

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

A REVIEW OF THE VIVIPAROUS OPHIDIOID
FISHES OF THE GENUS *SACCOGASTER*

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Over the past 5 years we have examined specimens of several species of small viviparous ophidioid fishes from the continental slopes, which seemed to defy rational placement in a scheme of classification. The opportunity to examine all of the species at the same time has resulted in the present paper, in which we recognize *Saccogaster* Alcock as a senior synonym of *Barbuliceps* Chan. We refer six species to the genus, four of which are described for the first time, and discuss the relationships of the species.

We are greatly indebted to all of the following, who have helped us by providing specimens and in other ways: N. Chirichigno, W. Eschmeyer, G. Krefft, A. G. K. Menon, N. Parin, C. R. Robins, J. Staiger, P. Struhsaker, A. Wheeler, P. Whitehead, the Smithsonian Oceanographic Sorting Center and the British Museum (Nat. Hist.). Robert H. Gibbs and Richard Winterbottom read and commented on a part of the paper. Bruce B. Collette criticized the entire manuscript.

The following abbreviations are used throughout the paper: SL, standard length; BMNH, British Museum (Natural History), London; IM, Instituto del Mar, Lima; IOM, Institute of Oceanology, Moscow; ISH, Institut für Seefischerei, Hamburg; USNM, National Museum of Natural History, Washington; ZMUC, Zoological Museum University of Copenhagen; ZSI, Zoological Survey of India, Calcutta.

Saccogaster Alcock

Saccogaster Alcock, 1889, p. 386. Type-species by monotypy, *Saccogaster maculata* Alcock, 1889.

Barbuliceps Chan, 1966, p. 4. Type-species by original designation, *Barbuliceps tubercularis* (lapsus pro *tuberculatus*) Chan, 1966.

Diagnosis: Barbels absent. Live bearing; male genitalia (so far as known) borne on a fleshy stalk, lacking ossified parts. Ventral fins each with a single ray immediately adjacent to each other. Dorsal, anal and caudal fins confluent. Pectoral fin rays supported by elongated radials. Scales lacking on head and reduced or absent on body. Anterior nostril directly above upper lip. Tongue with an anterior prowlike extension. Spine present on opercle. Branchiostegal rays 8; 4 attached to the outer surface of the epihyal and enlarged distal part of ceratohyal, 4 attached ventrally or medially along shaft of ceratohyal. Tail section of body not greatly elongated, anal fin originating posterior to the midlength of the fish. Teeth present on palatine. Maxillary vertically expanded posteriorly.

First neural spine smaller than those following. Ribs absent from first two centra. At least some neural spines with truncate or spatulate tips.

Description: Small fishes, largest specimen 140 mm SL. Relatively short-bodied, depth at vent 6.2 to 8.7 in standard length; head 3.0 to 4.4 in standard length. Musculature generally weak and flabby, virtually absent around the belly. Eyes small. Caudal fin with 12 rays inserted on 2 hypurals. So far as known, paired tooth patches at the bases of gill arches 3 and 5. Total vertebrae 51 to 57 (not including ural centra). Most specimens with a rayless, predorsal pterygiophore.

Relationships: *Saccogaster* appears to be closely related to the *Cataetix-Diplacanthopoma* group of genera (including also the nominal genera *Oculospinus*, *Pseudonus* and *Myxocephalus*), all of which contain viviparous species with conjoined median fins. The limits of these genera are not precisely defined at present; however, some characters shared with *Saccogaster* include a stalked intromittent organ in the male, eight branchiostegal rays and (so far as known) the parietals separated by the supraoccipital. *Saccogaster* particularly resembles *Diplacanthopoma* in its naked head and in the absence of ribs on the first two centra. *Diplacanthopoma* is more generalized in its complete complement of imbricate body scales but more specialized in its longer, tapering tail and single hypural.

Bythites (and a related undescribed genus, Nielsen and Cohen, in press) is also close to *Saccogaster*, resembling it in the same ways given above for the *Cataetix-Diplacanthopoma* group (although eight branchiostegal rays is not characteristic of all species in the *Bythites* group). Some differences are the presence in *Bythites* (and in the undescribed genus) of a complete complement of imbricate scales on the body and the absence of elongated pectoral radials.

The single most distinctive feature of the species of *Saccogaster* is

the presence of greatly elongated pectoral radials, a character shared with *Calamopteryx* and with *Sciadonus* and *Leucochlamys* among the aphyonid ophidioids. *Calamopteryx* has scales on the head and body, seven branchiostegal rays, ribs on the first two centra and an unstalked intromittent organ and does not seem very close to *Saccogaster*. The two aphyonid genera mentioned above also resemble several *Saccogaster* species in lacking scales; however, the aphyonids have a notably high number of abdominal centra (Nielsen, 1969). It seems obvious that elongate pectoral radials have evolved independently at least three times in ophidioid fishes.

Synonymy: *Barbuliceps* Chan, which we refer to the synonymy of *Saccogaster*, was recognized on the basis of comparison with the genera of scaleless ophidioids. Chan (1966) stressed relationship with *Spectrunculus* Jordan and Thompson, 1914, a deep-bodied pelagic form with a high vertebral count (79–80),¹ which undoubtedly represents the metamorphosing stage of some ophidioid. We cannot properly place *Spectrunculus* but doubt that it is close to the species discussed herein.

Barbuliceps differs in only one significant respect from *S. maculata*, the type-species of *Saccogaster*, and that is in the presence of incomplete body squamation in *S. maculata* and the absence of all scales in *B. tuberculata*. We do not consider this to be sufficient to warrant the recognition of a distinct genus.

Distribution: All of the known specimens of *Saccogaster* have been taken with bottom trawls at depths ranging from about 100 to ~~1200~~⁸²⁰ meters beneath tropical seas. *S. maculata* has been captured four times in the Bay of Bengal. *S. staigeri* is known from two specimens from different localities off Florida. *S. hawaii* is described from a single specimen taken off Maui in the Hawaiian Islands. *S. tuberculata* has been taken from the South China Sea and off Maui. The related *S. parva* is known only from the holotype taken off the coast of Brazil. The most highly specialized species, *S. normae* has been caught at two localities off the coast of northern Peru. Too little information is available to allow any conclusions to be drawn about distribution patterns.

KEY TO SPECIES

- 1a. Scales present on body.
 - 2a. Spine on opercle with a single point; pectoral fin rays 16 to 18; dorsal fin rays 75 to 88.
 - 3a. Gill filaments on first arch not notably reduced in size (Fig. 1a); palatine tooth row several teeth wide; dorsal fin rays 75 to 83 *S. maculata* Alcock.
 - 3b. Gill filaments on first arch notably reduced in size (Fig. 1b); palatine teeth in a single row; dorsal fin rays 87 to 88 *S. staigeri* new species.

¹ Based on our examination of the holotype of *S. radcliffei* Jordan and Thompson, 1914, the type-species of the genus, and one additional specimen.

- 2b. Spine on opercle with three points; pectoral fin rays 22; dorsal fin rays 92 *S. hawaii* new species.
- 1b. Scales absent.
- 4a. Gill opening extending above level of pectoral fin base; gill filaments on first arch short (Fig. 1d).
- 5a. Developed rakers on first gill arch 3; pectoral fin rays 20 to 23; jaw teeth granular; anal fin rays 57 to 59
..... *S. tuberculata* (Chan).
- 5b. Developed rakers on first gill arch 6; pectoral fin rays 14; some jaw teeth longer, needlelike; anal fin rays 64
..... *S. parva* new species.
- 4b. Gill opening not extending above level of dorsal margin of pectoral fin base. Gill filaments on first arch long (Fig. 1e) *S. normae* new species.

Saccogaster maculata Alcock

Figures 1a, 2

Saccogaster maculatus Alcock, 1889, p. 389 (orig. descr. based on 2 ♀ ZSI F 11673-4; Bay of Bengal, 20°17'30" N, 88°50' E, 193 fms. = 353 m.).—Menon and Yazdani, 1968, p. 150 (types in ZSI).

Saccogaster maculata Alcock, 1891a, p. 30, pl. 7, fig. 3 (♂ from Bay of Bengal, 439-505 m., 11.1°C.).—Alcock, 1891b, p. 226, fig. (longer descr. of previous spec.).—Alcock and McArdle, 1900, pl. 29, figs. 2, 2a (♂ intromittent organ).

Diplacanthopoma (Saccogaster) maculatum Alcock, 1899, p. 102 (descr. based on 5 spec. including types, Bay of Bengal).

Diagnosis: Scales present on sides of body; relatively long gill filaments on first arch (Fig. 1a); palatine tooth row several teeth wide; see Table 1 for comparisons of meristic characters.

Study material: All from Bay of Bengal. ZSI 11673, syntype (x-ray photograph only); ZSI 13527-8 (2 specimens); ZSI 13045 (1); IOM (1), "Vitiáz" cr. 33, stat. 4929, 16°56' N, 83°13' E, 600 m.

Description: Selected measurements are presented in Table 2. Body compressed, relatively short, greatest depth 4.6 to 5.6 in SL. Preanal 1.5 to 1.7 in SL. The skin is thin and transparent.

Scales are absent from the predorsal part of the body and from a band along the bases of the dorsal and anal fins except posteriorly where they cover the entire depth of the body. The most anterior scales are widely scattered; more posteriorly they are progressively more closely spaced, and on the rear part of the body they are regularly imbricate. The figure given by Alcock and McArdle (1900) is inaccurate with respect to the pattern of scale distribution.

The lateral line is in 2 non-overlapping sections along the body; an anterior, dorsal part with about 12 small papillae in a row extending from near the upper angle of the opercle to a point somewhat anterior to the level of the vent; and a lower, posterior section, which does not extend to

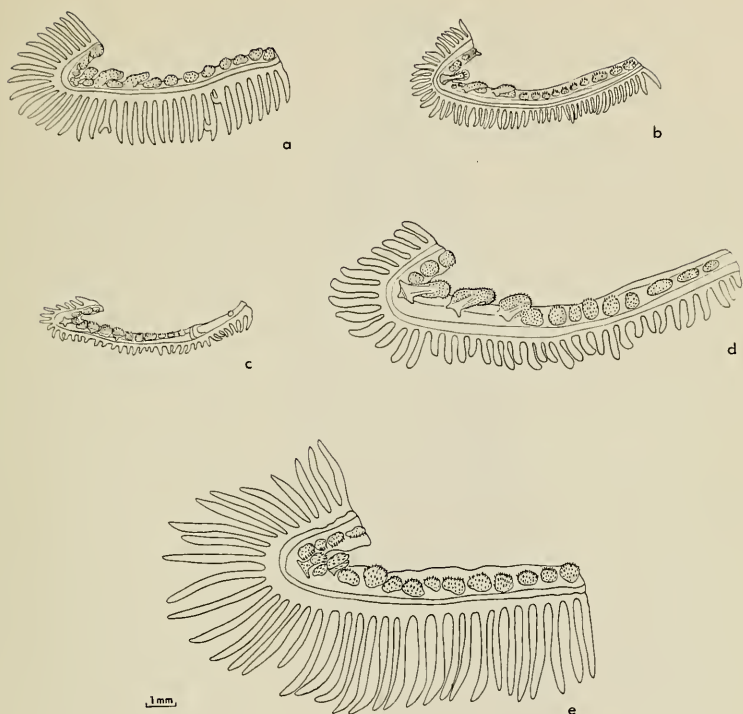


FIG. 1. Lateral view of first right gill arch in five species of *Saccogaster*. A, *maculata*, IOM; B, *staigeri*, USNM 207357, holotype; C, *hawaii*, USNM 207355, holotype; D, *tuberculata*, USNM 207354; E, *normae*, IM 421, paratype. All drawn to same scale, by Keiko H. Moore.

the very end of the body, consisting of 8 to 10 papillae in a row along the midline.

The lateral head canal has 1 pore above the angle of the gill opening; supraorbital pore 1, above the upper lip and medial to the tubular anterior nostril; infraorbital pores 5, 3 along upper lip posterior to anterior nostril and 2 very small pores above the posterior expanded part of the maxillary; mandibular pores 2 or 3, near the tip of the jaw; in addition, a pore is present slightly posterior to the rear margin of the maxillary.

Head compressed in postorbital region. Snout depressed, broadly rounded from above. Lower jaw slightly included. Small, darkly pigmented papillae and dermal fringes sparsely distributed on the snout, a few on the postorbital part of the head. An irregular row of widely spaced papillae on the mandible. The posterior tip of the opercle produced into a

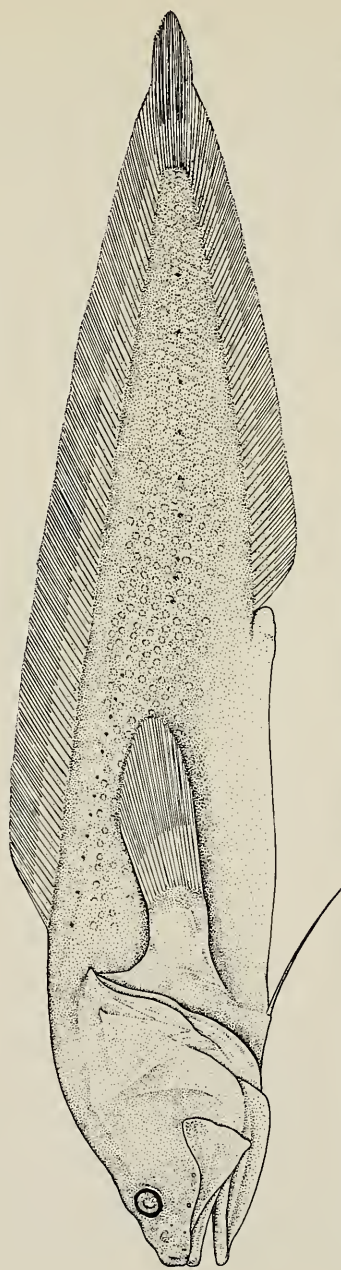


FIG. 2. *Saccogaster maculata*, IOM; 87.4 mm SL. Head pores and papillae not shown in detail. Drawn by Keiko H. Moore.

single blunt spine; in some specimens the ventral arm of opercle terminates as a short spine. The posterior, vertically expanded part of the maxillary is not sheathed posteriorly; the posteroventral corner is produced into a blunt projection.

First gill arch (Fig. 1a) with 3 developed rakers, 1 at the angle and 2 on the lower arm; both arms with low spiny pads. Gill filaments longer than developed rakers. Pseudobranch present, consisting of 2 filaments.

Dentition on premaxillary consisting of a narrow band of granular teeth. Medial to the band near the tip of the jaw is a series of 7 to 9 more elongate needlelike teeth in a widely spaced row. Vomer with a broadly V-shaped band of sharp pointed teeth. Palatine teeth similar, in a narrow band several teeth wide. Dentary with an irregular inner row of about 15 pointed teeth and an outer band 3 to 5 teeth wide of smaller teeth.

Dorsal fin originating over vertebral centra 6-7, anal fin under centra 21-23. Adpressed pectoral fin extending more than one-half the distance from the upper angle of the pectoral peduncle to the origin of the anal fin.

Peritoneum tough and silvery; swimbladder thin walled and clear. Pyloric caeca absent.

Intromittent organ of male borne on a thick, fleshy, posteriorly directed stalk with the vent on its ventral surface. The stalk has 2 prominent lobes at its tip; the cleft between the lobes leads to a pit, from which a penis protrudes. The penis in the "Vitiaz" specimen is 1.5 mm long; however, Alcock and McArdle (1900, fig. 2) show a longer one. Penis length may be correlated with degree of sexual maturity (as discovered in *Barathronus* by Nielsen, 1969). The paired testes of the "Vitiaz" specimen are not notably enlarged. A section of gonadal material shows spermatozoa arranged in spermatophores.

With the exception of a small amount of dusky pigmentation on the snout, there is no obvious color pattern in preserved specimens.

Abdominal centra 12. Centra 5-10 with neural spines variously truncate to spatulate, not sharp and needlelike. First parapophyses on centrum 7. Parietals separated by supraoccipital.

Distribution: All known specimens are from the Bay of Bengal and have been taken at depths ranging from 265 to 600 m.

Saccogaster staigeri new species

Figure 1b

Diagnosis: Scales present on sides of body, relatively short gill filaments on first arch (Fig. 1b); palatine teeth in a single row; see Table 1 for comparisons of meristic characters.

Study material: HOLOTYPE, USNM 207357 (formerly UMML 20757), "Gerda" stat. 657, 27°11'N, 79°49'W, 201-216 m, 10' otter trawl, 16 July 1965. PARATYPE, USNM 164144, "Oregon" 1005, 24°20' N, 82°55' W, 347 m, 40' shrimp trawl, 13 April 1954; bottom temp. 10.0°C. Neither specimen is suitable for illustrating.

Description: Selected measurements are presented in Table 2. Similar

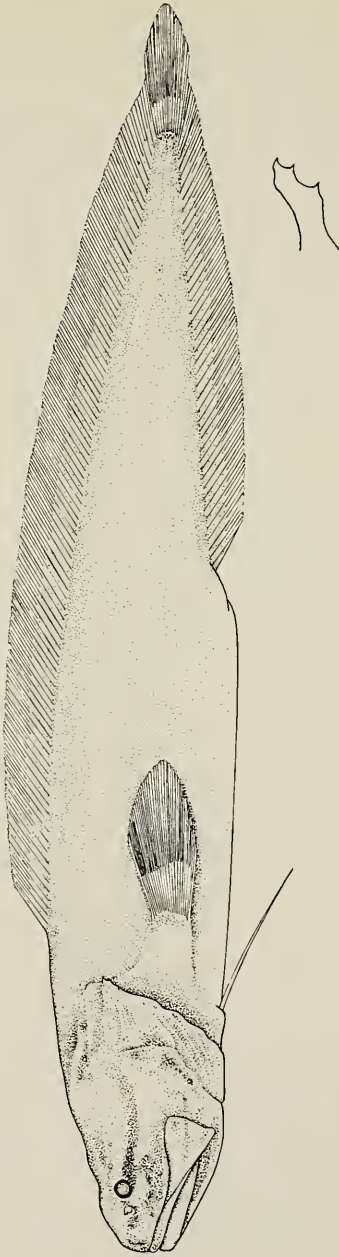


FIG. 3. *Saccogaster hawaii*, USNM 207355, holotype; 69.2 mm SL. Scales not shown. Lower right figure is enlarged view of opercle spine. Drawn by Keiko H. Moore.

TABLE 1. Frequency distributions of numbers of fin rays and vertebral centra in *Saccogaster*

	Dorsal rays																		
	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	
<i>maculata</i>	1 ¹				1 ¹			1											
<i>staigeri</i>													1	1					
<i>hawaii</i>																		1	
<i>tuberculata</i>											1	1	1 ²			1			
<i>parva</i>																	1		
<i>normae</i>									1				1						
	Anal rays																		
	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
<i>maculata</i>	1 ¹					1 ¹	1												
<i>staigeri</i>								1	1										
<i>hawaii</i>									1										
<i>tuberculata</i>											2		2 ²						
<i>parva</i>																			1
<i>normae</i>							1	1											
	Pectoral rays										Vertebrae ³								
	14	15	16	17	18	19	20	21	22	23	51	52	53	54	55	56	57		
<i>maculata</i>				1	2	1							1						
<i>staigeri</i>						2						1		1					
<i>hawaii</i>										1					1				
<i>tuberculata</i>								1	2 ²	1					1 ²	2	1		
<i>parva</i>		1													1				
<i>normae</i>					2										1	1			

¹ Not read from x-ray photograph.

² Holotype from S. China Sea; others from Hawaii.

³ Not including ural centra.

in most respects to *S. maculata*; only the differences are described in the following account. Greatest depth 4.6 in holotype, 6.2 in paratype.

Squamation of the holotype is similar to that of *maculata*; however, the paratype has fewer scales, which are doubtfully imbricate anywhere on the body. Whether greatly reduced squamation of the paratype is due to sex, size or individual variability we cannot say.

Lower part of the lateral line in the holotype with about 20 papillae; the lateral line cannot be traced in the paratype and head pores are indistinct.

Gill filaments on first arch shorter than developed rakers (Fig. 1b).

The enlarged, needlelike teeth at the tip of the premaxillary (about 20 in the holotype, 9 in the paratype) are in a cluster. Vomerine teeth about 10, similar to larger premaxillary teeth. Palatine with 8 to 12 sharp

TABLE 2. Measurements on *S. maculata* and *S. staigeri*

	<i>S. maculata</i>						<i>S. staigeri</i>			
	ZSI 13527		ZSI 13528		ZSI 13045		IOM		Holotype	Paratype
	♂ mm	% SL	♂ mm	% SL	♂ mm	% SL	♂ mm	% SL	USNM 207357	USNM 164144
Sex									♂	♀
SL	80.8		75.0		76.8		87.4		93.1	61.2
Snout to dorsal fin	28.9	35.8	24.9	33.2	23.5	30.6	28.7	32.8	29.1	31.2
Snout to anal fin	52.2	64.6	44.3	59.1	45.9	59.8	52.6	60.2	55.5	59.6
Snout to ventral fin	-	-	20.0	26.7	18.6	24.2	20.8	23.8	20.2	21.7
Body depth at vent	-	-	-	-	-	-	12.0	13.7	14.8	15.9
Head length	26.8	33.2	22.4	29.9	22.4	29.2	25.2	28.8	25.1	27.0
Snout length	5.0	6.2	3.8	5.1	3.7	4.8	5.1	5.8	6.1	6.5
Eye diameter ¹	2.4	3.0	2.3	3.1	2.3	3.0	2.1	2.4	2.0	2.1
Interorbital width ²	3.2	4.0	3.8	5.1	-	-	4.2	4.8	5.0	5.4
Upper jaw length ³	10.8	13.4	10.7	14.3	11.0	14.3	12.8	14.6	13.6	14.6
Depth of maxilla ⁴	4.1	5.1	3.8	5.1	3.7	4.8	5.2	5.9	4.5	4.8
Cleithrum to ventral fin ⁵	2.8	3.5	2.6	3.5	-	-	3.3	3.8	2.8	3.0
Ventral fin length	8.7	10.8	6.9	9.2	-	-	10.3	11.8	11.5	12.3
Pectoral peduncle length ⁶	5.0	6.2	4.1	5.5	4.1	5.3	6.0	6.9	5.1	5.5
Pectoral peduncle depth	4.6	5.7	3.2	4.3	4.3	5.6	4.2	4.8	4.5	4.8
Pectoral fin length ⁷	10.0	12.4	8.9	11.9	-	-	12.4	14.2	13.4	14.4

¹ Horizontal diameter of clear window.² Least distance between dorsal margins of clear windows (= fleshy interorbital).³ Snout tip to posterior margin of maxilla.⁴ Greatest depth, measured at rear of bone.⁵ Cleithrum to ventral fin.⁶ Upper angle of peduncle to origin of fin rays.⁷ Longest fin ray.

pointed, widely spaced teeth in a single row. Dentary with outer series of small teeth in a band 1 to 2 teeth wide.

Pyloric caeca of holotype developed as 2 hemispherical protuberances. Peritoneum transparent; swimbladder tough and silvery.

The holotype has a 9 mm long penis and the rear part of the body cavity occluded by great swollen testes. Eggs are visible through the body wall of the paratype; a fleshy, protruding genital papilla is present; it is cleft transversely to form anterior and posterior hoodlike structures, with the vent at the base of the anterior one.

Abdominal centra 14 in holotype, 13 in paratype.

Distribution: Known from two localities: off Jupiter Inlet on the east coast of Florida, and south of Tortugas in the Gulf of Mexico.

Etymology: Named for Dr. Jon C. Staiger, who first called this species to our attention.

Saccogaster hawaii new species

Figures 1c, 3

Diagnosis: Scales present on sides of body; very short gill filaments on first arch; opercular spine with 3 prongs; see Table 1 for comparisons of meristic characters.

Study material: HOLOTYPE, USNM 207355. "Townsend Cromwell" 40-62, 21°00' N, 156°47' W, 234 m, bottom temp. 15.9°C.

Description: Measurements are given in mm first followed by percent of standard length. Explanations of measurements are given in Table 2. SL 69.2; snout to dorsal fin 21.7 (31.3); snout to anal fin 42.8 (61.8); snout to ventral fin 15.5 (22.4); body depth at vent 8.4 (12.1); head length 17.9 (25.9); snout length 3.8 (5.5); eye diameter 1.5 (2.2); interorbital width 3.4 (4.9); upper jaw length 9.8 (14.2); depth of maxilla 3.5 (5.1); cleithrum to ventral fin 2.5 (3.6); ventral fin length 8.6 (12.4); pectoral peduncle length 4.0 (5.8); pectoral peduncle depth 2.6 (3.7); pectoral fin length 9.2 (13.3).

Body compressed, relatively elongate for a *Saccogaster*, greatest depth 6.9 in SL. Preanal 1.6 in SL.

Scales are absent from the predorsal part of the body and from a band along the bases of the dorsal and anal fins. The most anterior scales are widely scattered; more posteriorly they are progressively more closely spaced and on the rear of the body they are regularly imbricate.

The lateral line is obscure.

The head pore system cannot be described with any degree of precision due to the delicate condition of the extremely thin skin. However, subdermal neuromasts outlined in brown pigment are readily visible: lateral canal 5; supraorbital 5; suborbital 4 or 5; mandibular 4 or 5; preopercular 2 or 3.

Head slightly compressed in suborbital region. Snout depressed, broadly rounded from above. Lower jaw slightly included. Small darkly pigmented papillae are sparsely distributed on the snout, a few on the postorbital part of the head. A row of papillae is present along each mandible; the pores near the tip of the lower jaw are rimmed with denal fringe.

The posterior part of the opercle terminates in a flattened antlerlike 3-pronged spine (Fig. 3, inset). The posterior, vertically expanded part of the maxillary is not sheathed dorsally. A stout, short, anteriorly directed spine projects upward from ethmoid.

First gill arch with 3 barely developed rakers, scarcely longer than the spiny pads supported on the arch. Gill filaments on first arch short, a bare fringe (Fig. 1c). Pseudobranch absent.

Dentition on premaxillary a band of small granular teeth. Medial to the band at the tip of the jaw is a series of 8 elongate needlelike teeth in a widely spaced row. Vomer with 6 teeth similar to the longer premaxillary teeth, plus a scattering of shorter teeth. Palatine with 10–15 sharp pointed teeth in a single row. Dentary with an irregular row of about 15 longer, pointed teeth and an outer narrow band of shorter teeth.

Dorsal fin originating over vertebral centrum 7, anal fin under centrum 25. Adpressed pectoral fin extending about one-half the distance from the insertion of the pectoral rays to the vent.

Peritoneum thin walled and transparent.

No well-developed intromittent organ; probably an immature female. A pair of elongate gonads visible through the transparent belly skin.

Body generally pale, but with some fine brown pigmentation along the bases of the dorsal and anal fins. Similar pigmentation on the head, particularly on the snout and beneath the eyes. An intense dark brown band originating at the posteroventral segment of the eye and becoming more diffuse posteriorly. As noted above, neuromasts outlined in dark pigment.

Abdominal centra 16. Centra 5 to 12 with neural spines variously truncate, markedly so in the middle ones. First parapophyses on centrum 7.

Distribution: Off Maui, Hawaiian Islands.

Saccogaster tuberculata (Chan)

Figure 1d, 4

Barbuliceps tuberculatus Chan, 1966, p. 4, fig. 1, 1 (orig. descr., ♂; S. China Sea).

Diagnosis: Scales absent; relatively short gill rakers on first arch; teeth granular; see Table 1 for comparisons of meristic characters.

Study material: BMNH 1965.11.6.1, holotype, 6°01.8' N, 109°57.4'E, 823–834 m; USNM 207354 (2 ♀, 1 cleared and stained) and ZMUC P77540 (1 ♀), "Townsend Cromwell" 52–88, 21°06' N, 156°13' W, 585–640 m.

Description: Selected measurements are presented in Table 3. Body compressed, relatively short, greatest depth 5.3 to 5.9 in SL. Preanal 1.9 to 2.0 in SL. Skin relatively thick, loose and not transparent.

Lateral line continuous, marked by a narrow, unpigmented line along which 28 to 30 small papillae are arranged. The lateral line originates anteriorly above the angle of the gill opening and descends gradually to the midline, becoming obscure posteriorly.

The lateral head canal with 1 prominent pore above the angle of the

TABLE 3. Measurements on *S. tuberculata*

Sex	Holotype BMNH		USNM 207354		ZMUC	
	♂ mm	% SL	♀ mm	% SL	♀ mm	% SL
SL	107		134		98.0	
Snout to dorsal-fin	31.6	29.5	39.8	29.7	30.0	30.6
Snout to anal-fin	56.3	52.6	67.9	50.7	51.8	52.8
Snout to ventral-fin	21.8	20.4	26.1	19.5	—	—
Body depth at vent	15.2	14.2	17.4	13.0	12.2	12.4
Head length	29.4	27.5	33.5	25.0	26.1	26.6
Snout length	6.5	6.1	7.0	5.2	6.0	6.1
Eye diameter ¹	2.1	2.0	3.0	2.2	2.0	2.0
Interorbital width ²	5.9	5.5	7.5	5.6	5.7	5.8
Upper jaw length ³	14.7	13.7	17.3	12.9	13.6	13.9
Depth of maxilla ⁴	4.4	4.1	5.3	3.9	4.1	4.2
Cleithrum to ventral fin ⁵	4.2	3.9	4.2	3.1	4.0	4.1
Ventral fin length	10.3	9.6	15.8	11.8	11.7	11.9
Pectoral peduncle length ⁶	6.0	5.6	7.1	5.3	5.8	5.9
Pectoral peduncle width	5.2	4.8	6.8	5.1	4.9	5.0
Pectoral fin length ⁷	13.3	12.4	21.2	15.8	13.8	14.1

¹⁻⁷ See Table 2 for footnote references.

gill opening; supraorbital pore 1, above the upper lip and medial to the tubular anterior nostril; infraorbital pores 3, above the upper lip and posterior to the forward nostril; mandibular pores 2 or 3 near the tip of the jaw; also a single pore slightly posterior to the rear margin of the maxillary.

Head compressed in postorbital region. Snout depressed, broadly rounded from above. Jaws subequal, a slight bony protuberance at the symphysis of the mandibles. The holotype with small darkly pigmented papillae sparsely distributed about the head, more densely concentrated on the snout; the Hawaiian specimens with more and larger papillae, roughly arranged in several series: infraorbital, supraorbital, a V-shaped median one converging anteriorly between the eyes, and a roughly elliptical one around the ethmoid region; simple papillae along the mandible of the holotype and smaller Hawaiian specimen, the larger fish with more papillae, many of which have branched tips. Opercle with a single flattened spine. The posterior, vertically expanded part of the maxillary is barely or not at all sheathed.

First gill arch (Fig. 1d) with 3 developed rakers, 1 at the angle, 2 on the lower arm; both arms with low spiny pads. Some gill filaments on first arch shorter than developed rakers. Pseudobranch present, consisting of 2 filaments.

Dentition on premaxillary a band of granular teeth; similar teeth on dentary in a broader band, on vomer in a hemispherical to broadly V-shaped patch, and in a long narrow band on the palatine.



FIG. 4. *Saccogaster tuberculata*, BMNH 1965.11.6.1, holotype; four views of stalked intramittent organ of male, anterior to the right. A, lateral view; B, lateral view with stalk pushed forward; C, ventral view; D, ventral view; looking into distal end of stalk. Photographs by British Museum (Natural History).

Dorsal fin originating over centrum 7; anal fin under centrum 20 in the holotype, 22 in the Hawaiian specimens. Adpressed pectoral fin extending more than one-half the distance from the upper angle of the pectoral peduncle to the origin of the anal fin.

Peritoneum dusky in the holotype, less so in the Hawaiian fish. Swim-bladders of holotype and one Hawaiian specimen relatively thick walled, translucent; swimbladder of largest Hawaiian specimen thinner walled and nearly transparent. Pyloric caeca 2 hemispherical protuberances.

Intromittent organ of holotype (Fig. 4) on a thick, fleshy posteriorly directed stalk with the vent immediately anterior to its base; the distal rim of the stalk is swollen with anterior and posterior median clefts dividing the rim into two lobes; a fleshy mound in the posterior cleft gives rise to a short stringy penis; a section of gonadal material shows spermatozoa arranged in spermatophores. Largest Hawaiian fish with elongate (21.3 mm) separate ovaries containing several hundred (estimated) eyed embryos with attached yolk sacs.

Color of holotype generally pale, but with light smudges of dusky pigmentation on the body; the peritoneum showing darkly through the skin. Hawaiian specimens much darker. The largest Hawaiian fish has narrow pigmented lines running parallel to the dorsal and anal fin bases but terminating before the base of the caudal fin; the two subdorsal lines join in the predorsal region. Other specimens show traces of the same pattern but less well developed.

Abdominal centra 14. Centra 3 through 6 with ribs inserting directly on centra; the first pair of ribs slanting posteriorly at a more acute angle than those following. Pleural ribs absent beyond centrum 7. Centra 7 through 14 with stout parapophyses. Epipleurals associated with either the pleural ribs or parapophyses on centra 4 through 11. Neural spines on centra 4 to 13 variously truncate to spatulate.

The caudal fin skeleton is described and figured from an x-ray photograph of the holotype by Chan (1966) as a fused "bilobed hypural plate." On the basis of subsequent x-ray photographs of the holotype and examination of a cleared and stained Hawaiian specimen we find two separate hypurals, each supporting 6 caudal fin rays.

Parietals separated by supraoccipital.

Distribution: Described from the South China Sea at a depth of 823–834 m. Here recorded from off Maui in the Hawaiian Islands. Except for color, Hawaiian specimens seem remarkably similar to the type.

Saccogaster parva new species

Figure 5

Diagnosis: Scales absent; very short gill filaments on first arch; 6 developed gill rakers on first arch; see Table 1 for comparisons of meristic characters.

Study material: HOLOTYPE, ISH. "Walther Herwig" 90/68, 24°²¹33' S, 43°²²22' W, ~~1200~~ m, bottom trawl, 2 March 1968.

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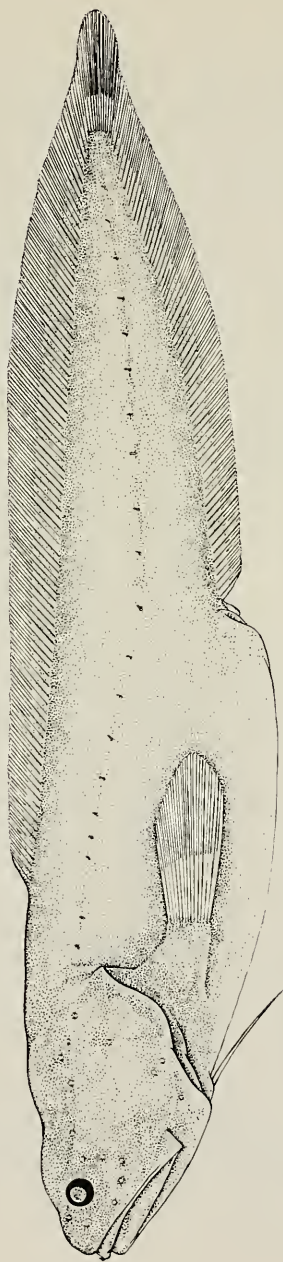


FIG. 5. *Saccogaster parva*, ISH, holotype; 58.0 mm SL, Head pores not shown. Drawn by Keiko H. Moore.

Description: Measurements are given in mm first followed by percent of standard length. Explanations of measurements are given in Table 2. SL 58.0; snout to dorsal fin 20.2 (34.8); snout to anal fin 34.0 (58.6); snout to ventral fin 11.0 (19.0); body depth at vent 9.3 (16.0); head length 14.9 (25.7); snout length 3.5 (6.0); eye diameter 2.0 (3.4); inter-orbital width 3.6 (6.2); upper jaw length 7.9 (13.6); depth of maxilla 2.7 (4.6); cleithrum to ventral fin 1.8 (3.1); ventral fin length 5.7 (9.8); pectoral peduncle length 3.7 (6.4); pectoral peduncle depth 2.2 (3.8); pectoral fin length 9.8 (16.9).

Body compressed, relatively short, greatest depth 5.3 in SL. Preanal 1.7 in SL. The skin is thin and delicate.

The lateral line is continuous, originating about midway between the upper angle of the gill opening and the dorsal profile; it descends gradually to the midline at about the level of the vent, whence it extends posteriorly. There are 9 papillae in the anterodorsal section and 11 or 12 in the midline.

The lateral head canal has 1 pore above the upper angle of the gill opening; supraorbital 1, above the upper lip and medial to the anterior nostril; infraorbital 2, on the upper lip below the posterior nostril; mandibular 4, 3 near the tip of the lower jaw and another near the angular. Neuromasts on the head are outlined in dark pigment and easily visible: lateral canal 5; supraorbital 5; suborbital 6; mandibular 4; preopercular 3.

Head compressed, snout blunt with subequal jaws. Very small papillae scattered on the snout, top of head and along mandibles. Opercle with a single flattened spine. The posterior, vertically expanded part of the maxillary strongly sheathed dorsally.

First gill arch with 6 developed rakers, 1 at the angle and 5 along the lower arm. Pseudobranch apparently lacking.

Dentition on premaxillary a narrow band of small granular teeth. Medial to the band near the tip of the jaw is a cluster of about 10 elongate needlelike teeth. Vomer with about 6 teeth similar to the longer premaxillary teeth and a scattering of smaller teeth. Palatine with 15 small, sharp-pointed teeth in a single row. Dentary with an irregular row of about 15 longer, pointed teeth and an outer narrow band of shorter teeth.

Dorsal fin originating over vertebral centrum 8, anal fin under centrum 23. Adpressed pectoral fin extending about one-half the distance from the insertion of the pectoral fin rays to the origin of the anal fin.

Peritoneum thin walled and transparent. Pyloric caeca developed as 2 hemispherical protuberances.

No well-developed intromittent organ. Paired ovaries joined posteriorly, packed with developing eggs.

Head and body evenly covered with a relatively dense concentration of fine brown chromatophores. According to data slip, "In life violet."

Abdominal centra 16. Centra 7 to 9 have neural spines with spatulate tips, not sharply pointed. First parapophyses on centrum 7.

Distribution: Off the coast of Brazil south of Rio de Janeiro.

Etymology: From the Latin *parvus*, little or small.



FIG. 6. *Saccogaster normae*, USNM 207356, holotype; 140 mm SL. Head pores not shown. Drawn by Keiko H. Moore.

Saccogaster normae new species

Figures 1e, 6, 7

Diagnosis: Scales absent; long filaments on first gill arch (Fig. 1e); gill opening restricted, not extending above level of pectoral peduncle; see Table 1 for comparisons of meristic characters.

Study material: HOLOTYPE, USNM 207356, "Anton Bruun" cruise 16, stat. 625A (Southeastern Pacific Biological and Oceanographic Program), 4°57' S, 81°23' W, 118–133 m, otter trawl, 2 June 1966. PARATYPE, IM 421 "Lance" Stat. 76, 5°04' S, 80°24' W, 150 m, 7 May 1969.

Description: Measurements are given in mm, holotype first followed by the paratype in parentheses. Due to the distorted nature of both specimens many measurements lack precision, particularly SL and other longer ones; hence, it does not seem worthwhile to present percentages of SL. Explanations of measurements are given in Table 2. SL 140 (138); snout to dorsal fin 41.1 (42.9); preanal 88.6 (84.5); snout to ventral fin 29.3 (31.3); body depth at vent 17.2 (17.8); head length 31.9 (31.8); snout length 7.6 (7.8); eye diameter 2.5 (2.9); interorbital width 6.6 (—); upper jaw length 16.0 (15.0); depth of maxilla 5.0 (5.0); cleithrum to ventral fin 8.4 (8.3); ventral fin length 15.7 (13.3); pectoral fin length 20.2 (20.5).

Body relatively elongate in appearance. Preanal about 1.7 in SL. Skin thick, loose and opaque.

Scales absent. Parts of the sides of the paratype have ridges of dark pigment that superficially resemble scale pockets. There are also areas containing fields of small irregular flattened pockets; none of these take up alizarin stain.

Lateral line continuous, with about 27 papillae in the holotype.

Lateral canal head pores 0; supraorbital pores 1, on the upper lip medial to the tubular anterior nostril; infraorbital pores 2, on the upper lip below the posterior nostril; mandibular pores 3, 2 near the tip of the lower jaw, 1 near the angular.

Head blunt, jaws subequal. Many small darkly pigmented filaments on the head and the predorsal part of the body, particularly densely distributed on the snout and dorsal region of the head. No externally developed opercular spine. The posterior part of the maxillary is buried dorsally in thick skin which restricts its free movement.

Gill opening restricted dorsally, not extending above the level of the dorsal base of the pectoral fin. This is a nearly unique condition among ophidioid fishes and so far as we know occurs among viviparous species only in the Australian *Dipulus caecus* Waite, 1905, a distantly related form. Obviously, a restricted gill opening has occurred independently on two occasions among ophidioids.

First gill arch (Fig. 1e) with 2 or 3 small clublike rakers that are barely more prominent than the spiny pads on the arch. Gill filaments on first arch notably elongate. Pseudobranch present, with 2 filaments.

Dentition on premaxillary a band of small granular teeth. Medial to the band at tip of the lower jaw is a cluster of larger teeth. Vomer with 15 to

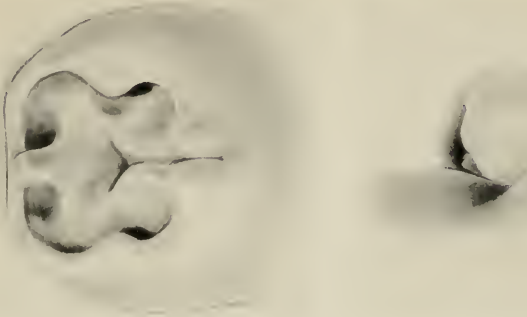


FIG. 7. *Saccogaster normae*, IM 421, paratype; 138 mm SL; two views of stalked intromittent organ of male, anterior to the left. Left, lateral view; right, looking into distal end of stalk.

20 small pointed teeth in a broadly V-shaped pattern on the vomer. Palatine teeth similar to those on vomer, in a narrow band 2 to 4 teeth wide. Dentary teeth in a band 4 to 8 teeth wide with inner teeth larger, but no clear distinction between large and small teeth.

Dorsal fin originating over centrum 7, anal fin under centrum 25. Adpressed pectoral fin extending less than one-half of distance from insertion of pectoral fin rays to vent. Although the ossified pectoral radials are elongated, as in other species of *Saccogaster*, they are for the most part imbedded in the body wall and not enclosed in a fleshy pectoral peduncle.

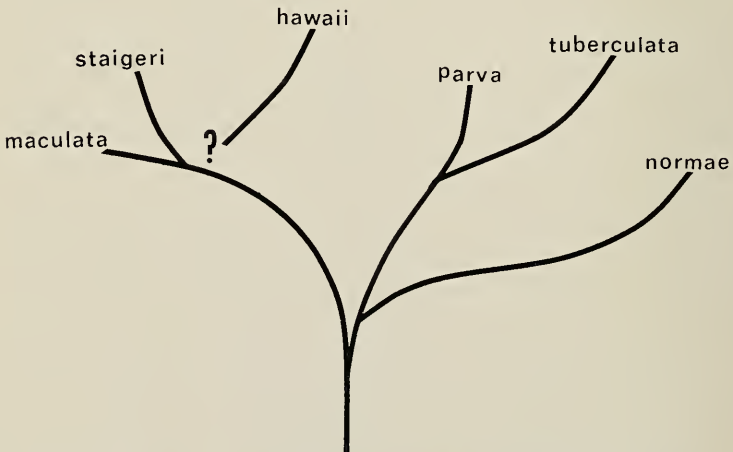


FIG. 8. Summary of possible relationships of species of *Saccogaster*.

Peritoneum thick, transparent to translucent. Pyloric caeca absent.

Intromittent organ of paratype on a thick, fleshy, posteriorly directed stalk with the vent on the anteroventral surface. The distal rim is inflated laterally giving a bilobed appearance. The two sides of the rim curve inward at the anterior midline and form an S-shaped ridge inside of the mouth of stalk, from which a short fleshy penis protrudes. A section of gonadal material shows spermatozoa arranged in spermatophores. The holotype, a female with a small fleshy intromittent organ, not in good condition.

Color chocolate brown, the fins darker.

Abdominal centra 15 or 16. Centra 6 to 12 with tips of neural spines variously truncate to spatulate. First parapophyses on centrum 7.

Distribution: Off the coast of Peru.

Etymology: Named for Miss Norma Chirichigno, Peruvian ichthyologist, who independently recognized this fish as an undescribed species and graciously placed her material at our disposal.

SPECIES RELATIONSHIPS

The characters that we have used to separate the species of *Saccogaster* are similar in magnitude to those which have been used to separate some ophidioid genera; however, no matter how divergent are these six species, they are nonetheless more closely related to each other than to any other ophidioid species. It seems more desirable to emphasize similarities rather than to multiply the number of mono- or bitypic genera.

S. maculata and *staigeri* appear to be the most generalized species. The others differ in at least some ways that might be considered as specializations of character states found in these two. We note, however, that for many characters, there is no way to know if we are dealing with general, primitive states or specialized, advanced ones. The same is true for the shared characters of *maculata* and *staigeri*. Reason demands that any two species which are as similar as are these two be considered as closely related. Two differences worthy of mention are the dentition on the palatine and the size of the gill filaments on the first arch. The palatine teeth are in a band several teeth wide in *maculata*, in a single row in *staigeri*. We do not know which is the generalized and which is the derived character state. For gill filament size, it seems most reasonable to assume that short gill filaments, as in *staigeri*, are derived from the more normal condition as seen in *maculata*. But this character must be used with caution, for in some fishes longer gill filaments are characteristic of species living in low oxygen water (for example the midwater stomiatoiid genus *Chauliodus*, Gibbs and Hurwitz, 1967).

S. hawaii has an opercular spine that is to the best of our knowledge unique among ophidioid fishes; we assume it is derived. It resembles *staigeri* in its single row of palatine teeth and short gill filaments.

The previous three species agree in having scales, surely a generalized character; however, the distribution pattern of the scales is a shared spe-

cialization that is derived from the more general pattern of squamation in ophidioid fishes. *S. maculata* and *staigeri* have interrupted lateral lines (no information on this character for *hawaii*), a character state that we interpret as being generalized among viviparous ophidioids. Each of the three species discussed below has a continuous lateral line and lacks scales. Absence of scales must be used with caution as there are numerous instances of independent loss of scales in ophidioids and other fishes.

S. tuberculata, which also has short gill filaments, differs from all *Saccogaster* species in having all teeth granular and even-sized, that is, in lacking the fairly uniform and consistent pattern of dentition described for the other species. We cannot say whether the teeth of *tuberculata* represent a primitive or advanced character state in *Saccogaster*.

S. parva, also with short gill filaments, is unique within the genus in having six, rather than three or fewer developed gill rakers. Because of the widespread occurrence of three or fewer developed gill rakers in viviparous ophidioids we think that this character state in *parva* may be derived.

S. normae is surely the most divergent of all *Saccogaster* species. The smaller gill opening and restricted maxillary must be derived conditions. A fleshy pectoral peduncle is lacking, superficially a primitive condition, but the presence of elongate pectoral radials indicates that absence of a peduncle has been secondarily derived from the condition as manifested in the other *Saccogaster* species. Notably long gill filaments are present on the first arch in *normae*, perhaps a character state derived from the *maculata* condition. In palatine dentition *normae* resembles only *maculata*.

In Figure 8 we present a diagram that summarizes a possible interpretation of the relationships of the known species of *Saccogaster*. As we have tried to demonstrate in the previous section, interpretation of character states is imprecise at best. Even so, an attempt at prediction seems worthwhile. We look forward to a test of our ideas, to be provided by more detailed knowledge of characters and by the likely discovery of as yet undescribed species.

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