FRESHWATER GAMMARUS SPECIES FROM EUROPE, NORTH AFRICA AND ADJACENT REGIONS OF ASIA (CRUSTACEA-AMPHIPODA)

PART I. GAMMARUS PULEX-GROUP AND RELATED SPECIES

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ABSTRACT

1) Within the genus Gammarus s.str., which is widely distributed throughout the northern hemisphere, more than 100 freshwater species can be distinguished.

2) These freshwater species can be classified in three artificial groups: (a) the G. pulex-group (species without dorsal carina and with dense setation on pereiopods 3 and 4 and uropods 3) and (b) the G. balcanicus-group (species without dorsal carina and poorly setose pereiopods 3 and 4 and uropod 3) and (c) the G. roeseli-group (species with dorsal carina). These groups are merely artificial ones since transitional (intermediate) species do exist. Moreover, the origin of the species is not known, so that polyphyly is not excluded.

3) In the present work the Gammarus pulex-group is revised, based on rich material from Europe, North Africa, Asia minor and adjacent areas.

4) The taxonomic differences between the various species are usually small but distinct and stable. This is especially evident in mixed populations of two or more species. In those populations no intermediates between the taxa have been observed.

5) In some cases, morphological differences between two species are hardly discernible although reproductive isolation is present (e.g. G. fossarum and G. wautieri).

6) Hybridization experiments can solve taxonomic problems and test the taxonomic value of morphological differences between populations. Such experiments between many Asiatic and European populations might clarify their taxonomic status.

7) The taxonomic characters may largely be variable within one population as well as in different populations of the same species.

8) Characters that are very stable in one species can be largely variable in other species (e.g. presence of calceoli, length of rami of uropod 3). Nevertheless we can distinguish certain stable characters (e.g. the structure of the mandibular palp), but also instable ones (e.g. the number of dorsal and lateral spines on the urosomites) in all species.

9) Gammarus pulex has given rise to several isolated populations, adapted to subterranean life (being blind or having enlarged eyes). These populations are considered distinct subspecies.

10) Within some taxa (e.g. G. fossarum and G. p. pulex) morphologically aberrant populations can be found. Since these populations do successfully cross-breed and are sympatric they must be considered mere variations.

11) We had serious problems to determine the identity of several Gammarus species, especially from Asia Minor, because of the impossibility to obtain literature and type material of some Russian authors. (So we cannot exclude the possibility that our species described from Asia might be identical with a species formerly described by a Russian author).

12) For all species, except the most common ones, complete lists of all localities studied are given. Moreover, in 3 maps the distribution of the various species and subspecies is illustrated.

13) It was not possible to illustrate all morphological details of every taxon mentioned in the present work. Only G. pulex, the type species of the genus Gammarus and the nominal form of the entire group, is figured completely. For the other taxa, only those parts are illustrated that are fundamentally different from those of G. p. pulex.

RÉSUMÉ

1) Au sein du genre Gammarus s.str. qui est largement répandue dans l'hémisphère nord, on peut distinguer plus que cent espèces d'eau douce.

2) On peut subdiviser ces espèces d'eau douce en trois groupes artisticiels: a) le groupe G. pulex (espèces sans carènes dorsales avec des péréiopodes 3 et 4 et uropode 3 très sétoses), b) le groupe G. balcanicus (espèces sans carènes dorsales et avec les péréiopodes 3 et 4 et uropodes 3 peu sétoses) et c) le groupe G. roeseli (espèces avec carènes dorsales). Ce ne sont que des groupes artisticiels, puisque des espèces transitives (intermédiaires) sont connues, comme n'est pas connu l'origine des espèces.


4) Les différences taxonomiques entre les différentes espèces sont légères, habituellement, mais distinctes et stables. Ceci est surtout évident dans des populations mixtes com-
portant deux ou plusieurs espèces. Dans ces populations l'on n'a jamais observé des spécimens intermédiaires entre deux espèces.

5) Dans certains cas, les différences morphologiques entre deux espèces sont difficiles à reconnaître, quoiqu'il existe une barrière reproductrice entre ces espèces (par exemple G. fossarum et G. wautieri).

6) Les expériences d'hybridation sont une bonne méthode pour résoudre des problèmes taxonomiques, et pour vérifier la valeur taxonomique de différences morphologiques qui existent entre des populations. Il serait recommandable d'effectuer des expériences d'hybridation entre un grand nombre de populations asiatiques et des populations européennes afin de vérifier leur valeur taxonomique.

7) Les caractères taxonomiques peuvent varier de façon considérable au sein d'une même population, ainsi que d'une population à l'autre.

8) Des caractères qui sont très stables dans une espèce peuvent être très variables dans une autre (par ex. la présence de calcéoles, la longueur des rames de l'europode 3). Néanmoins, nous pouvons distinguer des caractères stables (par ex. les palpes mandibulaires) et des caractères instables (par ex. le nombre d'épines de l'armature dorsale).

9) Gammarus pulex a créé plusieurs populations isolées, adaptées à la vie sous-ternaire (aveugles ou à yeux agrandis). L'on a considéré ces populations comme des sous-espèces distinctes.

10) Au sein de certaines unités taxonomiques (par ex. G. fossarum et G. p. pulex) l'on peut trouver des populations morphologiquement distinctes. Puisque ces populations s'inter-fécondent avec succès, et un mécanisme d'isolation géographique n'existe pas, l'on doit considérer ces populations comme des simples variations.

11) Pendant le présent travail nous nous sommes heurtés à de sérieux problèmes de détermination de beaucoup d'espèces du genre Gammarus, en particulier ceux de l'Asie Mineure, à cause de l'impossibilité d'obtenir la littérature et le matériel typique de certains auteurs russes. (Par conséquent nous ne pouvons pas exclure la possibilité que certaines de nos espèces asiatiques sont identiques avec des espèces décrites précédemment par des auteurs russes).

12) Pour toutes les espèces, sauf pour quelques espèces très communes (par ex. G. pulex, G. fossarum et G. lacustris) pour des raisons de limitation d'espace, des listes complètes du matériel étudié sont données. En plus l'aire de distribution connue est décrit et illustré à l'aide de cartes.

13) Il n'était pas possible de faire des figures de tous les détails de chaque unité taxonomique mentionné dans ce travail. Seulement G. pulex, l'espèce typique du genre Gammarus et la forme nominale de tout le groupe présenté ici a été dessiné entièrement. Pour tous les autres (sous)espèces, seulement les parties qui diffèrent principalement de celles illustrées pour G. p. pulex sont représentées.

INTRODUCTION

Among the various amphipod genera, Gammarus is probably the genus with the highest number of epigean freshwater taxa. The first members of this genus already were described during the Linnean period, about 200 years ago. In the following period, numerous different species, many of them now considered representatives of other genera were included in the genus Gammarus.

In the second half of the 19th and in the 20th century, many species at first attributed to the genus Gammarus were transferred to new genera. Nevertheless, up to this moment, the genus Gammarus is not yet satisfactorily delimited, while the taxonomy of the various species within this genus, especially of the freshwater forms, is not yet settled.

Because of the extreme variability at the one hand and the occurrence of convergent characters at the other hand, during a long time the opinion prevailed that only a limited number of very variable Gammarus species occurred in Europe and the adjacent parts of Africa and Asia.

Hybridization experiments as well as detailed studies on variability, distribution and ecology of the various morphologically different populations showed, that a very considerable number of inter-sterile Gammarus species inhabits the inland waters in the area studied.

During the second colloquium on the genera Niphargus and Gammarus in Lyon, 1973 it appeared that the present authors both tried to solve the complicated taxonomic position of the various freshwater species within the genus Gammarus. In order to make the situation not more complex than it was already, both authors decided that it would be wise to join forces. In this light they decided to study the genus Gammarus in Europe, North Africa and the adjacent countries of Asia using identical taxonomic criteria for all taxa involved. The study was based on the material from all the major museums and private collections from Europe, and a rich material collected by the second author.

Because of the large number of limnic Gammarus species living in the area studied, the genus was subdivided into three artificial species-groups. This paper is limited to members of the Gammarus pulex-group only. In following papers the members of the other groups will be discussed.

During this study the authors had to cope with many difficulties, the most important being the often very incomplete existing descriptions and the impossibility to obtain the type-material of
many species. This problem was especially serious with regard to the species described from the regions near the Black and Caspian Seas by Russian authors like Martinov, Derjavin and Birstein, since the descriptions and illustrations of these species are not always very detailed.

Because of this we cannot exclude the possibility that a limited number of published names has been fixed erroneously to taxa that we studied in this paper.

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Although the present paper is, we hope, a unity, each of the authors took special care for certain sections of it, which have been afterwards discussed with his co-author. Since both authors had enormous collections at their disposition, it was decided to start the study of the material separately. In a later stage of the work, during meetings in Titograd, in October 1974 and in Amsterdam, in October, 1975 the authors discussed each other’s results and compared the material of the various species they had at their disposition. They hope that through these methods the best results have been reached. Anyhow it must be stressed that both authors share the full responsibility for the total work.

TERMNOLOGY USED IN THIS PAPER

Standard terminology is used for the chitinous structures in the descriptions and diagnoses of all taxa described in this paper:

The head has two cephalic lobes which can be rounded, angular etc. The metasome and urosome segments are armed with dorsomedian and dorsolateral armature.

Antennae: peduncle, main flagellum, accessory flagellum.

Mandibular palp: third (distal) segment bearing numerous setae at interior margin (D-setae), and several long setae (E-setae) near the distal end; on the outer surface appear 1 or more groups of A-setae, on the inner surface 1 or more groups of B-setae; C-setae are absent (for terminology see Karaman, 1971).

Gnathopods 1 and 2 (P 1 and P 2) and pereiopods 3 through 7 (P 3 through P 7): segment 1 (coxal plate), segment 2 (basis), segment 3 (ischium), segment 4 (merus), segment 5 (carpus), segment 6 (propodus), segment 7 (dactylus).

Segment 6 (propodus or hand) of gnathopods 1 and 2: on the outer surface of the palm a medial palmar spine is implanted, on the posterodistal corner of the palm (palmar angle) several palmar angle spines are implanted on the outer surface and several submarginal spines on the inner surface.

On the distal part of the peduncle of the pleopods two coupling hooks (retinaculum) can be found.

The uropods consist of a peduncle and an inner ramus (endopodite) and outer ramus (exopodite).

THE GROUPS OF SPECIES WITHIN THE GENUS GAMMARUS

The genus Gammarus was established by Fabricius in 1775 with Cancer pulex Linnaeus, 1758, as a type species. In 1928, the generic name Gammarus was placed on the Official List of Generic Names in Zoology, as name no. 493, by the International Commission on Zoological Nomenclature.

During a very long period both marine Gammarus-like species as well as freshwater forms were considered members of the same genus Gammarus, an opinion which is still supported by many authors. Others, however, found it necessary to subdivide the genus Gammarus in two different genera, one for the marine and one for the freshwater species. Therefore Stanko Karaman, 1931,
introduced the generic name *Rivulogammarus* in which he and many authors after him included the freshwater members of the genus *Gammarus*. Stock, 1969, however, proved that *Rivulogammarus* must be rejected as a generic name in conformity with the International Code of Zoological Nomenclature.

Sket, 1971, established the new genus *Lagunogammarus* for the mixohaline species formerly included in *Gammarus* but his solution leaves many doubts about the taxonomic position of intermediate forms like *G. duebeni* Liljeborg, 1852. Golikov & Tzvetkova, 1972, likewise introduced new generic names for the marine and brackish water species within the genus *Gammarus*. It is clear, from the discussion that is going on at the moment that the utility of these generic names must be re-examined. Nevertheless it is clear that the oldest valid generic name for the freshwater forms is *Gammarus*. In order not to increase the confusion on the right taxonomic position of the marine and brackish water forms we will not treat that problem in the present work.

Although all freshwater species within the genus have many characters in common like the small rounded to reniform eyes, the mouthparts (all having a regularly comb-like row of D-setae on the 3rd segment of the mandibular palp), we can distinguish three artificial groups which can be more or less easily recognized on morphological features, viz. the *Gammarus roeseli*-group, the *Gammarus balcanicus*-group and the *Gammarus pulex*-group, the latter being the subject of the present study.

The members of the *Gammarus roeseli*-group can be distinguished from those of the other two groups by the presence of more or less developed carinae and dorsoposterior teeth on a number of metasome segments.

In both the *pulex*- and *balcanicus*-group dorsal carinae are completely absent. In the *G. balcanicus*-group setation on pereiopods 3 and 4 as well as on the outer margin of uropod 3 is very short or absent. In the *G. pulex*-group setation of both pereiopods 3 and 4 and uropod 3 is long.

Since this subdivision is a mere artificial one, it is sometimes possible to find intermediate forms between two groups, e.g. *G. kischineffensis*, which is intermediate between the *G. pulex*- and the *G. balcanicus*-group.

It must be emphasized that the definition of the *G. pulex*-group given in this paper is somewhat different from that given by Pinkster, 1970, since it now also includes species with long setae on the anterior margins of pereiopods 5 to 7.

**TAXONOMIC CHARACTERS USED IN THIS STUDY**

The following taxonomic characters were examined in the present study:

1. body length (viz. the distance from the tip of the rostrum to the tip of the third uropod);
2. the dorsal armature of meta- and uro- setae;
3. the shape of the eyes;
4. the shape of the lateral cephalic lobes;
5. the length and setosity of the peduncular and flagellar segments of antenna 1;
6. the shape and setosity of peduncular and flagellar segments of antenna 2;
7. the armature of the mouth-parts;
8. the shape of coxal plates 1 to 4;
9. the shape and armature of gnathopods 1 and 2;
10. the shape and armature of pereiopods 3 to 7, in particular of the basal segment of P5 to P7;
11. the number of retinacular hooks on the pleopods;
12. the shape and armature of the epimeral plates;
13. the shape and armature of uropods 1 and 2;
14. the shape and armature of uropod 3;
15. the shape and armature of the telson lobes;
16. sexual dimorphism;
17. colour of live specimen.

The characters 7 (except the mandibular palp), 11 and 13 are similar in all studied species. These characters will be described for the nominal form of this group, *G. p. pulex* only. If no details of certain characters are provided for other species, these characters must be assumed to be identical (similar) to those described for *G. p. pulex*. 
SEXUAL DIMORPHISM

Like in most other groups of amphipods, a marked sexual dimorphism can be found in all species of the *G. pulex*-group. Females differ from males in the following characters:

1. smaller body size;
2. relatively shorter antennae;
3. relatively shorter appendages, including uropod 3;
4. slightly but distinctly wider basal segment in pereiopods 5 to 7;
5. more slender antenna 2, with longer setae on peduncular segments 4 and 5;
6. calceoli are absent in all species even if the male has them;
7. absence of brush-like aspect of the setation on the flagellum of antenna 2;
8. smaller segment 6 (propodus) in gnathopods 1 and 2, with reduced total number of spines;
9. medial palmar spine always absent;
10. less abundant setation of pereiopods 3 and 4;
11. setation on the anterior margins of P 5-7, if present, as long as, or longer than in ♂.
12. less abundant setation of uropod 3, usually without plumose setae;
13. presence of oöstegites on the ventral surface of thoracic somites 2 to 5;
14. absence of 2 ventral copulatory processes on the ventral surface of the seventh thoracic somite.

CONSTANCY OF THE CHARACTERS

Some authors, e.g. Stock (1967, 1968), Roux (1967), Pinkster (1970, 1972, 1973), already showed that several characters in gammarids are very stable, while others can show an extreme variation.

A. Stable characters. — As far as can be concluded after studying many thousands of samples, belonging to various species described in this paper the following characters can be considered as more or less stable in adults (although there can exist some variability during the various developmental stages of the species).

1. the structure of the mandibular palp;
2. the setosity of antenna 1;
3. the shape and setation of peduncle and flagellum of antenna 2;
4. the presence or absence of a medial palmar spine or other spines on gnathopods 1 and 2;
5. the length of the setae at the posterior margin of pereiopods 3 and 4;
6. the presence or absence of setae on the inner surface of the basal segments of pereiopods 5 to 7;
7. the shape and the armature of pereiopods 5 to 7 and the presence or absence of long setae along their anterior margin;
8. the ratio inner versus outer ramus of uropod 3;
9. the presence or absence of setae on the dorsal surface of certain metasome segments.

B. Variable characters. — The following characters proved to be very variable:

1. the number of segments in the flagellum of antennae 1 and 2;
2. the shape of the epimeral plates of the pleon;
3. the setation of the gnathopods 1 and 2 and the telson;
4. the number of spines or setae on epimeres 2 and 3, on pereiopods 3 to 7, uropod 3, and telson lobes;
5. the number of elements implanted in the groups on the dorsal surface of the urosome segments.

Some characters which are very stable in one species can be extremely variable in other species like the shape of the eye (usually the eyes found in members of this group are small, almost round-ed: sometimes, however, according to changing light conditions the eyes can be much smaller or larger); the presence or absence of calceoli (a stable character in *G. p. pulex*, *komareki*, *rambouseki*, *birsteini* etc., but instable in *G. fossarum*, *laborifer* etc.); the shape of the epimeral plates.

Because of the very large variability within each species at the one side and the strong convergence of characters between the species at the other side, knowledge of ecological data, and data on the distribution of each species can be very useful for the identification of certain populations. Moreover,
the results of cross-breed experiments and the results of micro-geographical analyses (showing genetic and geographical barriers, respectively) can be of great help in evaluating the existing differences between different populations.

For the same reason it is important to take into consideration all other possible characters one has at his disposition when identifying a species. Since most of the specific characters are fully developed in adult specimens only, it is important to know (and record when collecting a sample) that precopulations (sexually mature specimens) are present in a sample. The distinction between genotypical and phenotypical characters is very difficult in the taxonomy of the genus *Gammarus*.

**PROBLEM OF “BLIND” SPECIES**

Within the *Gammarus pulex*-group, as in other groups of the genus *Gammarus*, populations can be observed in which the eyes are partially or even completely absent, usually because of their life in subterranean waters (springs, caves). In some cases, these populations are already completely isolated from relatives from superficial waters, thus forming new species like *G. vingai* Pinkster & Karaman, 1977 and *G. microps* Pinkster & Goedmakers, 1975 from caves in Turkey and Morocco, respectively. In other cases, however, the population living in subterranean waters are only partially isolated from other, epigean, populations of the same species, like *G. pulex polonensis* from a subterranean river in Poland.

In some populations from the Monfalcone springs in north-eastern Italy, we observed that specimens with normally developed eyes were accompanied by specimens with partially reduced eyes. On the other hand, in some populations of *Gammarus fossarum* from Croatia and Slovenia, Yugoslavia, specimens with normal developed eyes are often accompanied with specimens with enlarged eyes.

**HYBRIDIZATION EXPERIMENTS**

In order to form an idea about the significance of certain morphological differences in populations from different localities, some authors like Wautier & Roux, 1959; Roux, 1967; Meijering, 1972; Pinkster, 1972; Goedmakers, 1972; Goedmakers & Roux, 1975, started to do cross-breed experiments. These authors proved the existence of well established isolation mechanisms and were thus able to prove that *G. p. pulex*, *G. fossarum*, *G. wautieri*, and *G. monspeliensis* were good species. At the other hand it became clear that morphologically distinguishable forms like *G. p. gallicus* and *G. p. araurensis* were not genetically isolated from *G. p. pulex* but that nevertheless these populations could keep there own morphological features because of the existence of well-established geographical barriers. Thus these morphologically distinct forms must be considered subspecies of *G. pulex*. It was also shown (Goedmakers, 1972) that many morphologically distinct populations could exist within one species (*G. fossarum*) even without the existence of clear geographical barriers and thus are mere varieties of one and the same species. It will be clear that hybridization experiments can be a very useful instrument in solving such taxonomic problems. However, technical problems and the problem of transporting live animals from different parts of the world to the research-centre confine this type of taxonomic work.

**KEY TO THE (SUB)SPECIES OF THE GAMMARUS PULEX-GROUP MENTIONED IN THIS WORK (BASED ON ADULT MALES ONLY)**

1a) Eyes absent ............... 2
   b) Eyes present .............. 3
2a) Flagellum of A 2 slender .... *G. vingai* Pinkster & Karaman, 1977
   b) Flagellum of A 2 swollen . *G. pulex polonensis* n. spp.
3a) Eyes very small, round ........ *G. microps* Pinkster & Goedmakers, 1975
   b) Eyes normally developed, ovoid or reniform . 4
4a) Coxal plate 1 with dilated lower portion ........ .... *G. laitcordalis* n. sp.
   b) Coxal plate 1 not dilated ........ .... .... .... .... 5
b) Dorsal side of urosomites 1 and 2 not or only slightly elevated, never laterally compressed; postero-inferior corners of epimeres 2 and 3 never comma-shaped. 10

9a) Flagellum of A 2 swollen, with flag-like brush of setae; peduncle segments of A 2 poorly setose. .......................... G. agrarius G. Karaman, 1973
b) Flagellum of A 2 not swollen, poorly setose; peduncle segments of A 2 with long setae. .......................... G. syriacus Chevreux, 1895

10a) Basis of P 7 with very long setae along the posterior margin; epimeres 2 and 3 with numerous long setae along the ventral margin. .......................... G. rowxi Pinkster & Goedmakers, 1975
b) Basis of P 7 with short setae along the posterior margin; epimeres 2 and 3 with numerous long setae along the ventral margin. .......................... G. osellai n. sp.

11a) Inner ramus of 3rd uropod 1/3 to 1/2 the length of outer ramus. .......................... G. birsteinii nomen novum
b) Inner ramus of 3rd uropod at least half as long as outer ramus. .......................... 12

12a) Postero-inferior surface of basis of P 7 with setae. .......................... G. ibericus Margalef, 1951
b) Postero-inferior surface of basis of P 7 without setae. .......................... 13

13a) Peduncle segments of A 2 sparsely setose, calceoli present. .......................... G. pulex Lilljeborg, 1836
b) Peduncle segments of A 2 densely setose. .......................... G. rambouski S. Karaman, 1931

14a) Basis of P 7 without backward protruding lobe; urosome armed with many long setae. .......................... G. rambouski S. Karaman, 1931
b) Basis of P 7 with backward protruding lobe, urosome armed with (spines and) short setae. .......................... G. acalceolatus Pinkster, 1970

15a) Postero-inferior surface of basis of P 7 with setae. .......................... G. arduus G. Karaman, 1975
b) Postero-inferior surface of basis of P 7 without setae. .......................... 16

16a) Urosomites 1 and 2 dorsally elevated. .......................... 17
b) Urosomites 1 and 2 not (or only slightly) elevated. .......................... 20

17a) Urosomites 1 and 2 highly elevated, laterally compressed; epimeres 2 and 3 sharply pointed. .......................... 18
b) Urosomites 1 and 2 only moderately elevated, not compressed; epimeres 1 and 2 angular to moderately pointed. .......................... 19

18a) Flagellum of A 1 very long with 45 to 50 segments; flagellum of A 2 with flag-like brush of setae. .......................... G. pseudorynchus n. sp.

b) Flagellum of A 1 not very long; flagellum of A 2 without flag-like brush of setae. ..........................

19a) Peduncle of A 2 with long setae; flagellum not swollen. .......................... G. laborifer n. sp.

b) Peduncle on peduncle of A 2 short and scanty; flagellum swollen with brush of short setae. .......................... G. pulex gallicus S. Karaman, 1935

20a) Peduncle and flagellum of A 2 densely set with brushes of long setae. .......................... 21
b) Peduncle segments of A 2 with only a few brushes of setae. .......................... 24

21a) Peduncle segments of A 1 with only short setae. .......................... 22
b) Peduncle segments of A 1 with groups of long setae. .......................... 23

22a) Inner ramus of 3rd uropod longer than 3/4 of outer ramus; P 1 and 2 with straight setae; dorsal surface of urosome with short setae. ..........................

b) Inner ramus of 3rd uropod 1/2 to 2/3 as long as outer ramus; P 1 and 2 with many curled setae; dorsal surface of urosome with many long setae. ..........................

23a) Flagellum of A 1 with long setae. .......................... G. bergi Martinov, 1930
b) Flagellum of A 1 without long setae. .......................... G. frater n. sp.

24a) Propodus of P 1 and 2 with a strong spine in between the medial palmar spine and the palmar angle spines. ..........................

b) Propodus of P 1 and 2 without spines in between the medial palmar spine and the palmar angle spines. .......................... 25

25a) Posterior margin of P 3 and P 4 poorly setose, setae short; proximal portion of the outer margin of exopod in Ur 3 armed with spines only. ..........................

b) Posterior margin of P 3 and P 4 densely setose, setae long; setae are implanted along the entire outer margin of the exopod of Ur. 3. .......................... 26

26a) Epimeres 2 and 3 with sharply pointed postero-inferior corners. ..........................

b) Epimeres 2 and 3 rectangular to weekly pointed. .......................... 28

27a) Antennal gland cone distally recurved; P 3 to P 7 with short, stout dactylius. .......................... G. varroviensis Jazdowski, 1975
b) Antennal gland cone straight; P 3 to P 7 with long slender dactylius. .......................... G. laevis G. O. Sars, 1869

28a) Flagellum of A 2 without flag-like brush of setae. .......................... 29
b) Flagellum of A 2 with flag-like brush of setae. .......................... 32

29a) Inner ramus of Ur 3 longer than 3/4 of outer ramus; basis of P 7 with backward protruding lobe. ..........................

b) Inner ramus of Ur 3 shorter than 3/4 of outer ramus; basis of P 7 without backward protruding lobe. .......................... 30

30a) Peduncle segments 4 and 5 of A 2 with groups of setae being longer than the diameter of the segments on which they are implanted. ..........................

b) Peduncle segments 4 and 5 of A 2 with groups of setae being shorter than (or as long as) the diameter of the segments on which they are implanted. ..........................

31a) Antennae 1 and 2 very short; peduncle segments 4 and 5 with few groups of setae only. ..........................

b) Antennae 1 and 2 normally developed; peduncle segments 4 and 5 with many (more than 3) groups of setae. .......................... G. fossarum Koch (in Panzer, 1836)

32a) Flagellar segments of A 2 swollen, each segment bearing a dense row of 12 to 15 setae, together forming a flag-like brush. .......................... G. pulex pulex (Linnaeus, 1758)

b) Flagellar segments of A 2 less swollen, bearing only 6 to 8 setae on each segment. .......................... 33

33a) Setae on flagellar segments of A 2 longer than the length of the segments on which they are implanted, (epigean) .......................... G. p. aurantiensis Pinkster, 1972
b) Setae on flagellar segments of A 2 shorter than the length of the segments on which they are implanted, (hypogean) .......................... G. p. cognominis n. ssp.
**Gammarus p. pulex** (Linnaeus, 1758).

Figs. 1, 2, 3C-G, 4 and 5


*Rivulogammarus pulex pulex*; S. Karaman, 1931b: 101 fig. 6B; Cărușu, Dobreanu & Manolache, 1953: 82-85 figs. 44-47.

*Gammarus (Rivulogammarus) pulex*; Birstein, 1941: 259.

*Gammarus (Rivulogammarus) pulex pulex*; Schellenberg, 1937a: 499-502 fig. 7; 1937b: 276; 1942: 24-31 figs. 6-12; Birstein, 1945b: 153; Stephensen & Hynes, 1953: 291-296 fig. 1.

*Gammarus fluviatilis* Milne Edwards, 1830: 368.

*Gammarus fluviatilis var. zachariasi* Garbini, 1895: 205.

*Gammarus aquaticus* Leach, 1815: 359.

*Gammarus polymorphus* Helfer, 1914: 91.

**Diagnosis.** — A large form, making a robust impression (fig. 1A). Body smooth. Antenna 2 with a swollen compressed flagellum, bearing a flag-like brush of setae at the inner surface; calceoli present. Pereiopods 3 and 4 with long curled setae, pereiopods 5 to 7 almost without setae at the anterior margin of the segments.

Epimeral plates moderately pointed, armed with spines only. Uropod 3 densely setose, the inner ramus being about 3/4 to 4/5 times as long as the outer ramus. Urosome flat without dorsal elevations.

**Description.** — Male: Maximum length observed in many thousands of samples from all over the distribution area 23 mm. The urosome (fig. 3G) has a distinct though shallow excavation ("saddle"). Its general aspect is usually rather flat. The dorsal armature generally consists of a mid-dorsal group of elements and a lateral group on each side. These groups are usually a mixture of spines and setae which can be replaced by each other. Sometimes one or more of these groups can be completely absent.

The lateral cephalic lobes are usually rounded. The eyes are relatively small, always less than twice as long as wide, the upper margin of which is widely separated from the middorsal line (fig. 1E).

The first antenna (fig. 1B) is half as long as the body of the animal. The third peduncle seg-
ment is about half as long as each of the other two. The number of segments in the flagellum and accessory flagellum is largely variable, 22 to 35 and 3 to 6, respectively. The armature of both peduncle and flagellum is rather poor.

The second antenna (figs. 1C, 1D) shows one of the discriminating characters of the species. It is shorter than the first. The gland-cone is rather long, almost attaining the distal end of the third peduncle segment. Peduncle segments 4 and 5 are equally long and armed with tufts of short setae, implanted in three longitudinal rows. The length of these setae is shorter than the interval between the groups. The flagellum offers probably the most striking feature of this species; it consists of 12 to 18 segments, which are usually swollen and compressed; each segment is armed with a transverse row of setae on the inner surface, together forming a flag-like brush. In some populations, e.g. from Les Landes in France (figs. 1H and I) and from the southern part of Greece, the flagellar segments are less swollen and less compressed than in the typical form. Calceoli are always present on the first 6 to 9 segments.

The mouth parts of this species do not show obvious differences from other species within the genus *Gammarus* except in finer details of the mandibular palp. The upper lip (fig. 5E) is a little wider than deep, slightly emarginate near the apex. The mandibles have strongly dentate cutting edges, an accessory plate, a row of feathered setae and a strong molar (fig. 5F). The 3-segmented mandibular palp, like in all members of the *G. pulex*-group, has an unarmed first segment.
The inferior margin of the third segment is armed with a regular comb-like row of 25 to 38 D-setae and with 4 to 6 E-setae, some of them being plumose. In addition one group of A-setae and 1 or 2 groups of B-setae can be found (figs. 5G, H). The lower lip has no inner lobes (fig. 5D). Maxilla 1 with inner plate bearing long plumose setae, and outer lobe provided with stout serrate spines; palp of the right maxilla with spine-like teeth on the apex (fig. 5A), that of the left with setiform spines. Maxilla 2 is armed with rows of serrated bristles on both the inner and outer plates. The maxillipeds with the inner plate armed distally with strong spine-teeth; the outer plate with spine-teeth and long plumose spines; the palp is well developed. For further details see fig. 5C.

Coxal plates 1 to 7 are well developed; like in other members of the genus *Gammarus* the inferior corners of the 1st to 4th coxal plates are rounded (figs. 1F, 2A, 2C and 2D).

The propodus of the first gnathopod (figs. 1F, G) is pyriform, the palm being oblique and set with a strong medial palmar spine. A strong palmar angle spine together with some (usually 10 to 17) smaller spines can be found along the posterior margin and the inner surface of the hand. A varying number of setae can be found on the inner surface of the hand. The merus and carpus bear groups of long and often curved setae.

The propodus of the second gnathopod (figs. 2A, B) has about the same size as the first but is completely different in shape, because of its almost transverse palm. The strong medial palmar spine, which can be found in all members of this group, is separated from the palmar angle spines by a wide gap. The number of spines in the palmar

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Map III. The distribution of 11 (sub)species of the *Gammarus* pulex-group in Europe and northern Africa (the symbol for *G. pulex* refers actually to *G. pulex polonensis*).
Fig. 1. A-G. *Gammarus pulex pulex* (Linnaeus, 1758), $\delta$, 21 mm, from Lenstad, island of Öland, Sweden. A, habitus; B, first antenna; C, detail of second antenna; D, second antenna; E, head; F, first gnathopod; G, propodus of first gnathopod. H and I, *Gammarus pulex pulex* (Linnaeus, 1758), $\delta$, 16 mm from a small brook near Arès, dept. Landes, France. H, second antenna; I, detail of second antenna.
Fig. 2. *Gammarus pulex pulex* (Linnaeus, 1758), ♂, 21 mm, from Lenstad, island of Öland, Sweden. A, second gnathopod; B, detail of second gnathopod; C, third pereiopod; D, fourth pereiopod; E, fifth pereiopod; F, sixth pereiopod; G, pleopodal retinacula.
angle group is rather variable (from 3 to 5). Many groups of setae, variable in length and often curved, are implanted in the inner surface of the propodus.

The last three segments of the third pereiopod (fig. 2C) bear groups of long, often curved setae along the posterior margin. The number of setae and their length is somewhat variable, but usually 1.5 to 3 times as long as the diameter of the segments. The anterior margin of the merus is armed with 1 to 3 spines. The dactylus is rather short and stout.

The fourth pereiopod (fig. 2D) resembles the third one, although the setation is less dense and a little shorter.

The fifth pereiopod (fig. 2E) has a subrectangular basis with a more or less backward protruding lobe near its distal end always set with a spinule. In P6 and P7 (figs. 2F, 3C) the aspect of the basis gradually changes from almost quadrangular into more elongate. The armature of the distal segments of P5 to P7 usually consists exclusively of a varying number of spines. If setae are found, they are always shorter than the spines. In all pereiopods the relative length of the segments increases with age.

The inner ramus of the third uropod (fig. 3D) attains about 3/4 of the length of the first segment of the outer ramus. The greater part of the setae along the inner and outer margin of both endopodite and exopodite are plumose, except for those implanted near the top of the second exopod segment. The density of the setation and spinulation along the outer margin of the exopodite is largely variable throughout the distribution area of the species.

The posteroinferior corner of the first epimeral plate (fig. 3G) is always rounded, and set with some setules. In the second and third epimeres this corner is largely variable, varying from almost rectangular to moderately pointed; but never the sharp corner that can be encountered in G. lacustris or G. syriacus is found (vide infra). Although some long setae can be found along the anterior borders of the last two epimeral plates, their lower margins never bear setae.

The telson lobes (figs. 3E, 3F) are very variable in their armature (see also Pinkster, 1970). Along the outer margin 3 groups of elements can be found consisting of spines, setae or a mixture of both. A terminal group with 1 to 4 spines and a variable number of long setae is always present. In some populations, some setae or spines are implanted on the dorsal surface of the lobes.

Female: Smaller than male (maximum length observed 15 mm). Like in other groups of amphipods there exists a clearly marked sexual dimorphism which is visible in almost every appendage. The differences can be summarized as follows:

1) The setation of the peduncle segments of the first and second antennae is longer than in the male.
2) The characteristic brush-like aspect of the second antenna is almost absent (fig. 4A).
3) The propodus of the gnathopods (figs. 4B, C) is relatively smaller than in the male; medial palmar spines are always absent, and the total number of spines is reduced.
4) The setation of P3 and P4 is less abundant and shorter (figs. 4D, E).

Variability. — The variability observed in this species shows the same pattern as discussed in the general section on variability.

Material examined. — More than 2800 samples from all over the distribution area.
Loc. typ. — Island of Öland: Lenstad, brook with clear water. The δ neotype and many other topotypical specimens have been deposited in the collections of the Naturhistoriska Riksmuseet, Stockholm, under no. Amph. 3709.

Distribution. — In his 1972 paper Pinkster gave a review of the distribution of this species. During the present study material from some other areas is examined and at present the species has been found in southern Sweden, Finland, Denmark, Russia, Poland, Great Britain including Scotland and Ulster, the Netherlands, Belgium, France, Luxembourg, Germany, at lower altitudes in Switzerland and Austria, Bulgaria and Roumania, Yugoslavia, Turkey, Greece, Siberia including Lake Baikal, the greater part of China, the foot-hills of
the Himalaya mountains and Afghanistan (for refs. see Pinkster, 1972).

Remarks. — *Gammarus pulex pulex* is the type species of the genus *Gammarus*. Since it is well known and widely distributed, the species was also chosen as the nominal form of this species group.

Ecology. — Throughout its distribution area, *G. p. pulex* is a common inhabitant of middle and lower reaches of streams and rivers where stream velocities are moderate or low. Often it can also be found in the spring region of smaller streams where stream velocities are low and temperature fluctuations are limited (Meijering, 1971; Stock, Nijssen & Kant, 1966). When competing species are absent it can thrive throughout a stream (Goedmakers, 1974). Occasionally it has been found in stagnant pools and lakes especially when sufficient water movement due to wave action is present or in caves (Su Çiktigi Cave, Turkey).

It is often found together with other taxa of the genus *Gammarus* or with members of related genera like *Echinogammarus*, *Eulimnoamphipera* and *Pallasea*. Usually there is a strong competition between *G. p. pulex* and other gammarids, often resulting in a spatially separated distribution throughout a stream (Roux, 1967; Dennert, 1974).

Although the species usually occurs in freshwater it can live in a normal way in much higher salinities as was experimentally shown by Vincent, 1966, 1971. Schmidt, 1913 and Von Alten, 1915 reported the species from mineral springs with salinities up to 25370 mg/l. Pinkster, 1972 recorded a healthy *G. p. pulex* population from the exposed beach along the French channel coast. It can stand a rather high degree of organic pollution.

The reproductive period is largely variable throughout its distribution area and seems to be a function of both climatic and light factors.

The colour of live specimens is usually brown to greyish, although other colours can also be found, depending on the type of habitat.

In its large distributional area the species forms several geographically limited subspecies.

*Gammarus pulex araurensis* Pinkster, 1972.

Diagnosis. — A rather large form; except from some minor details in the second antenna (reduced number of setules on flagellum; flagellum segments not flattened) this subspecies closely resembles *G. p. pulex*.

Description. — Male: Maximum length observed 20 mm. The urosum is flat as in *G. p. pulex*, never showing dorsal humps as in *G. p. gallicus*.

The appendages of this subspecies are identical to those found in *G. p. pulex*, except for the second antenna, the peduncle of which is armed with more groups of setae, usually 3 to 4 on the fourth and 5 to 7 on the fifth segment, implanted in three longitudinal rows. The flagellar segments are never flattened, unlike the nominate subspecies. The setae, implanted on these flagellar segments are as long as in *p. pulex* but reduced in number (7 to 8 per segment) in comparison to the nominate subspecies (usually 12 to 15) (compare figs. 1C, D and figs. 3A, B).

Female: Females of this subspecies are not very characteristic and can be easily confused with females of *G. p. pulex*.

Material examined. — See Pinkster, 1972.

Loc. typ.: River Lamalou, near St.-Martin-de-Lamalou, France, dép. Hérault. The ♂ holotype, 9 allotype and about 100 paratypes have been deposited in the Zoölogisch Museum Amsterdam under cat. no. Z.M.A. Amph. 103.345.

Distribution. — At present this form is known from the upper regions of the rivers Lez, Hérault and Vidourle or their tributaries, a very restricted area in the French département Hérault (Pinkster, 1972).

Remarks and affinities. — Morphologically this subspecies is very close to both *G. pulex gallicus* and *G. p. pulex*, a notion confirmed by the results of hybridization experiments (Pinkster, 1972). However, the existence of geographical barriers creates the possibility that these closely related forms, although they can successfully cross-breed, can still maintain their own characteristics. Therefore we believe that this form (as well as *G. p. gallicus*) must be considered a distinct subspecies of *Gammarus pulex*. 
Fig. 3. A-B, *Gammarus pulex auroensis* Pinkster, 1972, ♀, 19 mm, from the river Lamalou, dept. Hérault, France. A, second antenna; B, detail of second antenna.

C-G, *Gammarus pulex pulex* (Linnaeus, 1758), ♀, 21 mm, from Lenstad, island of Öland, Sweden; E, do., ♂, 16 mm. C, seventh pereiopod; D, third uropod; E, F, telson; G, meta- and urosome.
Ecology. — This form has only been found in fast and moderately fast running stretches of some river systems (a biotope somewhat resembling that of *Gammarus wautieri*). It seems to avoid areas in which water temperatures in summer are too high. In few localities it has been found together with *Gammarus fossarum*. The colour of live specimens is brownish.
Fig. 5. *Gammarus pulex pulex* (Linnaeus, 1758), ♂, 21 mm, from Lenstad, island of Oland, Sweden. A, maxilla 2; B, maxilla 1; C, maxilliped; D, lower lip; E, upper lip; F, right mandible; G, mandibular palp, outer face; H, third segment of mandibular palp, inner face.
Gammarus pulex cognominis n. ssp. Fig. 6A-F.

Diagnosis. — Like *G. p. pulex* but differing in the less swollen and poorly setose flagellum of antenna 2, and the elongated pereiopods 5 to 7.

Description. — Male: Maximum length observed 15 mm. Body smooth. Uroscope very flat without any elevation. In the dorsal armature of the uroscope spines prevail; setae are usually absent; if present, their length does not exceed the length of the spines.

The lateral cephalic lobes are rounded, the eyes ovoid, nearly as long as the diameter of the peduncle of antenna 1.

The first antenna is slightly longer than half the body length and poorly setose. The main flagellum is long, having up to 45 segments. The accessory flagellum is 4- to 6-segmented. Each flagellar segment bears an aesthetasc increasing in length from 40 percent to 100 percent of the diameter of the segments on which they are implanted.

In A5, peduncle segments 4 and 5 have 4 to 5 and 6 to 7 transverse rows of short setae, respectively, the setae being as long as or shorter than the diameter of the segment on which they are implanted. The 14 to 17-segmented flagellum is less inflated than in *G. p. pulex*, slightly compressed dorsoventrally. Each segment is armed with 2 transverse groups of setae, as long as or shorter than the diameter of the flagellar segments. Calceoli are always present (fig. 6A).

The second segment of the mandible palp bears 4 to 5 setae in its proximal part and 8 to 9 setae in its distal part. The third segment bears 32 to 37 D-setae, 4 to 6 E-setae, 1 group of A-, and 1 group of B-setae.

The gnathopods are basically identical to those in *G. p. pulex*, but never bear curved setae.

The posterior margin of segments 4 and 5 in pereiopod 3 with numerous bunches of straight or curved setae (being as long as or slightly longer than the diameter of the segments on which they are implanted). The posterior margin of segment 6 is set with pairs of short spines, intermixed with several short setae.

The setation along the posterior margins of pereiopod 4 is slightly shorter than that of pereiopod 3. In P3 and P4 the dactyli are short. Pereiopods 5 to 7 (figs. 6B, C, D) are relatively long and slender, the margins of segments 3 to 5 have groups of spines only. Short setae can be found only at the posterior margin of segment 6. The basal segment of these legs never bears setae on the inner surface.

The epimeral plates are identical to those found in *G. p. pulex*. Uropod 3 is slender, with relatively narrow rami. The outer margin of the exopodite set with simple setae intermixed with several spines; the other margins of both rami bear both simple and plumose setae.

The telson lobes are relatively shorter than *G. p. pulex*, being wider than long (fig. 6E).

Female: Normal sexual dimorphism was observed. So, the setae on the peduncle of antenna 2 (fig. 6F) are slightly longer and more numerous than in the male; at the other hand the setation of the flagellum is less developed. The setation of pereiopods 3 and 4 is a little longer than in the other sex. Segment 4 of pereiopod 5 is in so far particular that several setae are implanted on its anterior margin intermixed with short spines; homologous setae are absent in P6 and P7.

Variability. — Apart from the usual variability the specimens from Ladžane, Bulgaria have an elongated telson compared with other populations, and resemble therefore, as far as this character is concerned *G. p. pulex*.

Material examined. — Bulgaria, prov. Loveč (type-lc.): — Devetska pšeterna cave, 18-III-1967, 8 holotype and 15 paratypes are deposited in the collection of G. Karaman, Titograd.

— Cave near village Devetaki, 25-VIII-1928, 3 specimens (Karaman Collection, Titograd = K.C.).

— Cave near village Ladžane, 16-X-1926, 5 specimens (K.C.).

Distribution. — Caves in the province of Loveč, Bulgaria.

Remarks and affinities. — *G. p. cognominis* is rather similar to *G. p. pulex*. It differs from it in the less setose antenna 2, in its more slender pereiopods 5 to 7, and in having sometimes a relatively shorter telson. It differs from *G. p. araurensis* by the less setose flagellum of antenna 2 in males; the flagellum is moderately swollen (not swollen in *araurensis*) and the setae on the flagellar segments are shorter. It differs from *G. p. gallicus*...
by the flat urosome (with elevations in gallicus), the rectangular epimeres 2 and 3 (moderately pointed in gallicus) and by the presence of a smaller number of setae on the flagellar segments of antenna 2. It differs from Gammarus microps in having a larger eye and less setose antenna 2.

Apparently, the widely distributed G. p. pulex has developed some more or less isolated subspecies adapted to subterranean life.

Gammarus pulex gallicus (S. Karaman, 1931).

Fig. 6G-1


Diagnosis. — Much smaller than G. p. pulex. Second antenna less swollen, and less setose than in the nominate subspecies. Urosome segments somewhat elevated. For the remainder, the species resembles p. pulex.

Description. — Male: Maximum length observed in more than 100 samples 14 mm. The body is smooth; the first urosome segment has an excavation like its larger relative. The other two urosome segments however show a low, but always distinct dorsal hump (fig. 6I).

The shape of the head, eyes, the mandibular palp and the first antenna resemble those of p. pulex.

The second antenna is different in so far that its flagellum is less swollen. Moreover, the setae implanted on the inner surface of the flagellar segments are shorter and reduced in number, never forming the flag-like brush which is so characteristic for p. pulex (figs. 6G and H).

The gnathopods and pereiopods 3 and 4 are like those in p. pulex. The fifth through seventh legs are less slender, resembling those of juvenile pulex pulex.

All other characters of this subspecies are more or less identical to those in p. pulex.

Female: Much smaller than the male. The maximum length observed in about 200 samples was 8 mm. This sex is not very characteristic since one of the discriminating characters, viz. the structure of flagellum of the second antenna, can only be found in the male. The only character in which females of this subspecies differ from females of other subspecies is the possession of elevated urosome segments. The colour of live specimens is usually a lighter or darker shade of brown.

Variability. — The variability pattern is identical to that encountered in Gammarus p. pulex.

Material examined. — More than 200 samples from the French départements Bouches-du-Rhône, Hérault, Gard, Var, Vaucluse and Basses-Alpes, including the type material.

Loc. typ.: Surroundings of Montpellier, France, dép. Hérault. The @ holotype and ± 30 paratypes are deposited in the collection of G. Karaman, Titograd.

Distribution. — This subspecies is known from a rather limited area in the southern part of France only.

Remarks and affinities. — From the description it will be clear that this subspecies is very close to G. p. pulex, showing only minor differences in the flagellum of the second antenna and in the somewhat dorsally elevated urosomites. Moreover, Roux, 1967, and Pinkster, 1972, proved that the two subspecies do easily cross-breed, and that the offspring from such hybridization experiments is morphologically identical to G. p. pulex. The only reason that this and other subspecies do not lose their identity in nature is the presence of geographical isolation barriers (Pinkster, 1972).

Margalef, 1944, mentioned this subspecies from the Spanish side of the eastern Pyrenees. Attempts to retrace this form failed however, so some doubts remain about its real identity. A sample from Margalef's locality, present in the collection of the M.C.S.N., Verona, proved to contain G. lacustris only.

Ecology. — Within its distribution area G. p. gallicus inhabits the lower stretches of river systems where stream velocities are usually low. It is often found accompanied by G. fossarum. In such localities G. fossarum inhabits the faster running parts of the stream while G. p. gallicus is restricted to the calmer, more slowly running waters near the bank. It can stand rather high summer temperatures, up to 26°C (own data).
Fig. 6. *Gammarus pulex cognominis* n. ssp. A-E, δ, 14.7 mm; F, θ, 10 mm; from Devetaška peštera cave, prov. Loveć, Bulgaria. A, second antenna; B, fifth pereiopod; C, sixth pereiopod; D, seventh pereiopod; E, telson; F, second antenna.


J-K, *Gammarus pulex polonensis* n. ssp., δ, 15 mm, from subterranean waterflow in old bed of river Warta, prov. Poznan, Poland. J, cephalic segment; K, second antenna.
Gammarus pulex polonensis n. ssp. Fig. 6J, K

Diagnosis. — Rather robust, smooth body. Eyes absent, antenna 2 with swollen, compressed poorly setiferous flagellum, calceoli present. Pereiopods 3 and 4 with long curled setae. Pereiopods 5 to 7 almost without setae along the anterior margin, their basis without setae on inner surface. Epimeres as in G. p. pulex. Inner ramus of uropod 3: 3/4 to 4/5 of outer ramus.

Description. — Male: Maximum length observed 16 mm. Body smooth, urosome almost flat with a shallow saddle on first segment. The elements on the urosome consist of some spines and setae as long as the spines.

The lateral lobes of the head are rounded. Eyes are completely absent (fig. 6J).

The first antenna is identical to that in G. p. pulex. The maximum number of segments observed in the flagellum is 25.

The second antenna is characteristic for this subspecies. The gland cone is short, attaining half the length of the third peduncle segment. Peduncle segments 4 and 5 are equally long, armed with a few groups of short setae only. The flagellum consists of 10 to 12 segments which are swollen and compressed. Compared with G. p. pulex the setae on the inner surface of these segments are reduced in length and number, thus never forming a flag-like brush (fig. 6K).

The third segment of the mandible palp bears 25 to 30 D-setae, 3 to 5 E-setae, 1 to 2 groups of B-setae and 1 group of A-setae.

Pereiopods 1 to 7, coxal plates, pleopods, uropods, telson and epimeral plates identical to those observed in G. p. pulex (see figs. 1F-G, 2, 3C-F).

Female: The normal sexual dimorphism was observed. The setae on peduncle segments 4 and 5 of A2 are little longer than in the male.

Variability. — Although we had only a small sample at our disposition it seems that the variability pattern is identical to that in G. p. pulex.

Material examined. — Poland, prov. Poznan (type-loc.), subterranean waterfall in old bed of river Warta, July, 1954, 10 specimens. The 8 holotype and 9 paratypes have been deposited in the collections of the Zoölogisch Museum Amsterdam under cat. no. Z.M.A. Amph. 104.012 a & b.

Distribution. — See sub material examined.

Remarks and affinities. — The swollen but poorly setiferous flagellum of the second antenna is a condition more or less intermediate between p. pulex and p. gallicus. The absence of eyes however makes this subspecies easily recognizable from all other subspecies of p. pulex. The other blind form within this group G. signai Pinkster & Karaman, 1977, has a very slender second antenna and very slender pereiopods, so any confusion with this species can be excluded. Since this subspecies was found within the distribution area of p. pulex and no reproductive isolation is proved so far we must consider this form an ecologically isolated subspecies of G. pulex.

Ecology. — In subterranean waters.

Gammarus microps

Pinkster & Goedmakers, 1975. Figs. 7 and 8

Ref.: Gammarus microps Pinkster & Goedmakers, 1975: 98-102, figs. 3-5.

Diagnosis. — Large animal with a smooth, slender body. Eyes very small, almost invisible. First and second antenna very long. All pereiopods very long, slender. Epimeral plates rectangular, sparsely armed. Transverse rows of spines are implanted on the inner surface of the propodus of P1.

Description. — Male: Maximum length observed 24 mm. The urosome (fig. 8G) has a distinct but shallow excavation (“saddle”) in the first segment. There are no dorsal elevations. The armature is poorly developed. In urosomite 3 the lateral group of elements seems to be absent.

The lateral cephalic lobes (fig. 8A) are more or less rounded. The eyes are very small, in some specimens almost invisible because of lack of pigment.

The first antenna is half as long as the body of the animal. The flagellum is very long having up to 46 segments in its main and 5 or 6 segments in its accessory flagellum (fig. 8B).

The second antenna (fig. 8C) is little shorter than the first. The gland cone is short. Peduncle segments 4 and 5 are both provided with groups of rather long setae, implanted in three longitudinal rows. The flagellum is shorter than the
Fig. 7. *Gammarus microps* Pinkster & Goedmakers, 1975, ♂, 23 mm, from Cave Ikhfou Ouan, prov. Taza, Morocco. A, mandibular palp; B, propodus of first gnathopod; C, third pereiopod; D, fourth pereiopod; E, fifth pereiopod; F, sixth pereiopod; G, seventh pereiopod.
Fig. 8. *Gammarus microps* Pinkster & Goedmakers, 1975, ♂, 23 mm, from Cave Ikhfou Ouan, prov. Taza, Morocco. A, cephalic segment; B, first antenna; C, second antenna; D, propodus of second gnathopod; E, third uropod; F, telson; G, meta- and urosome.
peduncle, its 15 to 19 segments are provided with a transverse row of 5 (on the first segment) to 10 (on the 7th and 8th segment) setae, usually longer than the length of the segments, giving the antennae a rather "hairy" impression. Calceoli are present on the first 8 to 10 segments.

The third segment of the mandibular palp bears about 25 D-setae, 4 or 5 E-setae, 1 group of A-setae and 1 or 2 groups of B-setae (fig. 7A).

The propodus of the first gnathopod (fig. 7B) is pyriform, very elongate, almost twice as long as wide. The dactylus is very long. The transverse rows of spines, implanted on the inner surface of the hand are characteristic for this species.

The propodus of the second gnathopod (fig. 8D) is large, making a swollen impression. Like in the first gnathopod the dactylus is long. In between the obtuse medial palmar spine and the palmar angle group of spines, characteristic for the *pulex*-group, another spine is implanted.

Except for their great elongation, P3 and P4 (figs. 7C and 7D) are not very characteristic; their coxal plates, like those of the gnathopods, have rounded inferior corners; the merus, carpus and propodus bear groups of long setae along their posterior margin.

The basal segment of the fifth pereiopod (fig. 7E) is slender, rectangular near its posterodistal end. The basis of P6 and P7 (figs. 7F, G) is more elongate than in P5. All segments of P5, 6 and 7 are very long and slender, armed with a varying number of very short spines sometimes intermixed with short setae.

The inner ramus of the third uropod (fig. 8E) attains about 3/4 of the length of the first segment of the outer ramus. The greater part of the setae, on the inner and outer margins of both endo- and exopodite are plumose.

The posteroinferior corner of the first epimeral plate (fig. 8G) is always rounded, set with some setules. The corners of the second and third plate are obtuse-angled to rectangular. A few spinules are implanted along the lower margins of the plates.

The telson lobes (fig. 8F) are slightly less than twice as long as wide. The armature is poorly developed and consists of some short terminal spines and setae.

Female: Smaller than the male (max. size observed 16 mm), most characters less pronounced. Even in this sex the species is still readily recognizable because of the very small eyes and the shape of the epimeral plates.

Material examined. — Cave Ikhouf Ouan (type-loc.), about 50 km S.W. of Taza, province of Taza, Morocco. Aug. 1972, 14 specimens. The ♂ holotype and 13 paratypes have been deposited in the British Museum (Natural History), London, under cat. no. 1974: 912 and 1974: 913, respectively.

Distribution. — See sub "material examined".

Remarks and affinities. — The very small eye, the long first antenna (with up to 46 flagellar segments), the shape and spinulation of the gnathopods, and the shape of the epimeral plates distinguish this species from all other species within this group.

Ecology. — Unknown.


Diagnosis. — A large blind species. The smooth body completely lacks pigment. The antennae and pereiopods make a slender impression. Epimeral plates are obtuse-angled to rectangular. Uropod 3 densely setose, the endopodite about 3/4 to 4/5 as long as the exopodite.

Description. — Male: Maximum length observed 22 mm. The urosome segments are low, not compressed, armed with a mid-dorsal group of elements and a lateral group on each side (fig. 9K, L).

The lateral cephalic lobes are rounded (fig. 9A). Eyes are completely absent. The first antenna is shorter than half the body length, peduncle segments 1 to 3 being progressively shorter. The maximum number of segments in the flagellum and accessory flagellum is 34 and 5, respectively.

The second antenna (figs. 9B and 9C) is relatively slender, its peduncle segments being poorly setiferous. The segments of the flagellum are also poorly setose, not swollen, the setae being always shorter than the segments on which they are implanted. Calceoli are always present. The antennal gland cone is as long as (in adult specimens) or
Fig. 9. A-L, *Gammarus vignai* Pinkster & Karaman, 1977, A-L, ♂, 20 mm; M, ♀, 12 mm; from a cave in the province of Konya, Turkey. A, cephalic segment; B, second antenna; C, detail of second antenna; D, third pereiopod; E, fourth pereiopod; F, fifth pereiopod; G, seventh pereiopod; G', dactylus of seventh pereiopod; H, third uropod; I, telson; J, epimeral plates; K, dorsal surface of urosome (lateral view); L, dorsal armature of urosome; M, second antenna.

*Gammarus vignai* Pinkster & Karaman, 1977, ♂, 20 mm; ♀, 12 mm; from a cave in the province of Konya, Turkey. A, cephalic segment; B, second antenna; C, detail of second antenna; D, third pereiopod; E, fourth pereiopod; F, fifth pereiopod; G, seventh pereiopod; G', dactylus of seventh pereiopod; H, third uropod; I, telson; J, epimeral plates; K, dorsal surface of urosome (lateral view); L, dorsal armature of urosome; M, second antenna.
longer than (in subadults) the third peduncle segment.

The third segment of the mandibular palp bears 34 to 37 D-setae, 3 to 5 long E-setae, 1 group of A-setae and 1 or 2 groups of B-setae.

The propodus of the first gnathopod is little shorter than that of the second. A medial palmar spine, two palmar angle spines and 3 or 4 smaller spines ("Stiftstacheln") can be found along the posterior margin and the inner surface of the hand. Segments 2 to 6 bear straight setae only.

Gnathopod 2 is slightly larger than gnathopod 1, its segments 4 and 5 being longer than the corresponding segments in the first. The propodus has almost parallel lateral margins. The armature consists of a medial palmar spine, 2 or 3 palmar angle spines and 2 or 3 smaller spines near the palmar angle.

Pereiopods 3 and 4 are slender and long. The posterior margin of segments 4 and 5 of P3 (fig. 9D) bear numerous long straight setae, the length of which never exceeds twice the diameter of these segments. In segment 6 these setae are much shorter, often replaced by short spines.

Except for the setae in the 4th and 5th segments, which are little shorter, P4 (fig. 9E) resembles P3. The dactyli of P3 to P7 are short, moderately slender (fig. 9G').

Pereiopods 5 to 7 (figs. 9F, G) are relatively slender and long. The basal segments are dilated, having a rectangular posterodistal corner.

Uropod 3 is moderately long with slender rami (fig. 9H). The endopod is 3/4 to 4/5 times as long as the exopod. The inner and outer margins of both rami are set with numerous tufts of simple and plumose setae. Apart from these setae, several spines are implanted on the outer margin of the exopod. The distal segment of the exopod is very short, shorter than the spines.

The posteroinferior corner of the first epimeral plate (fig. 9J) is rounded. In the second and third epimeres these corners are rectangular or slightly pointed. The distal margins of epimeres 2 and 3 bear 1 to 3 spines accompanied by 1 to 3 setae.

The telson lobes are slightly longer than wide, each lobe bearing a group of one spine and some setae along the distal margin and a group of setae on the dorsal surface; the outer margin is unarmed.

Female: The first and second antennae (fig. 9M) have more setose peduncular segments than in the male. Pereiopods 3 and 4 are less setose than in males. The telson lobes bear numerous long setae. Of course, females of this species are still very conspicuous, because of the absence of eyes.

Variability. — Although eyes are absent, sometimes small dots of red pigment can be found on the place of the eyes.

Material examined. — Turkey, province of Konya, cave called Camlik Dalayman Çocuk attıkları delik (type-loc.), April 24, 1974, 30 specimens. The ♂ holotype, ♀ allotype and 27 paratypes are deposited in the Museo Civico di Storia Naturale, Verona, Italy. One paratype is deposited in the collection of G. Karaman, Titograd, Yugoslavia.

Distribution. — See sub "material examined".

Remarks and affinities. — The absence of eyes and body-pigment, its slender antenna and its slender pereiopods make this species readily identifiable within the pulex-group. This absence of pigment and eyes and the long and slender extremities seem to be an adaptation to subterranean life. Similar adaptations have been found within the pulex-group (e.g. G. pulex polonensis, G. microps) and the balcanicus-group (G. albimanus G. Karaman).

Ecology. — Unknown.

Gammarus arduus Karaman, 1975. Fig. 10


Rivulogammarus komareki (non Schäferma); Cărășu, Dobrescu & Manolache, 1955: 86, figs. 48-51.

Diagnosis. — Like G. p. pulex, but with slender flagellum of antenna 2, with a setiferous distal margin of the second epimer and with a setiferous interior surface of the basal segment of pereiopods 6 and 7.

Description. — Male: Maximum body length observed 14.5 mm. Body dorsally smooth. Metasome segments 2 and 3 are sometimes armed with 2 to 4 short setae on the dorsal surface. The urosome and its armature are similar to that in G. p. pulex (fig. 10H).

The lateral cephalic lobes are rounded, the eyes are small, ovoid to slightly reniform, as long as or
shorter than the diameter of the first peduncle segment of antenna 1.

Antenna 1 is almost half as long as the total body length. Its peduncle as well as its flagellum are poorly setose. The main and accessory flagellum have 20 to 32 and 3 to 5 segments, respectively.

Peduncular segments 4 and 5 of antenna 2 (fig. 10A) bear several groups of setae which are as long as or little shorter than the diameter of the segments on which they are implanted. The flagellum is relatively slender, occasionally slightly swollen but always dorsoventrally compressed, it consists of 12 to 16 segments, armed with 1 or 2 transverse rows of setae along the inferior margin, the setae being as long as, or occasionally longer than, the diameter of the segments. Calceoli are almost always present in the first 8 to 12 segments. The tip of the gland cone almost reaches the distal end of the third peduncle segment.

The second segment of the mandibular palp bears up to 17 setae; the third segment is provided with 21 to 28 D-setae, 4 to 6 E-setae, 1 group of A-setae, and 2 groups of B-setae.

Coxal plates 1 to 4 have rounded inferior corners. Segments 2 to 6 of the first gnathopod are moderately setose, all setae being straight. The hand is set with a strong medial palmar spine, 2 to 4 palmar angle spines on the outer surface, and 3 to 6 submarginal spines on the inner surface. The dactylus is slender.

Segments 2 to 6 of gnathopod 2 are moderately setose, the setae being straight. The hand is slightly longer than in gnathopod 1. Apart from the usual medial palmar spine, 3 to 4 palmar angle spines and 2 or 3 submarginal spines can be found. The dactylus is slender.

Pereiopods 3 and 4 are slender, their dactyi short. Segments 3 to 6 of pereiopod 3 bear long, straight, or partially curved setae, 2 to 3 times as long as the diameter of the segments on which they are implanted. In pereiopod 4 these setae are less in number and shorter than in pereiopod 3 (1 to 1.8 times as long as the diameter of the segments).

Pereiopods 5 to 7 are moderately slender, the dactyi being short. The basis of P6 and P7 is set with a varying number of setae on the postero-interior surface. In P7 these setae are more numerous than in P6. In P7 the basal segment is about 1.5 as long as wide, its distoposterior end being wider than the proximal part of the next segment, forming a protruding lobe. The armature of segments 4 to 6 usually consists of spines only; if setae are present, they are always shorter than the spines (see figs. 10B, C and D).

Epimeres 1 and 3 are like those in G. p. pulex but epimere 2 is armed with numerous marginal and submarginal long setae. Epimere 3 bears spines at its inferior margin and occasionally 2 or 3 setae at its lower margin (fig. 10G).

Uropod 3 is moderately long, the inner ramus being 3/4 to 4/5 of the outer ramus. Both rami are armed with many groups of simple and plumose setae. In addition a varying number of spines can be found on the outer margin of the exopod (fig. 10E).

The telson lobes are 2 to 2.2 times as long as wide; each lobe has the usual distal group of spines and setae, the setae being about twice as long as the spines; several groups of setae, sometimes intermixed with a single spine, appear on the dorsal surface of each lobe (fig. 10F).

Female: Normal sexual dimorphism was observed. Some of the discriminating characters of the male are also present in the female, like the presence of setae on the inferior part of the second epimal plates and the presence of setae on the inner surface of the basal segment in pereiopods 6 and 7. Contrary to the situation in the male, long setae can be found on the anterior margin of segments 4 to 6 in pereiopods 5 to 7 (fig. 10J). The outer margin of the exopodite of uropod 3 only bears simple setae. The colour of live specimens is orange-brown to greyish.

Variability. — The metasome segments 2 and 3 are occasionally armed with 2 to 4 setae on the dorsal surface (specimens from Tekirdag, Horboz, and Sazli Dere, Turkey and from Ljubimec, Bulgaria). The number of setae on the inner surface of the basal segment of pereiopods 6 to 7 is rather variable and increases with age (2 to 15 setae on P7 and 0 to 7 setae in P6). The third epimere bears spines at the inferior part, occasionally accom-
Fig. 10. A-H, *Gammarus arduus* G. Karaman, 1975. A-H, ♂, 12.5 mm; I-L, ♀, 9.5 mm; from Krumovski izvori spring, Plovdiv, Bulgaria. A, second antenna; B, fifth pereiopod; C, sixth pereiopod; D, seventh pereiopod; E, third uropod; F, telson; G, second and third epimere; H, urosome; I, second antenna; J, seventh pereiopod; K, third uropod; L, telson.
panied by several setae in the anteroinferior part (in several populations from Bulgaria). The flagellum of antenna 2 is usually slender, occasionally slightly swollen (in populations from Dikilitaş, Bulgaria and Buru-Göl, Turkey).

Material examined.—

Turkey: Malkara, Tekirdag, N. of Marmara Sea, 6-VI-1970, many specimens (M.C.S.N.).

Buru Göl, fountain near house of Hor-Boaz, 17-XI-1942, 5 specimens (K.C.).

Sazli Dere, stream 20 km N. of Kircasalh, E. of Edirne, 1-VI-1973, 16 specimens, 2 precopulations (Z.M.A.).

Greece: Petuli, central Greece (21°31'E/37°21'N), alt. 1100 m, 26-X-1972, 1 specimen (K.C.).

Alephorion, Peloponnesus, (22°25'E/37°21'N), alt. 850 m, 15-IX-1972, 1 specimen (K.C.).

Platanousa, in Xerobouni Mountains (near Albanian border), 13-V-1932, 21 specimens (K.C.).

Brooklet fed by a well, 5 km W. of Alexandroupolis, 20-VI-1973, many specimens, many precopulations (Z.M.A.).

Stream called Pijë, at Agrinion (near Aya Sofia), 2-X-1973, many specimens, many precopulations (Z.M.A.).

Stream called Louros at Terrovo (near Ioannina), 2-X-1973, many specimens, many precopulations (Z.M.A.).

Stream called Trajos at Dara (near Tripolis), 29-IX-1972, many specimens (Z.M.A.).

Small stream crossing road from Karbounar to Kariña, 22-IX-1973, many specimens, 1 precopulation (Z.M.A.).

Small stream at Asopopolia (near Kalama), 22-IX-1973, many specimens, many precopulations (Z.M.A.).


Albania: Mountainous stream near Novi, alt. 1600 m, 13-VI-1952, 1 specimen (Z.M.A.).

Bulgaria: Spring near village Topolite, 14-V-1944, several specimens, accompanied by G. komareki (K.C.).

Opicvjat, 5-VI-1941, 20 specimens accompanied by G. cf. balcanicus (K.C.).

Spring near village Beikovo (near Plovdiv), 28-V-1940, 20 specimens (K.C.).

Krumovski izvori-spring, Plovdiv, 6-V-1940, several specimens, accompanied by G. komareki (K.C.).

Spring in village Topelii (W. of Ruse), 19-VI-1943, 19 specimens (K.C.).

Village Bigari (near Malko Trnovsko), Strandža Mountains, 29-V-1943, 10 specimens (K.C.).


Fountain, about 10 km from Dikilitaş, 14-IV-1944, 20 specimens (K.C.).

Small brooklet, 20 km W. of Sofia, 30-V-1973, 1 specimen (Z.M.A.).

Tributary of Marca at Popovica (27 km E. of Plovdiv), 31-V-1973, several specimens, 1 precopulation (Z.M.A.).

Small brook at Ljubimec (50 km E.S.E. of Haskovo), 31-V-1973, many specimens, many precopulations (Z.M.A.).

Localities cited.— Romania: Moneasa (reg. Arad); Hotarele (S.W. of Bucuresti); Izvarna (reg. Craiova); vide Cărăuşu, Dobreanu & Manolache, 1955.

Turkey: Malkara, Tekirdag, N. of Marmara Sea. G. Kara-

man, 1974.

Loc. typ. — Turkey, Malkara, Tekirdag (N. of Marmara Sea). The ♂ holotype and many paratypes are deposited in the Museo Civico di Storia Naturale, Verona, Italy.

Distribution: Romania, Bulgaria, Greece, European part of Turkey, Albania.

Remarks and affinities. — G. arduus is rather similar to Gammarus dulensis (S. Karaman) in the setiferous basal segment of P6 and P7 and in the presence of setae on epimere 2. It differs from this species in its much more setose antenna 2, P3 and P4, and uropod 3.

Cărăuşu, Dobreanu & Manolache, 1955: 86-90, figs. 48-51 gave a description of G. pulex koma-

reki auct. Comparison of this description with the type material of G. komareki and with G. arduus learns, however, that in reality they studied material of G. arduus. Gammarus komareki has a much more setose second antenna and moreover, this species never has setae on the interior surface of the basal segment in P6 and P7. The coexistence in one locality of both morphologically different forms is proof that they are good species.

Ecology. — This is a species from slowly to moderately fast running fresh waters, usually living between a dense vegetation of water-weeds. It is able to stand a rather high degree of organic pollution. In a few localities it has been found together with Gammarus komareki.

Gammarus inberbus n. sp. Fig. 11

Diagnosis. — A large, rather robust species, charac-

terized by the very poorly developed armature of almost all extremities.

Description. — Male: Body length up to 19 mm. Metasome and urosome segments smooth, without dorsal elevations or excavations. The dorsal armature of the urosome is poorly developed. In many specimens the dorsolateral groups of elements are absent from the first and third urosome segment. The lateral cephalic lobes are usually rounded. The eyes are relatively small, as in G. p. pulex.

The first antenna is about half as long as the body. Peduncle segment 3 is longer than half the length of each of the other two. The main and
Fig. 11. *Gammarus inberbus* n. sp., ♂, 18 mm, from Lake Issyk-Kul, Kazakhstan, U.S.S.R. A, first antenna; B, second antenna; C, mandibular palp; D, first gnathopod; E, propodus of first gnathopod; F, second gnathopod; G, propodus of second gnathopod; H, fifth pereiopod; I, seventh pereiopod; J, telson.
accessory flagellum have 20 to 25 and 4 or 5 segments, respectively. The peduncular and flagellar segment are very poorly setiferous (fig. 11A).

Antenna 2 is shorter than antenna 1. The gland cone attains the distal end of the third peduncle segment. Peduncle segments 4 and 5 are equally long bearing some tufts of short setae implanted in three longitudinal rows. The 10- to 13-segmented flagellum is armed with very few, short setae only. Calceoli are present in the first 6 to 8 segments (fig. 11B).

The second segment of the mandible palp bears up to 10 setae. The third segment bears 28 to 37 D-setae, 5 or 6 long E-setae, 1 group of A-setae, and 2 groups of B-setae (fig. 11C).

Gnathopod 1 is poorly setose (figs. 11D, E). The propodus is relatively short, armed with very few setae only. The dactylus is short. A strong pointed spine is implanted in between the median palmar spine and the palmar angle spine. Several spines, varying in number, occur along the posterior margin and along the inner surface of the hand.

Like the first, the second gnathopod is poorly setiferous (figs. 11F, 11G). The propodus is little longer than that of the first gnathopod. The dactylus is short. A strong pointed spine is implanted in between the medial palmar spine and the palmar angle group of spines. Two or three smaller spines are found on the inner surface near the palmar angle.

Pereiopods 3 and 4 rather slender. In P3 the setae on segments 4 and 5 are up to twice as long as the diameter of the segments. In P4 these setae are somewhat shorter and less numerous. The dactyls are short. Coxal plates 1 to 4 have rounded inferior corners.

Pereiopods 5 to 7 are slender. Their basal segment is relatively long and narrow, hardly forming a protruding lobe (figs. 11H, 11I); no setae have been observed on the inner surface. The armature of the other segments is poorly developed. The dactyls are short.

Epimeres 1 to 3 like those in G. p. pulex. The inferior margins never bear setae.

The third uropod is moderately long, its endopodite being about 3/4 of the exopodite. Both rami bear plumose and simple setae along the inner and outer margins. Some spines can be found in between the setae on the outer margin of the exopodite.

The telson lobes are elongate, more than twice as long as wide, bearing the usual group of apical spines and setae. These setae, like the few which can be found on the outer margin or the dorsal surface, are less than twice as long as the spines (fig. 11J).

Female: Normal sexual dimorphism was observed. Like in male all appendages are very poorly setiferous.

Variability. — As far as can be observed from the few samples we had at our disposal the variability does not show differences from the usual pattern within this group.


Loc. typ. — U.S.S.R., Republic Kazakhstan, Lake Issyk-Kul at Koïsara. The ♂ holotype, and 14 paratypes have been deposited in the collections of the Muséum national d'Histoire naturelle, Paris (France).

Distribution. — Until this moment this species is known from Lake Issyk-Kul only.

Remarks and affinities. — This species is characterized within this group because of the very poor setation of the appendages. Moreover, it has a strong spine implanted in between the medial palmar spine and the palmar angle (group of) spine(s) on both gnathopods. Within this group, this character is found in Gammarus crenulatus n. sp. only. The crenulate metasome of the latter species makes confusion almost impossible.

It is clear that this form must be considered a good species. However, we did not have the possibility to compare it with the material studied by Martinov, and one of his species might be identical to ours. So, the descriptions of G. ocellatus, Martinov, 1930 lines up with many details given here. However, Martinov at one hand does not mention the structure of the gnathopods and at the other hand he describes the eyes as large, reniform. Nevertheless some doubts remain about a possible synonymy of the two species.
Gammarus lacustris G. O. Sars, 1863.

Fig. 12A-D


Gammarus lacustris lacustris; Bousfield, 1958: 80.

Rivulogammarus lacustris; Dussart, 1948: 101-102; Straškraba, 1967: 208.

Gammarus (Rivulogammarus) lacustris; Schellenberg, 1937a: 490, figs. 2-6; 1937b: 276; 1942: 32-33, figs. 15-16; Birstein, 1945b: 154, fig. 2; Ruffo, 1951: 1, figs. 1-3; Pjäkić, 1963: 15-22, fig. 1; Vornatscher, 1965: 1.

Gammarus pulex; Dahl, 1915: 1-32, fig. 1; Stephensen, 1928 279, fig. 39 (1-6).

Gammarus pulex (part.); Sars, 1894: 503, pl. 177 fig. 2; Stebbing, 1906: 474.

Gammarus pulex De Geer morpha jenulcanensis Behning, 1921: 289 pl. 8 figs. 1-7.

Gammarus Scandinavicus S. Karaman, 1931b: 101, fig. 6a.

Gammarus bolkayi S. Karaman, 1934a: 325, fig. 1.

Gammarus weigeni Micherdziński, 1959: 598-599, fig. 81.

Squilla pulex; De Geer, 1778: 525, pl. 33.

Diagnosis. — A large, robust species. The habitus is pulex-like except for the relatively short but slender antennae, the sharper epimeres, and the slender dactyli of the pereiopods.

Description. — Male: Maximum length observed in more than 300 samples studied 25 mm (Lake Abant, Turkey). The metasome segments 2 and 3 bear some small setules along their posterior margins. The urosome (fig. 12A) has no excavations or elevations. The number of elements in the dorsal armature is reduced compared to p. pulex. The shape of the eyes and the lateral cephalic lobes are identical to those in p. pulex. The first antenna is relatively short, slightly longer than 1/3 of the total body length. The main and accessory flagella have 18 to 26 and 3 or 4 segments, respectively. The setation of both peduncle and flagellum is short.

Peduncular segments 4 and 5 of the second antenna (fig. 12B) are almost equal in length, armed with few tufts of setae, implanted in three longitudinal rows. The short flagellum (10- to 14-segmented) never has swollen segments or a flaglike brush as in G. p. pulex. The presence or absence of calcareous is variable, throughout the distribution area. We have the impression that in some populations calcareous disappear in certain periods of the year.

The third segment of the mandibular palp is armed with 25 to 34 D-setae, 3 to 5 E-setae, 1 group of A-setae, and 1 or 2 groups of B-setae.

The first and second gnathopods do not show important differences from those in G. p. pulex (see figs. 1F, 2A).

The setation of the third and fourth pereiopods is less dense than in p. pulex. The armature of pereiopods 5, 6 and 7 is basically the same as in G. p. pulex. A remarkable character of this species, already mentioned by Schellenberg, 1942 but erroneously not by Pinkster, 1972, and be found in the dactylus of P3 to P7 which is much more slender than in most other members of this group (see fig. 12C).

The structure of the epimeral plates is one of the discriminating characters of the species. The posteroinferior corner of the first is somewhat rounded, that of the second and third (fig. 12A) is always sharply pointed. Along the inferior margin of the last two epimeral plates a few spines and short setae may be implanted.

The endopodite of the third uropod reaches to about 3/4 of the first exopodal segment. The second segment of the exopodite is usually well developed. The setae along the inner and outer margins in both endo- and exopod are practically always plumose.

The telson lobes (fig. 12D) are sparsely armed, usually with no more than one or two terminal spines and some short setae. Rarely a subbasal spine can be found.

Female: Smaller than the male, most characters less pronounced than in the other members of this group. Females are still readily recognizable because of the sharp epimeral plates and the very slender dactylus in P3 through P7.

The colour of live specimens is greyish to brown or even greenish, depending on the habitat in which they are found.

Variability. — The variability pattern observed in this species does not show obvious differences with that observed in G. p. pulex.
Fig. 12. A-D, *Gammarus lacustris* G. O. Sars, 1863, ♂, 16 mm, from Loch Loyal, Scotland (G.B.). A, habitus; B, second antenna; C, seventh pereiopod; D, telson.

E-I, *Gammarus varsoviensis* Jazdzewski, 1975. E-H, ♂, 20 mm; I, ♀, 14 mm; from old bed of Vistula River, prov. Warsaw, Poland. E, second antenna; F, seventh pereiopod; G, telson; H, meta- and urosome; I, second antenna.
Material examined. — During the present study about 300 samples from all over the distribution area have been studied.

Loc. typ. — Sars, 1863 did not indicate a type-locality. Since this species was first published in his Beretning om en i Sommeren 1862 foregaten zoologisk Reise i Christianias og Trondhjems Stifter we must assume that he found his type material in the regions of Christiania (= Oslo) or Trondhjem. From his material, which is preserved in the collections of the Zoologisk Museet in Oslo a lectotype was selected. As restricted type-locality we selected: Norway, Selsvand, Vage. The lectotype has now been deposited in the Zoologisk Museum, Oslo under cat. no. F 382.

Distribution. — Pinkster, 1972, reviewed the known distribution of the species, based on data from literature and own material, as follows: Finland, Norway, Sweden, Scotland, Ireland, Denmark, Germany, northern Poland, Czechoslovakia, France, Switzerland, Italy, Austria and the entire Balkan region, U.S.S.R. (including Siberia), Turkey, Canada and the northern parts of the U.S.A. During the present study the species was also found in many mountain-lakes in Afghanistan and in India at the foothills of the Himalaya Mountains (material Z.M.A.), and on the Spanish side of the Pyrenees (material M.C.S.N.).

Remarks and affinities. — At first sight this species has no striking characters except for the structure of the epimeres and the slender dactyls. These characters suffice for discriminating this species. *Gammarus rouxi* is the only species with slender dactyls like *G. lacustris*, but differs from *lacustris* in almost all other characters. Sharp, pointed epimeres can be found in *G. monspeliensis*, *G. syriacus*, *G. agrarius*, *G. laborifer*, *G. osellai*, and *G. pseudosyriacus*. All these species have more or less elevated urosegmental nodes (versus flat in *lacustris*) but also differ from *lacustris* in the length and setation of the antennae or in the setation of the pereiopods (*syriacus, laborifer, agrarius, osellai*). The only species resembling strongly *Gammarus lacustris* is *Gammarus varsoviensis* Jaždżewski, 1975, which was hitherto confused with it. Jaždżewski, however, showed that differences were existing in (1) the relative length of the eyes; (2) the shape of the gland cone of A2; (3) the length of the flagella in A1 and A2; (4) the less slender dactyls; (5) the submarginal armature of the 2nd epimeral plates and the setosity of the urosome. Micherdziński, 1959, described *Gammarus wigrensis* as a distinct species, but Jaždżewski, 1975, proved that *wigrensis* was nothing but immature *lacustris*. Stráskraba, 1967 refers to *G. lacustris varvanticus* Behning. Since we were unable to study the types or the description of this subspecies we still are in doubt about its identity.

Ecology. — The species usually inhabits mountain and glacier lakes, but in some areas which have been glaciated during the last glacial periods, it also inhabits lowland lakes (e.g. Denmark, northern Germany and Poland). In some parts of its distribution area [Norway, (Økland, 1969), northern Sweden (Müller, in litt.); Eire (own observation), Poland (Jaždżewski, 1975, own observation), Canada (Bousfield, 1958; Hynes & Harper, 1972)] the species has been found in running waters. Økland suggested that this can be due to passive drift but the data from North America, Poland and Sweden (Bousfield, 1958; Hynes, 1972; Jaždżewski, 1975; Müller, in litt.) prove that this is not necessarily the case. In most cases this species is able to thrive in running waters because of the absence of competing species, a situation found in many parts of North America and the northern parts of Norway and Sweden. In Eire however, there is a strong competition with *G. duebeni celticus* Stock & Pinkster, 1970, as is suggested by the narrow zone of overlap between the species. *G. lacustris* in general seems to prefer stagnant waters with a rather high amount of organic sediment (Fryer, 1953; C. Roux, 1972). It can survive at low temperatures for a long time, but is rather susceptible to temperatures higher than 20°C.

*Gammarus varsoviensis* Jaždżewski, 1975.

Fig. 12E-I

Diagnosis. — Rather large species, resembling *G. lacustris*. The slender second antenna has a characteristic upwardly curved gland cone. Dactyli of pereiopods 3 through 7 as in *p. pulex*.

Description. — Male: Maximum length observed 20 mm. The body is robust, dorsally smooth. The posterior margins of the metasome segments are set with several fine, rather long setules (fig. 12H). Urosome segments almost flat with a very shallow saddle; their armature consists of one dorsomedian and one dorsolateral group on each side. Usually the setae in these groups are little longer than the spines.

The lateral cephalic lobes are more or less oblique, with rounded corners. The eyes are reniform, relatively large as compared with other members of this group, being about twice as long as wide.

Antenna 1: slightly more than half the body length. The number of segments in the main and accessory flagellum is 30 to 35, and 4 to 5, respectively. The armature of both peduncle and flagellum is very poor.

Antenna 2 is shorter than antenna 1. The gland cone offers one of the discriminating features of this species, being curved upwards (fig. 12E). Peduncle segments 4 and 5 are subequal in length, armed with few tufts of short setae, implanted in 3 longitudinal rows. The flagellum is slender, 13- to 17-segmented, with calceoli on the first 7 to 9 segments.

The third segment of the mandibular palp bears 23 to 28 D-setae, 4 to 6 E-setae, 1 group of A-setae and 1 group of B-setae.

The first and second gnathopods are basically identical to those in *p. pulex*.

Segments 4 to 6 of pereiopod 3 bear groups of very long, often curved setae along the posterior margin; the number of setae and their relative length increases with age. The dactylus is short, relatively stout. Pereiopod 4 is slightly shorter than P3, bearing somewhat shorter setae.

The shape and armature of pereiopods 5, 6 and 7 is basically the same as in *G. p. pulex*. The dactyli of these legs are relatively short, rather stout, less than 4 times as long as wide (fig. 12F).

The second and third epimeres are acute but less produced than in *G. lacustris*. The armature along the ventral margin consists of spinules only. Setae are never found.

The endopodite of the third uropod is about 3/4 of the exopodite. The setae along the outer margin of the exopodite are relatively long, more than twice as long as the diameter of the exopodite and often plumose.

The telson lobes (fig. 12G) are more than twice as long as wide. The armature resembles that of *G. p. pulex*. The apical setae are always longer than the spines.

Female: Although less pronounced, most of the characteristic features are as in the male.

Variability. — The variability was discussed at length by Jazdzewski, 1975. In general the variability pattern is identical to that encountered in *G. p. pulex*.


Other records. — See Jazdzewski, 1975: 76.

Loc. typ. — Old bed of the Vistula River in Secymin Nowy, Prov. Warszawa, Poland, 22-VIII-1969. The δ holotype, Ψ allotype and 6 paratypes have been deposited in the collections of the Zoologisch Museum Amsterdam under cat. no. Amph. 105.001 a, b and c. The remaining paratypes are deposited in the ZZOUL.

Distribution. — Northern Poland and the adjacent parts of the U.S.S.R. and Germany.

Remarks and affinities. — Until recently this species has been confused with *Gammarus lacustris*. Jazdzewski, 1975, however, made the differences clear. He found differences in the length/width ratio of the eye, the shape of the antennal gland cone, the number of the flagellar segments in the first and second antennae, the shape of the dactyli, the presence of setules on the metasome, the ventral armature of the epimeres, and the setosity of urosome and telson.
Ecology. — *G. varsoviensis* generally inhabits moderately flowing lowland rivers and streams. In some localities it has been found in lakes near the inflow or outflow of rivers. Often the species can also be found in flooded meadows or old river beds (see Jażdżewski, 1975).

**Gammarus laborifer** n. sp. Fig. 13

Ref.: *Gammarus syriacus* (part.); Chevreux, 1895: 160-164.

Diagnosis. — A rather large species. In general it looks more slender than most of the other species within the *pulex*-group. Relatively setose peduncles of antennae 1 and 2. Relatively short inner ramus of uropod 3.

Description. — Male: Maximum length observed 20 mm. The cephalic segment and the shape of the eyes are identical to those of *p. pulex*. The posterior margin of the third metasome segment is set with setules. The first and second urosome segments have well developed, laterally compressed dorsal elevations, almost resembling those in *G. syriacus* (fig. 13K). The dorsal armature consists of the usual middorsal and two lateral groups of spines and setae. The setae in these groups are often much longer than the spines.

The first antenna (fig. 13A) is half as long as or little longer than half the body length. It is slender, the third peduncle segment being much longer than half the length of the first or second peduncle segment. The inferior margin of the peduncle segments is armed with groups of rather long setae, a rather outstanding character within this group. The main and accessory flagellum have 32 to 40, and 3 or 4 segments, respectively.

The second antenna (figs. 13B, C) is also rather specific. Its gland cone is slender, attaining the tip of the third peduncle segment. The fifth peduncle segment may be a little longer than the fourth; both are armed with many groups of long setae along the inferior margin. The slender flagellum has a maximum of 15 segments, armed with a varying number of setae; these setae are longer than the diameter of the segments on which they are implanted. Calceoli may be found but are usually absent.

The mandibular palp has a second segment which is more densely setose than in most other members of this group. In the third segment the 25 to 30 D-setae are subequal in length, while the number of E-setae can be up to 8. Usually 2 groups of A- and 2 groups of B-setae can be found.

Except for some smaller details in the setation of the propodus (figs. 13E, F) (which never has curved setae) the first and second gnathopods resemble those in *p. pulex*. The same holds true for P3 and P4. The coxal plates of P1 to P4 are rounded.

The basal segment of P5 to P7 is relatively elongate, in P7 often more than twice as long as wide. The armature is poorly developed, in general consisting of a reduced number of small spines only (fig. 13G).

The first epimeral plate has a rounded to rectangular postero-inferior corner. In the second epimere this corner varies from rectangular to slightly pointed. The postero-inferior corner of the third plate is always sharper than the second but never as sharp as in *G. syriacus* or *pseudosyriacus*. The lower margin of the last two plates is set with some spinules only (fig. 13J).

The endopodite of the third uropod (fig. 13H) is rather short, hardly attaining 2/3 of the length of the exopodite. Long, often plumose setae are implanted on inner and outer margins of both endo- and exopodite.

The telson lobes, which are about twice as long as wide, show the same variable armature as in *p. pulex* (fig. 13I).

Female: Females of this species show the same dimorphism as in *p. pulex*. They are easily recognizable within the group because of the long setae on the pedunculus of the antennae, the setation of the mandibular palp, the elevations of the urosome, and the relatively short endopodite of uropod 3.

The colour of live specimens is brown to greenish.

Variability. — In addition to the pattern described for *p. pulex* variability can be observed in the height of the elevations of the urosome, the length of the setae on the peduncle of A1 and A2 and the
Fig. 13. *Gammarus laborifer* n. sp., ♂, 18 mm, from a small stream flowing into Lake Yamouné, Syria. A, first antenna; B, second antenna; C, detail of second antenna; D, mandibular palp; E, propodus of first gnathopod; F, propodus of second gnathopod; G, seventh pereiopod; H, third uropod; I, telson lobe; J, epimeral plates; K, urosome.
dactylus of P3 to P7 which can vary in slenderness. Probably this variability is age dependent.

Material examined. —
Nahr-el-Lebouch (Barraois), no date, 4 specimens (M.N.H.N.).
Lebanon: Running water near Yanconné, alt. 900 m, 25-VI-1972, 33 specimens (Z.M.A.).
Prov. Isparta, Egridir Lake, shore of the lake, 10-VII-1973, many specimens (M.C.S.N.).
Prov. Isparta, Egridir Lake, 4-VI-1970, many specimens (M.C.S.N.).
Prov. Isparta, water between Lake Egridir and Lake Byssehir, no date, 30 specimens (M.C.S.N.).
Loc. typ. — Mouth of small stream, running into Lake Yamouné, Syria. The holotype and 31 paratypes have been deposited in the collections of the Muséum national d’Histoire naturelle, Paris.

Distribution. — Actually this species is known from Lebanon, Syria, and the southern part of Asia Minor.

Remarks and affinities. — Chevreux identified part of the material as G. syriacus. However, this species is clearly different because of the absence of setae on the anterior margin of pereiopods 5 to 7. Moreover differences can be found in the setation of the mandibular palp, the second antenna and in the length of the inner ramus of the third uropod. It differs from G. pseudosyriacus and G. monspeliensis in the setation of the antennae and mandibular palp. Some populations have less elevated urosomes and/or less setose antennae and therefore can be confused with G. lacustris. However, in these cases the relative length of the endopod of Ur. 3 and the setation of the mandibular palp can be used as discriminating characters.

Ecology. — So far, this species has been found in the littoral zones of lakes or in the lower courses of rivers flowing into lakes. It can stand relatively high temperatures.

Gammarus gauthieri (S. Karaman, 1935). Fig. 14
Principal refs. — Rivulogammarus gauthieri Karaman, 1935: 47, figs. 1, 2.
Gammarus pulex subsp. gauthieri; Margalef, 1951: 267.
Gammarus (Rivulogammarus) pulex gauthieri; Schellenberg, 1937a: 503.
Gammarus gauthieri; Pinkster, 1971: 45-49, figs. 1, 2, 3A-I; 1972: 172, figs. 4A-D.

Diagnosis. — A medium large species. Except for some details in the second antenna and P5 to P7, the species resembles G. p. pulex in general appearance.

Description. — Male: Maximum length observed in 60 samples is 18 mm. The posterior margin of the third metasome segment is set with many setules. The urosome segments have no elevations or excavations. The armature shows the same variability as in G. p. pulex. The shape of the eyes and the lateral cephalic lobes are of the normal “pulex” type.

The first antenna (fig. 14A) is poorly setose, and almost half as long as the total body length. The peduncle segments are relatively short. The main and accessory flagella have 23 to 30, and 3 to 4 segments, respectively.

The second antenna (fig. 14B) is only sparsely armed with setae, most of them being rather short. The peduncle segments are strongly developed, about equal in length. The 12 to 15 flagellar segments are never swollen, the armature of which consists of some short setae only, implanted near the distal end of the segments. Calceoli are always present in adult males.

The third segment of the mandibular palp bears 25 to 30 D-setae, subequal in length, 5 or 6 E-setae, and one group each of B- and A-setae.

The morphology of the gnathopods and pereiopods 3 and 4 shows no differences with G. p. pulex. The distal end of the basal segments of P5 to P7 (figs. 14C, D and E) is always wider than the proximal end of the next segment, thus forming a protruding lobe. Occasionally a small setule can be found on this lobe; a spine like in the homologous position in G. waartieri has never been found. The armature of P5 to P7 is formed by spines, sometimes intermixed with short setae. The postero-inferior corner of the first epimeral
plate is rounded. In the second and third epimeres this corner is varying from almost rectangular to moderately pointed. Although some long setae can be found along the anteroinferior margin of the last two epimeres, their lower margin never bears setae (fig. 14I).

Uropod 3 (fig. 14F) closely resembles that of *p. pulex*. The telson lobes have a variable number...
of elements near their distal margin, together with some groups of setae on their dorsal surface (fig. 14G). Subbasal elements have never been found. Female: Shows a sexual dimorphism similar to that found in G. p. pulex. Because of the absence of very striking features (even in the male) the females of this species are hardly recognizable.

The colour of life specimens is usually greyish.

Variability. — The species is extremely variable (see Pinkster, 1971). The variability pattern, however, does not show fundamental differences from that encountered in other members of the pulex-group.

Material examined. — Over 60 samples from all over the distribution area including the type-material.

Loc. typ. — Oued Saida, at Saida, Morocco. The ♂ holotype, collected 24-III-1923, and 10 paratypes have been deposited in the Karaman Collection in Titograd.

Distribution. — This species is known from Tunisia, Algeria, Morocco and 31 more or less isolated localities in Spain (see Pinkster, 1971, and Goedmakers, 1974).

Remarks and affinities. — The species has no outstanding characters which separate it at first sight from other species within this group. Its most characteristic feature is found in the second antenna, with its relatively strong peduncle segments and very poor setation of the flagellum. This character, together with others like the wide basal segments and the absence of setae on the anterior margin of P5 to P7, the relative length of the endopodite of uropod 3, the flat urosome segments, and the slightly pointed epimeres 2 and 3 make this species distinguishable from all other species within this group.

The extreme intraspecific and intrapopulational variability were the reason for Goedmakers & Roux, 1975 to do hybridization experiments between some Spanish and a Moroccan population. Although they did not get any offspring from these crosses they could not conclude that two different species were involved because of the same negative results in their control experiments.

Ecology. — This species seems to prefer waters with a raised calcium ion content. Its localized occurrence in wells and upper reaches of streams in Spain (as well as the extreme variability within some populations (Pinkster, 1971)) are indications that these populations are relics of a formerly greater, probably more continuous distribution area in the Iberian peninsula. The occurrence of this species in several caves in Morocco (material studied during the present study) fits well in this “relict” theory. The species can stand high water-temperatures.


Diagnosis. — A medium large species making a rather robust impression because of its short antennae (fig. 15A). Pereiopods 5 to 7 are armed with spines only. The dorsal surface of the urosomites is flat.

Description. — Male: Maximum length observed 18 mm. The metasome segments are unarmed. The urosome segments have no dorsal excavations or elevations. The dorsal armature of the urosome is largely variable as in most species, always consisting of a dorsomedian and one or more groups of spines on either side. In between the spines some short setae can be implanted.

The shape of the cephalic segment and the eye are identical to those of G. p. pulex.

The first antenna is short, about 1/3 of the total body length. Peduncle segment 2 is about 2/3 of segment 1; peduncle segment 3 is about 2/3 of segment 2. The main and accessory flagella have 18 to 25, and 2 to 4 segments, respectively.

The slender gland cone of the second antenna (figs. 15B, K) attains the distal end of the third peduncular segment. Peduncle segments 4 and 5 are almost equal in length. Tufts of setae are implanted in three longitudinal rows on these segments. In every row 3 or 4 tufts are found. In younger animals, the tufts in the various rows are separated; in older animals tufts of different rows can merge, thus forming a kind of brush that surrounds the peduncular segment. The length of the setae, implanted in these tufts, increases from
Fig. 15. A-J, *Gammarus italicus* Goedmakers & Pinkster, 1977. A-G, ♂, 16 mm; H-J, ♀, 12 mm; from Torralba, Reg. Sardinia, Italy. A, habitus; B, second antenna; C, fifth pereiopod; D, sixth pereiopod; E, seventh pereiopod; F, third uropod; G, telson; H, second antenna; I, third uropod; J, telson.

about the diameter of the segment in the proximal groups to about 1.5 times the diameter of the segment in the distal groups. The 10- to 13-segmented flagellum is never flattened, sparsely setose, the setae being as long as the diameter of peduncular segment 5. Calceoli are often present.

The third segment of the mandibular palp is armed with 20 to 26 D-setae, 4 or 5 E-setae, 1 group of A-setae, and 1 or 2 groups of B-setae.

Gnathopods 1 and 2 as well as pereiopods 3 and 4 resemble those in *G. pulex* both in shape and armature. Coxal plates 1 to 4 have rounded inferior corners.

Pereiopods 5 to 7 (figs. 15C, D and E) have relatively short basal segments, varying from almost quadrangular in P5 to 1.5 times as long as wide in P7. The distal portion of the basal segments is always wider than the proximal portion of the next segment thus forming a backward protruding lobe. The interior surface of the basal segments is unarmed. The armature of the other segments consists of a varying number of spines or groups of spines, sometimes intermixed with short setae. The dactyli of all pereiopods are moderately slender.

The first epimeral plate has an almost rectangular posteroinferior corner. These corners are somewhat different in the second and third plate, being slightly pointed and sharply pointed, respectively. Their inferior margins are set with small spinules only (fig. 15A).

The third uropod is relatively short. Its endopod is 60% to 70% of the exopod. Plumose setae are found along the inner and outer margin of both endo- and exopod (fig. 15F, L).

The telson lobes (figs. 15G, M) overreach the pedunculus of the third uropod. Many (groups of) spines and setae can be found along the margins. Moreover, groups of spines and setae are implanted on the dorsal surface of the lobes. The setae, more in particular the terminal ones and those on the dorsal surface, are much longer than the spines.

Female: Normal sexual dimorphism was observed. Because of the absence of striking characters females of this species are easily confused with females of other species, especially with females of *G. wautieri*.

Live colour unknown.

Variability. — Apart from the usual pattern, variability was observed in the presence or absence of calceoli.


Loc. typ. — Italy, Sardinia, Torralba. The ♂ holotype and many paratypes have been deposited in the collection of the Museo Civico di Storia Naturale, Verona. 20 paratypes have been deposited in the Zoologisch Museum Amsterdam, cat. no. ZMA Amph. 105.477.

Distribution. — This species is widely distributed in the central part of Italy and the island Sardinia.

Remarks and affinities. — Most characters of this species are somewhat intermediate between *G. pulex* and *G. fossarum* as is the case in *G. wautieri*. However, it differs from the latter species because of its shorter antennae, the longer and more numerous setation of peduncle segments 4 and 5 of antenna 2 and in the presence of groups of spines and setae on the dorsal surface of the telson lobes.

Ecology. — This species is an inhabitant of wells and upper courses of rivers.


Figs. 16A-F


Diagnosis. — A medium large species. Except for differences in the structure and setation of the second antenna, this species makes the same impression as *G. p. pulex*. The flagellum of the second antenna is not swollen and bears no flag-like brush of setae. Calceoli are present. Urosomites 2 and 3 with minor elevations.

Description. — Male: Maximum length observed 16 mm. The first urosome segment has no dorsal excavation or elevation; the last two segments however have a low but distinct dorsal hump. The armature of the urosome as well as the shape of the head and eyes are as in *G. p. pulex*. 
The first antenna shows no special features and is poorly setose. Its main and accessory flagellum have 30 to 36, and 4 to 5 segments, respectively.

The gland cone of the second antenna (fig. 16A) is rather long, attaining the distal end of the third peduncle segment. The fifth segment is little longer than the fourth segment. Tufts of setae, varying in number, are implanted in three longitudinal rows on these segments. The flagellum is rather short, 10- to 13-segmented. The segments are never swollen and are less compressed than in G. p. pulex. A transverse row of at most 5 setae is implanted on each flagellar segment (fig. 16B), never forming a flag-like brush as in G. p. pulex. Calceoli are always present on the 2nd to 7th or 8th segments.

The mandible palp is identical to that in G. p. pulex. The gnathopods are as in typical p. pulex. The third leg is armed with many long setae, often curved in older males. The fourth leg is sparsely armed with rather short setae. Legs 5, 6 and 7 are of the normal pulex-type i.e. armed with spines only. The basal segment of the fifth leg always forms a backward protruding lobe (fig. 16C). In the seventh leg the basal segment is always set with a spinule (fig. 16D).

The shape of the epimeral plates is variable as in other species. Usually the posteroinferior corner is rounded in the first, almost rectangular in the second, and slightly pointed in the third plate. Spinules form the armature along the inferior margin of the second and third epimeres.

The endopodite of the third uropod is generally little shorter than 3/4 of the total length of the exopodite. Plumose setae can be found on the inner and outer margins of endo- and exopodite (fig. 16E).

The armature of the telson lobes is very variable like in many other members of this group. The terminal setae are always longer than the spines (fig. 16F).

Female: Females of G. wautieri lack most of the discriminating features present in the males. In mixed populations of p. pulex, wautieri and fossarum the females can still be distinguished because of smaller differences in the second antenna and third uropod (Roux, 1967), but this does not hold true for populations from different localities.

In that case intraspecific, interpopulational variability completely confuses the differences found in allopatric populations of the other species.

Variability. — As in p. pulex.


Loc. typ. — Roux, 1967 did not indicate a type locality. For the stability of nomenclature it is of the utmost importance that there is no doubt about the identity of the species. Consequently it is necessary to indicate a locality mentioned by Roux, 1967 as type-locality. We herewith restrict the type-locality to the river Vence, upstream of le Sappey-en-Sarreuse, France, dép. Isère. The δ neotype and many other specimens from the type-locality, collected on 28-III-1971 have been deposited in the collections of the Zoologisch Museum Amsterdam under cat. no. Z.M.A. Amph. 107. 190a, b.

Distribution. — The species was originally known from a rather limited area in the French Alps and Jura (see Pinkster, 1972). During the present study it was also found in some localities on the Italian side of the Alps. Jaždżewski, 1970 mentioned the species from certain localities in Poland. Cross-breed experiments carried out in Amsterdam between Polish populations and both Gammarus fossarum and G. wautieri from France proved that the Polish forms in reality belong to Gammarus fossarum as was already suggested by Goedmakers, 1972.

Remarks and affinities. — The morphological characters of this species are somewhat intermediate between G. p. pulex and G. fossarum. Dusaugey (1955) suggested that hybrids of these two species were involved. Cross-breed experiments by Wautier & Roux, 1959, Roux, 1967, and Pinkster, 1972 did not support this supposition and showed that G. wautieri is a good species.

Many morphological characters found in this species can also be found in Gammarus gauthieri, a species known from northern Africa and Spain (Pinkster, 1971). However, hybridization experiments by Goedmakers & Roux, 1975 gave so far negative results only, so we provisionally assume that wautieri and gauthieri are separate species.

Ecology. — Throughout its distribution area the species can be found in the middle reaches of river
systems with moderately fast running waters. This habitat is more or less intermediate between that of *G. fossarum*, the normal inhabitant of the upper reaches and that of *G. pulex*, the dominant form in the lower parts of the same river systems. There is always a broad zone of overlap between these three species. In localities where the three species coexist, the stony, fast running axis of the stream, where vegetation is nearly absent, is inhabited by *G. fossarum*, while *G. pulex* is predominantly found in the near-shore zone, where water currents are less strong and a rich vegetation can be found. *Gammarus waattieri* usually is the dominant species in between these two extreme microhabitats. In laboratory experiments Roux, 1967 proved that this species was also intermediate between *G. pulex* and *G. fossarum* in its oxygen consumption rate, its sensibility for high temperatures, and its resistance against water currents. These results perfectly agree with field observations.

**Gammarus kischineffensis** Schellenberg, 1937.

Figs. 16H-J, 17


Diagnosis. — Rather slender species. Easily recognizable because of the short setation of pereiopods 3 and 4. Moreover, the outer margin of the exopodite in uropod 3 is poorly setiferous. These characters are intermediate between the *G. pulex*-group and the *G. balcanicus*-group.

Description. — Male: Maximum length observed 17 mm. Body dorsally smooth without elevations or excavations. Some setules can be found along the posterior margin of metasome segments 2 and 3. The armature of the urosomites resembles that in *p. pulex* (fig. 17J).

The lateral lobes of the head are rounded (fig. 17A), the eyes being variable in size from almost round (type material) to reniform (in Polish material).

The relative length of the peduncle segments of the first antenna (figs. 17B, K) is variable, as is their armature (see under variability). The main and accessory flagella are 22- to 33-, and 3- to 4-segmented, respectively. They are poorly setose.

The second antenna has a short gland cone, being half as long as the third peduncle segment. Peduncle segments 4 and 5 are about equal in length. Their setation is rather variable as is shown in figs. 17C and 17L. The slender flagellum consists of 10 to 13 segments, all being poorly setose. Calceoli are found in the 2nd through 7th segments.

The third segment of the mandibular palp is armed with 26 to 32 D-setae, 3 to 5 E-setae, 1 group of A-setae and 2 groups of B-setae.

The first and second gnathopod are of the same type as found in *p. pulex* and moderately setose.

Pereiopods 3 and 4 belong to the distinguishing characters of this species, because of the short setation of segments 4 to 6 (figs. 17D, E). In P3 the setae are at most as long as the diameter of the segments on which they are implanted, in P4 they are always shorter than the diameter of the segments. The dactyls are short. The inferior corners of the coxal plates are rounded in P1 and P2 and quadrangular in P3 and P4.

Pereiopods 5 to 7 are moderately slender (figs. 17F, G and H). In P5 the basis is little longer than wide, in P7 about 1.5 times as long as wide. Sometimes short setules can be found on the inner surface of the basis in P6 and P7. The distoposterior end of these basal segments is always wider than the proximal end of the next segment, thus always forming a protruding lobe. The armature of the other segments of P3 through P7 mainly consists of spines. The dactyls are short.

The posteroinferior corner of the first epimeral plate is always rounded, in the second and third epimeres it varies from almost rectangular to moderately pointed (fig. 17J). The armature consists of spines only.

In addition to P3 and P4, the third uropod is one of the characteristics of this species in that the setation of the exopod is lacking in the lower half (as in the *G. balcanicus*-group). In the distal half few relatively short setae are implanted, only few of them being plumose. The inner ramus is about 3/4 of the outer ramus (fig. 16H).
Fig. 16. A-F, *Gammarus wautieri* A. L. Roux, 1967, ♂ 15 mm, from river Vence, dépt. Isère, France. A, second antenna; B, detail of second antenna; C, fifth pereiopod; D, seventh pereiopod; E, third uropod; F, telson; G, epimeres.

Fig. 17. A-J, *Gammarus kischineffensis* Schellenberg, 1937, ♂, 15 mm, from Kischineff, Ukrainian S.S.R. A, cephalic segment; B, first antenna; C, second antenna; D, third pereiopod; E, fourth pereiopod; F, fifth pereiopod; G, basal segment of sixth pereiopod; H, basal segment of seventh pereiopod; I, telson; J, meta- and urosome.

The telson lobes are about twice as long as wide. The armature consists of an apical group of elements together with some spines and/or setae on the dorsal surface or along the outer margin. The apical setae are up to twice as long as the spines (fig. 171).

Female: The setae of P3 and P4 (figs. 16I, J) are relatively longer than in the other sex, in P3 often longer than the diameter of the segment on which they are implanted. As in the male, the outer margin of the exopodite of Ur. 3 is poorly setose. Plumose setae have never been found along the outer margin.

Variability. — Apart from the normal variability observed within this group the following characters appeared to be variable throughout the distribution range: (1) The relative length of the peduncle segments of A1 (in Polish material the first and second segments are always equal in length, in the material from the type locality and the southern part of the U.S.S.R. the second segment is much shorter than the first one); (2) the setation of the peduncle segments of A1 and A2 (specimens from Poland are more setiferous than those from the type locality or from the U.S.S.R.).

Material examined. —


Distribution. — This species is known from southern Poland, Czecho-Slovakia, Roumania, Bulgaria, the southwestern part of the U.S.S.R., and the eastern part of Asia Minor (see also Jażdżewski & van Mansvelt, 1973; Dedju, 1967).

Remarks and affinities. — Because of the structure of P3, P4, and uropod 3 this species is more or less intermediate between the G. pulex-group and the G. balcanicus-group. It differs from the pulex-group by its remarkably less setiferous P3 and P4 and outer margin of the exopod of uropod 3. It differs from the balcanicus-group in the presence
of plumose setae on the outer margin of uropod 3. However, since these groups are merely artificial we decided to include the present species here as well as in a future revision of the balcanicus-group.

**Gammarus laticoxalis** n. sp. Fig. 18

Diagnosis. — A medium large species. Except from its characteristic first coxal plate, the species does not look very special. The inner ramus of the third uropod is about half as long as the outer ramus.

Description. — Male: Maximum length observed 16 mm. The last metasome segment is set with some setules along the posterior margin. The urosome segments have no dorsal elevations (fig. 18K). In many specimens a shallow excavation ("saddle") can be found on the first urosome segment. The dorsal urosome armature is poorly developed. On the first urosome segment only a middorsal group of small setae is found. On the last two segments the usual middorsal and two lateral groups can be found. The cephalic segment and the eyes are identical to those described for *p. pulex*.

The first antenna (fig. 18A) is little shorter than half the body length. The third peduncle segment is about half as long as each of the other two. The peduncle segments and the 27- to 35-segmented flagellum bear only a few setae. The accessory flagellum is 3- or 4-segmented.

The second antenna (fig. 18B) is shorter than the first. The gland cone does not reach the top of the third peduncle segment. Peduncle segments 4 and 5 are about equal in length and both are provided with tufts of short setae, implanted in three longitudinal rows. The length of these setae is usually less than the intervals between the tufts of setae. The flagellar segments are slightly swollen, somewhat compressed like in *pulex galicus*. However, the short setae implanted on these flagellar segments never form a flag-like brush like in *p. pulex*. Calceoli were found on the first 8 to 9 segments.

The third segment of the mandibular palp bears 25 to 30 D-setae and 5 or 6 E-setae along the inferior margin. Moreover 1 group of Α- and 1 group of B-setae can be found.

The first gnathopod is one of the discriminating characters of this species because of the shape of its coxal plate which has a dilated lower portion, a feature never observed in other members of this group (fig. 18C). This lower portion thus forms a forward protruding lobe which covers a large portion of the cephalic segment. The other segments of this gnathopod do not show important differences from those in *G. p. pulex*.

The second gnathopod, and pereiopods 3 through 7 resemble those of *G. pulex*. Coxal plates 2 to 4 have rounded inferior margins (see figs. 18D-H).

The first epimeral plate has a rectangular posteroinferior corner. In the second and third epimeres these corners vary from almost rectangular to slightly pointed. Small spinules along the inferior margin form the only armature of the second and third epimeres (fig. 18K).

The inner ramus of the third uropod (fig. 18I) is about half the length of the outer ramus, as in *G. fossarum*. Plumose setae are always found along the inner and outer margins of endo- and exopod.

The telson lobes are long, more than twice as long as wide. The armature consists of the usual distal group of elements together with smaller groups on the dorsal surface or lateral margins (fig. 18J).

Female: Shows the normal sexual dimorphism known in this group. The shape of the coxal plate in P1 and the short inner ramus of the third uropod make the species easily recognizable, also in the female sex.

Variability. — Shows the same pattern as in *p. pulex*.

Material examined. — Only known from the type-locality: Under the stones of a small well at Ain-Fidje, (Anti-Liban), Syria, 1911, 34 specimens. The 2 holotype and 33 paratypes have been deposited in the collections of the Muséum national d'Histoire naturelle, Paris.

Remarks and affinities. — Chevreux, 1915 identified these specimens as *G. syriacus*. From the description given here, it will be clear that this must be a mistake. The species neither has setae along the anterior margins of the 5th to 7th pereiopods nor the very sharp epimeral plates which are so characteristic for *G. syriacus*. Because
Fig. 18. *Gammarus laicoxalis* n. sp., ♀, 16 mm, from a well at Aïn Fidje, Syria. A, first antenna; B, second antenna; C, first gnathopod; D, second gnathopod; E, third pereiopod; F, fourth pereiopod; G, basal segment of fifth pereiopod; H, basal segment of seventh pereiopod; I, third uropod; J, telson; K, meta- and urosome.
of the armature of the pereiopods and the short inner ramus of uropod 3 (which is half as long as the outer ramus), the species could possibly be confused with _G. fossarum_, but the structure of the coxal plate of the first gnathopod is typical. Ecology and live colour unknown.

**Gammarus fossarum** Koch, in Panzer, 1836.

Figs. 19 and 20


_Rivulogammarus_ fossarum; Stráškraβa, 1967: 220.


_Gammarus (Rivulogammarus) fossarum_; Vornatscher, 1965: 1; Stráškraβa, 1962: 118.

_Rivulogammarus pulex fossarum_; Cárαšu, Dobreanu & Manolache, 1955: 90-92, figs. 52-53.

_Gammarus delebequei_ Chevreux & de Guerne, 1892: 136, figs. 1, 3, 5; Stebbing, 1906: 473; Spandl, 1924: 442; [non Margalef, 1944: 207. (= _G. gauthieri_)].


_Gammarus pulex danubialis_ f. _subterranea_ S. Karaman, 1931b 103.

_Gammarus pulex var. subterraneus_; Schneider, 1885: 1087.


_non Gammarus fossarum bodanicus_ Schellenberg, 1934: 216 (= _G. lacustris_).

_non Gammarus (Rivulogammarus) pulex fossarum_ f. _bodanica_ Schellenberg, 1942: 32, fig. 14 (= _G. lacustris_).

Diagnosis. — A relatively small species. Its habitus is less robust than that of _p. pulex_. The peduncle of the second antenna is more setose than in _p. pulex_. The inner ramus of the third uropod is about half as long as the outer ramus.

Description. — A redescription of topotypes of this species was given by Goedmakers, 1972. For the sake of completeness the most important characters will be repeated here.

Male: Maximum length observed in about 900 samples 14 mm. The dorsal surface of the urosomites shows neither excavations nor elevations. The dorsal armature is basically the same as in _p. pulex_.

The lateral cephalic lobes are rounded, the eyes are usually small, although some populations can have much larger eyes (see sub variability and figs. 20A, B and C).

The first antenna is almost half the body length of the animal. The main and accessory flagellum have 25 to 32 and 3 to 5 segments, respectively. The setation is poorly developed.

The setation of the second antenna (figs. 19A-D) is largely variable in density and length. The peduncle segments 4 and 5 of A2 bear many groups of setae implanted in three longitudinal rows. The length of these setae, although variable, is at least as long as, but usually longer than the diameter of the segments on which they are implanted. The segments of the slender 10- to 14-segmented flagellum are set with some setae near their distal ends, never forming a flag-like brush as in _p. pulex_. In some populations calceoli are always present, in others they are always absent. For a more complete discussion of the variability in the second antenna see Goedmakers, 1972.

The third segment of the mandibular palp is armed with a regular comb-like row of 28 to 35 D-setae and 4 to 6 E-setae, some of them being plumose. One group of A-setae and 1 or 2 groups of B-setae complete the armature of this segment.

The first and second gnathopods closely resemble those in _p. pulex_. The length of the setae implanted on P3 and P4 (figs. 20D-G) is rather variable as was demonstrated by Goedmakers, 1972 but not fundamentally different from other members in this group like _G. p. pulex_ or _G. lacustris_. The other appendages, except the third uropod, are similar to those of _G. p. pulex_ (figs. 20H, I).

The most characteristic feature of this species is the ratio length endopod versus exopod in uropod 3 varying from 0.4 to 0.6 in adult specimens. Although the setation is rather variable throughout its distribution area (see Goedmakers, 1972) this ratio stays rather constant (see figs. 19E and F).

The shape and armature of the telson lobes and the epimeral plates are basically the same as in _p. pulex_ (fig. 20J).

Female: As in other gammarid species the female is smaller than the male, and differs from it in the longer setation of the antennae, the shape of the gnathopods, the absence of medial palmar spines.
Fig. 19. A-H, *Gammarus fossarum* Koch, 1836. A, B, F, ♀, 12 mm; G, H, ♂, 9 mm; from a small stream near the Weichselmühle, S. of Regensburg, G.F.R. A, second antenna; B, detail of second antenna; F, third uropod; G, third uropod; H, second antenna.

C and E, *Gammarus fossarum*, ♂, 14 mm, from a mountain stream near Sarcenas, dept. Isère, France. C, second antenna; E, third uropod.

D, *Gammarus fossarum*, ♀, 14 mm, from a spring near Terziet, prov. Limburg, the Netherlands. D, second antenna.
Fig. 20. A, *Gammarus fossarum* Koch, 1836, ♀, 12.5 mm, from Žuženberg, Slovenia, Yugoslavia. Cephalic segment.
B and C, *Gammarus fossarum*, ♂, 8 mm, from Bocce del Timavo, Italy. Cephalic segments.
on the propodus of the gnathopods and uropods. Female *fossarum* can be easily told apart from females of other closely related species because of the longer setation in the second antenna (fig. 19H) and the short inner ramus of Ur. 3, which is often no more than 40% of the length of the outer ramus (see fig. 19G).

Colour of live specimens usually brownish, often with some red spots on the metasome segments.

Variability. — Goedmakers, 1972, already discussed the variability of this species. In general it can be said that the variability is about the same as in *p. pulex*. The variability of the setation in the second antenna and pereiopods 3 and 4 is even more pronounced than in the latter species. The presence or absence of calceoli, a stable character in many species, is a very variable character in *fossarum*. In some populations, e.g. from the Montfalcone springs in northeastern Italy great variability can be observed in the shape of the eyes, which can range from very small to very large. All transitions between these extremes can be found. In some areas e.g. in the French Pyrenees, the French Alps and the Greek island of Thasos the dorsal armature of the urosome is reduced in so far that the dorsolateral group of elements is usually lacking in the first urostyle segment.

Material examined. — More than 900 samples from all over the distribution area.

Loc. typ. — A small stream near the Weichselmühle, South of Regensburg a.d. Donau, Land Bayern, German Federal Republic. The δ neotype and many other specimens have been deposited in the collections of the Institute of Taxonomic Zoology (Zoölogisch Museum) Amsterdam under cat. no. Z.M.A. Amph. 103.337.

Distribution. — *Gammarus fossarum* is a widely distributed species, that has been found in France, eastern Belgium, Luxemburg, the southern parts of the Netherlands, southern and central Germany, southern Poland, Czecho-Slovakia, Austria, Switzerland, northern Italy, Jugoslavia, Hungary, Roumania, Bulgaria and northern Greece (see Goedmakers, 1972). During the present study the species was also found in the southern part of Greece and the northern part of Asia minor (coll. Z.M.A.).

Remarks and affinities. — Because of the extreme variability in the setation of its second antenna, its pereiopods 3 and 4 and its third uropod, many populations of this species have been described as new taxa (see synonymy). Goedmakers, 1972, proved that most of these morphologically different forms must be considered mere varieties of one and the same species: *G. fossarum*. Reexamination of the type material of *G. fossarum bodanicus* Schellenberg, 1934 learned that this subspecies must be considered subadult *G. lacustris*. Some doubt remains about the identity of *G. pulex* var. *subterraneus* Schneider, 1885. Since we were unable to study this material it is impossible to solve the problem in this work. However, reading the description of Schneider, we tend to believe that this subspecies is either subadult *G. p. pulex* or subadult *G. fossarum*. G. Karaman, 1973 described *G. cantor*, characterized by the absence of the dorsolateral armature of urosomite 1. Since this character proved to be variable in *G. fossarum* and many populations can be found in which the dorsolateral armature is reduced in the same way, we now consider this species a mere variety of *G. fossarum*. Margalef, 1944 and 1953 mentions *G. fossarum* from the Spanish province of Avila. However, systematic sampling throughout all provinces of Spain, did not reveal this species and we believe that Margalef in reality has studied material belonging to *G. gauthieri* or *G. ibericus*.

Ecology. — *G. fossarum* usually inhabits the upper reaches of streams (see e.g. Nijssen, 1963; Kallnbach & Meiijering, 1970). Its occurrence there is not only due to its capacity to withstand rather high current velocities and low temperatures, but moreover, to lower competition pressure by other related species like *G. p. pulex* (cf. Meiijering, 1971) or *G. roeselii* (cf. Besch, 1968). According to these authors, *G. fossarum* can be completely expelled from the lower reaches of streams by these species. In areas where it coexists with other species, it usually lives in those parts of the river where the highest stream velocities occur (e.g. A. L. Roux, 1967). It can stand rather high amounts of ions as was shown by Stock, Nijssen & Kant, 1966. The same holds true for organic pollution, although it is more susceptible for it than
G. p. pulex or G. roeseli (see Besch, 1968). The species can reproduce throughout the year when conditions are not too extreme. When summer temperatures are too high, it only reproduces in winter.

Gammarus uludagi G. Karaman, 1975. Fig. 21


Diagnosis: A small species, at first sight resembling Gammarus fossarum. The flagellum of the second antenna, however, is bearing a flag-like brush as in p. pulex. A rather characteristic feature is the relatively short telson, set with numerous long setae. Uropod 3 bears simple setae only.

Description. — Male: Maximum length observed 11 mm. Body smooth, urosome flat. The dorsal urosome armature prevalently consists of a great number of setae. All groups are present (fig. 21N).

The lateral cephalic lobes are rounded. The eyes are reniform to ovoid, as long as or shorter than the diameter of the peduncle of antenna 1 (fig. 21A).

The first antenna is poorly setose (fig. 21B), its length is up to 45% of the total body length. The main and accessory flagellum are 21- to 25- and 3- or 4-segmented, respectively.

The gland cone of the second antenna almost reaches the tip of the third peduncular segment. Peduncle segments 4 and 5 are equally long, both armed with 5 or 6 transverse rows of setae, as long as or longer than the diameter of the peduncular segments. The flagellum is slightly swollen, dorsoventrally compressed. The proximal 8 or 9 of the up to 12 flagellar segments bear two transverse rows of setae, twice as long as the flagellar segments, together forming a flag-like brush as in G. p. pulex. Calceoli are not always present (see fig. 21C, D and O).

The second segment of the mandibular palp bears 10 to 15 setae. The third segment bears 23 to 28 D-setae, 4 to 6 E-setae, 1 or 2 groups of A-setae and 1 group of B-setae.

Coxal plates 1 to 4 have rounded inferior corners. Gnathopods 1 and 2 are densely setose (figs. 21E and G), the setae being straight or curved, especially in segments 5 (= carpus) and 6 (= propodus). The dactyli are slender. The propodus of gnathopod 1 is armed with the usual medial palmar angle spines and a varying number of smaller submarginal spines ("Stiftstacheln") (fig. 21F).

The propodus of the second gnathopod is armed with a medial palmar spine, 2 or 3 palmar angle spines and 3 submarginal spines (fig. 21H).

Pereiopods 3 and 4 are basically the same as in G. p. pulex. In P3 the long, often curved setae along the posterior margin of segments 4 and 5 are 2 to 3 times as long as the diameter of the segments. In segment 6 these setae are fewer in number, slightly shorter than the diameter of the segments, and intermixed with short spines (fig. 21I). Pereiopod 4 is shorter than P3; the setae along the posterior margin of segments 4 to 6 are usually straight and shorter than in P3 (fig. 21J).

Pereiopods 5 to 7 are identical to those in G. p. pulex (see figs. 2E, 2F and 3C). The inner surface of the basis is unarmed. The dactyli of P3 to P7 are medium long and slender.

The epimeral plates are identical to those found in G. p. pulex (see fig. 21M), bearing spines along the ventral margins, sometimes intermixed with a short seta.

Uropod 3 is relatively short, its inner ramus varying from 60 to 70% of the length of the outer ramus. All setae are long and simple. Among the setae on the outer margin of the exopod some spines can be found (fig. 21K).

The telson lobes are short, varying from 1.1 to 1.5 times as long as wide bearing long setae along the distal and lateral margins as well as on the dorsal surface (fig. 21L).

Female: The normal sexual dimorphism can be observed. The armature of P3 to P7, urosome and telson is as in males. The peduncles of the first and second antennae bear longer setae than in the other sex. The brush-like flag of setae on the flagellum of A2 is absent in females. Because of the absence of striking characters females of G. uludagi can be easily confused with females of other species.

Variability. — Apart from the normal pattern, variability was observed in the presence or absence
Fig. 21. A-N, *Gammarus uludagi* G. Karaman, 1975, ♂, 10.5 mm, from Mt. Uludag, prov. Bursa, Turkey. A, cephalic segment; B, first antenna; C, second antenna; D, detail of second antenna; E, first gnathopod; F, propodus of first gnathopod; G, second gnathopod; H, propodus of second gnathopod; I, third pereiopod; J, fourth pereiopod; K, third uropod; L, telson; M, epimeral plates; N, urosome.

O, *Gammarus uludagi*, ♀, 12 mm, from the Island Lesbos, Greece. Second antenna.
of calceoli (the specimens from Lesbos, Greece never bear calceoli) and the relative length of the telson lobes.

Material examined. —
Turkey: — Prov. Bursa, Uludag Mountain, alt. 1750-2400 m, 14-VII-1972, several specimens (M.C.S.N.).
— do., alt. 2200-2400 m, 21-VII-1973, many specimens (M.C.S.N.).
— Prov. Aydin, Golcük, N. of Aydin, alt. 1000 m, shore of eutrophic lake, 3-VII-1973, several specimens (M.C.S.N.).
— Prov. Izmir, river in the surroundings of Izmir, V-1912, many specimens (M.N.H.N.).
— do., date unknown, 2 specimens (M.N.H.N.).
— do., brooklet 10 km S.E. of Kallon, 10-XI-1973, several specimens (Z.M.A.).
Loc. typ. — Turkey, Prov. Bursa, Uludag Mountain. The ♀ holotype and several paratypes are deposited in the Museo Civico di Storia Naturale, Verona, Italy.

Distribution. — Up to this moment the species is known from the western part of Asia Minor and the Island Lesbos off the coast of Asia Minor.

Remarks and affinities. — The characters of this species are somewhat intermediate between *G. p. pulex* and *G. fossarum*. It resembles *G. p. pulex* in the flag-like brush of setae on the flagellum of A2, shape and setation of P3 through P7 but it is different from *p. pulex* in the setation of the peduncular segments of A2, the relative length of the endopod of uropod 3 and the variability in the presence or absence of calceoli. It resembles *G. fossarum* in the setation of the peduncle of A2 but clearly differs from it in the structure of the flagellum of the same. It differs from *G. birsteini* in the structure of the uropod, the more setose telson and the absence of setae in segments 3 to 6 of P5 to P7. Ecology and colour of live specimens unknown.

**Gammarus pseudosyriacus** n. sp. Fig. 22

Ref.: *Gammarus syriacus* (part.) Chevreux, 1895: 160-164, figs. 5 and 7.

Diagnosis. — At first sight this species looks like *G. syriacus* because of its robust habitus, its sharp epimeres and its elevated uroscope segments. However, P5 to P7 never bear long setae along the anterior margin.

Description. — Male: Maximum length observed in the studied material 18 mm. The cephalic segment is of the normal "pulex"-type. The eyes are somewhat larger than in most other species within this group (fig. 22A). The posterior margin of the last two metasome segments is set with some small setules. The uroscope segments (fig. 22J) all bear a distinct dorsal hump which can be low in young animals, but very high in older ones, just as in *G. syriacus*. The dorsal armature consists of the usual middorsal and two lateral groups of elements.

The first antenna is little shorter than half the body-length. The third peduncle segment is about half as long as each of the other two. The main flagellum and accessory flagellum have 25 to 30, and 3 or 4 segments each. The number of elements on both peduncle and flagellum is low.

The second antenna (fig. 22B) is relatively slender. The gland cone reaches to the top of the third peduncle segment. Peduncle segments 4 and 5 are armed with groups of short setae, implanted in 3 longitudinal rows. The 12 to 15 segments of the slender flagellum are never swollen or compressed. The setae implanted near the top of each segment never form a flag-like brush. Calceoli can often be found in the first 6 to 8 segments.

The third segment of the mandibular palp is armed with the usual comb-like row of 24 to 32 D-setae and 4 to 6 E-setae along the inferior margin. In addition 1 group of A-setae and 1 or 2 groups of B-setae are found.

Except for some smaller details in setosity, the first and second gnathopods show no differences with those in *syriacus* or *p. pulex* (figs. 22C, D).

Pereiopods 3 and 4 are similar to those in *p. pulex*.

Pereiopods 5 to 7 show useful discriminating characters: the distal portion of their basal segment is always much wider than the proximal portion of the next segment, thus forming a protruding lobe (see figs. 22E, F and Chevreux, 1895); the anterior margin of these pereiopods never bears the long setae found in *G. syriacus*.

The first epimeral plate (fig. 22J) has a rectangular posteroinferior corner. In the second epimere this corner is moderately pointed against very sharp and pointed in the third one. In large spec-
Fig. 22. *Gammarus pseudosyriacus* n. sp., ♂, 16 mm, from pools in the surroundings of Damascus, Syria. A, cephalic segment; B, second antenna; C, propodus of first gnathopod; D, propodus of second gnathopod; E, fifth pereiopod; F, seventh pereiopod; G, third uropod; H and I, telson lobes; J, meta- and urosome.
imens this last epimeral plate is almost identical to that found in *G. syriacus* (see fig. 251). The armature of these epimeral plates consists of some spinules along the inferior margins and some setules along the posterior margins only.

The inner ramus of the third uropod is 2/3 of the outer ramus. Plumose setae are always found along the inner and outer margins of endo- and exopod (fig. 22G).

The telson lobes are about twice as long as wide. Apart from the distal group of spines and setae we can often find some other groups of elements on the dorsal surface and along the outer margin of the lobes (figs. 22H, I).

Female: The females of this species are easily recognizable because of the second antenna, the structure of pereiopods 5 to 7, the sharp epimeral plates and the dorsal elevations of the uroscope segments.

Colour of live specimens is brownish.

Variability. — Except for the normal variability encountered in this group, this species shows considerable variability in the dorsal elevations of the uroscope segments. Usually the height of these humps increases with age. As in *G. fossarum* calceoli are present in some populations but absent in others. In some localities (e.g. Spring of Soltan Seiṭ, near Ahlāṭ, Turkey and Doabi-Mekh-i-Zari, prov. Bamiyan, Afghanistan) the dactyli of the pereiopods are very slender while the dorsal elevations are less high than in the typical form.

Material examined. —

Syria: — Surroundings of Damascus, in small pools, 1911, 11 specimens (MNHN), accompanied by *G. syriacus* and *G. laborifer*.

Turkey: — Prov. Izmir, small river 3 km S. of Selçuk, 11-VII-1969, 5 specimens (ZMA).
— Prov. Bitlis, spring of Soltan Seiṭ, near Ahlāṭ, on W-coast of Van Göle, 26-IX-1957, 10 specimens (KC).
— Prov. Elazığ, small brook near İçme, 45 km of Elazığ, many specimens, many in precopulation (ZMA).
— do., Hazar Göle (lake), 6-VI-1970, 10 specimens (MCSN).

— do., warm spring at Qal-ā-Shaharak, in the Hazarajat region, date unknown (KC).
— Prov. Samangan, spring at Sar-i-Pul, 14-X-1957, 20 specimens (KC).
— Prov. Tariab, warm spring at Nichar, between Maimana and Belchirag, 28-X-1957 (KC).

Israel: — Banias, N.E. of Quiryat Shemona, 9-X-1968, 10 specimens (ZMA).
— Banias River, N.E. of Quiryat Shemona, 30-X-1972, 5 specimens (ZMA).
— Ein Ela, W. of Quneitra, 3-IX-1970, 5 specimens (ZMA).
— River Dan, E. of Quiryat Shemona, 3-XII-1970, 5 specimens (ZMA).

Loc. typ. — Syria, small pools in surroundings of Damascus.

Distribution. — This species is widely distributed in the “Near East” (see sub material examined). In some localities it was found together with *G. syriacus* and/or *G. laborifer*.

Remarks and affinities. — Up to now, this species has been confused with *G. syriacus* because of the incorrect description of *syriacus* by Chevreux (see sub *G. syriacus*). However, the presence of homogamous precopulations of both morphologically different forms in one sample proved that we had to do with an independent species. *G. monspeliensis* and *G. laborifer* are very close to this species in so far that they likewise share the combination of sharp epimeres, dorsal elevations of the uroscope and the absence of setae on the anterior margins of P5 and P7. However, both species show considerable differences in the setation of the second antenna.

Ecology. — This species is usually found in wells and oases in more or less desert-like areas. In some of these wells temperatures of up to 34°C have been recorded, a temperature fatal to almost all other gammarid species.
Gammarus monspeliensis Pinkster, 1972. Fig. 23
Ref.: Gammarus monspeliensis Pinkster, 1972: 177-179, figs. 6A-D.

Diagnosis. — A large species with a characteristic greenish colour, often striated with lighter bands. Like G. p. pulex the flagellum of the second antenna bears a flag-like brush of setae. Its first antenna is very long. The urosomites bear well developed dorsal humps.

Description. — Male: Maximum length observed 21 mm. The body is robust. The posterior margin of the last two metasome segments is set with a large number of setules. All urosomites have well developed dorsal elevations. As in G. syriacus these elevations are laterally compressed. The setae in the dorsomedian and dorsolateral armature are usually much longer than the spines (fig. 23E).

The peduncle segments of the first antenna are very poorly setose. The flagellum (fig. 23A) is very characteristic by its great length, consisting of 45 to 50 segments (against 22 to 35 in G. p. pulex).

The peduncle segments of the second antenna (figs. 23B, C) resemble those in G. p. pulex. The flagellum is slightly different since its segments are never swollen or compressed while the 11 to 13 setae on the inner surface of each segment are longer than in normal p. pulex, forming a flag-like brush like in p. pulex.

The propodus of the second gnathopod (fig. 23D) is slightly different from that of most other members in this group because of an increased number of spines near the palmar angle.

The first gnathopod, the pereiopods, the uropods and the telson are practically identical to those described for G. p. pulex.

The epimeral plates are distinctive: the second and especially the third plates have very sharp posteroinferior corners, almost resembling those found in G. syriacus. The only armature of these plates consists of some spinules along the inferior margin and some setules along the posterior margin (see fig. 23E).

Female: Shows the normal sexual dimorphism known for this group. It is easily recognizable because of the long flagellum in the first antenna, the dorsal elevations of the urosome and the sharp epimeres.

Variability. — The pattern is of the normal pulex type.

Material examined. —
France: dépt. Hérault: Source du Lez, N. of Montpellier, 8-1-1968, about 100 specimens, many of them in precopulation (ZMA).
— do., 1-V-1968, 7 specimens (ZMA).
— do., 1-VIII-1970, many specimens (ZMA).
— do., 26-III-1970, many specimens, many of them in precopulation (ZMA).
Loc. typ. — France, dépt. Hérault, Source du Lez, N. of Montpellier. The δ holotype, Φ allotype and many para-types, collected 8-1-1968, have been deposited in the Zoölogisch Museum Amsterdam under cat. no. ZMA Amph. 103.544.

Distribution. — This species is exclusively known from the upper reaches of the river Lez, North of Montpellier, France, dépt. Herault.

Remarks and affinities. — The morphological characters of this species resemble sometimes G. p. pulex (e.g. brush-like flagellum in second antenna, armature of pereiopods) or G. syriacus (presence of dorsal humps, sharp epimeres). Nevertheless it can be easily distinguished because of the special combination of these characters and its very long first antenna. Moreover, Pinkster (1972) proved that this species has developed an effective reproductive isolation from other populations within this species-group in the same part of Europe, so no doubt is left that we have to do with a good species. Recently G. Karaman, 1973 described G. monspeliensis agrarius. Comparison of this form with the nominate species, however, revealed important differences in the length of the first antenna and in the setation of pereiopods 5 to 7. Therefore it was decided that G. m. agrarius must be considered an independent species which is more closely related to G. syriacus than to G. monspeliensis.

Ecology. — The river in which this species is exclusively found is fed by an enormous resurgence, producing water with a high amount of Ca-ions.
The species is found under stones and between the vegetation, always together with *Echinogammarus thoni* (Schäferna), a species also characterized by the presence of dorsal humps.

Colour greenish, often with brighter bands.

**Gammarus syriacus** Chevreux, 1895. Figs. 24, 25


**Diagnosis.** — A large species with a rather robust habitus. The species is very conspicuous because of its setiferous pereiopods 5 to 7, its very sharp epimeres 1 to 3 and its well developed dorsal humps on urosomites 1 and 2.

**Description.** — Male: Maximum length observed in 36 samples is 23 mm. The cephalic segment and shape of the eyes are of the *p. pulex*-type. The posterior margins of the metasome segments are set
Fig. 24. A-K, *Gammarus syriacus* Chevreux, 1895, ♂, 17 mm, from pools near Damascus, Syria. A, first antenna; B, second antenna; C, detail of second antenna; D, first gnathopod; E, second gnathopod; F, third pereiopod; G, fourth pereiopod; H, fifth pereiopod; I, sixth pereiopod; J, seventh pereiopod; K, telson.

with many setules. The first two urosome segments show one of the more characteristic features of the species viz. well-developed, high, laterally compressed dorsal elevations. This character, which is very pronounced in adult specimens, can also be found in newly hatched juveniles. The armature of the urosome segments usually consists of a mid-dorsal group and 2 laterodorsal groups of elements. The number of spines and setae participating in these groups is largely variable (see figs. 25H, J).

The first antenna is long, poorly setose, about half the body-length. Peduncle segments 2 and 3 are about equal in length. The main and accessory flagellum have 32 to 40 and 4 to 6 segments, respectively (fig. 24A).

The second antenna (figs. 24B, C, 25B, C and L) has a short gland cone, reaching the middle of the third peduncle segment. The 4th and 5th peduncle segments, both of about the same length, bear many groups of setae, implanted in three longitudinal rows. The setae in these rows are usually much longer than the segments on which they are implanted. The 15 to 18 flagellar segments are never compressed or swollen and poorly setiferous. In most populations calceoli are found on the proximal 8 to 10 flagellar segments.

The third segment of the mandibular palp is armed with a regular comb-like row of 23 to 32 D-setae and 5 or 6 E-setae along the inferior margin. One group of A-setae and 1 or 2 groups of B-setae complete the armature of this segment.

The first and second gnathopods are of the usual type within this group (figs. 24D, E). However, the setation of the propodus can be greatly variable (from short to very long).

Pereiopods 3 and 4 bear long setae as in *pulex* (figs. 24F, G).

Pereiopods 5 to 7 are characteristic in so far that long setae occur along the anterior margin of the distal 3 to 4 segments. These setae are always longer than the spines intermixed with them. The basal segment of the pereiopods varies from relatively short in P5 to long and elongate in P7 (see figs. 24H-J, 25F).

The epimeral plates are among the most striking characters of this species. Unlike most other species within this group the posteroinferior corner of the first epimeral plate is sharp. This pointed aspect is even more pronounced in the second and third epimeres which end in very sharply pointed hooks. The armature of these epimeral plates is rather poor but variable in that in some populations setules can be found along the inferior margin of the 2nd and 3rd epimeres, while in other populations this margin is almost unarmed (see fig. 25I, K).

The endopodite of the third uropod (fig. 25G) is about 3/4 of the exopodite. Plumose setae are always found along the inner and outer margins of endo- and exopodite.

The telson lobes are elongate (figs. 24K, L), in adult specimens always more than twice as long as wide. The armature shows the same variability as in *G. pulex*. Usually, some groups of setae can be found on the dorsal surface of the lobes.

Female: As in most other members of this group female *syriacus* has longer setae on the antennae, smaller gnathopods and uropod 3 and it is devoid of the medial palmar spine on the propodus of gnathopods 1 and 2. Another character in which females of this species differ from the males is the much longer and denser setation of P5 to P7. Because of the very sharp epimeres, the setose pereiopods 5 to 7 and the high dorsal uroscope humps, females of *syriacus* can be easily separated from females of other species within this group.

The colour of live specimens is brownish to greenish.

Variability. — Except for the "normal" variability pattern this species shows variability in the length of the setae on the anterior margins of P5 to P7 and the height of the urosomal elevations. In general it can be said that the height of the dorsal humps as well as the pointed aspect of the epimeres increases with the total body length. In very large specimens the propodus of the gnathopods and the segments of the pereiopods are elongated (figs. 25D-F). Nevertheless considerable differences can be found between populations from different localities.

Material examined. —
Egypt: Lake Maryût (Lac Mariout), 1893, 3 specimens (MNHN).
— do., date unknown, 8 specimens (MNHN).
— Lake Maryût (Lake Mareotes), 8 XI-1911, 3 specimens (BMNH).
Fig. 25. A-I, *Gammarus syriacus* Chevreux, 1895, ♂, 22 mm, from Békaa, Ammik, Lebanon. A, cephalic segment; B, second antenna; C, detail of second antenna; D, propodus of first gnathopod; E, propodus of second gnathopod; F, seventh pereiopod; G, third uropod; H, uroscope; I, epimeral plates.
Israel: Lake Tiberias, date unknown, 6 specimens (MNHN).
- Bezet (Karkara), N. of Nahariya, 9-IV-1968, 4 specimens (ZMA).
- Aqua Bella, W. of Jerusalem, spring 1965, 8 specimens (ZMA).
- Ein-Dib, 29-XI-1968, 2 specimens (ZMA).
- Brekhart Ram, N. of Quneitra, 9-VII-1967, 4 specimens (ZMA).
- Banias, N.E. of Quiryat Shemona, 10-VII-1967, 3 specimens (ZMA).
- Ein Mata, S.W. of Jerusalem, 12-XII-1966, 5 specimens (ZMA).
- Khirbet Hanut, S.W. of Jerusalem, 12-XII-1966, 4 specimens (ZMA).
- Ein Pukin, S.W. of Jerusalem, 4-XI-1970, 3 specimens (ZMA).
- River Dan, E. of Quiryat Shemona, 3-XII-1970, 5 specimens (ZMA).
- Mevo Batar Ein Kube, S.W. of Jerusalem, 24-IV-1968, 4 specimens (ZMA).

Lebanon: Békaa, Amnik, alt. 830 m, VI-1972, 10 specimens (ZMA).
- Ain el- Baraké, alt. 1200 m, 25-VI-1972, 6 specimens (ZMA).
- Marc d’Addous, near Ba-albek, 1911, several specimens (MNHN).

Syria: Surroundings of Damascus, in small pools, many specimens (MNHN), accompanied by G. pseudosyracus and G. laborifer.
- Surroundings of Damascus, marsh-land, 1911, many specimens (MNHN).
- River Barrada, near Damascus, 1911, many specimens (MNHN).
- River Barrada, near Damascus, 28-VII-1914, 1 specimen (BMNH), accompanying species G. laborifer.
- Well at Koutaïf, N.E. of Damascus, 1911, 3 specimens (MNHN).
- River Barada, near Damascus, 4 specimens (MNHN).
- Surroundings of Damascus, small pools, 1911, many specimens (MNHN).
- Nahr el-Lebouch, 1898, 3 specimens (MNHN).
- Damascus, date unknown, 3 specimens (MNHN).
- Surroundings of Damascus, marsh-land, 8 specimens (MNHN).
- Small stream in the surroundings of Damascus, 1911, 8 specimens (MNHN).
- Mouth of small stream, running into Lake Yamouneh, 1911, several specimens (MNHN). Accompanying species: G. laborifer.

Loc. typ. — Small pools in the surroundings of Damascus, Syria. The δ neotype and many paratypes have been deposited in the collections of the Muséum national d'Histoire naturelle, Paris.


Distribution. — At this moment G. syriacus is known with certainty from the northern part of Egypt, Israel, the Sinaï, Lebanon, Syria and the southern part of Asia Minor. Although we have not actually seen material, it seems probable that this species also occurs in adjacent countries like Jordan and Iraq.

Remarks and affinities. — The original description of Chevreux has been a source of confusion. The samples from which Chevreux took his material proved to contain 2 and sometimes 3 morphologically different forms. None of these appeared to be identical with the description of Chevreux. A more detailed study revealed that Chevreux in his description mixed elements of two different forms. So the illustrations of the antennae, head eyes, third uropod and telson refer to one species, but the illustrations of the entire animal and the 7th pereiopod definitely refer to a second one. Since most of the specimens in Chevreux’s material belong to the form with setiferous pereiopods 5 to 7, but since Chevreux did not indicate any types, we decided that a neotype should be selected from specimens belonging to this form. The other two forms in question were separated as different species: G. pseudosyracus and G. laborifer, which differ from G. syriacus in the absence of setae on the anterior margin of P5 to P7. G. laborifer also differs from G. syriacus in the presence of long setae on both peduncle and flagellum of A2.

Other species that could be confused with G. syriacus (because of the sharp epimeres and elevated urosome segments) are G. montepeliensis and G. agrarius. G. montepeliensis differs from it in the brush-like aspect of the second antenna (δ) and the absence of setae on the anterior margin of P5 to P7. G. agrarius mainly differs from G. syriacus in the brush-like aspect of the second antenna (δ).

Ecology. — Data on the ecology of this species are very scarce. Most material has been found in small running waters up to altitudes of 1600 m. Chappuis, 1935, reports the species from a subterranean river in Lebanon.


**Diagnosis.** — A large species, with well-developed dorsal elevations on the urosome, very sharply pointed epimeral plates and a second antenna with a flag-like brush of setae as in *G. p. pulex*; pereiopods 5 to 7 bear medium long setae along the anterior margin of segments 3 to 6, intermixed with some spines.

**Description.** — Male: Maximum length observed 21 mm. The posterior margin of metasome segments 2 and 3 is set with some setules. The urosome segments 1 and 2 (and sometimes 3) have laterally compressed elevations forming distinct humps like in *G. syriacus* and *G. montspeliensis* (figs. 26N, O). The armature of the urosonites consists of a dorsomedian and 2 dorsolateral groups of elements. The composition of these groups is largely variable. The lateral cephalic lobes are rounded, the eyes small, ovoid, almost half as long as the diameter of the first peduncle segment of antenna 1 (fig. 26A).

The first antenna is nearly half the body length. The main and accessory flagellum are poorly setose and 31- to 38- and 4- to 5-segmented, respectively (fig. 26B).

The peduncle segments 4 and 5 of the second antenna (fig. 26C) are poorly setose, each segment with 4 to 5 transverse rows of short setae (shorter than the diameter of the peduncle segments). The tip of the gland cone almost attains the distal end of the third peduncular segment. The setae implanted on the swollen, dorsoventrally compressed flagellum form a flag-like brush like in *G. p. pulex*. Calceoli are always present (fig. 26D).

The third segment of the mandibular palp is armed with 29 to 34 short D-setae, 4 to 6 E-setae, 1 or 2 groups of B-setae and 1 group of A-setae (fig. 26E).

Gnathopods 1 and 2 are almost identical to those in *G. p. pulex*. They are moderately setose, bearing straight or partially curved setae. The dactyli are slender (figs. 26F, G).

The posterior margins of segments 3 to 6 in pereiopod 3 bear long straight or curved setae, 2.5 to 3 times as long as the diameter of the segments. In P4 these setae are a little shorter than in P3. The dactyli are moderately slender. Coxal plates 1 to 4 have quadrangular inferior corners.

Pereiopods 5 to 7 are moderately slender (figs. 26H-J). In addition to spines many setae are implanted on the anterior margin of segments 3, 4 and 5. These setae are usually longer than the diameter of the segments on which they are implanted. The basal segment of P5 through P7 never bears setae on the interior surface.

The first epimeral plate is slightly pointed, with numerous long setae on the anterior margin. In the second and third epimeral plates the sharply pointed aspect of the postero-inferior corner is even more pronounced, forming a sharp pointed hook as in *G. syriacus*. Many setae, sometimes accompanied by some spines, are found on the antero-inferior corner of these plates (see fig. 26M).

The endopodite of the third uropod is 3/4 to 7/8 of the exopodite. Plumose and simple setae, together with some spines are implanted on the inner and outer margins of endo- and exopodite.

The telson lobes (figs. 26K, L) are elongate, twice as long as wide, armed with a few distal spines accompanied with several long distal setae. Several small groups of setae can be found on the dorsal surface of the telson lobes.

Female: Normal sexual dimorphism was observed. Because of the shape of the urosonic segments and the shape of the epimeral plates females of this species can be distinguished from females of most other species. The flagellum of the second antenna is less setose than in the male, resembling the situation in *G. p. pulex*. The gnathopods and pereiopods 3 and 4 bear straight setae only.

The colour of live specimens is rather bright, more or less greenish.

**Variability.** — The pattern observed in this species is identical to the pattern discussed for the whole group.

**Material examined.** —


— do., rheocrene well, 28 km N. of Antalya, on foothills of Taurus Mts., 8-VIII-1969, many specimens, many in precopulation (ZMA).
Fig. 26. A, B, F-K, M, O and P, *Gammarus agrarius* G. Karaman, 1973, ♂, 17 mm, from Dinar Karakugu, Pinarbaşı, Turkey. A, cephalic segment; B, first antenna; F, propodus of first gnathopod; G, propodus of second gnathopod; H, fifth pereiopod; I, sixth pereiopod; J, seventh pereiopod; J', dactylus of seventh pereiopod; K, telson; M, epimeres; O, urosome; P, third uropod.

C-E, L and N, *Gammarus agrarius*, ♂, 21 mm, from well, N. of Antalya, Turkey. C, second antenna; D, detail of second antenna; E, mandibular palp; L, telson lobe; N, urosome.
— Prov. Konya, small ditch at Kaplica, near Ilgın, 10-V-1959, many specimens (ZMH).
— do., Dinar Karakugu at Düdenler, 7-V-1959, 12 specimens (ZMH; KC).
— Prov. Nigte, Nigte, 3-VIII-1947, several specimens (ZMH).

Loc. typ. — Turkey, Konya, Dinar Karakugu near Pinarbaşı. The 8° holotype and several paratypes have been deposited in the Zoologisches Museum, Hamburg. Some other paratypes have been deposited in the Karaman Collection, Titograd.

Distribution. — Southern part of Asia Minor.

Remarks and affinities. — This species has many characters in common both with *G. monspeliensis* and with *G. syriacus*. It differs from *G. monspeliensis* in its shorter antenna 1 and in the possession of setae along the anterior margin of P5 to P7. It differs from *G. syriacus* in the brush-like aspect of the flagellum of antenna 2. All other characters fall within the wide range of variability of these two species.

Ecology. — Known from running fresh waters with a high content of electrolytes and the shores of a lake; sometimes in enormous rheocrene wells similar to that of the type-locality of *G. monspeliensis* in the southern part of France. It seems to prefer a dense vegetation of waterweeds. It has been found accompanied by *G. accolaee* G. Karaman, *G. cf. argaeus* Vávra, *G. laborifer* n. sp., and *Echinogammarus thoni antalyae* G. Karaman.

**Gammarus acalceolatus** Pinkster, 1971. Fig. 27

Ref.: *Gammarus acalceolatus* Pinkster, 1971: 49-51, figs. 4-6.

Diagnosis. — A medium large species. The habitus is less robust than in most other members of the *pulex*-group. The very setiferous second antenna lacks calceoli. Very setiferous gnathopods 1 and 2 and setiferous pereiopods 5 to 7.

Description. — Male: Maximum length observed 17 mm. The lateral cephalic lobes are more or less rounded, the eyes are small. The posterior margins of metasome segments 2 and 3 are set with a number of short setules. The first urosome segment has a shallow excavation “saddle”; the other two urosome segments are somewhat variable. In older specimens a small dorsal hump can be present on the second segment as well. A dorsomedian and two dorsolateral groups of a variable number of elements are found on all urosomites.

The first antenna (fig. 27A) is more than half as long as the total body-length of the animal; the third peduncle segment is about half as long as each of the other two segments. Segments 2 and 3 bear some groups of setae along the dorsal surface. The main flagellum, with 36 to 41 segments, is long but poorly setose. The accessory flagellum has 4 to 5 segments.

The second antenna (fig. 27B) shows one of the discriminating characters of the species. Long setae are implanted on the inferior margin of peduncle segments 4 and 5. Groups of slightly shorter setae are implanted on the inner and upper surface of these peduncle segments. The 16 to 20 slender flagellar segments are armed also with numerous setae. These setae never form a flag-like brush as in *p. pulex*. Calceoli have never been found in the material examined.

The mandibular palp is armed with 23 to 28 D-setae and 6 E-setae on the inferior margin of the third segment. In addition 1 group of A-setae and 1 or 2 groups of B-setae can be found.

The propodus of the first gnathopod (fig. 27C) is slightly different from that in most other members of this group since the spines near the palmar angle form a kind of transverse row. Moreover, the spines along the posterior margin, the so-called “Stiftstacheln” are stronger and more numerous than in most other species in this group. The setation of the propodus is relatively long.

The propodus of the second gnathopod (fig. 27D) has the usual medial palmar spine and a palmar angle group of 2 strong spines with a group of 3 smaller spines at their insertion on the anterior surface. As in the first gnathopod the setation is relatively long.

The setae on segments 4 and 5 of pereiopods 3 and 4 are relatively long, often curled. Coxal plates 1 to 4 have rounded inferior corners.

The basal segments of pereiopods 5, 6 and 7 (figs. 27E-G) are relatively short (in P7 never more than 1.5 times as long as wide), always
Fig. 27. *Gammarus acaeleolatus* Pinkster, 1971, δ, 17 mm, from Aquelmane de St. Ali, prov. Meknes, Morocco. A, first antenna; B, second antenna; C, propodus of first gnathopod; D, propodus of second gnathopod; E, basal segment of fifth pereiopod; F, basal segment of sixth pereiopod; G, seventh pereiopod; H, epimeral plates.
having a protruding posterodistal lobe. Strong spines are implanted along the anterior and posterior margin of merus and carpus of this species. The setae, intermixed with these spines are always overreaching these.

The first epimeral plate has an almost rectangular posteroinferior corner. In the second and third epimeres these corners vary from almost rectangular to moderately pointed (fig. 27H).

The third uropod and telson lobes are similar to those described for G. p. pulex (see fig. 3D-F). Female: Shows the same sexual dimorphism as described for G. p. pulex. Moreover it must be noticed that the setae along the anterior margin in P5, P6 and P7 are longer and more densely implanted than in males.

Variability. — Although we only had one sample at our disposition it seems probable that the variability pattern is comparable to that of G. p. pulex.

Material examined. — One sample from the type locality. Loc. typ. — Morocco, prov. Meknes, A'quelmane de St. Ali, a lake between Midelt and Azrou. The ® holotype, 9 allotype and about 100 paratypes, collected 30-VII-1969, have been deposited in the collections of the Zoologisch Museum Amsterdam, cat. no. ZMA Amph. 102.739.

Distribution. — Known from the type locality only.

Remarks and affinities. — The presence of setae on the anterior margin of P5, P6, and P7 distinguishes this species from most other species in this group. It differs from G. syriacus and G. agrarius in the shape of the epimeral plates, the absence of dorsal urosome elevations, and the longer setation on the second antenna. G. ibericus also has setose pereiopods 5 to 7 but differs from acalceolatus in the absence of long setae on antenna 2 and the presence of calcieoli on the flagellum of antenna 2. Gammarus rambouseki differs from this species in the setation of the urosome segments and the relatively shorter endopod of uropod 3. Gammarus rouxi is easily distinguishable by its typical shape of the basis in P7.

Ecology. — No data available.

Gammarus ibericus Margalef, 1951. Fig. 28.

Refs.: Gammarus pulex (L.) subsp. ibericus Margalef, 1951 263, fig. 2; 1953: 198.
Gammarus ibericus; Pinkster, 1971: 51-52, fig. 7; 1972: 172, figs. 4E-G; Goedmakers, 1974: 211-214.

Diagnosis. — A relatively small species. Setose pereiopods. Relatively bald second antenna.

Description. — Male: Maximum length observed 14 mm. The shape of the head and the eyes are identical to those of G. p. pulex. The urosome has no distinct elevations or excavations. The armature is usually very poor. In many populations the first urosome segment is devoid of spines, only carrying a seta in the middorsal line. The armature of the other two segments consists of the usual middorsal and two lateral groups of elements.

The first antenna has a relatively long third peduncle segment, being almost as long as the second peduncle segment. The main flagellum and accessory flagellum are poorly armed, having 26 to 32, and 4 or 5 segments, respectively (fig. 28A).

Peduncle segments 4 and 5 of the second antenna (fig. 28B) are armed with few groups of medium long setae. The flagellum is slender, not compressed, poorly setose. Calcieoli are always present.

The third segment of the mandibular palp is armed with 18 to 23 D-setae, 4 to 6 E-setae, 1 group of A-setae and 1 or 2 groups of B-setae.

The first and second gnathopod including their propodi resemble those of p. pulex in shape and armature. The setation is relatively long as in G. acalceolatus.

The setae on the merus and carpus of P3 and P4 are relatively long, often curved, resembling those in p. pulex. Coxal plates 1 to 4 have rounded inferior corners.

The last three pereiopods (figs. 28C-E) show one of the discriminating characters of the species. Their basal segment is rather slender tapering toward the distal end, forming a more (P5) or less (P7) strongly protruding lobe. In larger males the basal segment of P7 can be more than twice as long as wide. The setae along the posterior margin of the basal segments are relatively long. The armature of merus, carpus, and propodus consists of spines and long setae along both anterior and
posterior margins. These setae are always longer than the spines. The setation is usually much denser than in *G. acalceolatus*.

The shape of the epimeral plates does not show differences from that found in *G. p. pulex* or *G. gauthieri*.

The endopod of uropod 3 (fig. 28F) varies from 2/3 to 3/4 of the length of the exopod. Simple and plumose setae can be found along the inner and outer margins of both rami. They are less densely implanted than in *G. gauthieri* or *G. p. pulex*.

The telson lobes (fig. 28G) almost twice as long as wide, distally have a group of spines and long setae. For the remainder, armature is almost absent.

Female: Shows the same sexual dimorphism as described for *G. p. pulex*. As in *G. acalceolatus* the setae on P5 to P7 are longer and more densely implanted than in male.

The colour of live specimens is brownish.

Variability. — The variability pattern of this species is of the same type as described for *G. p. pulex*. It must be emphasized here that this is also true for the dorsal armature. In most populations the first urosome segment is devoid of spines but nevertheless we cannot use this absence as a discriminating character (as Margalef did in his original description), since in some populations middorsal and lateral spines can be found.

Material examined. — Spain, prov. Cuenca: Fuentes de la Laguna “El Tobar” in
the Serrania de Cuenca, alt. 1100 m, date unknown, 2 specimens (collection Margalef, Barcelona).
— Fuente de los Tilos, 5 km W. of Betela, 20 km N.E. of Priego, 5-VI-1972, many specimens, many of them in precopulation (ZMA).
— Small brook, fed by several wells, 1 km N. of El Tobar, 30 km N.E. of Priego, 5-VI-1972, many specimens, many of them in precopulation (ZMA).

France, dept. Ardèche: Confluent of the Dorne, 1 km N.E. of Dornas, near le Chelyard, 6-IV-1972, 1 $^\circ$ (ZMA).
— Small brook, 5 km E. of Chirole, near Vals-les-Bains, 21-VI-1972, 26 specimens, 8 of them in precopulation (ZMA).

Dépt. Gard: Small brook, 2 km W. of St. Hippolyte, near Alès, 4-IV-1972, 2 specimens (ZMA).
— River Crespenou, 6 km E. of St. Hippolyte, near Alès, 4-IX-1972, 42 specimens, many in precopulation (ZMA).

— l'Hérault at Valrac, 1-IV-1972, 10 specimens, 1 precopulation (ZMA).
— l'Hérault, 0.5 km S.W. of Pont St. Etienne, 23-V-1972, 10 specimens (ZMA).
— l'Hérault, at St. Bausille de Putois, 23-V-1972, 8 specimens (ZMA).

Dépt. Cantal: l'Auze, 4 km S. of Mauriac, 70 km E. of Tulle, 21-VI-1972, many specimens, many in precopulation (ZMA).
— le Rioux Tort, 3 km W. of Pléaux, 30 km E. of Argentat, 21-VI-1972, 124 specimens, many in precopulation (ZMA).
— Confluent of la Cère, E. of Montvert, 20 km W. of Aurillac, 22-VI-1972, 61 specimens, many in precopulation (ZMA).
— Confluent of le Célé, 5 km E. of Mauris, 40 km S.S.W. of Aurillac, 18-VII-1972, 126 specimens, many in precopulation (ZMA).

— Confluent of Maronne, at la Broquerie, 7 km S.E. of Argentat, 22-VI-1972, 76 specimens, many in precopulation (ZMA).
— La Vienne, a few hundred meters from the spring, 3 km N. of Millevache, near Limoges, 18-V-1972, many specimens, many in precopulation (ZMA).
— Upper course of Triouzoune, 1 km N.E. of Meymac, near Clermond Ferrand, 18-V-1972, many specimens, many in precopulation (ZMA).
— l'Orange, 1 km E. of la Viallette, near Clermond-Ferrand, 18-V-1972, many specimens (ZMA).

Dépt. Lot: le Célé at bridge in road N 122, 500 m N.E. of Figeac, 67 km S.W. of Aurillac, 18-VII-1972, many specimens, many in precopulation (ZMA).

Loc. typ. — Spain, prov. Cuenca: Fuente de la Laguna "El Tobar" in the Serrania de Cuenca, alt. 1100 m. The types are deposited in the collections of Dr. R. Margalef, Barcelona.

Distribution. — Until recently this species was known from the type-locality in the Spanish province Cuenca only. Systematic sampling in large areas of Spain and France (Goedmakers, 1974) revealed that the species has a much wider distribution, not only in Spain but also in France.

Remarks and affinities. — *Gammarus ibericus* is a species with setiferous pereiopods 5 to 7, a character that can also be found in *G. acalceolatus*, *G. rambouseki*, *G. syriacus*, *G. agrarius* and *G. rouxi*. All these species however differ from *G. ibericus* in one or more aspects like the shape and setation of the second antenna (*acalceolatus*, *rambouseki*, *rouxi*), epimeres (*syriacus*, *agrarius*), dorsal armature (*rambouseki*), shape of the urosome (*syriacus*, *agrarius*), and several other smaller characters.

Ecology. — So far the species has always been found in springs and upper zones of rivers, a type of habitat closely resembling that in which *G. fos sarum* can be found.

*Gammarus osellai* n. sp. Fig. 29

Diagnosis. — A medium large species making a rather robust impression because of its short antennae. Pereiopods 5 to 7 have setose anterior margins. The inner ramus of uropod 3 is relatively short, 1/2 to 2/3 of the outer ramus.

Description. — Male: Maximum length observed 15 mm. The posterior margin of the last two metasome segments is set with some short setules. The urosome segments are almost flat, armed with a dorsomedian and two dorsolateral groups of spines and setae. The setae in these groups are always longer than the spines (fig. 29I).

The first antenna is relatively short, usually not longer than 1/3 of the total body length. The second and third peduncular segments are armed with some groups of setae (fig. 29A). The main and accessory flagellum are practically unarmed, 20- to 26- and 3- to 5-segmented, respectively.

The gland cone of the second antenna is short, reaching the middle of the third peduncular segment (fig. 29B). Peduncular segments 4 and 5 are equally long and both armed with many groups of setae, up to 1.5 times the diameter of the peduncular segments. The 10 to 12 flagellar segments are not swollen, armed with rather short setae. Calceoli have never been found.
Fig. 29. *Gammarus osellai* n. sp., ♂, 15 mm, from a stream near Pinarbaşı, prov. Kayseri, Turkey. A, first antenna; B, second antenna; C, third pereiopod; D, fourth pereiopod; E, fifth pereiopod; F, seventh pereiopod; G, third uropod; H, third uropod (part); I, meta- and urosome.
The third segment of the mandibular palp is
armed with 20 to 22 D-setae, 5 or 6 E-setae, 1
group of A-setae and 1 group of B-setae.

Gnathopods 1 and 2 are basically identical to
those in *G. p. pulex*.

The length of the setae implanted on P3 and
P4 is little shorter but not fundamentally different
from that in *p. pulex* (see figs. 29C and D).

Coxal plates 1 to 4 have rounded to quadran-
gular inferior corners.

The basal segments of pereiopods 5 to 7 (figs.
29E, F) vary from 1.5 times as long as wide in
P5 to more than twice as long as wide in P7. In
P7 some setae can be found on the postero inferior
surface of the basal segment. Apart from a number
of strong spines, segments 4 and 5 of P5 to P7
are armed with long setae along the anterior
margin.

The first epimeral plate is slightly pointed. In
the second and third epimeral plates this pointed
aspect of the postero inferior corner is even more
pronounced although never as much as in *G.
syriacus* (fig. 291).

The endopod of uropod 3 (figs. 29G, H) varies
from 1/2 to 2/3 of the length of the exopod.
Simple and plumose setae are implanted along the
inner and outer margins of both rami.

The telson lobes are about twice as long as wide,
distally armed with a few spines and several long
setae. Groups of long setae can be found on the
dorsal surface of the telson lobes.

Female: Normal sexual dimorphism was observed.
Most characters are less pronounced than in the
male and therefore females of this species are
easily confused with females of other species.

Variability. — Apart from the normal pattern, ex-
treme variability was observed in the ratio endopod
versus exopod in uropod 3. Within one population
it can vary from 1/2 to 3/4.

Material examined. —
Turkey: — Prov. Ankara, small brook, 20 km N.W. of Kirik-
kale, 57 km E. of Ankara, alt. 750 m, 6-VI-1973, many
specimens many in precopulation (ZMA). Accompanied
by *G. cf. balcanicus* (type locality).
— Prov. Kayseri, small stream fed by a well, 20 km N.E.
of Pinarbaşı, alt. 1710 m, many specimens, many in pre-
copulation (ZMA), 12-VI-1973.
The 8 holotype and many paratypes have been deposited
in the collections of the Zoologisch Museum Amsterdam,
cat. no. ZMA Amph. 105.209a, b.

Distribution. — Central part of Asia Minor.

Remarks and affinities. — Because of its setiferous
pereiopods 5 to 7 and its sharp epimal plates
1 to 3, this species resembles both *G. syriacus* and
*G. agrarius*. However, it clearly differs from these
two species in the absence of laterally compressed
elevations of the urosomites. Other species with
setiferous pereiopods 5 to 7 never have sharp
posterior inferior corners in all three epimal plates.
The species is dedicated to Dr. G. Osella of the
Museo Civico di Storia Naturale, Verona, who
collected many samples in Asia Minor.

Ecology. — Unknown.

*Gammarus effultus* G. Karaman, 1975. Fig. 30

Ref.: *Gammarus effultus* G. Karaman, 1975b: 324-330, figs
7-9.

Diagnosis. — A relatively small species; meta-
some segments dorsally armed with short setae;
urome segments not elevated. Antenna 2 slender,
the peduncle and flagellum armed with long setae.
Calceoli absent. P1 and 2 as in *G. p. pulex*. P5
to P7 with long setae on the anterior margins. The
inner rami of uropod 3 little longer than half
the outer rami.

Description. — Male: Maximum length observed
12 mm. The dorsal surface of the metasome seg-
ments and the first urome segment are set with
short setae. Uromsome segments without dorsal ele-
vations or excavations, armed with the usual groups
of elements (fig. 30O, P).

The lateral cephalic lobes are rounded; the eyes
are ovoid, slightly shorter than the diameter of the
first peduncle segment of antenna 1 (fig. 30A).

The first antenna is almost half as long as the
total body length. Both the peduncle and flagellum
are poorly setose. The second and third peduncular
segments have 2 to 3, and 1 or 2 groups of setae,
respectively, the main flagellum has up to 24 seg-
ments, the accessory flagellum only 2 or 3 (fig.
30B).

Peduncle segments 4 and 5 of antenna 2 bear
4 to 5 transverse rows of long straight setae, the
setae being twice as long as the diameter of the
segments on which they are implanted. The gland
cone is short. The flagellum is slender, 7- to 8-
Fig. 30. *Gammarus effultus* G. Karaman, 1975. A-P, δ, 11.2 mm; Q, 9, 7 mm; from spring in Kaleçik district, prov. Ankara, Turkey. A, cephalic segment; B, first antenna; C, second antenna; D, propodus of first gnathopod; E, propodus of second gnathopod; F, third pereiopod; G, fourth pereiopod; H, fifth pereiopod; I, sixth pereiopod; J, seventh pereiopod; K, third uropod; L, telson; M, epimeral plates; O, dorsal armature of meta- and urosome (lateral view); P, dorsal view of urosome; Q, seventh pereiopod.
segmented, dorsoventrally compressed, without calculi. The setae on the flagellar segments are longer than the diameter of the segments on which they are implanted (fig. 30C).

The third segment of the mandibular palp is armed with 25 to 28 D-setae, 4 to 6 E-setae, 1 group of A-setae and 2 groups of B-setae.

The first gnathopod has moderately long setae on segments 2 to 6. The propodus is armed with the normal medial palmar spine, 1 or 2 palmar angle spines and 2 or 3 submarginal spines. The dactylus is slender (fig. 30D).

The second gnathopod has the same type of armature as the first. The propodus shows the usual medial palmar spine, 3 palmar angle spines and 2 submarginal spines. As in gnathopod 1 the dactylus is slender (fig. 30E).

Pereiopods 3 to 7 are rather stout, having short dactyi.

The posterior margin of segments 4 and 5 of P3 is armed with rather short setae, intermixed with spines, the setae being little longer than the diameter of the segments (fig. 30F). The propodus is armed with groups of short spines and setae shorter than the diameter of the segment. In P4 the setation is even shorter (fig. 30G). Coxal plates 1 to 4 have rounded inferior corners.

The anterior margin of segments 3 to 5 in P5 to P7 is armed with spines and setae being as long as or longer than the diameter of the segments on which they are implanted. The basal segment of P5 is about as long as wide, forming a backward protruding lobe. In the next two pereiopods the basal segment is more slender, almost 1.5 times as long as wide. No setae have been found on the interior surface of these basal segments (see figs. 30H-J).

The epimeral plates as in *G. p. pulex* (fig. 30M).

Uropod 3 (fig. 30K) is moderately long, its inner ramus slightly longer than half the outer ramus. The setae on the outer margin of the exopod are never plumose.

The telson lobes (fig. 30L) are up to twice as long as wide. The setae in the distal group of elements are up to twice as long as the spines. Several groups of setae may be present on the dorsal surface of each lobe.

Female: The normal sexual dimorphism was observed. As in the males, short setae can be found on the dorsal surface of the metasome segments. The setae on the anterior margins of P5 to P7, the posterior margins of P3 and P4, and on the second antenna are longer than in males.

Variability. — Apart from the “normal” variability it was observed that the number of setae on the dorsal surface of the metasome and first urosome segments and length and number of setae on the anterior margins of P5 to P7 are rather variable.

Material examined. — One sample from the type-locality. Loc. typ. — Turkey, prov. Ankara, spring in Kalecik district. The ♂ holotype and many paratypes, collected 1-VII-1972, have been deposited in the collections of the Museo Civico di Storia Naturale, Verona. Several paratypes have been deposited in the Karaman Collection, Titograd.

Remarks and affinities. — *G. effultus* is somewhat similar to *G. birsteinii* nomen novum and *G. rouxi* Pinkster & Goedmakers. However, *G. birsteinii* always lacks the characteristic setae on the dorsal surface of the metasome segments and has a shorter inner ramus of the third uropod. *G. effultus* differs from *G. rouxi* by the presence of dorsal setae on all three metasome segments (in *G. rouxi* on segment 3 only), by the absence of setae on the ventral margins of epimeres 2 and 3, and in the shape of the basal segment in P7.

Ecology. — Unknown.

*Gammarus birsteinii* nomen novum. Fig. 31


*Gammarus brachyurus* G. Karaman, 1975a: 302-308, figs. 4-7; 1975b: 318-324, figs. 4-6.

*Gammarus argaeus var. brachyurus* Vávra, 1903: 111, pl. 3 fig. 13.

Diagnosis. — A small species. The slender peduncle and flagellum of antenna 2 bear long straight setae, calculei are always absent. Second segment of mandibular palp with increased number of setae. The dactylus of gnathopod 1 is often inflated medially. Pereiopods 5 to 7 with spines and setae along the anterior margin. Urosome flat. Uropod 3 very short, its inner ramus being only 1/3 to 1/2 of the outer ramus.
Fig. 31. *Gammarus birsteini* nom. nov. A-N, ♂, 10 mm; O, ♀, 8.7 mm; from a mountain stream, prov. Trabzon, Turkey. A, cephalic segment; B, first antenna; C, second antenna; D, mandibular palp; D', inner side of third segment of mandibular palp; E, propodus of first gnathopod; F, third pereiopod; G, fourth pereiopod; H, fifth pereiopod; I, sixth pereiopod; J, seventh pereiopod; K, third uropod; L, telson; M, epimeres; N, urosome; O, third uropod.

Description. — Male: Maximum length observed 11 mm. Body smooth, dorsally very flat. The dorsal urosome armature usually consists of a dorso-median and 2 dorsolateral groups of elements but in some populations the dorsolateral groups of elements may be absent on urosomite 1 (figs. 31N, S).

The lateral cephalic lobes are rounded. Eyes ovoid, as long as or shorter than the diameter of the first peduncle segment of antenna 1 (fig. 31A).

Antenna 1 is up to half as long as the total body length, both peduncular and flagellar segments being poorly setose. The main flagellum and accessory flagellum have 16 to 23, and 2 to 4 segments, respectively (fig. 31B).

Antenna 2 has a short gland cone, which never reaches the tip of the third peduncular segment. Peduncle segments 4 and 5 (figs. 31C, P) are almost equally long, each bearing 8 to 10 transverse rows of long straight setae at their ventral margin (being 2 to 3 times as long as the diameter of the segments). Each of the 8 to 10 segments of the slender, dorsoventrally compressed flagellum bears long straight setae, being 2 to 3 times as long as the diameter of the segments on which they are implanted. Calceoli have never been found.

The second segment of the mandibular palp bears up to 34 setae; the third segment (figs. 31D, D') is armed with 16 to 20 short D-setae, 4 to 6 long E-setae, 1 group of A-setae, and 1 or 2 groups of B-setae.

Segments 2 to 6 of gnathopod 1 are poorly setose, all setae being straight. The propodus is armed with a medial palmar spine, 1 to 3 palmar angle spines and 3 to 4 spines on the inner surface (fig. 31E). The dactylus is often dilated medially (fig. 31Q).

Segments 2 to 5 of the second gnathopod are also poorly setose. The propodus is set with straight or partially curved setae; apart from the medial palmar spine, 3 palmar angle spines and 2 or 3 submarginal spines can be found. The dactylus is slender.

Segments 4 to 6 of pereiopod 3 (fig. 31F) are set with long curled setae at the posterior margin, the setae being 1.5 to 2.5 times as long as the diameter of the segments.

Segments 3 to 6 of pereiopod 4 (fig. 31G) are poorly setose. Segment 4 bears several groups of straight setae, as long as the diameter of the segments on which they are implanted. Segments 5 and 6 bear 3 to 4, and 4 to 5 groups of short setae, respectively, intermixed with spines. Coxal plates 1 to 4 have rounded inferior corners.

Pereiopods 5 to 7 (figs. 31H-J) are moderately long, their basal segment being always more than twice as long as wide, lacking setae on the inner surface. Segments 4 to 6 are armed with the usual groups of spines along the anterior and posterior margins. In addition, groups of rather short setae (almost as long as the diameter of the segments on which they are implanted) can be found on the anterior margins of segments 4 and 5. The dactyls of all pereiopods are short.

The epimeral plates are identical to those in *G. pulex* (fig. 31M).

The most characteristic feature of this species is the structure of the very short third uropod (figs. 31K, O, R). The inner ramus is also very short, being 1/3 to 1/2 of the outer ramus only; a single spine is implanted at the distal end. The outer ramus is armed with long simple setae at the inner and outer margins and with some strong spines at the outer margin.

The telson lobes are wide and short, 1.4 times as long as wide. Each lobe has a single distal spine accompanied by several setae up to twice as long as the spines. Some setae appear on the dorsal surface of each lobe (fig. 31L).

Female: Normal sexual dimorphism was observed. Long setae appear on the peduncle and flagellum of A2 as in the male. The dactyls of both gnathopods are slender. Pereiopods 3 to 7, epimeral plates and telson are identical to those in the male. The third uropod is very short, the ratio between both rami like that in the other sex.

Live colour unknown.

Variability. — Except for the usual variability this species is variable in the relative length of the eyes. The dactylus of gnathopod 1 might or might not be dilated in the middle. The dorsal surface of urosomite 1 in some populations is armed with groups of spines and setae, in others it is not. The length of the inner ramus of uropod 3 usually
varies from 1/3 to 1/2 the length of the outer ramus.

Material examined. —
Turkey, prov. Artvin: Yanızçam gecidi (Yanızçam Silsilasi) mountain stream at 2000 to 2500 m, 9-VII-1971, several specimens (MCSN).
— Yanızçam gecidi, mountain stream at 2200 m, 8-VII-1971, several specimens (MCSN).
— Stream near Borcka, 18-VI-1964, 6 specimens (coll. MCSN, Verona).
— Stream near Hopa, 19-VI-1964, several specimens accompanied by _G. komareki_ (MCSN).

_Prov. Trabzon:_ Zigana gecidi, mountain stream at 1600 m, 12-VI-1969, several specimens (MCSN).
— Zigana Pass (S. of Trabzon) at 1500 m, 11-VI-1969, several specimens (MCSN).


Distribution. — Eastern part of Turkey near the Caucasus Mts., and the Talasskiy Alatau Mts., in Kazakhstan. Although no material is available we may assume that the species can also be found in the mountain chains in between these two widely separated areas.

Remarks and affinities. — The material we studied seems to be identical to that described as _Rivulogammarus brachyurus_ by Birstein, 1935, from the Syr Darya region (Talasskiy Alatau Mts.), although Birstein did not describe or figure some important characters like the second antenna and the shape and setosity of pereiopods 3 and 4. _Gammarus angusticoxalis_ Martinov, 1935, seems to be rather similar to _G. brachyurus_ Birstein, 1935. However, like Birstein for _brachyurus_, Martinov did not describe the second antenna. Since it was not possible to study material of the last species the question of a possible synonymy could not be solved.

During the present study it was found that the specific name _brachyurus_ was preoccupied by Vávra, 1905, for a variety of _G. argaeus_ Vávra. Therefore, it was necessary to change the preoccupied name _brachyurus_. As a new specific name we propose _G. birsteini_, in honour of the original author of this species.

Ecology. — No other data are available than that this species thrives in mountain streams at altitudes over 1500 m.

_Gammarus rambouseki_ (S. Karaman, 1931).

_Fig. 32_


Diagnosis. — Small species with stout extremities making a setiferous impression. Antenna 2 slender, densely setose, without calceoli. Pereiopods 3 and 4 with long setae along the posterior margin. Anterior margins of pereiopods 5 to 7 and uroscope with long setae.

Description. — Male: Maximum length observed 10 mm. The metasome segments bear short setae; the flat uroscope segments are armed with long setae, sometimes accompanied by single short spines (figs. 32K, L).

The lateral cephalic lobes are rounded; the eyes are small, ovoid, shorter than the diameter of the peduncle of antenna 1 (fig. 32A).

The first antenna (fig. 32B) is shorter than half the body length. The distal ends of the peduncle segments have a bunch of long setae on both the ventral and dorsal margin. In addition some groups of setae are implanted in the middle of the ventral margin of peduncle segment 2. The main flagellum has up to 26 segments, the accessory flagellum 3 or 4.

Peduncle segments 4 and 5 of antenna 2 (fig. 32C) are armed with 5 or 6 transverse rows of setae (being three times as long as the diameter of the peduncle segments). The up to 11-segmented flagellum is slender, weakly compressed dorsoventrally. Each flagellar segment is provided with 1 or 2 transverse rows of setae, up to twice as long as the diameter of the segments; calceoli are absent. The gland cone is short, hardly longer than half the peduncle of segment 3.

The third segment of the mandibular palp bears 20 to 25 D-setae, 4 to 6 E-setae, 1 group of A-setae and 2 groups of B-setae (fig. 32D).
Fig. 32. *Gammarus rambouseki* (S. Karaman, 1931), ♂, 10 mm, from Galičica Mt., Macedonia, Yugoslavia. A, cephalic segment; B, first antenna; C, second antenna; D, mandibular palp; E, fifth pereiopod; F, sixth pereiopod; G, seventh pereiopod; H, third uropod; I, telson; J, epimeres; K, urosome; L, dorsal view of urosome.
Gnathopods 1 and 2 are moderately setose, covered with straight setae only. The propodus of gnathopod 1 is armed with the usual medial palmar spine, 3 to 4 palmar angle spines and 2 to 4 submarginal spines. In gnathopod 2 a medial palmar spine, 3 palmar angle spines and 3 or 4 submarginal spines can be found. In both gnathopods the dactyls are slender.

Pereiopods 3 and 4 are short and stout, with short dactyls. Segments 4 and 5 of P3 bear long setae along the posterior margins (setae up to twice as long as the segments), on segment 6 the setae are shorter, about as long as the diameter of the segment and accompanied with pairs of short spines. Coxal plates 1 to 4 with rounded or quadrangular inferior corners.

In pereiopod 4 the setae along the posterior margin of segments 4 and 5 are as long as or slightly longer than the diameter of the segments; on segment 6 these setae are short.

Pereiopods 5 to 7 (figs. 32E-G) are short; the anterior margins of segments 4 and 5 are provided with numerous setae, as long as or longer than the diameter of the segments. Intermixed with the setae short spines can be found. The inner surface of the basis never bears setae. In P7 the basis is less than twice as long as wide.

The posterodistal corners of the epimeral plates vary from rectangular in the first to pointed in the second and third plates. Several pairs of setae, intermixed with spines, are found along the lower margins of the plates (fig. 32J).

Uropod 3 is relatively short (fig. 32H), its inner ramus being almost 2/3 of the outer ramus; all setae on uropod 3 are simple.

The telson lobes (fig. 32I) are short and broad, each lobe with 1 or 2 distal spines accompanied by several setae, up to twice as long as the spines. On the dorsal surface of each lobe 2 or 3 groups of long setae can be found.

Female: Normal sexual dimorphism was observed. Compared with other females within this group, female G. rambouseki is easily recognizable because of the presence of long setae on the second antenna, P3 to P7, the epimeres, uropod 3, and especially on the dorsal surface of the urosome. In this respect females of this species resemble the males.

Variability. — Apart from the usual variability, it was observed that the number of setae and spines on the epimeral plates was largely variable.

Material examined. —
Yugoslavia: Galičica Mountain in S. Macedonia, 1929 or 1930, several specimens (KC).
— Stream on foot of Perister Mountain near Bitola, S. Macedonia, alt. 500 m, 1960, 15 specimens (KC).
Greece: Torrent near Evrostini, Peloponnese (22°23'E 38°03'N), alt. 1200 m, 20-IX-1972, 4 specimens (KC).
— Ravine of Khakion, Mount Taygète, alt. 1300 m, 5-V-1966, 4 specimens (MCSN).

Loc. typ. — Galičica Mt., S. Macedonia, Yugoslavia. The ♀ holotype and several paratypes have been deposited in the Karaman Collection, Titograd.

Distribution. — Southern Yugoslavia and Greece.

Remarks and affinities. — G. rambouseki is a small species, well characterized by its setiferous body, especially urosome, and appendages (pereiopods 3 to 7 and antenna 2) and by the absence of plumose setae on the third uropod. In some respects, like the setiferous P5 to P7, this species resembles G. ibericus, G. acalceolatus, or G. syriacus. In these species, however, we never find the characteristic setation of the urosome. Furthermore, G. syriacus differs from the present species in having elevations on the urosome, very sharply pointed epimeres, and the relative length of the endopod of uropod 3.

In G. acalceolatus and G. ibericus the endopod of Ur. 3 is relatively longer and provided with plumose setae.

Schellenberg (1937a) mentioned a G. p. pulex f. bursuta (from Purnaro and Voialina, both in Greece) characterized by its very setiferous urosome. Probably this material also belongs to G. rambouseki.

Goedmakers (1972) suggested G. rambouseki to be identical to G. fossarum. This conclusion was based on the original description of S. Karaman. In this description S. Karaman failed to mention certain important characters like the setosity of P5 and P7. A renewed study of the type material learned, however, that G. rambouseki must be considered a good species.

G. crispus Martinov, 1932, from the foothills of the Caucasus Mountains near the Black Sea is
very similar to *G. rambouseki* in the setosity of the second antenna, uropod 3 and telson, but differs from it in its less setose uroscope and the shape of the epimeres. The restriction should be made that this opinion is based on the description of Martinov only. Unfortunately we were not in the opportunity to see the type material.

Ecology. — Living in mountain streams at altitudes over 500 m, sometimes accompanied by *G. cf. pavlovici* (G. Karaman).

**Gammarus komareki** Schäferna, 1922. Fig. 33

Refs.: *Gammarus komareki* Schäferna, 1922: 21-28, figs. 8, 9 and 10 ml-m4, tab. 1, 8, 8a1, 2, 8p1, 2; S. Karaman, 1930: 286 (part.); G. Karaman, 1975b: 350-352.


*Rivulogammarus komareki*; S. Karaman, 1931a: 60; 1934b 132.

*Gammarus pulex persicus*; S. Karaman, 1934b: 129, fig. 2.

*Rivulogammarus pulex komareki*; Kneva-Abadzieva, 1966 305.

*Gammarus (Rivulogammarus) pulex komareki*; Schellenberg, 1937a: 505.

non *Gammarus (Rivulogammarus) pulex komareki*; Cărăuş, Dobreanu & Manolache, 1955: 86-90, figs. 48-51 (= *G. arduus*).

Diagnosis. — A medium large species, very characteristic because of its densely setose peduncle and flagellum of antenna 2. Antenna 1 is poorly setose. The endopod of uropod 3 is 3/4 of the exopod.

Description. — Male: Maximum length observed 15 mm. The posterior margin of metastome segment 3 is set with some spinules. The uroscope usually has a distinct but shallow saddle; the dorsal armature of the uroscope consists of the normal dorsomedian and dorsolateral groups of short spines and short setae.

The lateral cephalic lobes are rounded. The eyes are small, reniform or ovoid, as long as or shorter than the diameter of the first peduncle segment of A1 (figs. 33A, B).

The first antenna is long, nearly 2/3 of the body length. The peduncle segments and the flagellum are poorly setose. The main and accessory flagella have 31 to 39, and 3 to 5 segments, respectively (fig. 33C).

The 4th and 5th peduncle segment as well as the flagellum of the second antenna are very densely setose. The setae in the transverse rows are up to three times as long as the diameter of the segment on which they are implanted. The gland cone is short, about half as long as the third peduncle segment (fig. 33D). The 10- to 13-segmented flagellum is slightly swollen and dorsoventrally compressed as in *p. pulex*. It never bears calceoli.

The third segment of the mandibular palp bears 40 D-setae, 4 to 6 long E-setae, 1 group of A-setae and 1 or 2 groups of B-setae (fig. 33E).

Gnathopods 1 and 2 are moderately setose, armed with straight setae. On the propodus of both gnathopods the usual medial palmar spine can be found. In gnathopod 1 a varying number of smaller spines are implanted along the posterior margin of the propodus and along the inner surface next to it. In the second gnathopod 3 strong palmar angle spines can be found.

Segments 4 to 6 of pereiopod 3 are very setose (fig. 33F) along their posterior margin. These setae can be 2 to 3 times as long as the diameter of the segments on which they are implanted. In segment 6 some spines are intermixed with the setae. In pereiopod 4 the setae are shorter and less numerous than in pereiopod 3 (fig. 33G). Coxal plates 1 to 4 usually have rounded inferior corners.

The basal segment of pereiopods 5 to 7 is rather slender with an unarmed interior surface, tapering towards the distal end, forming a more (P5) or less (P7) protruding lobe. The other segments are armed with numerous strong spines accompanied by a scarce number of short setae, being as long as or slightly longer than the segment on which they are implanted (figs. 33H-J).

The epimeral plates do not show obvious differences from those in *G. p. pulex* (fig. 33M).

The length of the inner ramus of the third uropod is about 3/4 of the outer ramus. The setation is less developed than in *G. p. pulex*. Plumose setae occur along the inner and outer margins of both rami (fig. 33K).

The telson lobes are slender, almost twice as long as wide. The setae occurring in the distal group of elements are only slightly longer than the spines. A few setae are implanted on the dorsal surface of each lobe (fig. 33L).

Female: The sexual dimorphism is basically different from that observed in other species within
Fig. 33. *Gammarus komareki* Schäferna, 1922. A, C-M, ♂, 12.7 mm; B, ♂, 10 mm; N-O, ♀, 8 mm; from spring in Asenovgrad, prov. Plovdiv, Bulgaria. A, cephalic segment; B, cephalic segment; C, first antenna; D, second antenna; E, mandibular palp; F, third pereiopod; G, fourth pereiopod; H, fifth pereiopod; I, sixth pereiopod; J, seventh pereiopod; K, third uropod; L, telson; M, second and third epimeres; N, second antenna; O, seventh pereiopod.
this group. So the setation on the peduncular segments of the antennae is reduced in length and number compared with the other sex. The same holds true for the setation of P3 and P4. At the other hand, the setation along the anterior margin of P5 to P7 is longer and more densely implanted than in males (see figs. 33N, O).

Variability. — Within this species the shape of the eye is somewhat variable. The same holds true for the length and the number of setae on antenna 2 and pereiopod 3. In general this number increases with age. In some populations setae are completely absent on the anterior margins of P5 to P7, whereas in others the terminal setae on the telson lobes can be up to twice as long as the spines. The colour of live specimens shows the same variability as in G. p. pulex.

Material examined. — About 100 samples from all over the distribution area.
Loc. typ. — Village Belovo near Pazarâlı, Bulgaria. The holotype and 15 paratypes have been deposited in the Zoologisches Museum Berlin (G.D.R.).
Localities cited. — Bulgaria: village Belovo, near Pazarâlı; Sliven; Camkôi monastery near Marica (all Schäferna, 1922); Stanimaki (= Asenograd) S.E. of Plovdiv; Tatarpazarâdik (both S. Karaman, 1934b); several localities in southern Bulgaria (Kneva-Abadzieva, 1966), many localities all over the country (G. Karaman, 1969, 1975b). Greece: Hordiotis Mt. near Saloniki (S. Karaman, 1931a); U.S.S.R.; Moldavia, mouth of river Ryniza (Schellenberg, 1937a); Iran: Viladereb (Mount Savalan, near Ardébil, Azerbaijan) (S. Karaman, 1934b, Karaman, 1969); Turkey: many localities (G. Karaman, 1975b).

Distribution. — G. komareki is known from Bulgaria, the northern part of Greece, the southern part of the U.S.S.R. around the Black Sea coast, the northern half of Turkey, and the northern part of Iran.

Remarks and affinities. — This species appears to be closely related to G. frater n. sp. and to G. bergi Martinov, 1930. It differs from G. frater by a less setose peduncle of A1 (in both sexes), by more setose pereiopods 3 and 4, and slightly more setose antenna 2 and uropods 3 (see also under G. frater n. sp.). Gammarus bergi differs from this species in the peduncle and flagellum of antenna 1 which are set with numerous very long setae, the size of the eye, and the absence of setae on the anterior margin of pereiopods 5 to 7 (in both sexes). Cărâsu, Dobreau & Manolache described a species under the name of komareki from Rumania; during the present study, it became clear that these records actually apply to Gammarus arduus n. sp., a species with setae on the inner surface of the basal segment in pereiopods 5 to 7.

Ecology. — The species is usually found in running waters or in springs. It seems to prefer a dense vegetation where water current velocities are rather low. It is able to stand a rather high degree of organic pollution. It has been found together with G. p. pulex, G. frater, G. pseudosyracus, G. birsteini and members of the G. balcanicus-group.

Gammarus frater n. sp. Fig. 34

Diagnosis. — Medium-large species with a densely setose second antenna. The first antenna bears some groups of setae on the peduncle segments. The setation along the posterior margin of pereiopods 3 and 4 is relatively short (in males). Uropod 3 without plumose setae along the outer margin of the exopod.

Description. — Male: Maximum length observed 14.5 mm. Body smooth, urospic segments without elevations. A distinct saddle is present on the first urospic segment. The dorsal armature consists of a dorsomedian and two dorsolateral groups of short spines and slightly longer setae (fig. 34K).

The lateral cephalic lobes are rounded, the eyes being reniform, slightly longer than the diameter of the first peduncular segment of antenna 1.

The first antenna (fig. 34A) is almost half the total body length. Peduncle segments 1 to 3 are armed with groups of setae at the ventral margin, varying in number from 2 on segment 1 to 5 on segment 2; segment 3 bears 3 groups of setae. These setae are never longer than the diameter of the segments on which they are implanted. The main and accessory flagella bear up to 35, and 3 or 4 segments, respectively.

Peduncle segments 4 and 5 as well as the flagellum of antenna 2 are densely set with transverse rows of long setae (fig. 34B). The 12- to 15-segmented flagellum is slightly swollen and dorso-ventrally compressed as in G. komareki. Each flagellar segment bears 1 or 2 transverse rows of
Fig. 34. *Gammarus frater* n. sp. A-K, ♂, 12.5 mm; L-O, ♀, 8.9 mm; from spring in Asenovgrad, prov. Plovdiv, Bulgaria. A, first antenna; B, second antenna; C, detail of second antenna; D, third pereiopod; E, fourth pereiopod; F, fifth pereiopod; G, seventh pereiopod; H, third uropod; I, telson; J, second and third epimeres; K, urosome; L, second antenna; M, third pereiopod; N, fourth pereiopod; O, seventh pereiopod.
setae being twice as long as the segments in the proximal half of the flagellum, gradually diminishing in length towards the distal parts of the flagellum. Calceoli have never been found. The gland cone is short, little longer than half the length of the third peduncular segment.

The third segment of the mandibular palp is armed with 32 to 38 D-setae, 4 to 6 E-setae, 1 group of A-setae and 1 or 2 groups of B-setae.

The first gnathopod is moderately setose, all setae being straight. The propodus has the usual medial palmar spine and up to 3 palmar angle spines. Several smaller spines ("Stiftstacheln") are implanted along the posterior margin.

The setosity of the second gnathopod is similar to that in the first. The propodus is armed with a medial palmar spine and usually 3 palmar angle spines. As in the first gnathopod the dactylus is slender.

Pereiopod 3 (fig. 34D) is poorly setose except for segment 4 which is armed with 5 to 7 groups of straight setae, which are about as long as the diameter of the segment on which they are implanted. In segments 5 and 6 both the length and number of the setae decrease.

The setation of pereiopod 4 (fig. 34E) is even poorer than that of P3, almost resembling the setation found in members of the *Gammarus balcanicus*-group. The length of the setae never exceeds the diameter of the segments on which they are implanted. Coxal plates 1 to 4 have rounded inferior corners.

Pereiopods 5 to 7 (figs. 34F, G) are identical to those in *G. komareki*. The basal segment never has setae on its interior surface. The armature usually consists of spines only. The dactylus is always short in P3 to P7.

The epimeral plates are like those of *G. komareki*. The posteroinferior corners vary from almost rectangular to slightly pointed. Spines form the only armature along the inferior margin.

Uropod 3 is moderately long; the inner ramus is about 3/4 of the outer ramus. The outer margin of the exopod is armed with a number of strong spines and a small number of simple setae (fig. 34H).

The telson lobes are short, little longer than wide. The setae in the distal groups of elements are up to twice as long as the spines. Several small groups of setae are implanted on the dorsal surface of each lobe.

Female: The sexual dimorphism in this species is slightly different from that in most other species (but identical to that in *G. komareki*). So the setation on the peduncle of antenna 2 is less developed than in the male (see fig. 34L). Unlike in the other sex, the pereiopods 3 and 4 make a rather setose impression. The setation of pereiopods 5 to 7 is better developed than in male, the setae being often 2 to 3 times as long as the diameter of the segments (figs. 34M-O). Both the number and length of the setae in the dorsal urosome armature is increased, compared with the male. Females of this species can be distinguished from females of many other species because of the setation of the peduncle of A1 and A2 and the long setation on pereiopods 5 to 7 (fig. 34O).

Variability. — Normal variability was observed.

Material examined. —
Bulgaria: Springlet in Asenovgrad (S.E. of Plovdiv), 4-IV-1942, 20 specimens (KC). Accompanying species: *G. komareki*.
— Backovski Monastery near Cervena Skala, in the Rodopi Mt. (S.W. of Plovdiv), 24-VII-1924 (KC).
Loc. typ. — Springlets in Asenovgrad, Bulgaria. The & holotype and 19 paratypes have been deposited in the Karaman Collection, Titograd.

Distribution. — S.W. part of Bulgaria.

Remarks and affinities. — At first sight this species looks very similar to *G. komareki* Schäfer- na, a species with which it has been found coexisting. However, both males and females can be easily distinguished because of the distinctly more setose peduncle of antenna 1, the less setose pereiopods 3 and 4, and the slightly less setose antenna 2. Martinov, 1932, described *G. crispus* from the Black Sea coast of the Caucasus, a species with a setose peduncle of antenna 1. *G. frater* is distinguished by its clearly less setose uropod 3 and telson. *G. frater* differs from *G. bergi* Martinov in the flagellum of A1 and the markedly less setose pereiopods 3 and 4.

Ecology. — Living in the spring region of small streams, sometimes accompanied by *G. komareki*. 


Gammarus bergi Martinov, 1930. Figs. 35, 36A–F

Diagnosis. — A rather small species which differs from most others in this group because of the setosity of both the first and second antennae.

Description. — Male: Body length up to 13 mm. Metasome and urosome segments smooth, without dorsal elevations or excavations. The dorsal armature of the urosome is poorly developed, consisting of a dorsomedian group of short elements and a dorsolateral group on each side. In the last urosome segment this dorsolateral group may be absent (fig. 36F).

The lateral lobes of the head are obtuse with rounded corners. The eyes are relatively large (fig. 35A).

Antenna 1 (fig. 35B) is about 1/3 of the body length. Peduncle segment 3 is about 2/3 of each of the other two. The inferior margin of peduncle segments 2 and 3 are armed with some tufts of long setae, being longer than the diameter of the segments on which they are implanted. The proximal 10 to 13 of the 18 to 22 segments in the main flagellum are armed with tufts of long setae along the inferior margin. The accessory flagellum has 3 to 4 segments.

Antenna 2 (fig. 35C) is nearly as long as A1. Peduncle segments 4 and 5 as well as the 9 to 11 flagellar segments are densely setose, the setae being up to 3 times as long as the diameter of the segments. The flagellum is not inflated, lacking calceoli. The antennal gland cone is short.

The third segment of the mandible palp has up to 24 D-setae, 4 or 5 long E-setae, 1 or 2 groups of B-setae and one group of A-setae.

The first gnathopod is basically identical to that in G. pulex; the propodus is set with long setae (fig. 35E).

The propodus of the second gnathopod is armed with an obtuse medial palmar spine and 3 palmar angle spines. The inner surface of the propodus is set with 4 spines near the palmar angle and many groups of long setae. The dactylus is slender (figs. 35F, 36A).

Pereiopods 3 to 7 are moderately slender with short stout dactyli. Segments 4, 5 and 6 of pereiopod 3 bear long, often curved setae, 2 to 3 times as long as the diameter of the segments. Some small spines can be found in between these setae (fig. 36B).

In pereiopod 4 (fig. 35G) the setae are slightly shorter and less numerous than in pereiopod 3. The coxal plates of P1 to P4 have rounded inferior corners.

In pereiopod 5 the basal segment is about 1.5 times as long as wide. Its distal end is wider than the proximal end of the next segment, thus forming a posteriorly protruding lobe. Setae are absent on the inner surface. Segments 3 to 6 are armed with a reduced number of short spines, sometimes intermixed with equally short setae (fig. 36C).

The basal segments of pereiopods 6 and 7 are relatively longer, more than twice as long as wide, distally not protruding. Setae are absent from the surfaces. The armature is identical to that in P5 (see figs. 35H, 36D).

The posteroinferior corner of the first epimeral plate is almost rectangular, that of the second and third (fig. 36F) is always sharply pointed. The inferior margin of the last two plates is armed with short spinules only.

Uropod 3 (fig. 35I) has an inner ramus which is more than 4/5 of the outer ramus. Plumose setae are found on the inner and outer margins of endo- and exopod.

The telson lobes are more than twice as long as wide. Each lobe has 2 to 3 apical spines accompanied by several setae, up to 3 times as long as the spines. A few setae are implanted along the outer margins of the lobes (fig. 36E).

Female: Unlike most members of the pulex-group the setation on the peduncular segments is less developed than in the male (as in G. komareki). The setation of A1, and P3 to P7 is identical to that in the male (unlike G. komareki). Females of this species can be distinguished from females of G. komareki because of the setiferous antenna 1 and non-setiferous P5 to P7. They differ from females of G. frater in the setiferous flagellum of antenna 1 and the absence of setae on P5 to P7.

Material examined. — 3 samples all from Lake Issyk Kul, Koïsara, U.S.S.R., 1906, containing 2 specimens each. (MNHN). Accompanying species in all 3 samples G. inberbus n. sp.

Loc. typ. — Koïsara, Lake Issyk Kul, Kazakhstan, U.S.S.R.
Fig. 35. *Gammarus bergi* Martinov, 1930, ♂, 13 mm, from Lake Issyk Kul, Kazakhstan, U.S.S.R. A, cephalic segment; B, first antenna; C, second antenna; D, mandibular palp; E, first gnathopod; F, second gnathopod; G, fourth pereiopod; H, sixth pereiopod; I, third uropod.
Fig. 36. A-F, *Gammarus bergi* Martinov, 1930, ♂, 13 mm, from Lake Issyk Kul, Kazakhstan, U.S.S.R. A, propodus of second gnathopod; B, third pereiopod; C, fifth pereiopod; D, seventh pereiopod; E, telson; F, meta- and uroscope.

Distribution. — Up to now this species is known from Lake Issyk Kul only.

Remarks and affinities. — At first sight this species is rather similar to *G. komareki* Schäferna and *G. frater* n. sp. It differs from *G. komareki* in the presence of long setae on the peduncle and flagellum of the first antenna, in its more rounded coxae 1 to 4, in the shape of the basal segments in P6 and P7, and in the shape of the epimera. Unlike *G. komareki*, the female of the present species has no long setae on the anterior margin of segments 4, 5 and 6 of P5 to P7. It differs from *G. frater* in the absence of setae on the flagellum of A1, the much longer setation of P3 and P4 (in males), the shape of the basal segments of P6 and P7, and the setation of the anterior margin of segments 4, 5 and 6 on P5 to P7 (in females only).

The material described here was originally identified as *G. p. pulex* by Chevreux. It is clear that this identification was wrong. In comparing the material with the description of *G. bergi* Martinov, 1930, from Lake Issyk Kul, we came to the conclusion that this material was identical. However, since we were unable to study Martinov’s type material, some doubt still remains. Ecology and colour of live specimens unknown.

**Gammarus rouxi** Pinkster & Goedmakers, 1975.

Figs. 36G-I, 37


Diagnosis. — A small but very characteristic species (fig. 37A) because of the short antennae which give the animal a rather robust impression, the slender dactyli of pereiopods 3 to 7, and the setation of pereiopods 6 and 7.

Description. — Male: Maximum length observed 10 mm. The dorsal surface of the third metasome segment is set with some small setules. The urosome segments have low but distinct elevations. The armature of the urospine consists of a dorsomedian and two dorsolateral groups of spines. The number of spines in each group is somewhat variable. Each group of spines can be accompanied by one or more setules, which almost equal the spines in length (fig. 36I).

The eyes are rather small, hardly longer than wide, the upper margin of which is widely separated from the mid-dorsal line (fig. 37A).

The first antenna is short (fig. 37B) about 1/4 of the total body length. The main and accessory flagella have 12 to 15 and 1 segments, respectively.

The second antenna (fig. 37C) is even shorter than the first. The gland cone is half as long as the third peduncle segment. The fourth and fifth peduncle segments are almost equal in length, both armed with some tufts of long setae along the inferior margin. The 7 or 8 segments of the flagellum are never swollen or compressed. Calceoli are always present in the 3 or 4 proximal flagellar segments.

The second segment of the mandibular palp is sparsely armed with setae (maximum number observed 13). The third segment has up to 20 D-setae, 4 or 5 long E-setae, 1 group of A-setae and 2 groups of B-setae.

The propodus of the first gnathopod bears a strong medial palmar spine which is separated from the palmar angle group of spines by a wide gap. The setation, if present, is very short.

The propodus of the second gnathopod is armed with an obtuse medial palmar spine which is separated from the palmar angle group consisting of 1 strong and 2 or 3 smaller spines. More so than in gnathopod 1, the propodus is set with groups of medium long setae.

The last three segments of pereiopod 3 (fig. 37D) bear groups of long sometimes curved setae along the posterior margin.

Pereiopod 4 closely resembles P3, although the setation is less dense (fig. 37E). Coxal plates 1 to 4 have almost rectangular inferior corners.

The basal segment of pereiopod 5 (fig. 37F) is little longer than wide. Its distal end is much wider than the proximal end of the next segment, forming a backward protruding lobe. The armature of merus and carpus consists of strong spines and many long setae intermixed with them.

The basal segment of pereiopod 6 (fig. 37G) is little longer than in P5 and set with some setae on its inner surface. For the remainder it resembles P5.

Pereiopod 7 (fig. 37H) is very characteristic in this species because of (1) the characteristic shape of its basal segment with its wide proximal and
Fig. 37. *Gammarus rouxi* Pinkster & Goedmakers, 1975. A-I, ♂, 10 mm; J, ♀, 6.5 mm; from Immouzer du Kandar, prov. Fez, Morocco, A, habitus; B, first antenna; C, second antenna; D, third pereiopod; E, fourth pereiopod; F, fifth pereiopod; G, sixth pereiopod; H, seventh pereiopod; I, dactylus of sixth pereiopod; J, basis of seventh pereiopod.
very constricted distal portion, as well as (2) the long setae both on the inner surface and the posterior margin. The other segments bear long setae in between the spines. The dactyl in all pereiopods are always very slender (fig. 37I).

The first epimeral plate has a rounded inferior corner. In the second and third epimeral plates these corners vary from almost rectangular to slightly pointed (fig. 36I). Setae are implanted along the inferior margins of all three epimeres.

The endopodite of the third uropod (fig. 36G) is little longer than half the exopodite. Although the setation is rather poorly developed we can always find some plumose setae along the outer margin of the exopodite.

The telson lobes (fig. 36H) overreach the peduncle of the third uropod. They are elongate, twice as long as wide and armed with a distal group of setae and spines and a varying number of setae on the dorsal surface.

Female: Much smaller than the male. Maximum length observed 6 mm. Apart from the usual dimorphism it was observed that the shape of the basal segment of P7 is even more characteristic than in the male. Females of this species therefore are easily recognizable.

The colour of live specimens is greenish.

Variability. — Comparable to that in *G. pulex*.

Material examined. — One sample from the type locality. Loc. typ. — Oued crossing road P24, upstream of Immouzzer du Kandar, province Fez, Morocco. The δ holotype, θ allotype and 50 paratypes, collected on 16-VI-1972, have been deposited in the collections of the Zoologisch Museum Amsterdam, cat. no. ZMA Amph. 105.002a-c. Accompanying species: *G. gauthieri*.

**Gammarus crenulatus** n. sp. Fig. 38

**Diagnosis.** — A medium large species, making a slender impression. It is readily recognizable because of the incisions of the dorsoposterior margins of the metasome segments, each incision bearing a long setule.

**Description.** — Male: Maximum length observed 16 mm. The metasome segments are very characteristic because of crenulations of the dorsoposterior margins (see figs. 38K, L). In each incision a long setule is implanted. Moreover, some setules are implanted on the dorsal surface of all metasome segments and the first urosome segment. Dorsomedian and dorsolateral groups of elements are found on all urosome segments. The setae in these groups are longer than the spines.

The lateral lobes of the head are rounded, the eyes being reniform, about twice as long as wide; the upper ocular margin is widely separated from the middorsal line (fig. 38A).

Antenna 1 is poorly setose. Its main and accessory flagellum have 24 to 31 and 4 to 5 segments, respectively.

The gland cone of the second antenna (fig. 38B) attains the distal end of the third peduncle segment. Peduncle segments 4 and 5 are equally long, armed with tufts of setae, implanted in three longitudinal rows. The slender flagellum has a maximum of 14 segments, none of them bearing calceoli. The setae, implanted in groups on these flagellar segments, are as long as or longer than the segments on which they are implanted, but never form a flag-like brush as in *G. p. pulex* (figs. 38B, C).

The second segment of the mandibular palp only bears 10 setae or less. The third segment has up to 30 D-setae, 6 or 7 long E-setae, 1 group of A-setae and 2 groups of B-setae (fig. 38D).

The first gnathopod is moderately setose (fig. 38E). The medial palmar spine is obtuse.

The hand of the second gnathopod is in so far characteristic (fig. 38F) that an obtuse spine is implanted between the obtuse medial palmar spine and the palmar angle (group of) spine(s). Numerous tufts of long setae are implanted on the inner surface of the hand. The dactylus is relatively long.
Fig. 38. *Gammarus crenulatus* n. sp., ♀, 14 mm, from river Soaditikos at Sofades, prov. Karditsa, Greece. A, cephalic segment; B, second antenna; C, detail of second antenna; D, mandibular palp; E, propodus of first gnathopod; F, propodus of second gnathopod; G, basis of fifth pereiopod; H, seventh pereiopod; I, third uropod; J, telson; K, metas- and uroscope; L, dorsal crenulations of metasome segments.
Pereiopods 3 and 4 do not show obvious differences from those in *G. p. pulex*. The inferior corners of coxal plates 1 to 4 are rounded to quadrangular.

Pereiopods 5 to 7 (figs. 38G, H) are relatively short. Their basal segment is also relatively short, varying from almost square in P5 to 1.5 times as long as wide in P7. In P6 and P7 the posteroinferior surface of the basis bears numerous setae. The armature of the other segments consists of a number of strong spines, sometimes intermixed with some short setae. The dactyli of P3 to P7 are short.

The first epimeral plate has an almost rectangular posteroinferior corner. In the second and third epimeres this corner is always sharp (fig. 38K). The lower margin of the second epimeral plate is set with some setules.

The endopodite of the third uropod (fig. 38I) attains about 3/4 of the length of the exopodite. Plumose setae are found along the inner and outer margins of endo- and exopodite.

The shape and setation of the telson lobes are identical to those in *G. pulex* (fig. 38J). Female: Normal sexual dimorphism was observed. So, the setation of the peduncular segments of A1 and A2 is longer than in the male. Females of this species are easily recognizable because of the crenulated metasome segments, the setules on the dorsal surface of the metasome segments and the setae on the posteroinferior surface of the basis of P6 and P7.

Variability. — Apart from the usual variability encountered in this group variability can be observed in the number of crenulations and setae on the metasome segments and in the number of setae on the posteroinferior surface of the basal segments of P6 and P7.


— Prov. Larissa, fountain of Daphne, about 30 km N. of Larissa, 5-X-1964, 10 specimens (ZMA). — Prov. Larissa, small brook 6 km N. of Tiranov, 14-X-1964, 2 specimens (ZMA).

Loc. typ. — Greece, Prov. Karditsa, river Soaditikos at Sofades. The holotype and 30 paratypes have been deposited in the collections of the Zoologisch Museum Amsterdam under cat. no. Z.M.A. Amph. 105.210a, b.

Distribution. — Thessalia, Greece.

Remarks and affinities. — Within the *G. pulex*-group, *G. crenulatus* is the only species with crenulated metasome segments and setae on the dorsal surface of all 3 metasome segments. Moreover, a strong spine is implanted between the medial palmar spine and the palmar angle group of spines in P2. The species is therefore easily recognizable within this group.

Ecology. — So far this species is known from the upper and middle reaches of freshwater streams with dense beds of vegetation. The colour of live specimens is greenish.

REFERENCES


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LIST OF (SUB)SPECIFIC NAMES USED IN THIS PAPER

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