

A REVISION OF THE EUROPEAN SPECIES OF THE GAMMARUS LOCUSTA-GROUP (CRUSTACEA, AMPHIPODA)

by

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With 26 text-figures

INTRODUCTION

In the past, many authors emphasized the great variability in the morphology of the members of the genus *Gammarus*. At the same time, such "varieties" were distributed in waters ranging from entirely fresh to purely marine. Both ideas, the morphological variability and the great salinity tolerance, have not been substantiated by more modern investigations. The descriptive and experimental work, first of all that of Sexton, has shown that the morphological characters of the various forms are very stable, at least at a given stage of maturity, and that very slight details suffice for their characterization. These closely related forms are intersterile (Spooner, 1947, 1951; Kinne, 1954; Wautier & Roux, 1959) and behave ecologically different (e.g. Spooner, 1947; Segerstråle, 1947; Kinne, 1954). Because of their intersterility and since the distribution areas overlap (cf. Segerstråle, 1947, fig. 6; Nijssen, 1963), most authors now follow Kinne, 1954, in considering the "forms" of *Gammarus* good species. The idea that the specific characters (more in particular, the "hairiness") would be brought forward through environmental factors, such as salinity, was disproved by Spooner (1947), who showed that the characteristic formation of the cuticular structures was independent of the salinity, and genetically determined.

Sexton (many papers), but especially Spooner (1947), Segerstråle (1947), and Kinne (1954) have done excellent work in straightening the taxonomic status of the marine and brackish water species of *Gammarus* of the Atlantic coasts of Europe. Their work chiefly, clarified the morphology and ecology of *Gammarus duebeni* Lilljeborg, 1851 and of a number of forms previously confused under the name of *G. locusta* (Linnaeus, 1758). The latter was subdivided into 4 different species: *G. locusta* (L.), *G. zaddachi* Sexton, 1912, *G. salinus* Spooner, 1947, and *G. oceanicus* Segerstråle, 1947.

It is clear from the literature, however, that the group of animals left untouched under the name of *Gammarus locusta*, does not form a homogen-

eous taxon. So, Pirlot, 1939, separated a West African form from *G. locusta*. His excellent description and figures show that he was clearly right in doing so, but at the same time he created a lot of confusion in applying the name of a Mediterranean species, *G. plumicornis*, which was admittedly poorly characterized by Costa (1853, 1856), to his West African material. As we will see in the sequel, Costa's species is entirely different from the animal studied by Pirlot, and a new name had to be chosen for the latter. In my 1966 paper, I proposed *G. crinicornis* as a replacement.

Apparently, Spooner (1947:15) was aware of this problem, since he did not attribute the name *plumicornis* to a "variety" of *G. locusta* found in Whitsand Bay (W. of Plymouth). In 1957, Spooner (1957:220) considered the material from Whitsand Bay (which he then called "*Gammarus* sp. allied to *locusta*") identical with "the predominant species in the Mediterranean". Den Hartog (1964:429) in the meantime synonymized these samples with *G. plumicornis* sensu Pirlot, and showed that similar forms occurred in the Netherlands. Re-examination of Dutch and West African material has convinced me that Den Hartog's and Pirlot's gammarids are indeed identical; their correct name should be *G. crinicornis*.

Other "varieties" of *Gammarus locusta* were described by Spooner (1947:16-17) from the Fleet (Dorset) and New England Creek (Essex). Margalef (1951:255) believed that these might be identical with *G. locusta* ssp. *aequicauda* (Martynov, 1931), which was originally described from the Crimea, and later on recorded from several places around the Mediterranean ¹⁾.

Both Margalef's identification (as *G. locusta aequicauda*) and Spooner's remark ("identical with the predominant species in the Mediterranean") involve Mediterranean species in the problem of the identity of Atlantic material. One thing, however, is clear: the taxonomy of the Mediterranean species of *Gammarus* is in a chaotic stage. Chevreux & Fage (1925:258) describe a "forme méditerranéenne" of *G. locusta*, which differs in certain characteristics from typical (Atlantic) specimens, and which is distributed in "mer, eau saumâtre, eau douce". A re-examination of their material proved that it consists of several distinct species, none of them *G. locusta*. Many authors have commented upon certain differences of their material with the real *G. locusta* (e.g. Colosi, 1921:5-6; Ruffo, 1936:25-28; Ruffo, 1938:137; Ruffo, 1941:115; Brian, 1955:1-6). Ruffo (1948:296-299) believed that there are several species involved in these discussions: the

1) I personally believe, Spooner's material might be *G. insensibilis*.

real *G. locusta*, *G. plumicornis* (sensu Pirlot), *G. zaddachi*, *G. aequicauda*, and *G. eduardi* Vecchi, 1931.

The record of *G. zaddachi* is based on Sexton (1942:602), who mentioned this species from the Crimea. It is my personal opinion that this record is doubtful and that it may be based on confusion with *G. aequicauda*. *G. eduardi* was described in April 1931 from Benghazi (Lybia); its description and topotypes that I examined for this present study, indicate that it is identical with *G. aequicauda* (described by Martynov in March 1931). Brian, 1955, proposed the same synonymy.

This would then reduce the number of Mediterranean species to three: *locusta*, *aequicauda* and *plumicornis*. This conclusion would seem to agree with Rancurel's results (1949:8-9); this author found 3 forms of *G. locusta* on the Mediterranean coast of France, which he called "forme saumâtre", "forme marine subtypique" and "forme typique". Margalef (1951:255-256) was of opinion that the "forme saumâtre" of Rancurel is identical with *G. aequicauda*, the "forme typique" with *G. locusta*, and that the "forme marine subtypique" is insufficiently characterized. However, the fifth to seventh legs of this form (as described by Rancurel) are so characteristic that confusion with *G. locusta* or *G. aequicauda* is absolutely excluded. These legs resemble the corresponding appendages of *G. plumicornis* (sensu Pirlot) in their widened basal segments; however, the second antenna is little setose ("peu poilue", Rancurel, 1949:5), whereas this appendage in *G. plumicornis* is "extremely richly ornamented with setae" ("la garniture de soies . . . est extrêmement riche", Pirlot, 1939:57). Freshly collected material from the Mediterranean has shown that two clearly different species are involved here (*G. subtypica* and *G. crinicornis*).

An abundant material has also convinced me, that both the real *G. plumicornis* (sensu Costa), and the so-called *G. plumicornis* (sensu Pirlot) exist in the Mediterranean. The first is a brackish water form, the second is a purely marine form, chiefly confined to sandy bottoms. In brackish waters around the Mediterranean, *G. aequicauda* is the predominant and (this time really) variable species. Black Sea material, thus collected near the type locality, has confirmed the identity of *G. aequicauda*.

None of the Mediterranean samples identified by previous authors as *G. locusta* is identical with that species. Even if all the forms mentioned above are weeded out, the remaining group differs so clearly from the Atlantic *G. locusta* that it is considered here as a distinct species, *G. insensibilis*. Much of this confusion is due to the fact that, apart from the excellent drawings of the head region and of the first two legs by Sexton (1942: pl. 3) no detailed drawings of the appendages of the real *G. locusta* are

available. Those of Chevreux & Fage (1925) are on a small scale, and are suspect because the authors confused three Mediterranean species²⁾ and three Atlantic species³⁾ under the name of *G. locusta*. The well-known plate of Sars (1894, pl. 176 fig. 1) is, at least partially, based on *G. oceanicus* and not on *G. locusta* (cf. Spooner, 1947:8). Della Valle (1893, pl. 24 fig. 20-34) illustrated *G. locusta* (but presumably it is *G. insensibilis*), although Pirlot (1939:53) believed that Della Valle had *plumicornis* before him⁴⁾. At any rate, it seemed useful to insert some drawings of the appendages of the real *G. locusta* (from the Channel coasts) in this paper, to make comparison possible.

THE CONSTANCY OF THE CHARACTERS

The old idea, that the species of *Gammarus* were extremely variable, and that only few species existed within the genus, is thoroughly disproved by ecological, systematic, and genetical work. Nevertheless, it must be admitted that some characters, such as the degree of setation of the legs, vary to a certain extent. Such "variations" are mentioned in the descriptive part under each species.

Very good, stable characters are the structure of the mandible palp, and the development of or absence of a compressed "keel" on the urosome segments.

The shape of the basal segments of the posterior legs is characteristic (a species with a "wide" basal segment never has a "narrow" one, and vice versa), although the length/width ratio of these segments may vary to a certain extent.

The number of spines, on the urosome, on the telson, and on the legs is largely variable. The number of subbasal spines on the telson is often used as a key-character, and, indeed practically all animals belonging to *G. aequicauda* have one such a spine, the majority of the specimens of *G. subtypicus* and *G. locusta* have three (but quite a few have one or two).

G. locusta and *G. insensibilis* are characterized by the long auxiliary flagellum of A₁, but smaller (though mature) individuals may have shorter flagella.

The "gradate condition" (Spooner, 1947) of the palmar spines of P₂ in *G. locusta* is a good character for entirely full-grown males. In *G. aequicauda*,

2) *Gammarus aequicauda*, *G. plumicornis*, *G. insensibilis* (present observations, based on re-examination of the original material).

3) *G. locusta*, *G. zaddachi* (cf. Sexton, 1942:583) and *G. salinus* (viz., Chevreux & Fage's material from the Loire; re-examination of the original material).

4) The material from Naples, examined by Pirlot, has been re-examined by me and belongs to *G. insensibilis* (6 specimens) and *G. subtypicus* (2 specimens).

however, some populations show this character more often than other populations, while it is absent in not a few "entirely full-grown" males.

It is certainly not true (as some authors believe, e.g. Brian, 1955) that specimens from waters with lower salinities tend to be more hairy. A form of *G. aequicauda* from a nearly fresh well in southern France, described in this paper, is much less setose than members of the same species from waters with a higher ion-content. Not known is up to now in how far the relative lengths of the branches of the uropods fluctuate in relation to the salinity; one gets the impression that in some populations of *G. aequicauda* these rami are subequal, whereas the inner ramus is clearly shorter than the outer in other populations.

Clinal variation is observed in at least one species (*G. crinicornis*). The central and eastern Mediterranean samples have the legs more hairy than the northern Atlantic samples; in the western Mediterranean, specimens closely resembling the Atlantic type have been found, whereas on the West African coast both setose and less setose specimens have been collected.

Many characters, such as the setation of the second antenna, the structure of the hand of leg 1 and leg 2, the degree of setation of the posterior legs and the length of the setae on urosome and telson, are much better developed in the male than in the female. For this reason, the present revision is mostly based on the characters of the adult male. A more detailed study of the females is necessary to determine which characters can be used for the identification of specimens belonging to that sex. It must be strongly emphasized that identifications in a group so difficult as *Gammarus*, especially when these identifications are made by workers unfamiliar with the genus, should be based on an abundant material, consisting of mature specimens, and containing males.

For critical identifications, not only one isolated character has to be taken into consideration, but a number of characters combined. Each individual character may show a certain unstability, but it never occurs that all characters together participate in these variations.

It is impossible to make out at present which species many of the older authors studied, even when their work is accompanied by figures, because most authors figured one or two characters only, which makes it hard to discover what species they had.

THE CHARACTERS OF THE LOCUSTA-GROUP

Spooner (1947), Segerstråle (1947), and Kinne (1954) summarized the more important features that separate *G. locusta* from the *zaddachi*-group (the latter comprises in temperate western Europe *G. zaddachi*, *G. salinus*

and *G. oceanicus*). Several Mediterranean species, e.g. *G. aequicauda*, break down these distinctions to a certain degree, but still the *locusta*-group appears to be characterized by the following combination of features (it should be noted that not all species share necessarily all of them):

1. Third segment of the mandible palp ventrally armed with a row of comblike spinules, which diminish regularly in size in proximal direction (no exceptions).
2. Pedunculus of the first antenna very little hairy (exception: *G. plumicornis*).
3. Sideplate 4 with a deep, almost rectangular lower portion (exceptions: *G. plumicornis*, *G. aequicauda*).
4. Urosome segments, especially 1 and 2, with angulate, strongly raised and laterally compressed dorsal elevations ("keel") (exceptions: *G. crinicornis*, *G. inaequicauda*).
5. Accessory flagellum long (exceptions: *G. plumicornis*, *G. aequicauda*).
6. Lateral lobes of head pointed (exception: *G. plumicornis*), sinus shallow.
7. The hindcorners of epimeres 2 and 3 are acutely produced (exceptions: *G. crinicornis*, *G. subtypicus*, some forms of *G. aequicauda*).
8. The median palmar spine of the second leg (adult ♂) is "flask-shaped" (no exceptions).
9. In the later mature stages, the median palmar spine of P₂ ♂ is succeeded, towards the palmar angle, by a regular series of spines graded in respect to size and distance between the successive spines (exceptions: some forms of *G. aequicauda*, *G. insensibilis*, *G. subtypicus*, *G. crinicornis*).
10. The inner ramus of the third uropod is 90 to 99% the length of the first segment of the outer ramus (exceptions: some forms of *G. aequicauda*, *G. plumicornis*, *G. inaequicauda*).

So, it appears that only characters (1) and (8) are shared by all species. *Gammarus plumicornis* and *G. aequicauda* possess only five of the above 10 characters, *G. crinicornis* seven, *G. subtypicus* and *G. inaequicauda* eight, *G. insensibilis* nine, whereas *G. locusta* has them all.

WHAT IS GAMMARUS PLUMICORNIS COSTA, 1853?

Central in the problem of the nomenclature of the species of the *G. locusta*-group, is the question which species was meant by Costa (1853, 1856) when he described and illustrated his *G. plumicornis*. Especially the rather extensive 1856 description, and the figures accompanying that description, however poor they are, contain some elements of key value that must

guide us in our attempts to fix the name *plumicornis* to one of the Mediterranean species.

The species to be called *G. plumicornis* must fulfil at least the following diagnostic features:

1. "antennis inferioribus plumosis" (Costa, 1856:215).
2. "il seconde e terzo anello addominale con l'angolo posteriore-inferiore prolungato in punta acuta" (: 215).
3. "Capo anteriormente ritondato" (: 215).
4. Peduncle segments 1 and 2 of first antenna with several (groups of) setae on the ventral margin (pl. 4 fig. 1a).
5. Accessory flagellum of A_1 short (pl. 4 fig. 1a).
6. Long setae on A_2 chiefly restricted to the ventral margins of the peduncle and flagellum segments (pl. 4 fig. 1a, 1b).
7. Third peduncle segment of A_1 elongate (pl. 4 fig. 1a).

Especially characters (1) and (3) are so salient in the taxonomy of *Gammarus*, that the identity of Costa's species is unmistakable as soon as one has the right material at hand. In the present publication (fig. 9-11), a brackish water species found in several localities in the western Mediterranean, is depicted, which fits all 7 points mentioned above.

No other *Gammarus* in the area under consideration has plumose setae on the A_2 (Costa used the word "plumosis" only in relation to *G. plumicornis*; in all other cases he used quite specific terms like "pilosus", "barbatus", "ciliatus"). No other *Gammarus* has rounded lateral lobes on the head (exception: certain forms of *G. aequicauda*). The other species of the *locusta*-group have the ventral margin of the A_1 peduncle nearly glabrous, only *plumicornis* has it rather hairy.

It must be admitted Costa's description could apply on *G. zaddachi*, as far as characters 2, 4, 5, 6, and 7 are concerned, but characters 1 and 3 do not agree.

Pirlot's interpretation of *G. plumicornis* (1939) lacks any ground, since it does not fulfil the requirements of any of the characters 1 to 7 of the above list.

G. insensibilis, of which the A_2 corresponds more or less with Costa's figures 1a and 1b, does not agree with characters 1, 3 and 5.

G. subtypicus does not agree with characters 1, 3, 4, 6, and 7.

Several of Costa's types are said to be preserved in the Museo Zoologico dell'Ateneo Napoletano, Naples, but attempts to locate the types of *G. plumicornis* there, or in other Italian institutions, failed. In order to

Now we have fixed the name *plumicornis* to a certain species, it is clear that the other taxa that have been called so, but which are different from the real *G. plumicornis*, have to receive other names. So, *G. plumicornis* of Pirlot, 1939, and Den Hartog, 1964, has been renamed *G. crinicornis*. The *G. plumicornis* in Riedl's (1963) "Fauna und Flora der Adria" is most probably *G. insensibilis*.

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1 Basal segments of P_5 , P_6 , and P_7 short and wide (in P_7 usually $1\frac{1}{4}$ to $1\frac{1}{3}$ times as long as wide). [Flagellum of A_2 short, segments of flagellum short. Third peduncle segment of A_1 short. Telson with (1 to) 3 subbasal spines. Epimeres 2 and 3 with subacute hindcorners] 2

— Basal segments of P_5 , P_6 , and P_7 longer and narrower (in P_7 more than $1\frac{1}{2}$ times as long as wide) 3

2 Posterior margin of basal segment of P_7 finely crenulate, with many spinules. P_7 densely setose. Fourth and fifth peduncle segments of A_2 normally armed with setae: those on the upper margin being shorter than those on the lower margin. Eye very large. Urosome with strong, compressed, dorsal elevations
. *G. subtypicus* Stock, 1966

— Posterior margin of basal segment of P_7 coarsely crenulate, with few spinules. P_7 spinose (in Atlantic specimens) or slightly setose (in Mediterranean specimens). Fourth and fifth peduncle segments of A_2 very richly armed with setae: those on the upper margin of segment 5 being as long as those on the lower margin. Eye of moderate size. Urosome with low dorsal elevations, not compressed.
. *G. crinicornis* Stock, 1966

- 3 Telson with long terminal setae (2 to 3 times as long as the spines). Fourth sideplate much longer than wide, its inferior margin curved. [Accessory flagellum of A₁ short, usually less than 9-segmented]. 4
- Telson with short terminal setae (not overreaching the spines). Fourth sideplate about as long as wide, its inferior margin straight or nearly so. 5
- 4 Plumose setae on A₁, A₂, all legs, urosome, and telson. Eyes large. Lateral lobes of head obtusely rounded. *G. plumicornis* Costa, 1853
- Simple setae on the body and appendages (with the exception of the pleopods and the third uropod). Eyes small. Lateral lobes of head usually angular
- *G. aequicauda* (Martynov, 1931)
- 5 A₂ without calceoli. Inner ramus of third uropod shorter (75-90%) than the first segment of the outer ramus. Posterior margin of third epimere with 0 or 1 setule 6
- A₂ with calceoli. Inner ramus of third uropod hardly shorter (90-100%) than the first segment of the outer ramus. Posterior margin of third epimere with several setules. *G. locusta* (Linnaeus, 1758)
- 6 Dorsal elevations of urosome not compressed. Lateral margin of exopod of third uropod virtually without plumose setae. Telson with 3 subbasal spines
- *G. inaequicauda* Stock, 1966
- Dorsal elevations of urosome compressed. Lateral margin of exopod of third uropod with numerous plumose setae. Telson with 1 (rarely 2 or 3) subbasal spines. *G. insensibilis* Stock, 1966

DESCRIPTIVE PART

All descriptions, unless the contrary is explicitly stated, apply to the adult male.

Gammarus locusta (L.) (fig. 1, 4b)

Even after the revisions by Spooner (1947) and Segerstråle (1947), seven different species, described in the sequel, were confused under the name of *G. locusta*. It is fair, however, to add at once that both Spooner and Segerstråle apparently had a fairly good idea of what the real *G. locusta* (s. str.) was. Spooner (1947) gave a detailed description of the real *G. locusta*, but discussed some other species (presumably *G. insensibilis* and *G. crinicornis*) in his paragraph "Notes on variation within the species".

Problems chiefly arise with the Mediterranean material, which has been called *G. locusta* by many authors, whereas, according to the present revision, the real *G. locusta* does not occur in the Mediterranean. In so far these forms are distributed outside the Mediterranean as well, they have been confused with *G. locusta*.

Most of these confusions are due to the fact that few trustworthy figures of *G. locusta* s. str. exist. The following illustrations may serve as a basis for the recognition of the species: Spooner (1947, fig. 1, 2 A, B, 3), Sexton (1942, Pl. 3 fig. 19-24), Kinne (1954, fig. 1 (top), 2 (6), 4 (top), 5 A-D, 6).

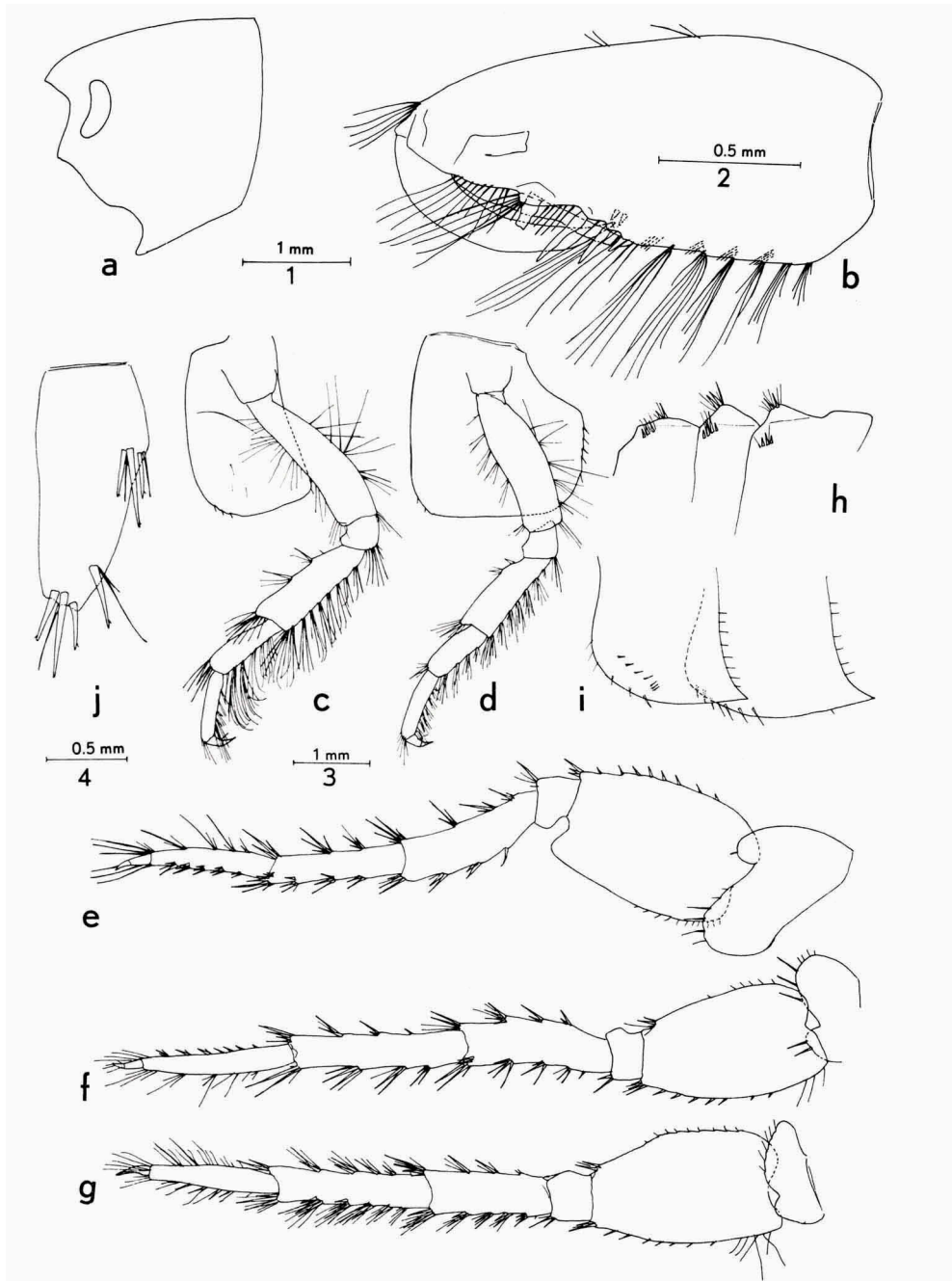


Fig. 1. *Gammarus locusta* (Linnaeus, 1758). ♂ from Roscoff, France. a, head (scale 1); b, hand of first leg (lateral) (2); c, third leg (3); d, fourth leg (3); e, fifth leg (3); f, sixth leg (3); g, seventh leg (3); h, urosome (lateral) (3); i, second and third epimeres (3); j, telson (4).

Several details not previously figured are illustrated in fig. 1 of the present paper.

In addition to Spooner's detailed description, the following notes can be made:

The first antenna (fig. 19 in Sexton, 1942) has only one group of 0 to 2 setules in the middle of the lower margin of peduncle segment 1, and one group of very short setules near the middle of the lower margin of segment 2; peduncle segment 3 is slightly less than half as long as segment 2, but it is of a rather elongate shape (i.e., about twice as long as wide). The accessory flagellum is long and has 8 segments at the onset of maturity, when it is about $1\frac{1}{2}$ times as long as peduncle segment 2, up to 15 segments in the oldest males, when it is distinctly more than twice as long as peduncle segment 2.

The second antenna (fig. 19 in Sexton, 1942) has slender fourth and fifth segments, whose lower margins are provided with 4 to 9, and 5 to 9 groups of setae, respectively. These setae are sometimes straight, but usually slightly curved at the tip. Owing to a printing error, which has caused confusion in several later papers (e.g., in Rancurel, 1949, and in Margalef, 1951), Sexton's (1942:600) table suggests that segment 5 is longer than segment 4. In fact, the text should read: "4th jt. about $\frac{1}{6}$ longer than 5th". The 7 to 11 most proximal segments of the flagellum are provided with calceoli.

The eyes (our fig. 1a) are small; the lateral lobes of the head are angular; the sinus is shallow.

The mandible palp has an unarmed first segment; segment 3 carries 4 terminal setae, two lateral groups of setae and a row of spinules along its lower margin. The spinules of this row diminish gradually but regularly in length (fig. 1 in Kinne, 1954).

Legs 1 and 2: see Sexton (1942, fig. 20-24) and Spooner (1947).

Leg 3 (fig. 1 c, present paper) has an elongate coxal plate with a rounded antero-inferior corner and an angular postero-inferior corner. The merus bears 2 groups of elements (each of 1 spine + some setae) on its anterior margin, about 8 groups of distally curved or curled setae on its posterior margin. The carpus has an unarmed anterior margin (except, of course, of the distal group of elements) and curved setae of increasing length on the posterior margin.

The fourth leg (fig. 1 d, present paper) has a characteristic coxal plate, which is as wide as long, or even wider than long; the inferior part is nearly rectangular, the inferior margin is straight; the posterior excavation is shallow. The merus bears 1 or 2 groups of anterior elements; these groups are implanted in the most proximal third of the segment; the posterior margin bears about 7 groups of elements (1 spine + several setae). The

carpus lacks anterior elements, but possesses 4 groups (1 spine + several setae) of posterior elements.

The fifth leg (fig. 1 e, present paper) has a subrectangular basal segment, which is slightly less than $1\frac{1}{2}$ times as long as wide (wider in females or younger specimens), its posterior margin nearly straight, the anterior margin not much curved. The merus and carpus bear groups of spines, with here and there an occasional seta, which is not much longer than the spines.

The sixth leg (fig. 1 f, present paper) has a slender basal segment with slightly convex posterior and anterior margins. The armature of merus and carpus resembles that of P_5 .

The seventh leg (fig. 2 A, 2 B in Spooner, 1947; fig. 1 g, present paper) has a rather elongate basal segment, which is usually slightly over $1\frac{1}{2}$ times as long as wide; its posterior margin bears several fine crenulations, each set with a spinule; often, the straight proximal part of the posterior margin shows a slight but distinct bend where it merges into the distal part. The distal hindcorner bears a few spines and a few setae, which are as long as or slightly longer than the spines. The anterior margin of the basal segment is slightly curved. The merus and carpus bear, both at their anterior and posterior margins, groups of elements consisting of spines and setae; the latter are longer than the spines, but less than twice as long.

The urosome segments, more particularly the first and second, bear strongly compressed dorsal humps; the dorsal and lateral armature consist of spines and setae, the latter are sparse and slightly longer than the spines (our fig. 1 h).

The second and third epimeres (our fig. 1 i) have both much produced, pointed posterior corners. Their posterior margins bear numerous setules.

The telson (our fig. 1 j) bears normally three subbasal spines, but not infrequently specimens with only one or two subbasal spines are found. One or two short setae are often found between the subbasal spines. Subterminally, the armature consists of one spine and one longer seta, sometimes also some shorter setae. The distal armature consists of three spines and one or two setae, the latter not overreaching the spines.

Distribution. — This species occurs in the temperate eastern Atlantic, where it is the most common purely marine form (for salinity range, see Den Hartog, 1964: 434). It lives in shallow waters (my own observations all range from the intertidal zone to about 30 m).

Since the species has often been confused, either with members of the *zaddachi*-group, or with one of the species treated in the sequel, all literature references should be considered with great reserve. I have seen samples of

this species from the Baltic and from the Atlantic coasts of Europe, as far north as Bergen (Norway), and as far south as Setubal (Portugal).

Accompanying species. — Usually alone. On sandy beaches sometimes, and in the Dutch Waddensea often, accompanied by *G. crinicornis*. Very rarely together with *G. zaddachi* (Veerse Meer, The Netherlands).

***Gammarus insensibilis* Stock, 1966 (fig. 2, 3, 4a, 5, 6)**

G. insensibilis Stock, 1966:2.

G. locusta (part.), Della Valle, 1893:759-762, pl. 2 fig. 1, pl. 24 fig. 20-34, pl. 45 fig. 1-11 (only Neapolitan records); Howes, 1939:414; Spooner, 1947:16.

G. plumicornis (part.), Pirlot, 1939:53 (only the Neapolitan record).

Material examined.

Mediterranean

France: surroundings of Banyuls, dépt. Pyrénées-Orientales, many specimens (LA); Étang de Leucate, dépt. Pyrénées-Orientales, 5 July 1963, 10 specimens (ZMA); Étang de Sigean, dépt. Aude, 8 September 1966, many specimens (ZMA); Marseille, Saumaty, dépt. Bouches-du-Rhône, 18 May 1966, many specimens (ZMA).

Italy: Gulf of Naples, "old collection", 6 specimens (SZN); Gulf of Naples, May 1939, 2 specimens (ZMA); Lago Fusaro, near Naples, 5 March 1963, 21 June 1963, 9 October 1963, 1 July 1965, many specimens (RMNH).

Yugoslavia: Golfo di Valdibora, near Rovigno, Istria, depth 11 to 15 m, 28 May 1961, 100 + specimens (1 ♂ **holotype**, the remaining specimens paratypes) (ZMA).

Greece: near the port of Porto Lago, depth 0-2 m, 29 June 1959, 2 specimens (RMNH).

Black Sea

Turkey: various localities on the Black Sea coast near Trabzon, depth 0-5 m, 1-8 June 1959, many specimens (RMNH).

Atlantic

France: Étang du Fret, north of Crozon, Brittany, a lagoon cut off from the sea by a dike with a sluice, chlorinity 18‰, among *Zostera marina*, 2 October 1966, many specimens (ZMA); a small loch, in connection with the sea, near Pointe du Binde (= Binde), Rade de Brest, Brittany, chlorinity 18‰, among green algae, 1 October 1966, 1 ♂, 6 ♀ (ZMA).

The general form, the colour, and the morphology of the appendages (long accessory flagellum of A_1 , setation of A_2 , shape fourth coxal plate, elongation of basal segments of P_5 to P_7) make that this species is most likely to be confused with *G. locusta*. The most easily observed difference is the absence, in the male of *G. insensibilis*, of calceoli on the flagellum of the second antenna (the specific name refers to this character).

Description (after specimens from Rovigno). — A large species (big specimens have a body length of about 19 mm).

The head (fig. 3 a) has acute lateral lobes, and a shallow sinus (somewhat deeper though than in *G. locusta*). The eye is distinctly larger than in *G. locusta*.

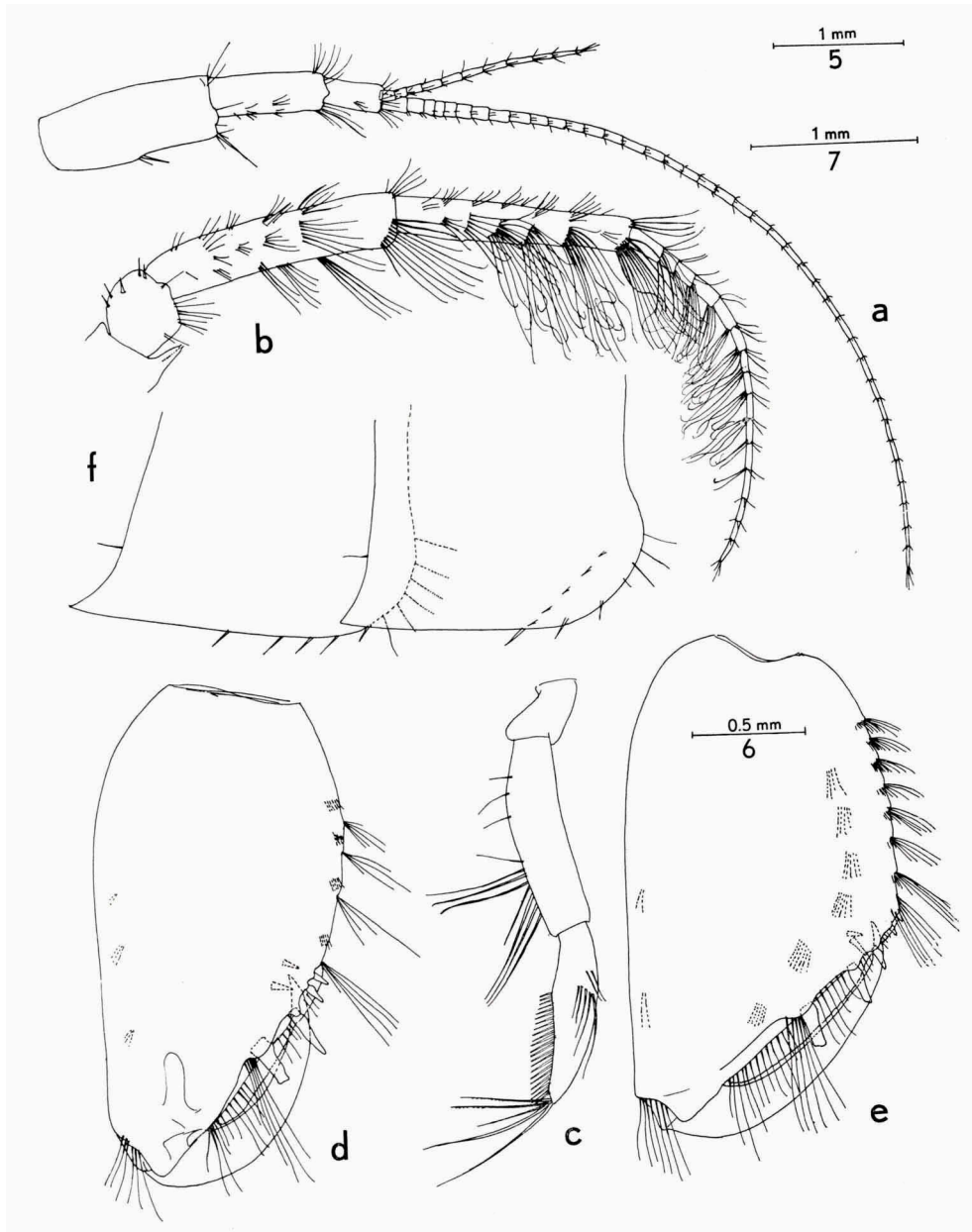


Fig. 2. *Gammarus insensibilis* Stock, 1966, ♂ from Rovigno, Yugoslavia. a, first antenna (scale 5); b, second antenna (medial) (5); c, mandible palp (2); d, hand of first leg (lateral) (2); e, hand of second leg (lateral) (6); f, epimeres 2 and 3 (7).

The first antenna (fig. 2 a) is rather similar to that of *G. locusta*. The accessory flagellum is long, nearly twice as long as peduncle segment 2 and has up to 12 segments. The flagellum is also long and overreaches that of A_2 .

The second antenna (fig. 2 b) has very slender and elongate peduncle segments 4 and 5. The gland cone, which is short in *G. locusta*, reaches halfway the third peduncle segment in *G. insensibilis*. The fourth and fifth peduncle segments bear several groups of setae (6 to 8 on segment 5); the setae of these groups are very long (especially those of the distal groups of segment 5) and somewhat curled or curved. The setae of the inferior side of the flagellum, especially of segments 2 to 10, are also very long. Calceoli are always absent.

The mandible palp (fig. 2 c) is of the usual type (gradate comb-like setae on the lower margin of segment 3, segment 1 unarmed).

The hand of the first gnathopod (fig. 2 d) is slightly more swollen than that of *G. locusta* (cf. fig. 1 b). The medial palmar spine is more or less flask-shaped. The posterior margin of the hand bears usually 4 (3 to 5) bunches of setae (in *G. locusta* 6 to 8).

The hand of the second gnathopod (fig. 2 e) is somewhat dilated towards the palm, whereas that of *G. locusta* has more or less parallel margins (cf. fig. 4 a and 4 b). The medial palmar spine is flask-shaped; even in the oldest specimens examined, it remains separated by a rather wide gap from the palmar angle spines.

The third leg resembles closely that of *G. locusta*.

The fourth leg (fig. 3 b) is also rather similar to that of *G. locusta*, but the coxal plate is always about as wide as long, never wider than long; the inferior margin of the plate is slightly curved. The anterior margin of the merus bears one spinule, which is implanted farther distally than in *G. locusta*.

The fifth leg (fig. 3 c) has a very slender basal segment (distinctly more than $1\frac{1}{2}$ times as long as wide); the merus and carpus bear, in addition to numerous spines, several long setae.

The sixth leg (fig. 3 d) has a much more slender basal segment than *G. locusta*; its posterior margin is slightly concave instead of convex. Long setae arise amidst the spines on the merus and particularly on the carpus.

The seventh leg (fig. 3 e) is also characterized by the slender basis (much more than $1\frac{1}{2}$ times as long as wide); the posterior margin of the basis is rather coarsely crenulate. The setae on merus and carpus attain sometimes twice the length of the spines.

The urosome (fig. 3 f) resembles that of *G. locusta*. The inner ramus

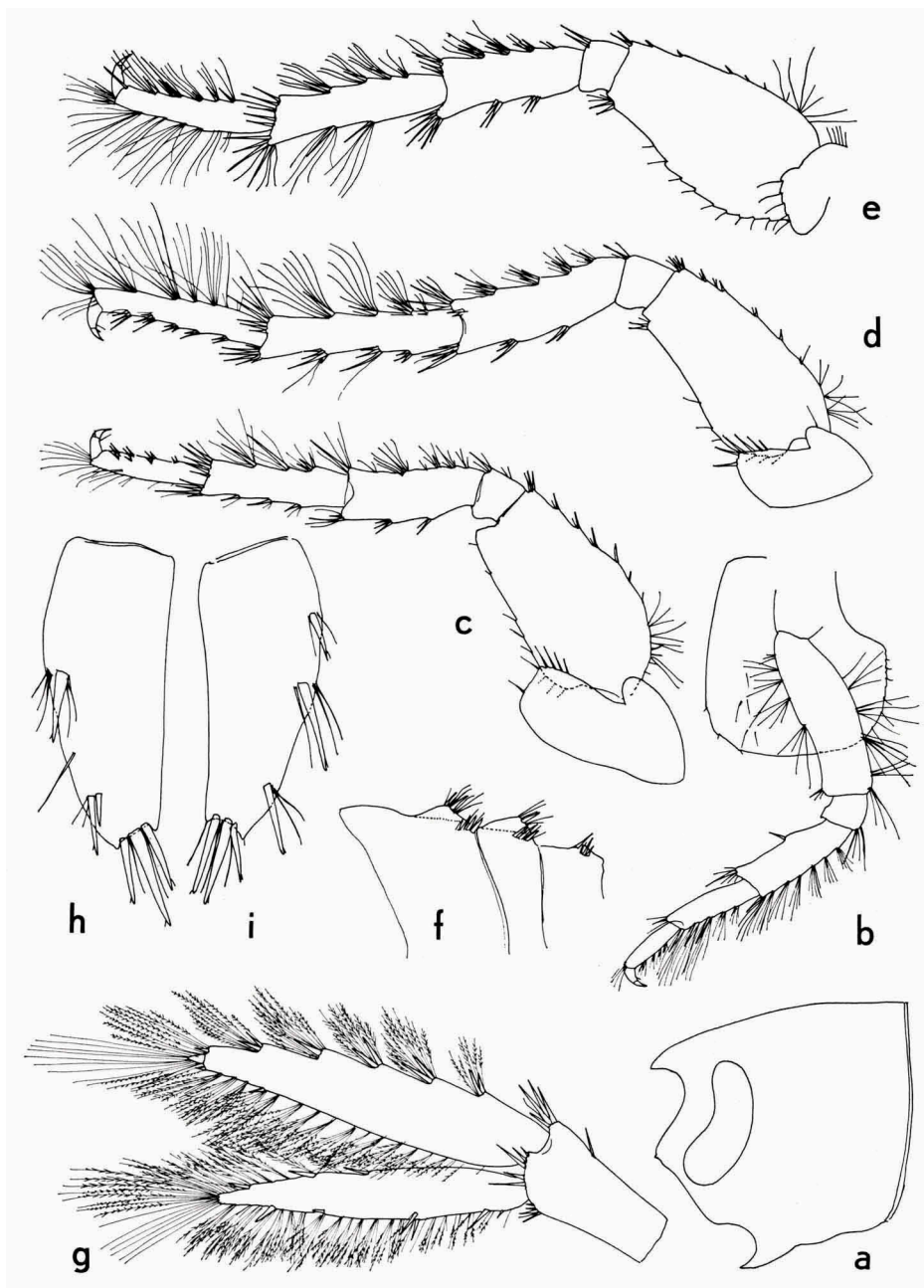


Fig. 3. *Gammarus insensibilis* Stock, 1966, ♂ from Rovigno, Yugoslavia. a, head (scale 1); b, fourth leg (3); c, fifth leg (3); d, sixth leg (3); e, seventh leg (3); f, urosome (lateral) (3); g, third uropod (5); h, i, left and right half of telson of the same animal (2).

of the third uropod is slightly shorter than the first segment of the outer ramus (usually 80 to 90% of that segment), a condition reminiscent of *G. inaequicauda*. In some specimens, the second epimere is subacute, the third is more strongly produced into a sharp point (fig. 2 f), but in many others the second and third epimeres are both strongly produced, thus resembling the situation found in *G. locusta*.

The telson is somewhat variable. Fig. 3 h and i show the two halves of the telson of one and the same male; it seems that fig. 3 h illustrates the more normal situation. At any rate only one subbasal spine occurs; the setae, which are sparingly found in the subbasal, subterminal, and terminal groups of elements, are not longer than the spines.

Variability. — Mediterranean specimens are larger (up to 19 mm) than Atlantic ones (up to 15 mm, but often much smaller). The carpus of P_3 ♂ often bears curved or curled setae in Mediterranean material (especially so in some samples from southern France), whereas the carpal setae are always straight in my Atlantic samples. The telson always bears one latero-basal spine only in Mediterranean specimens, whereas some Atlantic specimens have been observed with two or three such spines (in the Atlantic too, the vast majority has one latero-basal telson spine). The number of segments of the accessory flagellum can reach 12 in Mediterranean specimens, whereas 7 to 10 are the more frequently found numbers in the Atlantic. See also the discussion under *G. inaequicauda*.

Distribution and ecology. — The chart (fig. 6) shows the localities in which the species has been found. Many older Mediterranean records of *G. locusta* (see Della Valle, 1893) may be based in reality upon this species, but no certainty can be reached without re-examination of the original material, if still available.

Della Valle (1893) clearly figured the present species in his monograph on the Neapolitan Amphipoda; the armature of the antennae, the elongation of the basal segments of the posterior legs, and the length of the accessory flagellum leave no doubt on this point. Pirlot (1939:53) certainly was wrong in his opinion that Della Valle's illustrations were based on (what he called) *G. plumicornis* (= *G. crinicornis* in the present paper), since that species has very wide basal segments in P_5 to P_7 . Nevertheless, I have re-examined the sample, labelled "*G. locusta*" and present in what is called the "old collection" of the Stazione Zoologica, Naples. This is no doubt the sample Pirlot examined and to which he refers in his paper. The samples consisted

of 6 specimens of *G. insensibilis* and 2 of *G. subtypicus*. No material of *G. plumicornis* or *G. crinicornis* was present in the Naples collection.

The species is common in the Mediterranean. It has also been found in the Black Sea. Four Atlantic records are known to me: two in lochs or lagoons around the Rade de Brest (France, Brittany), one in the Fleet (England, Dorset) and one in New England Creek (England, Essex, south of Foulness Island). In the Mediterranean the species lives under fully marine conditions, but has a tendency to penetrate also in lagoons, bays and harbours with reduced salinity (polyhaline conditions). All Atlantic records are from waterbodies which are essentially landlocked.

The two French lochs have chlorinities of about 18‰ (during rainfall presumably less), the Essex locality has chlorinities ranging from 11.51 to 14.84‰ (Howes, 1939:389), the Dorset locality of about 14‰ (total salinity 26‰, cf. Spooner, 1947:16) (in the open sea the chlorinity is usually more than 19‰ in these places).

The occurrence of a Mediterranean species around the Rade de Brest (France) is not so surprising, since it is known that the northernmost distribution boundary of several species is reached in that area.

The bathymetrical range of *G. insensibilis* is 0 to 15 m.

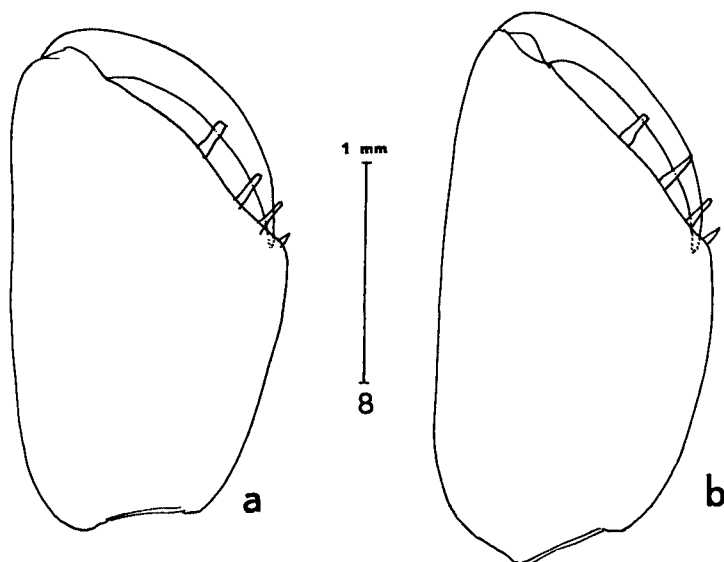


Fig. 4. Diagrammatic sketch of the hand of the second leg of *G. insensibilis* Stock (a) and *G. locusta* (L.) (b), to the same scale (scale 8).

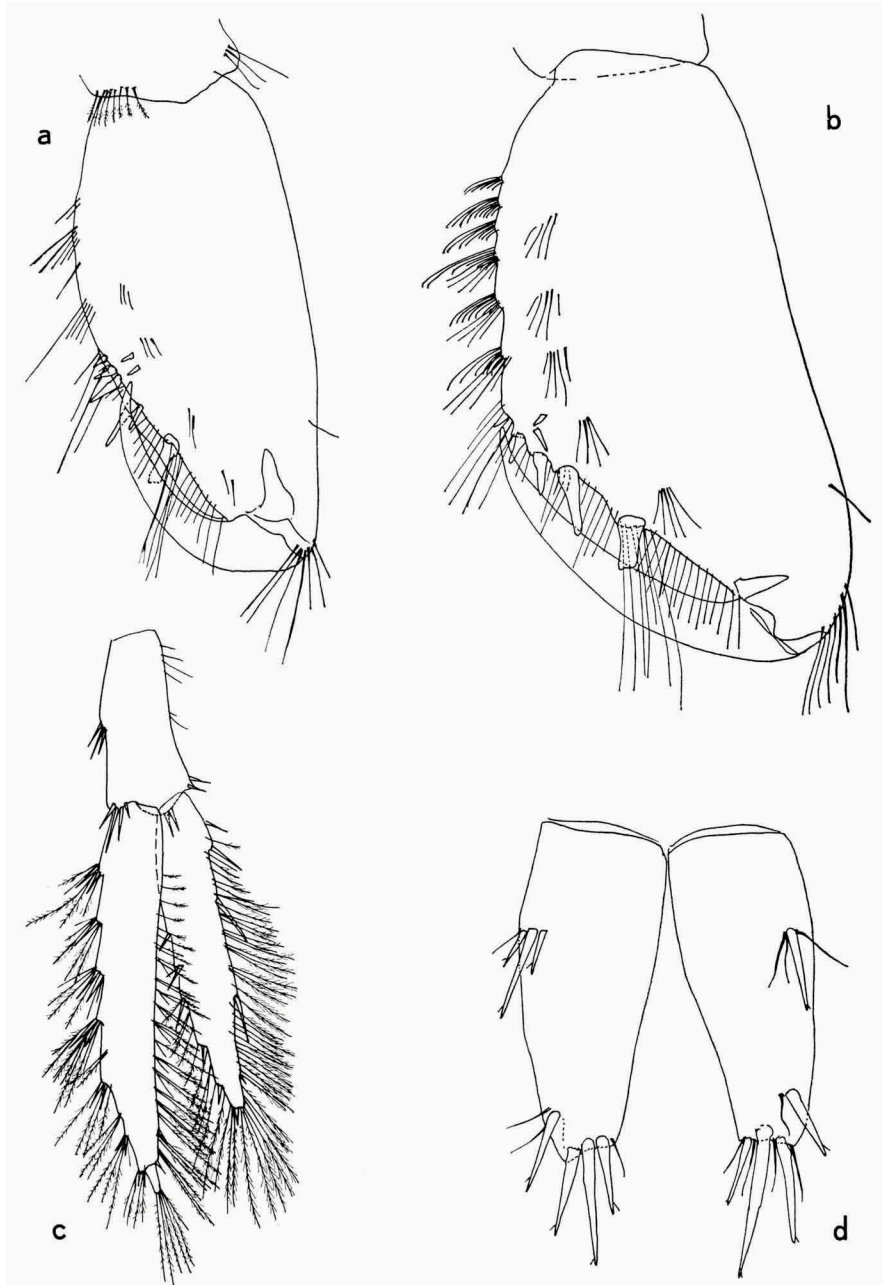


Fig. 5. *Gammarus insensibilis* Stock, 1966, ♂ from Le Fret, Brittany, France. a, hand of first leg (scale 14); b, hand of second leg (14); c, third uropod (12); d, telson (12). The right half of the telson has the normal subbasal armature (1 spine + 3 setae); the left half shows a rare anomaly: two of the setae are replaced by spines (scale 24).

Accompanying species. — *G. insensibilis* is usually found alone in the samples examined. Only in two samples, it was found together with *G. subtypicus*, and in one sample with *G. crinicornis*.

***Gammarus inaequicauda* Stock, 1966 (fig. 6-8)**

G. inaequicauda Stock, 1966:2; Stock & Kant, 1966:7-12, fig. 1-2.

G. campylops Sars, 1894 (non Leach, 1814): 500-502, pl. 176 fig. 2; Stebbing, 1906: 476-477; Oldevig, 1933:199, fig.

Material examined.

Moss, Christiania (= Oslo) Fjord, Norway, ex coll. G. O. Sars, 1 ♂ **holotype**, 5 ♂, 17 ♀ paratypes (Zool. Mus., Oslo).

Remarks. — G. O. Sars' material of, what he called, *Gammarus campylops* Leach, was recently redescribed by Stock & Kant, 1966. The unhappy nomenclatorial history of the name *campylops* is followed in detail in that paper. Since Leach's species was different from that of Sars, and since no other correct name was available, Stock, 1966, proposed the name *G. inaequicauda* for Sars' *G. campylops*.

G. inaequicauda is only known with certainty from the type-locality, Moss (Norway). Sars recorded it also from "an oysterbed on our south coast", but this material is no longer in existence, and thus cannot be checked. Sars' record from Denmark is incorrect (confused with *G. locusta* and *G. salinus*), as is his record from the British Isles (confused with *Marinogammarus campylops* (Leach)).

Since the publication of the notes of Stock (1966) and Stock & Kant (1966), a very abundant material of *G. insensibilis* became available, which was not collected in the Mediterranean (as all previous samples), but on the Atlantic coast of Brittany. This material, coming from halfway the type-locality of *G. inaequicauda* and the Mediterranean tends in certain respects to bridge the gap between *G. inaequicauda* and *G. insensibilis*.

The three groups of populations (Norway, Brittany, Mediterranean) agree with each other in several essential characters: the armature of A_1 ; the structure of the mandible palp; the shape and structure of P_1 , P_5 , P_6 and P_7 ; the reduction in length of the inner ramus of the third uropod; the reduction of the ornamentation of the posterior margin of the third epimere.

The differences between the males of the three populations are summarized in the following table, in which also the data concerning a population from New England Creek, Essex (derived from Howes, 1939, and Spooner, 1947) are inserted:

	<i>Moss</i>	<i>Le Fret</i>	<i>Rovigno</i>	<i>Essex</i>
setae on long segments of A ₂	straight	straight	often curved or curled	tendency to become curled
number of segments of accessory flagellum of A ₁	max. 8	max. 10	max. 12	max. 8
hand of 2nd leg	about twice as long as wide	about twice as long as wide	less than twice as long as wide	?
setae on carpus of leg 3	straight	straight	often curved or curled	?
urosome segments	not compressed	compressed	compressed	compressed
telson, number of latero-basal spines	3	1 (rarely 2 or 3)	1	?
setae on lateral margin of exopod of 3rd uropod	with incipient plumosity	plumose	plumose	?

From these data it would appear that *G. insensibilis* and *G. inaequicauda* are the southern and northern end, respectively, of a cline within a single species. Since so few Atlantic localities are known⁵⁾, however, it seems premature to synonymize them. Instead, I have preferred to retain the name *G. inaequicauda* for the original type-series from Norway, which is characterized by a few outstanding features not present in the British, French or Mediterranean populations. These features are the absence of compressed elevations on the dorsal side of the urosome, the absence or reduction of plumose setae on the lateral margin of the third uropod, and the presence of 3 latero-basal spines on the telson. These are characters used very often in the systematics of Gammaridae for specific diagnoses, and most authors agree as to their usefulness.

5) Four localities; material of 2 of them examined for the present study.



Fig. 6. Distribution of *Gammarus insensibilis* Stock, 1966 and of *G. inaequicauda* Stock, 1966.

More taxonomic work, by preference on material from intermediate localities, as well as experimental work (interfecundity tests) will be necessary to solve the question whether one polytypic species or two different species are concerned.

For a detailed description of *G. inaequicauda*, the reader is referred to the paper by Stock & Kant (1966) and to fig. 7 and 8 of the present paper.

***Gammarus plumicornis* Costa (fig. 9-12)**

G. plumicornis Costa, 1853:176; Costa, 1856:215-216, pl. 4 fig. 1 a-c; Stock, 1966:2.

Material examined.

Mediterranean coast of France: Étang de St. Nazaire, dépt. Pyrénées-Orientales, brackish water, chlorinity 5.3‰, 3 July 1956, many specimens, 1 ♂ selected as **neotype**

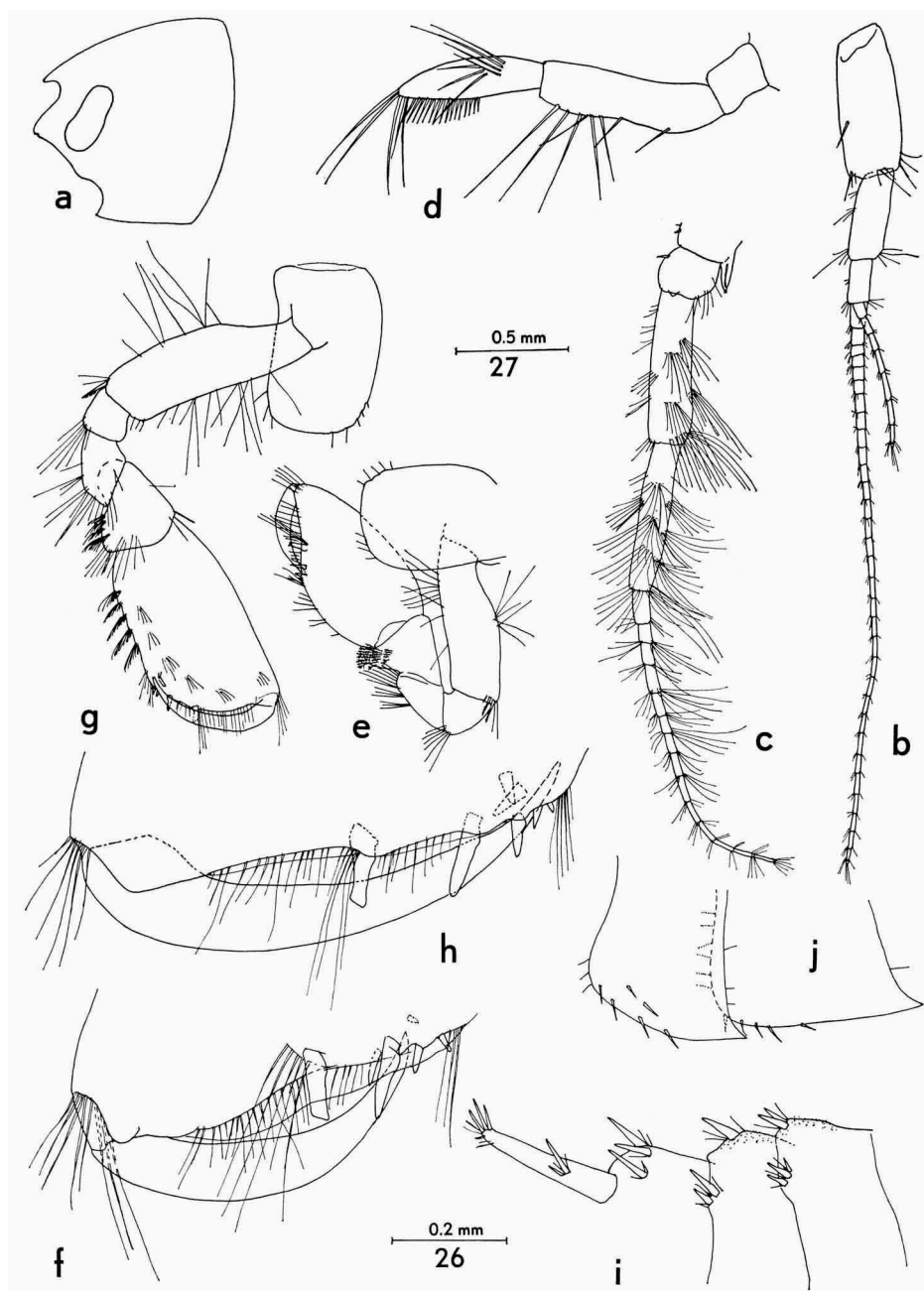


Fig. 7. *Gammarus inaequicauda* Stock, 1966, ♂, paratype, from Moss, Christiania Fjord, Norway. a, head (scale 12); b, first antenna (12); c, second antenna (12); d, mandible palp (24); e, first leg, lateral (12); f, palm of first leg, lateral (26); g, second leg, lateral (12); h, palm of second leg, medial (26); i, urosome (27); j, second and third epimeres (12).

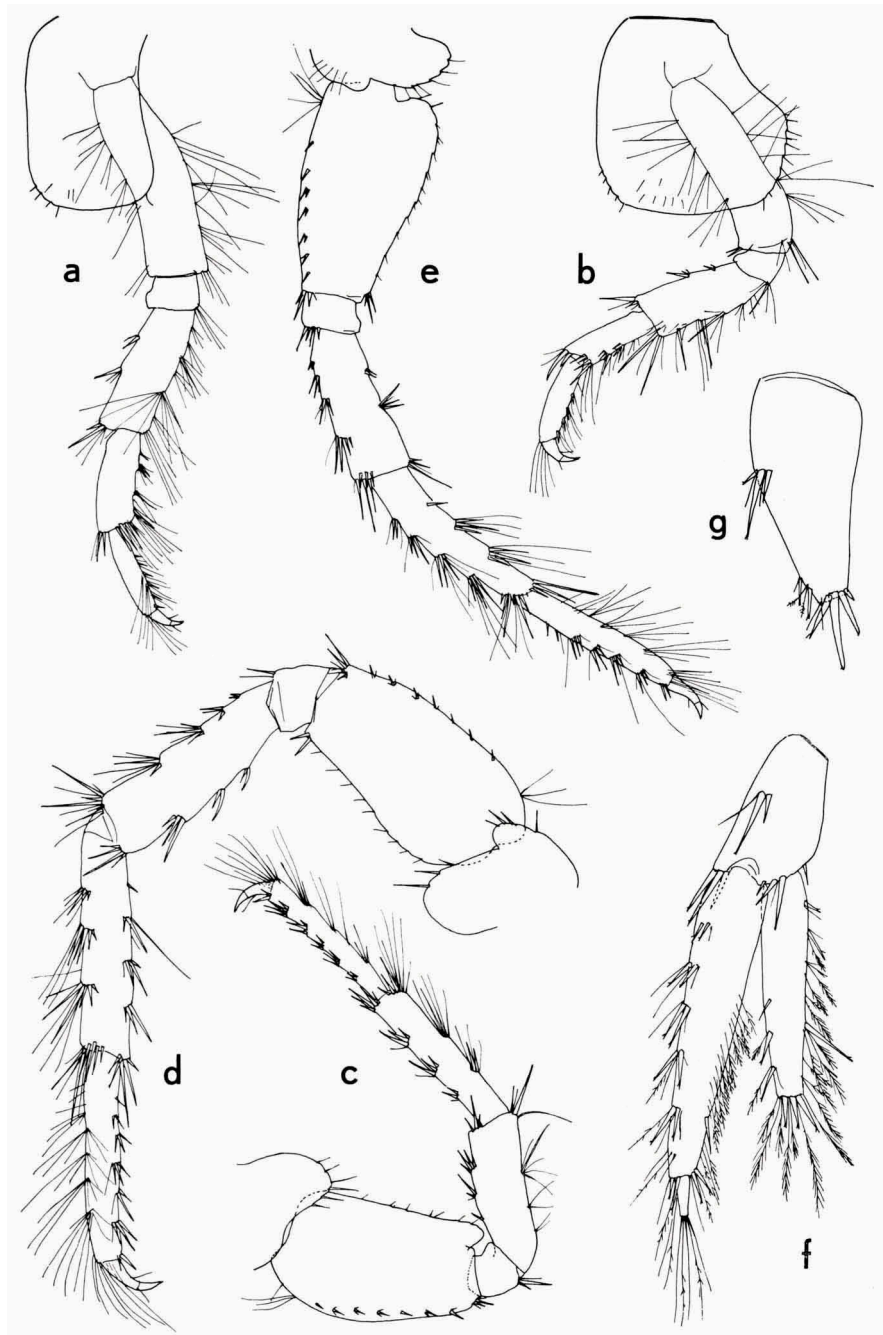


Fig. 8. *Gammarus inaequicauda* Stock, 1966, ♂, paratype, from Moss, Christiania Fjord, Norway. a, third leg (scale 12); b, fourth leg (12); c, fifth leg (12); d, sixth leg (12); e, seventh leg (12); f, third uropod (24); g, telson, left half (24).

(ZMA); Étang de Sigean, near Sigean, S. of Narbonne, dépt. Aude, brackish water, 25 September 1957, 1 ♂ (RMNH); Étang de Sigean, dépt. Aude, 8 September 1966, many specimens (ZMA); Camarque, submerged land along the Étang de Consécançière, 7 April 1966, 1 ♀ (ZMA); Étang de Biguglia, Corsica, May 1887, 1 specimen (MNHN); Étang de Diana, Corsica, May 1887, 3 specimens (MNHN).

Description. — Maximal length observed about 10 mm. The head is somewhat variable in shape (fig. 9 a, b), but the lateral lobe is never acute but always more or less rounded. The sinus is shallow; the eye is large.

The first antenna (fig. 9 c) has the third peduncle segment exactly half as long as the second, but since the third segment is more than twice as long as wide, it retains a very slender and elongate aspect. The ventral margins of the peduncle segments bear several groups of setae (especially segment 2); the general aspect of these segments is the more setose, since most of the setae are plumose. Plumose setae also occur on the flagellum and accessory flagellum. The flagellum is rather slender, the accessory flagellum is less than $1\frac{1}{2}$ times as long as peduncle segment 2, and counts 5 to 7 segments.

The second antenna (fig. 9 d) is fairly slender. Peduncle segments 4 and 5 are subequal. The gland cone is rather long. Silky setae occur on all segments; those on the ventral margin are the longest; mixed with glabrous setae, a varying percentage of plumose setae are found; the highest percentage of plumose setae is found in large males. The most proximal 5 to 7 segments of the flagellum bear calceoli in the male.

The mandible palp (fig. 9 e) shows the normal characteristics of the *locusta*-group.

All segments of the first leg (fig. 10 a), including the coxal plate, but with the exception of the merus, bear some plumose setae. Even in smaller males, the propodus always bears some plumose setae. The posterior margin of the propodus bears 4 to 6 groups of setae; the medial palmar spine is flask-shaped.

All segments of the second leg (fig. 10 b) are, at least in the adult ♂, provided with a varying number of plumose setae. The propodus has nearly parallel margins; the medial palmar spine is flask-shaped, but no "gradation" has been observed in the length or mutual space of the palmar spines.

The third leg is as illustrated (fig. 11 a); plumose setae are found on all segments, mixed with normal setae.

The fourth leg (fig. 11 b) has the coxal plate distinctly longer than wide; the posterior notch is shallow; the inferior margin is nearly semi-circular. The merus bears one posterior spine, implanted at $\frac{1}{4}$ of the length of the margin. The carpus bears also a posterior spine (absent in *G. locusta* and *G. insensibilis*). In this leg again, many setae are plumose.

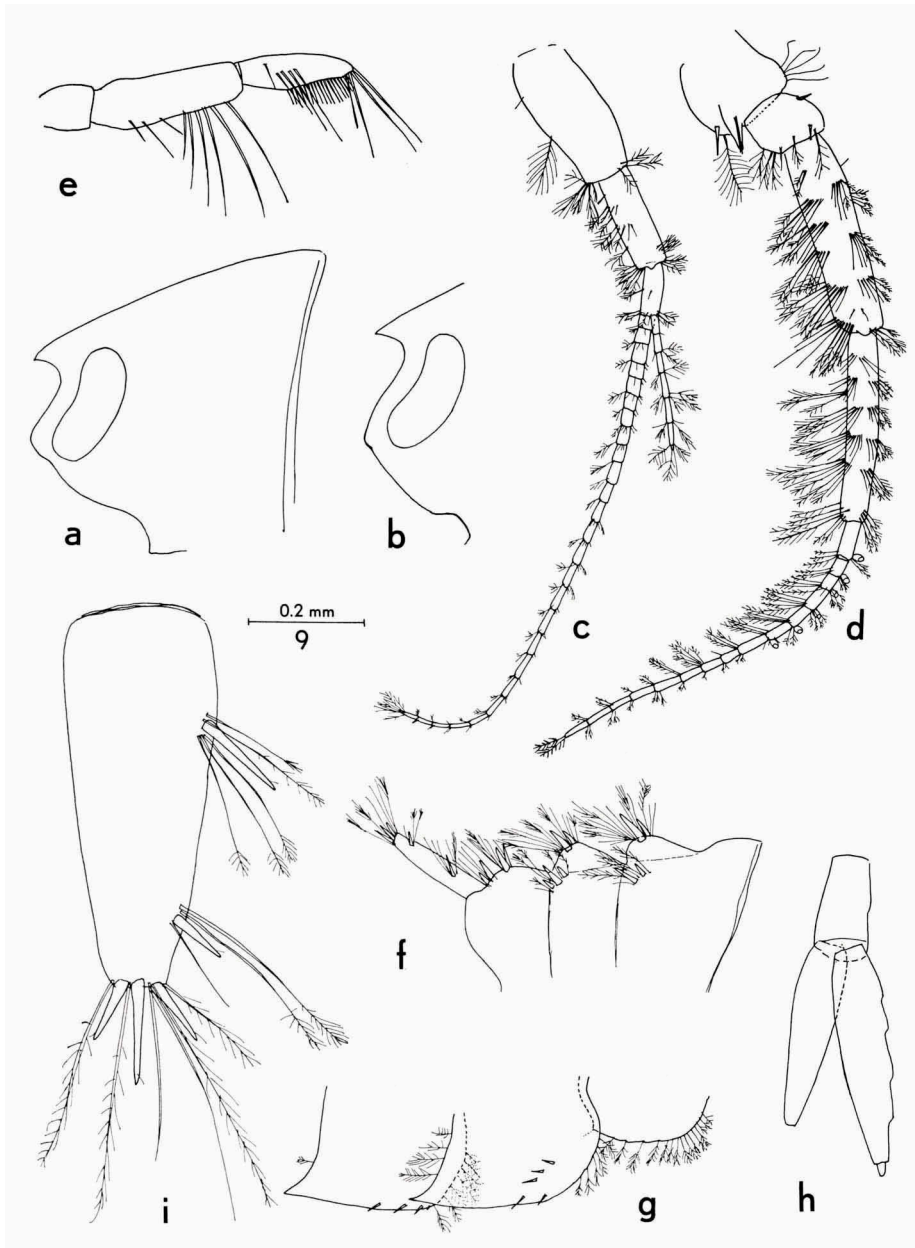


Fig. 9. *Gammarus plumicornis* Costa, 1853, ♂ from Etang de St. Nazaire, France. a, b, heads of two different specimens (scale 6); c, first antenna (7); d, second antenna (medial) (7); e, mandible palp (2); f, urosome (lateral) (1); g, epimeres (1); h, third uropod (all setae and spines omitted) (1); i, telson (dorsal) (9).

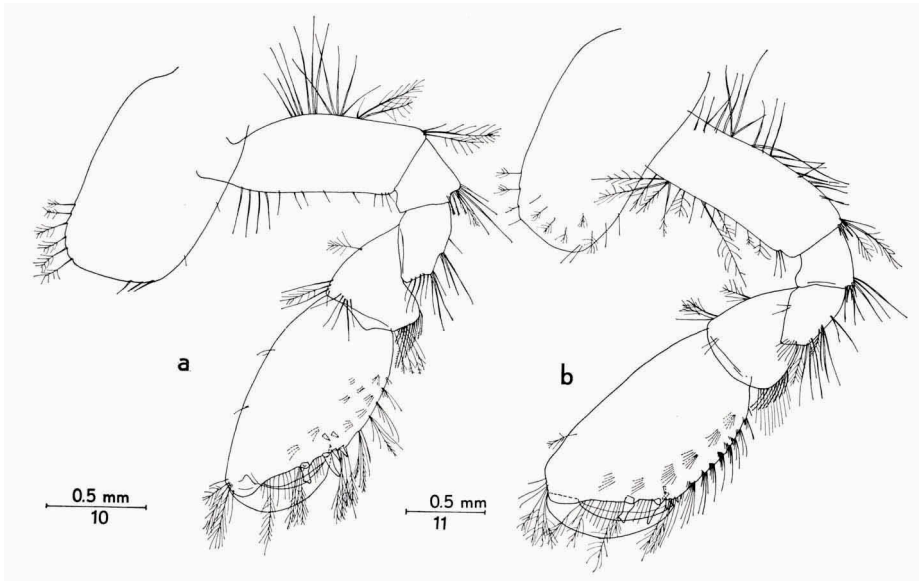


Fig. 10. *Gammarus plumicornis* Costa, 1853, ♂ from Etang de St. Nazaire, France. a, first leg (scale 10); b, second leg (11).

The fifth leg (fig. 11 c) has a rather slender basal segment (distinctly more than $1\frac{1}{2}$ times as long as wide). Although this leg is not very setose, some of the available setae are plumose.

The sixth leg (fig. 11 d) has a very slender basal segment, the posterior margin of which shows a tendency towards concavity. The setae (partly plumose) are longer, often fully twice as long as the spines occurring in the same group of elements.

The seventh leg (fig. 11 e) has a slender basal segment ($1\frac{3}{4}$ times as long as wide) with a straight anterior margin and a regularly curved posterior margin. The setae on the merus and carpus are often more than twice as long as the accompanying spines. Several setae are plumose, especially on the posterior margin of the basis, and on the propodus.

The urosome (fig. 9 f), more in particular segments 1 and 2, has conspicuous dorsal elevations, which are laterally compressed. The dorsal armature consists of 2:2:2 spines, the lateral armature of 2:3:2 spines. Long setae, twice as long as the spines, and partly plumose, occur between and outnumber the spines.

The epimeres (fig. 9 g) also bear plumose setae: the first on its ventral margin, the second and third on their anterior and posterior margins. Both

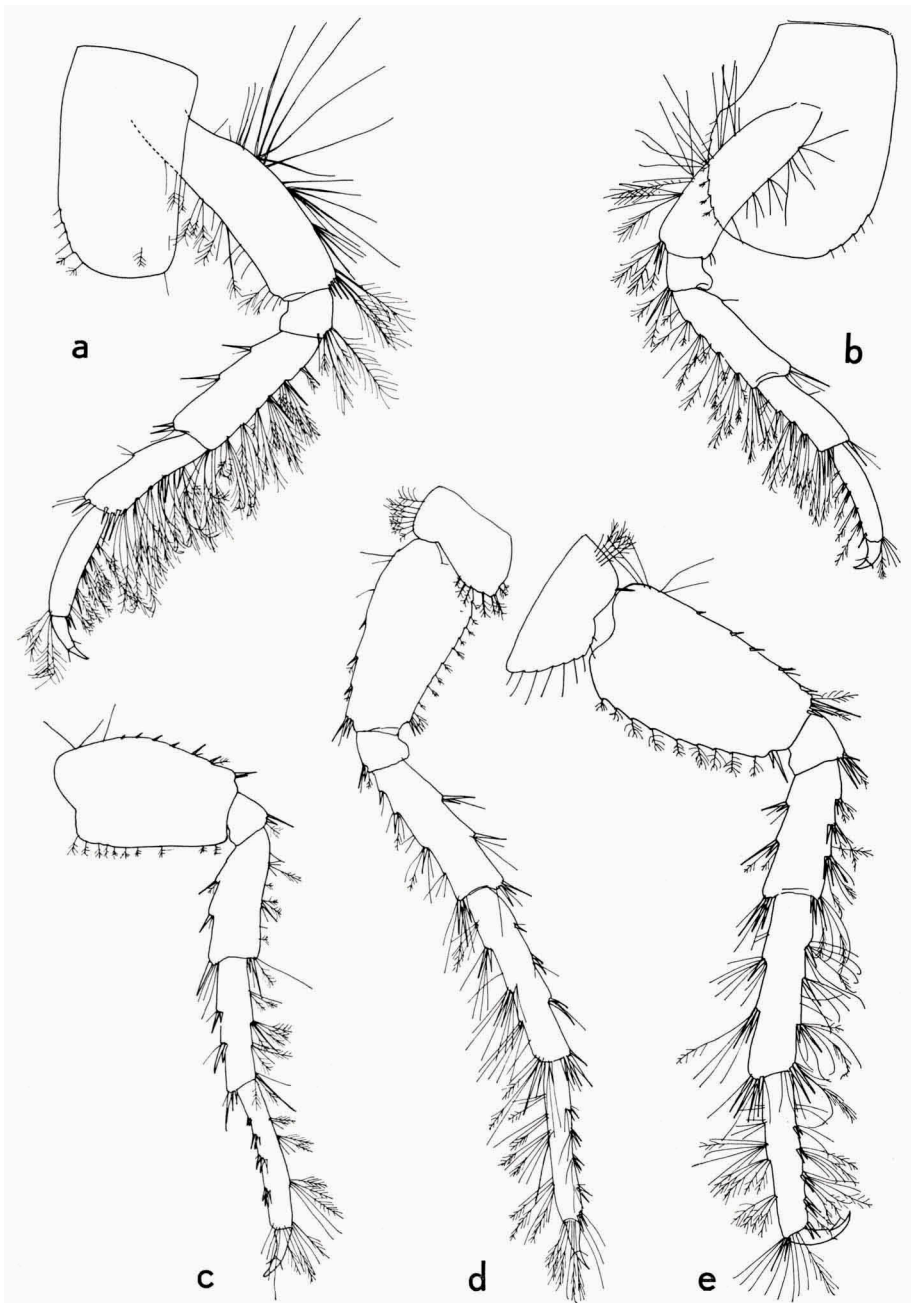


Fig. 11. *Gammarus plumicornis* Costa, 1853, ♂ from Etang de St. Nazaire, France. a, third leg (scale 1); b, fourth leg (1); c, fifth leg (1); d, sixth leg (1); e, seventh leg (1).

second and third epimere have the postero-inferior corner produced into a long, fine point. The posterior margin of the third epimere bears only one seta.

The third uropod (fig. 9 h) has the inner ramus markedly shorter than the basal segment of the outer ramus.

The telson (fig. 9 i) has the usual three groups of elements: subbasal — with one spine and several setae; subterminal — with one spine and two or three setae; terminal — with three spines and several setae. The setae are longer than the spines, the longest terminal ones even twice as long as the spines. Several setae are plumose.

Variability. — In the illustrated specimen (a large, adult male) a great percentage of the setae on the appendages is plumose. In other specimens (either younger males, or females) the simple setae are in the majority. Nevertheless, plumose setae are always present, between the simple ones, especially on the A_2 flagellum.

Distribution. — This species has been recorded from “étangs” (lagoons with brackish water, near the shore, and with or without permanent connection with the sea) in southeastern France and Corsica. The type-locality of Costa was the extreme point of Calabria. In several localities, *G. plumicornis* was accompanied by *G. aequicauda*. It does not seem to penetrate as far in waters with a low salinity as *G. aequicauda* does, nor has it been found in the estuarine waters of river mouths, where *G. aequicauda* is the predominant species.

Affinities. — With the exception of the most striking feature of the species — the presence of plumose setae on nearly all appendages — *G. plumicornis* is remarkably similar to *G. aequicauda*. It is, indeed, not easy to distinguish younger males or females (which are less “plumose” than older, larger males) from *G. aequicauda*. However, upon closer inspection, larger specimens of *G. aequicauda* have acute lateral head lobes, a longer inner branch on the third uropod, often a lower number (5 to 8) of segments in the accessory flagellum, and a less hairy A_1 peduncle.

It may be borne in mind, that the distinction of an Arctic gammarid, *G. setosus* Dementieva, 1931, is also chiefly based on the occurrence of plumose setae (cf. Segerstråle, 1947:241).

Hybridization attempts will be necessary to decide whether *G. plumicornis* is sufficiently separated genetically from *G. aequicauda*. Such experiments are now in preparation.

Brun (1963) observed that two *Gammarus* species of the *locusta*-group, found in brackish waters of southern France ("étangs saumâtres de Provence"), were sexually isolated. From Brun's work, it does not become clear which two species he had for his experiments; he designates them with the nomina nuda "*G. intermedius*" and "*G. camarguensis*", and comments that these are "que. . . . un nom provisoire, n'ayant pu préciser définitivement leur identité éventuelle avec des espèces déjà décrites dans d'autres pays" (Brun, 1963:2934). Judging from the locality, from which only two brackish water species are known, Brun worked with *G. plumicornis* and *G. aequicauda*. If this assumption is correct, the sexual barrier between the two species is affirmed by Brun's experiments.

***Gammarus crinicornis* Stock (fig. 12-16)**

G. crinicornis Stock, 1966:2; Stock, Nijssen & Kant, 1966:24.

G. plumicornis (non Costa), Pirlot, 1939:53-61, fig. 4-7; Den Hartog, 1964:429-433, fig. 6; Vader, 1966:105.

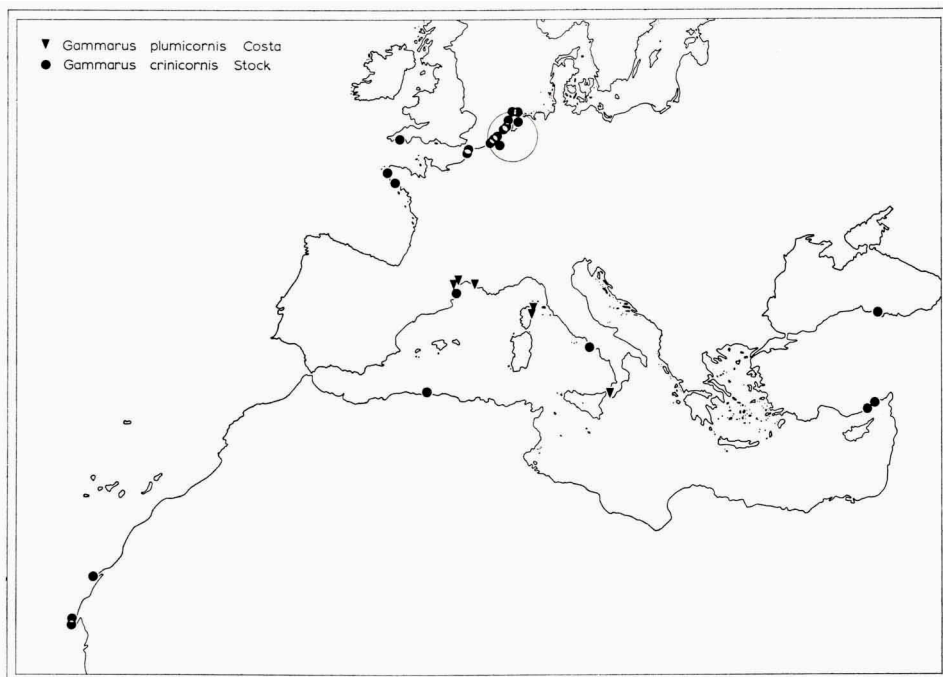


Fig. 12. Distribution of *Gammarus plumicornis* Costa, 1853 and of *G. crinicornis* Stock, 1966.

- ? "Variation of *G. locusta* from Whitsand Bay", Spooner, 1947:15.
 ? *Gammarus* sp. allied to *locusta*, Spooner, 1957:220.
 ? *Gammarus zaddachi* ssp. *oceanicus*, Toulmond & Truchot, 1964:22.

Material examined.

Mediterranean

France: coast near Banyuls, 1 ♂ (LA).

Algeria: Algiers, June 1928, many specimens (RMNH).

Italy: N. of Torregaveta, W. of Lago Fusaro, prov. Napoli, sandy bottom, 11 May 1950, many specimens (RMNH).

Turkey: coast near Kizkalesi, about 58 km S.W. of Mersin, depth 1-2 m, bottom fine sand with detached algae, overgrown rocks, 12 May 1959, 4 specimens (RMNH); Port of Mersin, depth 0.5-1.5 m, bottom fine sand, fished at night, 15 May 1959, 1 ♂ (RMNH).

Black Sea

Turkey: near Samsun, depth 0-2 m, rocks, 12 June 1959, many specimens (RMNH).

Atlantic Ocean

Spanish Sahara: Baie de l'Ouest, near Faux Cap Blanco, depth 35-50 m, April-August 1906, several specimens (ZMA); Faux Cap Blanco, 35-50 m, April-August 1906, several specimens (ZMA).

France: Petite Plage, Concarneau, Brittany, 21 April 1924, 1 ♂ (ZMA); Anse de Dinan, W. of Crozon, Brittany, 10 August 1951, 7 specimens (ZMA); Pointe de la Crèche, Boulogne, dépt. Pas-de-Calais, beach, under *Fucus* washed ashore, 26 October 1965, 7 specimens (ZMA); Langue de Chien, Ambleteuse, dépt. Pas-de-Calais, intertidal, under stones, 18-22 April 1965, 22 September 1965, many specimens (ZMA).

The Netherlands: Buitenhaven, in front of the Zoological Station, Den Helder, prov. Noord-Holland, 24 August 1949, 1 ♂ **holotype**, several paratypes (ZMA, Amph. 101.688); very numerous other specimens, both from the North Sea coast and the Waddensea (see chart, fig. 13).

Description. — The excellent description and fine illustrations of Pirlot, 1939, form a good basis for the recognition of the species.

Maximal length observed: about 20 mm. The lateral lobes of the head (fig. 14a) are acute; the sinus is shallow; the eyes are small.

The third peduncle segment of the first antenna (fig. 14b) is less than twice as long as wide and thus makes a "heavy" impression. The accessory flagellum is fairly long, and consists of 8 to 12 segments.

The setal armature of the second antenna (fig. 14c) is absolutely distinctive: dense transverse rows of setae are found on the inner surface of peduncle segments 4 and 5; the setae extending in ventral direction are the longest on segment 4, but on segment 5 the dorsally directed setae are as long as those directed ventrally. The fourth peduncle segment is rather heavy. The flagellum is very short, often not more than 10-segmented; the basal 4 or 5 segments carry calceoli.

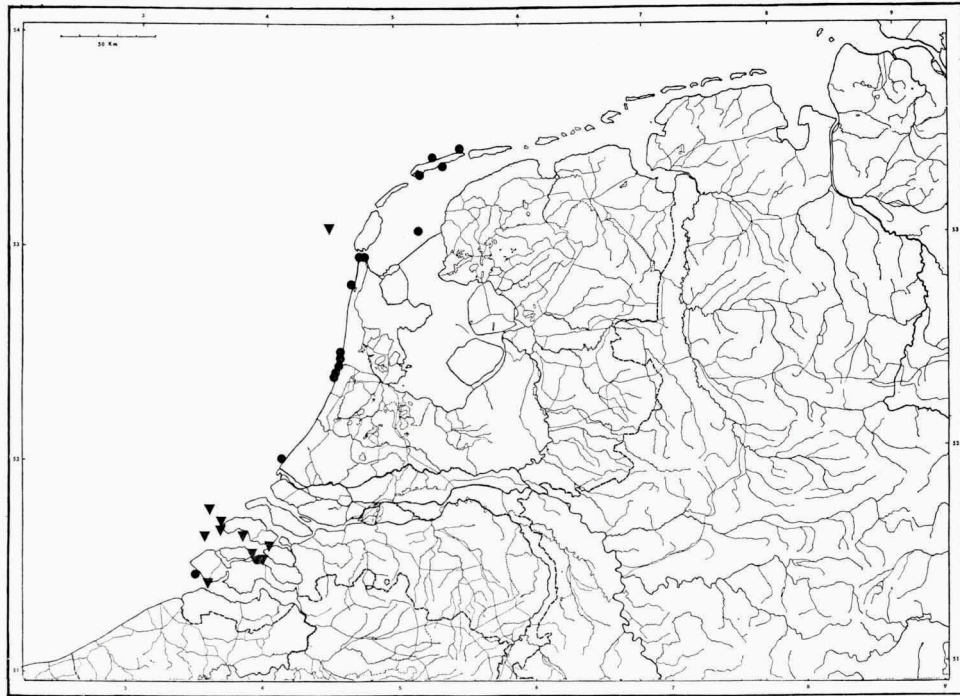


Fig. 13. *Gammarus crinicornis* Stock, 1966, in the Netherlands. Circles indicate the localities of the material examined for the present revision; triangles stand for records from Den Hartog, 1964, and Vader, 1966.

The mandible palp (fig. 15 a) resembles that of *G. locusta*.

The hands of the gnathopods (fig. 14 d, e) have flask-shaped medial palmar spines. The spines on the palm of leg 2 are not "gradate".

Leg 4 (fig. 15 b) resembles that of *G. locusta*. In legs 5 to 7 the very wide basis is characteristic (fig. 15 c, d, e). In leg 5, the basal segment is hardly longer than wide; in legs 6 and 7, this segment is $1\frac{1}{4}$ times as long as wide. The posterior margin of the basis of P_6 is strongly convex, that of P_7 shows a limited number (4 to 6), widely spaced and often coarse, denticulations, whereas the place where the proximal part of the margin passes into the distal part is marked by a distinct bend. A few setules, shorter than, or at most as long as, the spines, occur on P_5 . In Atlantic material from the coasts of Europe, P_6 and P_7 are spinous but do not bear any setae at all (except on the end of the propodus). In most Mediterranean and Black Sea samples, these legs are provided with several setae, longer than the spines (fig. 16 e). However, one Mediterranean sample (from

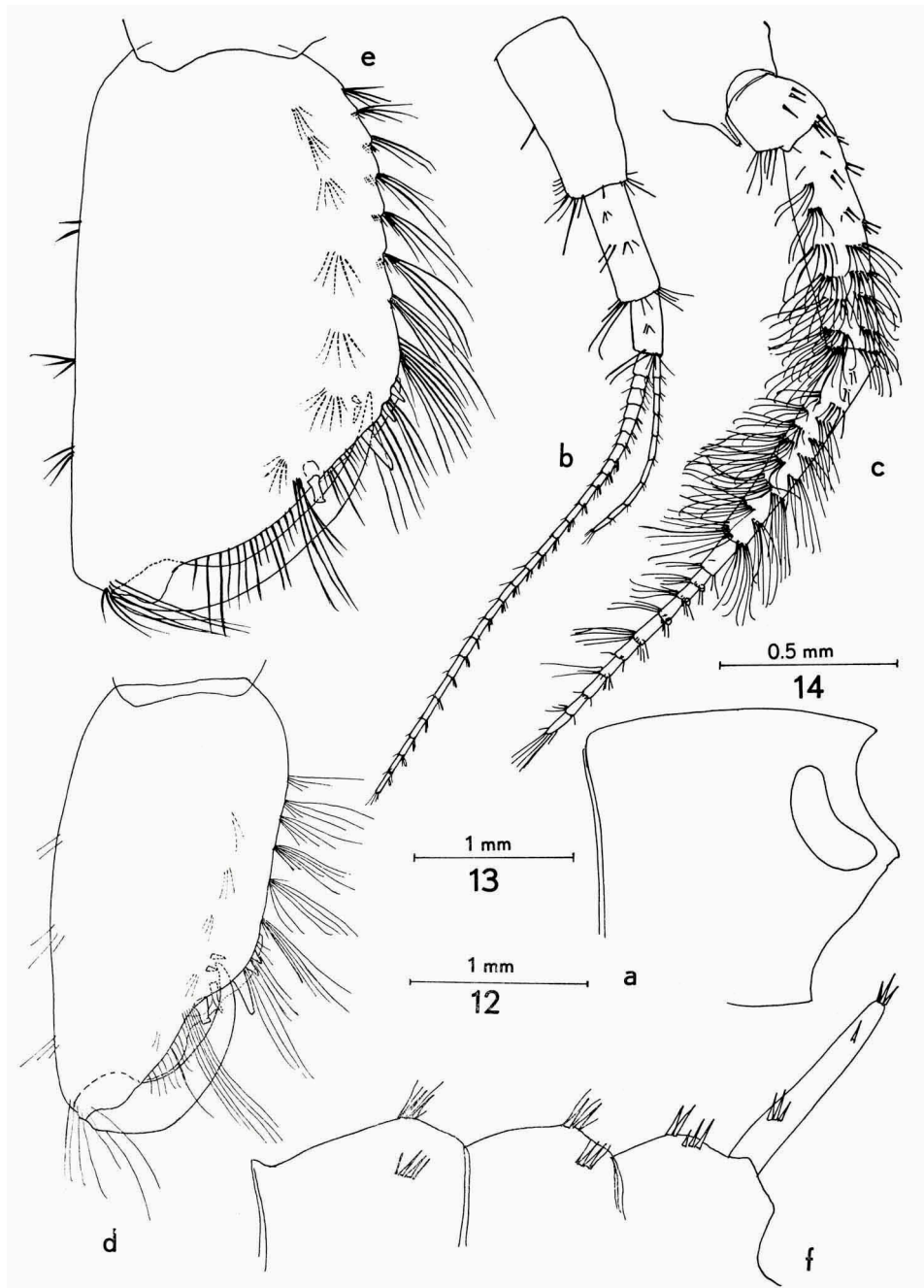


Fig. 14. *Gammarus crinicornis* Stock, 1966, ♂ from Den Helder, The Netherlands. a, head (scale 12); b, first antenna (13); c, second antenna (medial) (13); d, hand of first leg (lateral) (14); e, hand of second leg (lateral) (14); f, urosome (lateral) (12).

Banyuls) shows the Atlantic type of spination, and samples from West Africa are either of the hairy type (material from Faux Cap Blanco) or of the spinose type (material from Rio de Oro).

These variations in hairiness of the posterior legs, are correlated with more obvious setation of other parts of the body as well (dorsal part of urosome, cf. fig. 14 f and 16 f; telson, cf. fig. 16 b, c). Moreover, the second and third epimere are equally pointed in material from the northern parts of the range (fig. 16 a), whereas in material from the Mediterranean, the second epimere is less produced than the third (fig. 16 c). For the moment I do not attach any taxonomic value to these variations.

Apart from the setation of the second antenna, the low elevations on the urosome, which are hardly or not at all compressed (fig. 14 f, 16 f), separate this species at once from all other members of the *locusta*-group.

Accompanying species. — Usually found alone. In one sample, it occurred mixed with *G. subtypicus* and *G. insensibilis*. In the West African part of the range, it is not accompanied by any other *Gammarus*. On the temperate European Atlantic coasts, it inhabits the niche “exposed sandy beaches and bays” alone. In less uniform biotopes, it may occur together with *G. locusta* (especially so in the Dutch Waddensea), or with *G. salinus* and *G. locusta* (under stones on the “grève”, with estuarine influences, on the French Channel coast, cf. Stock, Nijssen & Kant, 1966).

Remarks on the synonymy. — The species recorded by Spooner under various names are discussed in the introduction. Both its description (“very dense setation on antenna 2” and “the elevations of the urosome segments are . . . less compressed than usual” = than in *G. locusta*), and the habitat (“on sandy ground”, “amongst algal detritus”) are strong indications that *G. crinicornis* is actually involved. Attempts to locate the original material, failed.

Toulmond & Truchot (1964: 22) recorded *G. oceanicus* (as *G. zaddachi oceanicus*) from Ile de Siec (W. of Roscoff). Since this locality is much too far south for *G. oceanicus*, it is very probable that another *Gammarus* is involved. The habitat (“détritus d'Algues sur plages sableuses à marée basse”) makes *G. crinicornis* the most likely species. The original material is no longer in existence (Truchot, personal communication, 29 September 1966). A renewed visit to their locality (Siec) has revealed only *G. locusta* (3 October 1966); still, I consider *G. crinicornis* as the most probable species hiding under their record of *G. oceanicus*.

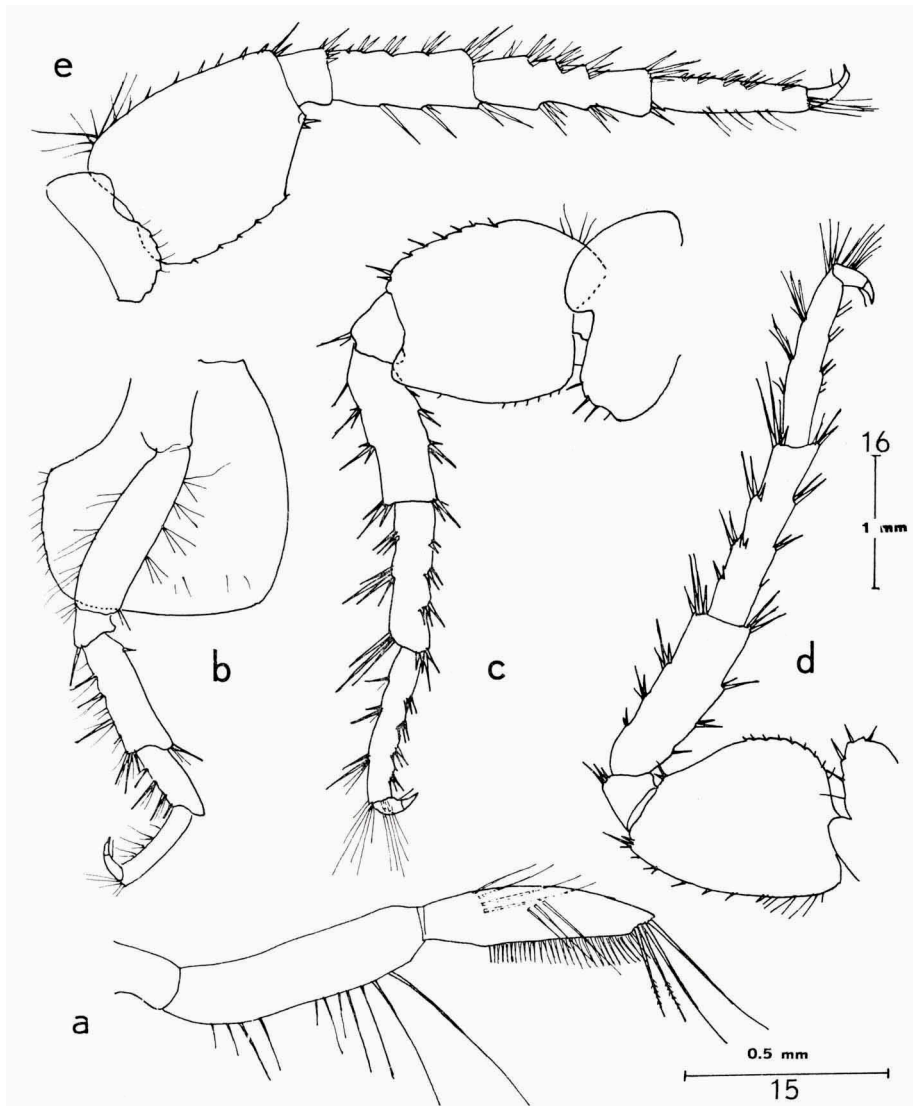


Fig. 15. *Gammarus crinicornis* Stock, 1966, ♂ from Den Helder, The Netherlands. a, mandible palp (scale 15); b, fourth leg (16); c, fifth leg (16); d, sixth leg (16); e, seventh leg (16).

***Gammarus subtypicus* Stock (fig. 17-21)**

G. subtypicus Stock, 1966: 3.

G. locusta forme marine subtypique, Rancurel, 1949: 3-6, 8-9, plate fig. F 9, F 10.

? *G. massiliensis* Brun, 1963: 2934 (nomen nudum).

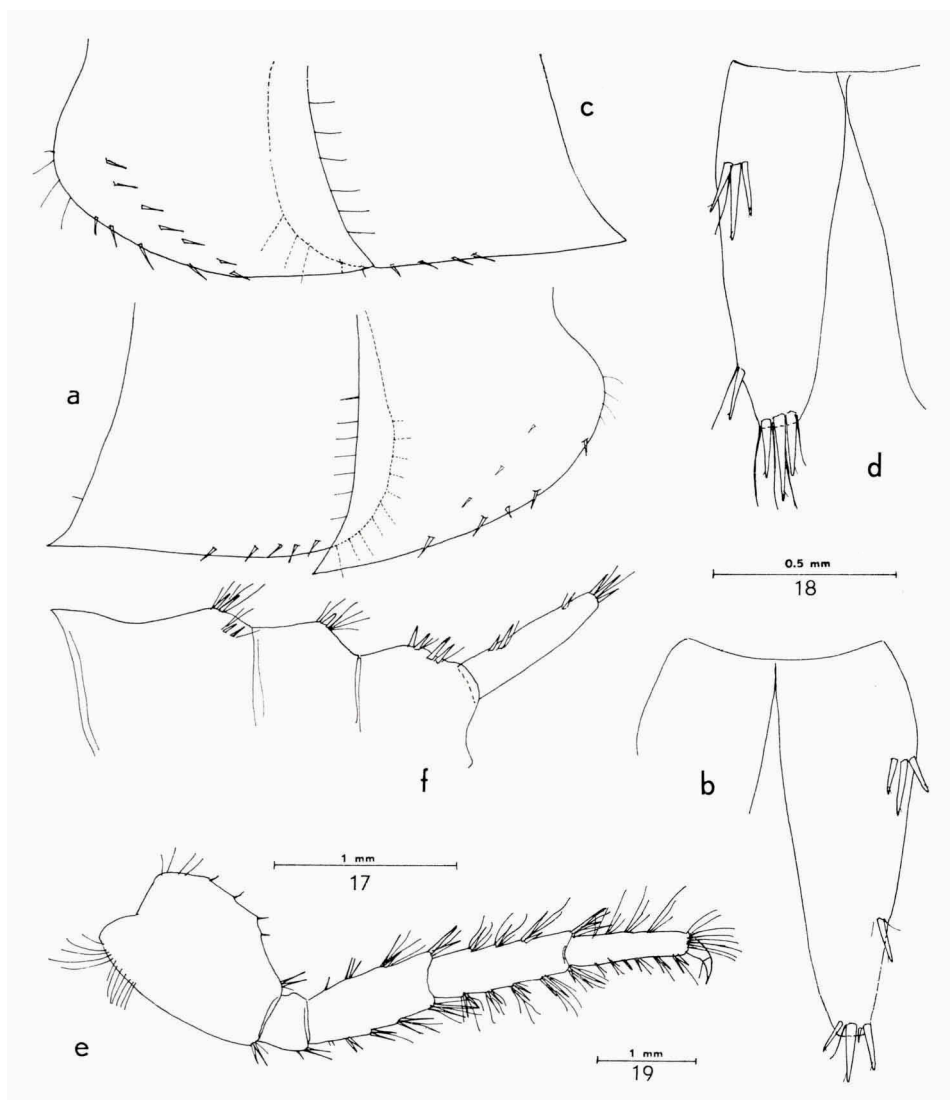


Fig. 16. *Gammarus crinicornis* Stock, 1966, ♂. a-b, from Den Helder, The Netherlands; c-f, from Algiers, Algeria. a, second and third epimeres (scale 17); b, telson (18); c, second and third epimeres (17); d, telson (18); e, seventh leg (19); f, urosome (lateral) (17).

Material examined.

Mediterranean

France: Baie de Banyuls, dépt. Pyrénées-Orientales, depth about 4 m, bottom with *Posidonia*, 4 July 1956, 1 ♂ **holotype**, 16 paratypes (ZMA); surroundings of Banyuls, many specimens (LA).

Spain: Cadaqués, summer 1946, 1 ♂ (ZMA); Estany de ses Gambes, Mallorca, a lagoon of about 800 m length without connection with the sea, 31 May 1951, 7 specimens (RMNH).

Turkey: Sea of Marmora near Florya, about 15 km W. of Istanbul, depth 0-0.2 m, under stones, 2 April 1959, 2 ♂, 2 ♀ (RMNH); Mediterranean coast near Kizkalesi, about 58 km S.W. of Mersin, depth 0-1 m, overgrown rocks, 12 May 1959, many specimens (RMNH).

Black Sea

Turkey: coast near Samsun, depth 0-2 m, rocks. 12 June 1959, 2 specimens, presumably this species (RMNH); near the port of Trabzon, depth 0-5 m, 17 June 1959, 10 specimens (RMNH).

Description. — Maximum length observed 21 mm.

The head (fig. 17 a) has acute lateral lobes and a shallow sinus. The eyes are large.

The first antenna (fig. 17 b) is characterized by a short third peduncle segment (much less than twice as long as wide) and a rather long accessory flagellum (7- to 9-segmented, about twice as long as peduncle segment 2).

The second antenna (fig. 17 c) has a short flagellum (19- to 24-segmented, shorter than the peduncle). The fourth and fifth peduncle segments bear several groups of lateral, medial, and mediodorsal setae, but the setae in each group are neither very long, nor very numerous. The ventral setae are distinctly longer than the mediodorsal ones. Calceoli are present, but relatively little numerous (4 to 7).

The mandible palp conforms entirely the *locusta* type (fig. 17 d).

The hands of both the first (fig. 18 a, b) and second leg (fig. 18 c, d) bear a flask-shaped (or at least truncate) medial palmar spine. The gap between the medial palmar spines and the lateral palmar spines is not large, but large enough to avoid the origin of a "gradate" pattern.

The third leg (fig. 19 a) with very many, long and curly, hairs on the merus and carpus. The anterior margin of the carpus often bears 3 groups of elements.

The coxal plate of the fourth leg (fig. 19 b) has a small posterior notch, and a partially straight lower margin. The merus is anteriorly armed with one group of elements (implanted in the proximal fourth of the segment) and posteriorly with numerous groups of stiff setae.

The legs 5 to 7 have a wide basal segment. In leg 5 (fig. 20 a) this segment is less than $1\frac{1}{2}$ times as long as wide; the merus and carpus of this leg

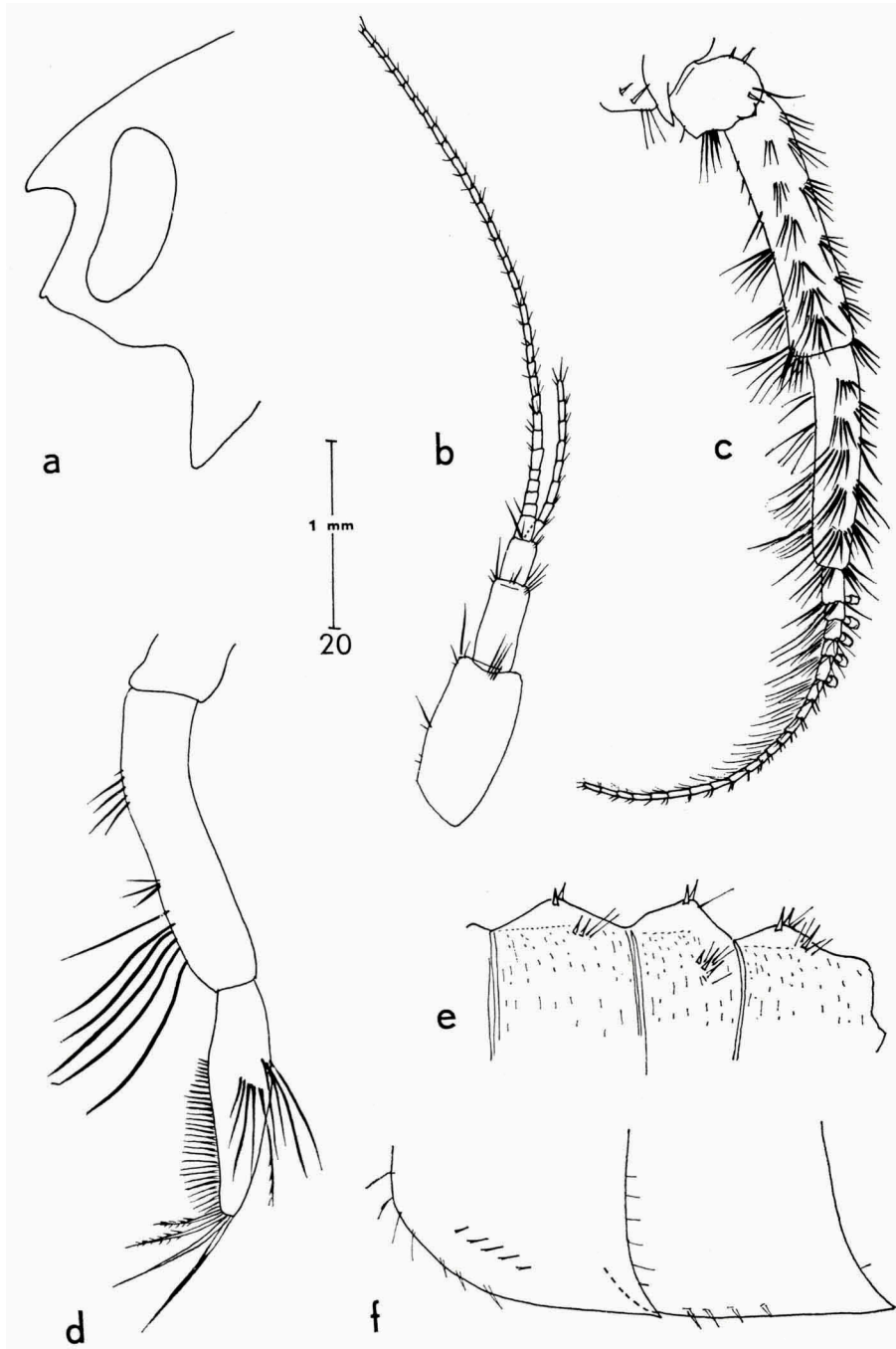


Fig. 17. *Gammarus subtypicus* Stock, 1966, ♂ from Banyuls, France. a, head (scale 20); b, first antenna (16); c, second antenna (medial) (16); d, mandible palp (15); e, urosome (lateral) (16); f, second and third epimeres (16).

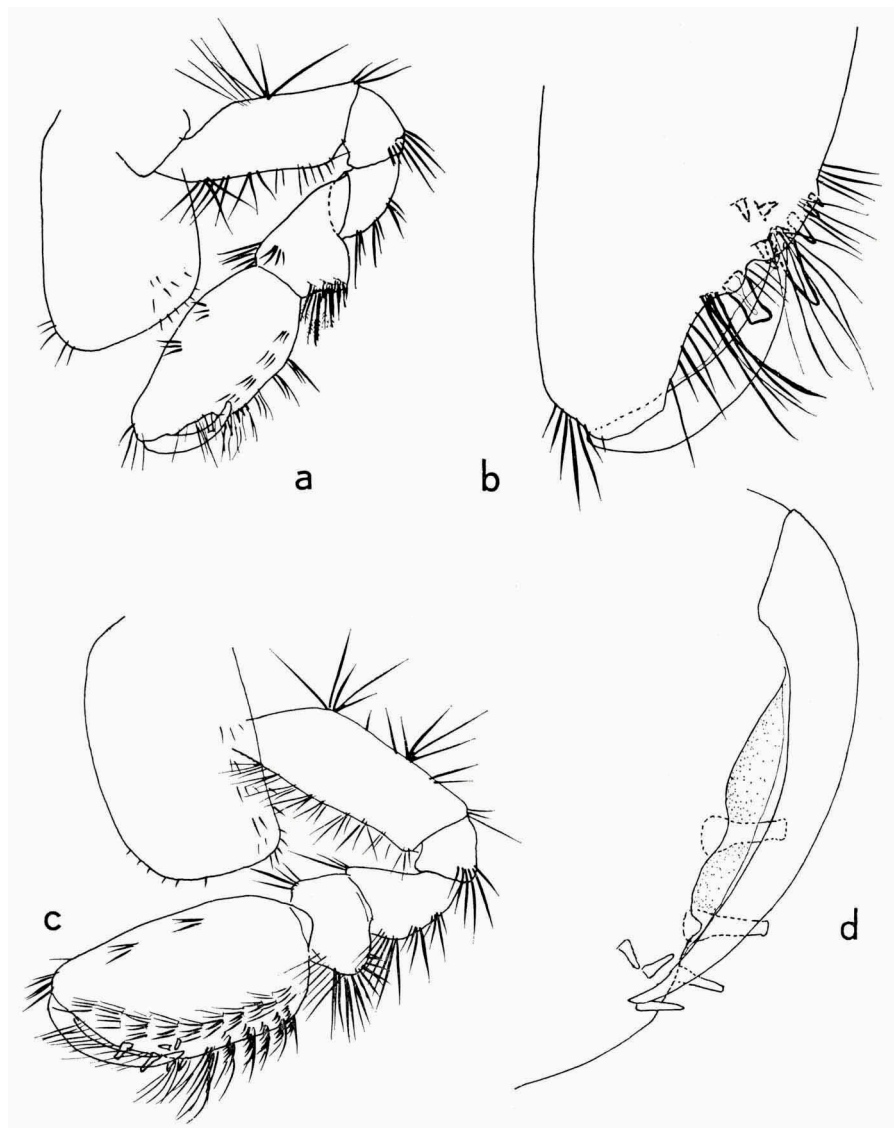


Fig. 18. *Gammarus subtypicus* Stock, 1966, ♂ from Banyuls, France. a, first leg (scale 16); b, palm of first leg (15); c, second leg (16); d, palm of second leg (setae omitted) (15).

are armed with spines only, sometimes with a short setule between it. The basal segment of leg 6 (fig. 20 b) has a convex anterior margin; the rather bulging proximal part of this posterior margin merges into a slightly concave distal part. Long setae, up to twice as long as the spines, are found on the merus and carpus. The basal segment of leg 7 (fig. 20 c) is less than $1\frac{1}{2}$ times as long as wide; its convex posterior margin shows a feeble bend where the proximal margin merges into the distal margin. The entire posterior margin of the basis bears many fine, spiniferous crenulations. Long setae, 2 to 3 times as long as the spines, occur on the merus and carpus.

The urosome (fig. 17 e) is dorsally produced into strong, compressed elevations, bearing 2 : 2 : 2 dorsal spines and 2 : 3 : 1 lateral spines (variation in the spine formula occurs from time to time). Very few, short setae, occur between the urosome spines.

The second and third epimeres (fig. 17 f) are pointed but not exceedingly produced. The posterior margin of the third epimere bears only one setule.

The third uropod has the inner ramus as long as the basal segment of the outer ramus (fig. 19 d).

The telson (fig. 19 c) is not elongate, rather wide in relation to its length, and provided with the usual three groups of elements (subbasal: two to three spines + some setae; subdistal: one spine + two to three setae; distal: three spines + three to four setae); the setae are slightly shorter to slightly longer than the accompanying spines.

Distribution. — Shallow waters of lagoons and bays, on sandy bottoms, with vegetation; Mediterranean and Black Seas. Not very common.

Associated species. — In one locality, a lagoon on Mallorca, *G. subtypicus* was found together with numerous specimens of *G. aequicauda*. Normally, the species lives in water of full marine salinity, and thus it is associated with *G. crinicornis* and/or with *G. insensibilis*.

Affinities. — Sometimes regarded identical with *G. locusta* (cf. Margalef, 1951:256), but at once characterized from the Atlantic *G. locusta* by the widened appearance of the basal segment in P_5 to P_7 , by the less produced epimeres, by the reduction (to a single seta) of the ornamentation of the posterior margin of the third epimere, by the short and wide third peduncle segment of A_1 , by the short flagellum of A_2 , by the greater hairiness of P_6 and P_7 , etc. The Mediterranean counterpart of *G. locusta*, *G. insensibilis*, differs moreover from *G. subtypicus* in the absence of calceoli on A_2 .

The most closely related species is *G. crinicornis*; this species lacks,

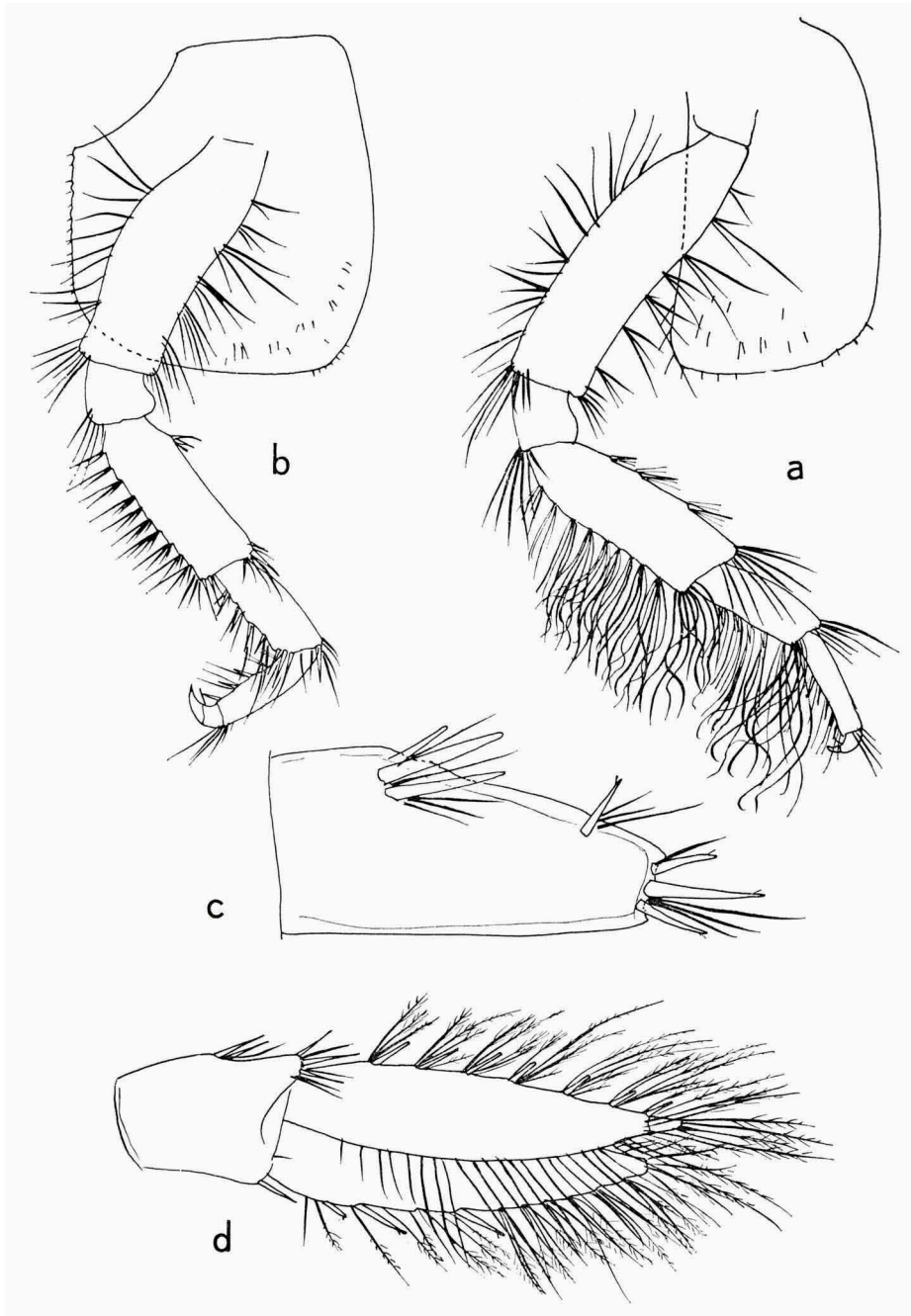


Fig. 19. *Gammarus subtypicus* Stock, 1966, ♂ from Banyuls, France. a, third leg (scale 16); b, fourth leg (16); c, telson (15); d, third uropod (simplified by omission of certain setae) (20).

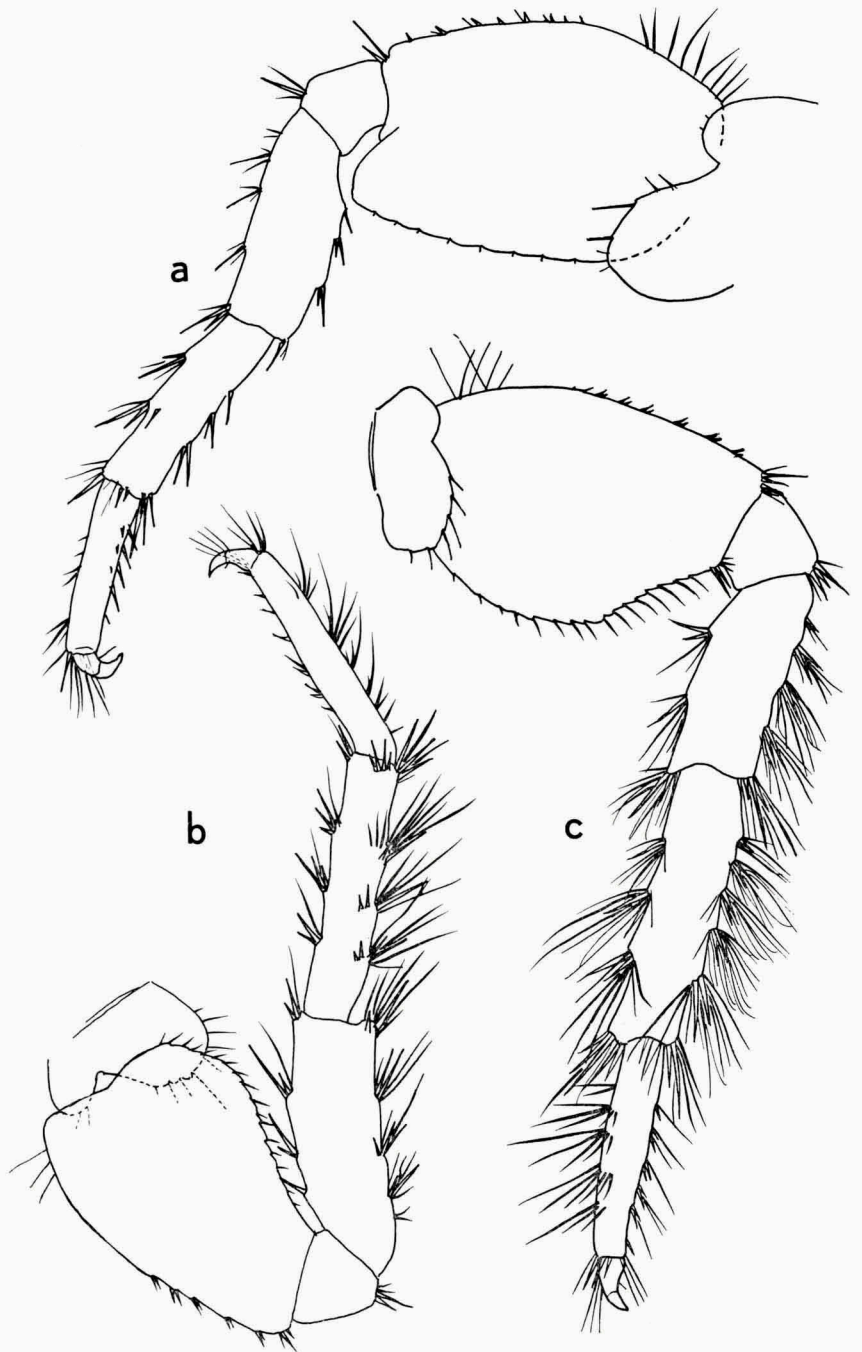


Fig. 20. *Gammarus subtypicus* Stock, 1966, ♂ from Banyuls, France. a, fifth leg (scale 16); b, sixth leg (16); c, seventh leg (16).

however, compressed dorsal elevations on the urosome and differs moreover in the hairiness of A_2 , in the armature of the basis of P_7 , in less hairy legs, etc.

***Gammarus aequicauda* (Martynov, 1931) (fig. 21-26)**

Carinogammarus aequicauda Martynov, 1931 (March): 593-602, fig. 29-39.

Gammarus locusta (nec Linnaeus), Colosi, 1921: 5-6, fig. 4a-b; Schellenberg, 1928: 648-649; Ruffo, 1936: 24-28, fig. 1; Ruffo, 1941: 115; Brian, 1955: 1-8, fig.; Walshe-Maetz, 1956: 525.

Gammarus locusta, forme méditerranéenne (eau saumâtre, eau douce), Chevreux & Fage, 1925: 258-259.

Gammarus eduardi Vecchi, 1931 (April): 57-62, fig. 1-4.

Gammarus aequicauda, Schellenberg, 1937: 269; Ruffo, 1948: 296-299; Sacchi, 1961a: 48, 54, 55, 58; Sacchi, 1961b: 17, 20, 27; Stock, 1966: 3.

Gammarus locusta forma b, Ruffo, 1938: 137.

Gammarus locusta aequicauda, Schellenberg, 1940: 40-42; Margalef, 1951: 255-263, fig. 1.

Gammarus plumicornis (nec Costa), Ruffo, 1946: 52.

Gammarus locusta forme saumâtre, Rancurel, 1949: 4-8, fig.

Gammarus locusta forme camarguaise, Guigues, 1961: 153-163, fig.

Material examined.

Mediterranean

France, dépt. Pyrénées-Orientales: Fontaine d'Estramar, N. of Salses, 25 September 1957, many specimens (RMNH); well on highway N 9, just south of the boundary with dépt. Aude, chlorinity 3.2‰, 9 September 1961, many specimens (ZMA); Étang de St. Nazaire, 3 July 1956, 7 specimens (ZMA); Etang de Leucate, 5 July 1963, 2 specimens (ZMA).

France, dépt. Aude: Etang de Lapalme, 25 September 1957, 7 specimens (RMNH); Résurgence de la Nouvelle, near La Nouvelle, S. of Narbonne, ditch with brackish water, 25 September 1957, 6 specimens (RMNH); south of Narbonne, ditch near saltpits of Sigean, 25 September 1957, 10 specimens (RMNH); Etang de Sigean, 8 September 1966, 5 specimens (ZMA).

France, dépt. Bouches-du-Rhône: Camarque, Salin de Badon, 26 May 1952, many specimens (ZMA); Camarque, Canal de Roquemaure, 26 May 1952, 1 specimen (ZMA); Camarque, Etang de l'Impérial, 7 April 1966, 7 specimens (ZMA); Camarque, Etang de Consécanière, 7 April 1966, many specimens (ZMA); Camarque, Etang de Tampan, 7 April 1966, many specimens (ZMA); Camarque, in small pool near Pertuis de Rousty, 7 April 1966, many specimens (ZMA); Rognac, pool with freshwater on the bank of the Etang de Berre, 8 April 1892, many specimens (MNHN).

France, dépt. Var: Fréjus, lagoon with slightly brackish water, 25 February 1891, many specimens (MNHN).

France, Corsica: Etang de Biguglia, May 1887, 11 specimens (MNHN).

Spain, Mallorca: Estany de ses Gambes, a lagoon of about 800 m length, without connection with the sea, 31 May 1951, many specimens (RMNH).

Italy, prov. Napoli: Lago di Patria, 40 km N. of Naples, Cl. 4.5‰, 22 March 1959, 4 specimens (RMNH).

Yugoslavia, Dalmatia: Strozancie, 5 km S.W. of Split, June 8 1961, many specimens (ZMA); Mouth of river Stobreč, about 5 km S.W. of Split, 40 to 80 m from the sea, chlorinity 683-836 mg/l, 6 June 1961, many specimens (ZMA).

Greece, Thessalia: Shallow lagoon near Salaora, Gulf of Arta, 2 June 1964, many

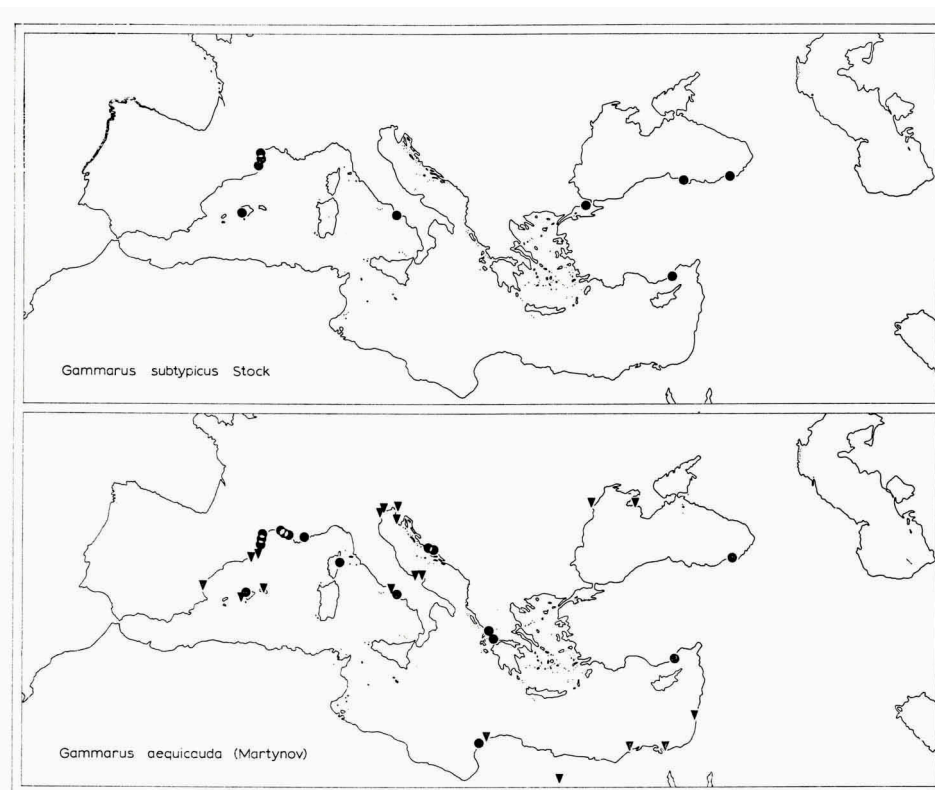


Fig. 21. Distribution of *Gammarus subtypicus* Stock, 1966, and of *Gammarus aequicauda* (Martynov, 1931). The larger dots in the lower figure indicate localities of the material examined for the present revision; the smaller dots stand for localities recorded in the literature.

specimens (RMNH); Lagoon of Missolonghi, S. of Magoula, 5 June 1964, many specimens (RMNH).

Lybia: near Benghazi, brackish pool, 28 March 1965, 5 specimens (RMNH).

Turkey: Kizkalesi, S.W. of Mersin, brackish pool on the shore, depth 2 m, 12 May 1959, 13 specimens (RMNH).

Black Sea

Turkey: Port of Trabzon, pelagic on light at night, 7 June 1959, 3 specimens (RMNH).

Remarks. — As is clear from the long list of references, this is the most abundant form of the *locusta*-group around the Mediterranean. It is a brackish water species, which can penetrate into the mouths of streams and rivers in places that are — at least temporarily — nearly fresh. Measurements in the environment of *G. aequicauda* show that it can sustain great salinity

variations (Sacchi, 1961a, 1961b). Perhaps due to the different ecological circumstances under which the species can live, a good deal of variation has been observed between various populations. Since I was unable to find any consistent line in these variations, all are considered one species in this paper. But it should be realized that further splitting might be necessary, especially when we have acquired more knowledge about the relation between the (changes in) salinity and the external morphology and when the results of interfecundity tests, already in course, are available.

For the moment, it suffices to give short descriptions and detailed illustrations of two "forms" of *G. aequicauda*. The first "form", from a brackish pool in Turkey, is closely resembling the types (from brackish waters in the Crimea); the second "form" is from nearly fresh water in southern France.

Description of the typical form. — Head with pointed lateral lobes, sinus shallow, eye rather small (fig. 22 a).

The first antenna (fig. 22 b) has the third peduncle segment not very slender. The accessory flagellum is short (1.2 times as long as peduncle segment 2) and has only 5 to 8 segments.

The second antenna (fig. 22 c) has a long gland cone. Peduncle segments 4 and 5 bear ventrally groups of long setae, the terminal end of which is often somewhat curved. Calceoli are present on the 7 to 9 most proximal segments of the flagellum.

The mandible palp (fig. 22 d) is of the *locusta*-type.

The posterior margin of the hand of leg 1 (fig. 23 a) is convex and armed with three to six groups of setae. The medial palmar spine (fig. 23 b) is flask-shaped.

The posterior margin of the hand of leg 2 (fig. 23 c) is very convex. The medial palmar spine is flask-shaped or at least truncate, but the lateral palmar spines are not (fig. 23 d); the palmar spines are not gradate.

The merus of leg 3 (fig. 23 e) bears two or three groups of elements on its anterior margin, no or one group on the anterior margin of the carpus. The posterior margins of these segments bear long, curled setae.

The coxal plate of leg 4 is distinctly longer than wide; its ventral margin is curved; the posterior notch is shallow (fig. 23 f). The merus bears rarely one, mostly two groups of anterior elements, the carpus rarely one, usually no group of such elements; the posterior armature consists of setae only.

The basis of leg 5 is less than $1\frac{1}{2}$ times as long as wide. Merus and carpus bear long hairs, often much longer than the spines (fig. 24 a).

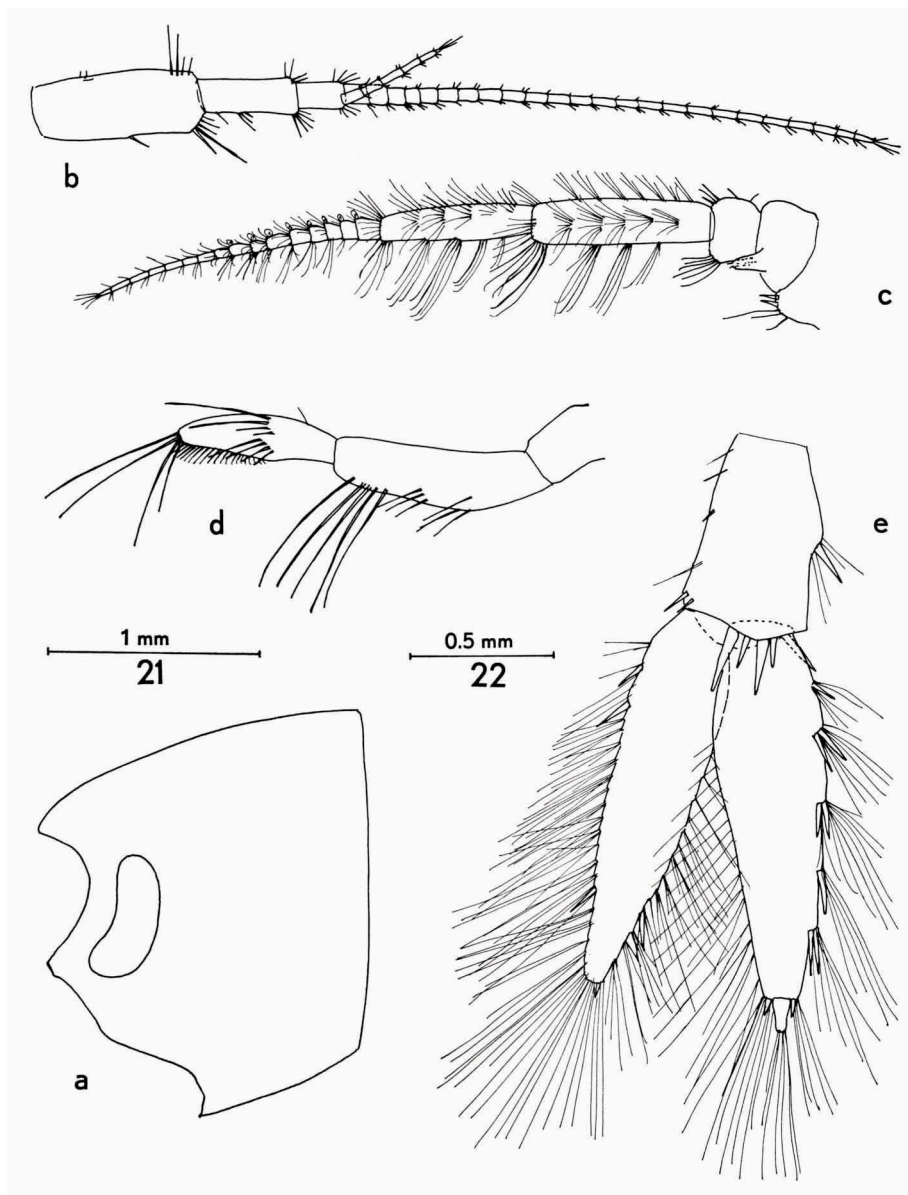


Fig. 22. *Gammarus aequicauda* (Martynov, 1931), ♂, typical form, from Kizkalesi, Turkey. a, head (scale 21); b, first antenna (13); c, second antenna (medial) (13); d, mandible palp (14); e, third uropod (practically all setae are plumose, but this plumosity is omitted in the drawing) (22).

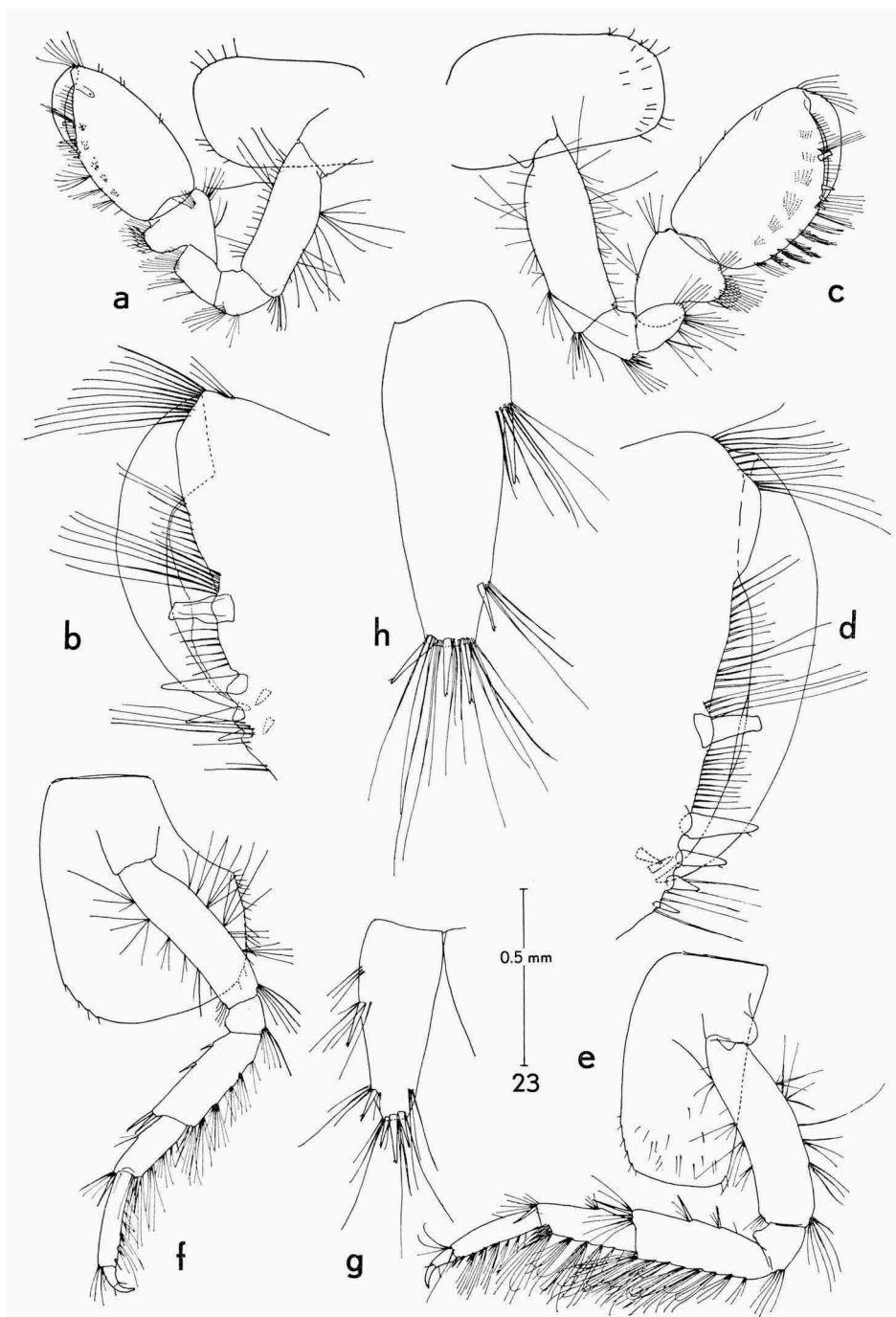


Fig. 23. *Gammarus aequicauda* (Martynov, 1931), ♂, typical form. a-g, from Kizkalesi, Turkey; h, from Camarque, France. a, first leg (scale 1); b, palm of first leg, lateral (9); c, second leg (5); d, palm of second leg, lateral (9); e, third leg (5); f, fourth leg (5); g, telson (2); h, telson (23).

The setae on the merus of leg 6 (fig. 24 b) are, at least on the anterior margin, much longer than the spines. The propodal sole bears several long setae in addition to the spines.

The basal segment of P_7 (fig. 24 c) has a regularly curved posterior margin. Long, slightly curled, setae (often twice as long as the corresponding setae) arm the merus and carpus.

The urosome segments are dorsally raised and compressed (fig. 24 d) armed with spines and numerous long setae (2 to 3 times as long as the spines).

The epimeres 2 and 3 are acute but not produced unduly (fig. 24 e); the third bears only one setule at its posterior margin.

The telson (fig. 23 g) bears sometimes, proximally of the subbasal spine, a group of setae; there is one subbasal spine, accompanied by several setae; the subdistal groups consist also of one spine and several setae, whereas there are three spines and many terminal setae. The setae, more in particular the terminal ones, are more than twice as long as the spines.

In other populations, the basal group of setae is lacking (fig. 23 h), but the long setae (2 to 3 times as long as the spines) still are characteristic.

The inner ramus of the third uropod (fig. 22 e) is as long as the basal segment of the outer ramus.

Description of atypical material, from the Fontaine d'Estramar (N. of Salses, dépt. Pyrénées-Orientales, France). — Although the antennae, the urosome and telson bear long setae just as in the typical form, the posterior legs are less hairy. This feature is most clearly shown by the merus of legs 6 and 7, which bear setae that are only 1 to $1\frac{1}{2}$ times as long as the spines (fig. 26 b, c). The propodal sole of leg 6 is scarcely, if at all, setose. The basal segments of legs 5 to 7 are more elongate; that of leg 5 (fig. 26 a) has a concave posterior margin; that of legs 6 and 7 have nearly straight posterior margins (fig. 26 b, c).

A curious feature of this population is the tendency to reach fairly early in the development the so-called "gradate" pattern in the propodal armature of leg 2. In fig. 25 c, the propodal segments of leg 2 of two males of identical size have been compared; the one male (dotted line in the figure) was collected in the Camarque (France, dépt. Bouches-du-Rhône) and approaches the typical form; the other male (uninterrupted line in the figure) came from the Fontaine d'Estramar. It can be seen from the figure that, although the remaining proportions of the propodus are virtually identical, in the latter male the gap between the medial and lateral palmar spines is noticeably smaller.

The epimeres 2 and 3 (fig. 25 d) of the members of this population are more produced than in typical material.

These differences, if they were consistently present, would seem of taxonomic importance. But several intermediates between the typical and atypical forms have been observed in hairiness and elongation of the posterior legs.

Another rather curious point in which *G. aequicauda* shows variation, is

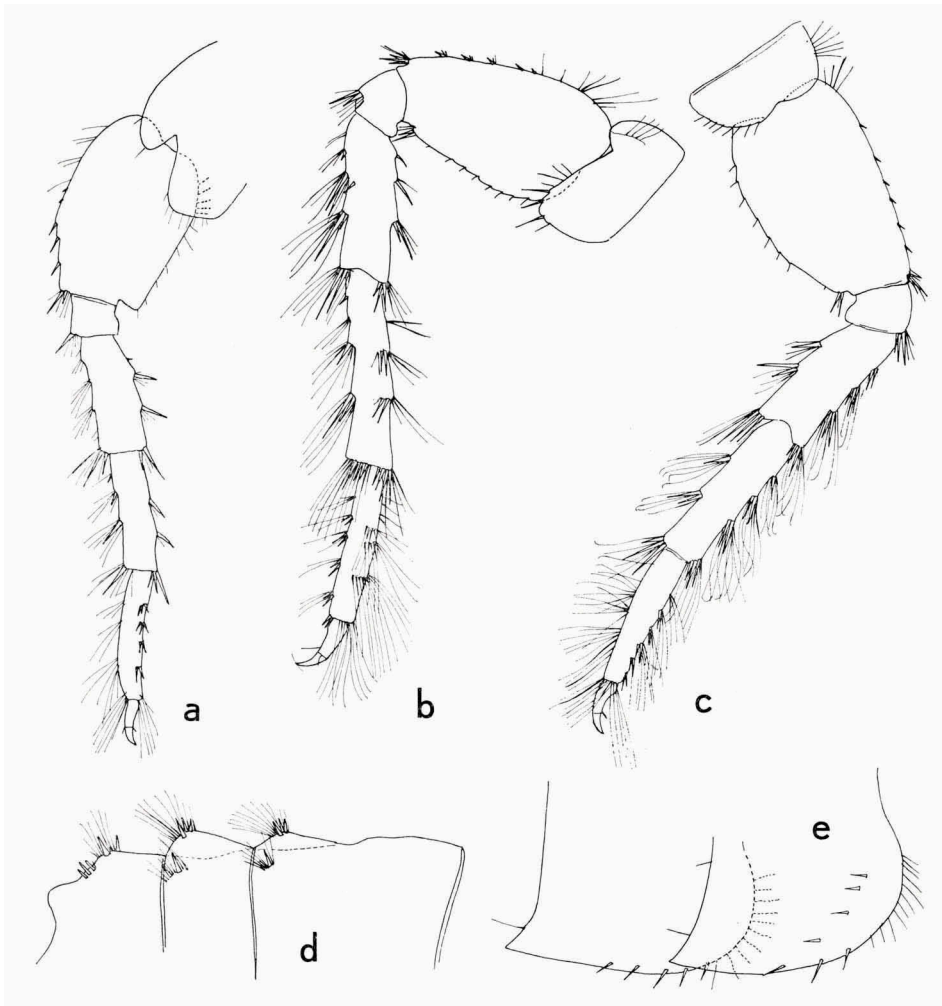


Fig. 24. *Gammarus aequicauda* (Martynov, 1931), ♂, typical form, from Kizkalesi, Turkey. a, fifth leg (scale 5); b, sixth leg (5); c, seventh leg (5); d, urosome (lateral) (21); e, second and third epimeres (21).

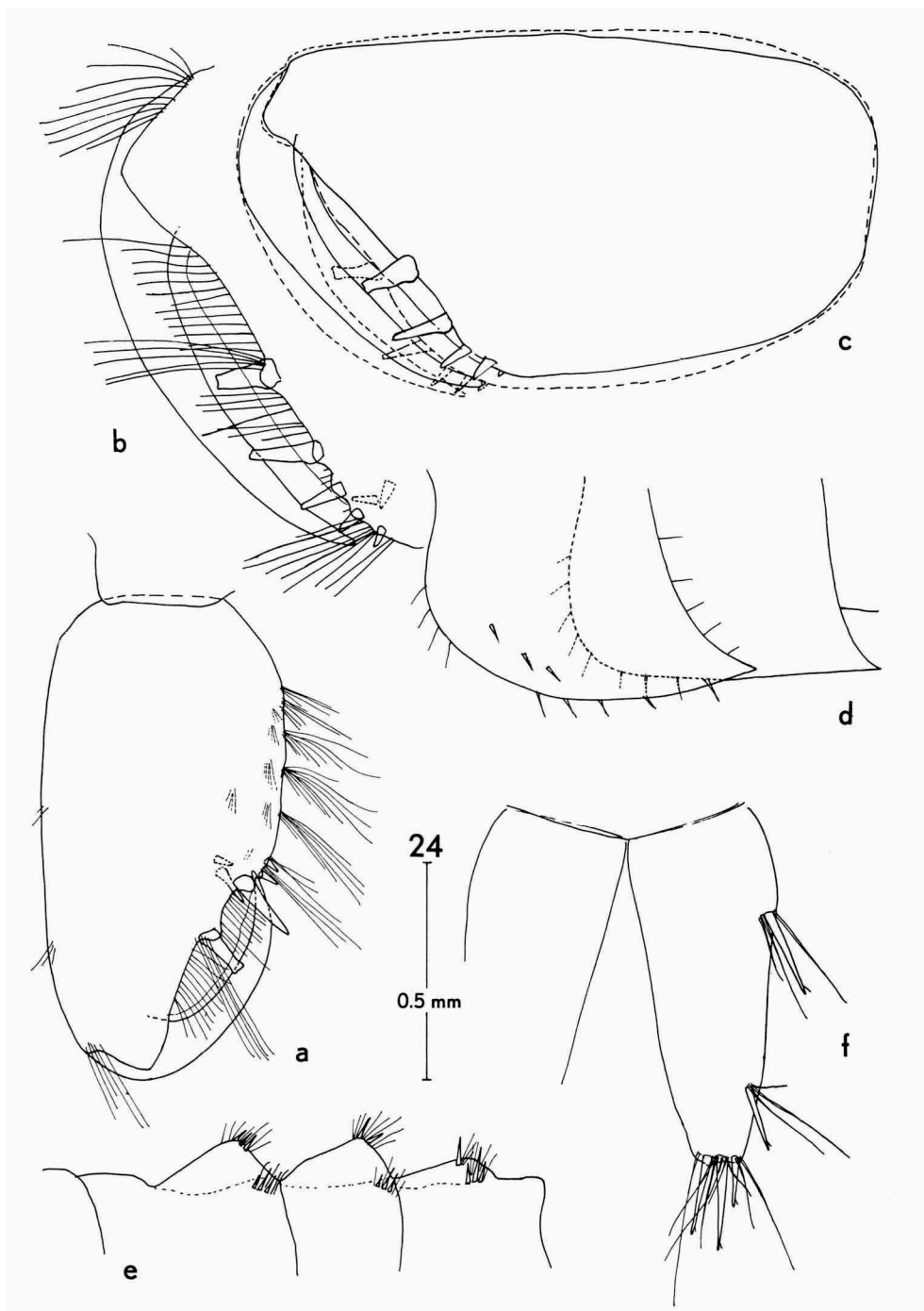


Fig. 25. *Gammarus aequicauda* (Martynov, 1931), ♂, less hairy form, from Fontaine d'Estramar, France. a, hand of first leg (scale 14); b, hand of second leg (lateral) (24); c, the hand of the second leg of two specimens of *G. aequicauda* of the same size: interrupted line — hairy form from the Camarque, uninterrupted line — less hairy form from the Fontaine d'Estramar (scale 14); d, second and third epimeres (12); e, urosome (lateral) (13); f, telson (24).

the shape of the lateral lobes of the head. Though acute in most adult males, some specimens (mostly females and juveniles, but sometimes also larger males) have more rounded lateral lobes, similar to those of *G. plumicornis*. The nature of the lateral lobes has been used, and still is in use, for the distinction of the genera (or subgenera) *Gammarus* s.str. and *Rivulogammarus*. The variation just mentioned would divide members of one population of apparently the same species over two different genera, a fact that enlarges only the suspicion I have always felt against the validity of *Rivulogammarus*.

Material from many localities, including the types, have the rami of the uropods subequal. There is a marked tendency, however, especially in females and younger specimens, towards a shortening of the inner ramus. This ramus may reach then a length of 80 to 90% of the first segment of the outer ramus.

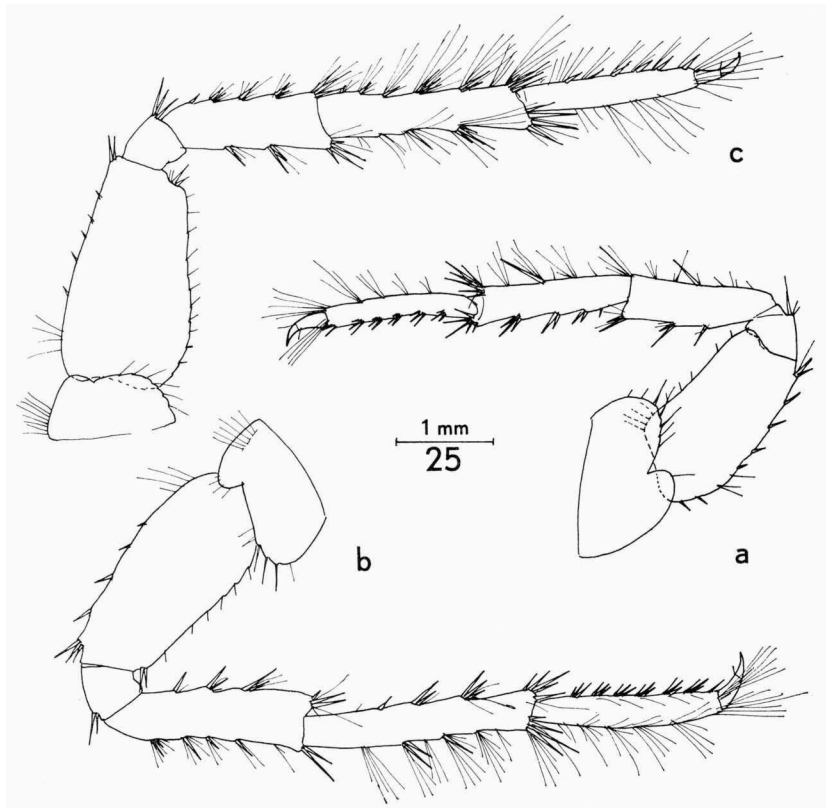


Fig. 26. *Gammarus aequicauda* (Martynov, 1931), ♂, less hairy form, from Fontaine d'Estramar, France. a, fifth leg (scale 25); b, sixth leg (25); c, seventh leg (25).

Distribution. — The species occurs all around the Mediterranean and Black Seas, always in very shallow waters (0-5 m). It prefers brackish, or (temporarily) nearly fresh waters; it was observed by Sacchi (1961a, 1961b) at 6.09-7.91 ‰ Cl (the chlorinity in Sacchi's observation area varied over a longer period between 3.88 and 19.77 ‰, at a temperature of 9.0 to 35.0° C). The chlorinities recorded in the present paper (see list of material examined) range from 3.2 to 8.4 ‰.

Associated species. — In the more saline part of its range sometimes accompanied by *G. plumicornis* Costa, rarely by *G. subtypicus* Stock.

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