

Anisochromis straussi, New Species
of Protogynous Hermaphroditic Fish,
and Synonymy of Anisochromidae,
Pseudoplesiopidae, and
Pseudochromidae

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and THOMAS H. FRASER

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ABSTRACT

Springer, Victor G., C. Lavett Smith, and Thomas H. Fraser. *Anisochromis straussi*, New Species of Protogynous Hermaphroditic Fish, and Synonymy of Anisochromidae, Pseudoplesiopidae, and Pseudochromidae. *Smithsonian Contributions to Zoology*, number 252, 15 pages, 2 figures, 4 tables, 1977.—*Anisochromis straussi* is described from the isolated St. Brandon's Shoals in the southwestern Indian Ocean. The species exhibits two types of color patterns, which are correlated to some degree with size and sex. Histological sections of the gonads indicate that all testes have a nonfunctional cavity that represents the remnant of the ovarian lumen, and all have remnants of oocytes among the acini. The smaller specimens are female, the larger, males. Evidence is presented that the Anisochromidae, Pseudoplesiopidae, and Pseudochromidae form a monophyletic group. Evidence is also presented that within this group the Pseudoplesiopidae and Anisochromidae form a monophyletic group and each of these two taxa is definable based on autapomorphies. The Pseudochromidae appear to be a possibly polyphyletic primitive residue group that is not definable on the basis of autapomorphies. The lowest phylogenetic level for which there is evidence of monophyly among the fishes currently assigned to the Anisochromidae, Pseudoplesiopidae, and Pseudochromidae was chosen as the level for family recognition. Pseudochromidae is the oldest family-group name available for this level.

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Introduction

This study was initiated by our collecting an undescribed species of the previously monotypic genus *Anisochromis*, currently assigned to the monotypic family Anisochromidae. Except for listings or discussions based on the original descriptions (J. L. B. Smith, 1954b) of *Anisochromis* and the Anisochromidae, there has been no new information presented on these two taxa. During preparation of the description of our new species, we became impressed by the similarity of *Anisochromis* to fishes of the family Pseudochromidae and Pseudoplesiopidae. We were thus prompted to investigate the systematic relationships of *Anisochromis*. We also noted that eggs were often present in the gonads of specimens exhibiting either of the two types of color patterns shown by our new species. J. L. B. Smith (1954b) had reported that each of the two color patterns exhibited by his species (which are quite similar to those of our species) was indicative

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of a different sex. This apparent discrepancy caused us to examine the gonads of the new species in more detail. The results of our investigations are reported below.

METHODS.—Vertebrae and dorsal and anal-fin ray counts were taken from radiographs. The osteological description of *Anisochromis* is based on four cleared and stained specimens (see "Comparative Material").

Gonadal tissue for cross sectioning was taken from specimens originally fixed in approximately ten percent formalin, washed in freshwater, and preserved in 75 percent ethanol. Sections were stained in Mayer's hematoxylin and eosin-phloxine solution.

ABBREVIATIONS.—ANSP = Academy of Natural Sciences of Philadelphia; AMNH = American Museum of Natural History, New York City; BMNH = British Museum (Natural History), London; CAS = California Academy of Sciences, San Francisco; RUSI = Rhodes University, J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa; USNM = acronym for former United States National Museum, collections of which are now in National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.

COMPARATIVE MATERIAL.—A wide variety of pre-

served whole specimens representing various families, genera, and species of fishes was examined, often by radiography, to determine osteological and other characters. With the exception of specimens of *Percichthys*, this material is not listed here. Four specimens of *Percichthys trucha* (USNM 52426) were radiographed to obtain information on dorsal, anal, and caudal-fin structure, and one specimen was dissected to obtain information on the branchial and hyoid arches (poor condition of the specimens precluded clearing and staining). It was not always possible to determine genus or species for the specimens of Pseudochromidae and Pseudoplesiopidae. Supplementary information on these two families was derived from the studies of Lubbock (1975, 1976), Schultz (1967), and J. L. B. Smith (1945a,b). The most relevant cleared and stained specimens examined are listed as follows (numbers in parentheses indicate number of specimens examined):

ACANTHOCLINIDAE: *Acanthoclinus* species, USNM 200546 (1); *Acanthoplesiops hiatti*, USNM uncataloged (2); *Belonepterygion fasciolatum*, USNM 211306 (2). ANISOCHROMIDAE: *Anisochromis straussi*, USNM 215859 (4). CEPOLIDAE: *Cepola pauciradiata*, USNM 213502 (1). GRAMMIDAE: *Gramma loreto*, USNM 199487 (3); *Lipogramma anabantoides*, USNM 216405 (2). OPISTOGNATHIDAE: *Opistognathus whitehursti*, ANSP 120714 (1); *Stalix moenensis*, USNM 211963 (1). PERCICHTHYIDAE: *Morone americana*, USNM 109851 (3). PLESIOPIDAE: *Assessor mcneilli*, USNM uncataloged (3); *Plesiops coeruleolineatus*, USNM 211304 (2); *Trachinops taeniatus*, USNM uncataloged (1). PSEUDOCROMIDAE: *Pseudochromis flavivertex*, USNM 211305 (2). PSEUDOGAMMIDAE: *Aporops* species, USNM uncataloged (3); *Pseudogramma polyacantha*, USNM 209575 (3). PSEUDOPLESIOPIDAE: *Chlidichthys auratus*, USNM 211780 (2); *C. rubiceps*, USNM 211777 (5); *Pseudoplesiops annae*, USNM uncataloged (2). SERRANIDAE: *Bostockia porosa*, AMNH uncataloged (2); *Epinephelus fasciatus*, USNM uncataloged (3); *Serranus cabrilla*, USNM uncataloged (2).

Twenty-one specimens of *Anisochromis kenyae* served as the basis for comparing that species with our new one: RUSI 824 (14), USNM 216415 (6), and ANSP 134469 (1).

ACKNOWLEDGMENTS.—We wish to thank the following individuals for providing loans of specimens or information on holotypes: M. Boeseman, Rijksmuseum van Natuurlijke Historie, Leiden; A. Kottaus, Hamburg; H. Nijssen, Zoölogisch Museum, Amsterdam; M. M. Smith and R. Winterbottom, RUSI; W. F. Smith-Vaniz, ANSP; P. J. P. Whitehead and A. C. Wheeler, BMNH.

A. Spreitzer, NMNH, provided laboratory assistance, and P. Melville, NMNH, prepared the histo-

logical sections of gonads for our study.

The specimens of the new species of *Anisochromis* were collected during the 1976 expedition to St. Brandon, which was conceived, produced, and funded by L. H. Strauss, Washington, D.C.

Drafts of the manuscript were read by, and benefited from the criticism of, G. J. Nelson and D. E. Rosen (AMNH), and W. L. Fink (Museum of Comparative Zoology, Harvard University).

Anisochromis straussi, new species

FIGURES 1, 2

DIAGNOSIS.—A species of *Anisochromis* with 25–27 segmented dorsal-fin rays (modally 26), 17–19 segmented anal-fin rays (modally 18), 33–35 total vertebrae (modally 34). Dorsal fin of terminal stage color pattern (Figure 1) lacking a discrete dark spot or blotch in interradiar membranes at anterior end of dorsal fin.

DESCRIPTION.—Osteology. Infraorbital bones 3–5 (includes lacrymal and relatively tiny dermosphenotic; lesser numbers apparently resulting from fusions); where five infraorbitals are present, third from anteriormost bears wide subocular shelf. One extrascapular (lateral) on each side (supratemporal canal passing only through skin medially; canals from opposite sides just failing to join middorsally). Orbitosphenoid absent. Basisphenoid present. Vomer toothed. Palatine toothless, well separated from foreshortened mesopterygoid and ectopterygoid (ectopterygoid reduced to small blade of bone without anteriorly extending process). Supramaxillaries absent. Sesamoid articulators (coronomeckelians) absent. Outer row of large teeth in each jaw; patch of much smaller teeth behind outer row anteriorly in upper jaw; irregular row of much smaller teeth behind outer row anteriorly in lower jaw.

Infrapharyngobranchial 1 absent; infrapharyngobranchials 2, 3, and toothplate of 4 present, toothed; no interarcual cartilage between cartilagenously tipped uncinat process of epibranchial 1 and infrapharyngobranchial 2; one or two well-developed gill rakers on epibranchial 1, two or three ceratobranchial 1; basibranchials 1–3 present, 4 present as cartilage; basibranchial 1 anteriorly ventral to basihyal; urohyal articulates with ventral surface of basibranchial 1. Basihyal toothless, with well-developed median keel anteriorly.

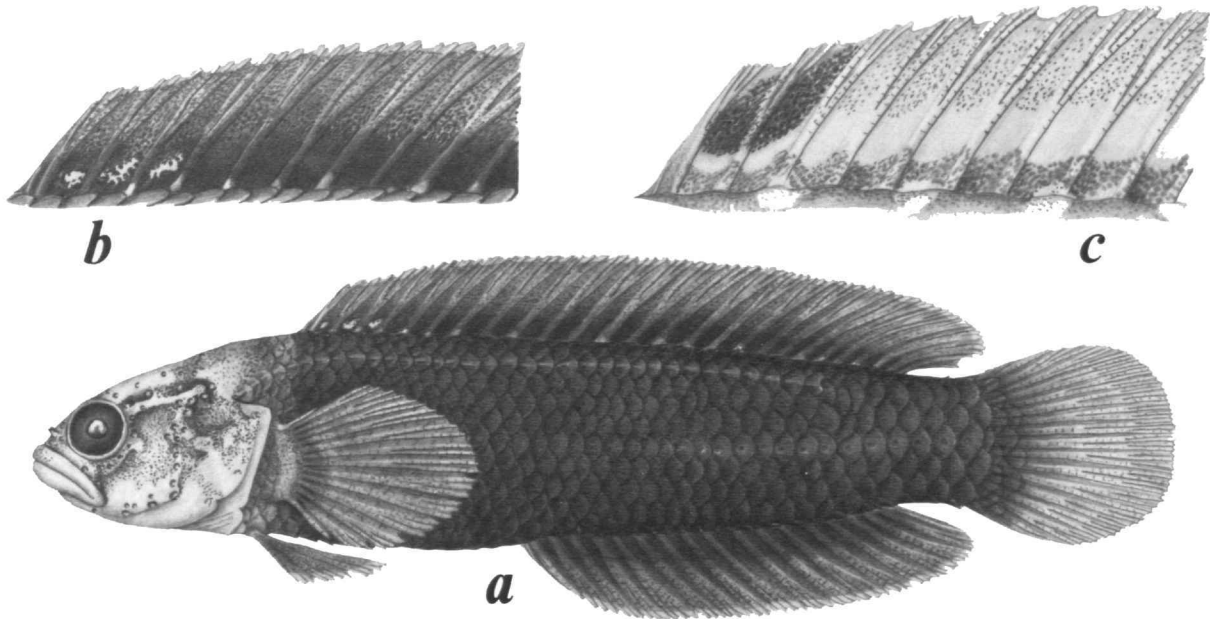


FIGURE 1.—*Anisochromis straussi*, terminal color pattern, USNM 216465, 22.6 mm SL: *a*, lateral view; *b*, anterior portion of dorsal fin enlarged. *Anisochromis kenya*, terminal color pattern, USNM 216415, 25.1 mm SL: *c*, anterior portion of dorsal fin enlarged (Drawn by J. R. Schroeder.)

Dorsal and ventral hypohyals present; ceratohyal (= anterior ceratohyal) without "beryciform" foramen, but with dorsal margin excavated; ceratohyal and epihyal (= posterior ceratohyal) form suturing joint on both medial and lateral surfaces; six branchiostegals: five attach on ceratohyal, one attaches at joint between ceratohyal and epihyal; anterior two branchiostegals attach to ventral notches in ceratohyal.

Dorsal and ventral postcleithra present. Pectoral-fin radials 4, ventralmost articulating only with coracoid; fin rays 14 (rarely 13 or 15 unilaterally); rays usually all branched except very short dorsalmost ray; two dorsalmost rays articulate with scapula; scapula foramen complete. Pelvic-fin rays I, 4; spine feeble, inapparent; innermost ray much reduced in size, simple, often nubbin-like, other rays branched. Dorsal and anal fins each comprise tiny spine and branched rays (see Table 1 for dorsal and anal-fin ray counts); last ray in each fin split to

base, both halves of ray articulating with same pterygiophore (two halves counted as one ray in enumerating dorsal- and anal-fin rays), posterior half of split ray usually much reduced in size, unbranched; all but anteriormost two pterygiophores of dorsal and anal fins consist of autogenous proximal, medial and distal radials; two anteriormost pterygiophores in each fin consist of fused proximal and medial radials, no (autogenous?) distal radials present in anteriormost pterygiophore in each fin, but distal radials autogenous in next to anteriormost pterygiophore; anteriormost dorsal-fin pterygiophore inserted in space between second and third neural spines; except for anteriormost two pterygiophores in each fin, dorsal or anal-fin pterygiophore-vertebra ratio is 1:1. Predorsal bones 2 (rarely 3). Caudal fin with 14–16 branched rays all of which articulate with hypurals; total rays, including procurrent elements, consistently 25; no procurrent spur (Johnson, 1975); parhypural and hypurals 1

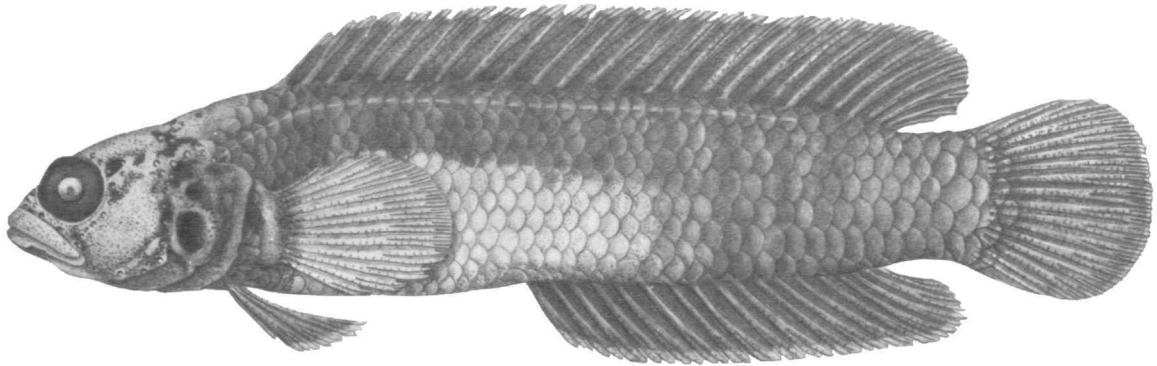


FIGURE 2.—*Anisochromis straussi*, ocellated color pattern, USNM 215859, 23.4 mm SL. (Drawn by J. R. Schroeder.)

and 2 fused into autogenous plate; hypurapophysis well developed; hypurals 3 and 4 fused to each other and to urostylar complex; hypural 5 autogenous; two epurals; no autogenous uroneurals; neural spine of preural vertebra 2 usually short, occasionally long.

Vertebrae 10 (rarely 11) + 23–25 = 33–35; epi-pleural ribs begin on first vertebra and continue posteriorly to vertebra 21 or 22; pleural ribs begin on third vertebra and continue posteriorly to vertebra 10, where they may be greatly reduced in size; no autogenous hemal spines.

No scales on head or dorsal, anal, pectoral, and pelvic fins. Body completely scaled except for portions of predorsal area and fleshy pectoral-fin base; caudal fin scaled basally. Scales cycloid anteriorly on body, becoming ctenoid posteriorly at about level of pectoral-fin axil (note: ctenii not shown in Figures 1 and 2). Tubed lateral-line scales 30–38. Of 28 specimens on which bilateral counts were made, 7 were bilaterally symmetrical, 9 had higher left side counts, 12 had higher right side counts; the difference between right and left counts ranged from 1 to 4 scales ($\bar{x} = 1.7$). Tubed lateral-line scales terminate well anterior to posterior insertion of dorsal-fin base; posteriormost tubed scale, unlike other tubed scales, often notched on posterior margin. Several scales of midlateral row on posterior half of body of some specimens each bearing a pit centrally; anteriormost pitted scale often well in advance of level of posteriormost tubed scale.

Color of freshly preserved specimens (based on

general recollections and color slides of one terminal stage and two ocellated stage specimens). Terminal stage. Head generally bright reddish orange with adjacent pale and black stripe-like markings extending posterodorsally from orbit at about two-o'clock position; indistinct, slender, dusky stripe extending from ventral margin of orbit to posterior tip of maxillary; diffuse, dusky markings elsewhere. Head color rapidly grading into black anteriorly on body. Body uniformly black. Black of body extending onto dorsal, anal, caudal, and pelvic fins, at least basally. Dorsal and anal fins dusky distal to black basal portions, distalmost margins immaculate. Caudal fin uniformly dusky distal to black area. Pelvic fin almost entirely black with immaculate distal margin. Pectoral fin: fleshy base dusky, rayed portion black basally, becoming pale dusky distally.

Ocellated stage. Head generally pale greenish ventrally, becoming olive brown dorsally; large, dark-dusky to black spot on opercle narrowly, irregularly margined with brilliant white; adjacent pale and black stripe-like markings extending posterodorsally from orbit at about two-o'clock position; with few scattered, irregular, pale and dusky marks; indistinct, slender, dusky stripe, bordered by pale spots or stripe, extending from ventral margin of orbit to posterior tip of maxillary. Body generally dusky orangish, grading into dusky greenish posteriorly; faint indications of several dusky bands present; prepectoral area olive brown with bright, pale spots. Dorsal and anal fins dusky greenish ante-

TABLE 1.—Frequency distributions for certain meristic characters of *Anisochromis straussi* and *A. kenyae*

Species	Segmented dorsal-fin rays				Segmented anal-fin rays				Total vertebrae				
	25	26	27	\bar{x}	17	18	19	\bar{x}	32	33	34	35	\bar{x}
<i>strausi</i>	9	70	2	25.91	5	74	2	17.96	11	69	1		33.87
<i>kenyae</i>	19	2		25.09	19	1		17.05	1	19	1		33.00

Species	Tubed lateral-line scales												
	28	29	30	31	32	33	34	35	36	37	38	\bar{x}	
<i>strausi</i> ¹				2	1	6	9	13	17	7	7	1	34.38
<i>kenyae</i> ²		1	1	4	2	2	1	1					30.84

¹Includes bilateral counts on 28 specimens.

²Includes bilateral counts on 3 specimens. Three additional specimens, data from which are not included in table, had unilateral counts of 29 or 30, 30 or 31, and 31 or 32.

riorly grading into dusky orangish posteriorly; distal margins immaculate. Caudal fin greenish in area covered by scales, rays greenish or orangish, membranes variably dusky. Pelvic fin irregularly dusky basally, immaculate distally. Pectoral fin pale greenish basally, pale dusky distally. Specimens obtained during collections are remembered as having greenish heads and bodies, often with broad orange-yellow area on side, and white-margined, dark spot on opercle.

Color pattern of preserved specimens. Terminal stage. Head relatively immaculate dorsally and ventrally; dusky and black markings on side of head as described for fresh specimens; adjacent black and pale stripes extending from eye may vary in intensity and distinctiveness, and may be present only as dark and pale spots; faint dusky stripe extending anteriorly from orbit at about nine o'clock position; occasionally a dusky spot ventrally on opercle. Black markings on body and fins essentially as in fresh specimens. Linear series of pale spots present, each spot at base of a dorsal-fin ray; occasionally a few pale spots basally in anterior interradiial membranes of dorsal fin and anterodorsally on body.

Ocellated stage. Dark and dusky markings as described for fresh specimens, white areas immaculate; faint, dusky stripe extending anteriorly from orbit at about nine o'clock position. Some specimens, especially smaller ones, exhibit black spots on caudal peduncle area, one or two of which are

usually at posterior end of dorsal-fin base; body rarely with many scattered tiny black spots; up to 12 diffuse, dusky bands present on sides, some restricted to dorsal portion; abruptly pale, roughly rectangular area often encompassing much of area from venter to midside dorsally and from pectoral-fin axil to level of anterior anal-fin rays posteriorly.

Many degrees of intermediacy in color pattern between the ocellated and terminal stages are represented by available specimens; however, the specimens were sorted into two groups, each believed to be homogeneous on the basis of color pattern, prior to our finding that only one species was involved. The size-frequency distributions for these sortings is given in Table 2. It is apparent from this sorting that specimens below 20.0 mm SL are all clearly ocellated stages and those above 25.9 mm (almost all above 24.9 mm) are terminal stages.

COMPARISONS.—*Anisochromis straussi* is very similar to *A. kenyae*, the only other species of *Anisochromis*, but differs from that species in coloration (particularly of the terminal stage) and in having higher mean numbers of dorsal and anal-fin rays, total vertebrae, and tubed lateral-line scales.

J. L. B. Smith (1954b) described the "male" (equals our terminal stage) of *A. kenyae* as having the dorsal and anal fins red with a dusky margin, a dark blotch anteriorly on the dorsal fin extending posteriorly to the fifth ray, the blotch anteriorly edged with yellow, and the fin ventral to the blotch

TABLE 2.—Frequency distributions for the two color-pattern types of *Anisochromis straussi* arranged by standard length classes

Color pattern	Standard length midclass (mm)												
	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5	26.5	27.5	28.5
Terminal					1	2	7	6	7	9	7	1	2
Ocellated	7	2	1	8	2	9	2	4	5	1			

yellow anteriorly grading into orange-red posteriorly. We noted no red or yellow color or dark blotch in the dorsal or anal fins of freshly preserved terminal stage specimens of *A. straussi*, in which the dorsal and anal fins appeared black and dusky, just as in preserved specimens. In terminal-stage specimens of *A. straussi* the dorsal fin (Figure 1a,b) has a wide, black basal stripe (punctuated with pale spots), the pigment of which may be intensified anteriorly, but does not form a noticeable blotch. Immediately above the basal stripe is a wide dusky stripe and the narrow, immaculate distal margin of the fin. In preserved terminal-stage *A. kenyae* (Figure 1c) the dorsal fin has a narrow, dusky basal stripe margined dorsally by a broader, immaculate stripe, which is margined dorsally by an even broader dusky stripe; an intensified dark blotch occupies much of the distal area of the membranes between the anterior two to four rays.

Frequency distributions and their means for certain meristic characters for the two species of *Anisochromis* are compared in Table 1. Each pair of means was compared by *t*-test and the *p*-value for each pair was less than 0.001, indicating that the differences are highly significant.

J. L. B. Smith (1954b) reported that *A. kenyae* had 11 precaudal vertebrae. All of the 21 specimens (including 20 paratypes) of *A. kenyae* we examined had 10 precaudal vertebrae, as did 80 of 81 specimens of *A. straussi* checked for this character (the exception had 11). Smith did not indicate how many specimens of *A. kenyae* were checked for precaudal counts nor how he defined precaudal vertebrae. We define precaudal vertebrae as those vertebrae that lack a hemal spine (the precaudal vertebrae of the four cleared and stained specimens of *A. straussi* we examined also lacked complete hemal arches).

TYPE SPECIMENS.—All types were collected at St. Brandon's Shoals within the area between 16°20' to 16°43'S and 59°35' to 59°41'E during the period

30 March to 11 April 1976. All three of us participated in all the collections, during which we were assisted by various other participants in the expedition to St. Brandon's: L. H. Strauss, P. West, C. Marshall, W. O. Nordlinger, P. W. Manhard. More detailed information is available from the original field data sheets filed in the Division of Fishes, National Museum of Natural History, Smithsonian Institution.

Holotype: USNM 216462, terminal-stage color pattern, 25.5 mm SL, field number VGS 76-7. Paratypes: USNM 215859, 26 specimens (including 4 cleared and stained), 18.7-26.1 mm SL, VGS 76-7; USNM 216463, 19 specimens, 16.4-27.8 mm SL, VGS 76-11; USNM 216465, 3 specimens, 22.6-23.9 mm SL, VGS 76-1; USNM 216464, 1 specimen, 26.8 mm SL, VGS 76-6; USNM 216466, 2 specimens, 26.5-28.3 mm SL, VGS 76-12; BMNH 1976.8.24.1-10, 10 specimens, 16.6-25.3 mm SL, VGS 76-10; CAS 37640, 15 specimens, 16.1-24.9 mm SL, VGS 76-9; AMNH 35892, 6 specimens, 22.0-28.0 mm SL, VGS 76-17; RUSI 862, 2 specimens, 17.2-25.5 mm SL, VGS 76-8.

ETYMOLOGY.—Named in honor of Lewis H. Strauss of Washington, D.C., who conceived, organized, produced, and participated in the expedition to St. Brandon's that netted a scientifically, highly valuable collection of fishes and other marine organisms.

DISTRIBUTION AND HABITAT NOTES.—*Anisochromis straussi* is known only from the isolated and relatively tiny area of St. Brandon's Shoals (= Caragos Carajos) in the southwestern Indian Ocean. Specimens were obtained only in rotenone collections. All of the 16 rotenone collections made at St. Brandon's were in rocky areas that included dead and live coral (live coral was uncommon at all but one of these areas). *A. straussi* was taken in nine of these 16 collections at an overall depth range of about 0.25-11 meters (recorded in the field as estimates of 0.5-35 feet), and all nine col-

lections were proximate to areas exposed at low tide. Of the seven rotenone collections where *A. straussi* was not obtained, four were made at depths greater than 15 meters and were well removed from areas exposed at low tide. The other three areas did not appear to differ much from stations where *A. straussi* was obtained. We often noted during collections that specimens of *A. straussi* were lying on the bottom adjacent to isolated, small (perhaps less than 0.5 meter in diameter), live coral heads with surfaces composed of tiny finger-like projections. Our presumption is that the *Anisochromis* were living on the corals.

Anisochromis kenyae, apparently unlike *A. straussi*, is widely distributed: occurring on the east African coast, at least from 3°–14° south latitude (J. L. B. Smith, 1954b; M. M. Smith, pers. comm.). *A. kenyae* was collected from pools in reefs at about low-tide mark (J. L. B. Smith, 1954b).

Reproductive Biology

The reproductive tract of *Anisochromis straussi* is of the usual perciform configuration, in which the right and left gonads fuse posteriorly to form a common oviduct that ends immediately behind the anus. There is no ovipore; the eggs apparently leave the body through a rupture in the connective tissue at the end of the common oviduct.

In *Anisochromis* each gonad is a hollow sac with a single dorsal ridge of germinal tissue. Transformation occurs when the germinal epithelium ceases to produce oocytes, and seminiferous crypts proliferate and begin to produce sperm. At this time sperm passages develop in the dorsal walls of the gonad and join in a common sperm duct in the dorsal and posterior wall of the common oviduct. In specimen USNM 216464-1, a ripe female that apparently spawned some time before it was collected (evidenced by oocytic debris in the germinal ridge), the sperm duct is visible near the union of the gonads but not farther posteriorly. This specimen does not have functional seminiferous crypts. Specimen USNM 216463-3 has functional crypts, early stage oocyte remnants, and a complete sperm duct that runs in close proximity to the ureter, but none of our serial sections are complete enough for us to determine if the urinary and sperm ducts exit separately or unite before leaving the body.

Specimen USNM 215859-9, a mature male with few oocyte remnants, was sectioned frontally. The posterior half of the testis has large crypts that are filled with a weakly staining clear material. This region appears similar to the so-called seminal vesicles that appear in certain gobies, toadfishes, and some serranoids. Their function is unknown.

The urinary bladder of both sexes is conspicuously enlarged with thick spongy walls. We are not aware of similar elaboration of the urinary bladder in any other fish, but this may not be significant.

Table 3 presents the results of histological examination of the gonads of 12 specimens of *Anisochromis straussi*. In general, specimens with ocelated stage color pattern are smaller and are females, and specimens with terminal stage color pattern are larger and are males, but there is considerable overlap. The overlap is not surprising and is comparable to that found in other transforming hermaphrodites (C. L. Smith, 1967). The presence of a nonfunctional lumen in the testis (remnants of the ovarian lumen) and oocyte remains among the testicular acini are further evidence that this species is a protogynous hermaphrodite.

Relationships of the Anisochromidae

J. L. B. Smith (1954b) described the Anisochromidae in the same paper in which he described the genus *Anisochromis*. Without explanation, Smith stated that the Anisochromidae were most closely related to the Pseudochromidae, in which he (1954a) earlier recognized two subfamilies. Pseudochrominae and Pseudoplesiopinae (Pseudochromidae was first proposed as a family-group name by Müller and Troschel, 1849, and Pseudoplesiopidae by Bleeker, 1875, who included a group Pseudoplesiopini among the three groups he recognized in his family Pseudochromidoidea). The only other important study treating the classification of the Anisochromidae was that of Böhlke (1960), who recognized three families Anisochromidae, Pseudochromidae, Pseudoplesiopidae—henceforth referred to jointly as the pseudochromoids) for the fishes treated by J.L.B. Smith (1954a, b), but Böhlke did not indicate whether he considered the families to be closely related. Most recently, Lubbock (1975,

TABLE 3.—Results of histological examination of gonads of *Anisochromis traussii* (oocyte stage as defined by C. L. Smith and Young, 1966)

Catalog number	Specimen number	Standard length (mm)	Color pattern stage	Gonad condition
CAS 37640	12	16.1	ocellated	immature female, stage 2 oocytes, no obvious male tissue
CAS 37640	10	19.2	ocellated	immature female, stage 2 oocytes, no obvious male tissue, no sperm duct
USNM 216463	11	21.4	ocellated	immature female, stage 2 oocytes, no obvious male tissue
CAS 37640	3	22.9	terminal	inactive male, some sperm, stage 2 oocytes
USNM 215859	9	24.2	terminal	active male, many sperm, few stage 2 oocytes
CAS 37640	6	24.9	ocellated	active female, stage 4 oocytes, no obvious male tissue
USNM 216463	2	25.3	terminal	immature female, stage 2 oocytes, no obvious male tissue
USNM 216463	3	26.3	terminal	transforming, sperm duct complete, many active sperm crypts, some sperm, stage 2 oocytes abundant
USNM 216463	1	26.7	terminal	inactive male, few sperm, stage 1 and 2 oocytes
USNM 216464	1	26.8	terminal	active female, oocyte debris, late stage 3 oocytes, partial sperm duct, no obvious male tissue
USNM 216463	4	27.8	terminal	active male, abundant sperm, stage 2 oocytes
AMNH 35892	2	28.0	terminal	highly developed male, many spermatocytes, few sperm, stage 2 oocytes

1976), in describing new species of *Pseudochromis* and *Chlidichthys* (which Böhlke placed in the Pseudochromidae and Pseudoplesiopidae, respectively), followed J. L. B. Smith (1954a) and did not recognize the Pseudoplesiopidae as distinct from the Pseudochromidae. Lubbock (pers. comm.) suggested to Springer the possibility that the Anisochromidae ought to be synonymized with the Pseudochromidae.

Böhlke's 1960 study was an attempt to define the families of serranoid fishes with disjunct lateral lines. The fishes of the seven families (pseudochromoids, Plesiopidae, Grammidae, Pseudogrammidae, Acanthoclinidae) Böhlke recognized in this group have a long and involved classificatory history. Most have been included in the Serranidae at one time or another, and all have specialized character states of the lateral line, including: interrupted, incomplete posteriorly, multiple lateral lines, and no lateral line at all (we consider the primitive state for the lateral line in perciforms to be a single, uninterrupted lateral line extending the entire length of the body). Without explana-

tion, however, Böhlke neglected to include some families (e.g., Owstoniidae and Opistognathidae) whose members have posteriorly incomplete lateral lines and which have been considered (for instance, Günther, 1860; Boulenger, 1901, Jordan and Snyder, 1902; Fowler, 1934) to be closely related to, or even included in, families he did treat in his study. Nevertheless, Böhlke's study, as the most recent and comprehensive treatment of the pseudochromoids, is a point of departure from which to attempt to determine if these three families are closely related and whether we should recognize one or more families for them. To answer the first of these two questions it was necessary to determine if the pseudochromoids form a monophyletic group among the fishes Böhlke treated. We believe the pseudochromoids are monophyletic and we distinguish them from the other compared families on the presence of two synapomorphies: the reduced number of dorsal-fin spines and the nature of the connection between the uncinat process of the first epibranchial and the second infrapharyngobranchial.

Based on the generalized perciform fishes *Percichthys* and *Morone* (Percichthyidae), we consider the presence of 10 dorsal-fin spines to be the unspecialized condition for perciform fishes, among which we include the serranoids (for a discussion of some of the most generalized perciforms, see Gosline, 1966).¹ Böhlke's families appear to fall into four groups based on number of dorsal-fin spines: Group I, Anisochromidae (1 spine), Pseudoplesiopidae (1 or 2, primitively 2), Pseudochromidae (2 or 3, primitively 3); Group II, Pseudogrammididae 6 to 8, primitively 8 (note: the anteriormost spine is vestigial, visible only in osteological preparations, and has been overlooked often by authors); Group III, Grammididae (11 to 13, primitively 11), Plesiopidae (11 to 14, primitively 11); Group IV, Acanthoclinidae (18 to 21, primitively 18). The Grammididae and Plesiopidae (Group III) appear to be least specialized for number of dorsal-fin spines, with specialization proceeding in two directions: increase and decrease in number of spines. The pseudochromoids have the fewest spines and are well separated in this character from the group (II) with the next most reduced number of spines.

In the pseudochromoids epibranchial 1 bears an uncinuate process that is cartilagenously tipped and is connected ligamentously directly to infrapharyngobranchial 2. A similar connection between these two bones occurs in the beryciform fishes and thus might be considered to be an unspecialized state when present in perciforms. In the Percichthyidae, however, there is an interarcual rod of cartilage between the uncinuate process of epibranchial 1 and infrapharyngobranchial 2. Rosen and Greenwood (1976:25) assert that the presence of this interarcual cartilage is a synapomorphy of the perciforms, and many perciforms exhibit the cartilage, including all the fishes Böhlke (1960) discussed except the pseudochromoids. The lack of an interarcual cartilage in the pseudochromoids represents either retention of a primitive, beryciform condition or a specialization, through loss, convergent on the beryciform condition. Many specialized (usually

benthic) perciform fishes lack an interarcual cartilage (for instance: blennioids, stichaeoids, cottoids, batrachoids, trichonotids, pholydichthyids, callionymids, trichodontids, uranoscopids; Springer and Freihofer, 1976). In view of the numerous specializations shared by the pseudochromoids and many perciforms with an interarcual cartilage (including, lack of an orbitosphenoid, fewer than six segmented pelvic-fin rays, fewer than 19 principal caudal-fin rays), we believe that the lack of an interarcual cartilage in the pseudochromoids is a specialization convergent with the primitive beryciform character state.

Interrelationships of the Pseudochromoids

Based on number of dorsal-fin spines, it might appear that the Pseudogrammididae are the sister group of the pseudochromoids, but we believe, as did Böhlke, that the pseudogrammidids are not closely related to any of the other families he treated.² Aside from a disjunct lateral line, we find no specialization common to the pseudogrammidids and any of the other families that is not also common to a large number of families Böhlke did not treat (a disjunct lateral line occurs also in the Nannoperccidae, some Blenniidae, and some Brotulidae, for instance, and may not necessarily indicate relationships). The Pseudogrammididae appear to be generally less specialized than the other families Böhlke treated, and do not exhibit some specializations that occur throughout the other families. For instance (primitiveness here based on character states in *Percichthys*), the pseudogrammidids are primitive in having seven branchiostegals, the epiphyal and ceratohyal not sutured together (but sutured on medial surface in the percichthyid genus *Morone*!), and in having hypurals 1-4 autogenous, whereas the other families are more specialized in having five or six branchiostegals, the epiphyal and

¹ The Perciformes is a widely accepted group for which monophyly has not been demonstrated. It cannot be demonstrated, therefore, that the pseudochromoids are a member of the Perciformes. Our out-group comparisons are based on the assumptions that the Perciformes is a monophyletic group and the pseudochromoids are a member of it.

² Böhlke (1960) believed that the pseudogrammidids were closely related to *Grammistops* (Grammistidae). Gosline (1960, 1966) synonymized the Pseudogrammididae with the Grammistidae, and Schultz (1966) agreed. C. L. Smith and E. H. Atz (1969) concluded on the basis of gonodal structure, and Randall, et al. (1971) on the basis of the toxin grammistin, that the grammistids and pseudogrammidids are not closely related. Kendall (1976) considered the grammistids and pseudogrammidids to form a portion of a subfamily Grammistinae, of the Serranidae.

ceratohyal sutured together (both surfaces), hypurals 1 and 2 fused together, and in having hypurals 3 and 4 fused together and also fused to the urostylar complex. It, therefore, seems more reasonable that one of the other families Böhlke treated would be a better candidate as a sister group for the pseudochromoids. This may be true, but we were unable to find a shared specialization that was unique to the pseudochromoids and one or two of the other three families, with one possible exception, *Lipogramma*, which Böhlke (1960) described and assigned, for lack of another possibility, to the Grammidae.

Lipogramma, which has no lateral line, exhibits one specialization (and possibly a second), which is found otherwise only in the pseudochromoids among all the fishes Böhlke treated (including the Pseudogrammidae): infrapharyngobranchial 1 is absent (specialized), and there is a cordlike ligament attaching the lateral surface of the ceratohyal to the dentary. We are uncertain of the ligament's existence in *Percichthys* (our specimens were in poor condition), but it is absent in *Morone*. The loss of infrapharyngobranchial 1, or its lack of ossification, has occurred independently in a wide variety of fishes (for instance, blennioids, cottoids, leptoscopids, stichaeoids) and may not necessarily indicate relationships. We have not searched widely for the ligament, which occurs in various character states in at least the Clinidae *sensu stricto* (but not other blennioids), Congrogadidae, and some Serranidae (but not others). Considerably more study will be necessary to determine whether *Lipogramma*, or any of the other fishes Böhlke discussed, is the sister group of the pseudochromoids.

Fowler (1934) placed *Parasphenanthias* Gilchrist (which Barnard, 1927:492, had synonymized with *Owstonia* of the Owstoniidae) in the Pseudochromidae. Myers (1935) indicated that although *Parasphenanthias* and *Owstonia* were closely related, they were not close to the Pseudochromidae, but Myers was using *Pseudogramma* as a basis for his comparison. Nevertheless, we agree with Myers that the owstoniids are not closely related to the pseudochromoids. We also agree with Okada and Suzuki (1956) that the Owstoniidae should be synonymized with and under the Cepolidae, and consider them as such in the following discussion.

The cepolids exhibit a number of specializations

that occur also in the pseudochromoids. Most of these specializations are shared as well with the other families of fishes that Böhlke treated, but one specialization, the presence of only two or three dorsal-fin spines, occurs only among the pseudochromoids. We believe that this character is convergent in the cepolids and pseudochromoids. The cepolids are less specialized than the pseudochromoids (or any of the other families Böhlke treated) in having autogenous hypurals 3 and 4 (these hypurals appear to be fused in some specimens or species of cepolids, but they are primitively autogenous within the family; Monod (1968, fig. 683) misinterpreted the hypurals of *Cepola*: his hypural 1 represents fused hypurals 1 and 2, his hypural 2 is 3, and his hypural 3 is 4). The cepolids are also less specialized than the pseudochromoids in having an interarcual cartilage between epibranchial 1 and infrapharyngobranchial 2 and an infrapharyngobranchial 1, and are perhaps less specialized in lacking the ceratohyal-dentary ligament. The cepolids are more specialized than the pseudochromoids (and other fishes Böhlke treated) in having: the first dorsal-fin pterygiophore inserted between the first and second neural spines (primitive condition: between spines 2 and 3), the last dorsal and anal-fin pterygiophores each supporting a single ray (primitive condition: supporting two elements; also known as the last-ray-split-to-the-base condition), a single postcleithrum on each side (primitive condition: two postcleithra, one dorsal and one ventral, on each side), and no predorsal bones (primitive condition: 3 bones; pseudochromoids have 2 or 3).

The conjunction of more primitive states for the caudal-fin hypurals, interarcual cartilage, infrapharyngobranchial 1, and ceratohyal-dentary ligament, together with the more specialized states for dorsal-fin pterygiophores, predorsal bones, and postcleithra, leads us to believe that the cepolids are not the sister group of the pseudochromoids.

The Opistognathidae have been considered to be close relatives of the Pseudochromidae (Günther, 1860:254; Boulenger, 1901; Jordan and Snyder, 1902) and Acanthoclinidae (Gosline, 1968, fig. 12, and pers. comm.), and although Böhlke (1960) omitted consideration of the opistognathids, their relationships must be examined. The opistognathids exhibit a number of specializations that are also

found in the pseudochromoids (lateral line incomplete and terminating below the dorsal fin, six branchiostegals, epihyal and ceratohyal sutured together, hypurals 1 and 2 fused, hypurals 3 and 4 fused to each other and to urostylar complex), but these are the same specializations that characterize the other families Böhlke (1960) treated. We found no specialization that the opistognathids shared with the pseudochromoids to the exclusion of the other families. We, therefore, have no basis for relating the opistognathids more closely to the pseudochromoids than to any of the other families. There is, in addition, no basis for excluding the Opistognathidae from Böhlke's serranoid group of fishes with disjunct lateral lines. (The opistognathids also possess an interarcual cartilage, 9–12 dorsal-fin spines, infrapharyngobranchial 1, no ceratohyal-dentary ligament, last dorsal and anal-fin pterygiophores each supporting two external elements, and first dorsal-fin pterygiophore inserted between the second and third neural spines. The opistognathids are more specialized than the other families Böhlke treated in having: the lateral line imbedded in the skin, rather than occurring on scales; no teeth on infrapharyngobranchial 2, a convergent condition occurring otherwise only in *Acanthoplesiops* of the Acanthoclinidae among the fishes Böhlke treated; and the condition of the segmented pelvic-fin rays is unusual: the anterior two are stout and simple, whereas the posterior three are weak and branched.)

In summary, considering the families Böhlke (1960) discussed, together with the Opistognathidae and Cepolidae, we believe that the pseudochromoid fishes form a monophyletic group, whose sister group we are unable to hypothesize reasonably.

Synonymization of the Anisochromidae and Pseudoplesiopidae

Assuming that pseudochromoids form a monophyletic group, we wished to determine whether each of the three families that the group comprises is monophyletic. We surveyed the members of each family for various characters in a search for autapomorphies, or synapomorphies shared by only two of the three families. Of numerous characters examined, the most useful are given in Table 4, together with the character states for each. We are unable to propose degree of specialization for char-

acters 8 and 10 in the table, but based on more generalized perciform fishes (particularly *Percichthys*), we propose the following directions for specialization of the other characters (least specialized condition presented first):

1. From 5 to 4 to 3 segmented pelvic-fin rays.
2. From all branched, to some branched, to all simple rays.
3. From 3, to 2, to 1 dorsal-fin spine, and from strong to weak spines.
4. From all branched to most simple segmented dorsal-fin rays.
5. From 3 to 2 to 1 anal-fin spine, and from strong to weak spines.
6. From scales to no scales on dorsal fin.
7. From few medial radials fused with proximal radials (or almost all medial radials autogenous), to several fused, to all fused with their respective proximal radials in each fin.
9. From ventralmost pectoral-fin radial joining only coracoid, to joining both coracoid and scapula.
11. From two (anterior and posterior) disjunct series of tubed lateral-line scales, to anterodorsally tubed series only, to only one tubed scale anterodorsally.
12. From head scaled to not scaled.
13. From palatine teeth present to teeth absent.
14. From more than 7 to less than 4 gill rakers on lower limb of first arch.
15. From branchiostegal membranes separate to membranes fused ventroposteriorly.
16. From parhypural autogenous to parhypural fused to hypural 1.
17. From preural hemal spine 2 autogenous to spine fused to centrum.
18. From ectopterygoid and mesopterygoid both articulating closely with palatine, to both well separated from palatine (resulting from shortening of the anterior processes of the ectopterygoid and mesopterygoid).
19. Ligament from ceratohyal: from connecting to dentary at symphysis, to connecting on coronoid (ascending) process of dentary (specialization inferred from condition in *Lipogamma* and the Clinidae, and less certainly in *Serranus*, where the ligament connects at the symphysis or point anterior to coronoid process).

The Anisochromidae exhibit at least five autapomorphies (12–15, 19) and can be considered to be

TABLE 4.—Comparison of certain characters in the three families of pseudochromoid fishes (family composition as defined by Böhlke, 1960; * denotes autapomorphic characters and, where the same character in another family is accompanied by two asterisks, further denotes that the phylogeny of the autapomorphy is presumed to have passed through the more primitive derived state exhibited by the character with two asterisks; ** denotes synapomorphic characters and, where the same character in another family is accompanied by a single asterisk, further denotes that the synapomorphy is presumed to have occurred, as a precursor, in the phylogeny of the family in which the character bears a single asterisk)

Characters	Families		
	Pseudochromidae	Pseudoplesioptidae	Anisochromidae
1. Pelvic-fin rays	I,5	I,3 or I,4**	I,4**
2. Segmented pelvic-fin rays	all branched	all simple*	3 branched, 1 simple**
3. Dorsal-fin spines	II or III, at least some strong	I or II, weak**	I*, weakest*
4. Segmented dorsal-fin rays	vary from all branched to most simple	most simple*	all branched
5. Anal-fin spines	III, at least some strong	I-III, weak**	I*, weakest*
6. Scales on dorsal fin	present or absent	absent**	absent**
7. Medial radials in dorsal and anal fins	several fused to proximal radials in each fin**	all, or almost all, fused to proximal radials*	few fused to proximal radials in each fin
8. Pectoral-fin rays	16-20	17-19	13-15 (14 modally)
9. Ventralmost pectoral-fin radial	joins coracoid	joins coracoid and scapula*	joins coracoid
10. Vertebrae	10-11 + 16-17 = 26-28	10-13 + 17-20 = 27-33	10 (rarely 11) + 22-25 = 32-35
11. Tubed lateral-line scales	2 disjunct series: 1 anterodorsally, 1 midlateral posteriorly	1 scale anterodorsally*	1 series anterodorsally**
12. Head scaled	yes	yes	no*
13. Palatine teeth	present	present	absent*
14. Gill rakers on lower limb of first arch	more than 7	more than 7	less than 4*
15. Branchiostegal membranes	margins on each side separate ventroposteriorly	margins on each side separate ventroposteriorly	ventroposterior margins fused across ventral surface of head*
16. Parhypural	autogenous	fused to hypural 1**	fused to hypural 1**
17. Hemal spine of preural centrum 2	autogenous	fused to centrum**	fused to centrum**
18. Ectopterygoid and mesopterygoid	articulate closely with palatine	articulate closely with palatine	well separated from palatine*
19. Ligament from ceratohyal attaches to dentary	at symphysis	at symphysis	on coronoid process*

monophyletic (not unexpected as only one genus is involved). The Pseudoplesioptidae exhibit at least four autapomorphies (2, 4, 9, 11) and may also be considered to be monophyletic (the presence of simple segmented dorsal-fin rays in pseudoplesiop-

ids and some pseudochromids is here considered to be a convergence as the unspecialized condition for rays is also present in pseudochromids and must be considered the primitive state for all pseudochromids). The Pseudochromidae, however,

lack autapomorphic characters; thus, there is reason to doubt their monophyly. The pseudochromids exhibit one possible synapomorphy (7) with the pseudoplesiopids but none with the anisochromids, and one might consider this a basis for recognizing the pseudochromids as the sister group of the pseudoplesiopids. The anisochromids, however, exhibit at least six synapomorphies (1,2,5,11,16,17) with the pseudoplesiopids and the likelihood that these two families form a sister group seems more plausible than the pseudochromid-pseudoplesiopid group possibility.

If the Pseudochromidae are a polyphyletic group it is probable that some member genera are more closely related to the Pseudoplesiopidae and others more closely related to the Anisochromidae. In any event, the Pseudochromidae presently appear to form a primitive residue pseudochromoid group and there is no basis for maintaining them as a distinct family. J. L. B. Smith (1954a) combined the Pseudochromidae and Pseudoplesiopidae (although maintaining them as subfamilies), and Lubbock (1975, 1976), currently the most active student of both groups, agreed (although he did not cite subfamilies in his studies). J. L. B. Smith (1954b) later recognized the Anisochromidae as distinct from his Pseudochromidae. Based on synapomorphies, however, the Anisochromidae and Pseudoplesiopidae are more closely related to each other than either is to the Pseudochromidae. Under the circumstances there seems little reason to recognize either two or three families among the pseudochromoids, and we here propose to combine them all under the oldest of the three family names, Pseudochromidae. Concurrently, we do not recognize subfamilies in the Pseudochromidae. In effect, we have chosen the lowest (least equivocal) phylo-

genetic level for which there is evidence for monophyly among the pseudochromoids as the level for family recognition.

Diagnosis of the Pseudochromidae

Small, often colorful, Indo-West Pacific reef-dwelling perciform fishes, seldom attaining 125 mm SL (to about 200 mm in *Labracinus*); many species under 75 mm. Dorsal fin I-III,21-37; spines often inconspicuous; segmented rays varying from all branched to most unbranched. Predorsal bones 2 or 3. Antermost dorsal-fin pterygiophore inserted between second and third neural spines. Terminal dorsal and anal-fin pterygiophore each supporting two external elements (last ray split to base). Pelvic-fin insertion below to well in advance of level of antermost insertion of pectoral fin. Pelvic fin consisting of a spine and: five branched rays, or three branched and one simple ray, or three or four simple rays. Vertebrae 10-13 + 16-25 = 26-35. Hypurals 1 and 2 (and sometimes parhypural) fused into autogenous plate. Hypurals 3 and 4 fused to each other and to urotylar complex. No autogenous uroneurals. No interarcual cartilage between uncinat process of epibranchial 1 and infrapharyngobranchial 2. Infrapharyngobranchial 1 absent. Six branchiostegals. Epihyal and ceratohyal suturally joined. Preopercle margin entire. Tubed lateral-line scales in two disjunct series (one dorsoanteriorly, one midlateral posteriorly), one series (dorsoanteriorly), or present as only one tubed scale anteriorly; centrally pitted scales often present following dorsal tubed scale series or preceding midlateral posterior series. Cordlike ligament present attaching lateral surface of ceratohyal either to coronoid process or symphysial area of dentary.

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Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of the manuscripts and art.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1 $\frac{1}{4}$ " margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5-9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9b." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9b." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.

