# BEAUFORTIA

#### SERIES OF MISCELLANEOUS PUBLICATIONS

# ZOOLOGICAL MUSEUM OF THE UNIVERSITY OF AMSTERDAM

No. 211

Volume 16

November 20, 1968

A revision of the European species of the *Echinogammarus* pungens - group (Crustacea, Amphipoda)

# JAN H. STOCK

#### ABSTRACT

A revision of the species belonging to the group of, or confused with "Gammarus" (now Echinogammarus) pungens H. Milne Edwards, 1840 is given. Not less than 7 species have, at one or more occasions, been confused with E. pungens. All of these, and a number of related forms, are described and illustrated in detail, in several cases after consultation of the original or of the type material. In order to stabilize the nomenclature of this group, a neotype is selected to replace the lost types of Gammarus pungens. A key to the species is provided. The subgenera Homoeogammarus and Parhomoeogammarus, as well as the genus Ostiogammarus, are synonymized with Echinogammarus. The subgenus, or genus, Marinogammarus is synonymized with Chaetogammarus. Since the species known as Gammarus or Marinogammarus olivii (now Chaetogammarus olivii) is frequently confused with various Echinogammarus species, this species and some of its allies are included as well in the present paper.

The variability and ecological preferences of each species are discussed.

#### Introduction

As the result of some 15 years of study in the gammarids, from various angles such as taxonomy, ecology, experimental tagging, breeding, interfertility, I finally have decided to publish the results of my observations on the "Gammarus" pungens group. In doing so, I strongly feel that this work is far from complete, but also that E. J. Phelps' words, from 1899, could have been written very well indeed for this kind of article: "The man who makes no mistakes does not usually make anything".

In the course of ecological work in the "étangs" (= brackish lagoons) along the French Mediterranean coast, several samples of *Echinogammarus* were collected that, according to the classical identification works, should be called *Gammarus pungens* H. Milne Edwards, 1840. It was observed that several morphologically different forms occurred in these samples; that

Received: July 24, 1968

furthermore these forms were constant and without intermediates, even in samples in which more than one form occurred; and that finally no couples in pre-copula were composed of heterogeneous types. These observations, together with the failure of interbreeding in experiments (G. & B. Brun, 1964; Razakandisa & Brun, 1964), made me aware of the fact that G. pungens apparently is the collective name for a group of sibling species.

In the following paper, an attempt is made to classify and to distinguish these sibling species. I follow in this revision closely the procedure of an earlier revision of mine (Stock, 1967), of the Gammarus locusta-group, i.e., all species are abundantly illustrated, of all species chiefly the males (which have more clearly demarcated characters) are treated, and material from all around the Mediterranean basin — as far as available in the collections of the museums in western Europe — has been incorporated. Moreover, an extensive study of the literature has been made, although it is often not easy, owing to lack of sufficient information therein, to determine what species that or that author meant with the name "Gammarus pungens". In several cases, the original material on which a publication was based, and — in the cases of Gammarus olivii, G. beieri, G. eisentrauti, and G. veneris — also the typematerial was studied to clarify the status of the taxa involved. In this way I hope to have partly avoided the shortcomings of some older publications, that treated only local groups of gammarids, without taking into consideration the taxa described elsewhere, or the variability existing elsewhere.

In contradistinction to the opinions of authors as S. Karaman, who believed that every river-system or every isolated lake possessed its own species or subspecies of gammarids, I found that most of the taxa have a large distribution, often circum-mediterranean. It might be remarked in parentheses that my previous study, on the *Gammarus locusta*-group, yielded similar biogeographic results. Like those in that species-group, the species of the *pungens*-group are choosy rather than unspecialized in their preference for the salinity of their environment. The various records of species occurring both in fresh- and seawater, invariably point to confusion of two or more taxa.

The following paper is an attempt to straighten out the question. It must be remarked that, although the collections of several museums were studied for this purpose (see: Acknowledgements), I examined relatively few samples from Italy, the Balkans and North Africa. For some of the more widely distributed species, especially *Echinogammarus veneris* and *E. foxi*, it might be advisable in the future to delimit subspecies.

A subdivision into two subspecies might be indicated also in the case of the two "forms" of *Echinogammarus pungens*: the one from waters with a rised ion-content around the Mediterranean basin, the other from fresh waters draining into the Atlantic Ocean. I regret that lack of sufficient material keeps me from proposing a definite, clear-cut solution in these cases, but I take consolation in the words of Hector (in Shakespeare's "Troilus and Cressida"): "Modest doubt is call'd the beacon of the wise".

# **ACKNOWLEDGEMENTS**

The author is indebted to the Directors and Curators of the following institutions for the loan of material used in this study: Dr. J. Eiselt and Dr. G. Pretzman of the Naturhistorisches Museum, Wien (abbreviated in the sequel NMW), Dr. J. Forest of the Muséum National d'Histoire Naturelle, Paris (MNHN), Dr. H.-E. Gruner of the Zoologisches Museum der Humboldt Universität, Berlin (ZMB), Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), Dr. F. D. Por of the Hebrew University, Jerusalem (HUJ), Dr. A. L. Rice and Mr. M. H. Thurston of the British Museum (Natural History), London (BMNH). Furthermore, the samples preserved in the Zoölogisch Museum, Amsterdam (ZMA), have been examined. Dr. B. Brun, Laboratoire de Biologie Animale, Marseille (LBM), Dr. L. Berner, Marseille, and Drs. S. Parma, Hydrobiologisch Instituut, Nieuwersluis (The Netherlands), have kindly provided several most interesting samples. Dr. R. Margalef, of the Fisheries Research Institute, Barcelona, was kind enough to have collected fresh material of E. pungens from a locality cited in the literature. Dr. A. Punt and some of his cooperators of the Laboratory of Animal Physiology of the University of Amsterdam, as well as Drs. P. J. H. van Bree of the Zoölogisch Museum, Amsterdam were most helpful in collecting gammarids in the département de Charente, France, on their various travels in that region. Mr. J. Paul, likewise of the Zoölogisch Museum Amsterdam, kindly collected some samples in southern Europe. Dr. Zora Karaman, Skopje, Yugoslavia, and Dr. G. S. Karaman, Titograd, Yugoslavia, were of great help in providing literature from the Balkans, unavailable in this country, and very worthwhile information on certain species described by the late Dr. S. Karaman.

Much material was collected by the author, on some trips assisted by Mr. S. Pinkster or Mr. P. Kant, in southern France. Subventions for the realisation of this fieldwork from the University of Amsterdam, from the Netherlands' Organization for the Advancement of Pure Research (Z.W.O.), The Hague, and from the Centre National de la Recherche Scientifique (C.N.R.S.), Paris, are gratefully acknowledged.

# CONSTANCY AND VARIABILITY OF CERTAIN CHARACTERS

The variability pattern in the *Echinogammarus pungens*-group is very similar to that encountered in the *Gammarus locusta*-group (Stock, 1967). Several characters are very stable, while several others are not. So, the structure of the mandible palp, the setation of the 2nd antennae, the presence or absence of compressed dorsal elevations on the urosome, and the shape of these elevations, as well as the morphology of the legs, are very constant features. The shape of the basal segments of legs 5 to 7, in particular of the latter, is age- and sex-dependent: in younger specimens and in females, this segment is wider and less elongate than in adult males. In adult males, however, the shape and armature of the basal segment are fairly constant characters.

The shape of the inner ramus of the uropod (scale-shaped versus more elongate) is a constant, but not easily visible character. The uropod should be observed always mounted under a coverglass, and care should be taken that the inner ramus is observed in flat position and not from the lateral side.

More variability is observed in the following cases:

1. The epimeral plates of the pleon. The degree to which their ventroposterior corners are produced into a point seems to change from population to population. Some populations of *Echinogammarus veneris* have the 2nd and 3rd epimeres very much produced (e.g. the population from Lake Tiberias, fig. 7b), others (like the type-specimens from the Venus-well on Cyprus, fig. 10c) have the lower back angle nearly rectangular. Similar variations are known from species within the *Gammarus locusta*-group, such as *G. crinicornis* (cf. Stock, 1967: 36) and *G. aequicauda* (cf. Stock, 1967: 51).

Roux (1967) has demonstrated that individuals with more or less rectangular and with strongly pointed epimeres in *Gammarus pulex*, are interfertile and thus belong to a single species.

2. The telson. The armature of the telson lobes is extremely variable, both within one population and between populations of different origin. In some populations a large percentage of the individuals lacks the baso-lateral telson spine (cf. figs. 31f and 33d). The presence or absence of this spine was taken by some authors, e.g. Karaman (1929b: 105—106) as a specific character, but my observations do not support this view. Not seldom, one finds individuals in which even the left and right telson halves show considerable differences; one such case is shown in fig. 7d for *Echinogammarus veneris*. It seems that, in addition to *E. veneris*, especially *E. thoni*, *E. stammeri* and *Chaetogammarus olivii* are susceptible for this type of variation.

The shape of the telson lobes, however, is not subject to noticeable variation.

- 3. The dorsal and lateral armature of the urosome. The number of elements participating in this armature can vary largely. Such variations have been described frequently in various species of the family Gammaridae by other authors as well. (The presence or absence of long setae between the spines, however, is a much more stable character).
- 4. The peduncle of the first antenna. The degree of "hairiness" of the peduncle is somewhat variable and age-dependent.
- 5. The setation of the appendages and of the body tends to be less in younger specimens.

This holds also true for the setation of the lower margin of the epimeres. In younger specimens of *E. acarinatus* and of *E. lusitanus*, this margin bears spines only, like in *Marinogammarus*. The anterior spines disappear first in older specimens, to make place for setae; in fully mature males, all spines are replaced by setae; in females, even mature ones, spines often remain. Although I have not actually observed this phenomenon in *E. tacapensis*, it is suspected to occur in that species as well, since Chevreux & Gauthier (1924) found only spinules on the lower margin of the epimeres, whereas Ruffo, 1939, observed setae.

6. The compressed keel on the pereion and pleion. Some species have a dorsal carina on the pereion and/or on the pleion. The number of pereion segments participating in this keel formation may vary, especially in *E. thoni* (Schäferna), where the keel might be restricted (according to Karaman, 1934: 329) to the pleion segments only. I have observed similar variations in *E. scutarensis* (Schäferna), where the development of the carina may change between nearly absent to very pronounced.

- 7. The sideplates 1 to 4 carry long setae on their lower margins in *E. pungens*; no variability as to this character has been observed by us. In *E. veneris*, however, the setules are shorter, and tend to disappear. In some of the eastern populations of the species (from near Damascus, Syria and from Cyrenaica), all coxal plates bear setules on their lower margin. In the more western populations (from Italy), the lower margin of all coxal plates is naked or armed with a limited number of setules only. Intermediate populations (from Israel, Cyprus and Yugoslavia) tend to be intermediate also as to the setation of the coxal plates, in the sense that the lower margin of the 4th plate starts losing its setation, then followed by the 3rd plate, etc.
- 8. The presence or absence of feathered setae on the antennae and legs is considered a character of some importance on specific level in Gammarus. In the present survey, I came across some populations of Echinogammarus that possessed very numerous feathered elements on all appendages, but that were otherwise indistinguishable from E. foxi. Moreover, intermediates were found that possessed a few feathered setae intermixed with more numerous "normal" setae. It might be significant that all those aberrant populations (i.e., the populations bearing at least some feathered setae) lived in the Black Sea, whereas those from outside the Black Sea had only simple setae. However, it may be repeated, not all Black Sea specimens are provided with feathered setae (see also point 9).
- 9. In this connection, it is perhaps significant that some Black Sea specimens of *E. foxi* lack calceoli on the second antennae in the male. The greater part of the material seen by me from the Black Sea, and all material from outside that region, do possess calceoli. There seems no relation between the presence or absence of calceoli and the nature of the setal armature (feathered or smooth) (see point 8). The presence or absence of calceoli is a charcater of specific importance in the genera *Gammarus* and *Chaetogammarus*, thus the lack of calceoli in some pontic specimens is a most disconcerting feature, which may need further study, based on a more abundant material.

# Chaetogammarus, A SENIOR SYNONYM OF Marinogammarus

The genus *Chaetogammarus* was described by Martynov, 1925. Although Martynov designates no type-species, there are sufficient indications to select herewith, from the species listed in Martynov's paper, the first cited and only described species as the type-species (in accordance with the Code of Nomenclature, rec. 69B, 9 to 12). The type-species thus selected is *Gammarus tenellus* G. O. Sars, 1896, nom.preocc. = G. ischnus Stebbing, 1899.

The genus Chaetogammarus, as diagnosed by Martynov (see also Martynov, 1932: 95), differs in only one respect from the subgenus Marinogammarus Schellenberg, 1937a: Martynov (for Chaetogammarus) calls the lateral lobes of the head "triangular, sometimes acute and extended", whereas Schellenberg (for Marinogammarus) describes them as "rundlich abgestumpft". When Sexton & Spooner (1940) treated Marinogammarus as a full genus, they repeated this character (in the description, not in the diagnosis):

"lateral lobes rounded". Later, Schellenberg, 1942, used this feature as the only distinguishing character between the genera *Chaetogammarus* and *Marinogammarus*. In my opinion, this feature has no importance whatsoever: in *Gammarus aequicauda* (Martynov, 1931) one finds in one population specimens with pointed and rounded lateral lobes (Stock, 1967: 53). Moreover, Martynov himself in the original description of *Chaetogammarus* in 1925, and later also Cărăusu, Dobreanu & Manolache (1955), included species with pointed as well as with rounded lateral lobes in *Chaetogammarus*.

It might be remarked here, as a side track, that the distinction between Gammarus s.str. and Rivulogammarus Karaman, 1931, also supports on the shape of the lateral lobes of the head, and that I consider those two genera also identical.

Cărăusu et al. (1955) were apparently aware of the impossibility of using the shape of the lateral lobes as a generic character, since they proposed two quite new features, the length of the 3rd uropod in relation to the length of the urosome, and the presence or absence of curled setae on the 2nd antenna of the male, as key characters. The uropod length, apart from being sex- and age-dependent, has very little significance. The presence of curled setae on the A2 is of no value either; first of all, the type-species of *Chaetogammarus* (C. ischnus) has straight setae; secondly, it is known that in Gammarus tigrinus Sexton, 1939, the antennal setae may be straight or curled, depending on age of the specimens and season of the year (Hynes et al., 1960); thirdly, the curly or straight state of the setae is shown to be dependent on the size of the specimens and the "activité génitale" in Gammarus pulex (Linnaeus, 1758) (cf. Roux, 1967: 43).

Summarizing, it must be concluded that *Chaetogammarus* Martynov, 1925, is a senior synonym of *Marinogammarus* Schellenberg, 1937.

# Homoeogammarus and Parhomoeogammarus, Junior synonyms of Echinogammarus

Schellenberg, 1937a, created a new subgenus, Homoeogammarus, for the species Gammarus simoni Chevreux, 1894, and G. tacapensis Chevreux & Gauthier, 1924. No type-species was indicated, thus the name Homoeogammarus is not available, according to article 13(b) of the Code of Nomenclature. This subgenus is, according to the original description, characterized against Marinogammarus and Echinogammarus by (1) a long palm in the first male gnathopod, provided with "Stiftstacheln"; (2) small eyes. The first of these characters is one of the outstanding features of Gammarus marinus (see Sexton & Spooner, 1940, fig. 1d), which is precisely the type-species (by monotypy) of Schellenberg's own subgenus Marinogammarus. Character (2) is, of course, without generic importance, since species with larger and smaller eyes are more often found within the same genus or subgenus (e.g., to take an example from Schellenberg's own paper, 1937a: Rivulogammarus duebeni (Lilljeborg, 1851) with large elongate eyes, and

R. pulex (Linnaeus, 1758) with small, rounded eyes). The other characters of certainspecies of *Homoeogammarus*, more in particular the setiferous lower margin of the epimeres (see Ruffo, 1939, fig. 5) make it clear that this subgenus is a junior synonym of *Echinogammarus* Stebbing, 1899.

Parhomoeogammarus Schellenberg, 1943, is said to differ from Homoeogammarus in (1) the more elongate eye; (2) the absence of "Stiftstacheln" on the palm of the first male gnathopod, and (3) the presence of a hind corner on the basis of P7. Now, characters (1) and (2) were exactly the only features separating Homoeogammarus from Marinogammarus and Echinogammarus; this means that Parhomoeogammarus is not distinguishable from these genera by these features. Character (3) is neither borne out by Schellenberg's figure 1d, nor by material examined during this study. Because of the setiferous P7 and setiferous male epimeres, Parhomoeogammarus lusitanus Schellenberg, 1943 (the type-species by monotypy) must be classified with Echinogammarus.

# THE DISTINCTION BETWEEN Chaetogammarus AND Echinogammarus

We have retained Marinogammarus and Echinogammarus here essentially in the sense of Schellenberg, 1937a (with the exception that Chaetogammarus is considered in this paper a senior synonym of Marinogammarus, and that Homoeogammarus and Parhomoeogammarus are united with Echinogammarus).

In close accordance with Sexton & Spooner's diagnosis (1940: 636) of Marinogammarus, the following diagnosis for Chaetogammarus is proposed:

Gammarus-like species; with a short inner ramus in uropod 3; almost completely lacking setae on the hind peraeopods, dorsally on the urosome, on the coxal plates 1 to 4, and on the ventral margin of the epimeral plates; hind margin of basis of 7th peraeopod not expanded, armed with very short setules; adapted for life in stony littoral habitats, although sometimes living intertidally in places with freshwater influence.

Type-species: C. ischnus (Stebbing, 1899).

Echinogammarus, in its emended and enlarged sense, can be diagnosed as follows:

Like Chaetogammarus, but with longer setae on one or more of the following parts: dorsal surface of urosome, coxal plates 1 to 4, ventral margin of epimeral plates, hind peraeopods, especially also hind margin of basis of 7th peraeopod; adapted for life in running fresh waters and lakes, often with a high Ca-content, or in estuarine and brackish conditions.

Type-species: E. berilloni (Catta, 1878) — by subsequent selection (Chevreux & Fage, 1925: 259).

Karaman's genus Ostiogammarus, with the same type-species, is a junior synonym of Echinogammarus.

# THE CHARACTERS OF THE Echinogammarus pungens-GROUP

The species treated in this paper are those related to or confused with *E. pungens* (H. Milne Edwards, 1840). These species can be defined as follows: members of *Echinogammarus*, with large, elongate eyes, without teeth-like projections on the metasome, without dense spinulation all over the metasome (some setules may occur, however, on the posterior margins of the metasome segments).

Thus defined, the following European species belong to the pungens-group: (1) E. pungens (H. Milne Edwards, 1830); (2) E. veneris (Heller, 1865); (3) E. scutarensis (Schäferna, 1922); (4) E. thoni (Schäferna, 1922); (5) E. pungentiformis (Schäferna, 1922); (6) E. foxi (Schellenberg, 1928); (7) E. acarinatus (Karaman, 1929); (8) E. stammeri (Karaman, 1929); (9) E. beieri (Karaman, 1930); (10) E. eisentrauti (Schellenberg, 1937a); (11) E. lusitanus (Schellenberg, 1943).

Since number (7) has currently been confused with *Chaetogammarus olivii* (H. Milne Edwards, 1830), the latter species has been included in the present discussions, as well as *Chaetogammarus dahli* nom.nov., a species in turn confused with *Chaetogammarus olivii*.

Re-examination of the type-material has shown that species number 9 is synonymous with number 2; number 5 (of which I have not seen material) is probably also a synonym of number 2.

E. lusitanus is included here, because it can be taken easily for a member of the pungens-group (especially since its dorsum is scarcely ornamented), but it belongs actually to the berilloni-group (see page 52).

Echinogammarus cari (Karaman, 1931a) is an incompletely known species, probably synonymous with E. simoni (Chevreux, 1894).<sup>1</sup>) A subspecies of E. cari, described by Karaman, 1934, as Ostiogammarus cari bosnensis is probably synonymous with E. stammeri, an opinion shared by Pljakić, 1962, after re-examination of topotypes of O. cari bosnensis.<sup>2</sup>)

KEY TO THE EUROPEAN SPECIES OF THE Echinogammarus pungens-GROUP AND TO CERTAIN Chaetogammarus SPECIES FREQUENTLY CONFUSED WITH Echinogammarus-SPECIES (BASED ON ADULT MALES ONLY).

Species marked with an asterisk (\*) do occur in European waters, but are not treated in this paper.

- 2a) Metasome keeled; urosome with very high, compressed, dorsal elevations.

  Echinogammarus thoni (Schäferna, 1922)
- b) Metasome without keel; dorsal elevations on urosome low or absent ....... 3
- 1) Pljakić, 1962: 15, thinks that *E. cari* is synonymous with his *Gammarus pungens* ssp. acarinatus (= E. stammeri in the present paper).
- 2) Pliakić records E. stammeri under the name of G. pungens ssp. acarinatus.

3a) Hand of gnathopod 1 with very oblique palm, practically invisibly merging into the posterior margin. Setae on 2nd antenna shorter than the diameter of the segments carrying them.

Echinogammarus lusitanus (Schellenberg, 1943)

- Eyes very elongate, sausage-shaped. Lateral lobes of head produced into a sharp point.

\*Chaetogammarus placidus (Grimm, in Sars, 1896)

5a) Telson lobes more or less triangular, as long as wide. First segment of mandible palp setiferous.

Chaetogammarus ischnus (Stebbing, 1899)

- 8a) Setae on the 2nd peduncle segment and on the flagellum segments of A1 very short (shorter than the diameter of the segments). Setules on the anterior margin of merus of P3 shorter than the spines. Posterior margin of basis of P5, P6, and P7 with exceedingly small setules. Carpus of P6 and P7 more than 2½ times as long as wide. [A2 with calceoli. First segment of A1 as long as segments 2 + 3 together.]

\*Chaetogammarus pirloti (Sexton & Spooner, 1940).

- b) Some of the setae on the 2nd peduncle segment and on the flagellum segments of A1 at least as long as the diameter of the segments. Setules on the anterior margin of merus of P3 longer than the spines. Posterior margin of basis of P5, P6, and P7 with 'normal' setules. Carpus of P6 an P7 less than 21/2 times as long as wide ... 9
- 9a) First segment of peduncle of A1 distinctly shorter than segments 2 and 3 combined. Peduncle and flagellum segments of A2 densely setose. Flagellum of A2 without calceoli. Second peduncle segment of A1 nearly 3 times as long as wide, third peduncle segment much longer than wide.

Chaetogammarus olivii (H. Milne Edwards, 1830).

b) First segment of peduncle of A1 about as long as segments 2 and 3 combined. Peduncle and flagellum segments of A2 sparingly setose. Flagellum of A2 provided with calceoli. Second peduncle segment of A1 about twice as long as wide, third peduncle segment hardly longer than wide.

Chaetogammarus dahli nov. sp.

10a) Third segment of mandible palp with regular (comb-like) armature on the lower margin. Setae on telson shorter than the spines. Flagellum segments of A2 of larger males compressed, robust, the proximal ones with calceoli.

Echinogammarus stammeri (Karaman, 1929)

b) Third segment of mandible palp with regular plus irregular setation on the lower

margin. Setae on telson longer than the spines. Flagellum segments of A2 not compressed, slender; calceoli absent.

Echinogammarus acarinatus (Karaman, 1929)

11a) Dorsal elevations of urosome not compressed. Basis of 5th leg with large posterodistal lobe. Merus of 5th leg unusually short and wide. Coxal plates 1 to 4 practically without setules on their lower margins.

Echinogammarus foxi (Schellenberg, 1928)

- - b) Telson distally with spines only. Propodus of legs 1 and 2 widened.

Echinogammarus eisentrauti (Schellenberg, 1937)

13a) Fourth and fifth peduncle segments of 2nd antenna with sparse tufts of setae; flagellum of 2nd antenna with short setae only. Hind margin of basis of 6th and 7th legs with very long, very densely set, setae. Lower margin of coxal plates 1 to 4 with long, densely set, setae.

Echinogammarus pungens (H. Milne Edwards, 1840)

b) Fourth and fifth peduncle segments of 2nd antenna richly armed with tufts of long setae all around the segment; flagellum with long setae. Hind margin of basis of 6th and 7th legs with shorter, often more widely interspaced setules. Coxal plates 1 to 4 partly naked, or armed with shorter and less densely inserted setae, on their lower margins.

Echinogammarus veneris (Heller, 1865)

#### DESCRIPTIVE PART

All descriptions, unless the contrary is explicitly stated, apply to the adult male. In all figures of the third uropod, the plumosity of the setae is omitted.

# Echinogammarus pungens (H. Milne Edwards, 1840). Figs. 1—4.

Gammarus pungens H. Milne Edwards, 1840: 47; Bate, 1862: 217; Ferrer Galdiano, 1921: 374—376, figs. 1—2; Karaman, 1929a: 99; Monod, 1931: 411; Margalef, 1944a: 201, figs. 10—14; Margalef, 1944b: 71, figs. 10—11; Petit, 1950: 477; Harant & Jarry, 1963: 262, 299; G. Brun, 1967: 22, 26, 28.

Gammarus pungens f. carinata (nom. nud.) Schäferna, 1920: 1-5.

Gammarus pungens f. carinata Schäferna, 1922: 28-33, 97-98, 102-103, figs. 11 (part.), 12 (part.), 13.

Gammarus pungens ssp. carinata Pljakić, 1962: 15-23.

Gammarus pungens du Rhône; Brun & Brun, 1964: 754—759, pl. I fig. R, pl. II fig. R. Gammarus Veneris (?G. pungens); Chevreux, 1899: 71; March, 1899: 12.

Gammarus (Echinogammarus) pungens; Schellenberg, 1937a: 272.

Ostiogammarus pungens; Karaman, 1929b: 105-107; Karaman, 1931: 45.

Gammarus pungens (part.); Della Valle, 1893: 296, 764, pl. 24 fig. 35; Stebbing, 1906: 471—472 (lit.); Ruffo, 1937: 53—60, figs.

Echinogammarus pungens (part.); Straškraba, 1967: 205.

?Gammarus (Echinogammarus) pungens; Ruffo, 1939: 60 (lit.).

#### Material examined. -

S p a i n : Lago de Bañolas, prov. Gerona, 6—15 Apr. 1968, many specimens (ZMA). Ebro estuary, near San Jaime de Enveja, 22 June 1968, 2 3, 1 9 (ZMA).

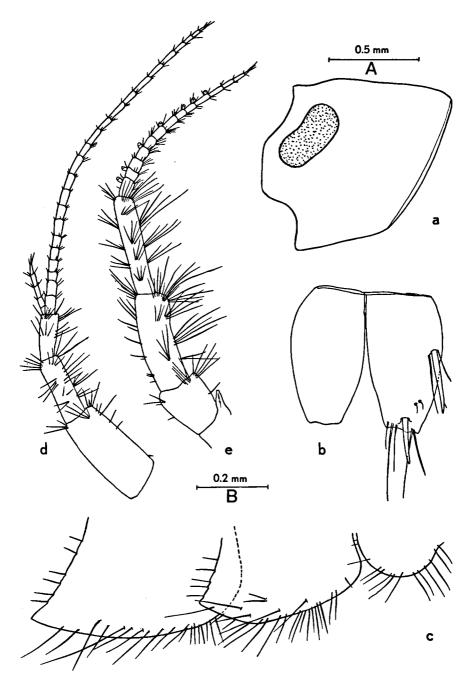


Fig. 1. Echinogammarus pungens (H. Milne Edwards, 1840), &, from Fontaine de Salses (France, Pyrénées-Orientales). a, head, lateral (scale A); b, telson, dorsal (B); c, epimeral plates 1 to 3 (A); d, first antenna (C); e, second antenna (C).

- France: Fontaine d'Estramar (= Fontaine de Salses), dépt. Pyrénées-Orientales, between waterweeds, 25 Sep. 1957, many specimens (RMNH); same locality, 20 Sep. 1956, 9 Sep. 1961, 10 Apr. 1967, chlorinity 2.16 %, many specimens (ZMA).
- Balaruc-les-Bains, near Sète, dépt. Hérault, in a brook, 16 Feb. 1897 and 9 Mar. 1897, many specimens (MNHN); in a source near Balaruc-les-Bains, Aug. 1897, many specimens (MNHN).
- River l'Hérault, dépt. Hérault, some 3200 m from the mouth, in drift-wood, 27 Apr. 1968, chlorinity 3.7‰, 9 specimens (ZMA).
- Port St. Louis-du-Rhône, dépt. Bouches-du-Rhône, in the river Rhône, about 200 m north of the bridge, 5 May 1967, chlorinity 0.075 ‰, 2 \( \text{ZMA} \).
- Mouth of the river Touloubre (in Etang de Berre), dépt. Bouches-du-Rhône, 30 Mar. 1961, L. Berner coll., 15 specimens (ZMA).
- Mouth of the river Argens, dépt. Var, near highroad N 98, in Enteromorpha, 4 Jan. 1968, chlorinity 1.99 ‰, 1 &, 1 \ (ZMA).
- Sources de la Touvre, le Bouillant (near la Ruelle, E. of Angoulême), dépt. Charente, under stones, 25 Apr. 1968, chlorinity 0.02 ‰, 11 specimens (ZMA); same locality, 21 Mar. 1968, 1 9 (ZMA).
- River Gers at Layrac, dépt. Lot-et-Garonne, large, fast-running river, 26 Apr. 1968, 1 Q (ZMA).
- River Gers near Fleurance, dépt. Gers, near bridge in road N 653, chlorinity 0.027‰, 22 Aug. 1968, 1 9 (ZMA).
- Italy: "Italy", without further specifications, 8 specimens, collection A. Della Valle (BMNH).
- Yugoslavia: Strožanac, 5 km S.E. of Split, 8 June 1961, 1 9 (ZMA); river Stobreć, near Strožanac, 40 m from open sea, chlorinity 0.835 %, 6 June 1961, 1 3 (ZMA).
- Small river debouching into Kotor Bay, S.W. of Risan, 18 June 1961, many specimens (ZMA).

Description of material from the neotype locality (Fontaine de Salses). — A small species; the largest male available (out of some 200 specimens) is about 11 mm long, females and most other males are 6 to 9 mm long. The lateral lobes of the head (fig. 1a) are truncate. The eyes are 13/4 times as long as wide, rather small; the distance from the upper margin of the eye to the mid-dorsal line is rather large (fig. 1a). The first antenna (fig. 1d) has the first peduncle segment slightly shorter than the 2nd and 3rd combined. Peduncle segment 1 with a few setae; more (tufts of) setae on segments 2 and 3. Accessory flagellum 5- to 6-segmented; main flagellum 22- to 26-segmented, long. Second antenna (fig. 1e) shorter than the first; gland cone short, straight, directed forward; peduncle segments 4 and 5 each provided with 4 tufts of long setae on the inferior margin; their median and dorsal surfaces bear 4 to 5 tufts of much shorter setae. The general impression of the peduncle is that of a scarce setation. The flagellum of the 2nd antenna is shorter than the peduncle, 12- to 16-segmented; calceoli are always present, usually rather numerous (6 to 10); the inferior side of the flagellum is ornamented with tufts of short setae (shorter than the tufts on the inferior margin of the peduncle).

The mandible palp has an unarmed first segment; the inferior margin of the third segment is armed with a regularly comb-like row of spinules (as in *E. foxi*, cf. fig. 14d).

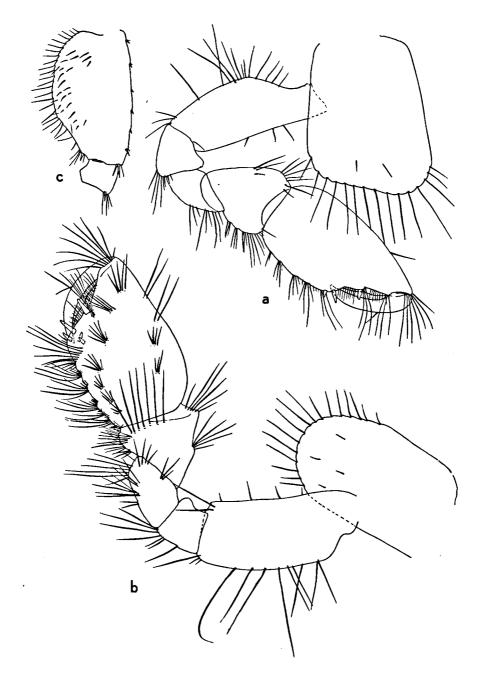


Fig. 2. Echinogammarus pungens (H. Milne Edwards, 1840), from Fontaine de Salses (France, Pyrénées-Orientales). a, first leg, & (scale A); b, second leg, & (A); c, proximal segments of seventh leg, \( \partial \) (C).

The coxal plates 1 to 4 have numerous small notches on their inferior margin; in each notch a long setule is implanted. Scattered setae occur moreover on the inner surface of these coxal plates. The first and second legs (gnathopods) are for the rest without peculiarities (figs. 2a, 2b). The 3rd leg (figs. 3a) is also very similar to that of related species, as E. veneris. The 4th leg (fig. 3b) has 5 tufts of setae on the anterior margin of the merus. The 5th leg (fig. 4a) has a more or less rectangular basal segment, the posterior margin of which bears numerous small notches, each notch with a short setule; the anterior margin of this segment bears, in addition to a number of spines, several tufts of setae, which are longer than the spines. The infero-posterior corner of the basis is nearly rectangular and does not project much. The basis of leg 6 (fig. 4b) is tapering; its posterior margin is crenulated and provided with numerous long setae. The basis of leg 7 is in the male (fig. 4c) nearly rectangular in its proximal part, tapering in its distal part; its posterior margin is densely crenulated, and provided with equally densely set, long setae; numerous shorter setules are scattered over the surface of the entire posterior part of this segment. In female, the basis is relatively wider (fig. 2c). Numerous long setae, which are much longer than the spines, occur on the distal segments of legs 5 to 7.

The dorsum of the pleosome is not keeled; it bears a few scattered setules. The first urosome segment shows a distinct dorsal concavity ("saddle") in front of the distinctly compressed dorsal elevation (fig. 3d). A lower compressed dorsal elevation is present on the 2nd urosome segment, a still lower elevation on the 3rd. The usual armature of the urosome segments is 1-2-1; 1-2-1; long setae (overreaching the spines) are implanted in each group of elements (fig. 3d).

The epimeral plates 1, 2, and 3 (fig. 1c) bear numerous long setae on their inferior margin. Shorter setae occur on the posterior margin of plates 2 and 3. The 2nd plate has a nearly rectangular postero-inferior corner, the 3rd a slightly pointed one.

The telson (fig. 1b) consists of two elongately elliptical halves; the sub-basal spine is usually present; there is often only one distal spine; long setae (the distal ones longer than the spine) accompany the spines.

The 3rd uropod has a very short, scale-like endopod. The exopod bears long setae on both margins; these setae are feathered, except for the exteroproximal ones (in fig. 3c all setae are illustrated without feathering).

Variability. — In some older specimens, and in some populations from the Balkans, the number of notches and the number of setae on the inferior margin of coxal plate 4 is lower than in the French material described above.

Remarks on the neotype. — Gammarus pungens was described by H. Milne Edwards (1840) in three lines only, as follows: "Espèce également trèsvoisine de la Crevette d'Olivi, mais ayant le petit appendice terminal des dernières fausses pattes tout-à-fait rudimentaire, et le grand appendice trèspoilu et à peine épineux". As type-locality is mentioned "les eaux thermales du mont Cassini en Italie". Della Valle (1893) wonders where this locality is

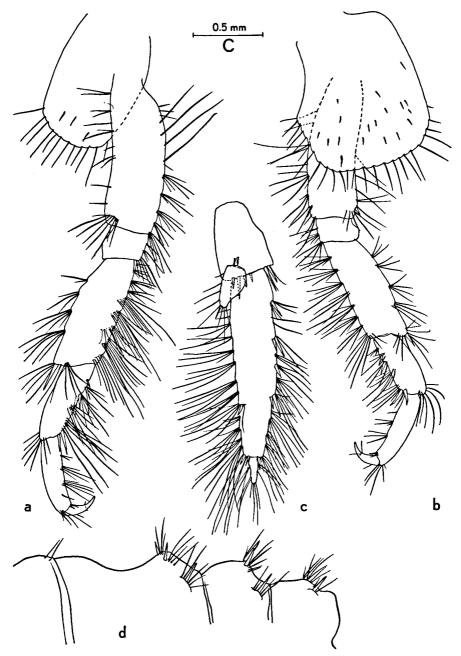


Fig. 3. Echinogammarus pungens (H. Milne Edwards, 1840), &, from Fontaine de Salses (France, Pyrénées-Orientales). a, third leg (scale C); b, fourth leg (C); c, third uropod (A); d, urosome, from the left (A).

in Italy; his attempts to collect gammarids on the Monte Cassino, Terra di Lavoro, failed; moreover, there are no thermal springs in that area.

The following four factors contributed to the enormous confusion that reigns nowadays in the *pungens*-group: (1) the quite insufficient original description, unaccompanied by illustrations; (2) the unfindable type-locality; (3) the occurrence of several closely related species in the type-area (Italy); (4) the absence of original type-specimens. As to point (4), all my attempts to locate the types in one of the museums in western Europe failed.

In this light, I have felt the necessity in the interests of stability of nomenclature, to designate a neotype for *Echinogammarus pungens*. In doing so, I had myself guided by the following reasons: (1) The first author, who was clearly aware that "Gammarus" pungens consisted of several closely related taxa, was Schäferna (1922), who distinguished G. pungens forma carinata (= the typical form), G. pungens forma acarinata (now Echinogammarus acarinatus), Carinogammarus pungentiformis (now Echinogammarus veneris) and Carinogammarus thoni (now Echinogammarus thoni). Since Schäferna's publication is well-illustrated, I propose to follow his usage and to restrict the name Echinogammarus pungens to the taxon called by him Gammarus pungens forma carinata. (2) In agreement with the Code of Nomenclature, art. 75 (C) (5), I have sought for a neotype coming from thermal waters, just as Milne Edwards' types. I thus selected a neotype from a sample collected in the Fontaine de Salses, a slightly thermal, mineral spring on the Mediterranean coast of France.

The neotype, a male, is deposited in the Zoölogisch Museum, Amsterdam, collection number Amph. 101910a.

Note on the synonymy. — Through the courtesy of Dr. R. Margalef of Barcelona, I could examine freshly collected material from the Lake of Banyolas, a locality well-known from the literature (cf. Ferrer Galdiano, 1921, and Margalef, 1944a, 1944b). The material proved to belong to *E. pungens*. Although the lake is "fresh" (i.e., it has a low chlorinity), it has a high ion-content, chiefly consisting of Calcium (CaO content 0.28—0.29 g/l, according to Margalef, 1944b: 30).

Notes on the specimens from outside the Mediterranean drainage basin. — Four samples are available (from the French départements Charente, Gers, and Lot-et-Garonne) from waters draining into the Atlantic Ocean, whereas all remaining samples come from waters draining into the Mediterranean. These "Atlantic" samples are very close to typical *E. pungens*, except in a few respects: (1) The first antenna (fig. 4d) is very robust (i.e., the 3rd segment of the peduncle is exceptionally short, the flagellum has only 12 to 15 segments, the short accessory flagellum has only 3 to 4 segments). (2) The flagellum of the second antenna is also short (only 8 to 10 segments). (3) The basis of leg 7 is more slender, and its posterior margin is straighter (fig. 4e). Since so few "Atlantic" samples are available, I have preferred for the moment to consider them merely as a slightly aberrant "form" of *E. pungens*. More material, and by preference hybridization tests, are necessary to clarify the taxonomic status of the Atlantic form.

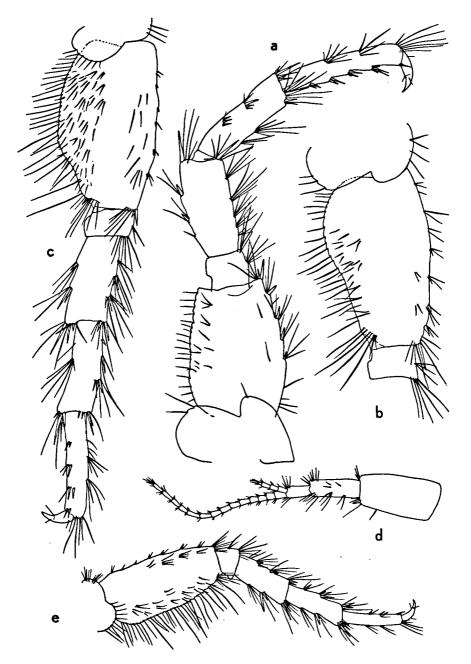


Fig. 4. Echinogammarus pungens (H. Milne Edwards, 1840); a-c, & from the Fontaine de Salses (France, Pyrénées-Orientales); d-e, & from the Sources de la Touvre (France, Charente). a, fifth leg (scale C); b, basal segments of sixth leg (C); c, seventh leg (C); d, first antenna (C); e, seventh leg (E)

It may be significant that all "Atlantic" collections have been made in so-called fresh waters (i.e., with a low chloride content), although these waters, being of Karstic origin, presumably have a high calcium content.

Ecology. — This is a species from running brackish waters (estuaries, mineral springs) or larger lakes (with substantial water-movement, through wave-action) with a high ion (particularly Ca<sup>++</sup>) content. In estuaries, it lives often accompanied by Gammarus aequicauda (Martynov). In places where the freshwater influence is already large, E. pungens is gradually crowded out by members of the Gammarus pulex-group, by Echinogammarus thoni (Schäferna), by E. berilloni (Catta), or by E. veneris (Heller). In mineral springs, it may live together with E. foxi (Schellenberg).

Distribution. — Known with certainty from Spain, France, Italy, and Yugoslavia.

# Echinogammarus eisentrauti (Schellenberg, 1937). Figs. 5—6.

Gammarus (Echinogammarus) eisentrauti Schellenberg, 1937a: 278—280, fig. 4. Gammarus pungens subsp. Eisentrauti; Margalef, 1950: 144—150, fig. 5. Gammarus pungens forma; Margalef, 1944a: 201.

Material examined. — Deyá, in the western part of the isle Mallorca<sup>3</sup>), in fresh water, 19 specimens of both sexes (syntypes, ZMB). A male has been selected by me as the *lecto-holotype* (ZMB 24695).

Description. — Largest male 11 mm long; other males and all females smaller (6—10 mm). The shape and size of the eye and the shape of the head is correctly shown in Schellenberg's illustration (1937a, fig. 4a). The first antenna is very similar to that of *E. pungens* (present paper, fig. 1d).

The second antenna (fig. 5a) bears 4 tot 5 bunches of setae on the inferior and medial margins of segments 4 and 5; each bunch contains only a limited number of setae. The flagellum is 13- to 17-segmented; its proximal 8 to 10 segments are provided with large calceoli; the proximal segments are robust; the setae on the flagellum are slightly longer than the length of its proximal segments. The gland cone is thumb-shaped, remarkably short.

The mandible palp has an unarmed first segment, whereas the lower margin of the third segment bears a regular, comb-like row of setules.

The coxal plates 1 to 4 resemble closely that of *E. pungens*. The carpus of leg 1 (fig. 5b) has a rounded, projecting posterior margin (this "lobe" is larger than in *pungens*). The hand (propodus) is much widened: the length of the posterior margin is less than the greatest width of the propodus (in *pungens*, the posterior margin is longer than the greatest diameter). The palm is very clearly demarcated, concave; the tip of the dactylus does not attain the palmar angle.

<sup>3)</sup> For the correct locality, see Margalef, 1950: 144.

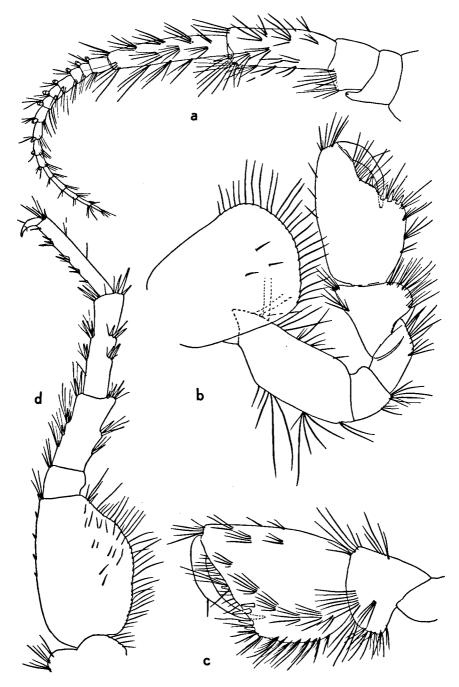


Fig. 5. Echinogammarus eisentrauti (Schellenberg, 1937), & paratype, from Deyá, Mallorca, a, second antenna (scale C); b, first leg (C); c, distal segments of second leg (C); d, seventh leg (E).

Leg 2 (fig. 5c) shows more or less the same features: the carpus has a projecting posterior lobe and the propodus is widened. Here again, the length of the posterior margin of the propodus is inferior to the greatest diameter, whereas in *E. pungens* the reverse situation occurs.

Legs 3, 4, and 5 are rather similar to those of *E. pungens*. The basis of leg 6 (fig. 6b) is slender; its concave posterior margin is finely notched, each notch being provided with a long setule.

In the male, the basis of leg 7 (fig. 5d) resembles, both in shape and in armature, that of *E. pungens*. The number and the length of the setae on merus and carpus of leg 7 is slightly less than in *E. pungens*. In the female, the basis of leg 7 (fig. 6c) shows strong sexual dimorphism, in that it is exceedingly widened. In the female of *E. pungens*, the basis of leg 7 likewise is wider than in male (fig. 2c), but the widening is much less pronounced than in *E. eisentrauti*. As far as I can judge, Margalef's figure (1950) labelled "p73" actually represents the 6th leg of a male.

The urosome (fig. 6a) has a distinct excavation ("saddle") on the first segment. The dorsal elevations are fairly low, that on segment 2 is only slightly compressed. The dorsal urosomal armature consists of a surprisingly high number of spines: 4:2:4 on segment 1, 4 to 6:2:4 to 6 on segment 2, and 3:0 to 2:3 on segment 3. Each group of spines might be accompanied by 1 or 2 setules; these setules are usually shorter than the spines, occasionally as long as these.

The epimeral plates are very setose, like those of E. pungens.

The telson (fig. 6d) bears distally 3 spines only; rarely one or two setae, that are shorter than the spines, are added to this terminal armature. A subbasal spine and setule are present.

Remarks. — It is clear, from the morphology of A1, A2, the coxal plates 1 to 4, P3 to P7, and the epimeral plates, that this species resembles closely E. pungens. It is hard to decide, whether Margalef was right in considering it a subspecies, endemic to fresh streams on Mallorca, of E. pungens, or that it represents a "good" species. Interfertility tests are required to make a final decision possible. For the moment, I followed Schellenberg (1937a) in considering E. eisentrauti an independent species. I have done so, since some characters of eisentrauti fall entirely outside the range of variation of pungens. This is true for the widened hands of legs 1 and 2 ( $\sigma$ ), the very concave palm of leg 1 ( $\sigma$ ), the extreme widening of the basis of leg 7 ( $\varphi$ ), the reduction of setal armature, and its replacement by extra spines, on the dorsum of the urosome, and the absence of long setae on the distal end of the telson.

Variability. — Margalef (1950) reports in great length on the variability of this species.

Distribution and ecology. — Endemic to Mallorca, not on Ibiza (Margalef, 1950). In fresh, running, calciferous waters.

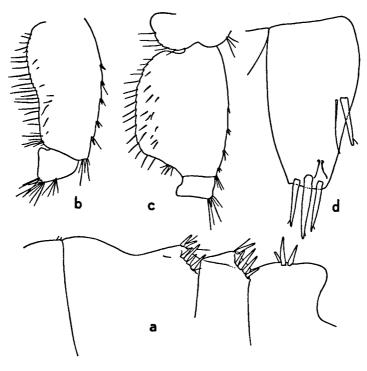


Fig. 6. Echinogammarus eisentrauti (Schellenberg, 1937), paratypes, from Deyá, Mallorca. a, contour of urosome, 3, from the left (scale A); b, proximal part of sixth leg, 3 (E); c, proximal part of seventh leg, 9 (C); d, telson, right half, 3 (B).

# Echinogammarus veneris (Heller, 1865). Figs. 7—10.

Gammarus veneris Heller, 1865: 981; Chevreux, 1894: 171—172, fig. 1 (types reexamined); Chevreux, 1895: 159—160.

Gammarus pungens (part.); Stebbing, 1906: 471-472; Ruffo, 1937: 53-60, figs.

Gammarus beieri Karaman, 1930: 283-286, fig. 1.

Gammarus (Echinogammarus) beieri; Schellenberg, 1937a: 271.

Echinogammarus beieri; Straškraba, 1967: 204.

Carinogammarus pungentiformis (nom. nud.) Schäferna, 1920: 1-4.

Carinogammarus pungentiformis Schäferna, 1922: 49-50: 70-71, 99-100, 102-103, pl. I fig. 6.

Ostiogammarus pungens pungentiformis; Karaman, 1934: 328-329.

Gammarus (Echinogammarus) pungentiformis; Schellenberg, 1937a: 271.

?Gammarus (Echinogammarus) pungens (non Milne Edwards); Ruffo, 1948: 300.

Gammarus pungens f. padanus Maccagno & Cuniberti, 1956: 176-177.

Material examined. — 55 specimens (syntypes), labelled "Venus Quelle bei Paphos, Cyper, 1862" (NMW, nr. 766). A lectoholotype (3) has been selected from the typeseries; it is preserved now also in the Vienna Museum. From the syntypes, 5 3 and 3 9, (now paratypes) have been donated to the Zoölogisch Museum, Amsterdam (ZMA Amph. 101.927). Moreover, 8 specimens, likewise paratypes, are present in the British Museum (Natural History), coll.nr. 1911: 11: 8: 19082—89.

Other records:

Italy: Verona (Garbini), 1 9, 2 & (MNHN).

Modena, in well of the Museum, 1886, 1 9 (MNHN).

Modena, in a well, 1886, 2 & (MNHN).

San Faustino, Modena, 1886, many specimens (MNHN).

Canal near Jesolo, E. of Venice, July 1968, 0.63 % Cl, 5 specimens (ZMA).

Pietrasanta (= NNW. of Pisa), Toscane, 17 Sep. 1911, 8 specimens (MNHN).

Chianti Mountains near Radda, alt. 600 m, cold spring, many specimens (BMNH).

Capo Sile, Veneto, fresh ditch, many specimens (BMNH).

Grotta del Mago, Tessino, 3 Oct. 1956, 1 & (MNHN).

Riete, fresh channel, many specimens (BMNH).

Fiume Conca near Pesaro, many specimens (BMNH).

Lake Bolsena, many specimens (BMNH).

Lake Piediluco, many specimens (BMNH).

Lake Bracciano, NW. of Roma, 2 &, 2 ♀ (MNHN).

Tiber Valley, N. of Roma, fresh stream, several specimens (BMNH).

Fiume Anapo, near Siracusa, May 1889, many specimens (MNHN).

Yugoslavia: Lake Skradin, near Skradin, about 10 km N. of Sibenik, Croatia, 31 May 1961, chlorinity 0.402 ‰, 2 specimens (ZMA).

Strožanac, 5 km E. of Split, 8 June 1961, 2 3 (ZMA).

River Stobreć near Strožanac, 40 m from open sea, 6 June 1961, chlorinity 0.780—0.835 %, 1 9, 2 3 (ZMA).

Ryeka Dubrovačka near Dubrovnik, about 500 m from the end of the bay, 12 June 1961, many specimens (ZMA).

"Dalmatia", without further specifications, leg. S. Karaman, 7 specimens (BMNH). Small river, debouching into Kotor Bay, S.W. of Risan, freshwater, 18 June 1961 (ZMA).

Greece: Kallegoni, island Levkas, Ionian Islands, in a spring, 12—19 Apr. 1929, 7 3, 7 9, (syntypes of Gammarus beieri Karaman, 1930) (NMW, nr. 999). 1 3 has been selected as the lectoholotype.

Near East: Brook N.E. of Damascus, Syria, 1911, many specimens (MNHN).

Djeroud near Damascus, Syria, 1911, many specimens (MNHN).

Aïn Tabigah, Syria, 6 specimens (MNHN).

Lake Tiberias, eastern shore, Israel, 7 May 1962, many specimens (ZMA); Lake Tiberias, Ein Gev, 22 March 1965, many specimens (HUJ); Lake Tiberias near Tiberias, 27 Feb. 1962, many specimens (ZMA).

Tabkha spring, western side of Lake Tiberias, Israel, Nov. 1963, many specimens (HUJ); 24 June 1968, 1 9 (ZMA).

Fulia springs, Israel, 27 Jan. 1964, many juveniles probably of this species (HUJ). "Palestine", without further specifications, 5 specimens (BMNH).

North Africa: Wadi-el-Glaa, Cyrenaica, Lybia, 10 July 1959, many specimens (BMNH) (probably this species).

Description. — A large species (normal size for males 11 to 13 mm, sometimes up to 18 mm), but some lake populations consist of much smaller specimens. It is easily confused with *E. pungens*; it seems practical, therefore, to stress the differences from that species. The urosome is very strongly "keeled" (i.e., the dorsal elevations are very clearly compressed), but the number of setae on its dorsal side is usually less than in *pungens* (fig. 7c). The epimeral plates 2 and 3 are pointed in some populations (e.g., in the popu-

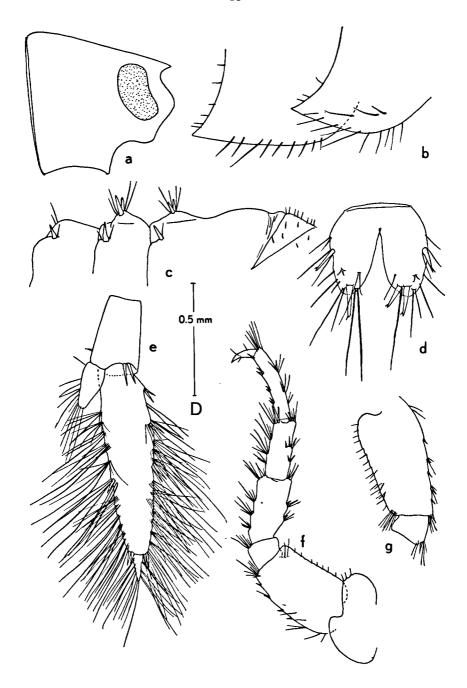


Fig. 7. Echinogammarus veneris (Heller, 1865), &, from Lake Tiberias. a, head, from the right (scale C); b, epimeral plates 2 and 3, from the left (C); c, urosome, from the left (C); d, telson, dorsal (A); e, third uropod (plumosity of the setae omitted) (D); f, fifth leg (E); g, proximal part of sixth leg (E).

lations from Lake Tiberias, fig. 7b), nearly rectangular in others (e.g., in the type-specimens of *E. veneris* from Cyprus, fig. 10c), but all intermediates occur. The coxal plates are less hairy than in *E. pungens*; in most specimens especially coxal plates 1 and 2 are less hairy than in *E. pungens* (this is the case in most Italian populations); in others, coxal plates 1 and 2 are sparingly setose, whereas plates 3 and 4 hardly bear any setules on their inferior margin (this is true for the Lake Tiberias population, figs. 8c, 8d, 9a, 9b).

The most easy distinction lies in the setation of the male antennae. The first antenna (fig. 8a) often (but not always) has longer and more numerous setae, both on the 2nd peduncle segment and on the flagellum. The second antenna (fig. 8b) invariably is much more hairy; peduncle segments 4 and 5 bear 5 or 6 tufts of long setae on their inferior margin; groups of nearly equally long setae occur on the inner and upper surface of these peduncle segments. The setae on the flagellum are also very long, whereas these are short in pungens. The general impression of the second antenna of of E. veneris is more brush-like than in E. pungens.

The merus of leg 4 usually bears spines and setae in *E. veneris* (fig. 9b). The basis of leg 5 (fig. 7f) is slightly more slender and lacks long setae on its anterior margin; the infero-posterior corner is as in *pungens*. The basis of leg 6 (fig. 7g) is also more elongate than in *E. pungens*. The basis of leg 7 (figs. 9c, 9d) is more regular in shape, and tapers only very slightly; its posterior margin bears fewer notches, the setae arising from these notches are shorter, the setation is less dense and more irregular in size than in *E. pungens*.

Variability. — A variable species. The A1 may or may not be more hairy than in E. pungens. The epimeres are pointed or rectangular (see discussion in the Introduction). The telson may or may not be provided with a subbasal spine (see Introduction). The setation of the coxal plates, though usually less than in E. pungens, may vary to a considerable extent.

Remarks on the synonymy. — I have re-examined Heller's type-specimens of "Gammarus" veneris as well as Karaman's type-specimens of "Gammarus" beieri. They belong to the same species. The types of G. beieri have the characteristic setation of the A2 &, the coxal plates 1, 2, and 3 bear setae. coxal plate 4 much less, P7 and the urosome are as in veneris. The telson of beieri bears spines that are shorter than, or sometimes as long as, the setae. The dorsum of the pleion is unarmed (contrary to Karaman's statement and contrary to Schellenberg's, 1937a, classification), except for the usual ornamentation with a few setules on the posterior margin of the pleon segments.

Although Chevreux, 1894, re-examined also the types of *veneris*, he failed in his later papers to discriminate between *E. pungens* s.str., *E. veneris*, and *E. thoni*.

I have not seen type-material of Carinogammarus pungentiformis Schäferna, 1922, and of Gammarus pungens f. pedanus Maccagno & Cuniberti. 1956, but the published accounts on these taxa, together with their ecological preferences, leave little doubt that they are synonymous with E. veneris.

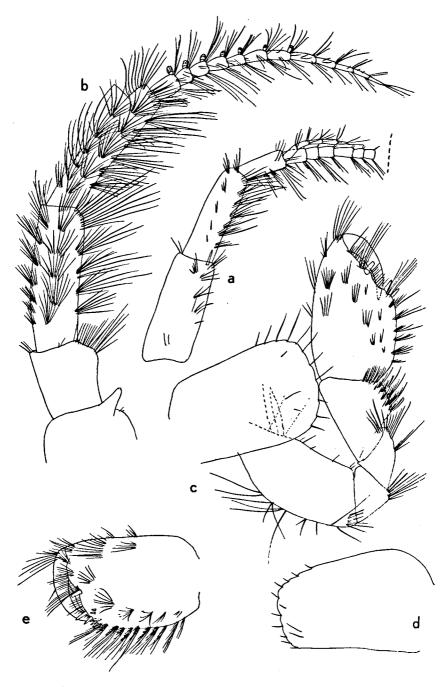


Fig. 8. Echinogammarus veneris (Heller, 1865), &, from Lake Tiberias. a, proximal portion of first antenna (the flagellum is 30-segmented) (scale C); b, second antenna (C); c, first leg (C); d, second coxal plate (C); e, hand of second leg (C).

Ecology. — This is a species from running fresh waters. It may live in wells and in rivers, where it sometimes descends to the beginning of the estuarine part of the stream. It occurs also in the littoral zone of larger lakes. Lives usually alone; sometimes together with members of the Gammarus pulexgroup; in the upper parts of estuaries sometimes competing with E. pungens.

Distribution. — Probably circum-mediterranean.

# Echinogammarus thoni (Schäferna, 1922). Figs. 11—13.

Carinogammarus thoni Schäferna, 1922: 42-45, 99, 102, figs. 19-21, pl. I fig. 4; Karaman, 1929a: 93-94.

Gammarus (Echinogammarus) thoni; Schellenberg, 1937a: 271.

Echinogammarus thoni; Straškraba, 1967: 205.

Gammarus pungens (de Montpellier); Chevreux & Fage, 1925: 252—253, fig. 263. Gammarus pungens du Lez; Brun & Brun, 1964: 754—759, pl. I fig. L, pl. II fig. L. Position uncertain: Ostiogammarus thoni semicarinatus Karaman, 1934: 329—330.

#### Material examined. -

France: Sources of the river Lez, N. of Montpellier, dépt. Hérault, about 150 specimens (RMNH); same locality, 8 Jan. 1968, chlorinity 0.062 ‰, many specimens (ZMA); same locality, 1 May 1968, many specimens (ZMA).

Le Lez, near Montpellier, 19 Feb. 1898 and 10 Sep. 1898, 5 specimens (MNHN). Bassins du promenade de Montpellier, many specimens (MNHN).

River Le Vidourle near Sommières, dépt. Gard, in cascade, 9 Jan. 1968, chlorinity 0.055 %, 13 specimens (ZMA); river Le Vidourle, near Marsillargues, dépt. Hérault, 27 Apr. 1968, chlorinity 0.03 %, many specimens (ZMA).

River Mosson, S.W. of Montpellier, dépt. Hérault, near highroad N 113, 8 Jan. 1968, chlorinity 0.037 % (ZMA).

Source near Balaruc-les-Bains, dépt. Hérault, Aug. 1897, 1 specimen (MNHN).

Description. — Resembles *E. pungens* in the shape of the head and eyes, in the setation of the coxal plates and epimeral plates, in the antennae and in the shape of the gnathopods. The most easily observable difference is, of course, the presence on all pleon segments of a distinctly compressed dorsal keel (fig. 12c). Even the 7th pereion segment bears an indication of a keel. The compressed elevations on the urosome are much taller than in *E. pungens* (fig. 12c). The urosome spines are accompanied by very few, short setules only. *E. thoni* is markedly larger than *E. pungens*: adult males average about 15 mm.

Other differences are the endopod of the 3rd uropod, that is tapering to a very narrow tip (fig. 12e); the telson (fig. 12f), which often (though not always) lacks a subbasal spine and in which the spines are longer than the setae; the basal segments of P5, P6, and P7 (figs. 13c, 13d, 11d) resemble in shape more closely those of E. veneris than those of E. pungens; the setation of the posterior margin of the basis of P7 is very similar, however, to that of E. pungens.

Remarks on the synonymy. — Re-examination of the material described by Chevreux & Fage, 1925, in the "Faune de France", demonstrated that it

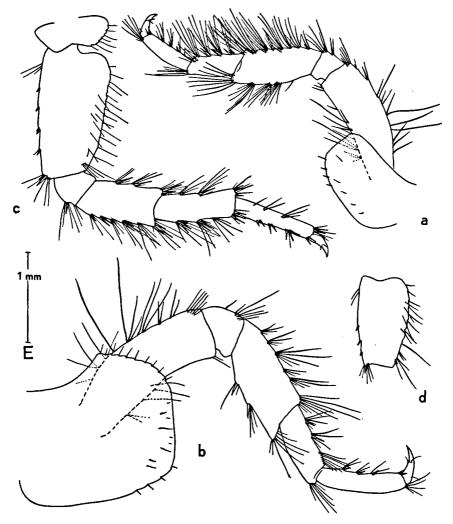


Fig. 9. Echinogammarus veneris (Heller, 1865), &, from Lake Tiberias. a, third leg (scale E); b, fourth leg (C); c, seventh leg (E); d, basis of seventh leg of a smaller male (E).

belonged to *E. thoni* instead of to *E. pungens*. The first authors who were aware of the fact that at least two different species were hidden under the name of *E. pungens* in southern France, were Brun & Brun, 1964, who conducted intersterility tests to demonstrate the specific status of *E. thoni* (under the name of "Gammarus pungens du Lez") and *E. pungens* (under the name of "Gammarus pungens du Rhône").

Ecology. — Sources and mid-courses of rivers, lakes, usually together with members of the *Gammarus pulex*-group. Rarely (Balaruc) accompanied by *E. pungens*.

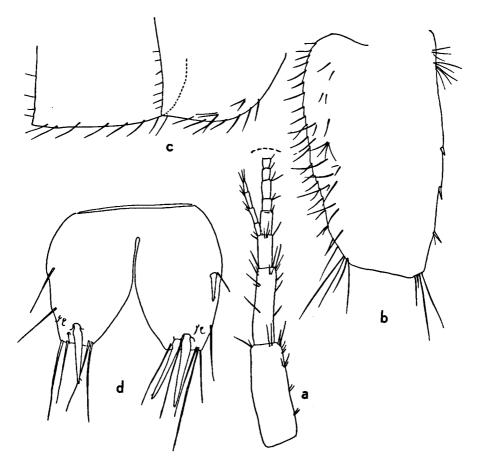


Fig. 10. Echinogammarus veneris (Heller, 1865), 3, paratype, from the Venus Spring, Cyprus. a, proximal portion of first antenna (scale C); b, basis of seventh leg (A); c, second and third epimeral plate (C); d, telson (B).

Distribution. — Known with certainty only from Dalmatia and Herzegovina (Yugoslavia) and from two départements in southern France: Hérault and Gard.

# Echinogammarus foxi (Schellenberg, 1928). Figs. 14—21.

Gammarus foxi Schellenberg, 1928: 649—652, fig. 201; Schellenberg, 1936: 15. Gammarus (Echinogammarus) foxi; Schellenberg, 1937a: 272. ?Gammarus Olivii (non Milne Edwards); Ruffo, 1937: 52—53.

#### Material examined. -

France: Fontaine de Salses, dépt. Pyrénées-Orientales, between aquatic plants, 20 Sep. 1956, many specimens (ZMA); same locality, 25 Sep. 1957, many specimens (RMNH); same locality, 9 Sep. 1961, many specimens (ZMA); same locality, 10 Apr. 1967, chlorinity 2.16 %, 10 specimens (ZMA).

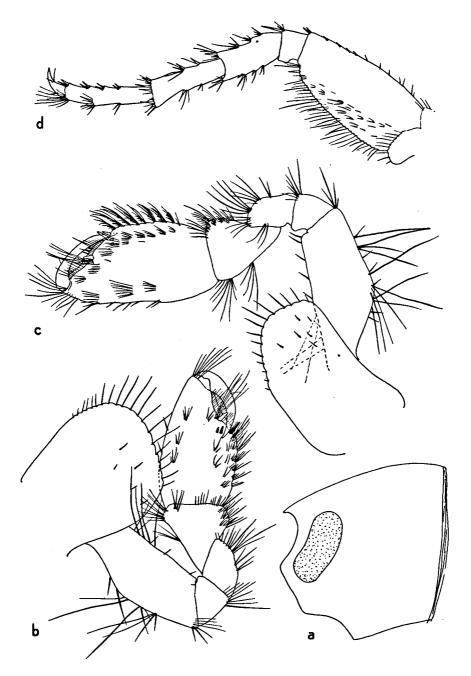


Fig. 11. Echinogammarus thoni (Schäferna, 1922), &, from the river Lez near Montpellier. a, head, from the left (scale C); b, first leg (C); c, second leg (C); d, seventh leg (E).

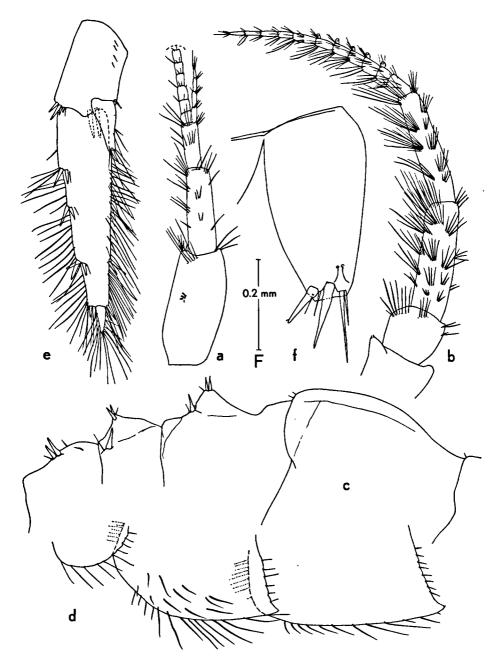


FIG. 12. Echinogammarus thoni (Schäferna, 1922), &, from the river Lez near Montpellier. a, proximal portion of first antenna (flagellum 24-segmented) (scale C); b, second antenna (C); c, profile of dorsum of the last pleon segment and of the urosome segments 1 to 3 (C); d, epimeral plates 1 to 3 (C); e, third uropod (plumosity of the setae omitted) (A); f, right half of telson (F).

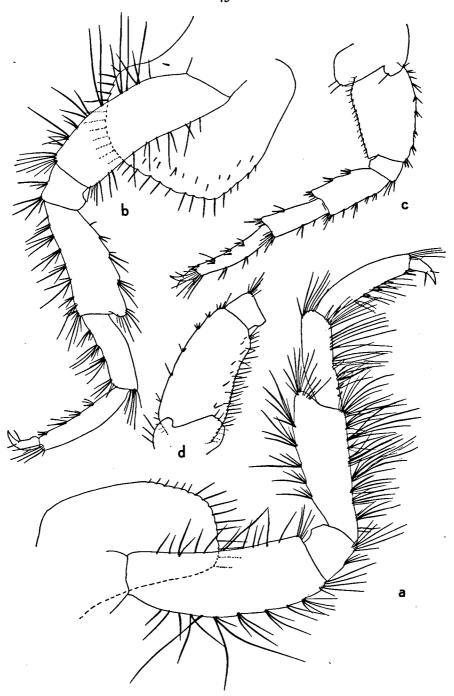


Fig. 13. Echinogammarus thoni (Schäferna, 1922), 3, from the river Lez near Montpellier. a, third leg (scale C); b, fourth leg (C); c, fifth leg (E); d, proximal segments of sixth leg (E).

La Durancole, near its mouth in the Etang de Berre, N.W. of Berre, dépt. Bouches-du-Rhône, in cascade, between green filamentous algae, 6 Jan. 1968, chlorinity 0.390 %, many specimens (ZMA); same locality, 28 Apr. 1968, many specimens (ZMA).

Mouth of the Gapeau, near Port-Pothuau, E. of Hyères, dépt. Var, 5 Jan. 1968, chlorinity 11.50%, many specimens (ZMA).

River Var, near the mouth, dépt. Alpes-Maritimes, autumn 1965, 11 specimens (LBM).

Italy: Affluent of the river Po at Chivasso, near Torino, July 1964, 8 specimens (LBM).

Yugoslavia: Dalmatian coast, 30 km S. of Jadranova, depth 0—2 m, 5 Aug. 1959, 10 specimens (RMNH).

Israel: Source Ein as Sa'ada (on the road Haifa-Nazareth near Acre Junction), 28 Feb. 1962, many specimens (ZMA).

Alexander River, no date specified, many specimens (HUJ).

Black Sea: Coast near Samsun, Turkey, rocks, 0—2 m, 12 Apr. 1959, 11 specimens (RMNH).

About 20 km W. of Trabzon, Turkey, 0—2 m, 4 Apr. 1959, many specimens (RMNH). Eforie-Sud, Roumania, just S. of boulevard, 6 Aug. 1965, many specimens (ZMA).

Sea of Marmora: Near Florya, about 15 km W. of Istanbul, under littoral stones, 2 Apr. 1959 (RMNH).

Description. — Large males (from the Black Sea) may attain a length of 13 mm; specimens from inland waters are always much smaller, 6—10 mm long.

The eye is slightly larger, and the lateral lobes are slightly more acute than in *E. pungens* and *E. veneris* (figs. 14a, 17a). The first urosome segment is dorsally only slightly excavated (the "saddle" is indistinct), whereas the urosome segment shows only inconspicuous, non-compressed dorsal elevations (figs. 14f, 17c). Very few setae accompany the dorsal urosome spines.

The peduncle segments of the first antenna, more in particular segment 2, carry several tufts of setae (figs. 14b, 18a). The second antenna has a rather slender peduncle, which is slightly more hairy than in *E. pungens*, but distinctly less than in *E. veneris*. Calceoli may be present (though small) or absent (see paragraph on variability in Introduction). Specimens from inland waters have only simple setae on the A2 (fig. 14c), but in material from the Black Sea and the Sea of Marmora, an important number of specimens have feathered setae. Sometimes (fig. 18b) only a few setae are feathered, sometimes most setae (fig. 18c). In the same sample "feathered" and "simple" specimens may occur, with all intergradations. The distal segment of the mandible palp bears a regular "comb" of setae (fig. 14d).

The coxal plates 1 to 4 have a smooth (i.e. without notches and setules) inferior margin; only on the anterior and posterior corners of the plates, one or a few setules arise. The setation of the merus and carpus of the 3rd and 4th legs is much less dense, and the individual setae are much shorter than in *E. pungens* (figs. 16a, 16b, 17b, 20a).

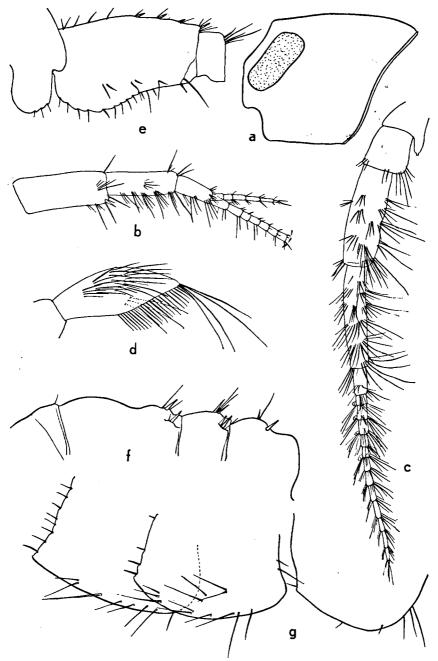


Fig. 14. Echinogammarus foxi (Schellenberg, 1928), &, from the Fontaine de Salses (France, Pyrénées-Orientales). a, head from the left (scale A); b, proximal portion of first antenna (flagellum 31-segmented) (C); c, second antenna (C); d, distal segment of mandible palp (F); e, proximal segments of sixth leg (C); f, contour of the urosome, from the left (C); g, epimeral plates 1 to 3 (A).

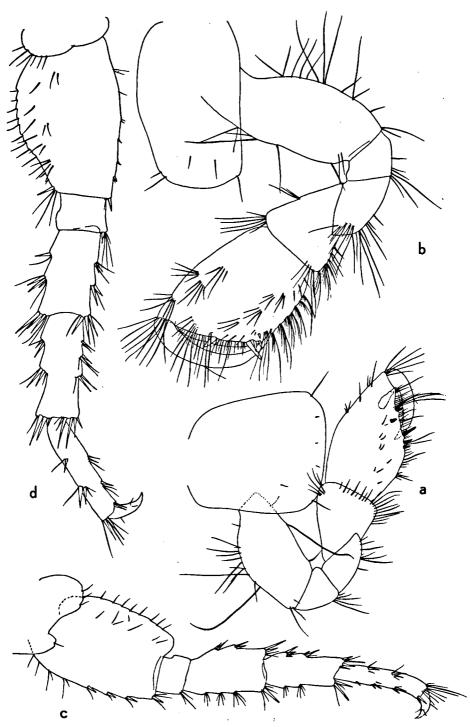


Fig. 15. Echinogammarus foxi (Schellenberg, 1928), &, from the Fontaine de Salses (France, Pyrénées-Orientales), a, first leg (scale A); b, second leg (A); c, fifth leg (C); d, seventh leg (C).

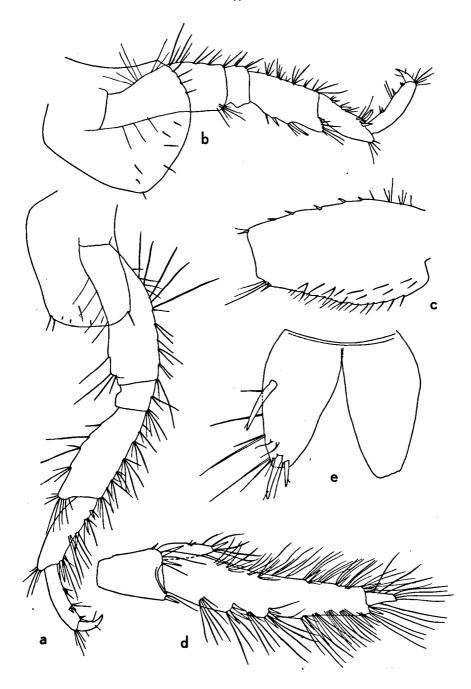


Fig. 16. Echinogammarus foxi (Schellenberg, 1928), &, from the Fontaine de Salses (France, Pyrénées-Orientales). a, third leg (scale C); b, fourth leg (C); c, basis of seventh leg of a large male (C); d, third uropod (plumosity of the setae omitted) (A); e, telson, spines and setae on right half omitted (B).

The 5th leg (figs. 15c, 18d) is remarkable in its basal segment and in its merus. The basis has only short setules on its anterior margin, and relatively few setules on its posterior margin; the broadly rounded infero-posterior corner, which projects far backward, is quite characteristic. The merus is shorter and wider than in *E. pungens* and *E. veneris*, has a more projecting infero-posterior lobe, and bears fewer and shorter setae.

The 6th and 7th legs (figs. 14e, 15d, 20b, 20c) are also distinctly less hairy on the level of merus and carpus. Their basal segments bear short, rather widely spaced, setules only on the posterior margin.

The epimeral plates (figs. 14g, 17d) have rectangular back corners; their inferior margins bear a row of setae.

The inner ramus of the 3rd uropod has an elongate shape. In specimens from inland waters, it is not very hairy (fig. 16d), in Black Sea specimens much more so (fig. 17e). The telson (figs. 16e, 20d) usually has a subbasal spine (small or lacking in some specimens); a few setae, overreaching the spines, are present on the telson.

Variability. — Rather variable in size, in presence or absence of calceoli, in setation of the 3rd uropod, and in the presence or absence of plumose setae on the A24). The shape of basis and merus of leg 5, the paucity of setation on legs 5 to 7 and on the urosome, the absence of compressed elevations on the urosome, and the smooth lower margin of the coxal plates, are constant and diagnostic features of this species. These differences are correlated in a rather loose way with the distribution; large size specimens, without calceoli, with setose 3rd uropods and plumose setae on the appendages, occur chiefly in the Black Sea. Since, however, "normal" specimens occur as well in the same populations, and since one can find every possible combination of characters present in at least some individuals, I have thought it wise to consider all these animals as belonging to one species, E. foxi. In doing so, particular stress is laid upon the similarities, and less attention is paid to the differences between these gammarids. At any rate, a "typical" E. foxi (from inland brackish water) and the Black Sea form are illustrated here in detail (figs. 14 to 16, and 17 to 20), in order to make it possible for future workers to form their own opinion.

Note on the synonymy. — I am unable to make out, whether the form briefly described, but not figured, by Ruffo, 1937, under the name of Gammarus Olivii, belongs to this species or to E. stammeri. The large size, the reduction of the setae on the coxal plates, and the shape and armature of the basis of leg 7 point in the direction of E. foxi. One of my samples (from a tributary of the river Po) was collected, like Ruffo's material, far from the sea, indicating that E. foxi is able to penetrate under certain conditions (probably a high Ca-content) far into inland waters.

<sup>4)</sup> In some very "plumose" specimens, feathered setae are not restricted to the A2, but occur also on peduncle segments 2 and 3 of A1, on the mandible palp, on the hand of legs 1 and 2, and on merus and carpus of leg 4.

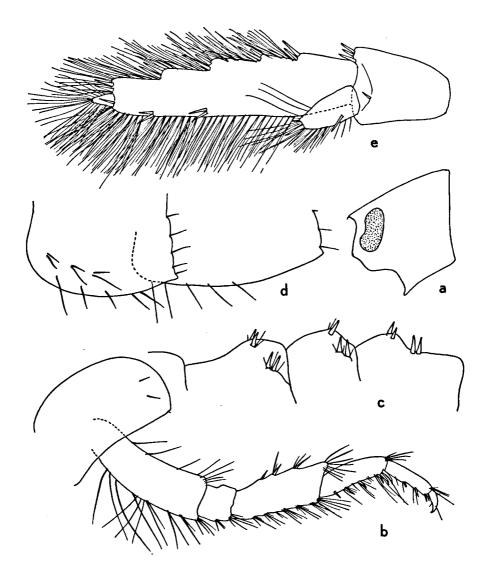


Fig. 17. Echinogammarus foxi (Schellenberg, 1928), modestly "plumose" &, from the Sea of Marmora. a, head from the left (scale E); b, third leg (E); c, contour of urosome from the left (C); d, second and third epimeral plates (C); e, third uropod (plumosity omitted) (C).

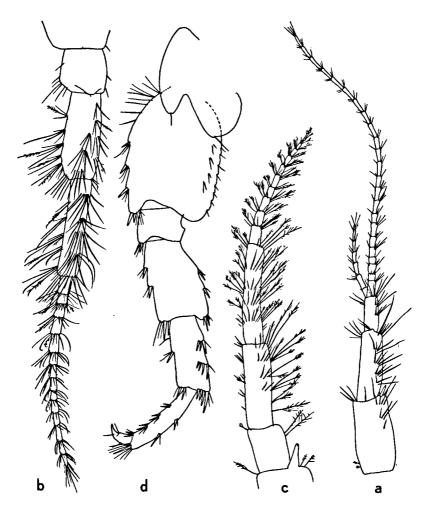


Fig. 18. Echinogammarus foxi (Schellenberg, 1928), &, from the Sea of Marmora (all, except c, from a modestly "plumose" specimen). a, first antenna (scale E); b, second antenna of a specimen with hardly feathered setae (E); c, second antenna of a rather "plumose" specimen (E); d, fifth leg (E).

Distribution and ecology. — Originally described from brackish lagoons near Lake Timsah, in the Suez Canal area of Egypt (Schellenberg, 1928), where it was found in localities with 1.40 and 21.72% maximal chlorinity, respectively. Later, Schellenberg (1936) recorded it from Lakes Maryût and Edku, near Alexandria, Egypt. In the latter localities, *E. foxi* was often accompanied by a brackish water gammarid, *Gammarus aequicauda*. Considered together with the present records, it seems that this species occurs in brackish coastal waters (lakes,running waters with high ion-content) around the Mediterranean, as well as in the open Black Sea. In France, *E. foxi* is accompanied in the more saline parts of its range by either *Gammarus* 

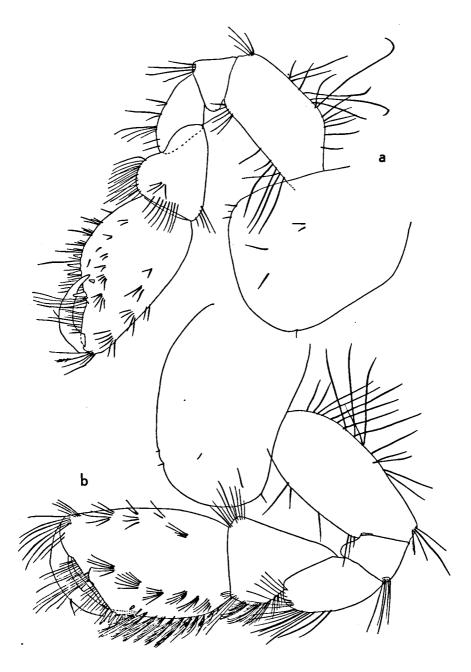


Fig. 19. Echinogammarus foxi (Schellenberg, 1928), modestly "plumose" &, from the Sea of Marmora. a, first leg (scale C); b, second leg (C).

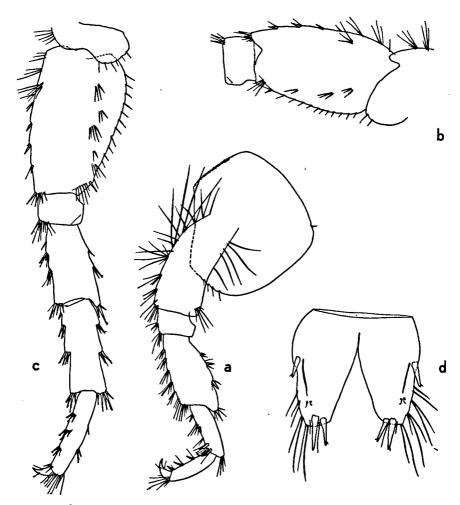


Fig. 20. Echinogammarus foxi (Schellenberg, 1928), from the Sea of Marmora. a, fourth leg (scale E); b, basal segments of sixth leg (E); c, seventh leg (E); d, telson, dorsal (A).

aequicauda (Martynov) or Ech. pungens (Milne Edwards), or both; in the fresher parts of its range by Gammarus pulex gallicus (Karaman). In the Black Sea, it is accompanied by Gammarus aequicauda or, rarely, by G. subtypicus Stock.

# Echinogammarus lusitanus (Schellenberg, 1943). Figs. 22—23.

Gammarus (Parhomoeogammarus) lusitanus Schellenberg, 1943: 2—4, fig. 1. Gammarus lusitanus; Margalef, 1955: 166—168, fig. 14.

#### ·Material examined. -

Spain: Above Alsasua, prov. Navarra, in a small brook, altitude about 600 m, 29 Apr. 1960, many specimens (RMNH).

Abadia, prov. Caceres, 5 May 1960, 7 specimens (RMNH).

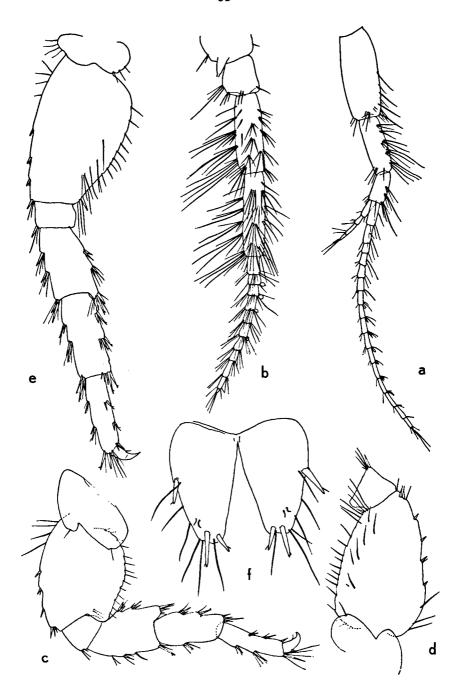


Fig. 21. Echinogammarus foxi (Schellenberg, 1928), &, from Samsun, Black Sea. a, first antenna (scale C); b, second antenna (C); c, fifth leg (C); d, proximal portion of sixtht leg (C); e, seventh leg (C); f, telson (B).

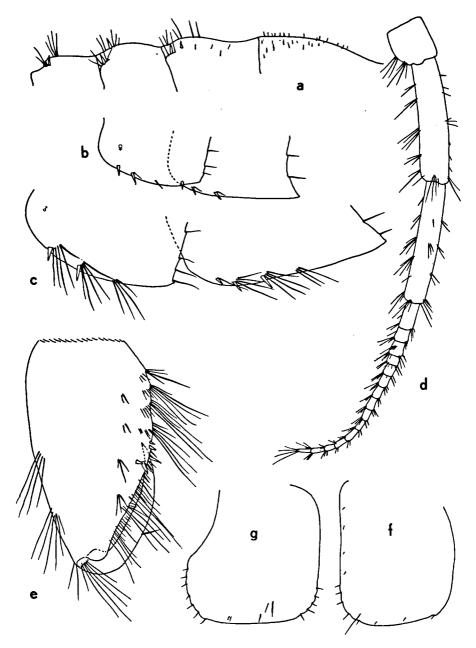


Fig. 22. Echinogammarus lusitanus (Schellenberg, 1943), from Alsasua, prov. Navarra, Spain. a, contour of last pleon and urosome segments, & (scale C); b, second and third epimeral plates, & (A); c, same of & (A); d, second antenna, & (C); e, hand of first leg, & (B); f, first coxal plate, & (F); g, fourth coxal plate, & (C).

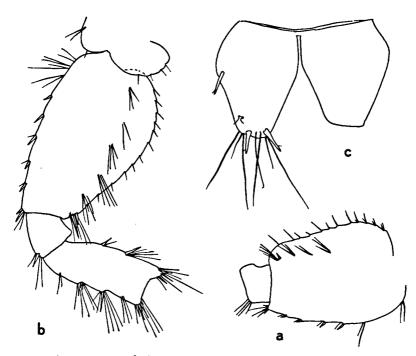


Fig. 23. Echinogammarus lusitanus (Schellenberg, 1943), 3, from Alsasua, prov. Navarra, Spain. a, basis of fifth leg (scale C); b, proximal portion of seventh leg (C); c, telson (B).

Remarks. — This species belongs actually to the berilloni-species group in the genus, as is demonstrated by the paucity of the setation of A 1 and A 2 d, by the very oblique palm of the first gnathopod d, by the considerable sexual dimorphism, and by the very wide telson lobes (approaching in shape those found in Chaetogammarus ischnus). It is included here to make clear its generic position (in Echinogammarus instead of in Parhomoeogammarus, see page 18). Moreover, the paucity of the ornamentation of the pleon, makes the relationship with E. berilloni not at once clear. The coxal plates 1 to 4 are not ciliated on their inferior margin. The basis of leg 5 has a small disto-posterior lobe. Leg 7 bears short, widely spaced setae on the posterior margin of the basis, whereas the merus is provided with spines and long setae. The epimeres 2 and 3 bear 2 to 4 spines each on their inferior margin; each of these spines is accompanied with a short setule only in female, but with a bunch of 3 to 5 long setae in male. The dorsum of the last metasome segments bears scattered setules; the dorsum of the urosome has only very low elevations and shows a reduction in armature, as already noted by Schellenberg. The 3rd segment of the mandible palp is ventrally armed with a comblike row of hairs.

Ecology. — Lives in small freshwater streams.

Distribution. — Northern Portugal, northwestern and western Spain.

## Echinogammarus scutarensis (Schäferna, 1922). Fig. 30c

Carinogammarus scutarensis Schäferna, 1922: 45—48, 99, figs. 22—23, pl. I fig. 5 Gammarus (Echinogrammarus) scutarensis; Schellenberg, 1937a: 271.

Ostiogammarus scutarensis; Karaman, 1934: 328—329, fig. 2.

Echinogammarus scutarensis; Straškraba, 1967: 205.

#### Material examined. -

Y u g o s l a v i a (Montenegro): Small brook embouching in Lake Skutari near Poseljani, 18 June 1961, many specimens (ZMA).

River Mórača, near Donja Gorica (south of Titograd), 19 June 1961, 9 specimens (ZMA).

Remarks. — This species is distinguished at once by the recurved antennal gland cone (see Schäferna, 1922, pl. I figs. 5, 5a2; and Karaman, 1934, fig. 2). The anterior coxal plates (fig. 30c in this paper) bear, just like the posterior ones, a few setules at their lateral margins, but none at their inferior margin. The dorsal keel on the pleon segments, though present in all specimens examined, is much stronger developed in the specimens from Donja Gorica, than in those from a brook near Lake Skutari.

Distribution and ecology. — Lives in rivers around Lake Skutari, Yugo-slavia, but apparently not in the lake itself. Accompanying species: Gammarus triacanthus (Schäferna) and Gammarus balcanicus Schäferna.

#### Echinogammarus acarinatus (Karaman, 1929). Figs. 24—26.

Ostiogammarus acarinatus acarinatus Karaman, 1929b: 105-107.

Ostiogammarus acarinatus Karaman, 1931: 43—45, figs. 6a, c, e, g; Karaman 1934: 327—328.

Gammarus pungens f. acarinata (nom. nud.) Schäferna, 1920: 3-4.

Gammarus pungens f. acarinata Schäferna, 1922: 33, 98 figs. 11 (P'5), 12 (pl. 5' 1—3). Gammarus olivii forme saumâtre; Razakandisa & Brun, 1964: 719—722, fig. 1 (bottom).

Echinogammarus olivii (part.); Straškraba, 1967: 205.

### Material examined. -

France: Mouth of river Orb, at Valras-Plage, dépt. Hérault, stones with Enteromorpha, 27 Apr. 1968, chlorinity 4.0 ‰, 2 specimens (ZMA).

Mouth of river l'Hérault, at La Tamarissière, dépt. Hérault, about 100 m upstream of the lighthouse, 27 Apr. 1968, chlorinity 6.8 %, many specimens (ZMA).

La Tamarissière, dépt. Hérault, under stones on the seaward side of the pier, 27 Apr. 1968, chlorinity 18.9 ‰, 1 &, 1 \( \) (ZMA).

River l'Hérault, dépt. Hérault, some 3200 m from the mouth, in dead trees, 27 Apr. 1968, chlorinity 3.7 ‰, 2 3, 1 \( \) (ZMA).

Etang de Citis, dépt. Bouches-du-Rhône, 9 Nov. 1967, many specimens (ZMA); same lake, near road D 51, shore, sandy mud, stones, shell, 6 Jan. 1968, chlorinity 1.58 %, 20 specimens (ZMA).

Mouth of river Touloubre (in Etang de Berre), dépt. Bouches-du-Rhône, 30 Mar. 1961, about 30 specimens (ZMA); same locality, muddy, 28 Apr. 1968, chlorinity 0.10 %, 1 & (ZMA).

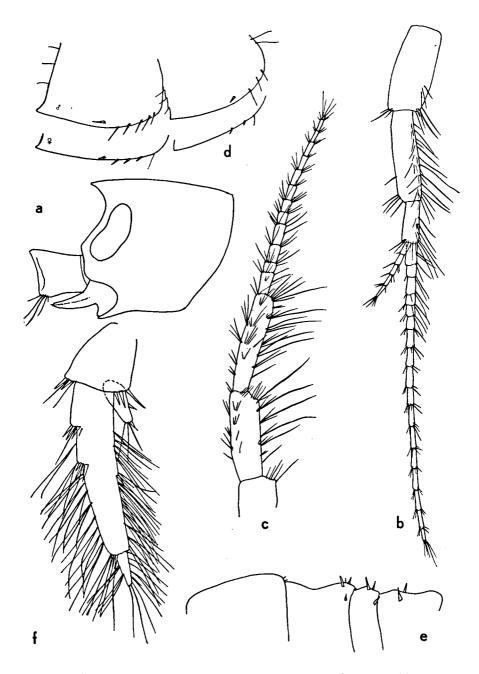


Fig. 24. Echinogammarus acarinatus (Karaman, 1929), from Étang de Citis (France, Bouches-du-Rhône). a, head and gland cone from the left, & (scale A); b, first antenna, & (C); c, second antenna (C); d, second and third epimeral plates from the right (top: &; bottom: Q) (A); e, contour of pleon and urosome segments (A); f, third uropod (plumosity of the setae omitted) (A).

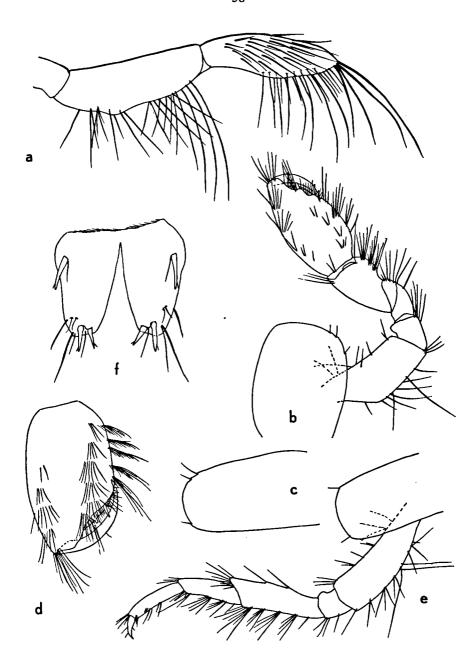


Fig. 25. Echinogammarus acarinatus (Karaman, 1929), &, from Etang de Citis (France, Bouches-du-Rhône). a, mandible palp (scale F); b, first leg (A); c, second coxal plate (A); d, hand of second leg (D); e, third leg (C): f, telson (B).

Y u g o s l a v i a: River Stobreć, about 5 km E. of Split near village Strožanać, some 40 m from the open sea, reed-vegetation, 6 June 1961, chlorinity 0.835 ‰. 1 \( \) (ZMA).

Description. — A small species: length of the adult male about 7 mm. The eye is rather elongate, the lateral head-lobes are not very acute (fig. 24a). The urosome bears very few, short spines, and hardly any setae (fig. 24e); the first urosome segment has only a shallow "saddle"; the dorsal elevations are low, rounded, and not compressed. The spine formula of the urosome is 0-1:2:0-1; 1:2:1; 1:0:1.

The first antenna (fig. 24b) has a very slender peduncle, which is rather setose. The second antenna (fig. 24c) has a slender, elongate 5th segment; segments 4 and 5 bear 7 to 8 bunches of long setae on their inferior margin; the median and dorsal setae on these segments are much less numerous and less long. The flagellum consists of slender, not compressed, segments, bearing relatively few, and short, setae. No calceoli. The gland cone is short and directed forward; it is gradually tapering into a narrow point (fig. 24a).

The mandible palp (fig. 25a) has an unarmed first segment; the third segment bears, in addition to the usual 4 long, distal setae, on the its ventral margin a row of shorter setae of a size, plus an extra row, inserted on the internal side of the segment quite near to the ventral margin, consisting of longer setae. The result of this is that the inferior margin of the 3rd palp segment does not show the usual comb-like aspect, but a more irregular armature, such as found in Gammarus zaddachi.

The coxal plates 1 to 4 bear setules only on their corners, not on their lower margins. The hands of legs 1 and 2 are rather feeble in comparison to other members of the genus (figs. 25b, 25d).

Legs 3 and 4 (figs. 25e, 26a) are, like those of *Chaetogammarus olivii*, very little setose, but they are much less robust and more slender than in that species. The same slenderness is present in legs 5 to 7 (figs. 26b, c, d); these legs bear only a very limited number of setae in addition to the spines. The posterior margin of the very elongate basis of leg 7 is provided with 5 to 8 notches, each with a short setule.

The epimeral plates 2 and 3 (fig. 24d) are provided with a limited number of elements (the anterior elements assume the shape of setules, the posterior ones the shape of spinules). In male, the setules outnumber the spinules, in female just the reverse is true.

The first uropod resembles that of E. stammeri (vide infra).

The 3rd uropod (fig. 24f) has a tapering, elongate endopod. The armature of exo- and endopod consists of a few spines and a rather small number of long, plumose setae.

The telson lobes (fig. 25f) are elongate; a subbasal spine is present in most of my specimens; the number of setae is small, but the distal ones are much longer than the spines.

Remarks. — This species bridges the gap between the genera *Echinogam-marus* and *Chaetogammarus*. It is much less setose than most other species

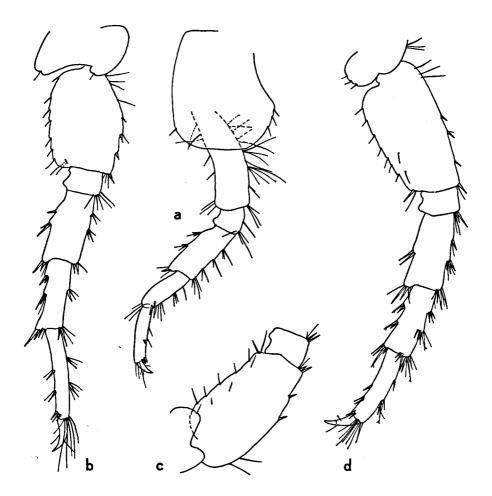


Fig. 26. Echinogammarus acarinatus (Karaman, 1929), &, from Etang de Citis (France, Bouches-du-Rhône). a, fourth leg (scale C); b, fifth leg (C); c, proximal portion of sixth leg (C); d, seventh leg (C).

of Echinogammarus (except E. stammeri) and approaches in this respect Chaetogammarus olivii. The only reason that I have included it in Echinogammarus is the constant presence of setules on the epimeral plates 2 and 3 in older males of E. acarinatus. The ecology of E. acarinatus (from marine to oligohaline waters) is also intermediate between that of the other Echinogammarus species (living in fresh and brackish waters) and Chaetogammarus olivii (in marine and polyhaline waters).

Distribution. — Known from stony and sandy habitats in estuaries and brackish lagoons in Yugoslavia and France. Its range in estuaries is quite considerable: from nearly full seawater to oligohaline conditions. Its optimum is apparently in mesohaline surroundings.

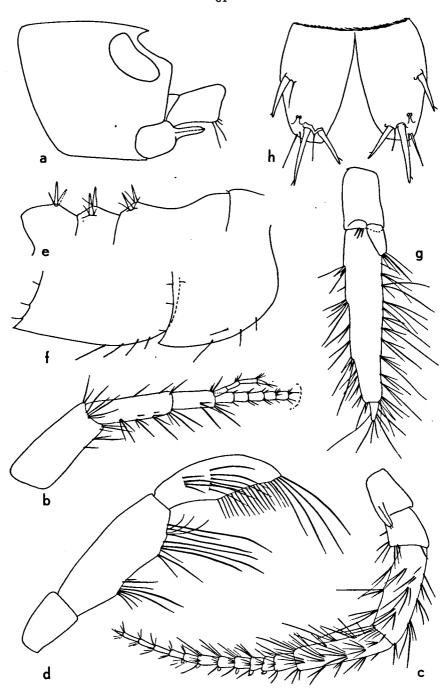


Fig. 27. Echinogammarus stammeri (Karaman, 1929), 3, from the Massif de la Sainte Baume (France, Bouches-du-Rhône). a, head and gland cone, from the right (scale A); b, proximal part of first antenna (flagellum 21-segmented) (A); c, second antenna (A); d, mandible palp (F); e, contour of urosome, from the right (A); f, 2nd and 3rd epimeral plates (A); g, third uropod (A); h, telson (F).

Accompanying species. — In the most saline part of its range, E. acarinatus sometimes is accompanied with Chaetogammarus olivii (H. Milne Edwards) and Gammarus crinicornis Stock. In the mesohaline part of its range, it may occcur simultaneously with Gammarus aequicauda (Martynov) or with Echinogammarus pungens (H. Milne Edwards).

## Echinogammarus stammeri (Karaman, 1929). Figs. 27—29.

Ostiogammarus acarinatus stammeri Karaman, 1929b : 105-107.

Gammarus pungens ssp. acarinatus Pljakić, 1962: 15-23, figs. 1-7.

Ostiogammarus cari bosnensis Karaman, 1934: 327—328 (teste Pljakić, 1962: 17, based on topotypes<sup>5</sup>).

Gammarus pungens (non Milne Edwards); Barbé, 1964: 648-649, fig. 3.

?Gammarus Olivii (non Milne Edwards); Ruffo, 1937: 52-53.

?Gammarus olivii (non Milne Edwards); Angelier, 1959: 17, 32, 33, 34, 47.

#### Material examined. -

France: Brue-Auriac, dépt. Var, in a well, 22 Aug. 1962, 1 & (ZMA); Brue-Auriac, Vallon de Font-Taillade, in a rivulet, 28 Apr. 1968, many specimens (ZMA).

Barjols, dépt. Var, Ruisseau des Ecrevisses, 29 Apr. 1968, many specimens (ZMA). Argens river, Vallon Sourn, near Châteauvert, dépt. Var, 29 Apr. 1968, many specimens (ZMA).

Le Gapeau, a rivulet near Montrieux-le-Jeune, dépt. Var, 29 Apr. 1968, 1 9, 1 8 (ZMA).

Ruisseau de Montrieux, near Montrieux-le-Jeune, dépt. Var, 13 Febr. 1968, 9 specimens (LBM); 29 Apr. 1968, 7 specimens (ZMA).

Affluent of Le Gapeau, about 2 km N. of Belgentier, dépt. Var, 29 Apr. 1968, many specimens (ZMA).

Solliès-Toucas, well in the village, dépt. Var, 29 Apr. 1968, many specimens (ZMA). Le Réal de Cuers, a rivulet near Cuers, dépt. Var, 29 Apr. 1968, 1 3 (ZMA).

Description. — A small, rather delicate species (adult male 6.0 to 7.5 mm, exceptionally up to 9 mm, long). The eye is kidney-shaped, situated rather near to the dorsal border of the cephalic segment; the lateral head lobes are acute (fig. 27a). The urosome (fig. 27e) has low, not compressed, dorsal elevations; the "saddle" on urosome segment 1 is only very shallow. Dorsally, the urosome bears long spines, usually according to the formula 1:1:1; 1:1; 1:0:1; short setae (shorter than the spines) complete the urosomal armature.

The first antenna (fig. 27b) has a slender peduncle; second peduncle segment only slightly shorter than the first, fully  $3\frac{1}{2}$  times as long as wide; third peduncle segment  $2\frac{1}{2}$  times as long as wide, half as long as the second. The accessory flagellum has 3 or 4 segments only, the main flagellum is 20- to 23-segmented; the peduncle segments are not very setose.

The second antenna (fig. 27c) is more robust than that of *E. acarinatus*; the setae on peduncle segments 4 and 5 are shorter, but they are implanted more densely, also in the inner surface of the segments. The flagellum consists (at least in larger males) of robust, slightly compressed, segments

<sup>5)</sup> Pljakić reckons O. cari cari also to this taxon, but in my opinion cari cari is synonymous with simoni Chevreux.

(reminiscent of the situation found in Gammarus pulex, though less distinct than in that species), bearing rather few, but not very short, setae. Calceoli present, usually 5 or 6 in number. The gland cone (figs. 27a; 27c) points forward and is finger-shaped, i.e., it has parallel margins and a bluntly rounded tip.

The mandible palp (fig. 27d) has an unarmed first segment, whereas the lower margin of the third segment is provided with a regular row ("comb") of setae of a size.

The coxal plates 1 and 2 bear 1 or 2 short setules on their lower margins (figs. 28b, 28c); those of legs 3 and 4 have the setation restricted to the posterior and anterior corners.

The hand of leg 2 (fig. 28a) is rather elongate; the palmar angle is poorly defined and merges gradually into the posterior margin. Palmar spines long.

Legs 3 and 4 (figs. 29a, 29b) very little setose. The merus of leg 3, but in particular that of leg 4 is very slender (even more than in *E. acarinatus*).

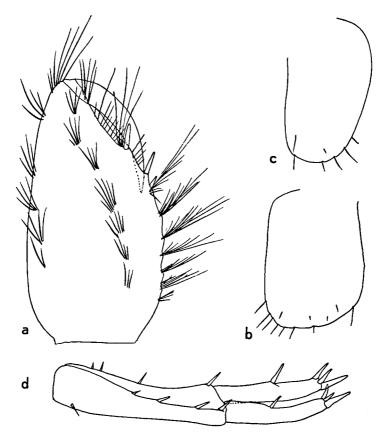


Fig. 28. Echinogammarus stammeri (Karaman, 1929), &, from the Massif de la Sainte Baume (France, Bouches-du-Rhône). a, hand of 2nd leg (scale B); b, first coxal plate (A); c, second coxal plate (A); d, first uropod (F).

The basis of leg 5 (fig. 29c) has a strongly projecting disto-posterior corner; its anterior margin is armed with spinules, its posterior margin with short setules. The basis of leg 6 is slender (fig. 29d). The basis of leg 7 (fig. 29e) is also slender, although more tapering and less parallel-sided than in acarinatus; its posterior margin bears very short setules only; the merus and carpus are usually armed with spines only, sometimes a few short setules (shorter than the spines) may be found.

The epimeral plates 2 and 3 (fig. 27f) are acute; their lower margins are provided with a limited number of fairly long setae.

Each of the rami of the first uropod (fig. 28d) is armed with only 1 marginal spine, in addition to the 3 terminal spines.

The 3rd uropod (fig. 27g) is, especially in smaller specimens, rather scantily setose.

The telson lobes are longer than wide (fig. 27h); subbasal spines present or absent; a subbasal setule may accompany the subbasal spine; if the spine is absent, this setule may be present or absent; distal spines long. Short setae (less long than the spines) complete the armature.

Variability. — The subbasal telson spine is present in some French populations, absent in others. It was absent in the material studied by Karaman, 1929b, from Trieste, and in that of Pljakić, 1962, from Yugoslavia. As discussed in the introduction, the presence or absence of this spine is not considered a character of taxonomic importance.

In one stream, the Ruisseau des Ecrevisses, in France, although not in direct connection with the sea, the water is salty (2.20-2.29% Cl.). The abundant population of E. stammeri in this stream has a markedly smaller body size (length adult male 3.0-5.0 mm) than the typical form, but it is otherwise undistinguishable from it.

Remarks. — This species is no doubt closely related to *E. acarinatus*, and Karaman, in its original description, considered it a subspecies of *acarinatus*. Since no data on interfecundity are known, it seems best for the moment to give *stammeri* full specific rank, the more so since it is clearly distinguishable from *acarinatus*, amongst others by the characters mentioned in the key. The only other species which might be confused with *stammeri* is *foxi*, which resembles it in the non-compressed urosomal elevations, and in the projecting basis of leg 5. Upon closer inspection, several clear differences exist between *foxi* and *stammeri*, such as the short merus of leg 5 in *foxi* (long in *stammeri*), the longer setation of the basis of leg 7 in *foxi*, the presence of setae on merus and carpus of leg 7 in *foxi*, and the presence of long setae on the telson of *foxi*.

As I remarked already under *E. foxi*, Ruffo's (1937) records of "Gammarus Olivii", from fresh waters in northern Italy might belong to *E. foxi*, although it is not at all excluded that also *E. stammeri* was present in Ruffo's samples.

It is not certain either to which species Angelier's records (1959) from Corsica belong. The name employed in his paper (G. olivii) is almost certainly

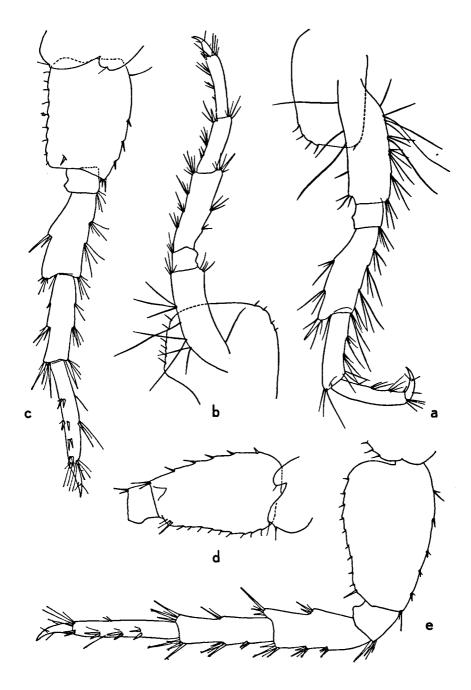


Fig. 29. Echinogammarus stammeri (Karaman, 1929), 3, from the Massif de la Sainte Baume (France, Bouches-du-Rhône). a, third leg (scale C); b, fourth leg (C); c, fifth leg (C); d, proximal portion of sixth leg (C); e, seventh leg (C).

not correct, since the ecological conditions of his findings (viz., fresh, running waters) do not point in the direction of *olivii*.

Distribution. — Fresh streams and upper courses of rivers, often far from the sea, in France, Italy, and Yugoslavia. In France, this species seems to be restricted to streams in the Massif de la Sainte Baume (dépt. Var).

Ecology. — Usually accompanied by Gammarus fossarum Koch, more rarely by other members of the Gammarus pulex-group. Lives under stones in clear, calciferous, running waters, but seems to avoid springs.

### Chaetogammarus ischnus (Stebbing, 1899). Figs. 30a, 30b.

I could examine only one sample of this species, belonging to the subspecies sowinskyi (Behning, 1914) (lit. and syn. see Straškraba, 1962: 124), from the Volga near Seratov (BMNH). This species is well-characterized by the shape of the telson lobes, which are as long as wide, more or less triangular in outline (fig. 30b). The mandible palp (fig. 30a) offers another distinctive feature; the basal segment is setiferous (this character separates C. ischnus sowinskyi from all other species treated in this paper), the third segment bears, in addition to the usual four, long, distal setae, on the inferior margin a distal row of regularly sized setae plus a proximal row of irregular setae. This armature is reminiscent of that found in Gammarus tigrinus Sexton.

### Chaetogammarus olivii (H. Milne Edwards, 1830). Figs. 31—33.

Gammarus Olivii H. Milne Edwards, 1820: 367, 372, pl. 10 figs. 9-10; H. Milne Edwards, 1840: 47.

Gammarus Olivii; Chevreux & Fage, 1925: 251—252, fig. 262. (p.p., part of their material belonged to Ch. dahli).

Marinogammarus olivii; Sexton & Spooner, 1940: 645—649 (p.p., only the syntypes record from Naples and the Cap d'Antibes record), figs. 4 f-o (not figs. 3 a-1 and 4 a-e, which apply to Ch. dahli).

Gammarus (Echinogammarus) olivii; Schellenberg, 1937a: 272.

Gammarus (Echinogammarus) Olivii; Ruffo, 1938: 138-141, figs. 1-6.

Echinogammarus olivii (part.); Straškraba, 1967: 205.

Gammarus olivii forme marine typique; Razakandisa & Brun, 1964: 719—722, fig. 1 (top).

Gammarus (Marinogammarus) atlanticus Dahl, 1958: 11-15, figs. 2-4.

Uncertain references (may apply to Ch. olivii or to Ch. dahli). -

Gammarus olivii; Reid, 1940: 335-337.

Marinogammarus olivii; Reid, 1944: 22, fig. 18.

Gammarus (Echinogammarus) olivii; Brian, 1939: 2-3.

Material examined. -

Spain: Cadaques, prov. Gerona, Playa Mayor, 4 Aug. 1950, 3 specimens (RMNH).

France: La Tamarissière (S. of Agde), dépt. Hérault, under stones on the beach near the pier, 27 Apr. 1968, chlorinity 18.9 ‰, 11 specimens (ZMA).

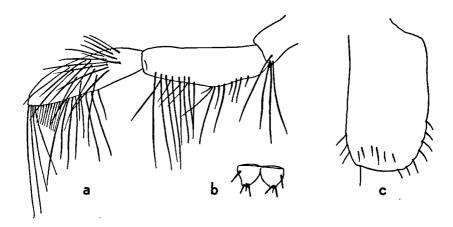


Fig. 30 a-b, Chaetogammarus ischnus sowinskyi (Behning, 1914),  $\mathcal{Q}$ , from the Volga near Seratov. a, mandible palp (scale F); b, telson (free hand sketch). c, Echinogammarus scutarensis (Schäferna, 1922),  $\mathcal{Q}$ , from Donja Gorica (Montenegro), second coxal plate (scale A).

Etang de Thau, shore near Balaruc-les-Bains, dépt. Hérault, under stones and in weeds, littoral zone, 27 Apr. 1968, chlorinity 20.5 %, many specimens (ZMA).

Fos-sur-Mer, Pointe St. Gervais, dépt. Bouches-du Rhône, shingle and stones in the littoral zone, 30 Apr. 1968, 13 specimens (ZMA).

Carro, Plage du Verdon, dépt. Bouches-du-Rhône, 17 July 1967, many specimens (ZMA).

Sausset, dépt. Bouches-du-Rhône, 8 May 1963, many specimens (ZMA).

Cassis, dépt. Bouches-du-Rhône, shore, 19 Nov. 1967, many specimens (ZMA).

Etang de Berre, dépt. Bouches-du-Rhône, near Martigues, at the tidemarks, between algae, stones and sand, 6 Jan. 1968, chlorinity 11.40 ‰, many specimens (ZMA); Etang de Berre, mouth of river Touloubre, 30 Mar. 1961, 1 specimen (ZMA); Etang de Berre, les Cabanes de Mauran, 22 Sept. 1967, many specimens (ZMA).

La Reppe at Sanary-sur-Mer, dépt. Var, non-permanent river, about 200 m from the open sea, reeds, stones, 5 Jan. 1968, chlorinity 17.0 %, 25 specimens (ZMA). Cap d'Antibes, dépt. Alpes-Maritimes, 8 specimens (BMNH).

Italy: Naples, collection H. Milne Edwards, 2 syntypes (MNHN). Rapallo, prov. Genova, 21 July 1950, many specimens (RMNH).

Y u g o s I a v i a: Adriatic coast E. of Opatija, 14 Apr. 1955, 1 Q (ZMA). Split, Marjan peninsula, 12—13 May 1956, many specimens (RMNH).

Split, beach, under cobbles, 25 Aug. 1960, many specimens (RMNH); same locality, 10 June 1961, many specimens (ZMA); same locality, in fine gravel at the water-line, 21 May 1956, 7 specimens (RMNH); same locality, shore, 13—21 May 1956, 6 specimens (RMNH).

Omiš, S.E. of Split, beach, 11 June 1961, many specimens (ZMA).

Morphology. — This species is very clearly described (under the name of *Marinogammarus atlanticus*) by Dahl, 1958. The reader is referred to that description, to the figures 4 f-o in Sexton & Spooner (1940), and to the figures 31—33 in the present paper.

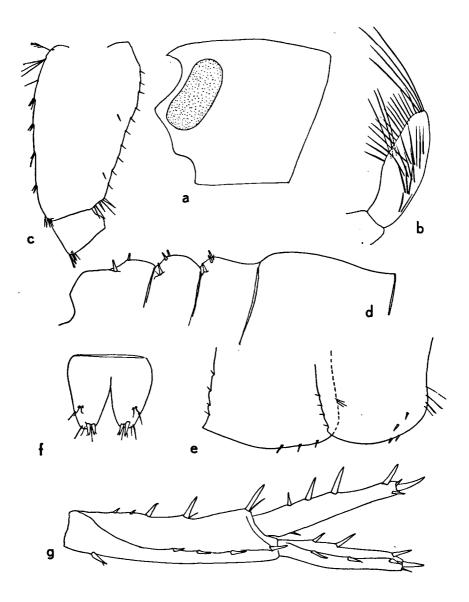


Fig. 31. Chaetogammarus olivii (H. Milne Edwards, 1830), 3, from Split, Yugoslavia (except for c, which is after a large 3 from Cassis, France and for g, which is after a 3 from La Tamarissière, France). a, head from the left (scale A); b, distal segment of mandible palp (F); c, basis of seventh leg (C); d, contour of last pleon and urosome segments (A); e, second and third epimeral plates from the left (A); f, telson (D); g, first uropod (A).

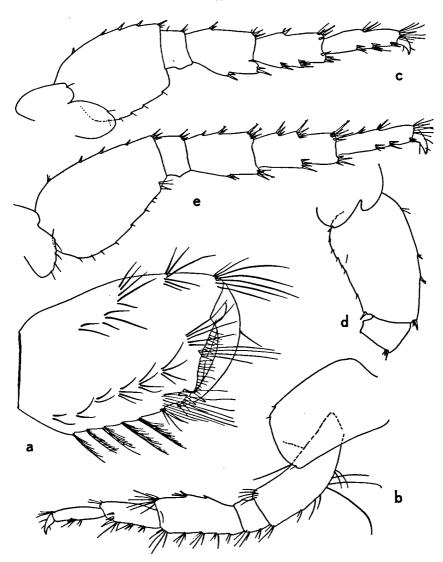


Fig. 32. Chaetogammarus olivii (H. Milne Edwards, 1830), 3, from Split, Yugoslavia. a, hand of second leg (scale B); b, third leg (C); c, fifth leg (C); d, proximal portion of sixth leg (C); e, seventh leg (C).

Remarks on the synonymy. — See under Chaetogammarus dahli.

Distribution and ecology. — This species is rather common in the Mediterranean basin, where it inhabits the littoral zone of cobble beaches, occurring sometimes even above the high-tide line. It can penetrate in polyhaline waters, as estuaries of small, non-permanent streams and lagoons.

I have had no opportunity to examine any material from outside the Mediterranean, although Dahl (1958) records this species from the Azores and

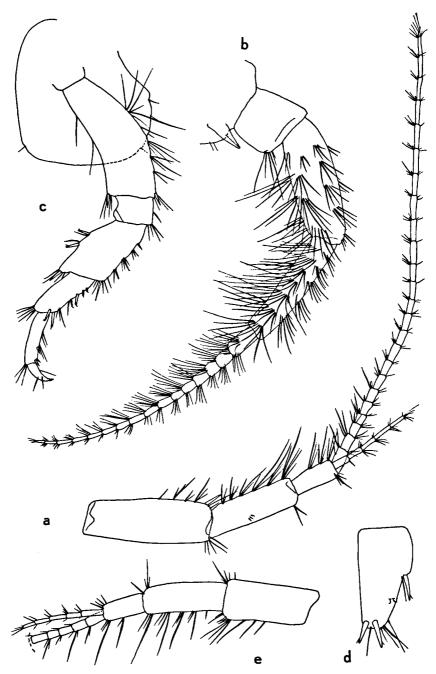


Fig. 33. Chaetogammarus olivii (H. Milne Edwards, 1830), from La Tamarissière (France, Hérault), except for c, which is from Split, Yugoslavia. a, first antenna. & (scale C); b, second antenna, &, median view (C); c, fourth leg, & (A); d. right telson lobe, & (D); e, first antenna, Q (A).

Madeira, Chevreux & Fage (1925) from Brittany, and Reid (1940, 1944) from Great Britain. As to the latter two records, my attempts to locate the actual material in one of the larger museums, failed.

Variability. — In most specimens, the armature of the inferior margin of epimeral plates 2 and 3 consists of spinules only in both sexes. Some specimens (all from estuarine localities), however, do possess a few short setules in front of the spinules, a condition reminiscent of that found in *E. acarinatus*.

The anterior margin of the merus of the 3rd leg sometimes bears strong spines and hardly any setae (as in the P3 illustrated in fig. 32b), sometimes spines are absent and replaced by longer setae, as in Ch. dahli (cf. fig. 35b).

### Chaetogammarus dahli nov. sp. Figs. 34-35.

Marinogammarus olivii (non Milne Edwards); Sexton & Spooner, 1940: 645—649, figs. 3 a-l and 4 a-e (their remaining figures apply to the real C. olivii).

Gammarus Olivii (non Milne Edwards); Chevreux & Fage, 1925: 252 (pro parte, the Algeria record only).

Gammarus olivii (non Milne Edwards); Dahl, 1958: 11--15 (in discussion on relationship with other species).

Material examined. -

I taly: Naples, without further details, Stebbing coll., 1 & (holotype) and 3 &, 5 \( \text{paratypes} \) [B.M.(N.H.), cat.no. 1928-12-1].

Algeria: Bône, on a beach, Dec. 1922, 5 &, 14 \( \rightarrow \) (MNHN).

Differential diagnosis. — C. dahli is closely related to C. olivii, with which it agrees in the remarkable shortness of the segments in legs 3 to 7, in the "spinose habitus" (i.e., with hardly any long setae on the posterior legs, on the epimeral plates, on the side plates, and on the urosome), and in the shortness of the 2nd peduncle segment of A1. C. dahli is a small species (length O 7 to 8 mm, rarely up to 10 mm). It has clearly been described by Sexton & Spooner (1940, see the above synonymy for the exact figure numbers) under the name of Marinogammarus olivii. The only discrepancy between Sexton & Spooner's description and their actual specimens, which are preserved in the British Museum (Natural History), is found in the armature of the urosome. Their statement that "each of the three (urosome) segments" presents the formula 2:1:1:2 is not correct: this formula applies to segments 2 and 3 only, whereas segment 1 presents the formula 0:1:1:0.

The following salient differences between C. olivii and C. dahli can be observed: (1) The 2nd peduncle segment of A1  $\sigma$  is  $2\frac{1}{2}$  to 3 times as long as wide in olivii, about twice as long as wide in dahli. (2) The 3rd peduncle segment of A1  $\sigma$  is at least twice as long as wide in olivii, only  $1\frac{1}{4}$  to  $1\frac{1}{2}$  times as long as wide in dahli. (3) The same segment in the female is much longer than wide in olivii, scarcely longer than wide in dahli. (4) The first segment of the peduncle of A1  $\sigma$  is shorter than segments 2 and 3 combined

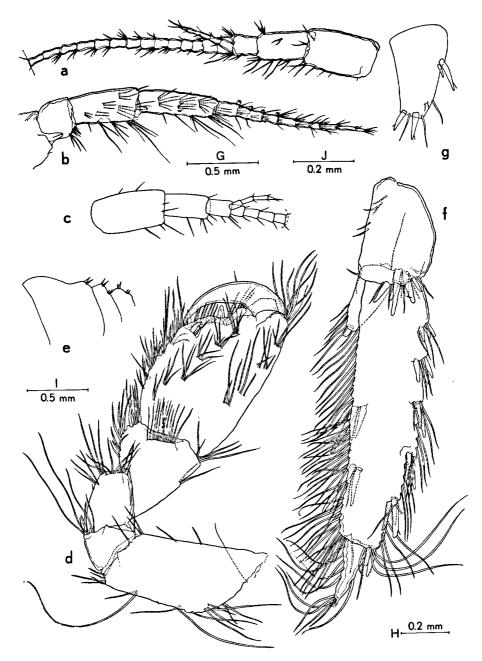


Fig. 34. Chaetogammarus dahli nov. sp., from Bône, Algeria. a, first antenna, & (scale G); b, second antenna, & (G); c, proximal part of first antenna, Q (H); d, second leg, & (H); e, contour of urosome, from the left, & (I); f, third uropod, & (plumosity of the setae omitted) (H); g, right telson lobe, & (I).

in olivii, as long as — or even longer than — these segments combined in dahli. (5) The peduncle and flagellum of A2  $_{\circ}$  bear numerous tufts of long setae, also on the inner and upper margin of the segments, in olivii, but are only feebly setose in dahli. (6) The proximal flagellum segments (3) are devoid of calceoli in olivii, provided with calceoli in dahli. (7) The merus of P3  $_{\circ}$  is between 2 and  $_{\circ}$  times as long as wide in olivii, twice — or even less than twice — as long as wide in dahli. (8) The merus in P4 through P7 is more than  $_{\circ}$  times as long as wide in olivii, less than  $_{\circ}$  times as long as wide in dahli. (9) The rami of the first uropod bear 2 to 4 marginal spines in olivii, one, rarely 2, marginal spines in dahli. (10) The first urosome segment bears a group of dorsal and one of lateral spines in olivii, whereas in dahli the lateral group is absent.

Of these characters, especially the items 1 to 6, and 10 are readily observable.

In some of its characters, C. dahli is intermediate between C. olivii and C. pirloti (Sexton & Spooner, 1940), a species known from various places in the west of the British Isles. C. dahli resembles C. pirloti in the presence of calceoli, as wel as in the robustness of the first peduncle segment of A1. The differences between dahli and pirloti can be found in couplet 8 of the key to the species in this paper, whereas in addition the much shorter and wider meral segments of legs 3 through 7 in dahli may be mentioned. The first urosome segment in dahli lacks the lateral group of spines, while this group is present in pirloti. Moreover, C. dahli usually has only 1 spine (rarely 2 spines) on each ramus of the first uropod, whereas pirloti usually has 2 spines. Finally, the lateral margin of the exopod of uropod 3 is devoid of plumose setae in pirloti, while these are present in dahli.

Remarks on the synonymy. — Two species were confused in the past, and notably by Sexton & Spooner, under the name of Gammarus (or Marinogammarus) olivii. Sexton & Spooner were probably aware of the morphological heterogeneity of their material, since they clearly illustrated the salient differences between the two species, but they adopted only one name for them, M. olivii. Unfortunately, the form amply described and more abundantly illustrated, does not correspond morphologically with Milne Edwards' type specimens (the two male syntypes in the Muséum National d'Histoire Naturelle, Paris, have been re-examined for this purpose; Sexton & Spooner incorporated in their paper also figures of these syntypes, which clearly bear out the fact that two species are confused).

Dahl (1958) was the first to recognize that two different species were hidden under the name of *olivii*. He retained the one amply described by Sexton & Spooner as the real *olivii*, and named the other *Marinogammarus atlanticus*. Although Dahl was right in his conclusion that two species are involved, he unfortunately continued to call the wrong one *olivii*.

As I could confirm through re-examination of the type material, the real olivii is identical with atlanticus.

It must be concluded then, that the species amply described by Sexton &

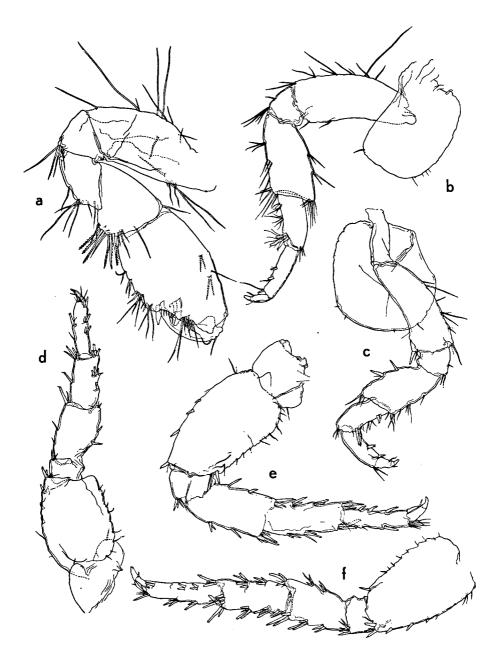


Fig. 35. Chaetogammarus dahli nov. sp., from Bône, Algeria, &. a, first leg (scale H); b, third leg (G); c, fourth leg (G); d, fifth leg (I); e, sixth leg (I); f, seventh leg (I).

Spooner as *olivii* must receive another name. Since no name is available for this species, I propose *Chaetogammarus dahli* for it, in recognition of Dr. Erik Dahl, of Lund, who was the first to recognize and stress the heterogeneous nature of the *olivii*-complex.

Ecology. — Unknown.

Distribution. — Only known from the two localities (Naples and Bône) cited in the paragraph on the material examined.

Variability. — Though most specimens examined have only one marginal spine on each of the rami of the first uropod, in some 3 or 4 specimens a smaller second, more proximal, spine is present.

#### REFERENCES

ANGELIER, E.

1959 Les eaux douces de Corse et leur peuplement. — Vie Milieu, suppl. 8: 1—56.

BARBÉ, L.

1964 Compléments concernant la distribution géographique de quelques Gammares de la faune française. — Bull. Soc. zool. France, 89: 644—650.

BEHNING, A.

1914 Gammarus sowinskyi n.sp. aus der Umgebung von Kiew. — Zool. Anz., 44: 42—44.

BRIAN, A.

1939 Gli Anfipodi della Laguna di Venezia. — Boll. Ist. Zool. Anat. comp. Univ. Genova, (2) 17 (110): 1—8.

Brun, G.

1967 Etude écologique de l'estuaire du "Grand-Rhône". — Bull. Inst. océanogr. Monaco, 66 (1371): 1—46.

Brun, G. & B Brun

1964 Sur la répartition et la taxinomie des Gammares du groupe Gammarus pungens dans le Sud-est de la France. — Bull. Soc. zool. France, 89: 754—759.

CĂRĂUSU, S., E. DOBREANU & C. MANOLACHE

1955 Amphipoda forme salmastre si de apă dulce. — Fauna Republ. pop. Romîne, Crustacea, 4 (4): 1—409.

CHEVREUX, E.

1894 Gammarus simoni nov. sp., Amphipode des eaux douces d'Algérie et de Tunésie. — Bull. Soc. zool. France, 19: 171—176.

1895 Amphipodes terrestres et d'eau douce, provenant du voyage en Syrie du Docteur Th. Barrois. — Revue biol. Nord France, 7 (4, 5): 154—164.

1899 Distribution des Gammarus d'eau douce. — Feuille jeunes Natural., (3) 29 (340): 71—72.

CHEVREUX, E. & L. FAGE

1925 Amphipodes. — Faune de France, 9: 1—488.

CHEVREUX, E. & H. GAUTHIER

1924 Description d'un nouveau Gammare. — Bull. Soc. Hist. nat. Afr. Nord, 15: 53—55, pl. I.

DAHL, E.

1958 Fresh and brackish water amphipods from the Azores and Madeira. — Boletim Mus. munic. Funchal, 11 (27): 5—25.

DELLA VALLE, A.

1893 Gammarini del Golfo di Napoli. — Fauna Flora Golf. Neapel, 20: i—xi, 1—948, 61 pls.

FERRER GALDIANO, M.

1921 Observaciones sobre los Gammaridae de agua dulce de España. — Real Soc. Esp. Hist. nat., Tomo extraordinario, 50° Aniversario: 371—378.

HARANT, H. & D. JARRY

1963 Guide du naturaliste dans le Midi de la France, 2: 1—369. (Delachaux & Niestlé, Neuchâtel).

HELLER, C.

1865 Kleine Beiträge zur Kenntnis der Süsswasser-Amphipoden. — Verh.k.-k. zool.-bot. Ges. Wien, 15: 979—984, pl. XVII.

HYNES, H. B. N., T. T. MACAN & W. D. WILLIAMS

1960 Key to the British species of Crustacea: Malacostraca occurring in fresh water. — Sci. Publ. Freshwater biol. Ass., 19: 1—36.

KARAMAN, S.

1929a II. Beitrag zur Kenntnis der Amphipoden Jugoslaviens. — Glasnika zemaljskog Muzeja Bosni Hercegovini, 41: 83—100.

1929b 4.Beitrag zur Kenntnis der Süsswasseramphipoden. — Bull. Soc. sci. Skoplje,9 (Sect. Sci. nat., 3): 93—107.

1930 Amphipoda. In: M. Beier, Zoologische Forschungsreise nach den Jonischen Inseln und dem Peloponnes. — Sitz.ber. Akad. Wiss. Wien, math.-naturwiss. Kl., (1) 139: 283—289.

1931a Gammarus cari n.sp. aus Westjugoslawien. — Zool. Anz., 94: 265—268.

1931b III. Beitrag zur Kenntnis der Amphipoden Jugoslaviens, sowie einiger Arten aus Griechenland. — Prirodoslovne Rasprave, 1: 31—66.

1934 VI. Beitrag zur Kenntnis jugoslawischer Süsswasseramphipoden. — Zool. Anz., 107 (11/12): 325—333.

MACCAGNO, T. P. & A CUNIBERTI

1956 Intersessualità in Gammarus pungens M. Edw. (Crostacei Anfipodi). — Atti Accad. Sci. Torino, (1) 90: 171—188.

MARCH, E.

1899 Distribution des Gammarus d'eau douce de la faune française. — Bull. Soc. Sci. nat. Ouest France, 9 (2): 11—12.

Margalef, R.

1944a Contribución al conocimiento de los crustacéos anfipodos que viven en las aguas dulces y salobres de España. — Bol. real Soc. Esp. Hist. nat., 42: 199—209.

1944b Materiales para el estudio de la biología del Lago de Bañolas (Gerona). — Publicaciones Inst. Biol. apl., 1: 27—76.

1950 Algunos crustáceos interessantes de las aguas dulces y salobres de España.
— Publicaciones Inst. Biol. apl., 7: 131—151.

1955 Contribución al estudio de la fauna de las aguas dulces del noroeste de España. — Publicaciones Inst. Biol. apl., 21: 137—171.

MARTYNOV, A. V.

1925 Etudes sur les Crustacés de mer du bassin du bas Don et leur distribution éthologique. — Annu. Mus. zool. Acad. Sci. Russ., 25: 1—115, pl. I.

1931 Zur Kenntnis der Amphipoden der Krim. — Zool. Jahrb. (Syst.), 60 (3—4): 573—606.

1932 A contribution to the knowledge of the fresh-water fauna of the Black Sea coast of Caucasus, I. Amphipoda. — Trav. Inst. zool. Acad. Sci. URSS, 1: 73—98, pls. I—V.

MILNE EDWARDS, H.

1830 Recherches pour servir à l'histoire naturelle des Crustacés Amphipodes. — Ann. Sci. nat., 20: 367.

1840 Histoire naturelle des Crustacés, 3: 1—638. — Collection Suites à Buffon (Roret, Paris).

MONOD, Th.

1931 Crustacés de Syrie. In: A. GRUVEL, Les états de Syrie: 397-435 (Paris).

PETIT, G.

1950 Deux stations de Gammarus pungens M. Edw. dans les Pyrénées-Orientales. Vie et Milieu, 1: 477.

PLJAKIĆ, M. A.

1962 Ein Beitrag zur Kenntnis der Taksonomie, Verteilung und Migration des Gammarus pungens M. Edw.... — Izdanya Inst. Pescicult. R. P. Macédoine, 3 (2): 15—26.

RAZAKANDISA, R. & B. BRUN

1964 Sur une espèce de Gammare d'eau saumâtre voisine de Gammarus (Marinogammarus) olivii Milne-Edward. — Bull. Soc. zool. France, 89 (5—6): 719—722.

REID, D. M.

1940 Three species of Amphipoda (Crustacea) new to Britain. — Ann. Mag. nat. Hist., (11) 6: 335—337.

1944 Gammaridae (Amphipoda); with key to the families of British Gammaridea.

— Synopses British Fauna, 3: 1—33. (Linnean Soc. London).

Roux, A. L.

1967 Les Gammares du groupe pulex (Crustacés Amphipodes). - Essai de systématique biologique. — Thèse Fac. Sci. Univ. Lyon, 447: i—vii, 1—172.

RUFFO, S.

1937 Studi sui Crostacei Anfipodi, III. Gammaridi della acque superficiali del Veneto.. — Memorie Mus. Stor. nat. Venezia Tridentina, 4 (1): 35—61, pls. I—V.

1938 Gli Anfipodi marini del Museo Civico di Storia Naturale di Genova, a. Gli Anfipodi del Mediterraneo. — Annali Mus. civ. Stor. nat. Giacoma Doria, 60: 127—151.

1939 Studi sui Crostacei Anfipodi, VII. Osservazioni sopra alcuni Gammaridi nord-africani. — Atti Soc. Ital. Sci. nat. Mus. civ. Stor. nat. Milano, 78: 55—62.

1948 Raccolte faunistiche compiute nel Gargano da A. Ghigi e F. P. Pomini. — Acta Pont. Acad. Sci., 12: (25): 293—308.

SARS, G. O.

1896 Crustacea Caspia, Amphipoda, supplement. — Bull. Acad. imp. Sci. St.-Pétersbourg, 4 (5): 421—489, pls. 1—12.

SCHÄFERNA, K.

1920 A contribution to the knowledge of the Gammarida of the Adriatic region and their geographical distribution. — Bull. internation. Acad. Sci. Bohême, 1920: 1—5.

1922 Amphipoda balcanica. — Věstník Kral. Č. Společnosti Nauk, 2: 1—110.

SCHELLENBERG, A.

1928 Zoological Results of the Cambridge Expedition to the Suez Canal, 1924, XXXV. Report on the Amphipoda. — Trans. zool. Soc. London, 22 (5): 633—692.

1936 The fishery grounds near Alexandria, 10. Amphipoda benthonica. — Notes Mem. Fish. Res. Directorate, Minist. Commerce Indust. Egypt. 18: 1—27.

1937a Schlüssel und Diagnosen der dem Süsswasser-Gammarus nahestehenden Einheiten... — Zool Anz., 117 (1—2): 267—280.

- 1937b Kritische Bemerkungen zur Systematik der Süsswassergammariden. Zool. Jahrb. (Syst.), 69: 469—516.
- 1942 Flohkrebse oder Amphipoda. Tierw. Deutschl., 40: i—iv, 1—252.
- 1943 Portugiesische Süsswasser-Amphipoden. Memórias Est. Mus. zool. Univ. Coimbra, 139: 1—7.
- SEXTON, E. W.
  - 1939 On a new species of Gammarus (G. tigrinus) from Droitwich District. J. mar. biol. Ass. U.K., (n.S.) 23: 543—551.
- SEXTON, E. W. & G. M. SPOONER
  - 1940 An account of Marinogammarus (Schellenberg) gen. nov. (Amphipoda), with a description of a new species, M. pirloti. J. mar. biol. Ass. U.K., (n.S.) 24: 633—682.
- STEBBING, T. T. R.
  - 1899 Amphipoda from the Copenhagen Museum and other sources, II. Trans. Linn. Soc. London, (2) 7 (8): 395—432, pls. 30—35.
  - 1906 Amphipoda, I. Gammaridea. Tierreich, 21: i—xxxix, 1—806.
- STOCK, J. H.
  - 1967 A revision of the European species of the Gammarus locusta-group (Crustacea, Amphipoda). Zool. Verhand. Leiden, 90: 1—56.
- STRAŠKRABA, M.
  - 1962 Amphipoden der Tschechoslowakei nach den Sammlungen von Prof. Hrabě. 1. — Věstník Českoslov. zool. spol., 26 (2): 117—145.
  - 1967 Amphipoda. In: J. ILLIES (ed.), Limnofauna Europea: 202—209. (Gustav Fisher, Stuttgart).

Prof. Dr. J. H. STOCK Zoölogisch Museum der Universiteit van Amsterdam Plantage Middenlaan 53 Amsterdam-C. — The Netherlands