OCCURRENCES OF THE ISOPODA FLABELLIFERA GNORIMO-SPHAEROMA RAYI HOESTLANDT ON THE COASTS OF JAPAN, EASTERN SIBERIA AND HAWAII, WITH A BRIEF NOTE ON ITS GENETIC POLYCHROMATISM

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With Text-figures 1-10

Contents

Page

1.	Introduction	31						
2.	Characteristics of the American Pacific species of the genus Gnorimosphaeroma	32						
3.	Study of Gnorimosphaeroma from Japan, Eastern Siberia and Hawaii	35						
	3.1. Localities	35						
	3.2. Study of Gnorimosphaeroma rayi							
	3.2.1. Morphological differences							
	3.2.1.1. Antennule	37						
	3.2.1.2. Maxillipede	38						
	3.2.1.3. Peraeopod I	39						
	3.2.2. Remarks	41						
3.3. Japanese species of the genus Gnorimosphaeroma								
4.	Short indications about the polychromatism of Gnorimosphaeroma rayi from Japan and							
Eastern Siberia								
5.	Conclusions							
6.	Summary							
Ref	References							

1. Introduction

At the time of our prospecting survey of the American Pacific coast, from Alaska to California, for the purpose of studying the genetic polychromatism of the Isopoda Flabellifera *Gnorimosphaeroma oregonense* Dana 1853, we discovered a new species, *Gnorimosphaeroma rayi* Hoestlandt 1969; it is a Sphaeromatid previously mistaken for *G. oregonense* (Menzies 1954; Riegel 1959); both are morphologically very similar to each other but their polychromatic types are utterly distinct¹⁰. We only found that species in one place in California at Tomales Bay (at 65 km north of San Francisco); there are two small pebbled beaches, situated on the south-west side of that bay and separated from each other by a distance of 1 km: Shallow Beach (38°08'25"

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¹⁾ Schultz (1969) and Rotramel (1972) had doubts about this new species, but without bringing any positive argument; therefore we cannot take such assertions into account.

Latitude North; 122°52'50" Longitude West) and Shell Beach (38°08'25" Latitude North; 122°52'30" Longitude West) (Hoestlandt 1969).

One could wonder whether it was not a Sphaeromatid imported accidentally from Japan, at the time of successive implantations of Japanese oysters (*Crassostrea* gigas Thunberg) in that bay from 1928 onwards (Bonnot 1935; Barret 1963). Now, on the coasts of Japan as well as of Eastern Siberia, it is the species *G. oregonense* which had been reported (Thielemann 1911; Nierstrasz 1931; Gurjanova 1933, 1935, 1936, 1938; Shiino 1944); it was therefore most interesting to examine again the Sphaeromatidae from the Japanese coasts.

We had the opportunity to have a look at a locality of the Japanese coast, at Awakominato (70 km south of Tokyo), then to receive a lot of samples from different localities in Japan, as well as from a locality in Eastern Siberia and a locality in the Hawaii Islands. We make a point of expressing our thanks and gratitude to Doctor Dollander, director of the "Maison Franco-Japonaise" in Tokyo, as well as to the Japanese professors M. Iwasa, T. Kikuchi, S.M. Shiino, T. Tokioka; we also thank Doctor T.E. Bowman of the National Museum of Natural History in the United States of America and Doctor R.J. Lincoln of the British Museum (Natural History) in Great Britain.

After recalling the distinctive characteristics of the American Pacific species of the genus *Gnorimosphaeroma* (Hoestlandt 1973), we will examine *Gnorimosphaeroma* received from Japan, Eastern Siberia and Hawaii and we shall compare them with other species of the same genus. We shall finally give a few concise indications about the polychromatism at a Japanese locality of *G. rayi*.

2. Characteristics of the American Pacific Species of the Genus Gnorimosphaeroma

On the American Pacific coast, the Sphaeromatid described by Dana in 1853 under the name of "Sphaeroma oregonensis" originated from Puget Sound (Oregon) and from the Bay of San Francisco (California). The latin description was too short to allow the distinction between the species closely resembling one another morphologically. So far, four principal species are clearly definite: all of them belong to the genus Gnorimosphaeroma created by Menzies (Menzies 1954) and have the following specific names, G. oregonense Dana 1853, G. luteum Menzies 1954, G. noblei Menzies 1954, and G. rayi Hoestlandt 1969. A fifth species, G. insulare Van Name 1940 was only found in an island off California (San Nicolas Island); it is closely related to G. luteum; we take no notice of it in the present survey, but we will soon publish a detailed study about it.

It is easy to distinguish G. noblei from the other three species, for G.n. is smallsized (3 mm in length at the most) and the basal segments of the right and left antennules approximate each other on the ventral midline of the cephalon; in the other three species the adults reach 8–12 mm in length and the basal segments of the antennules are ventrally separated by the rostrum. G.l. shows ecological and systematic differences from the other two species G.o. and G.r. In fact, G.l. is a species from brackish water whereas G.o. and G.r. are marine; on the other hand in the abdominal part of G.l., only two pleurites reach the lateral border of the pleon, for the third pleurite keeps hidden under the second one; in G.o. and G.r., the three pleurites reach the lateral border of the pleon (Fig. 1).

The morphological distinction between G.o. and G.r. refers mostly to the peraeopod I. In G.o., the sternal ridges of the ischiopodite, meropodite and carpopodite bear two or three rows of long setae (Fig. 2); in G.r. besides the sterno-distal setae of these segments, there can be found only one or two sternal setae solely on the ischiopodite (Figs. 8 and 9, pp. 39 and 41); there is not, as to this character, any difference

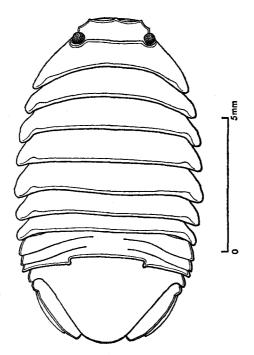


Fig. 1. Gnorimosphaeroma rayi (from Sugashima). Male, dorsal view.

between G.r. from California and G.r. from Japan.

The peraeopod I of G.l. is closely related to that of G.r., but the sternal ridges of the ischiopodite, meropodite and carpopodite do not bear any other setae but the sterno-distal seta (Fig. 3).

There exist other differences between G.o., G.l. and G.r.; they will be mentioned when we study the Gnorimosphaeroma from Japan.

It is now possible to present a key of determination of the four species considered here:

(1)	Basal segments of right and left antennules approximate each other on the ventral midline
	of the cephalonG. noblei
(1)	Basal segments of right and left antennules remaining separated ventrally by rostrum (2)

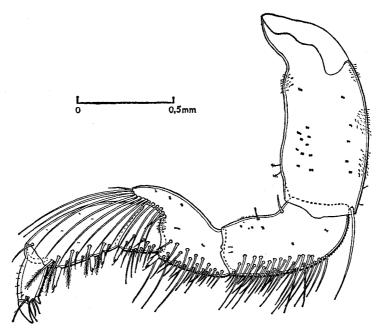


Fig. 2. Gnorimosphaeroma oregonense (from the American Pacific coast). - Peraeopod I.

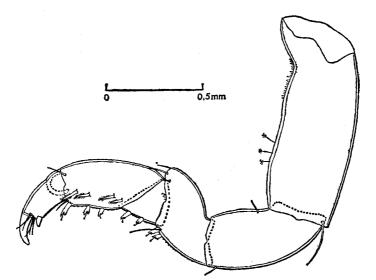


Fig. 3. Gnorimosphaeroma luteum (from the American Pacific coast). - Peraeopod I.

(2)	2 pleurites reach lateral border of pleonG. luteum
(2)	3 pleurites reach lateral border of pleon (3)
(3)	Sternal ridges of ischiopodite, meropodite and carpopodite of the peraeopod I bearing
	numerous setaeG. oregonense
(3)	Sternal ridges of ischiopodite, meropodite and carpopodite of the peraeopod I achaetous
	(except sterno-apical seta of each of the three segments and sometimes 1 or 2 setae on
	sternal ridge of ischiopodite)G. rayi

3. Study of *Gnorimosphaeroma* from Japan, Eastern Siberia and Hawaii

3.1. Localities. We examined specimens from eleven localities (nine from Japan, one from Eastern Siberia and one from the Hawaii Islands). The Japanese localities (Fig. 4) are those of Muroran and Hakodate in Hokkaido Island; of Awakominato, Misaki, Shimoda, Sugashima, Hatakezima and Lake Naka-Umi in Honshu Island; of Tomioka in the Amakusa Archipelago near Kyushu Island; the locality in Eastern Siberia (Fig. 4) is close to Petrov Island, in Syaukhe Bay, at 150 km east of

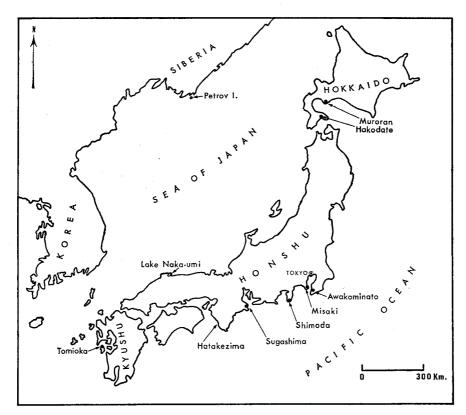


Fig. 4. Map of Japan and Eastern Siberia. The arrows show the localities where samples of *Gnorimosphaeroma rayi* were collected.

Vladivostok; the locality in the Hawaii Islands (Fig. 5) is in Maui Island in the place called Waianapanapa Caves.

In the specimens from these localities, we never found any G. oregonense, G. luteum nor G. noblei; whereas G. rayi is present as well as 2 Japanese species recently described (G. lata Nishimura 1968 and G. salebrosa Nishimura 1969).

3.2. Study of Gnorimosphaeroma rayi (Fig. 1, p. 33). All the specimens examined have been taken out of marine water under stones and pebbles exposed at low tide; only the samples from Petrov Island were captured at a depth of 5 m. As to the

specimens from Lake Naka-Umi, they live in a polyhaline brackish lagoon; marine animals live in the coastal area where G. rayi live; the specimens were accompanied among the Isopoda by Cleantis planicauda, Idotea metalica, Synidotea laevidorsalis and among the Amphipoda by Ampithoe valida, Anisogammarus annandalei, Caprella acutifrons (Kikuchi in litt.). In all the other inventoried localities the facies is always marine.

We examined closely 136 G. rayi from Japan, Eastern Siberia and Hawaii, which are divided as follows: Muroran: 8 young; Hakodate: $15\mathfrak{Q}$; Awakominato: $15\mathfrak{J}$, $8\mathfrak{Q}$; Misaki: $17\mathfrak{J}$; Shimoda: $10\mathfrak{J}$; Sugashima: $20\mathfrak{J}$, $10\mathfrak{Q}$; Lake Naka-Umi: $12\mathfrak{J}$; Tomioka: $6\mathfrak{J}$; Petrov Island: 8 young; Hawaii: $2\mathfrak{J}$, $4\mathfrak{Q}$, 1 young. Those G. rayi show the specific characters given in the key of determination of paragraph 3 (p. 34).

Very likely, the Sphaeromatids from the coasts of Japan and Eastern Siberia

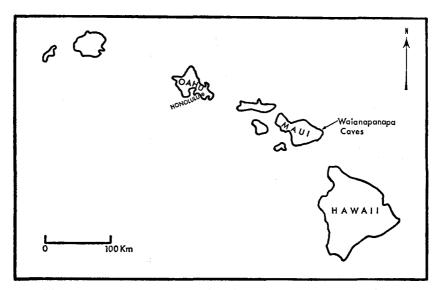


Fig. 5. Map of the Hawaii Islands. The arrow shows the locality where samples of *Gnorimosphaeroma rayi* were collected.

previously identified as G. oregonense are actually G. rayi. In fact, Gurjanova (1938) shows the presence of G. oregonense among the Isopoda captured in the Syaukhe and Sudzukhe Bays at the time of the Expedition of USSR in that country in 1934. Now, the 8 samples of the British Museum in London that we examined had been donated by Gurjanova and captured in the Sea of Japan "near the Petrov Island" in September 1934; since Petrov Island is situated in Syaukhe Bay, the specimens from the British Museum very likely originated from the Expedition of USSR in 1934. Therefore, the samples of the British Museum which are obviously G. rayi, are very probably from the same species as those quoted by Gurjanova (1938), samples he wrongly assimilated to G. oregonense of the American Pacific coast.

3.2.1. Morphological differences. If we are to study the main morphological differences between G.r., G.o. and G.l. of the various Pacific coasts, we must examine

the antennule (a_1) , the maxillipede (mxp) and the first peraeopod (P_1) . Our observations are carried out on adult males, when the samples allow it. Anyway, we did not notice any significant differences between the sexes, nor between the samples of adults or nearly fully-grown.

3.2.1.1. Antennule (Fig. 6). The number of segments was pointed out by a few

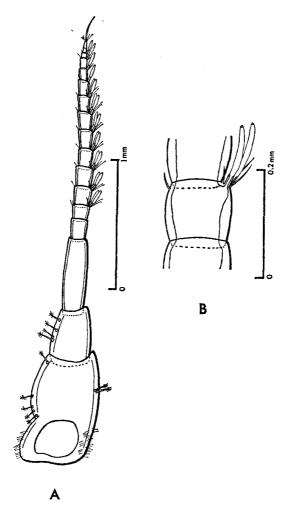


Fig. 6. Gnorimosphaeroma rayi (from Sugashima). — A: Antennule;
B: 3rd segment of flagellum of the antennule.

authors to characterize the species, but this number seems to be directly connected with the body length of the specimens; thus, G.r. (3 adults) from Sugashima which are large sized have on an average a flagellum of 13 segments whereas those from Tomioka (3 adults) are smaller and have only 9 segments.

The important character of the antennules is concerned with the length of the

aesthetes in comparison with the length of the segment in the median part of the flagellum (Fig. 6, B). We noticed that the ratio $\frac{\text{length of aesthete}}{\text{length of segment}}$ had the following value for the three closely related species of the USA (G.o., G.l., G.r.) and this, from samples of different geographic areas for G.o. and G.l. (Hoestlandt 1973): G.o.: $1,79\pm0,24$; G.l.: $0,72\pm0,28$; G.r.: $1,44\pm0,22$. Therefore, we notice that there is no value highly significant of this ratio between G.o. and G.l. For G.r. from Japan, (measurements of 80 individuals) we notice that the ratio $(1,10\pm0,40)$ is somewhat lower than for G.r. from Tomales Bay, and that the standard-deviation is higher, which

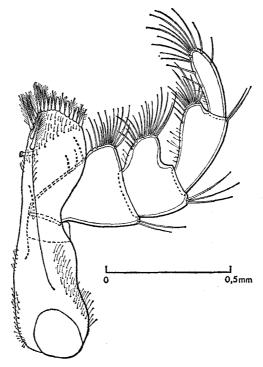


Fig. 7. Gnorimosphaeroma rayi (from Sugashima). - Maxillipede.

shows important individual variations. There is no more value highly significant of this ratio between G.r. from Japan and G.l. from USA; we can therefore set forth for this character, a tendency to a certain similarity between G.r. from Japan and G.l. from USA.

3.2.1.2. Maxillipede (Fig. 7). There exist several differences between the three species of the USA; let us point out the most important ones that are connected with the chetotaxy of the setae of the segments of the palp. Segment 1 bears two long setae in G.o., 1 short in G.l. and 1 long seta in G.r.; the outer border of segment 4 (except the distal end) does not bear any seta in G.o., bears 2 or 3 setae in G.l. and may have one seta in G.r.; at last the outer border of segment 5 (except the distal end)

bears 1 seta in G.o., 3 or 4 setae in G.l. and 2 or 3 setae in G.r. We notice in the G.r. studied in the present article the same characters as in G.r. from USA: the maxillipede shown in Fig. 5 is that of a sample from Sugashima which holds all the characteristics of G.r. from Tomales Bay. However, we must mention in many populations examined a slight tendency to a certain similarity with G.l., principally for the setae of the outer border of segment 4 (some rare individuals from Awakominato, Misaki, Shimoda, Petrov Island and Hawaii bear 2 setae, those from Lake Naka-Umi 2 or 3 setae). As to the ratio between the length of the setae of the inner border of segment 3 and the length of the segment itself, the G.r. from Japan and USA have hardly different values $(0.94\pm0.25$ for Japan and 1.03 ± 0.24 for the USA); this ratio is higher

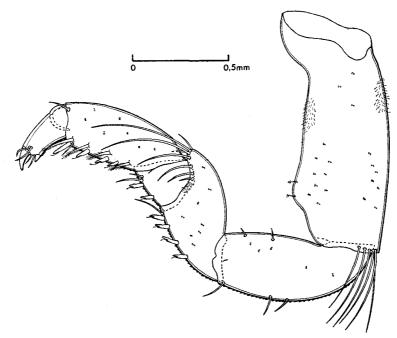


Fig. 8. Gnorimosphaeroma rayi (from Sugashima). - Peraeopod I.

for G.o. $(1,25\pm0,20)$ and lower for G.l. $(0,95\pm0,18)$ but without allowing any highly significant differences.

3.2.1.3. Peraeopod I. If the G.r. from Japan, Eastern Siberia and Hawaii are similar for the antennules and maxillipedes, they differentiate into two groups as to the characters connected with the peraeopods but obviously this differentiation remains within the range characteristic of G.r. One of these groups (Group I) (Fig. 8) includes the Japanese Gnorimosphaeroma of Muroran, Hakodate, Sugashima and the other group (Group II) (Fig. 9, p. 41) includes the Gnorimosphaeroma of the other Japanese localities (Awakominato, Misaki, Shimoda, Tomioka, Lake Naka-Umi) as well as of Petrov Island and Hawaii Archipelago.

The most distinct difference between those two groups is that of the number of

		Group I			Group II						
Localities	California	Muroran	Hakodate	Sugashima	Awakominato	Misaki	Shimoda	Tomioka	Naka-Umi	Petrov Island	Hawaii
Number of Gnorimosphaeroma rayi examined	12 ని	8 y.	15 우	20 ቆ	15 😚	17 3	10 3	68	12 😚	8 y.	2 ô 4 ♀ 1 y.
Number of setae of basipodite	7,50	5,16	6,40	6,25	1,53	1,46	1,20	1	1	1	1
	(0,64)	(0,98)	(0,22)	(1,41)	(0,49)	(0,49)	(0,40)	(0)	(0)	(0)	(0)
Number of setae of meropodite	8,83	7,80	7,46	8,10	5,33	5,62	4,80	4,66	3,72	4,62	5,57
	(0,68)	(0,40)	(0,71)	(0,60)	(0,59)	(0,60)	(0,59)	(1,10)	(1,13)	(0,99)	(1,29)
Length of largest seta of meropodite	1,73	1,21	1,32	1,55	0,77	0.78	0,68	0,96	0,83	0,71	0,65
Length of meropodite	(0,20)	(0,34)	(0,20)	(0,33)	(0,21)	(0,18)	(0,09)	(0,11)	(0,15)	(0,09)	(0,07)

Table 1. Number of setae of peraeopod I (with standard-deviation) for Gnorimosphaeroma rayi from different localities.

setae on the sterno-distal corner of the basipodite: 4–7 setae for Group I, 1–2 setae for Group II. In Table 1, we read the average results of the number of setae of the basipodite for respective locality (the subjacent number between brackets gives the value of the standard-deviation). If we calculate the average for each group, the difference noticed has a highly significant value: $5,95\pm2,76$ for Group I and $1,23\pm0,84$ for Group II.

Two other differences are less important, though they are very frequently observed, because they have no highly significant value: they are concerned with the setae of the tergo-distal lobe of the meropodite, either their number or their length. In Table 1, we read the average number of setae of this lobe as well as the ratio: $\frac{\text{length of largest seta}}{\text{length of meropodite}}$ (the subjacent numbers between brackets give the value of the standard-deviation). If we calculate the average for each group, the differences noticed have no highly

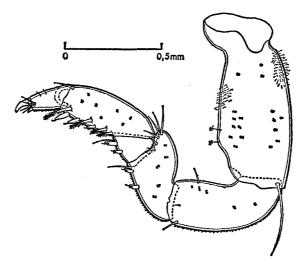


Fig. 9. Gnorimosphaeroma rayi (from Awakominato). - Peraeopod I.

significant value: for the number of setae, we get $7,82\pm1,33$ for Group I and $4,97\pm2,16$ for Group II; as to the ratio $\frac{\text{length of largest seta}}{\text{length of meropodite}}$, we get $1,43\pm0,64$ for Group I and $0,77\pm0,35$ for Group II. The important individual differences within each group do not give sufficient value to this double character to classify with certainty the specimens in one of the two groups; let us recall that the character connected with the sterno-distal setae of the basipodite allows to classify definitely all the *G.r.* from Japan, Eastern Siberia and Hawaii in one group or the other and that all the individuals of a same populations are all of the same group.

3.2.2. Remarks. The present geographic distribution of Groups I and II does not correspond to any definite delimitation (Fig. 4, p. 35). Undoubtedly in Japan, G.r. from Northern Japan (Hokkaido Island) belong to Group I and the whole of G.r. from the Central or Southern Japan as well as those from Eastern Siberia

and Hawaii belong to Group II but there is a population in the middle part of Japan (Sugashima) that belongs to Group I. Obviously, it would be necessary to study the populations of G.r. from the north-east coast of Honshu Island in order to determine more precisely the distribution of both groups.

As to the G.r. from California, Table 1 shows that they belong to Group I. Barret (1963) points out that the Japanese oysters implanted in Tomales Bay from 1928 on, came from Matsushima Bay (Miyagi Prefecture) which is at 400 km north of Tokyo. Therefore, there may exist populations belonging to Group I in that bay.

If we compare the peraeopod I in G.r. (Group II) (Fig. 9) and in G.l. (Fig. 3), we notice that there is hardly any difference, especially if we allow for the individual

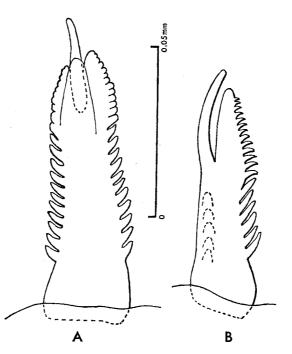


Fig. 10. Distal serrated bristle of the propodite of peraeopod I. — A: Gnorimosphaeroma luteum; B: Gnorimosphaeroma rayi.

variations. In fact, the average number of the sterno-distal setae of the basipodite is 1 (standard-deviation=0) for G.l. and $1,23\pm0,84$ for G.r. (Group II); as to the average number of the setae of the tergo-distal lobe of the meropodite, it is $2,90\pm1,14$ for G.l. and $4,97\pm2,16$ for G.r. (Group II); the average ratio $\frac{\text{length of largest seta of meropodite}}{\text{length of meropodite}}$ is $0,91\pm0,26$ for G.l. and $0,77\pm0,35$ for G.r. (Group II).

There remains however a very characteristic difference between P_1 of *G.l.* and of *G.r.* (Groups I and II), but that requires a microscopic study with highly magnifying power: it is the shape of the most distal serrated bristle of P_1 which is localized on the sterno-distal part of the propodite (Fig. 10). That serrated bristle ends in *G.l.* (also

in G.o.) by two crenate lappets enclosing a central flagellum (Fig. 10A); in G.r., that serrated bristle shows only one lappet (on the distal side of the limb) and one flagellum (on the proximal side of the limb) (Fig. 10B). In G.r., the other serrated bristle of P_1 can be similar to that of G.l..

If, for the whole of the morphologic characters, G.r. is more closely related to G.o. than to G.l., we must admit a tendency to a certain similarity between G.r. from Group II and G.l., especially for the whole of the characters of peraeopod I, except for servated bristle.

3.3. Japanese Species of the Genus Gnorimosphaeroma. Among the Gnorimosphaeroma from Japan that we examined, we found two other species. First, the samples received from the locality of Hatakezima (Tanabe Bay, Wakayama Prefecture, Honshu Island) (Fig. 4) are G. salebrosa Nishimura 1969; that species was described by Nishimura from specimens coming from the same area. Then, among the G.r. from the locality of Tomioka, there were a few samples of G. lata Nishimura 1968; the only specimens known previously are those which helped to define the species and which came from Tanabe Bay; it is therefore the first time that this species is captured in another part of Japan that is at 600 km west of Tanabe Bay.

There is another species G. ovata Gurjanova 1933, which was described for the first time from samples found in the Sea of Japan along the coast of East Siberia (Peter the Great Bay and Tartar Strait); that species was found in Japan at Akkeshi and Tsuiyama (Hyogo Prefecture) (Shiino 1957). We did not find that species among the samples that we examined.

It is easy to differentiate those three species (G.s., G.l., G.ov.) from G.r. for they are smaller (5 to 6 mm in length at the most); on the other hand, they are proportionately broader and more flattened, a confusion with G.r. therefore seems to be impossible.

4. Short Indications about the Polychromatism of *Gnorimosphaeroma rayi* from Japan and Eastern Siberia

Two short indications can be given here about the polychromatism of G. rayi studied in this article.

A preliminary study "in situ" of the locality of Awakominato²⁾ allowed us to notice the identity between the polychromatic types of this locality and Tomales Bay in California.

In fact, at Tomales Bay, we had found four types of structural polychromatism: furcosum, pluripunctatum, marmoratum and transversum (Hoestlandt 1974). At Awakominato, we found other samples of pluripunctatum, marmoratum and furcosum; furcosum seems to be rare and nearly uniform in aspect; pluripunctatum shows slight variations especially in regard to the small white lateral plates of the fifth tergite, often they are

²⁾ The circumstances allowed us but a short stay and therefore too short a study for this population.

lacking. On the other hand, at Awakominato, we observed polychromatic types unknown at Tomales Bay. The first of the cases is a type of structural polychromatism corresponding to both *bilineatum* and *posterolunulatum* of *G.o.* (Hoestlandt 1974). The second is two types of coloration polychromatism *rubrum* and *aurantiacum*. The last of the cases is the existence of types *furcosum* which are bicoloured in black and yellow or black and red pigments; in the species *Sphaeroma serratum* we had once observed bicoloured types in South Atlantic populations (Hoestlandt 1956, 1957, 1962). It is not surprising to find a richer polychromatic types in Japan than in California, for very likely, the few individuals settled in California together with the Japanese oysters had a genic pool more limited than that of the main populations in Japan.

It is interesting to add that exceptionally, among the G.r. preserved in alcohol that we observed, a few individuals from Petrov Island had kept clearly the polychromatic type *transversum* observed in the G.r. from California (Hoestlandt 1974) that we had not seen at Awakominato. We must also notice that morphologically G.r. from Awakominato and Petrov Island belong to Group II whereas those from California belong to Group I. The identity of polychromatic types between G.r. from California and G.r. from Awakominato or Petrov Island proves that Groups I and II belong to the single and same species and perhaps even to the single and same subspecies only.

5. Conclusions

The morphological and biological relations between G.o. and G.l. from the Eastern Pacific coasts and G.r. (Groups I and II) from the West Pacific coasts militate for the hypothesis of a common origin of those three species and that common origin can only be northern; in fact, G.o. and G.l. are present in Alaska (Hoestlandt 1973), G.o. was observed along the Aleutian Islands (Richardson 1905), G.o. (or perhaps G.r.) was found along the coasts of the Bering Sea (Richardson 1905; Thielemann 1911; Gurjanova 1936). Besides, those three species are cold temperate species living under the influence of the same ocean current, the Kuro-Siwo. Though the waters they live in have similar temperatures in winter (0 to 11° C), in summer the water temperature is higher in Japan (18° to 25°C) than in North America (9° to 14°C) (US Navy 1955); this shows that G.r. can bear warmer waters in summer than G.o. and G.l.

Between the Pacific Sphaeromatids of the genus Gnorimosphaeroma and the Atlantic Sphaeromatids of the genus Sphaeroma (European and North African coasts) (Lejuez 1966) living under the influence of the Gulf Stream, that is to say under a temperate climate whose water temperature is higher by 7°-8°C than that of the regions where live the quoted species of Gnorimosphaeroma, there are ecological relations as seen between G. oregonense or G. rayi and S. serratum or S. monodi, between G. luteum and S. rugicauda, and further between G. noblei and S. teissieri. If at present, impassable "barriers" (Atlantic Ocean, American Continent) separate Gnorimosphaeroma from Sphaeroma, one species may have been at the origin of each of these three ecological groups in a fairly recent past when the northern polar area was temperate; even perhaps only one species may be at the respective origin of the North Atlantic *Sphaeroma* and the North Pacific *Gnorimosphaeroma*; similar further adaptations, in similar ecological environments of the Atlantic or the Pacific, would have gone leading to the origin of the various Sphaeromatids studied.

6. Summary

Along the coasts of Japan, Eastern Siberia and Hawaii, the Sphaeromatid (Isopoda Flabellifera) *Gnorimosphaeroma rayi* is widely spread; it is an Isopoda previously discovered in California (Tomales Bay) where it had very likely been imported accidentally together with Japanese oysters.

G. rayi is very similar to the other two American Pacific species, G. oregonense and G. luteum; the differences between those three species are described.

In the inventoried localities (8 in Japan, 1 in Eastern Siberia and 1 in Hawaii) there are two types morphologically distinct (chaetotaxy of the peraeopod I), among which one is more northern than the other. The validity of G. salebrosa and G. lata is proved, too.

The polychromatism of G. rayi in Japan is more variable than that of G. rayi in California.

The three closely related species G. oregonense, G. luteum and G. rayi may have had a common origin in a comparatively recent past in more northern regions which were once temperate in climate.

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