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# The mesopelagic copepod Gaussia princeps (Scott) (Calanoida: Metridinidae) from the Western Caribbean with notes on integumental pore patterns

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## Abstract

The mesopelagic calanoid copepod Gaussia princeps (Scott, 1894) was originally described from the eastern Atlantic. It has been recorded in tropical and subtropical latitudes of the world, but has been reported only occasionally from the northwestern tropical Atlantic (NWTA). Comparative morphological studies, particularly of males, have not included specimens from the NWTA. Based on a collection of zooplankton from the Caribbean Sea, an adult male of G. princeps is illustrated in detail and its morphology compared with other sources in order to explore intra- and interoceanic differences within the species. The proportions and structure of the Caribbean specimens agree with the description of specimens from the eastern Atlantic and the Indian Ocean, except in details of the ornamentation of some appendages. Additional intra- and interspecific differences were found in the number of integumental pores on the male antennules, swimming legs 1–4, and fifth legs. Integumental pores are consistently fewer in the Caribbean male than in the Indo-Pacific and eastern Atlantic counterparts, but G. princeps remains as the species of the genus with the largest number of pores on the swimming legs, a potential species-defining character within the genus. The Caribbean record, at 25–50 m deep, is the shallowest occurrence known for this mesopelagic form in the NWTA and represents the first finding of the genus and species in the western Caribbean and in Mexican waters.

Key words: zooplankton, Mexico, marine diversity, integumental pores

## Introduction

The marine mesopelagic copepod genus Gaussia Wolfenden, 1905, which belongs to the calanoid family Metridinidae Sars, 1902, was a monotypic taxon for decades. Currently, this genus contains four bioluminescent species, which have different distributional patterns in the world's ocean (Vervoort 1965; Björnberg & Campaner 1988, 1990; Soh et al. 1998; Defaye 1998). The most widely distributed species is G. princeps (Scott, 1894), known from temperate and tropical latitudes of all major oceans (Vervoort 1965; Soh et al. 1998). The original description of this widespread species was based on a single male from the Gulf of Guinea, in the eastern Atlantic (Scott 1894); females have been briefly illustrated from different geographical areas (Owre & Foyo 1967; Saraswathy 1973b; Björnberg & Campaner 1988). The morphological differences distinguishing the known species of Gaussia are subtle but consistent (Defaye 1998; Soh et al. 1998).

Relatively little information is available about the males of these species; they have been only superficially treated for G. sewelli Saraswathy, 1973 and G. intermedia Defaye, 1998; the male of G. asymmetrica Björnberg & Campaner, 1988 remains unknown. A complete redescription of G. princeps, published by Soh et al. (1998), inclued adult males and females from the Indian Ocean and compared the male to the holotype from the Gulf of Guinea. There are no detailed illustrations or descriptions for male specimens of G princeps from the western Atlantic.

During a survey of the oceanic zooplankton of the western Caribbean Sea, a single male specimen of *G*. *princeps* was collected. This specimen is described and illustrated in full, including an analysis of the integumental pore pattern on all the appendages; it is compared with the existing descriptions and illustrations of this species but particularly with the redescription by Soh *et al.* (1998) in order to explore intraspecific differences between specimens from the Indo-Pacific,the eastern Atlantic, and the Caribbean. The variability of the pore pattern on the swimming legs, the right male antennule, and the male fifth legs is compared among the species of *Gaussia* for which this information is available.

## Material and methods

Zooplankton samples were collected by the NOAA Ship "Gordon Gunther" during a survey of the Mesoamerican Reef System, carried out in March, 2006. The cruise was directed at studying the ichthyoplankton distribution and physical oceanography of the Western Caribbean coast from the Yucatan Channel south to the Mexico-Belize border. Zooplankton was collected in different water strata using Multiple Opening and Closing Net Environmental Sensing System (MOCNESS) and standard plankton nets with a mesh size of 60  $\mu$ m. Most samples were obtained within the 0–100 depth range; one of the stratified samples, obtained from the 25–50 m layer (sta. 54) contained a specimen of a large black calanoid copepod identified as *Gaussia princeps*. Samples were fixed and preserved in ethanol. Copepods were sorted from the original sample and preserved in 70% ethanol.

The male specimen of *G. princeps* was prepared for taxonomic analysis by dissecting the appendages of the right side of the body to observe and count the integumental gland pores. Dissected appendages were mounted in glycerine and sealed with Entellan ®, the remaining parts of the specimen were preserved in 70% ethanol and deposited in the collection of Zooplankton at ECOSUR, Chetumal, Mexico (ECO-CHZ). Basic taxonomic observations were performed using an Olympus BX51 microscope with differential interference. Illustrations were prepared with the aid of a camera lucida at different magnifications.

The general morphological terminology of Huys and Boxshall (1991) was followed and Soh *et al.* (1998) was consulted for the comparison of position and number of integumental gland openings and other microcharacters.

## Systematics

Order Calanoida Sars, 1903

Family Metridinidae Sars, 1902

Genus Gaussia Wolfenden, 1905

Gaussia princeps (Scott, 1894) (Figs 1–4)

**Material examined.** One adult male, coll. 31 March, 2006 from sta. 054 (18°18'33.84" N; 87°25'06.96"W), oceanic waters, at a depth of 25–50 m, Mexican Caribbean Sea. Specimen partly dissected, ethanol-preserved, vial and slides deposited in the collection of Zooplankton of ECOSUR under catalogue number ECO-CHZ-003536.

**Description of adult male.** Body length 10.1 mm, including caudal rami. Length of prosome: 7.0 mm. Body with typical calanoid shape, relatively slender, prosome slightly narrower anteriorly and widest at first

process visible in lateral view (Fig. 1A–B). Prosome anteriorly an acute process; depression anterior to process visible in lateral view (Fig. 1C). Rostrum wide, with 2 long filaments each armed with short setules along both margins (Fig. 3G). Prosome apparently 5-segmented; first segment a complex of 5 cephalic somites and thoracic somites 1 and 2; 3–6 articulating. Fifth thoracic somite symmetrical, slightly produced posteriorly to form subtriangular processes (Fig. 1D).



**FIGURE 1.** *Gaussia princeps* (Scott, 1894) from the western Caribbean. Adult male. A. habitus, lateral view; B. habitus, dorsal view; C. cephalic area showing frontal process and depression, lateral view; D. fifth pedigerous and first urosomites, dorsal view; E. anal somite and caudal rami, dorsal view; F. same, lateral. Scale bars: A,B= 3mm, C–F=0.7 mm.



**FIGURE 2.** *Gaussia princeps* (Scott, 1894) from the western Caribbean. Adult male. A. left antennule segments 1–10; B. same, segments 11–16; C. same, segments 17–23. D. right antennule, segments 1–10; E. same, segments 11–20; F. detail of modified seta and aesthetasc; G. detail of segment 17 and distal acute process. Position of integumental pores indicated by solid circles. Scale bars: A-E=0.7 mm, F=0.05 mm, G=0.35 mm.

Urosome representing 30% of total body length, 5-segmented. Relative lengths of urosomites from anterior to posterior somites: 21.4: 21.5: 17.1: 15.6: 24.4 = 100. Anal somite with wing-like lateral processes reaching proximal 1/3 of caudal rami (Fig. 1E); dorsal rounded process visible in lateral view (Fig. 1F). Caudal rami relatively short, robust, symmetrical, about 1.3 times longer than wide (Fig. 1E); inner and outer margins lightly setose from proximal 1/3. Each ramus with five setae: 1 lateral, 1 subterminal and 3 terminal; all ramal setae biserially plumose.

Left antennule (Fig. 2A–C) 23-segmented, reaching beyond caudal rami by 2–3 segments. Armature per segments as follows (numerals = segment, numerals in parentheses = number of setae, ae = aesthetasc): 1(6+3ae), 2(2+ae), 3, 4(2+ae), 5(2+ae+ small spine), 6(2+ae), 7(6+3ae), 8-12(2+ae), 13(1+ae), 14(2+ae), 15(2+ae), 16(1), 17(2+ae), 18(1), 19(1), 20(2), 21(1+ae), 22(1), 23(5+ae).



**FIGURE 3.** *Gaussia princeps* (Scott, 1894) from the western Caribbean. Adult male. A. antenna; B. mandibular palp; C. mandibular blade showing detail of teeth and blade ornamentation; D. maxilla; E. maxilliped; F. first swimming leg. G. rostral area, ventral view. Some setae cut short. Position of integumental pores indicated by solid circles. A,B–G= 0.7 mm, C=0.2 mm.



**FIGURE 4.** *Gaussia princeps* (Scott, 1894) from the western Caribbean. Adult male. A. second swimming leg; B. detail of hook-like and spiniform processes on first endopodal segment of second swimming leg; C. third swimming leg; D. fourth swimming leg; E. fifth swimming leg, anterior view; F. basipod and exopod of left fifth leg, lateral view; G. detail of processes of second exopodal segment of left fifth leg; H. detail of distal exopodal segment of right fifth leg, showing ornamentation. Position of integumental pores indicated by solid circles. Scale bars A,C–E,H=0.7 mm, B,F,G=0.3 mm.

Right antennule 20-segmented, geniculated between segments 16 and 17 (Figs. 2D–E). Armature as follows: 1(7+4ae), 2(2+ae), 3–7(2+ae), 8, 9(1+ae), 10, 11(2+ae), 12(2+ae), 13(3+ae+short spiniform seta), 14(2), 15–17(2+spine), 18(4+ae), 19(1), 20 (5+ae). Segment 11 with additional modified, globose seta (Fig. 2F);

segment 17 with spiniform, acute distal ventral process reaching beyond distal end of segment (Fig. 2G). Antenna (Fig. 3A) coxa with1 long seta (not illustrated), basis with 2 subequal setae on outer distal margin. Endopod 2-segmented, proximal segment long, with 1 seta inserted at 2/3 length, second with 9 medial and 7 distal setae and subterminal patch of spinules. Exopod 8-segmented, segments 2–4 partially fused, segments armed with 1 seta on segments 1, 3–6, and 2 on segment 7; 4 setal elements on distal segment.

Mandible (Fig. 3B–C): Gnathobase with 8 wide-based bicuspidal or tricuspidal teeth distinctly separated from large distal tooth by a wide distemma. Bases of teeth 3–8 with clusters of spinules. Proximal seta with spinulose inner margin. Basis of mandibular palp with 4 medial subequal setae. Endopod 2-segmented; proximal segment with 4 setae; distal segment with 10 terminal setae. Exopod 5-segmented, with 1, 1, 1, 1, 2 setae.

Maxillule not illustrated, as in Soh *et al.* (1998): with praecoxal (= protopodal segment proximal to coxa) arthrite bearing 16 spiniform setae [12 ventral, 3 posterior, 1 on anterior]. Coxal epipodite with 9 setae, coxal endite with 5 setae. Basis with proximal and distal endites bearing 4 and 5 setae, respectively, basal exite with single seta. Endopod reduced, 1 articulating segment with 6 medial and 11 distal setal elements. Exopod oblong, with 11 subequal setae.

Maxilla (Fig. 3D) precoxa and coxa partially fused, with syncoxa and basis fused; praecoxal lobe with 6 setae, coxal lobe with 3 setae, proximal and distal lobes of basis with 3 setae each. Proximal segment of endopod large, with 4 setae, antepenultimate and penultimate segments small, with 2 setae each, distal segment small, with 2 long, curved setae. All setae biserially setulated.

Maxilliped (Fig. 3E) precoxa and coxa incompletely segmented, 4 endites with 1, 2, 4, and 4 setae, respectively; distal and subdistal endites each with patch of short spinules at base and tuft of hair-like setules between them. Basis and endopod partially fused; basis with 3 setae, dense longitudinal row of spinules along medial surface; neither proximal nor distal basal lobe developed. Endopod 6-segmented, distal segment small, partially inserted on penultimate one; endopod armed as follows: 2, 4, 4, 3, 3, 4. Gland openings on all endopodal segments of the maxilliped, except distalmost.

First swimming leg (Fig. 3F) with 3-segmented exopod and endopod; coxa with long plumose seta on internal margin reaching beyond distal margin of basipodal segment. Basipod with long, recurved seta on inner margin reaching middle of third endopodal segment. Outer margin of second and third exopodal segments with combined rows of denticles and short setules. Outer spines of same segments with terminal lash. Proximal and second segments of endopod with outer margin covered with minute spinules of different sizes; third segment with small patch of spinules on anterior surface. Second, third and fourth legs with 3-segmented exopods and endopods (Fig. 4A, C–D). Second leg with endopod bearing characteristic bifid process on distal inner margin; proximalmost hook shorter than distal one, both strongly chitinized. Same segment with slender, acute accessory process on medial-proximal position; process directed posteriorly (Fig. 4B). For armature formula of legs 1–4 see table 1.

**TABLE 1.** Armature formula of swimming legs 1–4 of male of *Gaussia princeps* from the western Caribbean. Roman numerals indicate spines and Arabic numerals are setae. Numerals to the left of a comma or dash indicate lateral elements; numerals between two commas are terminal elements, and numerals to the right of a comma or dash are medial elements.

	coxa	basis	exopod	endopod
leg 1	0-1	1-1	I-1; I-1; II,I,4	0-1; 0-2; 1,2,2
leg 2	0-1	0-0	I-1; I-1; III,I,5	0-0; 0-2; 2,2,4
leg 3	0-1	0-0	I-1; I-1; III,I,5	0-1; 0-2; 2,2,4
leg 4	0-1	0-0	I-1; I-1; III,I,5	0-1; 0-2; 2,2,3

Fifth legs modified, uniramous (Fig. 4E–H). Basis with short, slender seta inserted distally on outer margin. Endopod absent. Left leg exopod 2-segmented, proximal segment cylindrical, naked; second segment with 2 proximal processes, 1 on anterior surface, 1 on posterior surface of segment; former represented by long, triangular protuberance, naked; second process wide-based, distally covered with hair-like setules. Distal segment with 3 distal sensilla. Right leg with intersegmental sutures suggesting 3 segments, but second and third putative segments partially fused. Outer margin of terminal segment with proximal seta and small subdistal seta. Same segment with medial rounded protuberance and 2 distal sensilla.

**Remarks.** The Caribbean specimen was identified as *G princeps* by having a combination of the following characters (Soh *et al.* 1998): 1) cephalosome produced to form a stout process; 2) rostral area indented in lateral view; 3) proximally directed medial process of second exopodal segment of male left fifth leg relatively short, not reaching the distal margin of the basipodite; 4) in addition to hook-like process on lateral margin, spiniform process on proximal surface of first exopodal segment of second swimming leg present.

*Gaussia princeps* was originally described from a single male specimen 12.0 mm long, collected in the Gulf of Guinea, eastern tropical Atlantic (Scott 1894). The known range of the body length of the males from different geographical areas is between 9 and 12 mm (Scott 1894; Vervoort 1965; Saraswathy 1973b; Soh *et al.* 1998). The size of the Caribbean specimen (10.4 mm) falls within the overall average size range of the species. According to data presented by Vervoort (1965), males from the Indo-Pacific tend to be smaller than those from the eastern Atlantic. However, Saraswathy (1973b) suggested males from the Pacific are the largest (10.1–11.1 mm), and those from the Atlantic are the smallest (9.1–10.4 mm). According to these figures, the Caribbean specimen (10.2 mm) would be at the upper end of the range of the Atlantic males.

There are some morphological differences between the males from the Indian Ocean (and the holotype male), as described by Soh et al. (1998) with respect to the Caribbean male: 1) the shape and size of the accessory spiniform process of the first endoped of the second leg; this structure is relatively short and robust in the former group of specimens and it is slenderer, relatively longer in the Caribbean male; 2) the spiniform process on the right antennule segment 17 is more acute and relatively longer in the Caribbean specimen, it stretches well beyond the end of the distal margin of the segment, whereas it barely reaches this margin in the Indian Ocean specimens. This process is also short in G. sewelli (Saraswathy & Bradford 1980; fig. 1A), but it is well developed, also stretching beyond the same segment in G. intermedia (Defaye 1998; fig. 2D); 3) the globose setal element with cone-shaped distal protuberance inserted on segment 11 is slightly wider, shorter in the Indian Ocean specimens and the paired aesthetasc is short, slightly longer than the modified seta; in the Caribbean male, the globose seta is more slender and the accompanying aesthetasc is longer. Soh et al. (1998) also noticed a difference in the shape of this seta between the holotype male from the Eastern Atlantic and specimens from the Indian Ocean. In the Caribbean specimen, this structure is, in fact, more similar to that depicted by Saraswathy and Bradford (1980, fig. 2C) for G. sewelli, with a long accompanying aesthetasc. Soh et al. (1998) stated that the shape of the bulbous seta on segment 11 of the right male antennule has some range of variation within the species; these differences were also reported by Saraswaty (1973a). Apparently, this seta has a considerable range of intra- and interspecific variability and its morphology is not consistent within one species of Gaussia.

**Integumental pore patterns.** The pore pattern has been used in other marine calanoid copepods such as *Eucalanus* Dana (Fleminger 1973) and even in another genus of the family Metridinidae (*Pleuromamma* Giesbrecht) as a consistent character to separate species (Park & Mauchline 1994; Park 1995). The number and general distribution of the pores have been found to express important differences between congeners in *Gaussia*. In *G princeps* and *G sewelli*, these integumental structures are distributed on all the appendages (Barnes & Case 1972; Soh *et al.* 1998). In the other two known species, *G asymmetrica* and in *G intermedia*, pores are present on the antennules and the swimming legs only (see Björnberg & Campaner 1990; Defaye 1998). The presence of pores on all the appendages, including the mouthparts, was observed in the Caribbean specimen, thus agreeing with the general pattern of *G princeps*.

Soh *et al.* (1998) described and compared the pore patterns in groups of female specimens of *G. princeps* from Japanese waters and the Indian Ocean, without finding intraspecific differences. They did not comment on the pore pattern related to male sexual characters such as the right geniculate antennule and the fifth leg.

The Caribbean specimens showed a pore pattern that differs in number with that described from specimens from the Indian Ocean and Japan (Soh *et al.* 1998) on different appendages, as follows: (number of pores of Indian and Japanese waters vs number in Caribbean specimens between parentheses; appendages/ segments with identical patterns ommitted:

*Left antennule*. First segment 9(7); third segment 3(2); fifth and sixth segments 2(1); seventh segment 6(3); eleventh segment 1(0).

*Right antenule*. First segment 12(9); second and third segments 3(2); fourth segment 2(1); sixth and eighth segments 2(1); tenth segment 1(0).

Mandible. Basis 3(1).

Differences on swimming legs 1–4 in Table 4, on fifth legs, see Table 3.

All the other integumental pores depicted by Soh *et al.* (1998) were found in the Caribbean specimens. However, in some cases, the position was not the same, i.e. in the maxilliped, all five endopodal segments have a pore each, but in the Indian specimens two of these are in medial position, whereas all five pores are distal or subdistal in the Caribbean specimens.

As noticed by Soh *et al.* (1998), the number of gland openings is the largest among the species of Gaussia. This is true when considering the mouthparts, the male and female swimming legs 1–4, and the female antennules; however, this is not as clear in reference to the male fifth leg (see Table 3), or the right male antennule (see Table 4). Pores are present on the second endopodal segment of legs 2–4 and on the third endopodal segment of legs 3 and 4 of *G princeps* only (see Table 3). The Indian Ocean specimens (Soh *et al.* 1998) have the highest number of pores on the swimming legs 1–4. Overall, the Caribbean specimen has consistently fewer pores on all these appendages, but in each case, the figure is still higher than the other two species for which pores of swimming legs have been examined (*G asymmetrica, G intermedia*) (see Table 4). The Caribbean specimen has a single pore on the first endopodal segment of leg 2, a position not reported in any other specimens of *G princeps*; the only segment in which the Caribbean specimen has more pores than those found by Soh *et al.* (1998) is the third exopodal segment of the fourth swimming leg (7 vs 6), the remaining pattern agrees with their observations.

According to this comparative analysis, the species with the highest number of pores on the male right antennule is *G sewelli* (see Table 2; Saraswathy & Bradford 1980); *Gaussia princeps* has the highest pore number on the fifth leg, followed closely by G sewelli, but patterns remain undescribed for males of *G intermedia and G asymmetrica*. These patterns should be compared in order to state the overall range of interspecific variation involving secondary sexual characters.

**TABLE 2.** Comparison of pore number of male right antennule of *Gaussia princeps* from the Caribbean (this survey) (GpC), the Indian Ocean (Soh *et al.* 1998) (GpI), and *G. sewelli* (Saraswathy & Bradford 1980) (GsI) from the Indian Ocean. Antennule segments grouped in three sectors: first segment, segments 2–5, and 6–12.

	GpC	GpI	GsI
First segment	9	11	11
Segments 2–5	7	10	13
Segments 6-12	6	9	10
Total pores	22	29	34

	GpC	GpI	GsI
Сх	3	4	2
RBp	3	3	3
LBp	3	4	4
RExp1	1	3	4
LExp1	2	3	3
RExp2	4	4	5
LExp2	5	6	5
Total pores	21	27	26

**TABLE 3.** Comparison of pore number of male fifth leg of *Gaussia princeps* from the Caribbean (this survey) (GpC), the Indian Ocean (Soh *et al.* 1998) (GpI), and *G sewelli* (Saraswathy & Bradford 1980) (GsI) from the Indian Ocean. Enp= endopod; Exp=exopod; Cx=coxa; Bp=basipodite; R=right; L= left.

**TABLE 4.** Comparison of pore number of swimming legs 1–4 of *Gaussia princeps* from the Caribbean (this survey) (GpC), the Indian Ocean (Soh *et al.*, 1998) (GpI), *G asymmetrica* (Björnberg & Campaner 1990) (GaSA) from the south-western Atlantic Ocean, and *G intermedia* from the north Pacific (Defaye 1998) (GiNP). Enp= endopod; Exp=exopod; Cx=coxa; Bp=basipodite.

		GpC				GpI				GaSA				GiNP		
	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
Cx	_	2	1	1	_	1	1	1	_	1	1	1	_	1	_	_
Вр	1	2	1	_	2	2	1	_	_	1	1	1	-	1	_	_
Enp1	_	1	_	_	_	_	_	_	_	-	_	_	-	_	_	_
Enp2	_	1	1	_	1	1	1	1	_	_	_	_	_	_	_	_
Enp3	1	_	1	1	1	1	2	2	1	-	_	_	-	1	_	_
Exp1	_	2	3	3	_	3	3	3	_	1	2	1	_	1	3	3
Exp2	_	3	3	3	_	4	4	4	_	4	4	4	-	4	3	3
Exp3	1	7	10	8	2	7	9	9	1	7	9	9	2	3	7	9
Total	3	18	14	19	6	19	21	20	2	14	17	16	2	11	13	17

## Discussion

*Gaussia princeps* has been recorded from a wide range of depths (0–3000 m) including mesopelagic and bathypelagic waters (Soh *et al.* 1998). In the northwestern tropical Atlantic (NWTA) it has been recorded at depths between 250 and 1000 m (Wilson 1950; Owre & Foyo 1964, 1967). Owre & Foyo (1964, 1967) reported one female from 584 m and two males from 259 m and 595 m, respectively in the Caribbean and the Straits of Florida. Grice (1963) reported it from deeper samples (2000 m) in the eastern Caribbean. The finding of this mesopelagic form at the uppermost layer sampled during this survey (25–50 m) represents the shallowest occurrence in the region. Soh *et al.* (1998) relate the occurrence of this species at 400–500 m in Suruga Bay, Japan, with the presence of Intermediate Subarctic Water, of relatively low salinities. In the Indian Ocean Saraswathy (1973a) found *G princeps* consistently in the upper 200 m and noticed that it tends to avoid upwelling areas but is associated with deeper, colder waters. In the western Caribbean there are several records of deep-living species occurring in the upper layers, their occurrence probably related to upwelling (Suárez-Morales 1990). In the sample site from which *G princeps* was collected lies over a deep

depression of 1000–1500 m with colder intermediate water. The male from the Caribbean was captured at night (00:13 h), thus suggesting a vertical pattern that agrees with the known diurnal migratory behaviour of the species with a shallower occurrence at night (Childress 1976).

In the NWTA this species has been recorded in a few localities only (Vervoort 1965; Soh *et al.* 1998). It was found in the oceanic area south of Cape Hatteras (Wilson 1950), in the Florida Straits (Owre & Foyo 1967), off Hispaniola in the Caribbean Sea (Wilson 1950; Grice 1963), and in the oceanic area of the eastern Caribbean (Owre & Foyo 1964) (Fig. 5). This species has not been recorded in the adjacent Gulf of Mexico (Suárez-Morales *et al.* 2000) or in the western Caribbean Sea.



**FIGURE 5.** The northwestern tropical Atlantic with the location and authorities of the regional records of *Gaussia princeps* (Scott). 1. Wilson (1950); 2. Grice (1963); 3. Owre & Foyo (1964); 4 Owre & Foyo (1967); 5. this survey.

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