Report No. 1 from the Lund University Expedition in 1957
to the Azores and Madeira

FRESH AND BRACKISH WATER AMPHIPODS FROM THE AZORES AND MADEIRA

By ERIK DAHL 1)

The Swedish Zoological Expedition to the Azores and Madeira worked in the islands from the end of February to the end of April 1957. During that time the expedition, which was planned and led by Professor P. Brinck and the present writer, had the opportunity to work in six islands of the Azorean group, viz. Santa Maria, São Miguel, Terceira, Pico, Faial and Flores, and in the main island of Madeira. The expedition was made possible by the financial and official support of various Swedish funds and authorities, but the comparative success of our field-work was to a very large extent due to the understanding and helpfulness of the central and local Portuguese authorities and of various private persons in the islands.

The collections, mainly of terrestrial and fresh and brackish water fauna, brought back to Sweden were fairly large. The results will be published in various scientific periodicals.

Of fresh and brackish water amphipods only four species were obtained. Two of them were new to science, and despite the small number of species our results contribute materially to the knowledge and understanding of the aquatic amphipod fauna of the islands.

From the Azores only *Gammarus (Sarothrogammarus) guernei* Chevreux and a subterranean amphipod of dubious identity had previously been recorded from fresh and brackish waters. Besides collecting new material of the former species we could identify the latter as *Pseudoniphargus africanus* Chevreux and add a new estuarine species *Gammarus (Marinogammarus) atlanticus*, which will be described below.

From Madeira *P. africanus* had been recorded previously. We found no further material of that species but could add *G. (M.) atlanticus* and a new species *G. (Sarothrogammarus) madeirensis* which will also be described in the present paper.

I am particularly indebted to Mr. G. E. Maul for his kindness in publishing my report in this Boletim.

---

1) Zoological Institute of the University of Lund, Sweden

Genus Pseudoniphargus Chevreux

Pseudoniphargus africanus Chevreux 1901 a

Fig. 1.

Taxonomic remarks. In his survey of the Azorean fresh water fauna Barrois (1896, p.132) reported the presence of a subterranean amphipod which he identified as *Niphargus puteanus* Koch and which he obtained in wells in S. Miguel and Faial. Although some of the comments made by Barrois raised doubts about the specific identity of this amphipod the record was of great interest to us as the presence of a true *Niphargus* in the subterranean waters of the islands would have been most unexpected.

Thanks to the efforts of Dr. Vicente of the Museum of Ponta Delgada, the well at Rosto de Cão, where Barrois obtained his S. Miguel specimens, could be identified. It had, however, recently been closed because the salinity of the water made it unsuitable for drinking, and we could not sample the fauna. At Faial and Pico, on the other hand, we had the opportunity to collect

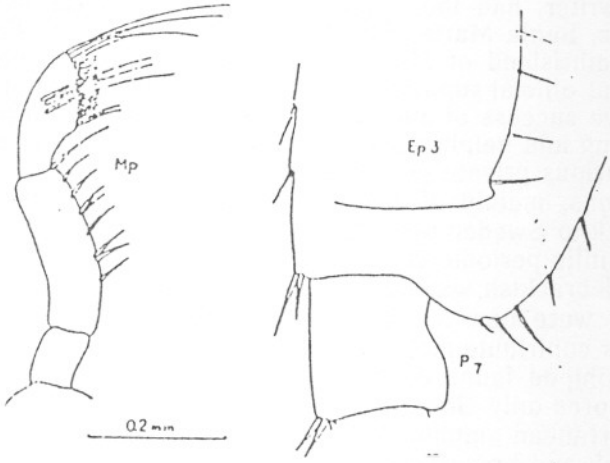


FIG. 1. — *Pseudoniphargus africanus*, ♂ from the Azores (Faial).

in several of these so-called «poços de maré» which are slightly influenced by the tide and where the salinity amounts to a few parts per thousand. Most of them contained amphipods of the species *Pseudoniphargus africanus* but no other species and as several of them are situated within the town of Horta where Barrois also obtained specimens, it appears as if the identity of his subterranean amphipod could be regarded as established.

The Azorean form agrees fairly well with *P. africanus* Chevreux and with our present knowledge of that species I cannot see any reason to give it even sub-specific rank. Schellenberg (1939, pp. 300 ff.) who surveyed the variability within the species *P. africanus* concluded (*l. c.*, p. 304) that there

is a definite tendency towards morphological variation even within different populations of a limited area. This is not surprising as the habitat frequented by the species favours the establishment of small and isolated populations.

On p. 303 of the quoted paper Schellenberg summed up in tabular form the morphological variation encountered in various localities. It concerns mainly the total body length, the length and number of segments of the antennula, the shape of the basis of the three posterior pereiopods, the structure of the last uropod, and the spinulation of the telson.

In all these various respects the Azorean specimens examined are rather uniform and could be characterized as follows: Comparatively large, total body length of larger specimens of both sexes 6-8 mm. Antennulae reaching approximately to end of mesosome, number of segments of flagellum generally 17 or 18. Distal posterior corner of basis of three posterior pereiopods broadly rounded, very slightly produced. Third uropod of female slightly longer than urosome, that of the most extreme male as long as metasome and urosome combined, outer ramus 6 times as long as peduncle. Telson with 4 terminal spines on each lobe.

Among the various populations analyzed in Schellenberg's table the Azorean specimens most closely approach the type and co-type from Bône in Algeria. The basis of the three posterior pereiopods (cf. fig. 1 and Schellenberg, *l. c.*, fig. 1 a, p. 301) and Chevreux (1901 a, fig. 1, p. 212) is identical, the relative length of the antennula is the same and the number of flagellar segments falls within the same range of variation. The total length of the third uropod is similar and the number of terminal spines on the telson is identical. On the other hand the ratio between the peduncle and the outer ramus of the third uropod in the male is very different (1:1 and 1:6 respectively) and the outer ramus of the same uropod of the female is somewhat longer in the Azorean specimens.

Some further points may be noted. The tooth on the posterior corner of the third epimeral plate in the Azorean specimens is indistinct, thus corresponding to the conditions found in most populations but differing from the population of Kef Djemel in Algeria and to a lesser extent also from the type. The posterior corner of the palm of the first gnathopod in the type is provided with 3 bifurcate spines (Chevreux, *l. c.*, fig. 2 E, p. 214) and Schellenberg (*l. c.*, p. 300) recorded 3 in specimens from Split in Yugoslavia. In the Azorean specimens there are 5 such spines. On the inner plate of the maxillipeds Chevreux (*l. c.*, p. 214) noted some hairs on the distal margin. Schellenberg believed that statement to be erroneous and recorded 3 straight spines and some hairs. On a dissected female from Faial I found 4 spear-shaped spines on the left and 5 on the right side together with some hairs. The mandibular palp would seem to differ considerably from that drawn by Chevreux (*l. c.*, fig. 2 A, p. 214) but apparently the proportions have been somewhat distorted owing to the fact that the appendage was not drawn in profile by Chevreux.

Schellenberg (*l. c.*, p. 304) concluded his survey of *P. africanus* as follows: "Ich lasse daher den ganzen Tierkomplex unter dem Namen *Pseudo-*

niphargus africanus vereinigt und überlasse es einer späteren Zeit, mit reicherem Material die Unterartfrage zu lösen». Since this was written the situation has not changed materially. The records of *P. africanus* are still comparatively few and scattered, the taxonomic evaluation of various taxonomic features, e. g. the third uropod of the male, is still impossible. Concerning the subterranean amphipods of the Azores it could only be said that, as far as now known, they all belong to one species which falls within the morphological range of *P. africanus*.

Occurrence and ecology in the Azores. As will be seen from the list of localities on p.10 we found *P. africanus* in slightly saline waters in wells just above sea-level at Faial and Pico, the only islands where we had the opportunity to examine this kind of habitat. As already pointed out Barrois (1896, p. 132) recorded what was almost certainly the same species from a similar locality at S. Miguel. In all we examined 10 «poços de maré» (9 in Faial and 1 in Pico) and found *P. africanus* in 7 of them (6 in Faial and 1 in Pico). Of the three wells where we did not find the species one was in the centre of Horta and very difficult to work owing to its construction, and two were in Almoxerife, north of Horta. The salinities measured in them were 1.1 and 0.9 parts per thousand respectively and consequently well within the normal range of the species. Despite these exceptions the species appears to be widely distributed and fairly common in the saline subterranean waters near the coast of at least some of the islands.

On the other hand *P. africanus* was not found in any of the numerous fresh-water wells, springs, streams, ponds, and lakes examined by us in six of the Azorean islands. The lowest salinity at which the species was obtained was 0.5 °/₀₀, in a well in the park of Horta, the highest value found by us was 3.8 °/₀₀ in one of the wells at Feiteira, in Faial, and in the well at Areia Larga, in Pico. But as those were the most saline subterranean waters we had the opportunity to investigate, the upper salinity limit of the species in the islands is not yet established. During the dry season the salinity of the wells examined by us is said to be higher.

Geographic distribution and general remarks. The geographic range of *P. africanus* covers both the northern and the southern margins of the Mediterranean basin from Yugoslavia and Algeria westwards. The species has also been recorded from caves in the Cantabrian mountains near Santander and San Sebastian in Spain, and from Funchal in Madeira.

Especially the earlier records of *P. africanus* were mostly from wells or other subterranean waters which were fresh or only slightly brackish. Schellenberg (*l. c.*, p. 300) therefore regarded it as coming originally from fresh waters and considered a derivation from the sea or from brackish waters as most unlikely. The occurrence in Madeira could in his opinion be explained by the existence of a land-bridge broken in the Miocene, as postulated by some geologists.

Later findings radically changed the foundations of these arguments. The species was obtained in a cave in Corsica where the pool where the

animals were found is partly fed by rain water but also communicates with the sea by means of fissures. During periods of drought, therefore, the salinity increases materially (Balazuc and Angelier, 1952, p. 311). Further numerous specimens were found among the marine psammon at Banyuls-sur-mer on the south coast of France in salinities up to 33 parts per thousand (*l. c.*, p. 310). Finally there are our own observations at the Azores where the species appears to be confined to those subterranean waters which are more or less influenced by the sea.

The general distribution of *P. africanus* with all known localities in the neighbourhood of the sea and partly with brackish waters, the occurrence of the species in marine caves and in the marine psammon forced Balazuc and Angelier (*l. c.*) to the assumption that *P. africanus*, like numerous other subterranean amphipods and isopods, entered fresh and brackish subterranean waters by way of the marine subsoil waters of the coast. As already indicated above the distribution of the species in the Azores strongly supports this view.

Balazuc and Angelier also made some attempts to fix the time when the open sea became «une barrière plutôt qu'un passage» (*l. c.*, p. 311) to *P. africanus*. They point out that the European mainland, Corsica, and the North African coast have in various ways been connected with each other up to post-Pliocene times. For Madeira they accept continental connections with the Iberian Peninsula up to the beginning of the Pliocene. Some geologists and zoogeographers apparently are not prepared to accept tertiary connections between Madeira and the mainland.

In the case of the Azores, current geological opinion seems to be in favour of their purely oceanic origin, probably as the result of submarine volcanic activity in the Miocene. There seems to be some evidence indicating that the areas of land in the central Atlantic were once considerably greater than now, but proof of continental connections appears not to be available.

The only Tertiary marine deposits of the Azores, the limestones of Santa Maria, are of Miocene origin. If provisionally we accept the oceanic origin of the Azores, it seems probable that *P. africanus* invaded the islands some time probably not earlier than the Miocene, when the species had already acquired the characteristics by which we know it to-day. By then the general ecology of the species must still have facilitated a transport (active or passive) over wide areas of open sea such as is typical of many of the present littoral amphipods. At present dispersal or accidental transport of the species across the sea appears extremely unlikely. On the other hand power of such dispersal may have been retained till long after the end of the Miocene. Thus, although it appears highly probable that *P. africanus* reached the Azores by way of the sea, it is impossible to say when the invasion of the islands took place.

Material examined:

Azores.

Faial, loc. 81, Horta, in the town, in well just S of Ribeira dos Flamengos. 2.IV.1957. 1 specimen.

» loc. 82, Horta, near the coast, in well just N of Ribeira dos Flamengos. Temperature of water, 3.IV.1957, 11.30 a.m., 16°.9, salinity 1.3 °/₀₀, 2.20 p.m. temperature 17°.0, salinity 1.3 °/₀₀ (high water 2.02 p.m.). 2. and 3.IV.1957. Numerous specimens.

» loc. 84, Horta, well near the park, temperature 17°.0, salinity 0.9 °/₀₀, 3.IV.1957. 3 specimens. Well in the park, temperature 17°.2, salinity 0.5 °/₀₀. 1 specimen.

» loc. 87, Feiteira, well W of stream bed, temperature 15°.0, salinity 2.1°/₀₀, 3.IV.1957. 1 specimen. Well E of the stream bed, temperature 16°.1, salinity 3.8 °/₀₀, 3.IV.1957. Many specimens.

Pico, loc. 107, Areia Larga, well 15 m. deep, temperature 17°.5, salinity 3.8 °/₀₀, 11.IV.1957. Many specimens.

Genus Gammarus J. C. Fabricius

Subgenus Marinogammarus Schellenberg

In 1940 Sexton and Spooner elevated the subgenus *Marinogammarus* as defined by Schellenberg (1937) to full generic rank. When Schellenberg published his key to the subgenera the only *Marinogammarus* known to him was *G. (M.) marinus* Leach. With some hesitation he also added *G. locustoides* Brandt, which later proved to be an *Anisogammarus* (Sexton and Spooner, *l.c.*, p. 637).

Sexton and Spooner extended the genus *Marinogammarus* to comprise six species of littoral amphipods, viz. *M. marinus* (Leach 1815), *M. olivii* (Milne-Edwards 1830), *M. stoerensis* (Reid 1938), *M. obtusatus* (Dahl 1938), *M. finmarchicus* (Dahl 1938), and *M. pirloti* Sexton and Spooner 1940.

Of these species *M. olivii* had been placed by Schellenberg (*l.c.*, p. 272) in his subgenus *Echinogammarus*. Sexton and Spooner did not enter into any general discussion of the interrelationships between *Echinogammarus* and *Marinogammarus* but confined themselves to stating that *G. olivii* Milne-Edwards is more closely related to *M. marinus* than to e.g. *G. pungens*. Unfortunately, however, this statement cannot be accepted without some further qualification. The genus *Marinogammarus* as defined by Sexton and Spooner provides no dividing line between the true *Marinogammarus* species and the *sectio glabra* of the subgenus *Echinogammarus* as defined by Schellenberg. It is also clear that according to the subgeneric definitions given by Schellenberg (1937) *M. pirloti* Sexton and Spooner should be regarded as an *Echinogammarus* and not as a *Marinogammarus*. The same might be said about a species encountered by us in the Azores and Madeira. It is obviously closely related to *pirloti* and *olivii* but easily distinguished from the other *Echinogammarus* and *Marinogammarus* species. It will be described below as a new species.

I was not in a position to make an investigation of the *Marinogammarus-Echinogommarus*-problem. Fortunately it is under consideration elsewhere. In view of what has been said above it may seem somewhat inconsequential to refer the new species to *Marinogammarus*, which I prefer to restore provisionally to its former status of subgenus. It seems to me, however, that this course is the one which is least likely to produce confusion.

Marinogammarus atlanticus n. sp.

Figs. 2-4.

Description of adult male. Head with lateral lobes somewhat produced, obtusely pointed. Eyes large, rather broad and distinctly reniform. Lower angle of head rounded, sinus rather deep.

Spinose humps on back of urosome segments indistinct, with rather few spines, which vary slightly in numbers:

Urosome segment	1	spine formula	2 (1), 2 - 1, (1) 2
»	»	2	»	2, 1 - 1, 2
»	»	3	»	2 (3), 1 - 1, (3) 2

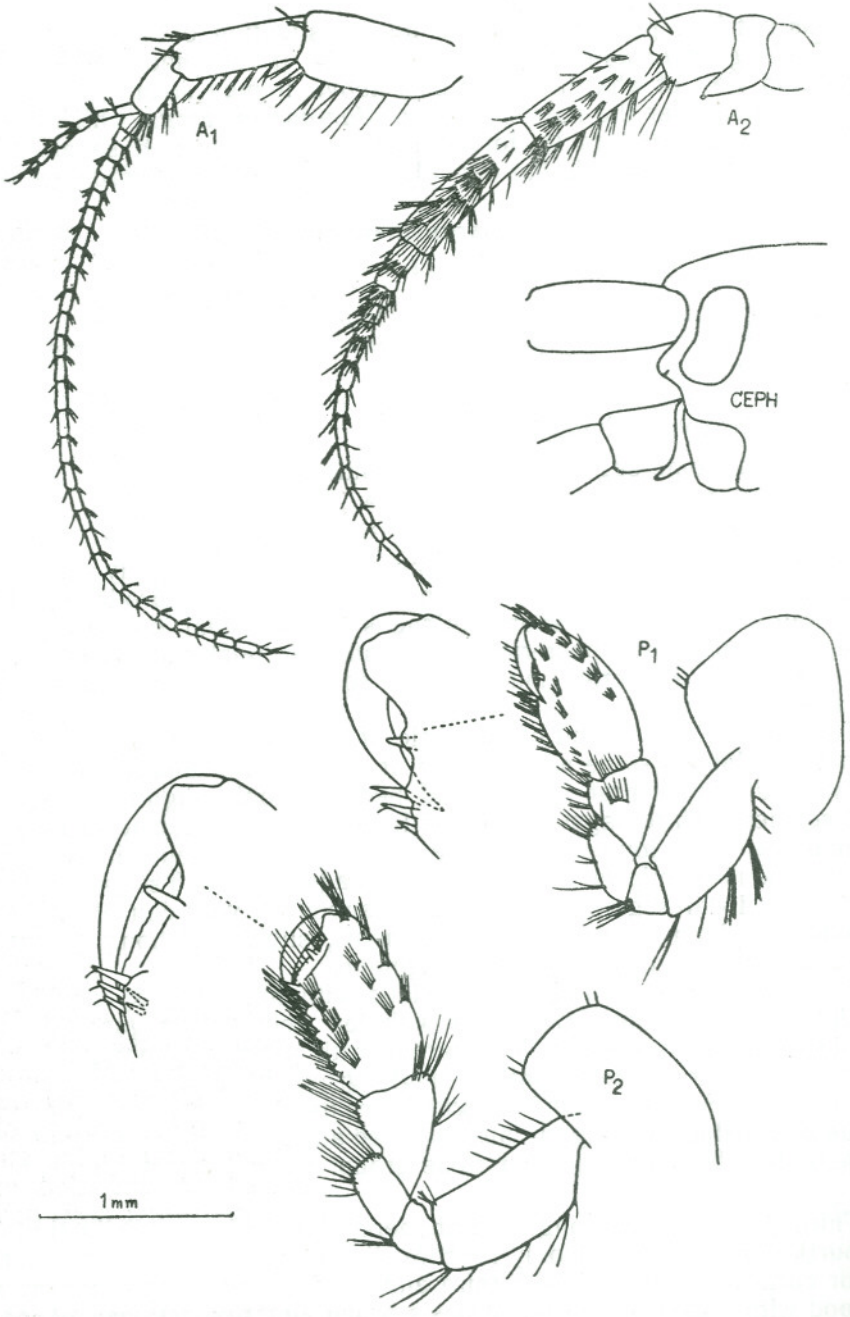
Second epimeral plate with hind margin straight or slightly sinuate with some short setae, posterior corner rounded or very slightly produced. On the anterior half of the plate a short oblique spine-row near the distal margin. Third epimeral plate with posterior margin straight, posterior corner distinct, slightly produced. Posterior margin with some short setae, distal margin with a few spines.

Telson reaching to end of peduncle of third uropod, deeply cleft, each lobe with one lateral spine and a group of distal spines and hairs.

Antennula with first segment of peduncle only slightly longer than second segment. Third segment half as long as second segment. Flagellum more than twice as long as peduncle, number of segments in type 30, in other specimens slightly variable. Accessory flagellum with 6 segments. Antenna with two distal segments of peduncle subequal, very densely setose on inner side, flagellum in type with 16 segments, slight variations observed in other specimens. No calceoli on any segments.

Pereiopods very strong and provided with numerous spines, but not strikingly short, three posterior pairs with few setae. First gnathopod with coxal plate expanding distally. Metacarpus with palm very oblique. Median palmar spine separated from palmar angle group by a wide gap. Dactylus curved inwards. Second gnathopod with margins of coxal plate parallel. Metacarpus with palm only slightly oblique, median palmar spine standing closer to hinge of dactylus than to palmar spine group, which comprises three spines only.

Third pereiopod as long as fifth pereiopod and very distinctly longer than fourth pereiopod which only reaches slightly past end of carpus of third. Anterior corner of merus of both third and fourth pereiopod produced. Fifth pereiopod with posterior corner of basis broad and rounded, corresponding


A1
A2
CEPH
P1
P2
1 mm

corner of sixth and seventh pereiopods not at all produced and provided with a group of spines and setae.

First uropod reaching slightly past second uropod. Third uropod with inner ramus small and narrow, provided with one terminal spine and several terminal plumose setae. Outer ramus densely setose with plumose setae both on inner and outer margin, second segment well-developed.

Male sensory setae of a type essentially similar to those described by Sexton and Spooner (1940) for *G. (M.) olivii* occur on the second antenna.

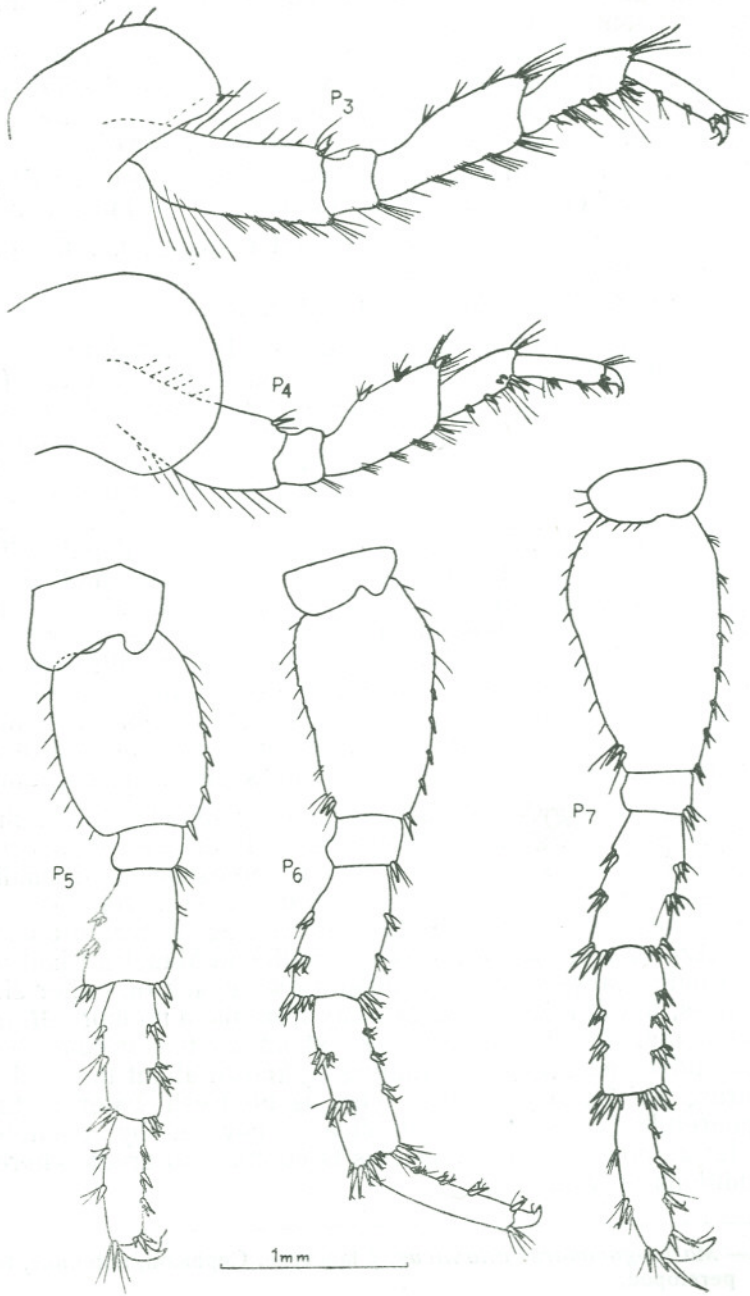
Female differing from male in the usual respects, i.e. the gnathopods are weaker and the antennae shorter.

Type in the Zoological Institute, Lund, No. 84.

Remarks. The present species is undoubtedly related to *G. olivii* and *G. pirloti*, which in their turn obviously stand close to eachother (cf. Sexton and Spooner, *l. c.*, p. 672). Nevertheless it differs from both species in so many respects that it must be kept separate at least at present. The proportions between the peduncular segments of the antennula are very similar in *G. pirloti* and *G. olivii* but the present species differs from both in having the second and third segments much longer proportionally. The antennular flagellum also is longer and consists of more segments. The flagellum of the antenna is provided with calceoli in both the species mentioned but not in the present one. The difference in length between the third and fourth pereiopods is greater in *G. atlanticus* than in either of the other two species. Otherwise the general proportions of the pereiopoda recalls those of *G. pirloti*, while all appendages are comparatively shorter and stouter in *G. olivii*. The third uropod, on the other hand, more closely resembles that of *G. olivii* in having plumose setae on both the inner and outer margin of the outer ramus and in having a well-developed second segment on the same ramus.

Occurrence and ecology. *M. atlanticus* was found both at the Azores (S. Miguel and Sta. Maria) and Madeira, but only in one very special type of habitat, viz. under stones in the tidal zone in the estuaries of small non-permanent streams. In some cases the species occurred in very great numbers in the narrow belt influenced by both sea and fresh water. In all three localities in the Azores and one of the two localities in Madeira I had the opportunity to examine large areas of boulderstrewn beach on either side of the small estuaries, but only a few yards away from them no more *M. atlanticus* were to be found. Nor did the species extend up the streams beyond the reach of the tides and breakers. Nothing is known about the ecology of the species during the dry season when there is no fresh water in the stream beds. Apparently it is then periodically covered by undiluted ocean water. As far as now known the species is confined to areas where poikilohaline conditions prevail.

FIG. 2. — *Marinogammarus atlanticus*, ♂ holotype. Cephalon, antennae, Ist and 2nd pereiopod.


P3
P4
P5
P6
P7
1mm

Material examined :

Azores

S. Miguel, loc. 27, Ribeira da Praia, 3km W of Vila Franca do Campo, under stones in the tidal zone in the estuary of a small, non-permanent stream. 13.III.1957. Numerous specimens, including *male holotype* and *female paratype.*

» loc. 2, Ribeira das Três Voltas, near Vila Franca do Campo, under stones in the tidal zone in the estuary of small non-permanent stream. 28.II.1957. 2 specimens.

Sta. Maria, loc. 47, Praia, under stones in the estuary of small non-permanent stream. 20.III.1957. 3 specimens.

Madeira

Funchal, loc. 111, in the western part of the town, under stones in the tidal zone in the estuary of a very small, non-permanent stream. 19.IV. 1957. Numerous specimens.

North coast, Faial, loc. 116, under stones in the tidal zone in the estuary of a small, non-permanent stream. 21.IV.1957. 5 specimens.

Subgenus **Sarothrogammarus** Martynov

THE RELATIONSHIP BETWEEN SAROTHROGAMMARUS MARTYNOV AND NEOGAMMARUS RUFFO.

Among the various subgenera of *Gammarus s.lat.* discerned by Schellenberg (1937) *Sarothrogammarus* is one of the most characteristic and uniform ones. Martynov (1935 p. 484) gave it full generic rank, but I prefer to follow Schellenberg and regard it as a subgenus.

Schellenberg (*l.c.*) recognized three species of *Sarothrogammarus,* viz. *S. guernei* (Chevreux 1889), *S. rhipidiophorus* (Chevreux 1901 b) and *S. asiaticus* Martynov (1935). In 1937 Ruffo described a new species, *Gammarus festae,* for which he created a new subgenus *Neogammarus,* and to this new subgenus he also referred *G. (S.) rhipidiophorus,* which agrees with *G. (N.) festae* in having the first uropod partially reduced.

During our visit to Flores we collected further material of *G. (S.) guernei* and at Madeira we found another, new species, which will be described below under the name *G. (S.) madeirensis.*

We have here a group comprising 5 species all of which are distinguished by the extreme development of the third pereiopod, which is much larger than the fourth pereiopod and nearly as long as the seventh pereiopod. It should be noted, however, that a similar although less extreme tendency occurs elsewhere within the genus *Gammarus,* e.g. among some species of the subgenus *Marinogammarus* (cf. p. 11).

In Table 1 a comparison is made between the five species dealt with here. It will be seen that while the other four species are obviously closely

FIG. 3. — *Marinogammarus atlanticus,* ♂ holotype. 3rd to 7th pereiopod.

related, *G. (N.) festae* differs in many respects. Alone it lacks dorsal spines on the urosome and the characteristic setae of the third pereiopod of the male. It also is the only species which has numerous setae on the third uropod. Despite the reduction of the first uropod *G. (S.) rhipidiophorus* agrees so

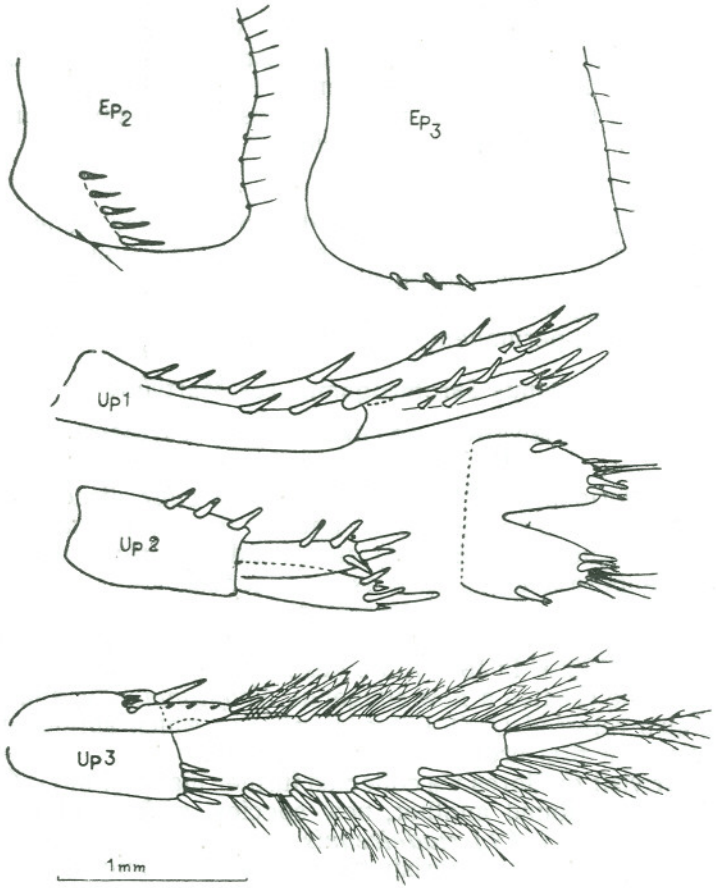


FIG. 4. — *Marinogammarus atlanticus*, ♂ holotype. Epimeral plates, uropods, telson.

closely with the three other *Sarothrogammarus* species in so many respects that I feel compelled to refer it once more to the latter subgenus and to reserve the subgenus *Neogammarus* for *G. (N.) festae*. This conclusion is mainly founded upon the study of the new material now available and implies no criticism of Ruffo (1937).

TABLE I.— *A Comparison between Species of* Sarothrogammarus *and* Neogammarus.

	Calceoli	Up 3 inner ramus segm. 2	Up 3 outer ramus, setae	Spines on dorsum of Us segment 1	2	3	Long setae on male P3	Difference in length between P5 and P7	Up 1
S. guernei	absent	present	absent	+	+	+	present	small	normal
S. rhipidiophorus	absent	present	absent	+	+	+	present	great	reduced
S. asiaticus	absent	absent	absent	—	+	+	present	small	normal
S. madeirensis	absent	present	absent	+	+	+	present	great	normal
N. festae	present	present	present	—	—	—	absent	?small	reduced

Sarothrogammarus guernei Chevreux 1889

Material examined:

Azores

Flores, loc. 108, Ribeira d'Além da Fazenda, under stones in a small spring on the bank of the stream, 14. IV. 1957. Numerous specimens.

Sarothrogammarus madeirensis n. sp.

Fig. 5.

Description of adult male. Colour (in life) yellowish, semi-transparent. Lateral lobes of cephalon broadly rounded. Eye small, oval, pigment dark brown, rather sparse. First and second urosome segments with one lateral and one medial spine on each side of dorsum, third segment with only one lateral spine. Posterior corner of third epimeral plate with a small tooth. Telson with one (otherwise sometimes two) lateral and three distal spines on each lobe, cleft to base.

Antennula considerably longer than antenna. First segment of peduncle somewhat longer than second segment, which in its turn is distinctly longer than third segment. Flagellum with 18 segments, accessory flagellum short, with 3 segments, the last of which is minute. Antenna with two distal segments of peduncle sub-equal, flagellum of 10 segments.

First coxal plate slightly expanding distally. First gnathopod with palm very oblique, concave and crenulate, with two strong spines at posterior corner, and one more near the corner. Second gnathopod slightly larger than first gnathopod, which it resembles with respect to spines and crenulation of the palm, which is, however, less oblique. Third pereiopod of the type characteristic of the subgenus, much larger than fourth pereiopod. The dense coating of plumose hairs on the posterior margin very well developed not only on merus and carpus but also on metacarpus. Fourth coxal plate deeply excavated behind. Fifth pereiopod distinctly shorter than sixth and seventh pereiopods, reaching only slightly past end of carpus of sixth pereiopod. Sixth and seventh pereiopods subequal, basis of seventh pereiopod narrow.

Pleopods well developed.

First uropod normal, reaching to end of second uropod. Third uropod very large, inner ramus reduced to minute scale.

Female with gnathopods weaker and dense growth of hairs on third pereiopod lacking. Several ovigerous females carried 2 eggs in marsupium.

Length of body abt. 6mm.

Type in Zoological Institute, Lund, No. 85.

S. madeirensis differs from *S. rhipidiophorus* in having a normal first uropod, from *S. guernei* in having the fifth pereiopod distinctly shorter than the sixth and seventh pereiopod and from *S. asiaticus* in having spines on the dorsal side of all urosome segments. Besides these diagnostic features there are many differences in other respects.

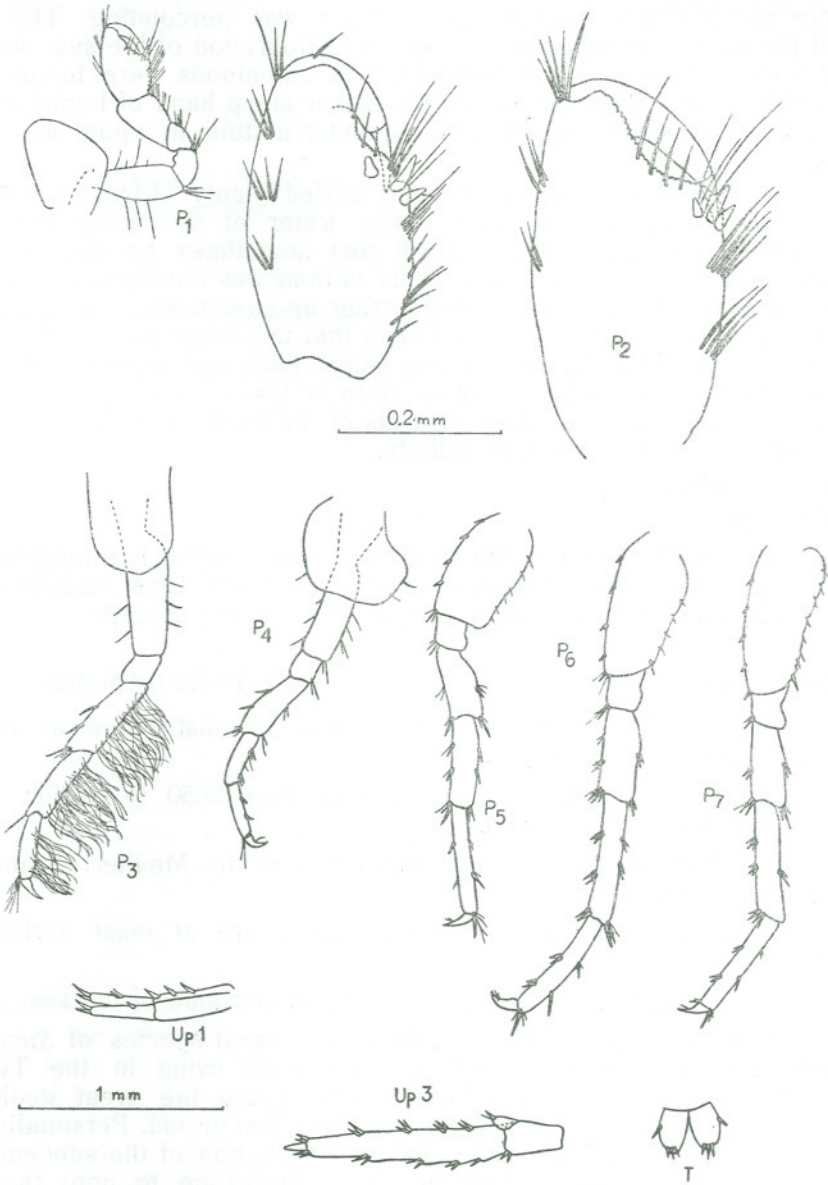


FIG. 5. — *Sarothrogammarus madeirensis*, ♂ holotype.

Occurrence and ecology. The species was only found on the north coast of Madeira under stones in and around small pools 20-50 m from the sea, in the estuary of a small stream. The shore consisted of a huge bank of stones and boulders through which water was percolating. The whole floor of the narrow stream valley in the neighbourhood of the sea was also largely made up of stones and boulders. The amphipods were found in the semi-subterranean habitat formed by the rather steep bank of bouldetrs near the sea, only one specimen was obtained under a stone in a pool wih muddy bottom.

At the time of our visit the stream carried plenty of fresh water after heavy rains in the mountains, and the water of the pools was fresh. There were indications, however, that it may sometimes be brackish. The vegetation was very poor even where the bottom was muddy and most species of the fresh water flora growing further up-stream were lacking. From inhabitants in the nearby village we learnt that the lower part of the valley is sometimes flooded by the sea during gales. Then and during dry periods when the stream and the pools dry up more or less completely and the amphipods have to withdraw to deeper levels of the bank of boulders they will have to live in water with a high salinity.

Material examined:

Madeira

North coast, loc. 129, Faial, at the mouth of Ribeira do Faial, among boulders in and around small pools near the sea, 26. IV. 1957. Numerous specimens including *male holotype* and *female paratype.*

THE DISTRIBUTION OF THE SUBGENUS SAROTHROGAMMARUS

The four species of *Sarothrogammarus* are distributed as follows, from east to west:

S. asiaticus. Mountain streams in Turkestan, 2650 to 2760m above sea level (Martynov 1935, p. 507).

S. rhipidiophorus. Widely distributed around the Mediterranean, partly in brackish waters.

S. madeirensis. Madeira, in waters which are at least periodically brackish.

S. guernei. Flores, in streams in the neighbourhood of the sea.

According to Martynov (*l. c.,* p. 508) the present species of *Sarothrogammarus* must have been derived from ancestors living in the Tertiary seas, which entered brackish and fresh waters during the great geological changes which befell the area in question during that period. Personally I can find no better way of explaining the present distribution of the subgenus. Its relict character seems very obvious, and it is interesting to note that two out of the four species live at least partly in poikilohaline waters. This makes

a derivation from the sea appear more probable still. It is also interesting to note that the more or less related species *Neogammarus festae* has only been found under stones on the shore of the Mediterranean near Genova (Ruffo 1937, p. 440).

Concluding Remarks

The collection of fresh and brackish water amphipods made by the Swedish Expedition comprises the following four species:

Pseudoniphargus africanus Chevreux. Azores, previously reported also from Madeira.

Gammarus (Marinogammarus) atlanticus n. sp. Azores and Madeira.

Gammarus (*Sarothrogammarus*) *guernei* Chevreux. Azores.

» » *madeirensis* n. sp. Madeira.

As far as known to me no other fresh or brackish water amphipod has ever been reported from the islands.

Of the four species mentioned above one, *M. atlanticus*, is closely related to the two marine littoral species *M. olivii* (Milne-Edwards) and *M. pirloti* Sexton and Spooner, and has connections also with other members of the *Marinogammarus-Echinogammarus* group. Its derivation from marine littoral amphipods, probably in comparatively recent time, is obvious and it is included in the present report only on account of its predilection for strongly poikilohaline littoral habitats.

Of the other species of the islands *P. africanus* was found to occur only in more or less saline subterranean waters. It could not be found in any pure fresh water locality and its upper salinity limit within the islands could not be established. Its general distribution and above all its occurrence in the marine psammon on the south coast of France clearly indicate a marine ancestry of the species.

There remain the two species of *Sarothrogammarus*. *S. guernei* is confined to running fresh waters in the neighbourhood of the sea, while *S. madeirensis* occurs in a more or less poikilohaline habitat. The general distribution and ecology of the subgenus *Sarothrogammarus* points to a derivation from marine ancestors during the Tertiary era and it could hardly be explained otherwise.

On the other hand no representative of the numerous old and widespread fresh water genera of the neighbouring continents has been found in any of the islands.

Consequently nothing in the present composition of the fresh and brackish water amphipod fauna of the Azores and Madeira favours the assumption of comparatively recent continental connections. On the contrary all available facts indicate that the amphipods in question reached the islands by way of the sea.

REFERENCES

Balazuc, J. & A. Angelier:
1952. Sur la capture, à Banyuls-sur-Mer (Pyréné-Orientales) de *Pseudoniphargus africanus* Chevreux 1901 (Amphipodes *Gammaridae*). *Bull. Soc. Zool. Fr.* 76.

Barrois, Th.:
1896. Recherches sur la faune des eaux douces des Azores. *Mem. Soc. Sci. Agr. et Arts de Lille,* ser. 5:4.

Chevreux, E.:
1889. Description d'un *Gammarus* nouveau, des eaux douces de Flores (Azores). *Bull. Soc. Zool. Fr.* 16.
1901 a. Amphipodes des eaux souterraines de France et d'Algérie. V. *Pseudoniphargus africanus* nov. gen. et sp. *Bull. Soc. Zool. Fr.* 26.
1901 b. D:o VI. ? *Gammarus rhipidiophorus* Catta. *Ib.*

Dahl, E.:
1938. Two new Amphipoda of the Genus Gammarus from Finmark. *K. Norske Vidensk Selsk. Forh.* 10.

Leach, W. E.:
1815. A tabular view of the external characters of four classes of animals, etc. I. Crustacea. *Trans. Linn. Soc. London* 11.

Martynov, A.:
1935. Amphipoda Gammaridea of the running waters of Turkestan. *Trav. Inst. Zool. Ac. Sci. URSS.* 2. (Russian with comprehensive English summary).

Milne-Edwards, H.:
1830. Recherches pour servir à l'histoire naturelle des Crustacés Amphipodes. *Ann. Sci. Nat.* 20.

Reid, D. M.:
1938. *Gammarus marinus* Leach, var. nov. *stoerensis* (Crustacea Amphipoda). *Ann. Mag. Nat. Hist.* ser. 11:1.

Ruffo, S.:
1937. Studi sui Crostacei Anfipodi. V. Una nuova specie di Gammarus del mar Ligure. *Ann. Mus. Civ. Stor. Nat.* Genova, 59.

Schellenberg, A.:
1937. Schlüssel und Diagnosen der dem Süsswasser-Gammarus nahestehenden Einheiten ausschliesslich der Arten des Baikalsees und Australiens. *Zool. Anz.* 117.
1939. Verbreitung und Alter der Amphipoden-Gattung Pseudoniphargus nebst Verbreitung der Gattung Niphargus. *Ib.*127.

Sexton, E. W. & G. M. Spooner:
1940. An account of *Marinogammarus* (Schellenberg) gen.nov. (Amphipoda), with a description of a new species, *M. pirloti*. *Journ. Mar. Biol. Ass.* 24.