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The American Museum of Natural History

INTRODUCTION

THE ORDER SYNENTOGNATHI is notable, among other things, for striking differences between the juvenile and adult stages of many of the species that comprise it. In at least three of the principal families, the Belonidae, the Hemiramphidae, and the Exocoetidae, there are forms that are provided with mandibular lappets or barbels when young. These are often accompanied by a dorsal fin which is dark and high posteriorly. Long before sexual maturity is established these barbels disappear, and the form and pigmentation of the dorsal fin alter radically. Various aspects of these changes have been discussed by Nichols and Breder (1928), Gudger (1929), Brunn (1935), and Breder (1932, 1938, 1948). Unlike so many characters of vertebrates that differ from young to adult, these characters are not in any way associated with maturing gonads, inasmuch as the whole transformation takes place well before any maturing process is evident.

Many of these juvenile developments are resorbed in an orderly manner as in the case of the long barbels of *Cypselurus cyanopterus* (Cuvier and Valenciennes), which at the height of their development are considerably longer than the fish itself. The reduction of these barbels, as figured by Breder (1938), indicates clearly that they regularly shrink in size to the point of complete disappearance. Certain others of these vanishing characters are reduced in rather odd ways. For example, Nichols and Breder (1928) thought that the juvenile beak of *Oxyporhamphus* might normally break off when the fish had reached a certain size. While this conjecture could not be fully confirmed by the further data of Brunn (1935) and Breder (1938), there is at least nothing in their data that could be used to invalidate it.

The present contribution is based on a closer examination of a curious mode of reduction than has been given to any such material in the past. It has long been known that the form of the dorsal fin of the juvenile *Tylosurus raphidoma* (Ranzani) differs in striking ways from that of the adult. The dorsal fin of the juvenile fish is high posteriorly and black, while that of the adult is light and high anteriorly. Breder (1932) studied certain features of this transformation, and was impressed by the fact that it could not be merely the outstripping of one end of the fin by the other in rate of growth. Some other detail of transformation was present, since a problem of absolute length of fin rays was involved.

Another feature of this fin is that the distal portion of the young dorsal which is absent in the adult is intensely melanic; the pigment actually outlines definitively the form that the adult fin is to take. These data were published in the above reference, based on work done at the no longer extant laboratory on Dry Tortugas, Florida, then operated by the Carnegie Institution of Washington. It was not until 1950 that suitable material was found which made possible further studies. The needed material was obtained at the Lerner Marine Laboratory on Bimini, Bahamas. This, together with corollary material that has been accumulated over the intervening years, forms the basis of the present contribution.

DESCRIPTION OF TRANSFORMATION

THE DETAILS OF THE MANNER in which the dark-colored, posteriorly high dorsal fin of the juvenile *Tylosurus raphidoma* is transformed into a light-colored, anteriorly high dorsal fin in the adult is best divided into two parts, the first concerned with the gross changes and the second with the cellular activity involved, based on histological analysis.

GROWTH AND HETEROGONY

Measurements of the length of the specimens used and the heights of the posterior and anterior portions of the dorsal fins are given in table 1, expressed in millimeters. The standard length (tip of upper jaw to base of tail) was used for the length of the fish. The two measurements made on each dorsal fin represent actually the longest posterior and longest anterior rays in the fin. These varied slightly from fin to fin and with the size of the fish, the longest anterior ray being either number 1 or 2, while the longest posterior ray ranged from 3 to 6, counting from the posterior end of the fin.

Table 1 shows that there is a rather large amount of variation in this material which is especially apparent in the second part of the table where the two fin heights are given in per cent of standard length. Part of this is real, especially that concerned with the middle values of the posterior height of the fin,

and part is artifact. The measurements of the fins are quite precise, but the standard lengths suffer from a number of unavoidable inaccuracies. Preserved material of this sort, especially if not fixed in a straightened-out position, is notoriously difficult to measure accurately. Like snakes, these fish stretch easily in rather unpredictable ways because of their extent in one dimension. Thus it should be borne in mind that where these data are treated graphically the abnormal displacement of points errs along the coordinates representing standard lengths and not along those representing fin heights. This does little more than make for unsightly graphs. The nature of the data and their handling are such that these departures from a narrow band have no bearing on any conclusions derived from consideration of the data.

The data expressing fin heights in per cent of standard length are represented graphically in figure 1. It is evident that while the anterior lobe of the fin increases regularly in height, at first very fast and later very slowly, the posterior lobe at first grows even faster than the anterior lobe. Just at the time that the growth of the anterior lobe slows down rather abruptly the posterior lobe grows smaller (relative to the length of the fish), and finally, as this relative decrement levels off, the posterior part of the fin is lower than in the youngest stages found.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF THE DEVELOPMENT OF THE DORSAL
FIN OF *Tylosurus raphidoma*

Standard Length	Posterior Dorsal Height	Anterior Dorsal Height	P.D.H./S.L.	A.D.H./S.L.
Southern Florida and Puerto Rico (A.M.N.H. Nos. 2902, 2083, 994)				
375	10	29	.027 −	.077 +
475	12	41	.025 +	.086 +
415	15	33	.036 +	.080 −
360	12	32	.033 +	.089 −
373	11	35	.029 +	.094 −
391	9	35	.023 +	.090 −
405	10	36	.025 −	.089 −
399	14	35.5	.035 +	.089 −
422	12	39	.028 +	.092 +
382	14	35	.037 −	.092 −

TABLE 1—(*continued*)

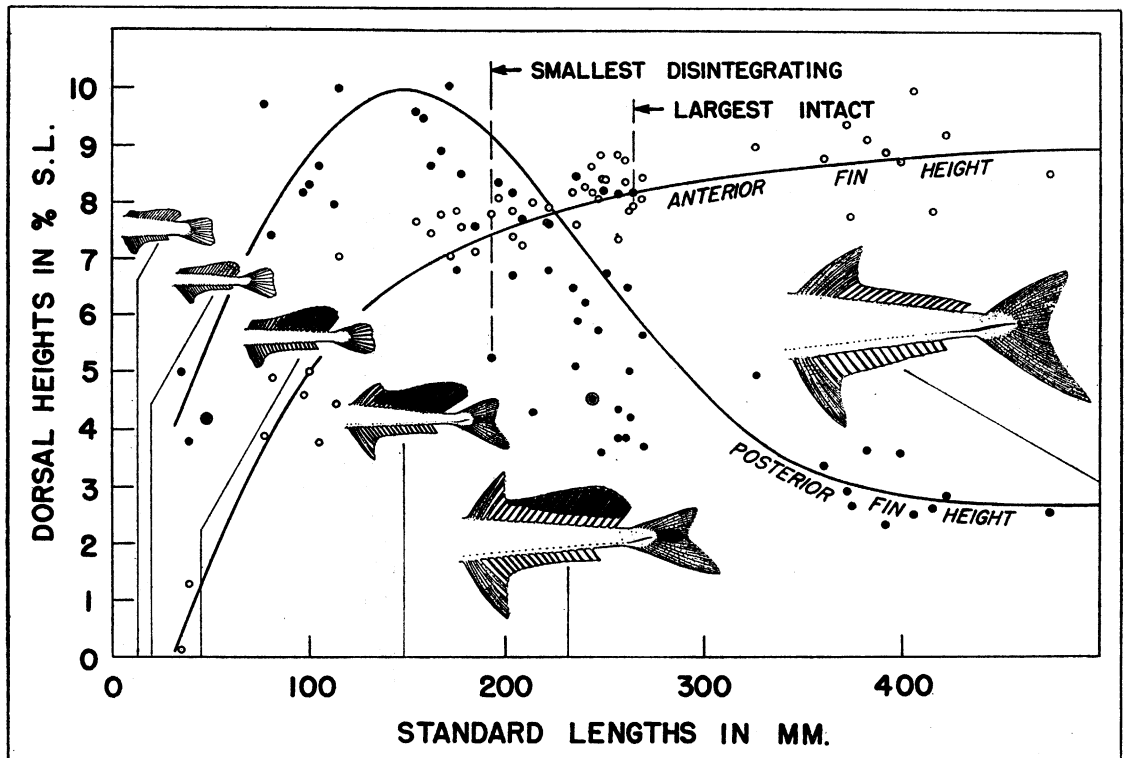| Standard Length	Posterior Dorsal Height	Anterior Dorsal Height	P.D.H./S.L.	A.D.H./S.L.
North Carolina (A.M.N.H. Nos. 4374, 4373, 5274)				
167	15	13	.090 −	.078 −
236	20	18	.085 −	.076 +
250	20.5	21	.082	.084
221	17	17.5	.077 −	.079 +
264	21.5	21	.081 +	.080 −
251	17	21	.068 −	.084 −
158	15	15.5	.095 −	.098 +
183	14	13	.077 −	.071 +
161	14	12	.087 −	.075 −
171	18	.12	.105 +	.070 +
156	15	12	.096 +	.077 −
114	11.5	8	.101 −	.070 +
198	16.5	16	.084 −	.081 −
208	16	15	.077 −	.072 +
234	15	19	.064 +	.081 +
258	21	19	.081 +	.074 −
203	16.5	16	.081 +	.079 −
177	15	13.5	.085 −	.076 +
Bimini (collected 1948, 1949, 1950)				
100	8.3	5	.083	.050
203	13.9	15	.068 +	.074 −
81	6	4	.074 +	.049 +
39	1.5	0.5	.038 +	.013 −
48	2	2	.042 −	.042 −
35	1.75	0.3	.050	.009 −
113	9	5	.080 −	.044 +
104	9	4	.087 −	.038 +
98	8	4.5	.082 −	.046 −
77	7.5	3	.097 +	.039 −
193	10	15	.052 −	.078 −
212	9	17	.042 +	.080 +
261	17	22	.065 +	.084 +
240	15	20	.062 +	.083 +
237	12	20	.051 −	.084 +
238	14	20	.059 −	.084 +
270	10	23	.037 +	.085 +
261	10	23	.038 +	.088 +
243	11	20	.045 +	.082 −
249	9	22	.036 +	.089 −
327	16	29	.049 −	.089 −
262	11	21	.042 −	.080 +
258	11	23	.043 −	.089 +
270	15	22	.056 −	.081 +
243	11	21	.045 +	.086 +
247	14	21	.057 −	.081 +
262	13	21	.050 −	.079 +
260	10	21	.038 +	.081 −
222	15	17	.068 −	.077 −
177	12	14	.068 −	.079 +

FIG. 1. Changes in anterior and posterior heights of the dorsal fin of *Tylosurus raphidoma* with increase of length of fish. Dorsal heights expressed as per cent of standard lengths. White circles represent anterior fin height. Black circles represent posterior fin height. Curves are free-hand approximations of the mean. No account is taken here of the mechanics of the changes in the posterior height. The illustrations of various indicated stages at their respective lengths have been taken from Breder (1932). Data from table 1.

Illustrations of the dorsal fin in series indicating where they belong in reference to the chart (fig. 1) should help in visualizing these changes. Theoretically such a change could be brought about by differential growth rates along the axis of the fin or by resorption of the long posterior rays. The second view would have to be invoked only if the longest posterior rays were longer in absolute terms at their greatest development than they were in the final adult form. This kind of relationship is clouded in a graph such as figure 1 where one character is expressed in per cent of the other, although for purposes of understanding the basic relationships it is a very useful method. The present case is so unusual, however, that certain of its features can be brought out clearly only by replotting the same data in such a way that both coordinate representations are independently

expressed in absolute units. Thus in figure 2 the growth of the anterior lobe is represented best by a straight line, and this part of the fin is found to be growing practically isogonically with the length of the fish.

The posterior lobe as indicated in the left-hand portion of figure 2 is clearly not growing isogonically. The portion left of the line marked "smallest disintegrating" is growing at a slower pace nearing 200 mm. in standard length than in the portion nearing 100 mm. Here it becomes clear that the change in the proportions of the fin cannot be simply in rates of fin-ray growth, and therefore some other process must be involved.

This graphic treatment is not enough to establish beyond a doubt whether the fin change is or is not a simple instance of resorption. To understand the nature of this difficulty recourse must be made to data not
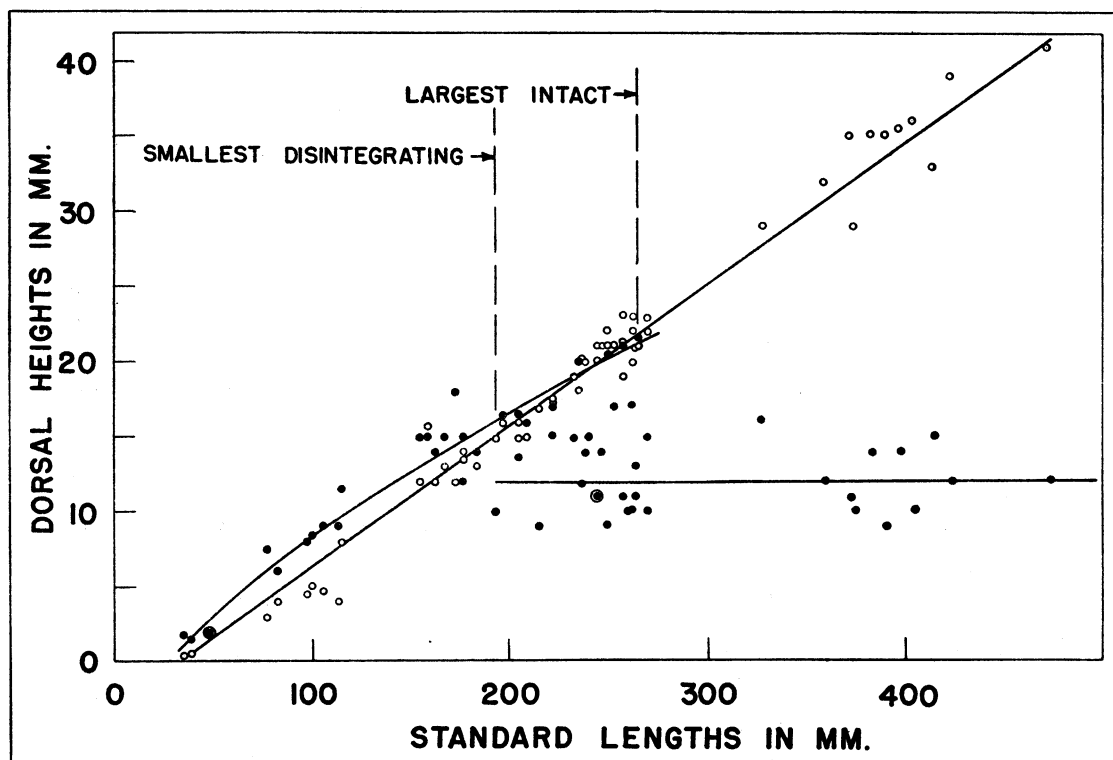
FIG. 2. Changes in anterior and posterior heights of the dorsal fin of *Tylosurus raphidoma* with increase of length of fish. Unlike figure 1, to which this should be considered complementary, the dorsal heights are expressed not in relation to the length but in absolute units. White circles represent anterior fin height. Black circles represent posterior fin height. Curves are free-hand approximations of the mean. Account is taken of mechanics of the posterior height indicating its disruptive nature. Data from table 1.

readily displayed by ordinary graphic means. This situation is caused by the fact that between the two vertical lines on both figure 1 and figure 2 marked, respectively, "smallest disintegrating" and "largest intact" two kinds of dorsal fins are encountered. In this area of overlapping of the two types of fins some are intact and are represented by the fifth drawing from the left in figure 1. Others between the two named boundaries are not intact and are represented by plate 1, figure 3. The area between these two boundaries may be appropriately called the "area of disintegration." Lest it be thought that these ragged fins are merely the results of rough handling of either the living or preserved fish it may be pointed out that many completely feral individuals in this size range have been seen to be in the same condition in the sea. They are not easy to capture except by night light, and even this method has never yielded

many of these fishes in any place where it has been tried by the authors. In any case, the histological evidence, which is presented below, makes elaborate explanation at this point unnecessary. This condition is of course the reason for the large amount of scatter in the points on the graph of the posterior dorsal heights in this area. In figure 1 it can be seen that this disintegrating distal portion of the fin is an area of intense melanin concentration, and that if the melanic area were trimmed off the outline of the adult dorsal would be left. The light proximal fin membrane is also shown in plate 1, figure 3.

It is thus evident that a single line of growth of the posterior lobe as in figure 1 cannot properly express this condition. Therefore in figure 2 in the area of disintegration there are mixed fins, some intact and some broken off. The latter form the bases of a new curve, in this instance a straight, hori-

TABLE 2

DATES OF COLLECTION AND STANDARD LENGTHS (IN MILLIMETERS)
OF *Tylosurus raphidoma*

Locality	Date	No. of Fishes	Min.	Modes[a] of Mean	Max.
Berry Islands,[b] Bahamas	2/18/30	9	320	*430*	440
Key West,[b] Florida	6/5 to 7/18	197	29	*50*	68
	8/30/26	2	195	196	197
	8/31/29	1	—	600	—
Tortugas,[b] Florida	6/20 to 7/6/29	22	479	*540*	632
		1	—	840	—
		4	106	*140*	232
		11	13	*18*	58
Cape Lookout,[b] North Carolina	7/25/13	19	114	*160, 260*	280[c]
Sandy Hook,[b] New Jersey	8/30/26	1	—	59	—
Bimini, Bahamas	1/27/48	1	—	212	—
	4/ 1/48	1	—	77	—
	6/14/48	3	98	105	113
	8/13/48	4	35	51—	81
	11/2/49	1	—	193	—
	6/2/50	2	100	151+	203
	7/—/50	18	177	*240*	327

[a] Where possible, modes are used in preference to means; the former are in italics.

[b] From Breder (1932).

[c] Material reëxamined and measured on a basis of standard lengths. Difference between the data in this table and those in table 1 indicates merely that some of the material suitable for one table was not suitable for the other, being incomplete in data, location, or date, or, on the other hand, defective in fin or beak.

zontal line. Such a horizontal line indicates no growth whatever, a condition that cannot persist much beyond the boundary of the graph. Evidently this line must turn upward when individuals larger than any of ours are considered and then must run more or less parallel with the line of the anterior lobe, since the dorsal heights, anterior and posterior, of large and very large fish are proportional to the length of the fish and to each other. It would seem that the fin, after this disruption, repairs itself and then rests for a while as the fish continues to grow as a whole. While it is clearly demonstrated that actual disintegration of the distal portion of the fin is the primary cause of the change from the juvenile to the adult fin outline, it must be remembered that the two other processes mentioned, differential growth and resorption, may be, and

to some slight extent probably are, going on simultaneously. To establish the relative values of these two methods, which here are clearly minor and almost negligible, much more work must be done and many more data be available.

As is mentioned above, the activity involving the described dorsal-fin changes takes place long before sexual maturity. The actual time of this fin change in the ontogeny of the fish can be best understood by analyzing the data of table 2. This analysis is expressed graphically in figure 3. Measurements of 279 specimens in standard lengths are plotted against the time they were caught. The larger sizes were advanced a year or more in figure 3, since it is evident from the sizes and times of collection of those in the first year that those relegated to the
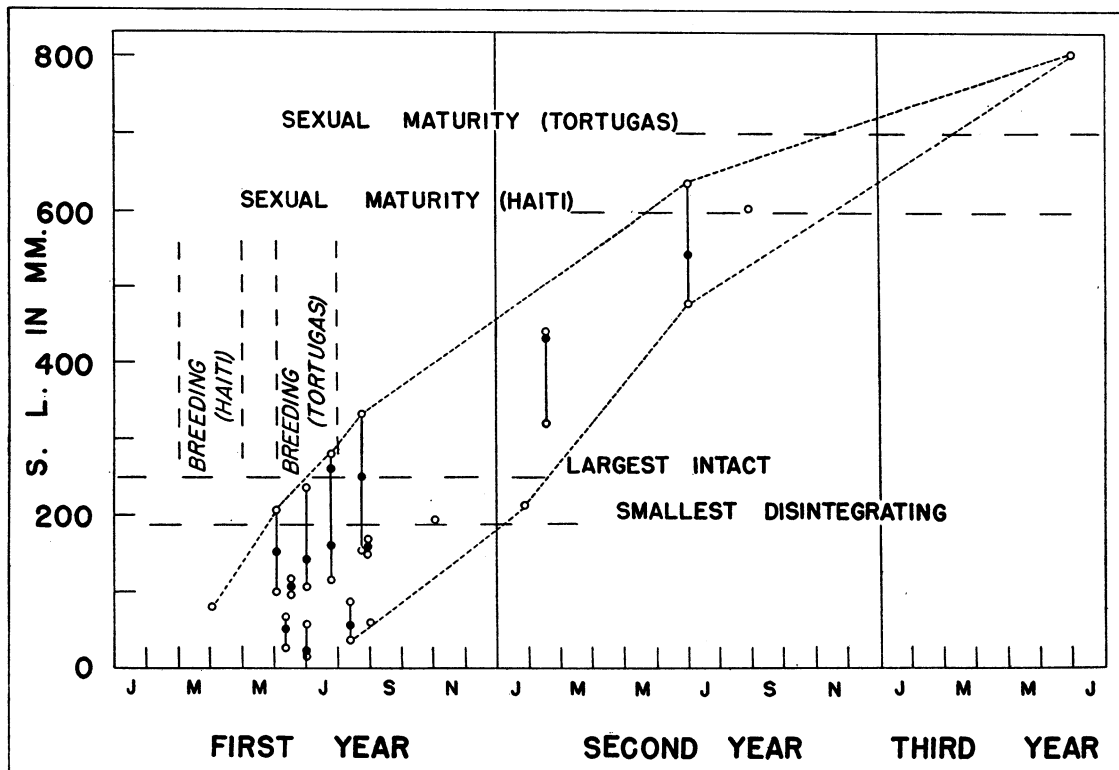
FIG. 3. Standard lengths of 279 *Tylosurus raphidoma* and their respective dates of occurrence. See table 2 for detailed data and location of each sample. Haitian data from Beebe and Tee-Van (1928), Tortugas data from Breder (1932).

second must have been hatched the year before. This, together with the several other confirmatory observations discussed below, makes, we believe, a reasonably acceptable growth curve.

Young fish below the area of disintegration in figures 1 and 2 were taken from April to August only. Fish in the area of disintegration were taken from June to January. Fishes a little above that area appear first in July, and the larger ones of course may be collected the year round. They can be seen any day even if not readily caught. Beebe and Tee-Van (1928) found ripe fish in breeding condition at Haiti in March and April, while Breder (1932) found the same situation at the Tortugas in June and July. The smallest sexually mature fish at Haiti were 600 mm., while none smaller than 700 mm. was mature at the Tortugas. These various data fit together very well. From the observations on both the presence of breeding fish

and the backward projection of growth to the base line, it appears that the bulk of the breeding took place from March to July inclusive. Sexual maturity seems not to appear before a year or a year and a half of age from the time of hatching and not under 600 mm. in standard length. The juvenile transformation of the dorsal fin appears to be completed before an age of about six months and under a size of 275 mm. in standard length. Thus in the most delayed juveniles, the transformation takes place well before they are half the length they are destined to attain by the onset of maturity.

CELLULAR ACTIVITY

In order to understand the manner in which this evident sloughing process took place, histological study was made of the two dorsal fins shown in plate 1, one before the sloughing process had begun and the other at its height. The fins, with some of the adja-

cent dorsal musculature, were removed from the fresh fish and fixed in Bouin's fluid. Each fin was divided into three pieces and these were sectioned three ways; respectively, at right angles to the long axis of the rays, at right angles to what had been the long axis of the intact fish, and longitudinal to the fin ray. The last method gave sections that contained longitudinal sections of the ray, and the first method gave transverse sections of the rays and the membrane between them. The second method proved most unsatisfactory, as it provided oblique sections of everything except the dorsal musculature. The sections were cut at 7 microns and stained with Harris' hematoxylin and eosin, and Masson's trichrome method. Three additional fins in the disintegrating stage that had been fixed in formalin were also sectioned, two transversely and one longitudinally. A fourth disintegrating fin was stained with alizarin and cleared in glycerin for a study of the bone structure.

For study of the involuting mandibular lappets, three formalin-fixed fish were used. Two of these were the same fish used for fin sections, the whole fish having been put in formalin after the fins were removed for Bouin fixation. The third fish was also in the disintegrating fin stage. The mandibular regions were removed, decalcified, embedded in paraffin, and sectioned at 7 microns. Alternate slides were also stained in hematoxylin and eosin, and Masson's trichrome stain.

One barbel was removed from a formalin-fixed specimen of *Cypselurus cyanopterus* (Cuvier and Valenciennes). The standard length of the fish was 155.5 mm. The right barbel was 51.5 mm. long. Sections were cut at 10 microns and stained with hematoxylin and eosin, Bodian's protargol method, and Masson's and Van Gieson's methods for the demonstration of connective tissue. One barbel was also removed from an old formalin-fixed specimen of *Cypselurus furcatus* (Mitchill). The standard length of the fish was 52 mm., and the barbel was approximately at the height of its development. Sections were cut at 7 microns and stained with Masson's trichrome method.

The structure of the fin rays of these fish conforms to the descriptions given by Goodrich (1904) and Blanc (1947) for various spe-

cies of teleosts. Each dermal ray is composed of a pair of segmented membranous bones, the lepidotrichia, which reach from their articulation with the radialia of the endoskeleton at the base to the margin of the fin. Actinotrichia were present in the small fish with the intact dorsal and in one other fish with a disintegrating fin. These numerous small bones extend distally from between the ends of the lepidotrichia and are evidently a character of youth. They were completely absent from the larger fish with the disintegrating fins. That this absence is not merely a part of the disintegrating process is evidenced by the fact that the actinotrichia were also absent from the anterior parts of the fin which are not involved in the disintegration.

The non-osseous tissues of the dorsal fin have been comparatively neglected in the literature. We have been unable to find any descriptive material comparable to that which follows, which is obviously necessary to a basic understanding of the matters under consideration. Scaleless epithelium covers the entire fin, and around each ray a loose connective tissue separates the lepidotrichia from the epithelium. The surface epithelium rests on a rather heavy basement membrane. The loose connective tissue, basement membrane, and epithelium are continuous between the rays and form the membrane of the fin (pl. 2, fig. 2). In the more distal portions of the fin, the membrane is exceedingly thin and delicate, and the basement membrane provides the heaviest supporting tissue present. Capillaries and melanophores are seen in the loose connective tissue. There are no epidermal melanophores in these fins; all pigment cells are confined to connective tissue areas. Melanophores are most numerous in the dermis but are frequently found between the ends of the opposing lepidotrichia and even within the core of the ray.

The core of the ray between the two lepidotrichia is filled mainly with collagenous connective tissue. Near the base of the fin two arterioles are found in the center of the core; nearer the margin of the fin only one arteriole is seen. Small venules are also present in the center of the core. Laterally, next to the concave surface of the lepidotrichia is an aggregation of tissue extending nearly throughout
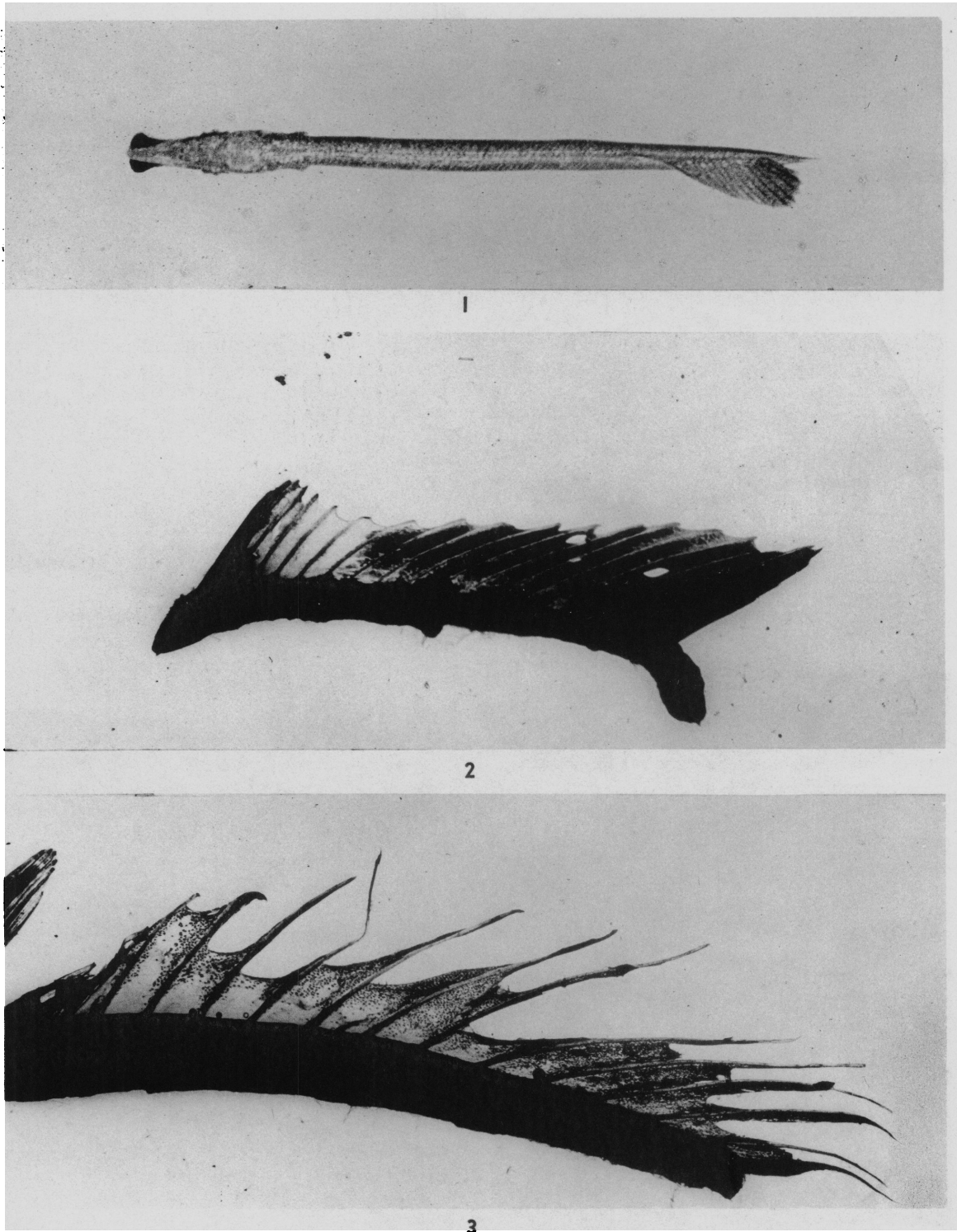
Dorsal fins of *Tylosurus raphidoma*. 1. Living example of *Tylosurus raphidoma*, 150 mm. in standard length, showing the dark, posteriorly high dorsal fin as it is customarily carried to one side. After Breder (1948). 0.71 × life size. 2. Lateral view of a fixed dorsal fin of *Tylosurus raphidoma* of 100 mm. in standard length, slightly before it has reached the zenith of its development. The two perforations were caused by spreading the fin with insect pins. 4.75 × life size. 3. Lateral view of a fixed dorsal fin of *Tylosurus raphidoma* of 203 mm. in standard length in the process of disintegrating. This is nearly the smallest size at which this event takes place. 4.75 × life size
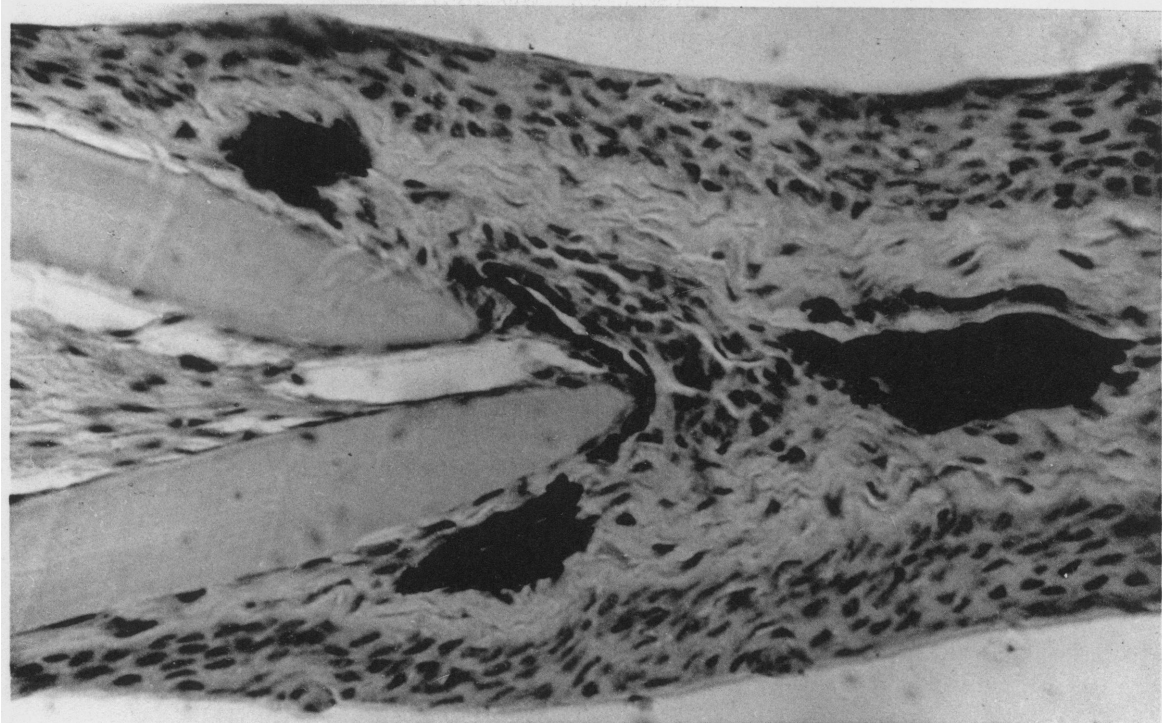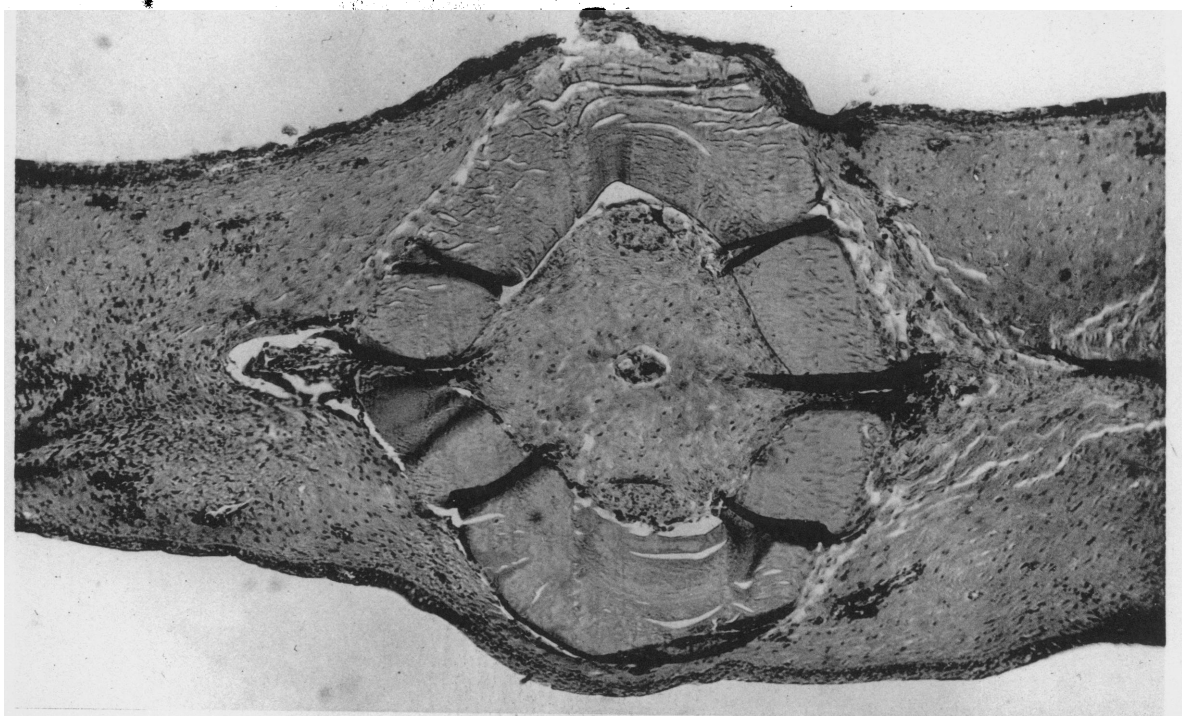
Tylosurus dorsal fins. 1. Section near base of heavy anterior rays which remain intact, showing arrangement of blood vessels and nerve tracks. 126 ×. 2. Section near base of posterior rays at a level below the point of disintegration, showing the sturdy construction of the fin at this place. 855 ×
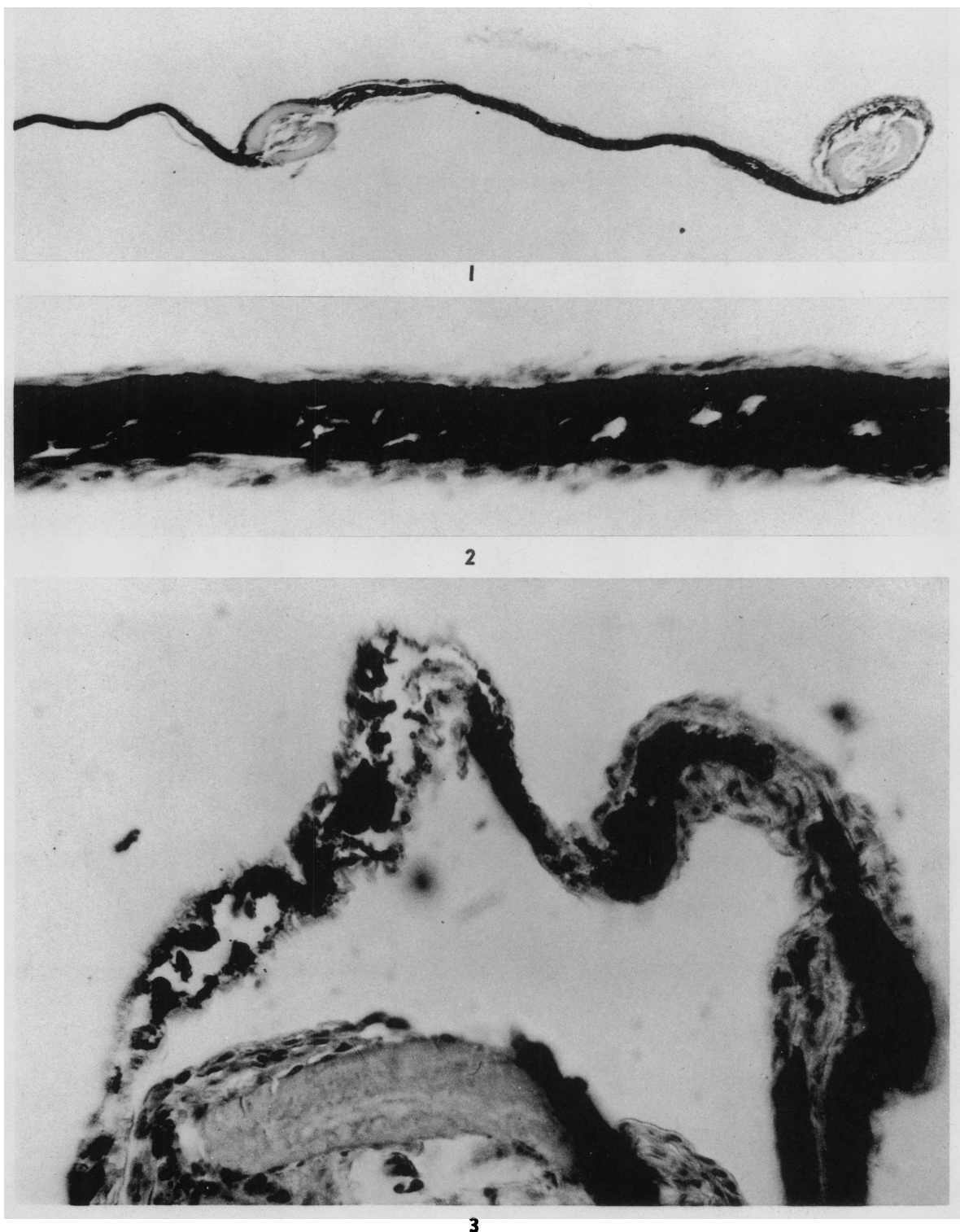
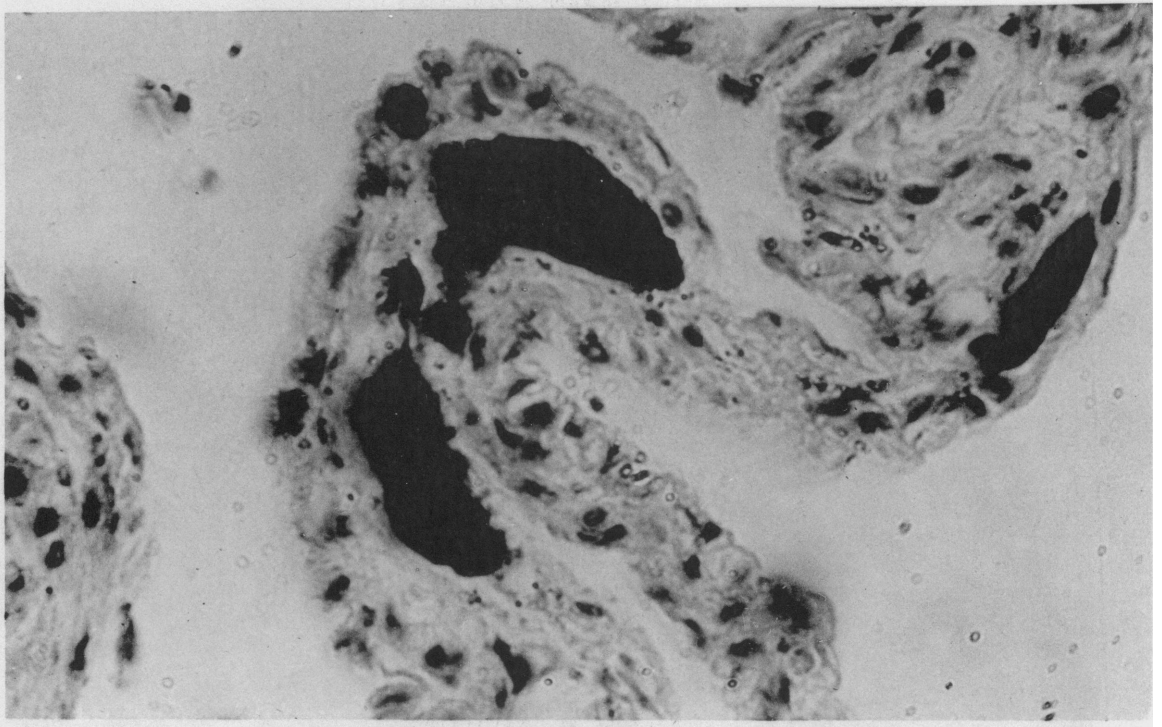*Tylosurus* dorsal fins. 1. Section of intact, heavily pigmented portion which later disintegrates. 167 ×. 2. Detail of interradial membrane before disintegration. 765 ×. 3. Detail of interradial membrane in the process of disintegration. 668 ×
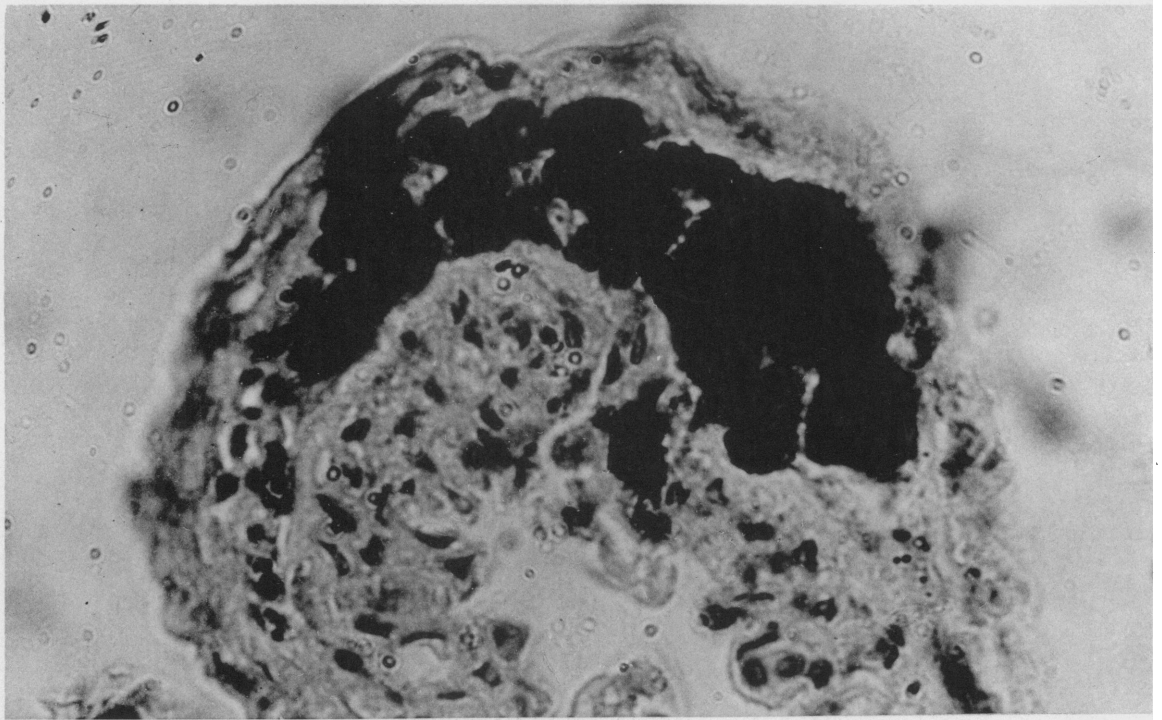
Tylosurus dorsal fins. 1. Further magnified portion, showing the loose melanin granules in the process of being extruded through the epithelium from ruptured melanophores. 2687 ×. 2. Another portion of the disintegrating fin in a slightly more advanced stage. 2687 ×

the length of the ray, containing nerve fibers and small venules and infrequent melanophores (pl. 2, fig. 1). An occasional capillary connects the central blood vessels with these lateral ones. Blood vessels are also found in the triangular-shaped area immediately outside the opposing sides of the lepidotrichia where the tissue narrows to become the fin membrane. These vessels also send branches into the core of the ray between the lepidotrichia.

In the distal portion of the fin, centrally, between two adjacent rays the membrane is reduced to a pair of single layers of epithelium and basement membranes, with a few connective tissue strands between them. In the young fish with the intact fin, sections of the membrane taken through the black area show two bounding layers of epithelium and two dense layers of melanophores between them. In such an area all other histological detail is completely obscured (pl. 3, figs. 1, 2). The melanic portion of the disintegrating fin resembles that of the younger intact fin in many places, but the melanic deposits are less dense. From examination of serial sections of the disintegrating fin it is clear that the melanophores become increasingly less numerous distally in the portion sloughing off (pl. 3, fig. 3). The epithelium becomes detached from the fin, leaving the underlying connective tissue and lepidotrichia naked. Nuclei of the shedding epithelium are pycnotic, and the cytoplasm appears shrunken and vacuolated. Nuclei of the connective tissue cells of the membrane appear somewhat pycnotic, while those enclosed by the lepidotrichia are less so. There is no evidence of any dissolution of the bone or of any inflammatory reaction or congregation of phagocytic cells that might be present if this tissue were undergoing resorption. There is no evidence of phagocytosis on the part of the abundant eosinophiles. Still nearer to the edge of the disintegrating fin, all the cells of the membrane are pycnotic, and the pigmented areas show a breakdown of the melanophores, with melanin granules scattered among the spaces that have appeared between the connective tissue fibers. The capillary walls have also broken down, and occasional erythrocytes and eosinophiles are present in this area together with much

cellular debris. Macrophages are conspicuously absent. The tissue encompassed by the paired lepidotrichia of the rays maintains its integrity longer than the tissue of the membrane.

At the same time that the dorsal fin is disintegrating the mandibular lappets (seen in pl. 1, fig. 1) are undergoing atrophy. No such disintegrating process takes place as is seen in the fin, but the process is more like that of the tadpole tail undergoing atrophy during metamorphosis. Bony elements are lacking, but there is much more connective tissue present than is found in the core of the fin. Sections from the mandibular region taken from the same small fish that furnished the intact black dorsal fin show an abundance of blood vessels in the connective tissue, many crowded with coarse eosinophilic granulocytes. The thin epithelial layer rests on a heavy collagenous basement membrane, and the finer collagenous fibers appear to run at right angles between the two layers of epidermis. The epithelium is three or four cell layers deep and does not contain either taste organs or mucous cells. Both these structures are present in the epithelial lining of the mouth.

In the lappets, the cell bodies of the melanophores are set deeper in the dermis than they are in the fin, and the dendritic processes proceed peripherally towards the surface from the main part of the cell body. These dendrites form a continuous surface of melanin under the basement membrane. The nuclei of the melanophores can be clearly seen in cells where the melanin granules are fully dispersed. Macrophages engorged with cellular debris and pigment granules are occasionally seen. The appearance of these cells in this location is another indication that the mandibular lappets in this young fish were already undergoing atrophy. Breder (1932) has already shown that the onset of involution of the lappets precedes that of the dorsal fin.

The mandibular region of the larger specimen with the disintegrating fin showed the lappets to be much reduced. The connective tissue at the base of the lappets contained numerous blood vessels. The peripheral vessels in what remained of the lappets were crowded with coarse eosinophiles; many more

of these cells were evident than in the small fish. Large macrophages filled with cellular debris were seen in the smaller blood vessels of the atrophying lappet. There appeared to be some decrease in the numbers of melanophores compared with the small fish, but this reduction was not a prominent feature of the involution process.

The mandibular region of a second fish with a fin in process of disintegration was sectioned. The same conditions obtained in this fish also, and the coarse granular eosinophiles were extremely prominent.

The barbel of *Cypselurus cyanopterus* is composed of a core of tissue resembling that which forms the *Tylosurus* lappet and in addition is provided with a thin fluted membrane on either side. The lappet membrane resembles the melanic membrane of the dorsal fin of *Tylosurus* in structure. The more distal portion of the membrane is formed by two layers of epithelium, two or three cells deep, which enclose a double row of melanophores and a few connective tissue fibers. The barbel itself is composed mainly of collagenous connective tissue, heavier in fibrous character than that found in the *Tylosurus* lappet. The core is richly supplied with blood vessels and nerves. Both small and large blood vessels are filled with coarse granular eosinophiles. The granules are stained intensely black when the sections are stained with Bodian's silver protargol. No parasites were noted in the sections of this barbel.

The large nerves run lengthwise of the barbel, and branches extend towards the periphery. In the sections stained with Bodian's method, fine fibers could be traced only into the melanophore area. None were seen peripheral to it, and no special sensory organs were demonstrated in the epithelium, although this is not proof of their absence. The epithelium contains mucous cells, but like the *Tylosurus* lappet, lacks taste buds. These appendages are distinguished in this respect from those of the catfish, goatfish, and others. Sato (1937, 1938) has described the histological structure of barbels in 18 different species of fishes, and in only one, the saw-shark, was the absence of taste buds noted. The rest of the species described consisted of fishes that retain the barbels in the adult form.

The epithelium of the *Cypselurus cyanopterus* barbel rests on a heavy collagenous basement membrane and immediately under this lies a wide layer of melanophores. Here, as in *Tylosurus*, the cell body lies nearest the center, and the dendritic processes for the most part extend peripherally and are considerably longer than those of *Tylosurus*. Macrophages engaged in phagocytic activity were not evident in the *Cypselurus* barbel. This is perhaps not surprising, for the reduction of the barbels of this form is evidently very slow as compared with that of *Tylosurus*. The barbels of *Cypselurus cyanopterus* reach their maximum development when the fish is about 50 mm. in standard length and are not lost completely until the fish is nearly 200 mm. in length. This is demonstrated pictorially and graphically by Breder (1938).

On the chin at the point of origin of the barbel, a wide band of smooth muscle lies between the epithelium and the connective tissue core of the barbel. This does not extend any great distance distal to the insertion of the barbel. There is no cartilaginous core in these appendages in *C. cyanopterus* such as is seen in the goatfish and other forms where the barbel epithelium contains taste organs.

One barbel of a small specimen of *Cypselurus furcatus* (52 mm. in standard length) was sectioned. This had been in formalin for many years, and the staining reaction of the tissue was considerably impaired. However, structural details could still be observed, showing the microscopical anatomy to be similar in character to that of the other barbels. This fish had been preserved at a time when the barbel had reached its approximate maximum size, as described by Breder (1932), which undoubtedly accounts for a lack of involution changes. Vascularization was noticeably less than in the involuting appendages of the other two forms described. The body of the barbel consisted of loose collagenous tissue in which blood vessels and nerves were found, a heavy collagenous basement membrane and epithelium two or three cells deep. No taste organs were evident in the epithelium covering either the main body of the barbel or the membrane. Coarse granular eosinophiles were also present within the small blood vessels and in the connective tis-

sue and epithelium, but these did not appear in any abundance. Macrophages were not observed. The structure of the membrane resembled that of *C. cyanopterus*, although it was not so heavily pigmented.

Several processes are involved in the disintegration of the melanic portion of the fin, and all of these point to a selective failure of blood supply. This point could be proved only by the use of micro-injection techniques in fresh material. However, the loss of blood supply is indicated by the death of the cells without any accompanying signs of wound healing or phagocytic activity. Inasmuch as the heavy pigmentation disappears before the fin is fully destroyed, the melanophores are among the first elements to be broken down. Because these cells represent such a large component of the structure of the thin membrane, their loss would considerably weaken the membrane. Ultimately the rest of the tissues become affected, the epithelium is stripped away, and the ragged membrane is broken off and washed away.

Similar processes of involution apparently take place in the larval form of *Fierasfer acus*. Bykowski and Nusbaum (1905) have attributed the loss of the filamentous juvenile tail to a process of resorption and the loss of the "vexillum" to a process of breaking off at the base. They also considered a failure of blood supply to be involved in the latter case, assuming that the central blood vessel of the organ was constricted by a thickening of the lateral supporting plates. The "vexillum" is considered to be a modification of the first ray of the dorsal fin in this species, and it is interesting to note that here also the disintegrating process is concerned with the same fin in which it appears in *Tylosurus*. Morse (1918) attributed the atrophy of the tadpole tail to an acidosis established in the tail regions by a depleted blood supply, assuming the blood supply to have been cut off by the rapidly developing urostyle. This hypothesis was not substantiated by Helff (1928).

No constriction of blood vessels by the lepidotrichia of the fins was noted in *Tylosurus*. If the loss of an adequate blood supply is responsible for the disintegration of the fin tissue, it must be accomplished in some other way. The physiology of such hereditary mechanisms is still obscure.

The structure of the black fin, before the disintegrating process is manifested grossly, bears a striking resemblance to what Reed and Gordon (1931) have designated the "second stage of melanosis" in the formation of melanomas in *Platypoecilus-Xiphophorus* hybrids. The *Tylosurus* fin shows a deterioration, if not complete destruction, of the connective tissue elements within the fin membrane. Where the melanophores are found in abundance, as in the melanotic *Platypoecilus* tissue, the binding quality of the connective tissue is lost and the parts of the fin readily separate. This tissue breakdown in the *Tylosurus* fin is plainly seen in plate 3, figure 3. The integrity of the epithelium of the *Tylosurus* fin is maintained for a longer period than the connective tissue. Destruction of muscle fibers described in the development of the melanomas is not shown by the *Tylosurus* fin. The area of the fin that is involved in the melanotic process is distal to the musculature at the base of the fin; in other words the line of pigment which delineates the proximal part of the black area is peripheral to the line of muscle insertion on the fin. The *Platypoecilus* hybrid may also show a loss of scales and fin rays in this stage of melanosis. However, the process of melanosis in the *Platypoecilus* hybrid goes on to become an overgrowth and a true neoplasm with typical invasive processes. The melanosis of the *Tylosurus* fin is confined within a definite area, and no evidences of overgrowth or tumor formation are present.

The appearance of the melanoma has been attributed by Reed and Gordon (1931) to activity of macromelanophores. There is no evidence to warrant the classification of melanin-bearing pigment cells in *Tylosurus* into macromelanophores and micromelanophores. Neither histological nor gross examination shows any great differentiation in size among the melanophores.

An examination of the fin rays, cleared and stained with alizarin, shows that the fin rays break off at the articulations of segments rather than through cellular disintegration. Thus the fin rays are reduced in length to a few basal segments. As with most dermal fin rays, the articulations near the distal ends allow more movement of segment on segment than those close to the base of

the fin, a feature that makes such fins progressively more flexible towards their outer edges. Evidently, as the membrane ruptures, dropping off or hanging in shreds, the exposed fin rays, which have both supported the membrane and been in turn supported by it, are in a sufficiently mechanically weakened condition to part at their looser, more distal articulations. If there is a concomitant physiological weakening of these joints, it is not evident from these studies. In most cases it seems that two or three segments remain, but in some rays there appears to be a single, extra long, basal segment which alone remains. Apparently there is considerable variation in the length of these segments. In fish just past this stage, there is evidence of growth almost as soon as healing over has taken place. The new growth, as is evident in fishes still a little more advanced, almost immediately bifurcates, so that by the time the fish are much larger there is the usual primary and often secondary dichotomy, characteristic of most teleost, posterior, low, dorsal rays. An attempt was made by statistical analysis to delimit more critically the number of the segments left, but it was found to be impossible to establish a sufficiently simple means that would be at once practicable and also insure statistical validity.

The elimination of melanin has long been recognized as a normal physiological process in fishes. Kuntz (1917), Murisier (1920–1921), Sumner and Wells (1933), and others have pointed out that the number of melanophores is reduced in fishes that are removed from a dark to a light background, and Odiorne (1937) has confirmed this work and popularized the concept of two methods of pigment reduction. One of these, concerned with the immediate reaction of concentration of pigment granules within the melanophores, he called a physiological process, and the other, concerned with the gradual elimination of actual melanophores, he called a morphological process. Most authors are agreed that the pigment is eliminated through the surface epithelium. Apparently there are two methods of such elimination. Odiorne (1936) has suggested that phagocytes ingest the pigment granules and move to the surface and are eliminated there. Smith (1931) has described phagocytes containing pigment detritus, and Gordon and Lansing (1943) have reported that the elimination of melanophores from the corium of melanotic *Platypoecilus* hybrids was accomplished by macrophages. In fact, macrophages containing pigment debris are common in sections of fish tissue.

A second method of pigment elimination is by direct migration of pigment granules through the surface epithelium. Osborne (1941) has reported that the elimination of pigment through the skin of blinded catfish is so great that the mucus that may be rubbed off the surface of the fish is black with melanin. The elimination of pigment by the fin of *Tylosurus* corresponds to this latter procedure (pl. 4, figs. 1, 2). There is no phagocytosis involved.

It is possible that one of the cellular elements found is a reaction to parasitic infection. In all the fins subjected to histological analysis occasional eosinophiles were seen in the blood vessels and connective tissue. In the sections of the larger Bouin-fixed disintegrating fin, enormous numbers of these cells were present within the blood vessels and connective tissue, particularly between the lepidotrichia. These granulocytes were much more numerous in the smaller blood vessels and capillaries than erythrocytes. Heavily staining chromatin and eccentricity of position characterize the nuclei. The cytoplasm was filled with very large, strongly eosinophilic, refractive granules of regular size. Similar granules, unenclosed by any cell wall, were found scattered among the fibers of the connective tissue. A second disintegrating fin showed an abundance of these cells, and in both cases the fishes had been afflicted with animal parasites.

Coarse granular eosinophiles have been described in various species of teleosts, but they are not always present in the circulating blood. This fact led many early observers to believe that the eosinophile was absent in teleosts. They are normally found in epithelial tissues (Catton, 1948) and in the peritoneal fluid (Drury, 1915). The present authors have noted these cells in various organs of the characin *Astyanax mexicanus* Fillipi, including the surface epithelium, the thymus, the spleen, the head-kidney, and the cranial cavity, but not in the blood

stream. Drury thought that their appearance in the blood might be an indication of a pathological condition. Durand and Toumanoff (1948) demonstrated a reaction of lymphocytes and eosinophiles by injecting bacteria into the abdominal cavity of *Plectorhyncus lineatus* (Linnaeus). Drury (1915) obtained considerable reduction in numbers of eosinophiles in the peritoneal fluid after bacterial injections in *Ctenolabrus rupestris* (Linnaeus) and *Pleuronectes platessa* Linnaeus. He also showed that bacilli or bacillary extracts caused a disintegration of eosinophiles in hanging drop preparations.

In view of the above evidence and the presence of parasitic worms in the dorsal fins showing disintegration, it seems possible that the presence of large numbers of eosinophiles is a reaction associated with parasitism and has nothing to do with the ontogenetic process of sloughing off melanic areas. The parasites in question consisted of the cysts of some unidentified species of worm. The cysts were found on the proximal parts of the ray and near the radialia at the base of the rays. All were in close proximity to blood vessels.

However, the possibility should not be overlooked that the coarse granular eosinophiles play some role in the resorption process. Jordan and Speidel (1931) have postulated a function for the coarse granulocytes having to do with the fat metabolism of the lung-fish. We have noted these same cells in histological material of various species of fish, both fresh-water and marine, and they have been shown to react positively to stains used for the demonstration of fat, such as osmic acid and Weigert's stain for medullated nerve fibers. Morse (1918) has described a liberation of fat from degenerating muscle tissues of the tadpole tail undergoing histolysis during metamorphosis. Brown (1946) disagrees with Morse and believes that the retraction and displacement of degenerating muscle fibers are responsible for the dark color which Morse attributed to released fat. Using Masson's stain which was not designed to demonstrate fat, Brown noted the same dense masses of tissue. However, the coarse granules in these eosinophiles in fishes, which stain with osmic acid, are not dissolved when techniques not designed to preserve the fat are used.

Since the involution of the mandibular lappets in *Tylosurus* appears to take place in a manner similar to the atrophying tadpole tail, it seems possible that the coarse granulocytes are involved in a process of preserving the fat released by the degenerating process for the further economy of the rapidly growing fish. The remarkable accumulation of these cells in the peripheral blood vessels and elsewhere in the involuting lappets and their relative scarcity in the deeper lying vessels of the mandibular region may be another indication of some function associated with the resorbing tissue.

Morse (1918) and Brown (1946) are agreed that phagocytosis plays only a secondary role in the process of atrophy. This is also in agreement with observations on the involuting *Tylosurus* tissues, where no phagocytes were found after extensive search in the disintegrating fin and were only occasionally seen in the involuting lappets. Helff (1926), in describing the histolysis of the operculum where the fore limb eventually breaks through in metamorphosing tadpoles, thought that the infiltration of lymphocytes into the thinning area was for purposes of phagocytosis. No such concentrations of lymphocytes were seen in the resorbing *Tylosurus* tissue.

Bykowski and Nusbaum (1905) have noted similar concentrations of leucocytes in the tissue of the filamentous tail region of *Fierasfer* undergoing resorption. These authors did not differentiate between different kinds of leucocytes, but they undoubtedly referred to lymphocytes. Their drawings show the cells to be lymphocytic in character. Had these cells contained coarse granules they would certainly have been so described by the authors, who described their material in the most minute detail. The function of the coarse granulocytes in *Tylosurus* is therefore still unknown.

DISCUSSION

SINCE IT HAS BEEN SHOWN by three separate approaches that the loss of the high, dark, posterior portion of the dorsal fin of *Tylosurus raphidoma* is not one of relative growth rates but one of direct sloughing off of the distal portion of the fin, some interpretation of the mechanism involved can be attempted. The three approaches summarized are: the proportional measurements of various dimensions of a large number of individuals of various sizes, the actual finding of fish in the sloughing stage, and the histology of the parts involved.

ONTOGENETIC SIGNIFICANCE

As this transformation occurs at least a year before the approach of sexual maturity, when the fish is not far from four months of age, it can hardly be associated with any hormonally induced modification such as is common in many other animals at the time of onset of sexual maturity.

Inasmuch as fish in the actual state of fin degeneration are not readily obtainable, it is evident that the stage is passed through with great rapidity, for those with a full black dorsal or with the adult type of fin are easily obtained. This is graphically indicated in the three text figures, especially figure 3. Such rapid involution leads naturally to the assumption that there was some selective value to shortening the period of transformation as much as possible. Actually such a requirement might be the basic reason for the development of an unusual sloughing-off process instead of a more conventional process of resorption. If this were true, one would expect to find some sharp change in behavior pattern at the time of the transformation. Actually, although the fish are still readily observed from docks, no obvious change in behavior is evident between those with their black "flag" and those that have lost it. The fish a year and a half or more old that are sexually mature are found more often in much deeper water, but no change in location or details of incidental feeding or other behavior is evident. At this time they can be seen making rushes into schools of *Jenkinsia* and *Atherina*, an observation which is confirmed and extended by the examination of

stomach contents indicated in table 3. Strangely, although the intestinal tracts of a dozen fish of 150 mm. standard length and less, bearing well-developed and fully intact black "flags," were examined, not one could be found that contained any recognizable remains. In an aquarium such fish feed readily on any organism small enough for them to engulf, as has already been noted by Breder (1932). These fish have a literally straight tube from gullet to anus serving as an intestinal tract. They are much more easily

TABLE 3

STOMACH CONTENTS[a] OF TRANSFORMING *Tylosurus raphidoma*

Number empty of recognizable remains	9
Number containing recognizable remains	9[b]
Jenkinsia (4 cases questionable)	5
Atherina	1
Synodus?	1
Shrimp sp. ?	3
Callinectid sp. ?	1
Number containing fish	7
Number containing Crustacea	4
Per cent eating fish	64
Per cent eating Crustacea	36

[a] Contents of 18 individuals of from 177 to 237 mm. in standard length taken in late August, 1950, at Bimini, British West Indies.
[b] The total of 11 instead of nine is due to the fact that the fish that contained *Synodus* also held a shrimp and the one with a callinectid also held a *Jenkinsia*.

starved than most fishes, and it would seem that they feed almost continually. With such a short tract it appears almost necessary for digestion to be more rapid, and digestive fluids to be more active, than in other fishes whose intestines offer greater areas of absorptive surface. When the fish are much smaller than the size at which they transform, they "hide" amid floating trash, usually small sticks which they closely resemble, as has been pointed out by Gudger (1929) and amplified by Breder (1946). At no place have the authors seen these fish undertaking this kind of "mimicry" when longer than 50 mm. At Bimini they have never been seen to associate with anything other than the "needles" of the so-called Australian "pine,"

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Casurina equisetifolia. The size of these needles makes them inadequate for purposes of protective association by longer fish. Incidentally, *Tylosurus raphidoma* was going through these stages long before the Australian pine was introduced in this area. One cannot but wonder what they did prior to this time. At the Tortugas they match *Cymodacea* "stems," as pointed out by Breder (1932), but on the Florida west coast they match miscellaneous bits of vegetation, as indicated by Breder (1946). At this stage they are capable of very considerable color change and customarily match the color of the objects that they attend very closely. All this behavior is lost long before they reach the size of transformation.

Whatever the biological significance of this transformation, from the above data it should be evident that we lack, as yet, sufficient information clearly to establish a function, although it seems likely that it may be associated with an abrupt change to predation on some form to which the black "flag" would serve as a warning. A considerable amount of stomach content analysis is necessary to establish this idea.

It has been abundantly demonstrated that dark objects within the visual field of many fishes induce the production of an increased number of melanophores, while a reduction in number is induced by light objects, e.g., Sumner (1939, 1943), Sumner and Doudoroff (1938), Sumner and Wells (1933), and Odiorne (1948). Since at the height of the development of the black "flag," the species under consideration associates with small, dark, and frequently virtually black twigs, it may be that the necessary optical fixation upon them is a factor in the maintenance of the intensity of melanin concentration. It is to be noted that occasional fish can be found without this intensely black area, for Breder (1932) reported one of 59 mm. lacking the melanic area. This individual was taken as a stray in New York Harbor, and it is not known with what it may have been associated. As already indicated, when the fish become too large to associate with the available twigs they still carry this area of melanin concentration on the dorsal fin. It is thought that the very density of the melanic concentration would normally take some

time to be noticeably reduced, perhaps the time between the end of association with dark twigs and the gross appearance of depigmentation, if the maintenance of the pigment is in fact based on the optical stimulation of the dark twigs.

The preceding is tantamount to saying that this morphological change may have a psychogenic basis. Such a view implies that when the fish reaches the stage in its behavioral life history where it ceases to "look at" small dark objects, the following chain of events is initiated. Without optical fixation on dark objects the intense melanophore concentration breaks down. This event in fact does precede the other changes. This may well be primarily responsible, on a mechanical basis, for the shredding of the interradial membrane which in turn may be responsible for the snapping of the lepidotrichia at the joints. Actually the change in optically instigated behavior is more marked at this period in the fishes' life than the above seems to indicate. The change is from the habit of association with dark objects to one in which the fish spends the rest of its life in open, clear water seeing mostly a bluish haze, its all but disappearing fellows, and mostly silvery food objects.

The problem of the utility of the synentognath barbel is inextricably involved in such considerations. As noted in the Introduction, these structures throughout the entire group, when present at all, are juvenile organs which disappear before the onset of sexual maturity. In most forms it is so long before, that the loss of them is not thought to be associated with maturation of the gonads. In the beaked groups, such as the Belonidae and Hemirhamphidae, the structure is represented by membranous flaps or lappets, but in the short-faced exocoetids, typical mandibular barbels are present. These show remarkable variation from species to species, in shape and general conformation, usually a pair being present in *Parexocoetus* and *Cypselurus*, although *Cypselurus comatus* (Mitchill) and *Exocoetus* have single symphyseal barbels, while *C. californicus* has about 14 more or less fimbriate ribbons as demonstrated by Hubbs and Kampa (1946).

The present finding that these elaborate appendages are controlled by smooth muscle

and are completely lacking in taste buds adds to the problem of their function. In addition to the examination of the structure in *Tylosurus*, the evident homologue in *Cypselurus cyanopterus* and in *C. furcatus* has been also selected for study, because the former possesses the most extensive development of this kind in the order, and the latter because it is the only form on which there is any report of a synentognath using these structures. Breder (1932) wrote as follows on their behavior: "The young fish to at least above 18 mm. are intimately associated with the Gulf weed and are never normally found far from it, at least at the Tortugas and Bahamas. Over this size they begin to range farther and farther until adult, when they seem to be fairly independent.

"Observations in aquaria show that they 'poke' into the clusters in a manner suggesting the use of the barbels as tactile or taste organs. At least they would rout out small organisms and then capture them. Such individuals were fed with miscellaneous plankton and always a considerable amount would fall to the bottom in a dying condition. After about a week in captivity, the little *Cypselurus* learned to feed from the bottom, swimming close to it and 'feeling' with their barbels after the manner of an *Ameiurus*." Small *Parexocoetus* without barbels, kept with the above, did not behave in this manner and although found in the same general locations never were seen to give the weed any attention. Muscular motion in the barbels of both species of *Cypselurus* here under consideration have been noted in aquarium material, especially when food was introduced.

If it is fair to assume that the smooth muscle that controls these barbels is not under voluntary control, we then have the curious situation in which these organs twitch or swing, independently of the volitional activity of the fish, on a tactile basis only. With the ubiquity of taste buds on teleost barbels and other exterior surfaces, it is a little difficult to account for their absence in these curiously elaborate transient structures in the Synentognathi. While obviously the examination of these mandibular growths in three species of synentognaths proves nothing about the rest, it seems more than likely that smooth muscle and the absence of taste buds will be found to be characters common to most, if not all, of the species. Nothing short of an extended survey of the order, which cannot be within the province of this contribution, would surely establish the extent of this unique combination of characters in teleost barbels.

PHYSIOLOGICAL SIGNIFICANCE

The significance of the condition of the tissues prior to and during the fin degeneration does not make the nature of the controlling mechanism clear, although some sort of circulatory failure is indicated. The interpretation is complicated by the fact that two specimens studied in the height of this degenerative activity were found to be parasitized. The presence of the great number of eosinophiles may or may not be associated with a reaction to the parasites or to the sloughing of the fin, or to both or neither. Because fish are so often host to a variety of parasites, it would be difficult indeed to obtain a specimen known to be completely free of any parasitic form. Since the parasites were observed in quiescent cysts, it is thought unlikely that they would be the direct cause of tissue destruction in the fin.

Although these highly melanic juvenile fins contain massive aggregations of melanophores, there is no evidence of melanosis, and evidently one of the first steps leading to the loss of the distal portion of the posterior part of the dorsal is a lessening of the number of melanophores in the area to be shed.

SUMMARY

1. SMALL JUVENILE *Tylosurus raphidoma* (Ranzani) concomitantly develop elongation of the posterior rays of the dorsal fins and mandibular lappets. Both structures are areas of intense melanin concentration.

2. Larger juveniles and sexually mature adults lack both these features, having no mandibular lappets and possessing a dorsal fin which is high anteriorly and low posteriorly and shows no concentration of melanophores at any place.

3. The metamorphosis from one form into the other is evidently rapid, for individuals in the state of transformation are not nearly so common as those above and below the size at which it occurs.

4. This transformation takes place when the fish are 200 mm. and 300 mm. in standard length and long before sexual maturity is attained which at the earliest is not under 600 mm.; therefore it is evidently not under the control of endocrine changes which take place at the attainment of sexual maturity.

5. The transformation takes place at an age of approximately six months, and sexual maturity is not attained until a year has passed.

6. Individuals in the transitional stage may be found in the summer and fall, most of the spawning evidently taking place in the first half of the year.

7. The black areas of the dorsal are re-duced not by resorption but by a process of sloughing off. The melanophores break down first, the fin membranes then disintegrate, and finally the fin rays snap off at their articulations.

8. Before the destructive changes take place, the final form of the fin is foreshadowed by the shape of the melanic area of the juvenile fin.

9. A change in behavior takes place before the process of sloughing off occurs, the young juveniles associating with floating twigs or stems about their own size and general color. After they stop this association, the changes described take place, and from then on they avoid such objects and live freely in open water.

10. Histological examination of the mandibular lappets of *Tylosurus* and the barbels of *Cypselurus* showed that these structures are eliminated by a process of resorption.

11. The presence of large numbers of coarse granular eosinophiles in all these involuting structures may be associated either with parasitism or with the resorption process.

12. No taste buds were found to be present in either the belonid lappets or the exocoetid barbels which are evidently homologous, a condition apparently unique among teleost oral appendages.

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