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

VICTOR G. SPRINGER, C. LAVETT SMITH, and THOMAS H. FRASER
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Anisochromis straussi, New Species of Protogynous Hermaphroditic Fish, and Synonymy of Anisochromidae, Pseudoplesiopidae, and Pseudochromidae

Victor G. Springer, C. Lavett Smith, and Thomas H. Fraser
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.
## Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Methods</td>
<td>1</td>
</tr>
<tr>
<td>Abbreviations</td>
<td>1</td>
</tr>
<tr>
<td>Comparative Material</td>
<td>1</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>2</td>
</tr>
<tr>
<td><em>Anisochromis straussi</em>, new species</td>
<td>2</td>
</tr>
<tr>
<td>Reproductive Biology</td>
<td>7</td>
</tr>
<tr>
<td>Relationships of the Anisochromidae</td>
<td>7</td>
</tr>
<tr>
<td>Interrelationships of the Pseudochromoids</td>
<td>9</td>
</tr>
<tr>
<td>Synonymization of the Anisochromidae and Pseudoplesiopidae</td>
<td>11</td>
</tr>
<tr>
<td>Diagnosis of the Pseudochromidae</td>
<td>13</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>14</td>
</tr>
</tbody>
</table>
Anisochromis straussi, New Species of Protogynous Hermaphroditic Fish, and Synonymy of Anisochromidae, Pseudoplesiopidae, and Pseudochromidae

Victor G. Springer, C. Lavett Smith, and Thomas H. Fraser

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 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 this material; hence, the specimens are not listed here. Four other characters. With the exception of specimens examined:

- **Acanthoclinidae**: *Acanthochilus* species, USNM 200546 (1); *Acanthoplepios hiatti*, USNM uncataloged (2); *Belonepteryx fasciolatum*, USNM 211306 (2); *Anisochromidae*: *Anisochromis straussi*, USNM 215859 (4); *Cepoideidae*: *Cepola pauciradiata*, USNM 213502 (1); *Grammateidae*: *Gramma loreto*, USNM 199487 (5); *Lipogramma anabantoides*, USNM 216405 (2); *Opistognathidae*: *Opistognathus whitehursti*, ANSP 120714 (1); *Stalix menensis*, USNM 211963 (1); *Percichthyidae*: *Morone americana*, USNM 109851 (3); *Pleisopidae*: *Assessor merelli*, USNM uncataloged (5); *Plesiops coeruleolineatus*, USNM 211304 (2); *Trachinops taeniatus*, USNM uncataloged (1); *Pseudochromidae*: *Pseudochromis flavivertex*, USNM 211305 (2); *Pseudo grammidae*: *Aporops species*, USNM uncataloged (3); *Pseudogramma polyacantha*, USNM 209575 (3); *Pseudopleisiopidae*: *Chlidichthys auratus*, USNM 211780 (2); *Cupiceps*, USNM 211777 (5); *Plesiops annae*, USNM uncataloged (2); *Serranidae*: *Bostockia porosa*, ANSP uncataloged (2); *Epinephelus fasciatus*, USNM uncataloged (5); *Serras phallus cebria*, USNM uncataloged (2).

Twenty-one specimens of *Anisochromis straussi* 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 interradial 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 medially). Orbitosphenoid absent. Basiphenoid present. Vomer toothed. Palatine toothless, well separated from foreshortened mesopterygoid and ectopterygoid (ectoterygoid reduced to small blade of bone without anteriorly extending process). Supramaxillaries absent. Sesamoid articulars (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 cartilageneously tipped uncinate process of epibranchial 1 and infrapharyngobranchial 2; one or two well-developed gill rakers on epibranchial 1, two or three cerato branchial 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.
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 1, 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
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; epipleural 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*

<table>
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<th>Species</th>
<th>Segmented dorsal-fin rays</th>
<th>Segmented anal-fin rays</th>
<th>Total vertebrae</th>
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</thead>
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<tr>
<td></td>
<td>25</td>
<td>26</td>
<td>27</td>
</tr>
<tr>
<td>straussi</td>
<td>9</td>
<td>70</td>
<td>2</td>
</tr>
<tr>
<td>kenyae</td>
<td>19</td>
<td>2</td>
<td>25.09</td>
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<table>
<thead>
<tr>
<th>Species</th>
<th>Tubed lateral-line scales</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>28</td>
</tr>
<tr>
<td>straussi</td>
<td>2</td>
</tr>
<tr>
<td>kenyae</td>
<td>1</td>
</tr>
</tbody>
</table>

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 orangish-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 interradial 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
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 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, 5 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 (= Cargados 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 216468–3 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 ocellated 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 Troshel, 1849, and Pseudoplesiopidae by Bleeker, 1875, who included a group Pseudoplesiopini among the three groups he recognized in his family Pseudochromidoides). 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 straussi* (oocyte stage as defined by C. L. Smith and Young, 1966)

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<th>Catalog number</th>
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<th>Gonad condition</th>
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<td>immature female, stage 2 oocytes, no obvious male tissue</td>
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<td>CAS 37640</td>
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<td>19.2</td>
<td>ocellated</td>
<td>immature female, stage 2 oocytes, no obvious male tissue, no sperm duct</td>
</tr>
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<td>21.4</td>
<td>ocellated</td>
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<tr>
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<td>22.9</td>
<td>terminal</td>
<td>inactive male, some sperm, stage 2 oocytes</td>
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<tr>
<td>USNM 215859</td>
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<td>24.2</td>
<td>terminal</td>
<td>active male, many sperm, few stage 2 oocytes</td>
</tr>
<tr>
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<td>active female, stage 4 oocytes, no obvious male tissue</td>
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<td>terminal</td>
<td>immature female, stage 2 oocytes, no obvious male tissue</td>
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<tr>
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<td>26.3</td>
<td>terminal</td>
<td>transforming, sperm duct complete, many active sperm crypts, some sperm, stage 2 oocytes abundant</td>
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<td>26.7</td>
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<td>inactive male, few sperm, stage 1 and 2 oocytes</td>
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<td>terminal</td>
<td>active female, oocyte debris, late stage 3 oocytes, partial sperm duct, no obvious male tissue</td>
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<td>27.8</td>
<td>terminal</td>
<td>active male, abundant sperm, stage 2 oocytes</td>
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<td>AMNH 35892</td>
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<td>28.0</td>
<td>terminal</td>
<td>highly developed male, many spermatocytes, few sperm, stage 2 oocytes</td>
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</tbody>
</table>

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 (pseudo-chromoids, Plesiopidae, Grammidae, Pseudogrammidae, Acanthochlinidae) 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 explanation, however, Böhlke neglected to include some families (e.g., Owstoniidae and Opistognathiidae) 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 uncinate 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 un
specialized condition for perciform fishes, among which we include the serranoids (for a discussion of some of the most generalized perciforms, see Gosline, 1966). Bohlke'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, Pseudogrammidae 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, Grammidae (11 to 13, primitively 11), Plesiopidae (11 to 14, primitively 11); Group IV, Acanthoclinidae (18 to 21, primitively 18). The Grammidae 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 pseudochromids 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 pseudochromids epibranchial 1 bears an uncinate 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 un-specialized state when present in perciforms. In the Percichthyidae, however, there is an interarcual rod of cartilage between the uncinate 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 Bohlke (1960) discussed except the pseudochromoids. The lack of an interarcual cartilage in the pseudochromids 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 pseudochromids and many perciforms with an interarcual cartilage (including, lack of an orbitosphenoid, fewer than six segmental pelvic-fin rays, fewer than 19 principal caudal-fin rays), we believe that the lack of an interarcual cartilage in the pseudochromids 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 Pseudogrammidae are the sister group of the pseudochromoids, but we believe, as did Bohlke, that the pseudogrammids are not closely related to any of the other families he treated. Aside from a disjunct lateral line, we find no specialization common to the pseudogrammids and any of the other families that is not also common to a large number of families Bohlke did not treat (a disjunct lateral line occurs also in the Nannopercidae, some Blenniidae, and some Brotulidae, for instance, and may not necessarily indicate relationships). The Pseudogrammidae appear to be generally less specialized than the other families Bohlke treated, and do not exhibit some specializations that occur throughout the other families. For instance (primitiveness here based on character states in *Percichthys*), the pseudogrammids 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

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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.

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 Bohlke 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 Bohlke (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 Bohlke 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 Bohlke discussed, is the sister group of the pseudochromoids.

Fowler (1934) placed Parapristanthesia Gilchrist (which Barnard, 1927:492, had synonymized with Oustonia of the Owstoniidae) in the Pseudochromidae. Myers (1935) indicated that although Parapristanthesia and Oustonia 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 Bohlke 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 Bohlke 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. 688) 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 Bohlke 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 Bohlke (1960) omitted consideration of the opistognaths, their relationships must be examined. The opistognaths exhibit a number of specializations that are also
found in the pseudochromoids (lateral line incomplete and terminating below the dorsal fin, six branchiostegals, epiphyal 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 Bohlke (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 Bohlke'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 Bohlke 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 Acanthoplesioptidae of the Acanthoclinidae among the fishes Bohlke 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 Bohlke (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 Pseudoplesioptidae**

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 characters 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.
8. From ventralmost pectoral-fin radial joining only coracoid, to joining both coracoid and scapula.
9. From two (anterior and posterior) disjunct series of tubed lateral-line scales, to anterodorsally tubed series only, to only one tubed scale anterodorsally.
10. From head scaled to not scaled.
11. From palpate teeth present to teeth absent.
12. From more than 7 to less than 4 gill rakers on lower limb of first arch.
13. From branchiostegal membranes separate to membranes fused ventrally.
14. From parhypural autogenous to parhypural fused to hypural 1.
15. From preural hemal spine 2 autogenous to spine fused to centrum.
16. 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).
17. From ligament from ceratohyal: from connecting to dentary at symphysis, to connecting on coronoid (ascending) process of dentary (specialization inferred from condition in Lipogramma 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)

<table>
<thead>
<tr>
<th>Characters</th>
<th>Pseudochromidae</th>
<th>Pseudoplesiopidae</th>
<th>Anisochromidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Pelvic-fin rays</td>
<td>I,5</td>
<td>I,3 or I,4**</td>
<td>I,4**</td>
</tr>
<tr>
<td>2. Segmented pelvic-fin rays</td>
<td>all branched</td>
<td>all simple*</td>
<td>3 branched, 1 simple**</td>
</tr>
<tr>
<td>3. Dorsal-fin spines</td>
<td>II or III, at least some strong</td>
<td>I or II, weak**</td>
<td>I*, weakest*</td>
</tr>
<tr>
<td>4. Segmented dorsal-fin rays</td>
<td>vary from all branched to most simple</td>
<td>most simple*</td>
<td>all branched</td>
</tr>
<tr>
<td>5. Anal-fin spines</td>
<td>III, at least some strong</td>
<td>I-III, weak**</td>
<td>I*, weakest*</td>
</tr>
<tr>
<td>6. Scales on dorsal fin</td>
<td>present or absent</td>
<td>absent**</td>
<td>absent**</td>
</tr>
<tr>
<td>7. Medial radials in dorsal and anal fins</td>
<td>several fused to proximal radials in each fin**</td>
<td>all, or almost all, fused to proximal radials*</td>
<td>few fused to proximal radials in each fin</td>
</tr>
<tr>
<td>9. Ventralmost pectoral-fin radial</td>
<td>joins coracoid</td>
<td>joins coracoid and scapula*</td>
<td>joins coracoid</td>
</tr>
<tr>
<td>11. Tubed lateral-line scales</td>
<td>2 disjunct series: 1 anterodorsally, 1 midlateral posteriorly</td>
<td>1 scale anterodorsally*</td>
<td>1 series anterodorsally**</td>
</tr>
<tr>
<td>12. Head scaled</td>
<td>yes</td>
<td>yes</td>
<td>no*</td>
</tr>
<tr>
<td>13. Palatine teeth</td>
<td>present</td>
<td>present</td>
<td>absent*</td>
</tr>
<tr>
<td>14. Gill rakers on lower limb of first arch</td>
<td>more than 7</td>
<td>more than 7</td>
<td>less than 4*</td>
</tr>
<tr>
<td>15. Branchiostegals membranes</td>
<td>margins on each side separate ventroposteriorly</td>
<td>margins on each side separate ventroposteriorly</td>
<td>ventroposterior margins fused across ventral surface of head*</td>
</tr>
<tr>
<td>16. Pachypteral</td>
<td>autogenous</td>
<td>fused to hypural 1**</td>
<td>fused to hypural 1**</td>
</tr>
<tr>
<td>17. Hemal spine of preural centrum 2</td>
<td>autogenous</td>
<td>fused to centrum**</td>
<td>fused to centrum**</td>
</tr>
<tr>
<td>18. Ectopterygoid and mesopterygoid</td>
<td>articulate closely with palate</td>
<td>articulate closely with palate</td>
<td>well separated from palatine*</td>
</tr>
<tr>
<td>19. Ligament from ceratohyal attaches to dentary</td>
<td>at symphysis</td>
<td>at symphysis</td>
<td>on coronoid process*</td>
</tr>
</tbody>
</table>

monophyletic (not unexpected as only one genus is involved). The Pseudoplesiopidae 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 autapomorphous 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) phylogenetic 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. Anteriormost 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 anteriormost 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. Hyurals 1 and 2 (and sometimes parhypural) fused into autogenous plate. Hyurals 3 and 4 fused to each other and to urostylar complex. No autogenous uroelectars. No interarcual cartilage between uncinate process of epibranchial 1 and infrapharyngobranchial 2. Infrapharyngobranchial 1 absent. Six branchiostegals. Epiphary and ceratothal suturally joined. Preopercle margin entire. Tubed lateral-line scales in two disjunct series (one doro-anteriorly, one midlateral posteriorly), one series (doro-anteriorly), 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 ceratothal either to coronid process or symphysial area of dentary.
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