ON MEMBERS OF THE *GAMMARUS PULEX*-GROUP (CRUSTACEA-AMPHIPODA) FROM WESTERN EUROPE

by

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RÉSUMÉ

La variabilité morphologique des Gammares du groupe *pulex* et la confusion concernant la position systématique des différentes formes de ce groupe, déjà démontrées par l'auteur en 1970, l'ont conduit à donner des descriptions de différentes formes du groupe et à discuter leur variabilité. Des expériences d'hybridation ont été faites entre des populations morphologiquement différentes, étroitement liées à, ou bien intermédiaires entre *G. pulex* et *G. wautieri* provenant de différentes localités d'Europe occidentale. Les résultats de ces expériences clarifient la position systématique de ces populations. Les données disponibles concernant l'écologie et la distribution des différentes espèces sont fournies.

ABSTRACT

The morphological diversity within the *Gammarus pulex*-group and the confusion concerning the systematic position of the various forms belonging to this group, already noticed by the author in 1970, formed the reason to give detailed descriptions of the different forms in this group and to discuss the variability within these forms. Hybridization experiments have been run between various morphologically different populations, closely related to, or intermediate between *G. pulex* and *G. wautieri* from different localities in Western Europe.
The results of these experiments, have an implication to the systematic position of these different populations. When available, information is given on the ecology and distribution of the various species.

INTRODUCTION

Gammarus species, belonging to the *pulex*-group have been a source of confusion for quite a long time, both amongst taxonomists as physiologists. The causes of this confusion can be found in the very poor original descriptions of the different species within the group, as well as in differences of opinion concerning the systematic position of certain forms.

So, *Gammarus fossarum* Koch, 1835, was alternately considered a subspecies of *Gammarus pulex* (Linné, 1758), (e.g. Schellenberg, 1937, 1942; Cărăusu, Dobreanu & Manolache, 1955; Straškraba, 1958), or an independant species (Koch, 1835; Schellenberg 1934; Wautier & Roux, 1959; Straškraba, 1962). The subsequent description of the same species, *G. fossarum,* under other names (e.g. *G. delebecquei* Chevreux & de Guerne, 1892; *G. pulex rambouseki* S. Karaman, 1931; *G. pulex danubialis* S. Karaman, 1931) made the whole situation still more confusing. The introduction of the generic name *Rivulogammarus* by Karaman, 1931 and the description of supposed intermediate forms between *Gammarus pulex* and *G. fossarum* (e.g. Dusaugey, 1955) contributed to the confusion.

Roux, 1967 aided to clear the situation to some extent in proving that the so-called intermediate forms between *G. pulex* and *G. fossarum* of Dusaugey, 1955, were certainly no hybrids between these two species but members of a good species, that could clearly be distinguished both on morphological and on physiological and ecological grounds. However, at the other hand, Roux did not give a complete description of this new species, which he called *G. wautieri.*

This situation instigated Stock, 1969 and Pinkster, 1970 to attack the problem at the bottom, the first by clearing the generic position of *G. pulex,* the second by giving a redescription of the species and by stabilizing the nomenclature through indication of a neotype.

At the same time systematic sampling was started in certain areas where members of this species-group occur. During the sampling, it became clear that, apart from the classical species, *G. pulex* (Linné, 1758), *G. fossarum* Koch, 1835, *G. wautieri* A. L. Roux, 1967, and *G. lacustris* G. O. Sars, 1863, several populations could be found, that showed distinct morphological deviations from these typical forms.

At the one hand, there was a group of populations, all very close to, but clearly distinguishable from *G. fossarum,* at the other hand there was a cluster of populations all very close to, or intermediate between, *G. pulex* and *G. wautieri*. It is worth noting that most of these aberrant forms are found in some few, rather restricted, areas, viz. the French Alps (in the départements Isère, Var and Alpes-Maritimes) and in the region around Montpellier (dept. Hérault). The present author started a large series of hybridization experiments, to clear the systematic position of these different forms. In these experiments seven populations were used, showing morphological affinity to *G. pulex* and *G. wautieri*. One of the populations, a typical *G. pulex*, came from the Netherlands; the other six, including a population of typical *G. wautieri*, came from southern France. In addition, other members of the research team of the Institute of Taxonomic Zoology (ITZ), Amsterdam, started other series of hybridization experiments (e.g. with populations morphologically close to *G. fossarum*, see Goedmakers, 1972). Where necessary the results of these experiments will be referred to.

This article will be an attempt to bring more clarity in the taxonomic status of the various "forms" within the *Gammarus pulex*-group and to understand the importance of the certain slight morphological differences, which make this group so difficult. Descriptions and illustrations are given of the western European species within the group. Variability will be discussed while figures are given of those characters in which the various populations differ from each other. Where available, information will be given on the ecology and distribution of the various species.

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THE CHARACTERS OF THE *GAMMARUS PULEX*-GROUP

Within the genus *Gammarus*, the *Gammarus pulex*-group is characterized by the following characters:

(1) small, kidney-shaped or rounded eyes, (always less than twice as long as wide), the upper margin of which is widely separated from the mid-dorsal line; (2) hands of gnathopods almost equal in size, though different in shape: the first one is always pyriform, the second one has an almost transverse palm; (3) both gnathopods are provided with a medial palmar spine in males; (4) P5 through P7 armed with spines only; (5) inner ramus of third uropod always at least half as long as the outer ramus; (6) first segment of exopod of third uropod armed with setae and spines along the outer margin.

Although some of these characters occur in other groups within the genus *Gammarus* as well, this combination of features is quite characteristic. So, the *Gammarus balcanicus*-group differs from the *pulex*-group in character (6) having the outer-margin of Ur 3 armed with spines only. *Gammarus roeseli* Gervais could also be considered as a member of the *pulex*-group, considering all the characters mentioned above, but nevertheless it is left out, because of the very characteristic teethlike projections on the metasome segments.

VARIABILITY

Within the *Gammarus pulex*-group, like in all other groups of gammarids, certain characters are very stable, while others can show an enormous variability.

As far as we could ascertain, after studying material of the various species, the following characters within this group are more or less stable:

1) The shape of the eye (always less than twice as long as wide).
2) The structure of the mandible palp (which always has a regular row of spines on the ventral margin of the third segment).
3) The setation of the flagellum of A2 (although

in general stable, there can be exceptions, e.g. in *G. fossarum).*

4) The shape of the hand of the gnathopods (the first one is always pyriform, the second one always has an almost transverse palm in this group. Both gnathopods are provided with a medial palmar spine in males).
5) The ratio between the endopod and the first exopodal segment of the third uropod (although this ratio changes during the development, it nevertheless is stable, within a certain range, and can often be used as a discriminating character).
6) The shape of the basal segment of legs 5 to 7 (although this character is age-dependant and the length/width ratio increases with age, a wide basal segment never changes into a narrow one).
7) The type of armature of legs 5 through 7 (usually consisting of spines only).

Variable characters are:

1) The number of the segments in the flagellum of both the first and second antenna. Generally this number increases with age, but it also shows geographical and ecological variation.
2) The shape of the epimeral plates.
3) The density of the setation along the outer margin of the exopod in uropod 3 and the number of plumose setae participating in it.
4) The armature and shape of the telson.
5) The number of spines and setae on the urosome, and on the anterior legs.

A similar pattern of variability can be found throughout this species group, and will not be discussed for every single species. Only if the variability pattern is different in one or more traits, this will be emphasized.

DESCRIPTIVE PART

The descriptions are comparative in relation to the redescription by Pinkster (1970) of *Gammarus pulex* (Linnaeus, 1758).

Gammarus lacustris G. O. Sars, 1863

Principal references. — Schellenberg, 1942 : 32—33; Reid, 1944 : 18—19; Fryer, 1953 : 155—156; Segerstråle, 1954 : 1—91; Micherdzinski, 1959 : 571—573; Menon, 1969 : 14—32; Pljakić, 1963 : 15—22; Bagge, 1964 : 292—294; Økland, 1969 : 11—152; Roux, 1972 : 287—296.

Material examined. — More than 80 samples from Scandinavia, Poland, Russia, Scotland, Eire and Canada.

A large species: the largest male out of 30 samples is about 20 mm.

Adult male. — Habitus (fig. 1A) rather robust, an effect that is intensified by the relative short antennae. The colour of live specimens is rather variable, from greyish to red-brown or greenish, depending on the composition of the bottom and the vegetation in which they are found. The eye is rather small (fig. 1B).

The first antenna is relatively short (fig. 1C), about 1/3 of the total body length of the animal. The main and accessory flagellum have 18 to 25 and 3 to 4 segments, respectively.

The second antenna (fig. 1D) is even shorter than the first. Its fourth and fifth peduncle segments are almost equal in length, both armed with some few tufts of setae, implanted in 3 longitudinal rows. The short (10- to 14-segmented) flagellum neither has flattened segments as in *G.p.pulex,* nor setae implanted in transverse rows. Calceoli are nearly always present in the 6 to 7 proximal flagellar segments.

The mandible palp (fig. 1E) has an unarmed first segment. The setae along the inferior margin of the third segment are equal in length, forming a regular comb.

The first and second gnathopods (figs. 1F, 1G) do not show important differences in comparison to those of *Gammarus pulex.* In both hands, a strong medial palmar spine is present.

The setation of the third and fourth legs is less dense and slightly longer, than normally found in *G. pulex* (figs. 2A, 2B).

Legs 5, 6, and 7 show no obvious differences from those in other species within this group (figs. 2C, 2D, 2E).

The inner ramus of the third uropod attains almost 3/4 of the length of the first segment of the outer ramus. The second segment of the exopod is rather well developed. The setae along the inner and outer margins of both endo- and exopod are practically always plumose.

The urosome (fig. 1A) has no elevations or excavations. The armature is usually very poor.

The telson lobes (fig. 2G) are scarcely armed. Rarely a subbasal spine, often present in *G. pulex,* can be found.

The structure of the epimeral plates (fig. 1H) is one of the discriminating characters of this species. The posteroinferior corner of the first one is somewhat rounded, that of the second and third are always sharply pointed. Although this character is variable in other species, and sharp epimeral plates can occur in some of them, they never show the constant, pointed corner encountered in the present species.

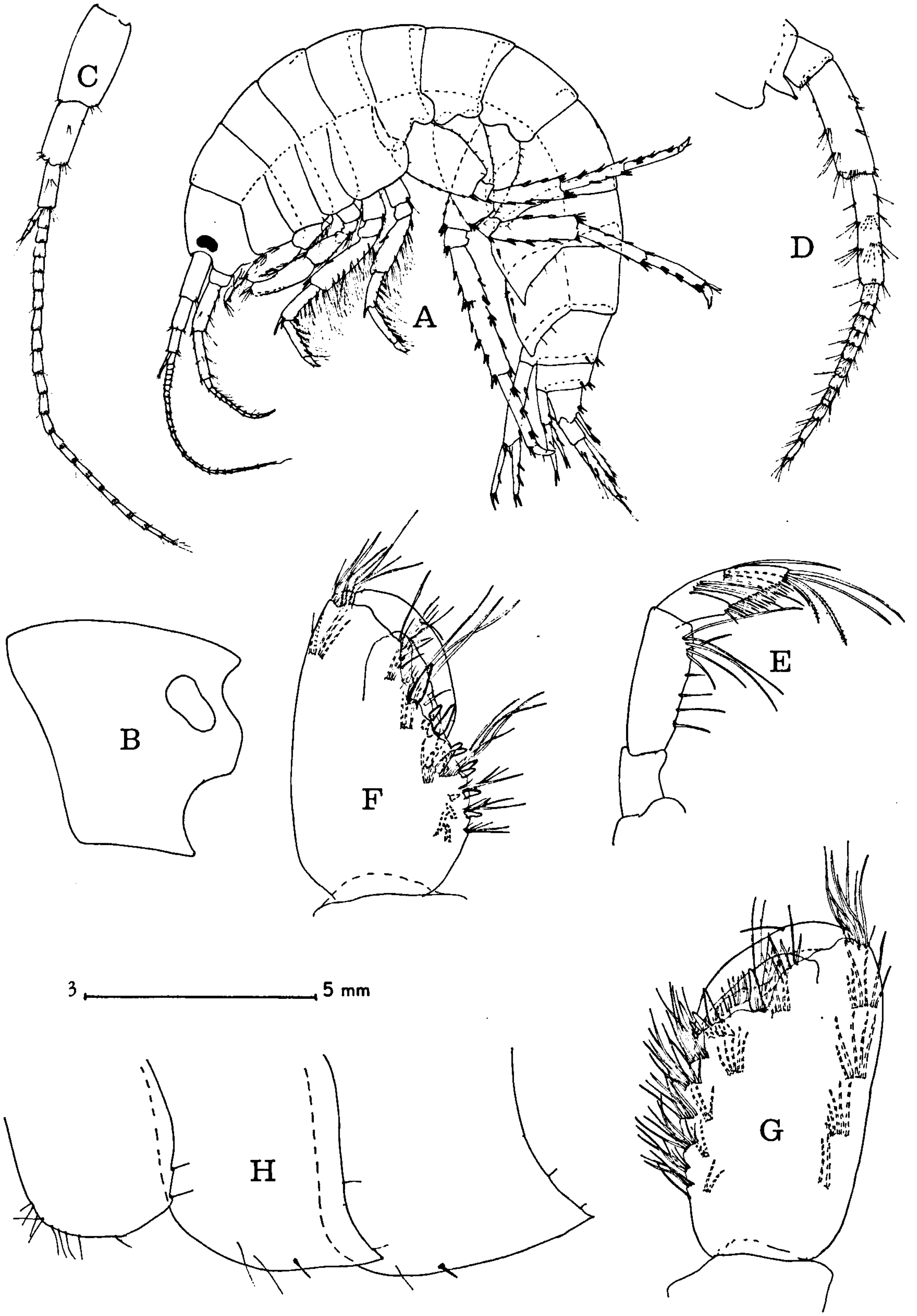


Fig. 1. *Gammarus lacustris* G. O. Sars, 1863, ♂, from Loch Loyal (Sutherland), Scotland. A, habitus (scale 3); B, head (1); C, first antenna (1); D, second antenna (1); E, mandible palp (2); F, hand of first leg (2); G, hand of second leg (2); H, epimeral plates (1).

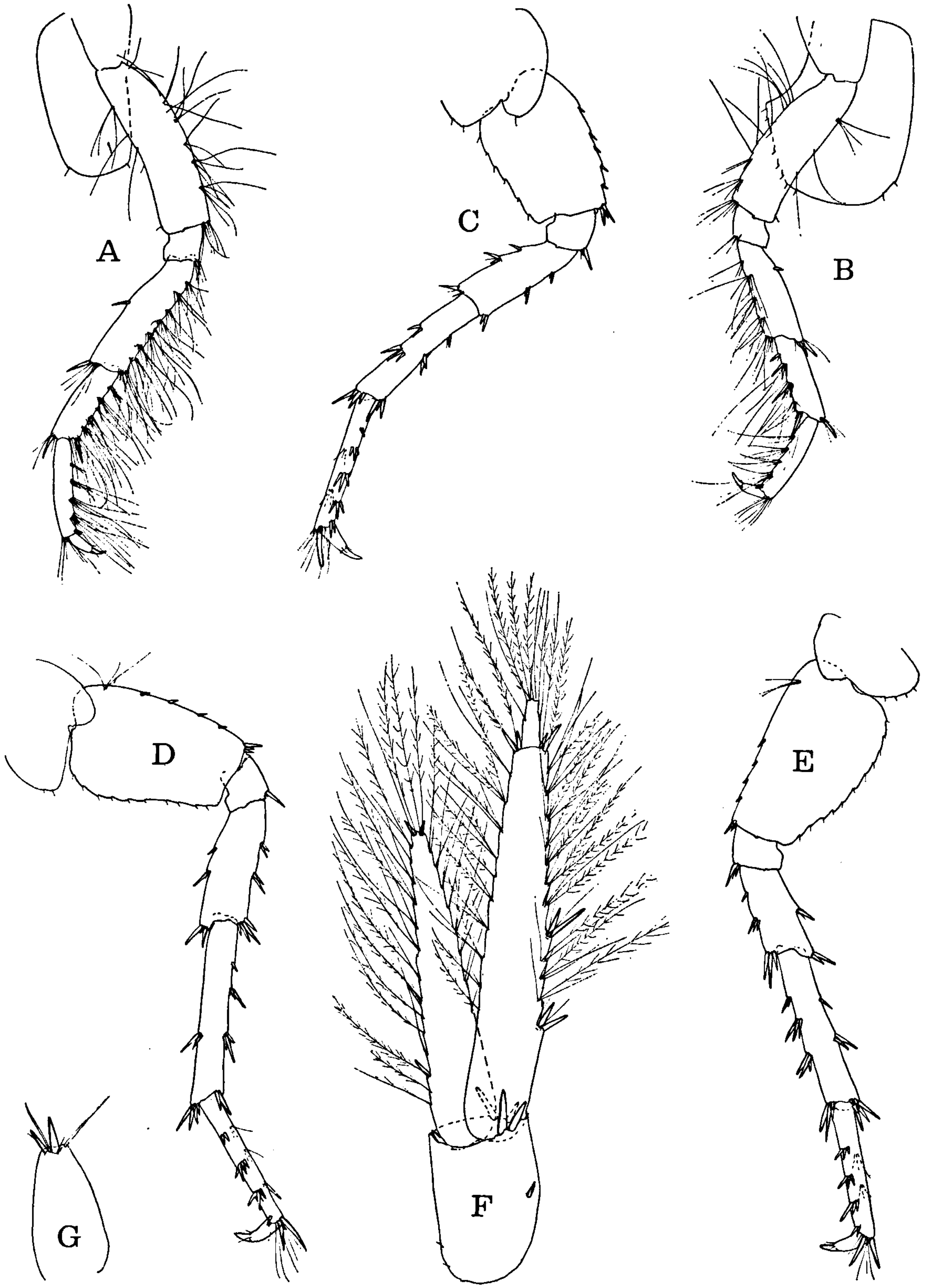


Fig. 2. *Gammarus lacustris* G. O. Sars, 1863, ♂, from Loch Loyal (Sutherland), Scotland. A, third leg (1); B, fourth leg (1); C, fifth leg (1); D, sixth leg (1); E, seventh leg (1); F, third uropod (2); G, telson (2).

Female. — Smaller than the male, most characters less pronounced, as in all other members of this group. Females are still readily recognisable, because of the sharp 2nd and 3rd epimeral plates.

Ecology and distribution. — The species usually inhabits mountain and glacier lakes, but in some areas (e.g. Denmark, northern Germany and Poland), it can also be found in lowland lakes and ponds as a relic of glacial periods. It has been found in Finland, Norway, Sweden, Scotland, Ireland, Denmark, Germany, northern Poland, Czechoslowakia, France, Switzerland, Italy, Austria, and the entire Balkan region, U.S.S.R. including Siberia, Turkey, Canada, and the northern parts of the U.S.A. (see Bagge, 1964; Fryer, 1953; Kaiser, 1958; Segerstråle, 1954, 1966; Micherdziński, 1959; Hynes, 1955; Reid, 1940; Dusaugey, 1955; Pljakić, 1952, 1963; Ruffo, 1951; Menon, 1969; Økland, 1969). Only occasionally (in Norway, Økland, 1969; Eire and Poland, own exploration) the species has been found in rivers, downstream of a lake, but this can be due to passive drift (Økland, 1969). In such rare cases only, there is a narrow zone of overlap with *G. pulex*. In other countries, e.g. France (Dusaugey, 1955), Italy (Ruffo, 1951) or Central Europe (Pljakić, 1952), the species has never been found together with other species of the *G. pulex*-group. It prefers stagnant waters with a relatively high amount of organic sediment (Fryer, 1953). It can survive at low temperatures for a long time, but is rather susceptible for temperatures higher than 20°C.

Gammarus wautieri A. L. Roux, 1967

References. — Dusaugey, 1955 : 9—18; Roux, 1967 1—172.

Material examined. — More than 250 samples from the french départements Isère, Vaucluse, Drôme, Hautes Alpes, Basses Alpes and Jura.

Male. — Medium large, the largest male out of a few thousands of specimens is about 16 mm long. In general appearance this species resembles *G. pulex*. The colour of live specimens is usually greyish to brown.

The shape of the head and eyes is of the same type as we find in other species within this group.

The first antenna is not very characteristic, having a main and an accessory flagellum of 30 to 36 and 4 to 5 segments, respectively. The fifth segment of the second antenna (figs. 3A, 3A') is little longer than the fourth segment. A variable number of setae, usually forming groups, is implanted on these segments in three longitudinal rows. On segment 5 a maximum of five groups is found. The flagellum is rather short, 10- to 13-segmented. The segments are never swollen and less compressed than in *G. pulex*. A transverse row of at most 5 setae is implanted on each flagellar segment, never forming a brush as in *G. pulex*. Calceoli are nearly always present on the 2nd to 8th segments.

The mandible palp (fig. 3B) does not show striking differences in comparison to other species in the group.

The first and second gnathopods are identical to those in *G. pulex*. The third leg is armed with many rather long setae, often curled in older males. The fourth leg on the contrary is sparingly armed with rather short setae.

Legs 5, 6, and 7 are of the normal type within the *Gammarus pulex*-group (see figs. 2C, D, E). The basal segment of the fifth leg always forms a backward protruding lobe. In the seventh leg, the basal segment is always set with a small spine (fig. 3C).

In general, the endopod of the third uropod is little shorter than ¾ of the total length of the exopod. Its setation is usually less dense than in *G. pulex*. Plumose setae are found on inner and outer margins of both endo- and exopod (fig. 3D).

The telson lobes (fig. 3I) do not show striking differences from those in *G. pulex*, and have the same variable armature.

The first urosome segment has no dorsal excavation ("saddle") or elevation; the last two urosome segments however, have a small dorsal hump. The dorsal armature has the normal mid-dorsal group of elements and a lateral group at either side.

The epimeral plates have variably shaped posteroinferior corners. Usually these corners are rounded in the first, almost rectangular in the second, and slightly pointed in the third plate.

Female. — As in the other species, females of *G. wautieri* lack most of the discriminating features present in the males. In mixed populations of *G. pulex* and *G. wautieri*, or of *G. wautieri* and *G. fossarum*, the females can still be distinguished because of slight differences in both the second antenna and third uropod (Roux, 1967), but this does not hold true for populations from different localities. In that case intraspecific, interpopulational variability completely overlaps that found in allopatric populations of other species.

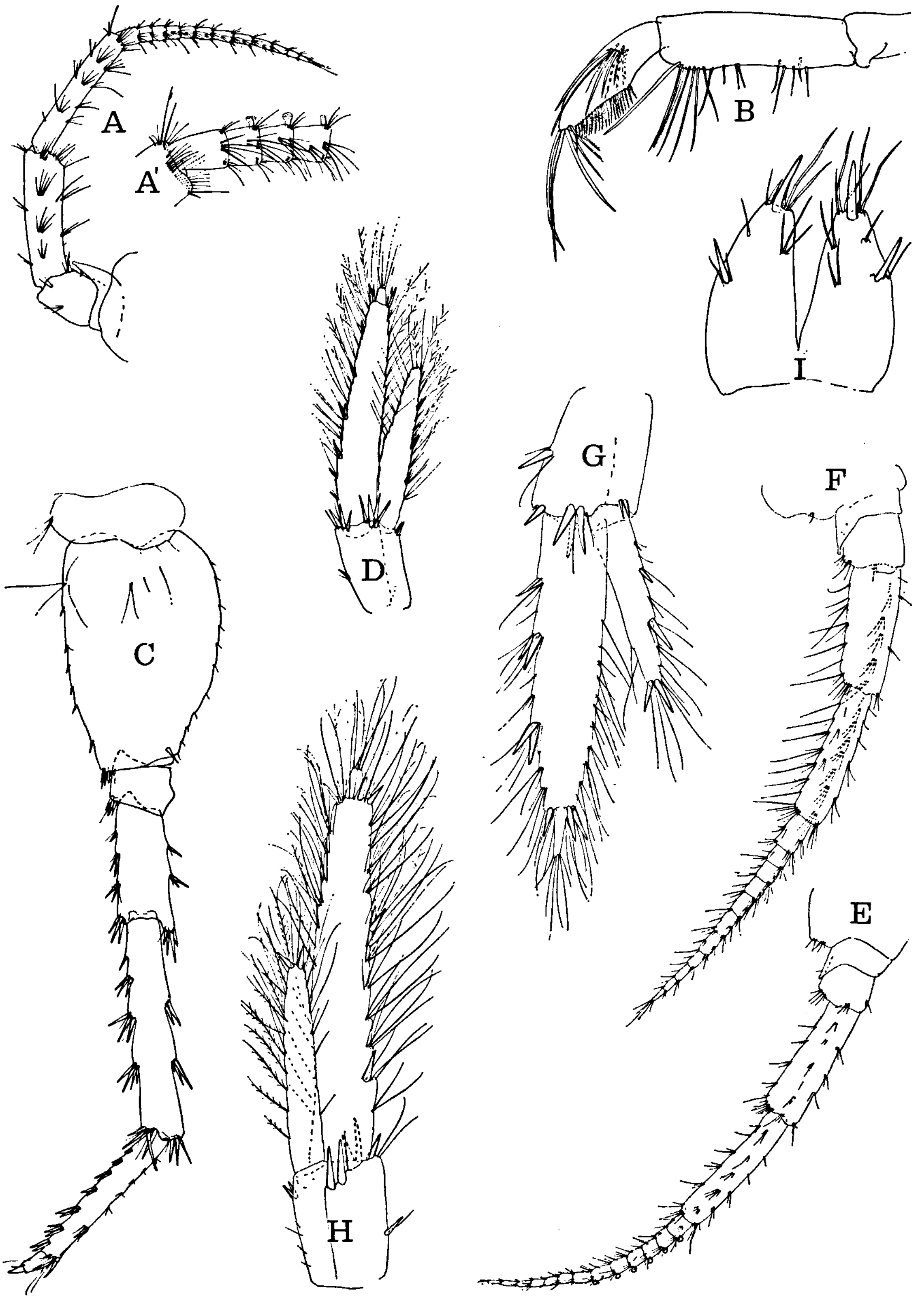


Fig. 3. A—D and I, *Gammarus wautieri* A. L. Roux, 1967, ♂, from the river Vence near le Sappey-en-Chartreuse, France, dépt. Isère. A, second antenna (1); A', detail of second antenna (2); B, mandible palp (2); C, seventh leg (1); D, third uropod (1); I, telson (2). E and H, *Gammarus fossarum* Koch, 1835, ♂, from a small brook near Ambleteuse, France, dépt. Pas-de-Calais. E, second antenna (1); H, third uropod (2). F and G, *Gammarus fossarum* Koch, 1835, ♂, from the river Amby, near Optevoz, France, dépt. Isère. F, second antenna (1); G, third uropod (2).

Distribution and ecology. — As far as we know at this moment, the species is limited to a rather small area in the French Alps, in the départements Isère and Rhône. Recently the species has been found in the french Jura. Jazdzewski, 1970, also mentions this species from certain localities in Poland. However, a study of this material and systematic sampling of the area concerned by one of the members of our team, learned that these Polish forms, although very similar to the typical *G. wautieri* in some characters, certainly show morphological differences from *G. wautieri* as well. Maybe hybridization experiments, which were started in spring 1972, can provide an answer to this new question. It is remarkable, that throughout its range the species is practically never found alone, but nearly almost together with other species of this group, viz., *G. pulex, G. fossarum,* or both of them (Dusaugey, 1955; and own results). Since the morphological characters of this species are somewhat intermediate between *G. pulex* and *G. fossarum,* Dusaugey (1955) supposed that hybrids of these two species were involved. Wautier & Roux (1959) and Roux (1967) clearly proved that this is not the case, and that *G. wautieri* is a good species, having a complete set of isolating mechanisms, a result that is completely confirmed by the present experiments. Moreover, Roux showed that the species was different in both its physiology and its ecology. It appeared to be intermediate between the two species in its oxygen consumption-rate (metabolism), its sensibility for high temperatures, as well as its resistance against water-currents. This is reflected in the distribution pattern in the alpine streams in which these species can be found. In the upper reaches, only *G. fossarum* is represented; in the mid-course *G. wautieri* is coming on the scene (although *G. fossarum* almost never disappears). In the lower parts it is replaced by *G. pulex.* In localities where *wautieri* coexists with other species of the group, the stony, fast running central axis of the streams, where vegetation is nearly absent, is inhabited by *G. fossarum,* while *G. pulex* is predominantly found in the nearshore zone, where water currents are less severe and a rich vegetation can be found. *G. wautieri* usually is the dominant species in between these two extreme microhabitats. In none of the zones however, one of the other species disappears completely (Roux, 1967; own results).

Gammarus fossarum Koch, 1835

Syn.: see Goedmakers, 1972.

Material examined. — About 600 samples from Germany, France, Yugoslavia, Austria, Switzerland, Belgium, Luxembourg, the Netherlands, Roumania, Poland and Czechoslovakia.

A redescription of this species was recently given by Goedmakers, 1972. Therefore only the most important characters will be summarized here.

Gammarus fossarum is a relatively small species within the *Gammarus pulex*-group. The maximum length observed (♂) is 14 mm. The colour of live specimens usually is a lighter or darker shade of brown. The peduncle segments of the second antenna bear the usual groups of setae, implanted in three different rows. The length of these setae, although variable, is at least as long as, but usually longer than the diameter of the segments on which they are implanted. The segments of the flagellum are set with some short setae near their distal end, never forming a flaglike brush as in *G. pulex.* In some populations calceoli are found, in others they are absent. Goedmakers already explained that considerable variation can be encountered in the setation of the 2nd antenna, especially in different populations (see also figs. 3E and 3F). The first and second gnathopods closely resemble those of the other species within this group. The length of the setae in P3 and P4 is somewhat variable (Goedmakers, 1972); these legs do not show fundamental differences from those of *G. pulex.* The other appendages, except the third uropod, are similar to those of other members of this group.

One of the most salient characters of this species is the ratio length endopod versus first segment of the exopod in Ur 3 which is about ½. Although the setation of the 3rd uropod is extremely variable throughout its distribution area (see figs. 3G, H, and Goedmakers, 1972), this ratio stays rather constant.

The smaller female shows the same sexual dimorphism as in other species.

Distribution and ecology. — See Goedmakers, 1972.

Remarks. — Goedmakers gives a survey of the variability of certain characters within one population and between populations. She points out that there is no correlation between the geographical region the population lives in and the absence or presence of certain characters. She proved, through hybridization experiments, that all morphologically different populations belong to the same species, *G. fossarum*. Meijering, 1972, pointed out that certain characters, considered to be discriminative between this species and *G. pulex*, e.g. the presence of plumose setae on the outer margin of the exopod in Ur 3 in the latter, also show up in very old males of *G. fossarum*.

Gammarus gauthieri (Karaman, 1935)

Rivulogammarus gauthieri Karaman, 1935 : 47.
Gammarus pulex subsp. *gauthieri;* Margalef 1951 : 267.
Gammarus gauthieri; Pinkster, 1971 : 45—49.

Material. — See Pinkster, 1971.

Pinkster, 1971, recently gave a redescription of this medium large species (maximum length observed 17 mm).

The head, eyes, first antenna and mouthparts are identical to those in other members of this species-group. The strongly developed fourth peduncle segment of the second antenna is almost equal in length to the fifth one (fig. 4A). They are armed with few groups of setae only. The only striking feature of the flagellum is the absence of special characters. Calceoli are always present in males.

The morphology of the first four legs never shows salient differences in comparison to other species within this group.

The distal end of the basal segments of legs 5 to 7 (figs. 4B, C) is always wider than the proximal end of the ischium, thus forming a protruding lobe, sometimes set with a small setule, but never having the small spine that is always found in the homologous position in P7 of *G. wautieri*. In adult specimens, the ratio endopod/exopod of Ur3 is almost ¾. Plumose setae are found on both inner and outer margins of the exopod. The telson has a variable number of elements near its top (fig. 4D). A subbasal spine, or group of spines, has never been found. The armature of metasome and urosome, as well as the shape of the epimeral plates closely resemble those in *G. pulex pulex*.

Female. — Shows the normal sexual dimorphism similar to females of other members of this group.

Remarks. — This species shows considerable intraspecific variation (Pinkster, 1971). Due to this, it is possible to find specimens that are morphologically almost completely identical to *Gammarus wautieri* A. L. Roux, 1967. Hybridization experiments, however, between populations of *G. gauthieri* from Spain and *G. wautieri* from France, started simultaneously by both Roux and Goedmakers, failed to give any positive results up to this moment.

Distribution and ecology. — This species is known from northern Africa and from many, more or less isolated localities in Spain (Pinkster, 1971). It seems to prefer waters with a raised calcium ion content. Its localized occurrence in wells and upper reaches of rivers in Spain, as well as the extreme variability within some populations, are an indication that these populations are relics of a formerly greater, probably more continuous, distribution in the Iberian peninsula.

Gammarus ibericus Margalef, 1951

Gammarus pulex ibericus Margalef, 1951 : 263; 1953 : 198.
Gammarus ibericus; Pinkster 1971 : 51—52.

Material. — See Pinkster, 1971.

Pinkster, 1971, already payed attention to this relatively small species within the *pulex*-group. Maximum length observed 11 mm. The species has many characters in common with *G. gauthieri*, but can be easily distinguished by the morphology of the fifth to seventh legs (figs. 4E, 4 F and 4G); the basal segments of these legs are rather slender, tapering towards the distal end, always forming a more or less protruding lobe. The armature of the distal four segments consists of spines, intermixed with setae, the latter being much longer than these spines. Such well-developed setation is not found in other described members of the *pulex*-group except for *G. acalceolatus* from northern Africa. The setation of the third uropod is less dense than in *G. gauthieri*.
The other characters differ from *G. gauthieri* in minor details only.

Distribution and ecology. — Up to now the species is known from the type locality only. Ecological data are not available.

Gammarus pulex pulex (Linnaeus, 1758)

Principle references. — Stebbing, 1906 : 474; Chevreux & Fage, 1925 : 253—254; Karaman, 1931 : 101—102; Schellenberg, 1942 : 24—31; Reid, 1944 : 17—18; Carausu, Dobreanu & Manolache, 1955 : 82—85; Roux, 1967 : 1—172; Stock, 1969 : 106—107; Pinkster, 1970 : 177—186; Vincent, 1971 : 1—132; Meijering, 1972 : 313—325.

Material examined. — More than 1000 samples from all over its distribution area.

A redescription of the nominal subspecies of this species has already been given by Pinkster, 1970. Since it is moreover the nominal form of the en-

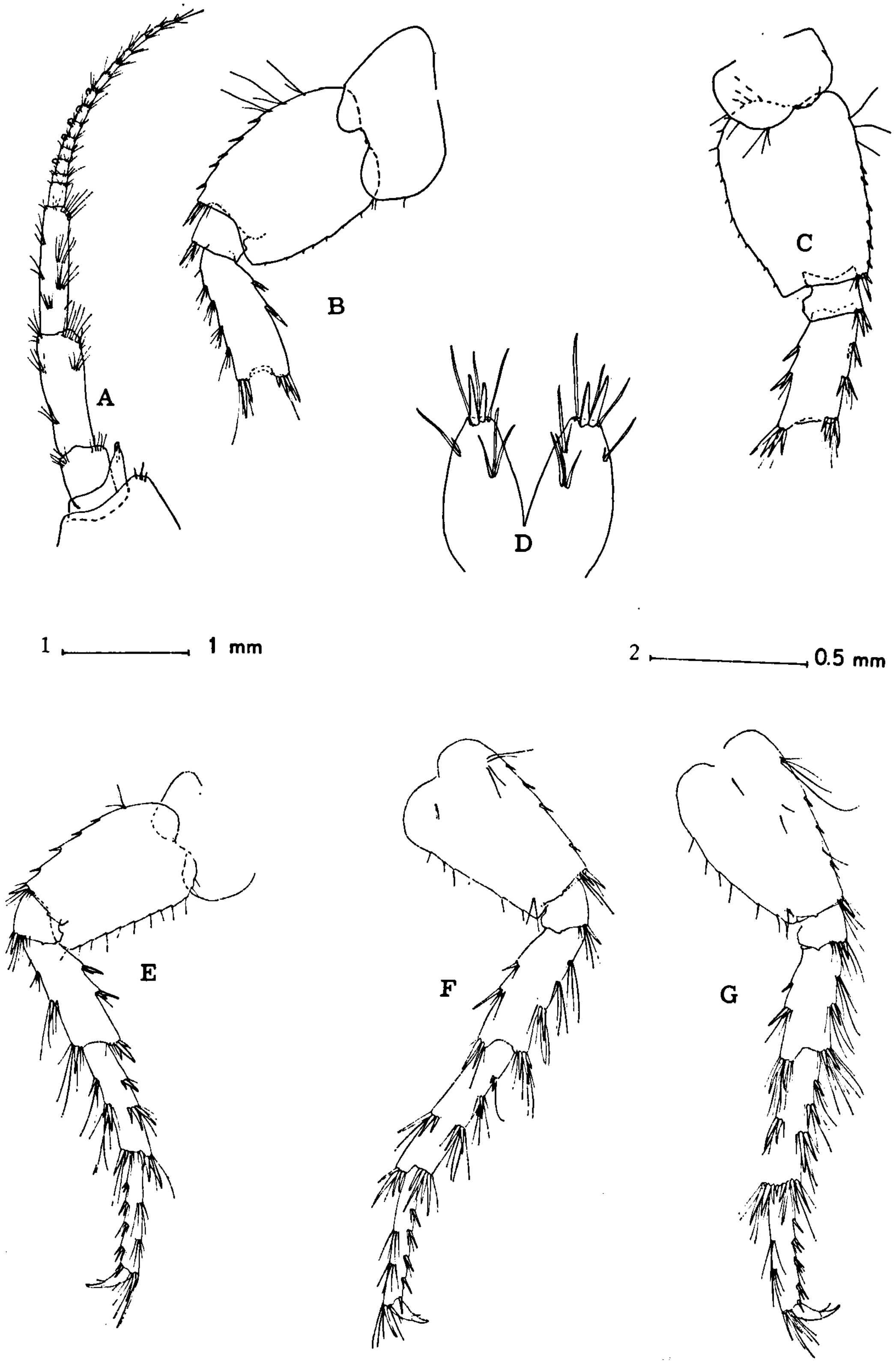


Fig. 4. A—D, *Gammarus gauthieri* Karaman, 1935, ♂, from Ifrane, Morocco. A, second antenna (1); B, fifth leg (1); C, seventh leg (1); D, telson (2). E—G, *Gammarus ibericus* Margalef, 1951, ♂, paratype from the Fuentes de la Laguna „El Tobar", Spain, prov. Cuenca. E, fifth leg (1); F, sixth leg (1); G, seventh leg (1).

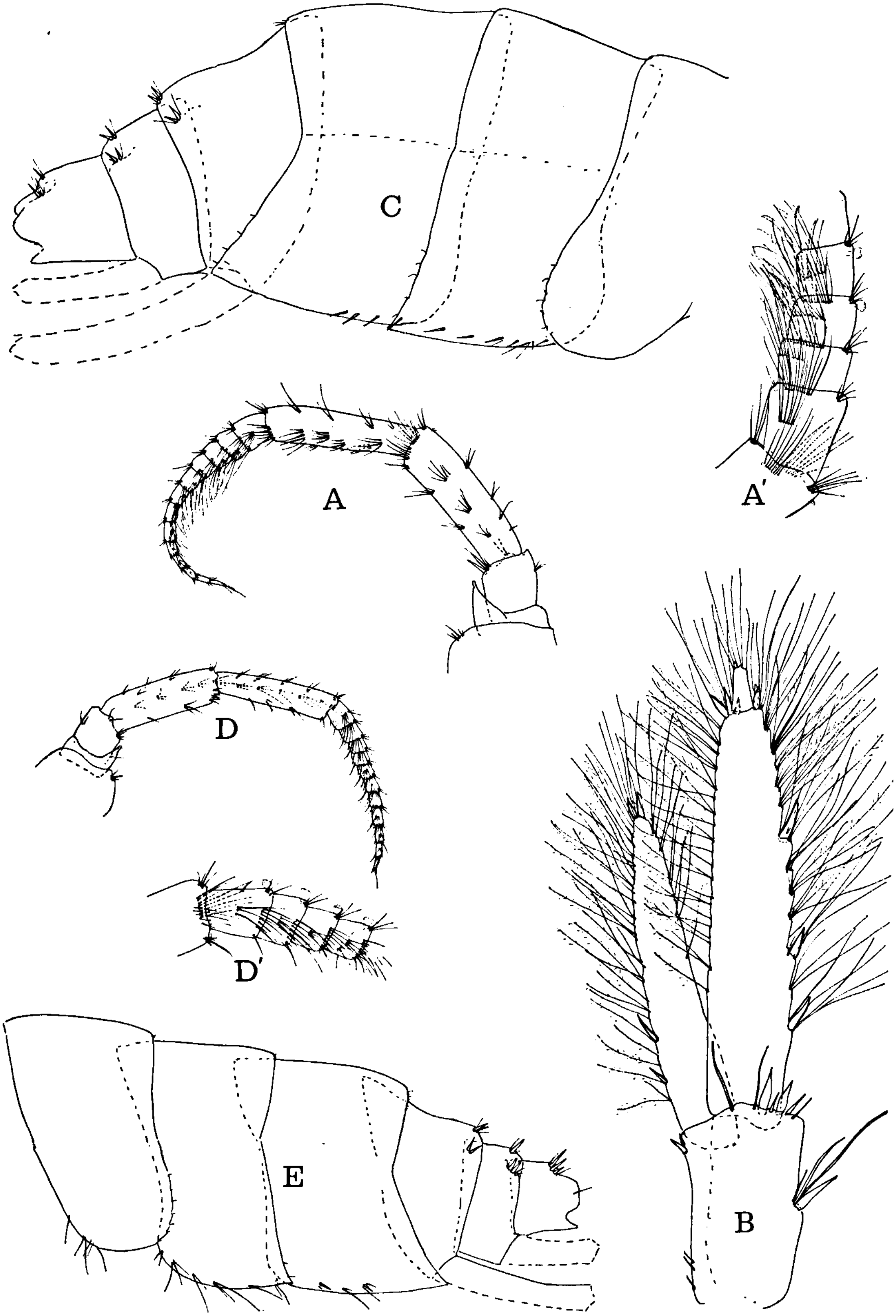


Fig. 5. A—C, *Gammarus pulex pulex* (Linnaeus, 1758), ♂, from the Hierdense Beek, the Netherlands, prov. Gelderland. A, second antenna (1); A′, detail of second antenna (2); B. third uropod (2); C, meta- and urosome (1). D—E, *Gammarus pulex gallicus* Karaman, 1931, ♂, from a small brook near Balaruc-les-Vieux, France, dépt. Hérault. D, second antenna (1); D′, detail of second antenna (2); E, meta- and urosome (1).

tire species-group, its characters will be summarized here.

Male. — Large, maximum length observed 23 mm, rather robust in general appearance with a greyish to brown or green colour, depending on the biotope in which it is found.

The third peduncle segment of A1 is about half as long as each of the other two; the 24-to 35-segmented flagellum has no particularities; the accessory flagellum is 4- to 6-segmented.

The second antenna (figs. 5A, A′) shows some of the discriminating characters of the species. Its peduncle segments 4 to 5 bear some groups of short setae, whose lengths are less than the distances between the groups, implanted in three longitudinal rows. The flagellum, probably the most characteristic part of the animal, has 12 to 16 wide, compressed segments making a swollen impression, each of them provided with a transverse row of 12 or more setae on the inner surface, together forming a flag-like brush. Calceoli are nearly always present on the outer margin of the second to tenth segment.

The mandible palp bears a regular comb-like row of spinules along the inferior margin of the third segment. The first gnathopod has a strong pyriform hand set with a strong medial palmar spine. A strong palmar angle spine together with several smaller spines (the so-called "Stiftstacheln") can be found along the posterior margin and the inner surface of the hand.

The hand of the second gnathopod has about the same size as the first but is completely different in shape, because of its almost transverse palm. The strong medial palmar spine is separated from the palmar angle group by a wide gap. The number of spines in the palmar angle group is rather variable. In specimens from the type locality, 1 strong and 4 smaller spines could be found, in populations from the Hierdense Beek, a brook in the Netherlands, 3 strong and 3 small spines were present.

The third and fourth legs bear a number of, often curved, setae on the distal three segments. In P3 these setae are generally longer than in P4. The coxal plates have rounded inferior corners.

The shape of the basal segments of legs 5, 6, and 7 gradually changes from wide in the fifth to elongate in the seventh leg. The armature of the distal segments usually consists of a varying number of spines exclusively.

The inner ramus of the third uropod (fig. 5B) attains about ¾ of the length of the first exopod segment. The greater part of the setae on the inner and outer margins of both endo- and exopod are plumose, except for those implanted near the top of the second exopod segment. The density of the setation and spinulation along the outer margin of the exopod is largely variable throughout the distribution area of the species (the same was shown by Goedmakers, 1972, for *G. fossarum).*

The telson, which overreaches the peduncle segment of the third uropod, is very variable in its armature (see Pinkster, 1970).

The first urosome segment has a distinct, though rather shallow excavation ("saddle"). The other segments do neither show elevations nor excavations. The dorsal armature generally consists of a middorsal group of spines and a lateral group on each side. Intermixed with these spines, small setae can be found. The posteroinferior corners of the epimeral plates (fig. 5C) are rather variable; generally the first one is rounded, the second and third ones rectangular or slighthly pointed, respectively.

Female. — Less characteristic than the male; the brush-like aspect of the flagellum of A2, very distinctive in the other sex, is usually absent here. In general, the setae on the peduncle segments of the first and second antennae are longer than in the males. All other features are less pronounced, a situation that can be met in all other species within this group.

Distribution and ecology. — As far as we know, *G. p. pulex* is known from southern Sweden, Finland, Denmark, and Russia (Segerstråle, 1954, 1955a, 1955b), Poland (Micherdziński 1959), Great Britain, including Scotland and Ulster (Hynes, 1955; Hamond, 1967; Macan & Mackereth, 1957; Reid, 1951), the Netherlands (den Hartog, 1964; Holthuis, 1956; Nijssen & Stock, 1966), Belgium (Stephensen & Hynes, 1953), France (Pacaud, 1952; Dusaugey, 1955; Roux, 1967; Vincent, 1971), Luxembourg (Hoffmann, 1963), Germany (Besch, 1968; Meijering, 1971; Schellenberg, 1942), the lower parts of Switzerland (own material), Bulgaria and Roumania (Cărăusu, Dobreanu & Manolache, 1955), Jugoslavia (Karaman, 1931), Siberia, including Lake Baikal (Sars, 1901; Bazikalova, 1945), Turkey and Greece (own material). In spite of an intensive research, the species has never been found in Norway (Økland, 1969), Eire (Sutcliffe, 1967), Italy and

Spain (own data), Czechoslovakia and Hungary (Straškraba, 1962, 1967).

In western Europe, *G. p. pulex* is the common freshwater species in the plains, where stream velocities are rather low. In this type of biotope it is often found together with *Echinogammarus berilloni* (Catta, 1878). There are no indications that a strong interspecific competition exists between these two species (Pinkster et al., 1970; Gras & Maassen, 1971). In mountainous areas, however, e.g. in the French Alps, or in certain parts of western Germany the species meets with strong competition of other species in this group, viz. *G. fossarum* and *G. wautieri*, or *G. fossarum* and *G. roeseli*, respectively (Roux, 1967; Meijering, 1971). This competition usually results in a distribution pattern with *G. fossarum* in the upper reaches of the stream, where water currents are strong and *G. p. pulex* in the lower reaches of the river systems. In the French Alps a third species, *G. wautieri*, can be found in a somewhat intermediate ecological position (Roux, 1967). Meijering, 1971, pointed out that *G. p. pulex* is more sensitive for lower temperatures and high stream velocities than *G. fossarum* and he makes clear that the combination of these two factors plays an important role in the competition between the two species. In source areas, where changes in temperature both during the year, as well as during the day-night cycle are relatively limited and the stream velocities are rather low, the species can successfully compete with *G. fossarum*. In those areas where *G. fossarum* is absent, *G. p. pulex* often inhabits the entire stream system, on condition that winter temperatures are moderate.

Although the species is usually found in fresh waters, it can thrive successfully at higher salinities. So, Schmidt (1913) and Von Alten (1915) report the species from mineral springs with salinities up to 25370 mg/l. In 1968, when some of these springs were revisited by some members of our team, this situation was still unchanged. Vincent, 1966, 1971, showed experimentally that *G. p. pulex* could live in a normal way in 40% seawater. Schmitz, 1959, and Schmitz, Besch & Kneissl, 1967, also record the adaptibility of this amphipod to higher salinities.

On the French Channel Coast, N. of Wimereux (France, dépt. Pas-de-Calais) healthy populations can be found on the open exposed beach, just above High-Water-Spring, in waters with a chlorinity that is often more than 1000 mg/l (own observation). These populations originally lived on top of the cliff, but reached the beach, when large portions of the cliff came down during gales in winter. The population that reached the beach this way, looked very healthy 18 months after the brusque change of habitat.

The reproduction period of this species is largely variable throughout its distribution area and seems to be a function of both climatical and light factors.

Gammarus pulex pulex, from les Landes

Material examined. — About 100 samples from the french département Landes (see also map III).

Populations from this part of France differ from "normal" *G. p. pulex* in the flagellum of their second antenna only (figs. 6F, 6F'), the segments of which never give the compressed and swollen impression that is so characteristic for the typical *G. p. pulex*. Moreover, the number of setae, participating in the flag-like brush along the inferior margin of the flagellum is somewhat reduced, in comparison with "normal" *G. p. pulex*. Notwithstanding this difference in the flagellum of the second antenna, this form must be considered a mere variety of *G. p. pulex*, as will be shown in the sequel.

Distribution and ecology. — This form is known from the French département Landes only (see map III), a region that is covered with extensive and dense pineries. Consequently the waters in this region are rather acid. So, in the spring of 1970 pH values of 4.5 or lower have been measured in more than 100 localities in which this form was found. Moreover, these waters are very poor in other important ions, such as chloride and calcium. In summer, these waters can partly dry up, because of evaporation and low precipitation.

Gammarus pulex gallicus (Karaman, 1931)

References. — Karaman, 1931 : 102; Roux, 1967 : 1—172.

Material examined. — More than 100 samples from the french départements Bouches-du-Rhone, Hérault, Gard, Var, Vaucluse and Basses Alpes.

Male. — This subspecies is much smaller than *G. pulex pulex*. The largest male observed amongst a few thousands of animals was 14 mm. Its general appearance, however, is very much like that of the other subspecies.

The main differences from *G. pulex pulex* are found in the second antenna of the male (figs. 5D, D′). The peduncle segments 4 and 5 resemble those of *G. p. pulex,* but the segments of the flagellum are different since they are less swollen than in *G. p. pulex* and moreover, the setae implanted on these segments are shorter and reduced in number, thus never forming a flag-like brush as its larger relative.

The fifth through seventh legs generally are less slender than in most other taxa within the group.

A slight excavation ("saddle") is visible on the first segment of the urosome. On the contrary, the other two urosome segments form dorsally a low but distinct hump (fig. 5E).

Although smaller in absolute size, the other appendages of this animal are similar to those in *G. p. pulex.*

Female. — Of small size, even in adult stages often no longer than 7 mm. This sex has no special characters and can easily be confused with juveniles of *G. p. pulex* or *G. wautieri.*

Distribution and ecology. — This species is known from a rather limited area in the southern part of France only (see map I). It usually inhabits the lower stretches of the river systems, where stream velocities are usually low. Often, e.g. in the french départements Var and Bouches-du-Rhone (own observation), it has been found together with *G. fossarum.* The distribution pattern in those river systems in which both *G. fossarum* and *G. p. gallicus* are found resembles that in other parts of Europe where *G. fossarum* and *G. p. pulex* occur together, and it seems that in this part of France *G. p. gallicus* occupies the same ecological niche as is usually occupied by *G. p. pulex* in other parts of western Europe, and shows a similar competition pattern with *G. fossarum.*

Margalef, 1944, mentions this subspecies from the Serrania de la Cerdaña on the Spanish side of the eastern Pyrenees. Attempts to retrace this form failed however, so some doubts remain about its real identity.

Straškraba, 1967, footnote 36, suggests that *G. p. gallicus* should be identical to *G. caucasicus* Martynow, 1932. However, comparison of our material with the descriptions and illustrations of Martynow does not support this suggestion.

Gammarus pulex araurensis nov. subspec.

Material examined. — 22 samples from the drainage systems of the rivers Hérault and Lez (France, dépt. Hérault) (see map II). About 100 specimens, collected 1-VIII-1970, in the river Lamalou, near St-Martin-de-Lamalou, France, dépt. Hérault, have been designated as types: the ♂ holotype, ♀ allotype and the paratypes have been deposited in the Zoölogisch Museum Amsterdam under cat. no. ZMA Amph. 103.345.

Male. — Rather large, up to 20 mm in length and resembling closely *Gammarus p. pulex* in almost every character except in the second antenna, the peduncle segments of which possess more groups of setae than in *p. pulex,* usually 3 to 4 on the fourth and 5 to 7 on the fifth segment, implanted in 3 longitudinal rows. The segments of the flagellum, however, are never flattened as in the nominal form. The setae, implanted near the top of each segment are as long as in *p. pulex,* but reduced in number (7 to 8) in comparison to *G. p. pulex* (12 to 15) (figs. 6E, 6E′).

The segments of the urosome never bear a dorsal hump as in *G. monspeliensis* or in *G. p. gallicus.*

This form, which was originally found in the drainage system of the river Hérault (Van Maren, 1972) (to which river the proposed name *G. p. araurensis* alludes), must be considered a new subspecies as will be shown in the sequel.

Ecology and distribution. — This form has been found in the upper regions of the rivers Lez, Hérault, and Vidourle, or their tributaries. Within these river systems, it inhabits the fast and moderately fast running stretches, a biotope that is sometimes shared with *Gammarus fossarum,* or with another still unidentified form, that resembles somewhat the Spanish *G. ibericus.* It never occurs jointly with *G. p. gallicus* (see map II).

Gammarus monspeliensis nov. spec.

Material examined. —

- France, dépt. Hérault: Source du Lez, N. of Montpellier, about 100 specimens, many of them in precopulation, 8-I-1968. The ♂ holotype, ♀ allotype and many paratypes have been deposited in the Zoölogisch Museum Amsterdam under cat.no. ZMA Amph. 103.344.
- Same locality, 1-V-1968. 7 specimens (ZMA).
- Same locality, 11 specimens, 13-X-1965 (ZMA).
- Same locality, many specimens, 1-VIII-1970 (ZMA).
- Same locality, many specimens, many of them in precopulation, 15-XI-1970 (ZMA).
- Same locality, many specimens, many of them in precopulation, 26-III-1970 (ZMA).
- France, dépt. Hérault: le Lez, W. of Prades-le-Lez, many specimens, many of them in precopulation, 1-VIII-1970 (ZMA).

Populations from the upper course of the river Lez, are clearly different from *G. p. pulex* or any

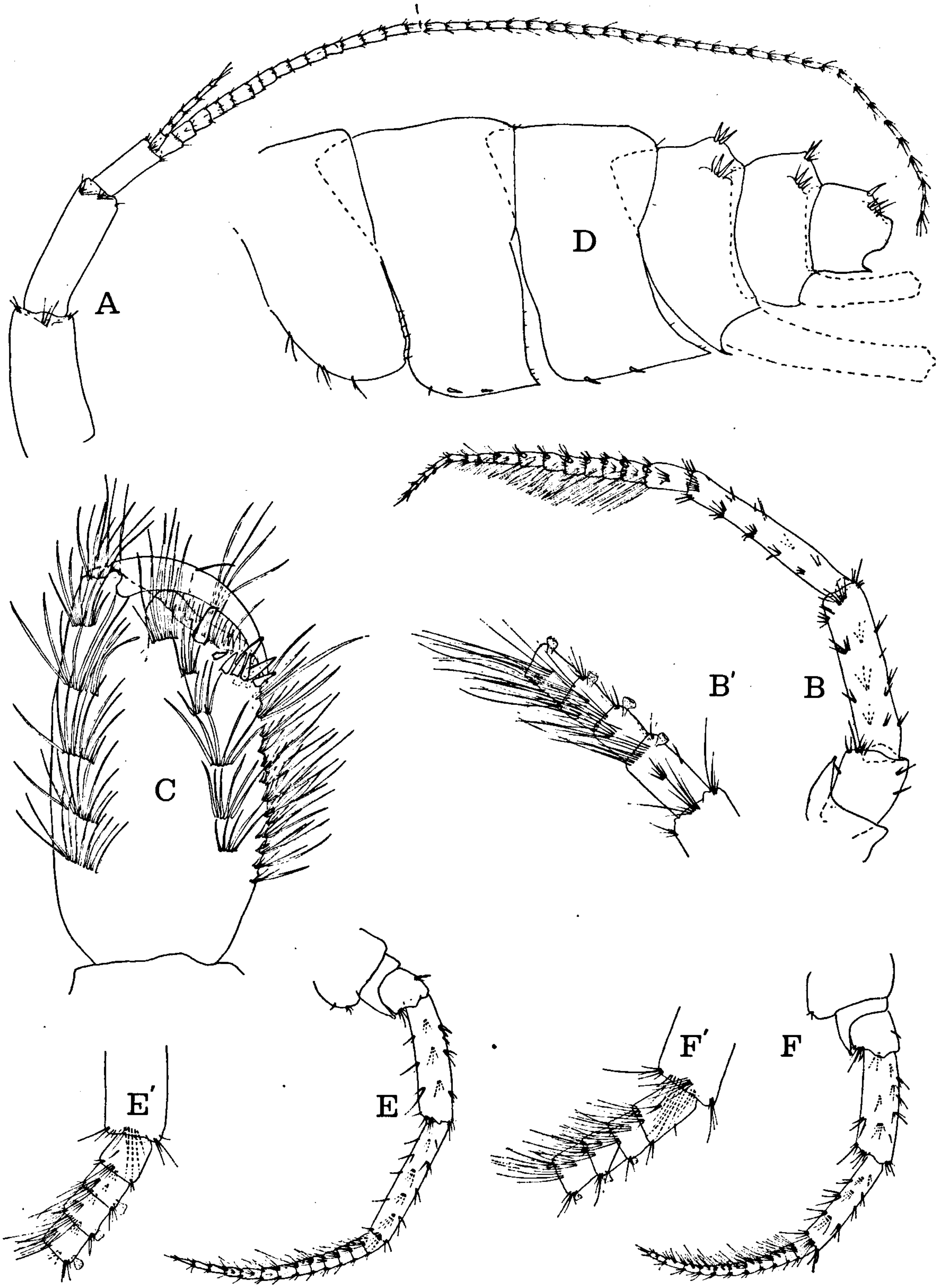


Fig. 6. A—D, *Gammarus monspeliensis* nov. spec., ♂, from the Sources du Lez, France, dépt. Hérault. A, first antenna (1); B, second antenna (1); B′, detail of second antenna (2); C, hand of second leg (2); D, meta- and urosome (1).

E and E′, *Gammarus pulex araurensis* nov. subspec., ♂, from the river Lamalou, France, dépt. Hérault. E, second antenna (1); E′, detail of second antenna (2).

F and F′, *Gammarus pulex pulex* (Linnaeus, 1758), ♂, from a small brook near Arès, France, dépt. Landes. F, second antenna (1); F′, detail of second antenna (2).

other member of the *pulex*-group in the rest of Europe in a few characters.

Male. — Maximum length 21 mm. Colour greenish, very often vertically striated with brighter bands.

The first antenna (fig. 6A) is remarkable because of the extreme length of the main flagellum, that often consists of 45 to 50 segments (against 24 to 35 in *G. p. pulex).*

The peduncle segments of the second antenna (figs. 6B, B′) resemble those in *G. p. pulex.* The flagellum is slightly different, since its segments are never compressed or swollen, while the 11 to 13 setae, implanted on these segments are even longer than in normal *pulex,* together forming a flag-like brush.

Compared with other members within this group, the number of spines near the palmar angle of P2 has increased (fig. 6C).

The other appendages, including the third uropod and the telson, do not show noteworthy differences from *G. p. pulex.*

A striking difference in comparison to the other members within this species-group, however, is the presence of well-developed dorsal humps on the segments of the urosome, almost resembling the situation found in *Echinogammarus thoni,* a species that likewise occurs in the source area of the river Lez and some adjacent river systems. These dorsal humps are not restricted to the adult stage, but occur already in just hatched juveniles, found in the female marsupium.

The special morphological characters and the result of the hybridization experiments (vide infra) were grounds to consider this form a good species.

Female. — Shows the normal sexual dimorphism, known for this group. The dorsal elevations of the urosome, so typical in the male, do also characterize the female quite clearly.

Ecology and distribution. — This form exclusively inhabits the upper reaches of the river Lez, North of Montpellier, France, dépt. Hérault (hence the specific name proposed, *monspeliensis*). This river is fed by an enormous rheocrene well, producing water with a high amount of electrolites, especially Ca-ions. The species is found under stones and between plants, always together with *Echinogammarus thoni,* a species that, although belonging to another genus, is provided with the same type of dorsal humps as the species in question.

HYBRIDIZATION EXPERIMENTS WITH VARIOUS POPULATIONS WITHIN THE *GAMMARUS PULEX*-GROUP.

Introduction. —

In order to form an idea about the significance of the morphological differences in populations from different localities, as described in the systematic part, the necessity of hybridization experiments came up. Other authors, e.g. Wautier & Roux, 1959, Roux 1967, and Meijering, 1972, already tried to cross-breed *Gammarus pulex pulex* and *Gammarus fossarum,* always with the same, negative results. Although precopulations can often be obtained between heterogeneous couples under laboratory conditions, and even ovoposition takes place in many cases (Meijering, 1972), an offspring has never been obtained. The development of the eggs always stops after a few cleavage stages and the eggs are removed by the females within a few days. Moreover, we must realize that the presence of eggs forms no proof that fertilization has taken place, since spontaneous ovoposition of unfertilized eggs has often been observed in females kept solitary (e.g. by Goedmakers, 1972). Anyhow, all these experiments leave no doubt that *Gammarus pulex pulex* and *G. fossarum* are intersterile. With these results in mind, and to reduce the number of possible crosses, the decision was made to leave *G. fossarum* out of our experiments. Seven populations of the *G. pulex*-group, including *G. pulex pulex* and *G. wautieri,* where chosen to start hybridization experiments with. These populations all show morphological differences, described in the systematic part, but have in common that the endopod of their third uropod is about ¾ of the length of the exopod. Other characters, like the structure of the second antenna and the contour of the urosome show differences in the various populations. Almost at the same time, series of cross-breeding experiments were carried out with some morphologically different populations of *Gammarus fossarum* (see Goedmakers, 1972) and with populations of *G. wautieri* at one side and *G. gauthieri* at the other, a series that is still going on. Most of the experiments have been carried out in collaboration with Mr. F. v. d. Beld, B.Sc., to whom I am greatly indebted.

Material. —

The experiments have been carried out with 1500 to 2000 individuals from each of the following localities (the names in italics have been used to indicate the populations in the tables and in the diagrammatic model of the results):

Gammarus p. pulex, from a small brook, N. of Arès, France, dépt. *Landes,* on road D 106; collected 13 November 1970; temperature 11.3°C, pH 4.5, chloride 34 mg/l. calcium 7.6 mg/l.

Gammarus p. pulex from the Hierdense beek, about 2 km. E. of *Hierden,* the Netherlands, prov. Gelderland; collected 15 December 1970 and 30 March 1971; temperature 7.4° (10.2)°C, pH 6.5, chloride 39 mg/l, calcium 31 mg/l.

Gammarus p. pulex from a tributary of la Laye, near a chapel called *Notre-Dame*-des-Anges, N.W. of Forcalquier, France, dépt. Basses-Alpes; collected 21 November 1970; temperature 9.8°C, pH 5.5, chloride 8 mg/l, calcium 84 mg/l.

Gammarus p. araurensis from the river *Lamalou,* France, dépt. Hérault, N.E. of St. Martin-de-Londres, 1 km W. of Pont de Januc; collected 14 November 1970 and 26 March 1971; temperature 12.8 (13.2)°C, pH 6.0 (6.5), chloride 7 (5) mg/l, calcium 70 (50) mg/l.

Gammarus monspeliensis from the "Sources du *Lez*", N. of Montpellier, France, dépt. Hérault; collected 15 November 1970 and 26 March 1971; temp. 13.5°C, pH 6.5-7.0, chloride 16 mg/l, calcium 103 mg/l.

Gammarus p. gallicus from a small brook near *Balaruc*-les-Vieux, N. of Sète, France, dépt. Hérault; collected 14 November 1970 and 25 March 1971; temperature 13.8 (12.8)°C, pH 6.5, chloride 122 mg/l, calcium 161 mg/l.

Gammarus wautieri from the river *Amby,* near Optevoz, E. of Lyon, France, dépt. Isère; collected 21 November 1970; temperature 10.2°C, chloride 13 mg/l, calcium 86 mg/l.

Gammarus wautieri from the river *Vence,* upstream of le Sappey-en-Chartreuse, France, dépt. Isère; collected 28 March 1971, temp. 5.6°C, pH 5.5, chloride 7 mg/l, calcium 88 mg/l.

Methods. —

All experiments were carried out in the Institute of Taxonomic Zoology of the University of Amsterdam (I.T.Z.), in an air-conditioned room, in which the day/night period could be controlled. During the present series of experiments a light period of 16 hours was alternated with a dark period of 8 hours. The various populations were kept in plastic storage basins of 25 x 25 x 10 cm, in 5 to 7 cm of water, with a constant circulation of air. Some pebbles were added to every basin as a hiding place for the animals. About 200 animals were kept in every basin. In the beginning, the water in these basins corresponded with the water from which the animals originated, but gradually they were adapted to normal Amsterdam tap water. Temperature in the different basins could be controlled by a combination of two different types of thermostates, one for cooling and one for heating. Most experiments have been done at a temperature of 15± 1°C. A problem, especially in the first series of experiments, which started in November 1970, was that the reproductive cycles of the various populations were not synchronous. Therefore, to introduce or reduce sexual activity, temperatures in some basins had occasionally to be raised or lowered. The animals were fed with *Stellaria media* Vill., a terrestrial weed, that can be found in all seasons. This plant is preferable to other types of food, since it is eaten completely by the animals leaving neither skeleton, nor slimy bacterial growth. As soon as precopulations were found in the storage basins, the couples were separated. Females were always checked to see if ovoposition had not already taken place. Next, precopulated males were put together with precopulated females from other populations, etc. So, some 10 to 50 heterogeneous couples were brought together in the same plastic storage basins mentioned above, in a mixture of water from which each of the two sexes originated. Gradually this water was replaced by Amsterdam tap water. In most cases precopulations were formed very soon again. As soon as females from such heterogeneous couples produced eggs, they were isolated in smaller plastic basins, 7 x 7 x 10 cm, again in 5 to 7 cm of water. Every two days these females were checked as to the presence or absence of eggs. As soon as hatching of the juveniles took place, the "empty" females were put back in the storage basins, in order to save the juveniles from being devoured by their own mother. The first two weeks the offspring of one female was kept apart in the smaller type of storage basin, but after that period it was put together with juveniles from identical crosses, to grow up. Mortality was usually rather high among these juveniles, mainly due to lack of place and time to attend properly to them. Nevertheless adults could be obtained from most of the fertile crosses.

Because of shortage of space, it was not always possible to run a control series with the same number of homogeneous couples. A proof, however, that the populations used did thrive under laboratory conditions, can be found in the fact, that new precopulations were formed in the storage basins, and that ovigerous females from the couples thus formed produced an offspring.

Results. —

Two series of crosses have been done: a first one

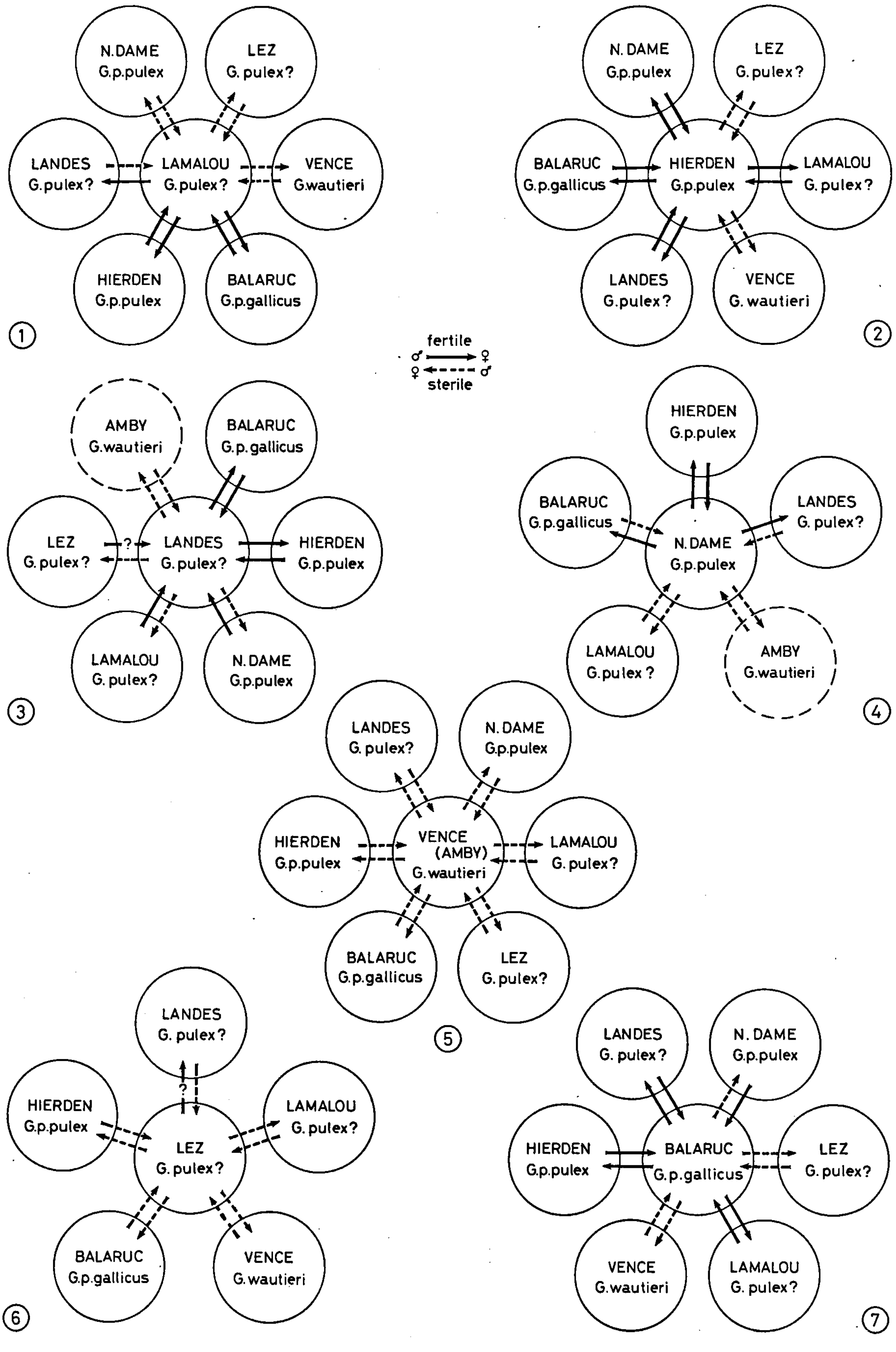


Fig. 7. Diagrammatic model of the hybridization experiments.

with material from les Landes, Balaruc, le Lez, le Lamalou, Notre-Dame-des-Anges, Amby, and Hierden. The results of this series, started in October 1970, together with the number of animals involved, the number of ovigerous females, and the number of females that produced an offspring are summarized in table I.

Table I

Results of the first series of hybridization experiments

Code	Number of ♂ used	Locality		Number of ♀ used	Locality	Number of ovig. ♀ after cross	Offspring produced
A	21	Lez	x	21	Balaruc	7	-
B	20	Balaruc	x	20	Lez	11	-
C	30	Lez	x	27	Landes	20	1*)
D	3	Landes	x	2	Lez	2	-
E	114	Balaruc	x	111	Hierden	69	12
F	69	Hierden	x	80	Balaruc	35	17
K	49	Balaruc	x	40	Landes	20	7
L	61	Landes	x	50	Balaruc	39	12
M	40	Lamalou	x	57	Hierden	33	-
N	20	Hierden	x	20	Lamalou	8	1
O	50	Lamalou	x	50	Balaruc	36	7
P	25	Balaruc	x	31	Lamalou	12	1
T	46	Lamalou	x	74	Landes	30	5
U	27	Landes	x	25	Lamalou	9	-
V	130	Landes	x	130	Hierden	58	6
W	52	Hierden	x	64	Landes	30	5
Y	15	Notre Dame	x	14	Lamalou	5	-
Z	20	Lamalou	x	25	Notre Dame	13	-
AA	2	Lamalou	x	3	Lez	1	-
AB	2	Lez	x	5	Lamalou	4	-
AI	39	Landes	x	28	Notre Dame	8	-
AJ	14	Notre Dame	x	19	Landes	14	9
AK	10	Balaruc	x	17	Notre Dame	11	-
AL	21	Notre Dame	x	28	Balaruc	43	12
AM	40	Hierden	x	39	Notre Dame	24	6
AN	60	Notre Dame	x	70	Hierden	35	7
G	35	Amby	x	50	Landes	11	-
H	25	Landes	x	25	Amby	19	-
AE	26	Notre Dame	x	26	Amby	13	-
AD	30	Amby	x	34	Notre Dame	20	-

*) after 24 hours †

The greater part of the crosses in which *G. wautieri* from Amby were involved, have been left out of this table, since a second inspection, after the end of the experiments learned, that the population was not homogeneous, and that sometimes *G. fossarum* or *G. pulex pulex* were mixed with *G. wautieri*. Therefore, in a second series of experiments, started in March 1971, this population was replaced by another, this time homogeneous, population of *G. wautieri* from the river Vence. Since the results with the population from les Landes had already given a good idea about the isolating mechanisms of these animals, parents from this origin were left out of the second series, to reduce the number of possible crosses. The results of the second series are summarized in table II, along with other data.

Table II

Results of the second series of hybridization experiments

Code	Number of ♂ used	Locality		Number of ♀ used	Locality	Number of ovig. ♀ after cross	Offspring produced
BA	70	Lez	x	91	Lamalou	26	-
BB	45	Lamalou	x	45	Lez	6	-
BC	77	Lez	x	85	Vence	29	-
BD	60	Vence	x	57	Lez	14	-
BE	40	Balaruc	x	43	Lez	31	-
BF	88	Lez	x	120	Balaruc	65	-
BG	47	Lez	x	65	Hierden	20	-
BH	51	Hierden	x	50	Lez	33	-
BI	70	Lamalou	x	85	Vence	15	-
BJ	85	Vence	x	96	Lamalou	39	-
BK	70	Hierden	x	95	Lamalou	43	6
BL	54	Lamalou	x	65	Hierden	27	8
BM	49	Vence	x	65	Hierden	18	-
BN	75	Hierden	x	80	Vence	15	-
BO	95	Balaruc	x	95	Lamalou	29	-
BP	92	Lamalou	x	120	Balaruc	30	3
BQ	75	Vence	x	120	Balaruc	43	-
BR	70	Balaruc	x	80	Vence	22	-

Finally, the combined results of both series of experiments are illustrated in a diagrammatic model (fig. 7). With the aid of this model and with the zoogeographical data we have at our disposition, one can easily understand the systematic status of the various populations used in these series of experiments.

These results will be discussed separately for every population.

Gammarus wautieri from the rivers Vence and Amby (France, dépt. Isère).

The results of the hybridization experiments make it clear, that a well-established reproductive barrier exists between this species and all other populations used in these experiments (see fig. 7 (5)). This is in complete agreement with the results obtained by Roux, 1967, and the fact that this species is very often found sympatric with other members of the *G. pulex*-group, viz., *G. pulex pulex* and *G. fossarum*. Moreover, *G. wautieri* is different from these species, in its morphology, as well as in its ecology and physiology.

Gammarus monspeliensis nov. spec. from the river Lez (France, dépt. Hérault).

The tables and fig. 7 (6) clearly show, that this population never produced an offspring when crossed with specimens belonging to other populations. Although ovoposition took place in many cases, the development of the eggs usualy stopped after some 5 to 15 days. In one case only, in crossing a male from the Lez, with a female from les Landes one juvenile was found, after 24 days, but this juvenile died within one day. Females from the river Lez, during this series of crosses, never produced any offspring with males from other populations. In the storage basins normal homogeneous reproduction took place. Considering these results, we must come to the conclusion that this population is not only different from the other forms and from *Gammarus pulex pulex* in its morphology, but also has established an effective reproductive barrier with other populations within the *pulex*-group. A geographical barrier is not always clear, since in the system of the river Lez, where this form is exclusively found, there might be a zone of contact with its relatives, *G. pulex gallicus* and *G. p. araurensis*. In conclusion, the morphological differences in the first and second antenna, the second gnathopod and the urosome, together with the effective reproductive isolation from other populations within the species-group, leave no doubt that this characteristic form must be considered a good, distinct species.

Gammarus pulex pulex from the Hierdense Beek, the Netherlands.

The results of the hybridization experiments with this population (tables I and II, fig. 7 (2) are completely different from those discussed before.

Offspring could be obtained in all crosses, except in those with *G. wautieri* from the river Vence, and with *Gammarus monspeliensis* from the river Lez. This is not astonishing since these two populations proved to be good species themselves. These results also mean, that the other populations must belong to the same species, *G. pulex*, as the Dutch material (of course they may belong to other subspecies).

Gammarus pulex gallicus from a small stream near Balaruc-les-Vieux, dépt. Hérault, France.

This form can be easily distinguished from *Gammarus pulex pulex*, because of the morphology of its second antenna. Hybridization experiments, however, clearly showed (Roux, 1967; present paper, tables I and II, fig. 7 (7)) that crosses between this subspecies and many other morphologically different populations within the species *G. pulex* are possible. So, a succesful offspring could be obtained in cross-breeding experiments between this form and animals from the Hierdense Beek (The Netherlands), from les Landes (France), from the river Lamalou (France, dépt. Hérault), and from a small brook near Notre-Dame-des-Anges (France, dépt. Isère). In the last case however, the crosses were successful in one way only: males from Notre-Dame×females from Balaruc produce an offspring but the reciprocal crosses did not work out. This is probably due to size differences; males of *G. pulex gallicus* are usually much smaller than females of *G. pulex pulex*, especially in this case, and there occur enormous "mechanical" difficulties in forming precopulations.

Roux, 1967, showed that juveniles, resulting from hybridization between *G. pulex pulex* and *G. pulex gallicus* were morphologically identical to *G. pulex pulex*, and therefore we must assume, that the genotype of the latter form is dominant over that of *G. pulex gallicus*. *G. pulex gallicus* has been found in a rather restricted area in the South of France only, an area in which no "typical" *G. pulex pulex* is found. It is almost sure, that in this case geographical isolation is the factor through which an aberrant morphology was developed without simultaneous development of a genetical isolating mechanism. Such a geographical isolation mechanism is easily demonstrable in most of the waters in which *G. p. gallicus* can be found, because of the mere absence of closely related forms. In some river systems in the french département Hérault, however, e.g. in the drainage systems of the rivers Hérault and Lez, the situation is a little more complicated. In these systems another very close relative, *G. p. araurensis*, can be found, a form which has been successfully crossed, not only with *G. p. pulex*, but likewise with *G. p. gallicus*. In these situations, *G. p. araurensis* usually inhabits the fast running or moderately fast running parts, while *G. p. gallicus* is found farther downstreams in the more slowly running parts of the river system.

Although these two forms have never been found together, there might be a possibility for them to get into contact with each other. Nevertheless, we still believe that an effective isolation mechanism is working here, since there is always a zone in between the two populations in which no gammarids do occur at all, or a zone that dries up completely from the early spring to the beginning of the rainy season, a period that roughly corresponds with the reproductive period of the populations in question (see map II).

In the river Lez, where a third member of the *Gammarus pulex*-group is found *(Gammarus monspeliensis)* and where the geographic barrier is not always so well established, an effective reproductive barrier has developed between *G. pulex gallicus* and *G. monspeliensis*. This is in complete agreement with the theory, that reproductive barriers between two closely related forms are always better developed in sympatric than in allopatric populations.

Gammarus pulex araurensis nov. subspec. from the river Lamalou (France, dépt. Hérault).

Regarding the results of the hybridization experiments with animals from this population (tables I and II, fig. 7 (1)) we see that combinations with *G. pulex gallicus* were successful in both directions. The combination with *G. pulex pulex* from N.-Dame-des-Anges, however, failed to give any success. This can be due to the rather small number of couples used, of course. As could be expected, the combination with *G. wautieri* and *G. monspeliensis* gave negative results. With the population from les Landes, the crosses were only partly fertile.

When studying the results of the experiments, it looks rather strange that two morphologically different forms (in absolute size, in the second antenna, and in the dorsal contour of the urosome) from the same river system, which do successfully crossbreed, can still maintain their own characteristic morphological features. Intensive sampling in the area in question in various seasons showed, however, that an effective isolation mechanism (desiccation during the reproductive period) is working here (see under *G. pulex gallicus).*

Since the reproductive barriers are still incomplete, the present morphologically aberrant and geographically isolated form must be considered a distinct subspecies of *Gammarus pulex.* Since it was exclusively found in the french département Hérault, the name *G. p. araurensis* is proposed.

Gammarus pulex pulex from les Landes.

Most of the crosses proved to be successful, except those with *Gammarus wautieri* from the river Amby (France, dépt. Isère) and with *Gammarus monspeliensis* from the river Lez. (Once a male from the river Lez x female from les Landes produced a juvenile, but this died within 24 hours). Only the combination male from les Landes × female from Notre-Dame-des-Anges appeared to be less succesful. However, we must conclude that an effective reproductive barrier has not yet been formed between this form and the other populations of *G. pulex* used in our experiments. Taking the geographical position of this form into consideration, we must come to the conclusion, that no sharp geographical barrier between this form and the normal *pulex* can be found. This form can be found in those regions of les Landes, where large pineries occur. However, once outside these woods, to the North, South or East, the typical *G. pulex pulex*, with the compressed and swollen antenna is reappearing. The only possible barrier would be of ecological nature, viz., the change in water composition, caused by the pineries. Indeed, the pH rapidly drops to very low values (4 to 4.5) as soon as a stream enters the woods. Probably, in this case, we have to do with some kind of morphological reaction, or with a special physiological race, in the sense of Vincent, 1971, particularly adapted for life in these acid waters. However, the fact that populations from those very acid waters do normally reproduce in Amsterdam tap water with a pH value of about 7 does not support this supposition. One should keep in mind that the pineries, which cause the extremely low pH values, were planted only a hundred years ago, so much too short a period was available to develop a new species or even a subspecies. Consequently, we must come to the conclusion that these populations from les Landes are mere variations of *G. pulex pulex.*

Gammarus pulex pulex from Notre-Dame-des-Anges.

In reviewing the results with this population we must bear in mind that they are possibly influenced by the small number of crosses executed. The results with this population are somewhat confusing. Morphologically, the animals are completely identical to those from the Hierdense Beek (the Netherlands) and crosses between these populations are rather succesful. However, with the other two subspecies, *G. p. gallicus* and *G. p. araurensis* the results are less convincing and we must conclude that reproductive barriers have already been formed or are being formed, between these subspecies and the populations in question. The same holds true for the crosses between this population and that from les Landes. However, since no morphological differences between this form and the typical *G. pulex pulex* could be found, and since no strong genetical barrier exists, we must consider this population as another (maybe physiologically different) form of *G. pulex pulex.*

DISCUSSION

When we consider the morphological diversity within the *Gammarus pulex*-group, and the results of hybridization experiments that have been run during the last few years (Roux, 1967; Goedmakers, 1972; present paper) it will be clear that speciation within this species-group is a rather complicated process. At the one hand, there is a number of good species like *G. pulex, G. fossa-*

rum and *G. wautieri*, all having successfully developed mutual reproductive barriers. These species, often coexisting in the same localities, can be clearly distinguished both on morphological and ecophysiological grounds. Their fairly large distribution areas seem to be an indication that these species developed quite a long time ago. At the other hand, however, evolution did not stop after this first speciation step. It is still going on, as is shown by the many morphologically aberrant forms of *G. fossarum* and *G. pulex*. One of the most important factors playing a rôle in this process of speciation is the degree of (geographic) isolation. Isolation, preventing a continuous gene-flow between the various populations, creates a possibility to develop special morphological characters within the isolates.

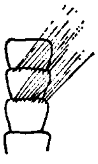
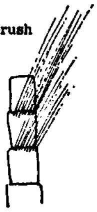
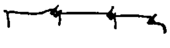
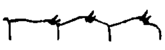
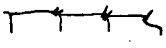
Morphological variability, which can be considered the first step towards speciation, is encountered in *G. fossarum* (see Goedmakers, 1972), a species subdivided into a considerable number of morphologically different populations. These populations usually inhabit the isolated upper reaches of stream systems, especially in mountainous areas, while the less isolated lower reaches are inhabited by other members of the *pulex*-group, e.g. *G. pulex pulex* and *G. wautieri*. Because of this distribution pattern, gene-flow will be reduced and every population could develop its own special characters. Goedmakers, 1972, proved that a number of populations tested still are conspecific, since they all did successfully cross-breed. The absence of reproductive isolation can easily be explained, since we know that the geographic isolation between the different populations must be a rather recent one, which developed after the melting of the glaciers that covered Europe during the glacial periods.

Within *G. pulex* the same process is going on, and all different steps on this way towards speciation can be found.

So in the french département Landes, which is almost completely covered with large pineries and where the waters are characterized by low pH-values, populations are found, that differ from normal *pulex* in one feature only. These populations can maintain their own morphological character, although considerable gene-flow, between this form and typical *pulex* is probable (they both inhabit the same stream systems, and the form from les Landes can successfully thrive in waters with normal pH-values). Probably, in this case, selection pressures corresponding to environmental factors are interfering with the regular exchange of gene material. However, time seems to have been too short to develop a new species or even a subspecies.

In some parts of southern France, especially in the département Hérault, the situation is even more complicated since not only one, but even three morphologically aberrant forms can be found, all occuring in the same river system. As we explained in the previous chapters, two of these forms, viz., *G. p. gallicus* and *G. p. araurensis* should be

Table III

Species / Character	G. p. pulex	G. p. gallicus	G. p. araurensis	G. p. pulex (Landes)	G. monspeliensis
Maximal length	23 mm	14 mm	20 mm	21 mm	21 mm
Number of segments in flagellum of A 1	24 - 35	24 - 32	31 - 37	26 - 34	45 - 50
Flagellum of A 2	swollen	slightly swollen	not swollen	not swollen	not swollen
Number of setae on proximal flagellar segments of A 2	12 - 15	7 - 8	4 - 6	8 - 10	11 - 13
Lengths of these setae (see fig.)	relatively long forming brush 	relatively short no brush 	relatively long no brush 	relatively long forming brush 	very long forming brush 
Dorsal contour of urosome					

considered as subspecies of *G. pulex*, while the third one, *G. monspeliensis* must be considered a full species. Very recently Miss A. M. C. Goedmakers discovered another aberrant form within the drainage system of the river Hérault. Since the identity of this form, whose morphology resembles somewhat the spanish *G. ibericus*, is not yet solved, it has been left out of this discussion. The development of these three forms, two of them endemic to this département, is not so surprising, since we know that this part of France is, geologically spoken, a very old one. Its old geological age is reflected in the presence of many endemic aquatic insects and other aquatic organisms (Harant & Jarry, 1963), and of an endemic species of fish, *Cottus petiti* Bacescu & Bacescu-Mester, 1964, in the Sources du Lez. (Bacescu & Bacescu-Mester, 1964). In the same region, we find a member of the *Echinogammarus pungens*-group, viz. *E.thoni*, likewise a species whose discontinuous distribution area is restricted to, geologically spoken, very old regions viz. Dalmatia and Herzogovina (Yugoslavia) and the french départements Hérault and Gard (Stock, 1968).

Since several different forms of the *G. pulex*-group are found in such a limited area, and since the morphological differences are usually very small, the salient differences between the various forms of *G. pulex* and *G. monspeliensis* are recapitulated in table III.

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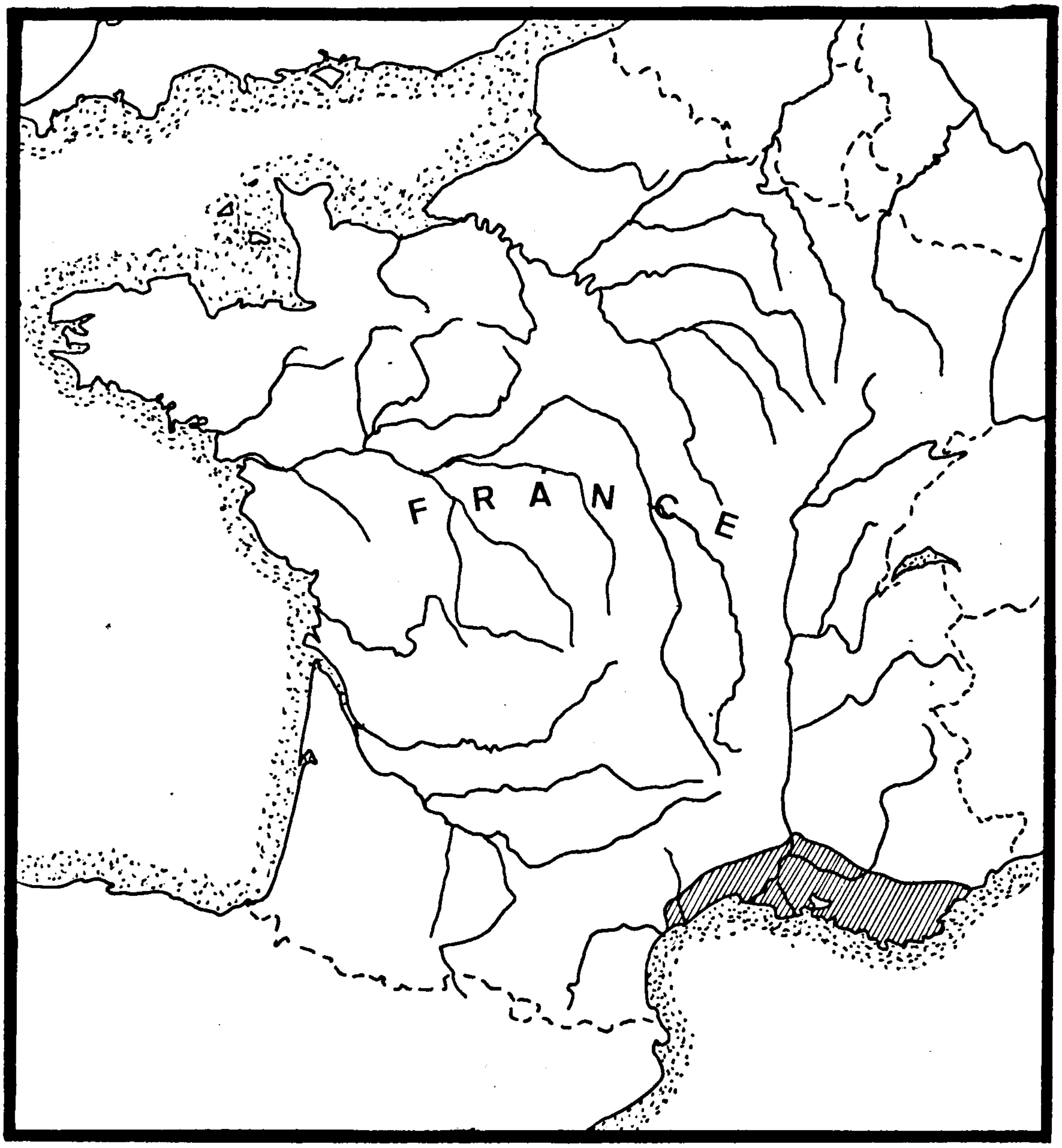
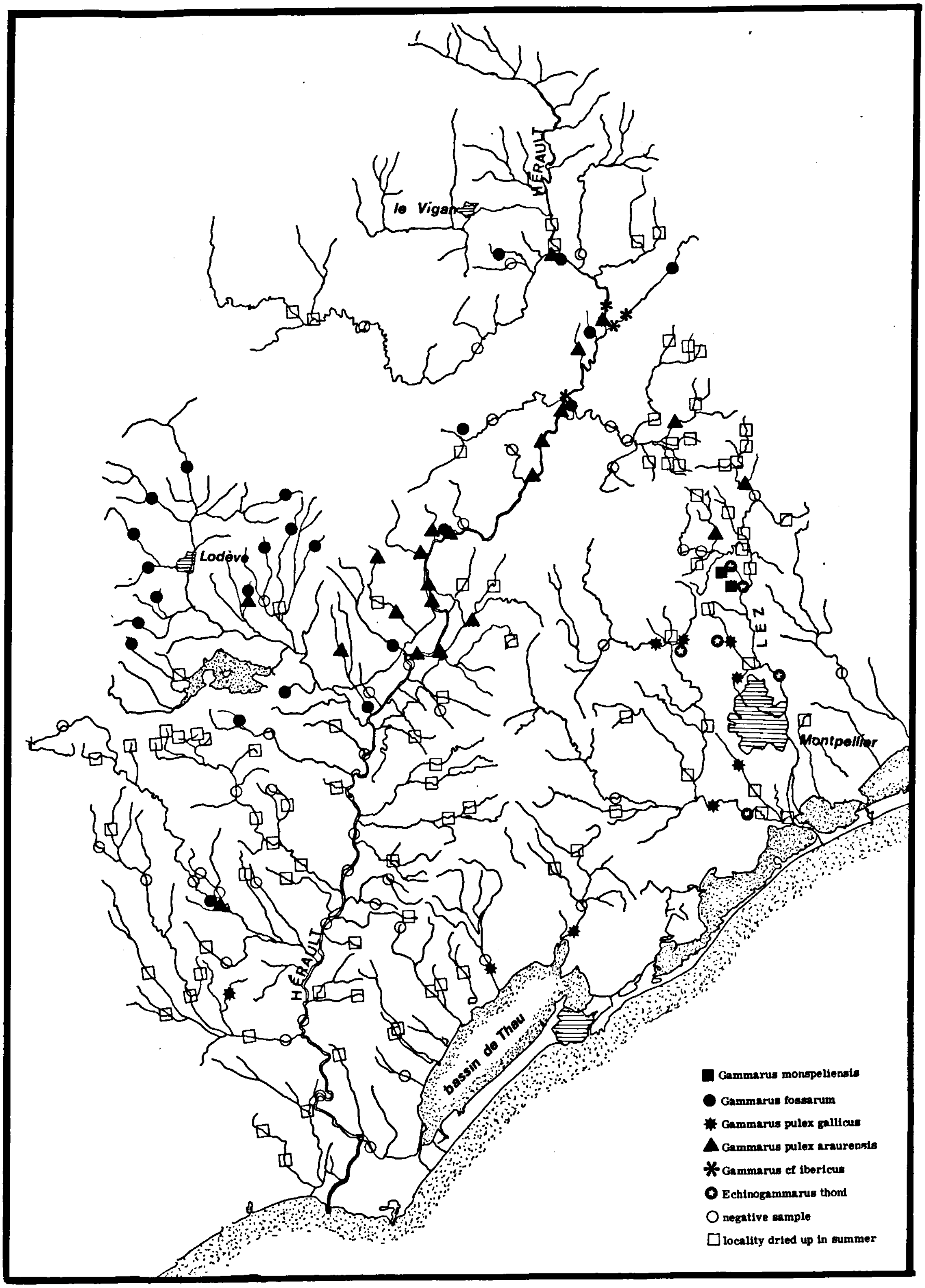


Map I. Distribution area of *Gammarus pulex gallicus* Karaman, 1931, based upon more than 100 samples.



Map II. The microgeographic distribution of the various members of the *Gammarus pulex*-group in the stream systems of the Hérault and Lez.

Map III. Distribution area of the aberrant form of *Gammarus pulex pulex* in the french département Landes.