

A new species of *Anthias* (Teleostei: Serranidae: Anthiinae) from the Galápagos Islands, with keys to *Anthias* and eastern Pacific Anthiinae

William D. Anderson, Jr. and Carole C. Baldwin

(WDA) Grice Marine Biological Laboratory, College of Charleston, 205 Fort Johnson, Charleston, South Carolina 29412-9110, U.S.A.; (CCB) Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0159, U.S.A.

Abstract.—*Anthias noeli*, new species, is described from 17 specimens collected off the Galápagos Islands in the eastern Pacific, keys to the species of *Anthias* and to the species of eastern Pacific Anthiinae are provided, and comments are presented on hermaphroditism in the Anthiinae. The specimens of the new species, described herein, constitute the first authentic record of *Anthias* from the Pacific; the genus is otherwise known only from the Atlantic where it is represented by seven species. The following characters in combination allow the separation of *Anthias noeli* from its congeners: soft rays in the dorsal fin 15 (rarely 16); tubed lateral-line scales 38 to 46; caudal-peduncle scales 22 to 25; lower jaw naked or with only a few scales posteriorly; gular region naked; total gillrakers on first gill arch 37 to 41; dorsal, anal, pelvic, and caudal fins each with some produced soft rays; anal fin angulate posteriorly; depressed anal-fin length 32 to 43% SL; longest dorsal-fin spine (fourth or fifth) 14 to 20% SL; upper caudal-fin lobe (39–60% SL) longer than lower (38–57% SL); no teeth on tongue.

During recent collecting trips to the Galápagos Islands, investigators aboard submersibles from the Harbor Branch Oceanographic Institution (Fort Pierce, Florida) have captured a number of new species, including 17 specimens of the new anthiine serranid described herein. Anthiines are small to medium size brightly colored fishes that occur worldwide in shallow to moderate depths of tropical, subtropical, and temperate seas. They are usually associated with coral reefs or rocky bottoms that provide refuge from predators. Individuals of most species feed upon zooplankton near the bottom and hastily seek shelter when approached by predators. Anthiines are often seen in aggregations, with males attending large harems. As far as is known, they are protogynous hermaphrodites, with

many species being sexually dichromatic and some being sexually dimorphic, especially in fin structure.

There are approximately 185 valid described species in the serranid subfamily Anthiinae, classified variously in at least 25 genera; additionally, there are a number of other known undescribed species of Anthiinae in museum collections, and there are undoubtedly other species that remain to be discovered.

Katayama & Amaoka (1986) restricted *Anthias* to include only Atlantic forms, removing Indo-Pacific species more appropriately regarded as representatives of *Pseudanthias*, *Franzia*, and *Mirolabrichthys*. Although not clearly stated, it appears that Katayama & Amaoka (1986:217–219, 221) considered *Anthias* to include the

following species: *anthias*, *asperilinguis*, *helenensis*, *menezesi*, *nicholsi*, *salmopunctatus*, *tenuis*, and *woodsii*. We modify their concept of the genus *Anthias* to exclude *salmopunctatus* and *tenuis*, which, as shown by Baldwin (1990), appear to be sister species and warrant placement in a genus distinct from *Anthias*. In addition, we include in *Anthias* both the new species described herein and *cyprinoides* formerly assigned to *Holanthias* by Katayama & Amaoka (1986).

Although we are not aware of any character that is clearly synapomorphic for the species of *Anthias*, all eight are extremely similar morphologically and appear to form a natural group. Herein we provide a diagnosis and description of the genus that distinguishes species of *Anthias* from all other serranid fishes.

Methods

Institutional abbreviations follow Leviton et al. (1985), except for HBOM (=Harbor Branch Oceanographic Museum). The methods used here are those of Anderson & Heemstra (1980), as modified by Anderson et al. (1990). Some of those methods are reiterated or clarified below. Tubed lateral-line scales were counted on both sides of each specimen of the new species; other scale counts, except those around the caudal peduncle, were made on either side, depending on condition of the specimen. Counts of caudal-peduncle scales were of the number of scales around the narrowest part of the peduncle. In making counts of rows of cheek scales and counts of scale rows and scales above and below the lateral line, small scales at orbit and at bases of dorsal and anal fins were excluded. (Scales excluded from those counts are distinctly and abruptly smaller than adjacent scales in the counted series.) Scales above the lateral line were counted in a ventroposterior direction from origin of dorsal fin to, but excluding, the lateral-line scale. Scales below the lateral line were counted in a dorsoan-

terior direction from origin of anal fin to, but excluding, the lateral-line scale. Gillrakers (including rudiments, when present) on the first gill arch were counted on the right side. We follow Mabee (1988) and use "supraneural" instead of "predorsal" to refer to the short series of bones anterior to the pterygiophores that support the dorsal fin, and we conform with Johnson & Patterson (1993: 557) and Patterson & Johnson (1995) in using the term "epineurals" for the intermuscular bones that conventionally have been called "epipleurals" in perciform fishes. Measurements are given as percentages of standard length (SL), except internarial distance which is also presented as the quotient of the snout length divided by the distance between the nares. Osteological data were recorded from radiographs. Standard methods for wax histology were used in preparing the gonadal sections for microscopic examination.

Anthias Bloch

Anthias Bloch, 1792 (type species *Labrus anthias* Linnaeus, 1758, by absolute tautonymy).

Aylopon Rafinesque, 1810 (type species *Labrus anthias* Linnaeus, 1758, by virtue of the fact that a replacement name retains the type of the prior name; *Anthias* incorrectly regarded as preoccupied by *Anthia* Weber, 1801, a genus of Coleoptera).

Diagnosis.—A genus of Anthiinae distinguishable from all other genera of the family Serranidae by the following combination of characters. No tooth plate on second epibranchial. Vertebrae 26 (10 precaudal + 16 caudal). Formula for configuration of supraneural bones, anterior neural spines, and anterior dorsal pterygiophores 0/0/2/1+1/1/ (using notation of Ahlstrom et al., 1976), except *A. nicholsi* rarely with slightly different placement of supraneural bones. Principal caudal-fin rays 15 (8 + 7); branched rays 13 (7 + 6). Dorsal-fin rays X, 13 to 16 (usually X, 14 or 15, most fre-

quently X, 15). Anal-fin rays III, 6 to 8 (usually III, 7). Pleural ribs on vertebrae 3 through 10. Epineurals associated with first 11 to 13 vertebrae. Scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni—see Hughes 1981; this type of scale called peripheral ctenoid by Roberts 1993); no smaller accessory scales (secondary squamation) at bases of body scales. Most of head, including maxilla scaly. Lateral line complete, extending to at least base of caudal fin (running parallel to dorsal body contour a few scale rows ventral to dorsal-fin base, curving rather abruptly ventral to posterior end of dorsal-fin base to run near midlateral axis of body). No supramaxilla. Anterior and posterior nares closely set on each side of snout; posterior border of anterior naris produced into a short flap, but never into a long filament. No fleshy papillae on border of orbit. Posterior margin of bony opercle with three spinous processes. Branchiostegal rays seven. Dorsal fin single, not deeply notched between spinous and soft portions. First caudal vertebra without parapophyses. Preopercle serrate, but without antrorse spines. Vomer and palatines with teeth; vomerine tooth patch without a well-developed posterior prolongation.

Description.—Characters included in the generic diagnosis form a part of the generic description and are not repeated. Premaxillae protrusile. Posterodorsal border of maxilla not covered by elements of circumorbital series when mouth closed. Outer teeth in jaws mostly conical; inner teeth mostly villiform or cardiform; some enlarged as canines. Endopterygoids usually toothless. Tongue usually without teeth (except present on tongue in almost all *A. menezesi* and *A. cyprinoides*). Pectoral fin approximately symmetrical, with 16 to 22 rays. Pelvic-fin rays I, 5. Gillrakers well developed, total on first arch 37 to 48. Lateral-line scales 31 to 48. Caudal-peduncle scales 16 to 25. No trisegmental pterygiophores associated with dorsal and anal fins. No

spur on posteriormost ventral procurrent ray (see Johnson 1975); penultimate ventral procurrent caudal-fin ray not shortened basally. Parhypural with well-developed hypurapophysis. Autogenous hypurals 5—no hypural fusions. Epurals 3. Uroneurals 1 pair (posterior pair absent). Modified scales (interpelvic process) overlapping pelvic-fin bases along midventral line.

Those species of *Anthias* in which the larvae have been described lack several characters found in the larvae of some American anthiines, viz., specialized larval scales and serrae on supraoccipital crest, pterotic ridge, articular, frontal ridge, parietal ridge, and fin spines. In addition, the known larvae of *Anthias* have a single serrate supraorbital ridge dorsal to each eye, in contrast with the larvae of at least two species of American anthiines that have three serrate supraorbital ridges on each side (Baldwin 1990).

Key to the Species of *Anthias*

- 1a. Lateral-line scales 31–34; sum of lateral-line scales plus total number of gillrakers on first gill arch, in individual specimens, 71–76; caudal-fin lobes moderate (length of upper lobe 31–49% SL) *Anthias nicholsi* Firth, 1933 (western North Atlantic)
- 1b. Lateral-line scales 36–48; sum of lateral-line scales plus total number of gillrakers on first gill arch, in individual specimens, 75–88; caudal-fin lobes moderate to well produced (length of upper lobe 32–110% SL) 2
- 2a. Longest dorsal-fin spine (usually the third) 13–30% SL, 19–30% SL in specimens more than ca. 100 mm SL; third dorsal-fin spine typically with well developed filament which may be up to 17% SL; lower caudal-fin lobe usually longer than upper
. *Anthias anthias* (Linnaeus, 1758) (eastern Atlantic, including the Mediterranean and Adriatic seas)
- 2b. Longest dorsal-fin spine 10–20% SL; fin membrane usually extending as a short filament at tip of each dorsal

- spine, but never produced to the extent seen in *A. anthias*; upper caudal-fin lobe usually longer than lower 3
- 3a. Soft dorsal-fin rays usually 14 (15 in 1 of 17 specimens); midline of gular region and lower jaw well covered with scales; pelvic-fin length 27–41% SL *Anthias woodsi* Anderson & Heemstra, 1980 (western North Atlantic)
- 3b. Soft dorsal-fin rays usually 15 (rarely 16); gular region naked; lower jaw naked or only partly covered with scales; pelvic-fin length 33–76% SL 4
- 4a. Pectoral-fin rays 19–21 (usually 20 or 21); longest dorsal-fin spine 10–13% SL; upper caudal-fin lobe 32–44% SL; pelvic-fin length 33–39% SL; known only from the eastern South Atlantic 5
- 4b. Pectoral-fin rays 17–20 (usually 18 or 19); longest dorsal-fin spine 12–20% SL; upper caudal-fin lobe 39–>70% SL; pelvic-fin length 33–76% SL; not known from the eastern South Atlantic 6
- 5a. Caudal-peduncle scales ca. 18; posterior margin of anal fin rounded; upper caudal-fin lobe 37–44% SL; no teeth on tongue *Anthias helenensis* Katayama & Amaoka, 1986 (eastern South Atlantic north of the Island of St. Helena)
- 5b. Caudal-peduncle scales 20–24; posterior margin of anal fin angular; upper caudal-fin lobe 32–37% SL; tongue usually with one or two small patches of teeth *Anthias cyprinoides* Katayama & Amaoka, 1986 (eastern South Atlantic west of the Island of Pagalu)
- 6a. Total gillrakers on first gill arch 41–48; tongue usually with teeth, teeth usually in narrow elongated patch . . . *Anthias menezesi* Anderson & Heemstra, 1980 (western South Atlantic)
- 6b. Total gillrakers on first gill arch 37–41; tongue usually without teeth 7
- 7a. Soft dorsal fin and usually soft anal fin without produced rays; caudal-peduncle scales 17 or 18; lateral-line scales 36–41; two of largest individuals examined (out of the 10 known specimens) with teeth on tongue

- *Anthias asperilinguis* Günther, 1859 (western North Atlantic)
- 7b. Two or more soft dorsal-fin rays and one or more soft anal-fin rays produced; caudal-peduncle scales 22–25; lateral-line scales 38–46; no teeth on tongue *Anthias noeli*, new species (Galápagos Islands, eastern Pacific)

Anthias noeli, new species
Rosy Jewelfish
Figs. 1–5; Tables 1, 2

Material examined.—Seventeen specimens, 62.1 to 173 mm SL; all collected off the Galápagos Islands in the eastern Pacific Ocean in depths of 184 to 351 m.

Holotype: USNM 353113 (167 mm SL, ♂); seamount SE of Isla San Cristobal—01°06.48'S, 89°06.70'W; 202 m; *Johnson-Sea-Link-I* dive no. 3937; Gilmore & Santos, 6 Nov 1995.

Paratypes: USNM 351335 (2, 127–150; ♀, ♂); off NE Isla Darwin—01°42'N, 92°00'W; 351 m; *Johnson-Sea-Link-II* dive no. 3103; McCosker & Pawson, 18 Jul 1998. CAS 86573 (1, 132; ♂); off Isla Darwin—01°41.39'N, 91°58.88'W; 335 m; *Johnson-Sea-Link-I* dive no. 3963; McCosker et al., 20 Nov 1995. USNM 351334 (2, 86–110; ♂, ♂); off Isla Marchena—00°24'N, 90°26.3'W; 303 m; *Johnson-Sea-Link-II* dive no. 3109; Baldwin & McCosker, 21 Jul 1998. GMBL 95-34 (1, 139; ♀) & HBOM 107:08471 (1, 123; ♀); off Cabo Douglas, Isla Fernandina—00°17.60'S, 91°39.00'W; 299 m; *Johnson-Sea-Link-I* dive no. 3956; Robison & Santos, 16 Nov 1995. CAS 201896 (1, 173; ♂); off Isla Plazas (=Plaza Sur in Fig. 2)—00°31'24"S, 90°09'0"W; 308 m; *Johnson-Sea-Link-II* dive no. 3096; McCosker & Day, 7 Jul 1998. USNM 351333 (2, 132–170; ?, ♂); 2 miles E of Isla Plazas (=Plaza Sur in Fig. 2)—00°32.25'S, 90°09.02'W; 308 m; *Johnson-Sea-Link-II* dive no. 3096; McCosker & Day, 7 Jul 1998. CAS 86807 (1, 163; ♂); seamount SE of Isla San Cristobal—01°06.03'S, 89°12.20'W; *Johnson-Sea-*

Table 1.—Data on morphometric characters for *Anthias noeli*. Standard lengths are in mm; other measurements, in percentages of standard length.

Character	<i>n</i>	Min.	Max.	Mean	Holotype
Standard length	17	62.1	173	—	167
Head, length	17	36.8	43.4	39.4	37.6
Snout, length	17	6.0	9.2	7.7	8.4
Orbit, diameter	17	11.3	15.1	13.5	11.4
Postorbital length of head	17	17.0	20.4	18.8	18.4
Upper jaw, length	17	17.0	19.0	17.9	18.2
Maxilla, width	17	5.9	7.4	6.6	7.0
Bony interorbital, width	17	7.6	9.1	8.3	8.6
Internarial distance	17	0.7	1.2	1.0	0.9
Body, depth	17	35.0	42.1	38.5	40.4
Body, width	17	13.1	19.1	15.9	17.6
Predorsal length	17	31.8	36.6	34.1	33.7
Prepelvic length	17	35.7	43.7	39.1	38.2
Preanal length	17	59.4	66.3	63.3	64.0
Caudal peduncle, length	17	21.9	26.7	24.6	25.6
Caudal peduncle, depth	17	11.8	13.6	12.6	13.6
Dorsal-fin base, length	17	54.4	61.7	57.0	61.7
Pectoral fin, length	17	28.2	33.4	31.2	31.4
Pelvic fin, length	11	32.6	55.1	42.7	53.7
Anal-fin base, length	17	16.1	18.5	17.3	18.2
Anal fin, length	15	32.3	42.9	37.0	41.9
Upper caudal-fin lobe, length	12	38.8	60.4	49.2	46.9
Lower caudal-fin lobe, length	13	38.2	57.4	46.8	46.3
First dorsal spine, length	14	6.1	8.5	7.0	7.4
Third dorsal spine, length	15	13.1	17.8	15.3	14.9
Fourth dorsal spine, length	11	14.3	19.9	16.6	14.7
Tenth dorsal spine, length	15	10.7	12.6	11.7	12.2
Longest dorsal spine, length	13	14.3	19.9	16.5	15.2
Longest dorsal soft ray, length	11	26.1	44.7	36.0	38.3
Pelvic spine, length	15	15.4	19.8	17.3	17.1
First anal spine, length	16	7.2	10.4	8.2	7.7
Second anal spine, length	14	12.0	20.4	15.6	14.4
Third anal spine, length	16	12.8	17.1	14.7	12.8
Longest anal soft ray, length	15	24.0	31.8	27.4	31.8

Link-I dive no. 3934; McCosker et al., 5 Nov 1995. UF 110990 (2, 68–134; ♀, ♀); seamount SE of Isla San Cristobal–01°06.23'S, 89°06.91'W; 184–215 m; *Johnson-Sea-Link-I* dive no. 3935; Robison & Liberatore, 5 Nov 1995. ANSP 177770 (3 specimens, 62.1–106 mm SL; ?, ♀, ♂); off Devil's Crown, Isla Floreana–01°12.50'S, 90°25.56'W; 232 m; *Johnson-Sea-Link-I* dive no. 3945; McCosker & Liberatore, 9 Nov 1995.

Diagnosis.—A species of *Anthias* distinguishable from all other species of the genus by the following combination of characters. Dorsal-fin rays X, 15 or 16 (usually

X, 15). Anal-fin rays III, 6 or 7 (usually III, 7). Pectoral-fin rays 18 to 20 (most frequently 19). Lateral-line scales 38 to 46 (usually 39–44). Total gillrakers on first gill arch 37 to 41 (usually 38–40; no rudimentary rakers). Sum of lateral-line scales plus total number of gillrakers, on individual specimens, 78 to 85. Caudal-peduncle scales 22 to 25 (usually 23 or 24). Caudal fin lunate to deeply forked (larger individuals tending to have more lunate fins). Dorsal, anal, pelvic, and caudal fins each with some produced soft rays. Upper caudal-fin lobe longer than lower. Anal fin angulated posteriorly. Gular region without

Table 2.—Frequency distributions of numbers of fin rays, scales, and gillrakers on first gill arch in *Anthias noeli*. Counts for the holotype are indicated by asterisks.

Character	15	16	6	7	18	19	20	Mean		
Dorsal soft rays	16*	1						15.06		
Anal soft rays			1	16*				6.94		
Pectoral-fin rays,										
Left side					1	14*	2	19.06		
Right side					2	10	4*	19.12		
	38	39	40	41	42	43	44	45	46	Mean
Tubed lateral-line scales,										
Left side	1	2	2	3	1	4	3*	—	1	41.82
Right side		1	2	4	4*	1	4	1		42.06
			22	23		24		25		Mean
Circum caudal-peduncle scales			1	7	5*		2			23.53
	10	11	12	Mean	27	28	29	30		Mean
Gillrakers										
Upper limb	4	12*	1	10.82						
Lower limb					5*	7	4	1		28.06
			37	38	39	40	41			Mean
Total gillrakers (upper limb + lower limb)			1	6*	5	4	1			38.88

scales. Endopterygoids and tongue without teeth.

Description.—Characters presented in the generic and species diagnoses and the generic description form part of the species description and are not repeated unless necessary for clarification. Data for morphometric characters appear in Table 1; those for some countable characters in Table 2. Mouth nearly terminal, lower jaw exceeding upper jaw very slightly. Maxilla falling short of vertical through posterior border of orbit. Maxilla usually widened distally, with a small shelf or rostrally directed hook on labial border (as in *Anatolanthias apimomycter*—see Anderson et al. 1990:926, fig. 2). Internarial distance 6–12, usually 7–10, times in snout length. Vertical limb of preopercle serrate; horizontal limb smooth or with several small serrae near angle; angle with a single spine, a serrated spinous process, or relatively large serrae. Distal margins of interopercle and subopercle usually

smooth or nearly so, occasionally with several small serrae.

Premaxilla with inner band of very small teeth and outer series of larger, mostly anteriorly directed, conical teeth; near symphysis, two to several teeth along medial margin of inner band enlarged as posteriorly directed conical teeth; outer row of larger conical teeth usually preceded by one or two enlarged canine teeth. Dentary with row of slender conical teeth along lateral edge of jaw; this row including one to three teeth, usually enlarged into recurved canines, at a point approximately one third length of row from its anterior end; band of very small teeth extending anteriorly from this row and reaching to near symphysis; one to several teeth on inner edge of band near symphysis enlarged and directed posteriorly; one or two enlarged exerted canines near symphysis.

Branchiostegal rays seven—anterior three inserting along ventral edge or ven-

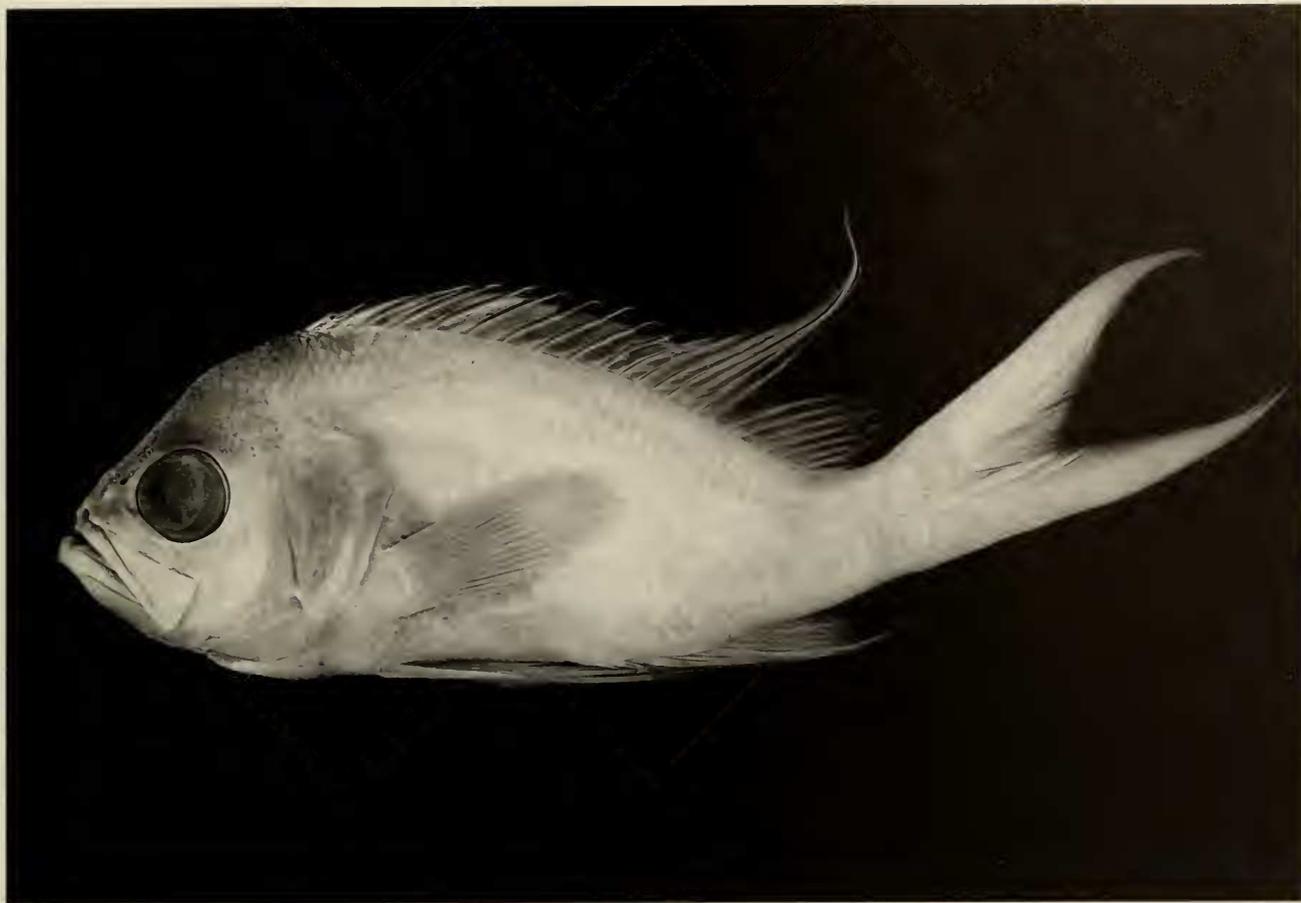


Fig. 1. Holotype of *Anthias noeli*, new species, USNM 353113, 167 mm SL; Galápagos Islands, eastern Pacific Ocean. Photograph by Donald Hurlbert, National Museum of Natural History, Smithsonian Institution.

tromedial aspect of hyoid arch, posterior four inserting on lateral surface of arch. Pseudobranch well developed, with ca. 22 to 33 filaments; number of filaments increasing with increase in SL (No. filaments = $a + b[SL]$; where $a = 17.03$, $b = 0.08$, $r^2 = 0.7522$).

Most of head, including most of dorsum of snout, interorbital region, and maxilla, scaly. Lateral aspect of snout, lachrymal, branchiostegals, branchiostegal membranes, and gular region naked (one specimen with a few scales on lachrymals). Dentary usually naked, but some specimens with a few scales posteriorly. Rows of scales on cheek 8 to 11 (usually 9 or 10; difficult to count). Dorsal and anal fins mostly scaleless, except columns of very small scales frequently present proximally on interradiial membranes between soft rays, particularly on larger specimens. Rows of scales between lateral line and mid-base of spinous dorsal fin 2 or 3. Scales between origin of dorsal

fin and lateral line 6 to 8. Scales between origin of anal fin and lateral line 17 to 20.

Longest dorsal-fin spine fourth or fifth. Second anal-fin spine more robust than first or third. Procurrent caudal-fin rays 9 (rarely 10) dorsally, 8 or 9 ventrally. Dorsal-fin membrane produced into a short filament posterior to each spine. Two or more soft dorsal-fin rays, one or more soft anal-fin rays, first two (and on occasion third) soft pelvic-fin rays (second longest), and caudal-fin lobes produced. Pectoral fin reaching posteriorly to at least as far as vertical through base of third anal spine, frequently as far as vertical through base of second anal soft ray or beyond; dorsalmost pectoral-fin ray always unbranched, ray next to dorsalmost ray and ventralmost ray occasionally unbranched. Pelvic fin reaching posteriorly at least to base of first anal soft ray to as far as well beyond posterior end of anal-fin base. Pelvic fin inserted beneath anterior part of pectoral-fin base.

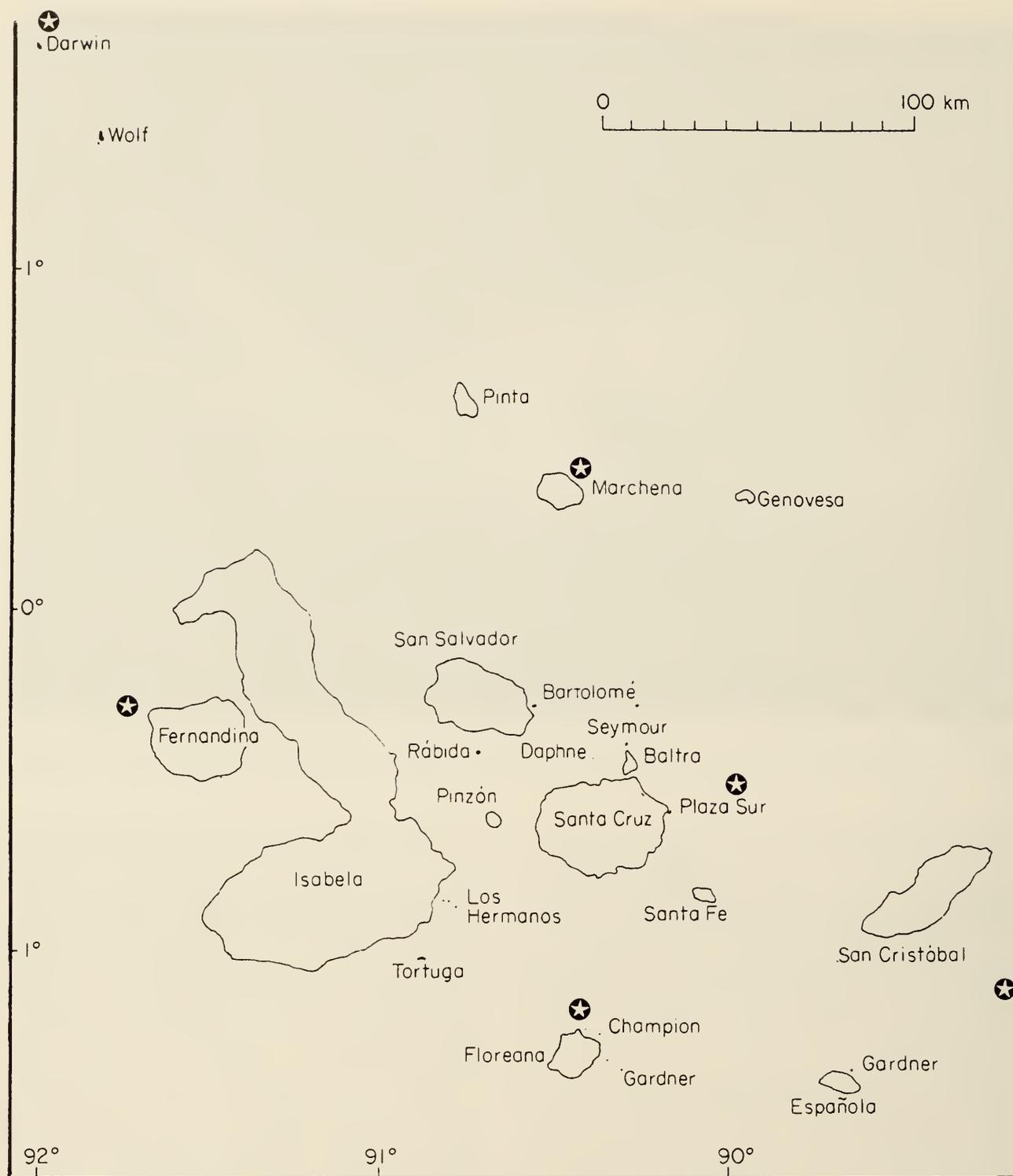


Fig. 2. Map of Galápagos Islands, eastern Pacific Ocean, showing localities of capture of *Anthias noeli*, new species. Modified from Grant 1984.

Coloration.—Description based on color photographs, taken shortly after capture, of two paratypes (CAS 201896, 173 mm SL; USNM 351333, 170 mm SL; see Fig. 3), and color notes, made by the second author in the field, of two other paratypes (USNM 351335, 127 & 150 mm SL). Head mostly rosy, a yellow streak extending across lach-

rymal and part of cheek and a broad yellow stripe extending from posterior margin of eye to posterior tip of opercle. Jaws rosy except small patch of yellow on upper lip near premaxillary symphysis. Iris yellow. Body mostly rosy dorsally, paler ventrally, a few yellow stripes or blotches on lateral and ventral aspects of body; black blotch

present at anterior base of spinous dorsal fin. Membrane covering dorsal-fin spines yellow except rosy distally; interradiial membranes mostly rosy; soft dorsal fin mostly rosy, except membranes separating three anteriormost dorsal soft rays mostly yellow or yellow distally and last four rays pale purple. Anal-fin spines and interradiial membranes yellow; anterior soft anal-fin rays and interradiial membranes yellow basally, yellow and rosy distally; posterior portion of soft anal fin rosy to pale purple. Pectoral fin rosy. Pelvic fin mostly pale rose, some yellow basally and on membrane between first and second rays. Caudal fin mostly rosy, some yellow on outer rays of dorsal and ventral lobes; produced distal ends of caudal-fin lobes rosy or lilac to purplish in color.

Coloration in alcohol.—Dark spot anterior to base of spinous dorsal fin usually persisting; dorsum of head frequently

dusky; fins mostly pallid; remainder of fish straw-colored.

Sexuality.—Histological examination of the gonads of all specimens of the new species (except for two for which no gonadal tissue could be found) showed that six individuals (68.0–139 mm SL) are females and nine (86.0–173 mm SL), including the five largest (150–173 mm SL), are males, suggesting that *Anthias noeli* is protogynous (see section on hermaphroditism in anthiines).

Sexual dimorphism.—In specimens more than about 120 mm SL, females (4 specimens, 123–139 mm SL) have shorter pelvic fins (33–36% SL vs. 43–55% SL), shorter longest dorsal soft rays (31–33% SL vs. 38–45% SL), shorter longest anal soft rays (24–28% SL vs. 28–32% SL), and shorter depressed anal-fin lengths (33–37% SL vs. 37–42% SL) than do males (5 specimens, 150–173 mm SL).



Fig. 3. Paratype of *Anthias noeli*, new species, USNM 351333, 170 mm SL; Galápagos Islands, eastern Pacific Ocean.

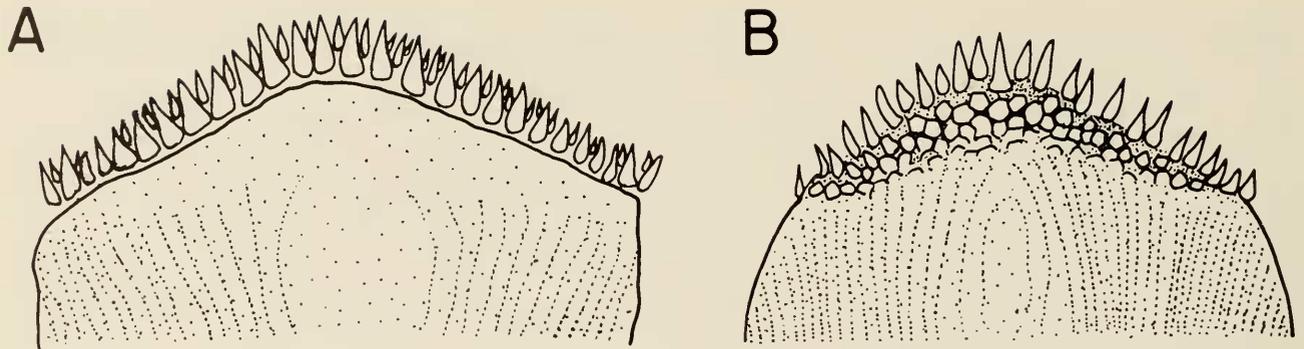


Fig. 4. Scales of anthiine fishes (posterior fields of scales towards the top of the page). A, ctenoid scale with only marginal cteni, as in species of *Anthias*; B, ctenoid scale with ctenial bases present proximal to marginal cteni.

Comparisons.—*Anthias noeli* is separable from other species of *Anthias* as follows: longest dorsal-fin spine fourth or fifth, third dorsal-fin spine with at most a short filament, and upper caudal-fin lobe longer than lower caudal-fin lobe in *A. noeli* versus longest dorsal-fin spine usually third, third dorsal-fin spine typically with well developed filament (up to 17% SL), and lower caudal-fin lobe usually longer than upper caudal-fin lobe in *A. anthias*; two or more soft dorsal-fin rays and one or more soft anal-fin rays produced and 22 to 25 caudal-peduncle scales in *A. noeli* versus soft dorsal fin and usually soft anal fin without produced rays and 17 or 18 caudal-peduncle scales in *A. asperilinguis*; upper caudal-fin lobe length 39 to 60% SL, 18 to 20 (usually 19) pectoral-fin rays, and tongue without teeth in *A. noeli* versus upper caudal-fin lobe length 32 to 37% SL, 20 or 21 pectoral-fin rays, and tongue usually with teeth in *A. cyprinoides*; 22 to 25 caudal-peduncle scales and anal fin angulated posteriorly in *A. noeli* versus ca. 18 caudal-peduncle scales and anal fin rounded posteriorly in *A. helenensis*; 37 to 41 total gillrakers on first gill arch and tongue without teeth in *A. noeli* versus 41 to 48 total gillrakers on first gill arch and tongue usually with teeth in *A. menezesi*; 38 to 46 lateral-line scales in *A. noeli* versus 31 to 34 in *A. nicholsi*; 15 or 16 (usually 15) soft dorsal-fin rays and gular region and dentary without scales (some specimens with a few scales on den-

tary posteriorly) in *A. noeli* versus 14 or 15 (usually 14) soft dorsal-fin rays and midline of gular region and dentary well covered with scales in *A. woodsi*.

In addition, *Anthias noeli* is distinguishable from the other species of Anthiinae found in the eastern Pacific by the following combination of characters: scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni; see Fig. 4A); maxilla scaly; dentary naked or with only a few scales posteriorly; gular region without scales; vomer with teeth; no teeth on tongue; anterior naris relatively close to posterior naris (internarial distance 6–12, usually 7–10, times in snout length); posterior border of anterior naris produced into a short flap, but never into a long filament; preopercle without antrorse spines; urohyal without anteriorly projecting spine; dorsal-fin rays X, 15 or 16 (usually X, 15); anal-fin rays III, 6 or 7 (usually III, 7); lateral-line scales 38 to 46; total gillrakers on first gill arch 37 to 41; diameter of bony orbit 11 to 15% SL. The most recent comparative treatment of the adults of eastern Pacific anthiines is that of Fitch (1982), which covers only four of those species, all found in the northern hemisphere. To facilitate identification of all 13 species of eastern Pacific Anthiinae, we present a key to those taxa (see below).

Distribution.—*Anthias noeli* is known only from the Galápagos Islands, eastern

Pacific Ocean, in depths ranging from 184 to 351 meters (see Fig. 2).

Etymology.—The specific name, *noeli*, is for Noel Archambault, IMAX® cameraman/stereographer, who lost his life on 26 June 1998 in a tragic plane crash in the Galápagos during one of the expeditions on which the new species was collected. Noel was a pioneer of modern 3-D film technology. It is appropriate to name in his memory a new species collected using the modern submersible technology that is allowing the exploration of oceanic regions previously inaccessible to scientific study.

Key to the Eastern Pacific Species of Anthiinae

- 1a. Scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni; Fig. 4A) 2
- 1b. Scales ctenoid with ctenial bases present proximal to marginal cteni (Fig. 4B) or in one species (*Trachypoma macracanthus*) scales cycloid 7
- 2a. Maxilla scaly 3
- 2b. Maxilla naked 5
- 3a. Vomer edentate; anterior naris somewhat remote from posterior naris; internarial distance 2.8–3.1 times in snout length . . *Anatolanthias apiomycter* Anderson, Parin, & Randall, 1990 (Nazca Ridge)
- 3b. Vomerine dentition well developed; anterior naris relatively close to posterior naris; internarial distance more than 5.0 times in snout length 4
- 4a. Posterior border of anterior naris produced into a filament, usually reaching posterior naris when reflected; ventral surface of dentary and midline of gular region with scales; bony orbit diameter 7–11% SL (8–11% SL in specimens <160 mm SL, 7–9% SL in specimens >165 mm SL); teeth usually present on tongue *Pronotogrammus multifasciatus* Gill, 1863 (southern California and the Gulf of California to northern Peru and the Galápagos Islands)
- 4b. Posterior border of anterior naris with-

out a filament, but produced into a short flap that almost always fails to reach posterior naris when reflected; dentary usually without scales, occasionally with a few scales posteriorly; gular region without scales; bony orbit diameter 11–15% SL (12–15% SL in specimens <140 mm SL, 11–13% SL in specimens >150 mm SL); no teeth on tongue . . . *Anthias noeli*, new species (Galápagos Islands)

- 5a. Lateral-line scales 60–71 (usually 62–68); specimens more than about 70 mm SL with sharp spine projecting anteriorly from ventral border of urohyal *Hemanthias signifer* (Garman, 1899) (southern California to northern Peru)
- 5b. Lateral-line scales 36–57 (usually 54 or fewer); urohyal without anteriorly projecting spine 6
- 6a. Lateral-line scales 36–40; total gillrakers on first arch 38–43; longest dorsal-fin spine most frequently the sixth, never the third; third dorsal-fin spine with short filament, but filament never well produced; middle rays of upper and lower lobes of caudal fin not longest in fin *Pronotogrammus eos* Gilbert, 1890 (mid-Gulf of California [28°N; Fitch 1982] to Colombia [6.5°N])
- 6b. Lateral-line scales 49–57; total gillrakers on first arch 31–35; longest dorsal-fin spine—the third; third dorsal-fin spine with well produced filament (at least in larger individuals); middle rays of upper and lower lobes of caudal fin longest in fin *Hemanthias peruanus* (Steindachner, 1875) (Hipólito Bank [27°N], Baja California Sur, in the Pacific and Cabo Lobos [ca. 30°N], Sonora, in the Gulf of California to Trujillo [8°S], Peru, and the Galápagos Islands [Fitch 1982; Grove & Lavenberg 1997])
- 7a. Spines in dorsal fin XI–XIII; ventral border of preopercle with strong antrorse spines 8
- 7b. Spines in dorsal fin X; ventral border of preopercle without antrorse spines, except in *Hypoplectrodes semicinctum*

- and occasionally in *Plectranthias exsul* 10
- 8a. Scales cycloid; spines in dorsal fin XII; soft rays in anal fin 6
..... *Trachypoma macracanthus*
Günther, 1859 (widely distributed in the South Pacific, including Easter Island and the Desventuradas Islands off the coast of Chile [Randall & Cea Egaña 1984; Pequeño & Lamilla 1996a,b; Rojas & Pequeño 1998a])
- 8b. Scales ctenoid; dorsal spines XI or XIII; soft rays in anal fin 8 or 9 ... 9
- 9a. Dorsal-fin rays XI, 17 or 18
..... *Acanthistius pictus* (Tschudi, 1846) (coasts of Peru and Chile)
- 9b. Dorsal-fin rays XIII, 14 or 15
..... *Acanthistius fuscus* (Regan, 1913) (Easter Island and Sala y Gómez Island [Rojas & Pequeño 1998a])
- 10a. Soft rays in dorsal fin 19–22 11
- 10b. Soft rays in dorsal fin 15 or 16 12
- 11a. Preopercle with 2 or 3 antrorse spines (one spine usually at angle or on ventral margin near angle, other spine[s] on ventral margin); total gillrakers on first gill arch 17–20; lateral-line scales 48–55 (most frequently 48–51) ...
..... *Hypoplectrodes semicinctum* (Valenciennes, 1833) (Juan Fernández Islands and San Félix Island [in the Desventuradas Islands] off the coast of Chile, and possibly Easter Island [Anderson & Heemstra 1989; Pequeño & Lamilla 1996b; Rojas & Pequeño 1998a])
- 11b. Preopercle serrate, but without antrorse spines; total gillrakers on first gill arch 34–37; lateral-line scales 58–65, usually 61–64 (counts only from eastern Pacific specimens)
.. *Caprodon longimanus* (Günther, 1859) (widely distributed in the Pacific—including Easter Island and the Nazca Ridge and from the Desventuradas and Juan Fernández islands off the coast of Chile, and “along the coast of South America” [Pequeño & Lamilla 1996a:931, 1996b])
- 12a. Scales on dorsum of head not extending anterior to nares (Randall 1996: 117); longest soft dorsal-fin ray ca. 26–35% SL; total gillrakers on first

- gill arch 26–28; in life, two orange-red bars on body (one just anterior to anal fin, the other terminating ventrally posterior to anal fin)
..... *Plectranthias parini* (Anderson & Randall, 1991) (Sala y Gómez Ridge and Easter Island [Randall 1996])
- 12b. Scales on dorsum of head extending anteriorly almost to upper lip, except for triangular premaxillary groove (Randall 1996:117); longest soft dorsal-fin ray ca. 16–>26% SL; total gillrakers on first arch 26–31 (usually 28 or 29); in life, brilliant red oblong area extending from bases of posterior rays of soft dorsal fin ventrally to just below midline and then posteriorly over middle of caudal peduncle to reach mid-ventral line near base of caudal fin ..
..... *Plectranthias exsul*
Heemstra & Anderson, 1983 (Juan Fernández Islands and Nazca Ridge; also reported from Desventuradas Islands by Rojas & Pequeño 1998a)

Plectranthias lamillai

Rojas & Pequeño (1998b) described a new species of *Plectranthias*, *P. lamillai*, from a single specimen (MNHNC P.7055, 139.6 mm SL) collected off Alejandro Selkirk Island in the Juan Fernández Islands off the coast of Chile. In the description provided by Rojas & Pequeño (1998b), we could find no characters that seem to reliably distinguish it from *Plectranthias exsul*, also known from off the Juan Fernández Islands. As a consequence, the first author made a detailed examination of the holotype of *P. lamillai* (now 136 mm SL) and compared it closely with two specimens of *P. exsul* (USNM 176577—a paratype, 158 mm SL, and USNM 312927, 122 mm SL) and found that the holotype agrees well with the original description of *P. exsul* and, with one exception, with the specimens of *P. exsul* with which it was directly compared. The interorbital region of the paratype of *P. exsul* examined in comparison is more flattened than that of the ho-

lotype of *P. lamillai*; this we attribute to ontogenetic differences or perhaps to sexual dimorphism. In contrast, the 122-mm specimen of *P. exsul* is essentially identical in head and body shape to the holotype of *P. lamillai*. It should be noted that the drawing with the original description of *P. lamillai* (see Rojas & Pequeño 1998b:fig 2) is not a particularly good representation of the holotype, especially of the head. *Plectranthias lamillai* and *P. exsul* have somewhat different patterns of coloration, but we think that the different patterns displayed are best interpreted as variations on a common theme. In view of the preceding and pending a more complete investigation, we deem it best to consider *P. lamillai* Rojas & Pequeño, 1998, as a junior synonym of *P. exsul* Heemstra & Anderson, 1983.

Comments on Hermaphroditism in Anthiine Serranids

Protogyny has been reported in species representing a number of anthiine genera, including *Hypoplectrodes* (*H. huntii* [as *Elterkeldia huntii*] and *H. maccullochi*; Jones 1980 and Webb & Kingsford 1992, respectively), *Hemanthias* (*H. vivanus* and *H. peruanus*; Hastings 1981 and Coleman 1983, respectively), *Pronotogrammus* (*P. martinicensis* [as *Holanthias martinicensis*]; Coleman 1981), *Pseudanthias* (*P. squamipinnis* [as *Anthias squamipinnis*]; Fishelson 1970 and Shapiro in a series of studies on the behavioral aspects of sex reversal—e.g., Shapiro 1986), *Sacura* (*S. margaritacea*; Reinboth 1963), and *Anthias* (*A. anthias*; Reinboth 1964). In addition, Heemstra (1973) provided evidence for protogyny in *Pseudanthias conspicuus* (as *Anthias conspicuus*), and Robins & Starck (1961) stated that *Plectranthias garrupellus* is probably protogynous. Thresher (1984) presented a summary (current through about 1981) of the information available on the reproductive biology of anthiines.

One might assume, from the publications on anthiines cited above, that all of them

are protogynous and monandric. Similarly, based on a number of studies, groupers (Serranidae: Epinephelinae), in general, have been considered to display monandric protogyny, but Sadovy & Colin (1995:961) found that sexuality in *Epinephelus striatus* (the Nassau grouper) “is essentially gonochoristic, with potential for sex change” and that “the juveniles pass through a bisexual stage of gonadal development,” thus illustrating the importance of not making a priori assumptions about the reproductive biology of serranid fishes. In a study of the Serranidae of the eastern Gulf of Mexico, Bullock & Smith (1991) presented evidence for protogyny in the anthiine *Hemanthias leptus*, but, based on finding a ripening male of 86 mm SL (p. 21, fig. 8b) and a sexually mature male of 61 mm SL (p. 207, pl. Id), entertained the idea that *H. leptus* may be diandric, acknowledging, however, that additional study is needed to confirm this.

In the subsection entitled Sexuality (under *Anthias noeli*, new species), we have presented evidence suggesting that *Anthias noeli* is protogynous. To gather a better appreciation of sexuality in the genus *Anthias*, William A. Roumillat, at our request, examined histological sections of the gonads of 20 specimens of the western Atlantic *A. nicholsi* and found 12 females (52.0–125 mm SL), one individual (73.0 mm SL) transforming from female to male, and seven secondary males (99.9–134 mm SL). These data strongly suggest that *Anthias nicholsi* is protogynous. *Anthias noeli* displays patterns of gonadal morphology similar to those seen in *A. nicholsi* (Fig. 5), lending further support to our contention that *A. noeli* is probably protogynous.

Sadovy & Shapiro (1987) gave criteria for diagnosing various types of hermaphroditism in fishes. Features that they identified as strongly indicating protogyny are: “membrane-lined central cavities in testes; transitional individuals; atretic bodies in stages 1, 2, or 3 of oocytic atresia within testes; sperm sinuses in the gonadal wall;

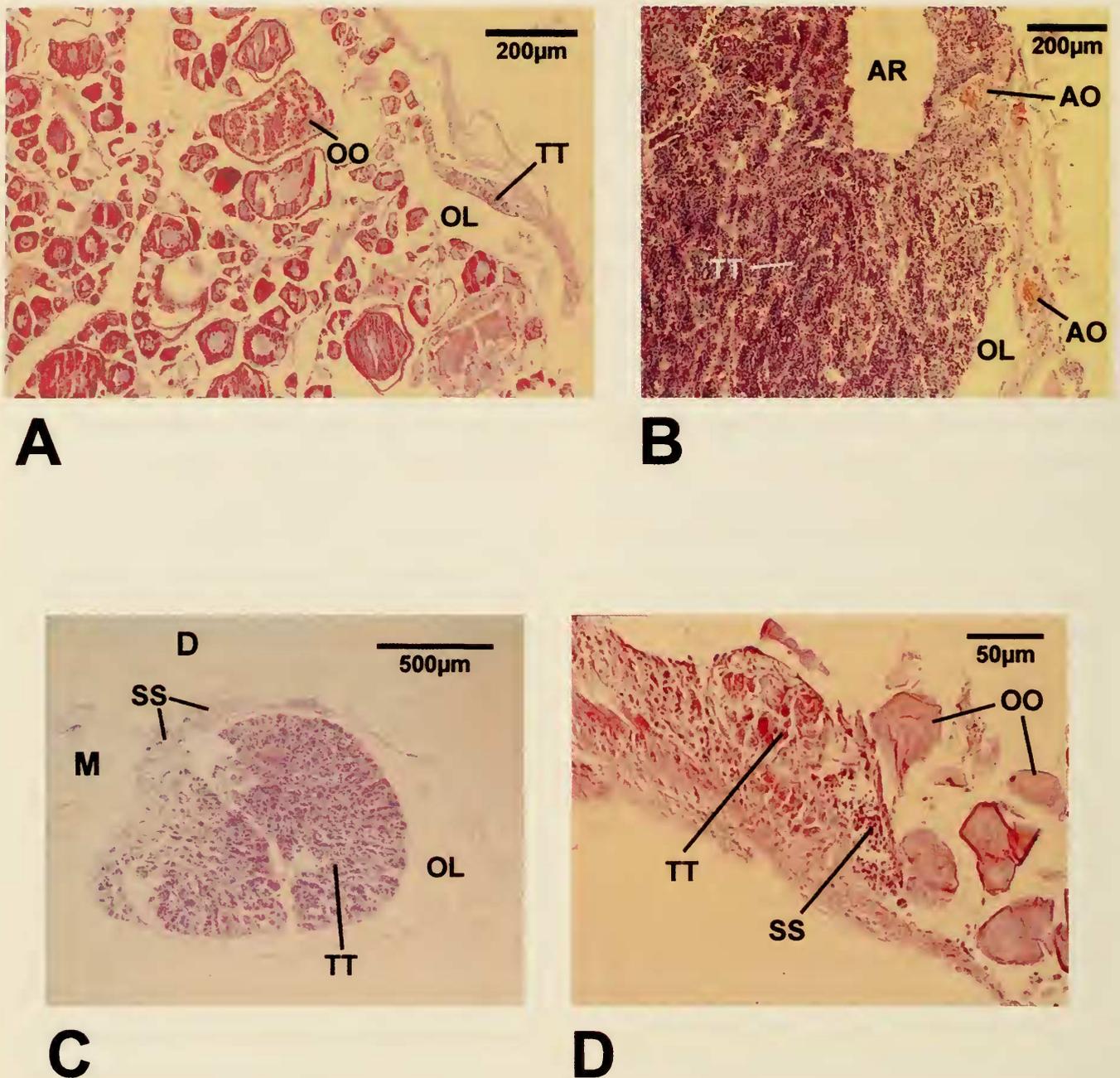


Fig. 5. Gonadal sections of specimens of *Anthias* stained with hematoxylin and eosin-Y. A, *A. noeli*, new species, HBOM 107:08471, 123 mm SL, mature female; B, *A. noeli*, new species, CAS 201896, 173 mm SL, secondary male; C, *A. noeli* new species, CAS 86573, 132 mm SL, secondary male; D, *A. nicholsi*, GMBL 59-32, 73.0 mm SL, individual transforming from female to male. Abbreviations: AR = artifact; AO = atretic oocyte; D = dorsal; M = medial; OL = ovarian lumen; OO = oocyte; SS = sperm sinus; TT = testicular tissue. Photomicrographs by William A. Roumillat, digital imagery by Karen Swanson, South Carolina Department of Natural Resources, Charleston.

and experimental production of transitional or sex-reversed individuals through manipulation of the social system" (Sadovy & Shapiro 1987:150). In our studies we found, with the assistance of Bill Roumillat, that *Anthias nicholsi* fulfills all of those criteria, except the last one which requires live material, and that *A. noeli* meets all but the last and the one involving transitional in-

dividuals (sensu Sadovy & Shapiro 1987: 147–148) which were not observed. We feel that it is reasonable to conclude that both species are protogynous.

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Literature Cited

- Ahlstrom, E. H., J. L. Butler, & B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic.—*Bulletin of Marine Science* 26:285–402.
- Anderson, W. D., Jr., & P. C. Heemstra. 1980. Two new species of western Atlantic *Anthias* (Pisces: Serranidae), redescription of *A. asperilinguis* and review of *Holanthias martinicensis*.—*Copeia* 1980:72–87.
- , & ———. 1989. *Ellerkeldia*, a junior synonym of *Hypoplectrodes*, with redescrptions of the type species of the genera (Pisces: Serranidae: Anthiinae).—*Proceedings of the Biological Society of Washington* 102:1001–1017.
- , & J. E. Randall. 1991. A new species of the anthiine genus *Plectranthias* (Pisces: Serranidae) from the Sala y Gómez Ridge in the eastern South Pacific, with comments on *P. exsul*.—*Proceedings of the Biological Society of Washington* 104:335–343.
- , N. V. Parin, & J. E. Randall. 1990. A new genus and species of anthiine fish (Pisces: Serranidae) from the eastern South Pacific with comments on anthiine relationships.—*Proceedings of the Biological Society of Washington* 103:922–930.
- Baldwin, C. C. 1990. Morphology of the larvae of American Anthiinae (Teleostei: Serranidae), with comments on relationships within the subfamily.—*Copeia* 1990:913–955.
- Bloch, M. E. 1792. *Naturgeschichte der ausländischen Fische*, vol. 6. Berlin, xii + 126 pp., pls. 289–323.
- Bullock, L. H. & G. B. Smith. 1991. Seabasses (Pisces: Serranidae).—*Memoirs of the Hourglass Cruises* 8 (pt. 2): 1–243.
- Coleman, F. 1981. Protogynous hermaphroditism in the anthiine serranid fish *Holanthias martinicensis*.—*Copeia* 1981:893–895.
- . 1983. *Hemanthias peruanus*, another hermaphroditic anthiine serranid.—*Copeia* 1983: 252–253.
- Firth, F. E. 1933. *Anthias nicholsi*, a new fish taken off Virginia in the deep-water trawl fishery.—*Copeia* 1933:158–160.
- Fishelson, L. 1970. Protogynous sex reversal in the fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the presence or absence of a male fish.—*Nature* 227:90–91.
- Fitch, J. E. 1982. Revision of the eastern North Pacific anthiine basses (Pisces: Serranidae).—*Contributions in Science, Natural History Museum of Los Angeles County* 339:1–8.
- Garman, S. 1899. Reports on an exploration off the

- west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding. XXVI. The fishes.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 24: Text: 1–431, Atlas: pls. 1–85 + A–M.
- Gilbert, C. H. 1890. A preliminary report on the fishes collected by the steamer Albatross on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species.—Proceedings of the United States National Museum 13(no. 797):49–126.
- Gill, T. 1863. Catalogue of the fishes of Lower California, in the Smithsonian Institution, collected by Mr. J. Xantus. Part IV.—Proceedings of the Academy of Natural Sciences of Philadelphia 15(2):80–88.
- Grant, P. R. 1984. Recent research on the evolution of land birds on the Galapagos. Pp. 113–136 in R. J. Berry, ed., *Evolution in the Galapagos Islands*. Academic Press, London & New York, 270 pp. [Reprinted from the *Biological Journal of the Linnean Society* (1984) 21(1,2):113–136.]
- Grove, J. S., & R. J. Lavenberg. 1997. *The fishes of the Galápagos Islands*. Stanford University Press, Stanford, California, xlvi + 863 pp.
- Günther, A. 1859. Catalogue of the acanthopterygian fishes in the collection of the British Museum, vol. 1. Gasterosteidae, Berycidae, Percidae, Aphredoderidae, Pristipomatidae, Mullidae, Sparidae. London, xxxii + 524 pp.
- Hastings, P. A. 1981. Gonad morphology and sex succession in the protogynous hermaphrodite *Hemanthias vivanus* (Jordan and Swain).—*Journal of Fish Biology* 18:443–454.
- Heemstra, P. C. 1973. *Anthias conspicuus* sp. nova (Perciformes: Serranidae) from the Indian Ocean, with comments on related species.—*Copeia* 1973:200–210.
- , & W. D. Anderson, Jr. 1983. A new species of the serranid fish genus *Plectranthias* (Pisces: Perciformes) from the southeastern Pacific Ocean, with comments on the genus *Ellerkeldia*.—*Proceedings of the Biological Society of Washington* 96:632–637.
- Hughes, D. R. 1981. Development and organization of the posterior field of ctenoid scales in the Platycephalidae.—*Copeia* 1981:596–606.
- Johnson, G. D. 1975. The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications.—*Occasional Papers of the California Academy of Sciences* 121:1–23.
- , & C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal.—*Bulletin of Marine Science* 52:554–626.
- Jones, G. P. 1980. Contribution to the biology of the redbanded perch, *Ellerkeldia huntii* (Hector), with a discussion on hermaphroditism.—*Journal of Fish Biology* 17:197–207.
- Katayama, M., & K. Amaoka. 1986. Two new anthiine fishes from the eastern tropical Atlantic.—*Japanese Journal of Ichthyology* 33:213–222.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—*Copeia* 1985:802–832.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tenth edition. Laurentius Salvius, Holmiae 1:1–824. [Photographic facsimile, 1956, printed by order of the Trustees British Museum (Natural History), London]
- Mabee, P. M. 1988. Supraneural and predorsal bones in fishes: development and homologies.—*Copeia* 1988:827–838.
- Patterson, C., & G. D. Johnson. 1995. The intermuscular bones and ligaments of teleostean fishes.—*Smithsonian Contributions to Zoology* 559:i–iv + 1–83.
- Pequeño, G., & J. Lamilla. 1996a. Desventuradas Islands, Chile: the easternmost outpost of the Indo-west Pacific zoogeographic region.—*Revista de Biología Tropical* 44(2):929–931.
- , & ———. 1996b. Peces de la familia Serranidae en las Islas Desventuradas, Chile (Osteichthyes, Perciformes).—*Boletín de la Sociedad de Biología de Concepción* 67:23–32.
- Rafinesque, C. S. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia, con varie osservazioni sopra i medesimi. Palermo.
- Randall, J. E. 1996. Two new anthiine fishes of the genus *Plectranthias* (Perciformes: Serranidae), with a key to the species.—*Micronesica* 29(2):113–131.
- , & A. Cea Egaña. 1984. Native names of Easter Island fishes, with comments on the origin of the Rapanui people.—*Occasional Papers of Bernice Pauahi Bishop Museum* 25(12):1–16.
- Regan, C. T. 1913. A collection of fishes made by Professor Francisco Fuentes at Easter Island.—*Proceedings of the Zoological Society of London* 1913 (pt. 3):368–374, pls. 55–60.
- Reinboth, R. 1963. Natürlicher Geschlechtswechsel bei *Sacura margaritacea* (Hilgendorf) (Serranidae).—*Annotationes Zoologicae Japonenses* 36:173–178.
- . 1964. Inversion du sexe chez *Anthias anthias*

- (L.) (Serranidae).—Vie et Milieu, Supplément 17:499–503.
- Roberts, C. D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei.—Bulletin of Marine Science 52:60–113.
- Robins, C. R., & W. A. Starck, II. 1961. Materials for a revision of *Serranus* and related fish genera.—Proceedings of the Academy of Natural Sciences of Philadelphia 113(11):259–314.
- Rojas, J. R., & G. Pequeño. 1998a. Revisión taxonómica de los peces de la subfamilia Anthiinae del Pacífico suroriental chileno (Pisces: Serranidae: Anthiinae).—Revista de Biología Marina y Oceanografía 33(2):163–198.
- , & ———. 1998b. *Plectranthias lamillai*, a new anthiine fish species (Perciformes, Serranidae) from the Juan Fernández Archipelago, Chile.—Scientia Marina 62(3):203–209.
- Sadovy, Y., & P. L. Colin. 1995. Sexual development and sexuality in the Nassau Grouper.—Journal of Fish Biology 46:961–976.
- , & D. Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes.—Copeia 1987:136–156.
- Shapiro, D. Y. 1986. Intra-group home ranges in a female-biased group of sex-changing fish.—Animal Behavior 34:865–870.
- Steindachner, F. 1875. Ichthyologische Beiträge. [I.] Sitzungsberichte der Akademie der Wissenschaften, Wien. Mathematische–Naturwissenschaftliche Klasse. Abt. 1. 70:375–390, 1 pl.
- Thresher, R. E. 1984. Reproduction in reef fishes. T. F. H. Publications, Inc., Neptune City, New Jersey, 399 pp., many unnum. illustrations.
- Tschudi, J. J. von. 1846. Ichthyologie. Pp. ii–xxx + 1–35, pls. 1–6, in Scheitlin & Zollikofer, 1844–1846, Untersuchungen über die Fauna Peruana, in 12 parts, St. Gallen.
- Valenciennes, A. 1833. In G. Cuvier & A. Valenciennes, Histoire naturelle des poissons. Tome 9. Paris, xxxii + 512 pp.
- Webb, R. O., & M. J. Kingsford. 1992. Protogynous hermaphroditism in the half-banded sea perch, *Hypoplectrodes maccullochi* (Serranidae).—Journal of Fish Biology 40:951–961.
- Weber, F. 1801. Observationes entomologicae. Kiliae.