

REVIEW OF THE SCORPIONFISH GENUS *MAXILLICOSTA*  
(PISCES: SCORPAENIDAE), WITH A DESCRIPTION  
OF THREE NEW SPECIES FROM THE  
AUSTRALIAN-NEW ZEALAND REGION

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ABSTRACT

The scorpionfish genus *Maxillicosta* Whitley, 1935, is expanded to include the genus *Cristula* De Buen, 1961. Each genus formerly consisted of a single species: *Maxillicosta reticulata* (De Buen, 1961) from Juan Fernández off the Chilean coast, *M. scabriceps* Whitley, 1935, from temperate waters of Australia. Besides these, two new Australian species, *M. whitleyi* and *M. lopholepis*, and a new species, *M. raoulensis*, from the Kermadec Islands in the southwestern Pacific, are described and illustrated. A key to the species is given. The closest relatives of the five species of *Maxillicosta* are fishes of the genus *Neosebastes*. Possible explanations of the distribution of *Maxillicosta* are discussed. A device for measuring interorbital depths is described.

The genus *Cristula* was proposed by Fernando De Buen (1961) for the species *C. reticulata* from Isla Más a Tierra of the Juan Fernández group 660 km off Chile. Examination by us of two specimens revealed that *C. reticulata* is not closely related to other southeastern Pacific species, but its relationships are with *Maxillicosta*, a genus based on a single species, *M. scabriceps* Whitley, 1935. *M. scabriceps* is known from temperate waters of Australia. Our examination of specimens of *Maxillicosta* indicated that there are three Australian species, two of which we here describe as new.

Twelve specimens of another new species were collected at Raoul Island of the Kermadec group in 1952 during the Danish GALATHEA Expedition. The Kermadec Islands are a remote group of small volcanic islands situated in temperate waters at about 30°S latitude and lying about 1000 km northeast of New Zealand, a location somewhat intermediate between Australia and Juan Fernández.

Comparison of the three Australian species and the Kermadec species with *C. reticulata* from Más a Tierra leads us to conclude that all species belong in the genus *Maxillicosta*, which is reviewed in this paper.

*Maxillicosta* is easily distinguished from all other scorpionfishes by the presence of two to seven ridges on the maxilla and about three ridges on the dentary. *Scorpaena loppei* Cadenat, 1945 (see Eschmeyer, 1969, Fig. 2e) is the only other scorpionfish having a ridged maxillary. In *S. loppei*, however, the ridge consists of but a single midlateral crest.

METHODS

Methods follow those of Eschmeyer (1969). Measurements are those commonly used to describe teleosts except pectoral fin length is measured from the base of the upper ray to the tip of the longest ray with the fin folded back. Measurements originating at the front of the specimen are taken on the left side beginning at the most anterior point of the left premaxillary.

Some head spines in species of *Maxillicosta* are not standard and elaboration is provided in the text.

The last ray of each median fin is usually a close-set double ray, counted as one.

Two species, *M. scabriceps* and *M. whitleyi*, could be visually distinguished on the basis of interorbital depth. An instrument was designed to quantify this difference. The interorbital depth gauge is a simple device which can measure accurately to

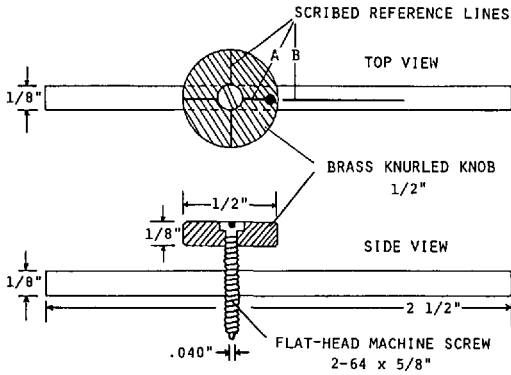


Figure 1. Interorbital depth gauge (see text for explanation).

within 0.1 mm and could be used for other measurements involving a depression (see Fig. 1 for specifications). After assembly, the quarter turn scribed line which comes closest to the scribed line on the bar when the screw is flush is marked (dot) to indicate the flush position. The bar is set across the interorbit at the middle of the eyes. The screw is turned until its tip touches the bottom of the interorbit. This is most easily seen by looking at the fish "head on." The number of turns needed to retract the screw to a position flush with the bar is counted to the nearest quarter turn. The clockwise quarter turns needed to line up the reference marks (A and B) are added to the full turns needed to withdraw the screw to the flush position (dot on reference line A will line up with scribed line B). With a thread size of 64 threads per inch, each quarter turn equals 0.099 mm, so that, for example, a three-quarter turn plus four full turns equals 19 quarter turns or 1.9 mm interorbital depth.

Abbreviations for repositories of material examined are: AMS—Australian Museum, Sydney; CAS—California Academy of Sciences, San Francisco; CSIRO—Commonwealth Scientific Industrial and Research Organization, Cronulla; SAM—South Australian Museum, Adelaide; SIO—Scripps Institution of Oceanography, La Jolla; USNM—National Museum of Natural His-

tory, Smithsonian Institution, Washington; WAM—Western Australian Museum, Perth; ZMUC—Universitets Zoologiske Museum, Copenhagen.

### *Maxillicosta* Whitley

*Maxillicosta* Whitley, 1935, p. 246 (type-species *Maxillicosta scabriceps* Whitley by original designation, monotypic). Marshall, 1965, pp. 419, 423 (in key, diagnosis).  
*Cristula* De Buen, 1961, pp. 24, 26 (type-species *Cristula reticulata* De Buen by original designation, monotypic).

**Diagnosis.**—Dorsal fin with 13 spines; dorsal soft rays 6-8; membrane of spinous dorsal fin deeply incised. Anal fin normally with 3 spines; anal soft rays 5. Caudal fin with 11-13 principal rays. Pectoral fin rays 20-27. Pelvic fin with 1 spine and 5 soft rays. Vertebrae 25-27, usually 26. Branchiostegals 7. Maxillary with several distinct ridges running longitudinally on posterior outer face; similar ridges also on underside of dentary. Scales modified, ending in a spine or soft point in some species. Scales present on cheek, behind eye, and on breast; none on maxillary or interopercle. Eye large. Supraocular margin with numerous spines. Gasbladder absent. Infraorbital bones with a large number of small pungent spines or spinules. Third infraorbital bone (second suborbital bone of Mastubara, 1943) with a somewhat modified T-shape but not broadly attached to preopercle. Villiform teeth in jaws, on vomer, and on palatines.

**Relationships.**—Though subfamilial placement is uncertain, the nearest relatives of *Maxillicosta* appear to be fishes of the genus *Neosebastes* in the subfamily Neosebastinae (established by Matsubara (1943) on the basis of an osteological examination of *N. entaxis*). Two workers, Scott (1962) and Mees (1964), combined *Maxillicosta* with *Neosebastes*. The genus *Neosebastes* is composed of six species and is restricted to the Australian region except for *N. entaxis*, which occurs in the South China Sea and Japan. *Maxillicosta* possesses a number of features seen in *Neosebastes*: third infra-

orbital bone of modified T-shape, becoming more or less narrow posteriorly, truncate at the posterior extremity; about 26 vertebrae; and such apparently specialized features as 13 somewhat elongate dorsal spines and about 7-8 dorsal soft rays (low for the family). *Maxillicosta* differs, however, in the possession of a number of specialized features not seen in *Neosebastes*: a somewhat higher pectoral ray count; ridges on the maxillary and dentary, a lower number of principal caudal rays, more fusion in the caudal skeleton, and the absence of a gas-bladder.

KEY TO THE SPECIES OF *MAXILLICOSTA*

- 1a. Body with reticulate brown pattern mirroring scale arrangement; dorsal fin mottled and banded with brown, without a prominent black spot; scales on back above lateral line (Fig. 2a) with exposed margin not notably elevated ..... *M. reticulata* (Fig. 9)
- 1b. Body without reticulate color pattern; dorsal fin with a black spot at about spines 4-9; scales, particularly those on head and above lateral line anteriorly, with exposed margin elevated and somewhat pointed ..... 2
- 2a. Scales above lateral line behind head variable but without a strong median ridge or serrated ridge and not ending in a well-developed round hard spine (some scales about as in Fig. 2b) ..... 3
- 2b. Scales above lateral line behind head with strong median ridge, either serrate or ending in a well-developed spine, running up and back through middle of exposed portion of scale (Fig. 2c-d) ..... 4
- 3a. Nasal bone with 2-3 spinous points; spines on ridge above eye well-developed and separate, numbering 8-13; interorbit deep (interorbital width/interorbital depth 1.7-2.2) ..... *M. scabriceps* (Fig. 3)
- 3b. Nasal bone with 4-9 spinous points; 12-19 weakly developed spinous points on ridge above eye; interorbit shallow (interorbital width/interorbital depth 2.5-3.3) ..... *M. whitleyi* (Fig. 5)
- 4a. Pectoral fin rays 21-22; gill rakers, including rudiments about 11; scales on back above lateral line with a strong spine on margin not preceded by a serrate ridge (Fig. 2c) ..... *M. lopholepis* (Fig. 6)
- 4b. Pectoral fin rays 25-27; gill rakers, including rudiments, 14-17; most scales on back above lateral line anterior to soft dorsal fin with serrate ridge across posterior field (Fig. 2d) ..... *M. raoulensis* (Figs. 7-8)

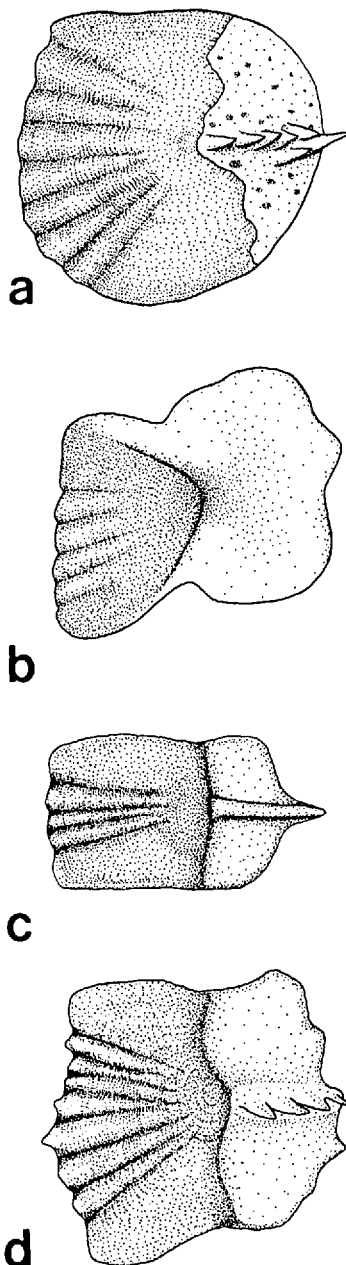


Figure 2. Scales from upper back behind head in species of *Maxillicosta*: a, *M. reticulata*; b, *M. scabriceps*, and *M. whitleyi*; c, *M. lopholepis*; d, *M. raoulensis*.

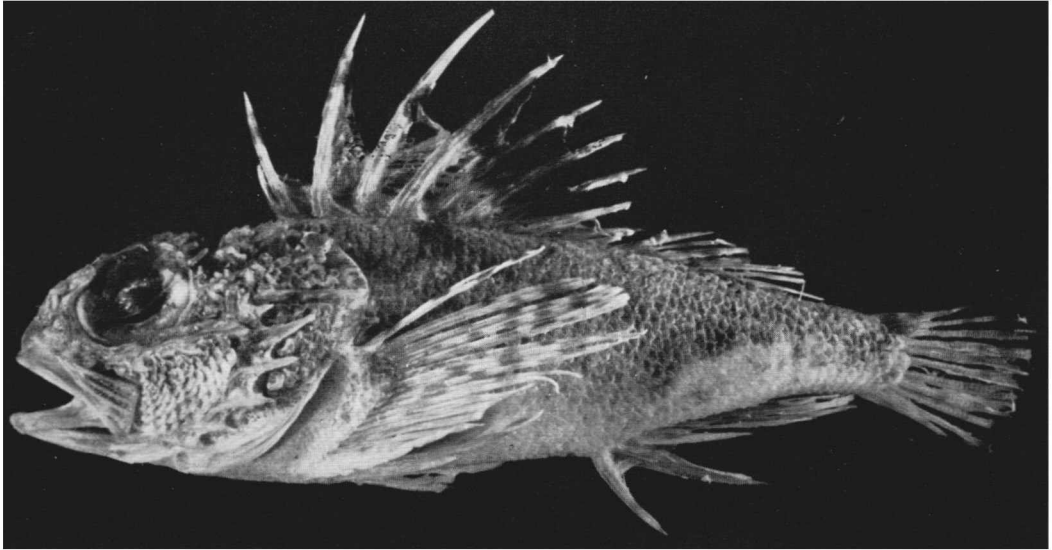


Figure 3. *Maxillicosta scabriceps*, WAM P5742, 78.8 mm S.L.

*Maxillicosta scabriceps* Whitley

Figure 3, Table 1

*Maxillicosta scabriceps* (in part) Whitley, 1935, pp. 246-247, Figs. 4-5 on Pl. XVIII [original description, holotype only; type locality Kingscote, South Australia; (paratypes of *M. scabriceps* are *M. whitleyi*)]. Whitley, 1938, p. 199 (new record for Western Australia (AMS IA7201)). Serventy, 1938, p. 299 (as food of cormorants at Fremantle, Western Australia (AMS IA7201)). Whitley, 1948, p. 29 (listed from Western Australia). Whitley, 1961, p. 66 (part of synonymy only). Whitley, 1968a, p. 38 (part of synonymy only).

*Neosebastes scabriceps*, Scott, 1962, p. 156, Fig. (compiled from Whitley, 1935; placed in *Neosebastes*; figure from Whitley). Mees, 1964, pp. 46-47 [in part; 1 specimen from Emu Point near Albany (WAM P5724) and 5 from Albany (WAM P5742), Western Australia; counts; comments].

*Maxillocosta scabriceps*, Whitley, 1964, p. 56 (listed; generic name misspelled).

**Material examined.**—AMS IA21 (1 specimen, 60.3 mm in standard length, holotype of *M. scabriceps*), Kingscote, Kangaroo Island, South Australia, 22 Feb. 1920. WAM P5742 (5, 63.7-87.2 mm), Albany, 1959. WAM P5724 (1, about 81 mm, mouth damaged), Emu Point near Albany, 3 April 1961. SAM F3831 (8, 59.3-76.1 mm), approximately 24 km west of Marino Light, South Australia. AMS IA7201 (1, about 62 mm, partially digested), Fremantle, registered in 1937. CSIRO A705 (1, 77.5 mm), Great Australian

Bight, Western Australia, trawled, 28 May 1951. CSIRO A764 (1, 62.3 mm) Smoky Bay, South Australia, dredge, 5 April 1953. CSIRO C2523 (1, 87.4 mm) Exmouth Gulf, Western Australia, prawn trawl, M/V LANCELIN, 1954. USNM 214626 (1, 36.8 mm), Gulf of St. Vincent, 34°47.9'S-34°48.3'S, 138°21.9'E-138°21.4'E, 17 m, ELTANIN Cruise 35, sta. 2304, 5 ft. Blake trawl, 7 Oct. 1968.

**Description.**—Counts and measurements are summarized in Table 1, body shape and color pattern in Figure 3.

Dorsal fin with 13 spines; dorsal soft rays usually 7 (1 with 6, 1 with 8); dorsal spine 4 longest. Anal fin with 3 spines, second longer than third; anal soft rays 5. Pectoral fin rays 21-24. Caudal fin with 10-12 principal rays, usually 11 (see remarks below). Gill rakers including rudiments 11-13, rarely 14; 3-4 on upper arch, with uppermost 2-3 rudimentary. Dermal appendages absent except sometimes a small tab between opaque and transparent portions of eye and flap on anterior nostril. Vertebrae 26 (16 specimens) or 25 (3). Gasbladder absent.

Head with numerous small spines, many spines multiple, often irregular. Lachrymal bone (first infraorbital bone) with several

Table 1. Counts\* and measurements for 10 specimens of *Maxillicosta scabriceps* (measurements are in mm, percent standard length in parentheses)

Character	Holotype AMS IA21	CSIRO C2523	WAM P5742 #5	WAM P5742 #4	WAM P5742 #3	CSIRO A705	WAM P5742 #1	WAM P5742 #2	CSIRO A764	USNM 214626
Standard length	60.3	87.4	87.2	78.8	78.3	77.5	73.8	63.7	62.3	36.8
Dorsal fin*	XIII,7	XIII,7	XIII,6	XIII,7	XIII,7	XIII,7	XIII,6	XIII,8	XIII,7	XIII,7
Anal fin*	III,5	III,5	III,5	III,5	III,5	III,5	III,5	III,5	III,5	III,5
Pectoral rays*	22,22	23,23	22,23	23,23	21,22	23,23	23,23	23,23	22,22	21,21
Branched left pectoral rays	2-8	2-9	2-7	2-8	2-6	2-7	2-11	2-8	0	2-7
Vertebrae	26	26	26	26	26	26	26	26	—	26
Gill rakers*	3 + 8 = 11	4 + 9 = 13	4 + 9 = 13	3 + 8 = 11	3 + 9 = 12	4 + 8 = 12	3 + 8 = 11	4 + 9 = 13	4 + 8 = 12	4 + 9 = 13
Head length	25.7(43)	36.5(42)	35.2(40)	32.8(42)	32.8(42)	31.2(40)	31.0(42)	26.5(42)	26.5(42)	17.0(46)
Body depth	19.2(32)	30.0(34)	26.3(30)	24.1(31)	24.9(32)	25.9(33)	23.3(32)	21.3(33)	22.3(36)	13.1(36)
Orbit diameter	9.0(15)	13.0(15)	13.0(15)	11.6(15)	11.9(15)	10.6(14)	10.8(15)	9.8(15)	8.8(14)	6.4(17)
Snout length	5.2(09)	7.1(08)	6.6(08)	7.0(09)	6.8(09)	6.2(08)	6.1(08)	5.2(08)	5.2(08)	3.3(09)
Interorbital width	2.7(04)	3.5(04)	3.9(04)	3.7(05)	—	3.1(04)	3.3(04)	3.0(05)	2.2(03)	1.8(05)
Interorbital depth	1.3(02)	2.0(02)	1.9(02)	1.7(02)	—	1.7(02)	1.9(03)	1.4(02)	1.3(02)	—
Jaw length	11.6(19)	15.8(18)	15.7(18)	14.3(18)	14.0(18)	14.6(19)	13.5(18)	12.1(19)	11.8(19)	7.5(20)
Predorsal fin length	21.0(35)	28.0(32)	27.9(32)	26.7(34)	26.4(34)	24.7(32)	24.8(34)	22.0(34)	20.5(33)	13.5(37)
Third dorsal spine length	13.7(23)	19.9(23)	—	20.0(25)	16.5(21)	—	15.1(20)	13.1(21)	15.5(25)	8.5(23)
First anal spine length	8.6(14)	10.2(12)	7.9(09)	11.3(14)	10.4(13)	8.6(11)	9.3(13)	7.3(11)	8.9(14)	4.3(12)
Second anal spine length	12.0(20)	16.8(19)	14.3(16)	15.6(20)	15.9(20)	14.9(19)	14.7(20)	13.0(20)	13.8(22)	7.1(19)
Third anal spine length	7.9(13)	10.9(12)	12.0(14)	12.7(16)	12.7(16)	10.5(13)	—	—	9.3(15)	5.2(14)
Least depth of caudal peduncle	5.7(09)	8.3(09)	8.5(10)	7.4(09)	7.5(10)	7.3(09)	6.7(09)	6.1(10)	6.2(10)	3.3(09)
Pectoral fin length	19.2(32)	28.2(32)	28.5(33)	26.6(34)	27.6(35)	25.0(32)	24.6(33)	22.0(34)	21.2(34)	12.8(35)
Pelvic fin length	15.2(25)	22.4(26)	22.5(26)	20.5(26)	21.1(27)	19.4(25)	20.0(27)	16.7(26)	16.8(27)	10.0(27)
Caudal fin length	—	25.2(29)	26.6(30)	24.1(31)	24.5(31)	23.3(30)	—	20.5(32)	21.2(34)	12.5(34)
Head length/orbital diameter	2.8	2.8	2.7	2.8	2.8	2.9	2.9	2.7	3.0	2.7
Head length/interorbital width	9.5	10.4	9.0	8.9	—	10.1	9.4	8.8	12.0	9.4
Orbit diameter/interorbital width	3.3	3.7	3.3	3.1	—	3.4	3.3	3.3	4.0	3.5
Orbit diameter/snout length	1.7	1.8	2.0	1.7	1.8	1.7	1.8	1.9	1.7	1.9
Interorbital width/interorbital depth	2.1	1.8	2.0	2.2	—	1.8	1.7	2.1	1.7	—

\* Counts on an additional eight specimens (SAM F3831) give the following totals. Dorsal fin, XIII,6 (2 specimens); XIII,7 (15); XIII,8 (1). Anal fin, III,5 (18). Left pectoral fin rays 21(2), 22(9), 23(7). Gill rakers 3 + 8 = 11(6), 3 + 9 = 12(2), 4 + 7 = 11(1), 4 + 8 = 12(3), 4 + 9 = 13(5), 4 + 10 = 14(1).

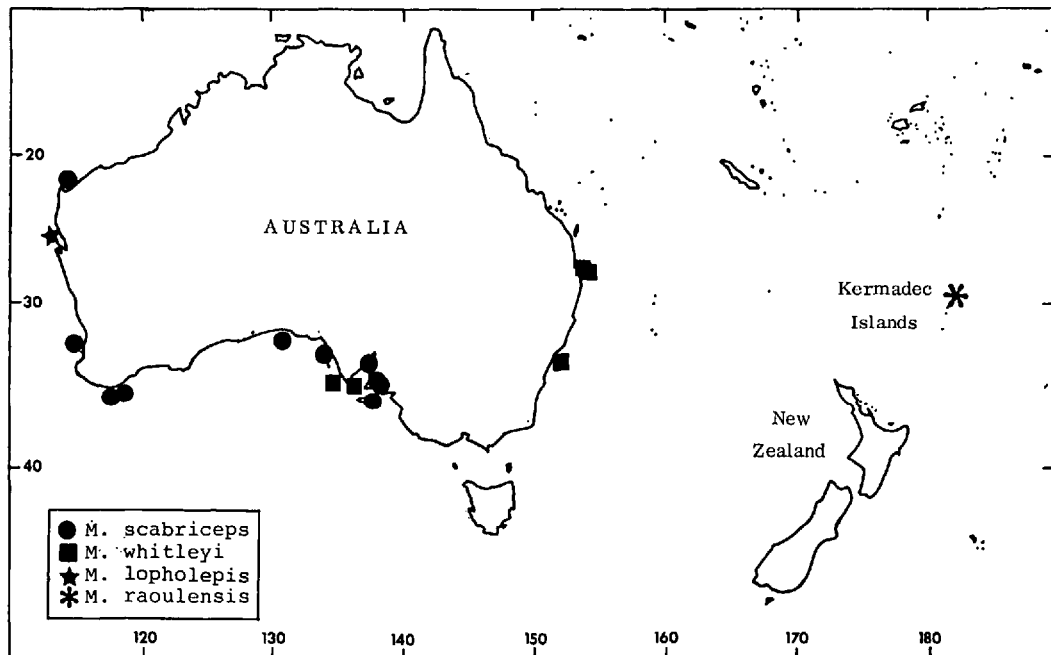


Figure 4. Distribution of species of *Maxillicosta* in Australia and the Kermadec Islands. The fifth species, *M. reticulata* occurs at Juan Fernández, 10,500 km east of the Kermadec Islands, at 34°S, 79°W.

spines on lateral face and on edge overlying maxillary; continuous with row of spines on ventral margin of suborbital ridge. Preopercle with 5 prominent pungent spines; a row of smaller spines on upper arm above first spine. Usually 2 spinous points on each nasal bone (3 in 1 specimen). About 8-12 spines around upper margin of orbit, a few of which are multiple. Small sphenotic and postorbital spines present. Opercle with 2 ridges ending in a spine, lower ridge especially prominent. Supracleithrum sometimes with spiny lumps. Cleithral spine well-developed. Occipital area depressed; bordered in front by 2 coronal spines near midline and a tympanic spine on each side slightly behind and lateral to coronal spine; bordered behind by a short ridge formed by the combined parietal and nuchal spines. Coronal spines large, single, with ridges on margins usually continuous with moderately developed interorbital ridges. Coronal

spines occasionally very close to or partially fused with tympanic spines. Upper and lower posttemporal spines as prominent ridges. Pterotic spine as a well-developed ridge. Interorbit narrow, 3.1-4.0 in orbit; deeply channeled, ratio of interorbital width to depth 1.7-2.2. Maxillary with 5-7 strong longitudinal ridges; upper longest and strongest. Dentary with 3 ridges on lower face.

Scales modified; longer than wide; exposed portion of most with small soft point on posterior margin; without ridges or spines (Fig. 2b). Vertical scale rows irregular and difficult to count, about 40-45 (35-53) rows. Lateral line scales indistinct, about 30 (28-33) tubules.

Color pattern as in Figure 3. Color (in alcohol) pale brown to grayish above, paler below. Spinous dorsal fin with prominent black spot between spines 4-9. Scattered dark patches present; dark pigment

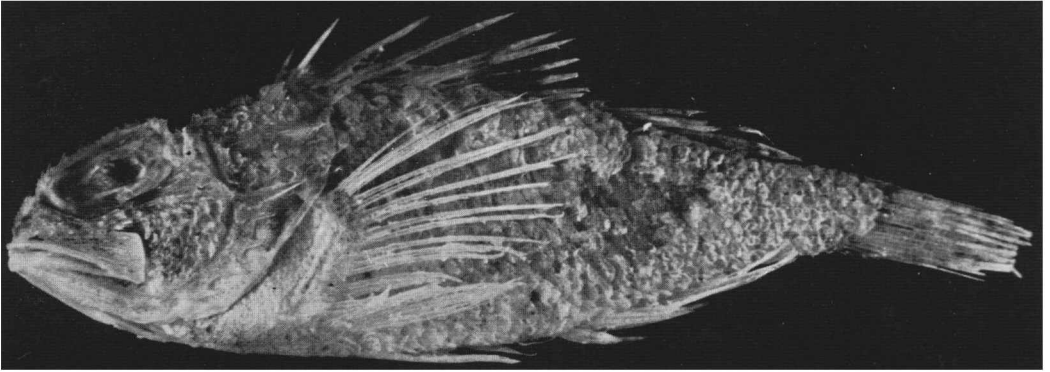


Figure 5. *Maxillicosta whitleyi*, holotype, AMS IB4409, 55.5 mm S.L.

along dorsal fin usually in faint saddles or bars, usually under spines 2-3, below about spine 6, under spines 9-10, and at beginning of soft dorsal fin, the latter extending down and forward well below lateral line. Dusky blotches and spots on sides below and between dark areas. Caudal fin with faint vertical bands, pelvic fin pale, pectoral rays banded. A broad dark area (some reddish color still retained in some preserved specimens) on upper part of eyes extending across interorbital area. Smallest specimen with caudal peduncle pale, abruptly browner anteriorly, a darker area under middle of spinous dorsal fin, and fewer scattered patches of dark pigment on sides. Pelvic fin dusky; pigment on pectoral fin more uniformly distributed.

*Distribution.*—*Maxillicosta scabriceps* is known from South Australia and Western Australia (Fig. 4). (Earlier records of this species from Queensland and New South Wales were based on *M. whitleyi*. The two specimens reported as this species by Mees (1964) from Bernier Island, Shark Bay, Western Australia, are *M. lopholepis*.) The depth range is virtually unknown; one small specimen was taken in 17 m but no information is available for the other specimens.

*Remarks.*—In the original description of *Maxillicosta scabriceps*, Whitley erred in stating that there are teeth on the tongue

and that the fish possesses 18 pectoral rays. The tongue has numerous small fleshy villi and the pectoral rays number 21-23 (22 on holotype). Whitley notes the presence of 10 main rays in the caudal fin, but most specimens have 9 branched (11 principal) caudal rays. The caudal fin of the holotype, however, is damaged and the rays cannot be counted. One specimen (WAM P5724) has 10 principal caudal rays but the count is the result of an abnormal fusion of two branched rays.

#### *Maxillicosta whitleyi* new species

Figure 5, Table 2

*Maxillicosta scabriceps* (not of Whitley), Whitley, 1935, pp. 246-247 (in part; his 2 paratypes of *M. scabriceps* are *M. whitleyi*; not description, which applies only to holotype of *M. scabriceps*). Whitley, 1961, p. 66 [2 specimens dredged from Southport, Australia; new record for Queensland; synonymy (most applies to *M. scabriceps*)]. Whitley, 1968a, p. 38 [part of synonymy; 1 specimen from Port Stephens, New South Wales (AMS IB7023)].

*Neosebastes scabriceps* (not of Whitley), Scott, 1962, p. 156 (in part; paratypes of *M. scabriceps* are *M. whitleyi*). Mees, 1964, p. 46 (in part; reference to Whitley, 1935, and Scott, 1962).

*Material examined.*—Holotype; AMS IB4409 (55.5 mm standard length), dredged off Southport, Queensland, registered in 1959.

Paratypes: AMS IB4406 (1 specimen, 48.7 mm), taken with holotype. AMS E988 (1, 65.0 mm), 80.5 km south of Cape Wiles, South Australia, in 137 m, ENDEAVOUR, 29 Aug. 1909. AMS

Table 2. Counts and measurements of the type specimens of *Maxillicosta whitleyi* and *Maxillicosta lopholepis* and two specimens of *Maxillicosta reticulata* (measurements are in mm, percent standard length in parentheses)

Character	<i>Maxillicosta whitleyi</i>				<i>Maxillicosta lopholepis</i>			<i>Maxillicosta reticulata</i>	
	Holotype AMS IB. 4409	AMS I. 10404	AMS E. 988	AMS IB. 4406	AMS IB. 7023	Holotype WAM P5736	WAM P25384-001	CAS 14004	SIO 65-659
Standard length	55.5	67.5	65.0	48.7	46.3	46.2	38.7	57.0	48.7
Dorsal fin	XIII,7	XIII,7	XIII,7	XIII,7	XIII,7	XIII,7	XIII,7	XIII,8	XIII,8
Anal fin	III,5	III,5	III,5	III,5	III,5	III,5	III,5	III,5	III,5
Pectoral rays	21,20	22,23	22,—	21,21	21,22	21,21	22,22	23,24	23,23
Branched pectoral rays	2-7	2-8	2-7	2-8	2-7	2-6	2-6	2-9	2-9
Vertebrae	26	26	25	25	26	26	26	26	26
Gill rakers	2 + 8 = 10	3 + 8 = 11	3 + 7 = 10	3 + 7 = 10	3 + 8 = 11	3 + 8 = 11	3 + 8 = 11	5 + 10 = 15	4 + 10 = 14
Head length	24.2(44)	28.0(41)	27.9(43)	21.2(43)	19.3(42)	21.3(46)	18.2(47)	23.7(42)	21.4(44)
Body depth	18.3(33)	20.6(30)	22.0(34)	16.8(34)	15.5(33)	16.0(35)	13.4(35)	18.7(33)	15.9(33)
Orbit diameter	9.2(17)	10.5(16)	10.1(16)	7.8(16)	6.9(15)	9.0(19)	7.1(18)	8.4(15)	8.3(17)
Snout length	4.1(07)	5.4(08)	5.0(08)	3.8(08)	3.6(08)	3.9(08)	2.8(07)	5.0(09)	4.7(10)
Interorbital width	2.3(04)	2.8(04)	3.3(05)	1.9(04)	2.0(04)	1.9(04)	1.2(03)	1.3(02)	1.3(03)
Interorbital depth	0.8(01)	1.1(02)	1.1(02)	0.7(01)	0.6(01)	0.5(01)	0.5(01)	0.5(01)	0.5(01)
Jaw length	10.3(19)	12.8(19)	13.0(20)	9.3(19)	8.0(17)	10.1(22)	8.5(22)	11.0(19)	10.0(20)
Predorsal fin length	20.5(37)	23.5(35)	24.0(37)	18.1(37)	15.8(34)	17.2(37)	14.9(38)	20.3(36)	18.9(39)
Third dorsal spine	11.0(20)	14.8(22)	14.7(23)	10.6(22)	9.1(20)	11.4(25)	9.3(24)	11.5(20)	10.5(22)
First anal spine length	6.3(11)	9.6(14)	8.2(13)	5.0(10)	5.0(11)	5.3(11)	5.3(14)	6.8(12)	5.8(12)
Second anal spine length	10.6(19)	15.0(22)	13.7(21)	8.8(18)	7.6(16)	9.8(21)	8.4(22)	12.3(22)	10.5(22)
Third anal spine length	8.2(15)	9.8(14)	9.3(14)	6.5(13)	5.8(12)	6.5(14)	5.7(15)	9.4(16)	5.6(11)
Least depth of caudal peduncle	5.7(10)	6.1(09)	5.8(09)	4.7(10)	4.4(09)	4.5(10)	3.5(09)	5.4(09)	5.4(11)
Pectoral fin length	17.0(31)	22.8(34)	20.2(31)	16.4(34)	15.0(32)	16.7(36)	13.1(34)	17.2(30)	15.7(32)
Pelvic fin length	14.9(27)	20.8(31)	17.4(27)	12.4(25)	12.7(27)	14.0(30)	12.7(33)	16.2(28)	15.0(31)
Caudal fin length	16.6(30)	21.7(32)	19.5(30)	—	14.7(32)	15.1(33)	11.7(30)	16.5(29)	15.0(31)
Head length/orbital diameter	2.6	2.7	2.8	2.7	2.8	2.4	2.6	2.8	2.6
Head length/interorbital width	10.5	10.0	8.4	11.2	9.7	11.2	15.2	18.2	16.5
Orbit diameter/interorbital width	4.0	3.8	3.1	4.1	3.4	4.7	5.9	6.5	6.4
Orbit diameter/snout length	2.2	1.9	2.0	2.0	1.9	2.3	2.5	1.7	1.8
Interorbital width/interorbital depth	2.9	2.5	3.0	2.7	3.3	3.8	2.4	2.6	2.6

I10404 (1, 67.5 mm), off Flinders Island, South Australia, in 68 m, ENDEAVOUR, 30 Aug. 1909. AMS IB7023 (1, 46.3 mm), trawled off Port Stephens, New South Wales, registered in 1964. Note: AMS E988 and AMS I10404 are also paratypes of *M. scabriceps*.

*Description*.—The description of this species is the same as that given for *Maxillicosta scabriceps* except for the differences noted below, in Figures 3 and 5 and in Tables 1-3.

*M. whitleyi* differs from *M. scabriceps* in four features. 1) The number of spines on the nasal bone is greater in *M. whitleyi* with 4-9 spinous points; *M. scabriceps* has 2-3 (usually 2). 2) The ratio of the interorbital width to interorbital depth is greater in *M. whitleyi* with a shallow interorbit than in *M. scabriceps* with a deeper interorbit (Tables 1 and 2). 3) The gill rakers are less numerous in *M. whitleyi* with 10-11 vs. 11-14 for *M. scabriceps* (Tables 1 and 2). 4) The spines on the head, particularly those on the supraocular ridge (Table 3) are more numerous and in general shorter in *M. whitleyi* than in *M. scabriceps*. The coronal spines are poorly developed in *M. whitleyi* and usually do not have ridges on their margins which connect with the poorly developed interorbital ridges.

Color pattern as in Figure 5. Color (in alcohol) essentially as in our smallest (36.8 mm) specimen of *M. scabriceps* but lacking dark pigment on pelvic fin.

*Distribution*.—*M. whitleyi* is known only from southeastern and southern Australia in the states of New South Wales and South Australia (Fig. 4). Known depths of capture are 68 and 137 m.

*Etymology*.—The species is named in honor of the Australian ichthyologist Gilbert P. Whitley.

### *Maxillicosta lopholepis* new species

Figure 6, Table 2

*Neosebastes scabriceps* (not of Whitley), Mees, 1964, p. 46 [in part, the 2 specimens from Bernier Island (WAM P5736)].

*Material examined*.—Holotype: WAM P5736 (46.2 mm standard length), Shark Bay, Western

Australia, 11.3 km west of Cape Couture, Bernier Island, 16 May 1960. Paratype: WAM P25384-001 (1, 38.7 mm), taken with holotype.

*Description*.—Counts and measurements are summarized in Table 2, body shape and color pattern in Figure 6.

Dorsal fin with 13 spines; dorsal soft rays 7; dorsal spine 4 longest. Anal fin with 3 spines, second longer than third; anal soft rays 5. Pectoral-fin rays 21-22. Caudal fin with 11 principal rays. Gill rakers including rudiments 11; 3 on upper arch, uppermost rudimentary; 8 on lower arch, 1-2 lowermost rudimentary. Dermal appendages absent except for flap on anterior nostril. Vertebrae 26 (2 specimens). Gasbladder absent.

Head with numerous small spines; many spines multiple. Lachrymal bone with numerous spines on lateral face, these continuous with row of spines on ventral part of suborbital ridge. Preopercle with 5 prominent pungent spines, first and uppermost longest and nearly reaching edge of opercular flap; a row of small spines on upper arm above first spine. Nasal bone with 5-10 spines. About 15 spines around upper margin of orbit, of which many are multiple. Opercle with 2 ridges each ending in a spine, lower ridge particularly prominent. Supracleithrum with spiny ridges. Cleithral spine well-developed. Occipital area slightly depressed, bordered in front by coronal spines near midline. Distinct, single tympanic spine on each side of occipital area anteriorly, well back and lateral to coronal spines. An upright spine (parietal plus nuchal) on each side at rear of occipital area, ridge smooth or with a few spinous points distally, followed behind by similarly shaped upper posttemporal spine. Lower posttemporal, sphenotic, and large pterotic spine also present, sometimes multiple.

Interorbit narrow, 4.7-5.9 in orbit, shallow, ratio of interorbital width to depth 2.4-3.8. Maxillary with 5-7 longitudinal ridges; upper and third or fourth from top longest and strongest. Dentary with 3 ridges on lower surface.

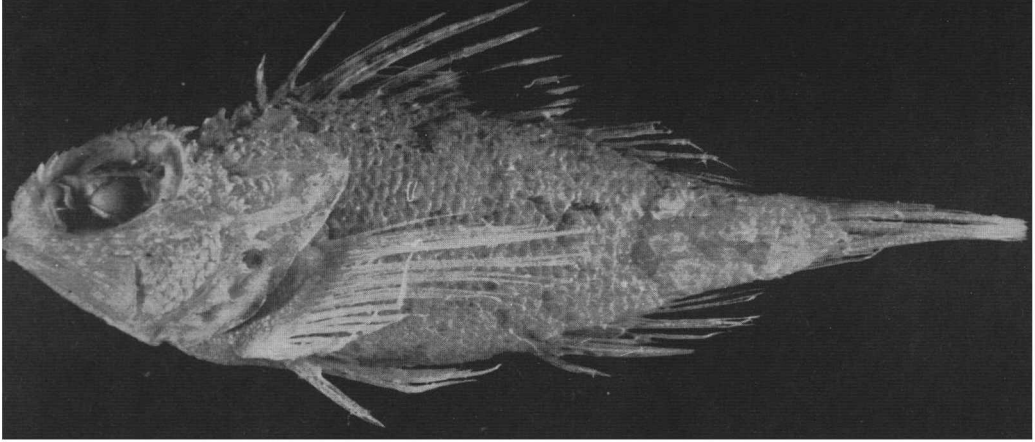


Figure 6. *Maxillicosta lopholepis*, holotype, WAM P5736, 46.2 mm S.L.

Scales modified; most about as long as wide; exposed portion with a small spine on posterior margin preceded by a ridge (Fig. 2c). Vertical scale rows about 38. Lateral line indistinct, 28-29 tubules; anterior ones with well-developed spinous ridge.

Color as in Figure 6. Mostly pallid in alcohol. Spots or small blotches on back and sides. Broad pale area across interorbit. Distinct brown bar traversing posterior portion of eye. Occiput pale. Pale triangular area between posterior margin of occiput and dorsal fin. Spinous dorsal fin with prominent black spot between spines 6-9. In smaller specimen a pale area under spines 4-6 extending to lateral line, followed by a darker saddle at about spines 6-10. An irregular dark bar on soft portion of anal fin. Probably mottled in life with much red.

*Distribution.*—*M. lopholepis* is known only from the type specimens from Bernier Island, Shark Bay, Western Australia (Fig. 4). No

depths of capture are available; presumably the specimens were trawled.

*Etymology.*—From the Greek, λόφος (lophos) = ridge + ληπις (lepis) = scale; referring to the spinous ridge on the scales above the lateral line.

#### *Maxillicosta raoulensis* new species

Figures 7-8, Table 4

*Sebastosemus* sp., Hallacher, 1974, pp. 74, 85 [gasbladder absent, gasbladder muscle present (based on one of our paratypes)].

*Material examined.*—Holotype: ZMUC P791068 (91.4 mm standard length), Raoul Island, Kermadec Islands, 29°15'S, 177°57'W, GALATHEA Expedition 1950-52, station 675, bottom trawl in 60 m, 2105 hours, 3 March 1952. Paratypes: All taken with the holotype, ZMUC P791069-76 (8, 37.8-101 mm). USNM 214627 (1, 84.1 mm), CAS 32173 (1, 100 mm), and CAS 32174 (1, 85.1 mm, cleared and stained).

*Description.*—Counts and measurements are summarized in Table 4; body shape

Table 3. Spines on supraocular ridge for *Maxillicosta scabriceps* and *Maxillicosta whitleyi* (right and left sides counted and entered separately)

	8	9	10	11	12	13	14	15	16	17	18	19	$\bar{x} \pm SE$
<i>M. scabriceps</i>	6	10	12	7	1	1							9.7 ± .20
<i>M. whitleyi</i>					1	0	1	2	2	3	0	1	15.8 ± .63

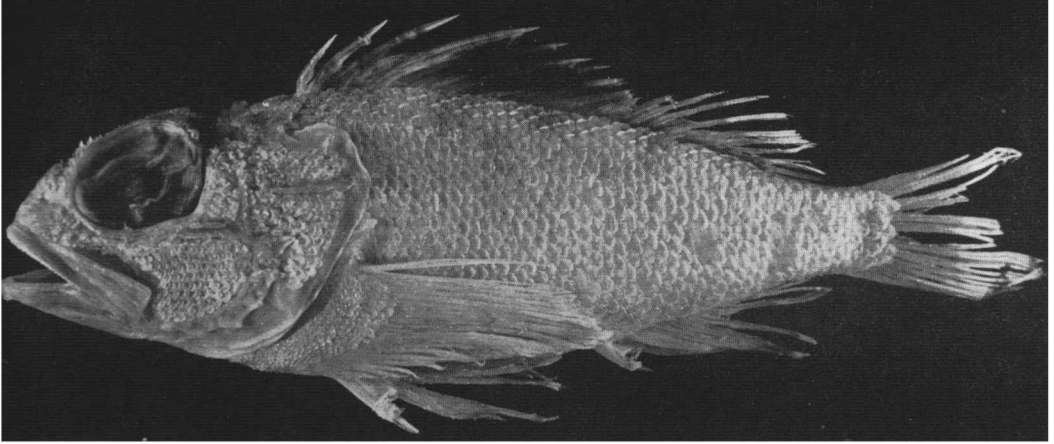


Figure 7. *Maxillicosta raoulensis*, holotype, ZMUC P791068, 91.4 mm S.L.

and color pattern in Figure 7; details of head in Figure 8.

Dorsal fin with 13 spines; dorsal spine 4 (11 specimens) or 5 (1 specimen) longest. Dorsal soft rays 8. Anal fin with 3 spines, second longer than third; anal soft rays usually 5 (1 specimen with 4). Pectoral-fin rays 25-27, rays 2-11 or 12 branched in larger specimens; smaller specimens with fewer branched rays, branching probably begins at about 35 mm SL; rays 7-9 from top longest. Caudal fin with 12-13 principal rays. Pelvic fin reaching to anus or to origin of anal fin. Gill rakers including rudiments 14-17; 4-5 on upper arch, with uppermost rudimentary. Dermal appendages absent except for small tab between opaque and transparent portions of eye and flap on anterior nostril. Small papillae on isthmus anteriorly. Vertebrae 26 (11 specimens) or 25 (1 specimen). Gas-bladder absent.

Head (Fig. 8) with numerous minute spines or spinules; becoming more numerous in larger specimens. Except for spines on preopercle, opercle, and cleithrum, all "spines" multiple and extremely variable in number of points, usually appearing as spiny ridges or patches of spinules. Lachrymal bone with numerous spines on lat-

eral face and on edge overlying maxillary, these continuous with broad band of spinules on suborbital ridge. Spinules on suborbital ridge more or less in rows posteriorly. Preopercle with 5 prominent broad spines; 1 or more supplemental spines at base of first; a band of smaller spines on upper arm above first spine. Ridge or spinous points on nasal bone, 5-16 spinous points. Ridge of spinules from preocular to postocular regions. Indefinite spines around and in area of occiput. Sphenotic, pterotic, posttemporal, parietal, and supracleithral bones with numerous patches of spinules; patch of nuchal spinules present. Occipital pit shallow, often with spinules and longitudinal row of modified scales inside pit. Interorbit narrow, 4.6-6.7 (mean 5.6) into orbit, slightly depressed in middle, with poorly developed interorbital ridges. Maxillary with 4-6 strong longitudinal ridges; one on lower edge sometimes absent; upper and third from top largest and strongest. Lower face of dentary with 2 or 3 lumpy ridges.

Scales modified; somewhat longer than wide; those above lateral line behind head with a serrate median ridge pointing up and back (Fig. 2d). Vertical scale rows somewhat irregular, 38-52. Scales on head peculiarly modified with posterior margins

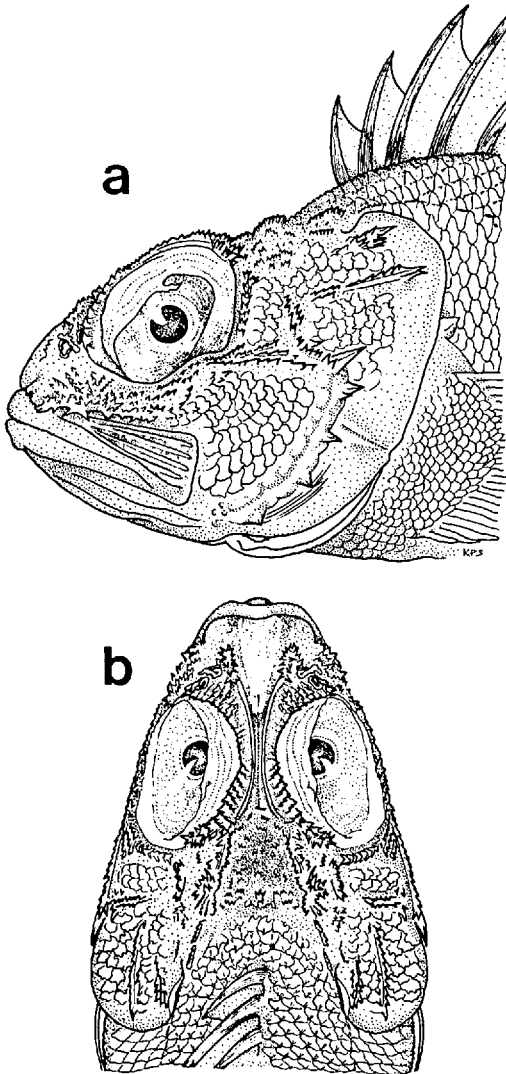


Figure 8. Head of *Maxillicosta raoulensis*: a, lateral view; b, dorsal view (drawings based mostly on holotype).

raised and curved somewhat outward. Lateral line scales indistinct, about 30 (28-30) tubules.

Color pattern as in Figure 7. Body in alcohol generally yellowish; most conspicuous feature black spot on dorsal fin between spines 4-9 or 10. Body with five broad saddle-shaped bands (brown in alcohol and well marked only in 1 specimen)

below dorsal fin, first under spines 1-4, second under spines 6 and 7, third under spines 9 and 10, fourth under dorsal soft rays 1-3, and fifth under rays 6-8. Brown spot present on body below eighth spine. Pectoral fin with scattered specks of brown on middle and upper portions. Dorsal, anal, and caudal fins banded by faint, extremely thin brown lines posteriorly, not well marked. In two small specimens pelvic fins with brown specks, darker posteriorly. Occiput darker than adjacent areas. Color in life probably mostly red.

*Distribution*.—*M. raoulensis* is known only from the type specimens from Raoul Island, Kermadec Islands, in 60 m (Fig. 4).

*Etymology*.—The specific name is based on the type locality, Raoul Island.

#### *Maxillicosta reticulata* (De Buen)

Figure 9, Table 2

*Cristula reticulata* De Buen, 1961, pp. 27-28, fig. 7 (original description; type locality Bahía Cumberland, Isla Más a Tierra, Islas Juan Fernández).

*Material examined*.—CAS 14004 (1 specimen, 57.0 mm standard length) and SIO 65-659 (1, 48.7 mm), Juan Fernández, southeast of Punta Bacalao, 33°38'20"S, 78°47'15"W, 0-26 m, fish poison and SCUBA, 16 Dec. 1965.

*Description*.—Counts and measurements are summarized in Table 2, body shape and color pattern in Figure 9.

Dorsal fin with 13 spines; dorsal spine 4 or 5 longest; dorsal soft rays 8. Anal fin with 3 spines, second longer than third; anal soft rays 5. Pectoral fin rays 23-25 (as reported for holotype), reaching origin of anal fin. Caudal fin with 12 principal rays. Gill rakers including rudiments 14-15; 4-5 on upper arch, uppermost 3 or 4 rudimentary; 10 on lower arch, lowermost 2 rudimentary. Dermal appendages absent except for small tab between opaque and transparent portions of eye and flap on anterior nostril. Vertebrae 26 (2 specimens). Gasbladder absent.

Head with numerous small spines. Most spines multiple except simple spines on pre-

Table 4. Counts and measurements for the type specimens of *Maxillcosta raoulensis* (measurements are in mm, percent standard length in parentheses)

Character	Holotype											
	ZMUC P791068	ZMUC P791069	CAS 32173	ZMUC P791070	ZMUC P791071	ZMUC P791072	CAS 32174	USNM 214627	ZMUC P791073	ZMUC P791074	ZMUC P791095	ZMUC P791096
Standard length	91.4	101	100	98.2	94.2	87.8	85.1	84.1	78.7	72.3	37.9	37.8
Dorsal fin	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8	XIII,8
Anal fin	III,5½	III,5	III,5	III,5	III,5½	III,4	III,5	III,5	III,5	III,5	III,5	III,5
Pectoral rays	27,26	27,26	27,27	27,27	26,26	27,27	26,26	26,26	26,25	25,25	26,26	27,27
Branched pectoral rays	2-11	2-11	2-12	2-11	2-11	2-11	2-11	2-12	2-11	2-10	some	2-9
Vertebrae	26	26	26	26	26	26	26	26	26	25	26	26
Gill rakers	4 + 11 = 15	4 + 11 = 15	4 + 10 = 14	4 + 10 = 14	5 + 11 = 16	4 + 13 = 17	4 + 11 = 15	4 + 10 = 14	4 + 13 = 17	4 + 10 = 14	4 + 10 = 14	5 + 11 = 16
Head length	38.8(42)	41.3(41)	41.0(41)	41.1(42)	38.5(41)	37.2(42)	38.9(46)	35.9(43)	33.7(43)	31.6(44)	17.8(47)	18.0(48)
Body depth	31.2(34)	36.2(36)	33.6(34)	37.0(38)	33.1(35)	34.4(39)	31.2(37)	30.4(36)	27.1(34)	25.2(35)	13.6(36)	14.0(37)
Orbit diameter	14.3(16)	15.2(15)	14.9(15)	15.2(15)	15.5(16)	13.7(16)	14.3(17)	13.5(16)	12.5(16)	11.8(16)	7.4(20)	7.0(18)
Snout length	8.1(09)	8.2(08)	8.5(09)	8.7(09)	8.6(09)	7.8(09)	7.8(09)	7.0(08)	6.4(08)	6.5(09)	3.5(09)	3.6(09)
Interorbital width	2.9(03)	3.3(03)	3.2(03)	2.8(03)	2.9(03)	2.7(03)	2.7(03)	2.8(03)	2.5(03)	2.1(03)	1.1(03)	1.2(03)
Jaw length	17.8(19)	19.5(19)	19.4(19)	19.4(20)	18.6(20)	17.8(20)	17.6(21)	17.4(21)	15.5(20)	14.6(20)	8.5(22)	8.5(22)
Predorsal fin length	32.7(36)	34.4(34)	35.4(35)	35.1(36)	32.8(35)	30.8(35)	33.8(40)	30.4(36)	28.4(36)	26.7(37)	15.0(40)	15.6(41)
Third dorsal spine length	16.6(18)	17.2(17)	17.5(17)	21.2(22)	18.1(19)	19.3(22)	19.8(23)	16.1(19)	15.1(19)	14.5(20)	8.4(22)	9.0(24)
First anal spine length	8.3(09)	11.0(11)	10.4(10)	10.0(10)	10.5(11)	9.0(10)	9.6(11)	7.9(09)	8.3(10)	7.3(10)	3.8(10)	4.7(12)
Second anal spine length	15.2(17)	18.3(18)	17.6(18)	17.3(18)	16.5(18)	16.2(18)	16.7(20)	14.3(17)	13.4(17)	12.9(18)	6.7(18)	7.0(18)
Third anal spine length	10.8(12)	12.8(13)	12.8(13)	12.3(12)	11.6(12)	11.6(13)	11.9(14)	9.3(11)	9.2(12)	8.8(12)	5.6(15)	5.0(13)
Least depth of caudal peduncle	9.7(11)	11.1(11)	10.9(11)	10.8(11)	9.3(10)	9.1(10)	9.7(11)	9.2(11)	8.3(10)	7.7(11)	3.9(10)	4.1(11)
Pectoral fin length	29.4(32)	33.3(33)	32.7(33)	32.3(33)	29.3(31)	28.2(32)	29.1(34)	28.5(34)	26.5(34)	24.7(34)	13.7(36)	13.3(35)
Pelvic fin length	25.3(28)	29.7(29)	28.1(28)	28.1(29)	26.8(28)	26.2(30)	25.6(30)	24.4(29)	23.7(30)	22.3(31)	11.8(31)	13.3(35)
Caudal fin length	25.1(27)	27.2(27)	27.7(28)	26.9(27)	25.0(26)	25.3(29)	26.3(31)	23.8(28)	22.0(28)	21.0(29)	13.3(35)	13.0(34)
Head length/orbit diameter	2.7	2.7	2.7	2.7	2.5	2.7	2.7	2.7	2.7	2.7	2.4	2.6
Orbit diameter/interorbital width	4.9	4.6	4.7	5.4	5.3	5.1	5.3	4.8	5.0	5.6	6.7	5.8
Orbit diameter/snout length	1.8	1.8	1.7	1.7	1.8	1.8	1.8	1.9	1.9	1.8	2.1	1.9

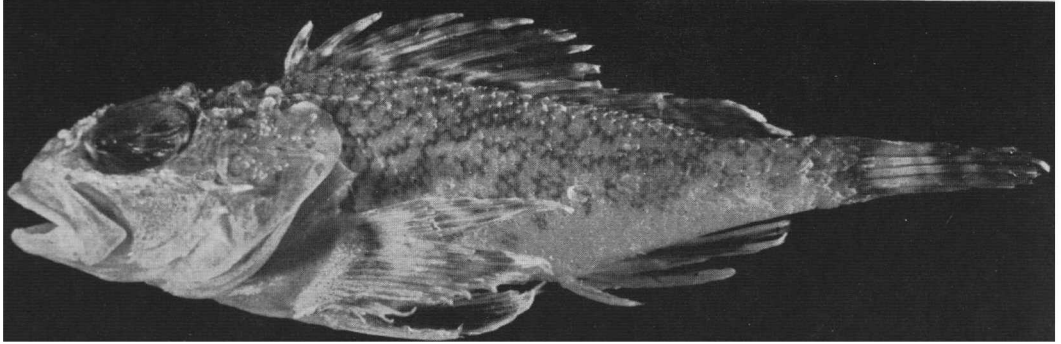


Figure 9. *Maxillicosta reticulata*, CAS 14004, 57.0 mm S.L.

opercle, opercle, and cleithrum. Lachrymal bone with several spines on lateral face; 2 moderately large spines on edge overlying maxillary, posterior spine curves down and back; continuous with a somewhat indistinct band of spines on suborbital ridge. Preopercle with 5 prominent broad spines; several small spines on upper arm of preopercle above first spine. A row of 2-4 spinules on nasal bone; group of about 5-6 spines in preocular area, smooth across mid-orbit but postocular to sphenotic region spiny. Indefinite spines around and in area of occiput. Ridge of nuchal spines present. Pterotic, posttemporal, parietal, and supra-cleithral bones each with discrete ridge of spinules. Occipital pit nearly absent; somewhat square; with small spines in and around margin. Interorbit very narrow, 6.4-6.5 into orbit. Maxillary with 2-4 weak ridges, first on upper edge longest and strongest, third ridge moderately developed, with rest indistinct. Dentary with 2-3 weak ridges.

Scales modified, those on back above lateral line with a few spines or serrate ridge on posterior field (Fig. 2a). Vertical scale rows 26-27. Lateral line with 32 tubed scales including 2-3 on caudal fin.

Color pattern as in Figure 9. Head and body light brown (in alcohol), underparts paler. Sides with reticulate dark brown pattern, becoming lighter below and disappearing at about midside. Dorsal fin mot-

tled and banded with brown; soft dorsal whitish distally. Specks forming indistinct patches of color (brown in alcohol) on pectoral fins. Caudal fin banded, especially distally. Pelvic fin and soft anal fin with diffuse patch of brown near center.

*Distribution.*—*M. reticulata* is known only from Isla Más a Tierra, Islas Juan Fernández: the holotype from Bahía Cumberland and the two specimens examined by us from southeast of Punta Bacalao in 0-26 m.

*Remarks.*—De Buen stated there are five branchiostegal rays. Specimens examined by us had seven branchiostegals. De Buen also notes the presence of 12 dorsal spines. The figure in the original description, however, shows 13 spines, the same as in our specimens. The 108-mm holotype was apparently lost when the collection of the marine biological station at Viña del Mar was destroyed.

#### DISCUSSION

The genus *Maxillicosta* contains five species: three confined to Australia, one from the Kermadec Islands, and one from Juan Fernández (Fig. 4).

*Maxillicosta raoulensis* is one of five species of scorpionfishes known from the Kermadec Islands. *Scorpaena cookii* Günther, 1873, *Pterois volitans* (Linnaeus, 1758), and two undescribed species are also known

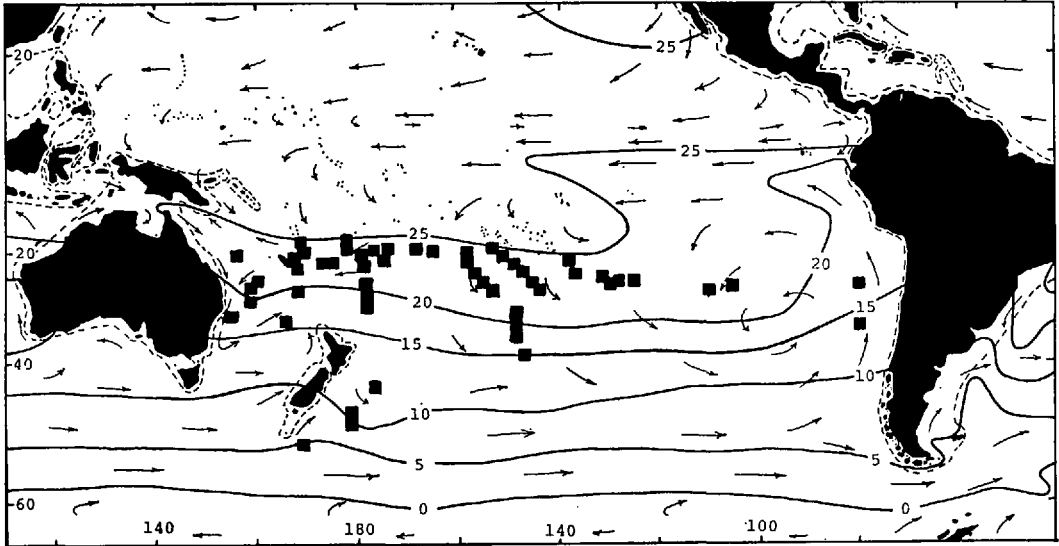


Figure 10. Squares indicate the locations of islands and near-surface seamounts available to ancestral temperate populations of *Maxillicosta* if 20°C isotherm shifted to present 25°C isotherm during a glacial period.

from Raoul Island [the specimen identified as *Scorpaena cirrhosa* from Raoul Island (Günther, 1860) is the holotype of *S. cookii*]. Of these *Pterois volitans* is the most wide-ranging species of a primarily tropical Indo-Pacific genus. *Scorpaena cookii* has been reported also from Lord Howe Island. Records of *S. cookii* from other areas are based on misidentifications (Eschmeyer and Randall, 1975). *S. cookii* shows relationships with *Scorpaena orgila* Eschmeyer and Allen, 1971, from Easter Island and with *Scorpaena thomsoni* Günther, 1880, from Juan Fernández and Isla San Ambrosio (Greenfield, 1974). One of the undescribed species is in the genus *Ocosia*. This genus was previously known from two species in Japan and one from the Philippines. The generic allocation of the second undescribed species is uncertain but its relationships are with *Aploactis*-like fishes. The Raoul Island scorpionfish fauna is a mixed one, but reflects strong ties to the Australian fauna. This agrees well with the general conclusions drawn for fishes by Waite (1910, 1911) and Whitley (1968b).

The fish fauna of Juan Fernández is not well known. Some 40 species have been reported from there by Rendahl (1921), who notes that about 50% are endemic. All scorpionfishes known from Juan Fernández and neighboring islands are endemic. Besides *Maxillicosta reticulata*, only two other scorpionfishes have been caught there, *Scorpaena fernandeziana* Steindachner, 1875, also found at Isla San Feliz, and *Scorpaena thomsoni* Günther, 1860, also found at Isla San Ambrosio. Specimens of *Scorpaena histrio* Jenyns, 1842, recorded from Juan Fernández (Steindachner, 1875) are likely based upon individuals of *S. thomsoni* (Greenfield, 1974). Like *Maxillicosta*, the closest relatives of these fishes inhabit waters of the southwestern Pacific.

Insomuch as four of the five species of *Maxillicosta* are found in the Australian-New Zealand region and five of the six species of *Neosebastes*, the closest relatives of the species of *Maxillicosta*, are also known from this region it seems likely that the common ancestor of the extant species of *Maxillicosta* arose there. The presence

of *Maxillicosta raoulensis* at the Kermadec Islands and *Maxillicosta reticulata* at Juan Fernández probably is explained by an eastward dispersal, involving larval transport and colonization by "ancestral" adults. It is apparent that the ancestors of the present species of *Maxillicosta* did not get to Juan Fernández in a single dispersal event, but ancestral populations must have occurred at intermediate locations where there are now no known descendants. Only a few poorly collected islands or seamounts present suitable habitats for *Maxillicosta* in the temperate waters of the South Pacific. If, during the Pleistocene or an earlier cold period, the present 20°C isotherm occurred about 500 km northward where the 25°C isotherm now lies, a number of near-surface seamounts, reefs, and islands which are now in tropical waters would have been available to support an ancestral temperate biota in the southern Pacific Ocean (Fig. 10). Subsequent warming would have then resulted in the present distribution by extinction of populations at intermediate localities. Alternately, during an earlier warm period, waters of the continental shelf of Antarctica may have been available to the ancestral species of *Maxillicosta*. Also, continental drift may have been a factor; a closer proximity of South America to the Australian New Zealand region might have facilitated the colonization eastward. Upon Pleistocene cooling the intermediate populations were exterminated, resulting in the present distribution.

Why an apparently significant number of species are found at Juan Fernández but not represented on the South American mainland is puzzling, and as McCosker (1971) points out, "This question remains unanswered with present information and would benefit from further study."

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