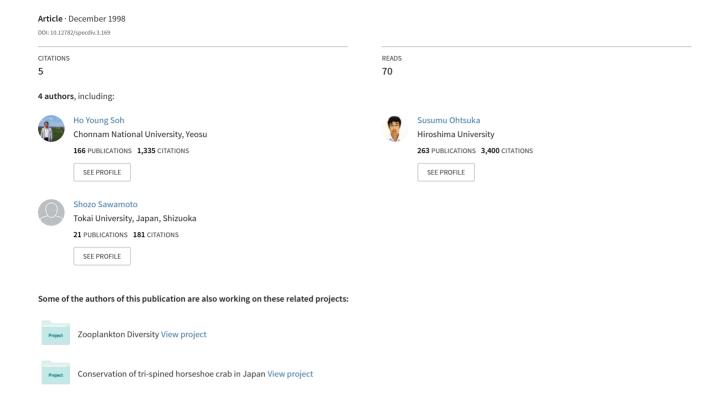
Gaussia princeps (Scott) (Copepoda, Calanoida, Metridinidae) from the Indo-Pacific, with Notes on the Zoogeography of the Genus



Gaussia princeps (Scott) (Copepoda, Calanoida, Metridinidae) from the Indo-Pacific, with Notes on the Zoogeography of the Genus

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Gaussia princeps (Scott, 1894) (Copepoda: Calanoida: Metridinidae) is redescribed from the Indo-Pacific region on the basis of two adult females, one adult male, and the fifth copepodid stage of both sexes and compared with the holotype from the Gulf of Guinea. The specimens of *G. princeps* from the Indo-Pacific region showed no remarkable differences from the holotype. The morphological differences from its two congeners are also discussed. The genital compound somite of the female of *G. princeps* carries paired gonopores and copulatory pores located antero- and postero-ventrally, respectively, without distinct seminal receptacles; this arrangement differs from those of other genera of the family Metridinidae. Present and previous data indicate that *G. princeps* is widely distributed in the mesopelagic zone of the oceans throughout the tropical to temperate regions, but there are some morphological evidences that the southeastern pacific population represents a distinct species.

Key Words: copepod, Gaussia princeps, genital systems, zoogeography.

Introduction

Gaussia Wolfenden, 1905, based on G. princeps (Scott, 1894) from the Gulf of Guinea, had been considered monospecific (Wolfenden 1911; Sewell 1932; Brodsky 1950). Later, Saraswathy (1973b) described G. sewelli from the Indian Ocean, and Björnberg and Campaner (1988) established G. asymmetrica from the Atlantic Ocean.

Gaussia princeps was originally described from a single male by Scott (1894), and then several authors (Esterly 1906; Wolfenden 1911; Davis 1949; Wilson 1950; Owre and Foyo 1967; Saraswathy 1973b; Björnberg and Campaner 1988) briefly treated the female, with illustrations only of the body and leg 5. These illustrations, however, are insufficient to provide the information needed for our phylogenetic studies on calanoid copepods (e.g., Ohtsuka et al. 1994), since strict homologies, considered essential in the study of phylogenetic relationships between taxa, cannot be traced. In Japanese waters the species was first reported, without illustrations, by Tanaka and Omori (1967), and has never been reexamined since then. Although the family Metridinidae consists of three distinct genera, Gaussia, Metridia Boeck, 1864, and Pleuromamma Giesbrecht, 1898, their phylogenetic inter-relationships have never been addressed. We intend to study the phylogenetic relationships between

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these genera based on a cladistic analysis. In advance of this study we here redescribe in detail the adults and the fifth copepodid stage of both sexes of *G. princeps* from the Indo-Pacific region, with remarks on the morphology and zoogeography of the genus. *Gaussia princeps* from Japanese waters is also compared with the holotype from the Gulf of Guinea.

Material and Methods

The present study is based on collections deposited in the Institute of Oceanic Research & Development of Tokai University, the Ocean Research Institute of the University of Tokyo, and The Natural History Museum, London. Sampling data and localities are summarized in Table 1. Copepod specimens were dissected and mounted in Gum-chloral medium, and observed and illustrated with a differential interference contrast microscope (Olympus BX-50) equipped with a drawing tube. The genital compound somite of the female was also examined with a scanning electron microscope (JOEL T-20). The morphological terminology follows Huys and Boxshall (1991).

Family **Metridinidae** Sars, 1902 Genus *Gaussia* Wolfenden, 1905

Diagnostic characters of the genus *Gaussia* are provided in addition to the definitions by Saraswathy (1973b) and Björnberg and Campaner (1988): urosome about half as long as prosome; genital compound somite of female with paired gonopores located anteroventrally and pair of small copulatory pores posteroventrally. Antennule with 23 segments, longer than body; antennular segments I-III and IX-XI completely and incompletely fused, respectively. First endopodal segment of leg 2 with or without small inner prominence proximal to large, subterminal hook. Coxae and intercoxal sclerite of male leg 5 completely fused. Exopod of left leg 5 two-segmented, with one inner and one outer strong process proximally; exopod of right leg 5 three-segmented, second and third segments incompletely fused.

Type species. Pleuromma princeps T. Scott, 1894.

Other species. *Gaussia sewelli* Saraswathy, 1973; *G. asymmetrica* Björnberg and Campaner, 1988.

Remarks. The family Metridinidae is composed of three genera: *Metridia, Pleuromamma*, and *Gaussia*. *Gaussia* is readily distinguished from the other genera by: (1) the absence of a rounded, black or dark-brown pigmented spot on the right or left side of the first pedigerous somite; (2) the genital compound somite of female being expanded anterolaterally; (3) the exopod of left leg 5 of the male being two-segmented. The female genital systems in this family are of two types. Both *Metridia* and *Gaussia* have an anteroventral pair of gonopores and a posteroventral pair of copulatory pores, whereas *Pleuromamma* has an anteroventral pair of gonopores and only a single copulatory pore ventromedially (Cuoc *et al.* 1997; present study). In addition, *Gaussia* lacks distinct seminal receptacles, whereas *Metridia* develops a pair of cylinder-shaped seminal receptacles just anterior to the

copulatory pores (cf. Giesbrecht 1892: plate 33). *Pleuromamma* carries a single well-developed seminal receptacle beneath the copulatory pore, which is connected to left or right gonopore through a receptacle duct (Ferrari 1984).

Gaussia princeps (Scott, 1894) (Figs 1-6)

Specimens examined are listed in Table 1.

Adult female. Body (Fig. 1A, B) 10. 47 mm (specimen from the Indian Ocean) and 10.90 mm (specimen from Suruga Bay) long. Prosome anteriorly produced into acute process; depression observed ventral to this process in lateral view (Fig. 1C); rostrum bearing two long, tapering filaments fringed with short setules; cephalosome and first pedigerous somite completely separate; fourth and fifth pedigerous somites completely fused; posterior corners of prosome almost symmetrically produced backwards into pointed, spine-like processes reaching middle of genital compound somite (Fig. 1D). Urosome three-segmented. Genital compound somite with small, conical process dorsally on right anterolateral swelling (Figs 1E, F, 2A); paired gonopores and copulatory pores (Figs 1E, F, 2A-C) located ventrolaterally in anterior and posterior regions, respectively; distinct seminal receptacles not found. Second urosomal somite small. Anal somite fringed with hairs ventrolaterally (Fig. 1A, B), also bearing pair of posterolateral papillae, each with three terminal gland openings. Caudal rami symmetrical, each with small posterodorsal papilla bearing one subterminal gland opening and fringed with fine setules along medial margin; with six plumose setae (Fig. 1A).

Antennules (Fig. 3A-E) symmetrical, with 23 segments, reaching beyond caudal rami by two or three segments; segments IX-X and XI incompletely fused; segments XI and XII, and XIV and XV almost separate (Fig. 3A, D). Fusion pattern and setal formula as follows: I-III-7 + 3 aesthetascs, IV-2 + aesthetasc, V-2 + aesthetasc, VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, XIII-2 + aesthetasc, XIII-2 + aesthetasc, XIII-2 + aesthetasc, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVII-2 + aesthetasc, XVII-2 + aesthetasc, XIX (-2 + aesthetasc on right side), XX-2 + aesthetasc, XXI-2 + aesthetasc, XXII-1, XXIII-1, XXIV-1+1, XXV-1+1 + aesthetasc, XXVI-1+1, XXVII-XXVIII-6 + aesthetasc. Segments I-XII fringed with fine hairs along posterior margin; segments I-XII and XIV-XV furnished with one or more gland openings along anterior margin (arrowheads in Fig. 3A-D).

Antenna (Fig. 3F, G): coxa with spinulose medial seta; basis bearing two unequal setae; endopod two-segmented, first segment carrying two setae of unequal lengths at two-thirds length, second with nine medial and seven distal setae and subterminal patch of spinules (Fig. 3G); exopod indistinctly eight-segmented, second through fourth segments incompletely fused; setal formula as follows: 1, 1, 1, 1, 1, 1, 1, 1, 4. First and second exopodal segments with gland opening on distal part of each (arrowheads in Fig. 3F).

Labrum (Fig. 3H) bilobed distally; paragnath furnished with six inner spinules on each side. Mandible (Fig. 3I): gnathobase with eight cuspid teeth and one spinulose dorsal seta, bearing tiny spinules at bases of teeth; basis of mandibular palp with four small medial setae and three subterminal gland openings; both rami of almost equal length; endopod two-segmented, first segment with four setae, second

Table 1. Sampling date, locality, depth, and gear used for collecting of Gaussia species.

Gear	ORI net	10-foot IKMT	10-foot IKMT	ORI net	ORI net	ORI net	10-foot IKMT	10-foot IKMT	10-foot IKMT	10-foot IKMT	10-foot IKMT	10-foot IKMT	10-foot IKMT
Depth	449 - 496	0 - 1200	0 - 1200	460	395	395	0 - 135	0 - 1650	0 - 880	0 - 880	0 - 1650	0 - 880	0 - 880
Locality	Suruga Bay (34°51.37'N, 138°38.00'E 34°51.11'N, 138°38.20'E)	Indian Ocean (0°04.4'N, 86°55.3'E 0°00.4'S, 86°54.6'E)	Indian Ocean (4°59.2'S, 87°01.0'E 4°48.6'S, 87°02.8'E)	Suruga Bay (34°50.29'N, 138°37.69'E 34°51.30'N, 138°37.99'E)	Suruga Bay (34°49.0'N, 138°37.3'E 34°47.3'N, 138°36.9'E)	Suruga Bay (34°49.0'N, 138°37.3'E 34°47.3'N, 138°36.9'E)	Indian Ocean (9°44.7'N, 86°43.2'E 9°45.9'N, 86°42.4'E)	Indian Ocean (9°46.4'N, 86°42.4'E 9°50.3'N, 86°40.2'E)	Indian Ocean (13°50.9'N, 86°59.8'E 13°54.1'N, 86°59.1'E)	Indian Ocean (13°50.9'N, 86°59.8'E 13°54.1'N, 86°59.1'E)	Indian Ocean (9°46.4'N, 86°42.4'E 9°50.3'N, 86°40.2'E)	Indian Ocean(13°50.9'N, 86°59.8'E 13°54.1'N, 86°59.1'E)	Indian Ocean (13°50.9'N, 86°59.8'E 13°54.1'N, 86°59.1'E)
Date	14 X 1988	28 I 1977	23 I 1977	13 XI 1992	27 III 1984	27 III 1984	10 II 1977	10 II 1977	11 II 1977	11 II 1977	10 II 1977	11 II 1977	11 II 1977
Number of specimens	1	1	1	1	1	1	63	4	12	က	1	1	2
Sex	o l	어	г ο	CV &	CV 4	CV ♂	아	아	아	√ 0	CV♀	CV ₽	CV o∕
Species	Gaussia princeps						G. sewelli						

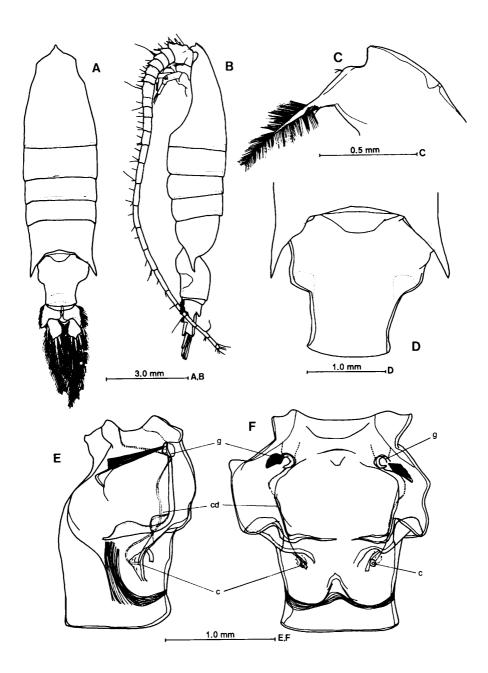


Fig. 1. *Gaussia princeps* (Scott, 1894), female from Suruga Bay. A, Habitus, dorsal view; B, Habitus, lateral view; C, Forehead, lateral view; D, Genital compound somite, dorsal view; E, Genital compound somite, lateral view; F, Genital compound somite, ventral view, c: copulatory pore; cd: copulatory duct; g: gonopore.

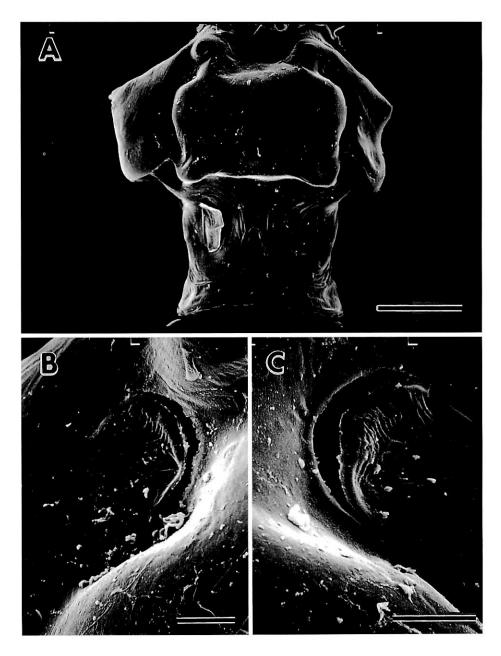


Fig. 2. *Gaussia princeps* (Scott, 1894), female from Suruga Bay. SEM micrographs of genital compound somite of female. A, Genital compound somite, ventral view, copulatory pores damaged; B, Right gonopore; C, Left gonopore. Scale bars = 0.3 mm (A); 0.05 mm = (B, C).

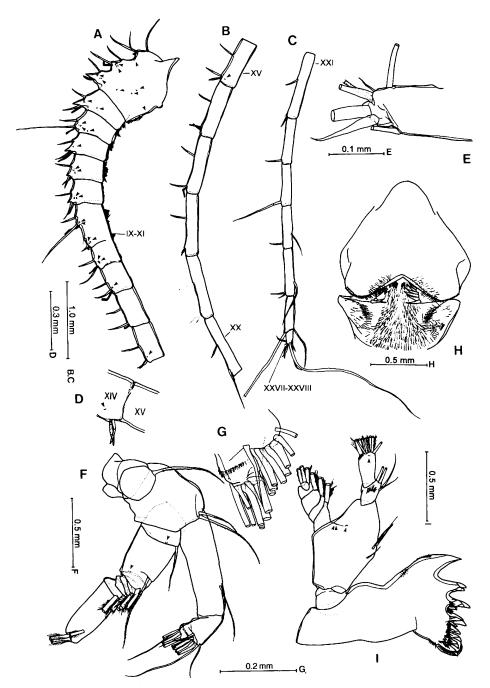


Fig. 3. Gaussia princeps (Scott, 1894), female from Suruga Bay. A, Left antennulary segments I-XIV; B, Left antennulary segments XV-XX; C, Left antennulary segments XXI-XXVIII; D, Left antennulary segments XIV and XV; E, Left antennulary segments XXVII-XXVIII; F, Antenna; G, Second endopodal segment of antenna; H, Labrum and paragnaths; I, Mandible. Arrowheads indicate gland openings.

with 10 setae distally, minute spinules terminally; exopod distinctly five-segmented, with setal formula of 1, 1, 1, 2.

Maxillule (Fig. 4A): praecoxal arthrite bearing 16 elements and gland opening (arrowhead in Fig. 4A); coxa with five plumose setae on endite, nine plumose setae on epipodite, and gland opening (arrowhead in Fig. 4A); first basal endite with four setae, second with five setae; basal exite with single short, plumose seta; endopod one-segmented, carrying six medial and 11 distal setae; exopod with 11 setae and gland opening (arrowhead in Fig. 4A), furnished with row of small hairs along medial margin.

Maxilla (Fig. 4B): first praecoxal endite bearing nine setae and one tiny spine, second praecoxal and two coxal endites each with three spinulose setae; basis having heavily sclerotized stout seta, three spinulose setae, and gland opening (arrowhead in Fig. 4B); setal formula of endopod: 4, 3, 2, 2; first endopodal segment with heavily sclerotized spiniform seta.

Maxilliped (Fig. 4C): praecoxa and coxa incompletely segmented, endites carrying one, two, four, and four setae, respectively; basis with three setae, row of minute spinules on medial surface, and gland opening (arrowhead in Fig. 4C); basis and first endopodal segment incompletely fused, setal formula of endopod: 2, 4, 4, 3, 3, 4. Second to sixth endopodal segments each with outer gland opening (arrowheads in Fig. 4C). Seta and spine formula of legs 1-4 as follows:

	coxa	basis	exopod segment	endopod segment
leg 1	0 - 1	1 - 1	I - 1; Ι - 1; Π, Ι, 4	0 - 1; 0 - 2; 1, 2, 2
leg 2	0 - 1	0 - 0	I - 1; I - 1; M, I, 5	0 - 0; 0 - 2; 2, 2, 4
leg 3	0 - 1	0 - 0	I - 1; I - 1; M, I, 5	0 - 1; 0 - 2; 2, 2, 4
leg 4	0 - 1	1 - 0	I - 1; I - 1; Ⅲ, I, 5	0 - 1; 0 - 2; 2, 2, 3

Leg 1 (Fig. 4D): basis furnished with tuft of short hairs on distomedial corner and small process on posterior aspect; outer margin of second and third exopodal segments fringed with row of spinules and short setules (Figs. 4D-a, b, c); outer spines on second and third exopodal segment each with terminal lash (Fig. 4D-d). Leg 2 (Fig. 5A): basis with minute spinules along lateral margin; first exopodal segment bearing patch of short spinules proximally; first endopodal segment carrying characteristic, double hook-like process subterminally and single simple prominence proximally (Fig. 5A-a). Legs 3 (Fig. 5B) and 4 (Fig. 5C): similar to those of *Gaussia asymmetrica* Björnberg and Campaner, 1990, but leg 4 having lateral basal seta and shorter terminal spine on third exopodal segment. Leg 5 (Fig. 5D): symmetrical, coxae completely fused with intercoxal sclerite; endopod absent; exopod three-segmented, first segment unarmed, second with long, curved seta on distomedial corner, third bearing medial spinulose seta and short terminal spine with curved terminal lash (Fig. 5D-a).

Copepodid V female. Body length 8.65 mm in two individuals. Urosome four-segmented. Antennule having 24 segments; segments IX and X completely separate, segments X and XI incompletely fused, and segments XIV and XV incompletely separate. Fusion pattern and setal formula as follows: I-III-5 + 2 aesthetascs, IV-2, V-2 + aesthetasc, VII-2, VII-1 + aesthetasc, VIII-2, IX-2 + aesthetasc, X-XI-4 + 2 aesthetascs, XII-2, XIII-2 + aesthetasc, XIV-2 + aesthetasc, XV-2 + aesthetasc, XVII-2 + aesthetasc, XVII-2 + aesthetasc, XVII-2 + aesthetasc, XIX-2 + aesthetasc, XIX-2

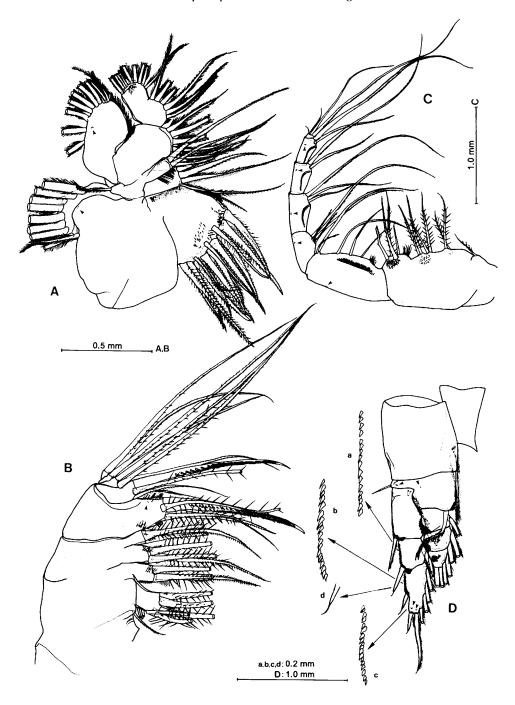


Fig. 4. *Gaussia princeps* (Scott, 1894), female from Suruga Bay. A, Maxillule; B, Maxilla; C, Maxilliped; D, Leg 1, anterior. Arrowheads indicate gland openings.

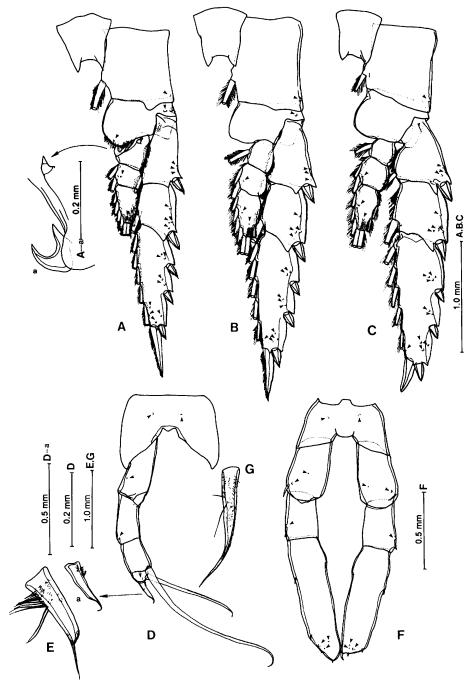


Fig. 5. *Gaussia princeps* (Scott, 1894), female from Suruga Bay (A-D) and from the Indian Ocean (E), copepodid V male from Suruga Bay (F); *G. sewelli* Saraswathy, 1973, female from the Indian Ocean (G). A, Leg 2, anterior; B, Leg 3, anterior; C, Leg 4, anterior; D, Leg 5, posterior; E,

XX-2 + aesthetasc, XXI-2 + aesthetasc, XXII-1, XXIII-1, XXIV-1+1, XXV-1+1 + aesthetasc, XXVI-1+1, XXVII-XXVIII-6 + aesthetasc. Second endopodal segment of antenna with eight medial and seven distal setae. Second endopodal segment of mandibular palp having nine setae distally. Endopod of maxillule carrying five medial and 10 distal setae; exopod with 10 setae. First praecoxal endite of maxilla bearing eight setae and one tiny spine. Second to fifth endopodal segments of maxilliped with setation formula: 3, 3, 2, 2. Legs 1 to 4 same as in adult female. Leg 5 as in *Gaussia sewelli* (see Sewell 1932: text-fig. 93); coxae completely fused with intercoxal sclerite; exopod two-segmented, first segment unarmed, second with two long, plumose medial setae and 1 short, plumose distal seta.

Adult male. Body 9.54 mm long (specimen from the Indian Ocean), similar to that of female except for posterior corners of prosome being produced posteriorly into short, blunt processes rather than long, sharp ones; prosome about 2.4 times as long as urosome. Urosome five-segmented. Right antennule (Fig. 6A-D) geniculate, having 20 segments: each of segments XII to XV incompletely separate, XVI and XVII incompletely fused. Posterior margin of segments I-XII without fine hairs. Fusion pattern and setal formula as follows: I-IV-7 + 4 aesthetascs, V-2 + aesthetasc, VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, XII-1 + process + aesthetasc, XII-2 + aesthetasc, XII-1 + process + aesthetasc, XIII-2 + aesthetasc, XIV-2 + aesthetasc (distal seta transformed into bulbous seta) (Fig. 6D), XV-1 (missing in Fig. 6B) + process + aesthetasc, XVI-XVII-4 (proximal seta of segment XVI missing in Fig. 6B) + 2 aesthetascs, XVII-2 + aesthetasc, XIX-1 + process + aesthetasc, XXIV-XXV-2+2 + process + aesthetasc, XXII-XXIII-2 + 3 processes + aesthetasc, XXIV-XXV-2+2 + process + aesthetasc, XXVI-1 + 1, XXVII-XXVIII-6 + aesthetasc. Those of left antennule same as in female.

Leg 5 (Fig. 6F) asymmetrical, uniramous; intercoxal sclerite fused to both coxae; basis with one small seta; endopod absent. Left leg: exopod two-segmented; first segment with distolateral spinules; second with two processes on proximal part, medial process (Fig. 6G) proximally directed, not reaching basis (arrowed in Fig. 6F), and having three spinules subterminally. Right leg: exopod incompletely three-segmented; second and third exopodal segments incompletely segmented; first segment with lateral spinule, second with slender medial seta proximally, third sinuous along medial margin, with three spinules.

Copepodid V male. Body length 8.2 mm. Urosome four-segmented. Left antennule as in copepodid V female; right not geniculate, segments XIX and XX each with one anterior process, segment XXI with two anterior processes. Appendages same as in CV female. Legs 5 (Fig. 5F) nearly symmetrical; coxae completely fused with intercoxal sclerite; basis bearing small outer spiniform seta on distal corner; endopod absent; exopod two-segmented, first segment with lateral spinule, second with three lateral, one terminal, and one medial proximal spinules.

Remarks. Gaussia princeps was originally described on the basis of a single male specimen 12.0 mm long, collected from the Gulf of Guinea (Scott 1894). The known range of body length of the males 9.0 to 12.0 mm (Scott 1894; Davis 1949; Saraswathy 1973b), while the female has been recorded with a range of 10.0-12.0 mm

Distal seta on third exopodal segment of right leg 5; F, Leg 5, posterior; G, Distal seta on third exopodal segment of right leg 5. Arrowheads indicate gland openings.

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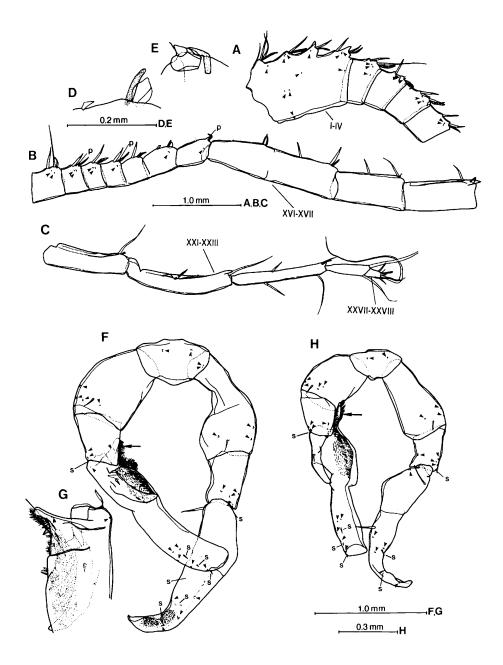


Fig. 6. Gaussia princeps (Scott, 1894), male from the Indian Ocean (A-D, F, G) and the holotype (E); G. sewelli Saraswathy, 1973, male from the Indian Ocean (H).

A, Antennulary segments I-VIII; B, Antennulary segments IX-XIX; C, Antennulary segments

XX-XXVIII; D and E, Anterior part of antennulary segment XIV; F, Leg 5, posterior; G, Medial process on second exopodal segment of left leg 5, anterior; H, Leg 5, posterior, distal two

in body length (Wolfenden 1911; Davis 1949; Tanaka and Omori 1967; Saraswathy 1973b; Björnberg and Campaner 1988). We reexamined the holotype of *G. princeps* deposited in The Natural History Museum, London and compared it with the specimens from Suruga Bay and the Indian Ocean. Except for sexual differences, these females from Suruga Bay and the Indian Ocean agree very closely with the holotype. However, the male from the Indian Ocean slightly differs from the holotype in the shape of a bulbous seta on the antennulary segment XIV (Fig. 6D, E). The morphological difference of the bulbous seta is also found in the specimens of *G. princeps* collected from the Indian Ocean by Saraswathy (1973b).

The adult female from Suruga Bay is 10.9 mm long and differs slightly from *G. princeps* collected from the southeastern Pacific (Björnberg and Campaner 1988, 1990) as follows: the former has a small, conical process dorsally on the right anterolateral swelling of the genital compound somite and a characteristic single prominence proximally on the first endopodal segment of leg 2, while the latter lacks both. There is another difference between *G. princeps* from the Indo-Pacific region and from the southeastern Pacific: the terminal spine of the third exopodal segment of female leg 5 of Suruga Bay and Indian Ocean specimens abruptly tapers as in *G. asymmetrica* (Fig. 5D-a, E), while the southeastern Pacific specimens resemble *G. sewelli* in having a smoothly tapering one (Fig. 5G). We think that these differences may be significant enough to indicate a separate species. However, it is also possible that these differences are involved in interspecific variation. Any conclusion is therefore put off until many more specimens of *G. princeps* from the world ocean are examined.

Discussion

Comparison between Congeners

Gaussia princeps is easily distinguished from its two congeners, G. sewelli and G. asymmetrica, by the combination of the following characters: (1) cephalosome anteriorly pointed to stout process; (2) last prosomal somite with almost symmetrical, posteriorly directed processes; (3) genital compound somite of female asymmetrical, with small anterodorsal prominence on right side; (4) proximally directed medial process of second exopodal segment of male left leg 5 relatively short, not reaching distal border of basis. There are several additional differences in the other appendages. Gaussia princeps from Suruga Bay and the Indian Ocean and G. sewelli bear a small medial prominence proximal to the large, subterminal, bifurcated hook on the first endopodal segment and a patch of minute spinules proximally on the first exopodal segment in leg 2, while G. princeps from the southeastern Pacific and G. asymmetrica lack these (Sewell 1932; Björnberg and Campaner 1990). Gaussia princeps and G. sewelli also have different numbers of setae on the antenna and mandibular palp of copepodid V: the former has eight medial and seven distal setae on the second segment of the antennary endopod and nine distal setae on the second segment of the mandibular endopod, whereas the latter bears seven, seven, and seven

exopodal segments of right leg torted. Arrowheads indicate gland openings. Arrows indicate inner process proximally directed on second exopodal segment. p: process; s: spinule.

setae on the counterparts, respectively (see Sewell 1932).

The number and distribution pattern of gland openings (presumably luminescent gland openings) also differ between congeners. In *G. princeps* and *G. sewelli* these openings are distributed on all appendages (Barnes and Case 1972; present study), whereas in *G. asymmetrica* they appear only on the antennules and all legs (Björnberg and Campaner 1990). The number of gland openings on the antennules and legs is largest in *G. princeps*. However, no intraspecific variations in gland openings were found between *G. princeps* from the Indian Ocean and from Suruga Bay. Therefore these could be diagnostic for each species of the genus *Gaussia*, as suggested for species of *Pleuromamma* (Park and Mauchline 1994; Park 1995) belonging to the same family. In additon to the morphological differences discussed in the remarks of *G. princeps*, observations on the gland openings also suggest that specimens of *Gaussia princeps* from the Indo-Pacific region and from the southeastern Pacific might not be conspecific.

Zoogeography of the Genus Gaussia

The distribution patterns of the three species of *Gaussia* are summarized in Fig. 7. *Gaussia princeps* is widely recorded throughout tropical and temperate regions of the oceans, while *G. sewelli* has been found exclusively in tropical regions of the northern Indian Ocean, particularly the central parts of the Arabian Sea and the Bay of Bengal. These facts were also confirmed in this study. *Gaussia asymmetrica* has

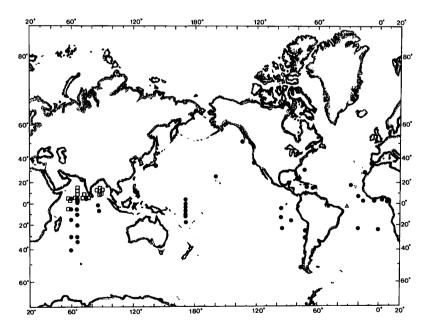


Fig. 7. Zoogeographical distribution of Gaussia princeps (●), G. sewelli (□), and G. asymmetrica (△) based on: Scott (1894), Wolfenden (1911), Sewell (1932), Lysholm et al. (1945), Davis (1949), Wilson (1950), Vervoort (1965), Owre and Foyo (1967), Grice and Hülsemann (1967), Tanaka and Omori (1967), Gueredrat (1969), Morris (1970), Roe (1972), Saraswathy (1973a), Björnberg and Campaner (1988), and present study.

Table 2. Depth distribution of genus Gaussia.

Species	Depth (m)	Literature					
Gaussia princeps	150 - 1000 Grice 1963; Kodama and Kubota 19 Kubota et al. 1992; Kubota and Sawam 1993; Morris 1970; Owre and Foyo 19 1967; Roe 1972; Scott 1894; Tanaka Omori 1967; Vervoort 1965						
	1500 - 3000 Wolfenden 1911						
	0 - 3660	Björnberg and Campaner 1988; Davis 1949; Grice and Hülsemann 1967; Gueredrat 1969; Saraswathy 1973a; Wilson 1950; present study					
Gaussia sewelli		Sewell 1932 Sewell 1947; present study					
Gaussia asymmetrica	0 - 212	Björnberg and Campaner 1988					

been recorded only in the tropical region of the southwestern Atlantic Ocean.

Table 2 shows the vertical ranges of the species of Gaussia. Gaussia princeps seems to be distributed mainly in the mesopelagic zone. In Suruga Bay this species was also collected from depths of about 400-500 m. These depths are the center of the Intermediate Cold Water with a minimum salinity of 34.25-34.30, originating from the Subarctic Water (Nakamura 1982). It is, however, unclear whether G. princeps depends on the salinity minimum layer, because only four specimens were found from three samples from just three of 19 cruises in Suruga Bay during 1980-1992. On the other hand, Saraswathy (1973a) suggested that the occurrence of Gaussia princeps in the upper 200 m in the Indian Ocean may be related to cold water originating from the Sub-Antarctic Intermediate Water and the Antarctic Bottom Water. Gaussia sewelli and G. asymmetrica were collected at depths of 0-1650 m and 0-210 m, respectively. It is uncertain in what hydrographic conditions these two species are distributed.

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References

Barnes, A.T. and Case, J.F. 1972. Bioluminescence in the mesopelagic copepod, *Gaussia princeps* (T. Scott). Journal of Experimental Marine Biology and Ecology 8: 53-71.

- Björnberg, T.K.S. and Campaner, A.F. 1988. On *Gaussia* Wolfenden (Copepoda, Calanoida, Metridinidae). Hydrobiologia 167/168: 351-356.
- Björnberg, T.K.S. and Campaner, A.F. 1990. On the genus *Gaussia* and the species *G. asymmetrica* (Copepoda, Calanoida). Crustaceana 58(1): 106-112.
- Brodsky, K.A. 1950. Calanoida of the far eastern seas and polar basin of the U.S.S.R. Opredeliteli po Faune SSSR 35: 1-442. (Translation: Israel Program for Scientific Translations, Jerusalem, 1967).
- Cuoc, C., Defaye, D., Brunet, M., Notonier, R. and Mazza, J. 1997. Female genital structures of Metridinidae (Copepoda: Calanoida). Marine Biology 129: 651-665.
- Davis, C.C. 1949. The pelagic Copepoda of the northeastern Pacific Ocean. University of Washington Publications in Biology 14: 1-118.
- Esterly, C.O. 1906. Additions to the copepod fauna of the San Diego Region. University of California Publications in Zoology 3 (5): 53-92.
- Ferrari, F.D. 1984. Pleiotropy and *Pleuromamma*, the looking-glass copepods (Calanoida). Crustaceana, supplement 7: 166-181.
- Giesbrecht, W. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Fauna und Flora des Golfes von Neapel 19: 1-831.
- Grice, G.D. 1963. Deep water copepods from the western north Atlantic with notes on five species, Bulletin of Marine Science of the Gulf and Caribbean 13: 493-501.
- Grice, G.D. and Hülsemann, K. 1967. Bathypelagic calanoid copepods of the western Indian Ocean. Proceedings of the United States National Museum 122: 1-67.
- Gueredrat, J.-A., 1969. Distribution de quatre espeéces de Copépodes bathypélagiques dans l'ouest du Pacifique équatorial et tropical sud. Deep Sea Research 16: 361-375.
- Huys, R. and Boxshall, G.A. 1991. Copepod Evolution. Ray Society, London, 468pp.
- Kodama, K. and Kubota, T. 1984. List of Calanoida and Cyclopoida (Copepoda) from Suruga Bay, Central Japan. Bulletin of the Institute of Oceanic Research & Development, Tokai University 6: 29-40.
- Kubota, T., Sawamoto, S. and Kishimoto, H. 1992. Macroplankton Project of Marine Biological Center, Institute of Oceanic Research & Development, Tokai University, 1980-1985. Bulletin of the Institute of Oceanic Research & Development, Tokai University 13: 105-120.
- Kubota, T. and Sawamoto, S. 1993. Macroplankton Project of Marine Biological Center, Institute of Oceanic Research & Development, Tokai University, 1985-1992. Bulletin of the Institute of Oceanic Research & Development, Tokai University 14: 151-163.
- Lysholm, B., Nordgaard, O. and Wiborg, K.F. 1945. Copepoda from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. Report of Sars North Atlantic Deep Sea Expedition 5:
- Morris, B. 1970. Calanoid copepods from mid water trawls in the north Pacific along 160°E. Journal of the Fisheries Research Board of Canada 27 (12): 2297-2321.
- Nakamura, Y. 1982. Oceanographic feature of Suruga Bay from view point of fisheries oceanography. Bulletin of Shizuoka Prefectural Fishery Experimental Station 17 (Special Number): 1-153.
- Ohtsuka, S., Boxshall, G.A. and Roe, H.S.J. 1994. Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. Bulletin of the Natural History Museum, London (Zoology) 60 (2): 105-172.
- Owre, H.B. and Foyo, M. 1964. Report on a collection of Copepoda from the Caribbean Sea. Bulletin of Marine Science of the Gulf and Caribbean 14: 359-372.
- Owre, H.B. and Foyo, M. 1967. Copepods of the Florida current. Fauna Caribaea 1, Crustacea, 1:

1-137.

- Park, J.S. and Mauchline, J. 1994. Evaluation of integumental pore signatures of species of calanoid copepods (Crustacea) for interpreting inter-species relationships. Marine Biology 120: 107-114
- Park, J.S. 1995. The development of integumental pore signatures in the genus *Pleuromamma* (Copepoda: Calanoida). Journal of the Marine Biological Association of the United Kingdom 75: 211-218.
- Roe, H.S.J. 1972. The vertical distributions and diurnal migrations of calanoid copepods collected on the Sond Cruise, 1965. III. Systematic account: Families Euchaetidae up to and including the Metridiidae. Journal of the Marine Biological Association of the United Kingdom 52: 525-552.
- Saraswathy, M. 1973a. Distribution of *Gaussia* (Copepoda, Metridiidae) in the upper 200m in the Indian Ocean. *In*: Zeitschel, B. (Ed.) *The Biology of the Indian Ocean*. Pp. 335-338. Springer-Verlag, Berlin.
- Saraswathy, M. 1973b. The genus *Gaussia* (Copepoda-Calanoida) with a description of *G. sewelli* sp. nov. from the Indian Ocean. Handbook int. Zooplankton Collection Indian Ocean Biological Centre 5:190-195.
- Scott, T. 1894. Report on Entomostraca from the Gulf of Guinea, collected by John Rattray, B. Sc. Transactions of the Linnean Society (Zoology) 2: 1-161.
- Sewell, R.B.S. 1932. The Copepoda of Indian Seas. Calanoida. Memoirs of the Indian Museum 10: 223-407, 3 pls.
- Sewell, R.B.S. 1947. The free-swimming planktonic Copepoda. Systematic account. Scientific Reports of the John Murray Expedition 8: 1-303.
- Tanaka, O. and Omori, M. 1967. Large-sized pelagic copepods in the northwestern Pacific Ocean adjacent to Japan. Information Bulletin on Planktology in Japan: 239-260.
- Vervoort, W. 1965. Pelagic Copepoda Part 2. Atlantidae Report 8: 9-216.
- Wilson, C.B. 1950. Copepods gathered by United States Fisheries Steamer "Albatross" from 1887 to 1909, chiefly in the Pacific Ocean. Bulletin of United States National Museum, 14 (4): 141-441.
- Wolfenden, R.N. 1911. Die Marinen Copepoden der Deutschen Südpolar-Expedition 1901-1903, II. Die pelagischen Copepoden der Westwinddrift des Südlichen Eismeeres. Deutschen Südpolar Expedition 12, Zoologie 4: 181-380.

Note Added in Proof

A new species of the genus *Gaussia, G. intermedia* Defaye, 1998 was described from the North Pacific. *Gaussia princeps* examined in the present study is clearly distinguished from the new species as follows: (1) the conical process on the right anterolateral swelling of the female genital compound somite is very small in *G. princeps* but large, curved posteriorly in *G. intermedia*; (2) the distal part of the inner bifurcate hook on the first endopod segment of leg 2 is of almost the same length as the proximal part in *G. princeps* but about four times as long as that in *G. intermedia*; (3) the two proximal processes on the second exopod segment of the male left leg 5 are more developed in *G. princeps* than in *G. intermedia*.

Additional Reference

Defaye, D. 1998. A new *Gaussia* (Copepoda, Calanoida, Metridinidae) from the North Pacific. Crustaceana 71(1): 81-91.