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A REDEFINITION OF THE SUBSPECIES OF *FODIATOR ACUTUS*

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ABSTRACT

Analysis of characteristics of 11 Atlantic and 54 Pacific specimens of *Fodiator acutus* showed that the two subspecies *F. a. acutus* and *F. a. pacificus* could not be distinguished on the basis of the original diagnosis, but that such distinction could be made on the basis of the eye and the snout expressed as a percentage of head length. It was also shown that *F. a. pacificus* Bruun and *Hemiexocoetus caudimaculatus* Fowler are synonyms of *Fodiator acutus rostratus* (Günther).

INTRODUCTION

The primitive flying fish species, *Fodiator acutus* (Cuvier and Valenciennes), was divided into two subspecies, *F. a. acutus* from the Atlantic and *F. a. pacificus* from the Pacific, by Bruun (1933) on the basis of 38 or 39 vertebrae in Atlantic specimens and 41 vertebrae in a single specimen from the Pacific, "along with a number of other smaller, yet distinct differences in proportions and fin-ray characters." Breder and Nichols (1934) noted vertebral counts of 39 in two specimens of *F. acutus* from the Pacific coast of Panama and therefore rejected the validity of the new subspecies. They also considered *pacificus* to be a *nomen nudum* because of the incomplete description. Later, Bruun (1935) gave a complete tabular description of

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the type of *F. a. pacificus*, comparing it with four specimens from the Atlantic Ocean off the coast of Angola, and with the type of Günther's *Exocoetus rostratus* (Günther, 1866) from Hawaii. Bruun's differential characteristics may be summarized as follows:

	ATLANTIC	PACIFIC
Dorsal rays	10 — 11	9
Anal rays	11	10
Pectoral rays	14 — 16	13
Predorsal scales	21 — 24	24 — 26
Vertebrae	38 — 39	41
Gill rakers	7 + 22	8 + 24

Subsequently, Breder (1938, p. 12-16) accepted the validity of this diagnosis, and noted several additional characters, as shown in his key:

"A. Gill rakers 7+22; predorsal scales 21 to 24; dorsal 10 or 11; anal 11; body depth 4.1 to 4.8; dorsal insertion 1.32 to 1.38; interorbital 3.6 to 3.7; pectoral rays 14 to 16. *Fodiator acutus acutus*

AA. Gill rakers 8+24 or 25; predorsal scales 24 to 26; dorsal 9 or 10; anal 10 or 11; body depth 4.85 to 6.0; dorsal insertion 1.31; interorbital 3.9 to 4.0; pectoral rays 13. *Fodiator acutus pacificus.*"

However, a specimen of *F. acutus* taken by the Yale South American Expedition at Cabo Blanco, Peru, on April 1, 1953, could not be ascribed to either subspecies on the basis of the characteristics given by Bruun and by Breder. This at once raised the suspicion that the two subspecies might not be valid, but might be merely the result of examining too few specimens. Accordingly, a study of a larger number of individuals was attempted. As far as Pacific specimens were concerned, the result was gratifying, but, although nearly every museum in the United States and western Europe was canvassed for material, the combined efforts of all could produce but 11 specimens from the Atlantic Ocean.

Materials

The following material has been available. The numbers in parentheses indicate the number of individuals included in each sample.

Pacific Material

Bingham Oceanographic Collection, Peabody Museum of Natural History

No. 704 (3) No locality
1004 (9) Concepcion Bay, Mexico
1011 (5) Concepcion Bay, Mexico
1012 (5) Concepcion Bay, Mexico
1040 (2) San Jose del Cabo, Baja California
1101 (3) Las Perlas Islands, Gulf of Panama
1193 (1) San Felipe Bay, Baja California

British Museum (Natural History)

No. 1898.12.31.40-41 (2) Sta. Elena Bay, Ecuador
1903.5.15.298 (1) Panama
1938.12.12.44 (1) Galapagos Islands
1938.12.12.45 (1) Galapagos Islands
1938.12.12.46-47 (2) Galapagos Islands
1939.7.10.17 (1) Galapagos Islands
1939.7.10.18 (1) Tehuantepec, Mexico

United States National Museum

No. 82006 (5) Chame Point, Panama
119729 (2) Concepcion Bay, Mexico

Chicago Natural History Museum

No. 2580 (2) Gulf of California
41516 (1) Galapagos Islands
41517 (1) Galapagos Islands
41703 (1) Galapagos Islands
49217 (3) Bahia Honda, Panama

Academy of Natural Sciences, Philadelphia

No. 7484 (1) No locality
7508 (1) Mazatlán, Mexico (Type of *H. caudimaculatus* Fowler)

Atlantic Material

American Museum of Natural History

No. 9023 (2) Angola

British Museum (Natural History)

No. 1906.8.24.128 (1) Angola
1938.10.10.23 (1) Nigeria
1938.10.20.24 (1) Nigeria

Chicago Natural History Museum

No. 4913 (2) Caribbean Sea, 14° 30′ N, 80° 30′ W

Zoologische Staatsinsitut und Zoologische Museum Hamburg

Nos. H1, 2,3,4 (4) West Africa (Measurements from Bruun, 1935).

There have thus been 54 specimens from the Pacific Ocean and 11 from the Atlantic available for study. It early became apparent that a considerable degree of allometric growth existed in most body proportions among the smaller individuals, but that this allometry had largely ceased at a standard length of about 100 mm. Consequently, the smallest specimen utilized in the comparison of these factors was 95 mm. in standard length. Hence, there were 39 Pacific and nine Atlantic specimens available for this purpose. Even though the size of the Atlantic sample still leaves much to be desired, it is more than twice as great as the amount of material that was available to Bruun. All the material, regardless of size, was utilized in analysing meristic characters.

Discussion

In the analyses of the various characteristics of the two groups, it was found that only two of the characteristics on which the subspecies were erected actually showed a significant difference between the groups ($P<0.02$). These characteristics were the number of predorsal scales and the width of the interorbital space. For the latter, it was found that a greater

degree of separation could be effected by expressing the width of the interorbital as a function of the length of the head rather than as a function of the standard length. In addition, there may be a difference in the number of pectoral rays. However, as will be shown later, the differences shown in these characters are not sufficient to warrant subspecific rank for the two groups. On the other hand, the length of the snout and the anterior-posterior diameter of the eye, in relation to head length, appear to be valid characters upon which the subspecies may be based.

The number of pre-dorsal scales varies between 20 and 25 in the Atlantic material, and between 22 and 28 in the Pacific, with mean counts at 22.3 and 24.5 respectively (Fig. 1A). It will be observed, however, that the standard deviations of the two distributions overlap by an amount equal to about 33 per cent of the smaller. Such a high degree of overlap is indicative of a corresponding degree of intergradation and is generally considered as indicating less than subspecific differentiation.

The width of the interorbital space, expressed as a percentage of the head length (Fig. 1B), ranges between 24.7 and 28.8, with a mean at 27.0 in the Atlantic material. In the Pacific specimens, however, these values are somewhat lower, the range spreading from 22.2 to 26.8, with the mean at 25.4. This distribution is skewed by the inclusion of a single specimen whose interorbital was only 22.2 per cent of the head length, the next lowest value being 24.0 per cent. Eliminating the single low value produces a considerable reduction in the range of the sample and almost entirely eliminates the skewness, but has no other marked effect. However, whether the sample is taken whole or without the one individual, the standard deviations again show considerable overlap, actually equal to 58.7 per cent of the smaller standard deviation. Clearly, this cannot be considered as indicating subspecific differentiation.

The distribution of the counts of pectoral fin rays in the Atlantic material is such that graphical representation is meaningless. A total of 16 counts showed 15 fins with 14 rays each and one with 16 rays. In the Pacific material, 94 counts showed 4.3 per cent of the sample with 12 rays, 63 per cent with 13 rays, and 33 per cent with 14 rays. The mean counts were 14.1 for the Atlantic specimens and 13.3 for the Pacific.

The distribution in the Atlantic material suggests that in a larger sample, more lower counts would be expected. Therefore, although the number of rays in the pectoral may actually be a good indicator of the subspecies, this cannot be determined from the present samples.

Some most interesting results were derived from a comparison of the snout as percent of head length in the two samples. The Atlantic and Pacific groups are clearly different (Fig. 1C), the former having a mean value of 36.3 per cent as compared with 39.6 per cent for the latter. The standard deviations of the two distributions do not overlap at all, even though the upper limit of range of the Atlantic sample includes the whole standard deviation of the Pacific material. This skewness of the Atlantic material is caused entirely by two individuals from the Caribbean Sea, whose snout lengths were 39.7 per cent and 41.4 per cent of their head lengths. As may be seen from a comparison of the upper and middle distributions in Fig. 1C, inclusion of these two specimens (the only ones from the western Atlantic) results in a discontinuous distribution. When the two Caribbean specimens are removed from consideration, the Atlantic material has the distribution shown in the upper line of Fig. 1C. There can be no doubt that the upper Atlantic group and the Pacific group are different. It also appears as though the Caribbean material may represent a population that is distinct from that of the west African coast, although the material is not large enough to draw reasonably reliable conclusions. However, this possibility is certainly not out of the realm of probability, especially when it is realized that *F. acutus* is generally confined to coastal waters and is therefore extremely unlikely to undertake long movements back and forth across the Atlantic. This is precisely the situation that could lead to separate, distinct races on either side of the ocean.

It will be seen from Fig. 1C that the standard deviations of the Pacific sample and the whole Atlantic sample do not quite meet, indicating a separation of a little more than 84 per cent. This degree of separation seems fully adequate to indicate subspecific differentiation. Comparing the west African material alone with the Pacific specimens. they are separated by a large

gap, indicating a pronounced degree of differentiation. With a larger sample, this could be interpreted as showing full specific rank for each group, but with the number so small this assumption is not warranted here.

The diameter of the eye, again expressed as a percentage of the head length (Fig. 1D), also provides a reliable character for the distinction of the two subspecies. The Atlantic material covers a range from 27.1 to 31.5 per cent, with the mean at 29.2 per cent. By contrast, in the Pacific material the eye is only 22.7 to 28.1 per cent of the head length, with the mean at 25.4 per cent. As with the length of the snout, the standard deviations of the two samples do not meet, showing that here, too, the samples represent separate subspecies.

Synonymy

The synonymy of the subspecies of *Fodiator* is no less involved than are the characters upon which the separation may be based. Bruun named his Pacific subspecies *pacificus*, and in his 1935 paper noted that there also occurred in the Pacific the at-least-nominal species, *Hemiexocoetus caudimaculatus* Fowler and *Exocoetus rostratus* Günther, both of which are clearly *Fodiator*. The type (and only) specimen of *H. caudimaculatus* is a juvenile, so that comparison with the adult material used here would be of no value. However, this specimen does not differ in any significant way from other juveniles of comparable size that are labelled *Fodiator acutus*. Bruun (1935) gave measurements of the type specimen of *Exocoetus rostratus*. It is undoubtedly a *Fodiator*, and almost certainly belongs in the Pacific subspecies. Thus, the eye is 24.3 per cent of the head, a Pacific characteristic; the snout, at 36 per cent of the head, could fall within either category; pectoral rays 13, while not a clear cut character, also suggests the Pacific subspecies; and the locality of capture, the Hawaiian Islands, prohibits any other conclusion.

Conclusions

The subspecies of *Fodiator acutus* have been shown to be inaccurately diagnosed, but analysis of various characteristics permits a redefinition of the subspecies, as follows:

A. Atlantic Ocean. Eye 29.2% (27.1 — 31.5%) of head; snout 35.1% (33.6 — 36.9%) of head in west African specimens, 40 — 41% in Caribbean.

Fodiator acutus acutus (Cuvier and Valenciennes)

AA. Pacific Ocean. Eye 25.4% (22.7 — 28.1%) of head; snout 39.6% (36.1 — 42.7%) of head.

Fodiator acutus rostratus (Günther)

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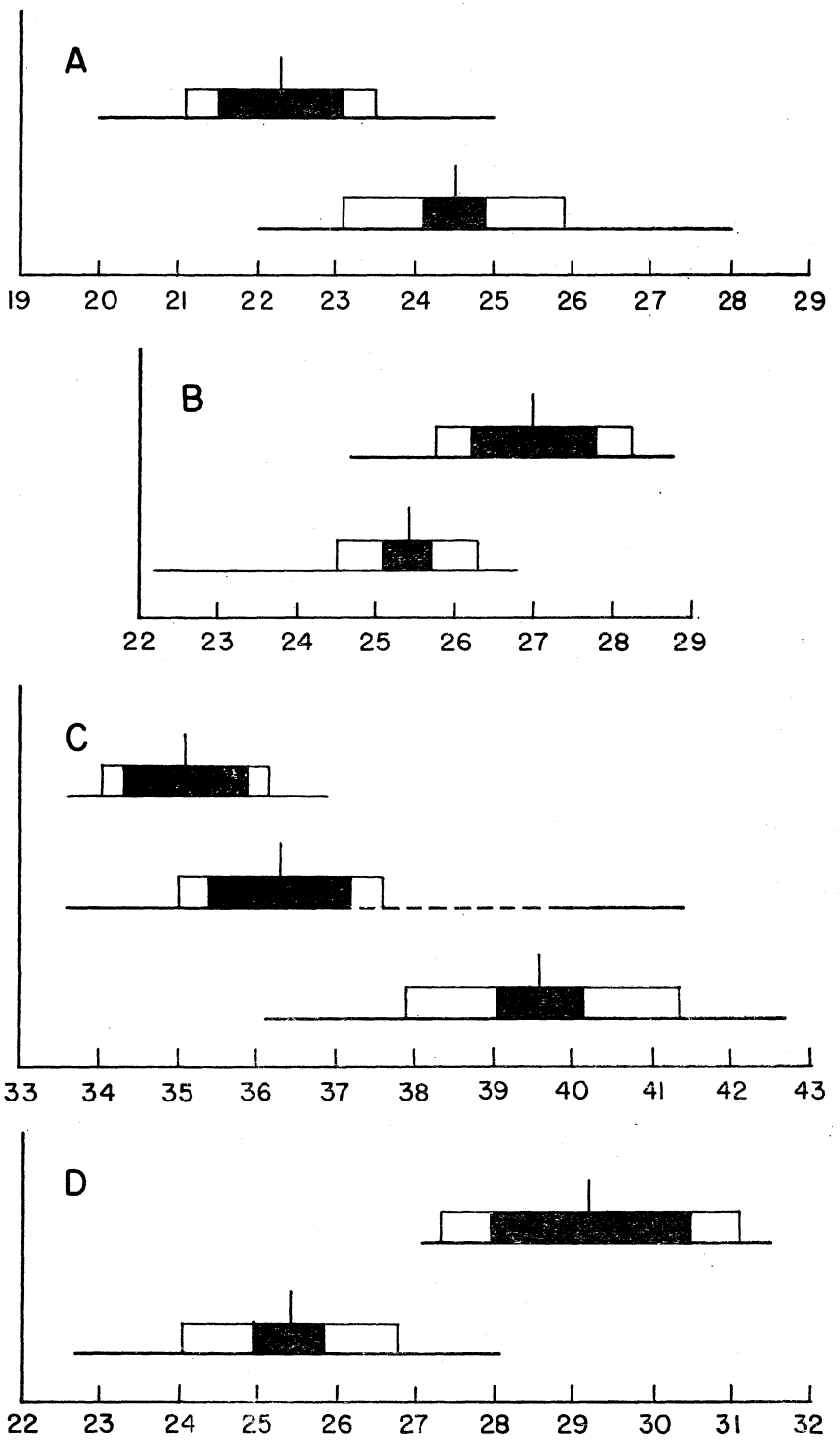
LEGEND FOR FIGURE

Figure 1. Distribution of several characteristics in *Fodiator acutus*. A. Pre-dorsal scales. Upper line, Atlantic sample; lower line, Pacific sample. B. Interorbital width expressed as percent of head length. Upper line, Atlantic; lower line, Pacific. C. Snout as percent of head length. Upper line, West African specimens; middle line, all Atlantic material (dashed base line shows discontinuity in sample); lower line, Pacific specimens. D. Eye as percent of head length. Upper line, Atlantic; lower line, Pacific specimens.


A
19 20 21 22 23 24 25 26 27 28 29
B
22 23 24 25 26 27 28 29
C
33 34 35 36 37 38 39 40 41 42 43
D
22 23 24 25 26 27 28 29 30 31 32