## PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Volume 61, No. 2, pp. 235–267, 12 figs. 10 tables (Appendix)

March 31, 2010

## A New Species of *Scorpaenodes* (Pisces: Scorpaenidae) from the Galápagos and Cocos Islands with Discussions of the Limits of *Scorpaenodes* and *Thysanichthys*

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Scorpaenodes rubrivinctus sp. nov. is described from seven specimens taken at the Galápagos Islands, bringing the number of scorpaenids known from the archipelago to 15 species in eight genera. The new species was observed and photographed at 203-412 m, often in association with sponges, and collected during two expeditions using the deepwater submersible Johnson Sea-Link in 1995 and 1998. The species has been photographed, but not collected, from Cocos Island, Costa Rica. In head spination, general appearance and many body proportions, the new species is similar to Thysanichthys crossotus, but shares with species of Scorpaenodes palatines that are devoid or nearly devoid of teeth and the presence of a large slit posterior to the posteriormost hemibranch. Among shallow reef species of Scorpaenodes, S. rubrivinctus is similar to S. albaiensis and S. minor, which are placed in the genus Hypomacrus by some authors. Like S. rubrivinctus, those species also have a relatively elongate snout and dorsalmost unbranched rays that are significantly and abruptly longer than the ventralmost branched rays. The latter condition is also seen in T. crossotus. However, the new species differs from S. albaiensis and S. minor in having more vertical scale rows and distinct vertical bars, in fin-spine lengths, and in body proportions. It differs in a number of respects from other deep reef species of Scorpaenodes, most notably in anal fin-spine lengths. We place S. rubrivinctus in Scorpaenodes, pending future cladistic study, but note that generic reassignment may prove necessary because limits of both Scorpaenodes and Thysanichthys are unclear. A 655 bp nucleotide sequence of the cytochrome c oxidase Subunit I (COI) gene is presented.

During 1995 and 1998, two of us (JM and CB) were fortunate to survey the Galápagos ichthyofauna using the one-atmosphere submersible *Johnson Sea-Link*. The volcanic nature, steep terrain, and strong currents of the Galápagos Archipelago provide a superb habitat for benthic scorpaenids, and at the same time makes deepwater fish collecting by traditional trawling and hook-and-line methods all but impossible. The maneuverability and observational opportunities of a manned submersible allowed us to observe and collect many new species and new records during dives to 1000 m (McCosker 1997), including the capture of six previously unknown and undescribed scorpionfishes. Amongst them was a dramatically-colored, elongate-snouted scorpionfish that we describe herein.

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Fifteen scorpionfishes are now known from the Galápagos archipelago. Charles Darwin collected the first Galápagos scorpaenid specimens at San Cristóbal Island, which were later described by Jenyns (1840) as *Scorpaena histrio*. Meek and Newland (1885) and Jordan and Evermann (1898) recognized *Scorpaena fucata* Valenciennes, 1846, and *Scorpaena pannosa* Cramer, 1897, as junior synonyms of *S. histrio*. Examination of the holotypes by one of us (SP) corroborates those synonymies. Garman (1899) described the midwater *Ectreposebastes imus* from waters off the archipelago. *Scorpaenodes xyris* (Jordan and Gilbert, 1882) and *Scorpaena mystes* Jordan and Starks, 1895, are widely distributed in the tropical eastern Pacific and at the Galápagos (Grove and Lavenberg 1997). *Pontinus strigatus* was described from the Galápagos by Heller and Snodgrass in 1903. *Taenianotus triacanthus* Lacepède,1802, was reported by Wellington (1978) based on a specimen photographed underwater at James Island, but this widespread Indo-Pacific species has yet to be collected and most likely is a vagrant (Robertson et al. 2004). The Scorpaenidae of the Galápagos were summarized by Grove and Lavenberg (1997), who inadvertently repeated the error of Seale (1940) in listing a misidentification of *Scorpaenodes xyris* as *Scorpaenopsis gibbosa* (Bloch and Schneider 1801), which does not occur in the archipelago (McCosker 1998).

Subsequently, McCosker (2008) described *Trachyscorpia osheri* and *Idiastion hageyi*, collected using the submersible *Johnson Sea-Link* at the Galápagos Islands. *Scorpaena cocosensis* Motomura 2004 was collected in nearshore waters at Tagus Cove during the 1998 expedition, extending its known distribution from Cocos Island (Motomura and McCosker 2009). Also collected using the submersible during the two expeditions were specimens of *Phenacoscorpius* (Motomura and McCosker, in prep.), *Pontinus vaughani* Barnhart and Hubbs, 1946, *P. clemensi* Fitch, 1955, and two additional undescribed species of *Pontinus* (Poss, McCosker and Lavenberg, in prep.). Those fourteen scorpaenids, along with the new *Scorpaenodes* which we describe herein, demonstrate the remarkable benefits of exploration using manned submersibles, as well as the diversity of the Galápagos scorpaenid fauna.

#### METHODS

Methods for taking counts and measurements follow those of Eschmeyer (1969b), as modified by Poss and Eschmeyer (1978), except that specimens were measured using digital rather than dial calipers. All measurements were recorded and analyzed to the nearest 0.01 mm, but reported to the nearest 0.1 mm. The last ray of both the dorsal and anal fins is typically split to its base, yet borne on a single pterygiophore. This last "double-ray" is counted here as  $1\frac{1}{2}$  to distinguish this condition from the much more infrequent condition in which it is not split to its base (and counted as 1), thereby avoiding the inconsistent counting of the fin-rays that has appeared in the literature of scorpaenoid species. As defined by Eschmeyer, the vertical scale-row count is the number of scale rows from the base of the supracleithral spine to the end of the hypural plate.

Abbreviations for depositories of specimens follow Leviton et al. (1985). A tissue sample from the USNM paratype is stored in 95% EtOH and deposited in the USNM fish collection.

Morphometric data from 44 body measurements and data for 4 variables derived from eight counts were maintained in separate database, input to the NTSYSpc numerical taxonomic analysis system (Ver. 2.20y), and analyzed independently. Sample sizes for the two multivariate analyses and the bivariate statistical contrasts included the 7 specimens of *S. rubrivinctus* and individuals of the following species: *Scorpaenodes albaiensis* (35 individuals in morphometric analysis, 30 in analysis of counts), *Scorpaenodes investigatoris* (2, 2), *Scorpaenodes littoralis* (28, 36), *Scorpaenodes minor* (28, 25), *Scorpaenodes smithi* (8, 8), *Scorpaenodes tribulosus* (3, 1), *Thysanichthys crossotus* (3, 3) and *Thysanichthys evides* (6, 6) for totals of 120 and 118 specimens in each analysis. These nearly always represent the same individuals. Except for one rare species, individuals

with damaged spines or missing scales were not analyzed. Lots from which counts and measures were taken are listed under comparative materials.

Bivariate comparisons based on the 43 measures used, as regressed against standard length (SL), are summarized in a separate section on morphometrics. Analyses of covariation were performed using the aoctool function in MATLAB (Ver. 7.04.365) of the MATLAB Statistical Toolbox and using two distinct models. The first testing, *via* ANCOVA, for the presence of different slopes among the species,  $Y = (\alpha + \alpha_i) + (\beta + \beta i) \cdot SL + \varepsilon$ , and the second testing, *via* ANCOVA, for the presence of different Y-intercepts, in the event slopes were found not to be significantly different,  $Y = (\alpha + \alpha_i) + \beta \cdot SL + \varepsilon$ . In nearly all cases, the latter model was found to provide the best fit, and slopes of nearly all variables were found not to differ significantly among species. Both Bonferonni and Sheffé adjustment procedures were employed in evaluating statistical significance in multi-way testing among species (Hochberg and Tamhane 1987). Neither correction differed in their effect and only probability values resulting from the Bonferonni procedure.are presented.

To assess better how *S. rubrivinctus* has differentiated morphometrically from its near relatives, size-adjusted principal components were obtained from a covariance matrix of log-transformed body (shape) measures by factoring out a 1 x 43 element isometric vector (1, 1, ..., 1), which served as an *a priori* representation of a pure size for Burnaby size correction (unit growth in each variable dimension defined; see Rohlf and Bookstein 1988). Principal components for data derived from counts were obtained separately using a correlation matrix of standardized variables. Five variables derived from 8 counts [total dorsal fin-rays (spines + soft rays), average number of pectoral fin rays (left + right/2), average number of total gill rakers (left + right/2), number of vertical scale rows, and average number of lateral-line scales (left + right/2)] were used in the principal components analysis (PCA) derived from a correlation matrix of these counts. Analyses of both datasets are discussed in a section titled Principal Components Analyses. NTSYSpc computes eigenvalues and eigenvectors using the QL algorithm with implicit shifts (Press et al. 1988) after standardization and tridiagonalization using Givens and Householder transformations.

#### Scorpaenodes rubrivinctus Poss, McCosker and Baldwin, sp. nov.

Figures 1-3, 4A, 7-9,11-12; Tables 1-10 (Appendix)

MATERIAL EXAMINED.— HOLOTYPE: CAS 90384, 100.8 mm SL, ♂, San Cristobal Id., seamount SE of San Cristobal Id. (01°06′24″S, 89°07′02″W), 203 m, *Johnson Sea-Link*, JSL Dive 3937, J.E. McCosker, 18 Oct 1995. PARATYPES: CAS 201883, 100.2 mm SL, ♂, Marchena Id. (00°24′00″N, 90°26′30″W), 303 m, JSL Dive 3109, J.E. McCosker and C.C. Baldwin, 21 Jul 1998. CAS 86532, 98.9 mm SL, ♂, Genovosa (Tower) Id. (00°21′48″N, 89°58′11′W), 280 m, JSL Dive 3974, J.E. McCosker et al., 24 Nov 1995. USNM 396088, 88.5 mm SL, ♂, 3 km E of Plazas Id. (00°32′24″S, 90°09′07″W), 305 m, JSL Dive 3096, J.E. McCosker and C.C. Baldwin, 9 Jul 1998. CAS 86511, 2(83.4-87.7 mm SL), ♀♀, Seymour Id. (00°23′15″S, 90°16′11″W), 308 m, JSL Dive 3980, J.E. McCosker, 27 Nov 1995. CAS 86524, 70.9 mm SL, ♂, Fernandina Id. (00°17′52″ S, 91°39′15″ W), 412 m, JSL Dive 3956, J.E. McCosker et al., 16 Nov 1995.

**DIAGNOSIS.**— A species of *Scorpaenodes* with the following characteristics: pectoral fin with 18–20 rays, the dorsalmost unbranched rays of which are abruptly longer than the ventralmost branched rays; an elongate snout (13–15%SL) (Figs. 1 and 2); relatively elongate dorsal spines; distinct broad, orange or orange red vertical bars on the body that extend onto the fins (Fig. 3); nasal spines short, and bifid or absent in some specimens; spines of the suborbital ridge extended laterally to form a shelf; 43-51 vertical scale rows.

**DESCRIPTION.**— Dorsal: XIII,  $8\frac{1}{2}$  (1), XIII, $9\frac{1}{2}$ \* (5), XIII,  $10\frac{1}{2}$  (2) [asterisk denotes holotype]. Anal: III, 5 (1), III,  $5\frac{1}{2}$ \* (7). Pectoral Fin-Rays (left): 18\*(2), 19(3), 20(3). Gill rakers (left): 4-6 (usually 5) + 1 + 9-12 (usually 10) = 15-17 (5 + 1 + 10 = 16 in holotype). Vertical scale rows: 43-51 (holotype with 48). Lateral-line scales (left): 22-25 + 1 = 23-26 (usually, 24 +1, including holotype). Vertebrae 9 + 15 = 24 (n = 5, including holotype; Figure 4A).

Head large (45-47% SL) (Figs. 1 and 2). Snout notably extended (13-15% SL), length slightly greater than orbit diameter (12-13% SL). All head spines sharp, well developed, except nasal spines, which are relatively short when present, and except those on the lacrimal (Figs. 1 and 2). Lacrimal with a rounded lobe anteriorly, followed by two relatively robust, but weakly pungent spines that overlap the premaxilla-the first directed nearly ventrally, the second posteroventrally; a sharper spine on lateral face at posterior end of lacrimal. Second infraorbital bone with a strong, laterally directed spine below center of eye, continuous with ridge at posterior end of lacrimal and immediately followed by a pronounced ridge on the third infraorbital bone that



FIGURE 1. Lateral view of *Scorpaenodes rubrivinctus*, holotype (CAS 90384, 100.8 mm SL).



FIGURE 2. Dorsal view of head of *Scorpaenodes rubrivinctus*, holotype (CAS 90384, 100.8 mm SL).

ends in a sharp spine. A single postorbital bone with 3-7 minute spinules. Preopercle with 4 or 5 prominent spines on its posterior margin; the uppermost spine largest in line with those along suborbital ridge, directed posterolaterally, with a prominent supplemental spine immediately anterior to it; second spine, when present, much smaller but sharp, immediately ventral to first; third spine pointing posteroventrally; fourth subequal to third, pointing primarily ventrally; fifth spine rudimentary. Nasal spine relatively short, sometimes bifid or nearly so (right side CAS 90384), or absent (right side of CAS 86532). Opercle with two pungent spines. Preorbital spine, suprarobital spine and postorbital spines present, with supraorbital spine much smaller than others. No small spines or spinules on posterodorsal margin of orbit immediately ventroposterior to postorbital spine. Interorbital ridges relatively weak, not ending in spines. Small, simple cirri usually present behind preorbital and supraorbital spines. Usually 2 coronal spines immediately anterior to occiput (missing in holotype and USNM 396088); one specimen (CAS 86524) with an enlarged coronal spine at the edge of a large "hole" in the cranium and with an additional coronal spine on right side. Tympanic spine prominent, pointed notably laterally, as well as dorsolaterally. Pterotic spine extremely well developed, as large as or larger than parietal spine. Nuchal and pareital spines prominent. Posttemporal with a single spine immediately anterior to that on supracleithrum. Supracleithral spine prominent. Cleithral spine very large, about equal in size to dorsalmost preopercular spine. Occiput slightly depressed, its anterior margin immediately posterior to the slightly raised supraoccipital commisure, its posterior margin between parietal spines (Fig. 2); anterior margin slightly wider than posterior margin. Minute teeth arranged in 4 or 5 irregular rows on the V-shaped vomer. Palatines toothless or possibly with at most a few scattered teeth. A prominent knob at symphysis of lower jaw; in dorsal view appearing as a rounded knob between widely spaced premaxillary bones. Two separated mandibular lateral-line pores immediately behind symphysis. Gill rakers relatively short, stubby. A well developed slit posterior to posteriormost hemibranch. Pseudobranch with 17-25 filaments. No cirri or tentacles on ventral surface of mandible. Swimbladder present.

Body laterally compressed, deepest between third dorsal spine and pelvic fin. Dorsal fin originating above supracleithral spine; third or fourth spines longest; penultimate shortest; fin membranes between spines notably incised. Anal fin with 3 prominent, slightly curved spines; second longest and thicker than first or third. Pectoral fin with 8-10, usually 9 ventralmost unbranched-rays, 9-10 branched rays in middle of fin, and a single



FIGURE 3. Coloration of holotype of *Scorpaenodes rubrivinctus*, (CAS 90384, 100.8 mm SL). Photograph was taken soon after its capture and before preservation.



FIGURE 4 A. Radiograph of *Scorpaenodes rubrivinctus* (USNM 396088, paratype). B. Radiograph of *Thysanichthys crossotus* (CAS 47297). Arrows indicate thickened procurrent caudal fin-ray.

unbranched ray dorsally. Longest ray of pectoral fin (dorsalmost unbranched ray) reaching to base of third anal spine, this ray notably longer than branched rays immediately above. Pelvic-fin spine relatively large, reaching more than half the distance from pelvic-fin insertion to the anal-fin origin. Caudal fin with 5 or 6 branched rays in ventral half and 6 or rarely 7 branched rays in dorsal half.

Color in life (based on field notes for CAS 201803, 100 mm SL paratype, made immediately after capture) pink with orange bars; first bar faint, behind head between first three dorsal spines;

second bar more distinct, beneath dorsal spines VIII-X; third bar distinct, between dorsal soft rays 1-8; fourth bar at base of caudal, extending narrowly onto fin (Fig. 3). Dorsal-fin membrane with orange blotches, soft dorsal with orange at basal 40%, then clear, becoming orange again distally. Anal fin faint orange, with third bar on body extending onto it. Pelvic-fin rays orange, membranes clear. Pectoral-fin rays checkered with orange, membrane clear. Caudal-fin rays orange, membrane clear. Belly and chest pale pink, becoming orange on ventral 40% of body. Body coloration in preservative pale, with several broad dark, rather well marked bars; first bar below first three dorsal spines, short, usually not reaching much below base of dorsal fin; second bar usually more prominent, below dorsal spines 5 or 6 and extending below lateral line almost to ventral midline near anus; third bar even broader and more prominent, extending ventrally from base of last dorsal spine and soft dorsal fin rays to base of anal fin; a fourth dark bar over posterior part of caudal peduncle. Posterior portion of caudal peduncle immediately anterior to caudal-fin base often with five to nine distinct, but relatively minute melanic spots that are sometimes seen in more anterior bars. The holotype and two paratypes (CAS 201883, CAS 86524) with black pigment on membranes between spines 7-11 subdistal to fin margin.

BODY MEASUREMENTS.— Measurements, in mm, followed parenthetically by the %SL, of the holotype and the 7 paratypes in the following order: CAS 90384 (holotype, 100.8 mm SL 3); CAS 201883 (100.2 mm SL); CAS 86532 (98.9 mm SL 3); USNM 396088 (88.5 mm SL 3); CAS 86511 (83.4, 87.7 mm SL 2♀); CAS 86524 (70.9 mm SL ♂). Head length: 45.2(44.8); 47.4(47.3); 45.4(45.9); 41.6(46.9); 41.5(47.3); 39.3(47.1); 32.2(45.4). Snout: 12.8(12.7); 14.3(14.3); 14.7(14.9); 12.4(14.0); 12.9(14.7); 12.2(14.6); 9.7(13.7). Orbit diameter: 11.8(11.7); 12.8(12.8); 12.4(12.5); 12.1(13.6); 11.8(13.4); 11.6(13.9); 8.7(12.3). Interorbital width: 4.0(4.0); 4.7(4.7); 6.2(6.3); 3.7(4.2); 4.0(4.6); 4.3(5.2); 3.5(4.9). Jaw length: 21.3(21.1); 20.1(20.0); 19.9(20.1); 17.9(20.2); 17.7(20.2); 17.6(21.1); 14.5(20.4). Postorbital length: 21.1(21.0); 21.4(21.4); 20.0(20.0); 18.9(21.3); 18.5(21.1); 16.5(19.8); 14.5(20.5). Greatest body depth: 34.3(34.0); 34.0(34.0); 32.6(33.0); 29.3(33.1); 29.7(33.9); 28.5(34.2); 25.1(35.4). Predorsal length: 40.9(40.6); 42.6(42.6); 42.7(48.1); 40.4(45.6); 39.0(44.5); 38.5(46.2); 30.0(42.3). Anal-fin length: 23.8(23.6); 26.2(26.2); 27.2(27.3); 22.7(25.9); 23.3(26.3); 24.8(29.7); 19.8(27.9). Caudal-fin length: 26.6(26.5); 22.7(22.7); 22.6(22.8); 20.5(23.1); 20.3(23.2); 20.9(25.1); 18.4(26.0). Pectoral-fin length: 26.4(26.2); 27.7(27.6); 36.3(36.7); 28.2(31.8); 21.4(24.4); 29.4(35.2); 24.8(35.0). Pelvic-fin length: 20.7(.20.5); 24.5(24.5); 27.1(27.2); 24.3(27.4); 20.9(23.8); 9.5(11.4); 16.8(23.7). First dorsal spine: 7.7(7.6); 7.1(7.1); 7.9(7.9); 7.3(8.3); 8.2(9.4); 7.6(9.1); 4.8(6.8). Second dorsal spine: 13.4(13.3); 9.4(9.4); 12.1(12.2); 11.2(12.6); 12.7(14.5); 12.0(14.4); 8.8(12.4). Third dorsal spine: 17.9(17.8); 16.2(16.2); 17.6(17.8); 14.4(16,3); 17.0(19.4); 16.4(19.7); 13.9(19.6). Fourth dorsal spine: 18.8(18.7); 16.6(16.6); 18.8(19.0); 15.4(17.4); 16.9(19.3); 15.3(18.3); 14.4(20.3). Fifth dorsal spine:16.8(16.7); 10.6(10.6); 16.0(16.2); 13.6(15.4); 14.7(16.8); 13.4(16.1); 12.7(17.9). Penultimate dorsal spine: 5.2(5.2); 6.1(6.1); 6.7(6.8); 6.9(7.7); 6.6(7.5); 4.4(5.3); 4.7(6.6). Last dorsal spine:13.0(12.9); 11.1(11.1); 11.7(11.8); 10.21(11.5); 11.9(13.6); 10.7(12.8); 8.0(11.3). First anal spine: 11.2(11.1); 9.6(9.6); 10.7(10.8); 8.4(9.4); 12.3(14.0); 8.0(9.6); 6.8(9.6). Second anal spine: 20.5(20.3); 19.2(19.2); 20.2(20.4); 17.1(19.3); 19.7(22.5); 17.7(21.2); 14.8(20.9). Third anal spine: 15.9(15.8); 14.8(14.8); 16.3(16.5); 12.9(14.6); 14.5(16.5); 13.6(16.3); 10.9(15.4). Caudal peduncle least depth: 9.4(9.3); 9.1(9.1); 9.1(9.2); 7.4(8.4); 8.5(9.7); 7.6(9.1); 6.9(9.7). Anterior tip of snout to base of second dorsal spine: 43.5(43.2); 44.5(44.4); 44.5(45.0); 41.1(46.4); 39.2(44.7); 40.8(48.9); 31.5(44.4). Snout to base of third dorsal spine: 46.2(45.8); 47.6(47.5); 50.9(51.5); 43.2(48.8); 41.1(46.9); 42.6(51.1); 33.5(47.2). Snout to base of fourth dorsal spine: 49.8(49.4); 51.8(51.7); 51.2(51.8); 46.3(52.4); 47.7(54.4); 45.3(54.3); 36.0(50.8). Snout to base of fifth dorsal spine:54.1(53.7); 55.8(55.7); 54.4(55.0); 49.2(55.6); 48.2(55.0); 49.2(59.0); 39.0(55.0). Distance between tip of fourth dorsal spine and membrane anterior to spine: 10.3(10.2); 10.0(10.0); 10.8(10.9); 8.67(9.8); 10.9(12.5); 8.1(9.7); 8.6(12.1). Distance between snout and pelvic insertion: 40.1(39.8); 44.4(44.3); 46.1(46.6); 40.0(45.2); 38.2(43.6); 33.7(40.4); 32.1(45.3). Distance between base of first and fifth dorsal spines:12.5(12.4); 13.1(13.1); 12.3(12.4); 11.1(12.6); 12.4(14.1); 12.9(15.5); 9.6(13.5). Distance between fifth dorsal spine base and pelvic-fin insertion: 36.2(35.9); 36.3(36.2); 36.5(36.9); 31.8(36.0); 30.5(34.8); 29.9(35.9); 27.6(38.9). Distance between first dorsal spine base and pelvic fin insertion: 33.8(33.5); 33.8(33.7); 33.8(34.2); 28.6(32.3); 29.0(33.1); 27.6(33.1); 24.5(34.6). Distance between bases of fifth and last dorsal spines: 25.9(36.5); 25.7(25.5); 25.4(29.0); 21.6(24.3); 22.6(22.6); 20.0(20.1); 18.6(18.8). Distance between base of last dorsal spine to base of last dorsal ray: 17.0(16.9); 15.0(15.0); 16.0(16.2); 14.3(16.1); 11.0(12.5); 15.0(18.0); 12.0(16.9). Distance between last dorsal ray and last anal ray: 13.2(13.1); 13.8(13.8); 12.2(12.3); 11.5(13.0); 10.6(12.1); 10.2(12.2); 10.0(14.1). Distance between anal-fin origin and base of last anal ray: 13.6(13.5); 13.4(13.4); 15.0(15.2); 12.7(14.3); 12.74(14.5); 11.0(13.2); 10.8(15.2). Distance between pelvic-fin insertion and anal-fin origin: 35.3(35.0); 33.0(32.9); 29.6(30.2); 27.7(31.3); 28.5(32.5); 26.0(31.2); 25.8(36.4). Distance between base of first dorsal spine and anal-fin origin: 47.4(47.0); 46.3(46.2); 45.9(46.4); 41.5(46.9); 41.6(47.4); 39.5(47.4); 33.2(46.8). Distance between base of last dorsal spine and pelvic-fin insertion: 46.2(45.8); 45.0(44.9); 43.0(43.5); 37.8(42.7); 38.7(44.1); 38.0(45.6); 34.2(48.2). Distance between last dorsal spine and last anal ray: 22.9(22.7); 21.8(21.8); 21.7(21.9); 20.1(22.7); 19.0(21.7); 19.9(23.9); 16.7(23.6). Distance between last dorsal ray and anal-fin origin: 25.1(24.9); 24.0(24.0); 26.9(27.2); 21.6(24.4); 20.5(23.4); 20.4(24.5); 18.4(26.0). Distance between base of last dorsal spine and anal-fin origin: 25.7(25.5); 26.6(26.7); 23.2(26.2); 27.2(27.5); 27.6(31.5); 21.6(25.9); 20.2(28.5). Distance between base of fifth dorsal spine and anal-fin origin: 41.0(40.7); 39.6(39.5); 39.8(40.2); 34.4(38.8); 33.2(37.9); 33.2(39.8); 28.2(39.8).

**ETYMOLOGY.**— The specific epithet is derived from the Latin combination *ruber* (red) + *vinc*-tus (banded), in reference to the color pattern of this species.

**DISTRIBUTION.**— The new species was observed and collected from rocky reefs upon the platform and along the margins of the Galápagos archipelago at depths from 200-412 m. It was also observed and photographed by Avi Klopfer, Shmulik Bloom, and John McCosker at Cocos Island, Costa Rica, at depths from 160-300 m. It is not an uncommon species at either location. *Scorpaenodes rubrivinctus* is known from deeper depths than yet reported for other species of *Scorpaenodes*. Four species of *Scorpaenodes* have been described from deep reefs (Eschmeyer 1969a; Eschmeyer and Rama Rao 1972). According to those authors, *S. muciparus* reaches depths of about 380 m in the Solor Straits at 8°27′S,122°54′E (ZMA 110.246). *Scorpaenodes investigatoris* has been taken to depths of 170 m, with the first specimen taken from stomach of a snapper (*Pristipomoides filamentosus*) caught in 200 m (Smith 1958). *Scorpaenodes tribulosus* reaches depths of 140 m. *Scorpaenodes smithi* has been recorded at depths to 110 m (BMNH 1933.8.11.4). Other species of *Scorpaenodes* necorded at depths, with *S. albaiensis* being taken from 1.5–85 m, *S. littoralis* to about 40 m (SAIAB 59759), and *S. minor* from 0–38 m. Nakabo (2002) reported *Thysanichthys crossotus* as occuring between 120 and 130 m.

To our knowledge this is the first report of a species of *Scorpaenodes* being collected by a submersible. Submersible dives were made across much of the Galápagos archipelago in a variety of habitats to a depth of 1000 m. The new species was observed between depths of 203-412 m during five submersible dives. It was typically found along steep volcanic slopes (60°-90°) that were not burdened with sediments. The fish were most abundant between 260-290 m and often associated with or residing upon rossellid sponges (Fig. 11), an association that collections data suggests may also be true for *S. smithi*. The fish were seen alone or in close proximity to each other, but were never observed to interact. With collection of the type series and with underwater observation of this species at Cocos Island (Fig. 12), *S. rubrivinctus* provides another example of the close association of the fish fauna of the Galápagos and Cocos Islands. Future use of submersibles is likely to greatly increase our understanding of this and other benthic deep reef species.

**SPECIES COMPARISONS.**— Scorpaenodes rubrivinctus is readily distinguished from S. xyris, the only other species of Scorpaenodes in the eastern tropical Pacific in having 47–51 vertical scale rows (39–47 in S. xyris), and a distinctly barred rather than variegated or somewhat more marmorated color pattern as seen in most shallow water species of Scorpaenodes. It can be readily distinguished from most other species of Scorpaenodes by its elongate snout (12.6-14.8% SL) vs.

(9.3-13.1%SL), except S. albaiensis and S. minor (Figs. 5A, 5B; Tables 3 and 4), which also exhibit elongate snouts (9.3-14.2% SL). The presence of wide, orange-red bars, and the head spination (Figs. 2, 6A) serve to distinguish it from all other Scorpaenodes species having bars, except perhaps S. muciparus. Although the fresh coloration of S. muciparus is unknown and the bars are known only from those observed in two drawings (see discussion below), S. rubrivinctus can be readily distinguished from it by its much longer snout, more elongate dorsal fin-spines, less numerous vertical scale rows (70-73 in S. muciparus) and longer anal fin spines. In the deep-water species S. investigatoris and S. smithi, like the shallow water S. albaeinsis and S. minor, the margins of the vertical bars are rather irregular and typically not well defined in adults. However, it should be noted that juveniles of S. albaiensis are notably more distinctly barred, like S. rubrivinctus, than are adults. Additional study of other Scorpaenodes species is needed to establish if this represents paedomorphosis. Unfortunately, juveniles of most species of Scorpaenodes, although often numerous, are extremely difficult to identify and pigmentation in preserved material typically fades with time.



FIGURE 5. A. Scorpaenodes albaiensis in lateral view (CAS 75357). B. Scorpaenodes minor in lateral view (CAS 214156). C. Thysanichthys crossotus in lateral view (CAS53360). D. Thysanichthys evides (FMNH 57082, holotype, 74.4 mm SL).

As can be noted in Table 1 (see Appendix), *S. rubrivinctus* has relatively small scales in 47–51 vertical scale rows (38–43 in *S. albaiensis*; 30–37 in *S. minor*; 39–40 in *S. investigatoris*; 33–46 in *S. littoralis*; 35–43 in *S. smithi*; 33-46 in *S. tribulosus*) and a relatively high pectoral fin-ray count: 18–20 (14–17 in *S. albaiensis*; 14–16 in *S. minor*; 19 in *S. investigatoris*; 17-19 in *S. littoralis*; 17–18 in *S. smithi*; 18-19 in *S. tribulosus*).

The new species is similar to Thysanichthys crossotus Jordan and Starks, 1904, in a number of

respects, including shape of the first three infraorbital bones, the shape and size of many cranial spines (Fig. 6B), the shape of the pectoral fin (Fig. 5C), and in body proportions (Fig. 5C, Figs. 7 and 8). However, T. crossotus differs in possessing 2 postorbital bones (infraorbitals 5 and 6) (Mandrytsa 1991 and 2001) vs. 1 in S. rubrivinctus, 15-17 pectoral fin-rays (vs. 18-20), a dorsal fin formula of XIII, 11<sup>1</sup>/<sub>2</sub> (vs. XIII,  $8\frac{1}{2}-10\frac{1}{2}$  in S. rubrivinctus), 10 + 15 = 25 vertebrae (vs. 9 + 15 = 24), a deeper body (38.7-39.9% SL vs. 33-35.4%), a slightly spine longer second anal (23-26% vs. 19-22.5%) (see Fig. 7H; Tables 2 and 5), a less developed ridge at the base of each opercular spine that is not much raised from the lateral surface of the opercle and in having dermal



FIGURE 6. A. Dorsal view of head of *Scorpaenodes albaiensis* (CAS 75357). B. Dorsal view of head of *Thysanichthys crossotus* (CAS 53360).

filaments along its head and lateral line. *Scorpaenodes rubrivinctus* also differs from *T. crossotus* in having a much longer upper preopercular spine, an enlarged pterotic spine and a moderately enlarged lower posttemporal spine. It also differs from *T. crossotus* in having the ridge of the posterior (second) spine on the third infraorbital bone (suborbital 2) relatively in line with the ridge of the more anterior spine, rather than distinctly offset ventral to it. In this respect it is more similar to *S. littoralis, S. albaiensis, S. minor* and the types of *T. evides*, as well as several other species of *Scorpaenodes*. It differs from the paratypes of *T. evides* in having a slightly, but significantly larger head (44.4–47.3% SL vs. 40.9–42.2% SL in *T. evides*; Tables 1, 4). It differs from both *T. crossotus* and *T. evides* in having a longer snout (13-15% SL vs. 10.8–11.5%SL in *T. crossotus* and 9.8–10.5%SL in *T. evides*).

GENERIC ASSIGNEMENT WITH REMARKS ON LIMITS OF SCORPAENODES AND THYSANICHTHYS.— Scorpaenodes Bleeker, 1857, contains 27 valid species, but has not been revised on a world-wide basis. Eschmeyer (1965) discussed the limits of Scorpaenodes and consigned Sebastopsis Gill, 1862, Setastopsis (not of Gill) Sauvage, 1873, Hypomacrus Evermann and Seale, 1907, Sebastella Tanaka, 1917, Metzelaaria Jordan, 1923, Parascorpaenodes Smith, 1957, and Paronescodes Smith, 1958 to its synonymy, noting that all differed from other members of the Scorpaeninae, except Hoplosebastes Schmidt, 1929, in having the combination of normally 13 dorsal spines and no palatine teeth. This contrasts with the diagnosis of Thysanichthys given by Jordan and Starks (1904), who distinguished the genus as having 13 dorsal spines, palatine teeth, dermal filaments on the head and lateral line, no enlarged preopercular spine or ridge on opercle, and more well-developed spines on the head and suborbitals. Eschmeyer's conclusion has been followed by most subsequent authors, although Mandrytsa (2001), resurrected Hypomacrus, thus following earlier workers (Herre 1952, 1953; Smith 1957, 1958; and Schultz 1966).

Although aspects of cladistic methodology employed in the work of Mandrytsa (2001) render some of his conclusions difficult to assess (Imamura 2004; Motomura, Sakurai, and Shinohara 2009), Mandrytsa did examine 13 species, one unidentified, as part of a cladistic study that focused primarily on the diversification of the cephalic lateral line. Mandrytsa concluded that Hypomacrus forms the sister-group to species of Scorpaenodes and the monotypic Hoplosebastes, but did not otherwise discuss intra-generic relationships among species of Scorpaenodes. Mandrytsa used six characters to infer the relationships between Hypomacrus and species of Scorpaenodes. Of these, five are based the presence of various discontinuities between branches of the cephalic lateral line, which he regarded as relatively apomorphic to the plesiomorphic condition seen in Scorpaenodes and some other Scorpaenidae in which these branches are completely confluent. The apomorphic condition of several of these characters appear in other more distantly related genera and subfamilies (eg. Phenacoscorpius, Idiastion, Setarchinae and Pteroinae), suggesting that the presence of such discontinuities may not be uniquely derived. Additionally, his single specimen of S. minor was relatively small (25 mm SL) and the development of the cephalic lateral line among many species of Scorpaeninae can change during ontogeny, typically becoming more bifurcate and interconnected with increasing size. Mandrytsa noted only a single character that he regarded as relatively apomorphic in species of Scorpaenodes as compared to species of Hypomacrus - pleural ribs beginning on the sixth rather than the fifth vertebra as observed in S. albaiensis and S. minor, a condition likewise seen among the Pteroinae. In S. rubrivinctus and in T. crossotus, the first pleural ribs begin on the fifth vertebra.

Other pertinent cladistic studies (Ishida 1994; Imamura 2004; Shinohara and Imamura 2007) and molecular phylogenetic studies (Smith and Wheeler 2004) have included too few species of *Scorpaenodes* and its near relatives to be informative as to the limits of the genus, with existing cladistic studies having reached substantially different conclusions with respect to the relationships of *Scorpaenodes* and its various potential sister-taxa.

Ishida (1994) placed Scorpaenodes as a sister group to Hoplosebastes and the Pteroinae and widely removed from Trachyscorpia, which he regarded as the sister-group to Plectrogenium. He considered the latter two genera as forming the sister group of the Sebastinae, which he elevated to family status, a conclusion widely followed. Ishida did not examine Thysanichthys. Imamura (1996) recognized Scorpaenodes as a member of an undifferentiated bush including species of Dendrochirus, Scorpaena, Scorpaenopsis, Pontinus, Trachyscorpia, and Setarches. Within an analysis of the Scorpaenidae that included other scorpaenoids, Mandrytsa (2001, Fig. 225) concluded that Scorpaenodes was one of 8 lineages of an undifferentiated bush at the base of the family, with Hoplosebastes the member of another lineage, and Hypomacrus forming a separate lineage including Idiastion and Phenacoscorpius, which together form a sister group to the genera Neoscorpaena, Trachyscorpia, Setarches, Ectreposebastes, and Lioscorpius. However, an analysis of relationships within the Scorpaenidae, exclusive of other scorpaenoids, led Mandrytsa (2001, Fig. 235) to conclude that Scorpaenodes is the sister group of Hoplosebastes. He considered them to form the sister group of Hypomacrus, while Trachyscorpia was recognized as the sister group of a clade composed of Idiastion and Phenaocoscorpius. Mandrytsa concluded that Thysanichthys forms the sister-group to a clade comprising the following genera: Adelosebastes, Hozukius, Helicolenus, Sebastiscus and Sebastes. In contrast, Imamura (2004) placed Scorpaenodes as the sister group to the Pteroine genera Pterois and Dendrochirus and regarded this clade as the sister group of a clade containing Pontinus, Trachyscorpia, Setarches, and Ectreposebastes, with both of these clades the sister group to Taenianotus. Completing representatives of the Scorpaeninae Imamura considered Scorpaenopsis as the next most proximate sister taxon to the combined clade, with Scorpaena representative of the next most ancestral sister lineage. Imamura concluded that all scorpaenoid clades are derived from a paraphyletic assemblage of species encompassing a loosely defined Sebastidae into which he tentatively placed *Thysanichthys*, although he did not examine species of *Thysanichthys* or *Hoplosebastes armatus*.

The molecular results of Smith and Wheeler (2004) embedded *Scorpaenodes scaber* in a clade of the Scorpaeninae, between *Scorpaenopsis macrochir* and three representative species of *Scorpaena*, and placed an unidentified species of *Thysanichthys* in a separate clade between *Trachyscorpia cristulata* and the sebastid genera *Helicolenus* and *Sebastes*. Unfortunately, the specimen identified by Smith and Wheeler as *Thysanichthys* sp. can not be located to verify its identity.

Although cladistic analysis and revision of *Scorpaenodes* and *Thysanichthys* and their near relatives is beyond the scope of this work, a number of observations pertinent to the generic placement of *Scorpaenodes rubrivinctus* are warranted. Our investigation suggests that the limits of these genera are poorly defined from a cladistic perspective and that *S. rubrivinctus* exhibits character combinations observed in several scorpaenid genera, most notably *Scorpaenodes*, *Thysanichthys* and *Hoplosebastes*. Although the unique combination of counts and measures in the new species suggest it may be more closely related to some species of *Scorpaenodes* than others, appropriate interpretation of various similarities in spination and morphometrics within a cladistic context is needed. Data from other species of *Scorpaenodes* are also needed before its relationships can be elucidated.

Subsequent to Eschmeyer (1965), the combination of 13 dorsal spines and the absence of palatine teeth has been widely employed to diagnose species of *Scorpaenodes*. However, this combination is also characteristic of species of the subfamily Pteroinae. Although 13 dorsal spines typically characterize *Scorpaenodes* and the Pteroinae and distinguish included species from those in the Scorpaeninae, which almost always bear 12 spines, specimens of *Scorpaenodes* species with 12 spines and Scorpaeninae species with 13 spines are observed infrequently. As discussed by Randall and Poss (2002), palatine teeth have been lost in multiple scorpaenoid lineages and their absence does not represent a uniquely derived character state.

The pectoral fin of *S. rubrivinctus* has the unusual shape also seen in *T. crossotus, S. albaiensis* and *S. minor*. In these species, the dorsalmost unbranched rays are abruptly longer than the ventralmost branched rays, a feature poorly figured in the original description of *T. crossotus*. A similar, but not as marked, discontinuity in fin-ray lengths is observed in other species of *Scorpaenodes* and in *T. evides*.

The presence of dermal filaments was used to originally diagnose *Thysanichthys*. However, a number of species of *Scorpaenodes*, most notably *S. hirsutus*, but also *S. albaiensis* and *S. minor* bear small, simple filamentous cirri on the head and body, as do species of *Thysanichthys*.

Besides *T. crossotus*, *T. evides* is the only other species in *Thysanichthys*. Late in this study, we included data for the five paratypes of *Thysanichthys evides*, as well as an additional specimen found in the lot containing the paratypes (SU 22611), but not designated as a paratype in the original description. Our analyses strongly suggest that *T. evides* is the senior synonym of *Scorpaenodes littoralis* Tanaka 1917. However, we are reluctant to formally reach such a conclusion without first examining the holotypes of *S. littoralis* (ZUMT 7439) and *T. evides* (FMNH 57082). Nonetheless, we note that with exception of but one measure, the paratypes cannot be distinguished from specimens identifiable as *S. littoralis* based on our data (Figures 2A, 2B; Tables 4, 10 [see Appendix]). Examination of a photograph and a radiograph of FMNH 57082 made available to us by the Field Museum (Fig. 5D) likewise fail to suggest notable differences between the nominal forms. W. Leo Smith informs us that palatine teeth are absent in the holotype of *T. evides*. Our data indicate that the paratypes of *T. evides* differ from material identified as *S. littoralis* only in the depth of the caudal peduncle (P< 0.05). However, none of our comparative materials of

*S. littoralis* are from Japan and this difference may reflect possible geographic variation within *S. littoralis*. Because Tanaka's name is in wide use, whereas that given by Jordan and Thompson has apparently been only used once (Matsubara, 1943; who explicitly mentions both species), we believe that such a potentially disruptive nomenclatural change should be made only after the holotypes and more extensive holdings of *S. littoralis* can be studied.

Although palatine teeth are present in *Hoplosebastes armatus* and *Thysanichthys crossotus*, these species also share with all species of *Scorpaenodes* and all members of the Pteroinae the presence of a prominent, spine-like, somewhat elongate and somewhat thickened unsegmented procurrent ray immediately dorsal to the dorsalmost segmented caudal fin ray. This procurrent ray is not particularly spinous, elongate, or thickened in other scorpaenoids. Among species that exhibit this condition, it is less developed in *Thysanichthys crossotus* and is typically more elongate and slender, yet distinctly pungent among pteroine species. If interpreted as a synapomorphy, the presence of this relatively hypertorphied, spinous, unsegmented procurrent-ray provides additional support for the recognition of clade K1 of Ishida (1994) or clade 10A of Imamura (2004), but also suggests the inclusion of *Thysanichthys*, which was not studied by either author. It also supports Ishida's and Mandrytsa's recognition of a relatively close relationship between *Hoplosebastes* and *Scorpaenodes*. Interestingly, many pteroines exhibit notable expansion and modification of bones in the region of the snout, with *Dendrochirus biocellatus* being notably similar to *S. rubrivinctus* in the shape of the head, body, and median fins.

Species of *Scorpaenodes, Thysanichthys* and *Trachyscorpia* (but not *Hoplosebastes*) all have relatively short rounded lobes on the ventral margin of the lacrimal, the posteriormost being slightly pointed in larger specimens. Although the anterior lobe is rounded in *S. rubrivinctus*, the second and third "lobes" are somewhat more pungent. This contrasts with nearly all other non-sebastid scorpaenoids, which usually bear distinct, pungent lacrimal spines. Among the Sebastidae (Sebastinae of some authors), the ventral margin of the lacrimal is usually largely devoid of distinct spines (except *Hozukius*), whereas in the Pteroinae the ventral margin can be relatively spineless or may lobed and bear numerous small spinules that increase in number with size.

Scorpaenodes rubrivinctus, like all other species of Scorpaenodes, Pteroninae, and Setarchinae, has a large cleft posterior to the posteriormost hemibranch. Among other Scorpaeninae, species of Pontinus have a small slit or cleft as do some species of Neomerinthe and Phenacoscorpius. This contrasts with the condition seen in Thysanichthys and most species of the Scorpaeninae in which this slit is absent at any size. In species of Trachyscorpia this cleft is present in smaller individuals, but is closed or absent in larger individuals.

Because of the presence of a heterogeneous assemblage of both relatively deep and shallow water species of *Scorpaenodes*, because of the substantial discordance between proposed relationships derived from molecular data and morphological data, and because of character incompatibility and size-related variation among some presumptively or potentially apomorphic states of the morphological characters discussed above, the relationships of species presently included in *Scorpaenodes* and *Thysanichthys* require further study before the phylogenetic relationships of *S. rubrivinctus* and its generic placement can be confidently established.

**MORPHOMETRICS.**— There are a number of morphometric differences that distinguish *S. rubrivinctus* from other species of *Scorpaenodes* and *Thysanichthys* (Tables 2–8 [see Appendix]; Figure 7A–O). Of these, only 4 measures reveal significant differences in slopes among the species compared. *Scorpaenodes investigatoris* shows more rapid growth of the predorsal length relative to SL than do *S. rubrivinctus* and other species compared. The caudal fin of *T. crossotus* appears to grow more rapidly relative to SL than it does in *S. rubrivinctus* or in other species compared, although its significance is based on only 3 specimens. A slightly more positive allometry in the



FIGURE 7. Regressions against SL for measurements that distinguish select species of *Scorpaenodes* and *Thysanichthys*. A – First Dorsal Spine. B – Second Dorsal Spine. C – Third Dorsal Spine. D – Fourth Dorsal Spine. E – Dorsal Spine Index (D1 + D2 + D3 + D4 + D5)/SL. F – Incision of Fin-Membrane at Fourth Dorsal Spine. G – First Anal Spine. H – Second Anal Spine. I – Snout to Pelvic-Fin Insertion. J – Penultimate Dorsal Spine to Anal-fin Origin. N – Base of First Dorsal Spine to Anal-fin Origin. O – Base of Last Dorsal Spine to Base of Last Anal Ray. *S. rubrivinctus*–filled circles; *S. albaiensis* – empty squares; *S. littoralis* – inverted empty triangles (apex down); *S. minor* – empty circles; *S. smithi* – empty diamonds; *Thysanichthys crossotus* – filled squares; *T. evides* – filled diamonds (paratypes). All lengths are in mm.



FIGURE 7. Regressions against SL for measurements that distinguish select species of *Scorpaenodes* and *Thysanichthys* (continued; see p. 245 for legend).

length of the pectoral fin relative to SL is observed in *T. crossotus* than in any of the other species examined. The incision of the dorsal fin at the fourth dorsal spine *vs*. SL shows positive allometry in *S. smithi* as compared to other species examined, including *S. rubrivinctus*.

For all other measured variables no significant differences in slope relative to SL were observed among species, with a pooled parallel slopes model of regression providing the best fit for our data. Numerous species exhibited significant differences from *S. rubrivinctus* in Y-intercept when compared under a parallel slopes model (Tables 2-8).



FIGURE 7. Regressions against SL for measurements that distinguish select species of *Scorpaenodes* and *Thysanichthys* (continued; see p. 245 for legend).

Each of the anteriormost 5 dorsal spines is longer at a given size in S. rubrivinctus than in other species of either Scorpaenodes or Thysanichthys (Fig. 7A-7D). Although the differences are slight (Fig. 7A-D), this is more readily apparent if the total lengths of the first 5 dorsal spines are added and their sum regressed against standard length (Fig. 7E). Scorpaenodes rubrivinctus has a more deeply incised dorsal fin membrane, as measured from the tip of the fourth dorsal spine to the membrane (Fig. 7F). Like T. crossotus, S. rubrivinctus has a relatively long first anal spine, which is notably longer than that seen in S. smithi (Fig 7G). However, the second anal spine of S. rubrivinctus is shorter than that of T. crossotus, but not significantly different in length from those seen in other species of Scorpaenodes compared, except S. smithi (and likely S. investigatoris, S. tribulosus and S. muciparus as materials become available). Scorpaenodes rubrivinctus has a slightly greater distance between the tip of the snout and the pelvic-fin insertion (Fig. 7I) than other species of Scorpaenodes. It differs from T. crossotus in having a shorter penultimate dorsal spine that is more typical of other species of Scorpaenodes (Fig. 7J). The distance between the base of the fifth dorsal spine and the pelvic-fin insertion is greater than observed in either S. albaiensis or S. minor, and less than in either S. smithi or T. crossotus, but not significantly different from that seen in S. littoralis (Fig. 7K). In contrast, the distance from the base of the first dorsal spine to the origin of the anal fin is as short as it is in S. albaiensis and S. minor, but slightly yet significantly shorter than that in S littoralis or S. smithi, as well as distinctly less than that in T. crossotus (Fig. 7K). In S. rubrivinctus the distance between the pelvic-fin insertion and anal-fin origin is proportionally the same as in S. albaiensis and S. minor, but slightly less than that observed in other species of Scorpaenodes examined (Fig. 7L). Scorpaenodes rubrivinctus also has the same proportional distance between the base of the first dorsal spine and the anal-fin origin as observed in S. albaiensis and S. minor, but significantly, albeit only slightly less than other species of Scorpaenodes compared, and notably less than observed in T. crossotus (Fig. 7M). The distance between the fifth dorsal spine and the anal-fin origin (Fig. 7N) is relatively shorter in the slender-bodied S. rubrivinctus, when compared to S. albaiensis, S. minor and S. littoralis, to the distinctly deeper bodied S. smithi, or to the much deeper-bodied T. crossotus. In contrast, the distance between the base of the last dorsal spine and the base of last anal ray relative to the SL is relatively less in the new species than in S. smithi and also much less than in T. crossotus (Fig. 7O). Two unexpected contrasts shows that the distances between the tip of the snout and the bases of the second and third dorsal spines are slightly shorter in S. albaiensis than in either S. rubrivinctus or S. minor.

PRINCIPAL COMPONENT ANALYSES.— When the measured variables are considered simultaneously using a size-corrected PCA their joint distributions reflect the distinctiveness of S. rubrivinctus from most other Scorpaenodes species. Although notably more slender in several measures of body depth, the new species is otherwise more similar to Thysanichthys crossotus in median-fin spine lengths than to other species of Scorpaenodes (Fig. 8). In particular, the elongate anal-fin spine lengths of S. rubrivinctus contrast markedly to the condition observed in other deep-reef species of Scorpaenodes in which they are relatively short. If specimens of Hopolosebastes armatus, which has greatly reduced anal-fin spines, are added to the morphometric ordination (not shown), they do not fundamentally alter the eigenstructure of the result and also plot in the same quadrant as specimens of S. investigatoris, S. smithi and S. tribulosus, although as even more distinctive outliers. The variables discussed above largely account for the clear separation within the ordination, as can be seen from the loadings of the size-adjusted principal components (Table 9).

The PCA derived from counts (Fig. 9; Table 10) shows a comparable result. However, there is a notable step-wise grouping of individuals nearly along the axis of the second eigenvector that results from the discrete distribution of values for a single variable (total dorsal-fin spines) with a high loading on this axis. Despite the presence of such artificial discontinuity, several disjunctions can be observed among the joint distributions of the variables.

Thysanichthys crossotus is separated from the other taxa studied by an unusual combination of more dorsal-fin rays, fewer pectoral finrays, and higher scale counts. That *S. albaien*sis and *S. minor* differ significantly in vertical scale counts is immediately apparent, and the combination of fewer scales and fewer pectoral-fin rays distinctly separate both from *S. rubrivinctus. Scorpaenodes rubrivinctus* is marginally disjoint in its combinations of counts from those observed in other deeper



FIGURE 8. Plot of largest 3 size-adjusted principal components, explaining 51.3% of the residual variance remaining after size-related variation, accounting for 91.8% of total variation, has been removed. S. rubrivinctus-filled circles; S. albaiensis - empty squares; S. littoralis - inverted empty triangles (apex down); S. minor - empty circles; S. investigatoris - filled triangles (apex up); S. smithi - empty diamonds; S. tribulosus - empty triangles (apex up; fin-spines of 3 known specimens in relatively poor condition); Thysanichthys crossotus - filled squares; T. evides - filled diamonds (paratypes). Loadings for most significant original variables contributing to each of the first three size-adjusted principal components are given in Table 9, with select original variables plotted against SL in Fig 7A-O. PC I accounts for 24.2%, PC II – 17.7% , and PC III – 9.5% of total residual variance after size adjustment respectively.



FIGURE 9. Plot of largest 3 principal components, explaining 88.3% of total observed variation in counts data (PC I - 58.0%; PC II - 18.5%; PC III - 11.8%). Symbols are as given in Figure 8. Factor loadings are given in Table 11.

water species (*S. investigatoris*, *S. smithi* and *S. tribulosus*). In contrast, the combination of counts observed in *S. littoralis* notably overlaps that seen in *S. rubrivinctus*, *S. albaiensis* and the group of deeper reef *Scorpaenodes*.

Although these results seem to suggest that the deeper reef species, including S. rubrivinctus, may not all belong to a single lineage, the combinations of counts in other species of Scorpaenodes require more rigorous testing before firm conclusions can be reached. Especially important will be the inclusion of additional materials of deeper reef species. The status of the poorly known Scorpaenodes muciparus emphasizes the importance of further study. This species was originally described as having a dorsal count of XIII, 91/2, a very high vertical-scale row count (70), 18-19 pectoralfin rays, and apparently relatively strong vertical bars, similar to those observed in S. rubrivinctus. The figure published in the original description (Alcock 1889) shows a dorsal count of XIII, 101/2, moderately elongate anal-fin spines, and a scale count that appears to approach about 50-60. However a later, more detailed figure (Fig. 10) that matched the original description was subsequently published by Alcock (1898). Although Eschmeyer and Rama Rao (1972) did not discuss this discrepancy nor did they provide additional counts or measures that could be used to assess joint distributions of counts with those in S. rubrivinctus, they did report three additional specimens identified as S. muciparus, not yet seen by us, and were able to confirm a scale row count of 70-73 on a specimen previously reported in Weber and deBeaufort (1962) as having 45-58 scales. Specimens of Hoplosebastes armatus have between 51 and 65 vertical scale rows.

The new species appears to grow relatively large for a species of *Scorpaenodes*, with our largest specimen measuring 100.8 mm SL. The largest known species of *Scorpaenodes* is *Scorpaenodes muciparus*, which reaches 146 mm SL (Eschmeyer and Rama Rao 1972; based on ZMA 110.246). To date, the largest specimens of *S. albaiensis* and *S. minor* examined by us



FIGURE 10. *Scorpaenodes muciparus* (Alcock 1889) as figured in Alcock (1898).



FIGURE 11. *Scorpaenodes rubrivinctus* associated with a rosselid sponge, photographed from submersible *Johnson Sea-Link* at 270 m off Seymour Island, Galápagos.



FIGURE 12. Photograph of *Scorpaenodes rubrivinctus* taken at Cocos Island during a submersible dive at 200 m, by *Undersea-Hunter/Deep-See*.

are 72.0 and 51.4 mm SL respectively, although Motomura, Sakurai, and Shinohara (2009) report a 78.5 mm specimen of the former from Okinawa (KAMUM-I 6429). Kuiter and Tonozuka (2001) reported S. albaiensis attains 120 mm TL or about 96 mm SL based on unspecified material. Larger species of Scorpaenodes include: Scorpaenodes guamensis (Quoy and Gaimard, 1824), which reaches about 85 mm SL (CAS 62573), although it may grow to about 112 mm SL (Leiske and Myers 1994; based on unspecified material 140 mm TL); Scorpaenodes carribaeus Meek and Hildebrand, 1924, attains about 85 mm SL (Eschmeyer 1969b, but largest specimen unspecified); Scorpaenodes elongatus Cadenat, 1950 (150 mm SL, Eschmeyer and Dempster 1990), Scorpaenodes immaculatus Poss and Collette, 1991, grows to at least 89 mm SL, Scorpaenodes insularis Eschmeyer, 1971, grows to 78.8 mm SL (USNM 267880). Scorpaenodes littoralis Tanaka, 1917, reaches about 88 mm (Randall 1995; based on unspecified material 110 mm TL), Scorpaenodes parvipinnis (Garrett, 1864) attains at least 93 mm SL (SAIAB 112; but may reach about 112 mm SL according to Leiske and Myers 1994; based on unspecified materials 140 mm TL), Scorpaenodes steeni Allen, 1977, attains about 99.8 mm SL. Scorpaenodes varipinnis Smith, 1957, reaches about 104 mm SL (Kuiter and Tomozuka 2001; based on unspecified material 130 mm TL), and Scorpaenodes xyris (Jordan and Gilbert, 1882) attains about 120 mm SL (Eschmeyer, Herald, and Hammon 1983; based on unspecified material 150 mm TL). Most near-shore species are smaller.

**BARCODE SEQUENCE.**— A 655-nucleotide sequence of the section of cytochrome c oxidase subunit I (COI) gene used for barcoding by the BOLD informatics database (Ratnasingham and Hebert, 2007) was obtained for one paratype (USNM 396088). This sequence was given the Genbank accession number GU357570. Although tissue from other *Scorpaenodes* species are listed in the BOLD database, COI gene sequences from these species have yet to be published. As recommended by the BOLD database management group, the 655 bp sequence (5'–3') of the paratype is presented as follows:

**COMPARATIVE MATERIAL EXAMINED.**— *Hoplosebastes armatus*: USNM 98898 (1, 86.3, holotype of *Hoplosebastes pristigenys* Fowler) 21°54'N, 114°46'E, vicinity of Hong Kong, 67.6 m. ZIN 22695 (1, 122.7. holotype of *Hoplosebastes armatus* Schmidt) Nagasaki. *Scorpaenodes albaiensis*: EGYPT: USNM 355353 (1, 48.1) Strait of Jubal, southern end of Sinai Peninsula at Ras Muhammad,. FIJI: CAS 206970 (1, 34.2) 19°9'38"S, 179°45'23"E, Lau Group, Matuku Id. CAS 206971 (5, 20.3–36.4) 18°58'57"S, 179°52'12"W, Totoya Id. CAS 206985 (1, 57.9) 172°6'S, 177°13'E, Naviti Id. CAS 214127 (1, 44.8) 18°09.52'S, 178°23.98'E, Barrier Reef off Suva. CAS 214150 (1, 51.7) 18°9.52'S, 178°23.98'E, Barrier reef off Suva. CAS 219009 (1, 37.8) 18°09.59'S, 178°23.96'E, Barrier reef off Suva. CAS 219648 (2, 48.2–48.4) 18°10.84'S, 178°28.14'E, Barrier reef off Suva. INDONESIA: USNM 210019 (1, 32.3) Moluccas Ids., Ceram, just offshore and just W of Tandjung Namatatuni. USNM 392573 (1, 49.6) 5°17'20"S, 122°04'E, Suluwesi Id, Big Damalawa Islet, Kabaena Id, Tallabassi Bay. MALAYSIA: CAS 207053 (4, 13.5–46.0) Borneo, Sabah State, east end of Borneo, Pulav Bohidulong. MOZAMBIQUE SAIAB

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397 (1, 40.3, paratype of Hypomacrus africanus) 14.2167°S, 40.7667°E, Mozambique, Pinda Id. SAIAB 398 (2, 65.2-67.8, paratypes of Hypomacrus africanus) 14.2167°S, 40.7667°E, Pinda I. SAIAB 400 (1, 62.2, paratype of Hypomacrus africanus) 11.1833°S, 40.6167°E, Querimba Archipelago. PAPUA NEW GUINEA: CAS 207058 (1, 54.4) New Britain, Dawapia Rocks. USNM 380226 (1, 26.5) 10°44'S, 165°49'30"E, Solomon Ids, Santa Cruz Id. USNM 380381 (2, 26.1-53.8 [scales damaged]) 1°30'30"S, 144°59'15"E, Hermit Ids. USNM 380946 (1, 42.5) 10°40'S, 165°47'30"E, Solomon Ids, Santa Cruz Id. USNM 382906 (1, 32.1) 10°49'30"S, 165°50'E, Solomon Is, Santa Cruz Is. USNM 383025 (4, 11.0-36.0) 10°42'30"S, 165°50'E. USNM 383806 (1, 19.6) 9°52'S, 167°09'30"E, Solomon Ids. USNM 384429 (2, 22.0-49.2) 10°48'30"S, 165°50'E. PHILIPPINES: CAS 211490 (2, 31.2-35.0) 13°42'N, 120°50'E, Caban Id. SU 20006 (1, 50.1, paratype of Hypomacrus albaiensis Evermann and Seale 1907) Sorsogon, Bacon. USNM 55902 (1, 48.9, holotype of Hypomacrus albaiensis, Luzon, Sorsogon, Bacon CAS 75357 (2,55.5-71.5), Luzon, Bulinao. USNM 344512 (8, 19.1-68.1) 10°35'05"N, 122°08'30"E, Panay Id. USNM 372602 (1, 48.7) 9°47'N, 118°44'E, Palawan Id, Puerto Princesa Bay. USNM 372637 (1, 52.8) 16°26'N, 119°50'E, Bolinao Lagoon. USNM 372638 (1, 45.8) 16°26'N, 119°56'E, Bolinao Lagoon. USNM 372662 (1, 53.2) 9°08'28"N, 123°29'40"E, Siquijor Id. USNM 372683 (1, 52.4) 10°52'30"N, 120°56'00"E, Bararin Id. USNM 372684 (1, 44.8) 9°02'27"N, 123°07'37"E, Negros Id, Bonbonon Pt. USNM 372685 (1, 42.1) 9°08'30"N, 123°29'22"E, Siquijor Id. SEYCHELLES: SAIAB 401 (2, 51.5–52.8, paratypes of Hypomacrus africanus) 4.6167°S, 55.4500°E, Mahe Id. SAIAB 402 (1, 46.2, paratype of *Hypomacrus africanus*) 9.4333°S, 46.3333°E, Aldabra Id. TAIWAN: ASIZ P0056237 (1, 45.5) [22.03°N, 120.72°E] Pingtung, Wanlitong. ASIZ P0056858 (2, 55.0-57.0) [22.67°N, 121.46°E] Nanlio, Lyudao. TANZANIA: SAIAB 323 (1, 62.4, holotype of Hypomacrus africanus) 6.1667°S, 39.1833°E, Zanzibar Id. SAIAB 399 (1, 72.0, paratype of Hypomacrus africanus) 6.1667°S, 39.1833°E, Zanzibar Id. SAIAB 403 (1, 53.2, paratype of Hypomacrus africanus) 5.1333°S, 39.6667°E, Pemba Id. TONGA: USNM 336568 (2, 29.3, 32.4) 21°19'30"S, 174°56'50"W, Eua. USNM 337718 (5, 16.8-30.8) 19°36'15"S, 174°28'15"W, Ha'apai Group, Ofolanga Id. VANUATU: USNM 348183 (1, 26.5) 17°41'39"S, 168°10'10"E, Efate. USNM 352337 (1, 26.0) 16°49'37"S, 168°22'15"E, Shepherd Ids, 11 Jun 1996. USNM 353504 (1, 42.5) 16°44'00"S, 168°07'35"E, Shepherd Ids, Epi Id. USNM 354461 (2, 39.7-41.7) 17°03'18"S, 168°21'43"E, Shepherd Ids, Emae Id. USNM 363285 (1, 26.2) 13°40'19"S, 167°39'04"E, Banks Ids, Mota Lava Id. USNM 363647 (1, 72.5) 13°40'19"S, 167°39'08"E, Banks Ids, Mota Lava Id. USNM 363767 (1, 47.3) 13°38'32"S, 167°30'18"E, Banks Ids, Rowa Id. USNM 364204 (1, 47.4) 16°43'36"S, 168°08'42"E, Shepherd Ids Epi Id. UNKNOWN: SAIAB 404 (2, paratypes of Hypomacrus africanus). Scorpaenodes investigatoris. INDIA: CAS 24264 (1, 71.1 holotype of Scorpaenodes investigatoris) 24°13'N, 65°52'E. USNM 204030 (1, 72.8, paratype of Scorpaenodes investigatoris) 17°25'N, 71°39'E. Scorpaenodes littoralis. AUSTRALIA: AMS I.17420005 (1, 59.4). AMS I.17422008 (1, 43.0). AMS I.27138019 (9, 19.5-65.6). AMS I.27148020 (15, 21.9-62.6). HAWAIIAN IDS.: CAS 33915 (1, 75.7) Oahu, Hauula Park. ISRAEL: HUJ 9349 (1, 35.3). TAIWAN: GCRL 23504 (1, 30.2). USNM 266431 (1, 55.3) Ma-Kong. NEW ZEALAND: NMNZ P.21812 (4, 51.4-80.9). Scorpaenodes minor: CAR-OLINE IDS.: USNM 224509 (1, 24.6) 6°52'N, 158°06'E, SW of Ponape. COMORES IDS: SAIAB 30868 (1, 30.8) 11.5833°S, 43.2667°E, Moroni. FIJI: CAS 206965 (1, 35.3) 18°54′0″S, 178°26′0″W, Lau Group, Yangasa Cluster. CAS 206969 (1, 23.3) 19°9'38"S, 179°45'23"E, Lau Group, Matuku Id. CAS 214151 (1, 18.3) 18°09.52'S, 178°23.98'E, Barrier Reef off Suva. CAS 214152 (1, 24.2) Barrier reef off Suva. CAS 214156 (1, 48.5) 18°9.52'S, 178°23.98'E, Barrier reef off Suva. CAS 218603 (2, 27.7-30.7) 18°09.835'S, 178°25.020′E, Barrier Reef off Suva. CAS 218609 (1, 28.6) 18°08.947′S, 178°23.932′E, Barrier reef off Suva. CAS 218620 (3, 17.3–17.2) 18°09.59'S, 178°23.96'E, Barrier Reef off Suva. CAS 219018 (7, 18.3–33.8) 18°09.59'S, 178°23.96'E, Barrier Reef off Suva. CAS 219027 (1, 25.4) 18°08.947'S, 178°23.932′E, Barrier Reef off Suva. CAS 219642 (2, 29.0-34.4) 18°09.52′S, 178°23.98′E, Barrier reef off Suva. FRENCH POLYNESIA: USNM 392263 (1, 19.6) 17°31'14"S, 149°45'44"W, Moorea. INDONESIA: USNM 99782 (1, 34.4, holotype of Hypomacrus brocki) Talisse Id. USNM 133077 (1, 29.5, paratype of Hypomacrus brocki) Patiente Strait. USNM 136438 (1, 26.7, paratype of Hypomacrus brocki) Gulf of Tonimi. MARSHALL IS.: USNM 140090 (1, 26.6, paratype of Hypromacrus brocki) Rongerik Atoll. USNM 140091 (1, 20.8, paratype of Hypomacrus brocki) Bikini Atoll, Arji Id. USNM 140228 (1, 27.2, paratype of Hypomacrus brocki) Rongelap Atoll, Kieshiechi Id. USNM 361009 (1, 20.4) Ratak Chain, Taka Atoll. MOZAM-BIQUE: SAIAB 320 (1, 34.9, holotype of Hypomacrus minor) Bazaruto. SAIAB 405 (1, 32.6) Tekomaji. SAIAB 406 (1, 39.1 ) Baixo Pinda. SAIAB 407 (1, 36.8) Baixo Pinda. SAIAB 408 (2, 35.1-38.9) Baixo Pinda. SAIAB 409 (7, 30.9-35.1) Bazaruto. NEW CALEDONIA: MNHN 1977-702 (2, 35.8-48.6). MNHN 1980-414 (1, 38.6) . MNHN 1980-572 (1, 29.9). USNM 324422 (1, 26.4) 20°37'19"S, 166°16'12"E, Loyalty Ids, Ouvea Atoll, Bagaat. PAPUA NEW GUINEA: CAS 207746 (8, 11.1-34.7) Trobriand Ids., Kiriwina Id. USNM 380373 (1, 24.2) 1°33'S, 144°59'E, Hermit Ids, Amot Id. USNM 384521 (1, 31.2) 10°44'12"S, 166°49'30"E, Solomon Ids, Ndendo. USNM 389540 (1, 21.2) 10°16'30"S, 166°16'30"E, Solomon Ids, Fenualoa Id. PHILIPPINES: USNM 99783 (1, 39.0, paratype of Hypomacrus brocki) Romblon. USNM 133076 (1, 34.1, paratype of Hypomacrus brocki) Manila Bay, Limbones Cove. USNM 298679 (1, 51.4) Batan Id. USNM 372689 (1 of 2, 30.4) 9°02'45"N, 123°07'37"E, Negros Id, off Bonbonon Point. RODRIGUES ID.: SAIAB 70479 (1, 31.8) 19°41'38"S, 63°17'36"E, off Ile aux Sables. SEYCHELLES: SAIAB 410 (2, 35.1-40.3, paratypes of Hypomacrus minor) Mahe. SAIAB 412 (2, 24.4-31.2, paratypes of Hypomacrus minor) Aldabra. TONGA: USNM 334501 (1, 23.4) 21°18'15"S, 174°26'20"W, Eua. WALLIS AND FUTU-NA IS.: USNM 365621 (3, 26.8-33.1) 13°21'30"S, 176°10'10 W, Uvea. USNM 373669 (1, 35.7) 13°16'50"S, 176°15'55"W, Uvea. USNM 373670 (7, 15.5-41.7[photo]) 13°16'50"S, 176°15'55"W, Uvea. USNM 373672 (1, 20.0) 13°16'50"S, 176°15'55"W, Uvea. USNM 376660 (9, 9.8 -24.5) 13°12'35"S, 176°14'45"W, Uvea. Scorpaenodes smithi. ALDABRA ATOLL: USNM 298642 (2, 24.3-28.4) Picard Id. AUSTRALIA: BMNH 1933.8.11.4 (1, 35.8, paratype of *Scorpaenodes smithi*) 11°30'00"S, 126°38'00"E, Samul [Sakul?] Bank. INDIA: BMNH 1932.2.15.15-20 (4 of 6, 25.1-48.3, paratypes of Scorpaenodes smithi) 6°1'20"N, 99°3'5"E, off Madras. CAS 13616 (1 of 4, 23.2-52.1, paratypes of Scorpaenodes smithi) 5°45'N, 98°20'E. Scorpaenodes tribulosus. KENYA: CAS 24267 (1, 51.2, holotype of Scorpaenodes tribulosus) 2°42'S, 40°53'E. CAS 75361 (2, 37.3-44.3) 02°42'S, 40°53'E. Thysanichichtys crossotus: JAPAN: USNM 50907 (1, 68.7, holotype of Thysanichichtys crossotus) no other data. TAIWAN: CAS 47297 (1, 91.7) Ta-chi, I-lan. CAS 53360 (1, 88.5). Thysanichthys evides: SU 22611 (6, 27.9-68.4, 5 of which are paratypes of Thysanichthys evides) Misaki.

#### ACKNOWLEGEMENTS

We wish to thank numerous colleagues who assisted us in this project, including but not limited to: Mark McGrouther (AMS); Kwang-Tsao Shao and Pi-Li Lin (ASIZ); David Catania, William Eschmeyer, Jon Fong, Tomio Iwamoto, and Mysi Hoang (CAS); Clive Roberts and Andrew Stewart (NMNZ); Eric Anderson, Ofer Gon, Phillip Heemstra, Elaine Heemstra, Wouter Holleman, Phumeza Mpambani, and Margie Shaw (SAIAB); Jeffrey T. Williams (USNM); Alexei Neylov and Arcady Balushkin (ZIN). We thank Eric Anderson and Hisashi Imamura for assistance with the translation of Mandrytsa's monograph and Hiroyuki Motomura, Yuo Sakurai and Gento Shinohara for making their results on Scorpaenodes albaiensis and S. minor available to us. Research efforts in the Galápagos were supported by the officers and crew of the Harbor Branch Vessel R/V Seward Johnson. We especially thank ace sub pilot Don Liberatore. For permission to study in Ecuador, we thank Eliecer Cruz, Arturo Izurieta Valery and Eduardo Amador, Parque Nacional Galápagos, as well as the staff of the Estacion Cientifica Charles Darwin. We thank Al Giddings, David Clark, the David and Lucile Packard Foundation, the Don Linker Foundation, the Discovery Channel, Ocean Films, the Smithsonian Institution's Discovery Center Project, and the IMAX corporation, Inc., for grants and other assistance. We also thank Avi Klopfer and Shmulik Bloom from Undersea-Hunter/Deep-See for providing underwater photographs and advice on the new species from Cocos Island; W. Leo Smith and Kevin Swagel (FMNH) for providing a figure and radiograph of the holotype of Thysanichthys evides; W. Leo Smith, H.J. Walker (SIO), John Hyde (NOAA, La Jolla), and Cindy Lawley (Illumina, Inc.) for their assistance in the hunt for an unidentified specimen believed to be Thysanichthys crossotus; and Shirley Pomponi (HBOI) and Henry Reiswig for their identifications of the Hexactinellida. Acknowledgement is also due to Lee Weigt, Amy Driskell and Andrea Ormos (USNM) for the COI sequence and to Sandra Raredon (USNM) for radiographs and photographs of the holotype of the nominal Hoplosebastes *pristigenys* Fowler. Last, but not least, thanks again are due to William N. Eschmeyer and also Michele L. Aldrich for their comments and editorial improvements.

### References

- ALCOCK, A.W. 1889. Natural history notes from H.M. Indian Marine Surveying Steamer 'Investigator,' Commander Alfred Carpenter, R.N., D.S.O., commanding. No. 12. Descriptions of some new and rare species of fishes from the Bay of Bengal, obtained during the season of 1888–89. Journal of the Asiatic Society of Bengal, ser. part 2, 58(17):296–305, 22 pls.
- ALCOCK, A.W. 1898. Illustrations of the zoology of the Royal Indian Marine Surveying Steamer 'Investigator', under the command of Commander A. Carpenter, R. N., D. S. O., and of Commander R. F. Hoskyn, R. N., Part 5, Fishes, pls. 18–24. Royal Indian Marine, Calcutta, India.
- BLEEKER, P. 1857. Bijdrage tot de kennis der ichthyologische fauna van de Sangi-eilanden. Natuurkundig Tijdschrift voor Nederlandsch Indië 13:369–380. [In Dutch]
- ESCHMEYER, W.N. 1965. Western Atlantic scorpionfishes of the genus *Scorpaena*, including four new species. *Bulletin of Marine Sciences* 15(1):84-164.
- ESCHMEYER, W.N. 1969a. A new scorpionfish of the genus *Scorpaenodes* and *S. muciparus* (Alcock) from the Indian Ocean, with comments on the limits of the genus. *Occasional Papers of the California Academy of Sciences*, no. 76. 11 pp., 1 fig., 1 table.
- ESCHMEYER, W.N. 1969b. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae). Occasional Papers California Academy of Sciences, no. 79. 143 pp., 13 figs.
- ESCHMEYER, W.N. 1986. Family No. 49: Scorpaenidae, Pages 463–478 in M.M. Smith and P.C. Heemstra, eds., *Smith's Sea Fishes*. MacMillan South Africa Ltd, Johannesburg, South Africa. 481 pp.
- ESCHMEYER, W.N., AND R.M. BAILEY. 1990. *Catalog of the Genera of Recent Fishes*. California Academy of Sciences, San Francisco, California, USA. 697 pp.
- ESCHMEYER, W.N., AND L.J. DEMPSTER. 1990. Pages 665–679 in J. C. Quéro, J. C. Hureau, C. Karrer, A. Post, and L. Saldanha, *Check-list of the Fishes of the Eastern Tropical Atlantic*. Clofeta. Vol. II. Junta Nacional de Investigação Científica e Tecnológica, Portugal.
- ESCHMEYER, W.N., E.S. HERALD, AND H. HAMMANN. 1983. A Field Guide to Pacific Coast Fishes of North America. Houghton Mifflin Company, Boston, Massachusetts, USA. 336 pp.
- ESCHMEYER, W.N. AND K.V. RAMA-RAO. 1972. Two new scorpionfishes (genus Scorpaenodes) from the Indowest Pacific with comments on Scorpaenodes muciparous (Alcock). Proceedings of the California Academy of Sciences, ser. 4, 39(18):337–382.
- EVERMANN, B.W., AND A. SEALE. 1907. Fishes of the Philippine Islands. *Bulletin of the United States Bureau* of Fisheries 26(1906):49–110, 22 figs.
- GARMAN, S. 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galápagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "*Alba-tross*," during 1891, Lieut. Commander Z. L. Tanner, U. S. N., Commanding. XXVI. The Fishes. *Memoirs* of the Museum of Comparative Zoology 24:1–431, 97 pls. (plates A–N in color).
- GILL, T.N. 1862. Notice of a collection of the fishes of California, presented to the Smithsonian Institution by Mr. Samuel Hubbard. *Proceedings of the Academy of Natural Sciences of Philadelphia* 14:274–282.
- GROVE, J.S., AND R.J. LAVENBERG. 1997. *The Fishes of the Galápagos Islands*. Stanford University Press, Palo Alto, California, USA. xliv + 863 pp.
- GÜNTHER, A. 1880. Report on the shore fishes procured during the voyage of H. M. S. *Challenger* during the years 1873–1876. *Zoology of the Challenger Expedition*, 1(6):1–82, pls. 1–32.
- HELLER, E., AND R.E. SNODGRASS. 1903. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. XV. New Fishes. Proceedings of the Washhington Academy of. Sciences 5:189–229, pls. 2–20.
- HERRE, A.W.C.T. 1952. A review of the scorpaenoid fishes of the Philippines and adjacent seas. *Philippine Journal of Science* 80(4):381–482. (dated 1951, but published in 1952)
- HERRE, A.W.C.T. 1953. Check list of Philippine Fishes. United States. Fish and Wildlife Service Research Reports, No. 20. 977 pp.

- HOCHBERG, Y., AND A.C. TAMHANE. 1987. *Multiple Comparison Procedures*. Wiley, Hoboken, New Jersey, USA. 450 pp.
- IMAMURA, H. 2004. Phylogenetic relationships and a classification of the superfamily Scorpaenoidea (Actinopterygii: Perciformes). *Species Diversity* 9:1-36.
- ISHIDA, M. 1994. Phylogeny of the suborder Scorpaenoidei. Bulletin of the Nansei National Fisheries Research Institute (27):1–111.
- JENYNS, L. 1840. Fish. In: The Zoology of the Voyage of H.M.S. Beagle, under the command of Captain FitzRoy, R.N. during the years 1832-1836. Edited and superintended by Charles Darwin. Smith, Elder and Co., London, UK. In 4 parts, i–xvi + 172 pp., pls. 1-29.
- JORDAN, D.S. 1923. A classification of fishes including families and genera as far as known. *Stanford University Publications, Biological Sciences, University Series* 3(2):77–243 + i–x.
- JORDAN, D.S., AND B.W. EVERMANN. 1898. The Fishes of North and Middle America, Pt. 2. *Bulletin of the United States National Museum* 47(2):i–xxx + 1241–2183, 2 figs.
- JORDAN, D.S., AND E.C. STARKS. 1904. A review of the scorpaenoids fishes of Japan. *Proceedings of the United States National Museum* 27:91–175.
- JORDAN, D.S., AND W.F. THOMPSON. 1914. Record of the fishes obtain in Japan in 1911. Memoirs of the Carnegie Museum. 45(4):205–313, pls. xxiv–xlii.
- KUITER, R.H., AND T. TONOZUKA. 2001 Pictorial Guide to Indonesian Reef Fishes. Part 1. Eels-Snappers, Muraenidae–Lutjanidae. Zoonetics, Australia. 302 pp.
- LIESKE, E., AND R.F. MYERS. 1994. Collins Pocket Guide. Coral Reef Fishes. Indo-Pacific and Caribbean including the Red Sea. Harper Collins, London, UK. 400 pp.
- MANDRYTSA, S.A. 1991. Морфлогичексие осбенности и положение в системе *Thysanichthys crossotus* (Scorpaeniformes, Scorpaenidae) [Morphological Characterization and Systematic Status of *Thysanichthys crossotus* (Scorpaeniformes, Scorpaenidae)]. *Proceedings Zoological Institute, Academy of Sciences, Union of Soviet Socialist Republics* 235:9–21. (In Russian)
- MANDRYTSA, S.A. 2001. Сейсмосенсорная Система И Классификация Скорпеиновидныь Рыь (Scorpaeniformes: Scorpaenoidei) [Lateral Line System and Classification of Scorpaenoid Fishes (Scorpaeniformes: Scorpaenoidei)]. Perm Permskogo University Press, Perm, Russia. 392 pp. (In Russian)
- MATSUBARA, K. 1943. *Studies on the Scorpaenoid Fishes of Japan. Anatomy, Phylogeny and Taxonomy* (I). Transactions of the Sigenkagaku Kenkyusho, Tokyo, Japan. 170 pp., 66 figs.
- MCCOSKER, J.E. 1987. The fishes of the Galápagos Islands. Oceanus 30:28-32.
- McCosker, J.E. 1997. A letter from the field: A half mile down. Pacific Discovery 50:42-45.
- McCosker, J.E. 1998. [Review of] Fishes of the Galápagos Islands, by J. S. Grove and R. J. Lavenberg, 1997. *Copeia*, 1998(3):809–812.
- MCCOSKER, J.E. 2008. *Trachyscorpia osheri* and *Idiastion hageyi*, Two new species of deepwater scorpionfishes (Scorpaeniformes: Sebastidae, Scorpaenidae) from the Galápagos Islands. *Proceedings of the California Academy of Sciences*, ser. 4, 59(3):113–123, 5 figs., 1 table.
- MEEK, S.E., AND R. NEWLAND. 1885. A review of the American species of the genus *Scorpaena*. *Proceedings* of the Academy of Natural Sciences of Philadelphia 37:394–403.
- MOTOMURA, H., AND J.E. MCCOSKER. 2009. Second specimen of the Costa Rican scorpionfish, *Scorpaena cocosensis* (Scorpaenidae): the first record from the Galápagos Islands, with fresh color notes on the Species. *Biogeography* 11:135–137.
- MOTOMURA, H., Y. SAKURAI, AND G. SHINOHARA. 2009. First records of a Scorpionfish, Scorpaenodes albaiensis, from East Asia, with a synopsis of S. minor (Actinopterygii: Scorpaeniformes: Scorpaenidae). Species Diversity 14(2):75–87
- NAKABO, T. 2002. Fishes of Japan with Pictorial Keys to the Species, English Edition, Vol. 1. Tokai University Press, Tokai, Japan. lxi + 866 pp.
- PRESS, W.H., B.P. FLAMMER, S.A. TEUKOLSKY, AND W.T. VETTERLING. 1988. *Numerical Recipes*. Cambridge University Press, New York, New York, USA. 1256 pp.
- POSS, S.G., AND B.B. COLLETTE. 1990. Scorpaenodes immaculatus, a new species of scorpionfish (Osteichthyes: Scorpaenidae) from Walters Shoals, Madagascar Ridge. Proceedings of the Biological Society of Washington 103(3):543–549, figs. 1–3

- Poss, S.G., AND W.N. ESCHMEYER. 1978. Two new Australian velvetfishes, genus *Paraploactis* (Scorpaeniformes: Aploactinidae), with a revision of the genus and comments on the genera and species of the Aploactinidae. *Proceedings of the California Academy of Sciences*, ser. 4, 41(18):401–426, 14 figs.
- RANDALL, J.E. 1995. *Coastal Fishes of Oman*. University of Hawai'i Press, Honolulu, Hawaii, USA. xiv + 439 pp.
- RANDALL, J.E., AND S.G. POSS. 2002. Redescription of the Indo-Pacific Scorpionfish Scorpaenopsis fowleri and Reallocation to the Genus Sebastapistes. Pacific Science 56(1):57–64.
- ROBERTSON, D.R., J.S. GROVE, AND J.E. MCCOSKER. 2004. Tropical transpacific shore fishes. *Pacific Science* 58(4):507–565.
- ROHLF, F.J., AND F.L. BOOKSTEIN. 1988. A comment on shearing as a method for "size correction". *Systematic Zoology* 36:356–367.
- SAUVAGE, H.E. 1873. Note sur le Sebastes minutus. Annales Sciences Naturel. (Zoologie), Paris, ser. 5, 17(5):1.
- SCHMIDT, P. 1929. On Hoplosebastes armatus, a new genus and new species of the family Scorpaenidae from Japan. Comptes Rendu Academie Sciences, l'URSS., Leningrad, USSR 8:194–196 pp., figs. 1–2.
- SCHULTZ, L.P. 1966. Fishes of the Marshall and Marianas Islands, vol. 3. Bulletin of the United States National Museum no. 202. vii + 176 pp., pls. 124–148, 155 figs.
- SEALE, A. 1940. Report on fishes from Allan Hancock Expedition in the California Academy of Sciences. Allan Hancock Pacific Expeditions 9(1):1–46.
- SHINOHARA, G., AND H. IMAMURA. 2007. Revisiting recent phylogenetic studies of "Scorpaeniformes". Ichthyological Research 54:92–99.
- SMITH, J.L.B. 1957. The fishes of the family Scorpaenidae in the western Indian Ocean. Part 1. The subfamily Scorpaeninae. *Ichthyological Bulletin*, J.L.B. Smith Institute of Ichthyology, Rhodes University, (4):49–72, pls. 1–4.
- SMITH, J.L.B. 1958. Fishes of the families Tetrarogidae, Caracanthidae, and Synanciidae from the western Indian Ocean with further notes on Scorpaenid fishes. *Ichthyological Bulletin*, J.L.B. Smith Institute of Ichthyology, Rhodes University, (12):167–181 pp., 2 pls.
- SMITH, W.L., AND W.C. WHEELER. 2004. Polyphyly of the mail-cheeked fishes (Teleostei: Scorpaeniformes): evidence from mitochondrial and nuclear sequence data. *Molecular Phylogeny and Evolution* 32:627-646.
- SNODGRASS, R.E., AND E. HELLER. 1905. Papers from the Hopkins-Stanford Galápagos Expecition, 1898–1899. XVII. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galápagos islands. Proceedings of the Washington Academy of Sciences 6:333–427.
- TANAKA, S. 1917. Eleven new species of fishes of Japan. Dobutsugaku Zasshi [Zoological Magazine], Tokyo, 29:7–12. [In Japanese]
- WEBER, M., AND L.F. DE BEAUFORT. 1962. The fishes of the Indo-Australian Archipelago, XI. Scleroparei, Hypostomides, Pediculati, Plectognathi, Opisthomi, Discocephali, Xenopterygii. E.J. Brill, Leiden, Netherlands. 481 pp.
- WELLINGTON, G.M. 1978. Undersea wonders of the Galápagos. *National Geographic Magazine* 154(3): 363–381.

# Appendix

Tables 1–10

scares on the caudal pedat	ורור מ	v 1031 and the count	טטוק פו	auty towy.							
		Total Dorsal Rays		Pectoral Fin-rays		<b>Total Gill Rakers</b>		Vertical Scale Rows	M	lean Lateral-line Scale	
				(Left+Right/2)		(Left+Right/2)				(Left+Right/2)	
	z	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean(Minimum)	SE
		(Minimum - Average)		(Minimum - Average)		(Minimum - Average)	•	(Minimum - Average)			
Scorpaenodes rubrivinctus	7	22.4(21.5-23.5)	0.308	19.1(18.0-20.0)	0.24	16.0(15.0-17.0)	0.289	47.7(43.0-51.0)	0.944	25.0(23.0-26.5)	0.408
Scorpaenodes albaiensis	30	22.4(17.5-23.5)	0.198	15.8(14.5-17.0)	0.919	14.9(12.0-19.5)	0.302	39.0(34.0-43.0)	0.473	22.5(18.5-24.5)	0.243
Scorpaenodes minor	25	21.7(20.0-22.5)	0.107	15.0(14.0-16.0)	0.098	13.1(9.5-15.5)	0.241	31.4(25.0-37.0)	0.64	19.9(15.0-23.5)	0.543
Scorpaenodes investigatoris	7	22.5(22.5-22.5)	;	19.0(19.0-19.0)	I	18.2(18.0-18.5)	0.25	39.5(39.0-40.0)	0.5	20.0(16.0-24.0)	4
Scorpaenodes smithi	8	22.0(21.5-22.5)	0.189	17.2(17.0-18.0)	0.134	17.2(16.5-18.5)	0.231	38.4(35.0-44.0)	1.224	21.8(14.5-24.5)	1.08
Scorpaenodes tribulosus1	б	21.5(21.5-21.5)	;	18.3(18.0-18.5)	0.167	14.7(13.0-15.0)	0.882	36.0(31.0-39.0)	2.517	20.2(14.0-21.0)	3.346
Thysanichthys crossotus	б	24.5(24.5-24.5)	;	16.6(16.5-17.0)	0.167	16.7(16.0-17.5)	0.441	45.7(43.0-48.0)	1.45	25.0(24.5-26.0)	0.5
Thysanichhtys evides	9	22.2(21.5-22.5)	0.211	18.0(17.5-18.5)	0.129	16.6(15.5-17.5)	0.665	42.7(38.0-46.0)	1.145	24.0(23.0-25.0)	0.341
Scorpaenodes littoralis	36	21.2(21.5-22.5)	0.076	18.2(17.0-19.0)	0.085	17.(14.5-20.0)	0.189	39.9(33.0-46.0)	0.59	24.0(20.5-25.5)	0.184

TABLE 2. Summary of regression statistics for body measures of *Scorpaenodes rubrivinctus* based on pooled parallel slopes model of regression. Mean %SL based on *S. rubrivinctus* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between *S. rubrivinctus* and other species of *Scorpaenodes* and *Thysanichthys* (n = 7).

Measured Variable	Mean %SL(Min-Max)	$(\alpha + \alpha i)$	β	S.E.	Probability
Head Length:	46.4(44.8-47.3)	2.03+2.39	0.415	0.301	P < 0.001**
Snout Length:	14(12.7-14.9)	0.111+2.00	0.117	0.187	P < 0.001**
Orbit Diameter:	12.9(11.7-13.9)	1.89+0.693	0.1	0.203	P < 0.001**
Interorbital Width:	4.74(3.97-6.27)	0.593-0.489	0.047	0.144	P < 0.001**
Jaw Length:	20.6(20.1-21.5)	0.217-0.654	0.211	0.197	P < 0.05*
Postorbital Length:	20.8(19.8-21.4)	0.289-0.246	0.208	0.242	P < 0.05*
Greatest Body Depth:	34(33-35.4)	1.18-1.42	0.342	0.431	P < 0.05*
Predorsal Length:	43.5(40.6-46.2)	1.79+1.59	0.397	0.353	P < 0.001**
Anal Fin Length:	26.9(23.6-29.7)	2.13-1.05	0.256	0.352	P < 0.05*
Caudal Fin Length:	24.3(22.7-26.4)	1.13-1.56	0.247	0.582	P < 0.05*
Pectoral Fin Length:	31.1(24.4-36.7)	3+0.114	0.275	1.1	
Pelvic Fin Length:	21(9.61-27.5)	0.747-3.35	0.239	0.864	
First Dorsal Spine Length (D1):	7.75(5.86-9.35)	0.822+0.817	0.059	0.283	P < 0.05*
Second Dorsal Spine Length (D2):	12.6(9.38-14.5)	1.51+1.58	0.092	0.368	P < 0.001 **
Third Dorsal Spine Length (D3):	18.1(16.2-19.7)	2.08+3.71	0.116	0.33	P < 0.001 **
Fourth Dorsal Spine Length (D4):	18.6(16.6-20.3)	2.02+3.47	0.124	0.31	P < 0.001**
Fifth Dorsal Spine Length (D5):	15.8(10.6-17.9)	1.71+1.37	0.122	0.41	P < 0.05*
Penultimate Dorsal Spine Length (PDS):	6.44(5.16-7.75)	-0.2209	0.067	0.26	
Last Dorsal Spine Length (LDS):	12.4(11.1-14.4)	0.255+1.53	0.104	0.296	P < 0.001 **
First Anal Spine Length:	10.8(9.43-14)	1.804	0.089	0.279	P < 0.001 **
Second Anal Spine Length:	20.6(19.2-22.5)	0.339	0.202	0.333	P<0.05*
Third Anal Spine Length:	16(14.6-17.8)	-0.427	0.163	0.241	
Caudal Peduncle Depth:	9.24(8.42-9.73)	0.29-0.74	0.097	0.127	P < 0.001 **
Snout Tip to Base of D2:	45.1(43.2-48.9)	1.92 + 2.01	0.408	0.358	P < 0.001 **
Snout Tip to Base of D3:	48.6(45.8-51.5)	2.11+2.59	0.434	0.455	P < 0.001 **
Snout Tip to Base of D4:	52.4(49.4-54.6)	2.00 + 2.64	0.471	0.436	P < 0.001 **
Snout Tip to Base of D5:	55.4(53.7-59)	2.06+1.98	0.51	0.409	P < 0.001 **
Tip of D4 to Fin Membrane:	10.7(9.71-12.4)	1.44 + 2.88	0.0591	0.235	P < 0.001 **
Snout Tip to Pelvic Fin Insertion:	43.2(39.8-46.6)	1.84+1.22	0.399	0.575	P < 0.05*
D1 Base to D5 Base:	13.3(12.4-15.5)	0.533+0.134	0.125	0.276	
D5 Base to Pelvic Fin Insertion:	36.6(34.8-38.9)	1.21-1.30	0.365	0.457	P < 0.05*
D1 Base to Pelvic Fin Insertion:	33.6(32.3-34.6)	0.855-3.13	0.361	0.791	P < 0.001 **
D5 Base to LDS:	25.6(24-27.3)	-2.88	0.287	0.601	
LDS Base to Last D. Ray Base (LDR):	16.1(12.5-18)	-2.062	0.183	0.452	P < 0.05*
LDR Base to Last Anal Ray (LAR):	13.1(12.1-14.2)	-2.743	0.161	0.357	P < 0.001 **
Anal Fin Origin to LAR:	14.3(13.2-15.2)	0.58-0.0453	0.136	0.489	
Pelvic Fin Insertion to Anal Fin Origin:	33.1(29.9-36.4)	-4.41	0.377	0.59	P < 0.05*
D1 Base to Anal Fin Origin:	47.2(46.2-49.2)	-3.278	0.507	0.478	P < 0.001 **
LDS Base to Pelvic Fin Insertion:	45.3(42.7-48.2)	-2.344	0.477	0.551	
LDS Base to Base of LAR:	22.8(21.7-24.1)	-2.411	0.253	0.326	P < 0.001 **
LDR Base to Anal Fin Origin:	24.8(23.4-27.2)	0.304-0.422	0.25	0.346	
LDS Base to Anal Fin Origin:	27.2(25.5-31.5)	0.200-0.916	0.28	0.48	P<0.001**
D5 Base to Anal Fin Origin:	39.9(37.9-42.4)	-3.439	0.437	0.389	P < 0.001**

TABLE 3. Summary of regression statistics for body measures of *Scorpaenodes albaiensis* based on a pooled parallel slopes model of regression. Mean %SL based on *S. albaiensis* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between this species and *S. rubrivinctus* (n = 35).

	·
Head Length: 43.6(40.5-50.5) 2.03-1.11 0.415 0.146 P <	0.001**
Snout Length: 12.3(10.2-16.0) 0.111+0.00 0.117 0.0907 P <	< 0.05*
Orbit Diameter: 12.0(9.78-16.4) 1.89-1.05 0.1 0.0983 P < 0.0000000000000000000000000000000000	0.001**
Interorbital Width: 4.71(4.01-7.33) 0.593-0.596 0.046 0.0699	
Jaw Length: 21.1(19.3-24.1) 0.217-0.253 0.211 0.0952	
Postorbital Length: 21.0(18.7-22.9) 0.289-0.156 0.208 0.117	
Greatest Body Depth: 30.5(26.8-37.0) 1.18-3.1 0.342 0.208	
Predorsal Length: 43.1(40.1-48.7) 1.79-0.211 0.397 0.171 P < 0.171	0.001**
Anal Fin Length: 27.1(22.7-31.2) 2.13-1.49 0.256 0.171	
Caudal Fin Length: 25.0(15.7-29.4) 1.13-1.09 0.247 0.282	
Pectoral Fin Length: 31.9(20.1-41.1) 3-0.941 0.276 0.534	
Pelvic Fin Length: 24.9(23.1-28.3) 0.747-0.256 0.239 0.418	
First Dorsal Spine Length (D1): 5.94(3.17-9.26) 0.822-0.874 0.0593 0.137 P < 0.0000000000000000000000000000000000	0.001**
Second Dorsal Spine Length (D2): 9.29(6.03-12.0) 1.51-1.52 0.0916 0.178 P < 0.0916	0.001**
Third Dorsal Spine Length (D3): 11.8(8.15-15.4) 2.08-2.1 0.116 0.16 P < 0.0000000000000000000000000000000000	0.001**
Fourth Dorsal Spine Length (D4): 12.8(10.0-16.5) 2.02-1.95 0.125 0.15 P < 0.15	0.001**
Fifth Dorsal Spine Length (D5): 12.9(9.87-16.7) 1.71-1.48 0.123 0.199 P < 0.103	0.001**
Penultimate Dorsal Spine Length (PDS): 5.05(3.79-8.44) -0.794 0.0666 0.126	
Last Dorsal Spine Length (LDS): 9.54(7.27-11.8) 0.255-0.71 0.105 0.143 P < 0.143	0.001**
First Anal Spine Length: 8.29(5.89-11.2) -0.586 0.0887 0.135 P <	< 0.05*
Second Anal Spine Length: 20.7(17.9-23.1) -0.197 0.202 0.161	
Third Anal Spine Length: 16.6(14.8-19.2) -0.222 0.164 0.117	
Caudal Peduncle Depth: 9.82(8.56-11.6) 0.29-0.256 0.0972 0.0614	
Snout Tip to Base of D2: 44.1(40.5-49.6) 1.92-0.325 0.407 0.174 P <	< 0.05*
Snout Tip to Base of D3: 46.8(41.5-52.4) 2.11-0.601 0.435 0.22 P <	< 0.05*
Snout Tip to Base of D4: 49.9(44.4-54.6) 2-0.829 0.473 0.211 P <	0.001**
Snout Tip to Base of D5: 53.4(48.8-58.4) 2.06-0.967 0.509 0.198 P < 0	0.001**
Tip of D4 to Fin Membrane: 5.84(4.07-8.1) 1.44-1.56 0.0593 0.114 P < 0.0000000000000000000000000000000000	0.001**
Snout Tip to Pelvic Fin Insertion: 41.5(36.3-49.2) 1.84-0.976 0.398 0.279 P < 0.0000000000000000000000000000000000	0.001**
D1 Base to D5 Base: 11.9(10.0-17.9) 0.533-0.866 0.125 0.133	
D5 Base to Pelvic Fin Insertion: 33.6(29.1-38.3) 1.21-2.77 0.366 0.221	
D1 Base to Pelvic Fin Insertion: 32.3(27.8-49.1) 0.855-2.82 0.361 0.383	
D5 Base to LDS: 26.4(21.2-30.8) -1.32 0.288 0.291	
LDS Base to Last Dorsal Ray Base (LDR): 15.5(9.98-19.1) -1.315 0.183 0.219	
LDR Base to Last Anal Ray (LAR): 14.3(10.5-17.1) -0.953 0.161 0.173 P <	< 0.05*
Anal Fin Origin to LAR: 12.1(9.72-14.5) 0.58-1.38 0.137 0.237	
Pelvic Fin Insertion to Anal Fin Origin: 35.2(29.2-41.5) -2.79 0.378 0.285 P <	0.001**
D1 Base to Anal Fin Origin: 46.2(41.4-49.9) -2.288 0.508 0.231	
LDS Base to Pelvic Fin Insertion: 44.3(33.1-49.4) -1.774 0.479 0.267	
LDS Base to Base of LAR: 22.5(20.2-24.9) -1.431 0.254 0.158	
LDR Base to Anal Fin Origin: 23.0(20.5-25.9) 0.304-1.31 0.25 0.168	
LDS Base to Anal Fin Origin: 24.4(20.8-27.6) 0.2-1.99 0.279 0.232	
D5 Base to Anal Fin Origin: 39.5(34.3-42.1) -2.089 0.437 0.188	

TABLE 4. Summary of regression statistics for body measures of *Scorpaenodes minor* based on a pooled parallel slopes model of regression. Mean %SL based on *S. minor* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between this species and *S. rubrivinctus* (n=25).

Measured Variable	Mean %SL(Min-Max)	$(\alpha + \alpha i)$	β	S.E.	Probability
Head Length:	44.2(41.5-48.4)	2.03-1.15	0.415	0.195	P < 0.001**
Snout Length:	12.2(10.5-14.7)	0.111+0.00	0.117	0.121	
Orbit Diameter:	12.2(10.1-14)	1.89-1.18	0.1	0.132	P < 0.001**
Interorbital Width:	4.92(3.95-6.58)	0.593-0.501	0.047	0.094	P < 0.001**
Jaw Length:	21.4(20.2-23.4)	0.217-0.116	0.21	0.127	
Postorbital Length:	21.8(19.2-24.4)	0.289 + 0.00	0.208	0.157	
Greatest Body Depth:	30.2(24.5-33.9)	1.18-2.53	0.342	0.279	
Predorsal Length:	43.8(40.2-48.3)	1.79-0.418	0.397	0.229	P < 0.001**
Anal Fin Length:	27.5(25-31.4)	2.13-1.5	0.256	0.228	
Caudal Fin Length:	25.9(21.4-28.2)	1.13-0.718	0.247	0.378	
Pectoral Fin Length:	31.7(21.1-40.9)	3.0-1.66	0.275	0.715	
Pelvic Fin Length:	24.9(21.5-29)	0.747-0.405	0.234	0.561	
First Dorsal Spine Length (D1):	5.87(4.56-7.69)	0.822-0.847	0.059	0.183	P < 0.001**
Second Dorsal Spine Length (D2):	9.09(6.69-11.1)	1.51-1.51	0.092	0.239	P < 0.001**
Third Dorsal Spine Length (D3):	11.6(8.98-13.4)	2.08-2.07	0.116	0.214	P < 0.001**
Fourth Dorsal Spine Length (D4):	12(9.63-14.6)	2.02-2.15	0.124	0.201	P < 0.001**
Fifth Dorsal Spine Length (D5):	11.7(8.99-14.3)	1.71-1.9	0.122	0.266	P < 0.001**
Penultimate Dorsal Spine Length (PDS):	4.14(2.72-6.45)	-0.856	0.067	0.169	
Last Dorsal Spine Length (LDS):	8.23(5.13-10.5)	0.255-1.02	0.104	0.192	P < 0.001**
First Anal Spine Length:	7.46(5.19-9.07)	-0.586	0.088	0.181	P < 0.05*
Second Anal Spine Length:	20.3(15.9-24.6)	-0.197	0.202	0.216	
Third Anal Spine Length:	15.6(12.3-17.7)	-0.2712	0.163	0.156	
Caudal Peduncle Depth:	10(8.42-11.4)	0.29-0.191	0.097	0.082	
Snout Tip to Base of D2:	44.6(42.2-47.7)	1.92-0.62	0.408	0.232	P < 0.05*
Snout Tip to Base of D3:	47.3(43.1-50.6)	2.11-0.822	0.434	0.295	P < 0.05*
Snout Tip to Base of D4:	50.6(47.2-57)	2-0.895	0.471	0.283	P < 0.05*
Snout Tip to Base of D5:	54.4(50.7-60.4)	2.06-0.912	0.51	0.265	P < 0.001**
Tip of D4 to Fin-Membrane:	5.94(3.89-8.96)	1.44-1.44	0.059	0.152	P < 0.001**
Snout Tip to Pelvic Fin Insertion:	40.4(38-44.2)	1.84-1.64	0.399	0.373	
D1 Base to D5 Base:	12.1(9.36-16.5)	0.533-0.691	0.125	0.179	
D5 Base to Pelvic Fin Insertion:	33.5(24.3-37.3)	1.21-2.27	0.365	0.296	
D1 Base to Pelvic Fin Insertion:	31.7(28.1-46.2)	0.855-2.26	0.361	0.513	
D5 Base to LDS:	26.3(19.4-43.3)	-1.32	0.287	0.39	
LDS Base to Last Dorsal Ray Base (LDR):	15.3(12.7-27)	-0.986	0.183	0.293	
LDR Base to Last Anal Ray (LAR):	14(10.3-24.5)	-0.953	0.161	0.231	P < 0.05*
Anal Fin Origin to LAR:	13.3(10.7-34.3)	0.58-0.614	0.136	0.317	
Pelvic Fin Insertion to Anal Fin Origin:	35.7(26-46.7)	-2.79	0.377	0.382	P < 0.001**
D1 Base to Anal Fin Origin:	45.7(42.3-48.5)	-1.708	0.507	0.31	
LDS Base to Pelvic Fin Insertion:	44.2(40.8-48.6)	-1.215	0.477	0.358	
LDS Base to Base of LAR:	21.6(18.2-24.5)	-1.284	0.253	0.211	
LDR Base to Anal Fin Origin:	22.7(19.5-25.2)	0.304-1.08	0.25	0.225	
LDS Base to Anal Fin Origin:	24.3(19.5-37.7)	0.2-1.36	0.28	0.311	
D5 Base to Anal Fin Origin:	38.2(30.7-45.7)	-1.819	0.436	0.252	

TABLE 5. Summary of regression statistics for body measures of *T. crossotus* based on a pooled parallel slopes model of regression. Mean %SL based on *T. crossotus* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between this species and *S. rubrivinctus* (n = 3).

Measured Variable	Mean %SL(Min-Max)	$(\alpha + \alpha i)$	β	S.E.	Probability
Head Length:	45.7(44.8-47)	2.03-1.11	0.415	0.386	P < 0.001**
Snout Length:	11.2(10.8-11.5)	0.111+0.00	0.117	0.24	P < 0.05*
Orbit Diameter:	14.2(14.1-14.5)	1.89-1.05	0.1	0.26	
Interorbital Width:	6.05(5.02-7.01)	0.593-0.596	0.047	0.185	P < 0.05*
Jaw Length:	19.5(18.9-20.6)	0.217-0.253	0.21	0.252	
Postorbital Length:	21.1(20.2-22)	0.289-0.156	0.208	0.31	
Greatest Body Depth:	39.4(38.7-39.9)	1.18-3.1	0.342	0.552	P < 0.001**
Predorsal Length:	42.8(41.2-45.2)	1.79-0.211	0.397	0.452	
Anal Fin Length:	29.8(28.1-31.9)	2.13-1.49	0.256	0.451	
Caudal Fin Length:	25.9(19.9-29.7)	1.13-1.09	0.247	0.746	
Pectoral Fin Length:	37.3(27.7-45.3)	3-0.941	0.275	1.41	
Pelvic Fin Length:	28.1(27-29.2)	0.747-0.256	0.234	1.11	
First Dorsal Spine Length (D1):	8.81(7.96-9.6)	0.822-0.874	0.059	0.363	
Second Dorsal Spine Length (D2):	14(12-15.1)	1.51-1.52	0.092	0.472	
Third Dorsal Spine Length (D3):	17.9(15.9-19.8)	2.08-2.1	0.116	0.423	
Fourth Dorsal Spine Length (D4):	18.1(16.2-19)	2.02-1.95	0.124	0.397	
Fifth Dorsal Spine Length (D5):	17.7(16.5-18.9)	1.71-1.48	0.122	0.526	
Penultimate Dorsal Spine Length (PDS):	8.58(7.2-9.94)	-0.794	0.067	0.334	
Last Dorsal Spine Length (LDS):	10.5(9.05-11.8)	0.255-0.71	0.104	0.379	
First Anal Spine Length:	10.6(8.94-11.4)	-0.586	0.088	0.357	
Second Anal Spine Length:	24.2(22.7-26.1)	-0.197	0.202	0.427	
Third Anal Spine Length:	17.9(16.9-19.1)	-0.222	0.163	0.309	
Caudal Peduncle Depth:	10.5(10.2-10.7)	0.29-0.256	0.097	0.162	P < 0.05*
Snout Tip to Base of D2:	44.1(42.2-46.4)	1.92-0.325	0.408	0.459	
Snout Tip to Base of D3:	46.9(44.8-49)	2.11-0.601	0.434	0.583	
Snout Tip to Base of D4:	50.6(49.2-52.2)	2-0.829	0.471	0.559	
Snout Tip to Base of D5:	55(53.2-57.2)	2.06-0.967	0.501	0.524	
Tip of D4 to Fin-Membrane:	10.7(9.81-11.2)	1.44-1.56	0.059	0.301	
Snout Tip to Pelvic Fin Insertion:	46(43-50.7)	1.84-0.976	0.399	0.738	
D1 Base to D5 Base:	14.1(13-15.1)	0.533-0.866	0.125	0.353	
D5 Base to Pelvic Fin Insertion:	40.9(40.6-41.1)	1.21-2.77	0.365	0.586	P < 0.001**
D1 Base to Pelvic Fin Insertion:	39.8(39.3-40.5)	0.855-2.82	0.361	1.01	
D5 Base to LDS:	28.3(25.6-32.2)	-1.32	0.287	0.771	
LDS Base to Last Dorsal Ray Base (LDR):	20.6(18.5-21.8)	-1.315	0.183	0.579	P < 0.001 **
LDR Base to Last Anal Ray (LAR):	14.5(13.5-15.8)	-0.953	0.161	0.457	
Anal Fin Origin to LAR:	13.8(12.2-14.8)	0.58-1.38	0.136	0.627	
Pelvic Fin Insertion to Anal Fin Origin:	32.7(30.6-36.8)	-2.79	0.377	0.756	
D1 Base to Anal Fin Origin:	57.2(55.2-59.7)	-2.288	0.507	0.612	P < 0.001 **
LDS Base to Pelvic Fin Insertion:	47.3(44.3-51.7)	-1.774	0.477	0.707	
LDS Base to Base of LAR:	29.7(28-30.7)	-1.431	0.253	0.418	P < 0.001 **
LDR Base to Anal Fin Origin:	25.1(23.4-27.5)	0.304-1.31	0.25	0.444	
LDS Base to Anal Fin Origin:	33.2(31.4-34.4)	0.2-1.99	0.28	0.615	P < 0.001 **
D5 Base to Anal Fin Origin:	49.2(48.1-50.8)	-2.089	0.436	0.498	P < 0.001**

TABLE 6. Summary of regression statistics for body measures of *T. evides* based on a pooled parallel slopes model of regression. Mean %SL based on *T. evides* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between this species and *S. rubrivinctus* (n = 6).

Measured Variable	Mean %SL(Min-Max)	$(\alpha + \alpha i)$	β	S.E.	Probability
Head Length:	41.4(40.9-42.2)	2.03-1.11	0.415	0.271	P < 0.001**
Snout Length:	10.2(9.87-10.5)	0.111+0.00	0.117	0.169	P < 0.001**
Orbit Diameter:	13.7(13.0-14.3)	1.89-1.05	0.1	0.183	
Interorbital Width:	5 11(4 73-6 07)	0 593-0 596	0.047	0.13	
Jaw Length	21.4(20.3-22.1)	0.217-0.253	0.21	0.177	
Destarkitel Langth	19 7(17 6 20 4)	0.220.0.156	0.21	0.219	
	18.7(17.0-20.4)	0.289-0.130	0.208	0.218	
Greatest Body Depth:	35.4(33.0-37.6)	1.18-3.1	0.342	0.388	D < 0.001**
Predorsal Length:	40.5(38.9-41.2)	1.79-0.211	0.397	0.318	P < 0.001***
Anai Fin Length:	30.0(27.0-33.0)	2.13-1.49	0.256	0.517	
Caudal Fin Length:	27.7(25.6-29.1)	2.0.041	0.247	0.524	
Petrio Ein Longth	32.3(23.2-30.0) 26.4(24.0.28.2)	3-0.941	0.275	0.995	
First Darsel Snine Length (D1)	20.4(24.9-26.5)	0.747-0.236	0.254	0.778	
First Dorsal Spine Length (D1):	11 2(8 88 12 0)	1.51.1.52	0.039	0.233	<b>P</b> < 0.05*
Third Dersel Spine Length (D2):	11.2(8.88-12.9)	2.08.2.1	0.092	0.332	P < 0.03
Fourth Dorsal Spine Length (D4):	14.2(13.0-13.1) 15 1(12 7 16 5)	2.08-2.1	0.110	0.297	$P < 0.03^{\circ}$
Fifth Dorsal Spine Length (D5):	15.1(13.7-10.5)	2.02-1.93	0.124	0.279	r < 0.05
Popultimate Dorsel Spine Length (BDS):	6 70(5 58 7 74)	0.704	0.122	0.309	
Last Dorsal Spine Length (LDS):	(0.79(0.38-7.74))	0 255 0 71	0.104	0.255	
East Dorsal Spine Length (LDS).	7 57(6 45 8 48)	0.235-0.71	0.104	0.200	
Second Anal Spine Length:	20.9(10.7.22.3)	-0.380	0.000	0.251	
Third Anal Spine Length	20.9(19.7-22.3)	-0.197	0.202	0.3	
I nird Anai Spine Length:	17.0(16.2-17.4)	-0.222	0.165	0.217	
Caudal Peduncle Depth:	11.2(10.1-12.2)	0.29-0.256	0.097	0.114	P < 0.05*
Shout Tip to Base of D2:	42.0(40.2-43.8)	1.92-0.325	0.407	0.323	P < 0.001**
Shout Tip to Base of D3:	45.2(42.8-47.0)	2.11-0.601	0.434	0.409	P < 0.001**
Shout Tip to Base of D4:	48.6(46.5-51.7)	2.00-0.829	0.471	0.393	P< 0.001**
Shout Tip to Base of DS:	53.0(50.8-55.0)	2.06-0.967	0.51	0.368	P < 0.05*
Tip of D4 to Fin Membrane:	6.88(6.03-8.46)	1.44-1.56	0.059	0.211	P < 0.001**
Snout Tip to Pelvic Fin Insertion:	41.5(39.7-45.2)	1.84-0.976	0.399	0.518	
D1 Base to D5 Base:	14.1(12.5-15.7)	0.533-0.866	0.125	0.248	
D5 Base to Pelvic Fin Insertion:	38.3(35.9-40.5)	1.21-2.77	0.365	0.412	
D1 Base to Pelvic Fin Insertion:	35.5(33.4-38.6)	0.855-2.82	0.361	0.712	
D5 Base to LDS:	28.9(26.8-30.3)	-1.32	0.287	0.542	
LDS Base to Last Dorsal Ray Base (LDR):	18.5(17.2-19.9)	-1.315	0.183	0.407	
LDR Base to Last Anal Ray (LAR):	16.4(15.0-17.2)	-0.953	0.161	0.321	P < 0.05*
Anal Fin Origin to LAR:	15.4(14.2-16.7)	0.58-1.38	0.136	0.44	
Pelvic Fin Insertion to Anal Fin Origin:	32.1(30.5-34.8)	-2.79	0.377	0.531	
D1 Base to Anal Fin Origin:	50.5(48.1-51.7)	-2.288	0.507	0.43	P < 0.05*
LDS Base to Pelvic Fin Insertion:	47.4(45.6-49.3)	-1.774	0.477	0.497	
LDS Base to Base of LAR:	26.5(25.6-27.7)	-1.431	0.253	0.293	P < 0.05*
LDR Base to Anal Fin Origin:	27.6(26.6-28.7)	0.304-1.31	0.25	0.312	
LDS Base to Anal Fin Origin:	28.8(27.5-30.0)	0.20-1.99	0.28	0.432	
D5 Base to Anal Fin Origin:	43.2(41.3-44.8)	-2.089	0.436	0.35	P < 0.05*

TABLE 7. Summary of regression statistics for body measures of *Scorpaenodes littoralis* based on a pooled parallel slopes model of regression. Mean %SL based on *S. littoralis* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between this species and *S. rubrivinctus* (n = 28).

Measured Variable	Mean %SL(Min-Max)	$(\alpha + \alpha i)$	β	S.E.	Probability
Head Length:	42.7(39.6-44.8)	2.03-1.11	0.415	0.149	P < 0.001**
Snout Length:	10.2(9.3-11.3)	0.111 + 0.00	0.117	0.092	P < 0.001 **
Orbit Diameter:	12.9(10.7-14.9)	1.89-1.05	0.1	0.1	P < 0.001 **
Interorbital Width:	5.07(4.07-5.94)	0.593-0.596	0.047	0.071	
Jaw Length:	22.2(19.9-23.9)	0.217-0.253	0.21	0.097	P < 0.001**
Postorbital Length:	19.7(16.2-21.7)	0.289-0.156	0.208	0.12	
Greatest Body Depth:	34.2(30.9-37.4)	1.18-3.1	0.342	0.213	
Predorsal Length:	40.0(37.2-42.6)	1.79-0.211	0.397	0.174	P < 0.001**
Anal Fin Length:	29.5(25.5-32.8)	2.13-1.49	0.256	0.174	
Caudal Fin Length:	27.4(24.3-29.8)	1.13-1.09	0.247	0.287	
Pectoral Fin Length:	32.0(26.6-37.8)	3-0.941	0.275	0.544	
Pelvic Fin Length:	25.1(8.21-29.1)	0.747-0.256	0.234	0.427	
First Dorsal Spine Length (D1):	7.23(5.97-13.0)	0.822-0.874	0.059	0.14	
Second Dorsal Spine Length (D2):	11.5(9.41-18.1)	1.51-1.52	0.092	0.182	P < 0.05*
Third Dorsal Spine Length (D3):	14.4(12.1-19.8)	2.08-2.1	0.116	0.163	P < 0.001 **
Fourth Dorsal Spine Length (D4):	15.1(12.7-18.8)	2.02-1.95	0.124	0.153	P < 0.001 **
Fifth Dorsal Spine Length (D5):	14.7(5.46-18.3)	1.71-1.48	0.122	0.203	
Penultimate Dorsal Spine Length (PDS):	6.18(4.25-10.1)	-0.794	0.067	0.129	
Last Dorsal Spine Length (LDS):	10.4(7.65-12.8)	0.255-0.71	0.104	0.146	P < 0.05*
First Anal Spine Length:	8.11(5.89-10.7)	-0.586	0.088	0.138	P < 0.05*
Second Anal Spine Length:	21.6(18.7-24.3)	-0.197	0.202	0.165	
Third Anal Spine Length:	16.1(14.0-18.0)	-0.222	0.163	0.119	
Caudal Peduncle Depth:	9.68(8.81-10.5)	0.29-0.256	0.097	0.063	
Snout Tip to Base of D2:	41.7(38.1-45.0)	1.92-0.325	0.408	0.177	P < 0.001**
Snout Tip to Base of D3:	45.2(42.3-49.3)	2.11-0.601	0.434	0.225	P < 0.001**
Snout Tip to Base of D4:	49.0(46.1-52.9)	2-0.829	0.471	0.215	P < 0.001**
Snout Tip to Base of D5:	52.7(50.0-57.2)	2.06-0.967	0.51	0.202	P < 0.001**
Tip of D4 to Fin Membrane:	7.25(5.88-9.11)	1.44-1.56	0.059	0.116	P < 0.001**
Snout Tip to Pelvic Fin Insertion:	40.4(37.2-49.5)	1.84-0.976	0.399	0.284	P < 0.05*
D1 Base to D5 Base:	13.1(11.3-15.3)	0.533-0.866	0.125	0.136	
D5 Base to Pelvic Fin Insertion:	36.9(32.3-40.5)	1.21-2.77	0.365	0.226	
D1 Base to Pelvic Fin Insertion:	34.6(31.2-37.8)	0.855-2.82	0.361	0.39	
D5 Base to LDS:	26.0(22.3-31.9)	-1.32	0.287	0.297	
LDS Base to Last Dorsal Ray Base (LDR):	16.2(13.6-22.4)	-1.315	0.183	0.223	
LDR Base to Last Anal Ray (LAR):	13.9(11.7-17.1)	-0.953	0.161	0.176	
Anal Fin Origin to LAR:	14.1(12.2-15.7)	0.58-1.38	0.136	0.241	
Pelvic Fin Insertion to Anal Fin Origin:	35.0(30.0-39.8)	-2.79	0.377	0.291	P < 0.05*
D1 Base to Anal Fin Origin:	48.4(33.9-52.1)	-2.288	0.507	0.236	P < 0.05*
LDS Base to Pelvic Fin Insertion:	46.2(43.3-50.8)	-1.774	0.477	0.272	
LDS Base to Base of LAR:	23.1(14.7-28.9)	-1.431	0.253	0.161	
LDR Base to Anal Fin Origin:	24.7(13.2-27.6)	0.304-1.31	0.25	0.171	
LDS Base to Anal Fin Origin:	26.0(13.2-29.6)	0.2-1.99	0.28	0.237	
D5 Base to Anal Fin Origin:	40.7(36.5-43.5)	-2.089	0.436	0.192	P < 0.001**

TABLE 8. Summary of regression statistics for body measures of *Scorpaenodes smithi* based on a pooled parallel slopes model of regression. Mean %SL based on *S. smithi* alone. P-values indicate significance levels for contrasts among Y-intercepts that are significantly different between this species and *S. rubrivinctus* (n = 8).

Measured Variable	% SL (Min - Max)	( <b>a</b> + <b>a</b> i)	β	S. E.	Probability
Head Length:	42.9(40.5-44.2)	2.03-1.11	0.415	0.244	P < 0.001**
Snout Length:	12(10.1-13.2)	0.0718+0.00	0.117	0.151	
Orbit Diameter:	13.3(12.1-14.9)	1.9-1.05	0.1	0.166	P < 0.001**
Interorbital Width:	6.96(6.13-7.68)	0.445-0.578	0.047	0.121	P < 0.001**
Jaw Length:	22.4(21.6-23.6)	0.381-0.265	0.21	0.165	
Postorbital Length:	19.9(18.5-20.8)	0.409-0.168	0.208	0.194	P < 0.001**
Greatest Body Depth:	40.3(37.2-42.8)	1.03-3.09	0.342	0.359	P < 0.001**
Predorsal Length:	41.9(39.9-44.6)	1.89-0.214	0.397	0.301	P < 0.05*
Anal Fin Length:	31.3(29.6-33.4)	2.18-1.49	0.256	0.284	
Caudal Fin Length:	26.8(25.1-29.5)	1.28-1.1	0.247	0.465	
Pectoral Fin Length:	29.6(27.1-33)	3.04-0.945	0.275	0.874	P < 0.05*
Pelvic Fin Length:	26(24.9-27.8)	0.9-0.278	0.234	0.685	
First Dorsal Spine Length (D1):	8.53(7.93-10.3)	0.828-0.875	0.059	0.227	
Second Dorsal Spine Length (D2):	11.6(9.14-13.1)	1.48-1.51	0.092	0.295	
Third Dorsal Spine Length (D3):	15.5(13.4-17.7)	2.14-2.11	0.116	0.265	
Fourth Dorsal Spine Length (D4):	16.4(13.4-18.9)	2.07-1.97	0.124	0.261	
Fifth Dorsal Spine Length (D5):	16.2(15.3-17.3)	1.68-1.49	0.122	0.336	
Penultimate Dorsal Spine Length (PDS):	4.95(3.47-7.46)	-1.029	0.067	0.218	P < 0.05*
Last Dorsal Spine Length (LDS):	10.2(8.91-12.4)	0.236-0.710	0.104	0.234	
First Anal Spine Length:	3.79(3.07-4.21)	-0.568	0.088	0.224	P < 0.001**
Second Anal Spine Length:	14.7(14-15.3)	-0.195	0.202	0.275	P < 0.001**
Third Anal Spine Length:	14.2(11.9-15.3)	0.02 + 0.00	0.163	0.2	P < 0.001**
Caudal Peduncle Depth:	11.2(10.6-12.3)	0.323-0.255	0.097	0.104	P < 0.05*
Snout Tip to Base of D2:	42.5(40.3-45.5)	2.12-0.342	0.408	0.304	P < 0.001**
Snout Tip to Base of D3:	45.6(42.4-49.1)	1.93-0.583	0.434	0.406	P < 0.05*
Snout Tip to Base of D4:	49.5(47.6-51.5)	1.77-0.803	0.471	0.387	P < 0.05*
Snout Tip to Base of D5:	53.5(51.5-54.9)	1.81-0.934	0.51	0.377	P < 0.05*
Tip of D4 to Fin Membrane:	8.21(7.48-9.04)	1.39-1.55	0.059	0.187	P < 0.05*
Snout Tip to Pelvic Fin Insertion:	44(39.2-53.8)	1.97-0.992	0.399	0.462	
D1 Base to D5 Base:	14.7(13.2-16)	0.48-0.847	0.125	0.23	P < 0.05*
D5 Base to Pelvic Fin Insertion:	42.5(40.1-46.2)	1.17-2.77	0.365	0.378	P < 0.001**
D1 Base to Pelvic Fin Insertion:	40.2(38.3-42.8)	1.01-2.83	0.361	0.632	
D5 Base to LDS:	26.2(23.7-30.4)	-1.18	0.287	0.479	
LDS Base to Last Dorsal Ray Base (LDR):	17.2(15.6-18.6)	-1.261	0.183	0.367	
LDR Base to Last Anal Ray (LAR):	15.6(13.6-17)	-0.962	0.161	0.288	P < 0.05*
Anal Fin Origin to LAR:	15.9(14.2-17.6)	0.763-1.39	0.136	0.39	
Pelvic Fin Insertion to Anal Fin Origin:	32.6(25.7-39.6)	-2.79	0.377	0.489	
D1 Base to Anal Fin Origin:	50.1(48.7-52)	-2.621	0.507	0.431	
LDS Base to Pelvic Fin Insertion:	49.1(43.6-53.1)	-2.016	0.477	0.451	P < 0.05*
LDS Base to Base of LAR:	25.5(23.2-27.5)	-1.57	0.253	0.271	P < 0.05*
LDR Base to Anal Fin Origin:	28.3(25.7-29.9)	0.334-1.31	0.25	0.275	P < 0.001**
LDS Base to Anal Fin Origin:	29.9(27.8-31.8)	-2.0038	0.28	0.389	
D5 Base to Anal Fin Origin:	42.2(40.8-43.7)	-2.129	0.436	0.312	

TABLE 9. Largest 10 positive and 10 most negative loadings on first size-adjusted principal component among 43 original measured variables used to compute size-adjusted principal components analysis. Original variables with relatively low, non-coincident, loadings on size-adjusted eigenvectors not shown. Note that same variables indicate significant differences among species, when regressed against standard length.

Measured Variable	PC I	PC II	PC III
First Anal Spine Length	0.0573	-0.0972	-0.0011
Second Anal Spine Length	0.0363	-0.0353	0.0013
Pelvic Fin Insertion to Anal Fin Origin	0.0342	0.0022	0.0004
Snout Length	0.0317	0.0056	0.0211
Postorbital Length	0.0282	0.0081	0.0128
Third Anal Spine	0.0268	-0.0129	-0.0013
Predorsal Length	0.0243	0.0074	0.0091
Snout Tip to Base of Second Dorsal Spine	0.0235	0.0052	0.01
Snout Tip to Base of Third Dorsal Spine	0.0203	0.0041	0.0095
Pelvic Fin Length	0.0192	0.0193	-0.0105
Greatest Body Depth	-0.0197	0.0142	-0.0074
Anal Fin Origin to Base of Last Anal Ray	-0.0207	0.0115	-0.0089
Last Dorsal Spine Length	-0.0221	-0.0198	-0.0087
Fifth Dorsal Spine Length	-0.0318	-0.0095	0.0105
Second Anal Spine Length	-0.0382	-0.0166	0.0141
Penultimate Dorsal Spine Length	-0.0338	-0.0413	-0.0726
Fourth Dorsal Spine Length	-0.0393	-0.0221	0.0166
Third Dorsal Spine Length	-0.0432	-0.0223	0.0122
First Dorsal Spine Length	-0.0491	-0.007	0.0227
Tip of Fourth Dorsal Spine to Fin Membrane	-0.0649	-0.0317	0.0344

TABLE 10. Loadings for variables of largest 3 principal components derived from countable features accounting for 88.3% of the total variation in the sample (PC I - 58.0%; PC II - 18.5%; PC III - 11.8%).

Counted Variable	PC I	PC II	PC III
Dorsal fin-rays	0.4797	0.8098	0.3267
Mean Pectoral Fin Rays (Left+Right/2)	0.8306	-0.3721	0.1307
Mean Gill Rakers (Left+Right/2)	0.7833	-0.3313	0.4186
Vertical Scale Rows	0.8531	0.1128	-0.2666
Mean Lateral Line Scales (Left+Right/2)	0.8065	0.104	-0.4535