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A STUDY OF THE SMALLEST SHARK-SUCKERS (ECHENEIDIDÆ) ON RECORD, WITH SPECIAL REFERENCE TO METAMORPHOSIS

BY E. W. GUDGER

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INTRODUCTION

The teleostean fishes of the family Echeneididæ are, because of the sucking disk on the upper surface of the head and because of their peculiar habits resulting from its possession, the most interesting of the marine fishes—not merely from a popular but even more from a scientific point of view. Their semi-parasitic, or better commensal manner of life, is rendered possible by this adhesive disk, which is plainly a morphologized first or spinous dorsal fin. The development of this disk is a wonderful problem in embryology, of the solution of which we unfortunately have never had even the least hint. Presumably the little fish undergoes a metamorphosis, and the study of the smallest known forms cannot fail to be of interest and value.

Having at hand specimens of the smallest shark-suckers ever taken of three genera (*Remora*, *Rhombochirus*, and *Echeneis*), and also an exceptional collection of graded young and small specimens of *Echeneis*, and

also having notes of the work of other investigators dealing with various small specimens of these and other genera, it has seemed worth while to bring all this data together and put it on record as a help to understanding the natural history of the sucking fishes.

Three of the specimens dealt with in this paper were exhibited and reported on at the meeting of the American Society of Zoölogists at New Haven on December 28, 1924, and a preliminary notice was published in the Anatomical Record, 1924, XXXI, No. 4. The nomenclature made use of herein is that of Jordan and Evermann in their 'Fishes of Middle and North America,' Washington, 1896–1900.

The members of the highly specialized but cosmopolitan family of sucking fishes fall naturally into two groups: the *Remora* group, with short rather stout bodies uniformly brown in color; and the *Echeneis* group, with long slender bodies striped on the sides. More complete definition of the characters of each group will be set forth under the group headings.

REMORA GROUP

The fishes of this group are short (rarely longer than 15 inches), robust, rather stout fishes; they have short and rounded pectoral and pelvic fins, and have the caudal forked in all stages; in color they range from brown to black without trace of stripes, and have normally from 13 to 26 lamellæ in the sucking disk. In this group three genera and five species are to be found according to Jordan and Evermann. Taking up this group, we will first study the young forms of the following.

Remora remora

The smallest sucking fish ever seen by man, so far as the records go, is a little *Remora remora* 30 mm. between perpendiculars, and 27 mm. to the end of the vertebræ (standard length). This little fish is a perfectly formed *Remora*, adult in every character save size and without a trace of larval structures—as may be seen in Fig. 1. As a specimen its history is rather interesting. It was taken by the U. S. Bureau of Fisheries Steamer 'Fishhawk' on September 3, 1914, in 34° 12′ 52″ N. Lat. and 76° 1′ 58″ W. long.—i.e., about thirty-five miles southeast of Beaufort Inlet, N. C.—at the surface in a stramen or heavy tow net.

Lewis Radcliffe, at the time of its capture director of the Fisheries Laboratory at Beaufort, showed me the little fish at Washington during the holiday season, 1914. It was loaned to me and was photographed and studied. Photograph and notes were then laid away until I could go

into the study more carefully. When the opportunity came I found that the fish itself was again needed, but in the meantime the great war had come, and in the changing work of the Bureau of Fisheries incident to the war the little *Remora* had disappeared. Search was made for it in the collections of the Bureau and even the vast collections of the United States National Museum were hunted through, but without avail. In the winter of 1924, Mr. S. F. Hildebrand, at present director of the Beaufort station, called at my office in New York and I asked him about the little *Remora* but he could give no information. However, in August, 1925, he found it in the collections at Beaufort and promptly loaned it to me for further study.

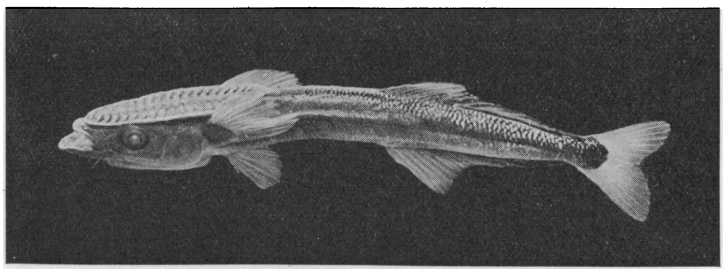

Fig. 1. *Remora remora*, the smallest known sucking fish—30 mm. over all, 27 mm. standard length. Taken in 1914 at the surface in the open ocean 35 miles southeast of Beaufort, N. C.
Collections U. S. Bureau of Fisheries.

The next smallest specimen to the above is one taken by Wm. Beebe on his first Galapagos expedition. While anchored in Key West harbor, on March 9, 1923, an 8.5 ft. shark was hooked, and when hauled on deck this little *Remora* was found adhering to it near the gills. This specimen is now in the collections of The American Museum of Natural History. The measurements in millimeters of these small specimens follow—No. 1 from Beaufort, No. 2 from Key West.

The first fish is in excellent condition save that it has been badly shrunken by strong preservatives, the second is in bad shape owing to too weak preservative. In both the disk has 18 lamellæ plainly countable, and in both the dorsal and anal fins are so small, or so torn and so collapsed that the fin rays cannot be counted without further damage to the fish. The measurements referred to when worked up into ratios vary somewhat from the proportions for adult fish as given by Jordan and Evermann (1898), as might be expected from such small specimens. In

	No. 1	No. 2
Length over all (between perpendiculars)	30	49
Length—tip of snout to end caudal vertebræ	27	43
Length of disk	9	14.5
Width of disk (greatest)	4	6
Width of head (at base of pectorals)	4	7.5
Number of lamellæ	18	18
Length of head	7.5	12
Length of base of soft dorsal fin	9.5	12.5
Length of base of anal fin	8.5	12

the next paragraph these differences will be set out, Jordan and Evermann's figures being put in parentheses.

For the Beaufort *Remora* the proportions are: head 3.8 (4); disk 3 (2.75); width between pectorals (greatest width of disk) 6.75 (5.25). The ventrals are not adnate to the abdomen in any degree whatever ("for more than one-half the length of their inner edge"). Disk slightly shorter than soft dorsal and slightly longer than anal—9.5 and 8.5—(not longer than both). Pectoral with about 20 rays, 5 mm. long or 0.3 of the length of head (not 0.6). For the Key West fish: head 3.6 (not 4); disk 3 (not 2.75); width between pectorals 5.7 (not 5.25). Ventrals not adnate to abdomen in any degree. Disk slightly longer than either dorsal or anal (both fins in such condition that there is a possibility of slight error in measurements). Pectorals in too bad condition to count rays. It should be stressed that these measurements are made from preserved specimens.

Color of Key West specimen brown. Lateral line in median region of side, running about straight forward to about hinder extremity of pectoral, where it bends abruptly upward at an angle of about 35°. On the Beaufort specimen were found on the sides of the body (in the comparatively freshly preserved fish) about 18 dark transverse bands, slightly angled forward like myomeres, not very distinct above the lateral line—

especially back of the beginning of dorsal and anal fins. Body color brown with a stippling of brown dots, becoming lighter below. After 12 years in formalin the body is much shrunk and the color is black. Lateral line very conspicuous and placed about mid-laterally. All fins transparent.

A Dane named Daldorf (he of the climbing fish story), on a journey in 1790–91 from Kjobenhavn to Tranquebar on the east coast of India, took from a shark in mid-tropical Atlantic two small grayish-brown sucking fish. These he described (1793) as being slightly over 2 "pollices" (inches?) long and having 15 lamellæ in the sucking disk. These little fishes seem to have been adult in everything but size. Daldorf named his fish *Echeneis squalipeta*, but to it is now assigned the name *Remora remora*.

In his section on Fishes (part IV of the 'Zoology of the "Beagle,"'), Jenyns (1842) says that near St. Paul's Rocks (in the tropical Atlantic about 1300 miles east of the mouth of the Amazon) Darwin got off a shark a small *Echeneis remora*. This little fish had 18 sections in its sucking disk and was slightly under 4 inches long. It was undoubtedly a *Remora remora*. There was no indication of any larval characters.

In 1867, Couch took from a shark on the English coast a 4.5 inch *Echeneis remora*. His brief description leads to the belief that it was a *Remora remora*, and that small as it was it was full grown in all but size.

Lütken (1875), among the 69 specimens of *Echeneis remora* (our *Remora remora*) in the museum of Copenhagen, found that his smallest fish was 42 mm. long. It then is smaller than Beebe's specimen and but 15 mm. longer than the 27 mm. fish from the U. S. Bureau of Fisheries. In fact it ranks as the second smallest specimen known. Finally the only other small sucker of this genus of which I have knowledge is a 4.25 inch (114 mm.) specimen which, according to Day (1881), was taken from a porbeagle shark near Mevagissey, Cornwall, England. Both these little fishes were normal in structure.

Just here it should be emphasized that neither in my specimens nor in those reported from the literature is there a single trace of a single larval or post-larval character. All these little Remoras were adult in every external feature. If they undergo a metamorphosis, it must be before they reach the very small size of one inch (25 millimeters).

Remora albescens

Günther (1860) inspected a 6-inch (151 mm.) specimen of this fish (his *Echeneis albescens*) collected in Chinese waters by Sir J. Richardson. He refers to no larval structures, although (as will be shown later) he

knew of such in other sucking fishes. The same remarks apply also to Temminck and Schlegel's (1850) 8-inch (203 mm.) specimen of this fish from the same waters. Both these fishes had 13 segments in the disk.

Remora brachyptera

Later in the very year that Lowe established the new species, *E. brachyptera* from Madeira, Storer (1839), under the name *E. quatuordecimlaminatus*, described a small specimen of the same fish from Massachusetts waters. This was a little fish 5.5 inches (140 mm.) long over all, which however presented no features not found in the adult. Its lamellæ numbered 14 as his specific name indicates. The name now used is that given above.

Temminck and Schlegel (1850) reported from Japanese waters two small sucking fishes which they denominated *Echeneis pallida*. These specimens had 16 lamellæ in their disks and were 5.5 (140 mm.) and 6 inches (151 mm.) long respectively, and showed no trace of larval characters. Jordan and Evermann (1898) identify these fishes under the name given above.

In the collections of the Copenhagen Museum, Lütken (1875) found two small suckers each about 4 inches in length, which he calls *E. pallida* but which he thinks may well be designated *R. brachyptera*. These were taken from the gills of a round-billed swordfish (*Tetrapturus*) captured in the Atlantic about 300 miles east of Cape San Roque. The caudal fin of this sucking fish according to Jordan and Evermann is normally "nearly truncate," but in these small specimens it was a "little convex."

Finally, there has just come to our Museum a 160 mm. (6.25 in.) *Remora brachyptera* taken from the gills of a 210-lb. marlin swordfish at Ceralvo Island, Gulf of California, by an expedition conducted by Mr. Keith Spalding of Pasadena. California. This fish has the caudal truncate. Perhaps the convexity in Lütken's specimens was an individual peculiarity, though, of course, it may be a larval character.

Before taking up the study of the last member of the *Remora* group, reference may be made to Dr. Murphy's note in Copeia (1914). In the north Atlantic (27° N. Lat. and 62° W. Long.) in 1912, he saw on a large Balistid fish "3 small, slender, dark-colored fishes (*remoras*) which appeared to be attached to the trigger fish's side." These were about 8 cm., 3.2 inches long. They were probably Remoras or Rhombochiruses —in any case their color indicates that they did not belong to the *Echeneis* group of the shark-suckers.

Rhombochirus osteochir (Cuvier)

Of this interesting form I have two small specimens—one from Long Key, Florida (No. 1 of the table), and the other from San Diego, California (No. 2 of the table). Their measurements in millimeters are as follows:

	No. 1	No. 2
Length over all	68	73
Length to base of last caudal vertebra	61	62
Length of disk	22	24
Width of disk (greatest)	9	10
Width of head at bases of pectorals	9	12
Number of lamellæ	17	18
Length of head	15	19
Length of base of soft dorsal fin	20	19
Length of base of anal fin	18	18

The smaller specimen, which has 17 lamellæ in its disk, was taken at Long Key, Florida, by Mr. N. Jerlaw of Chicago on February 23, 1924. It was preserved and forwarded to me by Mr. Hamilton M. Wright, a newspaper man of New York City, who kindly gave me the following data: "Mr. Jerlaw hooked and landed a 73.75 inch sailfish at the edge of the Gulf Stream . . . and this little sucking fish fell from its gills. . . They tell me down at Long Key that they seldom catch a sailfish that does not have one of these little sucking fish in its gills. They also say that they sometimes find them in the gills of the barracuda and other large fish." This little fish is portrayed in Fig. 2.

Compared with Jordan and Evermann (their figures in parentheses), we find the following variations in ratios, etc., between this fish and the Long Key specimen: head in length 4.1 (4.67); disk 2.77 (2.25); width between pectorals 6.8 (5). D. 17–23 (17–21 to 23), A. 22 (20 or 21).

Other differences are that the disk does not extend "forward beyond the tip of the snout," that the caudal fin is notched with the tips pointed instead of rounded, and that the central rays (i. e., those extending back to the notch) are much darker than the others. Further, the color is practically uniform above and below instead of being paler below. Finally, my specimen like Jordan and Evermann's was taken from a sailfish, but these authors are in error in calling it "parasitic" since it is a commensal or symbiont but never a parasite. The lateral line runs forward in mid-lateral region of the body to the hinder edge of the pectorals where it turns sharply upwards. Pectorals short and rounded;

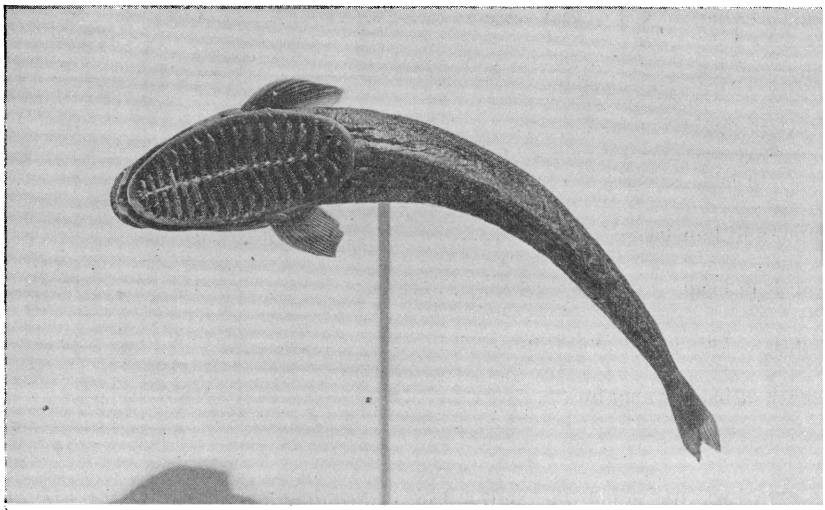

Fig. 2. The smallest known *Rhombochirus osteochir*—68 mm. over all, 61 mm. in standard length. Taken from the gills of a sailfish at Long Key, Fla.
Presented by Hamilton M. Wright.

rhomb-like, with stiff rays—*Rhombochirus*, rhomb (or rounded) hand (or pectoral).

In November, 1921, Prof. H. W. Norris had in Science a note on a small sucker taken from a tuna shark, *Isuropsis glauca*, at San Diego, California, just one year previous. The head of the shark had been cut off and carried to the laboratory, where in dissecting it this small *Rhombochirus* was found on the table—having fallen out of the mouth or gills. Prof. Norris's note in Science brought him a letter from me, and in reply he kindly sent the specimen, the measurements of which are given in the table above.

The proportionate measurements of this small specimen to Jordan and Evermann's fish (theirs set in parentheses) are as follows: head in length 3.3 (4.67) ; disk in length 2.6 (2.25); width between pectorals into length 5.4 (5). The disk does not extend even to the tip of the upper jaw ("extending beyond the tip of the snout"), The caudal fin is emarginate but has pointed (not rounded) tips as has the Long Key specimen, and the central rays, like those in the preceding, are markedly darker than the other rays. Color light brown above, somewhat darker below—much lighter than the Long Key fish. The ventrals are much longer and slenderer in this fish than in the preceding—9.5 mm. long by 2 mm. wide compared with 5.5 long by 2 wide for that above noted.

My next smallest *Rhombochirus* was sent me by a Pacific coast sportsman, Mr. A. R. Martin of Beverly Hills, California. It was taken from the gills of a one-hundred fifty-eight-pound marlin swordfish (*Tetrapturus mitsukuri*) at Santa Catalina. This *Rhombochirus* is 105 mm. (4.25 inches) long over all, and 92 (3.6 inches) in standard length. It has 18 lamellæ in its disk which is 24 mm. long by 15 wide. This disk (like the others) does not reach to the end of the upper jaw. The ventral fins in this fish are, like those of the specimen just described, somewhat longer, narrower, and more pointed (12 mm. long by 3 wide) than those of the smallest specimen. Evidently there is considerable variation here. Apparently there is variation also in the shape of the pectorals which seem to grow relatively shorter and rounder with age. The caudal fin is emarginate, and (unlike the two smaller fish) has the angles or points somewhat rounded. The whole fin is dark, but held against the light the central rays show up somewhat darker than the others. When this fish was received here, it was covered with a coating of blue-gray mucus precipitated on it by the formalin used as a preservative. It has not been possible entirely to remove all of this, but the underlying color seems to be a dark brown. The fins are black.

Poey (1856) was the first to describe from the western Atlantic this form of sucking fish. He had a number of specimens (the smallest 200 mm. long). All his specimens came from the sailfish *Tetrapturus* (probably *Istiophorus nigricans*), and he averred that this species is found only on that fish. Accordingly, he named it *Echeneis tetrapturorum*, or colloquially, "Pega de los Agujas," the sucker of the spearfishes. However, as has been noted above, it is taken on sharks as well and Mr. L. L. Mowbray of the New York Aquarium has taken it in the gills of the ocean sunfish, *Mola mola*, and from the barracuda.

Remilegia australis

This sucking fish, possibly the rarest form of the Echeneididæ, is remarkable for having a huge disk measuring nearly one-half the standard length of the fish and having from 24 to 27 lamellæ. Only one young specimen seems to be known. Lütken (1875) found in the Copenhagen Museum a specimen 46 mm. long and having 25 segments in its disk, which had been taken from a dolphin (the mammal not the fish) in 10° N. Lat. and 39° W. Long. This little sucker, though one of the smallest on record, presented no features not usual in the adult.

ECHENEIS GROUP

The sucking fishes of this group are long, slender and subcylindrical in form; their pectoral and pelvic fins are rather long and slender and decidedly pointed; the caudal in the young fish (as we shall see later) has a prolonged central lappet which progressively shortens down, becoming plumose, and finally somewhat concave behind. The color is generally slaty brown or greenish blue with a broad black stripe extending backward through the level of the eye and pectoral, along the middle of the side to the base of the caudal and in young specimens through this; above and below this are narrow white lines, while above and below these the dark body of the fish gives the impression of outer dark bands. Sucking fishes of this group attain the considerable length of about 36 inches. There are two species—one with 9–10–11 lamellæ in the disk, the other having from 20–28.

Phtheirichthys lineatus

So far as my personal experience goes this is the rarest of the sucking fishes. It was first described by Archibald Menzies in 1791 from a specimen "about 5 inches long" (125 mm.) taken from a turtle in the central tropical Pacific. Like *Echeneis* it has two narrow longitudinal white stripes on the sides separated by a broader dark one. And like the half-grown specimens of *Echeneis* it has a plumose or fan-shaped or spatulate caudal. It has, however, the smallest number of lamellæ (normally 10) known in the disk of any present day sucking fish. Menzies' illustration is herewith reproduced as Figure 3.

Poey (1856) had a still smaller specimen, 75 mm. (3 inches) long, which showed all the characters of Menzies' fish—10 lamellæ, slender body, stripes, etc. Poey notes the plumose caudal and says that this is a distinctive character of this genus, which he emphatically says is found

only in the gills of the big barracuda and from which it escapes when the later is caught.

Of this form Lütken (1875) tells us that he had 6 small specimens; 3 from the tropical and north central Atlantic, and 3 from the West Indies. These fishes ranged from 2.5 to 3.5 inches (63 to 89 mm.) in length. One sucker came from the stomach of a large mackerel-like fish, but no data was at hand for the sources of the other five. The pairs of plates in these various suckers were 9–10–11. For us, however his most interesting and significant statement is that, "In the very young fish, the middle rays of the caudal are, moreover, extended in a thread-like, fashion." In older fishes, the caudal is rhombic—i.e., shaped as in Menzies' figure. Here, then; is the first intimation of a metamorphosis or transformation in the tail fin of this member of the *Echeneis* group of

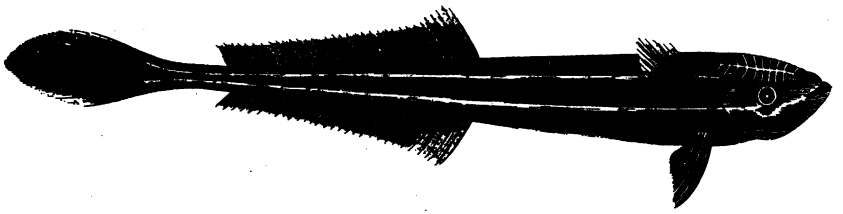

Fig. 3. *Echeneis lineata* (*Phtheirichthys lineatus*), the earliest known specimen—"about five inches long." Note the disk with ten segments, the striped sides, and the spatulate (or plumose) caudal. Specimen taken from a marine turtle in the tropical Pacific Ocean.

After Menzies, 1791.

the sharksuckers. Indeed, Lütken, comparing Poey's fish and his, definitely says ". . . this *E.* (*Phtheirichthys*) *sphyrænarum* is entirely identical with the young ones at hand of *E. lineatus*, and is undoubtedly nothing else but a step in the development of this species."

Günther (1876), in working over Andrew Garrett's fishes collected in the South Seas, describes an *Echeneis lineata* (synonymous with our species) and adds that in the British Museum is a small specimen with a peculiar caudal. This he says ". . . is different from that of the adult, in that in the young the middle rays are produced into a long thread." This he figures, and it is reproduced herein as Figure 4. On the same plate, he figures "an older specimen" with a plumose tail very like that on Menzies' fish. Unfortunately he gives no lengths for either fish, but in the figure the first is 61 mm. (2.5 inches) long in standard length and 85 mm. (3.4 inches) over all—the caudal being 24 mm. long and the prolonged central lobe 13 mm. (0.5 inch) long beyond the body of the

caudal. The larger fish is 235 mm. (9.4 in.) in standard length and 271 mm. (10.8 inches) over all as portrayed in the figure, and has a spatulate caudal almost identical with that of Menzies' fish (Fig. 3). Presumably these fishes are drawn natural size, although unfortunately our author nowhere so states. However, one thing is clear—i.e., that the larval and post-larval stages of this fish undergo a metamorphosis in the form of the caudal fin. Further on it will be seen that this is true of another genus also.

Franz (1910) described a specimen from Misaki, Japan, which was 15 cm. (5.9 inches) long and absolutely normal in every respect. Three

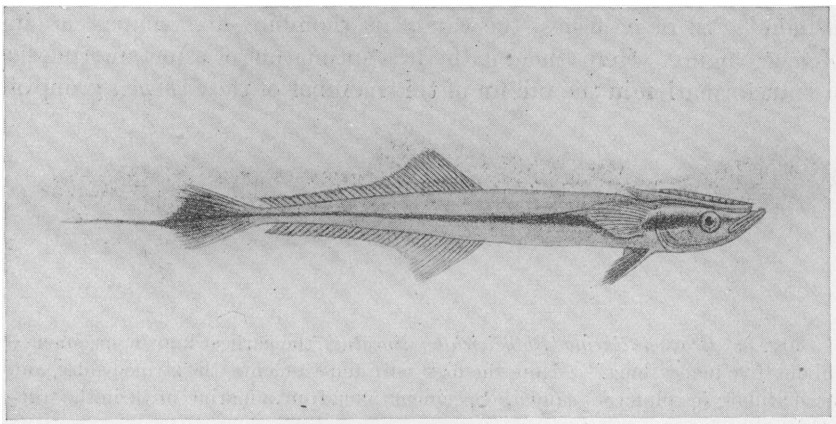

Fig. 4. A post-larval *Phtheirichthys lineatus* showing the prolonged central lobe of the caudal fin. From a specimen in the British Museum collections. Measurements not given, but presumably drawn life size—85 mm. total, 61 mm. standard length.

After Günther, 1876.

years later Tanaka (1913) described and figured another specimen of this form also taken near Misaki, Sagami, Japan. This fish was 21.2 cm. (8.4 inches) long from tip of upper jaw to tip of middle rays of caudal, of which he says, ". . middle rays produced so that the posterior margin is acutely rounded." From these accounts we may judge that the Japanese *Phtheirichthys* agrees in form of tail with the other known specimens of semi-adult fishes of this species and with Menzies' fish.

My personal knowledge of this form is confined to one possible experience. On July 4, 1914, at Tortugas, Florida, I took on a trolling line a 41-inch *Sphyræna barracuda*. When it had been brought on deck and subdued by being knocked on the head with a hammer, I found clinging

to the deck a beautiful little sucking fish, apparently (in stripes and plumose caudal) a counterpart of Menzies' fish. It was carefully detached, put in a jar of salt water, and later transferred into an aquarium of running salt water at the Laboratory of the Carnegie Institute of Washington. As it seemed sick and as the hour was late, examination of it was postponed until next morning. But when morning came no trace of the little fish could be found in the aquarium (where all the fishes were smaller than it), on the floor, in the waste pipe, or on the ground outside where the waste water fell. The only possible explanation is that it may have been abstracted by the cat from the lighthouse a quarter of a mile away. Yet never before or since has such a loss been had. Thus was lost the opportunity not only of identifying this specimen as Menzies' fish, but also of settling the question of whether it was identical with Poey's *Echeneis sphyrænarum*, "the sucker of the barracudas."

After my experience above noted, every boat that went out collecting at Tortugas had a trolling line swinging out behind, and I personally took every opportunity to go trolling. Numerous barracudas were taken, but not another of them had an adherent sucker when landed. There is, however, the strong possibility that these latter may have escaped in the strong fights put up by the barracudas before they were brought into the boat.

Echeneis naucrates

This sucking fish is the most abundant member of the family, the best known form (being represented in great numbers in collections), and has the greatest variation in the segments of its sucking disk (20–28).

The first reference to any peculiar structure in the caudal fin of juvenile forms of this fish is, so far as I know, found in the writings of Edward Rüppell (1835), He described from sharks and rays in the Red Sea a sucker which he named *Echeneis vittata*, but which is now believed to be correctly called *E. naucrates*. Rüppell, in his brief diagnosis, says: "Fin of the tail of the juvenile fish acuminate, that of the adult fish with elongate lateral points, and with the posterior margin cut in concave form." In his "description" he writes less clearly that ". . . the caudal fin in different ages of the fish undergoes great modifications in form. In young individuals this fin is bounded on the hinder edge by two lines that converge in a right angle. With increased growth, the points of the side edges in turn elongate so that in the full grown fish (about 3 ft. long) the hinder edge of the caudal fin appears to be cut in concave fashion."

The next notice of small specimens of this form has been found in the writings of Duméril (1858) where, on p. 375, he refers to the shape of the caudal "whose middle lobe, which is acuminate, exceeds in length the lateral lobes." That this is a larval structure will be pointed out later. In this paper Duméril sets forth the names of 46 species of sucking fishes based on examination of 161 specimens in the Museum d'Histoire Naturelle, Paris. He gives no sizes nor descriptions, but undoubtedly had some small specimens.

Early in 1860 Günther published volume II of his 'Catalogue of Fishes in the British Museum.' In this, under *E. naucrates*, he lists four young specimens, one of which (from New Guinea) was 6 inches long and had "the middle portion of the caudal considerably produced." The smallest was from California and measured "total length 4 inches; produced part of caudal 1½ inches." Later in the same year (1860) Günther published his 'History of *Echeneis*,' which is today the outstanding historical work on this most interesting family of fishes. Of the changes which take place in the caudal of *Echeneis naucrates* he makes the following explicit statement—the clearest on the subject known to me:

> The caudal fin undergoes extraordinary alterations with age. In *young specimens* about 4 inches in length, *the middle portion of the fin is produced into a long filiform lobe*. This lobe gradually becomes shorter, and the fin shows a rounded margin in fishes of middle age, with the middle portion sometimes distinctly projecting beyond the level of the margin. When, finally, the fish approaches the mature state, the upper and lower lobes are produced, and the fin becomes subcrescentic or really forked. Even in this state, I have observed specimens in which the middle part of the fin is slightly produced, so that it has the appearance of having three lobes.

Again, in 1876, Günther says of *E. naucrates:*

> In young individuals about 4 inches long the median rays of the tail fin are prolonged into a band-like lappet. With the growth of the fish, the lappet shortens and may entirely disappear, while the upper and lower points elongate backward on the edge. In fact one finds individuals with a concave or convex hinder edge to the caudal, and finally some in which the hinder edge is seen with three lappets or points.

Here then we have a definite statement of the metamorphosis of the tail-fin structure in *Echeneis naucrates*, aligning this fish with *Phtheirichthys* as noted by Lütken and by Günther. This matter will be gone into fully when description is given of my own material.

Although Lütken (1876) had 24 specimens of *Echeneis naucrates*, his smallest fish was only 5 inches long, and he gives no data whatever concerning the structure of the caudal—in striking contrast to his clear-cut statement as to the metamorphosis of this fin in *Phtheirichthys lineatus*.

Alleyne and Macleay (1877) caught a number of large specimens of *E. remora* (*E. naucrates*) at Darnley Island (in Torres Straits). "These were all full-grown fish and had slightly bilobed tails. Young specimens, about 7 inches long, taken at Cape York and Warrior Reef, present a different appearance. The middle rays of the tail are elongate."

Finally, Fowler (1903) will be quoted that a 5.16 inch (138 mm.) *E. albi-cauda* (synonym for *E. naucrates*) taken from a shark in Biscayne Bay, Florida, had a tail fin in which the "median caudal rays project." While Fowler is the last author to be quoted, it seems not improbable that if all the references to the sucking fishes could be looked up, other data might be noted on other small specimens of *Echeneis*. My personal observations will now be given based on a large collection of small Echeneises from Key West, Florida.

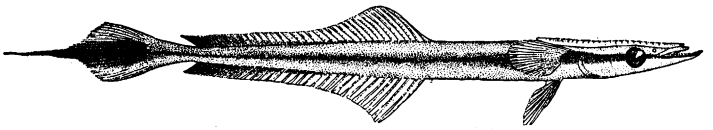

Fig. 5. A post-larval *Echeneis naucrates* (No. 2 of the table)—89 mm. in greatest and 70 mm. in standard length. Caudal 19 mm., lappet only 9.5 mm.
From a collection of 34 specimens of small forms from Key West, Florida.

In 1915, while working at the Marine Laboratory of the Carnegie Institution of Washington at Tortugas, Florida, I became interested in the metamorphosis of the tail in the genus *Echeneis*. My friend, Dr. Alfred G. Mayor, director of the laboratory, gave me a sum of money to be used in collecting small specimens of this fish. The interest was aroused of Mr. Peter Roberts, keeper of the fish market at Key West, and of the local fishermen, and during the months of July to October inclusive they got for me 34 specimens ranging from 70 to 123 mm. standard length (2.75 to 4.88 inches) and from 85 to 143 mm. (3.38 to 5.7 inches) over all. I plan later to work up short articles on the changes during growth of the caudal fin and on the variations in the number of the laminæ in the suctorial disk. But at this particular juncture the form of the caudal is the matter of particular interest.

Four of these little shark-suckers (unfortunately there is no data available as to the fishes from which they were taken) have a dark central prolongation of the caudal precisely as Günther figures for *Phtheirichthys*. The measurements in millimeters for these fishes are tabulated below. These measurements were not easy to make on these fishes, many of which

are bent, but they have been taken several times over with great care. All the fishes are in good condition (other than being bent) save No. 1, which was evidently dried up before it reached Mr. Roberts. The specimen shown as Figure 5 is No. 2 of the table.

Echeneis naucrates, juvenile forms from Key West, Florida

	No. 1	No. 2	No. 3	No. 4	No. 5
Length of caudal—base to tip median lappet..	16	19	18	20	26
Length—tip upper jaw to last verteb a.....	70	70	75	75	96
Length over all.....	86	89	93	95	122
Length of disk.....	20	19	20	20	24
Width of disk.....	7	7	8	8	9.5
Laminæ in disk.....	21	21	20	21	23
Length of head.....	15	14	15	15	18
Length of head in standard leng h.....	4.7	5	4.7	5	5.3
Length of disk in standard length.....	3.5	3.7	3.75	3.75	4
Depth in standard length.....		12.5	12.5	13.6	12.0

There is a remarkably uniform gradation in all the points recorded for the fishes in this series. The central lobe of the caudal is much subject to either wear or variation—the smallest fish has the shortest prolongation (6 mm.) of the central rays beyond the vertical through the ends of the dorsal and ventral white parts, and the largest fish has the longest (14 mm.). The lengths, both standard and total, are well graded. Fish No. 2 has a disk relatively shorter than the others, but the widths of the disks run uniformly. Fish No. 3 drops below the normal in number of laminæ, while No. 5 runs above, but both are well within the limits set by Jordan and Evermann of 20–28 (for the combined species *E. naucrates* and *naucratoides* which they doubtfully separate and which are now considered as one species, *naucrates*).

In relative proportions, my fish vary for length of head in standard length from 4.7 to 5.3, while Jordan and Evermann say 5.25; and for

length of disk in standard length from 3.5 to 4, while our authorities say 4 to 5. My depths are 12 to 13.6 in length, while theirs were 11 to 12. Fish No. 1 is shrivelled so badly that this latter measurement could not be accurately gotten. All the other fish are in excellent preservation save that in their eleven years in formalin their lateral stripes have all disappeared, except the central one, but the dark color of their dorsal and anal fins and of the median prolongation of the caudal still persists. The fish are of a uniform light-brown color, due to a meshwork of fine dots.

My other larger and older fishes from Key West have this central prolongation much shortened but still longer than the white dorsal and ventral outer portions of the caudal—the whole forming a spatulate fin like that on Menzies' fish—Figure 3.

It is now clear, from what various authors say and from what my materials show, that the young of *Echeneis* like the young of *Phtheirichthys* undergo a metamorphosis in the caudal fin. On the other hand nothing of the kind has been found in young Remoras down to as small a size as 27 mm.—hardly more than one-third as large as my smallest Echeneises.

This point forms another diagnostic character in separating the Echeneis forms from the Remoras. This was first noted by that great ichthyologist, Theodore Gill, as long ago as 1863 (p. 239) when he says of the "Echeneides [*Echeneis* and *Phtheirichthys*], caudal with median rays produced in the young, emarginated in the adult;" and of the "Remoræ [*Remora* and *Remilegia*], caudal generally more or less emarginated in the young, as well as in the old." Just what data he had on which to base these statements is not revealed in his article, but, since Dr. Gill had a most extraordinary knowledge of the literature of fishes, he presumably knew of the facts above quoted from articles antedating 1862.

Echeneis glaronensis

A Fossil Echeneid

In endeavoring to trace back the life history of the Echeneididæ, all the known young specimens have been studied, and, while they have been of very great interest, it must be confessed that they have led us back only as far at best as post-larval stages. At this point let us turn to palæontology to see if in that science we can get any hint as to the origin of this fish and its sucking disk. Here we find that only one fossil form has ever been figured and described. In 1886, Wettstein published a figure and description of *Echeneis glaronensis*, from the Tertiary strata of the canton of Glarus in Switzerland, preserved in the geological collections at Zurich.

Wettstein's description is quite technical but fortunately he gives an excellent life-sized figure, which is reproduced herein as Fig. 6. This skeleton is in natural size 225 mm. (9.2 inches) in length from tip of upper jaw to the end of the last caudal vertebra, and hence belonged either to a young fish or to a small species. It too shows no trace of larval characters. Only the hinder part of the sucking disk is shown but this, which certainly constitutes the major portion of that organ, contains 5 lamellæ which are separated by relatively wide interspaces. These measure, from before backward, as follows: spaces one, two, and three, 4.5 mm.; space four, 4 mm.; space five (from the last lamellæ to hinder edge of disk), 3 mm. These interspaces are about twice the width of those in the disk of a modern form of like size. In a preserved recent *Echeneis naucrates* of 220 mm. standard length the interspaces of the disk average about 2 mm. in width. Only in large modern specimens running from 30 to 36 inches will one find interspaces as wide as in this 9-inch fossil form. However, the present day *Remilegia australis*, which has a disk extending backward nearly one-half the standard length of the fish, has from 17–22 lamellæ. In a California specimen 280 mm. in standard length, the disk is 117 mm. long and has 18 lamellæ. Going from before backward, the space between lamellæ one and two measures 4 mm., that between nine and ten 6, and that between seventeen and eighteen measures 9 mm.

As may be seen in Wettstein's figure, the upper edge of the disk is an arc of a very flat curve which, before rounding to at the front end, might have embraced two or possibly three more lamellæ. Not so, however, the lower edge of the disk which forms part of a curve which, if continued in front, would not allow in a restoration for more than one, or at the very most, two other lamellæ.

We may go at the matter in another way. Begining at the right or front end of the disk, using a pair of dividers under a glass and taking the distance between lamellæ one and two as a unit, we find the space between two and three to be almost exactly the same; but between three and four the distance is slightly less, and between four and five noticeably less. This may, of course, be due to distortion, but for argument's sake taking it as normal and studying the curves of the outline of the disk, it will be seen that the disk could not have possessed more than two more lamellæ, or seven in all. The remains of one of these may be seen on either side just anterior to the present broken-off part of the disk. If the two anterior ends of these fragments are taken to represent the remains of another lamella and the dividers are applied it will be found

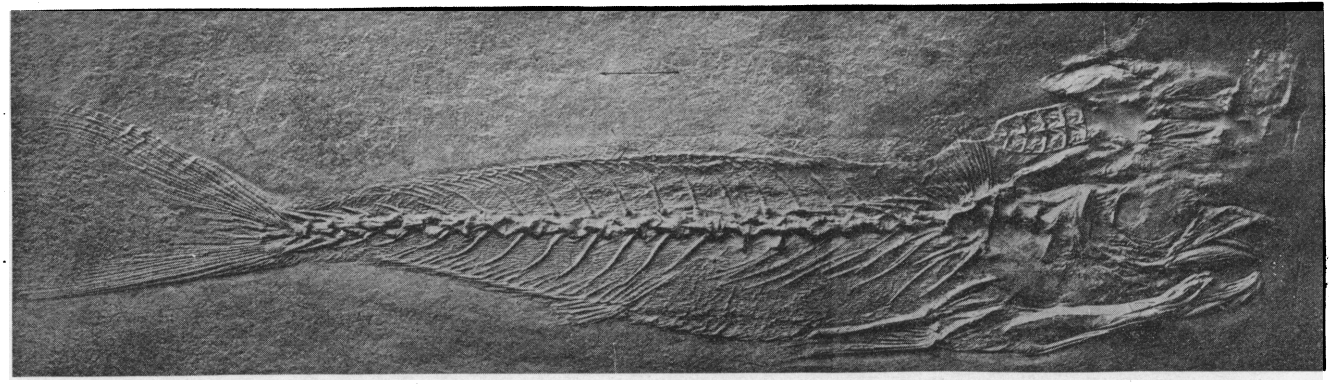

Fig. 6. *Echeneis glaronensis*, the only known fossil echeneid—natural size about 295 mm. in total, 225 mm. in standard length. From the Tertiary rocks of the canton of Glarus, Switzerland. Note the small number of lamellæ (5) and their wide separation. After Wettstein, 1886.

that the space between these fragments and the first perfect lamella is fairly close to that between lamellæ four and five. This leads to the conclusion that one more long, transverse, flat-angled partition and one other short, obtuse-angled lamella, as in present day forms, are all the additional segments which *E. glaronensis* possessed in its suctorial disk.

I have tried to figure it out that the parallel-sided structure in the right top corner of the figure represents the torn-away part of the disk. But it is too far away and not in what seems to be the line of application of the force which crushed and flattened the head, it is too wide, and finally it shows no sign of transverse lamellæ. It seems not improbable that in removing the slab lying on top of this skeleton, the front part of the disk came away with this slab leaving the depression now found where this part of the fossilized disk once was.

Taking all these facts into consideration, my judgment is that *Echeneis glaronensis* could not have had more than two additional segments in its sucking disk, or seven in all. Or making the largest possible allowance, not more than 3 additional lamellæ, or 8 in total count. This would ally it on the basis of a consideration of suctorial disk only to *Phtheirichthys* which has 10 lamellæ. Wettstein does not go into this speculation, which is certainly an interesting one, but allies his fish with *Echeneis remora* (*E. naucrates*) on points now to be considered.

Wettstein's figure is apparently made from a photograph, and he alleges that the disk (or its fragment) goes 13 times in the total length—I find it 14 (10.5 in standard length). He makes the width of the disk in its own length 2.3 times—I find it 2 exactly. Head in body 4.5, which is correct. Vertebral column with 10 abdominal plus 12 caudal vertebræ—I find 10 abdominal plus 13 caudal. He finds 18 main caudal rays which count seems to be correct. He does not count the pectoral and pelvic nor the soft dorsal and anal rays, which I make out to be about 15 and 7 respectively for pectorals and pelvics, and about 28 and 23 for soft dorsal and anal fins.

Disregarding the evidence from the disk, Wettstein places his fossil form near to *E. remora* of Linnæus, or in modern nomenclature *Remora remora*—this mainly on the basis of the number of vertebræ(12–15) in *Remora*. But *Remora* has 23 rays in the soft dorsal and 25 in the anal, whereas the fossil fish has about 28 and 23 respectively. Furthermore, *Remora* has 18 segments in the disk where the fossil has at most a possible 8 (*Phtheirichthys* has 10). The fossil and *Phtheirichthys* certainly approach in the number of segments in the disk, and I venture to suggest that if the caudal of the fossil were clothed in flesh it would probably

approach more nearly in general to the long plume-like form of that in *Phtheirichthys* than the shorter, blunter form in *Remora*. The rest is conjecture. Jordan and Evermann put *Phtheirichthys* and *Echeneis* in a group which their key says has 14 plus 16 equal 30 vertebræ. But so far as is known no man has ever counted the vertebræ in the first genus. There is not today a good description of the louse-fish, or even a complete fin ray count. Poey's gives a partial count only of the fin rays in his one specimen of *E. apicalis*, now known to be a synonym for *Phtheirichthys lineatus*. And so the matter stands as to the affinities of Wettstein's *Echeneis glaronensis*.

RÉSUMÉ

1. Nothing is known of the embryology of any Echeneid fish. The specimens studied in this paper are the youngest and smallest known. In the *Remora* group, where specimens run in size from 27 mm. up, there is no evidence whatever that the young have even a post-larval stage or undergo any metamorphosis whatever. The nearest approach to such is the rounding of the points of the emarginate caudal in the older young forms of *Rhombochirus*—a matter which seems not to have been noted before. (This statement has, of course, no reference to the origin and formation of the suctorial disk—of which we are profoundly ignorant). In the *Echeneis* group both genera—*Phtheirichthys* and *Echeneis*—in the young specimens from 61 mm. up have a post-larval stage in which the caudal has the median rays elongated to a greater length than the rest of the fin. As the fish grow older this becomes progressively shorter.

To get the embryology of one of these fishes, it would be necessary to go to a tropical region where sharks and rays (their largest and commonest hosts) abound, to catch numbers of the sucking fish and determine the period of ripening of their sexual products. Then, if artificial fertilization were found possible, the rest (in a properly provided laboratory with running water) ought to be fairly easy. Lacking such a laboratory, but with the breeding season established, one would have to fall back on "towing" and on the examination of the plankton gathered thereby. None of these things, so far as I know, has ever been done.

There is no embryological problem in all the realm of ichthyology today which is so unique and which offers so much of interest as the mode of formation of the sucking disk in any form belonging to the family Echeneididæ.

2. From time to time observations have been made and notes recorded as to the particular hosts on which certain species of sucker-fishes are found, and efforts have been made (notably by Poey) to estab-

lish the fact that certain suckers are commensal only on certain definite hosts. There seems to be some evidence that this is true of those suckers that are found in the mouths of whales, sharks, and rays, and among the gills of certain teleosts. However, too little is known to generalize. But in any case here is a field of investigation which promises most interesting results. A few years ago it seemed that I was going to be able to make a beginning. A friend of the department planned to go to one of the Florida Keys where an extensive pound-net fishery was carried on and there to collect suckers as the net was fished and record the fishes from which they were taken. However, ill health of the gentleman caused the plan to fall through.

3. But one fossil form is known—*Echeneis glaronensis*—from the Tertiary deposits of Switzerland. In it part of the sucking disk is broken off, but that which remains is perfect and, beyond having extremely wide spaces between the 6 remaining lamellæ, does not present any unusual structures. To the writer it seems to be nearer *Phtheirichthys* with 10 lamellæ than any of the existing genera. It throws no light whatever upon the origin or mode of formation of the sucking disk.

4. There is great need for a careful revision of the genera and species of the family Echeneididæ. In 1858, Duméril, having at hand 161 specimens in the Museum d'Histoire Naturelle of Paris, published a preliminary notice of such a work in which he named 46 species all belonging to the one genus *Echeneis*. The projected revision never saw the light.

In 1860, Günther, after a study of the 130 specimens of sucking fishes of all kinds in the collections of the British Museum, made one genus, *Echeneis*—as did Duméril—but only 10 species. In 1862, in a paper read before the Philadelphia Academy, Gill (1863) established 2 groups of these clinging fishes—the Echeneides composed of the genera *Echeneis* and *Phtheirichthys*, and the Remoræ with the genera *Remora* and *Remilegia*. In 1875, Lütken in his 'Museets Sugefiske' (Copenhagen) only in a general way followed Gill as to the 2 groups of "elongated" and "shorter" forms. In the first group he puts *Phtheirichthys* (1 species) and *Echeneis* (2 species) and in the second group 6 species, all also belonging under *Echeneis*, of which the Copenhagen Museum had 113 specimens of all kinds.

Finally, in 1898, Jordan and Evermann gave what is probably the best classification yet proposed. They establish the following genera: *Phtheirichthys* with one species; *Echeneis* with two species; *Remilegia* with one; *Remora* with three species; and *Rhombochirus* with one;—five genera with eight species. This is probably a sound classification, but

there needs to be made an intensive study of an extensive series of specimens—hundreds of specimens from all the great museums covering large numbers of localities and all stages of growth ought to be studied minutely and compared. From such a study would come a classification of these most interesting fishes which would approach the natural system and which would stand.

ADDENDUM

After this paper had been accepted for publication, I received from Dr. Å. Vedel Tåning of the Carlsberg Laboratory, Copenhagen, Denmark, an article entitled 'Position du Disque Céphalique chez les Echénéides au Cours de l'Ontogénèse' (1926, Comptes Rendus Académie Sciences, Paris, CLXXXII, pp. 1293–1295, 2 figs.). In this preliminary paper based on material from innumerable "towings" made in the Atlantic under the direction of Professor Johannes Schmidt, Tåning has described and figured post-larval stages of both *Remora remora* and *Echeneis lineata*. Of the former he figures the heads of specimens 5.6, 6.5, 9.8, 12, 18, and 25 mm. long; and of the latter he had young from 14 to 50 mm. over all.

In *Remora* no disk is visible in specimens below 8 mm. in length. In his 9.8 mm. specimen the disk is visible as a narrow oblong object lying in the region of the dorsal fin just behind the head. Lamellæ are not visible to the naked eye, but their beginnings are shown in sections. In a 12 mm. specimen about half of the disk lies on the head, and in older fishlets it is placed progressively farther and farther forward on the head. Of *Echeneis lineata,* Tåning had specimens ranging from 14 to 50 mm. in length, in which was found a state of things similar to that in *Remora* embryos of the same size. In a little fish 21.2 mm. long, the disk, visible to the naked eye, had so far progressed forward as to reach the hinder edge of the head. In a 32 mm. fish the anterior two-thirds of the disk was found on the head.

The heartiest congratulations of all ichthyologists and embryologists are due Tåning for his remarkable discovery, and his full paper will be awaited with the keenest interest. He apparently has at hand the material for the solution of the greatest and most interesting problem in the embryology of any marine fish. The present writer extends to Dr. Tåning his warmest felicitations on his extraordinary good fortune.

In the very hour that the page proof of this article was put on my desk there was brought to me a small *Phtheirichthys lineatus* measuring

64 mm. over all, 51 mm. in standard length, and having the caudal 13 mm. long with the central lappet extending 8 mm. beyond the other parts of the caudal fin, exactly as is shown in Günther's figure (my figure 4). This little fish was taken off a barracuda on February 13, 1926, at Hog Sty Island, Bahamas, by "The 'Ara' Expedition of 1926 to the Galapagos Islands" under the command of Commodore W. K. Vanderbilt of this city. Mr. Vanderbilt is greatly interested in fishes and had with him, to make colored drawings of the fishes taken by this expedition, Mr. Wm. E. Belanske, a skilful artist of this Museum, who has had much practice in making animal drawings. Among the paintings made by Mr. Belanske during the cruise of the 'Ara' is one showing this little fish in its life colors. This Mr. Vanderbilt purposes to reproduce in the book he is writing, descriptive of the expedition and of the fishes caught. Thus the scientific world will have a colored figure of *Phtheirichthys lineatus*, and, so far as I know, it will be the only colored figure of any shark-sucker ever published.

In size this is practically of the same length as the other small specimens. True Poey's fish was 75 mm. long, but Lütken had one measuring 63 mm., and Günther's presumed life-size figure measures 61 mm. over all. Furthermore, it is interesting to note that Mr. Vanderbilt's specimen was taken from a barracuda, as were Poey's and mine. It would be interesting to know if other sucking fishes are ever found on the barracuda, or if it harbors only what Poey calls "the sucker of the barracuda."

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