

A REVISION OF THE AMERICAN
GROUPERS: *EPINEPHELUS* AND
ALLIED GENERA

C. LAVETT SMITH

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INTRODUCTION

THE FAMILY SERRANIDAE, which includes some 300 species, forms an important segment of the marine shore fauna in tropical and subtropical areas. This family consists of some of the most generalized perciform fishes and apparently represents the stock from which many of the more specialized perciforms have evolved.

Because of the great number of species and because many reach large size and consequently are poorly represented in collections, the classification of the serranid fishes remains unsatisfactory. Moreover, such a classification can never be complete until the family is studied on a world-wide basis. Pending such a complete study, however, it seems advisable to investigate smaller units in which the direction and modes of evolution can be discerned. The American species of *Epinephelus* and related genera constitute such a unit and it is hoped that the results presented here will pave the way for future more extensive studies.

The present study has had two objectives: (1) to define the genera and species of the American groupers, (2) to discern relationships among these genera and species and trace the evolutionary trends in this section of the family. On the basis of this information I have attempted to synthesize a classification of these fishes and correlate previous literature with this classification.

Although it remains a matter of some debate as to which genera are closely allied to *Epinephelus*, the present study, for reasons given below, has been limited to the nominal genera *Alphistes*, *Cephalopholis*, *Dermatolepis*, *Epinephelus*, *Garrupa*, *Mycteroperca*, *Parepinephelus*, *Paranthias*, *Petrometopon*, *Promicrops*, and *Menephorus*. The area covered includes the Western Atlantic north of Uruguay and the Eastern Pacific north of Chile.

Some of the species that are well known or

commercially important have been given local common names. Many of these are widely accepted but others are so restricted that their inclusion herein could serve no purpose. In using common names, certain principles have been followed. All members of the family Serranidae are called sea basses. Members of the genus *Epinephelus* and its allies are called groupers. Certain species of groupers are known as jewfishes, hinds, leather bass, etc., and others are known by combination terms including the word grouper (red grouper, black grouper, yellowfin grouper). In accordance with the recommendations of the American Fisheries Society the term rockfish is not used for any member of this family in spite of its appropriateness and local acceptance. That name is reserved for certain Pacific scorpaenids.

It has been particularly helpful to have had the opportunity to see many of the species in the field, either freshly caught or under water in their natural habitat. Because of this I have been able to utilize subjective impressions based on their habits and life colors, in addition to features apparent from museum specimens.

METHODS AND MATERIALS

In order to conserve space in the lists of specimens examined, only locality and museum numbers are given. In the case of rare species or those poorly represented in collections, all available data are listed. Measurements are standard length in millimeters unless otherwise indicated. Specific localities are plotted on the distribution maps but localities falling within the radius of another spot are not replotted. The words PELICAN Station, OREGON Station and SILVER BAY Station indicate records obtained by the respective United States Fish and Wildlife Service research motor vessels.

ABBREVIATIONS

AMNH, the American Museum of Natural History
ANSP, Academy of Natural Sciences of Philadelphia
BOC, Bingham Oceanographic Collection
CAS, California Academy of Sciences
CBC, Chaplin Bahama Collection (Academy of Natural Sciences of Philadelphia)

CU, Cornell University
FMNH, Field Museum of Natural History
LACM, Los Angeles County Museum
MCZ, Museum of Comparative Zoology
SIO, Scripps Institution of Oceanography
TU, Tulane University

UCLA, University of California at Los Angeles
 UMIM, University of Miami Ichthyological Museum
 UMML, University of Miami Marine Laboratory

UMMZ, University of Michigan Museum of Zoology

If no museum number appears, the specimens were uncatalogued at the time I examined them.

ABBREVIATIONS IN FIGURES

ar, anal fin ray
 art, articular
 aspo, autosphenotic
 bb₁₋₃, basibranchials
 bh, basihyal
 boc, basioccipital
 bsp, basisphenoid
 c, vertebral centrum
 cb₁₋₅, ceratobranchials
 cha, anterior ceratohyal
 chp, posterior ceratohyal
 cl, cleithrum
 cor, coracoid
 d, distal pterygiophore
 ds, dorsal spine
 den, dentary
 dspo, dermosphenotic
 eb₁₋₄, epibranchials
 ect, ectopterygoid
 end, endopterygoid
 ep, epiplural ribs
 epo, epiotic
 exo, exoccipital
 fro, frontal
 ha, haemal arch
 hb₁₋₃, hypobranchials
 hs, haemal spine
 hyo, hyomandibular
 ih, interhyal
 int, intercalar
 iop, interopercular
 lac, lacrimal
 lat, lateral ethmoid
 lhh, lower hypohyal
 lsc, lateral skull crest
 met, metapterygoid

msc, median skull crest
 mx, maxilla
 n, neural spine
 na, nasal
 op, opercular
 p, proximal pterygiophore
 pa, parietal
 pal, palatine
 pas, parasphenoid
 pb₁₋₄, pharyngobranchial
 pcl, postcleithrum
 pel, pelvic bone
 plr, pleural rib
 pmx, premaxilla
 pop, preopercular
 pr, pelvic rays
 prb, predorsal bones
 pro, prootic
 ps, pelvic spine
 pto, pterotic
 pts, pterosphenoid
 ptt, posttemporal
 qu, quadrate
 ret, retroarticular
 sca, scapula
 scl, supracleithrum
 se, supraethmoid
 smx, supramaxilla
 soc, supraoccipital
 sop, subopercular
 sos, subocular shelf
 sym, symplectic
 ta, tabulars
 uh, urohyal
 uhh, upper hypohyal
 vo, vomer

COUNTS

In the present study relatively little emphasis has been placed on meristic data. Such counts as have been used are designed to establish the "normal" for the species and to give an indication of the range of variation. The material available has not been sufficient to justify exhaustive studies of geographic variation. Most groupers have fine scales that are irregularly placed around the lateral line and other usual reference points so that some of the standard counts are unsatisfactory. Fin ray counts, however, are quite useful as taxonomic characters

and are readily determined.

TRANSVERSE SCALE ROWS: In groupers, the lateral line emerges at irregular intervals through small intercalated scales so that the scale rows cannot be enumerated in the usual manner. Some authors have made a count above or below the lateral line, but this too is of limited value as the alignment of the scale rows changes along the body. The method employed here is to count the rows crossing a straight line from the lower posterior edge of the supracleithrum to the middle of the base of the caudal fin. Difficulty may be encountered in the region of the

caudal peduncle but with practice one can achieve reasonable accuracy. In larger specimens it is sometimes desirable to insert a pin at each end and stretch a rubber band between them to serve as a guide line.

SCALES ABOVE LATERAL LINE: Counted from highest part of lateral line to base of dorsal fin. Several counts are made at different positions and the lowest figure recorded.

SCALES BELOW LATERAL LINE: Counted from edge of anus obliquely backward and upward to lateral line. Some difficulty is experienced in enumerating the fine scales around the anus but this is a more definitive point than the origin of the anal fin.

SCALES AROUND CAUDAL PEDUNCLE: Scale rows on caudal peduncle are quite oblique and the most reliable figure is obtained by counting in a zigzag fashion around the smallest part of the caudal peduncle. The lowest accurate count is recorded.

FIN RAYS: Last dorsal and anal soft rays are considered to be branched to their base. Every pectoral element is recorded including the splintlike ray along dorsal edge. Pectoral count is most easily made from medial side of fin because folding of interradiial membranes makes it difficult to see the rays from the outer surface. Caudal rays are given as branched rays only, the addition of two rays to indicate the principal rays being, in my opinion, superfluous.

VERTEBRAL COUNTS: These are made on radiographs and ligamentary skeletons. The conical terminal centrum is included.

BRANCHIOSTEGAL RAYS: Branchiostegal counts listed here were made on specimens in which gill membranes were spread so that an accurate count was possible.

GILL RAKERS: Gill rakers as recorded include all countable elements. Where a distinction between developed rakers and rudiments was possible it is indicated by a plus sign. Gill rakers above and below the T-shaped element at the angle are similarly indicated.

PYLORIC CAECA: Whenever possible pyloric caeca were counted in fresh viscera in the field; the count is difficult to make in preserved material.

MEASUREMENTS

Measurements were made only on specimens that were not excessively distorted. Measure-

ments in groupers are in some respects more satisfactory than counts, because most specimens are large enough so that reasonable accuracy can be achieved. Moreover, the various species have distinctive characters that lend themselves to expression by means of measurements. All measurements are straight line distances, usually made with dividers and steel ruler, but a few small specimens were measured with dial calipers.

STANDARD LENGTH: Distance from tip of upper jaw to structural base of caudal fin. In specimens fixed with mouth open the tip of the snout is taken as the point where it would fall with mouth closed.

HEAD LENGTH: Distance from tip of snout to posterior extremity of opercular flap.

HEAD WIDTH: Width of head taken at a point just anterior to edge of preopercle with mouth and gill opening closed.

SNOUT LENGTH: From anterior edge of orbit to tip of snout with mouth closed.

SUBORBITAL WIDTH: Least fleshy width from lower edge of orbit to groove above maxilla.

INTERORBITAL WIDTH: Measured as least fleshy width.

POSTORBITAL HEAD LENGTH: From posterior edge of orbit to extreme tip of opercular flap.

ORBITAL DIAMETER: Anterior-posterior length of orbit.

LENGTH OF UPPER JAW: Distance from tip of upper jaw to midpoint of posterior end of maxilla.

LENGTH OF LOWER JAW: Distance from tip of lower jaw to middle of posterior end of maxilla with mouth closed.

SNOUT TO PREOPERCULAR ANGLE: From tip of snout with mouth closed to tip of preopercle below its notch.

LENGTH OF SUPRAMAXILLA: Greatest length of supramaxilla as visible externally.

WIDTH OF MAXILLA: Greatest width of maxilla excluding supramaxilla.

LOWER JAW TO GULAR NOTCH: From tip of lower jaw to anterior end of groove in tissue between rami of lower jaw. This measurement should be taken only when specimen has been fixed with mouth closed.

BODY DEPTH: Greatest depth of body taken just anterior to base of pelvic fins.

BODY WIDTH: Greatest width of body measured just behind shoulder girdle.

CAUDAL PEDUNCLE DEPTH: Least depth of caudal peduncle.

DORSAL ORIGIN TO TIP OF SNOUT: Measured from base of first dorsal spine to tip of snout with mouth closed.

SNOUT TO BASE OF PECTORAL: Measured from tip of snout with mouth closed to base of upper rays of pectoral fin.

TIP OF LOWER JAW TO BASE OF PELVIC FIN: From tip of lower jaw with mouth closed to base of pelvic spine.

LENGTH OF DORSAL FIN BASE: Measured from anterior edge of base of first dorsal spine to posterior edge of base of last dorsal soft ray.

LENGTH OF DEPRESSED DORSAL: From anterior edge of base of first dorsal spine to posteriormost tip of dorsal soft rays. In the usual position it is unnecessary to bend the fin, as the posterior rays lie horizontally.

LENGTH OF ANAL FIN BASE: From anterior side of base of first anal spine to posterior of base of last anal soft ray.

LENGTH OF DEPRESSED ANAL FIN: Measured from base of first anal spine to posteriormost tip of soft rays.

POSTDORSAL LENGTH: From base of last dorsal soft ray to midbase of caudal fin.

LENGTH OF CAUDAL PEDUNCLE: From base of last anal soft ray to midbase of caudal fin.

LENGTH OF PECTORAL FIN: From midpoint of pectoral base to tip of longest ray.

DORSAL SPINE LENGTHS: Lengths are taken for first, second or third (whichever is longer), and last dorsal spines. All spines are measured from point where they leave the body to the tip, rather than from their structural base which is difficult to locate in a large fish.

ANAL SPINE LENGTHS: All three spines are measured in same manner as dorsal spines.

CAUDAL FIN: Measured from middle of caudal base to tips of uppermost, lowermost, and middle rays. These measurements are rather subjective in those fishes with rounded tails and may be influenced by the extent to which the tail is spread. In spite of these difficulties the three measurements indicate the general outline of the fin.

As the present study is directed at the species level and above, the primary concern is with recognition of trends that indicate relationships and probable direction of evolution rather than small differences between populations. For this purpose it is deemed proper to use measurement

as well as meristic data. Most of the specimens are in the 100 to 700 mm. size range and probably represent a single growth stanza as understood by Martin (1949). Plotting the measurement against the standard length usually results in a straight line relationship, thus means and ranges are valid measurements of central tendency and dispersal of most measurement characters. Certain exceptions are noted.

BIOLOGY OF GROUPERS

Evolution in any group of animals is the product of the environment acting upon a genetic substrate. Mutations must be acceptable to the environment or they will be eliminated. The special requirements of any mode of life determine to a large extent the direction of evolution although different animals may meet the same requirements in different ways.

Adult groupers are reef fishes, that is, they live in relatively shallow water around hard, broken bottom such as rocks and corals which afford them abundant cover. The term coral reef fish often connotes special modifications of form or coloration such as those of the wrasses, butterfly fishes, box fishes, or trumpet fishes but groupers are not so modified and it would seem that a more precise definition must be based on behavior patterns that restrict them to the reef habitat.

Groupers, like other bottom dwelling fishes, are profoundly affected by the nature of the bottom. Stereotaxis is strongly developed and many species spend most of their time lying in contact with the bottom. They seem to have a compelling need for cover, being seldom seen far from a hole or crevice in which they seek shelter at the first approach of danger. They do not dig their own burrows but utilize almost any available opening big enough for them. The juveniles of a few species seek shelter in turtle-grass areas where attached vegetation affords sufficient protection, and large spotted jewfish are frequently caught among mangrove roots where there is little or no rock available.

The distance that an adult grouper will stray from shelter has not been investigated and there is probably some interspecific variation in this regard. Some species will swim upward to take a lure trolled near the surface but usually they remain near the bottom.

Wells (1957, p. 609 and pl. 9) has pointed out that coral reefs are best developed where mean

annual water temperature is 23°C. No significant reefs occur where the temperature during the year falls below 18°C. The same statement can be applied to groupers. They are generally confined to the area between the extended 70°F. (21.1°C.) isotherms although in the Northern Hemisphere, at least, the young of a few species have been taken north of these limits.

Most groupers are solitary but a small area of suitable habitat may harbor numerous individuals. The same fish may sometimes occupy one hole for extended periods but no active defense of territory has been recorded. I have often seen two or more Nassau groupers under the same ledge but they did not seem to affect one another. *Paranthias furcifer* is said to school and Hobson (1963, p. 19) has reported loose feeding aggregations in *Mycteroperca rosacea*.

The coloration of most groupers resembles that of their surroundings and some species undergo extensive color changes in response to the stimuli received. Under conditions of anoxia or during sleep, many groupers assume patterns of vertical or oblique bands. These temporary features of coloration are often seen in preserved specimens and have at times been considered significant taxonomic characters.

The coney, *Epinephelus fulvus*, also has an excitement color phase in which the fish is very dark above, and creamy white below, with a sharp line of demarcation running from the tip of the snout to the upper part of the caudal peduncle. Underwater, fish in this excitement pattern appear much slimmer than they really are.

A few species have highly distinctive deep and shallow water color phases. These are bright red or scarlet in deep water and green, olivaceous, or brown in shallow water. Sometimes the differences are so striking that distinctive names have been applied to them. There are no accompanying structural differences and the intergradation is so complete that it seems unlikely that these color phases have a genetic basis. Even those species without well-marked depth correlated color phases usually show increasing redness with increasing depth, presumably because of the metabolism of the pigments involved. It should be remembered that red blood appears green (to the human eye, at least) at depths over 30 feet, hence these "brilliant red" fishes are probably quite inconspicuous in their normal habitat.

Xanthic individuals occur in several species with considerable frequency and some grouper names are based upon these yellow variants which are probably the result of a single recessive gene.

Some groupers utilize their color pattern as the chief means of defense. I was able to touch one mutton hamlet (*Epinephelus afer*) repeatedly as it lay in a shallow depression in the reef at a depth of about 35 feet and its only response was to crowd deeper into its hiding place. Most species take cover at the first approach of an observer but once they are in their shelter they can usually be approached quite closely. Nassau groupers often make a series of grunts when disturbed, but I have not heard this from other species. Moulton (1958) and Hazlett and Winn (1962) have recorded and analyzed this sound which seems to be produced by certain anterior body muscles and the swim bladder. Marie Poland Fish has informed me that all the West Indian groupers tested by the Narragansett Laboratory have made sounds. At times *Epinephelus striatus* and *E. guttatus* go through a posturing in which they open their mouths and spread their gill covers to reveal the red lining of the mouth, possibly a threatening or warning pose.

Groupers seem to be generalized carnivores and fish and crustacea make up the bulk of the diets of most species. Some, such as *Epinephelus itajara*, seem to feed mostly on crabs and lobsters and those species have short, blunt canine teeth and large numbers of pyloric caeca. Others, notably species of *Mycteroperca*, have long, strong canine teeth and are probably primarily piscivorous. Perhaps the lack of specialization of feeding habits is a factor in their success in invading widely separated geographic areas where preferred food species may be absent.

Groupers apparently wander considerably in search of food, and depend largely on their sense of smell, for a well-baited trap attracts them from some distance. Food is generally swallowed whole; the fish opens its mouth and dilates its pharynx literally to inhale the food. Hungry fish in aquariums have been observed to grasp large pieces in their jaws and twist and pull with their bodies so as to tear off bites of a size that can be swallowed effectively.

Most, if not all groupers are protogynous hermaphrodites (Smith, 1959, 1965, 1967). This is undoubtedly a specialization related to the

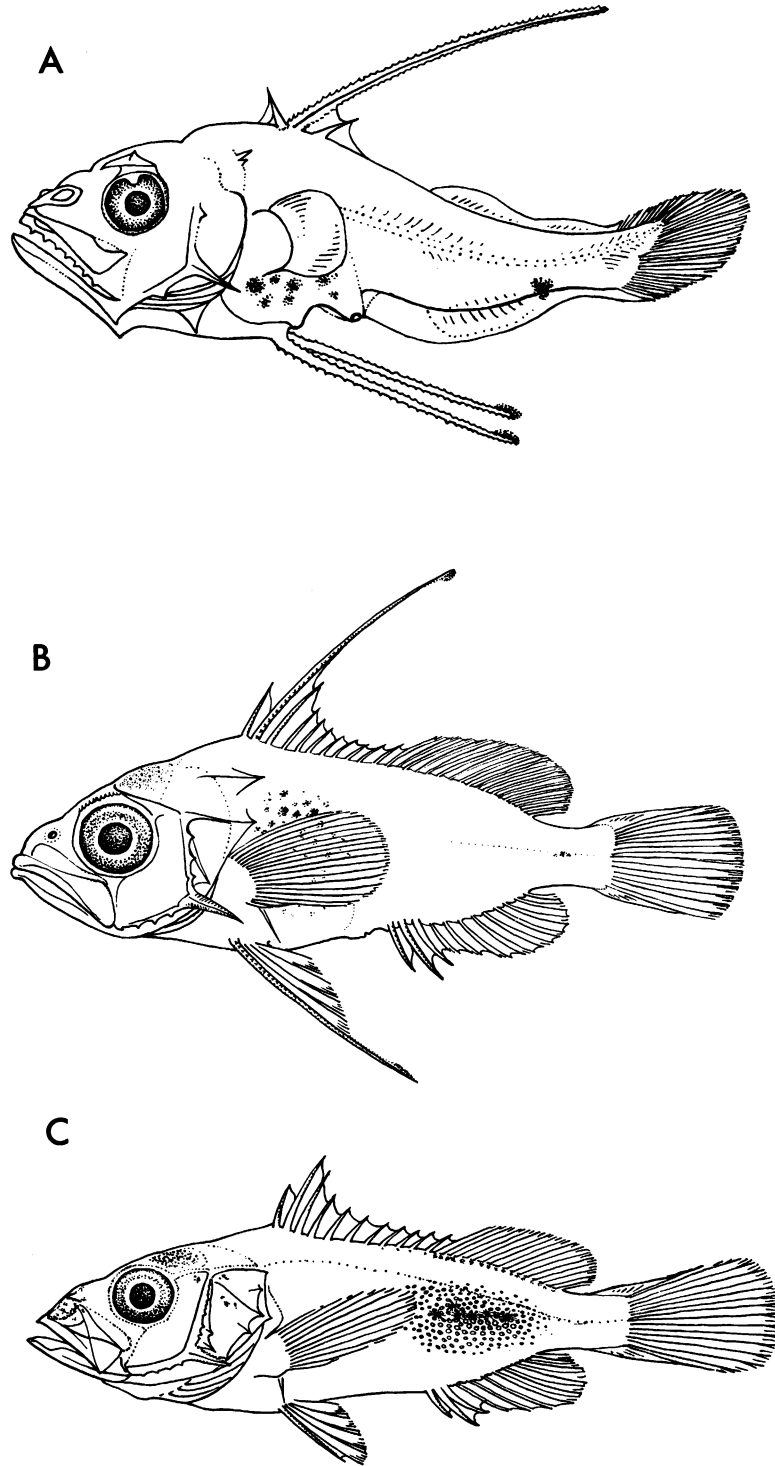


FIG. 1. Larval and juvenile groupers. A. Unidentified serranid larva from Bermuda, 5 mm. B. *Epinephelus* sp. from North Carolina, 14.4 mm. C. *Epinephelus striatus*, AMNH 24056, 24 mm.

synchronous hermaphroditism of some other serranids.

The spawning season seems to be temperature correlated, extending from the latter part of April to the middle of August in Bermuda and from December to April in Puerto Rico (Erdman, 1957 and personal commun.). Apparently spawning commences when the surface temperatures approach 70°F., at least in Bermuda waters. Randall and Brock (1960, p. 11) suggested that some Pacific groupers, especially *Epinephelus merra*, spawn intermittently, the peak of spawning occurring two to three days before the full moon. I have seen only one grouper (*Epinephelus fulvus*, 203 mm. long) from which eggs could be stripped, and it is likely that the situation is analogous to that in centrarchids where the eggs pass through the final stages of development so rapidly that the time during which the eggs can be expressed by pressure is very short, perhaps less than an hour (Sprecher, 1938, pp. 21-24).

I estimated that the ovaries of a *Mycteroperca bonaci*, 805 mm. long, contained more than five million large ova.

There is little information available on the place of spawning or on the spawning behavior in the wild, but Guitart Manday and Fernandez (1966) have described the spawning of *Epinephelus striatus* in the Cuban National Aquarium. The eggs are small (averaging 1.024 mm. in diameter) and numerous. They are released freely into the water and not guarded. Guitart Manday and Fernandez reported that there was no particular pairing, but the males butted their heads against the sides of the females for several days prior to spawning. The eggs were released in small lots during the night. Hatching began about 40 hours after spawning and the newly hatched larvae floated at the surface. Mito, Ukawa and Higuchi (1967) have given an account and detailed drawing of the early stages of *Epinephelus akaara*. Figure 1 shows the larval and postlarval stages of some West Indian species. It seems certain that the larvae are for a time pelagic.

In addition to the above mentioned studies, evidence for this hypothesis is as follows:

1. Some of the smallest groupers available for study (*Epinephelus striatus*, 19 mm. long) were collected at the surface near a light at night.

2. The young have greatly elongated second dorsal, pelvic, and preopercular spines, struc-

tures characteristic of pelagic larvae in which they serve as flotation devices. Small specimens of other serranid species also show elongation of these parts.

3. Two transparent late larvae were collected about 8 miles from land by Bermuda Biological Station personnel in 1954 and kept in aquariums until they transformed. They proved to be *Epinephelus afer*, 37.5 mm. and *Epinephelus striatus*, 45.6 mm. long. Much smaller individuals have been taken in shore collections, suggesting that metamorphosis can be delayed for a time if they do not reach a hospitable environment.

4. It is unlikely that the shelter-loving adults travel the long distances necessary to populate isolated oceanic islands. The Bermuda fauna includes more than 75 per cent of the known West Indian groupers even though Bermuda lies more than 800 miles from other coral reefs. Young of the year groupers are frequently taken as far north as Massachusetts where adult groupers are unknown. Such distributional patterns are best explained as the result of passive transport of larvae by oceanic currents associated with the Gulf Stream. Similar and even more striking patterns are found in the distribution of Indo-Pacific species where distances between islands are much greater. There is, however, a limit to the effectiveness of such transport as evidenced by the virtual absence of groupers in Hawaii (Gosline, 1955).

Upon transforming, the young grouper assumes a body form essentially like that of the adult. The elongate spines are lost and the pigmentation and scales develop. In at least two species of *Mycteroperca* (*tigris* and *interstitialis*) there is a juvenile color phase during which they are distinctly bicolored, dark above and white below with an abrupt line of demarcation. This pattern fades in *tigris* by the time the juveniles reach 50 mm. or so, but traces of it remain in specimens of *interstitialis* as long as 150 mm. Other species seem to lack this distinctive juvenile color phase.

OSTEOLOGY

It is appropriate that much of the generic classification of groupers is based on osteological characters. Most of the genera treated here can be distinguished on the basis of osteology alone, and combinations of osteological features characterize certain subdivisions within these genera.

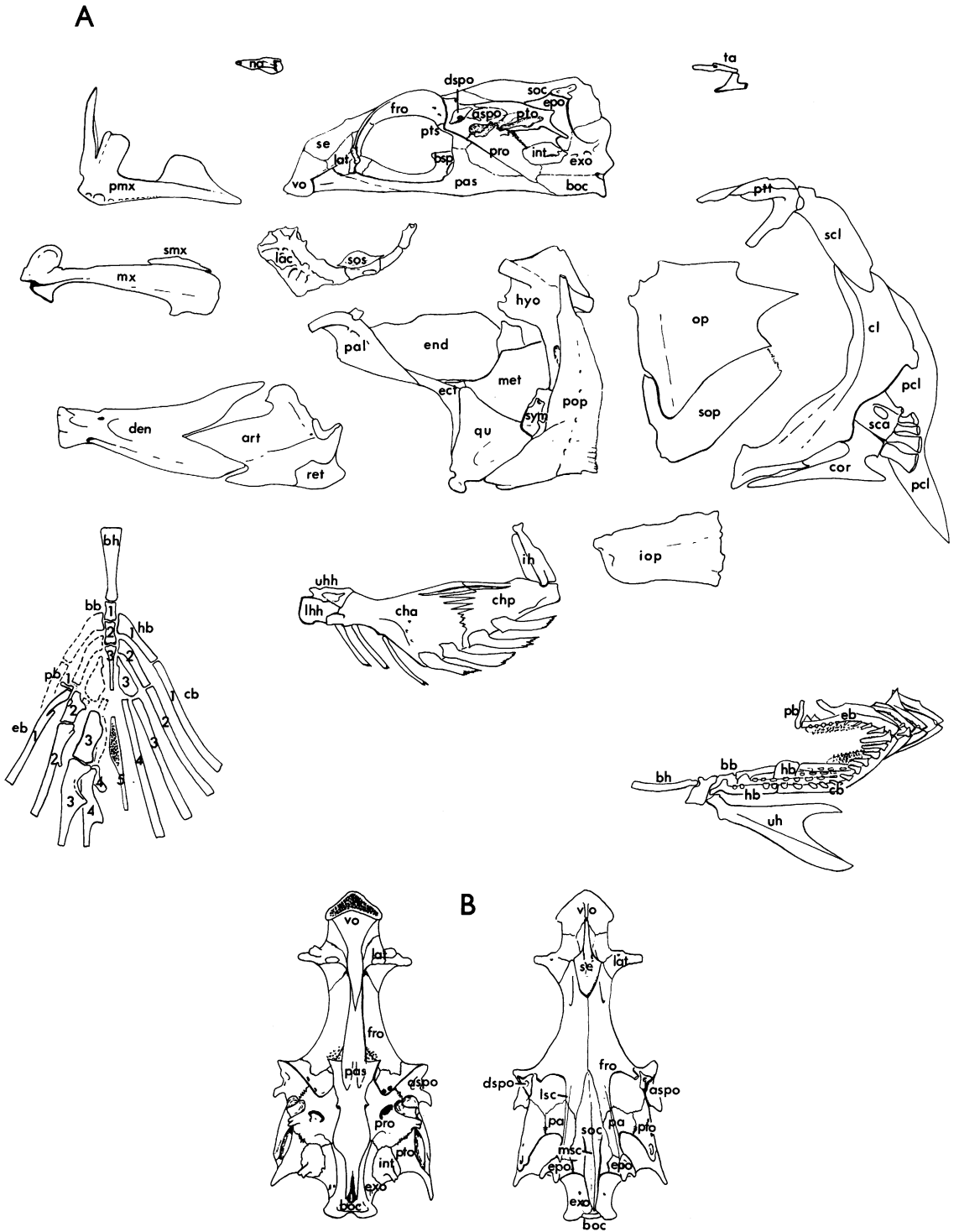


FIG. 2. *Epinephelus guttatus*. A. Cranial osteology showing lateral view of neurocranium and investing bones, dorsal view of branchial apparatus and lateral view of branchial apparatus. B. Ventral (left) and dorsal (right) views of neurocranium.

Almost all the diagnostic structures are in the skull; the postcranial skeleton is essentially the same in all groupers. The skeleton of *Epinephelus guttatus*, a species as unspecialized as any, is illustrated in figures 2 and 3. The following discussion is limited to those features that have taxonomic utility and are mentioned in the generic and specific diagnoses.

The fish skull must be considered as a functional unit, and it is to be expected that a change in one part will be followed by corresponding changes in adjacent or functionally related structures. To ignore this relationship would be to place undue emphasis on relatively small changes.

The most important taxonomic characters are found in the neurocranium. Particular emphasis has been placed upon the longitudinal crests of the dorsal surface which seem to be relatively

constant within a genus. There are three of these crests separating the groups of epaxial body muscles that insert on the dorsal surface of the skull. The median of these is the supraoccipital crest which sometimes continues forward onto the frontal bones. The lateral crests more or less parallel this median crest and are composed of sections of the epiotics, the parietals, and sometimes the frontals. In *Mycteroperca* these lateral crests are nearly straight and continue well forward on the frontals to merge with the dorsal rim of the orbit (fig. 32). In other genera these lateral crests converge anteriorly and then curve outward to a bony process of the frontal which surrounds a branch of the supraorbital lateral line canal at the rear of the orbit (fig. 2B). In *Mycteroperca*, the crests have no relation to the postorbital process.

Posteriorly, the lateral crests brace the facet of

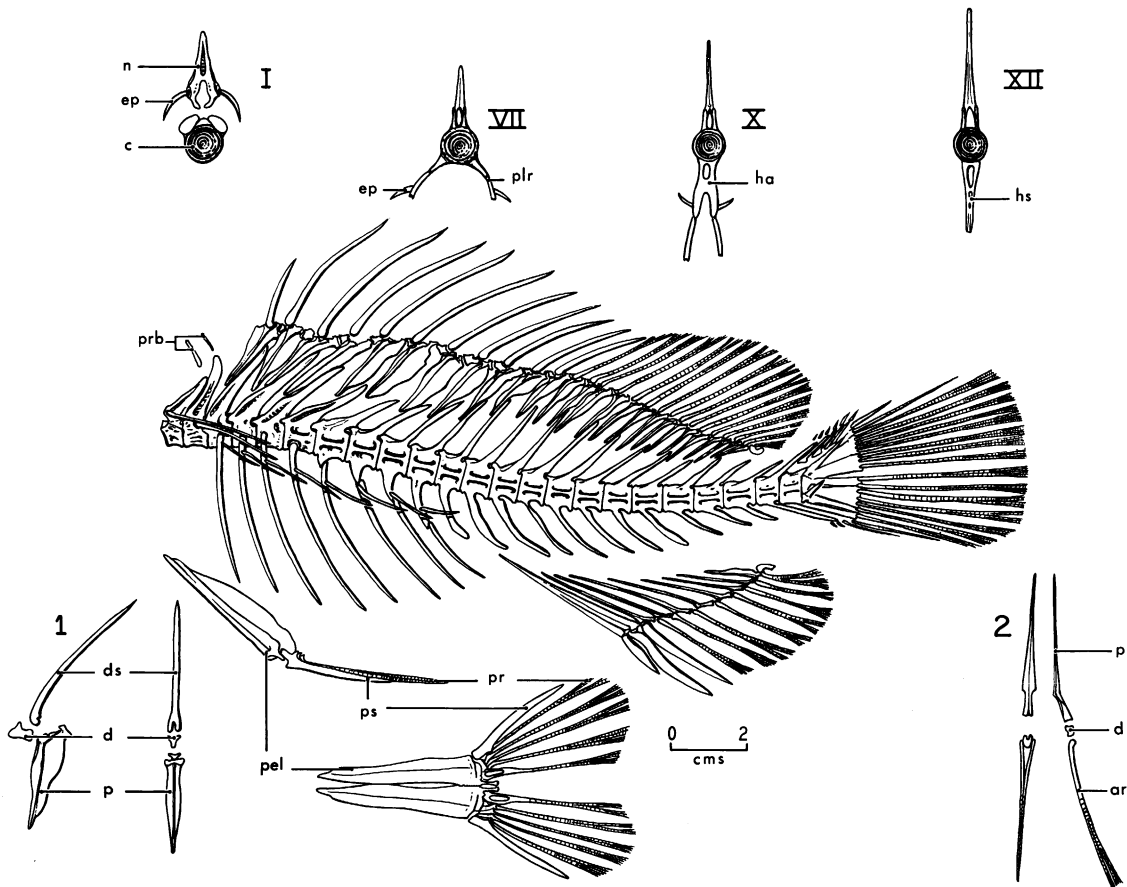


FIG. 3. *Epinephelus guttatus* osteology. Axial and appendicular skeleton with details of representative vertebrae (Roman numerals), a dorsal spine and an anal ray (1 and 2, respectively).

the epiotic where the superficial limb of the post-temporal attaches to the cranium. The shape of this epiotic facet is variable, but it is generally V-shaped with the apex of the V pointing forward. The arms of the V are nearly equal in size in some species of *Epinephelus*; in *Mycteroperca* the medial lobe is invariably shorter.

The nature of the supraethmoid is also of taxonomic significance. In some cases this bone forms the floor of a pit between the divergent anterior ends of the frontals. In other species the supraethmoid is nearly flush with the dorsal surface of the frontals, anterior to which it forms a massive transverse wall (fig. 17). The frontal pit is present or absent in *Epinephelus*, invariably absent in *Mycteroperca*. Its presence is correlated with a long premaxillary ascending process.

The form of the preopercle is a good character for some groupers. The subgenus *Alphestes*, for example, is distinguished by the presence of a strong hook on the lower limb just anterior to the angle. This is a complex structure that is itself serrated along its posterior edge. In other groupers there are definite serrae only on the vertical limb of the preopercle with an occasional irregular projection on the lower limb or with the lower limb entirely devoid of dentations. The outline of the preopercle serves to characterize certain infrageneric units within the genus *Mycteroperca*. Other characters of taxonomic value are quantitative, such as the relative height of the skull crests, proportional differences, etc. These are discussed where pertinent in species accounts.

GROUPER ILLUSTRATIONS

The production of good photographs of groupers is a trying task. Color variations cannot be depicted in a single photograph or drawing and large specimens are difficult to preserve for photographic purposes.

The following list of published illustrations will be helpful in the identification of American groupers:

- Paranthias furcifer*, Randall, 1968, p. 86, fig. 99 (color photograph)
Epinephelus fulvus, Randall, 1968, p. 62, fig. 67 (color photograph)
E. cruentatus, Randall, 1968, p. 62, fig. 68 (color photograph)
E. panamensis, Walford, 1937, pl. 15, fig. a (drawing from Steindachner, 1875)
E. striatus, Jordan and Evermann, 1920, facing p. 385 (monochrome photograph)
E. morio, Jordan and Evermann, 1920, facing p. 387 (monochrome photograph)
E. guttatus, Randall, 1968, p. 58, fig. 62 (color photograph)
E. niveatus, Böhlke and Chaplin, 1968, p. 277 (drawing)
E. flavolimbatus, Smith, 1961, p. 1:25, fig. 2-1 (monochrome photograph)
E. nigritus, Smith, 1961, p. 1:25, fig. 2-2 (monochrome photograph)
E. acanthistiis, Walford, 1937, pl. 64, fig. a (color photograph)
E. mystacinus, Böhlke and Chaplin, 1968, p. 278 (drawing)
E. guaza, Smith, 1961, 1:26, fig. 3-1 (monochrome photograph)
E. labriformis, Walford, 1937, pl. 61, fig. b (color photograph)
E. drummondhayi, Jordan and Evermann, 1920, p. 385 (drawing)
E. adscensionis, Jordan and Evermann, 1920, facing p. 282 (monochrome photograph)
E. analogus, Walford, 1937, pl. 61, fig. a (color photograph)
E. itajara, Jordan and Evermann, 1920, facing p. 392 (monochrome photograph)
E. inermis, Randall, 1968, p. 69, fig. 77 (monochrome photograph)
E. dermatolepis, Walford, 1937, pl. 14, fig. b (wash drawing)
E. afer, Randall, 1968, p. 63, fig. 69 (color photograph)
E. multiguttatus, Walford, 1937, pl. 15, fig. b (drawing after Günther, 1868)
Mycteroperca venenosa, Randall, 1968, p. 63, fig. 70 (color photograph)
M. bonaci, Randall, 1968, p. 65, fig. 71 (monochrome photograph)
M. jordani, Walford, 1937, pl. 12, fig. a (wash drawing)
M. tigris, Randall, 1968, p. 65, fig. 72 (monochrome photograph)
M. microlepis, Jordan and Evermann, 1920, facing p. 394 (monochrome photograph)
M. cidi, Cervigón M. and Velasquez, 1966, pp. 100, 101, figs. 6 and 7 (monochrome photographs)
M. interstitialis, Randall, 1968, p. 66, fig. 73 (color photograph)
M. phenax, Jordan and Evermann, 1920, facing p. 396 (monochrome photograph)
M. prionura, Walford, 1937, pl. 11, fig. c (wash drawing)
M. xenarcha, Walford, 1937, pl. 11, figs. a and b (wash drawings)
M. rosacea, Walford, 1937, pl. 60, figs. a and b (color photographs: called *M. pardalis*)
M. olfax, Walford, 1937, pl. 12, fig. b (wash drawing)
M. rubra, Randall, 1968, p. 67, fig. 75 (color photograph)

SYSTEMATICS

FAMILY SERRANIDAE

THE SERRANIDAE are generalized perciform fishes that are cosmopolitan in tropical and temperate marine and fresh waters. The fossil record for the family dates back to the Upper Cretaceous (Patterson, 1964, p. 470). Most marine species have 24 vertebrae (27 in *Polyprion*). The number of dorsal spines varies from eight to 15; there are usually three anal spines. Pelvic axillary processes are lacking. The lateral line is single and complete and does not extend onto the tail. There are two nostrils on each side, the posterior of which is sometimes enlarged. The pseudobranchiae are well developed. The gill membranes are separate and free from the isthmus and are strengthened with six to eight branchiostegal rays. Two pairs of extrascapulars, two pairs of postcleithra and a basisphenoid are present. The posttemporal is bifurcate, the lower strut articulating with the intercalar. The mouth is protractile and the maxilla is exposed for most or all of its length. The premaxilla has a dorsal posterior process lying internal to the shaft of the maxilla. There is a well-developed subocular shelf on the third circumorbital (second behind the lacrimal). There are persistent teeth on the vomer, palatines, premaxillae, dentaries, in some cases on the tongue and pterygoids, and on the superior and inferior pharyngeal bones. There is no excessive development of the lateral ridge of the preopercle. It is usually denticulate or serrate on its upper limb and in some cases on its lower limb.

These fishes are oviparous and protogynous or synchronously hermaphroditic. Early workers such as Cuvier (1829) and Gill (1862a) made little progress in the classification of perchlike fishes and the classification proposed by Regan (1913) has been adopted with slight modifications by most modern authors. However, the characters given above exclude the Plesiopidae, Theraponidae, Pseudochromidae, and a few other poorly known groups from the Serranidae. Gosline (1960) pointed out that the Plesiopidae and Pseudochromidae are closely related to the Grammistidae which he ranks as a family distinct from the Serranidae. Smith and Atz (1969) accorded the Pseudogrammididae full family rank

on the basis of the unique reproductive system in *Pseudogramma bermudensis*.

The Percichthyinae (auct.) lack so many serranid characters that their inclusion in the Serranidae is probably not warranted. They have 36 vertebrae (*Percichthys trucha*), and excessively cavernous head bones (as in some of the Sciaenidae).

If the limits of the family are nebulous, the subdivisions within it are even more so. Jordan and Eigenmann (1890) recognized six subfamilies: the Epinephelinae, Grammistinae, Anthiinae, Serraninae, Latinae, and the Percichthyinae. Boulenger (1895) included almost all of the Epinephelinae of Jordan and Eigenmann in the single genus *Epinephelus*, although he maintained *Paranthias* as a separate genus. Jordan and Evermann (1896b) split the Polyprioninae from the Epinephelinae and added the Liopropominae. Some authors have followed these schemes; still others have devised their own classifications. (Katayama [1960] included *Acropoma* and its relatives and recognized some 15 subfamilies from Japanese waters.)

It is premature to attempt a classification of this complex of genera until more information is available for the included species. Hence, the formulation of groups above the generic level is deferred and subfamily appellations are not used in order to avoid the implication of a degree of understanding which our present knowledge does not allow.

GROUPERS: *EPINEPHELUS* AND RELATED GENERA

Members of this complex are moderate-sized to large-sized serranid fishes with fine, usually ctenoid, scales numbering from 63 to 150 in lateral series. The lateral line is complete; its pores are irregular, usually several in each perforated scale. These scales are usually small and are intercalated between the larger and more regular unperforated scales. The cephalic lateral line pores are very numerous, the canals much divided. There are normally eight to 11 dorsal spines (nine or 11 in most genera) and usually 15 (eight plus seven) caudal rays. There are three anal spines and eight to 12 anal soft rays. The last pelvic ray is broadly connected to

the body by membrane. The pectoral is usually rounded or falcate with a fleshy, often fimbriate, flap just above the pectoral base. The superficial part of the posttemporal is not serrate. There are 24 vertebrae except in rare variant individuals.

The lateral line is arched but does not closely approach the base of the dorsal fin. The body is completely scaled and the scales extend to varying degrees onto the bases of the pectoral and caudal fins and the membranes of the soft parts of the dorsal and anal fins. The head is completely scaled except for the lips, which are naked, and the exposed part of the maxilla, which is variably naked or scaled. Usually there are a few scales along the branchiostegal rays and the anterior part of the mental area. The teeth are caniniform, usually largest toward the symphysis of the jaws, and are in two series in each jaw. The outer series consists of a single row of enlarged canines and the inner row of a band of smaller caniniform teeth. The eye is large, sometimes negatively allometric, and has a pear-shaped pupil. The anterior nostril is not tubular and there is a low flap between the nostrils. The preopercle is serrate along the upper limb and at the angle, usually unarmed along its lower limb. There are three opercular spines.

Caniniform teeth are variously developed on the vomer, palatines, premaxillae, dentaries, and branchial bones. On the lower limb of the first branchial arch are seven to more than 30 gill rakers. These are usually armed with strong teeth. The top of the skull in adults has the medial (supraoccipital) and lateral (frontoparietal) crests well developed and extending forward to the back of the orbit and in some cases farther. There is no smooth convex area behind the orbit except in juveniles. The supraethmoid is variously developed. The neural spine of the atlas is not coossified with its centrum. The first two vertebrae bear sessile epipleurals but no ribs. Haemal arches are present and complete on vertebrae eight through 23; haemal spines are present on vertebrae 11 through 23.

The coloration of groupers is various, often brilliant. Some species are represented by different color phases in deep and shallow water.

The eggs and larvae are presumed to be pelagic but for most species the larvae and spawning habits are unknown. Once the adult form is assumed, allometry is slight. Most species so far studied have been found to be protogynous.

Epinephelus and its allies are found in all warm seas. The present study is limited to those forms found in American waters—three genera, five subgenera, and 35 species. This procedure is considered sound because only three of these species have ranges extending beyond the limits of this area. The Western Atlantic and Eastern Pacific species are intimately related and together form a block within which we can discern phylogenetic lines and evolutionary trends.

A few other genera in the region under consideration resemble *Epinephelus* but have been omitted for various reasons. *Polyprion* and *Stereolepis* have not been included because of lack of material and because both of these genera lack the characteristic skull crests. Moreover, these genera have the dorsal soft rays fewer than or equal in number to the dorsal spines; *Epinephelus* and related genera have more soft rays than spines in the dorsal fin. The South American genus *Acanthistius* resembles *Epinephelus* externally but *Acanthistius* lacks the frontoparietal crests and has a low supraoccipital crest and several spines on the lower limb of the preopercle. In view of these differences, but chiefly because of inadequate material, *Acanthistius* is excluded from this study.

The American groupers represent three major lineages here treated as genera. *Paranthias* is probably monotypic or perhaps is a complex of a few weakly differentiated species. It has become specialized as a suprabenthic feeder and structurally bears the same relationships to *Epinephelus* that *Ocyurus* bears to *Lutjanus*.

Epinephelus is a large and unwieldy genus, but attempts to subdivide it have so far given unsatisfactory results. The relationships between the nominal genera *Petrometopon*, *Cephalopholis*, *Epinephelus*, *Promicrops*, *Dermatolepis*, and *Alphestes* seem to me best indicated by treating them as subgenera (except for *Petrometopon* which is considered a synonym of *Cephalopholis*). There are undoubtedly recognizable sublineages within the subgenera *Cephalopholis* and *Epinephelus* but these are not satisfactorily defined, and it seems best to avoid nomenclatural commitments by referring to them as informal species groups.

Mycteroperca seems to be a well-defined genus although the Atlantic species *rubra* is enigmatic and certainly not as closely related to the rest of the species as they are to each other.

The most important characters of the genera

TABLE 1
GENERIC AND SUBGENERIC CHARACTERS OF AMERICAN GROUPERS

	<i>PARANTHIAS</i>			<i>EPINEPHELUS</i>			<i>MYCTEROPERCA</i>		
	<i>Epinephelus</i>			<i>Promicrops</i>			<i>Alphistes</i>		
	<i>Cephalopholis</i>	<i>Promicrops</i>	<i>Dermatolepis</i>	<i>Alphistes</i>	<i>Promicrops</i>	<i>Dermatolepis</i>	<i>Alphistes</i>	<i>Alphistes</i>	<i>Alphistes</i>
Head length	short	long	long	long	long	long	long	long	long
Caudal	deeply forked	round or square	round or square	rounded	rounded	square	rounded	square or lunate	square or lunate
Supramaxillary bone	usually absent	present	present	present	present	present	present	present	present
Frontoparietal skull crests	high tilted outward	convergent anteriorly	convergent anteriorly	convergent anteriorly	convergent anteriorly	convergent anteriorly	parallel but with separate postocular process	parallel; no separate postocular process	parallel; no separate postocular process
Supraethmoid wall	absent	present or absent	absent	present	present	absent	absent	absent	absent
Suborbital width	narrow	wide	wide	wide	wide	wide	narrow	wide	wide
Postocular process	absent	present	present	present	present	present	present	absent	absent
Antrorse spine at angle of preopercle	absent	absent	absent	absent	absent	absent	absent	absent	absent
Dorsal rays	IX, 18-19	IX-XI, 14-18	IX, 13-16	IX, 15-16	XI, 15-16	XI, 17-20	XI, 16-20	XI, 15-19	XI, 15-19
Anal rays	III, 9-10	III, 7-10	III, 8-9	III, 8	III, 8	III, 9-10	III, 8-9	III, 10-13	III, 10-13
Total pectoral rays	39-40	32-40	32-38	36-38	36-38	36-39	33-38	30-36	30-36
Transverse scale rows	115-124	80-129	65-94	80-99	80-99	85-109	60-79	75-139	75-139
Total gill rakers	35-40	21-28	16-27	18-24	18-24	19-24	20-24	10-54	10-54

and subgenera considered herein are summarized in table 1 and in the following key.

KEY TO THE GENERA OF AMERICAN GROUPERS

1. Caudal deeply forked; dorsal and ventral profiles evenly curved, head short, less than 35 per cent of standard length (*Paranthias*)
Caudal rounded, truncate, or lunate, never deeply forked although some species may develop elongate lobes as large specimens. Dorsal profile more strongly curved than ventral. Head long, usually more than 35 per

- cent of standard length 2
2. Anal rays III, 11-14; body elongate, robust. Lateral skull crests straight, parallel and extending forward to join orbit rim anterior to middle of eye (*Mycteroperca*)
Anal rays III, 7-9 (occasionally 10); body compressed, deepest at origin of dorsal fin. Lateral skull crests usually converging anteriorly, then diverging to meet orbit rim at posterior part of orbit (*Epinephelus*)¹

¹Including subgenera *Epinephelus*, *Promicrops*, *Cephalopholis*, *Dermatolepis* and *Alphestes*.

CLASSIFICATION OF THE AMERICAN GROUPERS

Paranthias Guichenot, 1868

furcifer (Valenciennes, 1828)

Epinephelus Bloch, 1793

Subgenus *Cephalopholis* Bloch and Schneider, 1801

E. fulvus species-group

fulvus (Linnaeus, 1758)

E. cruentatus species-group

cruentatus (Lacépède, 1802)

panamensis (Steindachner, 1876)

Subgenus *Epinephelus* Bloch, 1793

E. striatus species-group

striatus (Bloch, 1792)

morio (Valenciennes, 1828)

guttatus (Linnaeus, 1758)

E. niveatus species-group

niveatus (Valenciennes, 1828)

flavolimbatus (Poey, 1865)

nigritus (Holbrook, 1855)

acanthistius (Gilbert, 1892)

mystacinus (Poey, 1852)

E. guaza species-group

guaza (Linnaeus, 1758)

labriiformis (Jenyns, 1843)

drummondhayi Goode and Bean, 1879

E. adscensionis species-group

adscensionis (Osbeck, 1771)

analogus Gill, 1864

Subgenus *Promicrops* Gill, 1868

itajara (Lichtenstein, 1822)

Subgenus *Dermatolepis* Gill, 1862

inermis (Valenciennes, 1833)

dermatolepis Boulenger, 1895

Subgenus *Alphestes* Bloch and Schneider, 1801

afer (Bloch, 1793)

multiguttatus (Günther, 1866)

Mycteroperca Gill, 1864

M. venenosa species-group

venenosa (Linnaeus, 1758)

bonaci (Poey, 1860)

jordani (Jenkins and Evermann, 1889)

tigris (Valenciennes, 1833)

M. interstitialis species-group

microlepis (Goode and Bean, 1880)

interstitialis (Poey, 1860)

phenax Jordan and Swain, 1885

cidi Cervigón M., 1966

xenarcha Jordan, 1888

prionura Rosenblatt and Zahuranec, 1967

rosacea (Streets, 1877)

olfax (Jenyns, 1843)

rubra (Bloch, 1793)

PARANTHIAS GUICHENOT, 1868

Brachyrrhinus GILL, 1863a, p. 236 (type-species: *Serranus creolus* Valenciennes [a subjective synonym of *Serranus furcifer* Valenciennes] by monotypy. Preoccupied in Coleoptera by *Brachyrrhinus* Latreille, 1802).

Paranthias GUICHENOT, 1868, p. 87 (type-species: *Serranus furcifer* Valenciennes by monotypy).

Creolus JORDAN AND GILBERT, 1883a, p. xxxvi (type-species: *Serranus furcifer* Valenciennes by monotypy. Appears in table of contents as if in addenda but not mentioned on cited page. Jordan, Evermann, and Clark [1930, p. 320] stated that it was withdrawn).

NOMENCLATURE: *Paranthias* is derived from the

Greek παρά, near, and *Anthias*, a genus of serranid fishes. *Paranthias* is of masculine gender.

DIAGNOSIS: Small groupers with robust body, moderately compressed; dorsal and ventral profiles nearly equally curved. Dorsal IX, 18 or 19; anal III, 9 or 10. Gill rakers 35-40. Head short, 26-30 per cent of standard length. Caudal fin deeply forked. Scales small, ctenoid. Lacrimal and suborbital width narrow. Supramaxilla vestigial or absent. Pyloric caeca 12.

Skull crests well developed; frontoparietal crests extending forward to posterior part of orbit, high and strongly canted laterally, highest posteriorly on parietals, lowest on posterior part

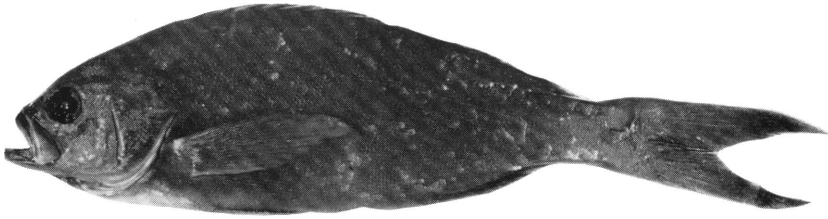


FIG. 4. *Paranthias furcifer*. AMNH 2735 from Isla San Benedicto, 186 mm.

of frontals, margins undulate (fig. 5). Supraethmoid forming floor of a deep pit between ends of frontals. Posterior part of parasphenoid bent abruptly upward. Anterior wing of hyomandibular well developed. One or two pairs of short, blunt, enlarged canines next to symphyses of upper and lower jaws.

Preopercle finely denticulate on upper margin, with few enlarged serrae at angle and several fine serrae on lower limb; no obvious notch above angle. Middle point of opercle slightly farther from upper point than from lower; posterior margin of operculum pointed, nearly symmetrical.

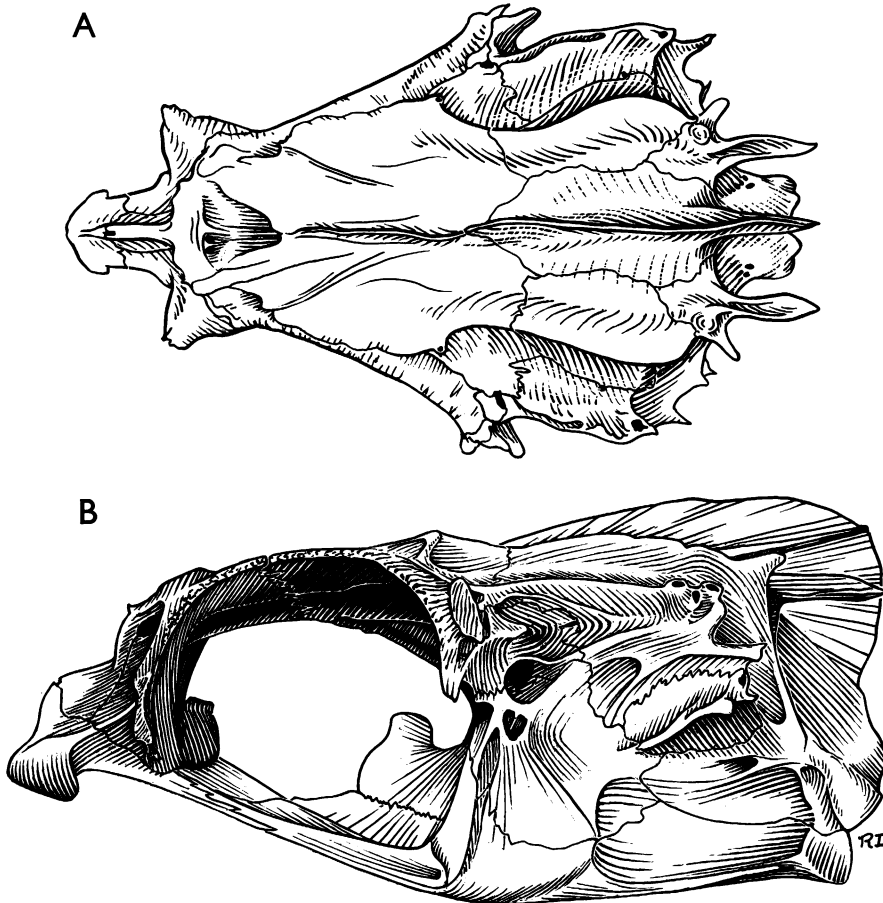


FIG. 5. *Paranthias furcifer* neurocranium. A. Dorsal view. B. Lateral view, from UMMZ 173418-S from Bermuda.

RELATIONSHIPS: This genus has been placed with *Anthias* and its relatives, but it seems more properly to belong with the groupers on the basis of skull structure and because it hybridizes with *Epinephelus fulvus*. McCully (ms) found significant similarities in the scales of *Cephalopholis* (auct.) and *Paranthias*. Smith (1966) presented evidence that the nominal genus *Menephorus* Poey was based on hybrids between *Epinephelus* (*Cephalopholis*) *fulvus* and *Paranthias* and summarized the evidence that *Paranthias* is related to *Epinephelus* and *Mycteroperca*.

INCLUDED SPECIES: *Paranthias* seems to be confined to American waters. Hildebrand (1946) recognized three species but the distinguishing characters seem of little value at the species level. Pending a thorough study of geographic variation, the American populations are treated here as a single species. A statistical comparison of specimens from the Atlantic and Pacific oceans using all of the features appearing in table 2 has failed to reveal any morphometric differences that can be construed as being of significance at the species level, although several were significantly different at the 0.05 level.

***Paranthias furcifer* (Valenciennes, 1828)**

CREOLE FISH

Figure 4

Rabirrubia de lo Alto PARRA, 1787, p. 43, pl. 20, fig. 2 (Havana). BERDEGUE A., 1956, p. 281 (Mexico, belongs to genus *Paranthias*).

Serranus furcifer VALENCIENNES, in Cuvier and Valenciennes, 1828, p. 264 (original description, Brazil).

Serranus creolus VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 265–266 (original description, Port-au-Prince; Martinique; Santo Domingo). VALENCIENNES, 1837, p. 31, pl. 18, fig. 1. STORER, 1846, p. 278. GUICHENOT, 1853, p. 149 (after Parra). GÜNTHER, 1859, pp. 100–101. POEY, 1864, p. 178; 1865 (1865–1866), p. 195. GÜNTHER, 1869, p. 409 (Atlantic coast of Central America). STEINDACHNER, 1876, p. 556 (Panama Bay and Lower California). COCKERELL, 1892, p. 8 (Jamaica).

Corvina oxyptera DEKAY, 1842, pp. 77–78, pl. 30, fig. 96 (original description, New York coast).

Serranus colonus VALENCIENNES, 1855, p. 300, pl. 2, fig. 1 (original description, Galápagos). GÜNTHER, 1859, p. 101 (after Valenciennes).

Centropristes nebulosus CASTELNAU, 1855, p. 5, pl. 1, fig. 4 (original description, Rio de Janeiro). GÜNTHER, 1859, p. 82 (after Castelnau).

Anthias furcifer: GÜNTHER, 1859, p. 91; OSORIO, 1893, pp. 136–140.

Epinephelus oxypterus: GILL, 1862c, p. 30 (after Storer); 1873, p. 806.

Brachyrhinus creolus: GILL, 1863a, p. 236; 1863b, p. 249 (Lower California). POEY, 1868 (1866–1868), p. 281 (Cuba). COPE, 1871b, p. 465 (St. Croix).

Paranthias furcifer: GUICHENOT, 1868, p. 87. JORDAN, 1885e, p. 98 (“probably not American”); 1886b, p. 377 (Cape San Lucas; Galápagos Is.; Panama); 1887a, p. 83; 1887c, p. 39 (Havana); 1887e, p. 580 (West Indies). JORDAN AND BOLLMAN, 1890, p. 181 (Albemarle, Chatham, Hood, Charles Is., Galápagos). JORDAN AND EIGENMANN, 1890, pp. 381–382. BOULENGER, 1895, pp. 273–274. JORDAN AND EVERMANN, 1896a, p. 378; 1896b, pp. 1221–1222. JORDAN AND MCGREGOR, 1899, p. 278 (San Benedicto, Socorro, Clarión Is.). GILBERT AND STARKS, 1904, p. 98 (not seen at Panama Bay). SNODGRASS AND HELLER, 1905, pp. 372–373 (Revillagigedo; Galápagos). BEAN, 1906, p. 55 (Bermuda). FOWLER, 1907, p. 267 (St. Croix). KENDALL AND RADCLIFFE, 1912, p. 110 (Taboguilla Is.). MIRANDA-RIBEIRO, 1915, p. 35 (Fernando de Noronha). EVERMANN AND RADCLIFFE, 1917, pp. 78–79 (Lobos de Afuera). METZELAAR, 1919, p. 52 (Bonaire and Curaçao). FOWLER, 1920, p. 144 (St. Croix). NICHOLS, 1921, p. 23 (Turks Is.). NICHOLS AND MURPHY, 1922, p. 508 (South Guanape Is., Peru). EVERMANN AND SEALE, 1924, pp. 30–31 (Barbados). MEEK AND HILDEBRAND, 1925, pp. 436–438 (Taboga Is.). VANDERBILT, 1927, p. 138, pls 11 and 12 (Tagus Cove and James Bay, Galápagos). BEEBE AND TEEVAN, 1928, p. 134 (Port-au-Prince Bay). NICHOLS, 1929, p. 257 (St. Croix, after Cope). JORDAN, EVERMANN, AND CLARK, 1930, p. 320. FOWLER, 1931, p. 273 (Grenada). BEEBE AND TEEVAN, 1933, p. 134 (Bermuda). BREDER, 1936, p. 25 (Cape San Lucas; Agua Verde). FOWLER, 1936, pp. 771–772, fig. 339. HERRE, 1936, pp. 160–161 (Cocos Is.; Albemarle Is., Galápagos). WALFORD, 1937, p. 118. BUTSCH, 1939, p. 24 (Barbados). SCHMITT AND SCHULTZ, 1940, p. 6 (Galápagos). SCHROEDER, 1941, p. 45 (Pensacola). FOWLER, 1942b, p. 75 (Cuba); 1944, pp. 246, 312, 343, 346, 350, 396, 411, 445 (Atlantic and Pacific records). NICHOLS AND MURPHY, 1944, p. 247 (St. Elena, La Plata Is., Ecuador). HILDEBRAND, 1946, p. 191 (Peru). FOWLER, 1953, p. 56 (Pacific coast of Colombia, compiled). SPRINGER AND BULLIS, 1956, p. 80 (Gulf of Mexico). MORROW, 1957, p. 29 (Lobos de Afuera). BRIGGS, 1958, p. 273. SMITH, 1958, p. 42, pl. 1 (Bermuda); 1959, pp. 114–117. BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:1, 1:2, 1:8, 1:23, fig. 6; 1966 (hybridizes with *Cephalopholis fulva*; relationships). CALDWELL,

1966, p. 43 (Jamaica). CERVIGÓN M., 1966b, pp. 290–291, fig. 113 (Porlamar, Cubagua and Los Hermanos, Venezuela). RANDALL, 1967, pp. 704–705 (food habits); 1968, pp. 84–85, fig. 99.

Paranthias creolus: GUICHENOT, 1868, p. 87.

Brachyrhinus furcifer: POEY, 1874, p. 34; 1875 (1875–1877), p. 19. JORDAN AND GILBERT, 1883a, p. 916; 1883e, p. 360 (Cape San Lucas).

Serranus castelnaui JORDAN AND EIGENMANN, 1890, p. 409 (replacement for *Centropristes nebulosus*, preoccupied in *Serranus*). JORDAN, 1891, p. 336. BOULENGER, 1895, p. 279 (redescription of the type, Paris Museum No. 7821). MIRANDA-RIBEIRO, 1915, p. 33 (Brazil).

Paranthias pinguis WALFORD, 1936, pp. 2–3 (original description, Guaymas, Mexico); 1937, p. 118, pl. 64, fig. h. HILDEBRAND, 1946, pp. 189–191.

Paranthias colomus: HILDEBRAND, 1946, p. 191 (Galápagos).

NOMENCLATURE: The type of *Serranus furcifer* was reexamined in the Museum d'Histoire Naturelle in Paris by Carl L. Hubbs on September 15, 1958. The specimen, 187 mm. long, is in good condition and agrees well with the description given below. It bears catalogue number 131 and according to the label was collected in Brazil by M. Delalande.

Serranus nebulosus Castelnau is identified with this species on the basis of the color pattern shown in Castelnau's plate. If the counts given by Boulenger (dorsal X, 12) are correct and not the result of some anomalous condition then this placement is incorrect. Only by reexamination of the type can the status of the name be established.

Certain Atlantic and Pacific specimens have one to several iridescent blue spots on the upper side of the body. If this pattern should prove constant, some populations may have to be accorded recognition.

The name *furcifer*, derived from the Latin *furca*, fork and *ferre*, to bear, refers to the deeply cleft tail.

DIAGNOSIS: As *Paranthias* contains only one known species, the characters of *P. furcifer* are those of the genus.

DESCRIPTION: In addition to head length, almost all other proportions are extreme (table 2). Special features of the skeleton have been discussed in the generic account.

The ground color of the head and body is rosy red, countershaded with black above and fading to pale pink on the lower sides and belly.

The lower parts of the head are washed with yellow. The maxillary and premaxillary grooves are lined with intense red. There is a pinkish-orange blotch behind each dorsal spine near the middle of the interradiation membrane; distal to this a greenish line runs obliquely backward and upward. Beyond this line there is a red blotch behind each spine, fading into the dark red ground color of the membrane. The basal fourth of the soft part of the dorsal fin is grayish red, fading to dark gray distally with a narrow orange margin. The anal fin is pink basally and distally with the intervening two-thirds of the fin bright red. The caudal is dark red, like the upper part of the body, with a narrow yellow margin. The pectoral is dark red with a triangular spot of bright red on the upper part of its base. The pelvics are orange-pink, somewhat more reddish across the middle. The iris is red.

RELATIONSHIPS: *Paranthias furcifer* does not seem to have close relatives in American waters. The true relationships of this species will perhaps become clearer when the serranid fishes are studied on a world basis.

ECOLOGY: In keeping with its structural distinctness, *Paranthias furcifer* differs from other groupers in its habits. It occurs in aggregations, usually in water over 50 feet deep. It commonly hovers near the bottom but not in crevices and other shelter as do most groupers. In both habits and morphology it holds among groupers the same position that the yellowtail, *Ocyurus chrysurus* (Bloch), does among snappers. Specimens taken on May 31, 1957 at Bermuda were in spawning condition. The maximum size is slightly more than 1 foot.

Randall (1967) presented data on the food habits of this species. He noted that it feeds on zooplankton in midwater, chasing and catching each food organism individually.

DISTRIBUTION: Record stations for *Paranthias furcifer* are plotted in figure 6. In the Western Atlantic it is known from Bermuda and Florida, the Gulf of Mexico, throughout the Antilles, Panama, and along the northern coast of South America to Brazil and Fernando de Noronha. On the Pacific coast it is found from Lower California to Peru and in the Revilla Gigedo, Cocos, and Galápagos island groups. Böhlke and Chaplin did not list it from the Bahamas nor have I seen it there, although there are specimens from Turks Island in the American Museum of Natural History.

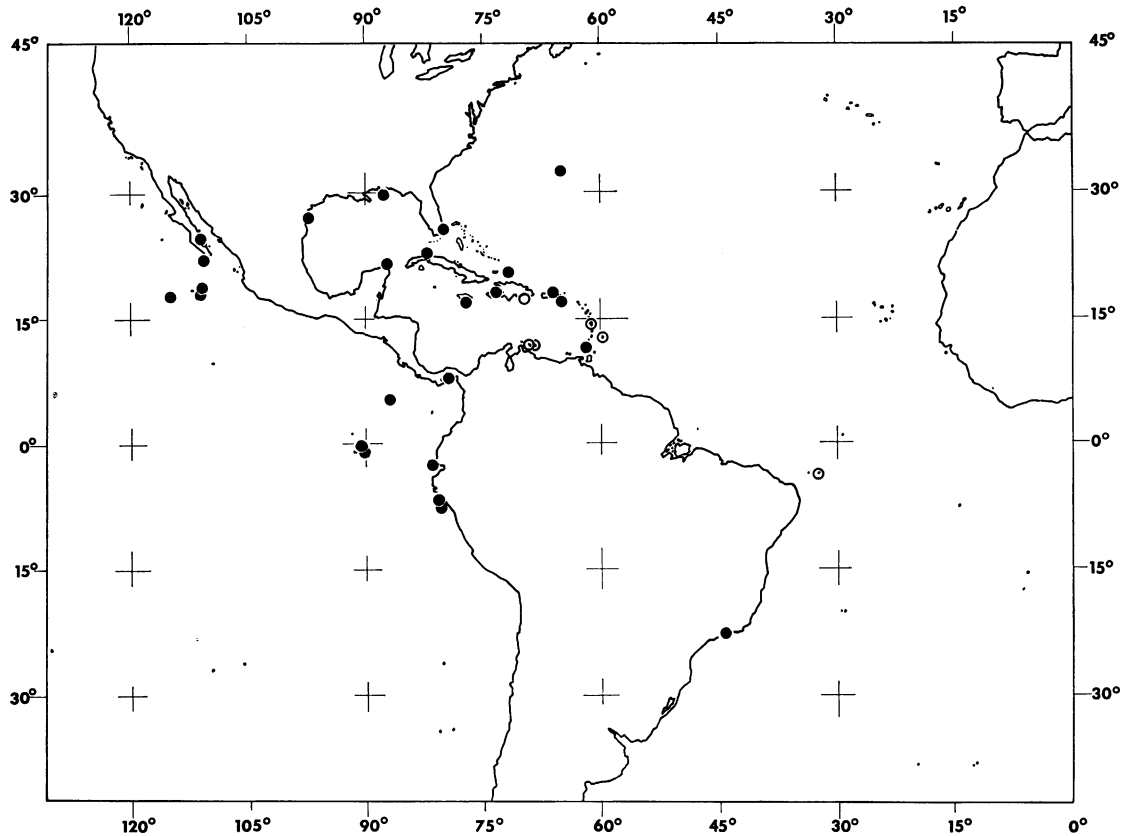


FIG. 6. *Paranthias furcifer* distribution records. Solid circles represent specimens examined, open circles are additional literature records. This species has also been reported from Fernando Poo in the Gulf of Guinea.

SPECIMENS EXAMINED

ATLANTIC RECORDS

Florida: Pensacola, MCZ 35129; off Bakers Haulover, 25° 54' N, 80° 07' W, UMML.

Texas: Padre Island, USNM 155189.

Mexico: Off northeast edge of Yucatan Peninsula, UMIM.

Brazil: Rio de Janeiro, MCZ 9764.

West Indies: No specific locality, USNM 33255, 9267; Grenada, ANSP 52468; St. Croix, ANSP 13458.

Puerto Rico: Carolina, USNM 108409.

Haiti: Port-au-Prince, USNM 120020, 122636, 133687; FMNH.

Jamaica: No specific locality, USNM 92678.

Cuba: No specific locality, USNM 12540, 19813; MCZ 10162; AMNH 988.

Bermuda: UMMZ 173418-S, 176109, 176172, 176563, 176629; FMNH 5265-67, 48419.

Bahamas: Turks Island, AMNH 7201, 7218, 7221, 7234, 7237, 7249.

PACIFIC RECORDS

Mexico: Baja California, Agua Verde, BOC 1155; Cape San Lucas, USNM 3688; San Lucas Bay, UCLA W52-259, W50-142; Isla San Benito, UCLA W53-104; Isla Cerralvo, UCLA W61-34; Isla Cerralvo, Los Frailes, LACM W51-105; Isla Carmen, UCLA W65-63; LACM W65-65, W65-77, W65-78, W65-81; Punta Pulpito, UCLA W65-75; LACM W65-51; Isla San Jose, LACM W65-49; Isla San Francisco, LACM W65-88; Santa Inez, LACM W65-66; Nayarit, Punta Los Custodios, south of San Blas, UCLA W58-37; Sinaloa, south of Bahía Topolobampo, LACM W56-118. Islas Revilla Gigedo, Isla San Benedicto, FMNH 52376; AMNH 2735; UCLA W55-121; Isla Socorro, FMNH 1756, 1782-83; USNM 46980-81; UCLA W55-125, W57-67, W53-47; LACM W56-202; Isla Clarión, MCZ 27897; USNM 46977-78,

TABLE 2
PROPORTIONAL MEASUREMENTS OF NINE SPECIMENS OF *Paranthias furcifer*^a

Measurement	1	2	3	4	5	6	7	8	9	Average
Standard length (mm.)	140.5	156	168	197	227	227	265	273	275	—
Head length	302	301	292	279	264	284	260	266	278	280.7
Head width	149	147	143	142	137	139	126	137	142	140.2
Head depth	235	250	232	221	198	207	192	198	213	216.2
Snout length	75	71	68	69	62	75	64	68	69	69.0
Suborbital width	25	22	21	20	18	22	17	18	18	20.1
Interorbital width	82	87	83	86	84	77	81	84	89	83.7
Length of: Orbit	78	74	63	63	57	59	60	53	56	62.6
Postorbital head	157	176	164	152	150	156	155	150	164	158.2
Maxillary	125	122	116	109	104	108	98	103	105	110.0
Lower jaw	121	125	119	109	104	106	96	103	105	109.8
Snout to angle of preopercle	217	212	208	188	189	196	183	181	189	195.9
Supramaxillary length	—	26	—	—	—	—	—	—	—	26
Maxillary width	39	38	42	36	40	33	34	35	35	36.9
Tip of lower jaw to gular notch	100	87	92	94	79	101	75	73	—	87.6
Body width	146	154	143	168	161	161	140	154	145	152.4
Body depth	335	372	345	338	302	319	298	306	316	325.7
Caudal peduncle depth	114	125	113	117	115	110	102	101	107	111.6
Tip of snout to dorsal origin	342	337	324	340	339	339	325	322	310	330.9
Tip of snout to pectoral base	288	285	286	254	264	282	257	271	276	273.7
Tip of lower jaw to pelvic base	352	359	345	335	326	339	335	346	355	343.6
Length of: Dorsal base	616	615	604	581	577	581	566	579	573	588.0
Depressed dorsal	683	679	670	640	641	628	608	632	613	643.8
Anal base	199	212	205	180	183	176	174	167	182	186.4
Depressed anal	288	308	298	249	269	240	223	223	223	259.0
End of dorsal to caudal base	153	170	164	170	152	161	158	163	149	160.0
Length of: Caudal peduncle	214	212	244	245	229	225	225	233	216	228.0
Pectoral	274	288	265	266	269	251	260	251	244	263.1
Pelvic	181	199	188	170	176	172	153	158	153	172.2
Dorsal spine I	64	61	57	46	44	48	49	46	53	52.0
Dorsal spine III	114	112	104	91	—	90	—	99	95	100.7
Dorsal spine IX	103	109	98	84	97	75	85	90	78	91.0
Anal spine I	57	58	54	41	44	40	36	37	38	45.0
Anal spine II	117	122	110	86	88	86	72	79	85	93.9
Anal spine III	110	122	110	94	88	93	91	90	96	99.3
Caudal base to tip of upper rays	388	359	327	414	370	348	351	326	300	353.7
Caudal base to tip of middle rays	142	147	140	122	128	119	115	117	122	128.0
Caudal base to tip of lower rays	377	333	354	360	341	348	336	310	318	341.9

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: 1-3, ANSP 27151-53 from the Galápagos Islands; 4-9, UMMZ from Bermuda.

125368, 94062, 47204, 47031-32, 46873-74;
UCLA W53-418, W55-161.
Clipperton Island: northwest corner, UCLA
W58-287; northeast side, LACM W56-236,
W56-237.
Costa Rica: Isla del Cocos, FMNH 22544-55;
Chatham Bay, UCLA W53-129, W58-378,
W53-126, W64-45, W64-46.
Ecuador: Islas Galápagos: Isla Isabela (Albe-
marle), FMNH 22540-43, 41448-54, 41440;
USNM 50039, 94059, 41411, 50052; UCLA

W53-158, W53-6, W54-225; Isla Genovesa
(Tower), FMNH 41290; Isla Fernandina
(Narborough), FMNH 41483-88; UCLA
W64-10, W54-415; Isla Santa Cruz (Inde-
fatigable), FMNH 49212; UCLA W64-21;
Isla Seymour, USNM 50038; Isla Española
(Hood), FMNH 41781-85; USNM 41244,
107073; Isla San Cristóbal (Chatham),
USNM 41441; UCLA W55-313; Isla Floreana
(Charles), USNM 50037; ANSP 81713; Isla
San Salvador (James), FMNH 41388, 41343-

45; Isla Santa Fé (Barrington), UCLA W64-30; no specific locality, USNM 107180; AMNH 8521-22, 8318; UCLA W53-178.
 Panama: Taboga Island, FMNH 20630-32; USNM 80254; Taboguilla Island, USNM 65605-06; MCZ 29573, 29636, 29675, 29699.
 Peru: Lobos de Afuera, USNM 77653; South Guanape Island, AMNH 7265.

EPINEPHELUS BLOCH, 1793

This is the most generalized genus of groupers, also the largest, consisting of more than 100 species, world-wide in the tropics and subtropics. In the American fauna it is represented by the following subgenera:

- Cephalopholis* Bloch and Schneider, 1801, of which *Petrometopon* Gill, 1865 is a synonym.
- Epinephelus* Bloch, 1793.
- Promicrops* Gill, 1868.
- Dermatolepis* Gill, 1861.
- Alphestes* Bloch and Schneider, 1801.

The generic characters are given in the key on page 84 and in table 1.

KEY TO THE SUBGENERA OF *Epinephelus*

- 1. Dorsal spines consistently 9, head spotted (*Cephalopholis*)

- Dorsal spines 10 or 11 (9 in *acanthistius* in which head and body are unspotted) 2
- 2. Head and body somewhat or quite compressed. Longest dorsal spines longer than anterior dorsal soft rays. Neurocranium not excessively depressed, frontals not touching parasphenoid 3
- Head and body not compressed, but nearly round in cross section. Longest dorsal spines (in specimens more than 300 mm. long) shorter than anterior soft rays. Neurocranium excessively broad and flat, frontals contacting parasphenoid and lateral crests scarcely evident (*Promicrops*)
- 3. Scales strongly ctenoid; head and body robust, not strongly compressed; color plain, barred, or spotted but not marbled (*Epinephelus*)
- Scales over most of body with reduced ctenii so that fish is smooth, except for area covered by folded pectoral fin. Head and body deep and strongly compressed. Color marbled 4
- 4. Color generally yellowish or brownish; preopercle with strong antrorse hook at its angle (*Alphestes*)
- Color generally blackish; sometimes spotted but usually marbled. Preopercle without strong antrorse spine (*Dermatolepis*)

Subgenus *Cephalopholis*

The species related to *fulvus* seem to form a

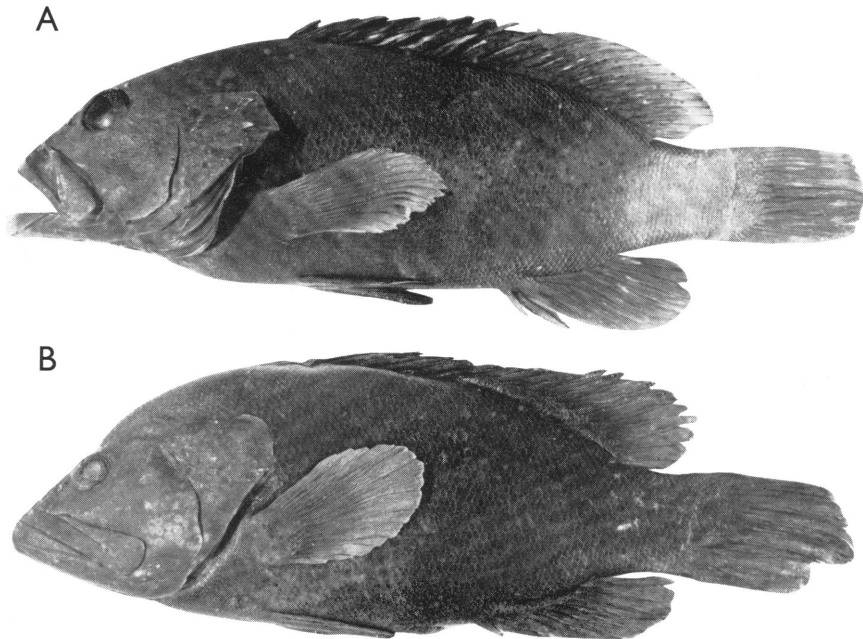


FIG. 7. Representative species of the subgenus *Cephalopholis*. A. *Epinephelus fulvus*, AMNH 23102, from Great Egg Island, Bahamas, 185 mm. B. *Epinephelus cruentatus*, AMNH field No. S63-16 from Bimini, Bahamas, 288 mm.

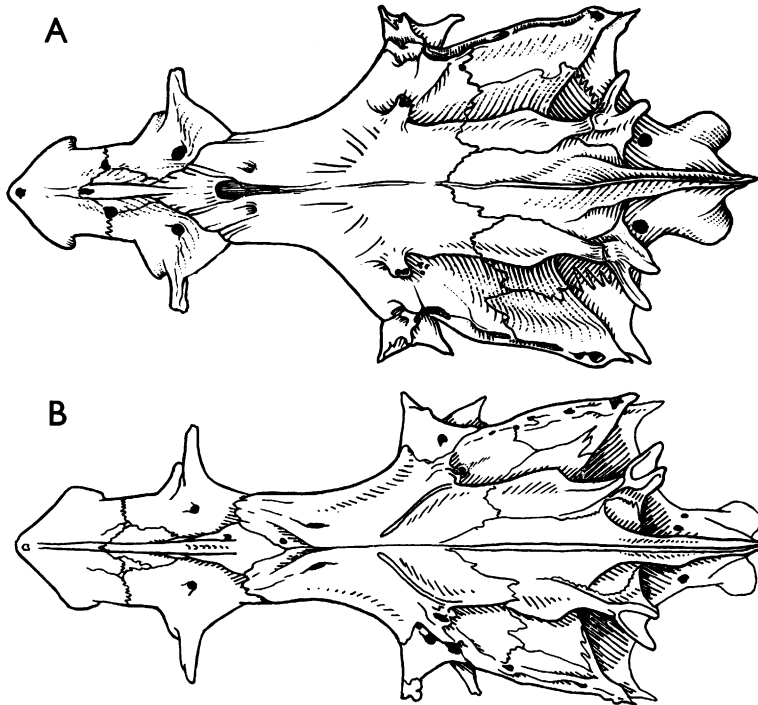


FIG. 8. Neurocrania of representative species of the subgenus *Cephalopholis*. A. *Epinephelus fulvus*, UMMZ 173404-S. B. *Epinephelus cruentatus*, UMMZ 172580-S.

more or less distinct lineage and share such features as small size, spotted color pattern, similar body shape, and nine dorsal fin spines. In every other respect, however, they are clearly related to *Epinephelus*. The discovery that the Eastern Pacific species *acanthistius* belongs to the subgenus *Epinephelus* rather than to *Cephalopholis* despite its having nine dorsal spines, is an indication that dorsal spine count alone is not a valid generic character. To continue to accord *Cephalopholis* full generic status would be to obscure its close fundamental alliance with the rest of the species of *Epinephelus*.

Petrometopon Gill, including *cruentatus* and *panamensis*, was based on the presence of transverse ridges connecting the anterior ends of the lateral skull crests (fig. 8). These ridges reinforce the anterior attachment of the dorsicranial musculature and are present in other genera such as *Variola* and *Plectropomus*. The Indo-Pacific *Epinephelus* (*Cephalopholis*) *urodelus* appears to bridge the gap between the nominal genera *Petrometopon* and *Cephalopholis*. In it the transverse ridges are only weakly developed; it has

the reticulated cheek pattern but has obtuse angles at the dorsal and ventral lobes of the caudal fin. Although these ridges undoubtedly have a functional significance and indicate a sublineage, I do not believe that they indicate divergence at even the subgeneric level. From published accounts it appears that several other Indo-Pacific species are closely related to *cruentatus* and *panamensis* but the generic name *Petrometopon* has seldom been applied to species outside American waters, and Katayama (1960, p. 54) includes *Petrometopon* in the synonymy of *Cephalopholis*.

I prefer to indicate relationships within the subgenus *Cephalopholis* by using the informal designation species-group. The *Epinephelus fulvus* species-group contains only that species in our area; the *Epinephelus cruentatus* species-group includes the American species *cruentatus* and *panamensis*.

SUBGENUS **CEPHALOPHOLIS**
BLOCH AND SCHNEIDER, 1801

Cephalopholis BLOCH AND SCHNEIDER, 1801, p. 311

(type species, *Cephalopholis argus* Bloch and Schneider, by monotypy).

Enneacentrus GILL, 1865, p. 105 (type species, *Serranus ouatalibi* Valenciennes [a subjective synonym of *Labrus fulvus* Linnaeus] by original designation).

Petrometopon GILL, 1865, p. 105 (type species, *Serranus guttatus* Poey [a subjective synonym of *Sparus cruentatus* Lacépède] by original designation).

Enneistus JORDAN AND EVERMANN, 1896b, p. 1147 (type species, *Bodianus acanthistius* Gilbert, by monotypy; proposed as a subgenus).

Bodianus BLOCH, 1790 (1790-1793), p. 31 (in part. Although several authors have restricted Bloch's name to species of *Epinephelus*, the inclusion of *Bodianus bodianus* [= *Labrus rufus* Linnaeus] constitutes designation of a type by absolute tautonymy, hence, *Bodianus* cannot be used for a serranid.).

NOMENCLATURE: The name *Cephalopholis* is derived from the Greek κεφαλή, head; φολίς, a horny scale. This name is properly feminine although it has usually been regarded as masculine.

DIAGNOSIS: Small groupers with robust, somewhat compressed bodies. Dorsal outline more strongly arched than ventral. Dorsal IX, 14-15; anal III, 8 or 9; gill rakers 17-27. Head moderate, 37 to 44 per cent of standard length. Caudal rounded, sometimes with angulate corners. Scales moderate, strongly ctenoid. Supramaxilla well developed. Lacrimal and suborbital wide.

Skull crests well developed, frontoparietal crests undulant, somewhat convergent anteriorly, then abruptly diverging; failing to reach orbit. Postorbital process included in frontoparietal crest. Some species with transverse crests crossing skull at 45-degree angle from anterior end of each lateral crest to midline. Supraethmoid forms floor of pit between frontals; no transverse wall. Parasphenoid straight or nearly so. Anterior wing of hyomandibular well developed. One or more enlarged canines on each side of symphysis of each jaw, or with median teeth of inner band enlarged.

Preopercle rounded, with shallow notch above angle; upper limb finely serrated, a few moderately enlarged serrations at angle, lower limb unarmed. Middle spine of opercle closer to lower than upper spine; opercular flap obtuse.

RELATIONSHIPS: The subgenus *Cephalopholis* seems to be an offshoot of the main *Epinephelus* line. It differs in having only nine dorsal spines and in small modifications of the skull.

Preliminary examination of certain Indo-

Pacific species indicates that the supposed distinction between *Petrometopon* and *Cephalopholis* is not constant and *Petrometopon* is here treated as a junior synonym.

INCLUDED SPECIES: Two species (*fulvus* and *cruentatus*) occur in the Western Atlantic and one (*panamensis*) lives in the Eastern Pacific. One or more species occur in the Eastern Atlantic and several in the Indo-Pacific region. The Eastern Atlantic species, *taeniops*, has been reported from the West Indies but these records do not seem to be supported by specimens and are probably misidentifications of *fulvus*.

The Eastern Pacific species, *acanthistius*, has long been regarded as a *Cephalopholis* because it has nine dorsal spines. On all other grounds, however, *acanthistius* is clearly assignable to the *Epinephelus niveatus* species-group of the subgenus *Epinephelus*.

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS *Cephalopholis*

1. Caudal rounded, without angles at upper and lower lobes. Skull with oblique transverse ridges connecting anterior ends of lateral crests with midline. No blue spots surrounded by black rings 2
- Caudal convex, but with definite obtuse angles at upper and lower lobes. Skull without transverse ridges connecting anterior ends of lateral crests. Body and head with small blue spots each surrounded by narrow black ring. In red phase from deep water these spots are replaced by small black spots without blue centers
. *Epinephelus (C.) fulvus*
2. Body with reddish spots about one-eighth inch in diameter, some with darker centers. No vertical cross bars; usually three or four distinct spots below base of dorsal fin. Western Atlantic
. *Epinephelus (C.) cruentatus*
- Body without reddish spots, but with nine or ten dark cross bands on lighter background. No conspicuous spots below base of dorsal. Eastern Pacific *Epinephelus (C.) panamensis*

Epinephelus fulvus Species-Group

Members of this species-group are characterized by having slightly convergent lateral skull crests not connected anteriorly by transverse ridges, a slightly emarginate caudal fin with definite, if obtuse angles, and generally a color pattern of small blue spots each surrounded by a black ring. Specimens from deeper water, however, have these spots reduced to small punctations and a generally red coloration with

reduced melanic pigments. This species-group includes the Eastern Atlantic species *Epinephelus* (*Cephalopholis*) *taeniops*, the Indo-Pacific *E. (C.) argus* and several others, all of which bear a close resemblance to *fulvus* of the Western Atlantic.

Epinephelus* (*Cephalopholis*) *fulvus (Linnaeus, 1758)
CONEY
Figure 7A

Caruna MARCGRAVE, 1648, p. 147 (Brazil).

Perca marina puncticulata CATESBY, 1743, p. 7.

Turdus cauda convexa CATESBY, 1743, p. 10.

Labrus fulvus LINNAEUS, 1758, p. 287 (original description, America, after Catesby).

Perca punctata LINNAEUS, 1758, p. 291 (original description, America, after Catesby). BONNATERRE, 1788, p. 130. GRAY, 1854, p. 109.

Guativere PARRA, 1787, pp. 7–8, pl. 5, figs. 1, 2 (Havana).

Perca punctulata GMELIN, 1789 (1788–1793), p. 1315 (original description, after Catesby).

Holocentrus auratus BLOCH, 1790 (1790–1793), p. 75 (original description, "East Indies").

Bodianus guativere BLOCH AND SCHNEIDER, 1801, p. 336 (original description, after Parra).

Gymnocephalus ruber BLOCH AND SCHNEIDER, 1801, p. 346, pl. 67 (original description).

Sparus punctulatus: LACÉPÈDE, 1802 (1800–1803), p. 155.

Serranus auratus: VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 364–365 (after Bloch). PETERS, 1866, p. 103.

Serranus ouatalibi VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 381–382 (after Parra). STORER, 1846, p. 278. MÜLLER AND TROSCHEL, 1848, p. 665 (Barbados). GUICHENOT, 1853, pp. 152–153 (Cuba). CASTELNAU, 1855, p. 2 (South America). GÜNTHER, 1859, pp. 120–121. POEY, 1864, p. 176. COPE, 1871b, p. 446 (New Providence; St. Kitts; St. Croix).

Serranus guativere: VALENCIENNES, in Cuvier and Valenciennes, 1828, p. 383. STORER, 1846, p. 278. MÜLLER AND TROSCHEL, 1848, p. 665 (Barbados). GUICHENOT, 1853, p. 153 (Cuba). POEY, 1864, p. 176. STEINDACHNER, 1866, pp. 776–777 (Cuba). COPE, 1871b, p. 466 (New Providence).

Serranus carauna VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 384–386 (original description, after Marcgrave). CASTELNAU, 1855, p. 1 (Brazil).

Enneacentrus ouatalibi: POEY, 1865 (1865–1866), p. 203 (Cuba).

Enneacentrus punctatus: POEY, 1868 (1866–1868), pp. 288–289 (Cuba). GOODE, 1876, pp. 59–60 (Bermuda); 1877, p. 292. BEAN AND DRESEL, 1885, p. 164 (Jamaica). COCKERELL, 1892, p. 7 (Jamaica). SMITH, 1896, p. 175 (Key Biscayne Bay).

Enneacentrus punctulatus: POEY, 1874, p. 34; 1875 (1875–1877), pp. 20–21; 1881, p. 319 (Puerto Rico).

Epinephelus punctatus: POEY, 1875 (1875–1877), p. 16 (Cuba). GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, p. 541. GOODE AND BEAN, 1886, p. 201. BOULENGER, 1895, pp. 183–184, fig. 16 (Bermuda; Jamaica; Santo Domingo; Barbados; Pernambuco, Bahía, Brazil; Lord Howe Island). METZELAAR, 1919, p. 231.

Enneacentrus punctatus guativere: GOODE, 1877, p. 292 (Bermuda).

Enneacentrus punctatus ouatalibi: GOODE, 1877, p. 292 (Bermuda).

Epinephelus fulvus var. *punctatus*: JORDAN, 1885c, p. 192 (identification of Catesby figure).

Epinephelus fulvus: JORDAN, 1885c, p. 194. JORDAN AND SWAIN, 1885b, pp. 402–405.

Enneacentrus fulvus var. *fulvus*: JORDAN AND SWAIN, 1885b, pp. 402–405.

Enneacentrus fulvus var. *punctatus*: JORDAN AND SWAIN, 1885b, pp. 402–405.

Enneacentrus fulvus var. *ouatalibi*: JORDAN AND SWAIN, 1885b, pp. 402–405.

Enneacentrus fulvus ruber: JORDAN, 1885 (1887a), p. 85; 1885d, p. 548; 1887c, p. 41; 1887e, p. 581 (West Indies).

Enneacentrus fulvus: JORDAN, 1887c, p. 41 (Havana); 1887e, p. 581 (West Indies). LEE, 1889, p. 671 (Rum Cay). HENSHALL, 1891, p. 388 (Key West). LÖNNBERG, 1895, p. 657 (Florida).

Enneacentrus fulvus rubra: LEE, 1889, p. 671 (Nassau; Watlings Is.).

Bodianus fulvus: JORDAN AND EIGENMANN, 1890, p. 379. HENSHALL, 1895, p. 216 (Key West). JORDAN AND EVERMANN, 1896a, p. 371; 1896b, pp. 1144–1145. JORDAN AND RUTTER, 1898, p. 104 (Jamaica). EVERMANN AND KENDALL, 1900, p. 73 (Key West; Tortugas; Florida Keys). BEAN, 1906, p. 52. BLOSSER, 1909, p. 297 (St. Croix). ROSÉN, 1911, p. 55 (Watlings Is.). MIRANDA-RIBEIRO, 1915, p. 26; 1918, pp. 91–92. JORDAN AND EVERMANN, 1920, opposite p. 382 (photograph).

Bodianus fulvus var. *fulvus*: JORDAN AND EIGENMANN, 1890, p. 379.

Bodianus fulvus var. *punctatus*: JORDAN AND EIGENMANN, 1890, p. 380. JORDAN, 1891, p. 319 (Bahía).

Bodianus fulvus var. *ruber*: JORDAN AND EIGENMANN, 1890, pp. 379–380.

Bodianus fulvus ruber: JORDAN, 1891, p. 336 (identification of *Serranus carauna* of Castelnau). JORDAN AND EVERMANN, 1896a, p. 371; 1896b, pp. 1145–1146. JORDAN AND RUTTER, 1898, p. 104 (Jamaica, copied). FOWLER, 1900, p. 118 (Port Antonio, Jamaica). BEAN, 1906, p. 52 (Bermuda). ROSÉN, 1911, p. 55 (Nassau). NICHOLS, 1912, p. 187; 1921, p. 22 (Turks Is.).

- Bodianus fulvus punctatus*: JORDAN, 1891, p. 336. JORDAN AND EVERMANN, 1896a, p. 371; 1896b, p. 1146. JORDAN AND RUTTER, 1898, p. 104 (Jamaica, copied). EVERMANN AND KENDALL, 1900, p. 73 (Key West; Biscayne Bay). BEAN, 1906, p. 52 (Bermuda). NICHOLS, 1921, p. 22 (Turks Is.).
- Bodianus punctatus*: LÖNNBERG, 1894, p. 127 (Key West). BLOSSER, 1909, p. 297 (St. Croix). EVERMANN AND MARSH, 1902, p. 150, fig. 43 (Puerto Rico). ROSÉN, 1911, p. 58 (Mastic Point and Clarence Harbor). EVERMANN AND SEALE, 1924, p. 29 (Barbados).
- Bodianus ruber*: EVERMANN AND MARSH, 1902, p. 150 (Puerto Rico). BLOSSER, 1909, p. 297 (St. Croix). EVERMANN AND SEALE, 1924, p. 28 (Barbados).
- Cephalopholis fulvus*: JORDAN AND THOMPSON, 1905, p. 239 (Tortugas). FOWLER, 1907, p. 252 (Bermuda; New Providence; Santo Domingo); 1920, p. 144 (St. Christophers; New Providence; Grand Inagua; Eleuthra; Fortune Island). MEEK AND HILDEBRAND, 1925, pp. 438-440 (Toro Point, Portobello, Panama). BREDER, 1925, p. 153 (Caledonia Bay, Panama); 1927, p. 39 (Royal Is.; Swan Is.; spelled *fulvis*). FOWLER, 1929a, pp. 153, 170 (St. Lucia; Key West). BREDER, 1929, p. 159. PARR, 1930, p. 49 (Green Cay; New Providence; Cat. Is.; Boobie Rocks; Hawks Nest, Turks Is.; spelled *fulvis*). JORDAN, EVERMANN, AND CLARK, 1930, p. 309. FOWLER, 1931, p. 272 (Grenada). BEEBE AND TEE-VAN, 1933, pp. 119-120 (Bermuda). BEEBE AND HOLLISTER, 1935, p. 215 (Union Is., Grenadines). FOWLER, 1936, pp. 749-750. BUTSCH, 1939, p. 23 (Barbados). LONGLEY AND HILDEBRAND, 1941, pp. 92-93 (color; rare at Tortugas). SCHULTZ, 1952, p. 121 (Venezuela). SPRINGER AND BULLIS, 1956, p. 77 (Gulf of Mexico). MARTIN SALAZAR, 1956, p. 103 (Gran Roque, Venezuela). RÖHL, 1956 (Venezuela). BRIGGS, 1958, p. 272. BARDACH, 1958, p. 140 (movements, Bermuda). SMITH, 1958, pp. 44-45, pl. 3 (Bermuda); 1959, p. 114, figs. 3-5 (hermaphroditic). BARDACH, 1959, p. 80 (standing crop, Bermuda). CERVIGÓN M., 1966b, pp. 292-293 (Gran Roque, La Tortuga, Los Hermanos, Venezuela).
- Cephalopholis fulvus ouatalibi*: FOWLER, 1907, p. 252 (New Providence; Santo Domingo; St. Croix; St. Kitts; Bermuda); 1920, p. 150; 1944, p. 444 (Nassau).
- Epinephelus (Bodianus) punctatus*: METZELAAR, 1919, pp. 46-47 (Curaçao; Bonaire; St. Eustacius).
- Cephalopholis punctatus*: FOWLER, 1920, p. 147 (Jamaica); 1929a, p. 158 (Port-au-Prince).
- Bodianus fulvus fulvus*: NICHOLS, 1921, p. 22 (Turks Is.).
- Cephalopholis fulvus ruber*: BEEBE AND TEE-VAN, 1928, pp. 124-125 (Port-au-Prince Bay). NICHOLS, 1929, pp. 248-249, fig. 112 (Puerto Rico, compiled). JORDAN, EVERMANN, AND CLARK, 1930, p. 309. FOWLER, 1938b, p. 310 (Haiti); 1942b, p. 68 (Cuba); 1944, pp. 444, 465 (West Indian records); 1953, p. 55 (Cartagena).
- Cephalopholis ruber*: FOWLER, 1929a, p. 164 (Puerto Rico).
- Cephalopholis fulvus punctatus*: BEEBE AND TEE-VAN, 1928, pp. 125-126 (Port-au-Prince). NICHOLS, 1929, p. 249, fig. 113 (Puerto Rico, compiled). JORDAN, EVERMANN, AND CLARK, 1930, p. 309. FOWLER, 1938b, p. 310 (Haiti). TORTONESE, 1939, p. 52 (Puerto Cabello). FOWLER, 1944, pp. 444, 465 (West Indian records); 1953, p. 55 (Cartagena).
- Cephalopholis fulvus fulvus*: FOWLER, 1942b, p. 68 (Cuba); 1944, pp. 444, 465 (numerous West Indian and mainland records).
- Cephalopholis ruber ruber*: FOWLER, 1950, p. 88 (St. Andrews Is.).
- Cephalopholis fulva*: BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:4, 1:14-1:15, 1:23, figs. 4.1, 13. RANDALL, 1963, p. 37 (Virgin Is., ecology). SMITH, 1965, p. 2 *et seq.* (gonad structure, hermaphroditism); 1966, pp. 1-11 (hybridization). CALDWELL, 1966, p. 39 (Jamaica). RANDALL, 1967, p. 696 (food habits). BÖHLKE AND CHAPLIN, 1968, p. 264 (Bahamas). RANDALL, 1968, p. 61, fig. 67 (general account; color photograph).

NOMENCLATURE: Some recent authors have used the trinomial to denote the three color phases. Since the modern definition of the subspecies implies genetic differentiation, and since these color forms are believed to be environmentally controlled, the species is treated in the binomial. Linnaeus based his description on the figures of Catesby; there is no type specimen.

The trivial name *fulvus* refers to the yellow color of the form described by Catesby.

DIAGNOSIS: Small species of *Epinephelus* with rounded preopercle, moderately robust body. Dorsal IX, 18; anal III, 9; pectoral 18; gill rakers 23-27. Anterior dorsal spines not elongate, dorsal interspinous membranes not excessively notched. Maxilla scaled. Three color phases: red (deep water), dark brown (shallow water), and xanthic (uncommon in deep and shallow water). Fish from shallow water have top and sides of body and head covered with small, bright blue spots each surrounded by dark rim. Two black spots on top of caudal peduncle and two at tip of lower jaw. Lower part of caudal fin colored like anal, upper part like soft dorsal.

This is the only American grouper with bright blue iridescent spots on the head and body. *Epinephelus (Cephalopholis) cruentatus* also has nine dorsal spines but differs in having red spots on reddish gray background and transverse ridges

connecting anterior ends of lateral skull crests (fig. 8B).

DESCRIPTION: Measurements of 10 specimens are given in table 3. The body proportions differ little from those of most species of *Epinephelus*.

The dorsal and anal lobes are rounded; the caudal is gently convex with rather sharp angles. The exposed part of the maxilla is scaled. The opercular flap is rather squarish. The nostrils are subequal.

The following color description is based chiefly on a living individual collected on the south shore of Bermuda on April 18, 1957, and was made after the fish had been held for two days in an aquarium. Ground color rich olive-brown. Body and head above a line from the lower part of the caudal peduncle to the tip of the snout densely spotted with light blue-green spots about 1 mm. in diameter; each spot surrounded by a narrow black ring. A black spot about 3 mm. in diameter, on dorsal part of each side of lower jaw near symphysis. Below these are three pale spots, one at tip of jaw, and one on each side of that one and separated from it by lines of ground color that extend vertically from the black spots. Two median black spots on top of the caudal peduncle, each about 3 mm. in diameter. Dorsal fin divided into three longitudinal bands of approximately equal width; base colored like the body, middle third pale olive, and outer third rich wine color. Basal two-thirds of fin spotted like the body, distal part immaculate. Tips of interspinous membranes black. Spinous and soft dorsal otherwise alike in coloration.

Caudal fin olive, darker at base and toward ventral margin. Dorsal margin and distal fourth of fin reddish brown, a little lighter than margin of dorsal fin.

Pectoral dusky olive at base and on membranes, gradually fading distally, the outer fourth quite pale. This margin and rays brownish orange.

Pelvic and anal fins similar in coloration, deep purple, shading to bright blue distally. Anal brightest blue on tips of anterior rays; pelvic brightest along anterior edge and tips of anterior rays.

A blue line along top of posterior half of lower jaw from articulation to midpoint of ramus.

Normally the body is only slightly counter-

shaded, but the shallow-water phases, at least, have a distinctive excitement pattern in which the body below a line from the tip of the snout to the posterior end of the dorsal fin is creamy white, whereas above this line it is dark brown. The excitement pattern shows a weakly defined dark band as wide as the eye extending from the front of the eye to the side of the upper jaw.

In the dark, and under certain other conditions, perhaps including anoxia, the body blanches so as to leave a pattern of irregular vertical bars. In this "sleep pattern" there is a tuning-fork mark on the head resembling that of *Epinephelus striatus*.

At depths of from 10 to 20 fathoms brownish olive phase intergrades with the deep-water phase, which is brilliant scarlet. The iridescent spots in the deep-water phase appear as black spots.

A less common color variant, in which the entire fish is bright chrome yellow, occurs in both deep and shallow waters; those from deep water are orange dorsolaterally, shading to scarlet on the back. Xanthic variants have fewer iridescent spots on the side but are otherwise similar to common phases. This variety is likely the result of a single gene.

RELATIONSHIPS: *Epinephelus fulvus* appears to be a close relative of the type species of *Cephalopholis* (*C. argus* Bloch and Schneider from the Indo-Pacific region) differing only in minor details of coloration and size. It is also quite similar to *E. (C.) taeniops* of the Eastern Atlantic, but that species lacks the distinct spots on the lower jaw and caudal peduncle.

ECOLOGY: This species seems to prefer clear water with little or no silt, for it was not found in the relatively murky water of Ferry Reach at Bermuda, although *E. striatus* and *E. guttatus* were. The coney is found in clear, shallow water on the south shore and to depths of over 30 fathoms on the Bermuda Banks. Shallow-water fish assume the excitement pattern at the first approach of danger and, also, at the first scent of food. Thus, it is an excitement phase rather than an alarm phase. In the excitement pattern the body appears to be elongate, almost wrasse-like in appearance. Coneys are readily caught on cut-fish bait, which attracts them from their daytime hiding places.

Because of their relatively small size, coneys seldom enter the Bermuda commercial catch, but their abundance makes them suitable for

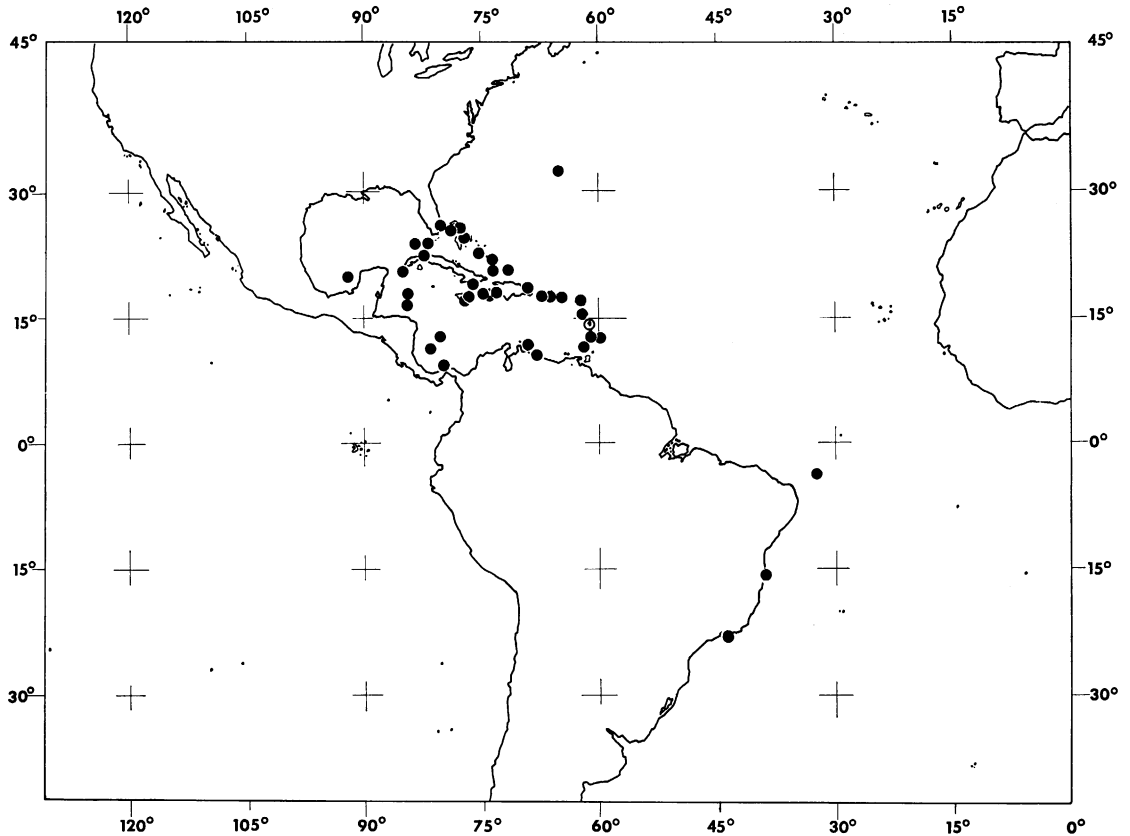


FIG. 9. *Epinephelus fulvus* distribution. Solid circles represent specimens examined, open circles are additional literature records.

use as bait. The species may assume increased importance in the future.

Spawning begins in May and continues until at least early August. The smallest male noted was about 8 inches long and the percentage of males increases to the maximum size of about 12 inches.

DISTRIBUTION: Coney occur in Bermuda, the Bahamas, and the Antilles, and from South Carolina to Panama, Colombia, and Brazil (Fernando de Noronha). The only records in the Gulf of Mexico are from the northern part of the Campeche Banks (fig. 9).

SPECIMENS EXAMINED

Florida: Off Miami, UMML; off Palm Beach, UMML 49-268; Bakers Haulover, UMML; Key West, ANSP 80007.

Gulf of Mexico: 20°05.7'N, 91°56.2'W, FMNH 46783.

Caribbean Sea: Misterioso Bank, FMNH 39790, 39791; Roncador Reef, ANSP; St. Andrews,

ANSP 81775; Swan Island, BOC 196; Royal Island, BOC 195.

Panama: Toro Point, FMNH 8387; USNM 80258; Portobelo, FMNH 8388-91; USNM 80319, 80255.

Venezuela: Porto Cabello, FMNH 6314; Curaçao, USNM.

Brazil: Bahia, USNM 43330; MCZ 4505; Rio de Janeiro, MCZ 874, 955-56; Maranhao, MCZ 10016; Fernando de Noronha, AMNH 18565.

Lesser Antilles: 18°07'N, 65°18'W, UMMZ 176964.

Grenada: ANSP 52473, 45091-92.

Barbados: USNM 131436.

St. Lucia: USNM 41298; Port Castries, ANSP 79297.

St. Kitts: ANSP 13415.

Sombrero Island: USNM 39835; MCZ 2835, 3074.

Virgin Islands: St. Croix, Frederiksted, FMNH; no specific locality, FMNH 52808-09, 54377;

ANSP 13410-13; MCZ 30151; St. Thomas, MCZ 10106, 10149.

Puerto Rico: Desecheo Island, FMNH; Arroyo, FMNH 3227; Porto Real, FMNH 3212; San Juan, UMMZ 172738, 172743; Mayaguez, TU 17182.

Hispaniola: Santo Domingo, MCZ 34700; ANSP 13406-09; Samaná Bay, USNM 88954; Pt. du Morne, FMNH 626; Petit Baraderes Bay, USNM 89648; Bigie Bay, USNM 89649-50; Port-au-Prince, USNM 133691; AMNH 19108, 19204; no specific locality, MCZ 2832; AMNH 19277.

Jamaica: Kingston, USNM 32083; Port Antonio, ANSP 18636; no specific locality, FMNH 2776, 2678.

Cuba: Guantanamo, BOC; Havana, ANSP 52092; off Cape Corrientes, TU 6314; Cienfuegos market, UMMZ 60552; no specific locality, USNM 9807, 9860, 9863, 2636, 3641, 129941; MCZ 10181-82, 10074-75, 10130, 10135-36, 10047, 10092, 10218, 26948, 10160, 10013; AMNH 18184.

Bahamas: Bimini, UMMZ 174399; FMNH 34213; BOC; New Providence, USNM 53134, 38493, 53132, 38495; MCZ 2811; ANSP 20553-4, 13385, 72280, 13416-17; CBC Stations 23, 192, 212, 225, 230, 242-43, 247, 257, 259, 431, 433; CBC lots 152-53, 172-73, 265, 340, 408; CBC accession 123; Rum Cay, USNM 38494, 38492; Exuma Cay, CBC Station 412; Cay Sal, FMNH 46132; Layton Cay, CBC accession 123; Watlings Island, USNM 53131, 38496; Long Island, USNM 53135; ?Tobago Cays, USNM 170193; Eleuthera, CBC lot 173; Royal Island, BOC 195; Turks Island, BOC 2356.

Bermuda: FMNH 4900-01, 48195, 4898-99; USNM 21402, 21897, 21386, 12710; MCZ 32869, 23784; ANSP 13418-19, 13622; AMNH 540, 1224; UMMZ 176054, 176056, 176106, 176116, 176128, 176140, 176144, 176162, 176166, 176173, 176361, 176502, 176505, 176529, 176580, 176604, 176614, 176622, 173400-S, 173404-S.

West Indies: No specific locality, USNM 9198, 33262, 33717.

No data: USNM 8130, 126876.

Epinephelus cruentatus Species-Group

The geminate American species *Epinephelus* (*Cephalopholis*) *cruentatus* of the Atlantic and *E.*

(*C.*) *panamensis* of the Pacific share the distinction of having prominent oblique transverse crests connecting the anterior ends of the lateral skull crests. Additional characters of the former genus *Petrometopon* Gill are: a rounded caudal fin without noticeable angles at the lobes, and a pattern of reddish spots on the cheek and opercular region separated by a dark reticular network of ground color.

Epinephelus* (*Cephalopholis*) *cruentatus

(Lacépède, 1802)

GRAYSBY

Figure 7B

Perca maculosa SEBA, 1761 (1734-1765), pp. 75-76, tab. 27, no. 6.

Perca guttatus (*non* Linnaeus): BLOCH, 1792 (1790-1793), pp. 89-91, pl. 312.

Bodianus guttatus: BLOCH AND SCHNEIDER, 1801, p. 330 ("Japan").

Sparus cruentatus LACÉPÈDE, 1802 (1800-1803), pp. 156-157, pl. 4, fig. 1 (original description, based on Plumier).

Serranus coronatus VALENCIENNES, *in* Cuvier and Valenciennes, 1828, pp. 371-373 (original description, Martinique). STORER, 1846, p. 280. MÜLLER AND TROSCHER, 1848, p. 665 (Barbados). GÜNTHER, 1859, p. 124 (Puerto Cabello; Cuba; Trinidad). COPE, 1871b, p. 446 (St. Croix; New Providence). GÜNTHER, 1880, p. 8 (Bermuda). COCKERELL, 1892, p. 8 (Jamaica).

Serranus guttatus: CASTELNAU, 1855, p. 1 (South America).

Serranus apiarius POEY, 1860 (1858-1861), pp. 143-144 (original description, Cuba).

Petrometopon coronatus: POEY, 1865 (1865-1866), pp. 198-199 (Cuba). FOWLER, 1929a, p. 158 (Port-au-Prince).

Petrometopon guttatus: GILL, 1865, p. 105. POEY, 1866 (1866-1868), p. 5; 1868 (1866-1868), p. 288 (Cuba); 1874, p. 34; 1875 (1875-1877), pp. 19-20 (nomenclature). GOODE, 1877, p. 292 (Bermuda).

Petrometopon apiarius: POEY, 1868 (1866-1868), p. 288 (Cuba); 1874, p. 34; 1875 (1875-1877), p. 20 (Cuba).

Serranus sp.: GOODE, 1877, p. 292 (Bermuda).

Enneacentrus guttatus: JORDAN AND SWAIN, 1885b, p. 398 (called *Epinephelus* in text). JORDAN, 1887c, p. 40 (Havana); 1887e, p. 581 (West Indies). LEE, 1889, p. 671 (Nassau, Rum Cay). HENSHALL, 1891, p. 388 (Key West; Garden Cay, Dry Tortugas). LÖNNBERG, 1895, pp. 657-658 (Florida).

Enneacentrus guttatus var. *coronatus*: JORDAN AND SWAIN, 1885b, p. 399.

Enneacentrus guttatus var. *guttatus*: JORDAN AND SWAIN, 1885b, pp. 398-399.

Epinephelus guttatus: JORDAN, 1884a, p. 78 (Key West);

TABLE 3
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus fulvus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	111	170	193	206	209	218	223	223	227	229	—
Head length	432	397	414	410	378	394	390	390	390	395	399.0
Head width	180	176	189	184	191	188	193	170	185	187	184.3
Head depth	279	259	280	272	244	271	269	258	253	275	266.0
Snout length	108	100	111	102	103	96	96	108	106	107	103.7
Suborbital width	41	47	49	46	48	46	49	52	48	46	47.2
Interorbital width	72	71	73	68	67	73	76	70	70	72	71.2
Length of: Orbit	86	76	70	68	65	64	65	63	62	66	68.5
Postorbital head	257	224	241	243	223	234	240	238	229	230	235.9
Maxillary	207	185	199	201	184	193	191	193	189	197	193.9
Lower jaw	216	176	212	204	184	202	202	202	189	205	199.2
Snout to angle of preopercle	306	265	285	274	256	289	278	260	262	282	275.7
Supramaxillary	63	53	49	61	55	55	58	58	64	57	57.3
Maxillary width	54	41	47	44	41	46	43	49	48	44	45.7
Tip of lower jaw to gular notch	135	165	145	165	148	124	126	143	156	144	145.1
Body width	180	191	187	194	179	186	198	159	174	186	183.4
Body depth	387	362	368	378	359	362	363	350	348	360	363.7
Caudal peduncle depth	153	135	140	138	134	140	139	137	137	138	139.1
Tip of snout to dorsal origin	441	356	414	379	373	408	386	381	366	382	388.6
Tip of snout to pectoral base	392	397	378	410	366	367	370	377	385	367	380.9
Tip of lower jaw to pelvic base	405	471	425	485	430	404	413	437	454	410	433.4
Length of: Dorsal base	595	523	554	521	531	550	529	558	537	533	543.1
Depressed dorsal	712	629	655	612	624	649	634	650	626	627	641.8
Anal base	189	176	181	187	175	183	188	188	170	166	180.3
Depressed anal	324	300	308	306	287	296	314	291	280	284	299.0
End of dorsal to caudal base	144	141	130	141	148	138	141	146	141	140	141.0
Length of: Caudal peduncle	216	182	181	194	181	188	193	191	192	188	190.6
Pectoral	297	259	277	271	249	257	265	240	258	253	262.6
Pelvic	243	200	205	209	194	193	206	197	203	197	204.7
Dorsal spine I	72	59	67	63	55	60	—	63	62	63	62.7
Dorsal spine III	149	124	130	129	110	119	130	119	117	109	123.6
Dorsal spine IX	135	124	119	126	120	112	126	117	115	105	119.9
Anal spine I	90	65	73	66	62	64	63	63	62	65	67.3
Anal spine II	167	135	129	121	115	124	135	112	115	118	127.1
Anal spine III	167	129	129	131	110	124	126	117	115	122	127.0
Caudal base to tip of upper rays	257	241	246	243	220	—	247	220	240	223	237.4
Caudal base to tip of middle rays	261	224	238	232	211	—	233	229	220	218	229.6
Caudal base to tip of lower rays	252	235	236	243	218	—	233	224	222	218	231.2

^aAll proportions are expressed in thousandths of the standard length. All specimens are UMMZ from Bermuda.

1885b, p. 125 (Key West). BOULENGER, 1895, pp. 176–177 (Atlantic coast).
Enneacetrus guttatus coronatus: JORDAN, 1887a, p. 85; 1887c, p. 41 (Havana); 1887e, p. 581 (West Indies).
Bodianus cruentatus: JORDAN, 1890, p. 648 (Port Castries, St. Lucia). HENSHALL, 1895, p. 216 (Florida). MIRANDA-RIBEIRO, 1915, pp. 26–27 (Brazil); 1918, p. 92.
Bodianus cruentatus var. *coronatus*: JORDAN AND EIGENMANN, 1890, p. 379.

Bodianus cruentatus var. *cruentatus*: JORDAN AND EIGENMANN, 1890, pp. 378–379.
Petrometopon cruentatus: JORDAN AND EVERMANN, 1896a, p. 371; 1896b, pp. 1141–1142. JORDAN AND RUTTER, 1898, p. 104 (Jamaica). EVERMANN AND KENDALL, 1900, p. 73 (Florida Keys). EVERMANN AND MARSH, 1902, p. 149 (Puerto Rico). EVERMANN AND GOLDSBOROUGH, 1902, p. 153 (Puerto Morelos, Mexico). BEAN, 1906, p. 54 (Bermuda). FOWLER, 1906, p. 96 (Marquesas Is.). ROSÉN, 1911, p. 55 (Andros Is.; Nassau; Rum Cay). NICHOLS, 1912,

- p. 187 (Havana). FOWLER, 1915b, p. 543 (St. George, Grenada); 1920, p. 144 (St. Croix). JORDAN AND EVERMANN, 1920, pp. 380-381. NICHOLS, 1921, p. 22 (Turks Is.). MEEK AND HILDEBRAND, 1925, pp. 441-442 (Toro Pt.; Colón, Porto Bello, Panama). BREDER, 1927, p. 39 (Swan Island; Glover Reef; Grand Cayman); 1929, p. 159. JORDAN, EVERMANN, AND CLARK, 1930, p. 308. PARR, 1930, p. 49 (Eleuthera; West Caicos; Turks Is.). FOWLER, 1931, p. 272 (Grenada). BEEBE AND TEE-VAN, 1933, p. 119 (Bermuda). Borodin, 1934, pp. 112-113 (Bermuda; Key West, Florida). HOWELL Y RIVERO, 1938, pp. 189-190 (type of *Serranus apiarius* Poey in MCZ). FOWLER, 1939, p. 12 (Kingston, Jamaica). BUTSCH, 1939, p. 23 (Barbados). FOWLER, 1942b, p. 68 (Cuba). SPRINGER AND BULLIS, 1956, p. 78 (Arcas Cay). SMITH, 1958, pp. 21, 42-43, fig. 14, pl. 2 (biology, Bermuda); 1959, p. 114 (hermaphroditic).
- Petrometopon cruentatus coronatus*: JORDAN AND EVERMANN, 1896a, p. 371; 1896b, p. 1142. EVERMANN AND KENDALL, 1900, p. 73 (Florida). FOWLER, 1915b, p. 533 (Port-au-Spain; copied); 1920, p. 150 (Nassau). BEEBE AND TEE-VAN, 1928, p. 126 (Port-au-Prince). NICHOLS, 1929, p. 248, fig. 111 (St. Croix). JORDAN, EVERMANN, AND CLARK, 1930, p. 308. FOWLER, 1944, pp. 444, 465 (Nassau; Rum Cay; Turks Is.; Roncador Bank; Courtown Cay; St. Andrews); 1953, p. 55 (Cartagena). BRIGGS, 1958, p. 273.
- Cephalopholis cruentatus*: JORDAN AND THOMPSON, 1905, p. 239 (Tortugas, compiled).
- Petrometopon cruentatum*: FOWLER, 1907, p. 252 (Viequas, Puerto Rico). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:4, 1:16-1:17, 1:23, fig. 14. RANDALL, 1963, pp. 34 *et seq.* (Virgin Islands, ecology). BRIGGS, 1964, pp. 451-452 (41 miles southeast of Port Aransas, Texas). CALDWELL, 1966, p. 43 (Jamaica). CERVIGÓN M., 1966b, pp. 293-294, fig. 115 (Cubagua, Venezuela). RANDALL, 1967, p. 705 (food habits); 1968, p. 64, fig. 68 (general account, color photograph). BÖHLKE AND CHAPLIN, 1968, p. 265 (Bahamas).
- Petrometopon cruentatum coronatum*: FOWLER, 1907, p. 252 (New Providence).
- Bodianus stellatus* BLOSSER, 1909, pp. 297-298, pl. 10 (original description, St. Croix, holotype Carnegie Museum No. 1473, now FMNH).
- Epinephelus (Bodianus) stellatus*: METZELAAR, 1919, p. 47 (Curaçao).
- Epinephelus (Petrometopon) coronatus*: METZELAAR, 1919, p. 46, fig. 16 (Curaçao).
- Petrometopon cruentatus cruentatus*: NICHOLS, 1929, pp. 247-248 (Santurce, Puerto Rico). FOWLER, 1944, pp. 444, 465 (Bahamas; Kingston; other West Indian localities). BRIGGS, 1958, p. 273.
- Cephalopholis stellatus*: JORDAN, EVERMANN, AND CLARK, 1930, p. 309.
- NOMENCLATURE: Two forms have been recognized: *coronatus* from deeper water, and *cruentatus* from the shallows. The *cruentatus* form has red spots with dark centers, which in preservative are left as dark spots. There are no other differences, and this pigmentary distinction is surely environmentally produced.
- The Linnean name *Perca guttata* has been applied to this species, but is now used for another species of *Epinephelus*, for reasons given under that species. Lacépède's name seems proper for the graysby.
- The species was based on a figure, hence there is no holotype. The type of *Serranus coronatus*, Paris Museum 890, has been examined by Carl L. Hubbs and its identification is confirmed by his observations. It is 193 mm. long and was collected at Martinique by Pleé.
- The adjectival name *cruentatus* (Latin) means dyed with blood.
- DIAGNOSIS: Species of *Epinephelus* with robust body, rounded preopercle, and large median canine teeth in posterior row. Dorsal IX, 14; anal III, 8; pectoral 16; gill rakers 18-21. A dense pattern of red or brown spots over reddish gray background. Four distinct spots along base of dorsal fin vary from black to white independently of rest of body color.
- The nine dorsal spines and convex tail immediately set this species apart from any other Atlantic grouper except *E. fulvus* which, however, has a color pattern of small blue or black spots on a red, brown, or yellow background in contrast to the pattern of the graysby of light red spots on the red-gray background. Three or four spots along base of dorsal usually stand out conspicuously and provide excellent recognition characters. The Pacific species, *panamensis*, is distinguished by lack of light spots on body, absence of contrasting spots along base of dorsal, presence of vertical bars, and large dark spot behind eye.
- DESCRIPTION: The general body form of the graysby is similar to those of *Epinephelus* (*Cephalopholis panamensis* and *E. fulvus* (table 4)).
- The dorsal and anal lobes are rounded; the dorsal spines are moderate in length, the fourth or fifth being longest. The caudal is rounded at all sizes. The maxilla is scaled and the gill rakers are moderate in length and reduced in number. The preopercle is gently rounded and has a shallow notch. In each jaw the medial canines in the posterior row are longer than those

in the anterior row. The pelvics are rounded; the last ray is adnate for only about a third of its length. The opercular flap is squarish; the uppermost opercular spine is longer than the lowest. The nostrils are subequal.

The following color description was made from a living specimen about 132 mm. long in the Lerner Marine Laboratory aquarium: ground color olive green, slightly lighter ventrally; covered with small, dark, reddish brown spots that are nearly uniform above and below. Smaller spots on maxilla, pectoral fin, and toward margins of other fins. A brilliant white stripe from tip of lower jaw across upper jaw and snout, continuing in the midline to a point halfway between orbit and dorsal origin. Four brilliant white spots along middorsal line; first near end of white stripe on predorsal region, second at base of third dorsal spine, third at base of sixth dorsal spine, and fourth at base of anterior soft rays. Each fin, except spinous dorsal, with an unspotted band of translucent gray that shades to reddish purple distally. The soft dorsal, anal, and caudal narrowly edged with pearly blue.

The sleep pattern consists of irregular vertical bars on the body with some longitudinal bars on the head. In preservative the red spots fade to pale white; some are irregular with dark centers. Such a specimen prompted the naming of *Bodianus stellatus*. The spots along the dorsal base change rapidly from pearly white to jet black.

Young as small as 20 mm. (FMNH) were taken by Donald S. Erdman in Haiti. In preservative they are uniform brown with dark spots on the head and on the body anteriorly. There seems to be no definite juvenile pattern in either this species or in *Epinephelus fulvus*.

RELATIONSHIPS: The two American species formerly known as *Petrometopon* are geminate forms which have evolved as a result of the isolation caused by the emergence of the Middle American Isthmus. They are well separated on the basis of color pattern but structural differences are minor.

ECOLOGY: This species is not abundant in Bermuda but is taken there in moderate numbers on the north reefs. It is quite numerous at Bimini where it is readily taken on hooks baited with cut conch (*Strombus gigas*). An individual 132 mm. long established itself in an aquarium in the Lerner Marine Laboratory

and challenged all comers, even larger fish than itself. Whether this demonstrated territoriality or mere food seeking was not determined. The sleep pattern of vertical bars apparently serves also as an excitement pattern.

The small size of *Epinephelus cruentatus* keeps it from being of commercial importance although it is presumably an excellent food fish.

DISTRIBUTION: The graysby occurs in Bermuda and from Florida to Brazil and throughout the Antilles and the Bahamas. The only Gulf of Mexico records are from Arcas Cay in the Gulf of Campeche and 41 miles south of Port Aransas, Texas (fig. 10).

SPECIMENS EXAMINED

Florida: Key West, MCZ 2837; FMNH 7032, 7008, 7045; USNM 35058, 62790-91, 143185, 83816; UMMZ 172579, 172580-S; Alligator Reef Light, USNM 57131; Triumph Reef, FMNH 46905; Miami, UMML; UMIM; UMMZ 172576; Cape Florida, UMIM 118-19, UMIM; Tortugas, USNM 117190.
Gulf of Mexico: Arcas Cay, FMNH 45480.
Caribbean Sea: Glover Reef, FMNH 39756-57; BOC 198; Grand Cayman, BOC 537; Swan Island, BOC 197.
Mexico: Puerto Morelos, USNM 50508.
Panama: Toro Point, USNM 80259, 80311, 128758-60; FMNH 20550-51; Portobelo, USNM 80312-13, 80249; Colón Reef, USNM 80261, 80314, 80322; no specific locality, FMNH 20552-56.
Venezuela: Puerto Cabello, FMNH 6310.
Grenada: ANSP 45086, 52474.
Barbados: USNM 120758.
Dominica: AMNH 1542.
Buck Island: USNM 78147.
St. Kitts: ANSP 13414.
Virgin Islands: St. Thomas, FMNH 2280; USNM 6761; St. Croix, FMNH 53048 (holotype of *Bodianus stellatus* Blosser, 156 mm., formerly Carnegie Museum 1273); MCZ 10215.
Puerto Rico: Vieques, ANSP 31728.
Hispaniola: Haiti, AMNH 18945, 19111; Port-au-Prince, FMNH; USNM 132540, 133693, 133696, 170019; UMMZ 142456; ANSP 76341, 77208; AMNH 19109, 18908, 19025, 19307; Gulf of Gonavé, FMNH; Jeremie, MCZ 2834; Santo Domingo, ANSP 77320, 77328; Samaná Bay, USNM 88953, 133696.

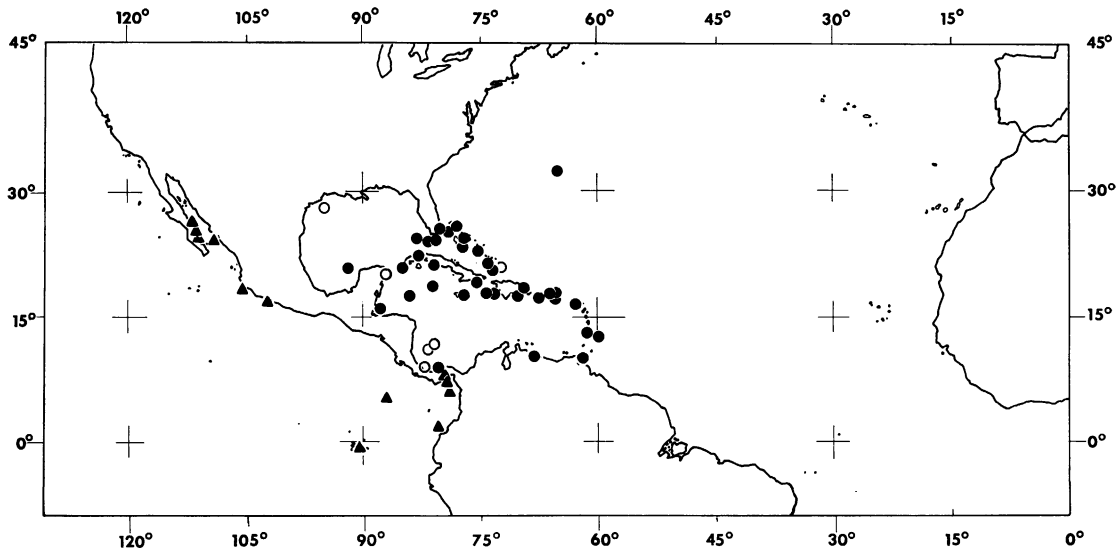


FIG. 10. Distribution records for *Epinephelus cruentatus* (circles) and *E. panamensis* (triangles). Solid symbols represent specimens examined, open symbols represent additional literature records.

Jamaica: St. Anne's Bay, BOC.

Cuba: Guantanamo Bay, BOC; Havana, USNM 35014-15, 38743, 129942-43; Cienfuegos Bay, MCZ 31708; Corrientes Bay, MCZ 39464; no specific locality, USNM 6775, 6921, 9816, 19801, 24779, 33661; MCZ 625, 9998, 10006, 10070, 10077, 10158 (type of *Serranus apiarius* Poey), 10186.

Bahamas: Bimini, FMNH; UMMZ 174394, 174396-S, 174400; Exuma, CBC lot 408-09, CBC Stations 410, 412; Green Cay, CBC Station 414; New Providence, USNM 38490, 53133; CBC Stations 181, 212, 219, 230, 232, 234, 241, 243, 246, 252, 255, 259, 292, 303, 410, 412; CBC lots 106, 118, 122, 128, 150, 155, 168, 172, 198, 265; ANSP 13467; MCZ 2831; FMNH 43098; Rum Cay, USNM 38491; Hawks Nest, Turks Island, BOC 2357; AMNH 7211; West Caicos, BOC 2319; no specific locality, USNM 6775.

Bermuda: FMNH 5270-71; USNM 169993, 170045, 21403; UMMZ 176413, 176532, 176617, 176630, 177496.

Epinephelus* (*Cephalopholis*) *panamensis
(Steindachner, 1876)

Serranus panamensis STEINDACHNER, 1876, pp. 551-554, pl. 1, fig. 1 (original description, Panama).

Enneacentrus panamensis: JORDAN AND SWAIN, 1885b, p. 398 (after Steindachner). JORDAN, 1886b, p. 377 (copied).

Bodianus panamensis: JORDAN AND EIGENMANN, 1890, p. 378 (copied).

Epinephelus panamensis: BOULENGER, 1895, p. 177.

Petrometopon panamensis: JORDAN AND EVERMANN, 1896a, p. 371; 1896b, p. 1141. GILBERT AND STARKS, 1904, p. 95 (Panama Bay). KENDALL AND RADCLIFFE, 1912, p. 107 (Taboguilla; Acapulco). OSBURN AND NICHOLS, 1916, p. 160 (Conception Bay, Lower California). MEEK AND HILDEBRAND 1925, pp. 443-440 (Balboa and Panama City markets). JORDAN, EVERMANN, AND CLARK, 1930, p. 308. WALFORD, 1937, p. 121, pl. 15, fig. a.

NOMENCLATURE: The adjectival name *panamensis* refers to Panama, the type locality.

I have been unable to determine whether Steindachner's type is still in existence.

DIAGNOSIS: Small species of *Epinephelus*, with robust body, rounded preopercle, and large, median caniniform teeth. Dorsal IX, 14; anal III, 8; pectoral 17 (18); gill rakers 16-19. Color pattern blue or yellow spots on side of head separated by dark reticulum. Body with black cross bands. Large black spot behind eye.

DESCRIPTION: The general shape is like that of *Epinephelus cruentatus* and its proportional measurements (table 5) are very similar except that the interorbital is slightly narrower. The preopercle is rounded, finely serrate above and without conspicuously enlarged serrae at the angle. The maxilla is scaled. The dorsal and anal soft lobes and the caudal are rounded; the

TABLE 4
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus cruentatus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	131	141.5	147	149	150	153	157.5	160.5	218	257	—
Head length	401	413	412	413	410	408	406	411	417	416	410.7
Head width	176	155	170	158	180	176	175	174	183	181	172.8
Head depth	267	283	265	275	273	281	267	277	298	309	279.5
Snout length	95	106	105	107	100	105	102	112	117	113	106.2
Suborbital width	34	37	34	40	37	39	41	37	41	43	38.3
Interorbital width	65	64	61	60	60	65	63	69	69	54	63.0
Length of: Orbit	69	71	71	70	73	69	67	65	64	74	69.3
Postorbital head	248	247	245	242	240	239	244	243	250	261	245.9
Maxillary	202	212	211	208	210	206	210	215	234	228	213.6
Lower jaw	210	223	218	211	207	209	206	209	236	237	216.6
Snout to angle of preopercle	290	293	296	295	297	294	295	302	317	—	297.7
Supramaxillary length	65	64	71	67	60	65	67	59	71	62	65.1
Maxillary width	42	53	48	47	50	49	50	44	50	51	48.4
Tip of lower jaw to gular notch	145	141	129	134	157	150	146	156	161	144	146.3
Body width	160	152	187	164	170	176	165	168	177	161	168.0
Body depth	366	367	344	359	370	382	378	377	399	381	372.3
Caudal peduncle depth	134	138	133	134	137	141	140	143	151	140	139.1
Tip of snout to dorsal origin	405	424	422	416	411	405	400	414	440	442	417.9
Tip of snout to pectoral base	378	385	378	379	400	392	397	399	408	381	389.7
Tip of lower jaw to pelvic base	405	403	395	413	440	425	429	417	420	409	415.6
Length of: Dorsal base	538	526	534	520	523	533	508	530	550	541	530.3
Depressed dorsal	653	654	660	638	633	637	616	657	658	654	646.0
Anal base	195	187	180	181	173	190	190	187	206	175	186.4
Depressed anal	347	311	316	326	313	337	337	340	333	302	326.2
End of dorsal to caudal base	137	134	133	134	133	137	133	143	119	128	133.1
Length of: Caudal peduncle	168	170	173	168	170	163	184	187	161	167	171.1
Pectoral	248	244	272	275	267	275	260	252	261	270	262.4
Pelvic	198	184	184	198	193	196	197	193	197	187	192.7
Dorsal spine I	65	64	68	67	57	56	54	59	64	64	61.8
Dorsal spine III	126	131	126	126	123	131	117	125	124	128	125.7
Dorsal spine IX	122	117	122	114	120	127	124	121	112	113	119.2
Anal spine I	73	74	75	77	73	85	70	72	71	82	75.2
Anal spine II	137	148	150	154	137	150	140	131	131	130	140.8
Anal spine III	145	145	146	131	143	147	127	128	138	132	138.2
Caudal base to tip of upper rays	225	237	214	232	227	222	229	231	239	230	228.6
Caudal base to tip of middle rays	248	254	245	248	247	252	241	243	257	239	247.4
Caudal base to tip of lower rays	218	216	218	221	230	216	216	218	218	222	219.3

^aAll proportions are expressed in thousandths of the standard length. All specimens are UMMZ from Bimini.

fourth or fifth dorsal spine is the longest. The last pelvic ray is adnate for its basal third only. The caniniform teeth are enlarged as in *E. cruentatus*. Transverse skull crests present.

The following is the color description of this species given by Meek and Hildebrand (1925, p. 443): "Color in life very dark red; sides with

about ten dark bars which are faint on upper part of the body; no round dark spots; sides of head with more or less distinct bluish spots, most prominent on lips; a dark blotch behind the eye is sometimes present; fins usually uniform dark brown; the dorsal and anal occasionally with bluish spots at the base on interradi-
al

membranes; the margins of the fins often blue." Walford (1937, p. 121) stated that the spots on the head and nape are orange and the spinous dorsal fin is brown at the tips, gray at the base.

RELATIONSHIPS: This species so strongly resembles *Epinephelus cruentatus* of the Western Atlantic that even without examination of the skull crests it is recognizable as a twin of *cruentatus*. The two species, however, are well differentiated and there is no question of their distinctness.

ECOLOGY: Meek and Hildebrand (1925, p. 443) stated that this is a fish of the rocks and is seldom taken in seines. It apparently never exceeds 1 foot in length.

DISTRIBUTION: *Epinephelus panamensis* is known from the Gulf of California to Gorgona Island off Colombia (fig. 10).

SPECIMENS EXAMINED

Mexico: Baja California, Puerto Marquez Bay, FMNH; Puerto Refugio, USNM 167566; Bahía Concepción, UCLA W53-97; AMNH 5464, 5481, 5485; Punta Concepción, UCLA W65-70; LACM W65-72; Muleje, UCLA W57-32; Sonora, Punta San Guillermo, UCLA W50-50, W50-33, W56-78; Puerto San Carlos, UCLA W52-41; LACM W58-41; Agua Verde, UCLA W61-123; LACM W65-60; Punta Pulpito, LACM W65-51, W65-75; Punta San Telmo, LACM W65-58; Isla Carmen, LACM W65-71, W65-63, W65-65, W65-77, W65-78, W65-79, W65-82; Isla Santa Cruz, LACM W65-86; Isla Santa Inez, LACM W65-66; Isla San Francisco, LACM W65-89, W65-90, W65-88; Isla San Jose, LACM W65-48; Cabeza de Mechudo, LACM W65-87; Colima, Playa de Santiago, northwest of Manzanillo, UCLA W56-232; Sinaloa, Isthmus de Isla Venados, UCLA W51-54; Acapulco, MCZ 29633, 29659, 29681.

Panama: Balboa Bay, FMNH 20557-70; USNM 50414, 65607-08, 80260, 128761; Canal Zone, Amador, Perico Island, UCLA W53-277; Taboguilla Island, MCZ 29574; USNM 65609; La Venta, USNM 128762; Taboga Island, USNM 80247-48; Archipiélago de las Perlas, AMNH 16758.

Costa Rica: Isla del Coco, Chatham Bay, LACM W64-47.

Colombia: Gorgona Island, USNM 101766.

Ecuador, Islas Galápagos: Isla Santa Cruz (Indefatigable), LACM W64-37.

SUBGENUS EPINEPHELUS BLOCH, 1793

- Epinephelus* BLOCH, 1793 (1790-1793), p. 11 (type species, *Epinephelus marginalis* Bloch [a subjective synonym of *Epinephelus fasciatus* Forskål], designated under plenary power of the International Commission on Zoological Nomenclature, Opinion 93).
- Cerna* BONAPARTE, 1835 (1832-1841), p. 10 (type species, *Serranus gigas* Brunnich [a subjective synonym of *Labrus guaza* Linnaeus], by original designation).
- Cynichthys* SWAINSON, 1839, p. 201 (type species, *Perca flavopurpurea* Bennet [a subjective synonym of *Holocentrus flavocaeruleus* Lacépède], by monotypy).
- Hyporthodus* GILL, 1862b, p. 98 (type species, *Hyporthodus flavicaudus* Gill [a subjective synonym of *Serranus niveatus* Valenciennes], by monotypy).
- Labroperca* GILL, 1863a, p. 236 (type species, *Serranus labriiformis* Jenyns, designated by Gill, 1864a, p. 80).
- Schistorus* GILL, 1863a, p. 236 (type species, *Serranus mystacinus* Poey, by monotypy).
- Merus* POEY, 1874, p. 39 (type species, *Serranus gigas* (Brunnich), Valenciennes [a subjective synonym of *Labrus guaza* Linnaeus], by orthotypy).
- Priacanthichthys* DAY, 1868, p. 193 (type species, *Priacanthichthys maderaspatensis* Day [a subjective synonym of *Epinephelus latifasciatus* Temminck and Schlegel], by monotypy).
- Homalogrystes* ALLEYNE AND MACLEAY, 1877, p. 268 (type species, *Homalogrystes guentheri* Alleyne and Macleay [a subjective synonym of *Epinephelus tauvina* (Forskål)], by monotypy).
- Itaïara* VAILLANT AND BOCOURT, 1877 (1915), p. 70 (type species, *Serranus itaïara* Lichtenstein, by monotypy [proposed as a subgenus]).
- Hyposerranus* KLUNZINGER, 1884, p. 3 (type species, *Serranus morrhua* Valenciennes, by monotypy).
- Garrupa* JORDAN, in Jordan and Eigenmann, 1890, p. 353 (type species, *Serranus nigrilus* Holbrook, by original designation [proposed as a subgenus]).
- Vivero* JORDAN AND EVERMANN, 1927, p. 505 (type species, *Epinephelus morio* Valenciennes, by original designation [proposed as a subgenus]).

NOMENCLATURE: The type of *Epinephelus* was selected by Jordan and Eigenmann in 1890 although these authors themselves were dubious whether their choice would stand, since it was not the first named species in Bloch's original *Epinephelus*. Fowler (1907), applying the "rule" that the first-named species should be the type of a genus, restricted the name to the subgenus here called *Alphestes*. This confusion has been resolved by a definite ruling of the International Commission (Opinion 93) fixing the type of *Epinephelus* as *E. marginalis* Bloch.

The name *Epinephelus* comes from the Greek ἐπινέφελος, clouded over, in allusion to the

TABLE 5
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus panamensis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	63	75	83	84	123	142.5	152	155	177	208	—
Head length	389	413	416	399	390	414	408	403	401	413	404.6
Head width	159	173	169	167	146	154	161	174	175	178	165.6
Head depth	254	253	271	268	264	274	280	274	271	276	268.5
Snout length	87	93	96	83	85	98	105	103	102	103	95.5
Suborbital width	25	33	42	36	37	39	43	39	42	50	38.6
Interorbital width	56	53	48	54	48	53	49	58	54	58	53.1
Length of: Orbit	87	67	84	77	77	81	69	77	68	70	75.7
Postorbital head	230	253	247	238	199	249	250	242	232	255	239.5
Maxillary	182	193	193	185	199	211	204	206	212	216	200.1
Lower jaw	190	200	205	202	203	218	211	213	212	226	208.0
Snout to angle of preopercle	278	293	295	286	289	295	289	294	288	303	291.0
Supramaxillary length	63	80	72	65	69	63	66	61	62	60	66.1
Maxillary width	40	47	42	48	45	53	43	48	45	48	45.9
Tip of lower jaw to gular notch	135	127	127	143	118	133	122	132	—	149	131.8
Body width	151	147	145	161	134	133	164	158	172	188	155.3
Body depth	335	367	361	363	354	347	368	361	362	363	358.1
Caudal peduncle depth	135	140	145	149	142	105	135	142	141	144	137.8
Tip of snout to dorsal origin	381	400	404	393	394	—	414	413	390	413	400.2
Tip of snout to pectoral base	381	373	373	381	374	379	378	384	381	404	380.8
Tip of lower jaw to pelvic base	397	393	404	452	390	407	395	410	441	445	413.4
Length of: Dorsal base	516	553	518	554	541	533	546	545	506	490	530.2
Depressed dorsal	619	680	639	690	663	642	664	639	616	606	645.8
Anal base	159	173	193	179	175	168	168	174	169	173	173.1
Depressed anal	310	333	343	345	321	305	316	306	294	310	318.3
End of dorsal to caudal base	151	147	145	137	150	137	138	135	141	139	142.0
Length of: Caudal peduncle	190	180	205	190	183	182	181	187	192	171	186.1
Pectoral	254	260	277	268	256	242	250	242	243	236	252.8
Pelvic	190	193	205	190	191	175	184	177	169	168	184.2
Dorsal spine I	56	60	60	65	61	53	56	58	59	55	58.3
Dorsal spine III	119	133	120	131	130	119	112	126	113	120	122.3
Dorsal spine IX	111	127	133	119	118	102	118	110	113	101	115.2
Anal spine I	56	87	78	65	65	70	62	71	71	65	69.0
Anal spine II	135	140	175	155	142	133	118	142	121	120	138.1
Anal spine III	135	140	151	131	138	123	122	126	116	108	129.0
Caudal base to tip of upper rays	222	240	247	238	224	225	217	213	206	197	222.9
Caudal base to tip of middle rays	254	267	283	268	236	239	230	226	218	224	244.5
Caudal base to tip of lower rays	222	247	229	226	224	228	187	229	201	207	222.0

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Column 1, USNM 167566; columns 2-4, USNM 80248; 5, 6, 8, USNM 50414; 7, 9, 10, USNM 128761, 128762, 80274 respectively. See text for data.

membrane believed to cover the eye of *Epinephelus ruber* (*Mycteroperca rubra*). The name is clearly masculine in gender.

DIAGNOSIS: Moderate to large-sized groupers with robust, compressed to nearly terete bodies. Dorsal outline usually more strongly arched than

ventral, body deepest at dorsal origin. Dorsal XI (X in a few species), 14 to 18. Anal III, 8 to 9. Gill rakers 19 to 28 on first arch. Head long, 34 to 47 per cent of standard length. Caudal rounded to slightly lunate. Scales moderate to small, strongly ctenoid. Lacrimal and suborbital

region wide. Supramaxilla present, well developed.

Skull crests well developed in most species. Frontoparietal crests convergent anteriorly then abruptly diverging to join postorbital process, ending behind orbit. Supraethmoid usually forming bottom of pit between frontals (expanded in a few species into transverse wall). Parasphenoid straight or nearly so. Anterior wing of hyomandibular well developed. Usually one or more pairs of enlarged canine teeth near symphysis of each jaw.

RELATIONSHIPS: The genus *Epinephelus* seems to represent the main stock of the groupers from which other genera have diverged. Various species of this genus have become specialized in diverse directions. Boulenger (1895) placed all of the groupers except *Paranthias* in a single genus. However, *Mycteroperca* certainly merits generic recognition and other groups of species stand apart from the main stem. I prefer to recognize them as subgenera, pending a complete revision of the Serranidae of the world.

INCLUDED SPECIES: This subgenus is circum-tropical in its distribution and includes nearly 100 species, of which 13 are from American coasts. The characters of the New World species are summarized in table 6 and the key below.

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS
Epinephelus

1. Pelvic fins shorter than pectoral fins, inserted below or behind ventral end of pectoral base . 2
Pelvic fins longer than pectoral fins, inserted well anterior to ventral end of pectoral base (*E. niveatus* species-group) 9
2. Body color pattern consisting of definite spots or vertical bars, or if body color is generally plain then dorsal interradial membrane is not notched between spines and there is no saddle-shaped blotch on caudal peduncle 3
Body color pattern generally plain reddish brown without well-defined spots or bars but sometimes with light reticulations or nebulous lighter spots 8
3. Dorsal spines 10; color pattern consisting of dark spots on lighter background. Eastern Pacific *Epinephelus analogus*
Dorsal spines 11. Western Atlantic species . . . 4
4. Color pattern spotted; either light spots on a dark background or dark spots on a light background 5
Color pattern plain reddish or with dark bars on a tawny background 7
5. Body, head, and fins everywhere covered with

- small, more or less stellate white spots (Florida and Bermuda) . . . *Epinephelus drummondhayi*
Body, head, and basal parts of vertical fins with dark spots on light background. 6
6. Maxilla usually scaleless (occasional specimens have small patch of scales on one or both sides); dark, saddle-shaped dorsal blotch on caudal peduncle and two indistinct blotches along base of dorsal fin. Outer third of vertical fins not abruptly darker than basal part. Dark spots on body largest ventrally, decreasing in size dorsally. Eastern and Western Atlantic *Epinephelus adscensionis*
Maxilla scaled; no saddle-shaped dorsal blotches. Outer third of soft dorsal, caudal, and anal fins abruptly darker than basal parts. Spots on body nearly constant size. Western Atlantic *Epinephelus guttatus*
7. Interradial membranes little notched between dorsal spines. Second dorsal spine longer than third. Color generally reddish brown, sometimes marbled with lighter spots. A few dark pinpoint spots on cheeks but not in regular row around eye, no saddle on caudal peduncle *Epinephelus morio*
Interradial membranes distinctly notched between dorsal spines. Third dorsal spine longer than second. Body color pattern consisting of about six more or less irregular and anastomosing vertical bars. Distinct squarish blotch on top of caudal peduncle. Single or double row of small black spots below and behind eye *Epinephelus striatus*
8. Color pattern generally reddish brown with varying degrees of lighter reticulations, sometimes forming wavy longitudinal lines. Small but distinct saddle-shaped blotch on dorsal surface of caudal peduncle. Eastern Pacific *Epinephelus labriformis*
No black saddle on caudal peduncle. Body with nebulous whitish spots that tend to form vertical rows. Eastern and Western Atlantic *Epinephelus guaza*
9. Dorsal spines 9 or 10 10
Dorsal spines 11 11
10. Dorsal spines 9. Eastern Pacific
. *Epinephelus acanthistius*
Dorsal spines 10. Western Atlantic and Eastern Pacific. Pectoral and caudal fins hyaline in individuals less than 150 mm. Sides with a few irregularly arranged pearly spots in individuals less than 300 mm. long. Large individuals immaculate reddish brown, with second dorsal spine the largest and interradial membrane deeply cleft *Epinephelus nigrilus*
11. Body color pattern consisting of 9 to 11 very regular dark vertical bars; no saddle-shaped blotch on caudal peduncle, but two bars on

TABLE 6
SOME CHARACTERS OF THE NEW WORLD SPECIES OF *Epinephelus*

Species	Dorsal Rays	Anal Rays	Pectoral Rays	Gill Rakers	Color Pattern	Caudal Peduncle Saddle	Spinous Dorsal Membrane	Longest Dorsal Spine	Caudal Fin Shape
<i>striatus</i>	XI, 16-18	8	35-38	22-26	5-6 vertical bars	very distinct, square	not notched	3-5	round or square
<i>morio</i>	XI, 16-17	9	33-36	22-25	red-brown, black points on sides of head	absent	not notched	2	square or slightly lunate
<i>guttatus</i>	XI, 15-16	9 (8)	32-36	24-28	red spots on light background	absent	indented	3-5	round
<i>guaza</i>	XI, 15-16	8	36-37	22-25	plain red, irregular white spots	absent	notched	3-5	round or square
<i>labriiformis</i>	XI, 16-17	9	35-39	23-26	red-brown, irregular white spots	small, distinct on top of peduncle	notched	3-5	round
<i>drummondhayi</i>	XI, 15-16	9	35-36	23-28	close-set white spots on head, body, and fins, except on pectoral	absent	notched	3-5	square or slightly lunate
<i>niveatus</i>	XI, 14-15	9	34-38	22-27	white spots in regular rows, continuous dark dorsal margin	extends below lateral line	notched	3-5	round
<i>flavolimbatus</i>	XI, 14(15)	9	36	23-26	white spots in regular pattern, dorsal margin yellow	ends at lateral line	notched	3-5	round
<i>acanthistius</i>	IX, 17	9	33-37	25-27	plain red	absent	deeply notched in adult	3-5	round
<i>nigritus</i>	X-XI, 14-15	9	36-39	21-25	scattered white spots	absent	deeply notched in adult	3-5	round or square
<i>mystacinus</i>	XI, 14-15	9	36-38	22-25	9-10 regular vertical bars	absent	notched	2 (3 in young)	square
<i>adscensionis</i>	XI, 16-18	8	35-39	24-28	red spots, which become darker ventrally	present on peduncle, two others along base of dorsal	notched	3-5	round or square
<i>analogus</i>	X, 17-18	8	39-40	26-28	red spots of even size	absent	notched	3-5	round or square

caudal peduncle may be fused to form wide band that is darkest dorsally. No black points around eye. Western Atlantic and Eastern Pacific *Epinephelus mystacinus*

Body without definite vertical bands but with well-defined pearly spots aligned in regular vertical and horizontal rows 12

- 12. Spinous and anterior part of soft dorsal with bright yellow margin (pale in preserved specimens). Dark dorsal blotch on caudal peduncle not extending below lateral line. Bright blue line from posteroventral part of orbit to angle of preopercle. Pearly spots disappear in individuals more than 300 mm. long. Western Atlantic . . . *Epinephelus flavolimbatus*
- Dorsal fin dusky to margin. Dark blotch on dorsal part of caudal peduncle extending well below lateral line. Western Atlantic and Eastern Pacific *Epinephelus niveatus*

Species-Groups in the Subgenus *Epinephelus*

Long accorded generic standing, the subgenus *Epinephelus* is clearly a natural unit of closely related forms. Nevertheless, there are certain clusters of similar species that surely represent discrete lines. Some of these are well marked and can be recognized at once. Others are less so and probably have extralimital relatives so that their status cannot be determined until the subgenus is studied on a worldwide basis, if then. Thus, the arrangement presented here is tentative and will undoubtedly be modified as new lines of evidence and new techniques for assessing relationships are applied to these fishes.

Epinephelus striatus Species-Group

Epinephelus striatus and *E. guttatus* are so similar that sun-bleached display specimens are difficult to identify although there are several meristic

characters that can be used to separate them. *Epinephelus morio* differs in fin outlines but otherwise strongly resembles the other two species. They are all moderately large fishes with tapering and somewhat compressed body outlines. *Epinephelus morio* has spotted and barred transient color phases and individuals in these color phases bear a remarkable resemblance to *E. striatus*. This is reflected in the Bermudan common name deer hamlet for *E. morio*, contrasting with hamlet (without a modifier) for *E. striatus*.

These three species are certainly close to each other and well separated from other American groupers.

Epinephelus (Epinephelus) striatus (Bloch, 1792)

NASSAU GROUPER

Figure 11

Grooper BROWNE, 1756, p. 448 (Jamaica).
Perca maxilla inferiore SEBA, 1761 (1734-1765), pl. 27, fig. 9.
Cherna PARRA, 1787, p. 50, pl. 24, fig. 1 (Cuba).
Anthias striatus BLOCH, 1792 (1790-1793), pp. 125-126, pl. 324 (original description, Atlantic Ocean).
 BLOCH AND SCHNEIDER, 1801, p. 305 (copied).
Anthias cherna BLOCH AND SCHNEIDER, 1801, p. 310 (original description, after Parra).
Sparus chrysmelanus LACÉPÈDE, 1802 (1800-1803), p. 160 (original description, Martinique).
Serranus gymnopareius VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 248-249 (original description, no locality; "perhaps *Anthias striatus* Bloch").
Serranus striatus: VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 288-291 (Gulf of Mexico).
 STORER, 1846, pp. 278-279. GUICHENOT, 1853, p. 153. GÜNTHER, 1859, pp. 110-111. POEY, 1864, p. 178 (after Parra). VAILLANT AND BOCOURT, 1915,

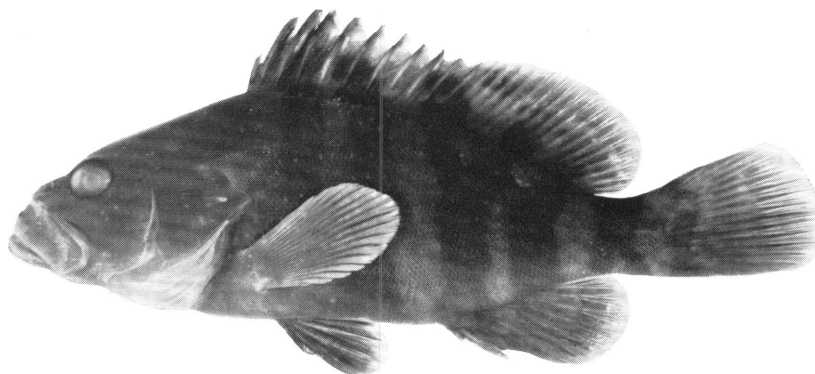


FIG. 11. *Epinephelus striatus*, AMNH field No. S66-112 from Berry Islands, Bahamas, 150 mm.

- pp. 76–80 (Antillean records). FOWLER, 1907, p. 255 (New Providence; St. Croix; Puerto Rico); 1927, p. 252 (Captiva Pass); 1929a, pp. 158, 164 (Port-au-Prince; Puerto Rico); 1938b, p. 310 (Haiti); 1939, p. 12 (Kingston, Jamaica); 1944, pp. 444–465 (St. Andrews; Colón, Panama; Kingston, Jamaica; Honduras); 1947, pp. 2–3 (Nassau); 1953, p. 56 (Cartagena, Colombia).
- Epinephelus striatus*: POEY, 1865 (1865–1866), p. 198 (Cuba); 1868 (1866–1868), p. 285 (Cuba). COPE, 1871b, p. 466 (New Providence; St. Croix). POEY, 1874, p. 34; 1875 (1875–1877), p. 15. GOODE, 1876, pp. 57–58 (Bermuda); 1879, p. 50. BEAN, 1881, p. 99 (Bermuda). POEY, 1881, p. 319 (Puerto Rico). GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, p. 918. JORDAN, 1884a, p. 77 (Key West); 1885b, p. 125 (Key West). BEAN AND DRESEL, 1885, p. 164 (Jamaica). JORDAN AND SWAIN, 1885b, pp. 384–385. JORDAN, 1887a, p. 84; 1887c, p. 40 (Havana); 1887e, p. 580 (West Indies). LEE, 1889, p. 671 (Nassau). JORDAN AND EIGENMANN, 1890, pp. 356–357 (St. Thomas). HENSHALL, 1891, p. 387 (Key West, Florida Keys). COCKERELL, 1892, p. 8 (Jamaica). LÖNNBERG, 1894, p. 127 (Key West); 1895, p. 657 (Haiti). BOULENGER, 1895, p. 235. HENSHALL, 1895, p. 216 (Key West). JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1157. SMITH, 1896, p. 175 (Florida). JORDAN AND RUTTER, 1898, p. 104 (Jamaica). BRICE, 1898, p. 283 (habits). EVERMANN AND KENDALL, 1900, p. 73. JORDAN AND EVERMANN, 1900, pl. 183, fig. 483. EVERMANN AND MARSH, 1902, pp. 152–153, pl. 12 (Puerto Rico). JORDAN, 1905, p. 324, fig. 258. JORDAN AND THOMPSON, 1905, p. 240 (Tortugas). TOWNSEND, 1905, p. 101 (longevity). FOWLER, 1906, p. 96 (Marquesas Is.; Jamaica). BEAN, 1906, p. 53 (Bermuda). ROSÉN, 1911, p. 54 (Bahamas). NICHOLS, 1912, p. 187 (Havana). JORDAN, 1917, pp. 157–159 (rheotropism). CROIZER, 1918, pp. 163–175 (tactile responses). FOWLER, 1918, p. 132 (Colón, Panama). TAYLOR, 1919, p. 9. METZELAAR, 1919, pp. 47–48 (Windward Is.; St. Martins). FOWLER, 1920, pp. 144, 147, 150, 153 (St. Croix; Jamaica; Nassau; Nutria; Key West). JORDAN AND EVERMANN, 1920, p. 384 (photograph). NICHOLS, 1921, p. 22 (Turks Is.). SCHROEDER, 1924, p. 14, fig. 9 (Key West). MEEK AND HILDEBRAND, 1925, pp. 460–461 (Panama). BREDER, 1925, p. 154 (Caledonia Bay, Panama); 1927, p. 39 (Royal Is.; Glover Reef; Swan Is.). BORODIN, 1928, p. 19 (Florida and Bahamas). BEEBE AND TEE-VAN, 1928, pp. 128–129 (Port-au-Prince). BREDER, 1929, p. 163. GUDGER, 1929, p. 171 (Tortugas). NICHOLS, 1929, p. 250, fig. 115 (San Juan and Ponce, Puerto Rico). JORDAN, EVERMANN, AND CLARK, 1930, p. 311. PARR, 1930, p. 50 (Nassau). BEEBE AND TEE-VAN, 1933, p. 123 (Bermuda; photograph).
- BORODIN, 1934, p. 112 (Florida Keys). BUTSCH, 1939, p. 23 (Barbados, uncommon). REED, 1941, p. 75 (Texas coast). LONGLEY AND HILDEBRAND, 1941, pp. 95–96, pl. 3, fig. 2; pl. 4, fig. 1 (Tortugas). HERRE, 1942, p. 292 (English Harbor, Antigua). FOWLER, 1942b, p. 68 (Cuba); 1942c, p. 11 (Honduras). BAUGHMAN, 1943, p. 770. MANTER, 1947, p. 371 (Tortugas; trematodes). SCHULTZ, 1952, p. 121 (Venezuela). HILDEBRAND, 1955, p. 208 (Campeche, Champoton, Mexico). RÖHL, 1956, p. 488 (Venezuela). BARDACH AND MENZEL, 1957, p. 108 (Bermuda growth rates). BARDACH, 1958, p. 140 (Bermuda, habits). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 48–49, figs. 6, 11, 17, pl. 8 (Bermuda, biology); 1959, p. 114 (hermaphroditic). BARDACH, 1959, p. 80 (Bermuda, standing crop). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:3, 1:8, 1:23, figs. 1.1, 7. SPRINGER AND McERLEAN, 1962, p. 394 (Florida, habits). RANDALL, 1963, pp. 34 *et seq.* (Virgin Is. ecology). RIVAS, 1964, pp. 28–29 (characters). RANDALL, 1965, pp. 13–16 (food habits). CALDWELL, 1966, p. 41 (Jamaica). CERVIGÓN M., 1966b, pp. 307–308 (La Blanquilla, Venezuela). RANDALL, 1967, pp. 699–700 (food habits). BÖHLKE AND CHAPLIN, 1968, p. 280 (general account, Bahamas). RANDALL, 1968, pp. 59–60, fig. 64 (general account, photograph).
- Cerna striata*: MIRANDA-RIBEIRO, 1915, p. 16 (Brazil); 1918, pp. 85–86.

NOMENCLATURE: The distinctive color pattern of this species has spared it from the nomenclatural confusion of less easily recognizable species. *Epinephelus striatus* Bloch (1793), however, is not this species but *Diplectrum formosum* (Linnaeus). Since *Anthias striatus* is the senior homonym, that name is available in *Epinephelus* for the Nassau grouper.

The adjectival name *striatus* is Latin for provided with stripes, in reference to the color pattern.

DIAGNOSIS: Moderate-sized species of *Epinephelus* with large eye, medium-sized scales, robust body. Nostrils subequal, posterior slightly enlarged, comma-shaped in adult. Dorsal XI, 16–17 with interspinous membranes notched; anal modally III, 8; gill rakers 24–25; pectoral 18. Vertical fins rounded. Skull crests well developed, convergent anteriorly. Supraethmoid forming floor of pit between anterior ends of frontals. Body with five vertical bars; row of small black spots behind and below orbit, distinct, large, quadrate, black blotch on top of caudal peduncle.

Only two American groupers have a body

pattern of vertical bars on a lighter background. *Epinephelus mystacinus* has nine to 11 regular, discrete bars; the last two, in some cases, fuse into a single wide band on the caudal peduncle. *Epinephelus striatus* has only five vertical bars, the third and fourth dividing dorsally where they are confluent. Posterior nostril in *E. mystacinus* greatly enlarged, whereas in *E. striatus* nostrils subequal. Moreover, *E. striatus* has several dark spots around eye which are lacking in *E. mystacinus*. Transient plain color phases of *E. striatus* somewhat resemble *E. morio*, but that species has second dorsal spine longer than third in the adult, and dorsal interspinous membranes not notched.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 7. In general, the body proportions are very similar to those of *E. morio* and *E. guttatus* but the upper jaw is somewhat shorter. The skull closely resembles that of *E. guttatus* but the median crest extends farther forward and the interorbital region is wider posteriorly than in that species. The supraethmoid does not form a transverse wall anterior to the frontals. There are 21–25 pyloric caeca.

The nostrils are subequal, the posterior becoming somewhat enlarged and slitlike or comma-shaped in larger individuals. The exposed surface of the maxilla is scaled. The third or fourth dorsal spine is the longest, the third definitely longer than the second except in newly transformed juveniles. The interspinous membrane is deeply cleft, with yellow fleshy tabs behind each spine. The vertical fins are rounded; the rounded caudal of the juvenile becomes increasingly angulate in larger fish.

The ground color of the body and head is tawny in individuals from shallow water, shading to pinkish or red in those from deeper water. Sometimes the body has a rather distinctive orange cast. The ground color is but slightly countershaded. The body is crossed by five vertical bars; the first is below dorsal spines three, four, and five; the second passes behind the pelvic fin; the third is above the anal spines; the fourth is above the last anal rays, and the fifth, which is sometimes double, is on the caudal peduncle. The third and fourth bars divide above the lateral line and their adjacent branches anastomose. A dark bar extends back from the tip of the snout through the eye, curving upward to meet its fellow just anterior to the

dorsal origin. Dorsally on the head there is a distinctive tuning fork-shaped bar that begins at the tip of the lower jaw and divides into two branches above the back of the orbit, the branches ending over the gill opening. There is an intense black quadrate blotch on the upper part of the caudal peduncle, and there are conspicuous discrete black points below and behind the orbit. The inside of the mouth is bright scarlet.

The range of color change is greater for this species than for other American groupers. Under proper stimuli a single individual can change from almost white to uniform dark brown in a few minutes. Only the blotch on the caudal peduncle and the points around the eye are immune. One individual in an aquarium at Bermuda momentarily reversed the vertical pattern so that the bars were lighter than the interspaces. Selective bleaching of certain areas on the body may give it a secondary pattern of white spots.

Specimens under 21 mm. lack the caudal peduncle blotch, but all fish over 35 mm. have it well developed. In these small juveniles there is a rather characteristic line of black spots along the bases of the dorsal rays posterior to the fifth spine. The pattern of vertical bars seems to develop at about 40 mm. in Bahaman specimens. In specimens under about 30 mm. the second dorsal spine is the longest.

The largest individual I have seen weighed slightly over 30 pounds; 50 or 60 pounds seems to be about the maximum. Most market fish are between 5 and 25 pounds.

RELATIONSHIPS: This species is structurally close to *E. guttatus* and *E. morio*, differing from the former in coloration and from the latter chiefly in fin structure and coloration. The three seem to form a closely related natural group that may be referred to as the *striatus* species-group.

ECOLOGY: *Epinephelus striatus* is found in depths ranging from only a few feet to at least 50 fathoms. East of the Gulf Stream it is one of the most common species but west of the Florida Straits it is outnumbered by *E. morio*. In Bermuda, *E. striatus* appears to be exceeded in abundance among groupers only by *E. guttatus* and, possibly, *E. fulvus*. The Nassau grouper seems to be rather wary and at the approach of an observer quickly retreats to some crevice, usually uttering a series of grunts as it does so (Moulton, 1958, p. 369; Hazlett and Winn,

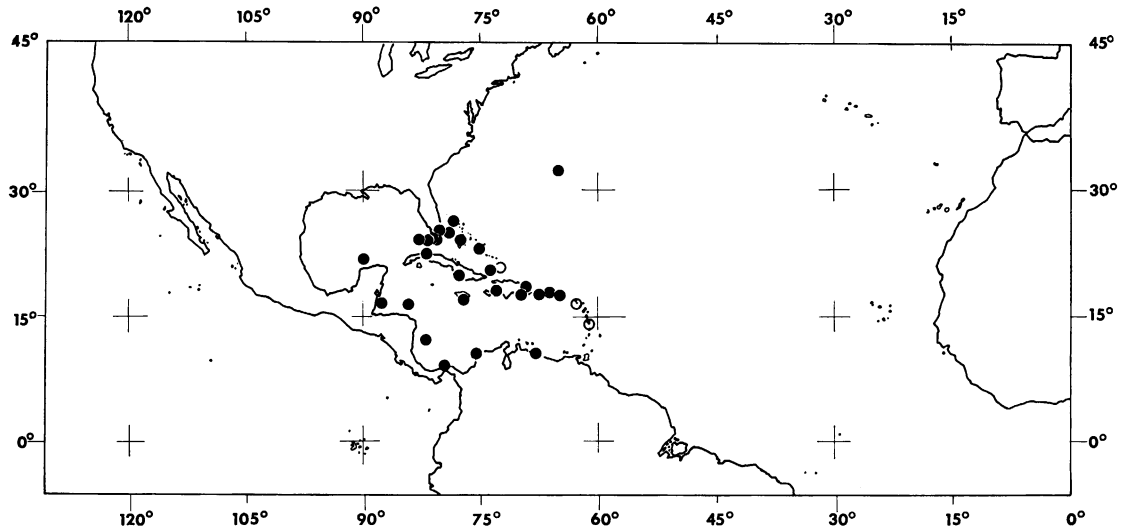


FIG. 12. *Epinephelus striatus* distribution records. Solid circles represent specimens examined, open circles are additional literature records.

1962). Individuals in the aquarium are distinctly barred at night, variable during daylight hours. The transformation from female to male takes place at a length of 30 to 80 cm., presumably indicating that more than one spawning season may be passed as a functional female. In Bermuda the spawning season lasts from early May to mid-August. The flesh is highly valued for food.

DISTRIBUTION: *Epinephelus striatus* is recorded from Bermuda and Florida, throughout the Bahamas and Antilles, and from the Yucatan Peninsula to Venezuela (fig. 12). It seems to be absent from the Gulf of Mexico, where it is replaced by *E. morio*.

SPECIMENS EXAMINED

Florida: Key West, FMNH 7031; CU 13297; USNM 47371, 170889, 170881; Islamorada, UMIM; Key Vaca, TU 17282; Tavernier Creek, USNM 57220; Broad Creek, USNM 53303; Tortugas, USNM 117189, 134894.

Campeche Bank: Alacran Reef, UMMZ 174174-S.

Honduras: USNM 34646.

Caribbean Sea: Swan Island, BOC 202; Glover Reef, FMNH 39719; BOC 203; St. Andrews, ANSP 74174.

Panama: Portobelo, FMNH 8405; USNM 80215; Colón, FMNH 8406-07, 8403-04; USNM 80269-70, 80286; Coco Solo, USNM 148669.

Colombia: Cartagena, MCZ 2822.

Venezuela: Puerto Cabello, FMNH 6312.

Virgin Islands: St. Thomas, USNM 39852, 35116, 34949, 35125; MCZ 3039, 10039, 10062, 10083, 10112; no specific locality, ANSP 80126.

Puerto Rico: Puerto Real, FMNH 52012; ANSP 23605; MCZ 28874; AMNH 2094; San Juan, FMNH 3190; USNM 50106; ANSP 29801; La Parguera, UMMZ 171776; Ponce, USNM 63068; no specific locality, USNM 125986.

Hispaniola: Haiti, MCZ 2823; AMNH 19004; Port-au-Prince, UMMZ 142450; ANSP 73314, 75281; USNM 133684, 132541; Santo Domingo, ANSP 77325, 77218; Samaná Bay, USNM 88957; Montecristi, AMNH 18755.

Jamaica: no specific locality, USNM 32044.

Cuba: Havana, UMMZ 65315; USNM 4771, 4671, 132970; Camaguey, USNM 132969; no specific locality, MCZ 9999, 3039, 26950, 23268, 10189, 2826, 10060, 10059, 9993, 39466; AMNH 999.

West Indies: no specific locality, USNM 33693; MCZ 10056.

Bahamas: near New Providence, FMNH 43097; USNM 53126-27, 38488; MCZ 2801, 2827; ANSP 72279, 72362; CBC Stations 34, 100, 182, 198, 203, 208, 209, 222, 277; CBC lots 142, 145; Bird Cay, CBC Station 363; Little Bahama Bank, UMIM; Royal Island Cay, BOC 200-01; Bimini, UMMZ 174431; BOC; Exuma Cays, CBC Station 352; Andros

TABLE 7
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus striatus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	45.58	159	168	176	241	242	251	254	323	332	—
Head length	425	402	405	418	402	401	414	409	402	389	404.7
Head width	172	157	161	148	154	165	159	175	180	187	163.1
Head depth	272	239	256	253	249	254	259	—	262	256	253.5
Snout length	97	88	101	108	108	112	112	106	108	102	105.0
Suborbital width	26	38	42	40	39	46	46	45	50	45	43.4
Interorbital width	70	57	65	57	56	64	66	63	65	60	61.4
Length of: Orbit	108	82	77	77	77	70	68	67	63	60	71.2
Postorbital head	227	230	238	239	232	235	243	238	246	238	237.7
Maxillary	202	167	190	182	178	192	189	181	186	176	182.3
Lower jaw	204	189	182	182	178	194	193	177	183	175	183.7
Snout to angle of preopercle	312	270	298	287	278	285	287	276	282	268	281.2
Supramaxillary length	56	57	60	51	46	64	60	59	59	60	57.3
Maxillary width	46	38	48	40	37	41	42	35	43	36	40.0
Tip of lower jaw to gular notch	135	113	—	148	—	—	—	130	—	—	131.3
Body width	125	164	167	165	145	151	155	152	176	179	162.0
Body depth	353	358	387	340	353	368	355	378	362	364	362.8
Caudal peduncle depth	111	116	125	122	110	120	120	112	115	117	119.7
Tip of snout to dorsal origin	441	396	434	437	427	430	414	411	415	399	418.1
Tip of snout to pectoral base	369	393	375	381	359	368	371	392	356	364	373.2
Tip of lower jaw to pelvic base	405	447	446	449	402	430	432	467	409	419	432.3
Length of: Dorsal base	585	541	565	520	519	533	552	543	560	536	541.0
Depressed dorsal	667	610	649	614	587	614	633	630	628	566	514.6
Anal base	174	167	173	170	156	165	167	157	158	157	163.3
Depressed anal	311	283	292	290	270	289	285	276	268	262	279.4
End of dorsal to caudal base	118	123	125	119	124	112	124	123	110	119	119.9
Length of: Caudal peduncle	171	170	196	188	195	178	191	189	187	185	186.6
Pectoral	254	238	244	233	232	238	231	228	228	208	231.1
Pelvic	219	198	208	199	197	202	201	201	195	184	198.3
Dorsal spine I	92	69	80	77	75	58	78	75	77	71	73.3
Dorsal spine III	186	160	176	168	164	169	171	165	164	184	169.0
Dorsal spine XI	139	126	131	142	108	122	129	118	115	120	123.4
Anal spine I	66	57	51	51	46	50	52	51	46	42	49.6
Anal spine II	140	119	119	111	108	93	100	102	96	87	103.9
Anal spine III	144	126	125	122	122	99	118	122	102	99	115.0
Caudal base to tip of upper rays	247	252	244	250	245	252	—	234	241	229	230.9
Caudal base to tip of middle rays	287	245	256	247	228	256	237	236	223	218	243.4
Caudal base to tip of lower rays	245	239	250	244	224	248	233	236	226	223	235.9

^aAll proportions are expressed in thousandths of the standard length. All specimens are UMMZ from Bermuda.

Island, CBC Station 393; AMNH 12070; Balmoral Island, CBC lot 138.

Bermuda: MCZ 26701, 34004; BOC; FMNH 48368, 48376, 48304, 4985-95; USNM 21954, 21366, 20184, 16807, 10341, 21954, 21366, 10341, 170035; UMMZ 172345, 172353, 172555-S, 172556-S, 172557-S, 173401-S, 176045, 176165, 176168, 176065, 176360,

176408, 176411, 176433, 176446, 176506, 176615, 176618-S, 176628; AMNH 532, 2975, 1787.

Epinephelus (Epinephelus) morio
(Valenciennes, 1828)

RED GROUPER

Serranus morio VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 285-286 (original description,

- New York; Santo Domingo). DEKAY, 1842, p. 23. STORER, 1846, p. 277. GUICHENOT, 1853, p. 150 (Cuba). GÜNTHER, 1859, p. 142. COCKERELL, 1892, p. 8 (Jamaica). FOWLER, 1907, p. 255 (Key West); 1929b, p. 611 (Barnegat Is.); 1932a, p. 399 (Cedros Is., Trinidad); 1936, pp. 759-760, fig. 335; 1938b, p. 311 (Haiti); 1953, p. 56 (Barranquilla, Cartagena, Colombia).
- Serranus erythrogaster* DEKAY, 1842, pp. 21-23, pl. 19, fig. 55 (original description, New York market). STORER, 1846, p. 282 (after DeKay). GÜNTHER, 1859, pp. 133-134 (Jamaica). HOLBROOK, 1860, pp. 32-35, pl. 5, fig. 2 (South Carolina).
- Serranus remotus* POEY, 1860 (1858-1861), pp. 140-141 (original description, Cuba).
- Epinephelus morio*: GILL, 1862c, p. 30. POEY, 1865 (1865-1866), pp. 197-198 (nomenclature); 1868 (1866-1868), p. 285; 1874, p. 34. GILL, 1873, p. 806. POEY, 1875 (1875-1877), p. 15 (Cuba). GOODE, 1879, p. 49. JORDAN AND GILBERT, 1879, p. 379 (Beaufort, N.C.). GOODE AND BEAN, 1880, p. 139 (Pensacola). BEAN, 1881, p. 99 (Bermuda). POEY, 1881, p. 319 (Puerto Rico). GOODE AND BEAN, 1883a, p. 238. JORDAN AND GILBERT, 1883a, p. 540; 1883d, p. 272 (Pensacola snapper banks). POEY, 1883, p. 118. BEAN, 1884, pp. 446, 503 (Key West). JORDAN, 1884a, p. 77; 1885b, p. 124 (Key West). JORDAN AND SWAIN, 1885b, pp. 381-383. JORDAN, 1887a, p. 84. JORDAN AND EVERMANN, 1887, p. 466. JORDAN, 1887b, p. 27 (Beaufort, N.C.); 1887c, p. 40 (Havana); 1887e, p. 580 (West Indies). JORDAN AND EIGENMANN, 1890, p. 361. HENSHALL, 1891, p. 387 (Florida). JORDAN, 1891, p. 319 (Bahía). KENDALL, 1891, p. 308 (Florida). LÖNNBERG, 1894, p. 127. BOULENGER, 1895, pp. 237-238. HENSHALL, 1895, p. 216 (Key West). JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1160. SMITH, 1896, p. 175 (Key Biscayne Bay). JORDAN AND RUTTER, 1898, p. 105 (Jamaica, compiled). BRICE, 1898, p. 283. SMITH, 1899, p. 880 (Katama Bay). EVERMANN AND KENDALL, 1900, p. 74 (Florida). JORDAN AND EVERMANN, 1900, pl. 184, fig. 485. SMITH, 1901, p. 309 (Woods Hole). SMITH, 1902, p. 32. EVERMANN AND MARSH, 1902, pp. 154-155, pl. 14 (Puerto Rico). JORDAN, 1905, p. 325, fig. 260. JORDAN AND THOMPSON, 1905, p. 240 (Hospital Key, Tortugas). BEAN, 1906, p. 53 (Bermuda). FOWLER, 1906, p. 97 (Bahía Honda; Snipe Key). KENDALL, 1908, p. 98 (Katama Bay, Mass.). ROSÉN, 1911, p. 54 (Mastic Point, Andros Is.). SUMNER, OSBURN, AND COLE, 1913, pp. 167-169. FOWLER, 1915a, p. 249 (Palm Beach). TAYLOR, 1919, p. 9. METZELAAR, 1919, pp. 48-49 (Aruba). FOWLER, 1920, pp. 147, 153 (Jamaica; Florida). JORDAN AND EVERMANN, 1920, pp. 385-386 (photograph). NICHOLS, 1921, p. 22 (Turks Is.). SCHROEDER, 1924, pp. 14-15, fig. 8 (Florida). MEEK AND HILDEBRAND, 1925, p. 455 (Colón, Panama).
- BREder, 1925, p. 154 (Caledonia Bay, Panama). NICHOLS AND BREder, 1927, p. 80, fig. 104. VANDERBILT, 1927, p. 136, pl. 8 (juvenile, Cat Island). BEEBE AND TEE-VAN, 1928, p. 128 (Port-au-Prince Bay). NICHOLS, 1929, pp. 251-252, fig. 117. GUDGER, 1929, pp. 171-172. JORDAN, 1929, p. 173. BREder, 1929, p. 162. JORDAN, EVERMANN, AND CLARK, 1930, p. 312. FOWLER, 1932a, p. 399 (off Cedros Point, Trinidad). BEEBE AND TEE-VAN, 1933, p. 121. LONGLEY, 1933, p. 294 (*angustifrons* a synonym). VLADYKOV, 1935, p. 8 (Halifax harbor). VLADYKOV AND MCKENZIE, 1935, p. 92 (after Vladykov). FOWLER, 1938b, p. 311 (Haiti). BUTSCH, 1939, p. 23 (Barbados). DELSMAN, 1941, p. 68 (Tortugas). LONGLEY AND HILDEBRAND, 1941, pp. 96-97, pl. 4, fig. 2; pl. 5, fig. 12 (Tortugas). REED, 1941, p. 76 (Texas coast). FOWLER, 1942b, p. 68 (Cuba). BAUGHMAN, 1943, p. 771 (Texas). FOWLER, 1944, pp. 444, 465. MANTER, 1947, p. 371 (Tortugas, parasites). FOWLER, 1952, p. 121 (Barnegat Is.). SCHULTZ, 1952, p. 120 (Venezuela). HILDEBRAND, 1955, p. 208 (off Campeche). MARTIN SALAZAR, 1956, pp. 102-103 (Gran Roque, Venezuela). SPRINGER AND BULLIS, 1956, p. 78 (Gulf of Mexico records). RÖHL, 1956, pp. 487-488 (Venezuela). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 48-49, pl. 7 (Bermuda). BAILEY ET AL., 1960, p. 25 (common name). MCALLISTER, 1960, p. 26 (after Vladykov). SMITH, 1961, pp. 1:2, 1:9, 1:23, fig. 8. MOE, 1963, p. 703 (albinism in Florida specimen). RIVAS, 1964, pp. 26-27 (characters). ALPERIN AND SCHAEFFER, 1965, pp. 3-5 (photograph, New York records). CALDWELL, 1966, p. 41 (compiled). CERVIGÓN M., 1966b, pp. 305-307, fig. 119 (Cubagua, Margarita, Porlamar, Punta de Pucha, Venezuela). RANDALL, 1967, pp. 698-699 (food habits); 1968, p. 60, fig. 65 (general account, photograph). BÖHLKE AND CHAPLIN, 1968, p. 279 (general account, Bahamas). MOE, 1969, pp. 1-95 (biology).
- Epinephelus erythrogaster*: GILL, 1862c, p. 30.
- Serranus angustifrons* STEINDACHNER, 1864, pp. 230-231, pl. 7, figs. 2, 3 (original description, Cuba).
- ?*Cherna americana*: JORDAN, 1884a, p. 78.
- Epinephelus angustifrons*: JORDAN, 1887e, p. 580. JORDAN, EVERMANN, AND CLARK, 1930, p. 311.
- Dermatolepis angustifrons*: JORDAN AND EIGENMANN, 1890, pp. 375-376 (after Steindachner).
- Epinephelus guativera* (non Parra): GARMAN, 1896, pp. 77-78 (Tortugas).
- Cerna morio*: MIRANDA-RIBEIRO, 1915, pp. 18-19 (Brazil); 1918, p. 88.

NOMENCLATURE: A check at the Paris Museum by Carl L. Hubbs revealed that the type specimen of this species has apparently been lost. However, Valenciennes's description is sufficiently clear to fix the name.

Although the name *Serranus angustifrons* Steindachner has long presented a problem (see Jordan and Eigenmann, 1890), Longley (1935) found that the type is *Epinephelus morio* and there is nothing in the original description to refute this.

Jordan and Eigenmann gave the derivation of the name *morio* as Moor, a translation of the name *nègre* used at Santo Domingo, but there is a Latin word *morio*, meaning monster or deformed person, and Valenciennes did not indicate the source of the name.

DIAGNOSIS: Moderate-sized species of *Epinephelus* with large eye, small scales, robust body. Nostrils subequal, posterior little larger than anterior. Dorsal XI, 16–17 with interspinous membrane not notched. Second dorsal spine longest. Vertical fins angulate in large fish. Anal III, 9; pectoral 17; gill rakers 23–25. Skull crests well developed, frontoparietal crests convergent anteriorly. Supraethmoid forming floor of pit between anterior ends of frontals. Body reddish brown with irregularly arranged white spots on sides. Sides of head with few scattered, very small, black spots. Vertical fins with darker marginal band. No blotch on caudal peduncle.

All other species of American grouper have dorsal interspinous membranes conspicuously notched. Furthermore, only *Epinephelus morio* and *E. nigritus* have second dorsal spine longer than third. *Epinephelus nigritus* has vertical fins rounded instead of angulate.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 8. In nearly all body proportions *Epinephelus morio* agrees closely with *E. striatus* and *E. guttatus* although the higher anal ray count is reflected in the length of the anal base.

The median skull crest is moderately high and extends far forward on the frontal bones. The frontoparietal crests are low but extend well ahead of the postorbital processes. The interorbital is wider than that of *E. striatus* or *E. guttatus*, narrowest between the anterior parts of the orbits. The preopercular angle is less expanded than that of *E. guttatus*. The medial canine teeth are low and rather blunt. The frontal pit is shallow, the supraethmoid not being expanded into a transverse wall. There are about 26 pyloric caeca.

The dorsal and anal fins are rather angulate in larger individuals. The caudal is square in

the young, becoming slightly lunate in older fish. The nostrils are subequal.

The head and body are reddish brown, shading to light pink or dirty white below. The edges of the soft dorsal, anal, and caudal fins are darker on the outer fourth, with a narrow white margin on the soft rays. The spinous dorsal is dusky throughout. The pectorals are dusky, somewhat lighter than the body, and the pelvics are light basally and dusky toward the tips of the anterior rays. The body is irregularly spotted with white, these spots becoming more numerous posteriorly. As in *E. striatus*, the lining of the mouth is scarlet. There are small black pin-point spots scattered over the sides of the head, especially on the cheek and sub-orbital areas; these points are not arranged around the eye as in *E. striatus*.

The color pattern is less variable than are those of some other species, but at times a few large light blotches can be seen, which correspond roughly to the light interspaces of the barred pattern of *E. striatus*. One individual observed in the Miami Seaquarium even had traces of the "tuning-fork pattern" on the head. A color variant from the Campeche Bank had an orange cast to the ground color similar to that of the few Nassau groupers from the same area. In all other respects it resembled red groupers taken with it.

Most red groupers weigh between 2 and 10 pounds; the maximum size is probably about 25 or 30 pounds.

RELATIONSHIPS: From the character analysis above it may be seen that this species is closely related to *E. striatus*. Where these species occur together (southern Florida, the West Indies, and the Campeche Bank) they remain distinct, but in general they replace each other geographically.

ECOLOGY: The young of *Epinephelus morio*, in color and form exact miniatures of the adults, are frequently seined among beds of turtle grass (*Thalassia*). Bermuda fishermen claim that this is a fish of sand holes, an explanation that is in accord with its distribution in the Gulf of Mexico. I have not observed it in its natural habitat, probably because it is not common in water less than 50 feet deep. It ranges to a depth of at least 60 fathoms. The early life history of *E. morio* is unknown. Moe (1969) has recently completed a thorough study of the red grouper in the Gulf of Mexico including

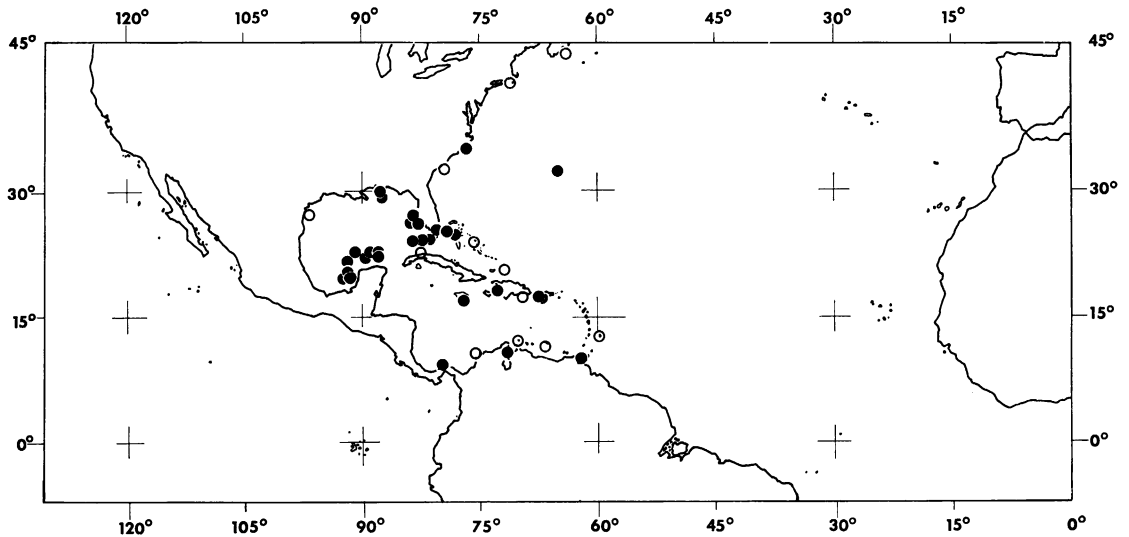


FIG. 13. *Epinephelus morio* distribution records.

data on age and growth, movements, and population dynamics.

DISTRIBUTION: The red grouper has its center of abundance in the Florida area and in the Gulf of Mexico, although there are records for most of the Antillean islands and along the northern coast of South America east as far as Trinidad (fig. 13). One specimen, ANSP 76304, from Trinidad has more rounded vertical fins than others of comparable size; it may represent a slightly differentiated population or it may be just a variant individual.

SPECIMENS EXAMINED

North Carolina: Beaufort, USNM 53401, 126094.

Florida: Miami, FMNH; Captiva Pass, FMNH 537; Key West, FMNH 7018; UMML 49-168; UMMZ 172578; USNM 75520, 75526-27, 75529, 129939, 170880, 32604, 62765, 34880; ANSP 16536; AMNH 2474; Fowey Rocks, USNM 170879; Cape Florida, USNM 62610, 170882, 62730; Bear Cut, UMIM; Islamorada, UMIM; Molasses Key, USNM 62575, 57134, 62765; Conch Key, USNM 170881; Florida Keys, no specific locality, MCZ 22828; Tortugas, USNM 117188, 6951; Palm Harbor, USNM 93698; Boca Grande, USNM 134893; Charlotte Harbor, USNM 33218; Lemon Bay, UMMZ 139276; Englewood, UMMZ 155062; Pass-a-Grille Beach, UMMZ 153740, 154039,

154072, 154303, 154832, 154834, 154957, 155062; Tampa, USNM 157590; Bonita Springs, CU 6636; Clearwater, CU 14707, 26361, 24983, 12876; "Snapper Bank," USNM 37309; west of Panama City, UMMZ 179122; no specific locality, USNM 6782, 22129.

Gulf of Mexico: 29°26'N, 87°32'W, TU 6315; OREGON Station 963, 27°07'N, 83°19'W, FMNH 61310; 29°26.5'N, 87°35'W, USNM 158598; 20°05'N, 91°51'W, UMMZ 176954; 20°05.6'N, 91°13'W, FMNH 45482; 300-380 mi. from Clearwater, Florida, USNM 158619; Campeche Bank, FMNH 46769, 46776; UMMZ 143113, 173989, 173979, 173979-S, 174061, 174067-S, 174125, 174173-S; USNM 39267, 39277, 37310; sight records from SILVER BAY Stations 341, 342, 352, 353, 358, 362, 364, 365, 366, 371, 374, 375, 383, 386, 391, 392, 394, 395, 398, 401, 402, 405, 406, 411, 412, 413, 414, 415, 416, 417, 419, 420, 422, 423, 424, 426, 427, 428, 435, 437; no specific locality, AMNH 8786.

Honduras: USNM 34645.

Panama: Colón, ANSP 49118; Fox Bay, FMNH 8401-02; Fort Randolph, USNM 128839, 80291.

Venezuela: Gulf of Venezuela, USNM 123135.

Brazil: Santos market, USNM 100885; Bahía, USNM 43332; Rio de Janeiro, MCZ 4507.

Trinidad: Cedros Point, ANSP 76304.

Puerto Rico: Puerto Real, FMNH 3208.

TABLE 8
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus morio*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	43.5	49.5	55.0	65.5	133.0	232.0	235.0	251.0	258.0	260.0	—
Head length	402	414	409	412	414	420	411	408	411	412	411.3
Head width	161	182	182	176	154	177	168	177	180	173	173.0
Head depth	241	263	273	260	263	276	272	257	262	260	262.7
Snout length	103	101	100	99	102	108	111	104	116	112	105.6
Suborbital width	23	20	27	31	38	45	47	46	47	46	37.0
Interorbital width	69	61	64	69	68	71	74	70	70	75	69.1
Length of: Orbit	115	111	109	99	98	84	80	82	70	83	93.1
Postorbital head	207	212	218	214	233	244	238	231	238	231	266.6
Maxillary	195	192	191	191	203	207	200	197	203	196	197.5
Lower jaw	184	202	200	183	203	211	200	185	209	187	196.4
Snout to angle of preopercle	299	303	291	290	301	302	294	291	293	288	295.2
Supramaxillary length	80	61	64	61	71	67	55	64	64	58	64.5
Maxillary width	46	51	45	46	49	47	49	46	43	46	46.8
Tip of lower jaw to gular notch	138	141	145	168	135	119	143	141	135	135	140.0
Body width	138	152	145	168	132	168	181	175	180	183	162.2
Body depth	345	364	345	336	342	371	377	347	353	354	353.4
Caudal peduncle depth	115	111	109	115	109	114	113	106	114	108	111.4
Tip of snout to dorsal origin	402	394	400	389	406	429	404	388	411	402	402.5
Tip of snout to pectoral base	414	414	400	382	380	375	379	398	370	377	388.9
Tip of lower jaw to pelvic base	460	465	455	450	414	407	417	450	411	419	434.8
Length of: Dorsal base	517	535	536	519	530	571	560	526	512	531	533.7
Depressed dorsal	598	616	591	595	602	640	626	598	570	590	602.6
Anal base	172	182	182	176	180	185	179	177	186	165	178.4
Depressed anal	287	313	300	290	297	284	274	267	285	256	285.3
End of dorsal to caudal base	115	121	127	130	120	129	128	135	124	123	125.2
Length of: Caudal peduncle	184	192	209	176	192	190	197	187	215	196	193.8
Pectoral	241	242	236	244	237	237	226	213	209	213	229.8
Pelvic	195	192	200	198	199	196	187	189	198	175	192.9
Dorsal spine I	69	71	82	84	79	67	83	78	66	73	75.2
Dorsal spine II	138	131	136	145	162	166	189	191	171	173	160.2
Dorsal spine XI	115	131	118	122	113	103	106	102	97	96	110.3
Anal spine I	57	71	64	76	56	45	43	48	52	42	55.4
Anal spine II	126	121	145	145	128	97	89	104	105	92	115.2
Anal spine III	126	121	136	130	128	106	106	98	97	88	113.6
Caudal base to tip of upper rays	207	232	218	221	259	278	294	236	246	260	247.8
Caudal base to tip of middle rays	241	232	236	229	233	222	219	207	205	204	222.8
Caudal base to tip of lower rays	207	232	218	214	256	261	257	251	221	246	236.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-4, UMML from Ft. Pierce, Florida; 5, UMIM 116 from Tortugas, Florida; 6-8 and 10, UMMZ 172578 from Key West, Florida; and 9, UMMZ 154303 from Boca Ciega Bay, Florida.

Haiti: Port-au-Prince, USNM 133683, 132112, 132542, 170014; ANSP 77204; AMNH 19020.

Cuba: no specific locality (probably Havana), USNM 9808.

Bahamas: Bimini, UMMZ 174253.

Bermuda: FMNH 4983-84; UMMZ 172561-S.

No locality: USNM 3537, 83456, 120518.

Epinephelus (Epinephelus) guttatus (Linnaeus, 1758)

RED HIND

Piraumba MARCGRAVE, 1648, p. 167.

Cugupuguacu CATESBY, 1743, p. 14.

Hyne BROWNE, 1756, p. 448 (Jamaica).

Perca guttata LINNAEUS, 1758, p. 292 (original description, America). BONNATERRE, 1788, pp. 130–131.

Cabrilla PARRA, 1787, p. 93, pl. 36, fig. 1 (Cuba).

?*Holocentrus punctatus* BLOCH, 1790 (1790–1793), p. 88, pl. 241 (original description).

Lutjanus lunulatus (non Park): BLOCH AND SCHNEIDER, 1801, p. 329 (after Parra).

Sparus atlanticus LACÉPÈDE, 1803, p. 158, pl. 5, fig. 1 (original description).

Serranus maculosus VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 332–333 (original description, no locality). VAILLANT AND BOCOURT, 1878 (1915), pp. 83–87 (Antilles). FOWLER, 1906, p. 97 (Florida Keys); 1907, p. 252 (New Providence; Santo Domingo; St. Martin; St. Thomas; St. Kitts); 1942a, p. 86 (Florida).

Serranus catus VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 373–375 (original description, Martinique). STORER, 1846, p. 280. MÜLLER AND TROSCHEL, 1848, p. 665 (Barbados). GUICHENOT, 1853, p. 151 (Cuba). COCKERELL, 1892, p. 8 (Jamaica). FOWLER, 1929a, p. 170 (St. Lucia); 1938b, p. 311 (Haiti); 1944, pp. 444, 465 (Nassau; St. Lucia; Port Antonio; Kingston; Roncador Bank).

?*Serranus nigriculus* VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 375–376 (original description, Martinique). GUICHENOT, 1853, p. 151 (Cuba). COCKERELL, 1892, p. 8 (Jamaica).

Serranus arara VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 377–378 (original description, not Parra's *Bonaci arara* which is *Mycteroperca bonaci*). POEY, 1865 (1865–1866), pp. 199–200 (nomenclature). GUICHENOT, 1853, p. 152.

Serranus lunulatus: VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 379–380 (after Bloch). STORER, 1846, p. 278. GUICHENOT, 1853, p. 152 (Cuba). POEY, 1864, p. 179. STEINDACHNER, 1866, pp. 775–776, pl. 14, fig. 1. GÜNTHER, 1869, p. 397. COCKERELL, 1892, p. 8 (Jamaica).

Serranus maculatus (non Bloch): GÜNTHER, 1859, p. 130 (West Indies).

Epinephelus lunulatus: POEY, 1866 (1865–1866),

pp. 200–202 (nomenclature); 1866 (1866–1868), p. 5; 1868 (1866–1868), pp. 286–287; 1874, p. 34. COPE, 1871b, p. 465 (St. Martin; St. Kitts; New Providence). POEY, 1875 (1875–1877), pp. 16–17. GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico).

Epinephelus cubanus POEY, 1866 (1865–1866), p. 202 (original description, Cuba); 1868 (1866–1868), p. 287; 1871, p. 34; 1875 (1875–1877), p. 17.

Serranus pixanga (non Valenciennes): POEY, 1866 (1865–1866), p. 203 (Cuba).

Serranus apua (non Bloch): STEINDACHNER, 1867, p. 349 (Barbados; Surinam). HENSHALL, 1891, p. 387 (Garden Key, Tortugas). GÜNTHER, 1899, p. 36 (identification of Linnaean specimen of *P. guttata*).

Epinephelus sp. dub. POEY, 1868 (1866–1868), p. 287 (Cienfuegos, Cuba).

Epinephelus guttatus: GOODE, 1876, pp. 58–59 (Bermuda); 1877, p. 292; 1879, p. 50 (Bermuda).

BEAN, 1881, p. 99. JORDAN AND GILBERT, 1883a, pp. 919–920. GOODE AND BEAN, 1886, pp. 194, 203.

JORDAN, 1886c, p. 396 (nomenclature). LÖNNBERG, 1894, p. 127 (Key West). JORDAN AND EVERMANN, 1900, p. 3197 (nomenclature). EVERMANN AND MARSH, 1902, pp. 153–154 (Puerto Rico). TOWNSEND, 1905, p. 101 (longevity). ROSÉN, 1911, p. 54.

METZELAAR, 1919, p. 48 (Curaçao; Aruba). JORDAN AND EVERMANN, 1920, p. 384 (photograph).

NICHOLS, 1921, p. 22 (Turks Is.). EVERMANN AND SEALE, 1924, p. 29 (Barbados). SCHROEDER, 1924, p. 14 (Florida Keys). MEEK AND HILDEBRAND 1925, p. 461 (not seen in Panama). BEEBE AND TEE-VAN, 1928, pp. 129–130 (Port-au-Prince). BREDER, 1929, p. 163. NICHOLS, 1929, p. 251, fig. 116 (Ponce market, Puerto Rico). JORDAN, EVERMANN, AND CLARK, 1930, p. 311. PARR, 1930, p. 49 (Bahamas; West Caicos Is.). BEEBE AND TEE-VAN, 1933, pp. 112–123 (Bermuda). BUTSCH, 1939, p. 23 (Barbados). LONGLEY AND HILDEBRAND, 1941, p. 97 (not seen at Tortugas). SPRINGER AND BULLIS, 1956, p. 77 (Alacran Reef). BARDACH AND MENZEL, 1957, p. 107 (Bermuda growth rates). BARDACH, 1958, p. 140 (habits in Bermuda). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 52–53, figs. 5, 12, 18, pl. 10 (Bermuda, biology). BARDACH, 1959, p. 80 (Bermuda, standing crop). SMITH, 1959, p. 114, fig. 2; pl. 1, figs. 6, 7 (hermaphroditic). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:3, 1:9, 1:23, figs. 1.2, 9. RANDALL, 1963, p. 37 (Virgin Islands, ecology). RIVAS, 1964, p. 28 (characters). CALDWELL, 1966, pp. 40–41 (Jamaica). CERVIGÓN M., 1966b, pp. 308–310, fig. 121 (Cubagua, La Blanquilla, Venezuela). RANDALL, 1967, pp. 697–698 (food habits). BÖHLKE AND CHAPLIN, 1968, p. 282 (Bahamas). RANDALL, 1968, pp. 57–58, fig. 62 (general account, color photograph).

Serranus stathouderi VAILLANT AND BOCOURT, 1877 (1915), p. 69 (substitute for *maculosus*, regarded by Günther as preoccupied).

- Epinephelus apua* (non Bloch): JORDAN AND GILBERT, 1883a, p. 973 (nomenclature). BEAN AND DRESEL, 1885, p. 164 (Jamaica). JORDAN, 1885c, p. 195. JORDAN AND SWAIN, 1885b, pp. 389-391. JORDAN, 1887a, p. 84; 1887c, p. 40 (Havana); 1887e, p. 581. COCKERELL, 1892, p. 8 (Jamaica). SMITH, 1896, p. 175 (Key Biscayne Bay).
- Epinephelus catus*: JORDAN, 1887c, p. 40 (Havana); 1887e, p. 581. JORDAN AND EIGENMANN, 1890, pp. 355-356. BOULENGER, 1895, pp. 210-211. HENSHALL, 1895, p. 216 (Key West).
- Epinephelus maculosus*: JORDAN AND EVERMANN, 1896a, p. 372; 1896b, pp. 1158-1159. JORDAN AND RUTTER, 1898, p. 104 (Jamaica). EVERMANN AND KENDALL, 1900, p. 73 (Florida). FOWLER, 1900, p. 118. EVERMANN AND MARSH, 1902, pl. 12 (figure legend only). JORDAN AND THOMPSON, 1905, p. 239 (Tortugas). BEAN, 1906, p. 52 (Bermuda). FOWLER, 1915a, p. 256 (St. Thomas). WILSON, 1916, p. 64 (Cartagena). FOWLER, 1920, pp. 137, 145, 147, 150, 153 (St. Martin; St. Kitts; Jamaica; Nassau; Key West). BORODIN, 1928, p. 19 (Bahamas).
- Cerna catus*: MIRANDA-RIBEIRO, 1915, pp. 16-17 (Brazil); 1918, pp. 86-87.
- Serranus guttatus*: FOWLER, 1929a, p. 170 (St. Lucia); 1938b, p. 311 (Haiti); 1939, p. 12 (Kingston, Jamaica); 1944, pp. 444, 465 (Nassau; St. Lucia; Jamaica; Roncador Bank); 1953, p. 56 (Cartagena).

NOMENCLATURE: Much of the confusion in the nomenclature of this species stems from difficulty in interpreting Linnaeus's original description, which was probably complex. At times the name has been applied to the species now called *Epinephelus* (*Promicrops*) *itajara* and *E. cruentatus* as well as to the present species. However, there is a specimen in the Linnaean collection which Linnaeus labeled *Perca guttata*. According to Günther (1899, p. 36), this specimen was received after the *Systema Naturae* was published so it cannot be the type. I follow recent convention in applying the name *Perca guttata* Linnaeus to the red hind.

The name *guttatus* (Latin) is an adjective meaning spotted.

DIAGNOSIS: Small-sized *Epinephelus* with large eye, moderate-sized scales, robust body. Nostrils subequal. Dorsal XI, 15-16; anal III, 9; pectoral 17; gill rakers 24-27. Dorsal interspinous membranes notched, vertical fins rounded. Skull crests well developed, frontoparietal crests convergent anteriorly. Supraethmoid forming floor of pit between anterior ends of frontals. Body pale yellow or light red, covered with darker red spots not appreciably larger ven-

trally. No saddle-shaped blotches along back. Soft dorsal, anal, and caudal fins very dark on outer third.

Epinephelus guttatus superficially resembles the rock hind, *E. adscensionis*, in having a pattern of reddish spots on lighter background, but there are no dark margins on fins of *adscensionis*. Unlike *E. guttatus*, *E. adscensionis* has three or four dark, saddle-shaped blotches along base of dorsal fin and on caudal peduncle. *Epinephelus analogus* of Eastern Pacific has reddish spots, but consistently only 10 dorsal spines.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 9. Its proportions are generally similar to those of *E. striatus*. The skeletal features of this species were discussed in the Introduction. The preopercular angle is expanded into a coarsely serrate lobe. The dorsal, anal, and caudal lobes are rounded. The dorsal interspinous membranes are moderately indented with fleshy tabs behind each spine. The nostrils are subequal, the posterior one not greatly expanded. The pyloric caeca are moderate in number, usually about 15.

The ground color of the head and body varies from brownish or greenish white to scarlet, somewhat lighter on the belly. The body and head are everywhere covered with bright red spots; even the gill membranes and maxillary grooves are spotted. On the body these spots are quite uniform in size but most have brown centers which become progressively larger dorsally until the upper ones are entirely red-brown. Such brown centers may be entirely lacking on the belly spots. The spinous part of the dorsal fin is olive, with bright yellow flags at the tips of the membranes. The fin is darker at the base and the distal edge. The soft dorsal is greenish olive in the middle, darker on the basal and distal thirds; there are a few red spots on the basal third and a few bluish spots in the central third, and there is a very narrow white margin as in most groupers.

The anal fin is similar to the soft part of the dorsal, having about five red spots along the base and a row of blue spots distal to these. The caudal is generally olive, darker distally and with a narrow white margin. There are scattered blue spots near the caudal base but no red spots. The pectorals are orange-red with randomly spaced darker red spots on the base. The pelvics are dusky white, becoming very dark on the distal parts of the anterior three rays and the

intervening membranes, with a few red spots on the basal third of the fin.

The inside of the mouth is white with scarlet patches on the pterygoid area, the corner of the mouth, and between the lower teeth and the posterior half of the lower lip. The area including the ceratohyals, tongue, gill arches, and gill rakers is red.

The sleep pattern of this species consists of rather irregular transverse bars that slope upward and backward. There is considerable variation in the number and size of the spots, but such differences seem to be random individual variations without consistent pattern. Individuals from deeper water are a more intense red and those from 40 or 50 fathoms seem to have smaller spots.

The spotted pattern is developed even at a length of 24 mm., but the dark margins of the fins are not as evident at this size. Identification of these small specimens can be verified by fin-ray count, the modal numbers of dorsal rays being 16 for *E. guttatus* and 17 for *E. adscensionis*. Like other small groupers, juveniles of this species have elongate second dorsal and preopercular spines.

ECOLOGY: In Bermuda this species is found in water from a few feet to more than 300 feet in depth. However, in Puerto Rico also I observed *E. guttatus* (but not *E. adscensionis*) in very shallow water. I did not see *E. guttatus* in shallow water around Bimini, where *E. adscensionis* is common

in depths of less than 20 feet, but *E. guttatus* is abundant there in water more than 30 feet deep. Longley and Hildebrand (1941) reported *E. adscensionis* as common in shallow water at Dry Tortugas, where *E. guttatus* was found at moderate depth. Thus, there is evidence that these two species may be ecological replacements.

Epinephelus guttatus is commonly seen in waters of Bermuda hovering around rocks and coral in the daytime. At the approach of the observer it quickly enters a hole or crevice. Its small size renders it of minor commercial importance but its abundance in Bermuda waters makes it useful as bait for larger species. Large individuals find a ready market, for it is an excellent food fish.

The nutrition of this species has been the subject of an extensive study by Menzel (1960). Captured individuals are frequently observed to regurgitate crabs and small fish and this species readily takes cut-fish bait.

The largest individual I have seen was 510 mm. long. The smallest male examined was 275 mm. and the largest female 400 mm. long.

RELATIONSHIPS: This species is very close to *Epinephelus striatus* and *E. morio*, but it is not intimately related to *E. adscensionis*, the other dark-spotted species in the Western Atlantic. Supporting discussion for this statement appears in the section on phylogeny.

DISTRIBUTION: Records of this species (fig. 14)

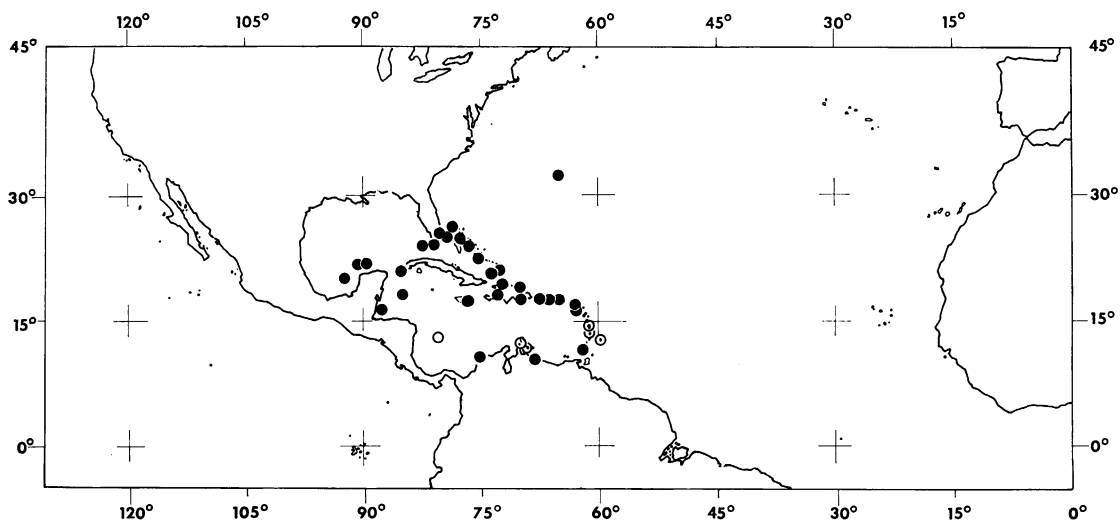


FIG. 14. *Epinephelus guttatus* distribution records. Solid circles represent specimens examined, open circles are additional literature records.

indicate that it lives in Bermuda, throughout the Bahamas and the Greater Antilles, and along the coast of the mainland from South Carolina to Panama and the north coast of South America. It reaches its greatest abundance in Bermuda and the West Indies; mainland records are few.

SPECIMENS EXAMINED

Florida: Key West, FMNH 7008; Garden Key, USNM 6770; Miami (sight record, January, 1957); Boynton, ANSP 69942.

Gulf of Mexico: Triangles, FMNH 46774; Alacran Reef, FMNH 46775, 46785; west of Campeche, USNM 158563; 22°22'N, 90°16'W, UMMZ 174087.

Mexico: Misterioso Bank, FMNH 39699; 20°05'N, 91°51'W, UMMZ 176955.

Caribbean Sea: Glover Reef, FMNH 49737, 39718, 39720; Roncador Bank, ANSP 81774.

Honduras: USNM 34647.

Colombia: Cartagena, FMNH 56821.

Venezuela: Porto Cabello, MCZ.

Lesser Antilles: 18°50.5'N, 64°38.1'W, UMMZ 176961.

Barbados: USNM 120738.

Grenada: ANSP 52467, 45093.

St. Kitts: ANSP 13413, 13370-71.

St. Martins: ANSP 13451.

Virgin Islands: ANSP 80122; St. Thomas, FMNH 2281; USNM 34925, 34954; MCZ 4804; ANSP 23360; St. Croix, FMNH 52807.

Puerto Rico: Arroyo, FMNH 3226; Aguadilla, USNM 50101; Puerto Real, FMNH 3262, 52051; AMNH 2022; Condado Rocks, UMMZ 172975.

Hispaniola: Santo Domingo, USNM 21213; ANSP 77329; Montecristi, CU 7247; Cul-de-Sac Plain, USNM 131197; Petit Baraderas Bay, USNM 89647; Samaná Bay, USNM 88955; west end of Hispaniola, UMIM; Haiti, AMNH 19115, 18947; Port-au-Prince, CU 13276; USNM 133694; ANSP 77207.

Jamaica: Port Antonio, ANSP 18652; no specific locality, FMNH 2794; USNM 30006, 38569.

Cuba: Havana, USNM 129940; ANSP 52093; San Antonio Knoll, TU 6316; Batabano, USNM 107441; Cienfuegos, UMMZ 60553; no specific locality, USNM 82431, 9845, 38742, 19814-15; MCZ 10058, 10133.

West Indies: no specific locality, USNM 38738, 34511.

Bahamas: Bimini, UMMZ 174432; FMNH; Great Bahama Island, FMNH 47926; vicinity

of New Providence, FMNH 43099; USNM 38489, 53128-29; ANSP 13368-69, 72361; CBC Stations 198, 212, 219, 242, 304, 341; West Caicos, BOC 2315; Cay Sal Bank, UMIM; Mangrove Cay, USNM 53130; no specific locality, MCZ 23785; USNM 6707.

Bermuda: MCZ 10200, 26702, 23767, 32867, 32855; FMNH 4905, 4982, 48141, 48182, 48171, 48238, 48259, 48332, 48394, 48452, 48546, 48703; USNM 16810, 20182; AMNH 17756, 9036, 2099, 549, 525, 531, 629; UMMZ 172298, 172352, 172401, 172541-S, 172542-S, 172543-S, 172544-S, 173402-S, 176034, 176055, 176057, 176105, 176117, 176129, 176139, 176164, 176409, 176412, 176432, 176447, 176462, 176524, 176534, 176592, 176605, 176613, 176627, 177490, 177491.

Epinephelus niveatus Species-Group

This complex of five species (*niveatus*, *flavo-limbatus*, *nigritus*, *acanthistius*, *mystacinus*) is well marked. The pelvic fins are large, usually longer than the pectoral fins and originate well in advance of the pectoral base. The species generally tend to be robust when young becoming more compressed as they get larger. The color is generally reddish brown, with pearly or bluish spots in the juveniles, although *E. mystacinus* has a pattern of bold, regular vertical bars throughout its life. Within the group two species have reduced numbers of dorsal spines; *Epinephelus nigritus* has 10 dorsal spines and *E. acanthistius* has nine, however, the dorsal ray count of *acanthistius* is also higher than in other members of the subgenus *Epinephelus*. Members of this species-group tend to be deep-water fishes and most species are known primarily from stray juveniles taken well outside the normal range of the adults.

Epinephelus (Epinephelus) niveatus

(Valenciennes, 1828)

SNOWY GROUPER

Figure 15

Serranus niveatus VALENCIENNES, in Cuvier and Valenciennes, 1828, p. 380 (original description, Brazil). CASTELNAU, 1855, p. 2 (Brazil). GÜNTHER, 1859, pp. 130-131. JORDAN, 1887d, p. 532 (nomenclature). FOWLER, 1907, p. 252 (Newport, R.I.; Katama Bay; Martha's Vineyard); 1944, p. 444 (New Providence); 1946b, p. 60 (Belmar, N.J.); 1948b, pp. 9-10 (N.J.).

TABLE 9
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus guttatus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	173	179	207	224	227	228	246	272	291	380	—
Head length	422	430	440	426	436	430	415	414	421	429	426.3
Head width	171	168	174	163	174	160	179	191	203	203	178.6
Head depth	257	246	263	250	262	248	238	259	258	263	254.4
Snout length	98	109	101	100	106	103	100	103	103	111	103.4
Suborbital width	35	36	38	36	40	40	39	39	41	47	39.1
Interorbital width	58	64	68	58	64	57	63	63	62	58	61.5
Length of: Orbit	95	92	94	87	84	92	81	79	77	68	84.9
Postorbital head	237	240	256	243	255	250	244	243	247	262	247.7
Maxillary	194	190	208	192	194	195	189	195	196	197	195.0
Lower jaw	197	184	193	192	200	200	187	197	186	203	193.9
Snout to angle of preopercle	295	302	307	299	302	303	280	287	285	300	296.0
Supramaxillary length	64	61	58	56	62	57	63	64	62	55	60.2
Maxillary width	46	45	48	40	44	46	47	44	41	43	44.4
Tip of lower jaw to gular notch	139	137	145	129	141	140	150	143	155	129	140.8
Body width	156	179	159	150	159	156	167	169	174	190	165.9
Body depth	370	341	357	326	357	338	339	360	354	357	349.9
Caudal peduncle depth	98	106	104	98	106	103	100	107	105	103	103.0
Tip of snout to dorsal origin	396	419	415	404	421	421	388	410	405	408	408.8
Tip of snout to pectoral base	376	399	394	375	388	390	404	399	399	375	389.9
Tip of lower jaw to pelvic base	434	439	435	442	438	432	459	463	460	430	443.2
Length of: Dorsal base	546	525	548	536	562	522	543	540	536	553	541.1
Depressed dorsal	639	598	621	605	643	596	603	592	603	611	611.1
Anal	173	173	164	156	167	158	167	162	158	162	164.0
Depressed anal	315	293	290	272	289	272	274	261	265	261	279.2
End of dorsal to caudal base	116	106	116	116	110	118	122	125	110	118	115.7
Length of: Caudal peduncle	197	184	188	176	189	195	183	199	196	187	189.5
Pectoral	266	246	244	223	240	219	224	232	241	218	235.3
Pelvic	205	198	205	194	196	191	187	184	186	176	192.3
Dorsal spine I	84	70	92	83	82	75	69	74	69	66	76.4
Dorsal spine III	185	145	188	156	181	167	157	165	180	168	169.2
Dorsal spine XI	121	117	123	116	119	110	110	101	108	100	112.5
Anal spine I	69	64	—	58	62	61	49	48	50	37	55.6
Anal spine II	136	140	140	129	119	118	122	99	107	95	120.5
Anal spine III	136	134	130	129	115	123	122	110	108	105	121.2
Caudal base to tip of upper rays	254	229	—	223	247	228	228	221	241	—	233.9
Caudal base to tip of middle rays	257	240	246	228	242	237	224	213	228	205	232.0
Caudal base to tip of lower rays	254	229	249	228	242	228	224	222	239	215	233.0

^aAll proportions are expressed in thousandths of the standard length. All specimens are UMMZ from Bermuda.

Serranus margaritifer GÜNTHER, 1859, pp. 131–132, pl. 9, fig. b (original description, South America).

Serranus conspersus POEY, 1860 (1858–1861), pp. 139–140 (original description, Cuba).

Hyporthodus flavicauda GILL, 1862b, pp. 98–99 (original description, Newport, R.I.). COPE, 1871a, p. 119. GILL, 1873, p. 806.

Epinephelus niveatus: POEY, 1865 (1865–1866), p. 202 (Cuba); 1868 (1866–1868), p. 286; 1874, p. 34; 1875 (1875–1877), p. 15. GOODE AND BEAN, 1879c,

p. 45. JORDAN AND GILBERT, 1883a, p. 541. JORDAN AND SWAIN, 1885b, pp. 386–387. JORDAN, 1885e, p. 98; 1887a, p. 84; 1887e, p. 580. JORDAN AND EIGENMANN, 1890, p. 357 (Cuba; Río de Janeiro). JORDAN, 1891, p. 336. BOULENGER, 1895, pp. 225–226, pl. 3, fig. b. JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1156. SMITH AND KENDALL, 1898, p. 171 (Woods Hole; R.I.). SMITH, 1899, p. 879 (common in Katama Bay in August and September, 1895). EVERMANN AND KENDALL, 1900, p. 73

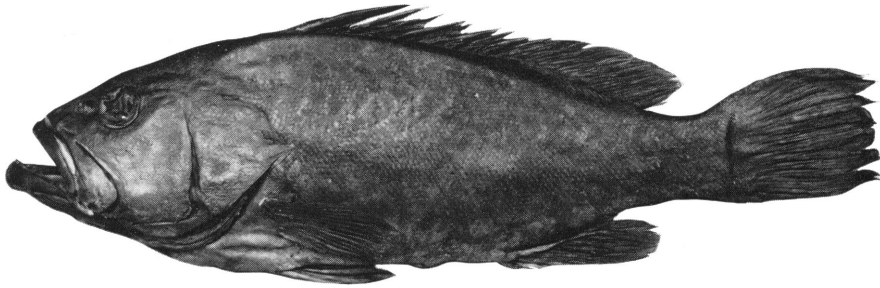


FIG. 15. *Epinephelus niveatus*, AMNH 20230 from Bimini, Bahamas, 810 mm. (paratype of *Alphestes scholanderi*).

(Florida). SMITH, 1901, p. 309; 1902, p. 32. JORDAN, 1905, p. 329, fig. 264 (photograph). KENDALL, 1908, pp. 97–98 (New England records). SUMNER, OSBURN, AND COLE, 1913a, p. 167; 1913b, p. 756 (Woods Hole). FOWLER, 1915b, p. 543 (St. Georges, Grenada); 1916b, p. 11 (N.J.); 1917b, p. 127; 1920, p. 150 (Nassau). JORDAN AND EVERMANN, 1920, pp. 383–384. MEEK AND HILDEBRAND, 1925, p. 458 (not seen in Panama). NICHOLS AND BREDER, 1927, p. 79, fig. 103. BREDER, 1929, p. 163. JORDAN, EVERMANN, AND CLARK, 1930, p. 311. BREDER AND NIGRELLI, 1934b, p. 195 (Long Beach, Long Island). HOWELL Y RIVERO, 1938, p. 190 (specimens in MCZ). LONGLEY AND HILDEBRAND, 1941, pp. 93–94 (Tortugas; some of these specimens are *E. flavolimbatus*). FOWLER, 1942b, p. 68 (Cuba). MANTER, 1947, p. 371 (Tortugas, parasites). FOWLER, 1952, p. 121. HILDEBRAND, 1954, p. 303 (Obregón, Mexico). BRIGGS, 1958, p. 272. BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:3, 1:10, 1:23, figs. 1.3, 10. LORET, 1962, pp. 21–22 (Long Island records, photograph of living specimen). RIVAS, 1964, p. 24 (characters). ALPERIN AND SCHAEFFER, 1965, pp. 4–5 (New York records). CALDWELL, 1966, p. 41 (Jamaica, compiled). CERVIGÓN M., 1966b, pp. 310–311, fig. 121 (Cubagua, La Tortuga, Venezuela). BÖHLKE AND CHAPLIN, 1968, p. 277 (Bahamas, based on *Alphestes scholanderi* Walters).

Serranus flavolimbatus (part): POEY, 1867 (1866–1868), p. 157 (*S. conspersus* in synonymy).

Epinephelus niphobles GILBERT AND STARKS, in Gilbert, 1897, pp. 442–443 (original description, Magdalena Bay, Lower California). JORDAN AND EVERMANN, 1898, p. 2853. JORDAN, EVERMANN, AND CLARK, 1930, p. 312. WALFORD, 1937, p. 109.

Garrupa niveata (part): MIRANDA-RIBEIRO, 1915, p. 19–20 (Brazil); 1918, pp. 88–89.

Epinephelus labriformis (non Jenyns): HIYAMA, 1937, p. 38, pl. 68 (Pacific coast of Mexico).

Epinephelus morio (non Valenciennes): GREELEY, 1939, p. 87 (Fire Island Inlet, New York).

Epinephelus mystacinus (non Poey): LONGLEY AND HILDEBRAND, 1941, pp. 94–95 (Tortugas).

NOMENCLATURE: Hubbs's careful reexamination and tabulation of characters on the six syntypes of *Serranus niveatus* in the Paris Museum confirms the correctness of the current use of this name. The syntypes are in four lots from Martinique and Brazil.

Howell y Rivero (1938, p. 190) stated that the types of *Serranus conspersus* are MCZ 10161, consisting of three specimens 87.5, 135, and 134 mm. long. The original description, however, was based on a single individual 200 mm. long. It stated that the spinous dorsal margin was dark and this was sufficient to identify *conspersus* as *niveatus*. MCZ 10161 includes both *niveatus* and *flavolimbatus*. The present location of the holotype, if still extant, is not known to me.

In an earlier paper (Smith, 1961) I considered *Alphestes scholanderi* Walters to be a synonym of *Epinephelus nigritus*. Rivas (1964) placed *scholanderi* in the synonymy of *E. niveatus* instead, and after examining the types of *scholanderi* in the American Museum of Natural History, I concur in his placement. In particular the neurocranium of *scholanderi* is much narrower than that of *nigritus* of comparable size and differs in a number of other proportions as well; *E. nigritus* almost invariably has 10 dorsal spines and only slightly enlarged posterior nostrils.

The holotype of *Epinephelus niphobles* (USNM 47582, from Lower California) and another lot of specimens from Panama Bay seem not to differ from typical Atlantic specimens. Hiyama (1937, pl. 68) also illustrated this species from the Pacific coast.

The trivial name *niveatus* is a Latin adjective meaning snowy, and refers to the color pattern of pearly spots.

DIAGNOSIS: Small species of *Epinephelus* with large eye, medium-sized scales, robust body. Nostrils subequal. Dorsal XI, 14 (15); anal III,

9; pectoral 18; gill rakers 23–26. Vertical fins rounded, dorsal interspinous membranes notched. Skull crests developed, frontoparietal crests convergent anteriorly. Supraethmoid forming floor of pit between frontals. Body with pearly-white spots in regular geometrical pattern. Black saddle on caudal peduncle reaches below lateral line. Dorsal fin margin dark.

This species may be easily distinguished from *E. flavolimbatus*, with which it has repeatedly been confused, by color pattern. *Epinephelus niveatus* has the dorsal interspinous membranes edged with narrow black band, whereas *flavolimbatus* has spinous dorsal and anterior part of soft dorsal with broad (occasionally narrow) yellow margin. Saddle on the caudal peduncle reaches below lateral line in *niveatus* but in *flavolimbatus* only to line. *Epinephelus niveatus* lacks narrow blue line from lower part of eye to angle of preopercle that is present in *flavolimbatus*. Young specimens of *E. nigritus* have light pectoral and caudal fins like young of both species, but *nigritus* never has definite geometrical pattern of pearly spots on sides, and lacks saddle on caudal peduncle at all sizes.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 10. In the depth of body and other measurements, *E. niveatus* resembles *nigritus*, *mystacinus*, and *flavolimbatus*, but *niveatus* has longer pelvics, a shorter caudal peduncle, and longer jaws and supramaxillae. The snout-to-preopercle distance is consistently greater than in these other species.

The pyloric caeca are numerous and are repeatedly branched. The soft dorsal, anal, and caudal lobes are rounded. The exposed part of the maxilla has a few embedded scales. The posterior nostril becomes enlarged in large individuals. The frontal pit is well developed; the lateral crests converge but little in the small specimens examined. The preopercle has several strong serrae at the angle.

The ground color of the head and body is chocolate-brown, slightly lighter below. The tips of the snout, lower jaw, and upper lip are dark. A dark mustache extends from the groove above the posterior tip of the maxilla onto the cheek. There is a large black spot on the caudal peduncle that is rounded below and extends well below the lateral line. The side of the body has several rows of pearly-white spots arranged as follows: a longitudinal row parallel to the curve of the back from below the dorsal origin

to the base of the tail; a row below this beginning on the nape and following the lateral line; two or three rows from the gill opening to the caudal peduncle; and, in some individuals, other rows spaced between these main rows. These spots are aligned in vertical rows as follows: over the upper end of the gill opening, under the third dorsal spine, at the middle of the pectoral fin, at the tip of the pectoral fin, under the last dorsal spines, under the anterior soft dorsal rays, under the middle dorsal rays, under the posterior dorsal rays, at the base of the caudal fin. There are no pearly spots on the dark caudal saddle, but most individuals have a row of spots on the middle of the dorsal fin. There also may be a few scattered spots on the head. The dorsal and anal fins are dusky throughout. The pectoral and caudal are clear, presumably yellow in life. The pelvic is black. There is variation in the number of pearly spots; some individuals lack spots anteriorly on the body and fins. Although few large specimens have been available for study, the largest examined (267 mm.) was like the smaller ones. Neither the caudal blotch nor the pearly spots seem to change consistently with age.

RELATIONSHIPS: *Epinephelus niveatus* is closely related to *E. flavolimbatus* with which it is sympatric at Tortugas, Cuba, and probably elsewhere. The species *niveatus*, *flavolimbatus*, *nigritus*, and *mystacinus* all have a low dorsal ray count (usually 14), and, together with *acanthistius*, seem to form a cluster which can be called the *niveatus* complex. *Epinephelus niveatus*, *E. nigritus*, and *E. flavolimbatus* resemble each other as juveniles, all three having pale pectoral and caudal fins and light spots on a darker brown background. *Epinephelus niveatus*, *E. nigritus*, and reportedly, *E. mystacinus* have many pyloric caeca. *Epinephelus mystacinus* and *E. nigritus* both have a developed supraethmoid wall.

ECOLOGY: Most of the specimens examined were small, under 100 mm., and were collected well to the north. About two-thirds were from the vicinity of Woods Hole. Presumably these juveniles had been carried northward on currents associated with the Gulf Stream from a mother population which, to the present, has not been located. The apparent absence from Bermuda suggests that the main population is restricted to the western side of the Gulf Stream and reinforces the evidence that it acts as a

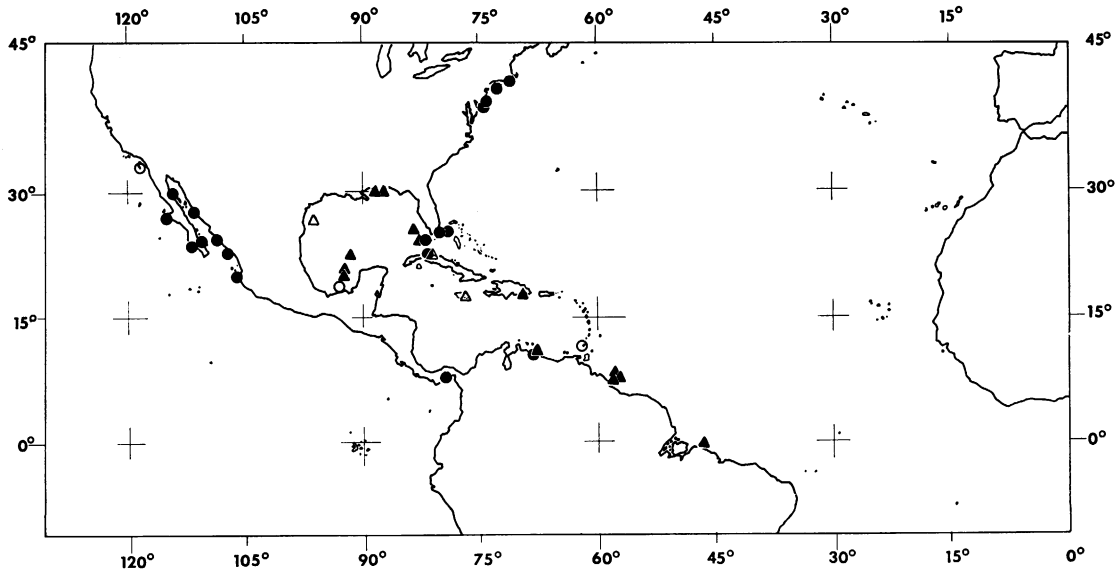


Fig. 16. Distribution records for *Epinephelus niveatus* (circles) and *E. flavolimbatus* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

barrier. Specimens collected at Tortugas were taken from between 47 and 94 fathoms (Longley and Hildebrand, 1941, pp. 94-95), and the types of *A. scholanderi* came from 1224 to 1500 feet.

DISTRIBUTION: *Epinephelus niveatus* is known from Woods Hole, New York, New Jersey, southern Florida, the Bahamas, Cuba, and Brazil. There are no records from the West Indies other than those from Cuba. On the Pacific coast there are records from Lower California and the Gulf of Panama (fig. 16).

SPECIMENS EXAMINED

ATLANTIC RECORDS

Massachusetts: Katama Bay, ANSP 23813-15; FMNH 7691; USNM 126985, 68076, 49658, 68075, 49668, 58836-38, 58877, 77786, 58835, 68074; Woods Hole, USNM 85777, 63915, 77785.

Rhode Island: Port Judith, USNM 39161; Newport, USNM 20759; ANSP 13294.

New York: Fire Island Inlet, USNM 108653; Atlantic Beach, AMNH 17466; Long Beach, AMNH 12512.

New Jersey: Clam Creek, ANSP 54602; Sea Isle City, ANSP 45478; Corsons Inlet, ANSP 45477.

Florida: Miami, UMML 49-80, 49-231; Tortugas, USNM 17716, 117141.

Venezuela: Puerto Cabello, FMNH 6313.

Brazil: Río de Janeiro, MCZ 10082, 10115, 10156.

Cuba: Havana, 24°25.3'N, 81°47'45"W, USNM 134225; no specific locality, USNM 6926, 9804; MCZ 10161 (types of *Serranus conspersus* Poey).

Bahamas: Bimini, AMNH 19924, 19925 (holotype and paratype of *Alphistes scholanderi* Walters).

PACIFIC RECORDS

Mexico: Baja California, Turtle Bay, UCLA W58-266; 24°35'30"N, 112°05'W, USNM 47582 (holotype of *Epinephelus niphobles* Gilbert and Starks); Baja Falso, UCLA W60-127; off San Luis Gonzago, UCLA W59-19; Bahía de la Paz, 24°19.3'N, 110°26.6'W, SIO 65-257-35A; Sinaloa, entrance to Bahía Topolobampo, UCLA W56-118; Sinaloa, vicinity of Mazatlán, LACM W51-40; Sonora, north of Bahía Guaymas, UCLA W50-53; entrance to Bahía Guaymas, UCLA W51-60; Bahía de Banderas 20°40.9'-41.5'N, 105°22.5'-24.2'W, SIO 62-52-35A.

Panama: Panama Bay, 08°16'30"N, 78°51'W, USNM 43400.

***Epinephelus (Epinephelus) flavolimbatus* Poey, 1865**

YELLOWEDGE GROUPER

Epinephelus flavolimbatus POEY, 1865 (1865-1866),

TABLE 10
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus niveatus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	73	76.5	106	114.5	117	144	147	182	185	267	—
Head length	425	444	453	437	453	410	422	429	430	423	432.6
Head width	179	196	198	188	171	187	167	168	168	184	182.6
Head depth	301	300	311	301	308	278	289	297	297	296	297.8
Snout length	110	98	104	105	111	108	109	104	103	120	107.2
Suborbital width	34	26	24	44	34	35	41	38	38	45	35.9
Interorbital width	89	72	68	83	68	83	75	77	81	84	78.1
Length of: Orbit	89	124	113	83	94	94	92	93	86	79	94.7
Postorbital head	233	229	241	266	239	229	242	245	195	242	236.1
Maxillary	212	222	222	210	218	208	214	209	216	208	213.9
Lower jaw	212	209	222	218	209	215	218	214	216	212	214.5
Snout to angle of preopercle	349	333	321	310	329	306	313	316	319	311	320.7
Supramaxillary length	62	78	75	70	81	62	71	69	65	67	70.0
Maxillary width	48	52	44	48	47	42	44	44	48	45	46.2
Tip of lower jaw to gular notch	171	170	146	118	162	174	133	143	146	135	150.8
Body width	192	163	184	166	154	191	167	162	157	174	171.0
Body depth	425	405	434	415	372	389	367	385	392	363	394.7
Caudal peduncle depth	137	118	123	127	124	115	122	118	122	121	122.7
Tip of snout to dorsal origin	370	412	396	397	415	368	398	387	389	401	393.3
Tip of snout to pectoral base	418	464	415	393	432	410	398	401	413	391	413.5
Tip of lower jaw to pelvic base	466	490	439	—	427	458	425	434	435	410	442.5
Length of: Dorsal base	569	529	538	585	517	538	537	517	535	519	538.4
Depressed dorsal	678	614	632	699	615	604	629	615	622	594	630.2
Anal base	192	190	179	175	171	177	173	170	178	165	177.0
Depressed anal	315	301	297	341	282	264	293	277	284	258	291.2
End of dorsal to caudal base	123	124	118	122	120	132	119	132	124	131	124.5
Length of: Caudal peduncle	178	176	151	166	179	191	167	173	162	189	173.2
Pectoral	247	261	255	249	231	226	231	220	222	213	235.5
Pelvic	240	274	274	284	165	260	245	258	235	230	256.5
Dorsal spine I	68	78	80	79	72	62	75	77	68	69	72.8
Dorsal spine III	192	190	189	175	154	153	167	170	146	137	167.3
Dorsal spine XI	130	156	146	162	128	132	133	129	124	112	135.2
Anal spine I	68	72	63	57	68	56	61	58	62	52	61.7
Anal spine II	130	150	132	118	128	118	—	129	122	109	126.2
Anal spine III	144	157	137	140	132	125	129	129	127	107	132.7
Caudal base to tip of upper rays	247	248	231	235	244	229	238	242	243	232	238.9
Caudal base to tip of middle rays	247	248	241	262	231	222	235	228	238	232	238.4
Caudal base to tip of lower rays	233	242	231	240	214	226	235	234	238	225	231.8

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Column 1, FMNH 7691 from Katama Bay; 3, FMNH 6313 from Puerto Cabello, Venezuela; 2 and 4, UMML from the vicinity of Miami, Florida; the others are UMIM from the vicinity of Miami, Florida.

pp. 183–184 (original description, Matanzas Bay, Cuba); 1867 (1866–1868), p. 157 (*niveatus* and *consersus* in synonymy); 1868 (1866–1868), p. 286; 1874, p. 15. JORDAN AND EIGENMANN, 1890, p. 357 (Pensacola). HENSHALL, 1895, p. 216 (Key West). JORDAN AND EVERMANN, 1896a, p. 372; 1896b,

p. 1155–1156. EVERMANN AND KENDALL, 1900, p. 73 (Key West; Pensacola). FOWLER, 1920, p. 147 (Jamaica). JORDAN AND EVERMANN, 1920, p. 383. JORDAN, EVERMANN, AND CLARK, 1930, p. 311. BREDER, 1929, p. 163. BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:3, 1:11, 1:23,

figs. 2.1, 10. RIVAS, 1964, p. 23 (characters). CALDWELL, 1966, p. 40 (Jamaica, compiled).
Serranus flavolimbatus: FOWLER, 1907, p. 252 (San Domingo); 1944, p. 465 (Jamaica).
Epinephelus niveatus (non Poey): JORDAN AND EVERMANN, 1887, p. 475 (Gulf of Mexico). LONGLEY AND HILDEBRAND, 1941, p. 94 (part, Tortugas). SPRINGER AND BULLIS, 1956, p. 78 (Gulf of Mexico records).
Serranus niveatus (non Poey): FOWLER, 1951, pp. 51-52 (N.J.).

NOMENCLATURE: The original describer, Poey, and several subsequent authors have confused this species with *E. niveatus* and relegated it to synonymy. The two species are readily separated at all sizes, however, and are clearly distinct. Poey apparently did not preserve the specimen on which the original description was based. It was 705 mm. long.

DIAGNOSIS: Moderate-sized species of *Epinephelus* with large eye, medium-sized scales, robust body. Nostrils subequal. Dorsal XI, 14 (15); anal III, 9; pectoral 18; gill rakers 23-26. Vertical fins rounded, dorsal interspinous membranes notched. Skull crests well developed, supraethmoid forming floor of pit between anterior ends of frontals. Body with pearly-white spots in geometric pattern and with dark saddle on dorsal surface of caudal peduncle, truncate below and limited by lateral line. Margin of spinous dorsal, anterior part of soft dorsal fin broadly yellow. Distinct blue line runs from orbit to angle of preopercle.

The resemblance between this species and *E. niveatus* has been discussed in the account of that species. The broad yellow margin on dorsal fin, caudal saddle ending at lateral line, and light blue stripe from eye to angle of preopercle are diagnostic characters of *flavolimbatus*.

DESCRIPTION: The body proportions (table 11) agree rather closely with *E. striatus* and *E. morio*. The upper and lower caudal rays average slightly shorter than in most other species of *Epinephelus* and the first dorsal spine is usually shorter than that of *niveatus*.

The preopercle has strong spines at the angle, the lowermost of which points nearly straight downward. In large individuals these coalesce into a flat, serrate lobe. The dorsal and anal fins are rounded, the caudal margin straight; the nostrils are subequal; the maxilla bears a few scales on its exposed surface. The frontoparietal crests are low and do not reach the

postorbital process; the median skull crest ends at the posterior part of the orbit; the frontal pit is well developed. The spinous dorsal is moderately notched between the spines. There are about nine pyloric caeca.

Individuals more than 250 mm. long are uniform reddish brown in preservative. The distal third or fourth of the spinous dorsal is light (yellow in life). This marginal band continues onto the anterior part of the soft dorsal fin. In large individuals the caudal blotch is obliterated. In smaller specimens there is a distinct narrow blue line from the posteroventral part of the orbit to the angle of the preopercle which may be lost in large adults. Specimens up to 100 mm. have pearly spots on the side of the body similar to those of *E. niveatus*. These spots are arranged in four longitudinal rows: one along the base of the dorsal fin, one along the lateral line, one behind the point of the opercle, and another behind the pectoral base. At the same time, these spots are aligned in seven vertical columns equally spaced between the gill opening and the caudal base. There are only one or a few such spots on the dorsal fin. The dark caudal saddle ends abruptly at the lateral line.

The basal part of the dorsal fin and the entire anal fin are dusky. The pectoral and caudal are clear in the young and the pelvic is very dark. A specimen collected by Al Pfeuger, 10 miles east of Alligator Reef Light, Florida, is 605 mm. long. This is the largest that I have seen.

ECOLOGY: *Epinephelus flavolimbatus* apparently inhabits moderately deep water. Poey stated that it was found at 150 to 200 fathoms. Numerous specimens were collected by the M/V OREGON at depths of 18 to 48 fathoms.

DISTRIBUTION: *Epinephelus flavolimbatus* is presently known from northern Gulf of Mexico, Cuba, southern Florida, and the northern coast of South America. Records are rather scattered (fig. 16), perhaps owing to inadequate sampling of the proper habitat.

SPECIMENS EXAMINED

Florida: Pensacola, USNM 37751 (470 mm., Silas Stearns); Tortugas, USNM 117166 (two specimens, 116.5-135 mm., 49 fathoms, Longley); 10 miles east of Alligator Reef Light, UMMZ (605 mm., Al Pfeuger); SILVER BAY Station 736, 26° 31' N, 83° 31' W, UMMZ 174574 (34 fathoms, Sept. 6, 1958).

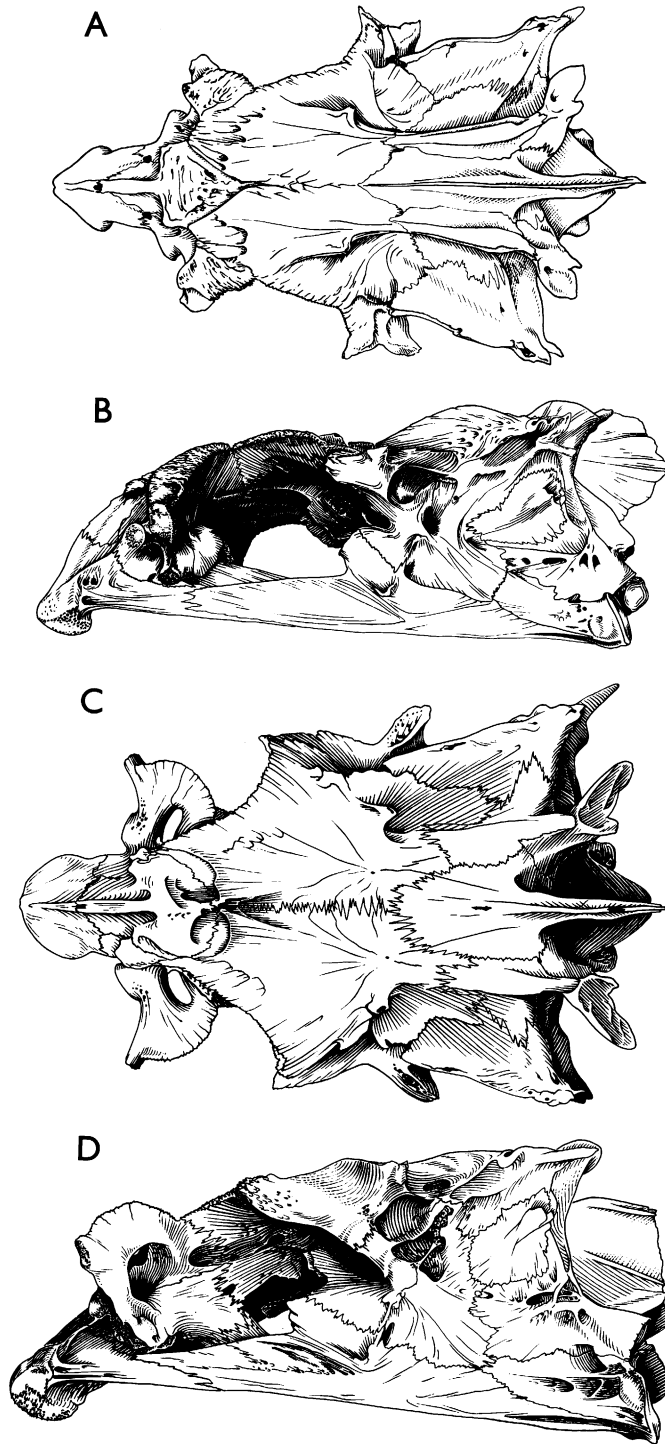


FIG. 17. *Epinephelus nigritus* and *E. itajara* neurocrania. A. *Epinephelus nigritus*, UMMZ 172588-S, dorsal view. B. Same, lateral view. C. *Epinephelus itajara*, AMNH 22454, dorsal view. D. Same, lateral view.

Mississippi: SILVER BAY Station 301, 29°20'N, 87°57'W, UMMZ 173969 (66 fathoms, March 15, 1958).

Texas: SILVER BAY Station 832, 27°46'N, 95°39'W, UMMZ 174573 (45 fathoms, Sept. 25, 1958).

Gulf of Mexico: OREGON Station 406,

22°14'N, 91°26'W, FMNH 46442 (80.5 mm., Aug. 16, 1951); OREGON Station 423, 19°36'N, 91°47.5'W, FMNH 46443 (123 mm., Aug. 19, 1951); OREGON Station 435, 20°05.7'N, 91°56.2'W, FMNH 46777 (294 mm.); OREGON Station 1303, FMNH 64174; PELICAN Stations 135-136, off Mobile

TABLE 11
PROPORTIONAL MEASUREMENTS OF NINE SPECIMENS OF *Epinephelus flavolimbatus*^a

Measurement	1	2	3	4	5	6	7	8	9	Average
Standard length (mm.)	80.5	99	102.5	116.5	135	294	339	470	638	—
Head length	435	424	424	429	422	425	419	415	390	420.3
Head width	199	172	166	159	170	207	189	174	141	175.2
Head depth	317	303	288	283	296	282	283	283	253	287.6
Snout length	99	96	102	94	89	119	115	113	111	104.1
Suborbital width	31	30	34	34	33	43	40	49	45	37.7
Interorbital width	65	71	63	60	56	73	63	70	69	65.6
Length of: Orbit	118	106	102	107	111	87	84	68	60	93.7
Postorbital head	236	232	234	232	237	235	236	243	224	234.3
Maxillary	211	212	210	206	200	199	201	200	181	202.2
Lower jaw	211	217	215	210	207	206	206	202	181	206.1
Snout to angle of preopercle	323	303	317	318	304	310	296	301	281	305.9
Supramaxillary length	56	71	63	60	63	66	59	56	56	61.1
Maxillary width	52	55	49	52	52	48	47	43	38	48.4
Tip of lower jaw to gular notch	143	116	127	129	115	119	140	113	128	125.6
Body width	174	157	156	146	152	168	177	170	138	159.8
Body depth	398	364	351	352	341	362	366	347	347	358.7
Caudal peduncle depth	118	121	117	120	119	122	117	128	110	119.1
Tip of snout to dorsal origin	416	399	390	378	385	418	388	417	393	398.2
Tip of snout to pectoral base	398	389	395	395	393	374	404	385	365	388.7
Tip of lower jaw to pelvic base	404	389	400	403	415	391	435	413	400	405.6
Length of: Dorsal base	540	530	546	515	533	554	521	532	523	532.7
Depressed dorsal	646	636	663	627	637	636	587	606	596	626.0
Anal base	168	192	176	189	181	180	173	171	147	175.2
Depressed anal	311	318	322	313	296	276	249	260	248	288.1
End of dorsal to caudal base	118	126	137	120	133	143	131	137	151	132.9
Length of: Caudal peduncle	180	197	185	180	193	197	201	204	191	192.0
Pectoral	279	263	263	258	244	228	215	211	201	240.2
Pelvic	277	253	293	270	256	214	192	—	169	240.5
Dorsal spine I	68	66	68	69	67	51	47	39	32	56.3
Dorsal spine III	168	157	161	163	148	119	124	100	91	136.8
Dorsal spine XI	174	146	146	150	141	116	112	109	—	136.8
Anal spine I	68	71	65	69	59	43	47	38	31	54.6
Anal spine II	155	136	141	150	130	94	97	74	60	115.2
Anal spine III	149	152	146	142	141	128	111	94	83	127.3
Caudal base to tip of upper rays	248	268	254	258	244	257	248	287	268	259.1
Caudal base to tip of middle rays	267	253	249	262	252	233	229	232	201	242.0
Caudal base to tip of lower rays	242	242	239	240	241	248	240	266	239	244.1

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1 and 6, FMNH 46442 and 46777; 2-5 and 7-8, USNM 11787, 117187, 117166, 117166, no number, 37751 respectively; 9, UMMZ from the vicinity of Miami, Florida. For data see text.

Bay, USNM 155194 (350 mm., 18 fathoms, March 1, 1939).
 Venezuela: Puerto Cabello, FMNH 6311 (190 mm., Feb., 1908, N. Dearborn).
 Brazil: FMNH 2020 (224 mm., Shedd Aquarium).
 Surinam: 06° 50' N, 54° 04' W, USNM (339 mm., 28 fathoms, Nov. 8, 1957).
 South America: OREGON Station 2229, 08° 33' N, 58° 50' W, UMMZ 174571 (two specimens, 67-100 mm., 38-41 fathoms, Aug. 28, 1958); OREGON Station 2231, 08° 32' N, 58° 42' W, UMMZ 174572 (100 mm., 45-48 fathoms, Aug. 29, 1958).
 Cuba: probably vicinity of Havana, MCZ 10161 (134 mm., F. Poey).
 Santo Domingo: eastern part, ANSP 13363 (296 mm., W. M. Gabb).

Epinephelus (Epinephelus) nigritus (Holbrook, 1855)

WARSAW GROUPER

Serranus nigritus HOLBROOK, 1855, p. 173, pl. 25, fig. 2 (original description, Charleston, S.C.); 1860, p. 177. GÜNTHER, 1859, pp. 134-135 (after Holbrook).

Epinephelus nigritus: GILL, 1862c, p. 30; 1873, p. 806. GOODE AND BEAN, 1878b, pp. 182-184 (Pensacola); 1879a, p. 139. GOODE, 1879, p. 50 (Pensacola). GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, pp. 540-541. SMILEY, 1884, p. 240 (Block Island). JORDAN AND SWAIN, 1885b, pp. 380-381. BEAN, 1884, p. 401. JORDAN, 1887a, p. 84; 1886a, pp. 208-209. BEAN, 1885, pp. 230-231 (Chesapeake Bay). JORDAN, 1887c, p. 580. JORDAN AND EIGENMANN, 1890, pp. 361-362. HENSHALL, 1891, p. 387 (southern Florida). KENDALL, 1891, p. 308. BOULENGER, 1895, p. 238. SMITH, 1896, p. 175 (Biscayne Bay). SCHROEDER, 1924, p. 15 (Key West). MEEK AND HILDEBRAND, 1925, pp. 462-463 (not seen in Panama). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:1, 1:3, 1:11, 1:23, figs. 2.2, 11. RIVAS, 1964, pp. 21-22 (characters, *A. scholanderi* not this species). ALPERIN AND SCHAEFFER, 1965, pp. 4-5 (New York record, photograph).

Centropristis merus POEY, 1868 (1866-1868), p. 288 (original description, Matanzas, Cuba); 1875 (1875-1877), p. 19.

Epinephelus merus: JORDAN AND EIGENMANN, 1890, pp. 362-363 (Rio de Janeiro, Rio Grande do Sul, "may be a variety of *nigritus*").

Garrupa nigrita: JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1161-1162. BRICE, 1898, p. 283 (Key West). SMITH, 1899, p. 880 (Woods Hole). EVERMANN AND KENDALL, 1900, p. 74 (Florida). SMITH, 1901, p. 309. FOWLER, 1907, p. 257.

KENDALL, 1908, p. 98 (Katama Bay). FOWLER, 1909, p. 408 (Carson's Inlet). SUMNER, OSBURN, AND COLE, 1913, p. 756. FOWLER, 1917b, p. 127 (Katama Bay). JORDAN AND EVERMANN, 1920, pp. 386-387. FOWLER, 1923, p. 21. BEEBE AND TEE-VAN, 1928, p. 130 (Port-au-Prince). BREDER, 1929, p. 164. JORDAN, EVERMANN, AND CLARK, 1930, p. 312. FOWLER, 1932b, pp. 86-87 (Clam Creek, Ocean Co., N.J.). BEEBE AND TEE-VAN, 1933, p. 125 (Bermuda, compiled). REED, 1941, pp. 76-77 (Texas coast). FOWLER, 1942a, p. 68 (Cuba). SCHULTZ AND REID, 1942, pp. 29-30 (Grande Isle, La.). BAUGHMAN, 1943, p. 771 (Texas). FOWLER, 1946a, p. 6 (Trinidad); 1952, p. 121 (N.J.). HILDEBRAND, 1954, p. 303 (off St. Joseph; Matagorda; Obregón, Mexico); 1955, p. 208 (off Campeche, Mexico). SPRINGER AND BULLIS, 1956, p. 78 (Gulf of Mexico records). BRIGGS, 1958, p. 272 (compiled distribution). SMITH, 1958, p. 50 (no Bermuda records).

Garrupa niveata (part): MIRANDA-RIBEIRO, 1915, pp. 19-20 (Brazil); 1918, pp. 88-89.

Epinephelus morio (non Valenciennes): GREELEY, 1939, p. 87 (Fire Island, N.Y.).

NOMENCLATURE: Holbrook's type, 310 mm. long, is ANSP 13468. The tail has been cut off but remains with the body and the specimen is otherwise in excellent condition.

The adjectival species name, *nigritus*, is from the New Latin *nigritus*, blackened, an apt characterization of the color pattern.

DIAGNOSIS: Large species of *Epinephelus* with medium-sized eye, moderate scales, robust body. Nostrils subequal, sometimes posterior somewhat larger than anterior. Dorsal X, 14-15; anal III, 9; pectoral 19; gill rakers 22-25. Vertical fins rounded; in large adults second spine much elongated and membranes deeply cleft between spines. Skull crests developed, low, frontoparietal crests convergent anteriorly. Supraethmoid expanded into transverse wall anterior to frontals. Body uniformly dark red to nearly black, counter-shaded but otherwise unmarked. Young with yellow caudal and pectoral and with a few whitish spots on side of body.

Young *Epinephelus nigritus* superficially resemble young *E. niveatus* and *E. flavolimbatus*. Under 100 mm. long, all three species have dark pelvic fins and light pectoral and caudal fins. At this size all three have white spots on body, those of *niveatus* and *flavolimbatus* arranged in precise patterns of vertical and horizontal rows, those of *nigritus* scattered more or less randomly. Both *flavolimbatus* and *niveatus* have

large dark saddles, *nigritus* a much smaller one. With increasing size, fins of *nigritus* become much darker and posterior nostril enlarges until diameter is two or three times that of anterior. Blotch on caudal peduncle in *E. flavolimbatus* is lost but nostrils remain nearly equal.

Very large individuals of *E. nigritus* have been confused with large *E. (Promicrops) itajara* but resemblance is principally one of size; *nigritus* has long dorsal spines and *itajara* has short ones. Body shape of the two species quite different; *nigritus* is more compressed, deepest somewhat behind dorsal origin. In coloration, *itajara* is greenish or gray, *nigritus* dark reddish brown.

DESCRIPTION: The robust body form is reflected in the body width measurement, and the extreme elongation of the dorsal spines is shown in the length of the second spine. This feature is allometric, however, and the second spine is shorter than the third until the body length reaches nearly 400 mm. Proportional measurements of 10 specimens are given in table 12.

The posterior nostril becomes somewhat enlarged and the dorsal membranes deeply cleft between the spines in specimens more than 350 mm. Caudal margin is straight with lobes gently rounded rather than angulate. There are a few scales on the exposed surface of the maxilla. Lobes of soft dorsal and anal are rounded. It is the only grouper in the western North Atlantic with 10 dorsal spines in a majority of individuals. Preopercle expanded into an irregular lobe at angle, with upper limb nearly at right angles to shorter lower limb.

Skull crests rather low. Lateral crests converge slightly and terminate behind postorbital process. There is a developed supraethmoid wall, as in *Mycteroperca* and in *Epinephelus mystacinus*. Pyloric caeca numerous as in *E. (P.) itajara*. Skull generally broad and flattened.

Body and head, which lack spots or bars, are deep chocolate-brown, sometimes nearly black, countershaded to dull reddish gray below. Dorsal, anal, and caudal are darkened distally, becoming almost black at margin. Pectoral gray and pelvic gray at base, darkening to blue-black toward margin. Anal fin has shades of iridescent blue. Juveniles have pectoral and caudal light, probably yellowish in life, and the soft dorsal lighter at margin. Body of juvenile with scattered white spots. Pelvic and anal are dark in young fish. No dark

blotch on caudal peduncle at any stage. Membranous margin of spinous dorsal is dark. There is a dark maxillary mustache present.

Except for *itajara*, this species reaches larger size than any other western North Atlantic grouper. Individuals approaching 100 pounds are brought into Miami pier frequently, and species is said to reach three times that weight. I have seen a specimen that weighed 285 pounds.

RELATIONSHIPS: This species is the type of a genus (or subgenus) *Garrupa* that includes no other species. In view of the close resemblance between the young of *nigritus* and those of *niveatus* and *flavolimbatus*, and because it has no distinguishing features unique among the species of *Epinephelus*, *Garrupa* seems unworthy of recognition. The development of the supraethmoid wall is shared by *itajara* (fig. 17) and *mystacinus* and the large number of pyloric caeca is shared by *niveatus*, *mystacinus*, and *itajara*.

ECOLOGY: The young of *Epinephelus nigritus* are taken in shore seining; series collected near Woods Hole, Massachusetts, are in the United States National Museum. The young are also known from the Gulf Coast as far west as Corpus Christi, Texas, but the time and place of spawning, like other details of the life history, remain unknown. This species is found in waters of 20 to 250 fathoms.

DISTRIBUTION: *Epinephelus nigritus* has long been included in Bermuda faunal lists on the basis of a photograph of a "four hundred pound" individual taken by Walter L. Beasley in May, 1905 (Townsend and Barbour, 1906, pp. 304-305). The photograph is not particularly helpful for identification and no explanation or description accompanies it. From comparison with the person standing by the fish, it seems doubtful that it weighed that much, and the round figure leads one to suspect that the weight was estimated. The dorsal spines seem too long for those of *itajara* but the body shape is more slender than that of *nigritus*. Bermudans use the name "black grouper" for *mystacinus* and there is a strong possibility that the picture is of that species or of a large example of *Mycteroperca bonaci*. In view of the uncertainty of the identification and the absence of other supporting evidence for its occurrence there, I have removed it from the Bermuda species list until actual specimens are available for study.

Elsewhere the species is known from Woods

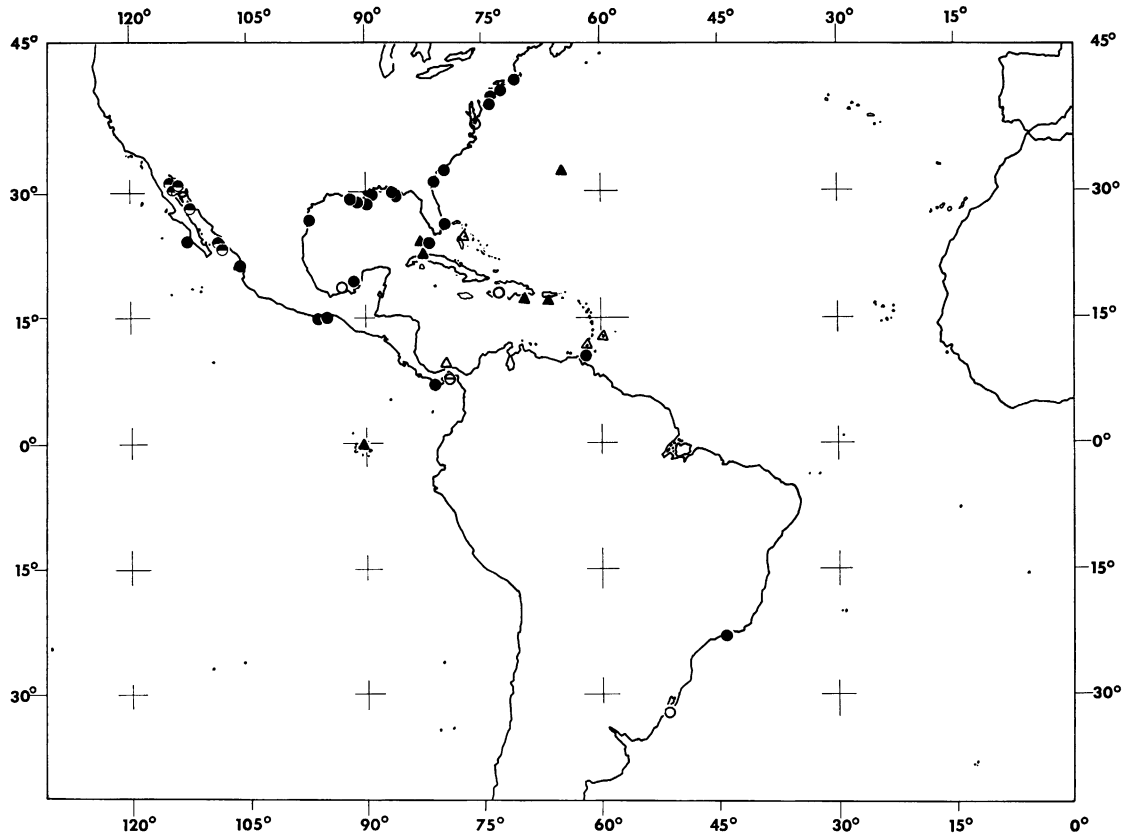


FIG. 18. Distribution records for *Epinephelus nigritus* (full circles), *E. mystacinus* (triangles), and *E. acanthistius* (half circles). Solid symbols represent specimens examined, open symbols are additional literature records.

Hole, Massachusetts, and from New Jersey south to Florida and throughout most of the Gulf of Mexico wherever suitable habitat is found (fig. 18). It is also known from Trinidad and Brazil. In the Eastern Pacific it ranges from Mexico to Panama.

SPECIMENS EXAMINED
ATLANTIC RECORDS

Massachusetts: Katama Bay, USNM 49675, 58840, 77784, 126640, 134891, 134892; ANSP 23882, 23883.
Rhode Island: Port Judith, USNM 134890; Triverton, USNM 39320.
New York: Fire Island Inlet, USNM 108652; Long Island, AMNH 17481; Coney Island, UMMZ 178597.
New Jersey: Belmar, ANSP 72095.
South Carolina: Charleston, ANSP 13468 (holotype of *Serranus nigritus* Holbrook).

Georgia: off Brunswick Sea Buoy, USNM 155192.

Florida: Miami, UMMZ 172588-S; Pensacola, USNM 21329; Panama City, UMMZ 179940-S.

Mississippi: Horn Island, USNM 134888; UMMZ 176996, 176969.

Louisiana: Chandeleur Island, TU 12827; off Grand Bayou, TU 6269; southeast of Fort Livingston, USNM 134886; Grand Isle, USNM 119701; Pass-a-Loutre, USNM 134889; Morgan City, USNM 131155; Ship Shoal, UMMZ 176971; no specific locality, USNM 134887.

Texas: Aransas Pass, USNM 86123; vicinity of Corpus Christi, FMNH 40265; USNM 94551.

Gulf of Mexico: 28°56'N, 89°27.6'W, FMNH 45479; 20°08'N, 91°30'W, FMNH 46450; 19°58'N, 91°42'W, UMMZ 174044, 174044-S.

TABLE 12
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus nigritus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	49	56.5	68	72.5	137	155	185	290	402	575	—
Head length	428	434	434	421	453	452	465	428	415	402	433.2
Head width	204	177	213	286	179	197	216	203	144	207	192.6
Head depth	306	327	324	290	314	316	311	293	274	297	305.2
Snout length	102	106	103	103	109	116	132	105	112	115	110.3
Suborbital width	31	27	37	28	40	45	43	48	44	49	39.2
Interorbital width	82	71	96	76	80	90	95	98	83	89	86.0
Length of: Orbit	92	106	88	97	88	84	76	55	75	49	81.0
Postorbital head	235	239	250	241	274	271	276	284	251	261	258.2
Maxillary	214	212	221	207	215	226	222	210	203	193	212.3
Lower jaw	204	212	221	207	212	226	222	210	162	197	212.7
Snout to angle of preopercle	316	319	309	303	314	319	319	297	299	282	307.7
Supramaxillary length	82	71	81	62	73	65	68	66	70	64	70.2
Maxillary width	61	48	51	41	51	52	49	48	47	43	49.1
Tip of lower jaw to gular notch	163	117	125	134	113	119	143	117	119	117	126.7
Body width	184	159	184	166	172	168	173	162	144	160	167.2
Body depth	398	434	404	421	391	394	395	386	328	386	393.7
Caudal peduncle depth	133	134	132	138	124	129	130	143	111	134	130.8
Tip of snout to dorsal origin	388	407	397	386	401	406	403	400	393	379	396.0
Tip of snout to pectoral base	418	398	375	407	394	394	405	383	387	362	392.3
Tip of lower jaw to pelvic base	439	363	368	386	401	390	397	397	432	385	395.8
Length of: Dorsal base	592	584	581	566	566	571	576	586	515	579	571.6
Depressed dorsal	673	735	699	690	675	697	673	700	686	657	688.5
Anal base	214	195	206	193	186	187	186	188	173	170	189.8
Depressed anal	327	372	360	352	318	332	313	309	264	259	320.6
End of dorsal to caudal base	133	154	125	124	135	135	130	152	162	139	138.9
Length of: Caudal peduncle	173	177	184	172	175	174	186	203	191	206	184.1
Pectoral	265	265	272	262	230	232	230	221	195	204	237.6
Pelvic	255	237	250	283	270	284	276	238	209	189	254.2
Dorsal spine I	92	88	81	83	73	65	70	66	51	71	74.0
Dorsal spine III	184	204	169	186	161	148	173	166	174	152	171.7
Dorsal spine X	163	168	162	152	150	135	154	122	106	107	141.9
Anal spine I	71	80	74	69	66	71	54	38	33	52	60.8
Anal spine II	143	159	140	138	117	123	114	83	73	86	117.6
Anal spine III	143	168	125	145	128	139	149	114	104	122	133.7
Caudal base to tip of upper rays	255	248	243	248	248	252	246	248	209	238	243.5
Caudal base to tip of middle rays	265	283	265	269	248	265	243	247	216	230	253.1
Caudal base to tip of lower rays	265	257	235	248	234	248	230	231	216	238	240.2

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1, 3, 5, 6, 10, USNM 126650, 126640, 131155, 131155, 21329 respectively; 2 and 4, FMNH 46450 and 40265; 7, UMM from Key West; 8, MCZ 9788; 9, UMMZ from the vicinity of Miami. For data see text.

Trinidad: Port-of-Spain, ANSP 76378.

Brazil: Rio de Janeiro, MCZ 9788.

PACIFIC RECORDS

Mexico: Golfo de Tehuantepec, off Salina Cruz,
15°41'N, 96°07.5'W, SIO 63-521-35A,

63-523-35A; 16°03.6'N, 95°19'W, SIO
65-166-35A; 15°52'N, 95°43'W, SIO 63-
525-35A; 15°56'N, 95°17.5'W, SIO 63-526-
35G; 15°50'N, 95°50.5'W, SIO 63-524-35C;
15°57.5'N, 95°00'W, SIO 63-504-35B;

15°57.5'N, 95°22.5'W, SIO 63-518-35B;
16°02.5'N, 95°02.5'W, SIO 63-503-35A;
Nayarit off San Blas, 21°50'-52.2'N,
106°09.4'-12.2'W, SIO 59-270-35B; off
Oaxaca, 15°48.5'N, 95°58'W, SIO 65-164-
35A; Baja California Sur, Magdalena Bay
near Sail Rock, SIO 62-85-35B.

Panama: off San Carlos, SIO 64-108-35A.

Epinephelus (Epinephelus) acanthistius
(Gilbert, 1892)

Bodianus acanthistius GILBERT, 1892, pp. 552-553
(original description, Cape Lobos, Gulf of Cali-
fornia). JORDAN AND EVERMANN, 1896a, p. 371;
1896b, pp. 1147-1148.

Epinephelus acanthistius: BOULENGER, 1895, p. 196
(after Gilbert).

Cephalopholis acanthistius: MEEK AND HILDEBRAND,
1925, pp. 440-441 (Panama City market). WAL-
FORD, 1937, pp. 116-117, pl. 14, fig. c. BERDEGUE
A., 1956, p. 269, fig. 185 (Mexico).

Enneistus acanthistius: JORDAN, EVERMANN, AND CLARK,
1930, p. 309. BREDER, 1936, pp. 20-21, fig. 8
(BOC 593, no locality).

Cephalopholis popino WALFORD, 1936, pp. 3-4 (original
description, Mazatlán, Mexico, holotype USNM
100979); 1937, p. 117, pl. 64, fig. a (west coast of
Mexico). HIYAMA, 1937, p. 38, pl. 21.

NOMENCLATURE: The characters by which
Walford distinguished *Cephalopholis popino* from
C. acanthistia are variable in other genera and I
see no reason to suppose that they are diagnostic
here. *Cephalopholis popino* is therefore placed in
the synonymy of *Epinephelus acanthistius*.

The holotype of *Bodianus acanthistius* is said
to be USNM 46940 from Cape Lobos, Gulf of
California; I did not see it at the United States
National Museum.

The name *acanthistia* is from the Greek *ἀκανθα*,
spine, and *ἵστίον*, sail, an allusion to the high
spinous dorsal.

DIAGNOSIS: Large species of *Epinephelus* with
rounded preopercle, robust body. Dorsal IX,
17; anal III, 9; gill rakers 14-17 on lower limb
of first arch. Anterior dorsal spines, especially
third and fourth, very long, membranes be-
tween them deeply cleft. Maxilla scaleless. Color
variation not well known. Body uniformly
brownish red, countershaded, but otherwise
unmarked.

DESCRIPTION: The head is large and massive
(table 13), the color nearly uniform brown
without conspicuous spots or other markings.
The dorsal spines are much elongated and the

dorsal membranes are deeply cleft between the
spines.

The preopercle is rounded; there are fine
serrations above the shallow notch and larger
ones at the angle. The posterior nostril is some-
what enlarged. The soft dorsal and anal lobes
are not falcate; the caudal is evenly convex.

RELATIONSHIPS: Examination of several speci-
mens in the collection at UCLA convinces me
that *acanthistius* is not a *Cephalopholis* but an
Epinephelus and further, that its affinities lie
with the *niveatus* complex, sharing with those
species the long pelvic rays, deep body, choco-
late-brown coloration and dark pelvic fins. The
niveatus complex has a low dorsal ray count of
14 or 15 and *acanthistius* has 17 dorsal soft rays
but only nine spines. If the loss of spines has
occurred at the posterior end of the spiny dorsal,
then it may be accompanied by the gain in this
line of two soft rays. The reduction in fin spines
in this line is presaged by the loss in the species
nigritus and *analogus*, which have 10 dorsal spines.

The resemblance to *Epinephelus flavolimbatus*
is heightened by the presence of a narrow dark
streak (presumably blue or silvery in life)
between the eye and the angle of the preopercle.

COLOR: Head and body generally chocolate-
brown; soft dorsal, anal, pelvic, and caudal
dark. Caudal nearly black beyond point of
branching of caudal rays. There is only minimal
countershading but the branchiostegal area is
light. The dark mustache above the maxillary
bone is prominent. A silver line from the eye
runs across the cheek toward the angle of the
preopercle. The pectoral axillary flap is dark.

ECOLOGY: The dark, reddish brown coloration
and the structure of the dorsal fin are so
similar to those of *Epinephelus nigritus* that the
habitat of *acanthistius* is perhaps also comparable.
Most of the known specimens were taken in
trawl or by hook and line in depths of 35 to 180
feet.

DISTRIBUTION: This species is known from
Cape Lobos and elsewhere in the Gulf of Cali-
fornia, Mazatlán and Panama (fig. 18).

SPECIMENS EXAMINED

Mexico: Sonora, west of Puerto San Carlos,
UCLA W50-33 (three specimens, 270-395
mm.); Sonora, Bahía Santa Barbara, UCLA
W50-42 (89 mm.); 2-3 miles off Punta San
Fermin, UCLA W52-45 (three specimens,
187-210 mm.); Sonora, 1 mile north of

entrance to Guaymas Harbor, UCLA W53-2 (217 mm.); Sonora, north of entrance to Guaymas Harbor, UCLA W51-60 (three specimens, 272-295 mm.); LACM W50-53 (two specimens, 270-395 mm.); Sonora, north of Punta Lobos, UCLA W56-28 (two specimens, 117-184 mm.); Baja California, 7 miles northwest of San Felipe, UCLA W55-1 (two specimens, 171-207 mm.); Baja California, Punta Diggs, UCLA W55-2 (129 mm.); Baja California, Bahía San Luis Gonzaga, UCLA W59-13, W59-14 (three specimens, 72-102 mm. and three specimens, 68-105 mm. respectively); Baja California, 1 mile off Bahía San Luis Gonzaga, UCLA W59-19 (two specimens, 175-195 mm.); Sinaloa, vicinity of Mazatlán, LACM W51-40 (two specimens, 440-460 mm.); Sinaloa, crest on island at Mazatlán, UCLA W51-59 (550 mm.); Mazatlán, USNM 100979 (380 mm.).

Panama: between Archipiélago de las Perlas and Isla Otoque, UCLA W53-311 (two specimens, 46-179 mm.).

Epinephelus (Epinephelus) mystacinus (Poey, 1852)

MISTY GROUPER

Serranus mystacinus POEY, 1852 (1851-1854), pp. 52-53, pl. 10, fig. 1 (original description, Cuba). GÜNTHER, 1859, p. 109. GILL, 1863a, p. 236 (type of *Schistorus*). FOWLER, 1931, p. 272 (Grenada); 1944, pp. 444, 465 (Nassau; Colón, Panama).

Schistorus mystacinus: POEY, 1867 (1866-1868), pp. 154-155; 1868 (1866-1868), p. 287; 1874, p. 34; 1875 (1875-1877), p. 18.

Epinephelus mystacinus: JORDAN AND SWAIN, 1885b, pp. 383-384 (Havana). JORDAN, 1887c, p. 40 (Havana); 1887e, p. 580 (West Indies). JORDAN AND EIGENMANN, 1890, p. 360 (after Jordan and Swain). JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1151. ROSÉN, 1911, p. 54 (Nassau, doubtful). FOWLER, 1918, p. 132 (Colón). JORDAN AND EVERMANN, 1920, p. 382. MEEK AND HILDEBRAND, 1925, pp. 455-456 (not seen in Panama). JORDAN, EVERMANN, AND CLARK, 1930, p. 310. BEEBE AND TEE-VAN, 1932, p. 120 (Bermuda); 1933, p. 120. HOWELL Y RIVERO, 1938, p. 190 ("type" in Museum of Comparative Zoology). BUTSCH, 1939, p. 23 (Barbados). FOWLER, 1942b, p. 68 (Cuba). ERDMAN, 1957, p. 330 (Puerto Rico). BRIGGS, 1958, p. 272 (compiled distribution). BÖHLKE AND CHAPLIN, 1968, p. 278 (Bahamas, along edges of banks). SMITH, 1958, p. 51 (Bermuda). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:4, 1:23, fig. 10. RIVAS,

1964, p. 22 (key, characters, common name). CERVIGÓN M., 1966b, pp. 311-312 (Puerto La Cruz, Venezuela). ROBINS, 1967, pp. 838-839 (42 mm. specimen from Florida).

Epinephelus septemfasciatus (part): BOULENGER, 1895, pp. 226-227 (West Indies references only). Seale, 1940, p. 21 (Galápagos Is.).

NOMENCLATURE: According to Howell y Rivero (1938, p. 190) MCZ 9991, 399 mm., is the holotype of *Epinephelus mystacinus*, but the original description is based on an individual 3 feet long. There is no indication on the specimen that it is the type although it was sent to the Museum of Comparative Zoology by Poey.

The specific name comes from the Greek *μύσταξ*, mustache, an allusion to the dark stripe within and behind the maxillary groove.

DIAGNOSIS: Large species of *Epinephelus* with large eye, medium-sized scales, robust body. Posterior nostril greatly enlarged in all but smallest fish, diameter about four times that of anterior nostril. Dorsal XI, 14-15; anal III, 9; pectoral 19; gill rakers 22-25. Vertical fins rounded, dorsal interspinous membranes notched. Skull crests well developed, frontoparietal crests converging. Supraethmoid expanded into transverse wall before frontal bones. Color pattern consisting of 10 regular vertical bars on lighter, chocolate-brown background. No saddle-shaped blotch on caudal peduncle, but posterior band may be darker above.

This species bears a superficial resemblance to *E. striatus*, but has more dark vertical bars on side of body; none is branched. In further contrast to *striatus* posterior nostril much enlarged. There are fewer dorsal soft rays.

DESCRIPTION: Proportional measurements of nine specimens are given in table 14. Most of these proportions show close agreement with those of the other species with 14 dorsal rays—*nigritus*, *flavolimbatus*, and *niveatus*.

The most notable modification in this species is the enlargement of the posterior nostril. The maxilla has a few scales on its exposed surface. The lobes of the vertical fins are rounded. The dorsal interspinous membranes are moderately notched between the spines and the third and fourth spines are the longest in the adult. The preopercle is similar to that of *Epinephelus nigritus*.

The ground color is chocolate-brown with nine or 10 vertical dark cross bars between the nape and the base of the tail. The last two may

TABLE 13
 PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus acanthistius*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Standard		
											Aver- age	Devia- tion	Error
Standard length (mm.)	64.9	71.3	85.0	86.6	96.4	101.8	116.5	126.0	172.0	210.0	—	—	—
Head length	415	421	424	427	424	423	427	333	436	435	416.5	29.986	9.482
Head width	191	184	171	165	183	172	184	198	197	195	184	11.60	3.67
Head depth	319	309	306	324	320	319	313	312	328	315	316.50	6.79	2.15
Snout length	96	98	98	102	96	96	86	99	100	104	97.50	4.84	1.53
Suborbital length	31	27	27	23	31	29	30	36	41	40	31.50	5.82	1.84
Interorbital width	63	70	69	66	73	63	62	74	79	77	69.60	6.08	1.92
Length of: Orbit	100	100	95	102	86	92	106	83	88	80	93.20	8.79	2.78
Postorbital head	227	238	236	236	247	236	250	198	261	257	238.60	17.78	5.62
Maxillary	199	208	208	208	210	196	209	190	215	210	205.3	7.70	2.43
Lower jaw	183	209	200	206	200	187	211	200	216	216	202.80	11.20	3.54
Snout to angle of preopercle	300	290	299	304	307	254	296	289	308	301	294.80	15.68	4.96
Supramaxillary length	69	87	80	82	71	70	68	72	78	71	74.80	6.48	2.05
Maxillary width	49	53	51	53	52	254	54	51	45	45	50.33	3.35	1.12
Tip of lower jaw to gular notch	146	161	—	157	133	152	115	129	147	150	143.3	14.81	4.94
Body width	154	173	153	167	157	163	166	159	173	173	163.8	7.83	2.48
Body depth	408	404	399	409	397	385	383	388	465	418	405.6	23.72	7.50
Caudal peduncle depth	125	119	127	126	126	126	129	133	128	141	128.00	5.75	1.82
Tip of snout to dorsal origin	379	393	382	398	396	379	406	393	400	405	393.10	10.05	3.18
Tip of snout to pectoral base	393	422	428	406	390	388	391	373	402	407	400.00	16.53	5.23
Tip of lower jaw to pelvic base	424	435	449	415	424	418	402	406	434	437	424.40	14.68	4.64
Length of: Dorsal base	552	539	535	565	539	540	539	552	530	524	540.5	12.54	3.96
Depressed dorsal	693	686	676	716	671	696	702	694	663	643	684.0	21.17	6.69
Anal base	200	195	206	202	196	195	187	198	191	201	197.1	5.5	1.75
Depressed anal	371	362	386	381	345	369	373	367	337	294	358.5	27.14	8.58
End of dorsal to caudal base	123	121	129	122	119	117	129	126	119	124	122.9	4.15	1.31
Length of: Caudal peduncle	174	182	181	189	187	177	182	186	182	200	184	7.18	2.27
Pectoral	308	309	329	321	296	300	313	310	295	298	307	11.14	3.52
Pelvic	276	281	275	300	257	281	277	283	245	243	271.8	17.99	5.69
Dorsal spine I	60	63	71	58	62	59	64	63	61	52	61.30	4.85	1.54
Dorsal spine III	162	154	153	149	168	141	177	150	157	157	156.8	10.22	3.23
Dorsal spine IX	163	168	171	162	164	163	172	167	163	146	163.9	7.22	2.28
Anal spine I	69	58	66	57	62	58	67	63	58	60	61.8	4.32	1.36
Anal spine II	142	126	81	186	140	126	127	127	116	104	127.5	27.16	8.58
Anal spine III	153	147	153	151	146	140	165	149	140	119	146.3	11.99	3.79
Caudal base to tip of upper rays	262	310	282	270	247	257	280	294	262	267	273.1	18.73	5.92
Caudal base to tip of middle rays	287	266	318	313	293	294	293	308	291	283	297	16.79	5.31
Caudal base to tip of lower rays	267	272	260	266	257	261	293	283	269	281	270.9	11.50	3.64

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-10 are SIO W59-14, W59-13, W59-42, W59-13, W59-14, W59-14, W56-28, W55-2, W55-1, and W55-1 respectively.

be fused on the caudal peduncle into a single wide band, somewhat darker above, and in keeping with the general countershading of the body. The maxillary mustache is rather prominent. There are several narrow, rather ill-defined dark lines crossing the side of the head. The dorsal, anal, and caudal are generally dusky and without definite dark margins. The pelvic is very dark.

The skull resembles that of *E. nigrilus*; the

supraethmoid is expanded into a transverse wall in front of the frontal bones. There is no pit between the anterior ends of the frontals. The frontoparietal crests converge slightly and terminate at the postorbital process.

The pyloric caeca are said by Poey to be numerous but I have not checked this. The functional significance of an increased number of pyloric caeca is not known, but *nigrilus*, *niveatus*, and *itajara* have many caeca.

TABLE 14
PROPORTIONAL MEASUREMENTS OF NINE SPECIMENS OF *Epinephelus mystacinus*^a

Measurement	1	2	3	4	5	6	7	8	9	Average
Standard length (mm.)	88.5	126.5	144	163	185	198	216	250	399	—
Head length	435	411	431	426	432	429	407	432	416	424.3
Head width	181	150	108	233	178	184	181	186	206	178.6
Head depth	311	273	295	294	286	303	285	306	263	290.7
Snout length	96	91	104	101	103	98	104	120	105	120.4
Suborbital width	28	32	38	37	43	35	37	40	45	37.2
Interorbital width	68	55	69	67	70	68	65	70	75	67.4
Length of: Orbit	124	95	97	98	97	88	76	88	73	92.9
Postorbital head	237	241	240	245	246	245	241	246	248	243.2
Maxillary	220	198	201	212	200	212	199	208	198	205.3
Lower jaw	225	209	205	221	189	215	201	216	203	209.3
Snout to angle of preopercle	328	304	316	313	311	311	292	310	296	309.0
Supramaxillary length	73	63	62	71	59	71	58	68	58	64.8
Maxillary width	51	47	49	49	49	51	46	50	45	48.6
Tip of lower jaw to gular notch	136	126	132	129	132	154	—	144	140	136.6
Body width	—	—	160	144	154	179	181	196	180	170.6
Body depth	395	379	389	368	414	389	412	392	348	387.3
Caudal peduncle depth	113	119	118	123	114	121	134	126	113	120.1
Tip of snout to dorsal origin	407	395	392	420	405	391	394	398	381	398.1
Tip of snout to pectoral base	395	379	392	405	414	402	410	412	388	399.7
Tip of lower jaw to pelvic base	429	395	424	429	441	414	463	460	426	431.2
Length of: Dorsal base	593	565	569	571	524	543	569	556	546	559.6
Depressed dorsal	667	672	674	663	600	634	657	638	614	646.6
Anal base	187	174	177	156	178	182	192	184	175	178.3
Depressed anal	299	296	319	294	—	306	310	292	272	298.5
End of dorsal to caudal base	124	142	104	117	97	116	106	112	128	116.2
Length of: Caudal peduncle	169	174	170	178	162	182	181	186	185	176.3
Pectoral	277	253	267	255	192	258	231	246	227	245.1
Pelvic	254	225	226	212	—	222	211	210	178	217.3
Dorsal spine I	90	75	76	67	70	71	62	60	63	70.4
Dorsal spine III	181	162	160	160	151	154	139	144	147	155.3
Dorsal spine XI	153	142	139	138	130	136	130	116	113	133.0
Anal spine I	68	71	62	61	51	66	49	54	49	59.0
Anal spine II	147	142	128	135	108	121	106	108	91	120.7
Anal spine III	141	142	128	135	111	141	113	124	107	126.9
Caudal base to tip of upper rays	243	—	243	248	—	263	250	220	214	240.1
Caudal base to tip of middle rays	254	—	260	242	—	265	259	242	228	250.0
Caudal base to tip of lower rays	254	—	236	233	—	247	248	224	219	237.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-3 and 9, MCZ 10174, 10081, 10009, and 9991 respectively; 4-6 and 8, USNM 4670, 34997, 4670, and 4670 respectively; 7, ANSP from Havana, Cuba.

RELATIONSHIPS: This species bears a close superficial resemblance to the Japanese species *septemfasciatus* and has been synonymized with it by Boulenger (1895). Several specimens of *septemfasciatus* in the UMMZ collection have fewer vertical bars (eight or nine instead of nine or 10) and consistently have a spine on the lower limb of the preopercle some distance from the spines at the angle. The single available skull of *mystacinus* has no such separated spine. Moreover, *E. septemfasciatus* is said to be a small fish of shore waters, whereas *E. mystacinus* reaches a weight of well over 100 pounds and inhabits water of 80 fathoms and deeper. The most intimate relationship of *E. mystacinus* is believed to be with the other members of the *niveatus* complex (*niveatus*, *flavolimbatus*, *acanthistius*, and *nigrinus*), whose affinities are strong.

ECOLOGY: The life history of *Epinephelus mystacinus* is unknown and young specimens are rare in collections. In Bermuda, fishermen told me that this species is never caught at less than 80 fathoms and it presumably lives at much greater depth. The possibility of exploiting this species commercially should be investigated more thoroughly.

DISTRIBUTION: *Epinephelus mystacinus* is known from Bermuda, Florida, Cuba, and Puerto Rico. Robins (1967) reported an adult 490 mm. long, from 12 miles east of Alligator Reef Light and a 42 mm. juvenile from latitude 24°25'N, longitude 82°56'W in 35 fathoms. Records are lacking for intervening regions. I saw several taken on the slope of Argus Bank, Bermuda, July 23-25, 1956. I have reexamined the specimen reported by Seale (1940) as *E. septemfasciatus* from the Galápagos and it seems to be *mystacinus*. Apparently this species like several other groupers occurs on both sides of the

Middle American Isthmus (fig. 18). The small size of the specimen indicates that there is a breeding population in the Galápagos.

SPECIMENS EXAMINED

ATLANTIC RECORDS

Cuba: USNM 4670 (three specimens, 163, 198, 250 mm., Poey); MCZ 10009 (144 mm., Poey); MCZ 9991 (399 mm., Poey); MCZ 10081 (126.5 mm., Poey); MCZ 10174 (88.5 mm., Poey); Havana, MCZ 1043 (270 mm., Poey); Havana, ANSP (216 mm., 1934, Howell y Rivero); Havana, USNM 34997 (185 mm., D. S. Jordan).
Bermuda: Argus Bank, UMMZ 172558-S (skull, July 23-25, 1956, C. L. Smith).
Caribbean: 18°31'N, 66°47'W, UMMZ 176965 (157 mm.).

PACIFIC RECORDS

Ecuador, Islas Galápagos: Isla San Salvador (James), Sullivan Bay, CAS 6891 (40 mm., Jan. 23, 1934).

Epinephelus guaza Species-Group

This is, at best, a dubious assemblage and the arrangement is primarily intuitive. On the other hand, there are no particular features to set these species apart from each other and it seems most expedient to consider them together as long as their association is clearly understood to be nebulous.

Epinephelus labriiformis and *E. drummondhayi* have rather similar color patterns consisting of small, stellate or linear spots on a dark red or greenish background. *Epinephelus labriiformis* has a dark saddle-shaped mark on the caudal peduncle but this is lost in a population from Alijos rocks. Although that population may

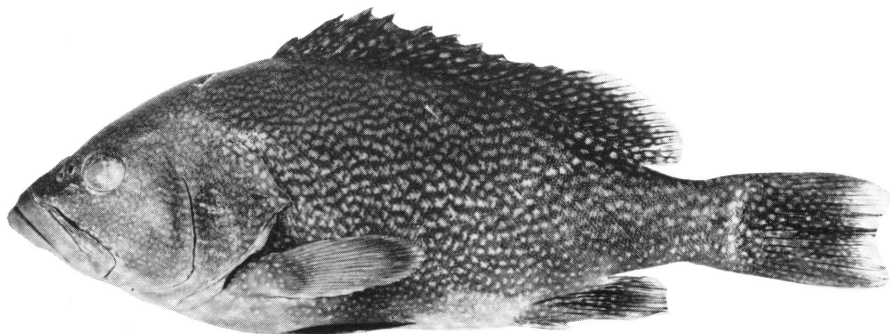


FIGURE 19. *Epinephelus drummondhayi*, AMNH 27711, from the Gulf of Mexico, 325 mm.

represent an undescribed species, it is quite close to the typical *labriformis* and was certainly derived from it. This suggests that in this case the dorsal saddle is not a reliable indicator of relationship.

Epinephelus guaza has not been well studied. It appears to be an Eastern Atlantic species with a population established along the coast of South America. Its placement here is primarily based on color pattern and general body shape.

Epinephelus (Epinephelus) guaza (Linnaeus, 1758)

- Labrus guaza* LINNAEUS, 1758, p. 285 (original description, "pelago").
- Perca gigas* BRUNNICH, 1768, p. 65 (original description, Marseilles). BONNATERRE, 1788, pp. 132–133 (Mediterranean).
- Holocentrus gigas*: BLOCH AND SCHNEIDER, 1801, p. 322 (after Brunnich).
- Holocentrus merou* LACÉPÈDE, 1802 (1800–1803), p. 377 (original description).
- Serranus dichropterus* VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 293–294 (original description, Brazil).
- Serranus gigas*: VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 270–278, pl. 33 (Mediterranean). GÜNTHER, 1859, pp. 132–133 (Cape of Good Hope). STEINDACHNER, 1877, p. 175. ROCHEBRUNE, 1882, p. 64 (St. Louis, Gorée, Dakar). OSORIO, 1909, p. 59 (Cape Verde Is.).
- Serranus mentzelii* VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 291–292 (original description, Brazil). GÜNTHER, 1859, p. 140 (after Valenciennes).
- Perca robusta* COUCH, 1832, p. 21, fig. 7 (original description, Cornwall).
- Serranus marginatus* LOWE, 1833, p. 142 (original description, Madeira).
- Serranus fimbriatus* LOWE, 1834, pp. 195–196, pl. 1, figs. 1, 2 (original description, Madeira). ROCHEBRUNE, 1882, pp. 64–65 (Barbarie; Cape Blanc; Cape St. Louis; Baie de Tant Almadie).
- Serranus ongus* (non Bloch): CASTELNAU, 1855, p. 2. GÜNTHER, 1859, pp. 142–143 (Bahía).
- Epinephelus brachysoma* COPE, 1871b, p. 466 (original description, Rio de Janeiro).
- Cerna gigas*: DODERLEIN, 1882 (not seen). MIRANDA-RIBEIRO, 1915, pp. 17–18 (Rio de Janeiro); 1918, p. 87.
- Epinephelus gigas*: JORDAN AND SWAIN, 1885b, p. 388. JORDAN AND EIGENMANN, 1890, pp. 359–360 (Rio de Janeiro). BOULENGER, 1895, pp. 231–233. METZELAAR, 1919, p. 232 (both sides of the Atlantic). BARNARD, 1927, pp. 482–483 (South Africa). CADENAT, 1950, p. 191, fig. 125 (Senegal). DEVINCENZI AND LEGRAND, 1936, pl. 28 (Uruguay).

PAES DA FRANCA AND VASCONCELOS, 1962, pp. 28–29 (Cape Verde Islands).

Epinephelus guaza: JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1154 (Brazil). JORDAN AND GUNN, 1899, p. 341 (Canary Is.). JORDAN AND EVERMANN, 1920, p. 383. JORDAN, EVERMANN, AND CLARK, 1930, pp. 310–311. SMITH, 1949, p. 195 (South Africa). SMITH, 1961, pp. 1:3, 1:13, 1:23, fig. 3.1. RIVAS, 1964, p. 29 (characters).

Serranus guaza: FOWLER, 1907, p. 253 (Italy; Syria); 1936, pp. 760–762, fig. 336. DELSMAN, 1941, p. 53 (French Guinea).

Serranus guaza mentzelii: FOWLER, 1907, pp. 253–254 (redetermination of the holotype of *E. brachysoma* Cope).

Epinephelus guaza mentzelii: FOWLER, 1920, p. 129.

NOMENCLATURE: I have seen few specimens from the Eastern Atlantic or Mediterranean and accept the name *guaza* on the authority of Jordan and Eigenmann and of Steindachner. Should the eastern and western populations prove separable, the name *mentzeli* is available for the Western Atlantic form.

The name *guaza* comes from the Spanish word for a large grouper.

The holotype of *Labrus guaza* Linnaeus is probably not extant.

DIAGNOSIS: Moderate-sized or large species of *Epinephelus* with small eye and moderate-sized scales. Body rather robust. Dorsal XI, 15 or 16; anal III, 8; pectoral 18; gill rakers 22–25. Skull crests well developed, frontoparietal crests convergent anteriorly, supraethmoid forming the floor of pit between frontals. Vertical fins rounded, dorsal interspinous membranes notched, third or fourth dorsal spine longest. Color mostly brownish red, with scattered indistinct white spots tending to form vertical rows on side of body. Vertical fins each with outer one-third dark.

Color pattern of *E. guaza* is suggestive of *E. morio*, from which it differs in the form of the first dorsal fin. The appearance is similar to that of the Pacific *labriformis* in that both have irregular white spots on the body, but *labriformis* has a distinct saddle on the caudal peduncle which *guaza* lacks. *Epinephelus guaza* differs from other American groupers in having an acutely-angled preopercle with a shallow notch above and serrations at the angle only slightly larger than those on upper limb. General body shape also quite distinctive.

DESCRIPTION: Table 15 gives the proportional measurements of six specimens of *E. guaza* from

Brazil. In proportions and in counts, *guaza* is aligned with the *striatus* complex.

The posterior nostril is little, if any, larger than the anterior one. The maxilla is nearly naked, with only a few scales on the exposed surface. The lobes of the vertical fins are rounded and the caudal margin is straight. The fourth and fifth dorsal spines are the longest.

I have not seen this species alive, but specimens in the Museum of Comparative Zoology are nearly uniform brownish above, lighter below. The side of the body is peppered with whitish spots of varying size and shape which tend to be aligned in vertical rows. There is a dark submarginal band and a narrow white margin on each median fin. The pectoral is dusky, particularly on the interradial membranes. The pelvic is dark at the tips of the anterior rays. According to the color plate in Smith (1949, pl. 18, pp. 435, 436), the belly and underparts of the head are yellow and the

dorsal parts of the head and body are brownish or greenish.

RELATIONSHIPS: *Epinephelus guaza* is an Eastern Atlantic and Mediterranean species which reaches the coast of Brazil. It is not closely allied with any other species in the western North Atlantic. *Epinephelus labriformis* resembles it somewhat, probably superficially.

ECOLOGY: No information is available on the ecology of this species in American waters.

DISTRIBUTION: This is properly a member of the Eastern Atlantic fauna and its range in the Western Atlantic is not known to extend north of Brazil. In the Eastern Atlantic it is known from the Cape of Good Hope to the British Isles (fig. 20).

SPECIMENS EXAMINED

Brazil: Santos market, USNM 100878 (172 mm., Cochran); Santos market, USNM 100886 (two specimens, 172-184 mm., April

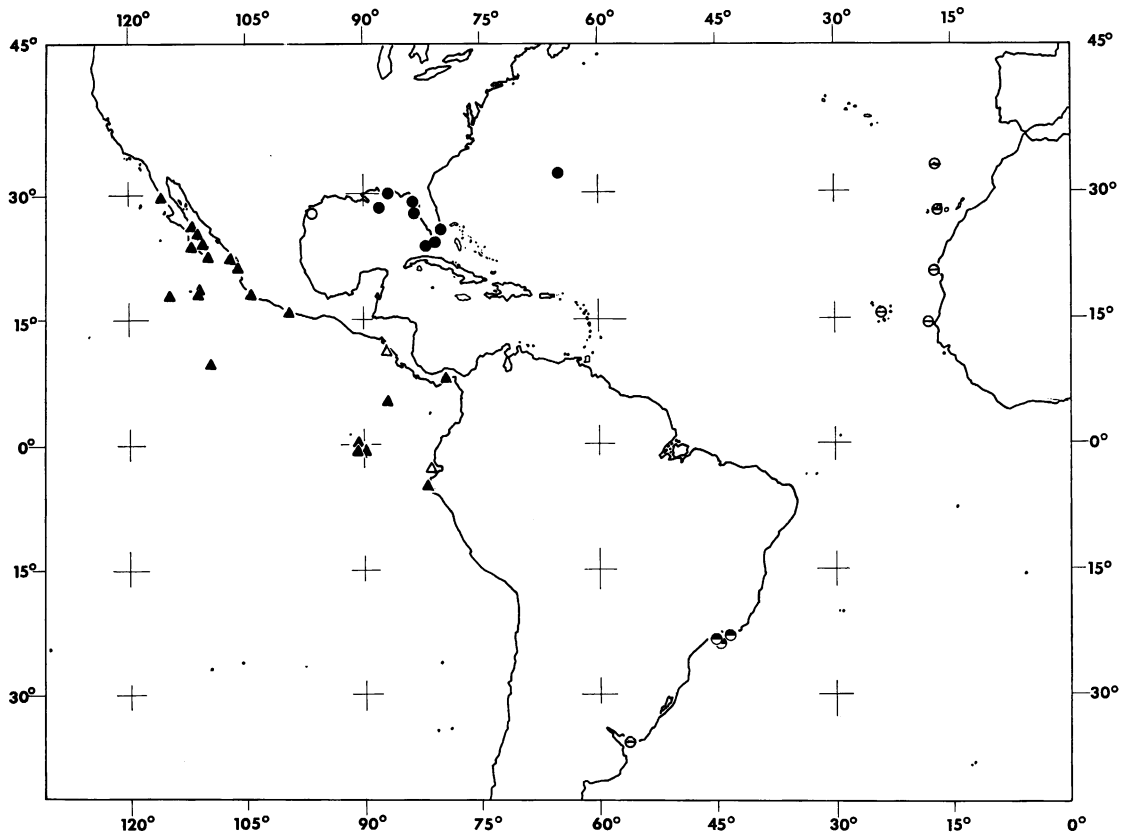


FIG. 20. Distribution records for *Epinephelus guaza* (half circles), *E. labriformis* (triangles), and *E. drummondhayi* (full circles). Solid symbols represent specimens examined, open symbols are additional literature records.

28, 1935, Cochran); Porto Inhauna, USNM 100823 (159.5 mm., May, 1935, Cochran); Santos Island, MCZ 10147 (193 mm.); Rio de Janeiro, MCZ 4506 (three specimens, 209, 274, 319 mm., L. Agassiz); Rio de Janeiro, MCZ 10196 (two specimens 181-205 mm., L. Agassiz); Rio de Janeiro, MCZ 10167 (163 mm., L. Agassiz); Rio de Janeiro, ANSP 13372 (147 mm., W. S. W. Ruschenberger [holotype of *Epinephelus brachysoma* Cope]).

Lebanon: Beirut, ANSP 13366 (242 mm.).

Epinephelus (Epinephelus) labriformis (Jenyns, 1843)

Serranus labriformis JENYNS, 1843, pp. 8-9, pl. 3 (original description, Galápagos). GÜNTHER, 1859, pp. 152-153 (Chatham Is.). FOWLER, 1944, pp. 176, 197, 224, 262, 273-274, 312, 327, 346, 350, 361, 396, 411 (Galápagos; Mexican coast; Panama; Pearl Is.).

Epinephelus sellicauda GILL, 1863b, p. 250 (original description, Lower California). JORDAN AND GIL-

TABLE 15
PROPORTIONAL MEASUREMENTS OF SIX SPECIMENS OF *Epinephelus guaza*^a

Measurement	1	2	3	4	5	6	Average
Standard length (mm.)	161	181	203	210	274	320	—
Head length	394	416	404	409	410	427	410.0
Head width	149	169	172	167	183	170	168.3
Head depth	255	258	259	252	254	281	259.8
Snout length	96	96	96	95	97	106	97.7
Suborbital width	34	34	39	38	41	41	37.8
Interorbital width	62	62	64	62	70	72	65.3
Length of: Orbit	68	79	69	71	57	73	69.5
Postorbital head	242	253	251	255	262	259	253.7
Maxillary	174	185	182	176	179	189	180.8
Lower jaw	177	188	187	181	179	191	183.8
Snout to angle of preopercle	280	295	288	286	283	306	289.7
Supramaxillary length	56	59	52	60	48	53	54.7
Maxillary width	37	45	39	40	43	47	41.8
Tip of lower jaw to gular notch	127	135	138	119	113	130	127.0
Body width	130	157	145	143	170	159	150.7
Body depth	351	357	352	348	355	356	353.2
Caudal peduncle depth	130	124	131	117	118	123	123.8
Tip of snout to dorsal origin	357	396	379	395	378	405	385.0
Tip of snout to pectoral base	363	382	369	374	357	392	372.8
Tip of lower jaw to pelvic base	410	421	416	414	394	438	415.5
Length of: Dorsal base	581	567	557	590	552	520	561.2
Depressed dorsal	674	663	645	674	624	603	647.2
Anal base	168	169	192	189	174	172	177.3
Depressed anal	304	306	325	302	276	281	299.0
End of dorsal to caudal base	130	118	118	129	118	113	121.0
Length of: Caudal peduncle	186	183	192	190	181	172	184.0
Pectoral	230	247	244	240	215	227	233.8
Pelvic	202	211	190	179	154	186	187.0
Dorsal spine I	68	65	62	67	61	54	62.8
Dorsal spine III	140	146	133	150	154	131	142.3
Dorsal spine XI	118	126	108	119	109	94	112.3
Anal spine I	68	62	69	57	50	42	58.0
Anal spine II	118	126	101	114	86	88	105.5
Anal spine III	121	140	99	129	100	100	114.8
Caudal base to tip of upper rays	227	244	222	243	206	222	227.3
Caudal base to tip of middle rays	242	261	236	245	215	216	235.8
Caudal base to tip of lower rays	224	242	217	248	215	230	229.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-6, MCZ 10167, 10196, 10196, 4506, 4506, and 4506 respectively. For data see above.

BERT, 1882, p. 229 (Braithwaite Bay, Socorro Is.); 1883b, p. 107 (Mazatlán); 1883c, p. 360 (Cape San Lucas); 1883f, p. 371 (Colima); 1883h, p. 625 (Panama). JORDAN AND SWAIN, 1885b, pp. 385-386 (description, synonymy). JORDAN, 1886b, p. 377; 1887a, p. 84.

Serranus sellicauda: GÜNTHER, 1864, p. 23; 1869, pp. 409-410. STEINDACHNER, 1876, p. 555.

Epinephelus ordinatus COPE, 1871b, p. 466 (original description, Panama).

Epinephelus labriformis: JORDAN AND SWAIN, 1885b, p. 387 (after Jenyns). JORDAN AND BOLLMAN, 1890, p. 180 (Indefatigable, Charles Islands, Galápagos). JORDAN AND EIGENMANN, 1890, p. 356 (*sellicauda* a synonym; Acapulco; Albemarle Is.). BOULENGER, 1895, p. 230 (Cordova Is., Nicaragua). JORDAN, 1895, pp. 443-444 (Mazatlán). JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1155. JORDAN AND MCGREGOR, 1899, p. 278 (Socorro Is.). GILBERT AND STARKS, 1904, p. 96 (Panama). SNODGRASS AND HELLER, 1905, pp. 367-368 (Galápagos; Cocos; Clipperton Is.). KENDALL AND RADCLIFFE, 1912, pp. 108-109 (Acapulco, Mexico; Taboguilla, Perica, Panama; Chatham Is.). EVERMANN AND RADCLIFFE, 1917, p. 69 (Lobos de Afuera). FOWLER, 1920, p. 128 (Panama City). JORDAN AND EVERMANN, 1920, p. 383. MEEK AND HILDEBRAND, 1925, pp. 459-460 (Taboga, Balboa, Panama). BORODIN, 1928, p. 19 (Galápagos Is.). JORDAN, EVERMANN, AND CLARK, 1930, p. 311. BREDER, 1936, p. 21 (Bahía Honda, Pearl Is.). HERRE, 1936, pp. 154-155 (Cocos Is.; Eden Is., Galápagos). WALFORD, 1937, p. 108, pl. 61b. HIYAMA, 1937, p. 38 (pl. 68 is *E. niveatus*). HILDEBRAND, 1939, p. 39 (upper chamber, Miraflores Locks, Panama). SCHMITT AND SCHULTZ, 1940, p. 5 (James Is., Charles Is., Galápagos; Socorro Is.). NICHOLS AND MURPHY, 1944, p. 248 (La Plata Is., Ecuador). HILDEBRAND, 1946, pp. 172-173 (Peru). MORROW, 1957, p. 28 (Lobos de Afuera, Peru). BERDEGUE A., 1956, pp. 276-277 (fig. 187 is not this species).

NOMENCLATURE: The types, collected by Charles Darwin, were originally deposited in the Museum of the Philosophical Society of Cambridge; I do not know whether they are still in existence. The holotype of the nominal species, *sellicauda*, is a specimen of *Epinephelus labriformis* 71.5 mm. long.

The name *labriformis* is derived from *Labrus*, a genus of wrasses, and the Latin termination *formis*, meaning form.

DIAGNOSIS: Small species of *Epinephelus* with moderate-sized eye, medium-sized scales, robust body. Nostrils subequal. Dorsal XI, 16-17; anal III, 8; pectoral 18 or 19; gill rakers 23-26. Vertical fins rounded, dorsal interspinous

membranes notched. Skull crests well developed, frontoparietal crests converging anteriorly. Supraethmoid forming floor of pit between anterior ends of frontals. Body reddish brown, with scattered irregular white spots. Distinct, small, black blotch on top of caudal peduncle.

The only other spotted Eastern Pacific species of *Epinephelus* are *niveatus*, which has pearly-white spots arranged in a geometrical pattern and a large saddle-shaped blotch on the caudal peduncle, and *analogus*, which has dark spots on a light background and 10 dorsal spines.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 16. The body shape is generally similar to that of *E. morio* and *E. striatus*. The preopercle is gently rounded with slightly enlarged serrae at the angle. The notch above the angle of the preopercle is rather shallow. There are scales on the exposed portion of the maxilla.

Preserved specimens are reddish brown with scattered white spots of varying sizes on the side. I have not seen the species alive but in the color plate of Walford (1937, pl. 61) the body and head are red and the soft dorsal, anal, and caudal are dark. The black blotch on top of the caudal peduncle is small, quadrate, and very distinct. According to Walford (1937, p. 108) the lining of the mouth is red. This species attains a length of about 20 inches.

RELATIONSHIPS: *Epinephelus labriformis* is a distinctive species, so well differentiated that it is difficult to be certain of its affinities. It generally resembles *E. guaza* in color pattern but structurally it seems closer to the *striatus* complex, agreeing with the species of that group in proportions and in having a red lining of the mouth and a lower dorsal fin. It is, of course, possible that this species is an immigrant from the Indo-Pacific region and has no close relatives in the American fauna. More probably, it is an early offshoot of the stock that gave rise to the *E. striatus* complex.

ECOLOGY: According to Walford, *E. labriformis* is common in shallow water close to shore.

DISTRIBUTION: *Epinephelus labriformis* lives on the Pacific coast of Central America from Lower California to Peru, and in the Revilla Gigedo, Cocos, and Galápagos Islands (fig. 20).

SPECIMENS EXAMINED

Mexico: Baja California, Cape San Lucas, USNM 7247 (holotype of *Epinephelus selli-*

cauda Gill), USNM 176143; Bahía de la Paz, USNM 46939; Isla Santa Catalina, LACM W65-85; Isla Santa Cruz, LACM W65-86; Isla San Francisco, LACM W65-89; Isla San José, LACM W65-48, W65-50; Baja California, Bahía San Lucas, UCLA W52-258; Bahía Frailes, UCLA W52-263; Bahía Magdalena, Yellow Bluff, UCLA W55-86; Baja California, Isla Carmen, LACM W65-63, W65-64, W65-78, W65-79, W65-80, W65-82; Baja California, LACM W65-57, W65-61, W65-67, W65-68; USNM 167146; Isla Ceralvo, southwest corner, LACM W61-35; Isla Ildefonso, LACM W65-83; Punta Concepción, LACM W65-71, W65-72, W65-73; Punta Pulpito, LACM W65-75, W65-76; Bahía Santa Inez, LACM W65-69; Puerto Mejía, LACM W59-183; south of Pulmo, LACM W59-248; Bahía Agua Verde, LACM W65-62; Punta San Telmo, LACM W65-58; Sonora, Puerto San Carlos, UCLA W58-41; south of San Carlos, UCLA W51-5; Punta Guillermo, LACM 51-11; Punta Mangles, LACM W65-84; Cabeza de Mechudo, LACM W65-87; Sinaloa, Mazatlán, Isla Venados, LACM W51-20; Mazatlán, USNM 28104, 86245, 101014; Mazatlán, Pala Point, UCLA W51-58; southwest of El Tule, LACM W61-30; isthmus of San Venados, UCLA W51-54; Colima, Playa de Santiago, northwest of Manzanillo, UCLA W56-232; Bahía Las Palmas, UCLA W59-251; Rancho El Tule, UCLA W61-29; Colima, USNM 9583; Colima, Ensenada Canizal, LACM W56-231; Nayarit, Ensenada Chacala, LACM W58-11; Bara de Talpeta, San Blas, UCLA W58-30; Guerrero, Acapulco, USNM 65487; MCZ 29631, 10041; Islas Revilla Gigedo, Isla Socorro, USNM 107179, 28237, 46985; LACM W55-155, W53-47, W52-199, W55-124; UCLA W55-126; Isla Clarión, LACM W55-54; UCLA W55-131, W55-163, W55-246; USNM 47201, 47203, 47033, 46870, 46887, 46983-84, 46888; MCZ 27895; Isla San Benedicto, UCLA W55-121.

Clipperton Island: UCLA W58-282; northeast side, UCLA W56-237, W58-357, W56-236, W58-371, W56-235, W56-238; north of Island, UCLA W58-281; south shore, UCLA W58-297, W58-285, W58-295; west end, UCLA W58-296, W58-291, W58-300; east side, south of Rock Pinnacle, UCLA W58-283;

end near Rock Pinnacle, UCLA W58-298; southwest shore, UCLA W56-241; southeast shore, near Rock Pinnacle, UCLA W56-240; northwest corner, UCLA W58-288.

Costa Rica: Isla del Coco, FMNH 41921-28, 41930-35, 22519-20; Chatham Bay, LACM W58-378, W63-145; UCLA W53-132.

Panama: Perico Island, USNM 65488; UCLA W53-277; Taboga Island, FMNH 20516-17; USNM 80222, 80267; Taboguilla Island, USNM 128765, 65693; Panama City, FMNH 20518-21, 20527-30, 20628; USNM 80268, 80282; Panama Bay, USNM 65495, 65486, 80217-18, 80220-21, 80284; Balboa, FMNH 20522-25; USNM 80219, 80283; ANSP 82200; Archipiélago de las Perlas, USNM 128770, 128501, 128768, 128776; Miraflores Locks, USNM 128767; Isla San José, UCLA W53-283; no specific locality, MCZ 5404, 3839; ANSP 13457 (holotype of *Epinephelus ordinatus* Cope).

Peru: Lobos de Afuera, USNM 77627; Paita, MCZ 10018.

Ecuador, Islas Galápagos: Isla Isabela (Albemarle), FMNH 41469, 41477; USNM 50070; Isla Marchena (Bindloe), ANSP 82192; FMNH 41292-94; Isla Floreana (Charles), USNM 41356, 107068; FMNH 41601-03; Isla San Cristóbal (Chatham), FMNH 41764; LACM W55-313; USNM 65489; UCLA W54-299; Eden Island, FMNH 22521; Isla Española (Hood), FMNH 41891; Isla Santa Cruz (Indefatigable), USNM 41420; FMNH 41717; UCLA W64-38, W64-15, W64-16, W64-19, W64-22, W64-26; Isla San Salvador (James), USNM 107067; UCLA W53-151; Isla Fernandina (Narborough), USNM 50024; UCLA W64-9, W64-5, W64-6, W64-1, W64-3; Isla Genovesa (Tower), UCLA W53-141; Isla Santa Fé (Barrington), UCLA W64-34; LACM W55-314; no specific locality, MCZ; between Islas Galápagos and Cedros, USNM 107181.

Epinephelus (Epinephelus) drummondhayi

Goode and Bean, 1879

SPECKLED HIND

Figure 19

Epinephelus drummond-hayi GOODE AND BEAN, 1879a, pp. 173-175 (original description, Bermuda and Florida); 1879c, p. 45; 1880, p. 139. GOODE, 1879, p. 50. GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, p. 540;

TABLE 16
 PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus labriformis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	108	206	212	240	248	249	284	297	308	327	—
Head length	426	447	432	427	407	426	417	401	435	425	424.3
Head width	176	192	200	208	185	209	181	168	211	187	191.5
Head depth	241	265	267	265	240	263	250	242	269	260	256.2
Snout length	93	109	101	104	99	108	109	94	107	101	102.5
Suborbital width	28	39	38	44	44	42	48	45	49	46	42.3
Interorbital width	51	87	66	58	63	62	60	59	68	66	64.0
Length of: Orbit	93	90	85	75	69	74	67	66	68	67	75.4
Postorbital head	241	265	259	263	250	261	254	254	266	266	257.9
Maxillary	185	194	193	192	185	191	190	182	185	200	189.7
Lower jaw	190	201	160	202	194	197	201	185	192	208	193.0
Snout to angle of preopercle	287	291	288	292	288	293	287	285	286	294	289.1
Supramaxillary length	56	56	59	63	60	56	55	47	55	64	57.1
Maxillary width	46	46	47	44	42	44	44	40	41	47	44.1
Tip of lower jaw to gular notch	130	126	156	129	119	131	120	118	141	121	129.1
Body width	167	167	222	206	157	191	146	145	205	165	177.1
Body depth	319	340	347	371	341	347	327	332	367	343	343.4
Caudal peduncle depth	116	102	113	119	109	114	106	113	109	102	110.3
Tip of snout to dorsal origin	380	405	392	404	393	386	391	384	383	404	392.2
Tip of snout to pectoral base	398	381	403	363	359	376	361	367	341	361	371.0
Tip of lower jaw to pelvic base	454	427	469	413	403	426	408	414	406	413	423.3
Length of: Dorsal base	602	570	571	610	589	590	577	586	594	587	587.6
Depressed dorsal	685	633	639	677	665	655	698	643	659	698	665.2
Anal base	171	163	177	171	169	159	158	168	167	162	166.5
Depressed anal	319	274	288	296	274	271	276	286	269	263	281.5
End of dorsal to caudal base	97	102	104	100	103	102	136	118	97	104	106.3
Length of: Caudal peduncle	185	184	179	181	188	177	199	189	180	199	186.1
Pectoral	241	218	217	219	206	213	208	210	211	191	213.4
Pelvic	194	172	170	179	165	157	162	155	156	156	166.6
Dorsal spine I	69	53	61	69	56	50	49	57	47	40	55.1
Dorsal spine III	148	133	134	154	127	133	120	133	110	125	131.7
Dorsal spine XI	134	100	113	104	103	102	90	93	91	135	106.5
Anal spine I	79	58	66	63	56	56	49	56	50	57	59.0
Anal spine II	144	112	123	110	125	102	90	106	91	92	109.5
Anal spine III	144	121	123	117	113	106	106	106	104	109	114.9
Caudal base to tip of upper rays	222	209	203	242	216	211	217	219	209	211	215.9
Caudal base to tip of middle rays	236	209	210	227	218	205	211	219	198	202	213.5
Caudal base to tip of lower rays	218	214	217	233	216	215	222	226	205	208	217.4

^aAll proportions are expressed in thousandths of the standard length. Locality data are as follows: Column 1, USNM 86245, Mazatlán, Mexico; 2-4, 6, 9, USNM 80266, 128770, 80283, 80284, 80267, from Panama Bay; 5, 7, 8, USNM 46887, 46985, 46870 respectively, Clarion Island; 10, USNM 46984 from Socorro Island.

1883d, pp. 272-273 (Pensacola Banks). BEAN, 1884, p. 503. JORDAN AND SWAIN, 1885b, pp. 388-389. JORDAN, 1887a, p. 84; 1887c, p. 581 (West Indies). JORDAN AND EVERMANN, 1887, p. 474 (*Pronotogrammus* in stomach). JORDAN AND EIGENMANN, 1888, p. 269 (Charleston); 1890, p. 356. HENSHALL, 1891, p. 387 (Key West). BOULENGER, 1895, pp. 224-225. JORDAN AND EVERMANN, 1896a, p. 372;

1896b, p. 1159. EVERMANN AND KENDALL, 1900, p. 73 (Pensacola, Key West). JORDAN AND EVERMANN, 1900, pl. 183, fig. 484. JORDAN, 1905, p. 325, fig. 259. BEAN, 1906, p. 53 (copied). FOWLER, 1906, p. 97 (Marquesas Keys). JORDAN AND EVERMANN, 1920, p. 385 (popular account, drawing). BREDER, 1929, p. 163. JORDAN, EVERMANN, AND CLARK, 1930, p. 312. BEEBE AND TEE-VAN, 1933, p. 124

(Bermuda, compiled). GUNTER, 1935, p. 40 (Gulf of Mexico off Louisiana). REED, 1941, p. 77 (Texas coast). BAUGHMAN, 1943, p. 771 (after Reed). SPRINGER AND BULLIS, 1956, p. 77 (Gulf of Mexico). BRIGGS, 1958, p. 272 (compiled distribution). SMITH, 1958, p. 51 (not seen in Bermuda). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:10, 1:23. RIVAS, 1964, pp. 24-26 (characters).

Serranus drummond-hayi: FOWLER, 1929a, p. 153 (Tortugas, 40 fathoms).

NOMENCLATURE: The holotype, USNM 16795, 315 mm. long, is in good condition. The original description refers to a drawing of the same species made at Bermuda by Col. H. H. Drummond-Hay but no Bermuda specimens were available to the describers. The specific name is in honor of Col. Drummond-Hay. This species is so well marked and so little known that it has escaped the synonyms that plague other American groupers.

DIAGNOSIS: Medium-sized species of *Epinephelus* with rather small eye, small scales, and robust, somewhat compressed body. Nostrils subequal. Dorsal XI, 16 (15); anal III, 9; pectoral 18; gill rakers 26-27. Vertical fins rather angulate, dorsal interspinous membranes notched. Skull crests well developed, frontoparietal crests convergent anteriorly. Supraethmoid forming floor of pit between anterior ends of frontals. Body reddish brown, everywhere covered with pearly, more or less stellate spots. No saddle-shaped blotch on caudal peduncle.

Color pattern alone is sufficient to distinguish this species from other American groupers. Some other species (e.g., *E. niveatus*, *E. morio*, young *E. nigritus*) have some white spots, but only *drummondhayi* has stellate spots over entire body, head, and fins.

DESCRIPTION: The body and head are deep and compressed, as reflected by the proportional measurements in table 17 and by figure 19. In most other proportions this species agrees rather well with *morio* and *striatus*, having a slightly longer snout, wider interorbital and suborbital, and shorter pectoral and anal fins. The postdorsal length is longer than for either *morio* or *striatus*.

The exposed part of the maxilla is scaled. The nostrils are about equal in size. All of the fins are rather angulate; the caudal angles are sharp. The serrations of the preopercle are even, those at the angle somewhat enlarged.

The ground color is dark reddish brown, shading to bluish purple on the underside of the head and body. All the fins except the pectoral, the upper part of the head, and the body except for the anterior part of the belly are covered with small, creamy white or pearly spots. The dorsal interspinous membranes are darker toward the margin but the other median fins and the pectoral are lightest distally. The pelvic is dark at the tip; the base is spotted like the body. Color changes in life, if any, have not been recorded.

There is a mounted specimen in the Bermuda Government Museum that is said to have weighed 35 pounds when alive. This is probably close to the maximum.

RELATIONSHIPS: This species appears to be unique among American groupers. The arrangement of color pattern suggests the Japanese species, *Epinephelus akaara* (Temminck and Schlegel), and the relationship of these species should be investigated. On the basis of the scanty existing evidence, *E. drummondhayi* may be provisionally regarded as an early derivative of the stock that gave rise to the *striatus* complex.

ECOLOGY: I have not seen small individuals of this species in museum collections and its life history seems to be unknown. Apparently, it seldom is taken in inshore waters. Jordan and Evermann (1896b, p. 1159) stated that it is common off Pensacola, Florida, but few specimens have been taken in the intensive exploratory fishing program of the U.S. Fish and Wildlife Service in the Gulf of Mexico. In January, 1957, I saw five individuals brought in to the Miami dock by a charter boat, presumably from the vicinity of Miami. I saw no fresh specimens in Bermuda although the fishermen know the species as "guinea chick hamlet."

DISTRIBUTION: The records for *Epinephelus drummondhayi* are from both coasts of Florida, Bermuda, and scattered localities in the Gulf of Mexico (fig. 20).

SPECIMENS EXAMINED

Florida: south Florida, USNM 16795 (315 mm., 1876, E. G. Blackford [syntype]); Cedar Keys, USNM 25112 (430 mm.); ca. 25 mi. from Clearwater, USNM 158620 (318 mm., June 29, 1948, R. D. Suttkus); Key West, BOC 606 (225 mm., March 10, 1926,

TABLE 17
 PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus drummondhayi*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	139	194.5	198	202	242	290	292	315	420	430	—
Head length	410	401	397	386	388	391	414	380	393	393	395.3
Head width	158	175	167	158	165	157	188	167	217	151	170.3
Head depth	281	272	280	287	293	307	291	298	305	286	290.0
Snout length	104	116	109	101	114	112	118	108	124	115	112.1
Suborbital width	36	46	40	45	48	47	50	51	49	51	46.3
Interorbital width	68	64	76	67	74	79	86	76	90	76	75.6
Length of: Orbit	90	77	83	72	70	69	67	63	60	58	70.9
Postorbital head	227	221	222	220	223	236	229	222	229	229	225.8
Maxillary	180	180	177	176	180	178	182	179	181	174	178.7
Lower jaw	187	180	187	176	182	169	183	187	183	178	181.2
Snout to angle of preopercle	299	285	275	275	283	278	291	275	271	270	280.2
Supramaxillary length	54	54	51	59	62	57	50	54	50	65	55.6
Maxillary width	50	49	45	45	50	48	43	48	45	42	46.5
Body width	155	162	174	163	165	148	212	152	206	144	168.1
Body depth	381	393	404	386	397	403	414	384	386	384	393.2
Caudal peduncle depth	115	116	114	119	118	116	120	121	114	112	116.5
Tip of lower jaw to gular notch	—	144	179	144	161	131	154	114	158	130	147.0
Tip of snout to dorsal origin	396	386	359	379	390	395	378	384	405	402	387.4
Tip of snout to pectoral base	403	383	394	364	366	383	397	357	352	358	375.7
Tip of lower jaw to pelvic base	450	422	455	408	409	433	457	413	412	409	426.8
Length of: Dorsal base	525	532	556	554	570	545	555	503	571	514	542.5
Depressed dorsal	601	601	614	621	630	609	616	546	612	572	602.2
Anal base	158	165	200	166	182	155	180	170	167	165	170.8
Depressed anal	263	262	263	250	269	238	260	248	231	233	251.7
End of dorsal to caudal base	140	139	141	141	138	138	123	146	143	149	139.8
Length of: Caudal peduncle	191	193	197	183	188	190	193	224	190	209	195.8
Pectoral	227	211	210	210	209	209	204	213	192	195	208.0
Pelvic	211	190	194	186	188	184	190	181	177	172	186.3
Dorsal spine I	83	69	66	69	68	68	58	46	54	47	62.8
Dorsal spine III	169	152	152	153	157	148	152	127	129	117	145.6
Dorsal spine XI	129	121	119	131	112	103	104	105	99	93	111.6
Anal spine I	68	59	61	57	62	55	50	49	44	47	55.2
Anal spine II	144	123	126	114	116	112	120	100	90	85	113.0
Anal spine III	144	123	129	124	126	117	120	101	100	107	119.1
Caudal base to tip of upper rays	255	224	258	248	236	255	257	243	218	227	242.1
Caudal base to tip of middle rays	227	208	205	223	207	255	205	200	195	227	215.2
Caudal base to tip of lower rays	245	226	250	238	227	240	240	232	221	221	234.0

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-5, UMMI presumably from the vicinity of Miami, Florida; 6, USNM 125714; 7, MCZ 35132; 8, USNM 16795, a syntype; 9, FMNH 46778; and 10, USNM 25112. See text for data.

PAWNEE); off Pensacola, MCZ 35132 (292 mm., 1931, W. C. Schroeder); Dry Tortugas, ANSP 74872 (229 mm., 40 fa.); vicinity of Miami, sight record (January, 1957). Gulf of Mexico: USNM 125714 (118 mm., Sept. 20, 1930, U.S. Fish and Wildlife

Service); 29°14.5'N, 88°20'W, USNM 158597 (434 mm., Feb. 15, 1951, M/V OREGON); 29°16'N, 88°20'W, USNM 158621 (352 mm., Feb. 26, 1951, M/V OREGON); OREGON Stations 472-484, FMNH 46778 (420 mm., Sept. 6-7, 1951).

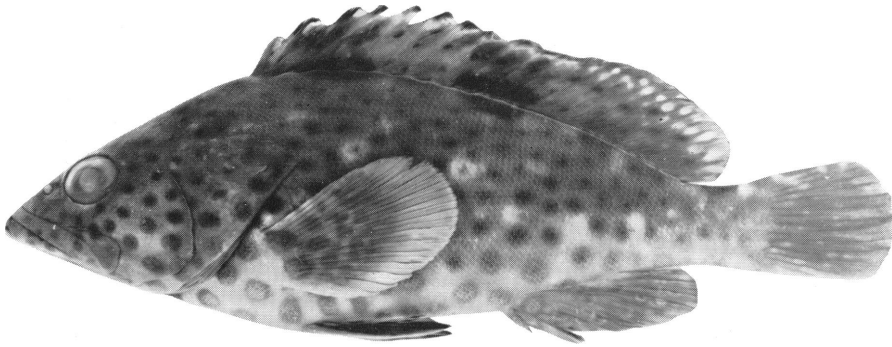


FIG. 21. *Epinephelus adscensionis*, AMNH field no. S63-6 from Bimini, Bahamas, 155 mm.

Bermuda: mounted specimen, Bermuda Government Museum.

Epinephelus adscensionis Species-Group

Epinephelus adscensionis and *E. analogus* both have spotted color patterns and a tendency toward a robust body shape. *Epinephelus analogus* reaches a large size, nearly a meter in length, and large individuals suggest *E. (Promicrops) itajara*. It does not, however, have the distinctive skull characteristics of *itajara*. Although they are well differentiated, *analogus* and *adscensionis* seem to be closely related. This group appears to be a natural one.

Epinephelus (Epinephelus) adscensionis

(Osbeck, 1771)

ROCK HIND

Figure 21

Perca tota maculis SEBA, 1758 (1734–1765), table 27.

Trachinus adscensionis OSBECK, 1771, p. 96 (original description, Ascension Is.). BONNATERRE, 1788, p. 46 (spelled *ascensionis*).

Perca adscensionis: BONNATERRE, 1788, p. 132.

Perca stellio WALBAUM, 1792, p. 349 (original description, after Seba).

Perca maculata BLOCH, 1792, pp. 92–93, pl. 313 (original description, Atlantic and Antilles).

Trachinus osbeck LACÉPÈDE, 1800 (1800–1803), p. 364 (original description, after Osbeck).

Serranus pixanga VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 383–384 (original description, after Marcgrave). POEY, 1865 (1865–1866), p. 203 (nomenclature).

Serranus nigriculus VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 375–376 (original description, Santo Domingo; Port-au-Prince). STORER, 1846, p. 280 (characters). GUICHENOT, 1853, p. 151.

?*Serranus luridus* RANZANI, 1840, pp. 356–359, pl. 36 (Brazil).

Serranus aspersus JENYNS, 1843, pp. 6–7 (original description, Porto Praya; St. Jago; Cape Verde Is.)

Serranus impetiginosus MÜLLER AND TROSCHEL, 1848, p. 665 (original description, Barbados). GÜNTHER, 1859, p. 142 (Trinidad); 1868, p. 225 (St. Helena).

Serranus capreolus POEY, 1860 (1858–1861), pp. 145–146 (original description, Cuba); 1866 (1866–1868), p. 201; 1867 (1866–1868), pp. 156–157.

VAILLANT AND BOCOURT, 1878 (1915), pp. 87–90. *Serranus varius* BOCOURT, 1868, p. 222 (original description, Gulf of Mexico; Central America).

Epinephelus impetiginosus: POEY, 1868 (1866–1868), p. 286 (Cuba); 1874, p. 34. JORDAN AND GILBERT, 1883a, p. 973. JORDAN AND EIGENMANN, 1890, p. 379.

Epinephelus punctatus (non Bloch): POEY, 1875 (1875–1877), p. 16; 1881, p. 319; 1883, p. 118. FOWLER, 1942b, p. 68 (name supposedly after Bonnaterre; Cuba).

Epinephelus atlanticus (non Lacépède): GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, p. 917.

Epinephelus capreolus: JORDAN AND GILBERT, 1883a, pp. 539–540.

Epinephelus ascensionis: JORDAN, 1884a, p. 78 (Key West). JORDAN AND SWAIN, 1885b, pp. 391–393. JORDAN, 1885b, p. 125; 1887a, p. 84; 1887c, p. 40 (Havana). BOULENGER, 1895, pp. 228–229. CUNNINGHAM, 1910, p. 97 (St. Helena). CLARK, 1916, p. 52. BARNARD, 1927, p. 481 (South Africa).

Epinephelus adscensionis: JORDAN, 1887e, p. 581 (West Indies). JORDAN AND EIGENMANN, 1890, pp. 354–355, pl. 60 (Bahía). HENSHALL, 1891, p. 387 (Key West). JORDAN, 1891, p. 319. HENSHALL, 1895, p. 216. SMITH, 1896, p. 175 (Biscayne Bay). JORDAN AND EVERMANN, 1896a, p. 372; 1896b, pp. 1152–1154. JORDAN AND RUTTER, 1898, p. 104 (Jamaica, copied). BRICE, 1898, p. 283. SMITH, 1899, p. 880 (Woods Hole). EVERMANN AND KENDALL, 1900, p. 73 (Florida records). SMITH, 1901, p. 390 (Katama Bay). EVERMANN AND MARSH, 1902,

p. 152, pl. 11 (Puerto Rico). JORDAN, 1905, p. 326, fig. 261. JORDAN AND THOMPSON, 1905, p. 239 (Tortugas). KENDALL, 1908, p. 97. JORDAN AND DICKERSON, 1908, p. 14 (Vera Cruz market). BLOSSER, 1909, p. 297 (St. Croix). NICHOLS, 1912, p. 187 (Havana market). SUMNER, OSBURN, AND COLE, 1913, pp. 167, 735 (Woods Hole). STARKS, 1913, p. 45 (Natal, Brazil). NICHOLS AND MURPHY, 1914, p. 263 (South Trinidad Islet). FOWLER, 1915b, pp. 533, 543 (Port-o-Spain, Trinidad; St. Georges, Grenada). METZELAAR, 1919, pp. 47, 232 (Willemstad, Curaçao; St. Eustacius). FOWLER, 1920, p. 150 (Nassau). JORDAN AND EVERMANN, 1920, pp. 382-383 (photograph). NICHOLS, 1921, p. 22 (Turks Is.). EVERMANN AND SEALE, 1924, p. 29 (Barbados). SCHROEDER, 1924, pp. 13-14 (Key West). MEEK AND HILDEBRAND, 1925, pp. 456-458 (Porto Bello, Panama). BREDER, 1925, p. 154 (Caledonia Bay, Panama). NICHOLS AND BREDER, 1927, p. 79, fig. 102 (Katama Bay). NICHOLS, 1929, pp. 249-250, fig. 114 (Puerto Rico). BREDER, 1929, p. 162. GUDGER, 1929, pp. 170-171 (Tortugas, ecology). PARR, 1930, p. 50 (Rum Cay, Boobie Rock, Tongue of the Ocean, Bahamas). JORDAN, EVERMANN, AND CLARK, 1930, p. 310. BEEBE AND TEE-VAN, 1933, p. 122 (Bermuda). BUTSCH, 1939, p. 23 (Barbados). LONGLEY AND HILDEBRAND, 1941, p. 93 (Tortugas). HERRE, 1942, p. 292 (Pelican Is., Barbados). BAUGHMAN, 1943, p. 770 (Texas Snapper Banks). MANTER, 1947, p. 371 (Tortugas, parasites). SMITH, 1949, p. 197, fig. 448 (Knysna to Cape of Good Hope). SCHULTZ, 1952, pp. 120-121 (Venezuela). SPRINGER AND BULLIS, 1956, p. 77 (Arcas Cay). RÖHL, 1956, p. 487, fig. 233 (Venezuela). BRIGGS, 1958, p. 272. SMITH, 1958, p. 52, pl. 9 (scarce in Bermuda). MOULTON, 1958, p. 369 (sounds produced by Bimini specimen). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:4, 1:11-1:12, 1:23, figs. 2.3, 12. RANDALL, 1963, p. 37 *et seq.* (Virgin Islands, ecology). RIVAS, 1964, p. 27 (characters). CALDWELL, 1966, p. 40 (Jamaica). CERVIGÓN M., 1966b, pp. 312-313, fig. 122 (Puerto Fermin, Cubagua, Venezuela). RANDALL, 1967, pp. 696-697 (food habits). BÖHLKE AND CHAPLIN, 1968, p. 281. RANDALL, 1968, p. 58, fig. 63 (general account, photograph).

Epinephelus aspersus: JORDAN AND EIGENMANN, 1890, p. 358 (after Jenyns).

Cerna adscensionis: MIRANDA-RIBEIRO, 1915, pp. 15-16; 1918, p. 85.

Serranus adscensionis: FOWLER, 1929a, p. 158 (Port-au-Prince).

?*Epinephelus analogus* (non Gill): BORODIN, 1934, p. 112 (Key West).

Serranus ascensionis: FOWLER, 1936, pp. 757-759, fig. 334.

Serranus punctatus: FOWLER, 1944, pp. 444, 465 (West

Indian records); 1953, p. 56 (Cartagena, Colombia).

NOMENCLATURE: The description of Osbeck is quite sufficient to fix the name of this species, and Fowler's action in rejecting his name in favor of Bonnaterre's *punctatus* seems unwarranted. Moreover, the name "*Trachine punctée*" is a common name and not available.

Osbeck's description made no mention of any specimens being kept and it is doubtful that the holotype is extant.

The trivial name *adscensionis* refers to Ascension Island, the type locality.

DIAGNOSIS: Small species of *Epinephelus* with moderate-sized eye, medium-sized scales, very robust body. Dorsal XI, 16-17 (18); anal III, 8; pectoral 19; gill rakers 25-28. Vertical fins rounded, dorsal interspinous membranes well notched. Skull crests well developed, only slightly convergent; supraethmoid forming floor of pit between anterior ends of frontals. Body light with large, dark, brownish red spots conspicuously larger ventrally. About three saddle-shaped blotches along base of dorsal fin and on top of caudal peduncle. Vertical fins without dark margins.

In the Atlantic only *E. guttatus* shares the pattern of reddish spots on a lighter background, but the red hind has smaller spots that are subequal throughout; the rock hind has larger spots increasing in size ventrally. Vertical fins of red hind have dark margins, but those of the rock hind do not. Rock hind has two or three dorsal saddle-shaped blotches; red hind has none. Relationship to Pacific *E. analogus* is close but that species has 10 dorsal spines and lacks dorsal saddles. *Epinephelus analogus* and *E. adscensionis* seem to be geminate species. *Epinephelus adscensionis* is unique in genus in consistently lacking scales on maxilla.

DESCRIPTION: Table 18 gives proportional measurements of 10 specimens of *E. adscensionis*. The robust body is reflected in body and head widths, as well as in the wide interorbital region. A length-weight relationship would demonstrate even more strikingly the difference in body form between this species and *E. guttatus* and its close relatives.

The exposed surface of the maxilla is scaleless. The posterior nostril is not enlarged, and the pectoral axillary flap is deeply indented posteriorly. The medial canines are only weakly developed. The fourth or fifth dorsal spine is

longest. The dorsal surface of the cornea has a pigmented point extending downward into the pupil. The preopercle has rounded, only slightly enlarged, teeth at its angle; the preopercular notch is a gentle indentation.

A specimen collected August 10, 1957, on the west side of North Bimini near Lerner Marine Laboratory, 130 mm. long, had the following color features: body and head greenish white shading to white below; everywhere covered with reddish brown spots, slightly lighter toward their margins but not definitely ringed with light red; spots largest below mid-side, smaller dorsally. A large black squarish spot below and on base of dorsal under last three spines and first two or three soft rays. A black saddle on top of caudal peduncle. Spinous dorsal with three rows of spots on membranes, the first just above the base, the second at middle of fin, and the third at edge of membranes and tips of spines. Flags on spinous dorsal membranes yellow. Soft dorsal like the spinous dorsal with lower row of spots on basal third and middle row of spots two-thirds of way out from base. Edge of dorsal lemon-yellow. Anal fin bluish with a row of four large red-brown spots along base. Two or three smaller spots near posterior margin. A black submarginal band equalling one-fourth of ray length with a narrow white margin. Pelvic with dusky blue membranes, five scattered large red spots, a dark submarginal band, and a narrow white marginal band. Ground color of pectoral like that of body. Two large red spots on prepectoral area. Base of pectoral rays with an oval, vertically elongate, red bar; beyond this, two rows of red-brown spots, six or seven in the first row and more in the outer row. Distal to these, a broad submarginal red-brown band covering one-third of ray length, surmounted by a yellow marginal band. Ground color of caudal fin like rest of body, densely covered with irregularly disposed large spots. Ground color shading to black submarginal band with narrow yellow marginal band. Iris yellow-brown.

The body spots in this species are usually without distinct dark centers. In a specimen taken at night from 45 feet at Arcas Cay there are definite dark centers in the spots above the mid-side of the body; the ventral spots have light centers and the dark spots in the dorsal fin are almost lacking. The marginal yellow band on the pectoral is much wider than in specimens

taken, as most have been, in shallow water during daylight hours. Sometimes white spots are scattered over the side of the body. The sleep pattern consists of irregular vertical bars.

In a 31 mm.-long specimen (USNM 170229) the preopercle has a single large, backward-pointing spine at the angle. The spots on the body are prominent but the dorsal saddles are not. The rounded tail, light fin margins, and robust body shape are distinguishable at this stage.

RELATIONSHIPS: *Epinephelus adscensionis* is widespread in the Atlantic Ocean and seems to represent a separate invasion of the West Indian area, for it has no really close relatives in the Western Atlantic fauna. In body proportions and color pattern it is similar to *E. merra* of the Indo-Pacific. *Epinephelus adscensionis* closely resembles the geminate species, *E. analogus* of the Pacific.

ECOLOGY: *Epinephelus adscensionis* was reported by Beebe and Tee-Van as an uncommon fish at Bermuda, perhaps because the temperature there is lower than optimum for the species. I did not collect specimens of this species there but one was on display in the Government aquarium and L. S. Mowbray assures me that their field collectors take them occasionally. Longley and Hildebrand (1941, p. 93) stated that in the Tortugas the species is found near coral stacks at depths of 10 to 15 feet. As this habitat type has been most thoroughly explored in Bermuda waters, I am sure that it is not common there. Its rarity, although possibly due to competition with *E. guttatus*, cannot be explained entirely on that basis as those authors reported that *guttatus* was the rarer species at Tortugas. The two species may be kept apart by some factor such as temperature tolerance, with *E. adscensionis* better adapted to more southern waters. I saw no rock hinds brought in at the Miami pier during the last week of January, but at least one specimen of *guttatus* was taken then by a party boat. In connection with the hypothesis that *adscensionis* is a fish of warmer water than is *guttatus*, Longley and Hildebrand reported that *E. guttatus* was found at medium depths at Key West. In Bermuda the same species is found in the shallows as well. The shallows at the Tortugas may be too warm for the red hind but well suited to the rock hind. In Bermuda, on the other hand, the cooler shallows may be well suited to the red hind. In Bimini the red hind, *E. guttatus*, is by far

the more common, as indicated by the catches of persons connected with the Lerner Marine Laboratory. It seems to be taken there in waters 30 feet or more in depth, but I did not see it among rocks close in on the west side of North Bimini when I collected *E. adscensionis* close to shore in waters only a meter or so deep.

As the common name suggests, *Epinephelus adscensionis* is a fish of rocks. I chased one small individual with a net and test tube for several minutes on each of two successive days until it finally sought shelter in a crevice, one entrance of which I blocked with the test tube while poking with a wire from the other end. During the chase, the fish repeatedly entered deep crevices where it was safe from capture, then would reappear a few minutes later allowing the chase to continue. Another individual taken from among the timbers of a wrecked ship lying in about 15 feet of water repeatedly ventured from a hole as I surfaced for air. As I approached the fish, it withdrew, but upon my retreat it came out to full view.

Apparently members of this species have well-established home ranges. An individual was seen to take shelter under the same rock on July 21, July 25, and August 6 (the area was not visited between these dates). On the last day the rock was disturbed in an unsuccessful attempt to capture the fish and it was not seen after that.

Moulton (1958) described sounds produced by this species as similar to those made by *Epinephelus striatus*.

DISTRIBUTION: This is one of the few wide-ranging groupers in the Atlantic, having been reported from the Azores, Canary Islands, Ascension Island, and south to the Cape of Good Hope. In the western part of its range it is known from Katama Bay, Massachusetts, and Bermuda, south through the Bahamas, the Antilles, and the Gulf of Mexico, and along the northern coast of South America to Brazil (fig. 22).

SPECIMENS EXAMINED

Massachusetts: Katama Bay, USNM 58857.
 Florida: Key West, USNM 26574, 26581, 34894, 47350; FMNH 1915; Pensacola, USNM 32635; Loggerhead Key, USNM 74400; no specific locality, MCZ 2830, 10127.
 Texas: within 50 miles of Corpus Christi, FMNH 40261.
 Gulf of Mexico: Arcas Cay, FMNH 45481;

UMMZ 174035; East Triangles Reef, FMNH 46441; Mexico City market, USNM 62267.

Caribbean: Serrana Bank, FMNH.

Panama: Portobelo, USNM 80293.

Venezuela: Pt. Macolla, Gulf of Venezuela, USNM 123133.

Brazil: Maceió, FMNH 3853, 3827; Recife (Pernambuco), USNM 104272; Bahía, USNM 43340; MCZ 10037; Río Grande do Norte, MCZ 9970; Río de Janeiro, MCZ 954; Natal, AMNH 3778.

Barbados: USNM 120766.

Dominica: USNM 170229.

Puerto Rico: Guanica, FMNH; Mona Island, FMNH; Playa de Ponce, USNM 50102.

Haiti: Port-au-Prince Bay, USNM 131204.

Cuba: reef flat between Cayo Hutia Light and Little Cay, northeast of light, USNM 82430; no specific locality, USNM 9803; MCZ 10110, 9996.

Bahamas: Cay Sal Bank, UMIM; Rum Cay, BOC 2306; New Providence and vicinity, CBC Stations 175, 182, 206, 207, 219, 230, 243, 250, 251, 263, 381; CBC lots 103, 111, 118, 150, 169, 173; ANSP 72424-27, 72618-19; Bimini, UMMZ 174378-S, 174379-80, 174392.

Bermuda: MCZ 3037.

***Epinephelus (Epinephelus) analogus* Gill, 1864** SPOTTED CABRILLA

Epinephelus analogus GILL, 1864b, p. 163 (original description, west coast of America). JORDAN AND GILBERT, 1882, p. 232 (Acapulco); 1883b, p. 107 (Mazatlán); 1883c, p. 110 (Panama); 1883g, p. 375 (Panama); 1883h, p. 625 (Panama). JORDAN AND SWAIN, 1885b, pp. 393-394. JORDAN, 1886b, p. 377 (Acapulco; La Unión; Mazatlán; Panama); 1887a, p. 84. JORDAN AND BOLLMAN, 1890, p. 181 (Charles Is., Galápagos). JORDAN AND EIGENMANN, 1890, p. 354. EVERMANN AND JENKINS, 1892, p. 144 (Guaymas). BOULENGER, 1895, p. 228 (Los Penas, Jalisco; Panama). JORDAN, 1895, p. 444 (Mazatlán). JORDAN AND EVERMANN, 1896a, p. 372; 1896b, p. 1152. JORDAN AND MCGREGOR, 1899, p. 278 (Clarión Is.). BOULENGER, 1899, p. 2 (Gulf of Panama). GILBERT AND STARKS, 1904, p. 96 (Panama Bay). SNODGRASS AND HELLER, 1905, p. 367 (Charles Is.; Clarión Is.). KENDALL AND RADCLIFFE, 1912, p. 107 (Panama). JORDAN AND EVERMANN, 1920, p. 382. MEEK AND HILDEBRAND, 1925, p. 454 (Balboa, Panama). JORDAN, EVERMANN, AND CLARK, 1930, p. 310. BREDER, 1936, p. 21. WALFORD, 1937, pp. 107-108, pl. 61, fig. a. HIYAMA, 1937, p. 38, pl. 67. SCHMITT AND SCHULTZ, 1940,

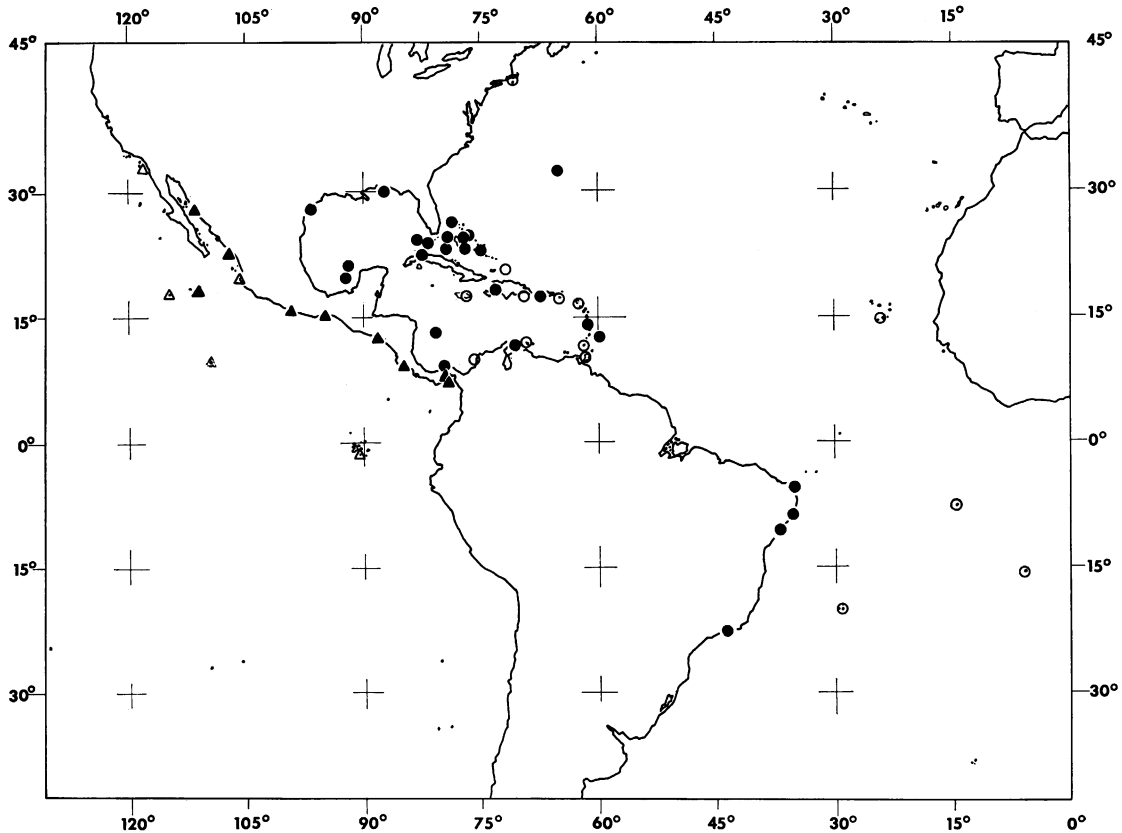


FIG. 22. Distribution records for *Epinephelus adscensionis* (circles) and *E. analogus* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

p. 5 (Socorro Is.). BERDEGUE A., 1956, pp. 277-278, fig. 188. BAILEY ET AL., 1960, p. 25 (common name).

Serranus courtadei BOCOURT, 1868, pp. 222-223 (original description, La Unión, El Salvador). VAILLANT AND BOCOURT, 1878 (1915), pp. 80-83, pl. 2, figs. 3, 3a.

Serranus analogus: GÜNTHER, 1869, pp. 410-411. STEINDACHNER, 1876, p. 555 (Acapulco; Mazatlán; Panama). FOWLER, 1944, pp. 172, 262, pl. 9 (Balboa, Ensenada Honda, Panama).

NOMENCLATURE: The type specimen, USNM 4944, is 250 mm. long and was collected by J. M. Dow on the west coast of Panama. The name *analogus* (Latin), similar, refers to its strong resemblance to *Epinephelus adscensionis*.

DIAGNOSIS: Small species of *Epinephelus* with moderate-sized eye and scales. Body rather robust. Nostrils subequal. Dorsal X, 17-18; anal III, 8; pectoral (19)-20; gill rakers 26-28. Skull crests well developed, convergent anteriorly;

supraethmoid forming floor of pit between anterior parts of frontals. Body ground color light, covered with dark red spots; no saddle-shaped blotches along back; no dark edges on fins; often with pattern of dark, transversely oblique bars.

Of the several species of *Epinephelus* in the Eastern Pacific, only *analogus* has a pattern of red or red-brown spots on lighter red or tawny background. It differs from most other species of *Epinephelus* in having only 10 dorsal spines. *E. analogus* resembles, and is a twin of the Atlantic *E. adscensionis*, but differs in color pattern, especially in lacking dorsal saddle-shaped blotches, in spine count, and in having scales on the maxilla.

DESCRIPTION: Proportional measurements are given in table 19. In general body shape it is close to *E. adscensionis*.

The dorsal membranes are notched between the spines. The posterior nostril is little en-

larged. The preopercle has a shallow indentation above the angle; the serrations at the angle are little enlarged. The dorsal, anal, and caudal lobes are rounded; the caudal is gently convex. The frontal pit is an extremely shallow depression; there is no supraethmoid wall.

The short lateral crests end well behind the postorbital processes. The exposed surface of the maxilla is scaled.

I have not seen this species alive; in alcohol the ground color is yellowish brown and the spots are dark brown or black. As in *E. adscensionis*

TABLE 18
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus adscensionis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	63.5	75	119	128	223	226	238	247	264	273	—
Head length	425	407	387	391	439	429	439	415	415	419	416.6
Head width	181	147	147	145	247	195	206	206	199	212	182.0
Head depth	251	229	218	211	209	247	252	249	241	249	235.6
Snout length	102	87	97	90	103	100	99	103	104	103	98.8
Suborbital width	24	27	34	31	36	40	36	40	42	40	35.0
Interorbital width	55	53	50	55	76	60	59	57	59	62	58.6
Length of: Orbit	94	93	81	82	83	82	80	73	66	75	80.9
Postorbital head	236	235	231	230	260	263	269	259	254	260	249.7
Maxillary	197	193	181	172	188	186	189	188	186	189	186.9
Lower jaw length	205	187	176	180	202	197	191	198	188	200	192.4
Snout to angle of preopercle	299	289	269	266	287	288	288	281	284	282	283.3
Supramaxillary length	55	67	55	—	52	58	57	59	63	46	56.9
Maxillary width	47	47	42	43	45	40	44	43	44	44	43.9
Tip of lower jaw to gular notch	118	129	139	113	128	115	145	126	146	139	129.8
Body width	173	149	151	164	211	175	181	182	191	181	175.8
Body depth	331	323	307	297	350	332	317	334	356	330	327.7
Caudal peduncle depth	110	127	109	113	121	119	113	111	119	110	115.2
Tip of snout to dorsal origin	394	363	366	355	415	394	395	387	386	388	384.3
Tip of snout to pectoral base	370	367	353	375	357	363	368	366	371	374	366.4
Tip of lower jaw to pelvic base	409	424	399	379	415	420	427	417	434	436	416.0
Length of: Dorsal base	654	607	567	586	628	582	578	583	591	575	595.1
Depressed dorsal	654	680	630	652	628	664	640	651	672	636	650.7
Anal base	173	193	189	184	152	186	164	168	165	176	175.0
Depressed anal	299	313	319	305	271	308	269	277	282	278	292.1
End of dorsal to caudal base	102	107	105	113	110	108	109	111	98	104	106.7
Length of: Caudal peduncle	181	193	193	195	177	197	191	196	170	187	188.0
Pectoral	268	260	235	242	222	235	218	223	222	220	234.5
Pelvic	213	215	189	191	173	184	181	178	182	176	188.2
Dorsal spine I	79	75	71	59	58	66	63	57	51	62	64.1
Dorsal spine III	157	153	139	129	135	133	122	123	117	123	133.1
Dorsal spine XI	142	135	130	125	108	117	107	99	108	106	117.7
Anal spine I	79	80	80	59	56	66	61	61	47	55	64.4
Anal spine II	165	155	151	129	108	119	107	101	100	103	123.8
Anal spine III	150	155	147	129	112	133	120	115	119	108	128.8
Caudal base to tip of upper rays	236	249	223	227	222	228	227	223	216	220	227.1
Caudal base to tip of middle rays	244	260	231	254	220	243	214	231	231	222	235.0
Caudal base to tip of lower rays	228	259	231	227	229	226	216	223	218	218	227.5

^aAll proportions are expressed in thousandths of the standard length. Locality data are as follows: Columns 1, 5, FMNH 46441, East Triangles; 2-4, 9, UMMZ 557141, 174392, 174378, 194380 respectively from Bimini; 6, 7, 10, UMIM, Anguilla Island, Cay Sal Bank; 8, UMIM from Miami.

sionis, the spots cover the entire head and body and diminish in size dorsally. There are about five faint vertical bars that slope downward and forward; each is about twice the breadth of a body spot. The spots extend onto the bases of all fins. The soft dorsal, anal, and caudal fins

are darker toward their margins. The underside of the head and body is unspotted. The pelvic fins are very dark on the distal half.

RELATIONSHIPS: *Epinephelus analogus* closely resembles *E. adscensionis*, and the two species are probably geminate. They are well differen-

TABLE 19
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus analogus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	53	59.5	80.5	103	127.5	128	161	174	246	250	—
Head length	415	403	385	417	408	410	401	405	413	426	408.3
Head width	170	176	174	184	176	195	199	207	199	189	186.9
Head depth	245	269	248	238	243	250	258	253	248	256	250.8
Snout length	94	84	81	92	94	94	93	89	91	94	90.6
Suborbital width	23	25	31	29	27	35	31	32	37	38	30.8
Interorbital width	66	67	56	58	63	78	68	66	77	76	67.5
Length of: Orbit	94	101	81	83	82	74	75	80	73	76	81.9
Postorbital head	245	235	224	248	239	238	258	253	262	272	274.4
Maxillary	189	185	174	180	184	180	177	190	189	192	184.0
Lower jaw	189	193	174	189	184	184	177	193	191	198	187.2
Snout to angle of preopercle	302	294	273	286	286	281	280	284	283	296	286.5
Supramaxillary length	66	59	56	58	59	55	40	55	53	58	55.9
Maxillary width	47	42	37	44	43	39	40	46	41	44	42.3
Tip of lower jaw to gular notch	104	109	106	107	133	129	124	118	106	108	114.4
Body width	142	134	155	160	169	191	193	175	171	176	166.6
Body depth	340	336	320	359	329	375	342	330	354	346	343.1
Caudal peduncle depth	113	118	136	117	114	133	115	115	114	120	119.5
Tip of snout to dorsal origin	387	378	360	388	369	363	357	368	368	392	373.0
Tip of snout to pectoral base	377	361	354	359	369	344	342	345	346	378	357.5
Tip of lower jaw to pelvic base	387	387	373	388	404	398	382	382	378	416	389.5
Length of: Dorsal base	585	597	553	607	592	602	612	601	618	588	595.5
Anal base	179	176	180	175	180	191	174	175	171	174	177.5
Depressed anal	330	319	304	311	314	328	307	310	280	302	310.5
Depressed dorsal	679	689	646	704	698	684	702	672	675	654	680.3
End of dorsal to caudal base	113	118	112	121	118	117	112	109	110	108	113.8
Length of: Caudal peduncle	198	193	199	180	204	207	205	207	199	210	200.2
Pectoral	249	244	230	257	227	234	227	236	217	218	233.9
Pelvic	198	218	174	204	200	195	189	193	179	184	193.4
Dorsal spine I	85	76	—	63	71	47	62	63	57	68	65.7
Dorsal spine III	160	151	149	136	153	125	121	129	134	132	139.0
Dorsal spine X	123	123	124	126	133	117	118	112	112	112	120.0
Anal spine I	66	67	75	83	59	55	50	60	47	46	60.8
Anal spine II	123	118	124	150	129	109	109	98	89	98	114.7
Anal spine III	123	118	118	136	137	117	115	109	114	108	119.5
Caudal base to tip of upper rays	245	227	230	252	251	234	236	241	228	248	239.2
Caudal base to tip of middle rays	245	244	242	267	263	250	255	253	242	240	250.1
Caudal base to tip of lower rays	226	227	230	233	235	227	233	239	220	244	231.4

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-5 and 7, USNM 80225; 6 and 8, USNM 128772; 9, USNM 41181; 10, USNM 4944. For data see text.

tiated; *analogus* has one less dorsal spine, one more pectoral ray, and no dorsal blotches.

ECOLOGY: *Epinephelus analogus* was taken commonly by Meek and Hildebrand in tide pools on the Pacific coast of Mexico. Walford (1937, p. 108) stated that it occurs over sandy bottom as well as about rocks. Several species of groupers in the Pacific are taken in tide pools, a habitat little utilized in the Atlantic, presumably because the greater tidal rise of the Pacific isolates larger pools at low tide.

This species is reported to have considerable commercial importance.

DISTRIBUTION: *Epinephelus analogus* is known from the Gulf of California to Panama and from Socorro and the Galápagos Islands (fig. 22).

SPECIMENS EXAMINED

Mexico: Salina Cruz, FMNH; southern Chiapas coast, FMNH; Mazatlán, USNM 101002, 28256; Bahía Topolobampo, UCLA W51-16, W51-18; entrance to Bahía Topolobampo, UCLA W56-118; south of Bahía Topolobampo, UCLA W58-46, W58-47; San Felipe, UCLA W50-188; Sonora, Guaymas harbor, UCLA W52-30; Guaymas, USNM 101020, 119845; Puerto Libertad, LACM W50-65; Acapulco, USNM 28235; FMNH; MCZ 28782; Bahía Almejas, UCLA W55-96; Durango, UMMZ 173657; Nayarit, Bahía Matenchen, UCLA W58-38; Isla Socorro, USNM 107070.

El Salvador: Cutuco, USNM 87340.

Costa Rica: Puntarenas, FMNH 7897.

Panama: Farfan Beach, USNM 128763; Taboga Island, USNM 128769; Venado Beach, USNM 128772; Chame Point, USNM 82230; Archipiélago de las Perlas, ANSP 82199; Panama City, USNM 78111, 80223-24, 128764; Panama City fish market,

UCLA W53-270; Golfo de Panama, Chiman, UCLA W53-317; Canal Zone, Balboa dock, UCLA W58-127; Balboa, USNM 80225, 128771; no specific locality, FMNH 20536-38, 20539-49, 20530-35; USNM 30993, 29284, 41181, 41426, 41447, 80263-65, 80268, 80288-89; MCZ 10101, 10113, 22265, 29649, 2838.

Central America: west coast, USNM 4944 (holotype).

SUBGENUS *PROMICROPS* GILL, 1868

Promicrops GILL, in Poey, 1868 (1866-1868), p. 287 (type species, *Serranus guaza* Poey [a subjective synonym of *Serranus itajara* Lichtenstein], by monotypy).

Itaiara VAILLANT AND BOCOURT, 1878 (1874-1915), p. 70 (type species *Serranus itajara* Lichtenstein, by monotypy [proposed as a subgenus]).

Epinephelus itajara and its Indo-Pacific counterpart *lanceolatus* are highly specialized and distinctive although their alliance with other species of *Epinephelus* is clear. On the basis of general body form they seem to be related to the widespread *Epinephelus tauvina* but this has yet to be confirmed. Most of the features that distinguish the subgenus *Promicrops* are associated with a broadening and depressing of the head and body. As a result, the neurocranium is flattened and reinforced so that the frontal and pterosphenoid bones come into contact with the dorsal part of the parasphenoid. Perhaps even more striking is a heavy strut of bone connecting the posterior face of each lateral ethmoid with the shaft of the parasphenoid (fig. 17). I have not found this in any other species of grouper. In conjunction with the depression of the skull the dorsal crests have been reduced to low ridges. Although these are not major differences, the general distinctness of the species leads me

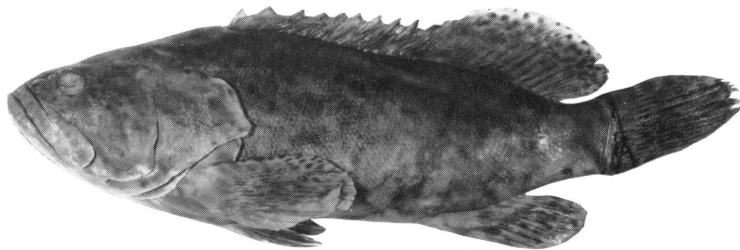


FIG. 23. *Epinephelus itajara*, UMMZ 155054 from Lemon Bay, Florida, 248 mm. Photograph by W. L. Brudon, courtesy Bermuda Fisheries Research Program.

to treat them as a rather weakly differentiated subgenus.

Epinephelus (Promicrops) itajara

(Lichtenstein, 1822)

JEWFISH
Figure 23

- Cugupuguacu* MARCGRAVE, 1648, p. 169 (Brazil). CATESBY, 1743, p. 14.
- Jewfish* BROWNE, 1756, p. 448 (Jamaica).
- Serranus itajara* LICHTENSTEIN, 1822, pp. 278–279 (original description, Brazil). PETERS, 1866, p. 110 (*S. galeus* a synonym).
- Serranus itaiara* (emended spelling): VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 376–377. VAILLANT AND BOCOURT, 1878 (1915), pp. 90–94, pl. 1, fig. 4; pls. 2, 4, 4a.
- Serranus galeus* MÜLLER AND TROSCHER, 1848, p. 621 (original description, British Guiana). GÜNTHER, 1859, p. 130 (after Müller and Troschel).
- Serranus guaza* (not of Linnaeus): POEY, 1861 (1858–1861), pp. 141–142, 354, pl. 13, fig. 8 (Cuba).
- Serranus quinquefasciatus* BOCOURT, 1868, p. 223 (original description, Pacific coast of Guatemala).
- Promicrops guaza*: POEY, 1867 (1866–1868), p. 154; 1868 (1866–1868), p. 287 (Cuba); 1874, p. 34. GILL, 1873, p. 806. POEY, 1875 (1875–1877), p. 18. GOODE, 1879, p. 50 (Key West). POEY, 1883, p. 118. JORDAN AND GILBERT, 1883a, p. 920 (“may be old *nigritus*”). JORDAN, 1887a, p. 84.
- Epinephelus quinquefasciatus*: JORDAN AND GILBERT, 1883b, p. 106 (Mazatlán); 1883c, p. 110 (Panama). GILBERT, 1883, p. 112 (Puntarenas).
- Epinephelus guaza*: GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). BEAN, 1884, p. 503.
- Epinephelus itaiara*: JORDAN, 1884a, p. 78; 1885b, p. 124 (Key West). BOULENGER, 1895, p. 252.
- Promicrops itaiara*: JORDAN AND SWAIN, 1885b, pp. 377–379. JORDAN, 1886b, p. 377 (Punta Arenas, TanESCO); 1887a, p. 84; 1887c, p. 40 (Havana); 1887e, p. 580. JORDAN AND EVERMANN, 1900, p. 3197. JORDAN, 1905, p. 323, fig. 257. JORDAN AND EVERMANN, 1920, p. 387 (photograph). NICHOLS, 1921, p. 22 (Turks Island). SCHROEDER, 1924, pp. 15–16, fig. 10 (Key West, Knights Key). MEEK AND HILDEBRAND, 1925, pp. 450–451. BEEBE AND TEE-VAN, 1928, pp. 130–131 (Port-au-Prince). BREDER, 1929, p. 162. JORDAN, EVERMANN, AND CLARK, 1930, p. 312. PARR, 1930, p. 50 (West Caicos Is.). BEEBE AND TEE-VAN, 1933, p. 126 (Bermuda). BREDER AND NIGRELLI, 1934a, pp. 162–164 (eel cyst in viscera). WALFORD, 1937, pp. 114–115, pl. 14, fig. a. HOWELL Y RIVERO, 1938, pp. 190–191 (Poey’s types of *Serranus guaza* are this species). HILDEBRAND, 1939, pp. 27, 39 (Gatun and Miraflores Locks). LONGLEY AND HILDEBRAND, 1941, p. 97 (Tortugas). REED, 1941, p. 76 (Texas). FOWLER, 1942b, p. 68 (Cuba). BAUGHMAN, 1943,

- pp. 771–772 (Texas coast). FOWLER, 1944, pp. 444, 465 (West Indian records). NICHOLS AND MURPHY, 1944, p. 247 (Credo, Colombia). MANTER, 1947, p. 371 (Tortugas, parasites). FOWLER, 1953, p. 56 (Cartagena). CALDWELL, 1954, p. 183 (Cedar Key). HILDEBRAND, 1954, pp. 303–304 (Obregón, Mexico; Padre Is., Texas). ERDMAN, 1957, p. 330 (Puerto Rico, lobsters in stomach). SPRINGER AND BULLIS, 1956, p. 78 (Gulf of Mexico). RÖHL, 1956, p. 487 (Venezuela). BRIGGS, 1958, p. 273. SMITH, 1958, p. 46, pl. 6 (not seen in Bermuda). MOULTON, 1958, p. 369 (no sounds from captive specimen). SMITH, 1959, p. 114 (hermaphroditic).

Epinephelus galeus: JORDAN, 1884b, p. 285.

- Promicrops guttatus* (non Linnaeus): JORDAN AND EIGENMANN, 1890, pp. 363–364, pl. 62 (Brazil). EVERMANN AND JENKINS, 1892, p. 143 (Guaymas, Mexico). HENSHALL, 1895, p. 215 (Key West). JORDAN, 1895, p. 444 (Mazatlán). JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1162–1164. EVERMANN AND BEAN, 1897, p. 244 (Indian River, Florida). BRICE, 1898, p. 283. JORDAN AND RUTTER, 1898, p. 105 (Jamaica). EVERMANN AND KENDALL, 1900, p. 74. JORDAN AND EVERMANN, 1900, pl. 185, figs. 485a, b, and c. GILBERT AND STARKS, 1904, p. 96 (Panama Bay). JORDAN AND THOMPSON, 1905, p. 240 (Tortugas). BEAN, 1906, p. 52 (Bermuda, after Townsend). FOWLER, 1906, p. 97. STARKS, 1913, p. 45 (Para, Brazil). FOWLER, 1915a, p. 249 (Stuart, Boca Grande Pass, Florida). MIRANDA-RIBEIRO, 1915, pp. 13–14 (Brazil); 1918, pp. 84–85. FOWLER, 1927, p. 252 (Captiva Pass, Fort Myers, Florida). BORODIN, 1928, p. 19. GUDGER, 1929, pp. 172–173, pl. 4, fig. 1 (Tortugas). HILDEBRAND, 1946, p. 171 (Callao, Peru). BERDEGUE A., 1956, pp. 282–283 (Mexico).

Epinephelus nigritus (non Holbrook): HENSHALL, 1891, p. 387 (Florida). LÖNNBERG, 1894, p. 124 (Key West). SMITH, 1896, p. 175 (Key Biscayne Bay).

Garrupa nigrita (non Holbrook): TAYLOR, 1919, p. 9, pl. 111 (killed in Florida).

Promicrops quinquefasciatus: JORDAN, EVERMANN, AND CLARK, 1930, p. 312.

Promicrops itajara: SCHULTZ, 1952, p. 121.

Epinephelus itajara: BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:1, 1:4, 1:12–1:13, 1:23, fig. 11. RIVAS, 1964, p. 25 (characters), CALDWELL, 1966, p. 41 (Jamaica, compiled). CERVIGÓN M., 1966b, pp. 313–314, fig. 123 (Porlamar, Punta de Piedres, Venezuela). RANDALL, 1967, p. 698 (food habits); 1968, pp. 60–61, fig. 66 (general account). BÖHLKE AND CHAPLIN, 1968, p. 283 (Bahamas).

NOMENCLATURE: Although Linnaeus’s *Perca guttata* may have been based partly upon the jewfish, I am following current practice and applying the name *guttatus* to the red hind, for

reasons given in the account of that species.

Serranus itajara Lichtenstein was based on a specimen which he thought was the *Itaiara* of Marcgrave. According to Jordan and Evermann (1896b, p. 1164), it is not. The specific name is commonly amended to *itaiara*, but I employ the original spelling.

I am unable to determine whether Lichtenstein's type is still in existence.

DIAGNOSIS: Very large species of *Epinephelus* with small eye, medium-sized, very rugose scales (in adult), and thick, almost terete, body. Dorsal XI, 15-16; anal III, 8; pectoral 19; gill rakers 22-24. Vertical fins rounded, dorsal spines short with interspinous membranes well notched. Skull crests weakly developed, low with frontoparietal crests converging anteriorly. Supraethmoid expanded transversely to form wall anterior to frontals. Head and body above with small black spots. Young with oblique, irregular vertical bars, adults nearly uniform gray or greenish.

The jewfish is largest of western North Atlantic groupers, readily distinguishable from all other species by its nearly terete shape, short dorsal spines, short canine teeth, and distinctive coloration; head extremely broad and flat, eyes small.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 20. This species is extreme in interorbital width, the low body, small allometric eye, short dorsal spines, and wide body and head. The pyloric caeca are exceedingly numerous and repeatedly branched.

The dorsal spines become tuberculate, the scales excessively roughened in large individuals. The dorsal and anal lobes are rather angulate in young but become rounded with age. The caudal fin is rounded at all sizes. There are prominent scales on the maxilla. The canine teeth are short and nearly indistinguishable from the smaller caniniform teeth which are strong and heavy. The lateral skull crests are obsolescent; the skull is extremely broad and flat with the median crest quite low and extending forward to just behind the orbit. There is a well-developed supraethmoid wall and the ascending process of the premaxilla is correspondingly shortened.

Large jewfish are gray or greenish with small, more or less distinct, black spots scattered over the upper parts of the head, body, and pectoral fin. Individuals under 3 feet long are greenish

or tawny, crossed by irregular but distinctly outlined bands. A specimen 107 mm. long from Shark River, Florida, is colored as follows: top of head and snout, suborbital region, and upper part of cheek dusky, irregularly spotted with small and medium-sized spots, especially along the edge of the preopercle. Upper lip dark at tip, crossed behind this by three dark lines. Two black spots on maxilla. Behind the head two vertical dark bars extend downward from the spinous dorsal, converge at the level of the upper margin of the pectoral, and become narrower below. A broad dark bar extends upward from the front of the anal fin to the margin of the anterior part of the soft dorsal; another runs from above the base of the posterior anal rays upward to edge of the posterior part of the soft dorsal fin. Dark bars cross the caudal peduncle just behind the dorsal and anal fins and at the end of the caudal peduncle; another lies on the basal third of the caudal fin. On each vertical bar there are several dark spots. Distal part of caudal fin with several irregularly placed black spots, each surrounded by a dusky circle in a darker background.

Dorsal fin crossed by extensions of body bars and with prominent black spots just above the bases of membranes two, three, four, seven, eight, nine, and 10. Anal fin dusky throughout with body cross bars extending onto the anterior and posterior parts, these dark bars connected at their distal ends by a dark marginal band on posterior anal rays. Pectoral crossed by four more or less regular rows of spots, otherwise pale. Pelvic dusky throughout with two dark spots near base. Underparts of head and body lighter, without conspicuous markings.

This species reaches a weight of more than 700 pounds; the rod and reel record is 693 pounds.

RELATIONSHIPS: Although *itajara* and the Indo-Pacific *lanceolatus* have long been considered as constituting a distinct genus, *Promicrops*, I believe that the characters that distinguish them from *Epinephelus* are not sufficiently distinctive to merit generic status. The terete body, excessively widened head, small eye, and rugose scales, common characters of these species, are all differences of degree. There is some question as to the specific distinctness of *itajara* and *lanceolatus*. On the basis of published illustrations of color pattern of young fish (e.g., that of Smith, 1949) the species appear to be

distinct. *Epinephelus itajara* has no close relatives in American waters. The record of *Promicrops itajara* from Siam (Smith, 1933, pp. 85-86) seems not to be *E. itajara* (Lichtenstein). I have been unable to determine the status of *Promicrops ditobo* Roux and Collignon (1954).

The eye size in *Epinephelus itajara* is strongly allometric, perhaps a reflection of the wide size range of study material. Other than a few proportions, including the longer dorsal spines, and more vivid coloration, juveniles as small as 87 mm. are not grossly different in appearance from adults.

ECOLOGY: In spite of its great size, the jewfish is an inhabitant of the shallow shore zone. In Florida it is often taken around docks and bridges and on set lines made fast to mangrove trees. A large portion of its food consists of crustaceans. Erdman (1957) and Longley and Hildebrand (1941) reported finding spiny lobsters in the stomachs, and two individuals from the Campeche Bank contained large

numbers of *Callinectes* or an allied crab. Presumably the poor development of canine teeth is a reflection of the crustacean diet although the jewfish will take fish bait.

Moulton (1958, p. 369) was unable to elicit sounds from a captive specimen at Bimini.

There is an indication that sex reversal occurs; the gonad of a 6-foot-long male from Bimini contained remnants of many ova.

DISTRIBUTION: The jewfish is known from both sides of Central America. In the Pacific it has been recorded from Puntarenas, Costa Rica, to Peru, and in the Atlantic from Florida throughout the Gulf of Mexico to Panama, Venezuela, Colombia, and Brazil. It is also known from Haiti, Cuba, Jamaica, Puerto Rico, and the Bahamas (fig. 24).

SPECIMENS EXAMINED

ATLANTIC RECORDS

Florida: Indian River Inlet, USNM 68437; off New Smyrna, USNM 62654; Key West,

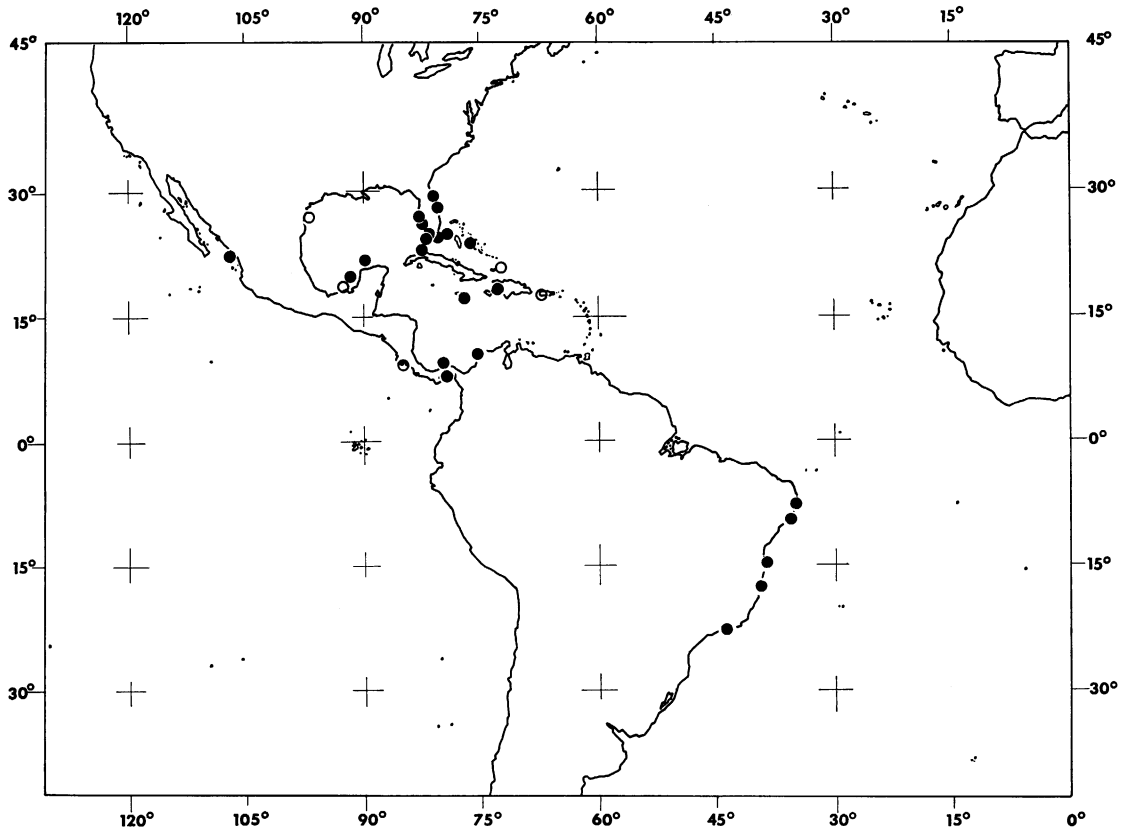


FIG. 24. *Epinephelus itajara* distribution records. Solid circles represent specimens examined, open circles are additional literature records.

TABLE 20
 PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus itajara*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	63	107.5	151	180	197	221	230	242	279	1602	—
Head length	428	400	401	414	419	421	415	413	419	345	407.5
Head width	214	186	172	208	213	208	204	217	235	202	205.9
Head depth	262	247	255	261	244	240	250	240	249	224	247.2
Snout length	95	84	86	94	87	88	87	83	97	73	87.4
Suborbital width	24	19	26	25	23	25	26	27	25	28	24.8
Interorbital width	63	74	70	86	74	81	83	81	91	93	79.6
Length of: Orbit	87	74	70	58	61	61	61	58	50	27	60.7
Postorbital head	270	251	265	272	284	281	278	285	283	255	272.4
Maxillary	198	186	199	192	193	201	196	198	159	169	189.1
Lower jaw	206	181	205	194	198	201	207	205	201	175	197.3
Snout to angle of preopercle	294	279	285	—	294	—	291	289	287	248	283.5
Supramaxillary length	71	65	56	61	66	59	57	66	66	49	61.6
Maxillary width	48	42	46	44	42	45	43	43	43	39	43.5
Tip of lower jaw to gular notch	151	121	116	131	135	—	113	118	136	119	125.7
Body width	183	172	175	206	180	188	189	209	226	206	193.4
Body depth	349	321	331	361	340	292	335	306	332	313	328.0
Caudal peduncle depth	127	130	126	136	129	127	130	124	129	131	128.9
Tip of snout to dorsal origin	397	372	387	378	393	389	396	384	369	341	380.6
Tip of snout to pectoral base	429	367	368	378	386	391	363	368	366	343	375.9
Tip of lower jaw to pelvic base	476	405	404	411	421	439	404	399	409	398	416.6
Length of: Dorsal base	532	563	573	561	566	532	528	556	570	513	549.4
Depressed dorsal	619	651	692	672	650	615	613	649	652	561	637.4
Anal base	175	177	166	175	162	165	167	163	179	159	168.8
Depressed anal	317	288	311	311	297	294	283	287	303	240	293.1
End of dorsal to caudal base	103	130	106	111	127	111	111	118	115	141	117.3
Length of: Caudal peduncle	167	172	175	178	152	186	187	174	186	185	176.2
Pectoral	254	233	238	228	234	219	228	221	231	185	227.1
Pelvic	206	195	192	192	183	183	176	182	188	142	183.9
Dorsal spine I	55	56	60	53	58	52	48	52	54	22	51.0
Dorsal spine III	143	112	123	94	112	104	109	103	90	93	108.3
Dorsal spine XI	135	121	116	108	112	100	104	99	100	62	105.7
Anal spine I	71	56	50	53	53	52	54	50	54	17	51.0
Anal spine II	135	121	123	103	102	—	—	97	95	31	101.1
Anal spine III	135	121	113	114	102	124	109	105	108	49	108.0
Caudal base to tip of upper rays	254	256	225	219	228	222	239	223	197	171	223.4
Caudal base to tip of middle rays	262	256	275	258	249	260	261	244	251	289	250.5
Caudal base to tip of lower rays	246	242	219	211	223	231	220	219	204	189	220.4

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1, 3, 5, 7, FMNH 8397, 8399, 3826, 2798 respectively; 2 and 8, UMMZ from Shark River and Cape Sable respectively; 4 and 6, CU 12891 and 6634; 9, 10, UMMZ 155054 and 174398-S. For data see text.

FMNH 33943; USNM 47387, 15305; Lemon Bay, UMMZ 155054; Clearwater, CU 12891; Bonito Springs, CU 6634; no specific locality, USNM 31910, 36967, 43927.
 Campeche Banks: Alacrán Reef, sight record, May 13, 1958, 19°58'N, 91°42'W, SILVER

BAY Station 363; 20°06'N, 91°40'W, SILVER BAY Station 369.
 Colombia: Cartagena, MCZ 9799.
 Brazil: Maceió, FMNH 830, 3826; Recife, USNM 104238; MCZ 10095, 10202; Rio de Janeiro, USNM 23241; MCZ 873,



FIG. 25. *Epinephelus inermis*, UMMZ 172574, from Miami, Florida, 214 mm. Photograph by W. L. Brudon, courtesy Food and Agricultural Organization of the United Nations.

10152-53; Bahía, USNM 39842; Canavieiras, MCZ 10145.
 Hispaniola: Port-au-Prince Bay, USNM 170017, 133692, 133685; AMNH 19003.
 Jamaica: FMNH 2798; USNM 37717.
 Cuba: MCZ 34157.
 Bahamas: Bimini, UMMZ 174398-S.

PACIFIC RECORDS

Mexico: Mazatlán, USNM 28307, 28318, 28358; Sonora, near mouth of Río Muerto, UCLA W50-27; Bahía San Carlos, UCLA W52-33; Sinaloa, Bahía Topolobampo, UCLA W51-18.
 Panama: Balboa, USNM 30277; Colón, FMNH 8399-400; USNM 80309; ANSP 49117; Mindi Cut, USNM 80272; FMNH 8397-98; Gatun Locks, USNM 128840; Canal Zone, Amador, Naos Island, LACM W53-266.

SUBGENUS *DERMATOLEPIS* GILL, 1862

Dermatolepis GILL, 1862a, p. 54 (type species, *Dermatolepis punctatus* Gill, by original designation).
Lioperca GILL, 1863a, p. 236 (type species, *Serranus inermis* Valenciennes, by monotypy).

NOMENCLATURE: The name *Dermatolepis* is from the Greek *δέρμα*, skin, and *λεπίς*, scale, in reference to the lack of strong ctenii on the scales. Its gender is feminine.

DIAGNOSIS: Moderate-sized serranid fishes with deep, strongly compressed bodies. Dorsal outline considerably more arched than ventral profile. Dorsal XI, 17-20; anal III, 9-10; gill rakers 19-24. Head moderately long, 37 to 43

per cent of standard length. Caudal rounded or slightly lunate. Scales small, smooth, ctenii reduced to blunt knobs. Skull crests as in *Epinephelus*, frontoparietal crests convergent anteriorly, not reaching supraoccipital ridge. Supraethmoid bent slightly upward posteriorly. Anterior wing of hyomandibular well developed. Jaws with slightly enlarged canines. Preopercle with upper limb finely serrate, a few strong serrae at angle; lower limb unarmed. Middle opercular spine closer to lower than upper spine. Operculum ending in obtuse point.

RELATIONSHIPS: The subgenus *Dermatolepis* differs from the closely related *Epinephelus* chiefly in scale structure, in which it is closely approached by *Alphestes*. Its dark color and deep compressed body shape set it apart from other subgenera but none of these features is distinctive in itself and even in concert they do not warrant recognition at more than the subgeneric level.

The neurocranium (fig. 26) is indistinguishable from that of the nominate subgenus. The subgenus *Dermatolepis* is most closely related to the subgenus *Alphestes*.

INCLUDED SPECIES: This subgenus includes four species: *inermis* from the Western Atlantic; *dermatolepis* from the Eastern Pacific; and two species, *striolatus* Günther and *aldabrensis* Smith from the Indian Ocean. The last two are possibly color phases.

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS *Dermatolepis*

Pectoral fin short, less than 25 per cent of standard

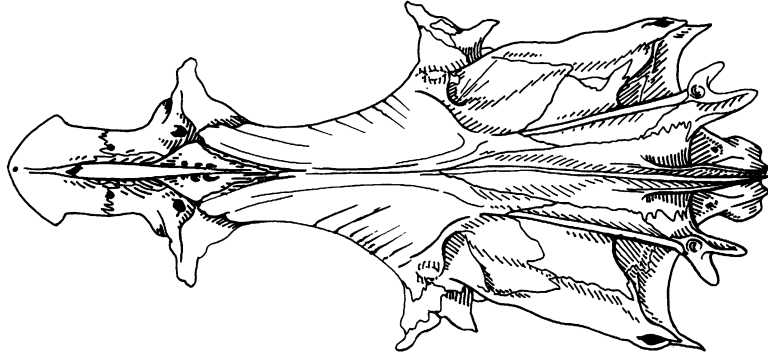


FIG. 26. *Epinephelus inermis*, AMNH 28045 from Puerto Rico. Dorsal view of the neurocranium.

length. Ground color gray, covered with irregular round white blotches and small dark spots; in some cases with vertical dark bars. Eastern Pacific. Dorsal XI, 18–19; pectoral 19 (20); gill rakers 21–24 *Epinephelus (Dermatolepis) dermatolepis*
Pectoral fin long, 29 to 35 per cent of standard length. Ground color black or very dark brown with rather large, sharply delimited white spots; never with vertical dark bars. Western Atlantic. Dorsal XI, 19 (20); pectoral 18–19; gill rakers 19–22 *Epinephelus (Dermatolepis) inermis*

Epinephelus (Dermatolepis) inermis

(Valenciennes, 1833)

MARbled GROUper

Figure 25

Serranus inermis VALENCIENNES, in Cuvier and Valenciennes, 1833, pp. 436–437 (original description, Antilles). STORER, 1846, p. 281 (copied). POEY, 1852 (1851–1854), pp. 54–55, pl. 4, fig. 2 (Cuba). GÜNTHER, 1859, p. 153 (Caribbean Sea; Cuba; West Indies). COCKERELL, 1892, p. 8 (Jamaica).

Lioperca inermis: GILL, 1863a, p. 236. POEY, 1865 (1865–1866), p. 198; 1868 (1866–1868), p. 282; 1874, p. 34; 1875 (1875–1877), pp. 17–18 (Cuba).

Dermatolepis inermis: JORDAN AND SWAIN, 1885b, pp. 405–406 (Havana). JORDAN, 1887c, p. 41 (Havana); 1887e, p. 581 (West Indies). JORDAN AND EIGENMANN, 1890, p. 376. JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1167–1168. OSBURN AND MOWBRAY, 1915, p. 3 (compared with *D. marmoratus*). MIRANDA-RIBEIRO, 1915, pp. 11–12 (figure, Brazil); 1918, p. 84. FOWLER, 1929a, p. 170 (St. Lucia). JORDAN, EVERMANN, AND CLARK, 1930, p. 313. BEEBE AND TEE-VAN, 1933, pp. 124–125 (compiled, “rare at Bermuda”). BUTSCH, 1939, p. 23 (Barbados). FOWLER, 1942b, p. 68 (Cuba). ERDMAN, 1957, p. 331 (La Parguera, Puerto Rico). BRIGGS, 1958, p. 271 (compiled). SMITH, 1958, pp. 46–47, pl. 5 (not seen at Bermuda). CALDWELL, 1959, p. 72 (Destin, Florida). BAILEY ET AL., 1960,

p. 25 (common name). SMITH, 1961, pp. 1:4, 1:14, 1:23, fig. 3.2. CALDWELL, 1966, p. 39 (Jamaica, compiled). CERVIGÓN M., 1966b, pp. 934–935, fig. 381 (La Blanquilla, Venezuela). RANDALL, 1968, p. 69, fig. 77 (general account, photograph). *Epinephelus inermis*: BOULENGER, 1895, p. 257.

Dermatolepis zanclus EVERMANN AND KENDALL, 1898, pp. 129–130, pl. 8, fig. 9 (original description, Key West, holotype USNM 48843). EVERMANN AND KENDALL, 1900, p. 74 (copied). JORDAN AND EVERMANN, 1898, pp. 2854–2855 (redescribed); 1920, p. 389 (general account, drawing). BREDER, 1929, p. 164. JORDAN, EVERMANN, AND CLARK, 1930, p. 313. BRIGGS, 1958, p. 271 (compiled).

Dermatolepis marmoratus OSBURN AND MOWBRAY, 1915, pp. 1–3 (original description, Key West). ANONYMOUS, 1915, p. 1209 (incorrect citation of original description). BREDER, 1929, p. 164.

NOMENCLATURE: The holotype of *Serranus inermis*, a mounted specimen (5633) is in the Paris Museum. According to C. L. Hubbs, it shows good agreement with figure 25.

Two nominal species from Key West seem to be based on individuals of *Dermatolepis inermis* with unusual color patterns. *Epinephelus zanclus* (Evermann and Kendall) was said to differ from *inermis* in having falcate dorsal and anal fins, but this is a normal condition in large *inermis*. The holotype of *zanclus*, USNM 48843, which I have examined, is 430 mm. long. It is lighter colored than most other specimens that I have seen and has small black spots, rather than large white blotches, over most of the body. This is believed to be a transient pattern such as is seen in other groupers; one specimen from Cuba has similar small black spots on the gill membranes in addition to the usual pattern of larger white spots.

The holotype of *Dermatolepis marmoratus* Osburn and Mowbray, AMNH 4775, has a color pattern similar to the type of *zanclus*. Also a large (24-inch) specimen, it has falcate dorsal and anal fins and a smaller eye but none of these features is diagnostic. I therefore place both *zanclus* and *marmoratus* in the synonymy of *inermis*. Contrary to the anonymous statement in the Bulletin of the New York Zoological Society for March 1915, the original description by Osburn and Mowbray was published as a separate leaflet by the New York Zoological Society; it never appeared in Zoologica.

The Latin adjectival name *inermis* means unarmed.

DIAGNOSIS: Large-scaled species of *Epinephelus* with vertical fins falcate in large individuals. Dorsal XI, 19 (20); anal III, 9; pectoral 18-19; gill rakers 19-22. Pectoral elongate, 29-35 per cent of standard length. Color usually dark brown or black with large, distinct white spots; white line through eye.

The Pacific species, *Epinephelus* (*D.*) *dermatolepis*, has smaller pectoral fins and lacks distinct white spots of *inermis*. It also has a distinctly barred phase which *inermis* apparently lacks. These two species distinguished from all other American groupers in lacking ctenii on scales.

DESCRIPTION: The pectoral fin of *inermis* is excessively developed, 29 to 35 per cent of the standard length, whereas in *dermatolepis* it does not exceed 25 per cent. Proportional measurements are given in table 21.

The preopercle is rather gently curved with a slight notch above the angle and slightly enlarged serrae at the angle. The body and head, except for the lips and the exposed surface of the maxilla, are covered with imbedded scales in which the ctenii are reduced to blunt stubs. The dorsal and anal fins (particularly the latter) become falcate with age. The caudal is rounded in small specimens, becoming square or even slightly lunate in large ones. The gill rakers are rather short.

The ground color is very dark brown in preservative, with the body and head variously spotted with distinct white spots, most of which are larger than the eye. There is little constancy in arrangement of these spots but most individuals seem to have one or more along the base of the anal fin and at the base of the caudal. A particularly conspicuous white spot lies

behind the end of the maxilla. The midline of the head is light from between the eyes to the occiput. Another distinct line extends forward from the upper part of the orbit toward, but not reaching, the tip of the snout. Still another bar connects the lower part of the orbit to the maxillary groove. There is another white bar that reaches from the orbit halfway to the opercular angle. There is a light line from the upper posterior part of the orbit that parallels the dorsal profile to a point anterior to the dorsal fin where it curves upward to the midline.

A white line crosses the upper lip at its tip and similar lines cross the upper lip and maxilla near their midpoints. The lower lip is crossed by a white line at the midline and has two spots on its upper surface lateral to this. All fins have small white spots that are most numerous toward the fin edges. Otherwise, the fins become darker toward their margins.

The rest of the body is so dark that there is little possibility of countershading. In LeDanois's picture of a living specimen of *inermis* (labeled *marmoratus*) the background is lighter, with rings of small dark spots surrounding the white spots. Some specimens (UMMZ 172574) have only a faint suggestion of this pattern. In the holotype of *E. zanclus* (USNM 48843) the body is evenly covered with dark spots separated by gray reticulation. There is an indication of this pattern in LeDanois's photo, suggesting that it is a color phase that is usually seen only in life. Possibly *Dermatolepis aldabrensis* J. L. B. Smith is a similar phase of *Dermatolepis striolatus*.

RELATIONSHIPS: The only American near relative of *E. inermis* is its Pacific congener, *Epinephelus* (*Dermatolepis*) *dermatolepis*. A specimen of *E. (D.) striolatus* (AMNH 19608, Shimone, Kenya) of the Indian Ocean seems to differ only in minor details of coloration.

ECOLOGY: Nothing seems to be known of this species in its natural habitat. Comments on habitat given by Osburn and Mowbray (1915, p.3) are probably based on *Epinephelus* (*Alphistes*) *afēr*.

DISTRIBUTION: *Epinephelus inermis* is known from Jamaica, Cuba, Puerto Rico, the Lesser Antilles, Río de Janeiro, and southern Florida (fig. 27). All of Bean's specimens from Bermuda have, upon re-examination, proved to be *E. (A.) afēr* and the occurrence of *E. inermis* in Bermuda is doubtful.

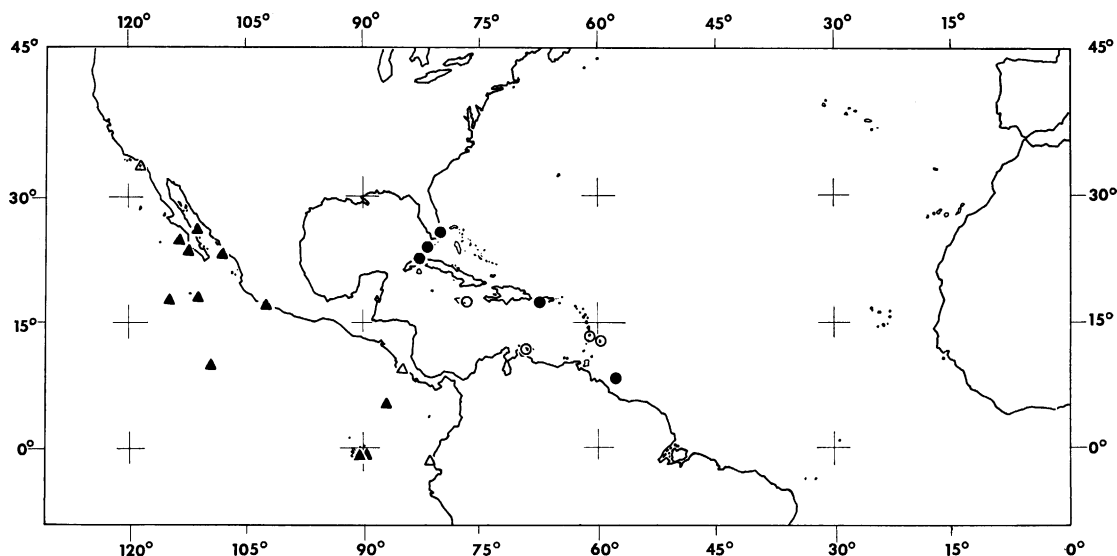


FIG. 27. Distribution records for *Epinephelus inermis* (circles) and *E. dermatolepis* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

SPECIMENS EXAMINED

Florida: vicinity of Miami, UMMZ 172574 (two specimens, 181-213 mm., early 1957, Al Pfeuger); Key West, USNM 48843 (430 mm., Evermann and Kendall [holotype of *D. zanclus* Evermann and Kendall]); AMNH 4775 (470 mm., Dec. 22, 1941, P. Roberts [holotype of *D. marmoratus* Osburn and Mowbray]).

West Indies: no specific locality, USNM 33629 (268 mm., J. C. Brevoort).

Puerto Rico: La Parguera, AMNH 28045 (290 mm., October, 1964, D. S. Erdman).

Cuba: Havana, UMMZ 171873 (206 mm., July, 1937, L. Howell y Rivero); MCZ 32809 (214 mm., 1931, L. Howell y Rivero); MCZ 37402 (163 mm., Poey); no specific locality, USNM 132425 (214 mm., Poey); MCZ 21779 (274 mm., Poey); MCZ 21780 (150 mm., Poey).

South America: OREGON Station 2234, 08°20'N, 58°30'W, UMMZ 174569 (151 mm., 23-26 fa., Aug. 29, 1958).

Epinephelus (*Dermatolepis*) *dermatolepis*

Boulenger, 1895

LEATHER BASS

Dermatolepis punctatus GILL, 1862a, p. 54 (original description, Cape San Lucas); 1863b, p. 250 (copied). JORDAN AND GILBERT, 1882, p. 229 (Braithwaite Bay, Socorro Is.). JORDAN AND SWAIN,

1885b, pp. 407-408 (Revillagigedo Is.). JORDAN, 1886b, p. 377; 1887a, p. 85. JORDAN AND EIGENMANN, 1890, p. 376. JORDAN, 1895, p. 444 (not seen at Sinaloa). JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1168-1169. JORDAN AND MCGREGOR, 1899, p. 278 (Clarión and Socorro Is.). SNODGRASS AND HELLER, 1905, p. 368 (Clarión; Cocos; Galápagos Islands). KENDALL AND RADCLIFFE, 1912, p. 110 (Acapulco). OSBURN AND MOWBRAY, 1915, p. 3 (comparison with Atlantic species). OSBURN AND NICHOLS, 1916, p. 162 (Santa Catalina Is.). FOWLER, 1917a, p. 3 (Puntarenas, Costa Rica). JORDAN, EVERMANN, AND CLARK, 1930, p. 313. BREDER, 1936, p. 23 (BOC 569, no definite locality). WALFORD, 1937, pp. 115-116, pl. 14, fig. b. NICHOLS AND MURPHY, 1944, p. 248 (La Plata Is., Ecuador). BERDEGUE A., 1956, p. 279 (Mexico).

Epinephelus dermatolepis BOULENGER, 1895, pp. 256-257 (new name to replace *punctatus*, preoccupied in *Epinephelus*).

NOMENCLATURE: I have been unable to locate the holotype, which was collected at Cape San Lucas by Xantus.

The adjectival specific name of the holotype, *Dermatolepis punctatus* Gill, is from the Latin *punctatus*, in allusion to the black spots on the body. The derivation of the new specific name, *dermatolepis*, is the same as that of the subgenus.

DIAGNOSIS: Small-scaled species of *Epinephelus* with vertical fins rounded at all sizes. Dorsal XI, 18-19; anal III, 9; pectoral 19 (20); gill rakers 21-24. Pectoral short, less than 25

TABLE 21
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus inermis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	150	183	214	214	256	264	274	304	305	339	—
Head length	390	396	393	397	379	375	376	385	383	370	384.4
Head width	147	175	145	178	154	144	126	171	164	155	155.9
Head depth	230	268	278	287	256	269	255	283	279	248	265.3
Snout length	93	93	89	103	94	85	95	97	92	89	93.0
Suborbital width	37	38	37	44	39	38	38	43	43	41	39.8
Interorbital width	57	57	54	63	59	53	53	62	59	52	56.9
Length of: Orbit	73	66	65	61	55	57	60	54	54	53	59.8
Postorbital head	240	249	243	250	242	244	243	252	249	242	245.4
Maxillary	160	148	154	159	152	144	146	156	147	146	151.2
Lower jaw	160	145	150	157	150	136	153	158	159	142	151.0
Snout to angle of preopercle	250	253	248	255	250	241	—	255	246	240	248.6
Supramaxillary length	50	55	47	54	41	49	44	49	49	46	48.4
Maxillary width	40	41	40	40	35	42	38	46	43	40	40.5
Tip of lower jaw to gular notch	123	161	140	152	146	—	131	118	—	143	139.2
Body width	140	156	150	180	162	—	124	181	159	155	156.3
Body depth	453	410	437	432	426	413	427	451	444	407	430.0
Caudal peduncle depth	113	128	126	138	141	134	137	145	131	137	135.0
Tip of snout to dorsal origin	373	391	369	414	383	366	396	400	379	378	384.9
Tip of snout to pectoral base	367	352	374	341	338	348	338	321	346	333	345.8
Tip of lower jaw to pelvic base	423	423	458	402	414	415	412	378	425	406	415.6
Length of: Dorsal base	600	—	610	640	615	599	597	625	598	577	606.6
Depressed dorsal	697	680	692	743	730	695	703	732	689	693	705.4
Anal base	180	199	192	192	191	191	192	194	189	186	190.6
Depressed anal	367	336	360	327	361	354	376	382	357	375	359.5
End of dorsal to caudal base	130	134	136	136	137	142	135	141	138	133	136.2
Length of: Caudal peduncle	217	205	203	182	209	216	210	225	228	207	210.2
Pectoral	347	303	343	290	328	318	332	326	326	313	322.6
Pelvic	227	210	234	196	219	231	235	230	228	221	223.1
Dorsal spine I	87	93	89	75	74	91	84	72	75	74	81.4
Dorsal spine III	180	178	168	166	160	172	151	169	171	167	168.2
Dorsal spine XI	123	145	117	131	117	116	109	115	116	106	119.5
Anal spine I	63	71	65	58	51	53	51	44	56	46	55.8
Anal spine II	120	109	100	100	90	118	93	92	98	86	100.6
Anal spine III	127	142	110	124	94	110	100	97	118	110	112.2
Caudal base to tip of upper rays	273	239	276	287	262	—	261	296	293	295	275.7
Caudal base to tip of middle rays	287	276	283	259	277	—	277	283	282	270	277.2
Caudal base to tip of lower rays	267	257	283	276	256	—	263	284	274	286	271.8

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1 and 7, MCZ 21780 and 21779; 2 and 4, UMMZ 172574; 3, USNM 132425; 5 and 10, UMML from Miami; 6, 8, and 9, UMIM from Miami. For data see text.

per cent of standard length. Color dark with black spots, usually with dark vertical bars; in some cases having few indistinct white blotches. A white line through eye from tip of snout to base of dorsal fin.

As in its Atlantic congener, the ctenii are much reduced and scales embedded so that the

body surface is smooth to touch. This species differs from Atlantic form chiefly in color pattern and in shorter pectoral fin.

DESCRIPTION: See table 22 for measurements of 10 specimens of leather bass. Noteworthy are the narrow interorbital, deep body, and small eye.

The preopercle is gently rounded, serrulate on the upper limb and with slightly enlarged serrae at the angle. The fins are gently rounded; the caudal is convex. There are no scales on the maxilla.

Most specimens are rather uniformly dark gray, everywhere peppered with discrete, round, black spots; some individuals show a definitely barred pattern. A specimen from Acapulco, Mexico, USNM 65474, 139 mm. long, has well-marked vertical bars on the body, each about as wide as the interspaces and with one to six light spots in its center. A faint column of dark spots is present in each interspace. There are four irregular vertical bars across the tail, and the body bands continue to the edges of the dorsal and anal fins; the pelvics and pectorals are crossed by similar dark bands. There is a dark submarginal band on the lobe of the soft dorsal fin. A light bar extends on top of the head from the snout nearly to the dorsal origin. Below this a light bar crosses the upper lip and reaches the upper part of the orbit, continuing behind the eye parallel to the back to a point over the upper end of the gill opening. A similar light bar crosses the middle of the upper jaw and continues upward to the lower part of the orbit. Another such bar extends from the lower, posterior part of the orbit to the angle of the preopercle and on across the interopercle. There are several white bars across the lower jaw and the breast. Irregular white blotches give the body a marbled appearance in most specimens. Walford (1937, p. 115) stated that the fins are narrowly edged with clear yellow.

RELATIONSHIPS: This is the only Eastern Pacific representative of the subgenus *Dermatolepis*. It is close to the Western Atlantic *E. inermis* but the two are well differentiated.

ECOLOGY: Nothing is known of the habits of *E. dermatolepis*.

DISTRIBUTION: *Epinephelus dermatolepis* is common on the Pacific coast of Mexico from Lower California to Acapulco and in the Revilla Gigedo, Cocos, and Galápagos Islands (fig. 27).

SPECIMENS EXAMINED

Mexico: Golfo de California, Sinaloa, Mazatlán, UCLA W52-103; Magdalena Bay, FMNH 49221; Guerrero, Puerto del Marques near Acapulco, UCLA W53-190; Acapulco Bay, USNM 65474; Acapulco, USNM 65704; MCZ 29638; Baja California, Thetis Bank,

25°55'N, 112°36'W, LACM W53-313; Islas Revilla Gigedo, Isla Socorro, USNM 28223, 107184; LACM W52-104; Berumers Cove, UCLA W55-126; Academy Bay, UCLA W55-155; Isla Clarión, USNM 46883.

Clipperton Island: Offshore around Island, UCLA W58-290; northeast side around Island, $\frac{1}{4}$ mile west of Wreck Bay, UCLA W58-294; 0-1 mile northwest of Wreck Bay, on northeast side of Island, LACM W56-236.

Costa Rica: Isla del Coco, USNM 49785, 119775; Chatham Bay, UCLA W53-126, W64-46; LACM W64-47.

Ecuador, Islas Galápagos: Isla San Cristóbal (Chatham), Wreck Bay, FMNH 41755; Isla Santa Cruz (Indefatigable), Academy Bay, LACM W64-21.

SUBGENUS ALPHESTES BLOCH AND SCHNEIDER, 1801

Alphestes BLOCH AND SCHNEIDER, 1801, p. 236 (type species, *Epinephelus afer* Bloch, designated by Jordan and Swain, 1885b, p. 394).

Prospinus POEY, in Gill, 1863a, p. 236 (type species, *Plectropoma chloropterus* Valenciennes [a subjective synonym of *Epinephelus afer* Bloch] by monotypy).

NOMENCLATURE: Poey rejected the genus *Alphestes* on the grounds that the original description was inadequate. Bloch and Schneider clearly stated, however, that *Epinephelus afer* Bloch was included, and that species is readily identifiable. Thus *Alphestes* should stand in spite of the ambiguity of the original description.

The name *Alphestes* comes from the Greek ἀλφηστίζς, a fish that swims in pairs. Its gender is masculine.

DIAGNOSIS: Small, rather strongly compressed groupers with dorsal profile much more strongly curved than ventral. Dorsal XI, 17-19; anal III, 9; gill rakers 21-24. Head moderate, 37 to 44 per cent of standard length. Caudal rounded. Scales moderate, strongly ctenoid. Supramaxilla present, well developed. Lacrimal and suborbital region narrow.

Skull crests well developed; frontoparietal crests parallel, intersecting supraorbital ridge. Postorbital process included in frontoparietal crest. No transverse wall on supraethmoid, which forms floor of pit between anterior ends of frontals. Parasphenoid straight or nearly so. Anterior wing of hyomandibular well developed. Moderately enlarged canine teeth near symphysis of upper and lower jaws.

TABLE 22
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus dermatolepis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	139	163	175	265	276	294	298	379	405	444	—
Head length	410	414	406	385	422	429	399	427	407	403	410.2
Head width	137	150	140	151	134	163	154	177	173	153	153.2
Head depth	291	301	303	287	322	306	284	325	269	295	298.3
Snout length	108	104	91	106	103	116	97	116	123	106	107.0
Suborbital width	43	46	43	47	51	49	47	50	47	50	47.3
Interorbital width	65	61	60	51	65	63	50	61	60	60	59.6
Length of: Orbit	79	77	74	53	65	58	57	58	53	50	62.4
Postorbital head	241	255	246	242	261	262	255	268	252	259	254.1
Maxillary	173	181	171	158	179	177	166	173	164	169	171.1
Lower jaw	176	184	177	160	178	179	154	170	165	164	170.7
Snout to angle of preopercle	281	282	274	253	288	281	260	290	277	270	275.6
Supramaxillary length	58	58	57	53	49	53	62	62	56	52	56.0
Maxillary width	43	46	46	43	51	39	42	44	40	43	43.7
Tip of lower jaw to gular notch	151	144	137	—	134	155	—	149	154	—	146.3
Body width	133	138	114	157	138	153	146	158	158	158	145.3
Body depth	482	466	437	438	444	415	416	422	407	412	433.9
Caudal peduncle depth	133	141	126	138	134	131	128	137	128	115	131.1
Tip of snout to dorsal origin	417	417	400	400	440	430	393	425	395	399	411.6
Tip of snout to pectoral base	356	365	360	374	371	378	399	377	390	394	376.4
Tip of lower jaw to pelvic base	421	414	400	411	404	425	470	407	432	468	425.2
Length of: Dorsal base	640	638	620	581	632	639	570	596	568	561	604.5
Depressed dorsal	737	712	694	619	692	714	628	660	610	599	666.5
Anal base	209	202	177	196	174	167	200	172	164	176	183.7
Depressed anal	338	334	326	291	281	269	290	268	252	250	289.9
End of dorsal to caudal base	115	123	126	132	127	126	117	121	126	127	124.0
Length of: Caudal peduncle	194	196	197	189	187	163	188	201	183	166	186.4
Pectoral	227	260	246	211	214	214	225	219	204	185	220.5
Pelvic	187	199	194	170	152	160	141	142	128	126	159.9
Dorsal spine I	94	80	83	47	105	61	74	58	51	47	70.0
Dorsal spine III	165	163	149	109	130	129	119	104	91	106	126.5
Dorsal spine XI	108	110	109	94	112	109	102	104	99	81	102.8
Anal spine I	68	58	63	53	62	48	62	45	48	50	55.7
Anal spine II	115	117	103	87	101	90	82	99	78	82	95.4
Anal spine III	122	129	143	100	—	92	117	103	93	98	110.8
Caudal base to tip of upper rays	230	264	240	219	241	235	232	226	225	202	231.4
Caudal base to tip of middle rays	248	264	246	219	217	221	230	216	206	193	226.0
Caudal base to tip of lower rays	252	251	234	219	225	214	221	210	215	185	222.6

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1 and 3–10, USNM 65474, 65704, 28223, 49785, 119775, 107184, 50075, 36883, 107184 respectively; 2, MCZ 29638. For data see text.

Preopercle with a right angle, upper limb evenly serrate, lower limb unarmed; at angle a strong spine is directed downward and forward; spine serrate on posterior edge. Three opercular spines nearly equidistant; opercular flap acutely pointed.

RELATIONSHIPS: Two osteological features distinguish the subgenus *Alphstes*: the dorso-

lateral skull crests are nearly parallel to each other and there is an antrorse spine at the angle of the preopercle. In all other respects, including the reduction of scale ctenii, both of its species closely resemble *Dermatolepis* and clearly belong within the genus *Epinephelus*.

Although the dorsolateral crests are parallel to each other they are more similar to those of

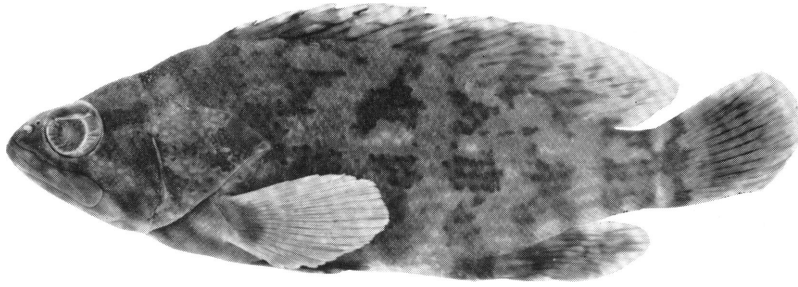


FIG. 28. *Epinephelus afer*, AMNH 18183 from Cuba, 146 mm.

Epinephelus than to those of *Mycteroperca* and the general aspect of the skull is clearly that of other species of *Epinephelus* (fig. 29). The postocular skull process bears the same relationship to the crest that it does in *Epinephelus* and is unlike that of *Mycteroperca*. The antrorse preopercular spine is like that of *Gonioplectrus*, which I interpret as a relative of *Polyprion*. These similar spines appear to be independently derived.

INCLUDED SPECIES: The subgenus is restricted to American waters and consists of *Epinephelus afer* in the Western Atlantic and Eastern Pacific and *Epinephelus multiguttatus* in the Eastern Pacific.

KEY TO THE AMERICAN SPECIES OF THE
SUBGENUS *Alphestes*

- Color brown or orange, side clouded with dark, irregular brown blotches that in some cases suggest vertical bars. Usually a dark stripe behind eye. Pectoral fin with seven or eight irregular bars. Gill rakers short, less than one-half length of gill filaments. Western Atlantic and Eastern Pacific . . .
. *Epinephelus (Alphestes) afer*
- Color brown, head and body densely covered with dark brown spots in some cases coalescent to form longitudinal stripes posteriorly. No black stripe behind eye. Pectoral fin with about five dark, regular, cross bars. Gill rakers long, about two-thirds length of gill filaments. Eastern Pacific . . .
. *Epinephelus (Alphestes) multiguttatus*

***Epinephelus (Alphestes) afer* Bloch, 1793**

MUTTON HAMLET

Figure 28

Epinephelus afer BLOCH, 1793, p. 12, pl. 327 (original description, locality given as Guinea but this is doubtful). BOULENGER, 1895, pp. 254–255, fig. 18 (skull, West Indies; Falkland Is.?).

Alphestes afer: BLOCH AND SCHNEIDER, 1801, p. 236 (type of *Alphestes*). PETERS, 1866, p. 105. JORDAN AND SWAIN, 1885b, pp. 396–397. JORDAN, 1887c,

p. 40 (Havana); 1887e, p. 581 (West Indies). JORDAN AND EIGENMANN, 1890, p. 350. JORDAN, 1891, p. 319 (Bahía). JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1164–1165; 1898, pl. 186, figs. 488–488a. BEAN, 1913, p. 121 (Bermuda). MIRANDA-RIBEIRO, 1915, pp. 10–11 (Brazil); 1918, pp. 83–84. JORDAN AND EVERMANN, 1920, p. 388. MEEK AND HILDEBRAND, 1925, pp. 463–464, pl. 43 (Panama). BORODIN, 1928, pp. 19–21 (West Indies; Bahamas). BEEBE AND TEE-VAN, 1928, p. 131 (Port-au-Prince). FOWLER, 1929a, p. 169 (St. Lucia). JORDAN, EVERMANN, AND CLARK, 1930, pp. 312–313. BEEBE AND TEE-VAN, 1933, pp. 126–127 (Bermuda). BUTSCH, 1939, p. 23 (Barbados). LONGLEY AND HILDEBRAND, 1941, p. 98 (habits, Tortugas). FOWLER, 1942b, p. 68 (Cuba); 1944, p. 465 (Fox Bay, Colón, Panama); 1953, p. 55 (Cartagena, Colombia). BRIGGS, 1958, p. 271 (compiled distribution). SMITH, 1958, pp. 7, 44, fig. 1B, pl. 4 (biology, Bermuda); 1959, p. 114 (hermaphroditic). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:5, 1:17, 1:23, figs. 4.2, 15. RANDALL, 1963, p. 34 (Virgin Is., ecology). CALDWELL, 1966, p. 39 (Jamaica, compiled). CERVIGÓN M., 1966b, pp. 315–316, fig. 124 (Puerto Fermin, Venezuela). RANDALL, 1967, p. 695 (food habits). BÖHLKE AND CHAPLIN, 1968, p. 276 (Bahamas). RANDALL, 1968, p. 64, fig. 69 (general account, color photograph).

Plectropoma chloroptera CUVIER, in Cuvier and Valenciennes, 1828, pp. 398–399 (original description, Antillean Sea; Martinique; Santo Domingo). STORER, 1846, p. 282. POEY, 1852 (1851–1854), pp. 73–74, pl. 9, fig. 3 (Cuba). CASTELNAU, 1855, p. 3 (spelled *chloroptera*; Rio de Janeiro). GÜNTHER, 1859, p. 164 (Caribbean Sea). POEY, 1865, (1865–1866), p. 265 (Cuba). VAILLANT AND BOCOURT, 1878 (1915), pp. 107–110 (Jamaica; Haiti; Martinique; Brazil).

Plectropoma monacanthus MÜLLER AND TROSCHEL, in Schomburgk, 1848, p. 665 (original description, Barbados). GÜNTHER, 1859, pp. 164–165. COCKERELL, 1892, p. 8 (copied; Jamaica).

Prospinus chloroptera: POEY, 1861 (1858–1861), p. 364.

- Prospinus chloropterus*: POEY, 1868 (1866–1868), p. 289 (Cuba); 1874, p. 34; 1875 (1875–1877), pp. 18–19 (Cuba).
- Prospinus* sp.: POEY, 1868 (1866–1868), p. 289 (differs in head coloration).
- Alphestes monacanthus*: COPE, 1871b, p. 467 (St. Martins).
- Serranus* sp.: GOODE, 1877, p. 292 (Bermuda).
- Alphestes chloropterus*: EVERMANN AND MARSH, 1902, pp. 155–156, fig. 44 (San Juan, Mayaguez, Puerto Rico). BEAN, 1906, p. 55 (Bermuda). FOWLER, 1915b, p. 543 (St. George, Grenada); 1920, pp. 137, 144 (St. Martins, St. Croix). NICHOLS, 1929, p. 252, fig. 118 (Ponce, Porto Rico).
- Dermatolepis inermis* (non Valenciennes): BEAN, 1906, p. 55 (Bermuda).
- Epinephelus chloropterus*: FOWLER, 1907, p. 258.
- Epinephelus lightfooti* FOWLER, 1907, pp. 258–260, fig. 3 (original description, Santo Domingo, holotype, ANSP 16514).
- Alphestes multiguttatus* (non Günther): EVERMANN AND RADCLIFFE, 1917, pp. 69–70.
- Epinephelus* (*Alphestes*) *afēr*: METZELAAR, 1919, p. 49 (Bonaire, Curaçao, St. Martins, St. Eustacius).
- Alphestes lightfooti*: JORDAN, EVERMANN, AND CLARK, 1930, p. 313.
- Alphestes immaculatus* BREDER, 1936, p. 22 (original description, Galápagos Is., holotype, BOC 596).
- Alphestes galapagensis* FOWLER, 1944, pp. 342–343, fig. 186 (original description, Chatham Is., Galápagos Is., holotype, ANSP 70138).
- Alphestes fasciatus* HILDEBRAND, 1946, pp. 163–166, fig. 36 (original description, Afuera Bay, Peru, holotype, USNM 127950). KOEPKE, 1955, p. 85. MORROW, 1957, p. 28 (Lobos de Afuera Is., Peru).

NOMENCLATURE: *Alphestes fasciatus* Hildebrand of the Pacific coast seems to be indistinguishable from the Atlantic *E. afēr*. *Alphestes immaculatus* Breder, an unmarked specimen, and *A. galapagensis* Fowler seem also to be the same. The original description of *fasciatus* credits it with 22 vertebrae, but this is likely in error as a paratype (USNM 107169) has 24 vertebrae as shown by X-ray.

According to Jordan and Evermann (1896b, p. 1165), the holotype of *Epinephelus afēr* Bloch was examined in the Berlin Museum. I do not know if it is still in existence but Peters (1866, p. 106) listed it as an alcoholic specimen 265 mm. long bearing number 143.

The name *afēr* means African; Bloch's type supposedly came from Africa. Metzelaar (1919, p. 49) has suggested, however, that the original locality may be an error for no further specimens have been recorded from there.

DIAGNOSIS: Rather small grouper with high dorsal and anal fins, compressed body, narrow suborbital region, and small scales. Dorsal XI, 18; anal III, 9; pectoral 17; gill rakers 21–24. Body brownish or orange with indistinct, darker brownish blotches that tend to form vertical bars and small orange spots.

Epinephelus afēr and *E. multiguttatus* are easily recognized by the strong antrorse spine of the preopercle. Color pattern and certain body proportions serve to distinguish the two species; *afēr* has nebulous dark blotches tending to form dark vertical bars, whereas *multiguttatus* has body covered with distinct dark spots.

DESCRIPTION: The eye of *Epinephelus afēr* averages slightly smaller than that of *multiguttatus*, otherwise the proportions are very similar (table 23.).

The nostrils are equal in size. All fins are rounded; the dorsal and anal are high, especially the soft parts. The maxilla is without scales on its exposed surface. The upper and lower limbs of the preopercle meet at right angles; the upper is finely toothed and there is a strong antrorse spine at the lower part of the angle that is serrate on its posterior edge. The eye is large, and the interorbital is rather narrow. The lateral skull crests are parallel and extend forward to the supraorbital ridge, as in *Mycteroperca*, with the postorbital processes plainly visible. The frontal pit is developed, and there is no supraethmoid wall (fig. 29).

The following color notes were made from a specimen 236 mm. long collected April 19, 1957, in Nonsuch Bay, Bermuda: ground color of body and head orange with white blotches on flanks, belly, and underside of head; irregularly marbled with brownish and dusky blotches on side and back. Head and body, except for under surface, covered with spots 1–3 mm. in diameter; these spots orange in light areas and brownish in darker areas. Pectoral fin yellow with dusky brownish reticulations lighter distally and obsolete at fin margin.

Spinous dorsal like the body at its base, with irregular brown and white blotches distally. Fleshy tips of interspinous membranes red. Soft dorsal, caudal, anal, and pelvic fins like body to middle of rays; distally, darker spots coalesce into reticulations surrounding white spots. On pelvic these reticulations are dark to fin margin; on other fins they disappear at margin.

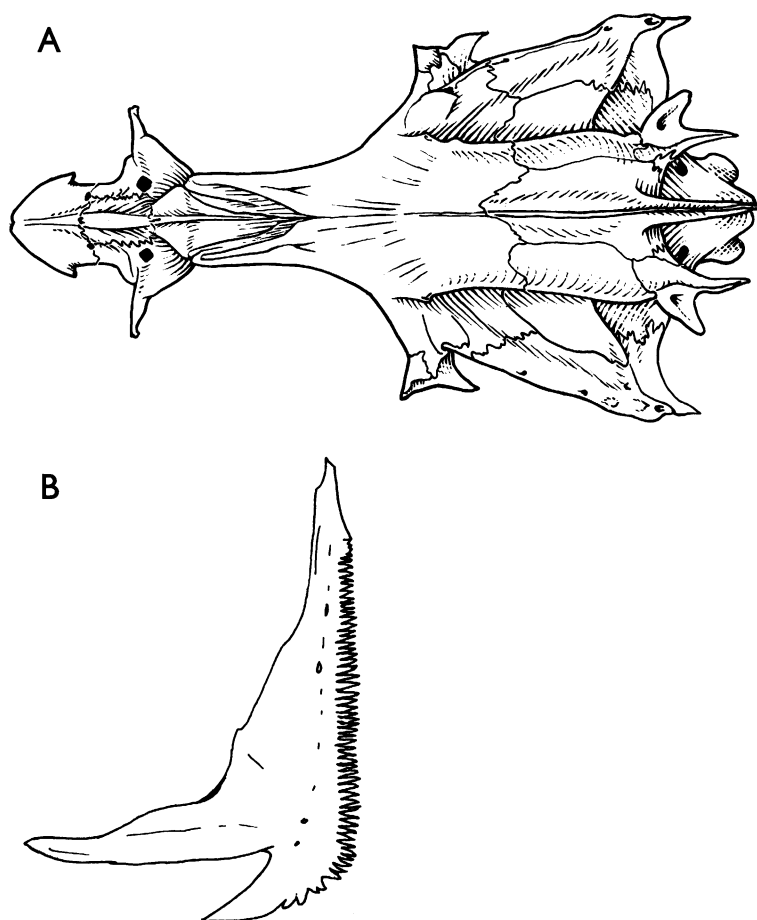


FIG. 29. Neurocranium and preopercle of *Epinephelus afer*. A. Dorsal view of neurocranium. B. Left preopercle, UMMZ 172523-S from Bermuda.

A Bermuda specimen kept in an aquarium during the summer of 1956 became brownish all over, retaining the pattern but losing the orange coloration. Usually the orange spots are not conspicuous in living fish but become so soon after death.

A small individual was collected at sea at a night light July 15, 1954. This fish, then a transparent larva, was retained in an aquarium at the Bermuda Biological Station until transformation when it was preserved at a length of 37.5 mm. The general appearance is similar to the adult but the preopercular angle has a spine directed straight downward and another directed straight backward; presumably the latter is a remnant of a strong spine that was present in the larva.

RELATIONSHIPS: *Epinephelus afer* differs from

E. multiguttatus chiefly in coloration. The differences are of the same order of magnitude as the distinction between allopatric geminate species of *Cephalopholis*, *Dermatolepis*, *Epinephelus*, and *Mycteroperca*. As both species of *Alphistes* live in the Galápagos Islands and have retained their distinctness, it seems probable, by analogy, that the other geminate pairs would also remain separate if they were sympatric.

ECOLOGY: *Epinephelus afer* relies heavily upon its protective coloration. One individual seen at a depth of about 35 feet was actually touched several times and its only response was to move a little farther into a clump of yellowish algae. It takes a hook readily and is especially plentiful on the south shore of Bermuda in shallow water only a few hundred yards from the edge of deep water. One specimen 47.5 mm. long (FMNH)

was collected on the Argus Bank, probably at the surface although it was fully transformed.

This species does not enter the commercial catch in Bermuda because of its small size and habits. I saw none caught in traps, which it either does not often enter or from which it is particularly adept at escaping.

This species has in the past been confused with *Dermatolepis* although the distinctive structure of the preopercle permits ready separation. All specimens of *inermis* reported from Bermuda by Bean have been reexamined; all are *Epinephelus afer*.

One ripe female was taken July 25, 1957, but the length of the spawning season has not yet been determined. The smallest male examined histologically was 193 mm. long; the largest individual seen (250 mm.) was a female, although there are histological indications that this species is protogynous.

DISTRIBUTION: In the Atlantic, *Epinephelus afer* ranges from Bermuda and Florida throughout the Bahamas and the Antilles. The species is found also in Panama, Cartagena Lagoon, and Brazil, but there are no records from the Gulf of Mexico. In the Pacific, *Epinephelus afer*

is known from the Gulf of California, Peru, and the Galápagos Islands (fig. 30).

SPECIMENS EXAMINED

ATLANTIC RECORDS

- Florida: Key West, FMNH 7076; Bakers Haulover, UMIM; Key Largo, UMIM.
- Panama: Colón Reef, USNM 80214.
- Brazil: Bahia, FMNH; USNM 43348; Recife (Pernambuco), USNM 104250, 104238; no specific locality, MCZ 9790-92.
- Grenada: St. Georges, ANSP 45085.
- St. Lucia: USNM 170218.
- St. Martins: ANSP 13312-14.
- Antigua: English Harbor, USNM 170297.
- Sombrero Island: MCZ 9800.
- St. Thomas: MCZ 4832.
- West Indies: USNM 33239; MCZ 9780.
- Puerto Rico: Guanica, FMNH; Puerto Real, UMMZ 143029; La Parguera, UMMZ 172528; Punta Congrejos, UMMZ 172563-S; Mayaguez, TU 17188; USNM 50202; Ponce market, AMNH 4904.
- Hispaniola: Santo Domingo, ANSP 16514 (holotype, *E. lightfooti* Fowler); Port-au-Prince, USNM 170026; AMNH 18944, 19029.

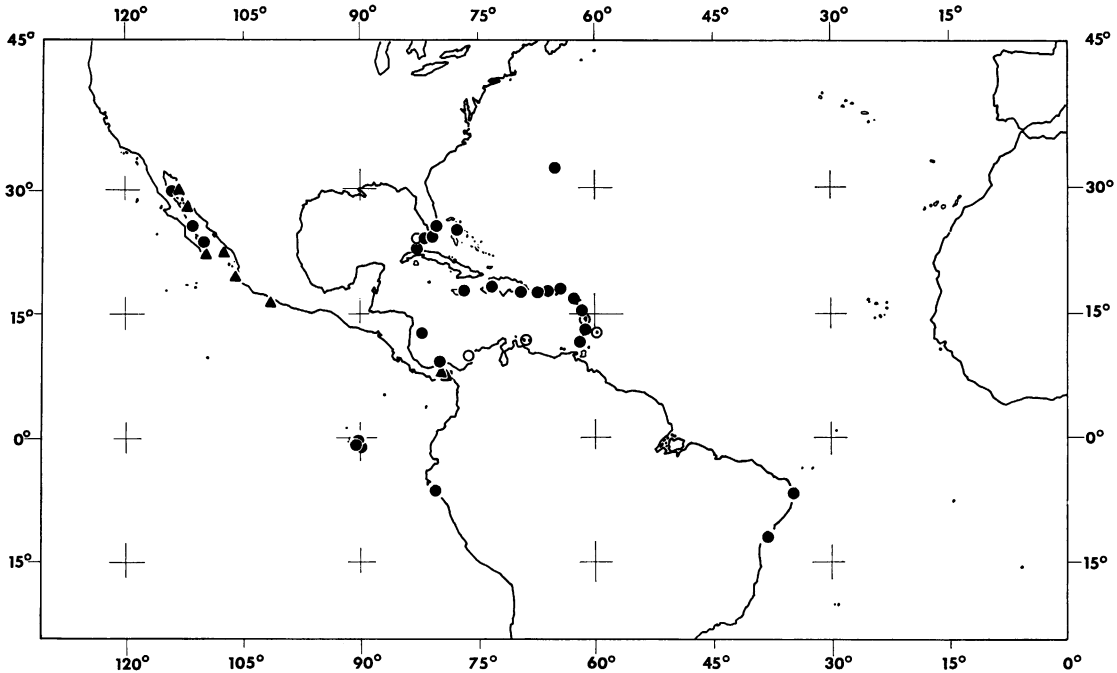


FIG. 30. Distribution records for *Epinephelus afer* (circles) and *E. multiguttatus* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

Jamaica: St. Ann's Bay, BOC.

Cuba: Havana, USNM 35057; MCZ 10079;

no specific locality, USNM 33082, 19082;

MCZ 9796-97, 9785; AMNH 18183.

Caribbean: Old Providence, USNM 38637.

Bahamas: vicinity of New Providence, CBC
Stations 238, 373, 379.Bermuda: FMNH 4972-74, 4838, 49037, 48868,
48249, 48869, 49047, 48276; UMMZ 172354,
172523-S, 175936, 176033, 176115, 176145,TABLE 23
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus afer*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	37.52	98.5	129	159	162	182	183	191	213	216	—
Head length	433	421	426	402	411	418	404	421	416	396	415.0
Head width	181	183	182	170	167	187	164	183	183	181	178.0
Head depth	285	249	256	245	241	234	257	246	239	241	249.0
Snout length	90	86	81	69	77	74	74	76	77	74	77.8
Suborbital width	19	20	16	19	19	19	19	21	21	19	19.2
Interorbital width	61	56	54	50	52	55	57	52	52	53	54.2
Length of: Orbit	127	102	97	88	86	85	85	84	82	74	85.1
Postorbital head	227	254	260	252	259	267	257	267	265	255	256.3
Maxillary	198	183	174	167	170	176	172	173	174	162	174.9
Lower jaw	196	188	171	167	170	170	175	178	176	162	175.3
Snout to angle of preopercle	317	289	287	267	278	275	279	280	282	269	282.3
Supramaxillary length	53	61	54	53	62	58	55	58	56	53	56.3
Maxillary width	43	46	39	38	37	41	38	39	35	37	39.3
Tip of lower jaw to gular notch	133	107	155	113	114	126	115	139	117	123	124.2
Body width	123	198	163	164	167	187	158	181	178	169	168.8
Body depth	323	386	415	396	398	404	393	403	387	391	389.6
Caudal peduncle depth	113	122	132	132	133	140	137	136	134	130	130.9
Tip of snout to dorsal origin	405	376	364	365	367	343	371	351	345	352	363.9
Tip of snout to pectoral base	368	355	399	349	352	354	347	385	357	345	361.1
Tip of lower jaw to pelvic base	391	406	488	402	426	423	407	469	416	433	426.1
Length of: Dorsal base	586	640	624	654	611	651	658	649	662	641	637.6
Depressed dorsal	691	741	744	767	716	736	770	720	761	748	739.4
Anal base	218	208	217	233	225	239	227	220	221	222	223.0
Depressed anal	356	360	360	390	370	365	374	348	364	359	364.6
End of dorsal to caudal base	94	86	109	104	93	88	98	89	87	83	93.1
Length of: Caudal peduncle	158	162	155	170	160	159	156	152	169	171	161.2
Pectoral	272	264	271	274	259	247	268	270	261	255	264.1
Pelvic	214	213	225	214	213	211	213	209	204	199	211.5
Dorsal spine I	91	91	89	88	77	63	82	79	61	74	79.5
Dorsal spine III	219	198	186	182	154	154	172	173	146	171	175.7
Dorsal spine XI	158	152	159	164	148	126	142	136	122	134	144.1
Anal spine I	93	107	89	82	93	88	82	86	75	74	86.9
Anal spine II	200	203	190	151	160	151	158	162	140	157	167.2
Anal spine III	182	183	182	176	160	151	158	162	155	153	166.2
Caudal base to tip of upper rays	218	233	260	242	241	253	221	249	246	241	240.4
Caudal base to tip of middle rays	269	264	291	283	278	275	251	288	282	271	275.2
Caudal base to tip of lower rays	194	233	256	252	253	258	219	270	272	252	245.9

^aAll proportions are expressed in thousandths of the standard length. All specimens are UMMZ from Bermuda; field and museum numbers as follows: Column 1, 1954-1; 2, 1955-1; 3, 70; 4, 69; 5, 71; 6, 172354; 7, VII: 27; 56; 8, 74; 9, 72; and 10, 73.

176358, 176349, 176525, 176582, 176621, 176488; MCZ 31037, 31038.

PACIFIC RECORDS

Mexico: Golfo de California, Sonora, Punta Guillermo outside Puerto San Carlos, UCLA W51-10; west end of Ensenada de las Tetras, UCLA W55-246; bay west of Las Tetras de Cabra, UCLA W55-243; Baja California, UCLA W65-75, W65-83; Punta Santelmo, UCLA W65-58; Punta Pulpito, UCLA W65-67; Bahía Magdalena, Turtle Inlet, UCLA W52-180; Isla Ceralvo, southwest corner, UCLA W61-35; Isla Carmen, UCLA W65-63; Isla Santa Cruz, UCLA W65-86; Isla San Francisco, UCLA W65-88; Angel de la Guarda, Puerto Refugio, UCLA W54-262.

Ecuador, Islas Galápagos: UCLA W53-178; Isla San Cristóbal (Chatham), ANSP 70138 (holotype, *A. galapagensis* Fowler); Isla Bartolomé, UCLA W64-42; Isla Santa Cruz (Indefatigable), north coast, UCLA W64-38; Academy Bay, UCLA W64-21, W64-26; Isla Fernandina (Narborough), south of Punta Espinosa, LACM W64-3.

Peru: Afuera Bay, USNM 127950 (holotype of *A. fasciatus* Hildebrand).

Epinephelus (Alphestes) multiguttatus
(Günther, 1866)

Plectropoma multiguttatum GÜNTHER, 1866, p. 600 (original description, Panama, holotype in British Museum [Natural History]).

Plectropoma afrom (non Bloch): GÜNTHER, 1869, pp. 411-412, pl. 67, fig. 3.

Alphestes multiguttatus: JORDAN AND GILBERT, 1883b, p. 107 (Mazatlán); 1883c, p. 110 (Panama); 1883g, p. 375 (Panama). JORDAN AND SWAIN, 1885b, pp. 395-396. JORDAN, 1886b, p. 377 (copied); 1887a, p. 84 (list only). JORDAN AND EIGENMANN, 1890, p. 349 (key, synonymy). JORDAN, 1895, p. 443 (Mazatlán). JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1165-1166. GILBERT AND STARKS, 1904, pp. 96-97 (characters, abundant in Panama Bay). FOWLER, 1916a, p. 409 (Panama). JORDAN AND EVERMANN, 1920, p. 388. MEEK AND HILDEBRAND, 1925, pp. 464-466, pl. 44 (Naos, Balboa, Panama City). JORDAN, EVERMANN, AND CLARK, 1930, p. 313. BREDER, 1936, p. 22 (San Diego Rocks). WALFORD, 1937, pp. 121-122, pl. 15, fig. b. SCHMITT AND SCHULTZ, 1940, p. 5 (Sullivan Bay, James Is., Galápagos). FOWLER, 1944, pp. 176, 245 (Balboa Harbor, Pearl Is.).

Epinephelus multiguttatus: JORDAN AND GILBERT, 1883h,

p. 625 (Panama). BOULENGER, 1895, pp. 255-256 (Las Penas, Jalisco); 1899, p. 2 (Gulf of Panama).

NOMENCLATURE: Boulenger listed the four syntypes of *Alphestes multiguttatus* collected by J. L. Dow on the Pacific coast of Panama in the collection of the British Museum.

The adjectival Latin name *multiguttatus*, meaning many spotted, refers to the dark spots on the head and body.

DIAGNOSIS: Small grouper with high fins, compressed body, narrow suborbital, and large scales. Preopercle with strong antrorse spine at angle. Body light, covered with dark brown spots which tend to coalesce to form longitudinal lines along the side posteriorly. Dorsal XI, 9; anal III, 9; pectoral 18; gill rakers 20-23.

Epinephelus multiguttatus is readily separable from *E. afer* by the distinct dark spots along the side that tend to coalesce into lines posteriorly. Pectoral is crossed by about six dark bars; *afer* has eight more or less irregular cross bars.

DESCRIPTION: For proportional measurements of 10 specimens see table 24. The proportions are similar to those of *E. afer*.

Exposed surface of maxilla scaled. Dorsal, caudal, and anal lobes rounded. Dorsal spines strong, with third to fifth longest; membranes not deeply notched between spines. Preopercle sharply angled with regular serrations on upper limb and a strong plectroid spine at angle. Nostrils subequal.

The following color description has been prepared from preserved specimens and from published accounts: ground color brown above and lighter below, densely covered with dark brown spots that tend to form lines posteriorly; pectoral crossed by five or six rather distinct dark cross bars on a yellow background; other fins and lower part of head and body unspotted, caudal fin with a narrow, pale yellow margin.

RELATIONSHIPS: *Epinephelus (Alphestes) multiguttatus* appears to be a twin of the only other species in the subgenus, *afer*. Apparently *Alphestes* has crossed the Central American Isthmus twice. The first invasion was followed by a separation sufficiently long to produce the differences noted between the two species. The second, much later, invasion of *afer* has been so recent that no appreciable differentiation has occurred.

ECOLOGY: Meek and Hildebrand (1925,

p. 466) found this species common along rocky shores of small islands in Panama Bay. They frequently took the young in tide pools.

DISTRIBUTION: Records of this species are from the Gulf of California to Panama and the Galápagos Islands (fig. 30).

SPECIMENS EXAMINED

Mexico: Golfo de California, Sonora, northeast of Punta de las Cuevas, UCLA W50-37; east side of Punta Paredones near Guaymas, UCLA W50-39; beach at La Libertad, UCLA W50-62; about 3 miles east of Puerto

TABLE 24
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Epinephelus multiguttatus*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	44	50	63	68	91.5	95	149	158.5	160	200	—
Head length	420	420	405	404	404	400	403	378	394	410	403.8
Head width	159	170	167	169	191	179	171	167	156	165	169.4
Head depth	250	260	262	265	257	253	238	243	228	243	249.9
Snout length	114	80	79	88	77	74	81	76	75	85	82.9
Suborbital width	16	20	16	22	22	16	20	21	19	23	19.5
Interorbital width	68	70	56	59	60	53	50	54	56	30	58.4
Length of: Orbit	102	110	95	96	93	89	87	79	88	80	91.9
Postorbital head	227	240	246	235	240	242	252	230	238	265	241.5
Maxillary	182	184	183	176	175	168	164	170	163	175	174.0
Lower jaw	182	190	190	184	180	174	174	177	166	185	180.2
Snout to angle of preopercle	284	290	286	272	273	268	275	262	266	275	275.1
Supramaxillary length	68	56	56	66	55	58	60	63	53	55	59.0
Maxillary width	45	50	40	37	44	42	40	44	44	45	43.1
Tip of lower jaw to gular notch	136	120	119	118	115	111	114	117	116	108	117.4
Body width	148	140	159	162	191	153	168	189	166	150	162.6
Body depth	364	340	349	360	372	363	369	356	331	350	355.4
Caudal peduncle depth	114	100	119	118	115	116	117	110	106	115	113.0
Tip of snout to dorsal origin	375	380	381	353	377	363	356	341	369	365	366.0
Tip of snout to pectoral base	375	350	365	353	344	342	362	328	341	350	351.0
Tip of lower jaw to pelvic base	409	390	389	397	383	389	430	391	400	415	399.3
Length of: Dorsal base	591	620	651	618	634	642	631	618	613	620	623.8
Depressed dorsal	659	700	746	728	727	732	705	707	700	695	709.9
Anal base	193	200	214	221	202	189	201	183	175	175	195.3
Depressed anal	330	340	349	353	339	326	329	303	300	308	327.7
End of dorsal to caudal base	102	100	87	96	98	89	87	88	91	90	92.8
Length of: Caudal peduncle	159	170	175	176	164	168	154	158	172	165	166.1
Pectoral	261	260	246	265	251	237	228	230	219	235	243.2
Pelvic	205	220	214	213	191	205	188	183	172	183	197.4
Dorsal spine I	68	84	71	66	71	63	64	60	59	58	66.4
Dorsal spine III	159	170	159	147	153	137	138	132	138	120	145.3
Dorsal spine XI	125	144	135	125	131	132	114	120	119	113	125.8
Anal spine I	91	80	87	81	82	74	70	66	72	70	77.3
Anal spine II	148	150	167	162	175	158	144	145	141	130	152.0
Anal spine III	148	160	167	176	158	153	154	145	138	130	152.9
Caudal base to tip of upper rays	227	230	246	250	234	237	248	202	219	225	231.8
Caudal base to tip of middle rays	250	240	270	272	257	263	245	227	231	250	250.5
Caudal base to tip of lower rays	250	200	238	235	240	242	228	196	206	218	225.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1, 2, USNM 81927; 3-6, USNM 128754; 7-10, USNM 29519, 76809, 128753, 29291 respectively. For data see text.

San Carlos, UCLA W50-36; northwest side of Punta de las Cuevas, UCLA W51-8; Punta Guillermo, near Guaymas, UCLA W51-11; Punta Guillermo, northwest side, UCLA W51-62; south of Puerto San Carlos, UCLA W51-260; Puerto Libertad, UCLA W50-66; bay between Las Tetas de Cabra and Punta San Antonio, UCLA W52-43; Bahía San Lucas, UCLA W52-259; Isthmus of Isla Venados, UCLA W51-54; Sinaloa, Esterodel Astillero, Mazatlán, UCLA W51-36; north of Punta Camarones, UCLA W51-41; Mazatlán, east side of Punta Pala, UCLA W51-58; Guerrero, Acapulco, MCZ 28783; San Diego Rocks, BOC 1075.

Panama: Panama, FMNH 20604, 20627, 20633-35; USNM 29291, 29519, 30954, 30988, 76809, 80210-11, 80273-76, 80296-97, 81926-28, 128753; MCZ 10170; Panama Bay, USNM 80207-08, 80294; Naos Island, USNM 80206; Balboa, USNM 80209, 80212-13, 80295, 128755; Venado Beach, USNM 128754; Canal Zone, Perico Island, east side, UCLA W53-277; Panama City market, UCLA W53-260, W53-270; east of Paitilla Point, large tide pool, UCLA W53-263; no specific locality, ANSP 45123-24; USNM 80321.

MYCTEROPERCA GILL, 1864

Mycteroperca GILL, 1864a, p. 80 (type species, *Serranus olfax* Jenyns by subsequent designation in Gill, 1865, p. 105).

Trisotropis GILL, 1865, pp. 104-105 (type species, *Johnius guttatus* Bloch and Schneider [a subjective synonym of *Perca venenosa* Linnaeus], by original designation).

Parepinephelus BLEEKER, 1876, p. 257 (type species, *Serranus acutirostris* Valenciennes [a subjective synonym of *Epinephelus ruber* Bloch], by monotypy).

Archoperca JORDAN AND EVERMANN, 1896b, p. 1171 (type species, *Mycteroperca bouleengeri* Jordan and

Starks [a subjective synonym of *Mycteroperca xenarcha* Jordan], by monotypy. [Proposed as a subgenus].

Xystroperca JORDAN AND EVERMANN, 1896b, p. 1181 (type species, *Mycteroperca pardalis* Gilbert [a subjective synonym of *Epinephelus rosacea* Streets], by monotypy. [Proposed as a subgenus]).

NOMENCLATURE: *Mycteroperca* is derived from the Greek *μυκτῆρος*, nostrils, and *πέρκα*, perch, in reference to the enlarged posterior nostril of the type species. This name is feminine.

DIAGNOSIS: Moderate to large groupers with elongate bodies that have dorsal profile more strongly arched than ventral. Body robust, somewhat compressed. Dorsal XI, 15-18; anal III, 10-13; gill rakers 10 to 54 on first arch. Head moderate, 33 to 41 per cent of body length.

Caudal fin square or lunate. Scales small, ctenoid. Lacrimal and suborbital region broad. Supramaxilla present, well developed.

Skull with dorsal crests well developed; frontoparietal crests parallel, joining supra-orbital ridge. Postorbital process outside of frontoparietal crest. Supraethmoid forming a transverse wall. Parasphenoid straight or nearly so. Anterior wing of hyomandibular reduced. Enlarged anterior canine teeth near the symphysis of each jaw.

Upper limb of preopercle serrate, lower unarmed; a few large teeth at angle below a more or less pronounced notch; angle sometimes forms a definite lobe. Middle opercular spine nearly equidistant from others; opercular flap ends in an acute, nearly symmetrical point. Some species have exerted rays in dorsal, anal, or caudal of adult.

RELATIONSHIPS: Although close to *Epinephelus*, the above combination of characters is deemed sufficient to warrant recognition of this group as a genus.

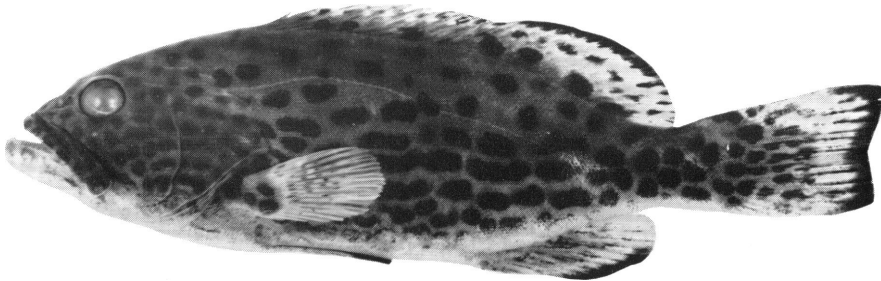


FIG. 31. *Mycteroperca venenosa*, AMNH field no. S66-112 from Berry Islands, Bahamas, 155 mm.

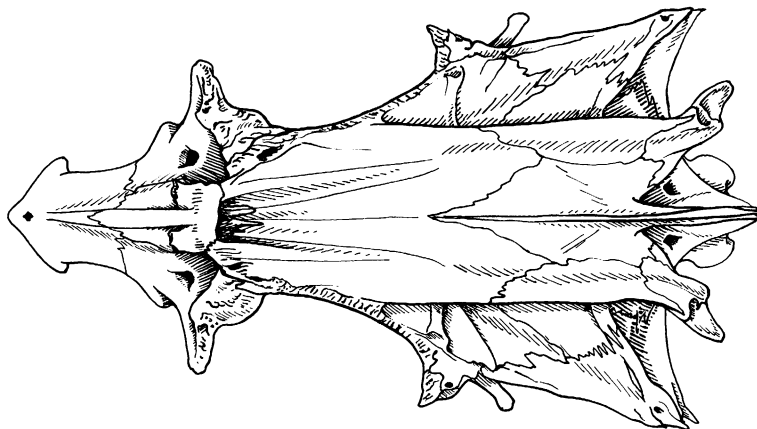


FIG. 32. *Mycteroperca venenosa*, UMMZ 172560-S, from Bermuda. Dorsal view of the neurocranium.

INCLUDED SPECIES: Thirteen American species of groupers belong to this genus, eight in the Western Atlantic and five in the Eastern Pacific. *Trisotropis dermopterus* (Temminck and Schlegel), a grouper found in the coastal waters of Japan, has some characters that suggest relationship with *Mycteroperca*. A specimen in the UMMZ collection has parallel frontoparietal crests but there is no transverse supraethmoid wall and the body shape is compressed and quite unlike that in the species of *Mycteroperca*. I do not believe that it is a member of this genus; until studied more thoroughly it may best be assigned to *Epinephelus*.

The Atlantic species have recently been reviewed by Cervigón M. and Velasquez (1966) and the Pacific forms were treated by Rosenblatt and Zahuranec (1967). The distinguishing characters of the species of *Mycteroperca* are summarized in the following key and in table 25.

KEY TO THE SPECIES OF *Mycteroperca*

1. Preopercle gently rounded, its upper and lower limbs meeting in a broadly obtuse angle or gentle curve, its notch more or less obsolescent, with no definite lobe below¹ . . . 2
- Preopercle angulate, the upper and lower limbs meeting at an angle of a little more than 90°, usually a marked indentation above the angle, below which is a definite, more or less serrate lobe 5

¹Specimens under 75 mm. long usually with a remnant of the larval spines at the preopercular angle, hence, for young specimens the key should be used with caution.

2. Developed gill rakers on lower limb of first arch four to eight (the rudiments more or less coalescent). Color pattern consisting of about 12 narrow, oblique lines crossing upper part of body. Posterior nostril greatly enlarged in specimens over 200 mm. long. Dorsal, anal, and caudal rays exerted in specimens over 350 mm. Western Atlantic *Mycteroperca tigris*
- Developed gill rakers on lower limb of first arch 11 to 16. Color pattern not as above. Dorsal, anal, and caudal rays not exerted 3
3. Distal third of pectoral bright yellow in life, sharply delimited from remainder of fin, which is variously marked with small dark spots. Large individuals with small, bright spots on lower part of body and head. Western Atlantic *Mycteroperca venenosa*
- Pectoral with narrow orange margin that is about one-fifth fin length and shades gradually into basal color pattern, which is dark and lacks discrete spots. No bright red spots . . 4
4. Side of head and lower part of body with brassy yellow spots surrounded by a light blue network. Anal fin gently rounded. Western Atlantic *Mycteroperca bonaci*
- Side of head without brassy spots. Anal fin falcate in large individuals. Eastern Pacific *Mycteroperca jordani*
5. Total gill rakers on first arch 45 to 54. Dorsal and anal fins falcate in large specimens. Eastern and Western Atlantic *Mycteroperca rubra*
- Total gill rakers on first arch 40 or fewer . . . 6
6. Total gill rakers on first arch 35 or fewer . . . 7
- Total gill rakers 36-40. Dorsal and anal fins falcate. Eastern Pacific . . *Mycteroperca rosacea*

TABLE 25
SOME CHARACTERS OF THE SPECIES OF *Mycteroperca*

Species	Dorsal	Anal soft rays	Pectoral rays	Gill rakers	Posterior nostril	Median fin rays	Color	Longest dorsal spine
<i>venenosa</i>	XI, 15-17	11	34	24-27	small	even	rows of rounded black blotches on greenish brown or red background, outer $\frac{3}{8}$ of pectoral yellow	3 or 4
<i>bonaci</i>	XI, 16-18	12	34	19-22	small	even	brassy spots on head, rows of square dark blotches on side, outer $\frac{1}{8}$ of pectoral orange	3 or 4
<i>jordani</i>	XI, 16-17	11	34	17-21	small	even	brownish with dark quadrate blotches	3 or 4
<i>tigris</i>	XI, 16-17	11	34	10-15	large	exserted	11 or 12 narrow oblique light lines on upper side	3 or 4
<i>microlepis</i>	XI, 16-18	11	33-34	21-28	slightly enlarged in adult	even	gray with darker vermiculations	3 or 4
<i>interstitialis</i>	XI, 17 (15-18)	11 (12)	34	23-27	large	exserted	dark brown or with pale reticulations on side	3 or 4
<i>cidi</i>	XI, 16	11	32-34	27-36	large	exserted	grayish brown	3 or 4
<i>phenax</i>	XI, 17 (16-18)	11	32-34	27-31	large	exserted	grayish brown with well-spaced dark spots	3 or 4
<i>xenarcha</i>	XI, 15-16	11	34	30-35	large	exserted	gray or blotched	3 or 4
<i>prionura</i>	XI, 16-18	11	30-32	34-38	not very large	exserted	tan with dark spots	3 or 4
<i>olfax</i>	XI, 16-17	11	32-34	25-29	very large	even	olive brown or purple-brown mottled with faint spots, or yellow	2
<i>rosacea</i>	XI, 16-18	11	32	37-39	large	even	covered with small dark spots or golden yellow	3 or 4
<i>rubra</i>	XI, 15-17	11	32	45-54	small	even	brownish with white spots and wavy undulating dark and light lines on side	3 or 4

7. First three dorsal spines elevated into a definite lobe. Galápagos Islands . . . *Mycteroperca olfax*
First three spines not elevated into a definite lobe 8
8. Dorsal, anal, and caudal without produced rays. Color predominantly gray, the side with a pattern of dark vermiculations. Western Atlantic *Mycteroperca microlepis*
Some rays of the soft dorsal, anal, or caudal produced in large specimens. Color brownish or gray with a pattern of spots or blotches . . . 9
9. Soft dorsal fin falcate in large specimens. Occurs in gray and pinto (blotched) color phases. Eastern Pacific *Mycteroperca xenarcha*
Soft dorsal fin not falcate with but some individual rays exerted in large specimens . . . 10
10. Body color light grayish brown, covered with small, well-spaced, brownish red spots. Exsertions on middle caudal rays irregular. Green submarginal band on caudal indistinct. Western Atlantic *Mycteroperca phenax*
Body dark reddish brown, sometimes broken into hexagonal spots separated by narrow, pale reticulations. Exsertions on middle caudal rays regular. Greenish submarginal band on tail distinct. Western Atlantic
. *Mycteroperca interstitialis*

Species-Groups in *Mycteroperca*

The genus *Mycteroperca* seems to be a tightly circumscribed complex of closely related species. Cervigón M. and Velasquez (1966) have pointed out that the Atlantic species fall into two weakly differentiated groups and I agree with this except that I would be inclined to place *M. microlepis* with *interstitialis* rather than with *venenosa* and *bonaci*. The evidence is not strong either way, however, and it is precisely for this reason that the groups should not be accorded subgeneric recognition.

Mycteroperca venenosa Species-Group

Members of this species-group have evenly curved preopercular bones without an abrupt angle and only a suggestion of a shallow notch near the posterior ventral corner. There is no well-developed serrated lobe at the angle of the preopercle. The supraoccipital crest is low, not extending above the plane of the dorsal margins of the lateral crests (fig. 37). Four species—*venenosa*, *bonaci*, *jordani* and *tigris*—are included here. Of these only *tigris* has strongly exerted fin rays in large adults.

Mycteroperca venenosa (Linnaeus, 1758)

YELLOWFIN GROUPER

Figure 31

- Piratiapia* MARCGRAVE, 1648, p. 158 (Brazil).
Perca marina venenosa CATESBY, 1743, p. 5, fig. 5.
Perca venenosa LINNAEUS, 1758, p. 292 (original description, America). BONNATERRE, 1788, p. 133 (America).
Bonaci cardinal PARRA, 1787, p. 29, pl. 16, fig. 1 (common name only).
Bodianus apua BLOCH, 1790, pp. 50–52, pl. 229 (original description, based on a drawing by Prince Maurice).
Johnius guttatus BLOCH AND SCHNEIDER, 1801, p. 77 (original description, based on Parra).
Bodianus marginatus BLOCH AND SCHNEIDER, 1801, p. 331 (original description, after Marcgrave).
Serranus apua: VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 287–288. GUICHENOT, in Ramon de la Sagra, 1853, p. 152 (Cuba). GÜNTHER, 1859, p. 140 (Caribbean; West Indies; Jamaica). GÜNTHER, 1880, p. 6 (St. Thomas).
Serranus cardinalis VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 378–379 (original description, after Parra). STORER, 1846, p. 279. GUICHENOT, in Ramon de la Sagra, 1853, p. 152. POEY, 1864, p. 177.
Serranus rupestris VALENCIENNES, in Cuvier and Valenciennes, 1833, pp. 437–440 (original description, St. Domingo; St. Bartholemy). STORER, 1846, p. 281. GÜNTHER, 1859, p. 145. POEY, 1865 (1865–1866), p. 200.
Serranus petrosus POEY, 1860 (1858–1861), pp. 136–138 (original description); 1867 (1866–1868), p. 155 (nomenclature, Cuba).
Trisotropis cardinalis: POEY, 1865 (1865–1866), p. 200 (nomenclature); 1866 (1866–1868), pp. 4–5 (suspected of causing ciguatera); 1868 (1866–1868), pp. 282–283; 1870, pp. 303–304; 1875 (1875–1877), p. 13.
Trisotropis petrosus: POEY, 1870, pp. 304–305 (Cuba); 1875 (1875–1877), p. 13. GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, p. 918. POEY, 1883, p. 118.
Trisotropis undulosus (non Cuvier): COPE, 1871b, p. 465 (St. Croix).
Trisotropis guttatus: GOODE, 1876, pp. 56–57 (Bermuda); 1877, p. 292. COCKERELL, 1892, p. 7 (Jamaica).
Epinephelus venenosus: JORDAN, 1884a, p. 68 (Key West); 1885c, p. 192 (nomenclature). BOULENGER, 1895, p. 259.
Mycteroperca venenosa: JORDAN AND SWAIN, 1885b, pp. 373–376. JORDAN, 1887a, p. 84; 1887c, p. 40; 1887e, p. 580. HENSHALL, 1895, p. 216 (South Florida Keys). JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1172–1173. BRICE, 1898, p. 283. EVERMANN AND KENDALL, 1900, p. 74 (Florida).

- JORDAN, 1905, p. 327, fig. 262. NICHOLS, 1912, p. 187. FOWLER, 1915b, p. 545 (Port Castries, St. Lucia). JORDAN AND EVERMANN, 1920, p. 391 (photograph). NICHOLS, 1921, p. 22 (Turks Is.). SCHROEDER, 1924, p. 16. BREDER, 1927, p. 39 (West Indies). BORODIN, 1928, p. 19 (Florida, spelled *Mictroperca*). BREDER, 1929, p. 160. LONGLEY AND HILDEBRAND, 1941, p. 99, pl. 6, fig. 1 (Tortugas, ecology). MANTER, 1947, p. 373 (parasites). ERDMAN, 1957, pp. 330-331 (Puerto Rico). SMITH, 1958, pp. 18, 54-55, fig. 10, pl. 12 (Bermuda, ecology); 1959, p. 114 (hermaphroditic). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:5, 1:17-18, 1:23, fig. 16. RANDALL, 1963, p. 37 (Virgin Is., ecology). CALDWELL, 1966, pp. 42-43 (Jamaica). CERVIGÓN M., 1966b, pp. 297-298 (Cubagua, Venezuela). CERVIGÓN M., AND VELASQUEZ, 1966, pp. 82-85 (general account, osteology). RANDALL, 1967, pp. 703-704 (food habits); 1968, p. 64, fig. 70 (general account, color photograph). BÖHLKE AND CHAPLIN, 1968, p. 287 (Bahamas).
- Mycteroperca venenosa* var. *venenosa*: JORDAN AND SWAIN, 1885b, pp. 373-375. JORDAN AND EIGENMANN, 1890, p. 369.
- Mycteroperca venenosa* var. *apua*: JORDAN AND SWAIN, 1885b, pp. 373-376. JORDAN AND EIGENMANN, 1890, p. 370.
- Mycteroperca venenosa* var. *guttatus* or *cardinalis*: JORDAN AND SWAIN, 1885b, pp. 373-376.
- Mycteroperca venenosa apua*: JORDAN, 1887c, p. 40 (Havana); 1887e, p. 580 (West Indies). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1173-1174. JORDAN AND RUTTER, 1898, p. 105 (Jamaica). EVERMANN AND KENDALL, 1900, p. 74 (Florida). JORDAN AND THOMPSON, 1905, p. 240. BEAN, 1906, p. 54 (Bermuda). FOWLER, 1907, p. 260 (St. Martin; St. Croix). ROSÉN, 1911, p. 54 (Green Turtle Cay). FOWLER, 1920, p. 137 (St. Martin). MEEK AND HILDEBRAND, 1925, p. 446 (not recorded from the Isthmus of Panama). BEEBE AND TEE-VAN, 1928, p. 127 (Port-au-Prince). BREDER, 1929, p. 160. GUDGER, 1929, p. 173 (Tortugas, parasites). PARR, 1930, p. 50 (Eleuthera). FOWLER, 1942b, p. 68 (Cuba); 1944, p. 445 (Nassau; Green Turtle Cay; Eleuthera); 1953, p. 55 (Cartagena). BRIGGS, 1958, p. 273.
- Mycteroperca venenosa guttata*: JORDAN AND BOLLMAN, 1889, p. 551 (Green Turtle Cay). JORDAN, 1890, p. 648 (St. Lucia). FOWLER, 1944, p. 445.
- Epinephelus apua*: LEE, 1889, p. 671 (Nassau). LÖNNBERG, 1895, p. 657 (Haiti).
- Mycteroperca bowersi* EVERMANN AND MARSH, 1902, p. 158, fig. 45 (original description, Culebra Is., Puerto Rico, holotype, USNM 49530). BEAN, 1906, p. 54. JORDAN AND EVERMANN, 1920, p. 394. EVERMANN AND SEALE, 1924, p. 29 (Barbados). NICHOLS, 1929, p. 253, fig. 120 (Puerto Rico). GUDGER, 1929, pp. 173-174 (Tortugas). JORDAN, EVERMANN, AND CLARK, 1930, p. 314. BEEBE AND TEE-VAN, 1933, p. 131, (Bermuda). BUTSCH, 1939, p. 24 (Barbados).
- Epinephelus (Mycteroperca) bonaci* (non Poey): METZEL-AAR, 1919, p. 50, figs. 17, 18 (Dutch West Indies).
- Mycteroperca apua*: JORDAN AND EVERMANN, 1920, p. 392.
- Mycteroperca venenosa venenosa*: BREDER, 1929, p. 160. FOWLER, 1944, p. 445 (Turks Is., copied).
- Trisotrophis venenosus*: JORDAN, EVERMANN, AND CLARK, 1930, p. 313. BEEBE AND TEE-VAN, 1933, p. 129 (Bermuda). BRIGGS, 1958, p. 273.
- Trisotrophis venenosus apua*: JORDAN, EVERMANN, AND CLARK, 1930, p. 313.
- NOMENCLATURE: The name *apua* has been used for the deep-water, red form but in the absence of structural differences I believe that it is better regarded as an environmentally produced color phase.
- Linnaeus based his description of *Perca venenosa* on Catesby's figure; hence, there is no holotype.
- The name *venenosa*, from the Latin *venenosus*, means full of poison and refers to the supposed poisonous property of the flesh.
- DIAGNOSIS: Moderate-sized species of *Mycteroperca* with robust body, medium-sized scales, rounded preopercle, with angle not produced. Dorsal XI, (15) 16; anal III, 11; pectoral 17; gill rakers 25-27. Posterior nostril not enlarged in small individuals but in specimens more than 500 mm. long it may be twice as large as the anterior (Cervigón M. and Velasquez, 1966, p. 85). Vertical fins without exerted rays. Dorsal with first three spines not elongate, no elevated lobe. Two color phases, deep-water red and a shallow-water greenish phase. Side of body with irregular rows of rounded dark blotches. Outer third of pectoral abruptly delimited, brilliant yellow. Lower part of body and head of large individuals with small, bright red spots.
- The yellowfin grouper is quite close structurally to *Mycteroperca bonaci*, with which it shares the rounded preopercle and subequal nostrils. *Mycteroperca venenosa* is more compressed and usually has one less ray in the soft dorsal and anal fins. Color patterns are different but bear a resemblance commensurate with their similar structure. In *venenosa* dark blotches on upper side of the body are rounded and arranged in ill-defined rows, whereas in *bonaci* the dark blotches are regularly quadrate. *Mycteroperca*

venenosa has deep-water and shallow-water color phases, but *bonaci* does not. Most distinctive feature of *venenosa* is the broad yellow margin of the pectoral fin in contrast to the narrow orange edge of the pectoral of *bonaci*.

DESCRIPTION: Proportional measurements of 10 specimens of *Mycteroperca venenosa* are given in table 26. The profile of the head is steeper than that of *M. bonaci* and the body is much deeper. Otherwise, the proportions are similar in the two species.

There are two color phases of the yellowfin grouper and I have seen some intermediates between them, although most individuals are clearly of one color phase or the other. The shallow-water form has a brownish or greenish ground color with the lower side of the body and head sparsely peppered with dark red spots, each about the size of the nostril. These do not develop until the fish is about 16 inches long. On the lower part of the body are irregular dark blotches that have salmon-red centers. The lining of the mouth is washed with orange. Along the midside there are irregular rows of oblong, rounded, dark blotches, each somewhat larger than the eye.

The spinous dorsal is pale for the middle third, dusky distally and proximally. The soft dorsal and anal fins are pale olive with one or more rows of small black spots that merge distally to form a black submarginal band. There are splashes of salmon red on the base of the anal. These fins are narrowly edged in pearly white. The caudal is like the rest of the body with darker blotches merging into a dark submarginal band and with a narrow blue margin. Sometimes there are salmon streaks along the upper and lower margins. The basal two-thirds of the pectoral is like the body, with irregular small dark spots. The sharply delimited outer one-third is yellow and immaculate. The pelvic is like the body on the basal half, with salmon-red blotches and with the leading edge white, the outer half of the anterior rays very dark, separated by lighter membranes. The inside of the mouth is orange. In larger individuals the red spots are carried onto the base of the pectoral. The above description is composite, based largely on an individual in the Miami Seaquarium in January, 1957.

The red, deep-water form is here described from a 595 mm.-long fish taken July 26, 1956, on Argus Bank, Bermuda, at a depth of 27

fathoms: top of head and body above the line from snout to upper base of caudal brilliant scarlet, below this shaded to grayish white. Grayish area and lower side of head sprinkled with red spots about 1-2 mm. in diameter, each surrounded by a yellow ring so that the whole spot is about 6 mm. across. Body pattern broken into blotches by lighter lines as in *Mycteroperca bonaci*, but blotches smaller and much less regular than in that species and more rounded, especially above the midline. Nine irregular light lines along side of body, four in red part and five below, with interspaces irregularly broken into rounded blotches. Anterior part of belly and breast irregularly mottled greenish with red spots. Posterior tip of premaxilla and cartilaginous edge of mandible bright yellow. Tip of chin gray. All dorsal spines black. Basal one-third to one-half of interspinous membranes scarlet, thence dark to margin with a yellow area behind each spine. Soft dorsal red for basal half, black at margin. Caudal fin entirely dark, nearly black at margin. Anal fin black for outer fifth of rays, proximal area grayish with scattered red spots surrounded by yellow (like those on the body but only one-half as large). Some yellow along spines. Outer third of pectoral brilliant yellow, sharply delimited from dark middle third. Base of fin grayish with some red spots. Outer third of pelvic black, remainder gray with a greenish orange wash on membranes.

In this species none of the fins has exerted rays. The soft dorsal and anal fins are slightly convex along their margins, their posterior angles rounded. The caudal is slightly lunate with moderately sharp lobes. The nostrils are subequal; the preopercle is evenly rounded with the notch reduced to a shallow emargination. The exposed surface of the maxilla is scaled; the upper lip is wide as in *Mycteroperca bonaci*. The skull closely resembles that of *bonaci* (figs. 32 and 37).

RELATIONSHIPS: *Mycteroperca venenosa* is closely related to *M. bonaci* and *M. jordani*. These three species and *M. tigris*, form a unit within the genus and are referred to here as the *venenosa* group.

ECOLOGY: Examples of the red form taken on Argus Bank on July 23-26, 1956, were nearly ripe. Erdman collected ripe eggs at Culebra Island on March 11, 1957.

The young of this species has not been re-

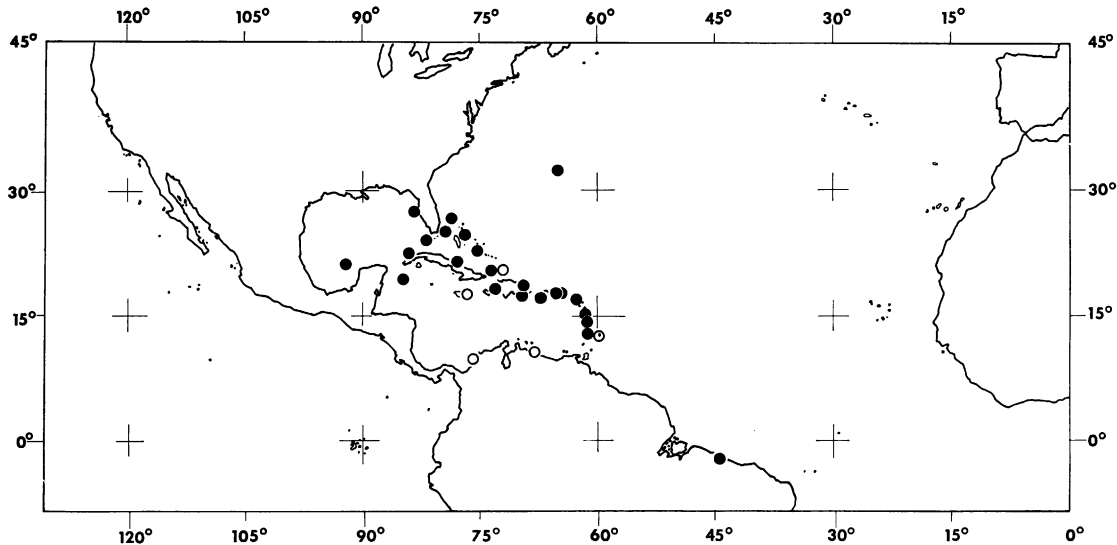


FIG. 33. *Mycteroperca venenosa* distribution records. Solid circles represent specimens examined, open circles are additional literature records.

ported. The smallest specimen examined was 57 mm. long and was in all respects like larger individuals.

DISTRIBUTION: The yellowfin grouper is known from Bermuda and southern Florida, throughout the Bahamas and the Antilles, on the Campeche Bank, and south to Brazil (fig. 33).

SPECIMENS EXAMINED

Florida: Key West, FMNH 31754; USNM 35084, 47349, 47395; Triumph Reef off Elliott Key, FMNH 46906; Clearwater, CU 26088; no specific locality, USNM 107194.

Mexico: Arcas Cay, sight record, May, 1958.
Caribbean Sea: Misteriosa Bank, FMNH 39860.

Brazil: Maranhão, MCZ 10148.

St. Lucia: USNM 41315.

Dominica: USNM 29862.

St. Martins: ANSP 13459.

St. Thomas: USNM 34956; MCZ 10151.

Puerto Rico: Culebra Island, USNM 49530 (holotype of *Mycteroperca bowersi* Evermann and Marsh); UMMZ 172529; La Parguera, UMMZ 172530, 173098; Las Croabas, UMMZ 173097.

Hispaniola: Santo Domingo, USNM 21214; Samaná Bay, USNM 88956; Port-au-Prince, USNM 133686; AMNH 18941.

Cuba: Havana, USNM 35103, 132968; FMNH 57543; no specific locality, USNM 6113, 9870; MCZ 10007, 10017, 10072, 10108, 22827, 26951.

Bahamas: Great Bahama Bank, FMNH; Walker Cay, FMNH 51378; vicinity of New Providence, CBC Stations 234, 246; Bimini, UMMZ 174397-S; no specific locality, MCZ 3099.

West Indies: no specific locality, USNM 15006, 33252.

Bermuda: FMNH 50577, 5227-28; USNM 170064-65; MCZ 31029; UMMZ 176445, 176626, 172560-S.

Mycteroperca bonaci (Poey, 1860)

BLACK GROUPER

Rockfish BROWNE, 1756, p. 448 (Jamaica).

Bonaci arara PARRA, 1787, p. 30, pl. 16, fig. 2 (Cuba).

Serranus arara STORER, 1846, p. 279 (after Parra, preoccupied by *Serranus arara* Valenciennes = *Epinephelus guttatus*). POEY, 1860 (1858-1861), p. 132 (Cuba). STEINDACHNER, 1867, p. 348 (Surinam and Barbados). COCKERELL, 1892, p. 8 (Jamaica).

Serranus bonaci POEY, 1860 (1858-1861), pp. 129-131 (original description, Cuba); 1861 (1858-1861), pp. 352-353; 1864, p. 177; 1867 (1866-1868), pp. 155-156.

Serranus brunneus POEY, 1860 (1858-1861), p. 131 (original description, Cuba); 1867 (1866-1868), p. 156.

Serranus decimalis POEY, 1860 (1858-1861), p. 138 (original description, Cuba).

TABLE 26
 PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca venenosa*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	156	172	197	200	214	225	254	321	327	489	—
Head length	378	366	373	380	362	373	354	346	355	358	364.5
Head width	147	145	157	158	159	160	146	159	167	155	155.3
Head depth	236	259	249	280	245	253	232	227	220	235	246.3
Snout length	93	105	94	88	96	102	98	93	101	104	97.4
Suborbital width	35	38	38	40	40	38	37	39	40	47	39.2
Interorbital width	74	78	66	80	68	71	69	67	76	78	72.7
Length of: Orbit	71	67	66	68	58	58	55	53	52	46	59.4
Postorbital head	228	215	226	233	222	222	213	218	220	232	222.9
Maxillary	179	180	180	185	173	176	169	165	168	171	174.6
Lower jaw	186	183	188	190	173	182	169	171	171	179	179.2
Snout to angle of preopercle	263	262	261	260	255	260	250	237	245	249	254.2
Supramaxillary length	58	55	56	60	51	56	57	56	58	51	55.8
Maxillary width	45	41	38	40	42	40	35	37	40	38	39.6
Tip of lower jaw to gular notch	99	—	96	103	117	127	102	100	104	102	105.5
Body width	135	—	145	155	145	149	146	156	150	155	148.4
Body depth	346	320	322	338	334	333	311	308	327	331	327.0
Caudal peduncle depth	125	116	117	123	117	111	110	112	119	117	116.7
Tip of snout to dorsal origin	378	372	383	373	371	369	353	355	370	380	370.0
Tip of snout to pectoral base	340	349	340	343	357	342	323	317	324	339	337.4
Tip of lower jaw to pelvic base	369	366	376	378	416	402	378	358	365	362	377.0
Length of: Dorsal base	583	538	551	553	514	542	528	520	544	556	542.9
Depressed dorsal	660	610	622	618	577	609	602	583	612	614	610.7
Anal base	199	203	198	205	192	204	205	193	205	186	199.0
Depressed anal	295	302	292	280	287	293	291	267	281	256	284.4
End of dorsal to caudal base	151	151	157	160	157	160	—	—	—	147	154.7
Length of: Caudal peduncle	183	198	198	218	194	200	205	185	202	198	198.1
Pectoral	205	203	211	195	—	204	195	182	183	—	197.2
Pelvic	186	186	198	180	194	184	177	167	168	168	180.9
Dorsal spine I	64	58	58	70	51	69	55	61	67	55	60.8
Dorsal spine III	125	116	137	—	119	136	126	126	138	106	125.4
Dorsal spine XI	103	110	96	110	107	104	118	93	119	90	105.0
Anal spine I	54	44	51	55	37	47	47	53	52	44	48.4
Anal spine II	83	84	84	95	75	89	79	79	86	88	84.2
Anal spine III	115	105	122	110	103	116	94	93	98	123	107.9
Caudal base to tip of upper rays	269	250	251	265	266	278	256	252	250	—	259.6
Caudal base to tip of middle rays	240	218	228	228	215	229	219	206	203	—	220.7
Caudal base to tip of lower rays	272	247	261	253	255	267	240	237	226	—	250.9

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1, 3, 5, 6, FMNH 57543, 31754, 46906, 50577 respectively; 2, 4, 10, UMMZ 172530, 173097, 174397-S respectively; 7-9, UMMZ from Bermuda, field numbers 156, 155, 154 respectively.

Serranus cyclopmatus POEY, 1861 (1858-1861), p. 353 (original description, Cuba); 1867 (1866-1868), p. 156.

Serranus lateopictus POEY, 1861 (1858-1861), p. 353 (original description, Cuba).

Trisotropis aguaji POEY, 1866 (1866-1868), p. 5 (suspected of causing ciguatera; *nomen nudum*); 1867 (1866-1868), pp. 229-231, 284 (original descrip-

tion, Cuba); 1870, p. 306; 1875 (1875-1877), pp. 13-14.

Trisotropis bonaci: POEY, 1867 (1866-1868), pp. 155-156; 1868 (1866-1868), pp. 283-284 (Cuba); 1870, p. 306 (nomenclature); 1875 (1875-1877), p. 13. BEAN AND DRESEL, 1885, pp. 164-167 (Jamaica). COCKERELL, 1892, p. 7 (Jamaica). JORDAN, EVERMANN, AND CLARK, 1930, p. 314 (synonymy). BEEBE

- AND TEE-VAN, 1933, pp. 129–130 (Bermuda). BEEBE AND HOLLISTER, 1935, p. 215 (Union Is., Grenadines). HOWELL Y RIVERO, 1938, p. 191 (Poey "types" in MCZ). BUTSCH, 1939, p. 23 (Barbados).
- Trisotropis brunneus*: POEY, 1868 (1866–1868), p. 284; 1870, pp. 305–306; 1875 (1875–1877), p. 13; 1883, p. 118. JORDAN AND GILBERT, 1883a, p. 538.
- Trisotropis undulosus* (non Cuvier): GOODE, 1876, pp. 55–56 (Bermuda); 1877, p. 292; 1879, p. 50.
- Epinephelus bonaci*: JORDAN, 1884a, p. 77 (Key West); 1885b, p. 124 (Key West). BOULENGER, 1895, pp. 265–266. MIRANDA-RIBEIRO, 1915, pp. 24–25 (Río de Janeiro and Angra dos Reis); 1918, pp. 90–91.
- Mycteroperca bonaci*: JORDAN AND SWAIN, 1885b, pp. 370–371. JORDAN, 1887a, p. 84; 1887c, p. 40 (Havana); 1887e, p. 580 (West Indies). HENSHALL, 1891, p. 387 (Key West); 1895, p. 216. SMITH, 1896, p. 175 (Key Biscayne Bay). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1174–1175; 1900, pl. 187, fig. 492 (skull). JORDAN AND RUTTER, 1898, p. 105 (Jamaica). SMITH, 1899, p. 880 (Woods Hole). EVERMANN AND KENDALL, 1900, p. 74 (Florida). SMITH, 1901, p. 310; 1902, p. 33. EVERMANN AND MARSH, 1902, p. 157 (Puerto Rico). TOWNSEND, 1905, p. 101 (an individual lived seven years in N.Y. Aquarium). BEAN, 1906, pp. 53–54 (Bermuda). KENDALL, 1908, p. 99 (Katama Bay). SUMNER, OSBURN, AND COLE, 1913, pp. 167, 756 (Woods Hole). FOWLER, 1915b, pp. 533, 543 (Port-of-Spain, St. Georges, Grenada); 1920, p. 153 (Key West; Charlotte Harbor). JORDAN AND EVERMANN, 1920, p. 392 (photograph). NICHOLS, 1921, p. 22 (Turks Is.). SCHROEDER, 1924, p. 16. MEEK AND HILDEBRAND, 1925, p. 447 (Toro Point, Colón, Porto Bello, Panama). NICHOLS AND BREDER, 1927, p. 80, fig. 105. BREDER, 1929, pp. 160–161. NICHOLS, 1929, pp. 252–253, fig. 119 (not common in Puerto Rico). FOWLER, 1942b, p. 68 (Cuba); 1942c, p. 11 (a juvenile of questionable identity from Honduras); 1944, pp. 445, 465; 1948a, pp. 73–74 (off Ventnor, New Jersey); 1953, p. 55 (Cartagena). SPRINGER AND BULLIS, 1956, p. 78. BARDACH AND MENZEL, 1957, p. 108 (Bermuda, growth rates). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 16, 22, 56–57, figs. 8, 16, pls. 13–14 (Bermuda, biology); 1959, p. 114, fig. 8 (hermaphroditic). TAVOLGA, 1960, pp. 97–100, fig. 1 (sounds produced). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:6, 1:18–1:19, 1:23, fig. 17. SPRINGER AND McERLEAN, 1962, p. 393 (Key Largo, ecology). CALDWELL, 1966, p. 42 (Jamaica). CERVIGÓN M., 1966b, pp. 296–297 (Cubagua, Venezuela). CERVIGÓN M. AND VELASQUEZ, 1966, pp. 86–89 (Venezuela, complete account). RANDALL, 1967, p. 702 (food habits); 1968, pp. 64–65, fig. 71. BÖHLKE AND CHAPLIN, 1968, p. 286 (Bahamas).
- Mycteroperca bonaci* var. *xanthosticta* JORDAN AND SWAIN, 1885b, pp. 371–373 (original description, Pensacola, Florida). JORDAN AND EIGENMANN, 1890, p. 370.
- Mycteroperca bonaci xanthosticta*: JORDAN, 1885a (1887a, p. 84). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, p. 1176. EVERMANN AND KENDALL, 1900, p. 74. BREDER, 1929, pp. 160–161.
- ?*Garrupa nigrita* (non Holbrook): TOWNSEND AND BARBOUR, 1906, p. 305 (Bermuda).
- ?*Promicrops guttata* (non Linnaeus): BEAN, 1906, p. 52 (Bermuda, after Townsend and Barbour).
- Mycteroperca xanthosticta*: JORDAN AND EVERMANN, 1920, p. 392. BRIGGS, 1958, p. 273.
- Mycteroperca bonaci bonaci*: BREDER, 1929, p. 161.

NOMENCLATURE: Felipe Poey seems to have described *Mycteroperca bonaci* no less than six times and in doing so has recorded the momentary color changes to which this species is subject. Howell y Rivero (1938, p. 191) stated that there are several syntypes of *M. bonaci* in the Museum of Comparative Zoology at Harvard University but the largest of the six specimens is 267 mm. long and, as the original description was based on an individual 425 mm. long, I do not believe that the holotype is included in the Harvard series.

In the Museum of Comparative Zoology are other specimens purported to be types of *Serranus brunneus* Poey and *Serranus cyclopomatus* Poey. The original description of *S. cyclopomatus* makes no mention of the size or number of individuals described but *S. brunneus* was based on a 350 mm. individual. Assuming that Poey gave the measurements of total length, the largest "type" at Harvard, 286 mm. standard length, could have been the holotype. In view of the discrepancies between the length and number of specimens mentioned in Poey's original descriptions and those of the series labeled as types, I believe that the status of the specimens should be regarded as doubtful and that identification of Poey's names should be primarily based upon the descriptions themselves. I did not find the type of *S. aguaji* Poey at Harvard although the original description stated that it was sent there. It was a large specimen, 1120 mm. long, with dark dorsal and anal margins, and round brownish spots. The color and size are both diagnostic of *bonaci*. The other Poey names, *decimalis* and *lateopictus*, and *arara* Storer, are also identifiable from the descriptions.

The holotype of *Mycteroperca bonaci xanthosticta*

Jordan and Swain is a large specimen in which the brassy spots are especially prominent. Such coloration is frequently seen in living specimens and appears to be without genetic significance.

The name *bonaci* is the vernacular in Cuba for large fishes of this genus.

DIAGNOSIS: Large species of *Mycteroperca* with robust body, relatively large scales, and rounded preopercle. Dorsal XI, 17; anal III, 12 (13); pectoral 17; gill rakers 20-26. Posterior nostril not enlarged. Vertical fins without exerted rays. First three dorsal spines low, not forming an elevated lobe. Does not have deep- and shallow-water color phases. Lower part of body and, especially, head with brassy spots separated by a blue reticulum. Pectoral with narrow orange margin. Upper side of body with pattern of large rectangular blotches transient and not visible in all color changes. Vertical fins jet black for their outer third.

Like other members of this genus, *Mycteroperca bonaci* is best recognized by the distinctive color pattern. Brassy yellow spots, each about 6 mm. in diameter, on side of head and body are distinctive. Subequal nostrils and rounded preopercle are best structural characters and must be relied on in identification of faded specimens. Dark spots on back, when present, are square and arranged in regular rows. Edge of pectoral orange, shading gradually into darker base of fin, without a wide band of bright yellow as in *M. venosa*.

DESCRIPTION: The body is of the usual shape in *Mycteroperca* without specialization of body form. Proportional measurements of 10 specimens are given in table 27.

The dorsal, anal, and caudal rays are never exerted even in the largest specimens. The nostrils are equal at all sizes. The preopercular angle is rounded, the notch only a gentle emargination. The gill rakers are moderate in length. The exposed surface of the maxilla is scaled. The upper lip is broad, as wide as or wider than the shaft of the maxilla at the midpoint of the supramaxillary groove.

The ground color is gray, darker above and covered with hexagonal bronze or brassy yellow spots on the side and head. These spots are especially prominent on the cheek and opercle and on the lower part of the head. They are absent from the midbelly and are obscured dorsally. Overlying this basic design is a transient pattern of grayish to black quadrate

blotches that are separated by about seven vertical and four or five longitudinal light lines. The first column of blotches lies above the opercle, the second is anterior to the dorsal origin, the third is beneath the third to fifth dorsal spines, the fourth is below the sixth to the seventh spines, the fifth is below the posterior dorsal spines, the sixth is below the anterior soft rays, the seventh is below the middle to the last soft rays, and the eighth is on the caudal peduncle.

The blotches are separated by longitudinal lines as follows: one following the dorsal profile a short distance below the dorsal fin base, one midway between the first line and the upper angle of the opercle, one just behind the upper angle of the opercle, and one behind the middle of the pectoral base. The lighter belly forms the edge of the lowest row of spots. The top of the head is dark. The inside of the mouth is dirty white.

The pectoral fin is dusky with a narrow orange border that is not sharply delimited from the rest of the fin. The rays are slightly darker than the membranes. The pelvic fin is dark.

The spinous dorsal fin has the same pattern as the body, with vertical rows of blotches extending out to the fin edge. The body pattern also extends out to the middle of the soft part of the dorsal and beyond this there is a row of dark spots on the membranes separated by the lighter rays. The outer third of the fin is dark, sometimes almost jet black, with a narrow white margin. The anal is similar to the soft dorsal. The caudal is generally dark with irregular blue streaks near its base and the outer one-third is jet black. It too has a narrow white margin.

Large individuals are reddish brown when taken from the water. Then the bronze spots stand out very distinctly. An 1100 mm. specimen caught on April 8, 1957, was a uniform dark brownish with rather distinct bronze spots when boated. As soon as it was struck with the killing pick, the light interspaces faded, revealing the pattern of quadrate blotches. In a few seconds even these faded and the entire fish became pale except the black margins of the soft dorsal, anal, and caudal fins. The light reticulations were still prominent even when all other overlying patterns were blanched. The size of the brassy spots remains approximately

constant throughout life, the spots becoming more numerous rather than larger in size.

An individual 88 mm. long was taken at a light at night on April 7, 1957. There is a suggestion of the dark vertical bars, but they are not distinct except on the base of the dorsal fin. The body is generally golden brownish with pale, pearly-white lines and reticulations. The pectoral fin is almost all light yellowish; the other fins are as in the adult. The gill and gular membranes are whitish without trace of yellow spots. There is a well-developed black mustache above the maxilla. Some of the hexagonal spots are joined to produce chainlike patterns. The juvenile has no bicolored phase like that of *Mycteroperca interstitialis* and *M. tigris*.

The color pattern of *Mycteroperca bonaci* is similar to that of *M. venenosa*. That evidence further supports the interpretation of close relationship of these species.

RELATIONSHIPS: The black grouper is closely

related to the sympatric *Mycteroperca venenosa* and to *M. jordani* of the Eastern Pacific, sharing with them the rounded preopercle, entire edges of the soft median fins, and subequal nostrils. It is closest to *jordani* which appears to be a geminate species.

ECOLOGY: In Bermuda spawning seems to take place from about the first of May to early August. Some individuals were in spawning condition on the Campeche Banks in mid-May. Females reach 30 to 50 pounds; larger individuals are usually males. Fifty- to 60-pound specimens are common. Mowbray (1950, p. 30) reported that this species reaches 180 pounds. The black grouper is one of the chief commercial fishes in Bermuda, where it frequently reaches a weight of 100 pounds. The vernacular name in Bermuda is rockfish.

DISTRIBUTION: *Mycteroperca bonaci* is common in Bermuda and southern Florida. It ranges through the Bahamas and the Antilles and was

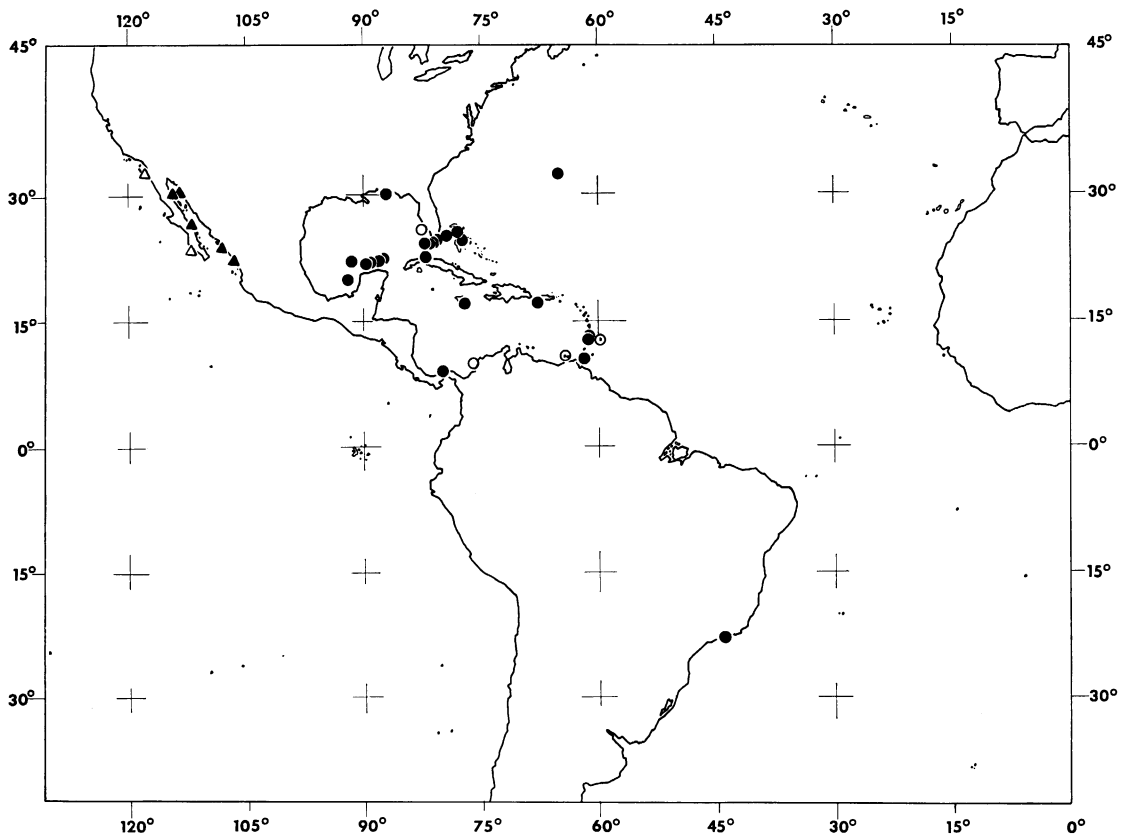


FIG. 34. Distribution records for *Mycteroperca bonaci* (circles) and *M. jordani* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

recorded by Fowler from Cartagena Lagoon. It is also common at Panama and on the northern part of the Campeche Banks (fig. 34). The records of Springer and Bullis (1956) all fall north of the verified range in the Gulf of Mexico and perhaps do not apply to this species. The type locality of *M. bonaci xanthosticta* is given as Pensacola but it was a large specimen, probably from a commercial fishing boat, and may have been taken farther south or even on the Campeche Banks.

SPECIMENS EXAMINED

Florida: Key West, FMNH 1937, 2056, 7008, 31753; USNM 26553, 26561 (cotype of *Trisotropis stomias* Goode and Bean), 35024, 35148, 38713, 47386, 75516-17, 83815, 111860, 134898; CU 596; AMNH 2805; Grassy Key, TU 16978; Big Pine Key, USNM 117470; Alligator Reef Light, USNM 57132; Key Largo, USNM 167627; Little Salt Pond Key, USNM 134897; Pensacola, USNM 127407, 35083 (holotype of *M. bonaci xanthosticta* Jordan and Swain).
 Louisiana: no specific locality, USNM 134899.
 Honduras: Bonaca Island, ANSP 71822.
 Panama: FMNH 20504-15, 20519-20; USNM 80241-44, 80278, 80304-07, 80320, 128756.
 Campeche Banks: 20°08'N, 91°41'W, UMMZ 174048, SILVER BAY Station 376; 22°21'N, 90°39'W, SILVER BAY Station 392; 22°24'N, 90°17'W, SILVER BAY Station 394; 22°22'N, 90°16'W, SILVER BAY Station 395; 22°32'N, 89°55'W, SILVER BAY Station 400; 22°13'N, 89°46'W, SILVER BAY Station 406; 22°13'N, 89°45'W, SILVER BAY Station 408 (Alacrán Reef); 22°18'N, 88°54'W, SILVER BAY Station 413; 22°31'N, 88°39'W, SILVER BAY Station 416; 22°51'N, 88°08'W, SILVER BAY Station 421; 22°30'N, 88°13'W, SILVER BAY Station 422; 22°21'N, 89°56'W, UMMZ 174114, 174114-S.
 Brazil: Rio de Janeiro, MCZ 958, 4508.
 Trinidad: Port of Spain, ANSP 45052.
 West Indies: no specific locality, MCZ 10226.
 Grenadines: Bequia Island, ANSP accession 162.
 St. Lucia: USNM 170145.
 Puerto Rico: Puerto Real, USNM 50169.
 Jamaica: USNM 29991.
 Cuba: Havana, USNM 35012; ANSP; no specific locality, MCZ 10000 (cotype of *Serranus bonaci* Poey); 10032-34 (cotypes of

S. bonaci), 10180 ("types" of *S. cyclopomatus* Poey), 10184 ("type" of *S. brunneus* Poey), 10195, 33937.

Bahamas: North Bimini, FMNH; vicinity of New Providence, CBC Station 209; CBC lot 277; Mores Island, AMNH 28219.

Bermuda: FMNH 48614, 49078, 5217-21, 5223-24; UMMZ 172554-S, 173405-S, 172553-S, 175998, 176142, 176169, 176007, 176406, 176623; USNM 12704, 21351-52, 21361, 164689, 190006; MCZ 34005.

Mycteroperca jordani (Jenkins and Evermann, 1889)
 GULF GROUPER

Epinephelus jordani JENKINS AND EVERMANN, 1889, pp. 140-142 (original description, Guaymas, Sonora; type USNM 39628). BOULENGER, 1895, p. 263. BÖHLKE, 1953, p. 69 (paratype, Stanford University 416).

Mycteroperca jordani: JORDAN AND EIGENMANN, 1890, p. 371. EVERMANN AND JENKINS, 1892, pp. 143-144, pl. 1, fig. 2. JORDAN, 1895, pp. 449-450 (characters, color, Mazatlán). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1176-1177; 1920, p. 392 (general account). WALFORD, 1936, p. 8 (nomenclature); 1937, p. 105, pl. 12, fig. a (Cerralvo Is.). HIRYAMA, 1937, p. 38, pl. 22 (characters, color plate). SCHMITT AND SCHULTZ, 1940, p. 5 (off San Jose del Cabo Bay). BERDEGUE A., 1956, pp. 273-274 (Mexico). BAILEY ET AL., 1960, p. 25 (common name). ROSENBLATT AND ZAHURANEC, 1967, pp. 233-255 (full account).

Mycteroperca venadorum JORDAN AND STARKS, in Jordan, 1895, pp. 446-447 (original description, Isla Blanca, type in British Museum [Natural History]). JORDAN AND EVERMANN, 1896a, p. 375; 1896b, p. 1186 (general account). OSBURN AND NICHOLS, 1916, p. 162 (Angel de la Guarda). JORDAN AND EVERMANN, 1920, p. 394. JORDAN, EVERMANN, AND CLARK, 1930, p. 314.

Trisotropis jordani: JORDAN, EVERMANN, AND CLARK, 1930, p. 314. BREDER, 1936, p. 23 (San Francisco, Gonzago Bay, San Felipe).

NOMENCLATURE: *Mycteroperca jordani* was described on the basis of a specimen 360 mm. long that had oblong brown spots. *Mycteroperca venadorum*, based on a larger individual had no such spots but was otherwise similar to *jordani*. By analogy with other groupers that show similar color variations, I concur with Walford's placement of *venadorum* in the synonymy of *Mycteroperca jordani*. The holotype of *M. jordani*, USNM 39628, was collected by Jenkins and Evermann at Guaymas, Mexico.

TABLE 27
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca bonaci*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	65	100	161	291	295	306	328	376	421	585	—
Head length	400	400	388	361	385	359	369	382	356	381	378.1
Head width	154	155	149	151	146	147	149	146	157	—	150.4
Head depth	231	240	227	223	219	209	220	218	220	—	223.0
Snout length	100	110	99	96	112	98	107	93	100	115	103.0
Suborbital width	31	35	37	41	37	39	40	40	39	46	38.5
Interorbital width	77	75	71	70	68	69	72	64	72	68	70.6
Length of: Orbit	92	80	68	53	56	54	53	51	50	42	59.9
Postorbital head	223	220	230	227	225	222	220	225	213	230	223.5
Maxillary	177	190	174	172	170	162	171	168	171	181	173.6
Lower jaw	185	180	183	182	180	168	168	178	178	190	179.2
Snout to angle of preopercle	277	275	269	251	254	245	253	249	249	265	258.7
Supramaxillary length	46	60	62	55	54	56	50	51	57	59	55.0
Maxillary width	38	40	37	38	42	38	37	40	37	41	38.8
Tip of lower jaw to gular notch	146	135	96	112	120	105	110	104	105	147	118.0
Body width	162	155	152	144	141	139	143	144	143	171	149.4
Body depth	308	320	301	302	307	288	293	287	289	292	298.7
Caudal peduncle depth	123	120	118	113	112	111	110	109	107	108	113.1
Tip of snout to dorsal origin	385	385	385	378	395	379	377	372	371	369	379.6
Tip of snout to pectoral base	385	385	342	347	351	333	332	329	315	379	349.8
Tip of lower jaw to pelvic base	431	480	391	392	403	382	386	378	372	429	404.4
Length of: Dorsal base	492	500	519	502	519	533	537	579	532	489	520.2
Depressed dorsal	585	600	621	574	588	605	604	583	596	538	589.4
Anal base	200	205	205	223	214	211	220	202	209	212	210.1
Depressed anal	308	315	323	309	303	297	297	281	290	272	299.5
End of dorsal to caudal base	154	150	155	144	164	150	152	153	150	153	152.5
Length of: Caudal peduncle	169	195	199	203	202	186	177	200	192	183	190.6
Pectoral	231	230	220	192	190	186	177	202	177	166	197.1
Pelvic	185	190	193	175	180	170	165	169	165	171	176.3
Dorsal spine I	54	70	68	64	69	62	67	53	62	60	62.9
Dorsal spine III	123	130	130	112	129	118	134	110	127	—	123.7
Dorsal spine XI	100	110	115	96	108	95	96	93	—	111	102.7
Anal spine I	46	55	47	48	46	42	40	40	—	34	44.2
Anal spine II	92	100	90	79	80	69	73	61	62	56	76.2
Anal spine III	108	105	109	105	97	88	98	90	91	92	98.3
Caudal base to tip of upper rays	238	260	255	—	254	242	—	226	198	242	252.0
Caudal base to tip of middle rays	246	250	239	247	237	239	—	219	233	197	245.2
Caudal base to tip of lower rays	238	245	248	225	227	214	—	—	220	231	205.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Column 1, UMML from Ft. Pierce Inlet; 2, UMML from off Miami; 3, UMIM from off Islamorada, Florida; 4-10, from Bermuda, field numbers 151, 185, 157, 158, 184, 183, 182 respectively.

This species is named for David Starr Jordan.

DIAGNOSIS: Rather large, heavy-bodied grouper with rounded preopercle and moderate-sized scales. Dorsal XI, 16; anal III, 11; pectoral 17; gill rakers 17-21. Posterior nostril not enlarged. No exerted fin rays. First three dorsal spines not forming an elevated lobe.

Color generally gray, sometimes with quadrate blotches on side. Pectoral with narrow orange margin.

Mycteroperca jordani is closely related to *M. bonaci* and shares with that species the evenly rounded preopercle and subequal nostrils. It differs from *bonaci* in coloration, apparently never

having orange or brassy yellow spots on lower head and body. There are no other Pacific species of groupers in which preopercular angle is not salient, or in which gill rakers are fewer than 13 on lower part of first arch. Fin margins entire, without exerted rays.

DESCRIPTION: For proportional measurements of four specimens see table 28. There are only trivial measurement differences between this species and *bonaci* and *venenosa*.

The nostrils are equal at all sizes. There is no exertion of the dorsal, anal, or caudal rays. The maxilla is scaled. The lobes of the soft dorsal and anal fins are rounded. The caudal is truncate or slightly convex; the anal fin is angulate but not falcate.

"Small specimens are a warm brown or olive gray with more or less distinct oblong dark spots; dark stripes radiate from the eye. These spots and stripes gradually become less distinct with age until the entire body becomes plain dark greenish brown on the back and sides, paler on the underparts. The tips of the fins in both small and large specimens are broadly edged with blackish and, narrowly, with white." (Walford, 1936, p. 8.)

RELATIONSHIPS: *Mycteroperca jordani* appears to be the geminate of *M. bonaci*, which it resembles in several important characters. It is a member of the *venenosa* complex.

ECOLOGY: This species reaches a weight of more than 100 pounds and a length of between 5 and 6 feet. Walford (1937, p. 105) recorded an individual taken at Ceralvo Island, April, 1935, which measured 4 feet 8 inches and was a nearly ripe female. Apparently *jordani* parallels *bonaci* in size as well as in structure.

DISTRIBUTION: *M. jordani* occurs in the Gulf of California and on the northern Mexican coast (fig. 34); it occasionally reaches the coast of southern California, according to Carl L. Hubbs (personal commun.).

SPECIMENS EXAMINED

Mexico: Golfo de California, Baja California, Bahía Concepción, UCLA W53-94; USNM 100992 (268 mm., April 11, 1935, L. A. Walford); Bahía San Luis Gonzago, UCLA W60-60; BOC 1116 (176 mm., May 17, 1926, PAWNEE); Bahía Boco-chibampo, UCLA W51-3; Sinaloa, Bahía Topolobampo, UCLA W56-115; Mazatlán, USNM 47467 (235 mm., D. S. Jordan).

No data: USNM 100988 (460 mm., L. A. Walford).

Mycteroperca tigris (Valenciennes, 1833)

TIGER GROUPER

- Serranus tigris* VALENCIENNES, in Cuvier and Valenciennes, 1833, pp. 440-441 (original description, Santo Domingo). STORER, 1846, pp. 281-282 (copied). GÜNTHER, 1859, p. 112. COCKERELL, 1892, p. 7 (Jamaica).
- Serranus camelopardalis* POEY, 1860 (1858-1861), pp. 132-134 (original description, Cuba); 1861 (1858-1861), pp. 353-354 (color).
- Serranus felinus* POEY, 1860 (1858-1861), p. 134 (original description, Cuba).
- Serranus rivulatus* POEY, 1860 (1858-1861), p. 135 (original description, Cuba); 1867 (1866-1868), p. 155 ("same as *T. felinus*").
- Serranus repandus* POEY, 1860 (1858-1861), pp. 135-136 (original description, Cuba); 1867 (1866-1868), p. 155 (same as *S. felinus*).
- Trisotropis reticulatus* GILL, 1865, p. 105 (original description, Barbados).
- Trisotropis camelopardalis*: POEY, 1866 (1866-1868), p. 4 (suspected of causing ciguatera); 1868 (1866-1868), p. 283; 1870, p. 307; 1875 (1875-1877), p. 14.
- Trisotropis felinus*: POEY, 1866 (1866-1868), p. 4 (suspected of causing ciguatera); 1867 (1866-1868), p. 155; 1868 (1866-1868), p. 283.
- Trisotropis tigris*: POEY, 1870, p. 307; 1875 (1875-1877), p. 14.
- Mycteroperca tigris* var. *tigris*: JORDAN AND SWAIN, 1885b, pp. 364-365. JORDAN AND EIGENMANN, 1890, p. 369.
- Mycteroperca tigris* var. *camelopardalis*: JORDAN AND SWAIN, 1885b, pp. 364-365. JORDAN AND EIGENMANN, 1890, p. 369.
- Mycteroperca reticulata*: JORDAN AND SWAIN, 1885b, p. 373. JORDAN, 1887e, p. 580 (West Indies).
- Mycteroperca tigris*: JORDAN, 1887c, p. 39; 1887e, p. 580 (West Indies). JORDAN AND EVERMANN, 1896a, p. 375; 1896b, p. 1187. JORDAN AND RUTTER, 1898, p. 105 (Jamaica). BEAN, 1906, p. 54 (Bermuda). JORDAN AND EVERMANN, 1920, p. 394. NICHOLS, 1921, p. 23 (Turks Is.). BREDER, 1927, p. 39; 1929, p. 161. JORDAN, EVERMANN, AND CLARK, 1930, p. 315. PARR, 1930, p. 50 (Washerwoman Cut). BEEBE AND TEE-VAN, 1933, pp. 131-132 (Bermuda). LONGLEY, 1935, p. 283 (*M. camelopardalis* in synonymy). HOWELL Y RIVERO, 1938, pp. 192-193 (Poey "types" in MCZ). LONGLEY AND HILDEBRAND, 1941, p. 101 (rare at Tortugas, photograph). FOWLER, 1944, pp. 445, 465 (Turks Is.; Kingston, Jamaica). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 8, 12, 21, 54-55, figs. 2a, 4, 15, pl. 11 (Bermuda, biology); 1959, p. 114, fig. 1

TABLE 28
PROPORTIONAL MEASUREMENTS OF FOUR SPECIMENS OF *Mycteroperca jordani*^a

Measurement	1	2	3	4	Average
Standard length (mm.)	235	285	368	511	—
Head length	383	364	386	393	381.5
Head width	136	158	149	186	157.3
Head depth	243	221	239	256	239.8
Snout length	104	104	109	121	109.5
Suborbital width	38	39	41	47	41.3
Interorbital width	68	67	77	88	75.0
Length of: Orbit	55	56	56	47	53.5
Postorbital head	236	242	242	245	241.3
Maxillary	177	—	186	188	183.7
Lower jaw	181	188	197	196	190.5
Snout to angle of preopercle	268	268	283	282	275.3
Supramaxillary length	51	53	56	49	52.3
Maxillary width	40	39	41	43	40.8
Tip of lower jaw to gular notch	106	112	99	106	105.8
Body width	134	142	144	176	149.0
Body depth	291	293	307	323	303.5
Caudal peduncle depth	123	119	115	125	120.5
Tip of snout to dorsal origin	368	374	382	395	379.8
Tip of snout to pectoral base	355	358	349	348	352.5
Tip of lower jaw to pelvic base	396	400	378	372	386.5
Length of: Dorsal base	526	519	530	554	532.3
Depressed dorsal	617	589	598	613	604.3
Anal base	185	193	181	180	184.8
Depressed anal	306	281	285	274	286.5
End of dorsal to caudal base	145	137	154	158	148.5
Length of: Caudal peduncle	170	181	196	180	181.8
Pectoral	217	200	198	200	203.8
Pelvic	170	167	170	178	171.3
Dorsal spine I	62	40	56	49	51.8
Dorsal spine III	117	119	107	105	112.0
Dorsal spine XI	100	74	77	79	82.5
Anal spine I	43	40	31	30	36.0
Anal spine II	77	63	71	62	68.3
Anal spine III	89	96	98	96	94.8
Caudal base to tip of upper rays	245	246	240	237	242.0
Caudal base to tip of middle rays	234	232	220	217	225.8
Caudal base to tip of lower rays	228	239	220	231	229.5

^aAll proportions are expressed in thousandths of the standard length. All specimens are as follows: Columns 1-4, USNM 47467, 39628, 100988, and 46884 respectively. For data see text.

(hermaphroditic). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:6, 1:19-1:20, 1:23, fig. 18. RANDALL, 1963, p. 37 (Virgin Is., ecology). CALDWELL, 1966, p. 42 (Jamaica, compiled). CERVIGÓN M. AND VELASQUEZ, 1966, pp. 89-92 (Venezuela, osteology). RANDALL, 1967, pp. 702-703 (food habits); 1968, p. 65 (photograph, general account). BÖHLKE AND CHAPLIN, 1968, p. 285 (Bahamas).

Mycteroperca tigris camelopardalis: JORDAN, 1887c, p. 39 (Havana). JORDAN AND EVERMANN, 1896a, p. 375; 1896b, p. 1187. FOWLER, 1942b, p. 68 (Cuba).

Epinephelus tigris: BOULENGER, 1895, pp. 259-260.

MIRANDA-RIBEIRO, 1915, pp. 24-25 (Maranhão, Brazil); 1918, p. 91. BORODIN, 1928, p. 19 (Florida).

Mycteroperca hopkinsi JORDAN AND RUTTER, 1898, p. 105 (original description, Jamaica). JORDAN AND EVERMANN, 1898, pp. 2855-2856. JORDAN, EVERMANN, AND CLARK, 1930, p. 314. FOWLER, 1944, p. 465 (copied). BÖHLKE, 1953, p. 70 (type, Stanford University 5073).

Mycteroperca camelopardalis: JORDAN AND EVERMANN, 1920, p. 395. JORDAN, EVERMANN, AND CLARK, 1930, p. 315.

Mycteroperca tigris tigris: FOWLER, 1942b, p. 68 (Cuba).

NOMENCLATURE: Carl L. Hubbs has examined the type of this species in the collection of the Paris Museum (7178) and reported that it was in good condition. It was collected by Ricord in Haiti (Santo Domingo?). The color pattern is still evident.

The Latin name *tigris* means tiger, a reference to the stripes.

The nominal form *Mycteroperca camelopardalis* (Poey), seems to be based on females, which are smaller and tend to be more reddish than males.

DIAGNOSIS: Moderate-sized *Mycteroperca* with medium-sized scales and robust body. Preopercle broadly rounded, without lobe or projection. Posterior nostril much enlarged in fish more than 300 mm. long. Dorsal XI, 16-17; anal III, 11; pectoral 17; gill rakers very few, 10-15. Vertical fin rays exerted in large adults. First three dorsal spines low, not forming an elevated lobe. Canine teeth especially long and strong. Only a single color phase known. Color generally dark greenish to black with lighter rivulations, especially ventrally. Back crossed by about 11 narrow pale lines which slope downward and forward. Inside of mouth dusky orange-yellow in life.

The extreme reduction to eight developed gill rakers on lower limb of first arch sets this species apart from all other species of *Mycteroperca*. Body form exceptionally robust for this genus. Color pattern of narrow stripes sloping downward and forward across back not duplicated in any other American grouper.

DESCRIPTION: The last dorsal spine is shorter than in other species except *Mycteroperca olfax*, otherwise there are no outstanding measurable characters (table 29).

The posterior nostril is enlarged in individuals more than 300 mm. long. The medial canines in both jaws are very strong. Individuals more than 600 mm. long have the rays of the soft dorsal, anal, and caudal unevenly exerted, giving the fins a ragged appearance. The preopercle is evenly rounded as in *Mycteroperca bonaci* and *M. venenosa*, and the exposed surface of the maxilla is densely scaled. The lower jaw projects strongly as in other species of this genus.

A living specimen, about 300 mm. long, held in an aquarium at the Bermuda Biological Station was observed to have the following color

pattern: ground pattern of body with reticulations of pale bluish surrounding brownish hexagonal spots of diameter about equal to eye, somewhat smaller on lower part of head. Spots also present on maxilla, lower jaw, and branchiostegal gular membranes. In the excitement phase only the above pattern shows. Normally spots on upper part of body obscured by dark overlying pattern of dark brownish, sometimes with a greenish cast; upper side crossed by light bars that are nearly vertical anteriorly but slope downward and forward posteriorly. These cross bars lie: 1) above middle of opercle; 2) in front of dorsal origin; 3) below base of third dorsal spine; 4) just below base of fifth spine; 5) below eighth spine; 6) below first soft ray; 7) below middle soft rays; 8) below posterior soft rays; 9) just behind dorsal fin; and 10) in front of upper procurrent caudal rays. Sometimes a faint bar just behind orbit. Pectoral membranes dark, the rays distinctly lighter. Pelvic with dark membranes, lighter blue rays, a white distal margin, and a narrow white margin along anterior edge. Dorsal dark at base of spinous part, tips of spines yellow. Bars extended onto basal part of fin. Body pattern continued onto middle of soft dorsal. A line of blue spots at midpoints of rays, fin darker distally to narrow white margin. Rays somewhat lighter than membranes. Inside of mouth dusky yellow-orange.

RELATIONSHIPS: *Mycteroperca tigris* is perhaps the most distinctive species of the genus. It has the rounded preopercle characteristic of the *venenosa* complex and the large posterior nostril common to the *interstitialis* group. I interpret this combination of characters as evidence that the species diverged from the *venenosa* stem soon after the two main lines split to give rise to those groups.

ECOLOGY: A specimen of *Mycteroperca tigris* 40.5 mm. long taken August 27, 1956, off the north shore of St. Georges, Bermuda, was sharply bicolored, dark above and light below, and had a yellow cast. There was a strong spine at the angle of the preopercle. The pattern of narrow oblique light lines was present.

This is one of the most easily observed groupers in Bermuda. During daylight hours individuals can be seen hovering a foot or two above the surface of the coral. They can be approached closely before they move away. They are voracious feeders, taking cut bait readily, and

are often caught on lures trolled near the reefs. On several occasions we have observed *Aulostomus* aligned with the long axis of the grouper and a few inches above it. At Bermuda I observed small wrasses, *Thalassoma bifasciatum* and *Bodianus rufus*, feeding on ectoparasites on a large specimen of *Mycteroperca tigris* and at Arcas Cay in the Gulf of Mexico I saw a *tigris* being "inspected" by *Gobiosoma (Elacatinus)* sp.

This species is not known from the Bermuda Banks where the minimum depth is 22 fathoms. It is possible that the young must spend the earliest bottom-dwelling stages in very shallow water.

Color change in this species is minimal, the only noticeable variation being in the intensity of the light markings. In the occasional specimens noted in which the light stripes are not evident, light hexagonal reticulations stand out quite clearly over most of the body.

DISTRIBUTION: Although *Mycteroperca tigris* is common in Bermuda, records for it elsewhere are spotty. It is known from the Bahamas, Cuba, Haiti, Tortugas, Arcas Cay, and Barbados (fig. 35).

SPECIMENS EXAMINED

Florida: Key West, FMNH 31752.

Gulf of Mexico: Arcas Cay, sight record, May 4, 1958.

West Indies: no specific locality, USNM 33618.

Barbados: USNM 6708 (type of *Trisotropis reticulatus* Gill *vide* Jordan and Swain, 1884b).

Cuba: no specific locality, USNM 9788, 19800, 32093; MCZ 9994-5, 10004, 10035, 10071, 10073, 10076, 10134, 10192, 10207, 26952.

Bahamas: Bimini, UMMZ 174254; New Providence, CBC Station 230; Andros Island, CBC Station 390.

Bermuda: FMNH 5226, 48375; USNM 21350; UMMZ 172548-S, 172549-S, 172550-S, 172551-S, 172552-S, 176035, 176048, 176069, 176108, 176127, 176138, 176147, 176170, 176171, 176383, 176407, 176410, 176434, 176444, 176475, 176503, 176509-S, 176583, 176625, 176660.

Mycteroperca interstitialis Species-Group

This species-group is distinguished chiefly by the form of the preopercular bones all of which have a distinct notch above a definite serrated lobe at the angle. The vertical and horizontal limbs are almost at right angles to each other. The supraoccipital skull crest is usually angled upward so that it extends above the plane formed by the top of the lateral skull crests (fig. 37). This group contains *microlepis*, *interstitialis*, *phenax*, *cidi*, *xenarcha*, *prionura*, *rosacea*, *olfax*, and *rubra*.

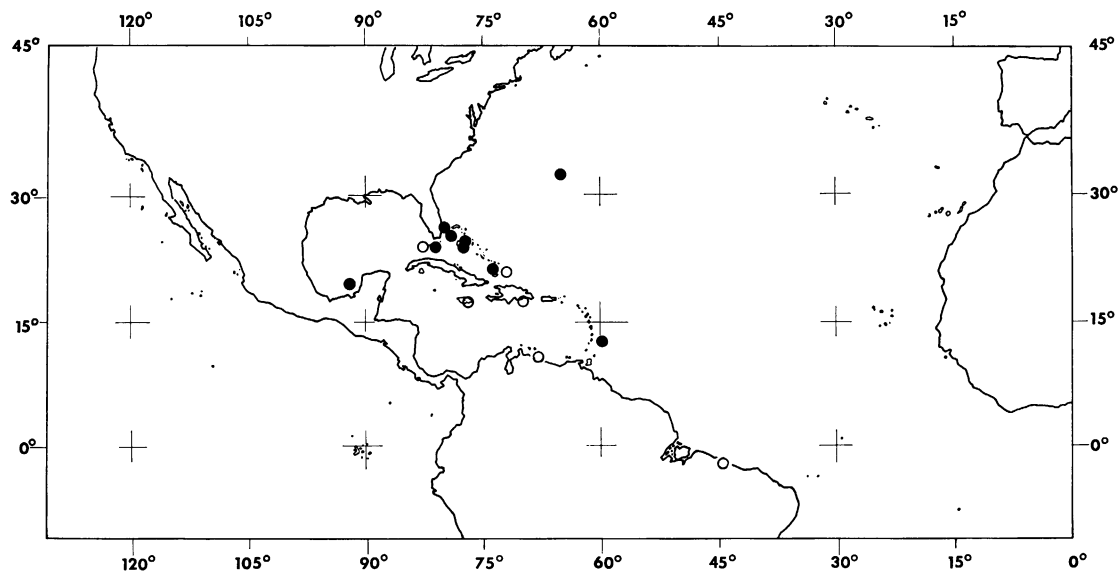


FIG. 35. *Mycteroperca tigris* distribution records. Solid circles represent specimens examined, open circles are additional literature records.

TABLE 29
 PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca tigris*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	226	271	282	292	322	350	384	384	397	426	—
Head length	392	369	358	366	371	374	376	381	380	388	375.5
Head width	159	159	145	147	146	140	180	158	174	188	159.6
Head depth	235	229	225	223	225	217	224	238	239	248	230.3
Snout length	115	100	99	103	107	106	109	108	106	113	106.6
Suborbital width	35	35	35	33	34	37	36	40	40	40	36.5
Interorbital width	69	70	67	69	68	67	65	70	71	70	68.6
Length of: Orbit	55	55	53	57	53	51	52	52	50	47	52.5
Postorbital head	235	231	227	226	230	229	234	241	242	244	233.9
Maxillary	181	177	174	180	175	180	182	178	185	190	180.2
Lower jaw	181	177	179	—	186	180	—	187	196	197	185.4
Snout to angle of preopercle	277	262	259	262	266	267	263	264	268	—	265.3
Supramaxillary length	44	44	46	48	50	51	60	56	43	56	49.8
Maxillary width	35	36	41	34	37	37	34	38	34	38	36.4
Tip of lower jaw to gular notch	139	124	110	127	137	131	125	118	118	122	125.1
Body width	159	166	152	149	152	140	158	151	171	168	156.6
Body depth	305	308	301	288	280	276	289	303	292	305	294.7
Caudal peduncle depth	115	114	112	113	107	109	107	120	113	113	112.3
Tip of snout to dorsal origin	398	387	387	394	382	383	378	406	380	395	389.0
Tip of snout to pectoral base	389	351	346	354	345	354	354	349	348	354	354.4
Tip of lower jaw to pelvic base	425	395	376	401	388	403	396	385	385	395	394.9
Length of: Dorsal base	—	531	489	486	503	493	518	506	504	530	506.7
Depressed dorsal	571	594	553	550	550	497	565	555	564	580	557.9
Anal base	195	203	188	188	186	183	180	187	190	185	188.5
Depressed anal	268	275	255	250	251	237	234	245	256	265	253.6
End of dorsal to caudal base	146	153	147	144	143	146	146	147	141	147	146.0
Length of: Caudal peduncle	199	190	183	175	183	183	187	195	191	182	186.8
Pectoral	190	203	179	185	177	177	177	182	176	177	182.3
Pelvic	168	159	152	154	149	143	142	143	145	148	150.3
Dorsal spine I	62	52	57	58	59	54	56	57	60	59	57.4
Dorsal spine III	113	113	117	110	112	111	104	120	106	120	112.6
Dorsal spine XI	93	85	85	79	81	74	—	89	87	77	83.3
Anal spine I	49	44	39	41	39	37	35	46	45	45	42.0
Anal spine II	78	77	71	53	71	76	73	79	76	73	72.7
Anal spine III	86	92	82	69	90	90	83	85	88	99	86.4
Caudal base to tip of upper rays	239	240	238	245	221	231	232	225	—	235	234.0
Caudal base to tip of middle rays	208	208	197	195	183	186	190	187	—	192	194.0
Caudal base to tip of lower rays	232	234	229	229	208	217	219	219	—	231	224.2

^aAll proportions are expressed in thousandths of the standard length. All specimens are as follows: UMMZ from Bermuda with field numbers, in the order of the columns, as follows: 148, 132, 138, 137, 133, 134, 150, 144, 143, and 139.

Mycteroperca microlepis (Goode and Bean, 1880)
 GAG

Serranus acutirostris (*non* Valenciennes, 1828): VALENCIENNES, in Cuvier and Valenciennes, 1833, p. 432 (misidentification of a specimen from Charleston, S. C.). DEKAY, 1842, p. 23 (copied, extralimital). STORER, 1846, p. 281. GILL, 1862c, p. 30.

Trisotropis acutirostris: GILL, 1873, p. 806.

Trisotropis microlepis GOODE AND BEAN, 1880, pp. 141–

143 (original description, west Florida, holotype, USNM 5137). GOODE AND BEAN, 1883a, p. 238. JORDAN AND GILBERT, 1883a, pp. 538–539. LÖNNBERG, 1894, p. 126 (Key West). JORDAN, EVERMANN, AND CLARK, 1930, p. 314. BEEBE AND TEE-VAN, 1933, p. 127 (Bermuda; drawing may be *M. interstitialis*). REED, 1941, p. 76 (Texas coast).

Trisotropis brunneus (*non* Poey): GOODE AND BEAN, 1880, p. 143.

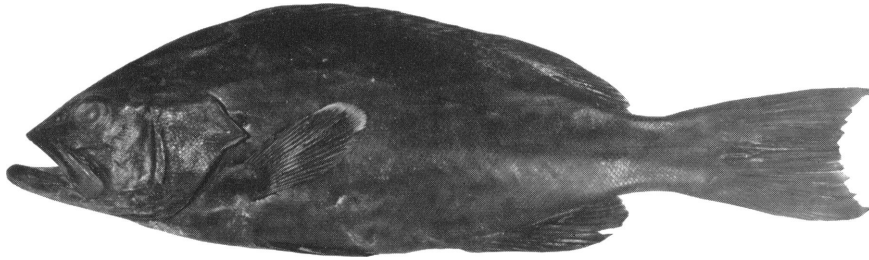


FIG. 36. *Mycteroperca interstitialis*, UMMZ 176148 from Bermuda, 326 mm. Photograph by W. L. Brudon, courtesy Bermuda Fisheries Research Program.

Trisotropis stomias (*nomen nudum*) GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico).

Trisotropis stomias GOODE AND BEAN, 1883b, pp. 427–428 (original description, complex). JORDAN AND GILBERT, 1833a, p. 918; 1883d, p. 273 (Pensacola). BEAN, 1884, p. 447. LÖNNBERG, 1894, p. 126 (Key West).

Epinephelus microlepis: JORDAN, 1884a, p. 77 (Key West). JORDAN AND SWAIN, 1885b, pp. 367–368. JORDAN, 1885b, p. 124; 1885e, p. 102 (nomenclature). BOULENGER, 1895, pp. 260–261. MIRANDA-RIBEIRO, 1915, pp. 23–24 (Brazil); 1918, p. 90.

Epinephelus stomias: JORDAN AND SWAIN, 1885a, p. 232 (Cedar Keys). JORDAN, 1885a, p. 35.

Mycteroperca microlepis: JORDAN, 1887a, p. 84; 1887b, p. 27 (Beaufort, N. C.); 1887e, p. 580. JORDAN AND EIGENMANN, 1890, p. 371, pl. 63. HENSHALL, 1891, p. 387 (Key West, west coast of Florida); 1895, p. 216 (Key West). SMITH, 1896, p. 175 (Key Biscayne Bay). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1177–1178. BRICE, 1898, p. 283. EVERMANN AND KENDALL, 1900, p. 74. BEAN, 1906, p. 54 (Bermuda). EVERMANN AND HILDEBRAND, 1910, p. 161 (Old Point Comfort, Virginia). FOWLER, 1915a, p. 249 (Palm Beach, Florida); 1920, p. 153. JORDAN AND EVERMANN, 1920, p. 392 (general account, photograph). EVERMANN AND SEALE, 1924, p. 30 (Barbados). SCHROEDER, 1924, p. 16 (Pensacola; Beaufort). HILDEBRAND AND SCHROEDER, 1928, p. 250. BREDER, 1929, p. 161. FOWLER, 1938a, p. 298 (mouth of Chesapeake Bay). LONGLEY AND HILDEBRAND, 1941, pp. 100–101 (Tortugas, habits). BAUGHMAN, 1943, p. 772 (Texas). MANTER, 1947, p. 373 (parasites). FOWLER, 1952, p. 121 (New Jersey). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 58–59, pl. 15. BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:7, 1:20, 1:23, fig. 66. HOESE, RICHARDS, AND CASTAGNA, 1961, pp. 104–105 (Virginia records). McERLEAN AND SMITH, 1964, pp. 301–302 (protogyne). ALPERIN AND SCHAEFER, 1965, pp. 4–5 (New York records, photographs). CERVIGÓN M., AND VELASQUEZ, 1966, p. 93 (not found in Venezuela, osteology).

Mycteroperca bonaci (*non* Poey): FOWLER, 1948a, pp. 73–74, fig. (New Jersey).

NOMENCLATURE: Two syntypes of *Mycteroperca microlepis* are USNM 5137 from west Florida.

I have examined the existing cotypes of *Trisotropis stomias* Goode and Bean in the United States National Museum. The series includes three species as follows: 26561 (Key West, 209 mm.) = *Mycteroperca bonaci*; 26587 (Key West, 307 mm.) = *M. phenax*; 16902 (Florida, 478 mm.) and 15462 (no locality, 607 mm.) = *M. microlepis*. A notation in the Catalogue states that 21336, also a syntype, has been destroyed. It is evident that the description was based on more than one specimen; the anal count is given as 10 (11). The statement that the caudal is lunate applies to all specimens except that of *M. bonaci* but the assertion that there are no canines in the lower jaw is true only of the example of *phenax* which has 11 (not 10) anal rays.

The name *stomias* is of more recent date than *microlepis*. In order to preserve conventional nomenclature I select as lectotype of *Trisotropis stomias* Goode and Bean USNM 16902 and thus relegate *stomias* to the synonymy of *Mycteroperca microlepis*.

The name *microlepis* (Greek μικρός, small, and λείψ, a scale) is an allusion to the fine scales.

DIAGNOSIS: A moderate-sized species of *Mycteroperca* with very small scales and robust body. Posterior nostril enlarged in large specimens. Preopercle with a pronounced lobe below notch. Dorsal XI, 16–17 (18); anal III, 11; pectoral 17; gill rakers 21–29. Vertical fins without exserted rays. First three dorsal spines not elevated into a lobe. Without depth-correlated color phases. General color gray, side

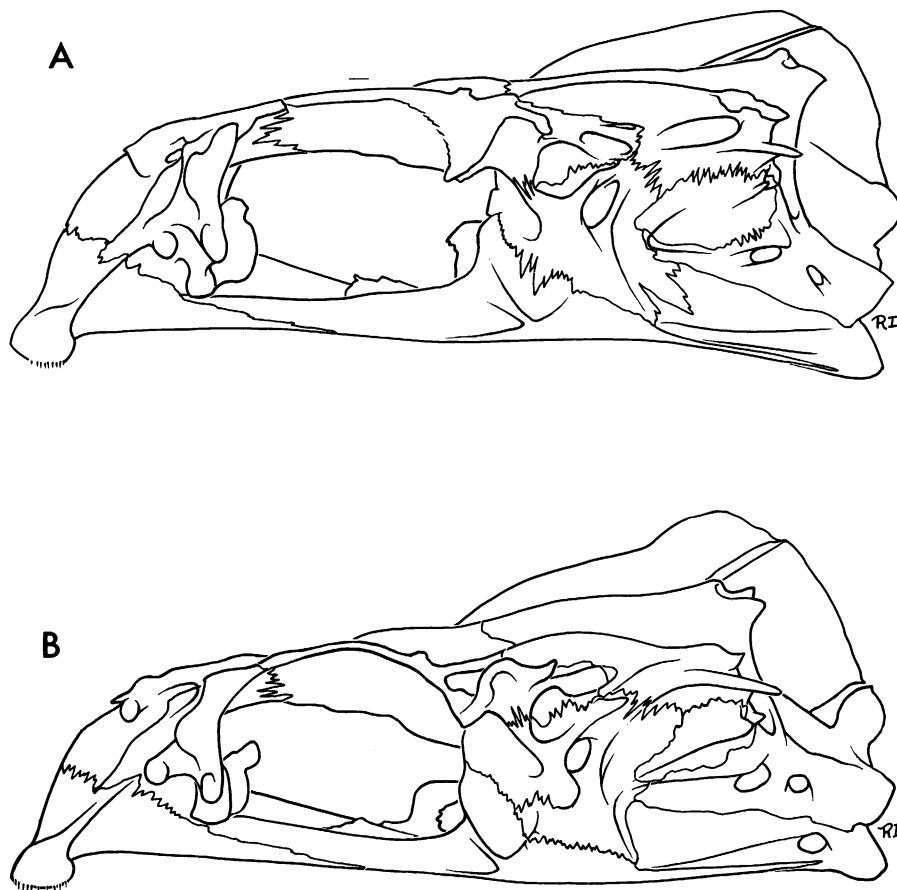


FIG. 37. Lateral views of the neurocrania of *Mycteroperca venenosa* and *M. interstitialis* showing the development of the supraoccipital crest. A. *Mycteroperca venenosa*, UMMZ 172560-S from Bermuda. B. *Mycteroperca interstitialis*, UMMZ 174005-S from Bermuda.

with darker vermiculations that are frequently grouped into quadrate blotches. Pectoral fin with a narrow light margin.

Mycteroperca microlepis resembles *M. bonaci* although its affinities lie with the *interstitialis* group rather than with the *venenosa* group. The posterior nostril does not enlarge until a length of about 600 mm. The preopercular angle is salient, with strong teeth below notch, but in this character it is less extreme than other members of the *interstitialis* group. This is the best character for determination of bleached or discolored specimens.

In life the fish is distinctive. Body mottled with dark vermiculations, sometimes arranged in several rows of quadrate patches. General gray color contrasts with brassy spots of *bonaci* which it otherwise strongly resembles.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 30.

The preopercle is finely serrate above, slightly notched, and has strong teeth below and a developed lobe at the angle. The median skull crest is high, ending behind the orbit. The lateral crest meets the supraorbital ridge over the posterior third of the eye. There is a high supraethmoid wall. The posterior nostril becomes much enlarged in large individuals. The dorsal and anal margins are convex; the caudal is slightly lunate. The upper lip is wide, as in *Mycteroperca bonaci*. The pharyngeal teeth are much coarser than in *bonaci* or *venenosa*.

The body is grayish, darker above with dark vermiculations on the side, sometimes with irregular dusky lines radiating from the eye. The vermiculations fade completely at times and

sometimes are arranged in definite rows or transverse bars, which may be broken into quadrate groups. The dorsal fin is dark at the base, shades to dusky toward the margin, and is narrowly edged with white. The caudal is similar to the dorsal. The anal is dusky for the basal third, becomes much darker toward the margin, and has a white margin which is widest on the anterior rays.

The pectoral fin is nearly clear but the upper corner has a few melanophores that in large specimens are numerous and form a conspicuous spot. The pelvic is light along the anterior edge and white on the margin; otherwise, the fin is dusky, being darkest on the outer third of the anterior rays. In life the anal and pectoral have an iridescent blue wash.

RELATIONSHIPS: In most features this species seems to bridge the gap between the *venenosa* species-group and the *interstitialis* group. Cer-

vigón M. and Velasquez (1966) placed it with the former on account of its weak preopercular lobe and the lack of exerted fin rays, but I am inclined to place it with the *interstitialis* group because some individuals show a strong preopercular lobe, and the outline of the preopercle is more angulate than in members of the *venenosa* group. This species is perhaps one of the best reasons for avoiding subgeneric recognition of the two groups.

ECOLOGY: On the Campeche Banks *M. microlepis* was taken at depths of 26 to 44 fathoms. No information is available on its life history. Specimens as short as 67 mm. show no trace of a bicolor pattern, and it seems unlikely that such a pattern is ever present in this species.

DISTRIBUTION: *Mycteroperca microlepis* regularly occurs farther north on the coast than any other grouper (fig. 38). However, it seems to be restricted to the Gulf of Mexico, the Atlantic

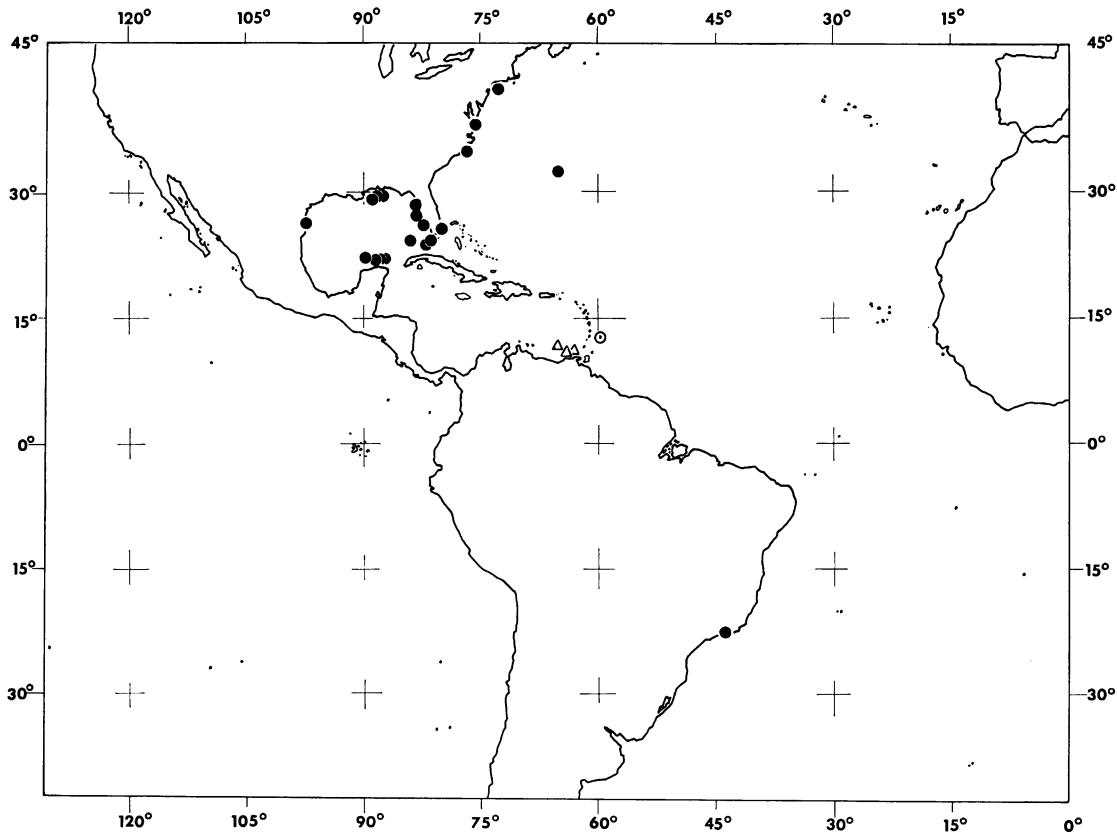


FIG. 38. Distribution records for *Mycteroperca microlepis* (circles) and *M. cidi* (triangles). Solid symbols represent specimens examined, open symbols are additional literature records.

coasts and Bermuda. There are no records from the West Indies.

SPECIMENS EXAMINED

New York: 40° 19' N, 68° 34' W, MCZ 39737.
 Chesapeake Bay: Old Point Comfort, USNM 67921; no specific locality, USNM 21353, 26415, 68183.
 North Carolina: Beaufort, USNM 19512, 51921-22, 53402, 61458, 62771, 63771, 111857, 111859; Cape Lookout, AMNH 5221.
 Florida: Boca Grande, FMNH 38423; Key West, FMNH 7007, 7037; CU 567; USNM 26579, 35021, 38682, 62771, 170887, 170891; ANSP 71177; AMNH 2471, 2534; Key Largo, FMNH 43960; Charlotte Harbor, USNM 33199; CU 10278, 13194, 22655; Channel Key, USNM 120512; Clearwater, CU 12892, 24982, 24923; USNM 158618; Cape Florida, USNM 62731; Captiva Pass, CU 13175; Broad Creek, USNM 57395; Miami, CU 25267; UMMZ 172587, 172587-S; off Cape Sable, USNM 39870; Angel Fish Creek, USNM 53285; Pass-a-Grille Beach, UMMZ 153508, 153636, 153757, 154000, 154156, 154835; Englewood, UMMZ 155053; Rhodes Creek, USNM 57175; Tortugas, UMMZ 87953; USNM 117192; Pensacola, USNM 31894, 30164; Cedar Keys, USNM 176238; Little Salt Pond Key, USNM 134896; no specific locality, CU 4987; USNM 5137 (syn-types of *Mycteroperca microlepis* [Goode and Bean]), 15462 and 16902 (cotype and lectotype of *Trisotropis stomias* Goode and Bean, respectively).
 Alabama: Mobile Bay, MCZ 2836.
 Mississippi: Horn Island, FMNH 31852; UMMZ 176967, 176968, 176970.
 Louisiana: off Chandeleur Island, TU 12822.
 Texas: Port Isabel, FMNH 11298-99.
 Gulf of Mexico: 24° 26.5' N, 87° 35' W, USNM 158599.
 Campeche Banks: off Progreso, UMMZ 143114; 22° 30' N, 90° 00' W, SILVER BAY Station 399; 22° 18' N, 88° 54' W, SILVER BAY Station 413; 22° 31' N, 88° 39' W, UMMZ 174122, SILVER BAY Station 416; 22° 34' N, 88° 36' W, UMMZ 174124, SILVER BAY Station 417; 23° 04' N, 88° 02' W, SILVER BAY Station 428; Alacrán Reef, UMMZ 17498-S.
 Brazil: Río de Janeiro, MCZ 958, 10126.
 Bermuda: FMNH 5216, 5222; USNM 134895.

Mycteroperca interstitialis (Poey, 1860)

YELLOWMOUTH GROUPER

Figure 36

Serranus interstitialis POEY, 1860 (1858-1861), pp. 127-129 (original description, Cuba).
Serranus dimidiatus POEY, 1860 (1866-1868), p. 129 (original description, Cuba).
Serranus falcatus POEY, 1860 (1858-1861), pp. 138-139 (original description, Cuba).
Mycteroperca calliura POEY, 1865 (1865-1866), pp. 181-183 (original description, Cuba). JORDAN AND SWAIN, 1885b, pp. 366-367. JORDAN, 1887e, p. 580 (West Indies). JORDAN AND EIGENMANN, 1890, pp. 368-369. JORDAN AND EVERMANN, 1896a, p. 375; 1896b, p. 1186. JORDAN AND EVERMANN, 1920, p. 394. JORDAN, EVERMANN, AND CLARK, 1930, p. 315. HOWELL Y RIVERO, 1938, p. 192. FOWLER, 1942b, p. 68 (Cuba, in Museo Poey).
Trisotropis chlorostomus POEY, 1867 (1866-1868), pp. 231-233 (original description); 1868 (1866-1868), p. 385; 1870, p. 308; 1875 (1875-1877), pp. 14-15.
Trisotropis calliurus: POEY, 1868 (1866-1868), p. 285; 1870, pp. 307-308; 1875 (1875-1877), p. 14.
Trisotropis interstitialis: POEY, 1868 (1866-1868), p. 285; 1870, p. 308; 1875 (1875-1877), p. 14. JORDAN, EVERMANN, AND CLARK, 1930, p. 314.
Trisotropis dimidiatus: POEY, 1868 (1866-1868), p. 385; 1870, p. 308; 1875 (1875-1877), p. 15. JORDAN, EVERMANN, AND CLARK, 1930, p. 314. BEEBE AND TEE-VAN, 1932, p. 120 (Bermuda); 1933, p. 138. HOWELL Y RIVERO, 1938, p. 192 ("types" in MCZ).
Trisotropis falcatus: POEY, 1868 (1866-1868), p. 385; 1870, p. 309; 1875 (1875-1877), p. 15. GOODE AND BEAN, 1883a, p. 238 (Gulf of Mexico). JORDAN AND GILBERT, 1883a, p. 538 (part, West Indian records only).
Trisotropis sp.: POEY, 1875 (1875-1877), p. 14 ("close to *calliurus*"). GOODE, 1877, p. 292 (Bermuda).
Mycteroperca falcata var. *falcata*: JORDAN AND SWAIN, 1885b, pp. 362-363. JORDAN AND EIGENMANN, 1890, p. 368.
Mycteroperca interstitialis: JORDAN AND SWAIN, 1885b, pp. 365-366. JORDAN, 1887c, p. 39 (Havana); 1887e, p. 580. JORDAN AND EIGENMANN, 1890, pp. 371-372. JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1178-1179. SUMNER, OSBURN, AND COLE, 1913, p. 167 (Woods Hole). FOWLER, 1917b, p. 127 (Katama Bay). JORDAN AND EVERMANN, 1920, p. 393. BREDER, 1929, p. 161. LONGLEY, 1935, p. 283 (synonymy, part of which refers to *M. phenax*). FOWLER, 1942b, p. 68 (Cuba); 1944, p. 445 (Turks Is., after Nichols). ERDMAN, 1957, p. 330 (Puerto Real, Puerto Rico). BRIGGS, 1958, p. 272 (Florida). BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:6, 1:21, 1:23, figs. 4.3, 5.1, 19. CALDWELL, 1966, p. 42 (Jamaica, compiled). CERVIGÓN M. AND VELASQUEZ, 1966,

TABLE 30
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca microlepis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	78.1	120	145	146	154.5	169	171	177	192.5	266	—
Head length	401	387	390	384	392	391	386	390	384	400	390.5
Head width	167	154	131	140	129	142	137	147	135	165	144.7
Head depth	234	237	241	236	236	231	240	234	239	233	236.1
Snout length	106	96	103	99	97	109	96	93	101	117	101.7
Suborbital width	31	33	38	34	32	33	35	40	35	41	35.2
Interorbital width	72	62	62	72	65	65	67	68	65	71	66.9
Length of: Orbit	73	79	62	68	74	68	67	59	60	55	66.5
Postorbital head	227	225	231	229	230	228	228	237	229	241	230.5
Maxillary	204	183	190	182	184	186	187	184	182	188	187.0
Lower jaw	204	196	197	185	188	189	187	195	179	199	191.9
Snout to angle of preopercle	298	279	283	274	278	287	281	277	265	286	280.8
Supramaxillary length	68	62	66	51	58	56	58	56	57	56	58.8
Maxillary width	44	42	47	38	39	38	41	37	42	38	40.6
Tip of lower jaw to gular notch	118	142	117	134	107	104	123	147	130	120	124.2
Body width	138	133	141	140	149	139	137	144	148	173	144.2
Body depth	312	308	300	336	304	305	330	305	312	289	310.1
Caudal peduncle depth	115	112	114	127	117	112	117	119	120	109	116.2
Tip of snout to dorsal origin	421	379	369	366	379	388	401	364	369	387	382.3
Tip of snout to pectoral base	369	387	366	370	366	361	363	373	366	370	369.1
Tip of lower jaw to pelvic base	387	450	393	397	398	388	386	412	395	398	400.4
Length of: Dorsal base	536	542	528	548	505	518	515	494	522	500	519.0
Depressed dorsal	612	612	607	634	576	604	661	579	611	566	606.2
Anal base	195	192	186	205	188	183	208	192	198	177	192.4
Depressed anal	293	292	286	295	291	296	298	288	286	259	288.4
End of dorsal to caudal base	130	146	155	154	149	154	152	161	148	147	149.6
Length of: Caudal peduncle	187	200	200	195	184	189	196	201	185	195	193.2
Pectoral	212	217	214	209	207	207	213	203	198	197	207.7
Pelvic	182	187	172	182	188	183	184	169	169	165	178.1
Dorsal spine I	52	62	59	58	61	65	67	59	55	60	59.8
Dorsal spine III	115	121	117	110	117	118	118	110	107	122	115.5
Dorsal spine XI	114	96	100	106	97	101	99	93	94	83	98.3
Anal spine I	47	50	52	41	42	41	47	48	39	45	45.2
Anal spine II	86	100	79	89	91	83	94	71	83	75	85.1
Anal spine III	106	112	90	99	91	101	114	99	94	90	99.6
Caudal base to tip of upper rays	234	254	255	264	259	263	260	240	239	256	252.4
Caudal base to tip of middle rays	227	217	234	223	230	225	231	212	208	209	221.6
Caudal base to tip of lower rays	—	246	231	253	252	251	251	220	234	237	241.7

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 2 and 6, UMMML; 1, 3, 4, 5, 7, 8, 9, 10, UMMZ 87953, 154156, 153948, 143115, 153757, 154156, 153757, 155053 respectively. For data see text.

- pp. 93–96 (osteology, Venezuela). RANDALL, 1967, p. 702 (food habits); 1968, p. 66, fig. 73 (general account, color photograph). BÖHLKE AND CHAPLIN, 1968, p. 284 (Bahamas).
- Mycteroperca dimidiata*: JORDAN AND SWAIN, 1885b, p. 367 (after Poey). JORDAN, 1887e, p. 580. JORDAN AND EIGENMANN, 1890, p. 372. JORDAN AND EVERMANN, 1896a, p. 374; 1896b, p. 1179. FOWLER, 1915b, p. 534 (Port-of-Spain). JORDAN AND EVERMANN, 1920, p. 393. HOWELL Y RIVERO, 1938, p. 192 (Poey "types" in MCZ).
- Mycteroperca falcata*: JORDAN, 1887c, p. 39 (Havana); 1887e, p. 580 (West Indies); 1891, p. 318 (Bahía). JORDAN AND EVERMANN, 1896a, p. 375; 1896b, pp. 1184–1185. BEAN, 1906, p. 54 (Bermuda, copied). FOWLER, 1915b, p. 543 (St. Georges, Grenada). JORDAN AND EVERMANN, 1920, pp. 393–394. NICHOLS, 1921, p. 23 (Turks Is.). JORDAN, EVERMANN, AND CLARK, 1930, p. 315. BEEBE AND TEE-VAN, 1933, pp. 130–131. HOWELL Y RIVERO, 1938, p. 192 (cotypes of *S. falcatus* in MCZ). BUTSCH, 1939, p. 23 (Barbados). FOWLER, 1942b, p. 68 (Cuba). BARDACH AND MENZEL, 1957, p. 108 (Bermuda, growth rates). BRIGGS, 1958, p. 272. SMITH, 1958, pp. 8, 10, 16, 58, figs. 2b, 3, 9, pl. 16 (Bermuda, biology); 1959, p. 114 (hermaphroditic).
- Epinephelus falcatus*: BOULENGER, 1895, pp. 261–262 (Bermuda; Jamaica; Grenada). MIRANDA-RIBEIRO, 1915, p. 23 (Brazil); 1918, p. 90.
- Epinephelus calliura*: BOULENGER, 1895, p. 264 (coast of Cuba).
- Epinephelus dimidiatus*: BOULENGER, 1895, pp. 264–265.
- Epinephelus interstitialis*: BOULENGER, 1895, p. 266. SCHULTZ, 1952, p. 120.
- Mycteroperca venenosa* (non Linnaeus): SMITH, 1902, p. 33 (Woods Hole area).
- Epinephelus* (*Mycteroperca*) *interstitialis*: METZELAAR, 1919, p. 51, fig. 19 (may be *M. phenax*).
- Mycteroperca falcata falcata*: BREDER, 1929, p. 161.
- Mycteroperca roquensis* MARTIN SALAZAR, 1956, pp. 100–102 (original description, Gran Roque, Venezuela).

NOMENCLATURE: Long known as *Mycteroperca falcata*, this species was described simultaneously by Poey under the name *interstitialis*. Longley (1935) was the first to indicate their identity, and his selection of the name *interstitialis* stands as the first reviser's choice. A third name of the same date, *Serranus dimidiatus*, is based on the distinctive juvenile color pattern.

The name *interstitialis* is from the Latin *interstinctus*, having interstices, apparently in reference to the color phase in which the ground pattern is broken into brown spots separated by a reticulum of light lines.

Poey's description makes no mention of the

deposition of a type specimen of *Mycteroperca interstitialis* in any museum.

DIAGNOSIS: Rather small *Mycteroperca* with compressed, deep body, small scales, and very pronounced preopercular lobe. Dorsal XI, 17; anal III, 11 (12); pectoral 17; gill rakers 24–28. Vertical fins with greatly exerted rays in adult. Posterior nostril greatly enlarged in large fish. First three dorsal spines not forming an elevated lobe. Color generally brownish, without depth-correlated phases, ground sometimes broken into fine, close spots separated by a lighter reticulum. Pectoral dark with a narrow white margin.

The salient preopercular angle and enlarged posterior nostril are characteristic of this species-group of *Mycteroperca*. Distinctive features of *interstitialis* are the color pattern of uniform brown or gray, close-set spots separated by a reticular network of narrow lines, and the form of exerted rays of dorsal, anal, and caudal fins. In structure of gill rakers and in meristic characters *interstitialis* is close to *phenax* but that species has exerted rays even longer and those of caudal much less regular. Color pattern of *interstitialis* similar to that of *phenax* but lacks brownish red, well-separated spots on a gray background. Juveniles of the two species very different; those of *interstitialis* are bicolored, those of *phenax* are not.

DESCRIPTION: The body of *Mycteroperca interstitialis* is deeper and more compressed than those of other species of the genus. This may account for the Bermudan name, "salmon rockfish." The proportions are very similar to those of *phenax*. Measurements of 10 specimens appear in table 31.

The preopercle is greatly expanded below the notch with strong but irregular serrae on this expansion. The skull crests are very high; the lateral crest extends forward to above the middle of the orbit (fig. 37). The median crest ends abruptly at the anterior end of the supraoccipital bone. The supraethmoid wall is well developed. The median canines are strong in both jaws. The posterior nostril is much enlarged, even in specimens of about 275 mm. The gill rakers, although not especially numerous, are long and rather slender. The upper lip is narrower at its midside than the breadth of the adjacent part of the maxilla. This character is useful in the separation of small specimens from those of *Mycteroperca bonaci*.

Some soft dorsal and anal rays start to exert when the fish is about 300 mm. long. This exertion is pronounced in the middle anal rays (six, seven, and eight) and the caudal rays, but less so in the dorsal fin. In large specimens the caudal rays are evenly exerted; each central ray ends in a symmetrical point. Toward the dorsal and ventral margins these points are skewed and are slightly longer.

The body color is brownish, only slightly paler below. The dorsal and anal fins are almost uniformly dusky, slightly darker on the outer third with a narrow white margin. The dorsal interspinous membranes are greenish. The caudal is dark throughout, with no light margin, but has a yellowish green submarginal band that fades soon after death. The pectoral membrane is light with the rays distinctly darker so that the outer third of the fin where the rays branch is darkest. There is a sharply delimited white margin about one-tenth as wide as the fin length.

The jaws are washed with yellow just anterior to the angle of the mouth. The inside of the mouth is white. Some individuals also have a greenish stripe from the anterior part of the eye to the nostril.

Some specimens show a transitory pattern in which the background is broken into small dark spots by a regular network of light lines. In another such pattern there are five or six vertical cross bars separated by light interspaces that are about one-fourth as wide as the bars; these bars are in turn disrupted into quadrate blotches similar to those of *bonaci* but more regular.

The young of *Mycteroperca interstitialis* are sharply bicolored, dark above and white below. The smallest individual seen was 37 mm. long. At 90 mm. the lower parts show some markings; the anterior part of the anal fin is sprinkled with melanophores and the upper and lower margins of the caudal fin are jet black. On the caudal peduncle the upper part is blackest just above the edge of the white area and on the caudal base there is a distinct oval spot set off by a halo of pale gray. This spot persists until the fish reaches a length of 150 mm. by which time the bicolored pattern is obsolescent. The dorsal fin of the young is washed with yellow but the green submarginal band is not present. The smallest individuals retain the large preopercular spine of the larvae. The series of young on which the above account is based is illustrated

in Bardach, Smith, and Menzel (1958, p. 110, fig. 3).

RELATIONSHIPS: The species of *Mycteroperca* that have the preopercular angle expanded into a prominent lobe and an enlarged posterior nostril seem to form an intimately related group that is here called the *interstitialis* species-group. The included species are *olfax*, *microlepis*, *phenax*, *rubra*, *rosacea*, *interstitialis*, *cidi*, *xenarcha*, and *prionura*. Several of these have exerted rays in the median fins, a feature shared in the genus only with *tigris*. *Mycteroperca interstitialis* is most closely related to *M. phenax*.

ECOLOGY: *Mycteroperca interstitialis* is apparently more common in Bermuda than the commercial catch would indicate because it is seldom taken in pots. It takes a hook readily. In Bermuda it is taken on the Banks as well as on the inshore reefs.

In Bermuda *M. interstitialis* gonads begin to ripen the last of May and spawning continues at least until the first of August. Juveniles become common inshore in August. The maximum weight is about 8 pounds.

DISTRIBUTION: *Mycteroperca interstitialis* is abundant in Bermuda and ranges through the Bahamas, the Antilles, and the Caribbean south to Bahía, Brazil. It is chiefly a geographical replacement of *M. phenax*, but the two are sympatric on the Campeche Banks (fig. 39).

SPECIMENS EXAMINED

Florida: off Miami, CU 25267.
 Caribbean Sea: Glover Reef, FMNH 39714; Alacrán Reef, UMMZ 174115, 174172-S.
 Brazil: Bahía, USNM 43388.
 Barbados (?): USNM 170117.
 Cuba: no specific locality, USNM 4669; MCZ 10011 (cotype of *Mycteroperca calliura* Poey), 9992, 10012, 10014 (cotype of *Serranus falcatus* Poey), 10078, 10183 (cotype of *S. falcatus*), 10188 (cotype of *S. falcatus*), 26953, 34158 (cotype of *S. falcatus*).
 West Indies: no specific locality, USNM 33593.
 Bahamas: Bimini, UMMZ 174419; New Providence, CBC 212.
 Hispaniola: Haiti, AMNH 19028.
 Bermuda: USNM 21406, 169989, 169998, 170007, 170008; MCZ 32856, 32870; FMNH 5225, 48296, 48370, 48388, 48726, 48819, 48853, 48864, 48867, 49084, 50578; UMMZ 172545-S, 172546-S, 172547-S, 176046,

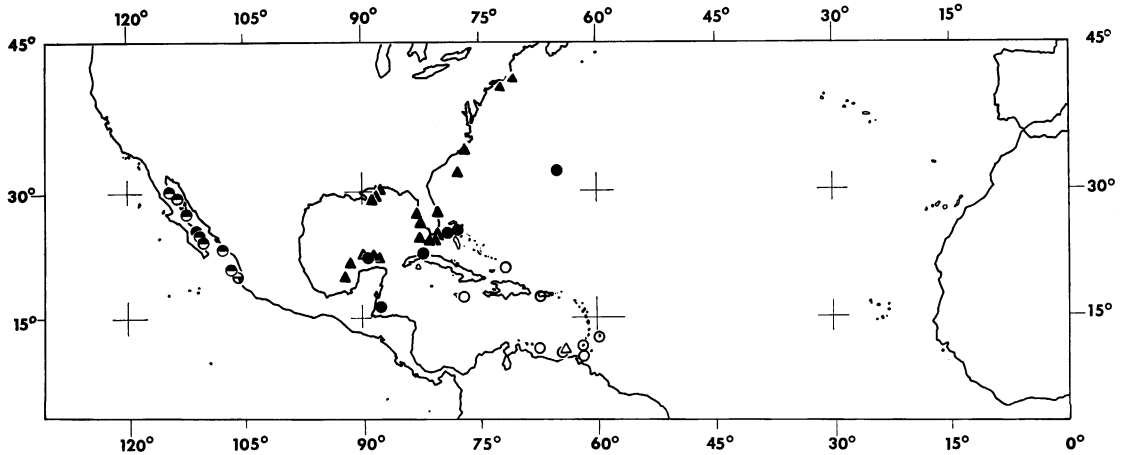


FIG. 39. Distribution records for *Mycteroperca interstitialis* (full circles), *M. phenax* (triangles), and *M. rosacea* (half circles). Solid symbols represent specimens examined, open symbols are additional literature records.

176107, 176148, 176167, 176359, 176474,
176504, 176507, 176589, 176601, 176624;
AMNH 17774.

Mycteroperca phenax Jordan and Swain, 1885
SCAMP

Trisotropis falcatus (non Poey): GOODE AND BEAN, 1880, pp. 141–142 (Pensacola). JORDAN AND GILBERT, 1883a, p. 538 (Florida records only); 1883d, p. 273. POEY, 1883, p. 118. LÖNNBERG, 1894, p. 126 (Florida).

Epinephelus falcatus: JORDAN, 1884a, p. 77 (Key West); 1885b, p. 124 (Key West, Pensacola).

Mycteroperca falcata: BEAN, 1884, p. 503. HENSHALL, 1895, p. 215 (Key West). PARR, 1930, p. 50 (Florida). BAUGHMAN, 1943, p. 772 (Texas coast). SPRINGER AND BULLIS, 1956, p. 78 (Gulf of Mexico). BRIGGS, 1958, p. 272 (part, Florida records).

Mycteroperca falcata var. *phenax* JORDAN AND SWAIN, 1885b, pp. 363–364 (original description, Pensacola, syntype USNM 34992). JORDAN AND EIGENMANN, 1890, p. 368.

Mycteroperca falcata phenax: JORDAN, 1887a, p. 84. HENSHALL, 1891, p. 387 (Key West, Ironwood Key, Key Largo). JORDAN AND EVERMANN, 1896a, p. 375; 1896b, p. 1185. SMITH, 1896, p. 175 (Key Biscayne Bay). BRICE, 1898, p. 283. EVERMANN AND KENDALL, 1900, pp. 74–75 (Florida). SCHROEDER, 1924, p. 17 (Key West). BREDER, 1927, p. 39; 1929, p. 161.

Mycteroperca interstitialis (non Poey): SMITH, 1899, p. 880 (Woods Hole); 1901, p. 310 (Katama Bay). KENDALL, 1908, p. 99. SUMNER, OSBURN, AND COLE, 1913, pp. 167, 756. NICHOLS AND BREDER, 1927, p. 80 (Woods Hole record doubted). LONGLEY, 1935, p. 283 (part). LONGLEY AND HILDEBRAND,

1941, p. 100, pl. 7, fig. 2 (only part of the synonymy is this species, figure mislabeled *M. venenosa*).

Mycteroperca venenosa (non Linnaeus): SMITH, 1902, p. 33 (Woods Hole).

Mycteroperca phenax: JORDAN AND EVERMANN, 1920, p. 394. JORDAN, EVERMANN, AND CLARK, 1930, p. 315. BRIGGS, 1958, p. 272. BAILEY ET AL., 1960, p. 25 (common name). SMITH, 1961, pp. 1:6, 1:21, 1:23, figs. 5.2, 19. ALPERIN AND SCHAEFER, 1965, pp. 5–6 (New York record, photograph). CERVIGÓN M., 1966b, pp. 298–300, fig. 116 (Cubagua, Venezuela), CERVIGÓN M. AND VELASQUEZ, 1966, pp. 96–99 (Venezuela, osteology). RANDALL, 1968, pp. 66–67, fig. 74 (general).

NOMENCLATURE: *Mycteroperca phenax* is treated as a full species rather than as a subspecies in spite of the strong resemblance to *M. interstitialis*. The young of these species are quite different and the two forms are sympatric on the northern part of the Campeche Bank.

There is one syntype of *Mycteroperca phenax* in the United States National Museum (USNM 34992, 234 mm.), and another is in the British Museum (Natural History).

The specific name is derived from the Greek *φένναξ*, imposter, equivalent to the common name “scamp.”

DIAGNOSIS: Moderate-sized, deep-bodied species of *Mycteroperca* with medium-sized scales and pronounced preopercular lobe. Posterior nostril enlarged in larger fish. Dorsal XI, 17; anal III, 11; pectoral 16 (17); gill rakers 26–31. Vertical fins with greatly exerted rays in adult. First three dorsal spines not forming an

TABLE 31
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca interstitialis*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	220	244	250	251	252	255	271	279	322	366	—
Head length	359	359	342	339	351	349	339	346	342	344	347.0
Head width	132	139	132	131	127	121	125	142	141	133	132.3
Head depth	223	238	234	223	230	235	210	237	217	238	228.5
Snout length	98	104	100	98	95	98	94	90	96	103	97.6
Suborbital width	32	29	30	28	32	29	30	29	28	29	29.6
Interorbital width	70	78	80	75	71	76	74	77	73	74	74.8
Length of: Orbit	62	61	62	62	63	63	59	61	53	53	59.9
Postorbital head	198	201	196	191	206	198	199	204	200	197	199.0
Maxillary	163	168	164	163	167	171	159	170	160	173	165.8
Lower jaw	168	172	170	167	175	180	173	176	169	176	172.6
Snout to angle of preopercle	252	252	246	249	248	255	236	249	242	251	248.0
Supramaxillary length	52	43	50	48	52	51	52	50	47	49	49.4
Maxillary width	36	39	34	40	38	39	35	36	33	34	36.4
Tip of lower jaw to gular notch	105	107	100	112	87	90	—	90	—	98	98.6
Body width	141	158	152	139	138	149	148	143	152	150	147.0
Body depth	314	320	318	320	319	317	303	326	323	336	319.6
Caudal peduncle depth	111	115	110	111	111	114	109	115	112	107	111.5
Tip of snout to dorsal origin	363	360	356	349	345	349	347	358	348	354	352.9
Tip of snout to pectoral base	350	346	332	325	—	—	325	332	315	337	332.8
Tip of lower jaw to pelvic base	416	406	388	392	—	—	375	387	391	396	393.8
Length of: Dorsal base	502	522	550	554	536	504	528	541	534	530	520.1
Depressed dorsal	573	581	616	598	599	569	592	598	584	578	588.8
Anal base	191	193	202	211	194	208	199	208	211	197	201.4
Depressed anal	268	258	276	279	258	275	269	280	261	277	270.1
End of dorsal to caudal base	180	166	168	171	181	180	162	168	166	178	172.0
Length of: Caudal peduncle	225	209	210	215	216	220	212	204	208	206	212.5
Pectoral	—	189	188	189	190	192	188	190	177	179	186.9
Pelvic	—	168	172	169	161	165	162	168	154	160	164.3
Dorsal spine I	68	66	68	70	69	69	70	61	71	61	67.3
Dorsal spine III	118	119	112	116	119	114	120	111	126	116	117.1
Dorsal spine XI	91	92	92	94	91	92	107	—	99	90	94.2
Anal spine I	36	39	38	36	50	47	44	39	47	45	42.1
Anal spine II	77	82	70	70	77	69	81	75	70	66	73.7
Anal spine III	95	90	92	92	99	92	96	90	93	98	93.7
Caudal base to tip of upper rays	286	289	292	279	282	273	273	305	267	272	281.8
Caudal base to tip of middle rays	—	213	216	207	214	204	210	228	205	205	210.8
Caudal base to tip of lower rays	—	277	272	267	261	259	266	290	264	265	269.0

^aAll proportions are expressed in thousandths of the standard length. All specimens are UMMZ from Bermuda with field numbers, in the order of the columns, as follows: 43, 45, 46, 44, 41, 1956, 153, 47, 152, S56-59.

elevated lobe. Color light brownish gray with small, well-separated spots. Pectoral dark with narrow light margin.

The scamp resembles *Mycteroperca interstitialis* but differs in having exertions of vertical fin rays longer and more irregular, and spots on body widely spaced on a light background. I have never seen a specimen in which there were

quadrate blotches on the upper part of the body although in some, especially smaller individuals, spots tend to be more pronounced in certain areas. The scamp has green submarginal band on dorsal and caudal fins as in *interstitialis* and, like that species, has a yellowish wash on the jaws.

DESCRIPTION: The proportions of this species

(table 32) are similar to those of *interstitialis* except that the longer rays of the vertical fins are reflected in the depressed dorsal and anal measurements and in the caudal proportions.

The gill rakers are long and slender, and in adults the posterior nostril is several times as large as the anterior nostril. The dorsal, anal, and caudal fins have some greatly elongate soft rays in specimens more than 300 mm. long. These prolongations exceed those of *Mycteroperca interstitialis*. The exertion of the anal fin rays in large specimens may equal or exceed the distance from the base of the rays to the normal edge of the fin. The maxilla is scaled on its exposed side. The pectoral is rounded; the pelvic has the last ray united by membrane to the body for less than half its length.

The body is light grayish brown, somewhat darker above, covered with well-spaced spots (each about 4 mm. in diameter) except on the belly. The outer two-thirds of the anal and pelvic are dark with a bluish cast, and the caudal and soft dorsal each have a greenish submarginal band. The angle of the mouth is yellowish; the inside of the mouth is white. The pectoral is light at the base and has light membranes with dark rays; the fin appears darkest about three-fourths of the way to the broad white margin. The pelvic is brownish dorsally, dark toward the tips, with the leading edge white. The margin of the anterior part of the fin is white. *Mycteroperca phenax* shows little color variation other than in intensity.

A specimen 72 mm. long, MCZ 31075, was pale with small but distinct spots on the sides of the body. Some spots were arranged in rings and connected with dusky lines suggesting the groups of spots in adult specimens. There was no indication of the bicolored pattern of the young of *interstitialis*.

RELATIONSHIPS: *Mycteroperca phenax* and *M. interstitialis* are geminate species that seem to have arisen through isolation by the Gulf Stream, *interstitialis* in the Bahamas and West Indies, *phenax* in the Gulf of Mexico. These species are sympatric on the Campeche Bank, where they retain their identity.

ECOLOGY: This species was taken often on the Campeche Bank in depths of 35 to 50 fathoms. It is apparently common there and on the Florida coast. It is highly esteemed as a food fish, reaching a weight of about 20 pounds.

DISTRIBUTION: *Mycteroperca phenax* is widely

distributed throughout the Gulf of Mexico and along the mainland coast to North Carolina (fig. 39); the young are taken occasionally off the Massachusetts coast.

SPECIMENS EXAMINED

Massachusetts: Katama Bay, USNM 49674; ANSP 23884; Woods Hole, MCZ 31075.

North Carolina: Beaufort, USNM 53403, 126482.

South Carolina: 32° 16.5' N, 77° 32.5' W, USNM 152088.

Florida: Pensacola, FMNH 643; MCZ 35133; Key West, FMNH 7052; USNM 164648, 34992 (holotype of *Mycteroperca falcata phenax* Jordan and Swain), 38708, 26587 (cotype of *Trisotropis stomias* Goode and Bean); Florida Keys, BOC 199; Charlotte Harbor, USNM 33219; Tampa, USNM 47316; Indian River Inlet, USNM 25113; Miami, UMMZ 172586.

Gulf of Mexico: OREGON Station 1795, FMNH 64195; 29° 26.5' N, 87° 35' W, USNM 158591; 29° 16' N, 88° 20' W, USNM 158592; no specific locality, USNM 125717.

Campeche Bank: Alacrán Reef, 22° 13' N, 89° 45' W, SILVER BAY Station 408; 21° 50' N, 91° 31' W, UMMZ 173993, SILVER BAY Station 343; 19° 47' N, 91° 45' W, UMMZ 174005-S, SILVER BAY Station 347; 20° 04' N, 91° 47' W, UMMZ 174007-S, SILVER BAY Station 350; 20° 09' N, 91° 51' W, SILVER BAY Station 353; 20° 02' N, 91° 57' W, UMMZ 174031, SILVER BAY Station 355; 20° 01' N, 91° 41' W, UMMZ 174042-S, SILVER BAY Station 361; 19° 58' N, 91° 42' W, SILVER BAY Station 363; 19° 57' N, 91° 45' W, SILVER BAY Station 364; 19° 57' N, 91° 40' W, SILVER BAY Station 365; 20° 10' N, 91° 43' W, UMMZ 174050, SILVER BAY Station 371; 20° 12' N, 91° 45' W, SILVER BAY Station 372; 20° 03' N, 91° 51' W, SILVER BAY Station 374; 21° 05' N, 91° 50' W, SILVER BAY Station 379; 21° 11' N, 91° 47' W, SILVER BAY Station 383; 21° 35' N, 91° 20' W, SILVER BAY Station 384; 22° 24' N, 90° 17' W, SILVER BAY Station 374; 22° 22' N, 90° 16' W, SILVER BAY Station 395; 22° 17' N, 90° 18' W, SILVER BAY Station 397; 22° 29' N, 90° 03' W, SILVER BAY Station 398; 22° 34' N, 89° 56' W, SILVER BAY Station 401; 22° 31' N, 88° 39' W, SILVER BAY Station 416; 22° 49' N, 88° 13' W, SILVER BAY Station 420; 22° 30' N,

TABLE 32
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca phenax*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	60	63.5	87.5	198	222	234	334	342	428	573	—
Head length	392	394	371	359	367	380	368	374	359	358	372.2
Head width	158	150	160	134	135	139	139	145	136	142	143.8
Head depth	242	236	263	240	223	237	225	243	236	246	239.1
Snout length	108	94	97	88	99	103	108	104	98	102	100.1
Suborbital width	33	25	29	33	29	32	30	36	37	37	32.1
Interorbital width	75	87	69	66	68	62	72	70	69	71	70.9
Length of: Orbit	83	87	74	68	65	68	60	56	54	48	66.3
Postorbital head	208	220	211	202	205	218	210	218	222	222	213.6
Maxillary	183	189	189	167	178	177	166	175	175	163	176.2
Lower jaw	192	189	183	177	171	184	181	184	187	175	182.3
Snout to angle of preopercle	283	291	257	253	255	271	260	268	259	250	264.7
Supramaxillary length	58	63	63	53	54	56	51	50	56	52	55.6
Maxillary width	42	39	34	38	36	36	36	35	33	37	36.6
Tip of lower jaw to gular notch	150	102	137	106	128	94	114	98	92	85	110.6
Body width	133	150	143	139	153	141	132	145	121	145	140.2
Body depth	333	323	331	328	304	335	295	329	329	333	324.0
Caudal peduncle depth	117	118	126	116	115	122	105	120	129	125	119.3
Tip of snout to dorsal origin	400	394	354	374	367	374	364	371	371	371	374.0
Tip of snout to pectoral base	367	370	377	343	340	353	355	335	339	337	351.6
Tip of lower jaw to pelvic base	400	402	457	399	401	406	398	398	397	382	404.0
Length of: Dorsal base	550	528	526	538	523	573	533	532	533	542	537.8
Depressed dorsal	652	583	606	616	595	650	582	611	624	607	609.9
Anal base	192	213	200	202	196	201	177	178	167	186	191.2
Depressed anal	292	331	297	313	293	299	259	300	301	307	299.2
End of dorsal to caudal base	142	134	154	146	159	154	154	159	168	159	152.9
Length of: Caudal peduncle	183	197	194	199	205	201	198	200	206	187	197.0
Pectoral	225	236	234	212	200	207	175	189	189	171	203.8
Pelvic	192	205	183	182	185	184	157	186	181	184	183.9
Dorsal spine I	58	79	57	51	61	62	58	66	60	35	58.7
Dorsal spine III	117	126	120	119	124	128	118	132	—	—	123.0
Dorsal spine XI	92	110	91	88	99	111	82	95	84	72	92.4
Anal spine I	50	47	46	43	52	47	37	37	28	33	42.0
Anal spine II	100	102	103	86	90	94	61	80	69	51	83.6
Anal spine III	117	102	114	93	86	109	84	91	83	74	95.3
Caudal base to tip of upper rays	250	276	269	326	304	327	260	325	381	307	302.5
Caudal base to tip of middle rays	200	244	229	215	198	226	177	202	192	188	207.1
Caudal base to tip of lower rays	242	236	269	295	282	288	257	306	329	289	279.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: 1, 2, 3, 4, 6, 9, 10, USNM 126482, 49674, 53403, 33219, 34992, 47316, 25113, respectively; 5, UMMZ 172586; 7, 9, UMIM without data, presumably from southern Florida. For data see text.

88° 13' W, SILVER BAY Station 422; 22° 27' N,
88° 11' W, SILVER BAY Station 423.

Mycteroperca cidi Cervigón M., 1966

Mycteroperca sp.: CERVIGÓN M., 1966b, pp. 300–302,
fig. 117 (Cubagua, Venezuela).

Mycteroperca cidi CERVIGÓN M., 1966a, pp. 653–660,
fig. 1–3, (original description, Venezuela). CERVIGÓN M. AND VELASQUEZ, 1966, pp. 100–104,
figs. 6, 7 (description, osteology, biology, habitats
and relationships). RANDALL, 1968, pp. 68–69,
fig. 76 (general account).

NOMENCLATURE: Apparently this species was unknown before 1961 and no earlier literature records apply to it.

DIAGNOSIS: Like its near relatives *interstitialis* and *phenax*, *cidi* has a compressed body, prominent lobe at angle of preopercle and, when large develops exerted fin rays. Dorsal XI (XII), 15-17; anal III, 10-12; pectoral 16; gill rakers 9-13+1+17-22; transverse scale rows 120-126. Posterior nostril enlarged in specimens more than 400 mm. long. Caudal peduncle slender for a *Mycteroperca*.

The high gill raker count sets it apart from both *phenax* and *interstitialis*.

DESCRIPTION: From the account and figures by Cervigón M., and Cervigón M. and Velasquez this species looks very much like *interstitialis*. Young individuals apparently have a color pattern suggestive of that of *M. microlepis* (see Cervigón M. and Velasquez, 1966, fig. 6) but larger individuals are uniform gray-brown. Occasionally there is a dusky yellowish wash around the mouth. Spiny dorsal clear dusky gray with a dark subterminal band and a narrow white margin. Anal similar. Pectoral yellowish gray with a clear distal margin. Pelvic grayish black with a white border. Gular region light.

The neurocranium closely resembles that of *interstitialis* and *phenax* (Cervigón M. and Velasquez, 1966, figs. 25, 27, 29).

RELATIONSHIPS: Cervigón M. and Velasquez assign to this species a close relationship with *phenax* and *interstitialis*.

ECOLOGY: Small individuals are abundant in depths of 3-4 fathoms. Larger specimens are restricted to deeper water.

DISTRIBUTION: Coast of Venezuela, abundant at Margarita and neighboring islands, less common at La Blanquilla (fig. 38).

SPECIMENS EXAMINED

None. The foregoing account is taken from Cervigón M. and Velasquez, 1966.

Mycteroperca prionura

Rosenblatt and Zahuranec, 1967

Mycteroperca prionura ROSENBLATT AND ZAHURANEC, 1967, pp. 241-244 (original description, Gulf of California).

Mycteroperca xenarcha (non Jordan): WALFORD, 1936, p. 6 (part, "spotted phase" only). WALFORD, 1937, p. 103, pl. 11, fig. c (in part, "spotted phase" only).

The following data are from Rosenblatt and Zahuranec, 1967:

DIAGNOSIS: Moderate-sized grouper with preopercular lobe and exerted caudal rays in adults. Total gill rakers 34-38; pectoral rays 15 or 16; dorsal X-XI, 16-18. Color pattern consisting of large, round, reddish brown, dark spots on light tan background, spots becoming more numerous, irregular, and relatively smaller with growth.

DESCRIPTION: A full description of this species, including proportional measurements, appears in Rosenblatt and Zahuranec (1967).

RELATIONSHIPS: *Mycteroperca prionura* is obviously a member of the *interstitialis* species-group. It appears to be most closely related to *M. interstitialis*, as evidenced by the pointed dorsal and anal fins, the color pattern and the serrated margin of the caudal fin.

ECOLOGY: According to Rosenblatt and Zahuranec, this species may be restricted to greater depths than other Eastern Pacific species. Only a few juveniles have been taken at depths shallower than 25 feet, and the species is known to range to 150 feet.

DISTRIBUTION: Gulf of California and northwestern coast of Mexico from Isla Santa Inez to Inner Gorda Bank, Baja California and from Bahía de Banderas, Jalisco (fig. 40).

SPECIMENS EXAMINED

Mexico: Baja California, Bahía de La Paz, Isla Lobos, AMNH 26000 (five paratypes, Aug. 24, 1965, Rosenblatt and party); Bahía de Banderas, USNM 101061 (paratype, 526 mm., March 21, 1935, L. A. Walford).

Mycteroperca xenarcha Jordan, 1888

BROOMTAIL GROUPEE

Mycteroperca xenarcha JORDAN, 1888, p. 387 (original description, James Is., Galápagos). JORDAN AND EIGENMANN, 1890, p. 372. JORDAN, 1895, pp. 450-451 (Venados Is.). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, p. 1180. ABBOTT, 1899, p. 348. SNODGRASS AND HELLER, 1905, p. 368. EVERMANN AND RADCLIFFE, 1917, p. 70 (Payta, Peru). JORDAN AND EVERMANN, 1920, p. 393. MEEK AND HILDEBRAND, 1925, p. 449 (close to *boulengeri*; not yet taken in Panama). WALFORD, 1936, pp. 6-7 (part, "plain phase only," *boulengeri* in synonymy); 1937, p. 103 (in part, "plain phase only," Banderas Bay, just north of Cape Corrientes). NICHOLS AND MURPHY, 1944, pp. 247-248 (St. Elena, Ecuador). HILDEBRAND, 1946, pp. 170-171 (Peru, no recent

specimens). BERDEGUE A., 1956, pp. 274-275 (commercial species in Mexico). BAILEY ET AL., 1960, p. 25 (common name). ROSENBLATT AND ZAHURANEC, 1967, pp. 239-241 (general account). *Epinephelus xenarchus*: BOULENGER, 1895, pp. 266-267. *Mycteroperca boulengeri* JORDAN AND STARKS, in Jordan, 1895, pp. 445-446, pl. 38 (original description; syntypes, Stanford University 1621). JORDAN AND EVERMANN, 1896a, p. 373; 1896b, pp. 1171-1172 (general account); 1898, p. 2856 (Mazatlán, a needless addendum); 1900, pl. 187, fig. 490. GILBERT AND STARKS, 1904, p. 97 (Panama Bay). JORDAN AND EVERMANN, 1920, p. 391 (key, characters, drawing). MEEK AND HILDEBRAND, 1925, pp. 448-449 (Corozal, Panama). BÖHLKE, 1953, p. 70 (three syntypes in Stanford University collection, 1621). *Trisotropis boulengeri*: JORDAN, EVERMANN, AND CLARK, 1930, p. 313. BREDER, 1936, p. 23 (Gonzago Bay; Cape San Lucas). *Trisotropis xenarchus*: JORDAN, EVERMANN, AND CLARK, 1930, p. 314. BREDER, 1936, p. 23 (Rey Is., Pearl Is.).

NOMENCLATURE: The holotype, MCZ 24198, from James Island in the Galápagos Islands was examined at the Museum of Comparative Zoology by Rosenblatt and Zahuranec (1967).

The name *xenarcha* is from the Greek ξένος, strange, and ἀρχός. Jordan (1896b, p. 1180) gave the meaning of the latter Greek word as "anus." However, Mrs. Rothman has pointed out that in most lexicons the meaning of *archos* is leader, and that the Anglo-Saxon "arse" is actually derived from a different word, probably ὄρος (*oros* or *orrhos*), rump.

DIAGNOSIS: Medium-sized species of *Mycteroperca* with robust body, moderate-sized scales, and a distinct preopercular lobe. Posterior nostril enlarged in large fish. Dorsal XI, 15-16; anal III, 11; pectoral 17; gill rakers 29-35. Dorsal and anal falcate in adult, caudal rays irregularly exserted, ragged in appearance. First three dorsal spines not forming an elevated lobe.

DESCRIPTION: Table 33 gives the proportional measurements of three specimens. The caudal fin of larger specimens is exserted, giving that fin a ragged or toothed appearance. The soft dorsal and anal fins are falcate; some of the central rays are elongate (dorsal rays eight to 10; anal rays four and five). Walford (1936, p. 6) reported that the species reaches a length of 3 feet.

According to Walford (1936, p. 7, and 1937, p. 103 and pl. 11), there are three phases:

TABLE 33
PROPORTIONAL MEASUREMENTS OF THREE SPECIMENS
OF *Mycteroperca xenarcha*^a

Measurements	1	2	3	Average
Standard length (mm.)	165	211	600	—
Head length	388	379	378	381.7
Head width	139	156	175	156.7
Head depth	252	254	248	251.3
Snout length	100	102	113	105.0
Suborbital width	30	33	38	33.7
Interorbital width	70	78	88	78.7
Length of: Orbit	67	64	45	58.7
Postorbital head	224	225	233	227.3
Maxillary	176	168	178	174.0
Lower jaw	182	178	182	180.7
Snout to angle of preopercle	267	258	267	264.0
Supramaxillary length	58	52	56	55.3
Maxillary width	39	38	39	38.7
Tip of lower jaw to gular notch	112	133	109	118.0
Body width	145	156	172	157.7
Body depth	327	341	345	337.7
Caudal peduncle depth	136	133	135	134.7
Tip of snout to dorsal origin	358	358	360	358.7
Tip of snout to pectoral base	355	367	352	358.0
Tip of lower jaw to pelvic base	403	419	412	411.3
Length of: Dorsal base	545	531	525	533.7
Depressed dorsal	648	626	633	635.7
Anal base	197	206	185	196.0
Depressed anal	345	348	333	342.0
End of dorsal to caudal base	158	152	162	157.3
Length of: Caudal peduncle	200	199	192	197.0
Pectoral	224	220	187	210.3
Pelvic	206	199	150	185.0
Dorsal spine I	64	62	48	59.0
Dorsal spine III	127	128	89	114.7
Dorsal spine XI	109	118	81	102.7
Anal spine I	55	50	—	52.5
Anal spine II	97	104	—	100.1
Anal spine III	115	121	78	104.7
Caudal base to tip of upper rays	285	275	267	275.7
Caudal base to tip of middle rays	255	258	198	237.0
Caudal base to tip of lower rays	273	273	242	262.7

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-3, USNM 47481, 80252, and 83923. For data see text.

a plain gray or brown phase with no color markings, called by him the gray phase; a gray phase in which there are irregular oval and quadrate blotches with lighter centers (pinto phase); and a spotted phase in which the body is covered with red-brown spots (spotted phase). Rosenblatt and Zahuranec (1967) have recently discovered that the spotted phase is a distinct species, *Mycteroperca prionura*, but it seems that the gray and pinto phases, like those that occur in other groupers such as *Mycteroperca interstitialis* most likely result from instantaneous changes produced by environmental stimuli. I therefore agree with Walford's action in synonymizing *boulengeri* (the pinto phase) with *xenarcha* (the gray phase).

RELATIONSHIPS: *Mycteroperca xenarcha* is an Eastern Pacific member of the *interstitialis* group. It seems to be closer to *interstitialis* than is either *rosacea* or *olfax* and presumably represents a

more recent separation from the parent Atlantic stock.

ECOLOGY: Walford (1937, p. 103) found that two specimens taken just north of Cape Corrientes in late March, 1935, were maturing females. This species reaches a weight of at least 60 pounds (Walford, *loc. cit.*).

DISTRIBUTION: *Mycteroperca xenarcha* ranges along the Pacific coast from San Francisco Bay to Peru (fig. 40). The type locality is given as the Galápagos Archipelago but Rosenblatt and Zahuranec state that no other specimens have been reported from the Galápagos. They suspect switched labels but are unable to confirm this suspicion.

SPECIMENS EXAMINED

Mexico: Baja California, Magdalena Bay, USNM 83923 (600 mm., August 31, 1916, ALBATROSS); Magdalena Bay, Turtle

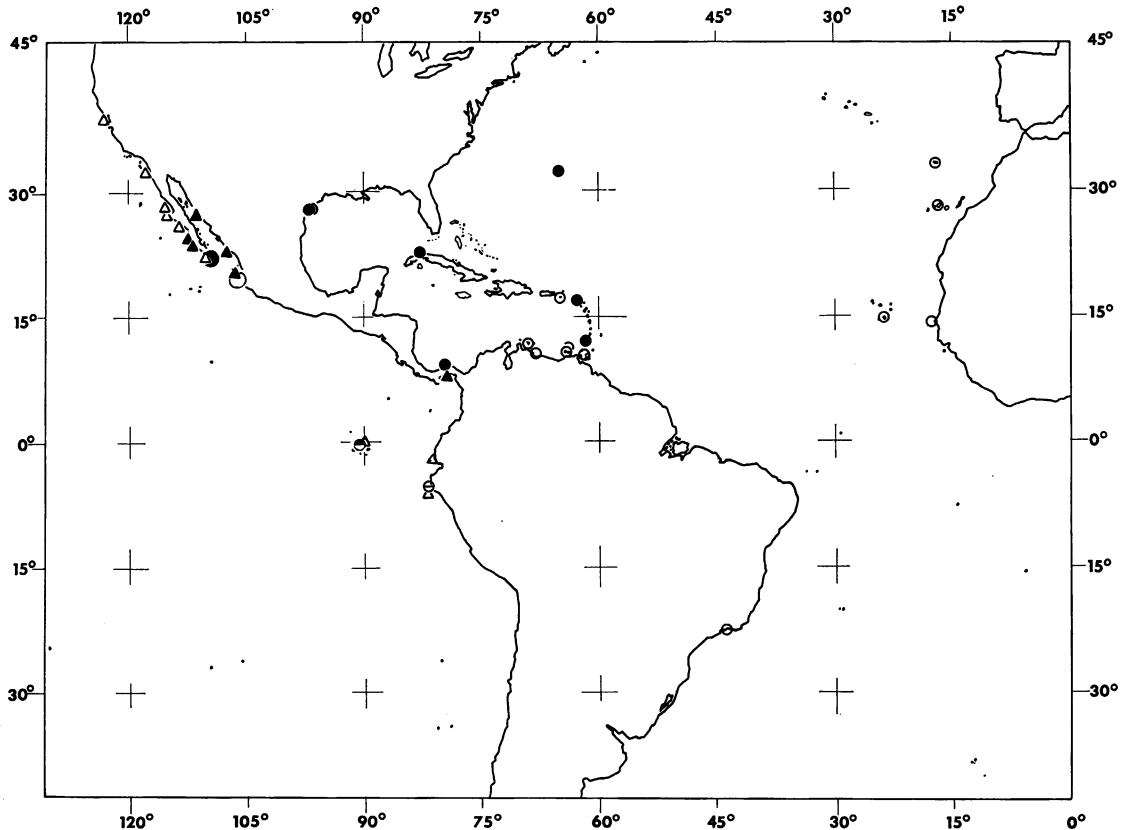


FIG. 40. Distribution records for *Mycteroperca prionura* (large circles), *M. xenarcha* (triangles), *M. olfax* (small half circles), and *M. rubra* (small full circles). Solid symbols represent specimens examined, open symbols are additional literature records.

Inlet, LACM W55-91; Bahía Santa Maria, Santa Maria lagoon, UCLA W50-134, W55-100, W53-320; Sinaloa, Mazatlán, USNM 47481 (165 mm., D. S. Jordan); Sonora, Bahía San Carlos, UCLA W52-35; Nayarit, Chacala, UCLA W58-5.
Panama: Corozal, USNM 80252 (212 mm., April 20-21, 1911, Meek and Hildebrand); Farfan Beach, USNM 128757 (303 mm., Feb. 24, 1937, S. F. Hildebrand.).

***Mycteroperca rosacea* (Streets, 1877)**

Epinephelus rosaceus STREETS, 1877, pp. 51-52 (original description, Angel Is., Gulf of California). BOULENGER, 1895, p. 262.

Trisotropis rosaceus: JORDAN AND GILBERT, 1883b, p. 107 (Mazatlán).

Mycteroperca rosacea: JORDAN AND SWAIN, 1885b, pp. 361-362 (Mazatlán, USNM 28131, characters). JORDAN, 1886b, p. 377 (after Streets); 1887a, p. 84. JORDAN AND EIGENMANN, 1890, p. 368 (synonymy, two specimens known). JORDAN, 1895, p. 446 (Mazatlán). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, p. 1184 (general account). OSBURN AND NICHOLS, 1916, p. 162 (Angel de la Guardia, orange to yellow). JORDAN AND EVERMANN, 1920, p. 393 (general account). JORDAN, EVERMANN, AND CLARK, 1930, p. 314. BREDER, 1936, p. 23 (San Francisquito, Gonzago Bay, San Felipe). ROSENBLATT AND ZAHURANEC, 1967, pp. 237-238 (general account).

Mycteroperca pardalis GILBERT, 1892, pp. 551-552 (original description, La Paz Bay, Lower California). JORDAN, 1895, pp. 447-448 (Mazatlán, color description). JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1181-1182 (general account, type of *Xystroperca*, new subgenus). OSBURN AND NICHOLS, 1916, p. 162 (Gulf of California: Carmen Is., San Joseph Is., Conception Bay, San Francisquito Bay, Estobar Is., Ceralbo Is.). JORDAN AND EVERMANN, 1920, p. 393 (general account). WALFORD, 1936, p. 7 (*rosacea* in synonymy); 1937, pp. 104-105, pl. 60, figs. a, b. BERDEGUE A., 1956, p. 275 (commercial species in Mexico).

Epinephelus pardalis: BOULENGER, 1895, p. 268.

Xystroperca pardalis: JORDAN, EVERMANN, AND CLARK, 1930, p. 315. BREDER, 1936, p. 24 (Gonzago Bay, Salina Bay, Espiritu Santos Is., San Francisco Bay [Mex.], Conception Bay, Carmen Island, Angelus Bay).

NOMENCLATURE: The name *Mycteroperca rosacea* seems to apply to the yellow form (or perhaps to a deep-water red form); *M. pardalis* was based on the spotted, shallow-water type. Walford (1936, p. 7) recognized that these

nominal forms were conspecific but employed the junior synonym *pardalis*.

The Latin trivial name *rosacea* comes from *rosa*, rose, and the adjectival suffix *aceus* means pertaining to or having the nature of, in allusion to the color pattern.

DIAGNOSIS: Moderate-sized species of *Mycteroperca* with robust body, medium-sized scales, and well-developed preopercular lobe. Posterior nostril enlarged in adults. Dorsal XI, 17; anal III, 11; pectoral 16; gill rakers 37-39. Anal somewhat falcate in adult. First three dorsal spines not forming an elevated lobe. A spotted and a yellow or reddish color phase.

This is the only Pacific grouper with 21 or more gill rakers below the angle of the first arch. The anal fin is rather strongly falcate; the dorsal fin may have middle soft rays slightly elongate so that the outline is angled rather than smoothly convex, but it is never really falcate. The caudal fin margin is smooth with no exerted rays.

DESCRIPTION: Proportional measurements of 10 specimens are given in table 34.

The preopercular angle is lobate and the posterior nostril is enlarged in large specimens. These characters indicate the affinities of *rosacea* with the *interstitialis* group, but the increased number of gill rakers sets it apart. The maxilla is scaled. The fins are rounded, although some specimens (i.e., the individual figured by Walford, 1937, pl. 60, fig. a) have a definite angle in the dorsal margin produced by moderate elongation of the middle rays.

According to Walford (1936, 1937) there are two color phases, the normal spotted form and a golden form, as found also in *Mycteroperca olfax*. The normal spotted form has a ground color of mottled olive-green, brownish gray, and golden brown, everywhere covered with golden brown spots that are smaller than the eye. The top of the head has four gray transverse stripes, the fourth extending across the anterior end of the dorsal fin (Walford, 1936, p. 7). The golden phase is lemon-yellow to warm orange; it is usually immaculate but some individuals have a few irregularly placed jet black spots and some have the entire dorsum black, changing abruptly to orange on the side (Walford, *loc. cit.*).

RELATIONSHIPS: The higher gill raker count suggests an alliance with *Mycteroperca rubra* but this is likely due to parallelism, for in most other respects, *rosacea* resembles *interstitialis* and it is

certainly closer to other members of the *interstitialis* group than it is to *M. rubra*.

ECOLOGY: *Mycteroperca rosacea* is apparently very common in parts of the Gulf of California and sometimes assembles in considerable aggregations. Walford (1937, p. 104) reported that stomachs of captured specimens contained plankton and small fish in about equal quantities. His specimens, taken in March and April, contained ripening eggs indicating the approach of the spawning season.

DISTRIBUTION: *Mycteroperca rosacea* occurs from Lower California and the Gulf of California south to Mazatlán. It is not known from offshore islands (fig. 39).

SPECIMENS EXAMINED

Mexico: Golfo de California, USNM 101059-60; Baja California, LACM W65-67, W65-84; Isla San Marcos, USNM 39047; Bahía de la Paz, USNM 46939; Los Frailes, USNM 101065; Bahía San Luis Gonzago, BOC 924; Isla Carmen, Bahía Ballenas, BOC 950; Bahía Salina, BOC 1242; Isla Carmen, AMNH 5446; LACM W65-79, W65-63, W65-64, W65-65, W65-77, W65-82; Isla Espiritu Santo, BOC 1243; Bahía San Francisco, BOC 1244; Isla Santa Cruz, AMNH 5483; Bahía Concepción, AMNH 5484, 5482, 5480; entrance to Bahía Concepción, rock point south of Punta Gallito, UCLA W57-33; Punta Concepción, LACM W65-70, W65-71, W65-72, W65-73; Punta Pulpito, LACM W65-40, W65-75, W65-76; Angel de la Guarda, Puerto Refugio on west side of northwest corner, UCLA W56-20; Angel de la Guarda, UCLA W53-71; Isla San José, LACM W65-48, W65-50; Punta Napolo, LACM W65-51, W65-52, W65-56; Punta San Telmo, LACM W65-57, W65-58, W65-59; Bahía Agua Verde, LACM W65-60, W65-61, W65-62; Isla Santa Inez, LACM W65-66; Isla Ildefonso, LACM W65-83; Isla Santa Catalina, LACM W65-85; Isla San Francisco, LACM W65-88, W65-90; San Francisquito Bay, AMNH 5494; Isla Ceralvo, AMNH 5479; Baja California, Cabeza de Mechudo, UCLA W65-87; Tiburón, UCLA W60-16; Isla San Luis, LACM W52-74; Bahía Las Animas, LACM W60-52; Puerto San Carlos, UCLA W52-41; Sonora, LACM W51-61; Sonora, off Punta de las Cuevas, UCLA W50-38, W50-48a, W51-8;

Bahía Bocochibampo, UCLA W51-3; Sonora, Punta Guillermo, UCLA W51-10, W51-62; Guaymas harbor, UCLA W52-3; north of Bahía Guaymas, LACM W50-53; west of Las Tetras de Cabra, UCLA W55-243; Nayarit, Chacala, LACM W58-5; Las Tres Marias, USNM 101062; Bahía Muertos, LACM W58-244; Sinaloa, LACM W51-48; Mazatlán, USNM 28131; Sinaloa, Isla Ignacio Farallon, LACM W56-109, W52-111.

Mycteroperca olfax (Jenyns, 1843)

- Serranus olfax* JENYNS, 1843, pp. 9-11, pl. 4 (original description, Galápagos Archipelago). GÜNTHER, 1859, p. 153 (characters, synonymy, Chatham Is.).
- Mycteroperca olfax*: GILL, 1864a, p. 80. JORDAN AND SWAIN, 1885b, p. 376 (after Jenyns). JORDAN AND BOLLMAN, 1890, p. 181 (Abingdon, Charles Is.). JORDAN AND EVERMANN, 1896a, p. 374 (synonymy); 1896b, p. 1183. SNODGRASS AND HELLER, 1905, p. 368-369 (Cocos; Tagus Cove, Albemarle; Elizabeth Bay, Narboro; Duncan, Barrington, Wenman, and Culpepper Is.). JORDAN AND EVERMANN, 1920, p. 393 (key, general account, doubtful photograph). JORDAN, EVERMANN, AND CLARK, 1930, p. 314. HERRE, 1936, p. 159 (Tagus Cove, Albemarle Is.). WALFORD, 1936, pp. 7-8 (characters, synonymy); 1937, pp. 105-106, pl. 12, fig. b (popular account). SCHMITT AND SCHULTZ, 1940, p. 5 (Albemarle; Hood Is.). BERDEGUE A., 1956, pp. 275-276 (commercial species). ROSENBLATT AND ZAHURANEC, 1967, pp. 235-237 (full account).
- Mycteroperca olfax* var. *olfax*: JORDAN AND BOLLMAN, in Jordan and Eigenmann, 1890, p. 367.
- Mycteroperca olfax* var. *ruberrima*: JORDAN AND BOLLMAN, in Jordan and Eigenmann, 1890, p. 367 (original description, Abingdon Is.).
- Epinephelus olfax*: BOULENGER, 1895, pp. 263-264.
- Mycteroperca olfax ruberrima*: JORDAN AND EVERMANN, 1896a, p. 374; 1896b, p. 1183 (general account).
- Mycteroperca ruberrima*: SNODGRASS AND HELLER, 1905, p. 370 (characters, synonymy; Wenman, Culpepper, Duncan Is.; Tagus Cove). JORDAN AND EVERMANN, 1920, p. 393 (general account).

NOMENCLATURE: Walford's action in relegating *ruberrima* to the synonymy of *olfax* seems sound, since *ruberrima* is apparently only a deep-water color phase comparable with that in *Mycteroperca venenosa*.

The name *olfax* is derived from the Latin *olfacto*, to smell, a reference to the enlarged posterior nostril.

I have been unable to determine the location of Jenyn's holotype. It is not listed in Boulenger's Catalogue (1895) and is perhaps still in the

TABLE 34
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca rosacea*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	76	110	110	122	331	380	399	420	428	608	—
Head length	375	377	368	359	360	364	351	359	369	362	364.4
Head width	131	147	141	144	137	164	145	183	157	143	149.2
Head depth	241	266	257	252	246	247	232	245	252	248	248.6
Snout length	98	95	171	94	109	110	103	111	114	112	111.7
Suborbital width	22	31	27	26	36	39	—	43	42	48	34.9
Interorbital width	72	76	76	74	79	80	76	75	83	80	77.1
Length of: Orbit	84	73	72	78	54	51	56	51	47	44	61.0
Postorbital head	199	205	205	195	213	218	207	211	224	222	209.9
Maxillary	170	168	168	169	163	167	165	165	167	179	168.1
Lower jaw	182	176	179	174	160	166	163	163	171	184	171.8
Snout to angle of preopercle	270	265	260	260	251	255	246	254	262	260	258.3
Supramaxillary length	69	49	60	58	54	57	45	46	58	51	54.7
Maxillary width	35	39	36	41	36	39	38	35	36	39	37.4
Tip of lower jaw to gular notch	113	105	96	103	115	116	113	115	90	97	106.3
Body width	126	133	130	137	148	149	145	143	166	133	141.0
Body depth	316	327	332	343	352	366	331	336	339	322	336.4
Caudal peduncle depth	118	124	126	121	134	126	125	129	133	120	125.6
Tip of snout to dorsal origin	388	375	378	379	379	387	363	385	404	378	381.6
Tip of snout to pectoral base	354	345	348	342	338	367	356	352	346	340	348.8
Tip of lower jaw to pelvic base	401	387	397	391	399	437	411	407	388	391	400.9
Length of: Dorsal base	519	526	540	539	517	534	514	540	530	503	526.2
Depressed dorsal	611	592	619	618	574	605	571	593	598	561	594.2
Anal base	195	184	210	178	178	188	182	187	178	178	185.8
Depressed anal	296	276	308	306	272	312	259	286	287	289	289.1
End of dorsal to caudal base	156	142	143	154	160	139	152	156	157	150	150.9
Length of: Caudal peduncle	191	196	199	206	218	179	201	192	199	181	196.2
Pectoral	239	223	218	214	182	185	190	176	189	176	199.2
Pelvic	210	196	201	210	157	178	152	150	164	—	179.8
Dorsal spine I	59	45	67	56	60	53	53	—	55	42	544.5
Dorsal spine II	131	115	131	124	98	114	86	—	112	101	112.4
Dorsal spine XI	121	114	120	108	86	107	79	—	81	75	99.0
Anal spine I	50	36	64	38	33	44	29	45	40	35	41.4
Anal spine II	100	83	95	92	69	78	56	73	74	69	78.9
Anal spine III	123	101	120	103	82	92	84	93	77	87	96.2
Caudal base to tip of upper rays	275	182	279	271	269	274	258	286	266	240	260.0
Caudal base to tip of middle rays	242	242	250	240	202	230	204	210	222	191	223.3
Caudal base to tip of lower rays	262	231	254	261	251	274	254	245	271	220	252.3

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1-4, SIO W65-87, W56-20, W65-87, W57-33; columns 5-10, USNM 101065, 101060, 46939, 39047, 101062, and 22131 respectively. For data see text.

Museum of the Cambridge Philosophical Society.

DIAGNOSIS: Large species of *Mycteroperca* with robust body, medium-sized scales, and pronounced preopercular lobe. Posterior nostril greatly enlarged in adult so that olfactory rosette is largely exposed. Dorsal XI, 17; anal

III, 11; pectoral 17 (16); gill rakers 25-29. First three dorsal spines elongate, forming an elevated lobe. Vertical fins without exerted soft rays. Brown and xanthic color phases are known.

A unique feature in *Mycteroperca olfax* is the elevation of anterior dorsal spines into a definite

lobe with the second spine longer than the third. Enlargement of posterior nostril is also extreme for the genus. Tail lacks exerted rays of *xenarcha*, and the soft dorsal is rounded. There are only about 13 gill rakers on lower part of first arch compared with 21 in *rosacea*.

DESCRIPTION: For proportional measurements of eight specimens see table 35.

The posterior nostril is greatly enlarged in large specimens. The soft dorsal is rounded but the anal fin is somewhat falcate. The caudal is square. The anterior three spines of the dorsal fin are elongate, forming a high lobe. The second dorsal spine is longer than the third. The preopercular angle is salient.

As in *Epinephelus fulvus* this species has a yellow phase that is predominantly chrome-yellow: the back is orange, the head orange-yellow, the lower parts lighter lemon-yellow, and the fin membranes chrome-yellow. Some specimens have been described as reddish (Walford, 1936, p. 8). Possibly these came from deeper water.

Mycteroperca olfax "is typically dark olive-brown on the back, sides, and head, spotted with purplish and lighter brown, belly grayish brown. There is considerable variation in the color, however, even within a small geographical area. Some specimens may be plain dark brown; others may have the body covered with faint circular dark brown spots, which seem to disappear with age." (Walford, 1936, pp. 7-8.) Similar variations are present in other groupers and may usually be seen in the same individual within a few minutes.

RELATIONSHIPS: This species is very distinctive but seems to belong to the *interstitialis* group. Presumably the parent stock of the group reached the Galápagos rather early and isolation has been sufficient to permit well-marked differentiation.

ECOLOGY: Walford (1937, p. 106) stated that *Mycteroperca olfax* is often found in shallow lagoons, sometimes in large schools. It reaches a length of 3 feet.

DISTRIBUTION: Although Jordan and Evermann (1896b, p. 1184) included Panama in the range of this species, I have seen definite records otherwise only from the Galápagos Islands (fig. 40). Rosenblatt and Zahuranec (1966, pp. 236-237), have discounted Seale's (1940) records from Panama and the Gulf of Cali-

fornia and cast doubt on the data of the MCZ specimen from Paita, Peru.

SPECIMENS EXAMINED

Ecuador, Islas Galápagos: Isla Genovesa (Tower), UCLA W53-141; Darwin Bay, FMNH 41213, 41168 (head only); south side of Isla Pinta (Abingdon), FMNH 41341 (skin); Isla Pinta, USNM 41274 (type of *Mycteroperca olfax ruberrima* Jordan and Bollman); Isla Isabela (Albemarle), USNM 49786, 50079, 50046; UCLA W53-6, W54-225, W52-279; Tagus Cove, FMNH 41434; Isla Floreana (Charles), USNM 41273; ANSP 81520; Port Charles Bay, USNM 89723; Isla San Salvador (James), USNM 50078; Isla Fernandina (Narborough), LACM W51-155, W53-178; UCLA W53-162, W64-1; Isla Santa Cruz (Indefatigable), UCLA W53-10, W54-416; Isla Darwin (Culpepper), UCLA W52-279; no specific locality, MCZ 10176, 10220; USNM 107066, 19895, 39857.

Mycteroperca rubra (Bloch, 1793)

COMB GROUPER

- Epinephelus ruber* BLOCH, 1793, pp. 22-23, pl. 331 (original description, "Japan," type in Berlin Museum). BLOCH AND SCHNEIDER, 1801, pp. 299-300. BOULENGER, 1895, pp. 267-268 (Palermo; Algiers; Madeira; Pta. Cabello; Rio de Janeiro). MIRANDA-RIBEIRO, 1915, pp. 21-22 (Brazil); 1918, pp. 89-90. METZELAAR, 1919, p. 233.
- Serranus acutirostris* VALENCIENNES, in Cuvier and Valenciennes, 1828, pp. 286-287 (original description in part; Brazil). VALENCIENNES, 1839 (1835), p. 11 (Canaries). GÜNTHER, 1859, p. 135. ROCHEBRUNE, 1882, pp. 66-67 (Senegal).
- Serranus undulosus* VALENCIENNES, in Cuvier and Valenciennes, 1828, p. 295 (original description, Brazil). CASTELNAU, 1855, p. 2 (Rio de Janeiro). GÜNTHER, 1859, pp. 143-144 (West Indies, Brazil). STEINDACHNER, 1877, p. 175 (Rio de Janeiro).
- Serranus fuscus* LOWE, 1834, p. 196 (original description; Madeira). ROCHEBRUNE, 1882, pp. 65-66. OSORIO, 1909, p. 59 (Cape Verde Is.).
- Serranus emarginatus* VALENCIENNES, 1839 (1835), p. 10 (original description; Canary Islands).
- Serranus ruber*: PETERS, 1866, p. 107 (type in Berlin Museum reexamined).
- ?*Trisotropis undulosus*: POEY, 1870, p. 305. COPE, 1871b, p. 465 (St. Croix; St. Martin).
- Epinephelus chalinus* COPE, 1871b, pp. 465-466 (original description; St. Martin).
- Parepinephelus acutirostris*: BLEEKER, 1876, p. 257 (type

TABLE 35
PROPORTIONAL MEASUREMENTS OF EIGHT SPECIMENS OF *Mycteroperca olfax*^a

Measurement	1	2	3	4	5	6	7	8	Average
Standard length (mm.)	272	280	281	325	356	410	557	592	—
Head length	386	377	379	371	347	365	366	378	371.1
Head width	147	143	128	143	131	137	156	182	145.9
Head depth	250	254	235	238	221	235	260	264	244.6
Snout length	105	104	110	108	97	102	116	122	108.0
Suborbital width	40	41	41	42	39	41	46	47	42.1
Interorbital width	77	71	75	80	70	77	87	91	78.5
Length of: Orbit	61	57	57	55	59	52	48	52	55.1
Postorbital head	237	223	215	222	206	217	221	223	220.5
Maxillary	173	168	171	171	157	167	176	184	170.9
Lower jaw	182	173	178	178	163	176	183	189	177.8
Snout to angle of preopercle	268	255	263	252	242	256	262	272	258.8
Supramaxillary length	53	52	53	62	56	57	54	56	55.4
Maxillary width	42	43	37	40	37	38	40	37	39.3
Tip of lower jaw to gular notch	107	105	109	98	93	90	101	107	101.3
Body width	151	152	139	143	125	144	158	177	148.6
Body depth	342	329	319	322	315	320	312	338	324.6
Caudal peduncle depth	132	130	126	126	124	124	122	127	126.4
Tip of snout to dorsal origin	382	396	404	408	386	388	395	399	394.8
Tip of snout to pectoral base	360	350	361	351	343	348	359	348	352.5
Tip of lower jaw to pelvic base	397	368	402	385	383	393	395	390	389.1
Length of: Dorsal base	544	554	523	538	548	495	494	515	526.4
Depressed dorsal	603	639	580	606	—	—	546	552	587.7
Anal base	176	171	178	200	160	183	178	182	178.5
Depressed anal	276	264	272	303	—	—	291	279	280.8
End of dorsal to caudal base	143	161	151	149	169	155	145	154	153.4
Length of: Caudal peduncle	217	187	185	197	205	220	201	215	203.4
Pectoral	200	202	189	200	183	171	180	182	188.4
Pelvic	169	155	164	166	142	149	138	139	152.8
Dorsal spine I	66	75	80	80	77	79	70	81	76.0
Dorsal spine III	143	112	139	143	135	156	152	149	141.1
Dorsal spine XI	—	89	89	98	84	80	59	79	82.6
Anal spine I	44	39	52	48	46	40	35	41	43.1
Anal spine II	85	89	89	108	67	66	66	66	79.5
Anal spine III	107	96	103	98	87	78	81	90	92.5
Caudal base to tip of upper rays	248	243	231	263	—	—	235	218	239.7
Caudal base to tip of middle rays	217	227	214	229	—	—	189	179	209.2
Caudal base to tip of lower rays	232	239	235	246	—	—	217	215	230.7

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1, 2, 4, 5, 6, 7, 8, USNM 49786, 50079, 50078, 19895, 19895, 39857, 41273 respectively; 3, ANSP 81520. For data see text.

of new genus). JORDAN, EVERMANN, AND CLARK, 1930, p. 315. WOODS, 1942, p. 191 (Corpus Christi). BAUGHMAN, 1943, p. 772.
Trisotropis acutirostris: GOODE AND BEAN, 1880, p. 143 (no United States records).
Mycteroperca scirenga: JORDAN AND SWAIN, 1885b, pp. 360–370 (after Rafinesque “but his description may apply to *Epinephelus alexandrinus*”). JORDAN, 1887d, p. 532 (West Indies); 1887e, p. 580.
Mycteroperca rubra: JORDAN AND EIGENMANN, 1890,

pp. 372–374. JORDAN AND EVERMANN, 1896a, p. 374; 1896b, pp. 1180–1181. FOWLER, 1915b, p. 533 (Port-of-Spain); 1920, p. 144 (St. Croix). JORDAN AND EVERMANN, 1920, p. 393. MEEK AND HILDEBRAND, 1925, pp. 445–446 (Porto Bello, Panama). FOWLER, 1936, pp. 762–764. TORTONESE, 1939, p. 52 (Colón). FOWLER, 1944, p. 465. CADENAT, 1950, p. 191, fig. 124 (Senegal). FOWLER, 1953, p. 55 (Colombia). SMITH, 1961, pp. 1:6, 1:21, 1:23, figs. 5.3, 18. CERVIGÓN M., 1966b, pp. 302–

304, fig. 118 (Cubagua, Venezuela). CERVIGÓN M. AND VELASQUEZ, 1966, pp. 104-108 (Venezuela, osteology). RANDALL, 1968, p. 68, fig. 75 (general account, color photograph).

Mycteroperca acutirostris: FOWLER, 1907, p. 261. FOWLER, 1920, p. 137.

Epinephelus (Mycteroperca) ruber: METZELAAR, 1919, pp. 51-52 (Venezuela; Curaçao; Wacao).

NOMENCLATURE: Bloch's type of *Epinephelus ruber* was said to be from Japan, but this locality is presumed to be in error. The holotype is probably still in the Berlin Museum. Peters (1866, p. 107) reexamined the holotype and reported that it was No. 161, 465 mm. long. The specific name comes from the Latin *ruber* (fem. *rubra*), meaning red. It was without color and was presumed to have been red; more likely it was yellow or it had been bleached by exposure to sunlight (Jordan and Eigenmann, 1890, p. 372).

DIAGNOSIS: Small species of *Mycteroperca* with rather compressed body, large scales, and slightly projecting preopercular angle. Nostrils subequal. Dorsal XI, 16; anal III, 11; pectoral 16; gill rakers very numerous, 45-54. First three dorsal spines not forming an elevated lobe. White spots and a series of irregular wavy lines on ventrolateral surface, especially above anal fin. This species can be distinguished from all other members of the genus by the high gill raker count.

DESCRIPTION: Proportions of 10 specimens are given in table 36. The body shape is rather distinctive in several measurements.

The preopercle is moderately salient, and there is little, if any, enlargement of the posterior nostril. The dorsal and anal lobes are rounded; the caudal is slightly concave, with no exerted rays. The snout is rather pointed and the ventral profile of the body is slightly more curved than that of most other species. The lateral skull crests converge slightly on the posterior part of the frontals, then continue forward to the supraorbital crests. The supraethmoid wall is only moderately well developed but there is no pit, at least not in the small specimen examined (MCZ 10198, 127 mm.).

The colors in life of this species have not been recorded but alcoholic specimens are dark brown above, lighter below, with reticulations that join to form wavy lines on the lower side. There are dark lines on the side of the head as follows: one from the posterior part of the orbit,

across the upper limb of the preopercle just below its upper end, thence to the opercular margin; one from the lower part of the orbit to the edge of the preopercle just above its notch and continued a short distance onto the opercle; and an extension of the usual maxillary mustache to the angle of the preopercle. There are also other indistinct markings on the head and in some specimens a definite line crosses the opercle just below the level of its point. The body is sprinkled with white spots, each about the size of the pupil, that seem to be randomly arranged.

RELATIONSHIPS: *Mycteroperca rubra* is not close to the *venosa* group and is placed with the *interstitialis* group on the basis of skull structure. The great number of gill rakers is probably a specialization but the large scales, weakly developed supraethmoid wall, and body shape suggests that this species may be an early offshoot of the *interstitialis* line.

ECOLOGY: I have found no account of the habits of *Mycteroperca rubra*.

DISTRIBUTION: *Mycteroperca rubra* is properly a species of the Eastern Atlantic and the Mediterranean fauna but there are museum specimens from Río de Janeiro and scattered records from elsewhere in the western North Atlantic (fig. 40).

SPECIMENS EXAMINED

Texas: within 50 miles of Corpus Christi, FMNH 40260 (186.5 mm., C. T. Reed); Harbor Island, Corpus Christi, USNM 134900 (103 mm., Oct. 5, 1926, J. C. Pearson), 134901 (111 mm., Oct. 11, 1926, J. C. Pearson).

Panama: Portobelo, FMNH 8386 (87 mm., April 24, 1911, Meek and Hildebrand); USNM 80251 (two specimens 90-97.5 mm., April 24-28, 1911, Meek and Hildebrand).

Colombia: Sabanilla, New Granada, USNM 131474 (117 mm., March 16-22, 1884, ALBATROSS).

Brazil: Río de Janeiro, USNM 83464 (125 mm., Wilkes Exploratory Expedition), 23243 (177 mm., Thayer Expedition); MCZ 10138 (seven specimens), 4085 (four specimens, Hassler Expedition), 4509 (five specimens), 10198 (five specimens); Santos market, USNM 100887 (163 mm., Cochran).

St. Martins: ANSP 12768 (91 mm., R. E. van Riggersma [type of *Epinephelus chalinus* Cope]).

Cuba: MCZ 10016 (four specimens, Poey);
USNM 38589 (two specimens, 77-83 mm.,
Poey).

Grenadines: Belmont Beach, Bequia Island,
ANSP accession 116 (74.5 mm., April 11-12,
1952, R. A. and S. P. Montgomery).

Bermuda: FMNH 48453 (131.5 mm., L. L.
Mowbray).

TABLE 36
PROPORTIONAL MEASUREMENTS OF TEN SPECIMENS OF *Mycteroperca rubra*^a

Measurement	1	2	3	4	5	6	7	8	9	10	Average
Standard length (mm.)	87	118.5	125	132	140	142.5	152.5	186.5	201.5	238	—
Head length	397	397	384	356	386	382	393	383	370	376	382.4
Head width	155	131	128	125	139	126	128	137	149	126	134.4
Head depth	264	262	240	223	257	242	256	267	241	244	249.6
Snout length	103	105	96	95	107	98	111	102	99	113	102.9
Suborbital width	29	34	32	30	32	32	39	35	35	36	33.4
Interorbital width	75	68	76	72	71	67	72	—	72	71	71.6
Length of: Orbit	86	84	76	77	82	74	72	70	65	67	75.3
Postorbital head	213	219	212	193	214	214	223	220	206	210	212.4
Maxillary	184	186	172	159	182	182	177	174	174	181	177.1
Lower jaw	195	194	180	167	193	189	190	188	181	191	186.8
Snout to angle of preopercle	282	287	272	254	282	277	282	279	266	277	275.8
Supramaxillary length	57	55	56	45	57	49	52	51	50	59	53.1
Maxillary width	40	42	40	38	43	42	43	40	40	42	41.0
Tip of lower jaw to gular notch	126	105	104	98	100	102	111	102	97	113	105.8
Body width	149	127	132	114	136	—	125	150	151	126	121.0
Body depth	368	338	320	326	336	344	325	373	345	349	342.4
Caudal peduncle depth	132	131	132	121	129	137	125	142	139	139	132.7
Tip of snout to dorsal origin	391	405	384	371	404	396	384	399	382	401	391.7
Tip of snout to pectoral base	374	367	352	337	361	358	364	383	335	357	358.8
Tip of lower jaw to pelvic base	414	409	396	386	396	393	410	413	390	412	401.9
Length of: Dorsal base	540	532	524	523	521	540	525	536	538	527	530.6
Depressed dorsal	632	637	624	606	625	625	610	649	638	561	620.7
Anal base	207	194	208	197	204	204	203	196	201	185	199.9
Depressed anal	322	338	340	292	350	337	321	314	325	294	323.3
End of dorsal to caudal base	138	143	136	163	132	147	141	123	149	151	142.3
Length of: Caudal peduncle	195	181	184	205	182	189	193	193	194	212	192.8
Pectoral	253	241	232	216	232	221	223	220	206	206	225.0
Pelvic	207	215	208	182	218	207	210	214	203	185	204.9
Dorsal spine I	66	59	72	68	64	53	72	62	60	48	62.4
Dorsal spine III	138	127	120	125	136	126	141	134	114	113	127.4
Dorsal spine XI	121	127	112	117	129	119	125	118	144	101	121.3
Anal spine I	49	51	40	45	61	46	49	46	45	40	47.2
Anal spine II	115	101	100	95	107	102	108	91	84	76	97.9
Anal spine III	132	118	112	114	118	105	111	110	99	99	111.8
Caudal base to tip of upper rays	276	262	278	250	282	270	275	273	268	271	270.5
Caudal base to tip of middle rays	264	253	252	242	254	256	252	247	253	221	249.4
Caudal base to tip of lower rays	264	266	256	261	279	274	269	260	270	261	266.0

^aAll proportions are expressed in thousandths of the standard length. Specimens are as follows: Columns 1, 4, 8, FMNH 8286, 4845, 40260 respectively; 2, 3, 5, 6, 7, 9, 10, MCZ 10016, 4509 (10198), 10016, 10016, 10016, 4509 (10198), 4805 respectively. For data see text.

DISCUSSION

PROPORTIONAL MEASUREMENTS

IF AVAILABLE, 10 specimens of each species were measured to establish body proportions. Measurements were converted to thousandths of standard length and are given in tables 9 through 36. As it is not a purpose of the present study to investigate geographic variation, specimens have been selected for measurement without reference to provenance. The 38 measurements were chosen to permit reconstruction of the outline of the fish. To facilitate comparison with other specimens, measurements are given for individuals rather than as averages.

Some measurements prove to be rather constant for all species of groupers; others reveal trends within a genus or show resemblances within species-groups. Thus, they are accessory generic and species-group characters. Most of the measurements of *Paranthias furcifer* differ from those of all other species. The species of *Mycteroperca* show relatively little variation both among and within species. This is perhaps indicative of their recent origin and close relationship. Conversely, in *Epinephelus* the various species and species-groups show considerable divergence in some characters.

Thirteen of the most revealing measurements are discussed below:

HEAD WIDTH: There are no particularly sharp differences in this character. *Paranthias*, *Mycteroperca*, and the subgenus *Dermatolepis* have low values; the other species are slightly higher. *Epinephelus itajara*, a species distinguished by its broad head, is widely overlapped in this character by *E. nigrurus* and to a lesser extent, by several other species. A sharper distinction between *itajara* and the other species is obtained with the ratio of head width to head depth.

HEAD LENGTH: In this feature *Paranthias* is extreme and is separated by a wide gap from other species. The rest of the groupers all have long heads, the head length averaging more than 40 per cent in all but *Epinephelus inermis*, *E. drummondhayi*, and the species of *Mycteroperca*. In this character as in many others, *Mycteroperca* stands somewhat apart from the other genera.

MAXILLARY LENGTH: *Paranthias* differs conspic-

uously from all other genera. The five species of the *niveatus* species-group are sharply differentiated from other forms of *Epinephelus*. The two species of *Dermatolepis* show no overlap in this character and *Mycteroperca tigris* is distinct from other members of its genus.

SUBORBITAL WIDTH: *Alphestes*, which resembles *Epinephelus* in most other characters, is isolated from all except *Paranthias* in this character. *Epinephelus itajara* has a much narrower sub-orbital than most other species. There is relatively more diversity among the species of *Mycteroperca*, but there is no break between *Mycteroperca* and the other genera.

INTERORBITAL WIDTH: *Epinephelus nigrurus* is extreme but is broadly overlapped by *itajara*, *niveatus*, *drummondhayi*, and *labriformis*. In view of the excessive widening of the skull of *itajara*, it is surprising that *nigrurus* has the wider interorbital. Members of the *Mycteroperca interstitialis* species-group tend to have higher values than those of the *venosus* group, with considerable overlap. The interorbital width of *Paranthias* is similar to that of some species of *Mycteroperca* but the subgenera *Alphestes*, *Cephalopholis*, and *Dermatolepis* all have lower values.

SNOUT TO ANGLE OF PREOPERCLE: *Paranthias furcifer* is extreme in this character, a direct reflection of the short head. There are no other really sharp breaks but the five species of the *Epinephelus niveatus* species-group are well differentiated from other species.

BODY DEPTH: Most species of *Epinephelus* have deeper bodies than do those of *Mycteroperca*, with overlap among some forms. The two species of the subgenus *Dermatolepis* have the deepest bodies of all. *Paranthias* agrees with *Mycteroperca*.

PECTORAL FIN LENGTH: In this measurement most species of *Mycteroperca* stand apart from those of other genera. *Mycteroperca rubra*, however, has a longer fin than its congeners and thus agrees with the species of *Epinephelus*, excluding *Dermatolepis*. The extreme elongation of the pectoral fin of *inermis* sets it apart from all other species of *Epinephelus*.

PELVIC FIN LENGTH: The members of the *Epinephelus niveatus* species-group are well defined by this measurement: it is negatively allometric

in them. As most measured fish are relatively small, the averages are not at the centers of the ranges. Again, *Mycteroperca rubra* stands apart from other members of the genus and the two species of *Dermatolepis* show little overlap.

THIRD DORSAL SPINE LENGTH: In this measurement (more properly termed longest

anterior dorsal spine) there are a few trends, and deviation by individual species seems to be the rule. Most species of *Mycteroperca* have low values but *M. olfax*, which has the anterior part of the fin elevated into a distinct lobe, and *M. rubra*, have higher averages. *Paranthias*, *Cephalopholis*, and *Epinephelus itajara* also have short spines

TABLE 37
FREQUENCY DISTRIBUTION OF DORSAL RAYS IN AMERICAN GROUPERS

Species	Dorsal Spines				Dorsal Soft Rays							
	IX	X	XI	XII	13	14	15	16	17	18	19	20
<i>Paranthias</i>												
<i>furcifer</i>	9	—	—	—	—	—	—	—	—	6	3	—
<i>Epinephelus</i>												
(<i>Cephalopholis</i>)												
<i>fulvus</i>	129	—	—	—	—	8	118	2	—	—	—	—
<i>cruentatus</i>	23	—	—	—	1	19	3	—	—	—	—	—
<i>panamensis</i>	10	—	—	—	—	9	1	—	—	—	—	—
(<i>Epinephelus</i>)												
<i>striatus</i>	—	1	41	—	—	—	—	18	22	1	—	—
<i>morio</i>	—	1	28	—	—	—	1	16	12	1	—	—
<i>guttatus</i>	—	1	101	—	—	—	22	77	1	—	—	—
<i>niveatus</i>	—	—	63	—	—	50	11	2	—	—	—	—
<i>flavolimbatus</i>	—	—	12	—	—	11	1	—	—	—	—	—
<i>nigritus</i>	—	35	1	—	—	25	11	—	—	—	—	—
<i>acanthistius</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>mystacinus</i>	—	—	8	—	—	4	4	—	—	—	—	—
<i>guaza</i>	—	—	6	—	—	—	4	2	—	—	—	—
<i>labriformis</i>	—	—	13	—	—	—	—	6	7	—	—	—
<i>drummondhayi</i>	—	—	8	—	—	—	1	7	—	—	—	—
<i>adscensionis</i>	—	—	31	—	—	—	—	7	23	1	—	—
<i>analogus</i>	—	11	—	—	—	—	—	—	9	2	—	—
(<i>Promicrops</i>)												
<i>itajara</i>	—	—	11	—	—	—	5	6	—	—	—	—
(<i>Dermatolepis</i>)												
<i>inermis</i>	—	—	13	—	—	—	—	—	1	—	10	2
<i>dermatolepis</i>	—	—	10	—	—	—	—	—	—	5	4	1
(<i>Alphestes</i>)												
<i>afer</i>	—	—	20	—	—	—	—	1	4	14	2	—
<i>multiguttatus</i>	—	—	10	—	—	—	—	—	—	1	8	1
<i>Mycteroperca</i>												
<i>venenosa</i>	—	—	12	—	—	—	4	7	1	—	—	—
<i>bonaci</i>	—	—	22	—	—	—	—	1	18	3	—	—
<i>jordani</i>	—	—	4	—	—	—	1	22	5	—	—	—
<i>tigris</i>	—	—	39	—	—	—	—	18	21	—	—	—
<i>microlepis</i>	—	2	61	1	—	—	—	17	38	8	—	—
<i>cidi</i>	—	—	331	1	—	—	5	297	3	—	—	—
<i>interstitialis</i>	—	—	22	—	—	—	1	5	15	1	—	—
<i>phenax</i>	—	—	11	—	—	—	—	1	9	1	—	—
<i>prionura</i>	—	—	—	—	—	—	—	52	41	2	—	—
<i>xenarcha</i>	—	—	5	—	—	—	19	14	—	—	—	—
<i>rosea</i>	—	—	6	—	—	—	—	1	4	1	—	—
<i>olfax</i>	—	—	10	—	—	1	—	2	7	—	—	—
<i>rubra</i>	—	—	23	—	—	—	6	16	1	—	—	—

and the individual species of *Dermatolepis* and *Alphestes* can be distinguished by this character.

FIRST ANAL SPINE LENGTH: This measurement exhibits little variation. The species of *Alphestes* and *Cephalopholis* have higher values than the others.

ANAL FIN BASE LENGTH: In most other characters the species of *Mycteroperca* have lower values than those of *Epinephelus* but here, in concordance with the higher number of anal rays, the reverse is true. The anal base length is not always correlated with the number of rays, however, because *Epinephelus afer*, which has only nine anal soft rays, has the longest anal base of any species of American grouper.

POSTDORSAL LENGTH: *Alphestes* has a shorter postdorsal length than any other subgenus or genus and *Mycteroperca* and *Paranthias* have the longest. Otherwise there are no significant trends in this character.

Similar trends are found in other measurements and their presentation here would serve no further purpose. More precise analysis of the morphometric characters of groupers should be attempted only after further data have been accumulated.

MERISTIC CHARACTERS

A few of the countable characters of groupers are so constant that they are useless for distinguishing genera and species. The branched caudal rays are nearly always $8/7=15$, the pelvic rays are constantly I, 5 and, with the exception of rare variant individuals, there are 24 vertebrae and seven branchiostegal rays. Vertebral counts on 116 specimens are recorded as follows (numbers in parentheses are the numbers of specimens counted): *Paranthias furcifer*, 24 (four); *Epinephelus striatus*, 24 (nine); *E. morio*, 24 (nine); *E. guttatus*, 24 (13); *E. drummondhayi*, 24 (one); *E. niveatus*, 24 (four); *E. flavolimbatus*, 24 (two); *E. nigritus*, 24 (one); *E. guaza*, 24 (two); *E. adscensionis*, 24 (three); *E. analogus*, 24 (one); *E. itajara*, 24 (two); *E. inermis*, 24 (two); *E. fulvus*, 24 (10); *E. cruentatus*, 24 (10); *E. afer*, 24 (eight); *Mycteroperca venenosa*, 24 (three); *M. bonaci*, 24 (three); *M. tigris*, 24 (seven); *M. microlepis*, 24 (two); *M. interstitialis*, 24 (nine); *M. phenax*, 24 (two); *M. xenarcha*, 24 (one); *M. olfax*, 24 (one); *M. rubra*, 24 (seven).

Counts of the olfactory rosette lamellae reveal some differences but the number appears to

vary with age and seems to present no information not revealed as well by other characters.

Like all taxonomic characters, meristics may vary independently without regard to relationships. Thus the loss of a dorsal spine in *Epinephelus analogus*, *E. nigritus*, and *E. acanthistius* and

TABLE 38
FREQUENCY DISTRIBUTION OF ANAL SOFT RAYS IN
AMERICAN GROUPERS

Species	Anal Soft Rays									
	6	7	8	9	10	11	12	13	14	
<i>Paranthias</i>										
<i>furcifer</i>	—	—	—	8	1	—	—	—	—	—
<i>Epinephelus</i>										
(<i>Cephalopholis</i>)										
<i>fulvus</i>	—	—	2	127	—	—	—	—	—	—
<i>cruentatus</i>	—	—	23	—	—	—	—	—	—	—
<i>panamensis</i>	—	1	8	1	—	—	—	—	—	—
(<i>Epinephelus</i>)										
<i>striatus</i>	—	—	42	—	—	—	—	—	—	—
<i>morio</i>	—	—	1	27	1	—	—	—	—	—
<i>guttatus</i>	—	—	2	100	—	—	—	—	—	—
<i>niveatus</i>	—	—	1	61	1	—	—	—	—	—
<i>flavolimbatus</i>	—	—	1	11	—	—	—	—	—	—
<i>nigritus</i>	—	—	—	36	—	—	—	—	—	—
<i>acanthistius</i>	—	—	—	—	—	—	—	—	—	—
<i>mystacinus</i>	—	—	—	8	—	—	—	—	—	—
<i>guaza</i>	—	1	5	—	—	—	—	—	—	—
<i>labriiformis</i>	—	—	13	—	—	—	—	—	—	—
<i>drummondhayi</i>	—	—	—	11	—	—	—	—	—	—
<i>adscensionis</i>	—	—	28	3	—	—	—	—	—	—
<i>analogus</i>	—	—	11	—	—	—	—	—	—	—
(<i>Promicrops</i>)										
<i>itajara</i>	—	—	11	—	—	—	—	—	—	—
(<i>Dermatolepis</i>)										
<i>inermis</i>	—	—	—	13	—	—	—	—	—	—
<i>dermatolepis</i>	—	—	—	9	1	—	—	—	—	—
(<i>Alphestes</i>)										
<i>afer</i>	—	—	—	21	—	—	—	—	—	—
<i>multiguttatus</i>	—	—	1	9	—	—	—	—	—	—
<i>Mycteroperca</i>										
<i>venenosa</i>	—	—	—	—	2	9	1	—	—	—
<i>bonaci</i>	—	—	—	—	—	—	17	5	—	—
<i>jordani</i>	—	—	—	—	—	4	—	—	—	—
<i>tigris</i>	—	—	—	—	1	38	—	—	—	—
<i>microlepis</i>	—	—	—	—	1	59	4	—	—	—
<i>cidi</i>	—	—	—	—	31	282	5	—	—	—
<i>interstitialis</i>	—	—	—	—	—	15	7	—	—	—
<i>phenax</i>	—	—	—	—	—	10	—	—	—	—
<i>prionura</i>	—	—	—	—	—	—	—	—	—	—
<i>xenarcha</i>	—	—	—	—	1	3	1	—	—	—
<i>rosacea</i>	—	—	—	—	1	5	—	—	—	—
<i>olfax</i>	—	—	—	—	1	9	—	—	—	—
<i>rubra</i>	—	—	—	—	2	20	1	—	—	—

the increased number of gill rakers in *Mycteroperca rubra* can be evaluated only within the framework of all of the characters of these and related species.

Discussion of pertinent characters will be found in the accounts of genera and species.

Frequency distributions of the significant meristic characters are given in tables 37 through 44.

ZOOGEOGRAPHY

ORIGIN: The greatest diversity of living species of groupers is found in the Indo-Pacific region,

TABLE 39
FREQUENCY DISTRIBUTION OF PECTORAL RAY COUNTS
(The right and left fins are summed)

Species	Pectoral Ray Count										
	30	31	32	33	34	35	36	37	38	39	40
<i>Paranthias</i>											
<i>furcifer</i>	—	—	—	—	—	—	—	—	—	1	8
<i>Epinephelus</i>											
(<i>Cephalopholis</i>)											
<i>fulvus</i>	—	—	—	—	3	5	107	5	3	—	—
<i>cruentatus</i>	—	—	23	—	—	—	—	—	—	—	—
<i>panamensis</i>	—	—	—	1	8	—	1	—	—	—	—
(<i>Epinephelus</i>)											
<i>striatus</i>	—	—	—	—	—	1	30	2	1	—	—
<i>morio</i>	—	—	—	2	22	3	2	—	—	—	—
<i>guttatus</i>	—	—	1	6	80	3	1	—	—	—	—
<i>niveatus</i>	—	—	—	—	2	5	50	2	3	—	—
<i>flavolimbatus</i>	—	—	1	—	—	—	11	—	—	—	—
<i>nigritus</i>	—	—	—	—	—	—	6	6	23	1	—
<i>acanthistius</i>	—	—	—	1	—	3	3	3	—	—	—
<i>mystacinus</i>	—	—	—	—	—	—	1	2	5	—	—
<i>guaza</i>	—	—	—	—	—	—	5	1	—	—	—
<i>labriformis</i>	—	—	—	—	—	1	3	2	5	2	—
<i>drummondhayi</i>	—	—	—	—	—	1	10	—	—	—	—
<i>adscensionis</i>	—	—	—	—	—	1	4	3	22	1	—
<i>analogus</i>	—	—	—	—	—	—	—	—	—	3	8
(<i>Promicrops</i>)											
<i>itajara</i>	—	—	—	—	—	—	1	2	8	—	—
(<i>Dermatolepis</i>)											
<i>inermis</i>	—	—	—	—	—	—	2	2	6	—	—
<i>dermatolepis</i>	—	—	—	—	—	—	—	—	6	4	—
(<i>Alphestus</i>)											
<i>afer</i>	—	—	—	1	16	—	3	—	—	—	—
<i>multiguttatus</i>	—	—	—	—	—	1	7	1	1	—	—
<i>Mycteroperca</i>											
<i>venenosa</i>	—	—	1	—	10	1	—	—	—	—	—
<i>bonaci</i>	—	—	—	—	15	2	1	—	—	—	—
<i>jordani</i>	—	—	—	—	3	1	—	—	—	—	—
<i>tigris</i>	—	—	—	1	29	4	2	—	—	—	—
<i>microlepis</i>	—	—	4	6	51	2	—	—	—	—	—
<i>cidi</i>	19	—	231	—	35	—	1	—	—	—	—
<i>interstitialis</i>	—	—	—	2	18	—	—	—	—	—	—
<i>phenax</i>	—	1	4	4	2	—	—	—	—	—	—
<i>prionura</i>	16	—	86	—	—	—	—	—	—	—	—
<i>xenarcha</i>	—	—	1	1	3	—	—	—	—	—	—
<i>rosacea</i>	—	—	6	1	—	—	—	—	—	—	—
<i>olfax</i>	—	1	1	2	5	1	—	—	—	—	—
<i>rubra</i>	1	1	19	1	—	—	—	—	—	—	—

TABLE 40
FREQUENCY DISTRIBUTION OF TOTAL GILL RAKER COUNTS IN AMERICAN GROUPERS

Species	Total Gill Rakers												
	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>Paranthias</i>													
<i>furcifer</i> ^a	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Epinephelus</i>													
(<i>Cephalopholis</i>)													
<i>fulvus</i>	—	—	—	—	—	—	—	2	16	44	58	7	—
<i>cruentatus</i>	—	—	3	10	8	1	—	—	—	—	—	—	—
<i>panamensis</i>	1	6	2	1	—	—	—	—	—	—	—	—	—
(<i>Epinephelus</i>)													
<i>striatus</i>	—	—	—	—	—	—	2	3	13	17	1	—	—
<i>morio</i>	—	—	—	—	—	—	1	4	16	8	—	—	—
<i>guttatus</i>	—	—	—	—	—	—	—	—	10	42	37	10	1
<i>niveatus</i>	—	—	—	—	—	—	2	26	21	11	3	1	—
<i>flavolimbatus</i>	—	—	—	—	—	—	—	3	4	3	2	—	—
<i>nigritus</i>	—	—	—	—	—	1	2	6	16	10	—	—	—
<i>acanthistius</i>	—	—	—	—	—	—	—	—	—	3	5	1	1
<i>mystacinus</i>	—	—	—	—	—	—	2	1	2	3	—	—	—
<i>guaza</i>	—	—	—	—	—	—	1	3	—	2	—	—	—
<i>labriformis</i>	—	—	—	—	—	—	—	2	5	4	2	—	—
<i>drummondhayi</i>	—	—	—	—	—	—	—	1	—	1	6	2	1
<i>adscensionis</i>	—	—	—	—	—	—	—	—	1	6	12	9	2
<i>analogus</i>	—	—	—	—	—	—	—	—	—	—	9	1	1
(<i>Promicrops</i>)													
<i>itajara</i>	—	—	—	1	—	—	2	7	1	—	—	—	—
(<i>Dermatolepis</i>)													
<i>inermis</i>	—	—	—	4	5	2	1	—	—	—	—	—	—
<i>dermatolepis</i>	—	—	—	—	—	1	5	3	1	—	—	—	—
(<i>Alphestes</i>)													
<i>afer</i>	—	—	—	—	—	1	7	9	3	—	—	—	—
<i>multiguttatus</i>	—	—	—	—	2	3	4	1	—	—	—	—	—
<i>Mycteroperca</i>													
<i>venenosa</i>	—	—	—	—	—	—	—	—	2	2	3	3	—
<i>bonaci</i>	—	—	—	1	1	2	6	—	—	—	2	—	—
<i>jordani</i>	1	—	1	1	—	1	—	—	—	—	—	—	—
<i>tigris</i> ^b	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>microlepis</i>	—	—	—	—	—	1	—	2	10	26	16	7	1
<i>cidi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>interstitialis</i>	—	—	—	—	—	—	—	3	5	5	4	1	—
<i>phenax</i> ^c	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>prionura</i> ^d	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>xenarcha</i> ^e	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>rosacea</i> ^f	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>olfax</i> ^g	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>rubra</i> ^h	—	—	—	—	—	—	—	—	—	—	—	—	—

^a35 (one), 36 (one), 37 (two), 38 (two), 39 (one), 40 (one).

^b10 (seven), 11 (seven), 12 (six), 13 (nine), 14 (one), 15 (one).

^c26 (five), 27 (two), 28 (two), 31 (one).

^d34–38 (Rosenblatt and Zahuranec, 1967).

^e29 (one), 30 (one), 31 (one), 32 (one), 35 (one).

^f37 (two), 38 (one), 39 (three).

^g25 (one), 26 (two), 27 (two), 28 (two), 29 (one).

^h45 (one), 48 (one), 49 (two), 50 (three), 51 (three), 52 (five), 53 (six), 54 (two).

TABLE 41
FREQUENCY DISTRIBUTION OF SCALES ABOVE LATERAL LINE

Species	Number of Scales																					
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>Paranthias</i>																						
<i>furcifer</i>	—	—	—	—	1	3	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Epinephelus</i>																						
(<i>Cephalopholis</i>)																						
<i>fulvus</i>	1	11	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>cruentatus</i>	—	2	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>panamensis</i>	2	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(<i>Epinephelus</i>)																						
<i>striatus</i>	—	—	—	—	—	1	5	7	10	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>morio</i>	—	—	—	—	—	—	—	—	—	—	—	3	10	5	4	2	2	1	—	—	—	—
<i>guttatus</i>	—	—	—	1	13	7	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>niveatus</i>	—	—	—	—	—	—	—	—	—	2	3	—	—	—	—	—	—	—	—	—	—	—
<i>flavolimbatus</i>	—	—	—	—	—	—	1	—	2	—	2	2	—	—	—	—	—	—	—	—	—	—
<i>nigritus</i>	—	—	—	—	—	—	—	—	3	3	4	5	2	2	—	—	—	—	—	—	—	—
<i>acanthistius</i>	—	—	—	—	—	—	4	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>mystacinus</i>	—	—	—	—	—	—	—	1	1	3	2	—	—	—	—	—	—	—	—	—	—	—
<i>guaza</i>	—	—	—	—	—	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>labriformis</i>	—	—	—	1	2	3	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>drummondhayi</i>	—	—	—	—	—	—	—	—	2	—	—	—	—	1	—	3	—	1	—	—	—	—
<i>adscensionis</i>	—	—	—	3	15	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>analogus</i>	—	—	—	—	—	—	2	3	2	—	—	1	—	—	—	—	—	—	—	—	—	—
(<i>Promicrops</i>)																						
<i>itajara</i>	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(<i>Dermatolepis</i>)																						
<i>inermis</i>	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—
<i>dermatolepis</i>	—	—	—	—	—	—	—	—	—	—	1	5	2	1	—	—	—	—	—	—	—	—
(<i>Alphestes</i>)																						
<i>afer</i>	—	—	2	7	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>multiguttatus</i>	—	—	—	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Mycteroperca</i>																						
<i>venenosa</i>	—	—	—	—	—	—	—	—	—	1	4	—	1	—	—	—	—	—	—	—	—	—
<i>bonaci</i>	—	—	—	—	—	—	—	—	—	—	3	1	—	—	—	—	—	—	—	—	—	—
<i>jordani</i>	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	1	1	—	—	—	—	—
<i>tigris</i>	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—	—	—	—	—	—	—
<i>microlepis</i>	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	3	7	4	4	1	—	—
<i>cidi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>interstitialis</i>	—	—	—	—	—	—	—	—	—	—	—	3	1	3	2	—	2	—	—	—	—	—
<i>phenax</i>	—	—	—	—	—	—	—	—	—	—	2	1	3	1	—	—	—	—	—	—	—	—
<i>prionura</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>xenarcha</i>	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—	—	—
<i>rosacea</i>	—	—	—	—	—	—	—	—	—	—	1	5	—	—	—	—	—	—	—	—	—	—
<i>olfax</i>	—	—	—	—	—	—	—	—	—	—	6	2	—	—	—	—	—	—	—	—	—	—
<i>rubra</i>	—	—	—	—	—	—	—	6	10	6	1	—	—	—	—	—	—	—	—	—	—	—

and that great faunal area is probably parental for all groupers. Of the three genera that occur in American waters, *Paranthias* is confined to this hemisphere and *Mycteroperca* is nearly so. These two genera probably reached their present level of differentiation here although the lack of intermediate forms suggests that the ancestral

stocks were well separated by the time they arrived.

Several subgenera and species-groups within *Epinephelus* are likewise so well defined that they probably represent different invasions of the American fauna.

DISPERSAL AND ISOLATION: It has been pointed

TABLE 42
FREQUENCY DISTRIBUTION OF TRANSVERSE SCALE ROWS

Species	Number of Scale Rows															
	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124	125-129	130-134	135-139
<i>Paranthias</i>																
<i>furcifer</i>												3	2			
<i>Epinephelus</i> (<i>Cephalopholis</i>)																
<i>fulvus</i>					6	9	5									
<i>cruentatus</i>		2	3	1												
<i>panamensis</i>		3	7													
(<i>Epinephelus</i>)																
<i>striatus</i>								9	2	1						
<i>morio</i>											4	8	9	6		
<i>guttatus</i>							4	13	8							
<i>niveatus</i>								2	3							
<i>flavolimbatus</i>					2	1	2	2								
<i>nigritus</i>						4	9	7								
<i>acanthistius</i>					6											
<i>mystacinus</i>							5	2								
<i>guaza</i>					3	2	1									
<i>labriformis</i>					1	6	1	1	3		1					
<i>drummondhayi</i>																
<i>adscensionis</i>					7	13	4	1								
<i>analogus</i>						1	3	4								
(<i>Promicrops</i>)																
<i>itajara</i>											1					
(<i>Dermatolepis</i>)																
<i>inermis</i>						2	1	1								
<i>dermatolepis</i>						1	1	1	3	3						
(<i>Alphestex</i>)																
<i>ofer</i>		4	6	1												
<i>multiguttatus</i>	1	3														

TABLE 42—Continued

Species	Number of Scale Rows															
	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	115-119	120-124	125-129	130-134	135-139
<i>Mycleroberca</i>																
<i>venenosa</i>	—	—	—	—	—	—	—	—	—	3	—	1	3	—	—	—
<i>bonaci</i>	—	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—
<i>jordani</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1
<i>tigris</i>	—	—	—	—	—	—	—	—	—	—	—	5	8	4	1	—
<i>microlepis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>cidi</i>	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	1
<i>interstitialis</i>	—	—	—	—	—	—	—	—	—	—	3	6	—	1	—	—
<i>phenax</i>	—	—	—	—	—	—	—	—	—	1	1	4	—	—	—	—
<i>prionura</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>xenarcha</i>	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
<i>rosacea</i>	—	—	—	—	—	—	—	1	4	—	—	—	—	—	—	—
<i>olfax</i>	—	—	—	—	—	—	—	2	1	—	2	—	—	—	—	—
<i>rubra</i>	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—

TABLE 43
FREQUENCY DISTRIBUTION OF SCALES BELOW LATERAL LINE

Species	Number of Scales						
	20-24	25-29	30-34	35-39	40-44	45-49	50-54
<i>Paranthias</i>							
<i>furcifer</i>	—	2	5	1	—	—	—
<i>Epinephelus</i>							
(<i>Cephalopholis</i>)							
<i>fulvus</i>	4	16	—	—	—	—	—
<i>cruentatus</i>	1	5	—	—	—	—	—
<i>panamensis</i>	9	1	—	—	—	—	—
(<i>Epinephelus</i>)							
<i>striatus</i>	—	—	19	5	—	—	—
<i>morio</i>	—	—	—	—	4	22	—
<i>guttatus</i>	—	—	16	9	—	—	—
<i>niveatus</i>	—	—	—	2	3	—	—
<i>flavolimbatus</i>	—	—	3	3	1	—	—
<i>nigritus</i>	—	—	1	17	2	—	—
<i>acanthistius</i>	—	—	9	1	—	—	—
<i>mystacinus</i>	—	—	—	2	5	—	—
<i>guaza</i>	—	—	5	1	—	—	—
<i>labriformis</i>	—	1	7	5	—	—	—
<i>drummondhayi</i>	—	—	—	—	—	1	4
<i>adscensionis</i>	—	14	11	—	—	—	—
<i>analogus</i>	—	—	3	5	—	—	—
(<i>Promicrops</i>)							
<i>itajara</i>	—	1	1	—	—	—	—
(<i>Dermatolepis</i>)							
<i>inermis</i>	—	—	—	2	2	—	—
<i>dermatolepis</i>	—	—	—	—	4	3	2
(<i>Alphestes</i>)							
<i>afer</i>	—	9	2	—	—	—	—
<i>multiguttatus</i>	—	4	—	—	—	—	—
<i>Mycteroperca</i>							
<i>venenosa</i>	—	—	—	6	—	—	—
<i>bonaci</i>	—	—	3	1	—	—	—
<i>jordani</i>	—	—	—	1	3	—	—
<i>tigris</i>	—	—	—	1	2	—	—
<i>microlepis</i>	—	—	—	—	11	11	—
<i>cidi</i>	—	—	—	—	—	—	—
<i>interstitialis</i>	—	—	—	—	8	3	—
<i>phenax</i>	—	—	—	6	1	—	—
<i>prionura</i>	—	—	—	—	—	—	—
<i>xenarcha</i>	—	—	—	3	—	—	—
<i>rosacea</i>	—	—	1	5	—	—	—
<i>olfax</i>	—	—	1	7	—	—	—
<i>rubra</i>	—	1	22	—	—	—	—

out that, in spite of the dependence of adults on the reef environment, groupers can effectively cross immense distances in the open sea as pelagic larvae. The Bermuda fauna attests to the effectiveness of this method of transport, for more than 85 per cent of the known West Indian grouper fauna has been reported from that remote archipelago, which lies more than

800 miles from other suitable grouper habitats. This transport of larvae has surely been abetted by, and is perhaps entirely due to, the Gulf Stream. In the absence of comparable currents, Johnston Island in the Pacific has no groupers although many species inhabit the Line Islands some 400 miles away (Gosline, 1955).

In the face of effective transport, one may

TABLE 44
FREQUENCY DISTRIBUTION OF CAUDAL PEDUNCLE CIRCUMFERENTIAL SCALES

Species	Number of Scales											
	32-34	35-37	38-40	41-43	44-46	47-49	50-52	53-55	56-58	59-61	62-64	65-67
<i>Paranthias</i>												
<i>furcifer</i>	—	—	—	1	2	5	—	—	—	—	—	—
<i>Epinephelus</i>												
(<i>Cephalopholis</i>)												
<i>fulvus</i>	—	—	10	10	—	—	—	—	—	—	—	—
<i>cruentatus</i>	—	—	1	4	1	—	—	—	—	—	—	—
<i>panamensis</i>	—	1	8	1	—	—	—	—	—	—	—	—
(<i>Epinephelus</i>)												
<i>striatus</i>	—	—	5	14	4	—	—	—	—	—	—	—
<i>morio</i>	—	—	—	—	—	4	14	7	1	—	—	—
<i>guttatus</i>	—	6	19	—	—	—	—	—	—	—	—	—
<i>niveatus</i>	—	—	—	1	1	2	1	—	—	—	—	—
<i>flavolimbatus</i>	—	—	—	—	3	3	1	—	—	—	—	—
<i>nigritus</i>	—	—	—	—	2	6	8	—	1	—	—	—
<i>acanthistius</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>mystacinus</i>	—	—	—	—	1	6	—	—	—	—	—	—
<i>guaza</i>	—	—	—	—	—	5	1	—	—	—	—	—
<i>labriiformis</i>	—	—	—	2	4	4	2	—	—	—	—	—
<i>drummondhayi</i>	—	—	—	—	—	—	—	—	4	1	—	—
<i>adscensionis</i>	—	—	10	14	—	1	—	—	—	—	—	—
<i>analogus</i>	—	—	—	—	4	4	—	—	—	—	—	—
(<i>Promicrops</i>)												
<i>itajara</i>	—	—	1	1	—	—	—	—	—	—	—	—
(<i>Dermatolepis</i>)												
<i>inermis</i>	—	—	—	—	1	2	—	—	—	—	2	2
<i>dermatolepis</i>	—	—	—	—	—	—	—	—	—	—	1	2
(<i>Alphestes</i>)												
<i>afer</i>	—	1	5	5	—	—	—	—	—	—	—	—
<i>multiguttatus</i>	2	1	1	—	—	—	—	—	—	—	—	—
<i>Mycteroperca</i>												
<i>venenosa</i>	—	—	—	—	—	—	—	3	1	1	1	—
<i>bonaci</i>	—	—	—	—	—	3	1	—	—	—	—	—
<i>jordani</i>	—	—	—	—	—	—	—	—	2	1	1	—
<i>tigris</i>	—	—	—	—	—	—	—	—	2	—	—	—
<i>microlepis</i> ^a	—	—	—	—	—	—	—	—	—	—	1	4
<i>cidi</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>interstitialis</i>	—	—	—	—	—	—	—	6	2	3	—	—
<i>phenax</i>	—	—	—	—	—	—	1	1	3	2	—	—
<i>prionura</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>xenarcha</i>	—	—	—	—	—	—	—	1	1	—	—	—
<i>rosacea</i>	—	—	—	—	1	—	3	1	1	—	—	—
<i>olfax</i>	—	—	—	—	—	—	—	1	4	2	—	—
<i>rubra</i>	—	—	—	—	—	3	14	6	—	—	—	—

^a68-70 (12), 71-73 (four), 74-76 (one).

consider what sorts of barriers serve to isolate segments of the population so that evolution can proceed. Transportation by oceanic currents is unidirectional, and in the case of the Bermuda fauna seems to have been continuous, for there are no endemic groupers (and few endemic

shore fishes of any kind), indicating that the gene flow to the islands has been sufficient to prevent differentiation.

It is readily apparent that the Western Atlantic and Eastern Pacific shore faunas are presently separated by the Middle American

Isthmus. According to geological evidence (as summarized by Mayr, 1946, and Simpson, 1950), this isolation has been continuous since the Late Pliocene. Earlier there were four gaps, any or all of which may have been open to shore fishes. The Colombian gap was open from Middle Eocene to Late Oligocene, the Panamanian gap from Late Eocene to, possibly, Late Oligocene, the Nicaraguan gap from Late Eocene to Middle Miocene, and the Tehuantepec gap from Middle or Late Miocene to Middle Pliocene. One or more of these gaps may even have been open as early as Late Paleocene. From the evidence at hand it is not possible to tell which of these gaps were utilized by particular species nor can we be certain when the crossings were made. Much of the evidence for the times and even the existence of these gaps is indirect, resting on the inability of terrestrial animals to cross them. The mere presence of a gap does not insure that it can be used by marine fishes because such ecological conditions as temperature, salinity, or direction of currents may render it impassable. It is abundantly clear that no crossings have been made since the gap closed, however, and this is sufficient to indicate the rate of evolution of groupers. Four species have remained essentially unchanged since Late Pliocene time. Two pairs of geminate species (*Epinephelus adscensionis* and *E. analogus*; *Mycteroperca bonaci* and *M. jordani*) date from closure of this separation.

In the Western Atlantic it appears that there were two centers of differentiation, the Gulf of Mexico and the West Indies. Some species are almost restricted to the Gulf, whereas others are nearly excluded from it. All other species for which there are sufficient collections are conspicuously more abundant in one of these areas than in the other. Thus, it appears that the Gulf Stream, although effective in transporting groupers for long distances, acts at the same time as a faunal barrier.

Not all groupers in a given area are equally differentiated from their relatives in adjacent faunal centers. Such variation is most readily apparent in the Eastern Pacific species and their Western Atlantic counterpart. Four levels of differentiation can be observed between related stocks: 1) six species (e.g., *Epinephelus itajara*, *nigritus*, *niveatus*, *mystacinus* (?), *afer*, and *Paranthias furcifer*) have not even reached the species level of differentiation; 2) some species (e.g.,

Mycteroperca bonaci and *M. jordani*) are distinct but close enough to be considered geminate species; 3) others (e.g., *Epinephelus inermis* and *E. dermatolepis*) are quite well differentiated but are readily recognizable as members of the same species-groups; and 4) a few (e.g., *Epinephelus labriformis*) are so distinct that their affinities are difficult to determine.

Similar levels of differentiation can be observed between those pairs of Atlantic forms which evolved in the Gulf of Mexico and to the east of the Gulf Stream, respectively. Distribution, interpretation of relationship, and level of differentiation are indicated in figure 41.

It is possible that these degrees of differentiation are due entirely to variable rates of evolution. The evaluation of morphological distinctness of two given species is admittedly subjective. At the same time, it seems probable that these different levels of separation result, at least in part, from differential times of isolation and indicate that there have been several crossings of the Middle American Isthmus. The finding of comparable levels of differentiation between Gulf of Mexico and West Indian forms in the Western Atlantic suggests that the submergence of Central America so modified the Gulf Stream that its effectiveness as a barrier was lessened and that it then acted as a filter bridge permitting interchange with the adjacent area.

Some of the four gaps across Middle America were open simultaneously and cannot be correlated directly with the postulated repeated crossings of the isthmus. It is impossible now to reconstruct with precision the exact timing of transfer of populations across barriers or to measure rates of differentiation. At present we have evidence only that barriers exist that divide American coastal waters into three distinct faunal regions (four, if the Galápagos Islands, where *Mycteroperca olfax* appears to have differentiated, are included). Groupers have crossed these barriers periodically, sometimes with resulting differentiation.

STRUCTURAL TRENDS IN THE AMERICAN GROUPERS

In order to apply the findings of the present study to groupers in other parts of the world it is necessary to discern and evaluate the trends among the comparatively well-known American

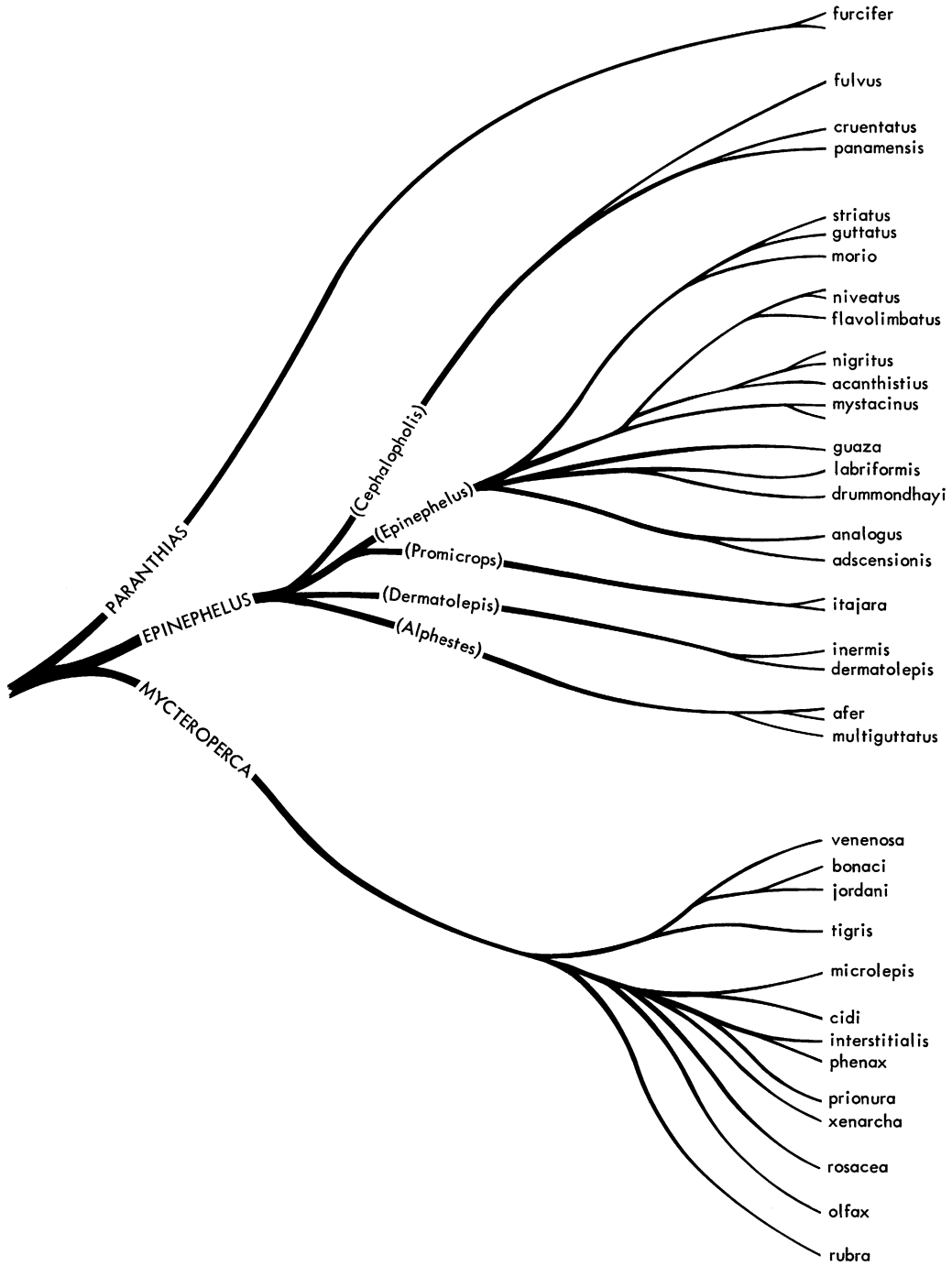


FIG. 41. Dendrogram showing inferred relationships of the American groupers.

species. The "primitiveness" of any structural feature in ancestral groups of fishes is of less interest here than is the direction of its evolution within this particular family. Hence, an attempt was made first to determine the relationship of the species involved on the basis of the ensemble of their characters and then each character was analyzed for trends within this framework.

BODY SIZE: The extremely large size obtained by some species of *Epinephelus* and *Mycteroperca* is a specialization which has arisen independently within these two genera. The potentiality for such size specialization can be considered a peculiarity of the groupers, which are among the largest teleost fishes.

BODY SHAPE: The elongation of the body in *Mycteroperca* is probably a secondary specialization from the compressed, ovate form of *Epinephelus* which is, in turn, derived from an elongate ancestral serranid stock. It is possible, however, that the form of *Mycteroperca* has been retained and that the compressed, ovate form is the only specialization.

POSTERIOR NOSTRIL: The enlargement of the posterior nostril is also an apparent specialization which has arisen independently in *Mycteroperca* and in *Epinephelus*. In *Mycteroperca* it has arisen but once, and in this genus it indicates relationship.

SCALES: The general trend among groupers is toward smaller scales (e.g., *Mycteroperca microlepis*, *Epinephelus drummondhayi*). The excessive rugosity of the scales of *Epinephelus itajara* is a specialization.

FIN SHAPE: Rounded soft dorsal and anal fins are generalized and those groupers having falcate or acutely lobed fins are specialized.

The exerted rays in the median fins of some species of *Mycteroperca* are specializations. The same condition appears in several other genera of serranid fishes; thus a basic genetic similarity seems to be indicated.

The elongate second dorsal spine of *Epinephelus morio* is apparently a retained paedomorphic character. The primitive caudal fin was probably moderately forked and the deeply forked caudal of *Paranthias furcifer* seems to be a direct specialization. Most groupers have rounded or square tails, representing specialization in the opposite direction. The lunate caudal fins of such species as *Epinephelus morio*, *E. drummondhayi*, and *Mycteroperca phenax* seem

to be the result of a secondary elongation of the caudal lobes.

FIN RAY COUNTS: Most groupers have 11 dorsal spines. The few that commonly or constantly have nine or 10 are believed to be secondarily descended from species having 11 spines. Most other serranid fishes have 10 spines in the dorsal and this number seems to be primitive for the family.

The primitive pectoral ray count seems to be 17 with secondary reduction to 16 or increase to 18-20.

The short anal fin of *Epinephelus* (eight or nine soft rays) seems to be primitive and higher numbers are considered more advanced. Most other serranids have only seven or eight soft rays.

GILL RAKERS: The most common and probably unspecialized number of gill rakers in groupers is 9-10+1+15-16. Reduction in *Mycteroperca tigris* and increase as in *M. rosacea* and *rubra* are presumed to be specializations.

PYLORIC CAECA: Low numbers of pyloric caeca (under 20) are usual, and the high number in some species is a specialization, perhaps for more efficient utilization of organisms such as crustaceans whose skeletons are composed largely of chitin.

COLOR: Somber, dark red coloration is interpreted as primitive; spots and bars represent modifications. This statement is based on the observation that gaudy color patterns have evolved in widely different directions, hence, are not likely to be primitive. The capacity to develop depth-correlated color phases is also considered a specialization.

SKULL CRESTS: The parallel crests of *Mycteroperca* are regarded as modifications of the convergent type of crests of *Epinephelus*. Primitively distinct postorbital processes are incorporated in the frontoparietal crests in more advanced forms. The high inclined frontoparietal crests of *Paranthias* are specialized in keeping with the foreshortened skull and angulate parasphenoid. The very low crests of *Epinephelus itajara* are specializations in another direction, and the transverse ridges seen in *Cephalopholis* are a recent innovation.

SUPRAETHMOID: In the more conservative species, the supraethmoid forms the floor of a pit between the anterior ends of the frontals. The development of a transverse wall anterior to the frontals is a specialization which has arisen

once in *Mycteroperca* and again, independently, in the *niveatus* species-group of *Epinephelus*.

HYOMANDIBULAR: The anterior wing of the hyomandibular is reduced in *Mycteroperca* from the expanded condition seen in *Epinephelus*.

PREOPERCLE: The strong antrorse spine at the angle of the preopercle of *Alphestes* is clearly developed from the condition found in *Epinephelus* and does not indicate alliance with those serranid fishes having strong spines on the lower limb of the preopercle. The lobate angle and the smoothly rounded preopercle are both believed to be derived from the intermediate condition.

TEETH: The jaw teeth of all groupers are in two rows, the outer row with enlarged teeth near the symphysis. In *Mycteroperca* the enlargement of these median canines is a specialization for a fish diet. In *Epinephelus nigritus* and *E. itajara* the canines are not enlarged, an adaptation to a crustacean diet.

SEXUALITY: Protogyny has been derived from synchronous hermaphroditism.

PHYLOGENY

To be useful in the determination of phyletic lines, the characters employed should be consistent both within and between groups involved and should be subject to a minimum of individual variation. In groupers meristic characters are useful and skeletal features are very important. Some proportional measurements serve to separate major groups and also indicate trends within these groups better than other characters. Coloration provides the most useful field characters but is of limited value in indicating phylogeny. Juvenile pattern, in particular, is useful in aligning certain species. Considerable reliance is placed on the general appearance of the animals but such subjective impressions can usually be supported by other features amenable to more precise quantification.

The picture of evolution within *Epinephelus* itself is far from complete but in American waters there are at least seven distinct lineages. *Epinephelus guaza*, an Eastern Atlantic species that reaches Brazil, seems to have no close relatives in American waters and is tentatively associated with *labriiformis* and *drummondhayi*. Their affinities lie with some Indo-Pacific species-group, possibly one that includes *E. summana*. *Epinephelus adscensionis* and its Eastern Pacific twin, *analogus*, are also without close

relatives in the Americas and probably evolved in the Indo-Pacific region. The *niveatus* and the *striatus* species-groups each encompass several species and probably evolved in American waters.

The *niveatus* group, comprising *niveatus*, *flavolimbatus*, *nigritus*, *acanthistius*, and *mystacinus*, is distinguished by long pelvic fins and a low dorsal count (14 or 15 soft rays except in *acanthistius*). All but *flavolimbatus* have numerous pyloric caeca and all but *mystacinus* have similar juvenile color patterns. *Epinephelus nigritus* and *E. mystacinus* have a transverse wall developed on the supraethmoid. Thus, some characters are common to all members of the group, whereas others link certain species. *Epinephelus niveatus* and *E. flavolimbatus* seem to be geminate species; the rest are earlier derivatives. Within the *striatus* group, *Epinephelus guttatus* and *E. striatus* seem closest, with *E. morio* slightly more distinct.

Epinephelus itajara (subgenus *Promicrops*), related to the Indo-Pacific species *lanceolatus*, must have been well differentiated by the time it reached the Western Hemisphere.

Another line, identified by secondary reduction of the number of dorsal spines to nine, gave rise to the subgenus *Cephalopholis*. The subgenus includes several Indo-Pacific forms in addition to the three American species treated here. Of the latter, *cruentatus* and *panamensis* are closely related; *fulvus* is more distant and appears to be more closely related to the Indo-Pacific *argus* and the Eastern Atlantic *taeniops*.

The subgenus *Dermatolepis* differs from *Epinephelus* in scale structure, body shape, and coloration but appears to be a recent descendant from *Epinephelus* stock. The two American species of *Dermatolepis* seem to be the result of differentiation following isolation by the Middle American Isthmus. One or two other species occur in the Indian Ocean.

The subgenus *Alphestes* is said to be characterized by having parallel skull crests and a frontal pit. The skull crests, however, are basically of the type seen in *Epinephelus* and are nearly identical with those of a skull of a small *E. adscensionis*. They include the postorbital processes, which those of *Mycteroperca* do not. The over-all aspect of the skull is that of *Epinephelus* rather than *Mycteroperca*. In its gross appearance *Alphestes* is close to *Dermatolepis*. The mottled color pattern with white spots in some temporary phases, dark spots in others, the rather

smooth scales, and certain similarities in body proportions lead me to believe that *Alphestes* and *Dermatolepis* are close relatives. This has been borne out by McCully's (ms) findings of similarities of scale structure. *Alphestes*, however, differs from other *Epinephelus*-like species in having an antrorse spine at the angle of the preopercle. This is a consistent structure implying a degree of genetic control quite unlike the disorganized spurs seen occasionally on the lower limb of the preopercle of some other forms, including *Dermatolepis*. Apparently the *Alphestes-Dermatolepis* line split off from the main *Epinephelus* line somewhat later than *Mycteroperca* did.

The genus *Mycteroperca*, consisting of 13 closely related species, seems to be the result of an early split of the *Epinephelus* stem. *Mycteroperca* is distinguished by the parallel skull crests, the well-developed supraethmoid wall, and the long anal fin. Two lines are distinguishable within the genus *Mycteroperca*, the *venenosa* group and the *interstitialis* group. *Mycteroperca tigris* stands somewhat apart but is still placeable in the *venenosa* group. Members of the *venenosa* group have rounded preopercles, subequal nostrils, and entire median fins. *Mycteroperca bonaci* and *M. jordani* are Atlantic and Pacific geminates. *Mycteroperca venenosa* is more distinctive and probably diverged a little earlier.

All species of the *interstitialis* group have lobate preopercles and enlarged posterior nostrils as adults. *Mycteroperca interstitialis*, *M. phenax*, *M. xenarcha*, *M. cidi* and *M. prionura* have exerted rays in the dorsal, anal, and caudal fins. *Mycteroperca microlepis*, *M. rosacea*, *M. olfax*, and *M. rubra* have these fins entire or merely falcate. *Mycteroperca olfax* has the greatest enlargement of the posterior nostril of any species of the genus and is unique in the development of a lobe at the anterior end of the dorsal fin. These specialized features suggest that it is the result of early isolation (in the Galápagos Islands) from other populations of this species-group. *Mycteroperca rosacea* and *M. rubra* also seem to have diverged early and are specialized in their high gill raker count. *Mycteroperca rubra* is the only species in the genus that is not restricted in its distribution to American waters. It is also extreme in scale size and body shape, characters in which it is primitive. *Mycteroperca interstitialis* and *M. phenax* are geminate species and *M. xenarcha* is close to them.

Mycteroperca microlepis superficially resembles members of the *venenosa* group in coloration, the lack of exertions on the median fins, and in general body proportions. These like characters are probably retained from common ancestry. The enlargement of the posterior nostril and the lobate preopercle in *microlepis* demonstrates its true affinity with the *interstitialis* complex.

The lineage most remote from the main stem of the groupers is that which gave rise to *Paranthias*. This genus is extreme in nearly all characters, especially body proportions, and probably in its habits. Some authors have even considered it to be allied with an entirely different section of the Serranidae that includes *Anthias* and related genera. *Paranthias* belongs with the groupers on the basis of the strong skull crests, the occasional development of the supramaxilla, and its hybridization with *Epinephelus fulvus*.

Discussions of the individual species relationships are to be found in the accounts of the species.

HYPOTHETICAL ANCESTRAL GROUPER

On the basis of the trends discussed above, it is possible to postulate the probable appearance of the ancestral grouper. Even if this diagnosis is incorrect in one or a few respects, the over-all characterization is believed to constitute a close representation. It was a moderate-sized or small fish, perhaps reaching a length of 300 mm. The body was robust, somewhat compressed, and deepest at the origin of the dorsal fin but not tapering strongly behind that. The dorsal profile was only slightly more arched than the ventral. The dorsal fin was low, the third or fourth spine the longest in the adult. The caudal was slightly forked, the soft dorsal and anal rounded. None of the vertical fins had exerted rays. The preopercle was rounded with only a slight notch above the angle. Its upper limb was serrate, the lower unarmed; the serrae at the angle were but slightly enlarged. Counts were approximately as follows: dorsal XI, 16-17; anal III, 8; pectoral 17; gill rakers 10+1+14; pyloric caeca about 12. The skull was much like that of *Epinephelus striatus*, the frontoparietal crests convergent, postorbital processes prominent, and median crests low and ending behind the orbit. The frontal pit was well developed.

Teeth were in two rows in the jaws, the outer single row having moderately enlarged canines near the symphysis. The posterior nostril was slightly enlarged in adults. Scales were rather large, 60-80 in the lateral line. The color was dark red without conspicuous bars, stripes or spots; the inside of the mouth was white. This ancestor was a protogynous hermaphrodite.

The ancestral grouper, in turn, was descended from a *Serranus*-like form that probably had these characteristics: a synchronous hermaphroditism; forked tail; large scales (about 40-50 in the lateral line); small, elongate, slightly compressed body; equal nostrils; few pyloric caeca. The counts were, probably: dorsal X, 15; anal III, 7; pectoral about 16.

SUMMARY

1. THE AMERICAN SPECIES of groupers constitute a block of serranid fishes which have been studied as a unit. Field investigation of their biology and life colors has supplemented laboratory studies on morphology, variation, and geographic distribution as indicated by existing museum specimens and literature records. Keys to the genera and species are given and previous literature is summarized in a synonymy for each species.

2. The groupers are moderate-sized to large-sized serranid fishes of warm seas. Most are solitary, reef-dwelling carnivores. In some areas they are the object of intensive, but local, commercial fisheries. Spawning takes place in the winter to late spring, depending on the latitude, but the manner of spawning is not known. The eggs are small, buoyant, and numerous. All of the species so far studied are protogynous. There is a pelagic larval stage during which the groupers can traverse great distances, but the adults are rather sedentary and probably rarely stray far from coral or rock reefs.

3. Groupers undergo considerable color variation of three types: "instantaneous," under nervous control; bathymetric, correlated with the environment, some species having strikingly different deep-water and shallow-water color phases; and xanthic, a yellow color phase under genetic control that characterizes small parts of the populations in a few species. A juvenile color phase different from that of the adult is present in some, but not all, species.

4. Osteological characters are useful in grouper classification and the osteology of *Epinephelus guttatus* is described in detail as a basis of comparison.

5. Subfamily names are not used in this report because present knowledge does not permit compartmentalization at that level.

6. The genus *Paranthias* is considered monotypic, with allopatric Western Atlantic and Eastern Pacific populations.

7. Twenty-one American species of *Epinephelus* are recognized. Seven distinct lines seem to be present. The nominal genera *Cephalopholis*, *Petrometopon*, *Alphestes*, *Dermatolepis*, *Promicrops* and *Garrupa* are placed in the synonymy of

Epinephelus. *Epinephelus niphobles* is a synonym of *E. niveatus*, which thus has Atlantic and Pacific populations. Other species that occur on both sides of the Isthmus of Panama are *Epinephelus nigrilus*, *itajara*, and probably *mystacinus* although the only Pacific record seems to be a small specimen from the Galápagos and this could be a locality error.

8. Two American species of the subgenus *Dermatolepis* are well differentiated, one on each side of the Central American Isthmus.

9. The Eastern Pacific species previously known as *Cephalopholis acanthistia* is clearly a member of the *E. niveatus* species-group.

10. The transverse skull crests of *Petrometopon* are not sufficient grounds for recognizing it at either the generic or subgeneric levels. It is combined with *Cephalopholis* as a subgenus of *Epinephelus*.

11. *Epinephelus afer* occurs in the Pacific Ocean as well as in the Atlantic; *E. multiguttatus* is confined to the Eastern Pacific. Apparently the subgenus *Alphestes* has twice invaded the Eastern Pacific from the Western Atlantic.

12. Thirteen species of *Mycteroperca* are recognized. These fall into two species-groups.

13. Some proportional measurements are relatively constant among most species of groupers. Others provide good generic and species-group characters and a few furnish useful species characters. Tables of measurements are given for each species except *Mycteroperca prionura* and *M. cidi*.

14. Barriers to dispersal and methods of transport of groupers are discussed. Three centers of distribution seem apparent: the Eastern Pacific, the Gulf of Mexico, and the West Indies. There is a sharp faunal break across the Straits of Florida and the Gulf Stream seems to be an effective, although incomplete, barrier. There appear to be several levels of differentiation between species in these regions. These may be due in part to different rates of evolution, but are more probably a reflection of different periods of isolation. The last closure of the Middle America gap was Late Pliocene and four species remain unchanged since that time.

15. A phylogeny of the American groupers is

proposed that is based on the information available at this time.

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