frequent as doubled haemal spines.

In spite of the work that has been done on pleuronectiform caudal osteology, there is still little agreement on interpretation of some structures. We cannot solve these problems here or discuss them in great detail. Most of these differences in interpretation concern certain epaxial elements. More detailed comparative work needs to be done on these elements before homologies can be determined. For example, there is one interpretation that uroneurals occur only in *Psettodes* (Ahlstrom). However, what appear to be remnants of a stegural may remain in *Citharoides, Lepidoblepharon, Scophthalmus,* and some achirines (Fig. 361; Amaoka, 1969; Hensley, pers. observ.). Although sufficient comparative work has not been done to treat these dorsal structures across all lines of flatfishes, within certain groups we can be fairly sure of homologies, due to certain consistent patterns of placement and shape and to some larval work where fusions have been observed.

In regard to neural and haemal spines of the second preural centrum, the parhypural, and hypurals, our knowledge rests on firmer ground. Characteristics of these structures have been widely surveyed and there is much more agreement on interpretation of homologous states. We interpret autogenous neural and haemal spines on the second preural centrum, retention of a parhypurapophysis and haemal arch on the parhypural, and articulation of the parhypural with the terminal half centrum as plesiomorphic for the order.

Several patterns of fusions occur in regard to hypurals 1–4. Hypural 5 moves to an epaxial position during ontogeny in flatfishes (Figs. 360, 362), and its fate is more properly discussed in reference to fusion (or lack of it) with epurals. The most primitive condition is where hypurals 1–4 are not fused to the terminal half centrum or among themselves (pattern 1; Figs. 359, 363 upper).

There are three patterns which are slightly different from each other. The interpretation of these is not so obvious, and we are hesitant here to make statements concerning homologies between groups. One of these (pattern 2) is where hypurals 3 and 4 are fused to the terminal half centrum (Fig. 361). This pattern is shown by *Citharoides* and apparently some Achirinae. In some achirines, a somewhat different pattern (3) occurs where hypurals 2, 3, and 4 are fused to the terminal half centrum (Fig. 363 middle). A fusion of hypurals 1–4 to the terminal half centrum (pattern 4) is found in the Soleinae, Cynoglossidae, one citharid (*Eucitharus*), and two genera of Rhombosoleinae (*Peltorhamphus, Rhombosolea*; Figs. 362, 363 lower). Caudal-fin development in a soleine is illustrated in Fig. 362.

Another pattern of hypurals (5) is unique to the Samarinae (Fig. 364). There are two ways to interpret this pattern. Here the central hypurals (2 and 3 or 2–4) are fused to the terminal half centrum. However, unlike the patterns previously de-

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Fig. 360. Caudal-fin structure of *Engyophrys senta* larvae (A–F), juveniles and adults (G–H). Standard lengths of specimens: (A) 4.6 mm; (B) 5.5 mm; (C) 7.0 mm; (D) 7.6 mm; (E) 7.7 mm; (F) 15.3 mm; (G) 45.7 mm; (H) 82.4 mm. NC = notochord, other abbreviations as in Fig. 359. Redrawn from Hensley (1977).
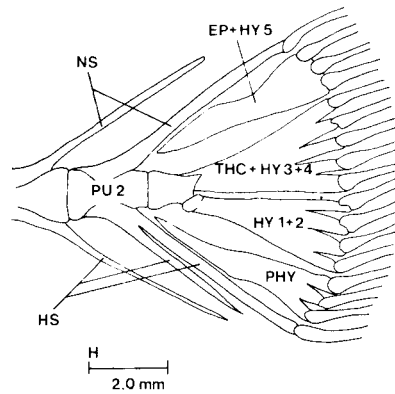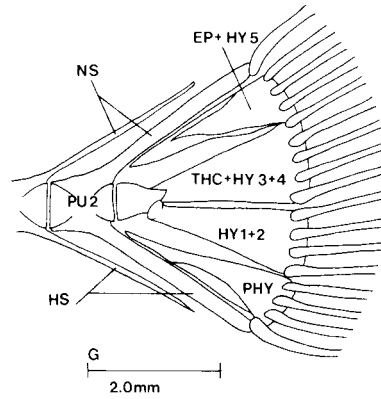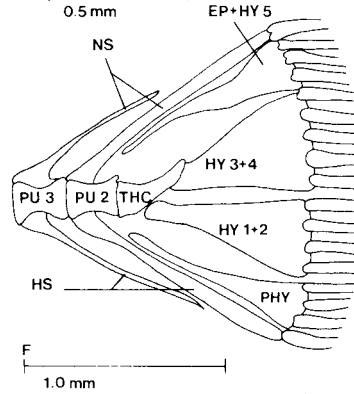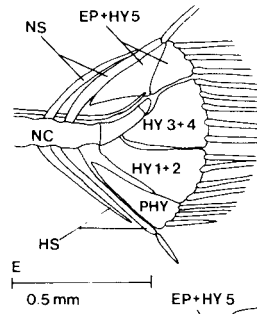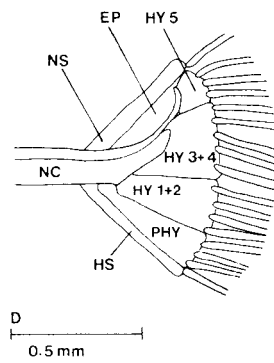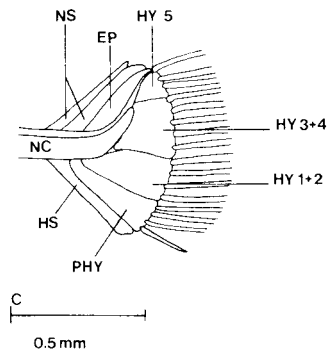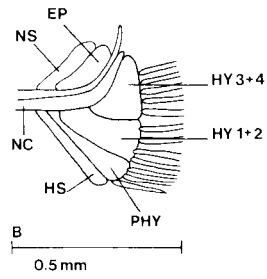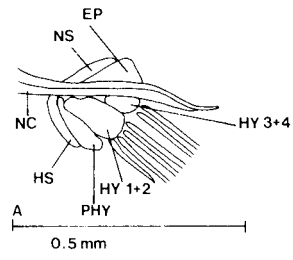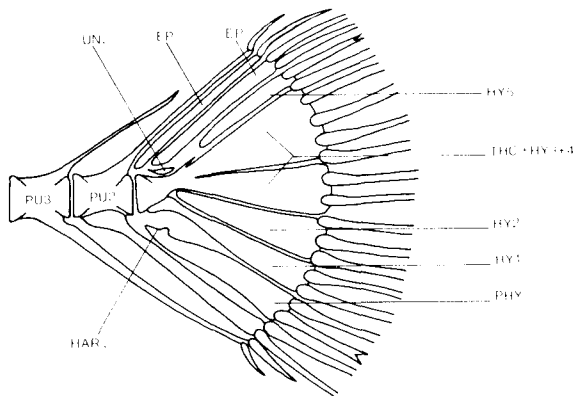
Fig. 361. Caudal skeleton of *Citharoides macrolepis*. Hypural pattern 2. HAR = haemal-arch remnant, other abbreviations as in Fig. 359. "V" on distal end of fin ray indicates dorsal- and ventralmost branched ray.

scribed, in the samarines hypural 1 does not articulate with the terminal half centrum.

The last pattern of hypurals (6) is characterized as follows (Figs. 360, 364 middle and lower): hypurals 1 and 2 are fused together forming one element which articulates with the posteroventral surface of the terminal half centrum; and hypurals 3 and 4 are fused together and to the terminal half centrum. This pattern occurs in the Pleuronectinae. Paralichthyidae (except *Tephrinectes* and *Thysanopsetta*), Scophthalmidae, one citharid (*Brachypleura*), and the Bothidae (except *Mancopsetta*). We interpret this pattern as homologous between these groups, derived, and indicative of a monophyletic origin. We will refer to these fishes as the bothoid group. Caudal-fin development in a bothid is illustrated in Fig. 360.

Although there is still some doubt concerning interpretations of certain epaxial caudal elements in flatfishes, some patterns are apparent. Most of the information indicates that at least in most pleuronectiform groups, the basal epural number is two. However, there is a small third element that appears in many species (Fig. 361; first uroneural of Amaoka, 1969). This element does not appear to be paired and its interpretation and fate in some groups is questionable. The two larger epural elements are still present in some flatfishes (Figs. 361, 363 upper), the citharids *Lepidoblepharon* and *Citharoides* and the paralichthyid *Tephrinectes*. The fate of these from the perspective of the entire order is questionable. However, it is obvious that these epurals have been reduced to one or zero in several groups. Which of these reductions are homologous is unknown. Within groups defined by other specializations, however, we are probably justified in assuming these epural reductions took the same course and are homologous states.

Although space does not allow a more detailed discussion of other caudal-fin characters, some obvious trends should be men-

tioned: Symmetrization—There is a marked trend among flatfishes toward dorsoventral symmetry in the caudal fin and skeleton. This has occurred by various types of fusions, losses, and secondary divisions of elements. These secondary divisions occur as scissures of varying depths in many caudal elements (Figs. 360H, 362F, 363 lower, 364 upper). Reduction of total and branched caudal rays—It has long been recognized that more primitive flatfishes tend to have larger numbers of total and branched caudal rays. Thus, *Psettodes* has a total caudal ray count of 24–25, 15 of which are branched. In many groups, caudal rays have been reduced to less than 18 and branched rays to 0–13.

Infraorbital lateral-line canal on ocular side.—In his study of sinistral flounders (i.e., Psettodidae and Pleuronectoidei) of Japan, Amaoka (1969) found ocular infraorbital bones present in the Psettodidae, two citharid genera (*Citharoides, Lepidoblepharon*), and the Paralichthyidae; they were absent from Japanese bothids. We have since done some survey work on this character in other groups not treated by Amaoka and found ocular infraorbital bones missing in additional groups (Table 179).

Examination of the Regan-Norman model using adult characters

In the following discussion, the groups and classification resulting from the current model for pleuronectiform evolution will be reexamined. The limited analysis presented here sheds much doubt on the monophyly of many of the currently recognized groups and their interrelationships. In a few cases, the evidence favoring different interpretations is so strong that these should be recognized in classifications. However, most of this analysis has produced questions and alternative suggestions that need additional study.

Psettodoidei, Psettodidae.—Nearly all of the character states used to define this group (*Psettodes*, two species) are symplesiomorphies or have been interpreted as such. Two exceptions, gill arches with groups of teeth and barbed jaw teeth, are states that Hubbs (1945) proposed as synapomorphies. Although we have no reason to doubt that *Psettodes* is a natural group, it should be redefined using character states which have been shown to be synapomorphies.

Soleoidei.—The differences between the Soleoidei and Pleuronectoidei were noted and expressed in important classifications before the works of Regan and Norman (e.g., Jordan and Evermann, 1896–1900) and they are obviously evident in the current model and classification. In most previous systematic research on pleuronectiforms, the author has concerned himself with one or the other group and assumed that the two were related only through a common ancestor near the early pleuronectiform line. The possibility, for example, that some soleoids may be most closely related to some pleuronectoids has only rarely been addressed. In any cladistic analysis of pleuronectiform interrelationships, character states used to unite the soleoids will need to be reinterpreted. Some character states

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Fig. 362. Caudal-fin structure of *Solea solea* larvae (A–C), juveniles and adults (D–F). Total lengths of specimens: (A) 6.0 mm; (B) 6.8 mm; (C) 8.1 mm; (D) 11.5 mm; (E) 18 mm; (F) 470 mm. HA = haemal arch, NA = neural arch, other abbreviations as in Figs. 359, 360. Redrawn from Fabre-Domergue and Biétrix (1905).

A   0.5 mm

B   0.5 mm

C   0.5 mm

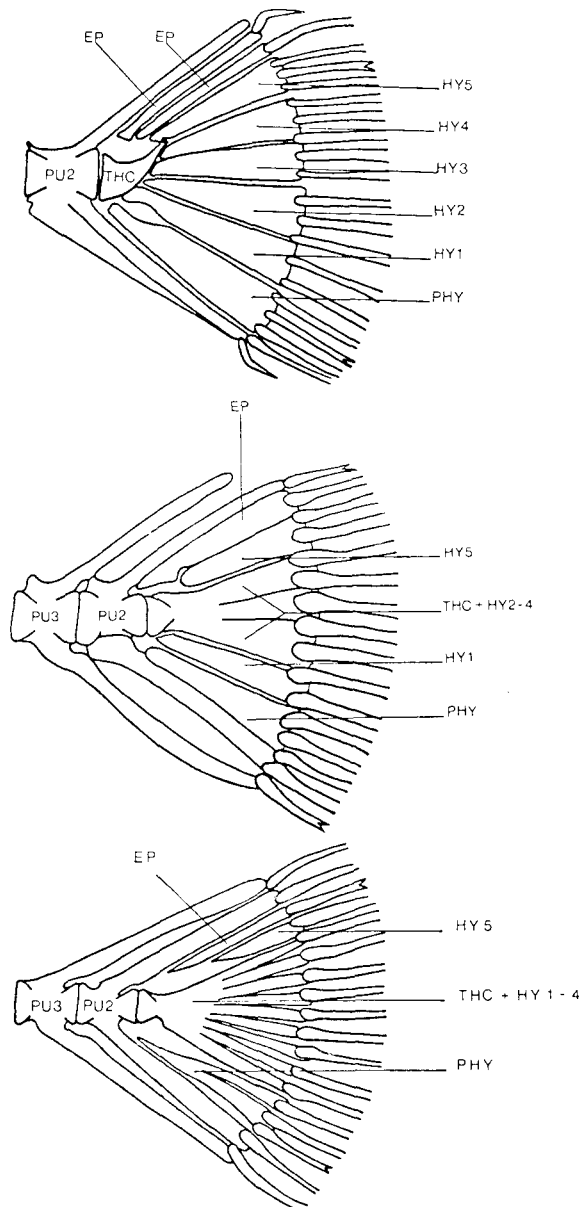D   0.5 mm

E   0.5 mm

F   0.5 mm
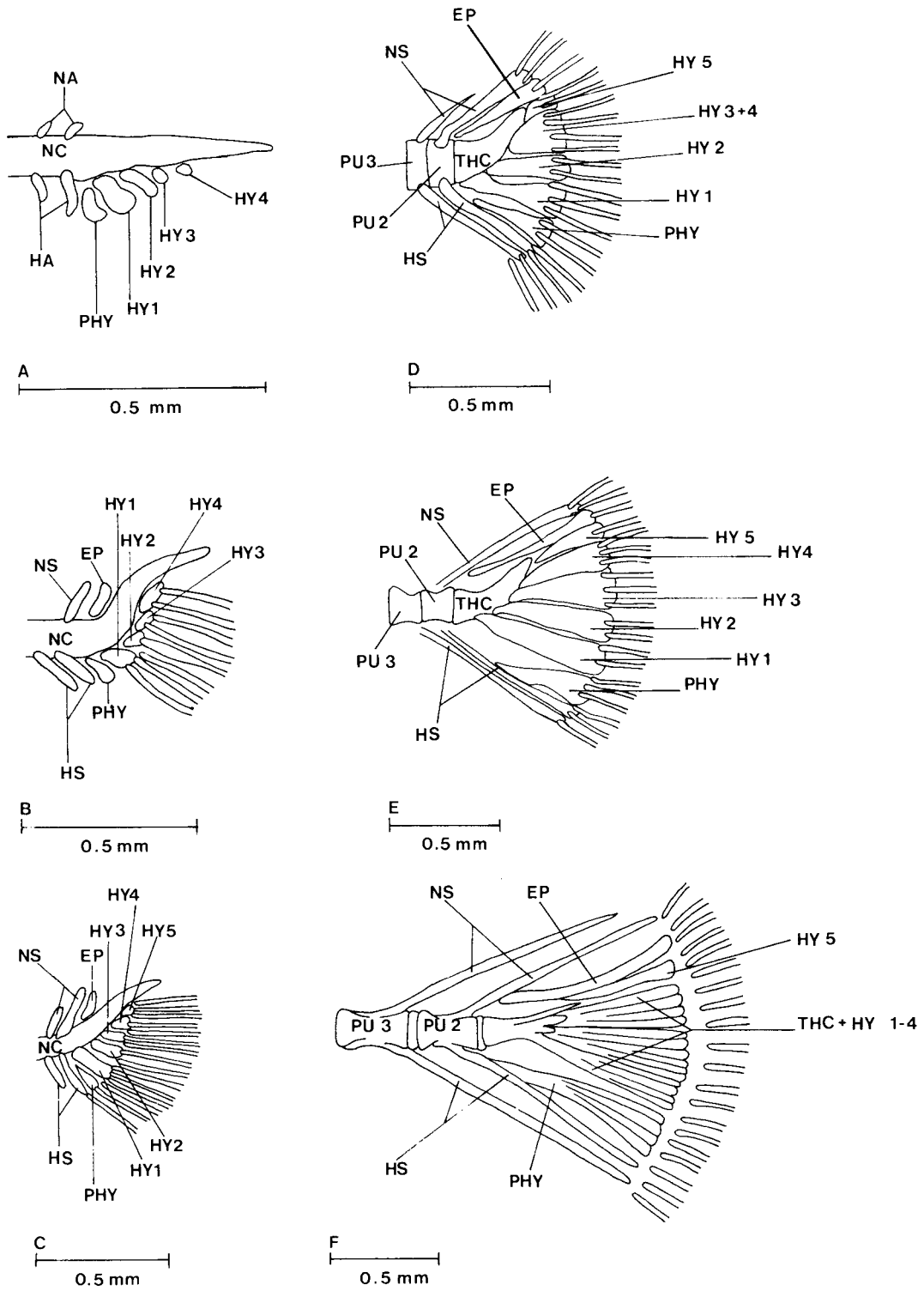
Fig. 363. Caudal skeleton of *Tephrinectes sinensis*. Hypural pattern 1 (upper); caudal skeleton of *Trinectes fimbriata*. Hypural pattern 3 (middle); and caudal skeleton of *Rhombosolea plebeia*. Hypural pattern 4 (lower). Abbreviations as in Fig. 359. "V" on distal end of fin ray indicates dorsal- and ventralmost branched ray.

used as evidence that soleids and cynoglossids are most closely related are plesiomorphic for the order (symmetrical nasal organs, dimorphic optic chiasmata), found in some pleuronectoids but dismissed as parallelisms [lower jaw not prominent, absence

of postcleithra, several "soleoid characters" found in rhombo-soleines, (see Norman, 1934)], or are incorrect (absence of all ribs). Other states used to unite the soleoid families include: (1) a preopercular margin covered by skin and scales; and (2) skin covering the dentary and interopercular bones being continuous across the chin, hiding the isthmus and branchiostegal rays (Norman, 1966). A covered preopercular margin is not limited to soleoids; it occurs in some rhombosoleine genera (Chabanaud, 1949; Hensley, pers. observ.). The second state as well as the absence of pleural ribs are possible synapomorphies for the group.

Cynoglossidae.—There is little doubt that the tonguesoles are monophyletic. They are unique in having the ventral fin of the blind side oriented along the midventral line and the ocular fin placed more dorsally or missing. The relationship of this family to other groups, however, is obscure (see Soleidae).

Soleidae.—The main character state proposed as uniting the two soleid subfamilies (Soleinae, Achirinae) appears to be that all species are dextral. This is still a poorly known group, and we are not prepared to make much of a contribution here. However, there are some marked differences between these subfamilies. In several characters, the Achirinae are more primitive than originally thought. Some species have hypural pattern 1, the most primitive. In species where hypural fusions have occurred, the first hypural remains free and articulates with the terminal half centrum (Fig. 363 middle). The haemal spine of the second preural centrum is autogenous (i.e., the plesiomorphic state for the order) in achirines. Uroneurals may still be present in some species. Although postcleithra are lacking in adult soleoids, at least one achirine species has them during larval development (Futch et al., 1972). Soleines differ from achirines in these characters in that they show what appear to be more derived states. The Soleinae have hypurals 1–4 fused to the terminal half centrum (Fig. 362F), the haemal spine of the second preural centrum is attached, there is no indication of uroneurals, and postcleithra have not been reported in larvae or adults. Soleines share these states with the Cynoglossidae. In addition, both groups have vertebral transverse apophyses, which are missing in achirines. The possibilities that the Soleidae are not monophyletic and the Soleinae are more closely related to the Cynoglossidae should be more thoroughly explored.

Pleuronectoidei.—Some of the character states used to define this group are plesiomorphic for the order: (1) preoperculum with free margin; (2) presence of postcleithra; and (3) presence of pleural and epipleural ribs. Some apomorphic states for the order are not limited to pleuronectoids; e.g., loss of dorsal and anal spines. The Regan-Norman model has used the position of the nasal organ of the blind side to separate pleuronectoids from soleoids and psettodids. In pleuronectoids, this nasal organ follows the migrating eye during metamorphosis. After metamorphosis, it remains near the dorsal edge of the head. This was interpreted as a specialization of pleuronectoids, except that this state does not occur in all Rhombosoleinae (i.e., nasal organs remain symmetrically placed). Thus, it is not a synapomorphy for the group, unless it can be shown that the nasal-organ symmetry in these rhombosoleines was secondarily derived from the asymmetrical state. We have not done a survey of nasal-organ symmetry, but incidental observations indicate that the supposed differences between these states (i.e., symmetrical vs

asymmetrical placement) are not as great as formerly thought. Loss of a truly dimorphic optic chiasma would appear to be the only synapomorphy proposed to date uniting the pleuronectoids. However, as previously discussed, a basically dimorphic or monomorphic optic chiasma has been demonstrated in very few pleuronectoid species.

One might expect that we are well informed about the interrelationships among pleuronectoids. Unfortunately, all of the past work has used the eclectic approach. Thus, scophthalmids and citharids have been related horizontally as primitive pleuronectoids, and bothids, paralichthyids, and pleuronectids as higher groups. Again, an important character here is the optic chiasma. Two states were recognized in pleuronectoids: (1) the primitive one (for pleuronectoids) where the nerve of the migrating eye is always dorsal regardless of eye position (i.e., the basically dimorphic state); and (2) the monomorphic state characteristic of "higher" pleuronectoids where the chiasma is fixed regardless of reversals. It has been assumed that all bothids, pleuronectids, and paralichthyids show the monomorphic state. Some evidence from other characters indicates this assumption is not valid.

Due mainly to the work of Amaoka (1969) and one of us (Ahlstrom), we have a good survey of the caudal-fin complex of pleuronectoids. Patterns of hypurals 1–4 are fairly well known. The distributions of these patterns call into question much of the current evolutionary model and classification of the Pleuronectoidei. There are five patterns of hypurals in this group as defined in the Regan-Norman model: Pattern 1 (Fig. 363 upper)—This is plesiomorphic for the order. Pattern 5 (Fig. 364 upper)—This pattern is limited to the Samarinae. We interpret this pattern as a synapomorphy uniting the samarines. Pattern 2 (Fig. 361)—Within pleuronectoids this pattern seems to be limited to Citharoides. It is apparently derived from pattern 1. Pattern 6 (Figs. 360, 364 middle and lower)—This is an apomorphic pattern which is very distinctive. We consider it homologous in pleuronectoids where it occurs and a synapomorphy uniting these groups. Again, we are calling this group the bothoids and it includes the Pleuronectinae, Paralichthyidae (except Tephrinectes and Thysanopsetta), Scophthalmidae, Bothidae (except Mancopsetta), and Brachypleura. Pattern 4 (Fig. 363 lower)—Within the pleuronectoids this pattern is limited to certain genera of Rhombosoleinae and Eucitharus. Based on other characters, the homology of pattern 4 between these groups is probably not true.

Citharidae.—Many character states used to define this family (Hubbs, 1945, 1946) are plesiomorphic for the order: (1) retention of pelvic spines; (2) retention of supramaxillae (Eucitharus and Citharoides); (3) urinary papilla close to anus; (4) no union of branchiostegals; (5) retention of vomerine teeth (Eucitharus, Brachypleura, Lepidoblepharon); and (6) retention of short-based ventral fins. Some are plesiomorphic for the Pleuronectoidei: (1) basically dimorphic optic chiasma (at least in Citharoides); (2) gill membranes showing some degree of union, but still fairly widely separated; and (3) loss of dorsal and anal-fin spines. The only possible character state proposed to date that could be interpreted as a synapomorphy for this family is the position of the anus on the ocular side. Although we have not examined many specimens for this character, it appears that deflection of the anus to the ocular side is probably slight. Amaoka (1972b) examined Brachypleura and attempted to redefine the Citharidae. However, he still showed no synapomorphies for the group.
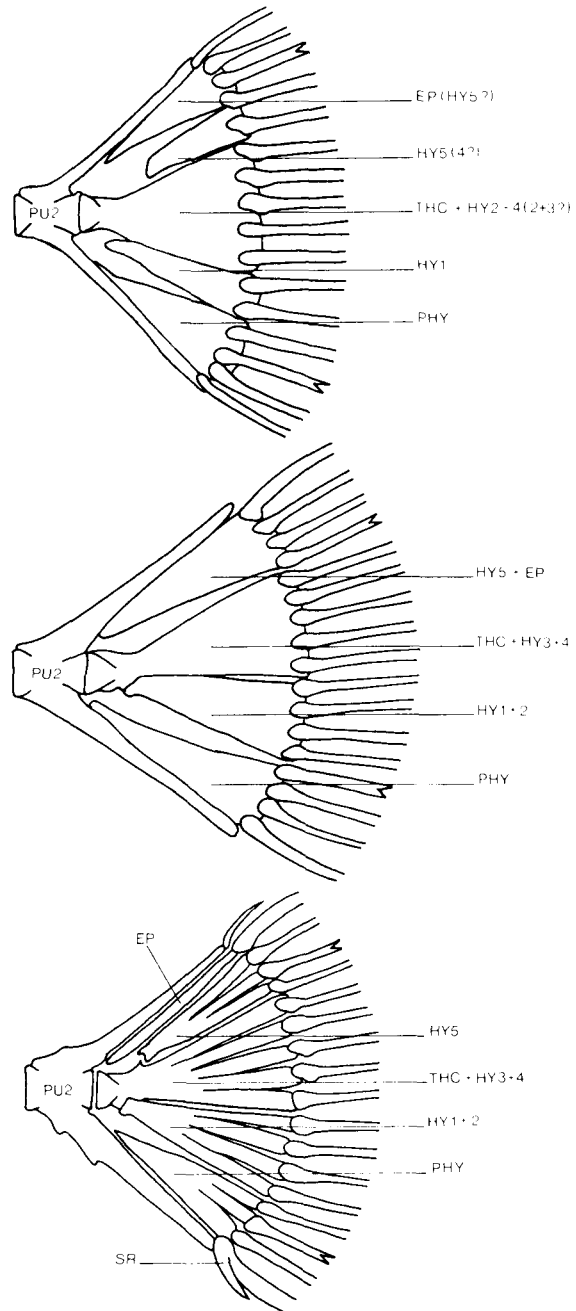

Fig. 364. Caudal skeleton of Samariscus triocellatus. Hypural pattern 5 (upper), caudal skeleton of Citharichthys macrops. Hypural pattern 6 (middle), and caudal skeleton of Hippoglossina oblonga. Hypural pattern 6 (lower). SR = splinter ray, other abbreviations as in Fig. 359. "V" on distal end of fin ray indicates dorsal- and ventralmost branched ray.

The family Citharidae as presently defined is a grade. Examination of the caudal osteology has shown two derived and one plesiomorphic pattern of hypurals. *Lepidoblepharon* shows pattern 1, which is plesiomorphic for the order. *Citharoides* shows pattern 2, a derived pattern (Fig. 361). This pattern could represent a state on a line leading toward pattern 6, which is shown by *Brachypleura*. *Eucitharus* shows pattern 4, which possibly developed independently in some rhombosoleines. The most obvious result of this is that *Brachypleura* belongs to the bothoid group, which shares the derived hypural pattern 6. In this interpretation, the character states shown by *Brachypleura* that are primitive for the order (e.g., vomerine teeth, ventral-fin spines) are also primitive for bothoids.

Scophthalmidae.—Based on ventral-fin morphology, the Scophthalmidae appear to be monophyletic. There are certain similarities in ventral-fin morphology between this family and the achirines, but these are probably superficial. Scophthalmids were previously thought to be closely related to and derived from the Citharidae (Hubbs, 1945). This hypothesis was based on certain symplesiomorphies, e.g., the low degree of fusion of the gill membranes and the presence of vomerine teeth. The Scophthalmidae show hypural pattern 6 and are thus members of the bothoid group.

Paralichthyidae.—Norman (1934) basically defined the Paralichthyinae (=Paralichthyidae with modifications) on external pelvic-fin morphology and vertebral structure (absence of transverse apophyses). The group was supposed to have the ventral fins nearly symmetrical in position and base lengths, or the ocular fin on the midventral line and its base slightly extended anteriorly. Symmetries in ventral-fin position and base lengths are plesiomorphic for the order and bothoids. Norman's paralichthyid genera with an ocular ventral fin on the midventral line and its base extended anteriorly are bothids (i.e., *Trichopsetta, Engyophrys, Taeniopsetta, Monolene, Perissias*).

Amaoka (1969) presented a more thorough, detailed definition of the family. However, many or most of the character states he used appear to be plesiomorphic for bothoid fishes (i.e., those defined by hypural pattern 6). A second limitation of Amaoka's work on this group is that it was limited to three genera (*Paralichthys, Pseudorhombus, Tarphops*). An important change in Norman's classification was made by Amaoka when he removed *Taeniopsetta* from the Paralichthyidae and placed it in the Bothidae. Hensley (1977) and Futch (1977) did the same for *Monolene, Engyophrys,* and *Trichopsetta.*

We have now examined some characters in the remaining Paralichthyidae, and additional changes are required in the composition of this group. In a survey of caudal-fin structure, it was found that *Thysanopsetta* and *Tephrinectes* show the most primitive type of hypural pattern (1; Fig. 363 upper). These two genera are much more primitive than expressed in the current classification and definitely do not belong to the bothoid group.

Within the remaining Paralichthyidae another group is discernable. This is composed of *Cyclopsetta, Syacium, Citharichthys,* and *Etropus,* i.e., the *Cyclopsetta* group. States for two complexes of characters, ventral-fin morphology and urinary-papilla position, are unique to this group and interpreted as synapomorphic. Arrangement of caudal-fin rays in the *Cyclopsetta* group is also unique and probably apomorphic (Fig. 364 middle). All species have 17 caudal rays, none of which are

supported by preural, neural or haemal spines. It should also be noted that the fifth hypural has fused with an epural. This fusion has been observed in larval development (Tucker, 1982; Ahlstrom, pers. observ.). However, fusion of the fifth hypural and one or more epurals has apparently occurred several times in pleuronectiforms, possibly including the bothoids (e.g., see Fig. 360). A detailed analysis of relationships between the *Cyclopsetta* group and other bothoids is not possible here. However, some character states may indicate a close relationship with bothids (absence of first neural spine, presence of vertebral transverse apophyses).

Amaoka (1969) and one of us (Ahlstrom) recognized another group within the Paralichthyidae composed of *Pseudorhombus, Tarphops,* and *Cephalopsetta,* i.e., the *Pseudorhombus* group. We interpret these genera as more specialized in certain characters than most other members of the family. Species of this group usually have a total caudal ray count of 17, the epural is fused to the fifth hypural, and they lack a splinter ray on the ventralmost caudal-fin ray. With the exceptions noted above (the primitive non-bothoid genera *Tephrinectes* and *Thysanopsetta* and the *Cyclopsetta* group), the remaining paralichthyids of the Regan-Norman classification (what we are calling the *Paralichthys* group) have the apparently plesiomorphic states of 18 caudal rays, at least one free epural (except in one species of *Hippoglossina* (Sumida et al., 1979)), and a splinter ray on the ventralmost caudal-fin ray (Fig. 364 lower). The splinter ray is probably a remnant of a ray lost through fusion with an adjacent ray (Okiyama, 1974). The *Pseudorhombus* group may be definable by synapomorphies but a detailed analysis has not been done.

After removal of the bothids (*Trichopsetta, Engyophrys, Taeniopsetta, Monolene, Perissias*) and the primitive non-bothoid genera (*Tephrinectes, Thysanopsetta*), recognition of the *Cyclopsetta* group as monophyletic, and recognition of the *Pseudorhombus* group as possibly monophyletic, few of the original paralichthyid genera remain. We have been referring to these as the *Paralichthys* group (*Ancylopsetta, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Verecundum,* and *Xystreurys*). At least most of the character states known for these remaining genera are plesiomorphic for the order (e.g., symmetrical ventral-fin states) or for bothoids (e.g., usual presence of at least one free epural). The *Paralichthys* group is probably not monophyletic.

Bothidae.—Norman (1934) defined the Bothinae (=Bothidae with modifications) on the basis of a high degree of ventral-fin asymmetry and the presence of vertebral transverse apophyses. The ocular ventral fin was said to be on the midventral line with its base extending anteriorly to the urohyal. Norman excluded *Taeniopsetta, Engyophrys, Trichopsetta, Monolene,* and *Perissias* from this group because the base of the ocular ventral fin, although on the midventral line and somewhat longer than that of the blind side, does not extend to the urohyal.

Amaoka (1969) examined many bothid genera and redefined the family using more characters. Most of the characters stressed by Amaoka have now been examined in other bothoids. These are discussed below:

Ventral-fin asymmetry.—In bothids the ocular fin base is on the midventral line, elongated, and has its origin anteriorly placed relative to the base of the blind fin. Within the bothoids this combination of states appears to be derived and unique.

Preorbital on blind side.—This bone is absent in the Bothidae. It appears to be present in all other bothoids (Pleuronectinae not examined for this character). Based on this comparison, we interpret the loss of this bone a derived state within the bothoids defining the family Bothidae.

Infraorbital bones of the ocular side.—All bothids have an ocular preorbital bone but lack the remainder of the series. The presence or absence of the ocular preorbital has not been surveyed in most bothoid groups. However, an ocular infraorbital lateral line is present in most bothoids. In addition to the Bothidae, it is missing in *Brachypleura* and the *Cyclopsetta* group.

Intermuscular bones.—We interpret the presence of at least two of the series of these bones (myorhabdoi) as a derived state unique to and defining the Bothidae.

First neural spine.—Although the first neural arch is present, the neural spine is missing in the Bothidae. It is present in all other bothoids except the *Cyclopsetta* group.

Vertebral transverse apophyses.—All bothids have two pairs of transverse apophyses on most vertebrae. As previously discussed, how to interpret these on the pleuronectiform level and within the bothoid group is questionable. Within the bothoids well-developed and very similar structures occur only in the Bothidae and Scophthalmidae. Very small transverse apophyses also occur in the *Cyclopsetta* group.

Based on these characters, the Bothidae appear to be monophyletic and definable by synapomorphies in at least three characters or complexes: (1) loss of the preorbital on the blind side; (2) presence of myorhabdoi; and (3) asymmetrical states of ventral-fin morphology.

Since Amaoka's (1969) work, we have examined the remaining genera not examined by him that have been considered bothids (i.e., *Grammatobothus, Lophonectes, Pelecanichthys, Mancopsetta*). All of these except *Mancopsetta* are bothids. *Mancopsetta* exhibits the following character states: (1) hypural pattern 1, i.e., the most primitive type; (2) presence of pleural and epipleural ribs, but no myorhabdoi or other intermuscular bones in the caudal region; (3) at least one free epural (none in adult bothids); (4) anus on midventral line (clearly on blind side in bothids); (5) no vertebral transverse apophyses; and (6) seven rays in the ocular ventral fin, 5–7 in that of the blind side (six in both fins in bothids). These are all characters in which *Mancopsetta* differs from the Bothidae. Due to the primitive hypural pattern, it is not a bothoid (see Rhombosoleinae).

Amaoka (1969) analyzed intergeneric relationships of Japanese bothids. However, his analysis was eclectic and did not include all genera (i.e., *Engyophrys, Trichopsetta, Monolene, Perissias, Grammatobothus, Lophonectes,* and *Pelecanichthys* were not examined). He recognized two subfamilies, the Taeniopsettinae and Bothinae. He erected the first subfamily for *Taeniopsetta.* Hensley (1977), Futch (1977), Evseenko (1977, 1981), and Amaoka (1979) implied that *Engyophrys* and *Trichopsetta* should be included in the Taeniopsettinae. This was done on the basis of larval characters and ventral-fin morphology. Most of the states used to define the Taeniopsettinae were considered by Amaoka (1969) to be plesiomorphic at the family level. Three characters were emphasized: (1) degree of anterior

extension of the base of the ocular ventral fin; (2) shape of the ventral (sciatic) area of the urohyal; and (3) number of suborbital bones on the blind side. In the taeniopsettines, the origin of the blind ventral fin is at the same transverse level as the second ray of the ocular ventral fin, i.e., the base of the ocular fin is only slightly elongated. In the Bothinae, extension of the base of the ocular fin is greater and the origin of the blind fin is on the same transverse level as the third or fourth ray of the ocular fin. Obviously, the taeniopsettine state here is the more plesiomorphic. *Engyophrys, Trichopsetta, Monolene,* and *Perissias* show this state. *Taeniopsetta* has a broad, truncate margin on the sciatic part of the urohyal. In bothines, this area of the urohyal is pointed. Amaoka (1969) clearly showed that the plesiomorphic state for bothoids is closer to the condition shown in taeniopsettines. *Engyophrys, Trichopsetta,* and *Perissias* show the taeniopsettine condition. *Monolene* the bothine state. Amaoka (1969) noted an apparent trend among bothoids in reduction of the number of suborbital bones of the blind side. This reduction may have occurred in several bothoid groups and interpretation of this character is not clear. Thus, infraorbital counts for bothoids are as follows (preorbital + suborbitals): Scophthalmidae 1 + 5; *Brachypleura* 1 + 0; *Paralichthys* group 1 + 4–5; *Pseudorhombus* group 1 + 5–7; *Cyclopsetta* group 1 + 5–6; and Bothidae 0 + 3–5. Pleuronectines were not examined for this character. The most common count in bothoids other than bothids is 1 + 5–7. Thus, there is some evidence that the basal or plesiomorphic count for bothids may be five suborbitals on the blind side. Among bothids this count apparently occurs only in *Taeniopsetta* and *Pelecanichthys. Engyophrys, Trichopsetta, Perissias,* and *Monolene* have three suborbitals on the blind side. In summary, there is good evidence, at least for the first two characters discussed above, that the Taeniopsettinae show states that are plesiomorphic for the family and may not be monophyletic.

Pleuronectidae.—Norman (1934) considered this family to be one of the "higher" flatfish groups, i.e., those with a monomorphic optic chiasma. Hubbs (1945) basically followed this interpretation, but showed that two of Norman's pleuronectid genera, *Brachypleura* and *Lepidoblepharon,* possessed some primitive states not shown in other pleuronectids. These two genera were removed by Hubbs and placed in his family Citharidae.

Norman (1934) defined the Pleuronectidae as being dextral and having eggs without oil globules. Basic to his concept of this family were the assumptions that all members were monomorphic in regard to the optic chiasma and that nearly all species were discriminately dextral. He divided the family into five subfamilies. All members of the Poecilopsettinae, Paralichthodinae, Samarinae, and Rhombosoleinae, as presently interpreted, are discriminately dextral, i.e., sinistral individuals occur so rarely in any one species that they can be considered anomalies. Most species of Pleuronectinae are also discriminately dextral. The few exceptions have probably returned to indiscriminate ocular asymmetry secondarily (Hubbs and Hubbs, 1945). We have no reason to doubt Norman's or Hubbs' assumption that the Pleuronectinae have a monomorphic optic chiasma. However, as previously discussed, there are no data showing this for the other pleuronectid subfamilies. Uniting these groups in the family Pleuronectidae appears to have rested only on ocular asymmetry. We have surveyed these subfamilies for various

characters and are confident that the Pleuronectidae as currently defined are not monophyletic. In fact, four of the pleuronectid subfamilies are not bothoids as we define the group. However, what the true relationships of these groups are is unknown. We discuss these subfamilies individually:

Poecilopsettinae.—We have examined radiographs of specimens of *Poecilopsetta* and *Nematops*. These genera have hypural pattern 1, at least one free epural, 20 caudal rays, and what appears to be a haemal-arch remnant on the parhypural. The caudal structure here is primitive compared to the bothoids and these fishes do not belong to that group. Poecilopsettines are poorly known and character states defining the group or relating it to others have not been investigated.

Paralichthodinae.—*Paralichthodes algoensis* has hypural pattern 1 (Ahlstrom, pers. observ.) and does not belong to the bothoid group. Its relationships to other groups are unknown.

Samarinae.—Since Hubbs' (1945) removal of *Brachypleura* and *Lepidoblepharon* from this group, it has been composed of *Samaris* and *Samariscus*. We have not done a detailed study of these genera, but some characters we have examined are worthy of note: (1) These genera show a unique hypural pattern (5; Fig. 364 upper). We interpret this pattern as derived relative to pattern 1 and as indicative that the group is monophyletic. Using this pattern to relate the group is more difficult; however, one of us (Ahlstrom) noted that in late-stage larvae of *Samariscus*, hypural pattern 1 is present, and fusions resulting in pattern 5 must occur very late in development. This is evidence that pattern 5 may have evolved directly from pattern 1 and does not represent a modification of the bothoid pattern 6. (2) Samarines are the only pleuronectiforms known other than the Bothidae to have intermuscular bones, although they do not have the two series of myorhabdoi as found in bothids. We have not done a detailed study of these bones in samarines, but they appear very similar to the epimerals, epicentrals, and hypomerals of bothids. (3) Samarines, cynoglossids, and soleines have an anterior pair of well-developed transverse apophyses on many vertebrae. Two pairs of these structures are found in the Bothidae and Scophthalmidae. (4) The Samarinae, Soleoidei, and *Mancopsetta* lack postcleithra, at least in adults. How to interpret these last three character states is open to question. Are three of the series of intermuscular bones homologous in samarines and bothids? Are the anterior vertebral transverse apophyses homologous between all of the groups? Do some of these character states indicate a close relationship between samarines and some soleoids (i.e., cynoglossids and soleines)? Our tentative hypothesis is that the samarines are a line that is at least independent from the bothoids. Here we are obviously stressing caudal characters. The corollary of this is that we are interpreting similarities between samarines and bothoids in intermuscular bones and vertebral transverse apophyses as homoplasies.

Rhombosoleinae.—The main character states used by Norman (1926, 1934) to define this subfamily were the high degree of asymmetry in the ventral fins and the absence of pectoral radials. The ocular ventral fin is on the midventral line and its base is considerably extended. The blind ventral fin is short based or missing. Another interesting characteristic of this group is that

several genera show high numbers of fin rays in the ocular ventral fin. There is a great deal of morphological diversity in rhombosoleines. Some genera appear fairly generalized in many characters (*Oncopterus, Psammodiscus, Rhombosolea, Azygopus,* and *Pelotretis*); others are more specialized (*Colistium, Peltorhamphus,* and *Ammotretis*). Many of the specializations in the latter genera are similar to those in some soleoids. This has been interpreted as parallel evolution (Norman, 1934; Hubbs, 1945). Norman apparently had some doubts about aligning this group with the Pleuronectinae. He realized that Parker's (1903) examination of one specimen of *Oncopterus darwinii* in his survey of optic chiasmata did not prove the group to be monomorphic in this character. This group has still not been studied in detail. It may be monophyletic, but its relationship to other flatfishes is unknown.

We have examined the caudal skeleton of all rhombosoleine genera except *Psammodiscus*. They show hypural patterns 1 and 4 (Fig. 363 upper and lower). Assuming the group is monophyletic, there are two implications here: (1) The primitive pleuronectiform hypural pattern 1 is also plesiomorphic for the Rhombosoleinae, and the derived pattern 4 arose within the group independently from the same pattern in the Soleinae, Cynoglossidae, and *Eucitharus*. (2) The Rhombosoleinae are not bothoids and should not be aligned with the Pleuronectinae.

The possibility has recently become apparent that *Mancopsetta* may be most closely related to the Rhombosoleinae. All known specimens of *Mancopsetta* are sinistral and it has been considered a bothid. However, it shares certain character states with at least some rhombosoleines. This genus has ventral-fin ray counts of 7 on the ocular side and 5–7 on the blind side. Although not strictly limited to the rhombosoleines, these high counts, at least in the fin of the ocular side, are characteristic of at least four rhombosoleine genera. The eyes are densely scaled in *Mancopsetta* and in *Azygopus* and *Pelotretis*. However, scaled eyes are found in some genera of other groups also (e.g., some pleuronectines). Andriashev (1960) and Penrith (1965) have both remarked on a fleshy lip-like structure which overhangs the anterior end of the upper jaw in *Mancopsetta*. One of the soleoid-type characteristics exhibited by the more specialized rhombosoleines is the dorsal fin originating in a rostral hook that overhangs the mouth. In the more generalized genera, there is no rostral hook and the dorsal fin originates at some posterior position. In at least one of these generalized genera (*Azygopus,* the only one examined for this character) there is a fleshy structure (possibly a precursor to the rostral hook?) overhanging the anterior end of the upper jaw which is very similar to that in *Mancopsetta*. Obviously more comparative work needs to be done here. However, it is possible that *Mancopsetta* and the Rhombosoleinae may form a monophyletic group with an indiscriminately dextral or sinistral common ancestor.

Pleuronectinae.—Norman (1934) stressed two character states in defining this subfamily: (1) lateral line well developed on both sides of the body; and (2) olfactory laminae parallel (except in *Atheresthes*), without rachis. A well-developed lateral line on both sides of the body is plesiomorphic for the order and bothoids. We have not examined olfactory laminae or attempted to analyze distributions of states for the character.

We have shown that the Pleuronectidae is probably not monophyletic, due to the inclusion of the four non-bothoid subfamilies. The subfamily Pleuronectinae is the only bothoid group

in Norman's Pleuronectidae. Members of this subfamily are dextral or apparently secondarily indiscriminate (Hubbs and Hubbs, 1945). They apparently have a monomorphic optic chiasma. However, most character states which species of this subfamily share appear to be plesiomorphic for the order or bothoids, e.g., symmetrical or nearly symmetrical ventral-fin placement and fin-base lengths, anus on or close to the mid-ventral line. We have examined the caudal osteology of about half of the pleuronectine genera. All have the bothoid hypural pattern (6) and one or possibly two free epurals. We have found no synapomorphies in the caudal fin for this group.

Larval characters

In the previous discussion, many doubts were raised concerning pleuronectiform interrelationships as expressed in the Regan-Norman model. Unfortunately, larvae for many of these groups are unknown. A second problem is that surveys for many characters where larvae are known have been incomplete and inconsistent. Most descriptive larval research has dealt with characters useful for identification and has not involved comparative work of sufficient detail to determine homologous states. Such work is sorely needed before distributions of homologous states can be determined for many characters.

Below is a list and discussion of certain characters and complexes. Selection of these was based mainly on the amount of available information.

Preopercular spines.—The presence of preopercular spines appears to be plesiomorphic for the order and some pleuronectiform groups. This is based on the observation that the state is widespread among flatfish and percomorph larvae.

Neurocranial spines.—Spines occur in some regions of the neurocranium in some pleuronectiform larvae. Most of these are said to occur in the otic or frontal regions. However, determining homologies here is difficult due to a general lack of detailed osteological study of the bones carrying these spines. Spines in the otic and frontal regions appear to be of two types. One of these is where spines are associated with neurocranial ridge systems. These are known for larvae of achirines (Houde et al., 1970; Futch et al., 1972), some scophthalmids (Jones, 1972), and some pleuronectines (Pertseva-Ostroumova, 1961). In the second type, spines occur singly or in small groups but are not part of a pronounced ridge. These have been said to occur on various bones of the otic region (epiotics, autosphenotics, autopterotics) or on the frontals. Tucker (1982) was not able to determine the origin of such spines in the larvae of *Citharichthys* and *Etropus* and referred to them as frontal-sphenotic spines. Although thorough studies are needed before neurocranial spines can be used to infer or test pleuronectiform interrelationships, certain patterns are noteworthy: (1) Spines that are not part of some pronounced ridge system appear to be limited to some bothoids (some species of the *Paralichthys* group, *Cyclopsetta* group, *Pseudorhombus* group, Scophthalmidae, Pleuronectinae, and Bothidae). (2) Within the Bothidae, only the larvae of *Engyophrys*, *Taeniopsetta*, and *Trichopsetta* (Taeniopsettinae; larvae of *Perissias* are unknown) are known to have otic spines (Amaoka, 1979). In these genera, the spines are on the same bones (epiotics and autosphenotics) and are probably homologous. (3) Within the *Cyclopsetta* group, a relatively well-de-

veloped otic or frontal spine occurs in *Cyclopsetta* and *Syacium* (Aboussouan, 1968b; Gutherz, 1970; Ahlstrom, 1971; Futch and Hoff, 1971; Evseenko, 1979), while series of small spines occur in *Citharichthys* and *Etropus* (Tucker, 1982).

Urohyal, basipterygial, and cleithral spines.—Spines on these bones are limited to certain genera of the Bothidae. Thus, they are considered apomorphic at the pleuronectiform and bothoid levels of universality.

Early-forming elongated dorsal-fin rays.—The presence of elongated dorsal-fin rays in pleuronectiform larvae has been extensively and justifiably used for identification purposes. However, use of these structures for phylogenetic interpretations is presently difficult and generally premature. There are several reasons for this. Surveys for these characters are inadequate, since larvae for many groups are unknown. Characters and character states have never been adequately defined to allow proper comparisons to be made. The only pattern here that is clear and phylogenetically interpretable is the state in bothids. All species of this family for which larvae are known show elongation of only the second dorsal-fin ray. This state is known only in this family and thus appears to be apomorphic within the order and bothoids.

Early-forming elongated ventral-fin rays.—Ocular ventral-fin rays which are elongated relative to those of the blind side are limited to certain species of the *Cyclopsetta* group. Due to the restricted occurrence of these, they are probably apomorphic for the order and bothoids. However, within the *Cyclopsetta* group, the distribution of elongated ocular ventral-fin rays does not conform to generic groups based on adult morphology. At least one species of cynoglossid is known to have elongated rays in the ventral fin of the blind side (Kyle, 1913; Padoa, 1956k).

Size at metamorphosis.—Most flatfishes metamorphose in the size range of ca. 10–25 mm. When size at metamorphosis has been discussed in regard to evolution in pleuronectiforms, the usual hypothesis has been that certain species and groups have evolved mechanisms for prolonging larval life for greater dispersal, and others have actually shortened larval life for recruitment to limited habitats (Amaoka, 1979; Moser, 1981). There are several implications in this hypothesis that are relevant here: (1) There is some size range for transformation that is plesiomorphic for the order. This is usually implied to be ca. 10–25 mm because most pleuronectiforms metamorphose in this range. (2) Metamorphosis at markedly smaller (e.g., Achirinae) or larger (e.g., Bothidae, some pleuronectines) sizes are derived states. (3) According to the Regan-Norman model, prolonged larval development must have developed independently in several lines. Although metamorphosis at large sizes is most common in bothids, it is also known for some Pleuronectinae, the Poecilopsettinae, some species of the *Cyclopsetta* group, and some cynoglossids.

Size at metamorphosis is an important character for larval identification, but its use for inferring phylogenetic relationships in most instances is premature. Exceptions may exist in the Bothidae, where the extremely long premetamorphic lengths exhibited by some genera are probably apomorphic within the family and can be used for phylogenetic information.

Relative time of caudal-fin formation. — In most known larvae of flatfishes and other teleosts, formation of the caudal fin precedes or occurs with that of the dorsal and anal fins. The only exceptions known in pleuronectiforms are the cynoglossids. In this family, the caudal fin does not develop until the dorsal and anal fins are nearly completely developed. This pattern of development is considered apomorphic in pleuronectiforms.

Eye migration and dorsal-fin position at metamorphosis. — Eye migration has been observed in some flatfish groups. In the Psettodidae, Pleuronectinae, Paralichthyidae (excluding the *Cyclopsetta* group), Scophthalmidae, and apparently some Soleidae, the first ray of the dorsal fin is above or posterior to the eyes. At metamorphosis, the migrating eye crosses anterior to the dorsal-fin origin. These types of eye migration and dorsal-fin position appear to be plesiomorphic for the order. Several derived states for these characters occur. In at least one species of cynoglossid, a fleshy rostral beak is formed anterior to the dorsal-fin origin. Eye migration takes place between the rostral beak and the interorbital region. In some soleids, the dorsal-fin origin projects above the snout and the eye migrates between this projection and the neurocranium. In the Bothidae, the dorsal fin is anterior to the eye and attached to the ethmoid region. During migration, the eye goes between the base of the dorsal fin and the ethmoid region. A path for the migrating eye is created by detachment of the anterior section of the dorsal fin from the ethmoid region so that a narrow slit is formed, or some tissue in the path of the migrating eye is absorbed. A very similar type of eye migration occurs in some species of the *Cyclopsetta* group. However, in other members of this group, the eye migrates around the dorsal-fin origin (Gutherz, 1970; Tucker, 1982).

Phylogenetic information provided by larval characters

Although larvae of some critical groups are unknown or poorly known, some comments about phylogenetic relationships can be made in regard to groups where our knowledge is on a higher level.

Bothoids. — Spines in the otic or frontal regions of the neurocranium which are isolated or in small clusters appear to be limited to various groups of bothoids. If these spines prove to be homologous between these groups, they may be apomorphic within the order. In this interpretation, they would be primitive for bothoids and lost in various lines.

Paralichthyidae. — As discussed in the section on adult characters, this family as currently interpreted is polyphyletic due to the inclusion of *Tephrinectes* and *Thysanopsetta.* We do not consider these genera bothoids as defined by the caudal-fin complex. Their larvae are unknown.

We have interpreted the *Cyclopsetta* group as monophyletic based on some adult character states which are probably apomorphic. Although larvae of this group show certain states which appear to be apomorphic within bothoids (e.g., elongated left ventral-fin rays), not all species in this group show these.

The *Pseudorhombus* group is possibly definable by adult synapomorphies. In larvae of this group, we see no character states that are presently interpretable with certainty as synapomorphies.

In examining adult characters of the *Paralichthys* group, it appeared likely that this group had no synapomorphies. Larvae

tend to support this. They show the following character states which appear to be plesiomorphic for the order: (1) presence of preopercular spines; (2) origin of the dorsal fin behind the eyes; (3) metamorphosis in a size range of 7.5–14.2 mm; and (4) eye migration anterior to the dorsal fin. In addition, at least some species show the following states which may prove to be plesiomorphic at least within the bothoids: (1) four or five elongated, early-forming dorsal-fin rays; and (2) presence of otic spines.

Bothidae. — With the exclusion of *Mancopsetta* and inclusion of *Perissias,* this family is definable by adult synapomorphies. Larvae of the Bothidae are probably better known than for any other family of flatfishes. However, larvae of many genera are still unknown (i.e., *Parabothus, Asterorhombus, Tosarhombus, Neolaeops, Japonolaeops,* and *Perissias*). Amaoka (1979) reviewed larval characters of most genera for which larvae are known. Known bothid larvae show the following character states which are interpreted as synapomorphies: (1) metamorphosis at a relatively large size (ca. 15–120 mm); (2) eye migration below the dorsal fin; (3) dorsal-fin origin anterior to eyes just prior to metamorphosis; (4) elongated, early-forming second dorsal-fin ray; and (5) lack of preopercular spines.

Larvae of some bothid genera have various combinations of otic-region, urohyal, cleithral, and basipterygial spines. It is tempting to use the presence of these spines to define bothid groups, and therefore, assume that they are apomorphic within the family. Spines in the otic region within the Bothidae are limited to the Taeniopsettinae as presently defined. However, spines in this region occur in other bothoid groups. Although sufficient comparative osteological work has not been done to show that these spines are homologous between taeniopsettines and other bothoids, use of these spines to infer close relationships between *Engyophrys, Taeniopsetta,* and *Trichopsetta* is questionable. Urohyal, cleithral, and basipterygial spines are known only from larvae of nine bothid genera. They occur in various combinations inter- and intragenerically. Amaoka (1969) presented a model of intergeneric relationships for Japanese bothids based on adult characters. Occurrence of these larval spines is scattered among the bothid lines hypothesized by Amaoka. This could indicate two possibilities: (1) the spines are apomorphic within the family, and Amaoka's model is incorrect; or (2) Amaoka's model is correct and the spines are plesiomorphic within the family and have been lost in several lines. Two major problems exist with Amaoka's phylogeny based on adult characters; it was constructed using eclectic methods and it did not include all genera. Interpretation of urohyal, basipterygial, and cleithral spines should await a cladistic analysis of bothid interrelationships based on adult characters.

Pleuronectidae. — Based on adult characters, we interpret this family as polyphyletic. Larvae of the four non-bothoid subfamilies are poorly known, and hence, of little aid in determining relationships of these groups. However, there are certain similarities in general body morphology between the few known samarine and poecilopsettine larvae. In regard to the Pleuronectinae, many adult states that are shared are plesiomorphic for pleuronectiforms or bothoids. This also appears to be true for most larval characters. The position of the dorsal-fin origin (posterior to the eyes) and the type of eye migration (anterior to the dorsal-fin origin) are plesiomorphic for the order. Some pleuronectine larvae have preopercular spines, which again, are

probably plesiomorphic for flatfishes. Some genera show spines in the otic region of the neurocranium; these are possibly plesiomorphic for bothoids. All known pleuronectine larvae lack elongated dorsal-fin rays. However, this state is not limited to this group and a phylogenetic interpretation of it would be premature. In short, at present, we know of no character states that are unique to pleuronectine larvae or that can confidently be interpreted as apomorphic.

Egg characters

Except in certain groups, eggs of flatfishes are still too poorly known to be of much value in phylogenetic studies. One character of pleuronectiform eggs was used by Regan (1910) and Norman (1934) to interpret phylogeny, the presence of one oil globule in bothid eggs to separate them from those of pleuronectids which lack oil globules. We now have more information about the occurrence of oil globules in flatfish eggs, and the distribution of these character states is not exactly that predicted by the Regan-Norman model (preceding article, this volume). The obvious pattern here is that bothoids have 0–1 and soleoids, rhombosoleines, and *Mancopsetta* multiple oil globules. There are published exceptions to this. Watson and Leis (1974) identified three types of eggs with multiple oil globules as those of bothids. However, these authors expressed some doubt about the identifications of at least two of these egg types. These eggs are probably some other group (poecilopsettines or samarines?). Brownell (1979) identified some eggs which lacked oil globules as the soleid *Heteromycteris capensis*. This is the only soleid we are aware of that lacks multiple oil globules.

It is probably premature to use the oil-globule character for phylogenetic information until eggs from other groups are known. However, it is interesting and possibly significant that the soleoids, rhombosoleines, and *Mancopsetta* are so sharply separable from the bothoids in this character. One oil globule appears to be the most common state in the eggs of percomorph fishes (based on accounts in Watson and Leis, 1974; Russell, 1976; Fritzsche, 1978; Hardy, 1978b; Johnson, 1978; and Brownell, 1979). This may indicate that this state is plesiomorphic for pleuronectiforms. Corollaries of this would be that oil globules were lost in most pleuronectines, and multiple oil globules developed in a line leading to the soleoids, rhombosoleines, and *Mancopsetta*.

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LITERATURE CITED

ABE, T. 1954. New, rare or uncommon fishes from Japanese waters. IV. Records of rare fishes of the families Lophotidae, Nomeidae, Icosteidae. Jpn. J. Ichthyol. 3:90–95.

———. 1957. Notes on fishes from the stomachs of whales taken in the Antarctic. Sci. Rep. Whales Res. Inst. (Tokyo) No. 12:225–233.

———, AND S. KAJI. 1972. A record of *Oreosoma atlanticum* (Oreosomatidae, Zeiformes, Teleostei) from Tasman Sea. U.O. No. 8:5–7.

ABLE, K. W. 1984. Variation in spawning site preference of the mummichog, *Fundulus heteroclitus.* Copeia 1984:522–525.

———. MS. Comments on the distribution and reproductive seasonality of snailfishes and lumpfishes in the estuary and Gulf of St. Lawrence.

———, J. D. FELLEY AND D. POWERS. MS. Taxonomy of Bermuda *Fundulus* (Pisces: Fundulidae).

———, D. F. MARKLE AND M. P. FAHAY. MS. Development of larval liparidine snailfishes from the western North Atlantic.

———, AND D. E. McALLISTER. 1980. Revision of the snailfish genus *Liparis* from Arctic Canada. Can. Bull. Fish. Aquat. Sci. No. 208.

———, AND J. A. MUSICK. 1976. Life history, ecology and behavior of *Liparis inquilinus* (Pisces: Cyclopteridae) associated with the sea scallop, *Placopecten magellanicus.* Fish. Bull. U.S. 74:409–421.

ABOUSSOUAN, A. 1964. Contribution à l'étude des oeufs et larves pélagiques des poissons téléostéens dans la Golfe de Marseille. Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars. 32(48):87–173.

———. 1965. Oeufs et larves de téléostéens de l'ouest africain. 1. *Acanthurus monroviae* Steind. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 27:1183–1187.

———. 1966a. Sur quelques larves pélagiques de téléostéens récoltées à Tulear. Recl. Trav. Stn. Mar. Endoume-Mars. Suppl. 5:149–164.

———. 1966b. Sur quelques larves pélagiques de téléostéens récoltées à Tulear. Cent. Oceanogr. Fac. Sci. Mars. 1966:147–159.

———. 1966c. Oeufs et larves de téléostéens de l'ouest africain. III. Larves de *Monacanthus hispidus* (L.) et de *Balistes forcipatus* Gm. Bull. Inst. Fondam. Afr. Noire, Ser. A 28:276–282.

———. 1966d. Oeufs et larves de téléostéens de l'ouest africain. IV. *Galeoides polydactylus* (Vahl) [Polynemidae]. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 28:1037–1040.

———. 1967. Oeufs et larves de téléostéens de l'ouest africain. V. *Caranx rhonchus* Geoffroy Saint-Hilaire (Carangidae). Affinités avec *Trachurus trecae* Cadenat. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 29:1039–1050.

———. 1968a. Oeufs et larves de téléostéens de l'ouest africain. VI. Larves de *Chloroscombrus chrysurus* (Linné) et de *Blepharius crinitis* (Mitchill) (Carangidae). Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 30:226–237.

———. 1968b. Oeufs et larves de téléostéens de l'ouest africain VII. Larves de *Syacium guineensis* (Blkr.) [Bothidae]. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 30:1188–1197.

———. 1968c. Oeufs et larves de téléostéens de l'ouest africain. VIII. Larves de *Bregmaceros macclellandi* Thompson (Bregmacerotidae). Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 30:1590–1602.

———. 1969. Sur une petite collection de larves de téléostéens récoltée au large du Brésil (Campagne "Calypso" 1962). Vie Milieu, Ser. A Biol. Mar. 20:595–610.

———. 1972a. Oeufs et larves de téléostéens de l'ouest africain. X. Larves d'Ophidioidei (*Oligopus, Ophidion* et *Carapus*) et de Percoidei (*Pseudupeneus*). Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 34:169–178.

———. 1972b. Oeufs et larves de téléostéens de l'ouest africain. XI. Larves serraniformes. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 34:485–502.

———. 1972c. Oeufs et larves de téléostéens de l'ouest africain. XII. Les larves d'Heterosomata récoltées aux environs de l'ile de Gorée (Sénégal). Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 34:974–1003.

———. 1975. Oeufs et larves de téléostéens de l'ouest africain. XIII. Contribution à l'identification des larves de Carangidae. Bull. Inst. Fondam. Afr. Noire, Ser. A Sci. Nat. 37:899–938.

———. 1980. Description d'une larve geante "rubaniforme," attribuée au genre *Brotulataenia* (Pisces, Gadiformes, Ophidioidei, Ophidiidae) et récoltée à l'est des nouvelles Hebrides. Cybium, 3rd Ser., (10):51–64.

ADAMS, J. A. 1960. A contribution to the biology and postlarval development of the sargassum fish, *Histrio histrio* (Linnaeus), with a discussion of the *Sargassum* complex. Bull. Mar. Sci. Gulf Caribb. 10:55–82.

AGASSIZ, A. 1882. On the young stages of some osseous fishes. Proc. Am. Acad. Arts Sci. 16(Pt. 3):271–303.

———, AND C. O. WHITMAN. 1885. The development of osseous fishes. I. The pelagic stages of young fishes. Mem. Mus. Comp. Zool. Harv. 14(1):1–56.

AHLSTROM, E. H. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl. Serv. SSRF 23.

———. 1956. Eggs and larvae of anchovy, jack mackerel, and Pacific mackerel, p. 33–42. *In:* Progress Rep., Calif. Coop. Oceanic Fish. Invest., 1 April 1955–30 June 1956, Sacramento.

———. 1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 10:31–52.

———. 1968. Review of "Development of fishes of the Chesapeake Bay region, an atlas of egg, larval and juvenile stages. Part I". Copeia 1968:648–651.

———. 1969. Remarkable movements of oil globules in eggs of bathylagid smelts during embryonic development. J. Mar. Biol. Assoc. India 11:206–217.

———. 1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fish. Bull. U.S. 69:3–77.

———. 1972a. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fish. Bull. U.S. 70:1153–1242.

———. 1972b. Distributional atlas of fish larvae in the California Current region: six common mesopelagic fishes. Calif. Coop. Oceanic Fish. Invest. Atlas 17.

———. 1974. The diverse patterns of metamorphosis in gonostomatid fishes - an aid to classification, p. 659–674. *In:* The early life history of fish. J. H. S. Blaxter (ed.). Springer-Verlag, Berlin.

———. 1976. Maintenance of quality in fish eggs and larvae collected during plankton hauls, p. 313–318. *In:* Zooplankton fixation and preservation. H. F. Steedman (ed.). Unesco Press, Paris.

———, AND O. P. BALL. 1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. Fish. Bull. U.S. 56:209–245.

———, J. L. BUTLER AND B. Y. SUMIDA. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26:285–402.

———, AND R. C. COUNTS. 1955. Eggs and larvae of the Pacific hake *Merluccius productus.* Fish. Bull. U.S. 56:295–329.

———, AND ———. 1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. U.S. Fish Wildl. Serv. Fish. Bull. 58:363–416.

———, AND H. G. MOSER. 1969. A new gonostomatid fish from the tropical eastern Pacific. Copeia 1969:493–500.

———, AND ———. 1975. Distributional atlas of fish larvae in the California Current region: Flatfishes, 1955 through 1960. Calif. Coop. Oceanic Fish. Invest. Atlas 23.

———, AND ———. 1976. Eggs and larvae of fishes and their role in systematic investigations and in fisheries. Rev. Trav. Inst. Peches Marit. 40:379–398.