AN ANNOTATED LIST OF THE SYNENTOGNATHI*

WITH REMARKS ON THEIR DEVELOPMENT AND RELATIONSHIPS

Collected by the Arcturus

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(Figs. 156-176 incl.)

The present paper is based on specimens of the order Synentognathic collected by the S. S. Arcturus, under the direction of William Beebe. Both Atlantic and Pacific forms are represented in the collections of that expedition (February to July, 1925).

We have laid emphasis on the larval and post larval development of the various species, partly because the material allowed of it, but chiefly because we believe that a study of the young stages will do much to clarify the relationships of the forms encompassed in this order. This has been our main objective and as a consequence we have written in as much of the indications of phylogeny as our studies of the specific ontogenies would permit. It should be added that material showing the changes between young and adult flying fishes is rare in collections, and more of it must be assembled before the group will be satisfactorily known.

Family BELONIDAE

Strongylura ardeola (Cuvier and Valenciennes).

Specimens 280, 285, 320 mm. standard length (Atlantic), No. 5047.

This is a clearly recognizable species, synonymized with poorly described ardeola (Cuvier & Valenciennes) by Jordan & Evermann. Jordan (1919, Proc. U. S. Nat. Mus. LV, p. 397) synonymizes ardeola with T. argalus Le Sueur (1823, Journ. Acad. Phil., II, p. 125, fig.) which is, however, not our fish. Belone depressa Poey (1860) has priority over Belone depressa Gunther (1866). In our material, which we identify with ardeola (following Jordan and Evermann, 1896, not Jordan, 1919), the jaws are very long and slender, in the 280 mm. specimen the lower jaw extending 15 mm. beyond the tip of the upper. Lower jaw measured from eye, 3.6 times rest of head.

Close to *pterurus*, Osburn & Nichols, 1916, which differs in more posterior insertion of ventrals, nearer base of caudal than eye, versus equidistant between the two, and also has about 2 less rays in the anal.

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Strongylura pterura (Osburn and Nichols).

A specimen 293 mm. standard length (Pacific), No. 5724.

Strongylura fodiator (Jordan & Gilbert).

A specimen 710 mm. standard length from Cocos Id., No. 5840.

Strongylura pacifica (Steindachner).

A specimen 68 mm. standard length, No. 5184.

Snout 11.5 mm. (measured from front of eye), beyond which the lower jaw extends 18.5 mm. more. Compared to the standard length of the fish, the lower jaw (measured from front of eye) is half again as long as in *S. marina* of the same standard length, but the upper jaw (snout) is about the same as in that species. See Breder, 1926, Copeia No. 153, p. 123. Peduncle prominently depressed but with no evident keel at this size.

Ablennes hians (Cuvier & Valenciennes).

Atlantic—Station 22, 9 examples 48 to 143 mm. standard length, No. 5044a; 2 examples 165 to 141 mm. standard length. Pacific—A specimen 730 mm. standard length, No. 5629.

The following table indicates the comparative rates of growth of the upper and lower jaws and the sizes of our specimens.

Standard length (mm.)	Upper jaw (mm.)	Lower jaw (mm.)	Difference (mm.)	Percentage
730	1 <u></u> 1.1.1			and the second second
165	39.75	49	10.75	81+
143	31	34	3.00	91 +
141	33	40	7.00	82 +
100				
80		34		· · · · · · · · · · · · · · · · · · ·
68	12	<u> </u>		<u> </u>
65.5	13			
63	12	22.5	10.50	53 +
62	10.5			
56.5	10	20.5	10.50	48 +
48(?)		19		Calendar

Family HEMIRAMPHIDAE

Hemiramphus brasiliensis (Linn.).

One from Bermuda 160 mm. standard length, No. 5000. Also another example from the Atlantic, 180 mm. standard length, No. 5045, and one from the Pacific 340 mm. standard length, No. 5349, which according to Gilbert and Starks, 1904, should be *H. saltator* Gilbert & Starks. However, the alleged differences these specimens display for the Atlantic and Pacific appear to be age characters. All three specimens fall in *saltator*, as defined by Meek and Hildebrand. Comparison of adequate material may show the Pacific form to be distinguishable as a race, but we are unable to separate it. The critical

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measurements of our material are as follows, expressed in hundredths of standard length:

Measurement	Atlantic	. Atlantic	Pacific
Standard length in mm.	160	180	330
Eye	.06 9/10	.06 3/10	.04 4/5
Pectoral length	.19	.19	.19
Dorsal height	.10 3/10	.08 4/5	.08 7/10
Dorsal to ventral insertion	.15	.16	.18
Postorbital part of head	.08 7/10	.10 1/2	.10 9/10
Depth	.12	.15	.16
Head	.24	.23	.23
Gill-rakers	28	27	27
Ventrals	midway base	midway base	midway base
	caudal & basal	caudal & axil	caudal & axil
	4th of pect.	pect.	pect.
Scales	58	61	60

Gilbert & Starks give .18-.21 for the pectoral length of H. saltator and .16-.17 for brasiliensis, whereas all our examples have .19. The lower mandible differences we believe to be fortuitous. It is to be especially noted that Gilbert & Starks (1904) compare fishes of different size groups in their table. That is, their H. saltator range from 213 to 283 mm. and their H. brasiliensis range from 190 to 222. This fact seems to strengthen our opinion that the alleged differences are due to age.

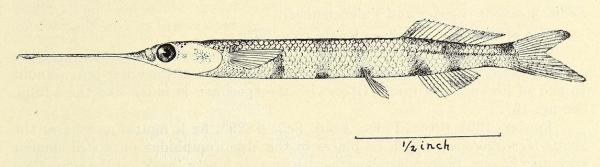


Fig. 156. Young Hemiramphus from the Pacific, of 50 mm. total length

We also have some juvenal fish of this species. Nos. 5184, 6215, 5102, 5248, 50 mm. to 13 mm. standard length. The largest may be described as follows: Sides flat, back convex, belly flat. Posterior dorsal rays elevated, black. Lower jaw extends beyond snout 20 mm., black. Ventrals and caudal dusky bordered with pale. Series of about 9 dark blotches on sides, 4 cross marks on belly.

Hyporhamphus, sp.

Specimens up to 35 mm. standard length, Pacific, No. 5248.

Juvenal specimens from the Atlantic, Nos. 5076 and 5072, and two from Bermuda, Feb. 16, 90 mm. standard length. The material is too small to be significant in a discussion of the distinctness of the two or three nominal American species of this genus.

Euleptorhamphus longirostris (Cuvier).

One from Hood I., Galapagos, No. 5461. Also Nos. 5459, 5455, 5726, 5456, 370 mm. to 293 mm. standard length.

The example of 370 mm. has the lower jaw measuring 147 mm. from eye to tip.

The ventral of *Euleptorhamphus* is forked in a peculiar manner (superficially like the caudal of a small fish). A tendency to bilobed ventrals may be traced through the Hemiramphidae to the Exocoetidae. See fig. 168.

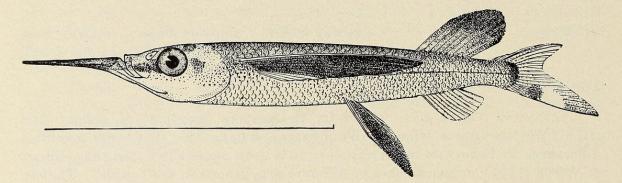


Fig. 157. Fodiator acutus (Cuvier and Valenciennes) of 34.5 mm. standard length

EXOCOETIDAE

Fodiator acutus (Cuvier and Valenciennes).

One of 34.5 mm. standard length, No. 5572.

This single small specimen differs from the existing descriptions of the species, based on larger examples in the greater length of the lower jaw. Snout to end of lower jaw 9 mm. Otherwise the specimen is much like the adults. See fig. 157.

Fowler, 1901 (Proc. Phila. Acad. Sci., p. 293, fig.), figures and bases the genus *Hemiexocoetus* which he places in the Hemiramphidae on a still smaller specimen 25 mm. in standard length, with an even longer 'beak,' at the same time calling attention to its resemblance to *Fodiator*. We have no hesitation in identifying our intermediate specimen with *Fodiator*, and very little hesitation in identifying it with *Hemiexocoetus* Fowler.

Evolantia microptera (Cuvier & Valenciennes).

Specimens numbered 5310, 5543, 5545, 5560, 5690a, 5743, 5953, 5962b, 6033b, 6049, 6059a, ranging from 155 mm. to 4 mm. standard length.

The smaller examples up to 58 mm. (or more) show a pronounced prolongation of the lower jaw. This becomes more pronounced with decrease in size reaching its maximum at about 17 mm. Below this it is less pronounced. The very small (4 mm.) specimens do not show more than a sharp point to the jaw. At 8 mm., specimens are intermediate between the condition of 17 mm. and 4 mm. See Figs. 158 and 159.

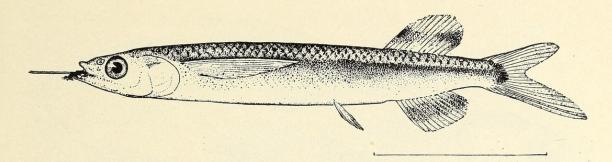


Fig. 158. Two stages of Evolantia microptera (Cuvier and Valenciennes), juv.

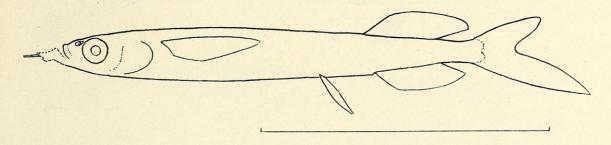


Fig. 159. Two stages of Evolantia mictoptera (Cuvier and Valenciennes), juv.

The temporary beak, consists of a pair of slender prolongations of the dentary, which seem to break through the skin as it approaches maximum length (the bones project from the skin in all our specimens), and later to break off normally and be lost in that way, while the loose skin heals to the chin.

Parexocoetus mesogaster (Bloch).

Two specimens from the Atlantic, 110-109 mm. standard length, No. 5044.

Halocypselus evolans (Linn.).¹

Specimens from Cocos, 158 mm. standard length, No. 5768; from the Atlantic, 83 and 85 mm., No. 6461, and 97 mm. No. 5165. Also, one of 34 mm. No. 5187. Smaller specimens as follows: 5249, 5279, 5420, 5938, 5965, 6046, 6056, 6071, 6137.

This species is separable from H. obtusirostris when small in that the latter has a large simple barbel on the chin, while H. evolans lacks it.

The following characters while slight and sometimes overlapping, also help to separate the two species.

evolans

obtusirostris

In advance of dorsal.

Anal origin—behind dorsal.

Distance from snout to ventrals equal to or greater than ventrals to last dorsal ray. Less than ventrals to last dorsal ray.

¹ See Nichols 1922, Copeia, page 50; Jordan 1924, Copeia, p. 89.

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Fig. 160. Halocypselus obtusirostris (upper), H. evolans (lower) of comparable size.

evolans cont'd.

Scales, dorsal to lateral line— $6\frac{1}{2}$. $7\frac{1}{2}$ or 8. Rarely 6 or 7.

Pectoral color-dark with a pale mar- Pale with a narrow dark margin. gin $(2\frac{3}{4}$ to 4 inch fish).

Halocypselus obtusirostris (Günther).

Specimens with the following numbers: 5166, 5397, 5542, 5710, 5938, 5965, 6137, 6400, 6419-the largest 57 mm. standard length.

obtusirostris cont'd.

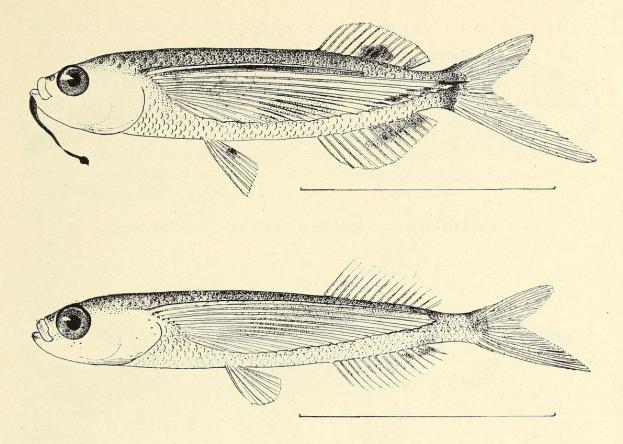


Fig. 161. Halocypselus obtusirostris (upper), H. evolans (lower) of comparable size.

Exonautes rondeletii (C. & V.).

One without data, 62 mm. standard length.

Juvenals, Nos. 5157, 5321, 5570, 5572, 5887, 6040, 6415.

We refer to this species a number of small flying fish 16 mm. and less in standard length with robust bodies and blackish paired fins.

Exonautes marginatus, sp. nov.

A number of specimens, the largest 40-50 mm. standard length, Nos. 5164, 5185, 6072.

We have some hesitation in giving a new name to this material. It may possibly be the young of E. affinis or speculiger, but seems not to be such. The smallest specimens have pectorals pale with narrow dark borders. At a somewhat larger size pectorals are streaked with dark. There are two broad dark broken bands across the breast, the anterior one at base of pectorals.

Description of type: No. 9234, American Museum of Natural History, current rip, Lat. $2^{\circ} 36'-2^{\circ} 8'$ N. Long. $85^{\circ} 1'-86^{\circ} 31'$ W., collected by Arcturus Expedition.

Length to base of caudal 45 mm. (59 mm. to tip lower caudal lobe). Depth in length, 6.7; head 4.3; pectoral 1.35; ventrals 2.3. Eye in head 2.3; snout 4; interorbital 3; maxillary 3.2; maximum width of body (at base of pectorals 1.3);

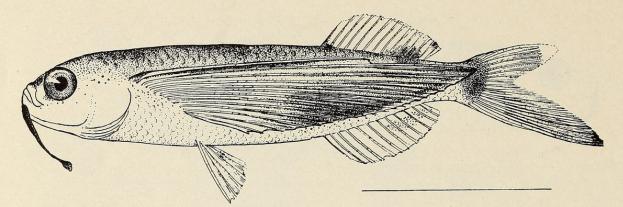


Fig. 162. Halocypselus obtusirostris of 57 mm. standard length.

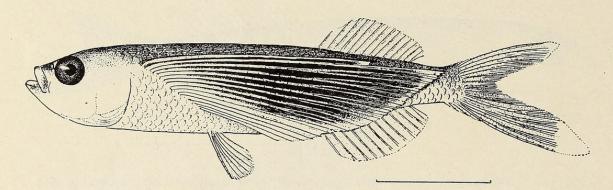


Fig. 163. Halocypselus evolans of 97 mm. standard length.

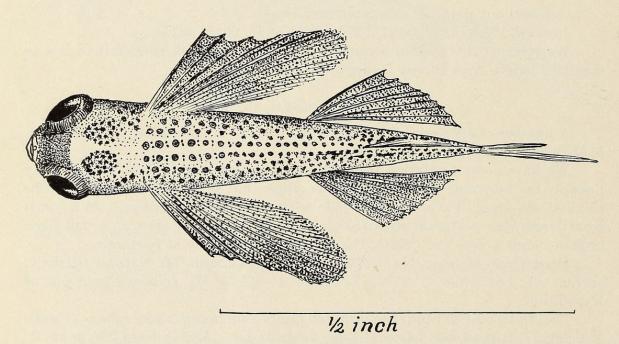


Fig. 164. Exonautes rondeletii of 16 mm. standard length.

length of peduncle 1.5; its depth 2.9; longest dorsal ray 1.5; longest anal ray 1.8; lower caudal lobe 0.7.

Dorsal 11; anal 12. Scales about 43.

No barbels. Maxillary nearly vertical, not reaching orbit; orbital rim slightly raised. Dorsal origin at $\frac{2}{3}$ the distance from margin of opercle to caudal base, slightly behind that of anal; origin of ventrals about equidistant from base of caudal and edge of preopercle. Depressed pectorals reach to middle of peduncle, ventrals to base of caudal. First pectoral ray not quite $\frac{2}{3}$ length of second, second slightly more than $\frac{1}{2}$ the third, third simple, slightly shorter than fourth (divided) which is the longest.

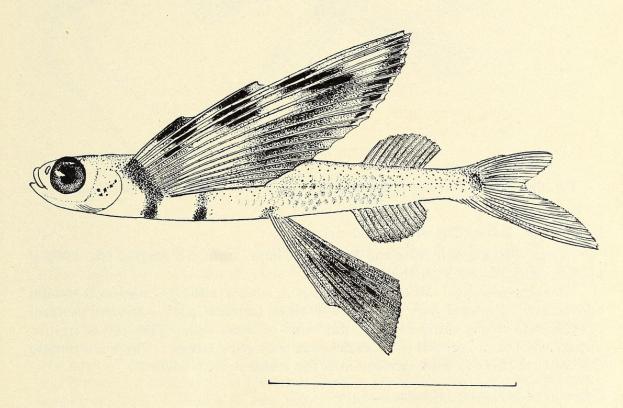


Fig. 165. Exonautes marginatus, type, 45 mm. standard length.

Cypselurus furcatus (Mitch.).

Two specimens from the Atlantic of 130 to 140 mm. standard length, and juvenals. Nos. 6453, 6461.

Large examples show the wings striped differently from the figure in Fowler, 1906, Repts. & Amphibs, N. J.

Cypselurus nigricans (Bennett).²

Three specimens 30 to 50 mm. standard length, Pacific, No. 5183. Dorsal, high black; wing stripe not bold. Very small specimens apparently this species, Nos. 5124, 5321, 5329, 5708, 5962, 6410.

² Nichols, 1924, Zoologica, V, p. 63.

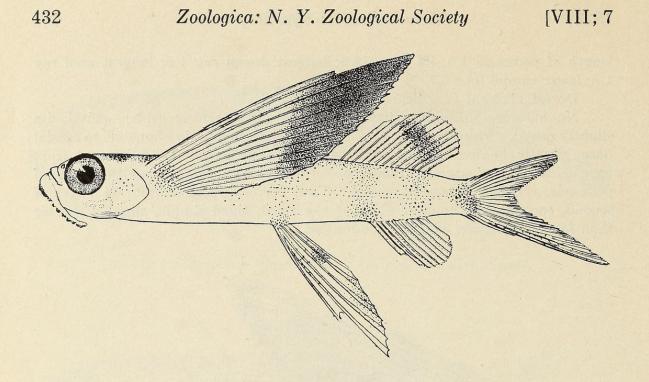


Fig. 166. Cypselurus bicolor (Cuvier and Valenciennes) of 33 mm. standard length.

Cypselurus bicolor (Cuvier and Valenciennes).

A small flying fish from the Pacific, 36 mm. standard length, No. 5960 is provisionally placed with this species.

Barbels present. More slender than is similar sized C. nigricans; caudal lobe larger. Pectoral pale with abrupt black terminal part. Second pectoral ray longest, versus third as in C. nigricans of same size. This ray is simple, apparently becoming split in these fishes as they grow larger. There is a remote chance that this fish may develop into the common C. bahiensis.

Cypselurus bahiensis (Ranzani).

A number of specimens mostly from Gardners Bay, Hood I., 300-320 mm. standard length, Nos. 5350, 5441, 5458, 5463, 5464, 5465, 5469.

Cypselurus callopterus (Günther).

Specimens 229 to 273 mm. standard length, mostly from Gardners Bay, Hood I., -Nos. 5462, 5466, 5467.

Cypselurus monroei, sp. nov.

In comparing Arcturus material with flying fishes in the American Museum of Natural History from other sources, we find a small specimen from Florida so unlike any adult known to us that we venture to describe it as new. The type, No. 8678 Am. Mus. Nat. Hist., Cocoanut Grove, Florida, Jan. 22, 1921, collected by Comm. R. M. Monroe, is 48 mm. in length to base of caudal. Depth in length, 6; head, 4.6; pectoral, 1.7; ventral, 2.5; Eye in head, 2.7;

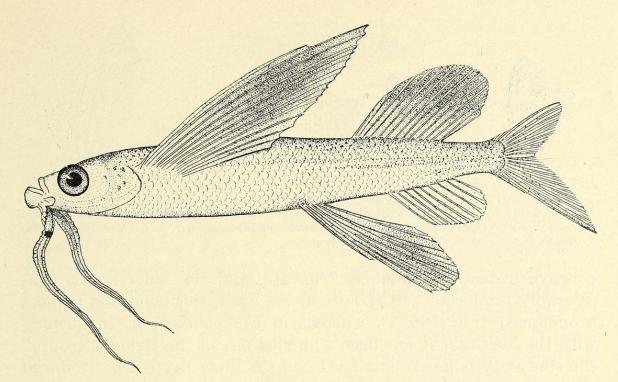


Fig. 167. Cypselurus monroei, type, 48 mm. standard length.

snout, 3.8; interorbital, 5.4; maxillary, 4; width of head, 2.1; greatest width of body, 2; barbels, 0.5; depth of peduncle, 2.7; lower caudal lobe, 0.7; longest dorsal ray, 1.2; anal ray, 1.5.

Dorsal rays, $13\frac{1}{2}$; anal, 9. Scales about 40 or 45.

Body subeliptical in cross-section, very like that of *Parexocoetus mesogaster*; head narrowed forward. Ventrals inserted midway between edge of preopercle and base of caudal; dorsal inserted at $\frac{2}{3}$ the distance from anterior margin of pupil to caudal base; anal well behind dorsal. Pectorals reach beyond middle of dorsal; ventrals to middle of peduncle. Two long simple fleshy tapering mandibular barbels, separate to base, each elliptical in cross section, pale colored with a dark fluted membrane at either side. Color in alcohol,—body palish; pectorals dusky, blacker posteriorly, base and inner margin pale; ventrals nearly uniformly dusky; dorsal dusky; anal pale, slightly dusky centro-marginally; caudal grayish.

DIFFERENTIATION OF VENTRAL FINS

The ventral fins of the synentognathi show some interesting differentiations which fit in readily with the phylogenetic tree here based on other characters. In the primitive Belonidae the ventrals are quite "normal," that is, of an outline common to most generalized fishes (Fig. 168, 1). In the derived Hemirhamphidae these fins are

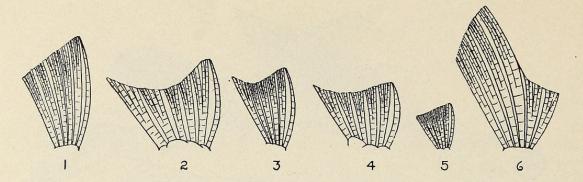


Fig. 168. Synentognath ventrals (right side viewed from below). 1. Strongylura ardeola; 2. Hemiramphus brasilensis; 3. Euleptorhamphus longirostris; 4. Evolantia microptera; 5. Halocypselus evolans; 6. Cypselurus callopterus.

concave instead of obliquely truncate, and the inner ray is considerably produced. In *Hemiramphus* itself, this condition is most pronounced (Fig. 168, 2), whereas in Euleptorhampus, in keeping with the idea that it has been "hurried out of the Belonid group," the concavity is less pronounced and the inner ray is less produced (Fig. 168, 3). Also, the length of the fin is greater in proportion to the breadth as in the Belonidae and not shortened as much as in Hemiramphus. In the "two-winged" flying fishes Evolantia and Halocypselus the fin is very like that of Hemiramphus, the chief difference in Evolantia being a flattening out of the concavity and a very slight lengthening of the fin (Fig. 168, 4). Going on to Halocypselus, the margin is practically straight again and the fin longer (Fig. 168, 5). In the "four-winged" group where these fins are used definitely as planes, there has been a great lengthening of the third ray as in Cypselurus (Fig. 168, 6). Fodiator is quite intermediate between the ventral fin condition of Hemiramphus and Cypselurus. The other genera of the "four-winged" group are essentially similar to the one figured and other genera in each family not figured or mentioned above are similar to their nearest allies which are figured.

The significance of these transformations is not clear, although it is evident that in the "four-winged" group of flying-fish the larger surface enables the ventrals to function to greater effect as planes.

CONCERNING THE PRESENCE OF GILL-RAKERS

Whereas we consider the Belonidae as basal in the Synentognath group, they have certain specialized characters not shared by its

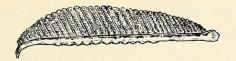


Fig. 169. Ablennes hians. First gill arch of a 52 mm. example (standard length) showing vestigial gill rakers still present.

other members. For instance, all but *Belone*, which may be looked upon as the most primitive member of the family, lack gill-rakers. It is therefore interesting to find, in examining young *Ablennes hians* not over 52 mm. long that distinct traces of gill-rakers are present (Fig. 169). At a slightly larger size these disappear, and we believe their presence to be a juvenal retention of a less specialized character, perhaps correlated with juvenal feeding habits. On either side of each vestigeal gill-raker a tiny spine is located the function of which we do not attempt to interpret. Without knowledge of how generally vestigeal gill-rakers are present in young Belonidae, our hypothesis that Hemiramphidae are fixed larval Belonids in no way precludes their origin from forms which have lost gill-rakers in the adult.

SCHLESINGER ON THE SCOMBERESOCIDAE

The unquestioned relationship, diversity of forms, and seemingly tangled phylogenetic lines within the Synentognathi, are reflected in the considerable discussion of this group in the literature. The only paper to which we wish particularly to refer is by Schlesinger, 1909, "Zur Phylogenie und Ethologie der Scombresociden."³ Scomberesocidae is here used in a broad sense for the whole group. The paper is a comprehensive one touching on various aberrant and exotic genera which we have not seen, and generalizing from what seems to us a rather imperfect knowledge of the habits of various forms, certainly of those with which we are familiar. On the other hand, considerable sound data is brought forward and well presented for recognition of two main divisions of the group, Microsquamati (needle fishes, etc.) and Macrosquamati (halfbeaks and flying fishes) which we consider as subordinal. Phylogenetically the cleavage between Belonidae and Hemiramphidae would seem to be a deep one. From which series the specialized genera Euleptorhamphus and Scomberesox are derived and which they parallel is

³ Verh. Zool.-Bot. Ges. Wien, LIX, p. 302-339.

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open to question, or perhaps they spring from an intermediate series, now mainly lost.

FLYING-FISH EVOLUTION

In constructing an hypothetical phylogeny of the needlefishflying fish group, a sound initial step is to select the basic or most primitive member. This would seem to be the needlefish, an elongate predaceous form with toothed jaws, and the leaping habit. The needlefish tail may be either homocercal or reversely heterocercal, which later character has persisted throughout its derivatives, *Hemirhamphus* and the flying fishes, which have also the leaping habit, seized on and carried to an extreme, correlated with specialized fin (wing) structure in the flying fishes.

The half-beak tendency is foreshadowed in the young of the needlefishes with a shorter upper jaw. This might be brought forward as evidence of the half-beaks' being ancestral to the needlefishes, but such knowledge as we have of evolutionary drift in marine surface fishes leads us to interpret it otherwise. Larval fish forms are not as a rule parallel to the phylogeny of the adult but specialized adaptations (correlated with different feeding habits, etc.) to the different environment which the young must meet due to its small size. Instances are not lacking where such specialized larval forms become established as the adult form, making an evolutionary step upward, and it is just this which seems to have taken place in the transition from needlefish to half-beak.

An apparently superficial character frequent with larval needlefishes, but one which should be given weight due to its persistance in other members of the group, is elevation of the vertical fins, especially of the dorsal, which at the same time is usually dark colored. In small fishes there frequently seems to be correlation between such fin development, which has no very obvious advantage and would tend to impede the progress of the bearer through the water, correlated with the habit of drifting in ocean currents. It is interesting to find an appreciable manifestation of this tendency to an enlarged dorsal in the young of Hemiramphus, and it is a persistent character in certain primitive flying fishes,-Fodiator, It is not unreasonable to suppose that it is in these Parexocoetus. cases perhaps an indication of phylogenetic affinity. There is another point that should be referred to in considering the develop-

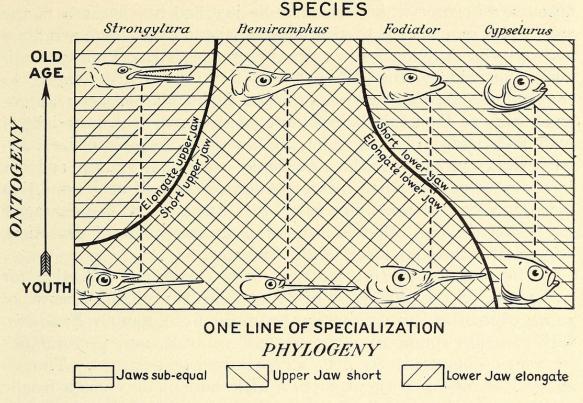


Fig. 170. Diagram of half-beak condition in phylogeny and ontogeny.

ment of the halfbeaks from needlefishes: the halfbeaks may not be strictly monophylatic, but may arise from approximate parallel lines with closely related ancestors. It is conceivable that *Hemiramphus* arose from those needlefish with lunate caudals and enlarged dorsals in the young; *Hyporhamphus* from other species.

At any rate it is from the *Hemiramphus* type of half-beak that the flying fishes would have developed, and in this connection it is interesting that very small *Hemiramphus* have a superficial character in common with various flying fishes of equally small size in the peculiar bands of dark color which cross the ventral surface.

Leaving the half-beaks we come to two primitive flying fishes quite unlike in character and will first mention *Fodiator* a rather short winged species with elevated dorsal, projecting chin and a short body with an elliptical cross-section. The present collection contains an individual which seems to be smaller than any previously figured as such, and this has the chin prolonged into a very respectable half-beak which we consider an ontogenous character reflecting flying fish phylogeny. Notice the difference in interpretation of the same half-beak condition in young flying fishes and young needlefishes, a difference which seems to be justified by the facts of the case. Not only are the toothed needle-fishes a priori more primitive and the winged flying fishes a priori more specialized than the half-beaks, but whereas the half-beak condition is peculiarly adapted to the feeding habits of very small fishes, flight is a character appropriate only to the adult as it is more or less dependent on weight of body and rigidity of wing which are functions of absolute size. Attention may be called to the—we think—somewhat unusual concept corollary to our accepted interpretation of the half-beak condition in young needlefish and flying fish.—It is, namely, that this character has lasted through different fish forms in the course of evolution, only part of the time as an adult character.

The most interesting material in the Arcturus collection for its bearing on the phylogeny of flying fishes is probably a series of young of another quite dissimilar primitive form, namely Evolantia, with elongate compressed body, small ventrals, and pectoral fins (or wings) comparatively little strengthened or enlarged. Though as fry Evolantia is without such, a little later it develops a fragile temporary beak on the lower jaw, which seems to be regularly lost at an early age by the enclosing fleshy skin breaking away from two slender supporting rods, the rods then breaking off and the skin being reduced leaving only a black spot on the chin. Such skin of a vestigial half beak furnishes us with a possible homology whereto to pin the peculiar barbels which occur as larval characters on the chins of this or that species of flying-fish, certainly with no obvious The pectorals of Evolantia increase in relative adaptive correlation. size with the growth of the fish. This form seems to stand rather close to the line of evolution from half-beak to flying-fish, a line which again was very likely polyphylatic. The affinities of Evolantia are perhaps with the typical flying fish Halocypselus, while those of Fodiator are more with Parexocoetus. Fodiator is already decidedly short bodied, one reason for looking upon it as rather aside from the main half-beak to flying fish trend which involves shortening of the body.

The singular form *Euleptorhamphus*, with half-beak condition at the apex of its development, combined with decidedly elongate and compressed body, must be a collateral specialization. We are unable to assign to it any significant position in the evolution of the group, though we can conceive of a not illogical sounding hypothesis

Nichols-Breder: Synentognathi

which would make of it a common ancestor and violate a surprisingly large number of seemingly sound concepts as to the nature of fish life and evolution. Perhaps the most satisfactory interpretation of this aberrant fish is that it was hurried out of the Belonidae by the same trends and forces which have controlled the general evolution of its group, too rapidly to differentiate on the basis of, or to correlate the characters involved.

Another aberrant form, *Scomberesox*, with half-beak young, may be looked upon as a throwback from the half-beaks towards needlefish ancestors, but we prefer to interpret it as a relic from near the line of differentiation between these two families, on which have been superimposed certain specialized characters peculiar to itself.

SYNENTOGNATH RELATIONSHIPS

A phylogenetic tree of the Synentognathi based on our studies is shown in Figure 171. It is nearly self explanatory and the following notes are consequently brief.

MICROSQUAMATI

As understood by Schlesinger the most trenchant division of the order separates the large scaled forms from the small. Thus we have the families Belonidae and Scomberesocidae below the transverse line separating these divisions.

Belonidae

This family is certainly the most primitive of the group and although the others have come up through it, its separation as such from the main "trunk" has been early. Of the Belonidae, *Belone* with its retention of gill-rakers certainly is closest to the base of the needle-fishes' line of ascent. After the gill-rakers were lost we have another early split sending off the compressed and more specialized *Ablennes*. Moving on to *Strongylura* we have its fresh-water specialization *Potamorraphis* with convex caudal, as an offshoot.

Scomberesocidae

This family has clearly arisen within the Belonidae, probably at some place close to where the modern Belonids separated from the stem leading to the Macrosquamati. Differentiation within it is simple and clear, *Cololabis* being a recognizable fixed larva of *Scomberesox*.

1928]

Treating the large scaled forms, there is one especial note to be made regarding *Euleptorhamphus* which we show as arising at some place between the Belonidae and Hemiramphidae (also at the line of differentiation between the Micro- and Macrosquamati) and following a line of its own within the Hemiramphidae. This, of course, makes the Hemiramphidae polyphyletic, and doubtless some students on such a basis would erect a new family for it, which actually would not be altogether unwarranted. However, we feel that it is better to leave it within the family on account of the hypothetical nature of such inferred relationships. It is also to be noted that of the Macrosquamati *Euleptorhamphus* has probably the smallest scales, which, with the other primitive characters it possesses, despite its specializations, is our reason for placing it adjacent to the Microsquamati line.

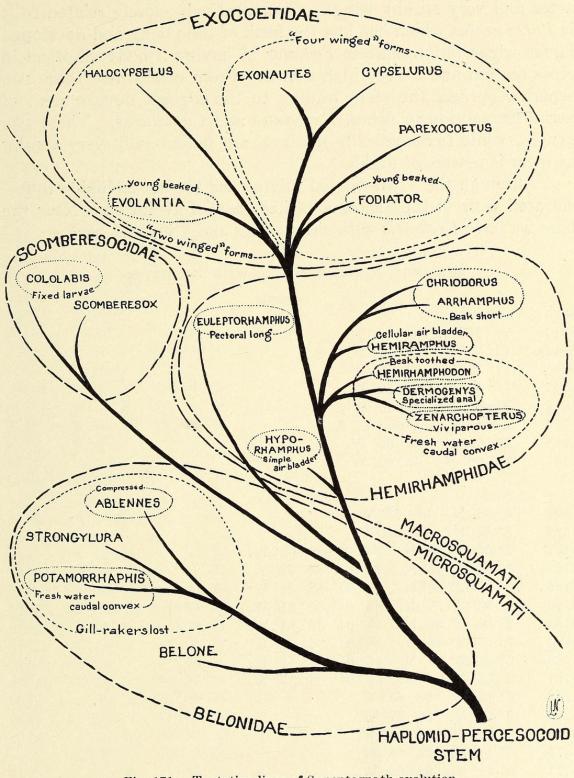
Hemiramphidae

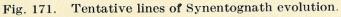
The stem leading to *Euleptorhampus* is discussed above. Regarding the main stem, although considerably divided, we do not feel that it is difficult to trace. *Hyporhamphus* is clearly near the base of this line of specialization possessing a simple air bladder. *Hemiramphus* like its allies variously retains primitive characters and gains others of a highly specialized nature. In the group that has taken to fresh-water and developed a convex caudal (analagous to *Potamorraphis* among the Belonidae) we have *Hemirhamphodon* still bearing teeth on its long unapposed lower jaw as the most primitive. *Dermogenys* on the other hand has developed a curiously modified anal, the possible use of which we do not know, but along with it as a still further development we have the viviparous *Zenarchopterus* in which the male anal is an intromittent organ.

Along another line there are *Chriodorus* and *Arrhamphus* which have the beak reduced. In the former it is so far reduced as to give the fish an appearance not unlike an Atherinid.

Exocoetidae

It is clear that the flying fishes arose from some form more or less intermediate between *Hyporhamphus* and *Hemiramphus*. They early split into two types leading to the "two-winged" and "fourwinged" species respectively. At the base of the latter stem we have





Fodiator which has a well developed "half-beak" as a larval character and very stubby wings. Comparatively closely related to it is *Parexoceotus* which has lost the beak of the young and developed larger wings but resembles *Fodiator* in having a body elliptical in cross section and a very high dorsal. From near where these two separate springs the stem leading to the highest development of aerial locomotion in fishes, *Exonautes* and *Cypselurus*. These two genera, while taxonomically distinct, are functionally very similar as regards powers of flight.

Although the "two-winged" flying fish are not as highly differentiated *inter se* they show a rather parallel evolution. Near the base we have *Evolantia* with short wings and a juvenal beak.

SPECIMEN NUMBERS CITED, WITH LOCALITIES.

Atlantic

Allunite
Bermuda
17° 56' N. 63° 12' W.
Limon Bay, Colon, C. Z.
Limon Bay, Colon, C. Z.
30° 00' N. 60° 00' W.
30° 00' N. 60° 00' W.
Pacific
5° 03' N. 81° 08' W.
3° 42′ N. 83° 03′ W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
2° 36'-2° 08' N. 85° 01'-86° 31' W.
0° 19' N. 89° 57' W.
0° 19' N. 89° 57' W.
0° 05′ S. 91° 11′ W.
0° 14' N. 91° 18' W.
0° 31' N. 91° 00' W.
0° 31' N. 91° 00' W.
0° 19' N. 89° 57' W.
0° 19' N. 89° 57' W.

5397	2° 00′ S.	89° 30' W.
5420	2° 00′ S.	89° 48' W.
5441	1° 22′ S.	89° 39' W.
5455	1° 22′ S.	89° 39' W.
5456	1° 22′ S.	89° 39' W.
5458	1° 22′ S.	89° 39' W.
5459	1° 22′ S.	89° 39' W.
5461	1° 22′ S.	89° 39' W.
5462	1° 22′ S.	89° 39′ W.
5462 5463	1°22′S.	
5464	1° 22′ S.	89° 39' W.
5465	1° 22′ S.	89° 39′ W.
5466	1° 22′ S.	89° 39′ W.
5467	1° 22′ S.	89° 39′ W.
5469	1° 22′ S.	89° 39' W.
5542	0° 22′ N.	88° 11′ W.
5543	3° 52′ N.	86° 43′ W.
5545	3° 52′ N.	86° 43′ W.
5560	4° 56' N.	84′ 35° W.
5570	3° 52' N.	86° 43' W.
5572	6° 16' N.	80° 48' W.
5629	Panama	
5690a	6° 27' N.	86° 54' W.
5708	6° 27' N.	86° 54' W.
5710	6° 30' N.	83° 33′ W.
5724	Cocos	
5726	Cocos	
5743	Cocos	
5768	Cocos	
5814	Cocos	
5840	Cocos	
5887	4° 50′ N.	87° 00' W.
5938	4° 50′ N.	87° 00' W.
5953	4° 50′ N.	87° 00′ W.
5960	4° 50′ N.	87° 00′ W.
5962	4° 50′ N.	87° 00′ W.
5962b	4° 50' N.	87° 00′ W.
5965	4° 50′ N.	87° 00' W.
6033b	4° 50′ N.	87° 00' W.
6040	4° 50' N.	87° 00' W.
6046	4° 50' N.	87° 00' W.
6049	4° 50' N.	87° 00' W.
6056	4° 50' N.	87° 00' W.
6059a	4° 50' N.	87° 00' W.
6071	4° 50' N.	87° 00' W.
6072	4° 50' N.	87° 00' W.
6137	2° 12′ N.	89° 01' · W.
Contraction of the		

443

444

10 2 2 3

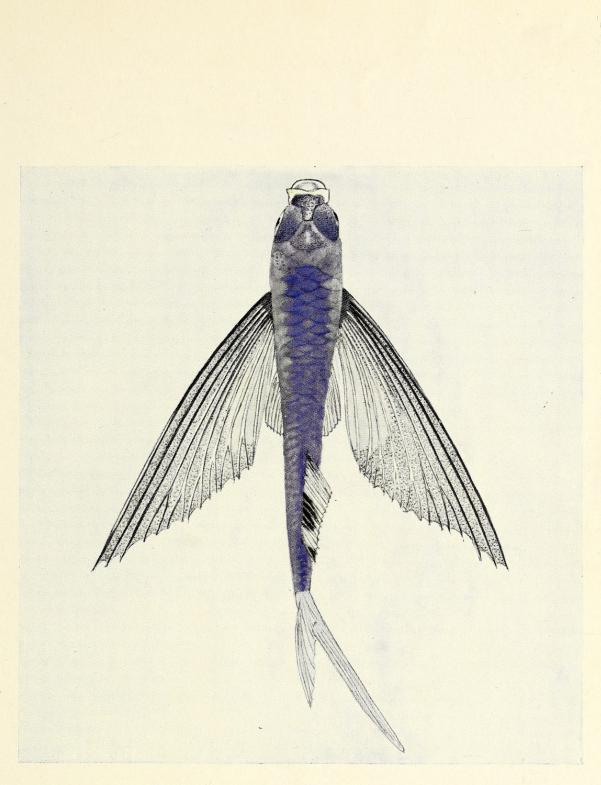


Fig. 172. Two-winged flying-fish (*Halocypselus evolans*) of 80 mm. standard length. From 'Natural History'. Drawing in colors. By Helen D. Tee-Van.

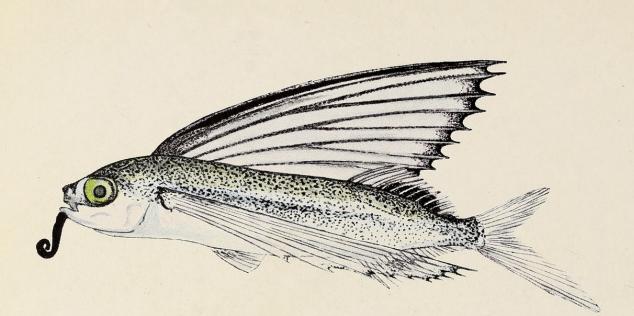


Fig. 173. *Halocypselus obtusirostris*. Drawing in colors. By Isabel Cooper.



Fig. 174. Exonautes marginatus (Field No. 5148) Drawing in colors. By Isabel Cooper.

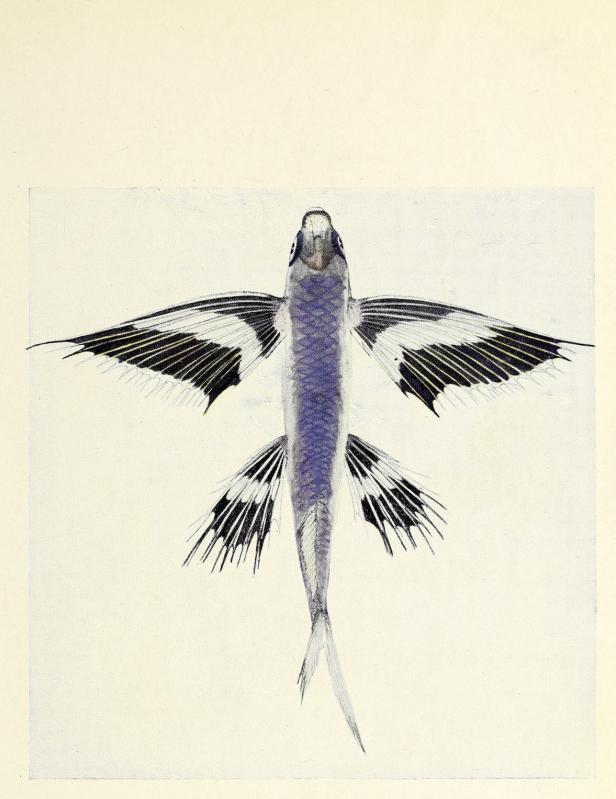


Fig. 175. Four-winged flying-fish (Cypselurus furcatus) of 160 mm. standard length. From 'Natural History'. Drawing in colors. By Helen D. Tee-Van.





Nichols, John T. and Breder, Charles M. 1928. "An annotated list of the Synentognathi, with remarks on their development and relationships." *Zoologica : scientific contributions of the New York Zoological Society* 8(7), 423–444. <u>https://doi.org/10.5962/p.184694</u>.

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