

THE *ECHINOGAMMARUS BERILLONI*-GROUP, A NUMBER OF PREDOMINANTLY IBERIAN AMPHIPOD SPECIES (CRUSTACEA)

by

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ABSTRACT

The morphological diversity within the species *Echinogammarus berilloni* (Catta, 1878), stressed by Spandl (1926), Margalef (1956) and Pinkster (1969) was a motive to sample systematically in drainage systems of the Iberian peninsula and of great parts of France. It became clear that *E. berilloni* in reality was the collective name for a group of at least 10 species, all of them with their own, restricted distribution area. Only one of these species, the real *E. berilloni*, inhabits a much larger area, including the major part of France, the Channel islands, Belgium, Luxembourg, the southern part of the Netherlands, and south-western Germany. In this study the characters of the *E. berilloni*-group are discussed and comparative descriptions are given of all species, along with a key for their identification. The variability and ecological preferences of each species are discussed.

An attempt has been made to relate the distribution pattern of this group and of other species groups in the Iberian peninsula (e.g. the *E. simoni*-group, members of the *G. pulex*-group, and the genus *Eulimnogammarus*) to geological data.

RÉSUMÉ

La variabilité morphologique de l'espèce *Echinogammarus berilloni* (Catta), remarquée par Spandl (1926), Margalef (1956) et Pinkster (1969) a mené à un échantillonnage systématique dans les systèmes d'eaux de la Péninsule ibérique et dans presque toute la France. Il a été prouvé que *E. berilloni* était en réalité le nom collectif pour un groupe d'au moins 10 espèces, dont chacune a son aire de distribution limitée. Il n'y a qu'une seule de ces espèces, le vrai *E. berilloni*, qui occupe une aire beaucoup plus étendue, comprenant la plus grande partie de la France, les îles de la Manche, la Belgique, Luxembourg, la partie méridionale des Pays-Bas, et la partie sud-ouest de l'Allemagne.

Dans cette note les caractères des *Echinogammarus* du groupe *berilloni* sont discutés et des descriptions comparatives de toutes les espèces sont données, ainsi qu'une clef de détermination. En outre la variabilité et les préférences écologiques de chaque espèce sont indiquées.

Enfin l'auteur propose un modèle de distribution du groupe et des autres groupes d'espèces de la Péninsule ibérique (p. ex. le groupe *E. simoni*, les membres du groupe *G. pulex* et le genre *Eulimnogammarus*) par rapport aux données géologiques.

INTRODUCTION

During the last 10 or 15 years a group of staff-members and students at the Instituut voor Taxonomische Zoölogie of the University of Amsterdam, coached by the enthusiasm of Prof. Dr. J. H. Stock, has been working on both systematic and ecological problems of fresh and brackish water amphipods. As a young member of this team, I collected some gammarids in the western Pyrenees in 1968. While studying this material it became clear, that *E. berilloni* (Catta) was not only a very variable species, as already noticed by Spandl (1926) and Margalef (1956), but in reality a collective name for a group of closely related species, each variable in itself. This resulted in the description of a new species, *E. aquilifer*. Pinkster, 1969, and likewise it was the start for a more intensive study of the subject.

One of the most fertile methods to solve systematic problems, especially when a group of variable species is involved, is to sample systematically and intensively in the area inhabited by the group in question. In doing so variability within and between various populations of one species, as well as interspecific differences may become clear. Consequently systematic sampling has been done, in the years 1969, 1970 and 1971, in all drainage systems of the Iberian peninsula (see map I) and in many parts of France (Pinkster et al., 1970; Pinkster & Stock, 1971).

Since morphological characters are changing during the development, and consequently, various stages of different species often are very much alike (see Dennert et al., 1969), sexually mature specimens can be used only. In order to obtain more information about the ecology of the different members of the group, analyses of water samples were made at nearly every station for the factors temperature, pH, chlorinity and calcium

ion concentration. Moreover, the width and depth of the streams inhabited, bottom type, vegetation, and degree of pollution were noted.

As a result of this systematic inventarisation, it became clear that the name *E. berilloni*, as used up to 1969 (see Pinkster, 1969), in reality is the collective noun for a group of at least 10 closely related, but distinct forms. Nine of these species are restricted to rather small areas in the northern half of the Iberian peninsula or the adjacent part of France. Only one species, *E. berilloni* s.str. has a much wider distribution, inhabiting the middle reaches of streams and rivers in France, the Channel Islands, Belgium, Luxembourg, the southern part of the Netherlands and south-western Germany. In Spain the species seems to be restricted to a rather narrow zone along the north-west coast.

In spite of our intensive sampling, no members of the *E. berilloni*-group were found in the southern part of the Iberian peninsula. In this area they seem to be completely replaced by members of the African *E. simoni*-group (Pinkster & Stock, 1972).

In this paper complete descriptions of all members of the *E. berilloni*-group and a key for their identification are given. The distribution of the various species is discussed and illustrated in maps, and where possible, notes are given on the variability and the ecological range of the different species. In a final chapter, the distribution of all groups of amphipods inhabiting inland waters in the Iberian peninsula and its zoogeographical aspects are discussed.

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THE CHARACTERS OF THE *ECHINOGAMMARUS BERILLONI*-GROUP

Stock (1968) and Pinkster & Stock (1972) summarized the most important characters discriminating the *Echinogammarus pungens*-group and the *E. simoni*-group from other representatives within the genus *Echinogammarus*. In this paper species are treated which are all closely related to, or confused with, *Echinogammarus berilloni* (Catta), and are defined by the following characters: (1) the eyes are large and elongate; (2) the hands of the first gnathopods are much smaller than those of the second; (3) all legs are armed with groups of setae, sometimes accompanied by some smaller spines; (4) the carpus of the second leg is always much shorter than the propodus; (5) the segments of both metasome and urosome are armed with spines and groups of, often very long, setae; (6) calceoli are always absent; (7) the first segment of the mandible palp is always unarmed, the third segment always bears a regular comb-like row of setae. These characters also occur in the females, although less pronounced than in the males. Although in some species (e.g. *E. calvus* and *E. echinosetosus*) characters (3) and (5) are less pronounced than in most other members of this group and tend to become intermediate between this group and the *Echinogammarus pungens*-group, I still believe, after weighing the various characters against each other that the members of the *E. berilloni*-group can be distinguished from the other species-groups within the genus *Echinogammarus*.

Considering the characters cited above, *Echinogammarus pacaudi* (Hubault & Ruffo, 1956) should be placed within this group of species, but the dorsal ornamentation of the metasome, very characteristic by its sharp, teeth-like projections, makes this species so different from all other species within the genus *Echinogammarus* that I prefer to separate it as a special group. When reading the description of *E. klaptoczi ebusitanus* Margalef, 1951, one hesitates as to whether this form should be placed within the *E. berilloni*-group or not. Examination of the type material provided the answer to this problem. The taxon

ebusitanus cannot be included in the *berilloni*-group because of the long, elongate carpus of the second leg, a character shared by the genus *Eulimnogammarus* and the *Echinogammarus simoni*-group.

THE VARIABILITY OF CHARACTERS

The original idea of *Echinogammarus berilloni* (Catta) being an extremely variable species does not hold after the present study. Of course, each of the 10 species in which the old „*berilloni*” is subdivided, is quite variable in some characters but not in others. Moreover, and this is probably the greatest difficulty in this group, the characters may change in the course of the development and growth. So the most characteristic features are found in the setation of the antennae, the legs, the metasome, urosome and epimeral plates. However, the number and length of setae increase with age and become fully characteristic only when the animal is full-grown. Younger stages are often very hard to distinguish. The same holds true for females of all species in the *E. berilloni*-group, not only because of the absence of discriminating setae, but likewise because of the characteristic spines on the hands of the gnathopods.

Therefore, all discussions concerning the specific characters and their variability are valid for adult males only.

Stable characters are the shape of the eyes, the setation of the second antenna, the absence of calceoli, the structure of the mandible palp, the presence or absence of medial palmar spines on the hands of the gnathopods, the morphology of the legs, the shape of the inner ramus of the third uropod, and the presence or absence of groups of setae on the dorsal surface of the telson, on the metasome and urosome segments (the number and length of these setae is less stable, however).

Furthermore variability can be observed in

- 1) The number of segments in the flagellum of the antennae.
- 2) The shape of the epimeral plates of the pleon; the angle of the ventroposterior corners can vary largely (see also Roux, 1967; Stock, 1968; Pinkster, 1970).
- 3) The number of spines participating in the armature of the telson. In some populations subbasal spines are present, in others they are absent. Even in a single specimen differences can be found between the contralateral telson lobes (see also Stock, 1968; Pinkster, 1970).
- 4) The number of spines on the metasome and

urosome segments.

- 5) The number of setae on the legs; in general, this number increases with age.

KEY TO THE SPECIES OF THE *ECHINOGAMMARUS BERILLONI*-GROUP. BASED ON ADULT MALES ONLY.

- 1 a) Peduncle segments 4 and 5 and flagellum of A2 provided with long, slightly curved setae, forming a flag-like brush. Hand of both first and second gnathopods without medial palmar spines
Echinogammarus meridionalis n. sp.
- b) These characters not combined 2
- 2 a) Flagellum of A2 provided with long setae forming a flag-like brush 3
- b) Flagellum of A2 armed with solitary setae only, never forming a flag-like brush 4
- 3 a) Dorsal surface of metasome and urosome armed with numerous hooked spines. Hand of first and second gnathopods armed with a medial palmar spine. Live specimens with vertical dark stripes
Echinogammarus zebrinus Pinkster & Stock, 1971
- b) Dorsal surface of metasome and urosome armed with small tufts of short setae only. Hand of second gnathopod without medial palmar spine. No vertical stripes
Echinogammarus aquilifer Pinkster, 1969
- 4 a) Setae on the peduncle segments of A1 and A2 longer than the diameter of these segments
Echinogammarus feminatus n. sp.
- b) Setae on the peduncle segments of A1 and A2 shorter than, or as long as, the diameter of these segments 5
- 5 a) Metasome and urosome covered with clusters of long, curved setae with small spines in between them. Epimeres with long setae along the ventral and posterior margins, as well as on the lateral surface
Echinogammarus berilloni (Catta, 1878)
- b) Metasome armed with small spines only, urosome with a few tufts of setae. Epimeres with setae along the ventral and posterior margins only 6
- 6 a) P1 to P7 set with many groups of very long setae. In P5 to P7 these setae are always much longer than the diameter of the segments on which they are implanted. Urosome segments with some groups of very long setae 7
- b) Setae on P1 and P7 short, in P5 to P7 always shorter than the diameter of the segments on which they are implanted. Urosome segments with short setae 8
- 7 a) The setae implanted along the external margin of the exopod of Ur3, are many times longer than the diameter of the exopod. The setae on the hand of the gnathopods are very long
Echinogammarus longisetosus n. sp.
- b) The setae implanted along the external margin of the exopod of Ur3, are about as long as the diameter of the exopod. The setae on the hand of the gnathopods are short
Echinogammarus tarragonensis n. sp.
- 8 a) Epimeres 2 and 3 with very long setae along the lower margin; their posterior margin and lateral

surface unarmed. Telson lobes elongate, more than 1.5 times as long as wide, their dorsal surface never armed with setae

Echinogammarus calvus (Margalef, 1956) new rank.

- b) Epimeres 2 and 3 with small groups of short setae both along the ventral and posterior margins and often on the lateral surface. Telson lobes short, less than 1.5 times as long as wide, their dorsal surface with one or more groups of short setae 9
- 9 a) A large species, adult male 18 mm. Hand of second gnathopod large, with a swollen lower portion. Flagellum of A1 very long, normally with more than 35 segments. Setae on legs, telson, and dorsal surface of metasome and urosome short, almost spiniform. Setae along the lower margin of the third segment of the mandible palp implanted in a comb-like way with some longer setae in between them; inner surface of the second segment without setae.

Echinogammarus echinosetosus n. sp.

- b) A small species, adult male 10–11 mm. Hand of second gnathopod rather small. Flagellum of A1 short, always less than 20 segments. Second segment of mandible palp with some setae on the inner surface; third segment with regular comb-like setae along the lower margin, increasing in length towards the distal end

Echinogammarus margalefi n. sp.

DESCRIPTIVE PART

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

Echinogammarus berilloni (Catta, 1878).

Figs. 1–3, 4 G-H

Principal references. —

Gammarus berilloni Catta, 1878 : 68, fig. 1; Chevreux, 1896 : 29, figs. 1–3; Margalef, 1953 : 193, fig. 235.

Gammarus (Echinogammarus) berilloni; Schellenberg, 1942 : 36–37, fig. 19; Stephensen & Hynes, 1953 : 301.

Echinogammarus berilloni; Chevreux & Fage, 1925 : 259, fig. 269; Boecker, 1926 : 5–8; Vandel, 1926 : 35–39; Spandl, 1926 : 128–132, figs. 1–4; Le Roux-Legeux, 1927 : 34–43; Legeux, 1927 : 67–68; Pacaud, 1944 : 36–44; Margalef, 1944 : 202–206, figs. 7–9; Pacaud, 1952 : 101–103; Holthuis, 1956 : 83–95, fig. 8; Hoffmann, 1963 : 96–98, figs. 29–37; Vincent, 1964 : 809; Vincent, 1967 : 2248; Pinkster, 1969 : 137–150; Margalef, 1970 : 169; Pinkster & Stock, 1971 : 37–51; Vincent, 1971 : 1–131, fig. A; Gras & Maasen, 1971 : 54–55.

Material examined. —

More than 500 samples from the entire distribution area (see Map II).

Description. —

A redescription of this species was already given by the present author in 1969. Since *E. berilloni* is considered the ancestor of this species-group, the most important characters will be summarized.

Male: A large species, maximum length observ-

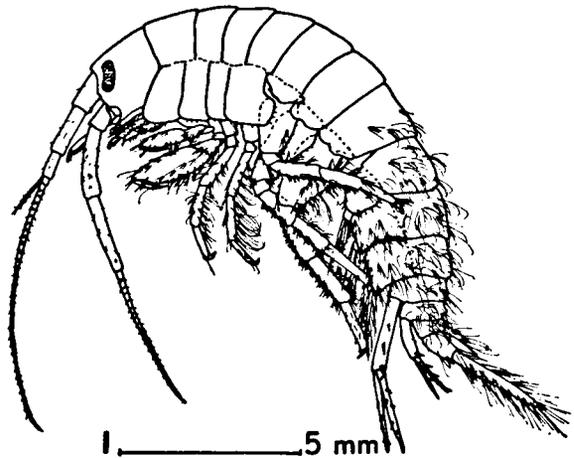


Fig. 1. *Echinogammarus berilloni* (Catta, 1878), habitus of a male from the neotype locality (scale 1).

ed about 20 mm. In general appearance, the species makes a slender impression (fig. 1). The lateral lobes of the head are truncated. The eyes are reniform, more than twice as long as wide. Both the first and second antennae are long, very slender without characteristic setation. Their flagelli have 32 to 40, and 18 to 22 segments, respectively.

The mandible palp has an unarmed first segment; the inferior margin of the third segment is armed with a row of spinules, subequal in length.

The first gnathopod has a piriform hand with a very oblique palm (fig. 2A). A strong medial palmar spine, clearly separated from the palmar angle spines, is always present. The hand of the second gnathopod is stronger than the first (fig. 2B). Its oblique palm is also provided with a strong medial palmar spine. The fifth to seventh legs are very characteristic. In these legs, the anterior margin of basis, merus and carpus are armed with densely implanted tufts of short setae, the number of them increasing with age. The posterior margin of basis and merus, as well as the lateral surface of the basis, is set with groups of very long setae, increasing in length and number from P5 to P7 (see fig. 2C).

Uropod 1 extending as far as, or slightly farther than, uropod 2. The inner and outer rami of uropods 1 and 2 are almost equal in length. They are armed with a variable number of spines (see figs. 4G, H).

Uropod 3 has a very short endopodal segment. The exopod is armed with clusters of setae (sometimes intermixed with 1 or 2 spines) on the inner

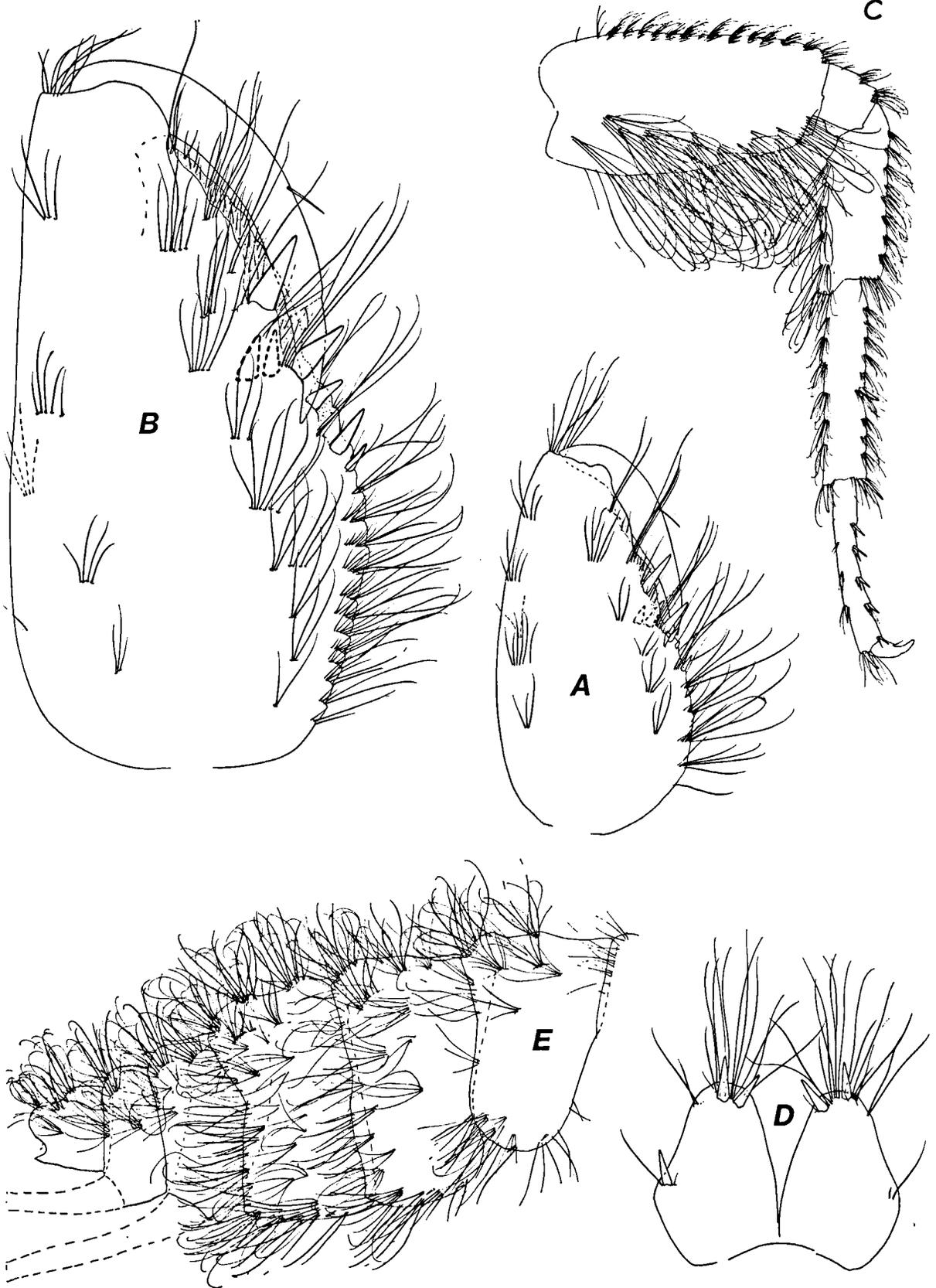


Fig. 2. *Echinogammarus berilloni* (Catta, 1878), ♂, from the neotype locality. A, hand of first leg (scale III); B,

hand of second leg (II); C, seventh leg (II); D, telson (III); E, plesome and urosome (II).

and outer margin. The second segment of the exopod is reduced and is as long as the terminal spines (see fig. 3H).

The telson is a little shorter than the peduncle of uropod 3; each lobe bears a lateral group of 1 spine (rarely lacking) and 2 to 3 setae, and an apical group of 1 to 3 spines and many long setae; its dorsal surface is never armed (fig. 2D).

The metasome segments, urosome segments and the epimeral plates are armed with clusters of long, very often curved setae, sometimes with small spines in between them. Almost invisible underneath these setae, the meta- and urosome segments bear a dorsal hump (fig. 2E).

Female: Smaller than the male (maximal length observed after examination of about 500 samples: 16 mm). Like in other groups of amphipods, there exists a clearly marked sexual dimorphism. So, the setation on the peduncle segments of both A1 and A2 is more strongly developed than in the male (figs. 3A and 3B). The hand in gnathopods 1 and 2 is less developed and has an almost transverse palm, without the medial palmar spine usual for the male (for figures see Pinkster, 1969). For the remainder, it can be stated that the characters found in the male are less pronounced in the female. So, the number of setae on the metasome, the urosome, and especially on the basal segments of P5 through P7 is much reduced (see Pinkster, 1969, and fig. 3J).

Immature: In general the setation of the legs is less developed in juveniles; the number of segments in the antennae is still low and the armature of the dorsal surface of metasome and urosome consists of small spines and short setae only. During the course of the development, the setae grow out to obtain their characteristic appearance at the age of sexual maturity (see figs. 3D through 3K). The medial palmar spine of P1 can be absent in very young males (fig. 3C).

Variability. — In general the variability pattern is similar to that discussed in a previous chapter.

Ecology. — *E. berilloni* is a species from the middle courses of streams and rivers in a large area of western Europe. When estuarine species are absent, such as *Gammarus chevreuxi*, e.g. in certain places in north-western Spain, it is sometimes able to penetrate into the estuarine region of river systems. Throughout its distribution area the

species has never been found in upper reaches of streams. Although there is no indication for a strong interspecific competition, the species is always replaced by other members of the family Gammaridae in the upper reaches, viz. *E. aquilifer* in the western parts of the Pyrenees, *E. calvus* in the spring zone of the Río Ebro, *Gammarus duebeni* in the western part of Brittany (Bretagne), and members of the *G. pulex*-group in the rest of Europe.

In the Nive, a stream that originates on the top of Mont Mondarrain (France, dépt. Basses-Pyrénées) — the type locality of *E. berilloni* — only *E. aquilifer* was found in the narrow fast running upper stretch of the river; as soon as the stream gets wider, *E. berilloni* appears. The zone of overlap, about 4 km long, points to the absence of severe competition between the two species (see also Stock et al., 1966; Pinkster et al., 1970; Gras & Maassen, 1971).

Vincent, 1971, in his thesis, comes to the conclusion that low temperatures and a low concentration of Ca-ions are limiting factors for this species. This view is supported by ecological data collected in the mid-western parts of France and by many laboratory experiments. In the region prospected by Vincent, *E. berilloni* was never found in waters in which the amount of Ca-ions was lower than 15 mg/l. In his experiments Vincent proved that at lower temperatures (4° C), *E. berilloni* was unable to recompensate the loss of Ca-ions during the moult, when the outside concentration of Ca-ions was below 20—25 mg/l. At higher temperatures (15° C) the minimum outside concentration of Ca-ions, necessary to harden the carapace, was considerably lower (6 mg/l).

This interaction between the hardness of the water and its temperature certainly helps to explain the absence of *E. berilloni* in spring areas of the rivers in the western Pyrenees, such as on the top of Mont Mondarrain. However, it does not explain the distribution pattern of this species in western France, e.g. its presence in regions such as Brittany (Bretagne) and its absence in the water system of the rivers Vilaine and Loire. In western Brittany very dense populations of *E. berilloni* have been found in very soft waters, even with less than 6 mg Ca/l (see Pinkster et al., 1970). On the other hand, *E. berilloni* has not been found (Gras & Maassen, 1971) in the drainage systems of the rivers Vilaine and Loire, where high amounts of Ca-ions are available and the yearly changes in temperature are rather moderate. *E. berilloni* is

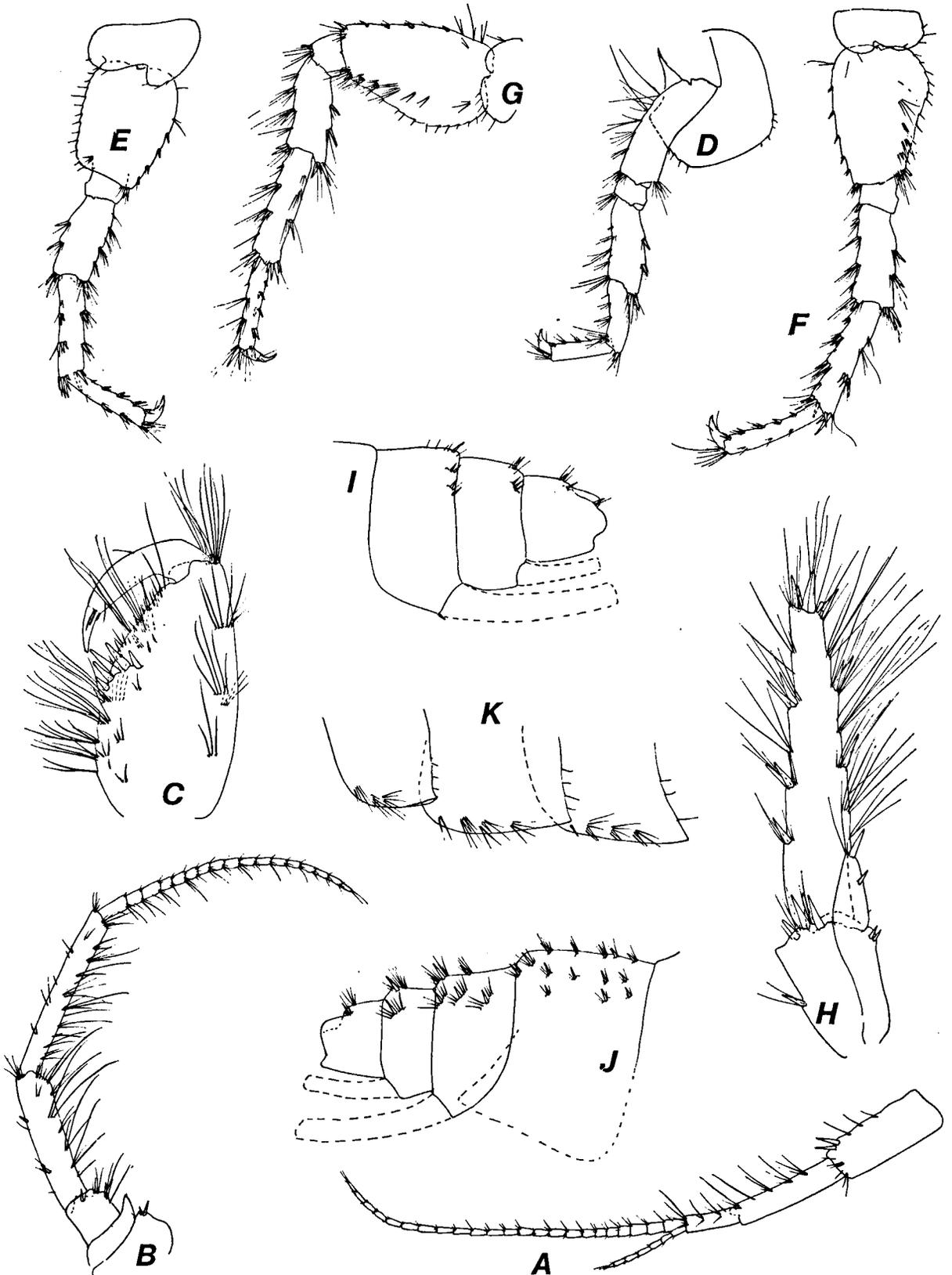


Fig. 3. *Echinogammarus berilloni* (Catta, 1878), A, B, and J, ♀, from the neotype locality; C—K, juvenile from the neotype locality. A, first antenna (scale II); B, second antenna (II); C, hand of first leg (III); D, fourth leg (II);

E, fifth leg (II); F, sixth leg (II); G, seventh leg (II); H, third uropod (III); I, urosome (II); J, urosome (II); K, epimeral plates (II).

also absent from certain parts of Les Landes (S.W. France).

In the light of the results of Vincent and our own field observations, we must assume that in *E. berilloni*, as in other gammarid species (e.g. *Gammarus pulex*, see Vincent, 1971) physiological races occur, adapted to waters with high or with low amounts of Ca-ions. The same holds true for the factor pH. In exploring western Europe, members of our research team found *E. berilloni* in waters varying in pH from 4.5 (in Bretagne) to 8 (localities in the Vendée) (Pinkster & Stock, 1970; Gras & Maasen, 1971).

The occurrence of *E. berilloni* in the estuarine part of some rivers in north-western Spain and underneath pebbles on sandy beaches (near Playa de San Antolin, Spain, Prov. Oviedo) are an indication that the species can stand rather high salinities as well as considerable changes in salinity. This was confirmed by experiments of Vincent, 1971, showing that *E. berilloni* behaved "normally" in more concentrated media, up to 80% sea-water (= approx. 24.8‰ S, or 15.680 mg Cl/l).

From samples from all parts of western Europe it became clear that this species can withstand a substantial amount of organic pollution and high temperatures. In some parts of Spain it has been found in waters having summer temperatures around 31° C.

Distribution. — *E. berilloni* is known from the north-western part of Spain (see Map III; own exploration); the western part of the Pyrenees; those parts of France which drain into the Atlantic, except for the higher Plateau Central and the drainage systems of the Loire and Vilaine (see map II; own exploration); the Channel Islands (own exploration); Belgium (Stephensen & Hynes, 1953); Luxembourg, (Hoffmann, 1963); the south-eastern provinces of the Netherlands (Holthuis, 1956); the south-western parts of the German Federal Republic (Boecker, 1926; Schellenberg, 1942; Besch, 1968). In spite of intensive exploration outside this area by the present author and other members of the research team of the Institute of Taxonomic Zoology of the University of Amsterdam, the species has never been found outside this area (see Map II).

Echinogammarus calvus (Margalef, 1956) new rank.

Figs. 4 A-F

Gammarus berilloni subsp. *calvus* Margalef, 1956 : 33, fig. 2.

Echinogammarus berilloni subsp. *calvus*; Margalef, 1970 : 170, figs. 2 A, B.

Material examined. —

Spain

prov. Santander:

- Río Ebro, W. of Reinosa, 5-VII-1969, rather fast running stream, Cl 7 mg/l, Ca 36 mg/l, many specimens (ZMA).
- Springs of the Ebro in Fontibre, 5-VII-1969, Cl 2 mg/l, Ca 18 mg/l, many specimens, many of them in precopulation (ZMA).
- About 20 m downstream of the springs of the Río Ebro, 5-VII-1969, Cl 2 mg/l, Ca 18 mg/l, many specimens (ZMA).
- Tributary of Río Besaya, near village Arenas de Iguña (halfway Reinosa and Torrelavega), 16-VII-1969, shallow, about 3 m wide, Cl 15 mg/l, Ca 66 mg/l, Ca + Mg 54 mg/l, many specimens (ZMA).
- Río Saja, S. of Renondo (= S. of Cabuérniga), 5-VII-1969, large, fast running river, Cl 8 mg/l, Ca 18 mg/l, Ca + Mg 0 mg/l (ZMA).
- Cascade in tributary of the Río Saja, on road C 625, 14 km S. of Cabuérniga, 5-VII-1969, clean, fast running, Cl 7 mg/l, Ca 8 mg/l, many specimens, many of them in precopulation (ZMA).
- Upper reaches of Río Besaya, near village Lantuene (= N.E. of Reinosa), 16-VII-1969, 40–50 cm wide, bottom of lime-concretions, Cl 7 mg/l, Ca 82 mg/l, many specimens (ZMA).

prov. Burgos:

- Río de Riaza, on road N 122 near Fuentecén Aranda del Duero, 20-VI-1970, fast running, clear, 30 cm—1 m deep, 10 m wide, temp. 13.4°C, pH 6.5, Ca 57 mg/l, Cl 11 mg/l, many specimens, many of them in precopulation (ZMA).
- Small brook in Quintanaelez (on road Pancorbo-Oña), 5-VII-1969, Cl 9 mg/l, Ca 50 mg/l, many specimens (ZMA).
- Tributary of the Ebro near Quintana de Valdivielso (= S.W. of Medina), 5-VII-1969, Cl 7 mg/l, Ca 84 mg/l, many specimens (ZMA).
- Nameless tributary of Río Arlanzon, W. of Las Quintanillas, 21 km W. of Burgos, about 3 m wide, Cl 12 mg/l, Ca 62 mg/l, many specimens, many of them in precopulation (ZMA).
- Río Pisuerga on road N 120 near village Melgar de Fernamental, 16-VII-1969, more than 20 m wide, Cl 8 mg/l, Ca 78 mg/l, many specimens (ZMA).
- Tributary of Río Arlanzon near village Sarracín (7.5 km S. of Burgos), 3 m wide, Cl 20 mg/l, Ca 74 mg/l, 16-VII-1969, many specimens (ZMA).
- Río Hormazuela, near village Villanueva de Arganó, on road N 120, 16-VII-1969, about 3 m wide, Cl 6 mg/l, Ca 86 mg/l, many specimens (ZMA).

prov. Logroño:

- Río Najerilla, about 5 km S. of Najera (along road C 113), major river, 16-VII-1969, Cl 2 mg/l, Ca 50 mg/l, many specimens (ZMA).
- Río Najerilla, S. of village Bobadilla (near road C 113), 16-VII-1969, large river, Cl 6 mg/l, Ca 28 mg/l, 20 specimens (ZMA).
- Río Tiron, near road N 232 and village Tirgo (= S.W. of Haro), 16-VII-1969, major river, deep, Cl 15 mg/l, Ca 134 mg/l, many specimens (ZMA).
- Río Oja near village Casalaceina on road N 232 (S.W. of Haro), 16-VII-1969, large river, Cl 9 mg/l,

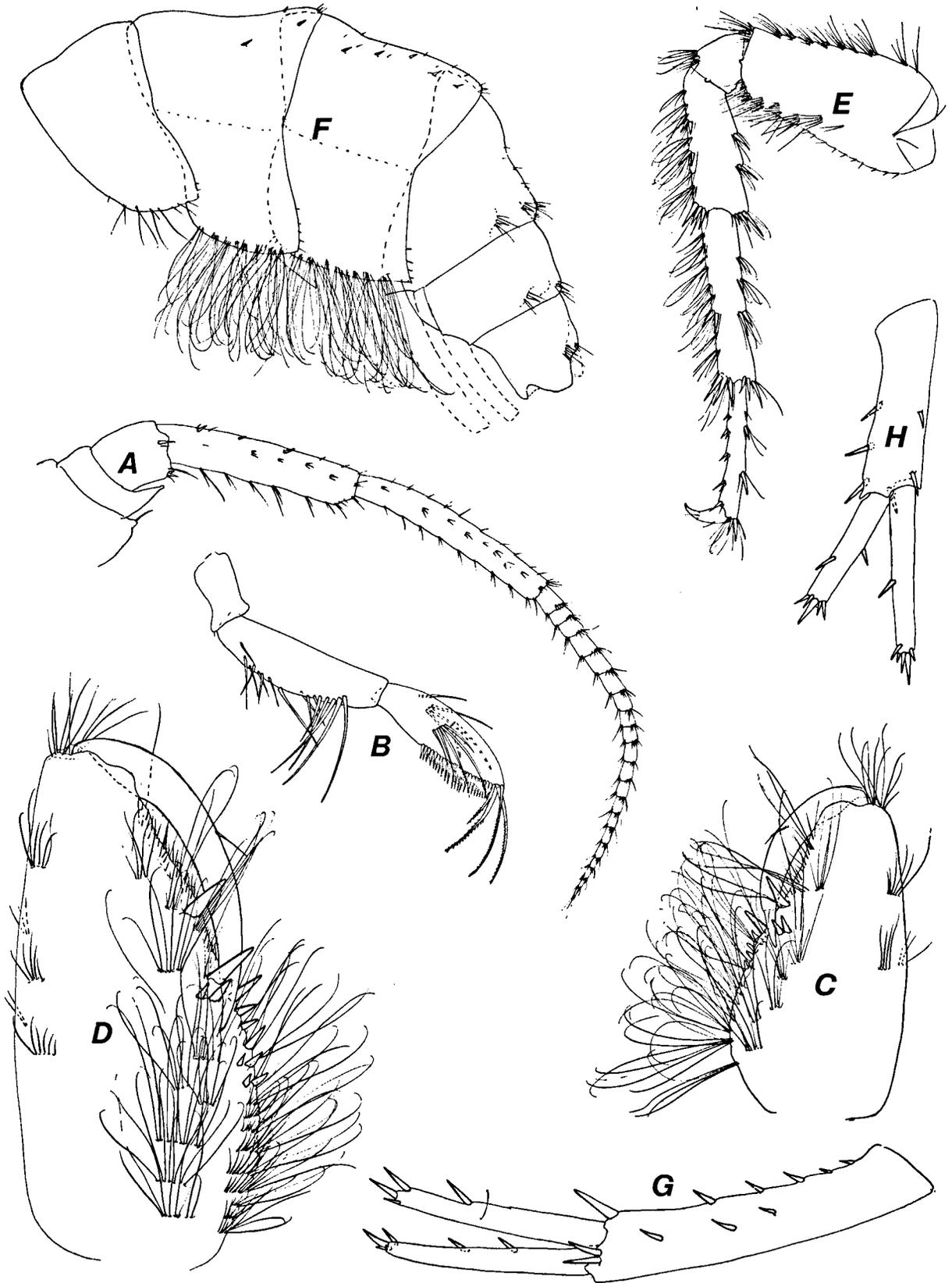


Fig. 4 A—F. *Echinogammarus calvus* (Margalef, 1956), ♂, from the sources of Río Ebro. A, second antenna (scale II); B, mandible palp (III); C, hand of first leg (III); D, hand of second leg (III); E, seventh leg (II);

F, pleosome and urosome (II). G—H. *Echinogammarus berilloni* (Catta, 1876), ♂, from the neotype locality. G, first uropod (scale II); H, second uropod (II).

Ca 34 mg/l, many specimens (ZMA).

prov. Vizcaya:

- Nameless confluent, 0.5 km E. of Bolivar (= 3.5 km S.W. of Marquina), 17-VII-1969, 2—3 m wide, fast running, Cl 14 mg/l, Ca 58 mg/l, many specimens (ZMA).
- Tributary of the Río Butrón, near village Gámiz (= N.E. of Bilbao), 17-VII-1969, stagnant, deep, Cl 22 mg/l, Ca 84 mg/l, 15 specimens (ZMA).

prov. Alava:

- Río Omecillo, S. of Espejo, 4-VII-1969, few specimens (ZMA).
- Río Araya, 2 km S. of Araya, about 30 km E. of Vitoria, 15-VII-1969, about 3 m wide, slowly running, Cl 5 mg/l, Ca 84 mg/l, many specimens (ZMA).
- Río Bayas, S. of Subljana, 4-VII-1969, Cl 9 mg/l, Ca 72 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. longisetosus* (see table I).

prov. Palencia:

- Río Pisuerga near village Olleros, 16-VII-1969, large river, about 10 m wide, deep, Cl 7 mg/l, Ca 82 mg/l, many specimens (ZMA).

prov. Vitoria:

- Spring area of Río Deva near Sallnas de Léniz (N. of Vitoria), 4-VII-1969, moderately fast running, Cl 68 mg/l, Ca 120 mg/l, many specimens (ZMA).

prov. Valladolid:

- Tributary of Río Duero, W. of Fuensaldana, near Valladolid, 5-IX-1970, slowly running, clear, 30 cm deep, 50 cm wide, temp. 20.8°C, pH 6, Cl 188 mg/l, Ca 16 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *Gammarus gauthieri*.

Description. —

Male: large, largest specimen observed 20 mm long. The shape and size of the eye, the shape of the head and the morphology of the antennae and mouth parts are almost identical to those of *E. berilloni* (for figures see Pinkster, 1969, and present paper figs. 4 A, B). The first gnathopod (fig. 4C) differs slightly from those in *E. berilloni*, in that the setae, implanted on the lateral surface of the propodus, are much longer. The same applies to the second gnathopod (fig. 4D).

The third and fourth legs closely resemble those of *E. berilloni* except for the setation which is a little shorter.

The fifth through seventh legs are fundamentally different from those in *E. berilloni* in the number and length of the setae, found on the basal segments: the long setae, implanted on the posterior margin of this segment, characteristic for *E. berilloni*, are completely absent in *E. calvus*. Instead of the many groups of long setae, which

are implanted on the basal segment of P7 in *E. berilloni*, only a few groups of short setae remain (fig. 4E).

The telson and third uropod resemble, both in shape and armature, those of *E. berilloni*.

The second and third epimeral plates show the most characteristic features for this species, since they have very long suspended setae along the ventral margin, while the lateral surface is completely unarmed. Along the posterior margin only a few setules occur (fig. 4F).

The urosome segments are armed with small spines and additional setae only (fig. 4F). The armature of the metasome segments is still more poorly developed. This baldness was a reason for Margalef (1956) to give this form the subspecific name *calvus*.

Female: The females of this species closely resemble those of *E. berilloni*.

Variability. — This species, originally described as a subspecies of *E. berilloni*, is a rather stable one. Although some features are variable to some extent as discussed in the previous section on variability, the discriminating characters, such as the armature of the epimeral plates, the absence of long setae on the dorsal side of the body and the setation of the legs, are very stable. Since both *E. berilloni* and this form are distributed in the same river system (Rio Ebro) showing a certain area of overlap (table I), and since no isolating mechanisms can be indicated, we believe that this form, like *Echinogammarus berilloni*, must be considered to be a good species: *Echinogammarus calvus*.

Distribution. — Up to now the species is known from a rather limited area in the northwestern part of Spain only (see map III).

Ecology. — *Echinogammarus calvus* is a species from the upper and middle reaches of rivers, where it seems to prefer rather fast running waters. The chlorinity and hardness (Ca concentration) of the waters inhabited seem to have little influence on the occurrence of the species. It was found in waters with Cl concentrations from 2 to 70 mg/l and with Ca concentrations from 8 to 134 mg/l. Neither the presence or absence of vegetation, nor the nature of the bottom seems to affect the animal since dense populations have been found under extremely varying conditions.

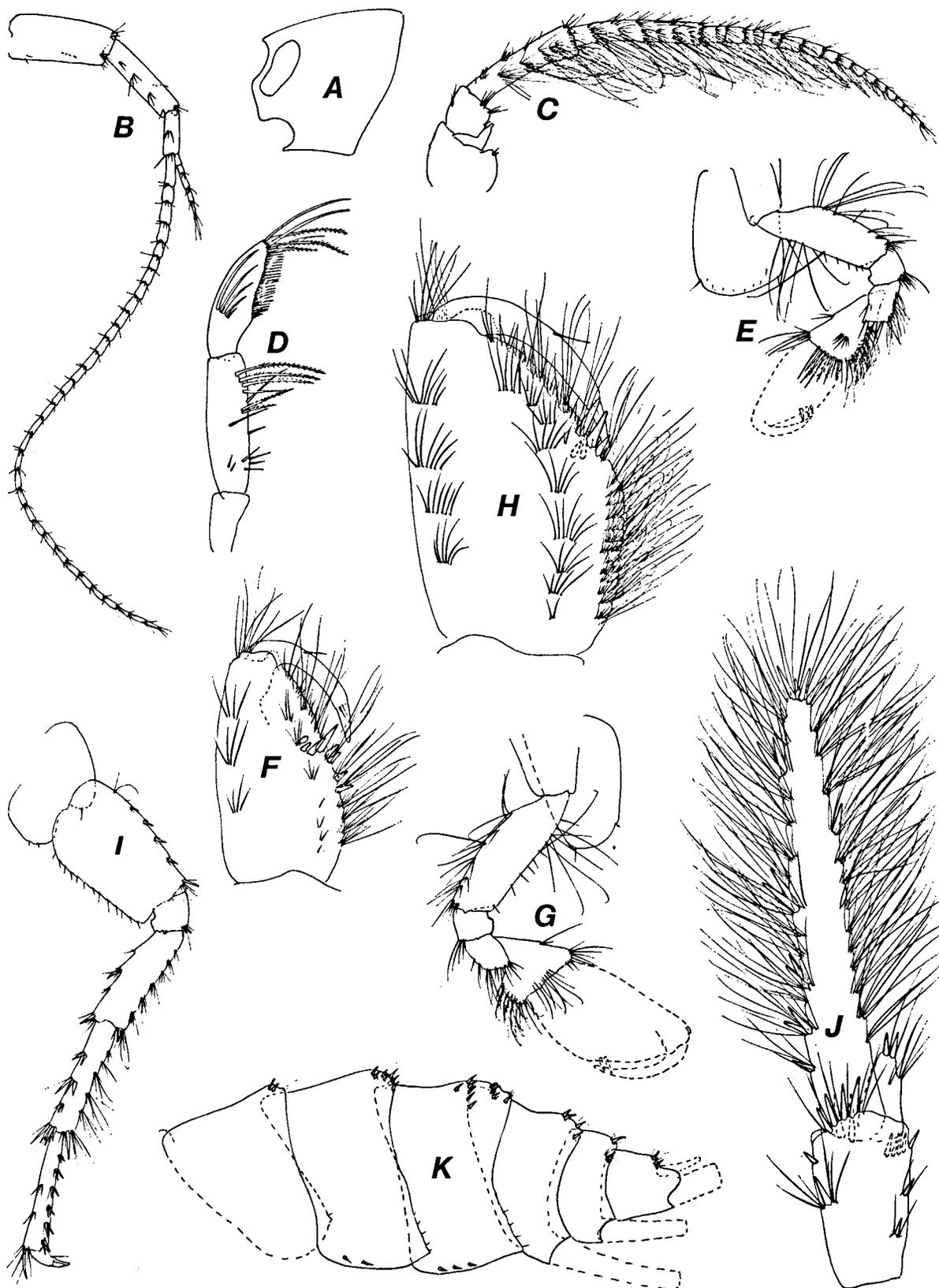


Fig. 5. *Echinogammarus meridionalis* n. sp., ♂, from the type-locality. A, head (scale II); B, first antenna (II); C, second antenna (II); D, mandible palp (III); E, first leg (II); F, hand of first leg (III); G, second leg (II); H, hand of second leg (III); I, fifth leg (II); J, third uropod (III); K, plesome and urosome (II).

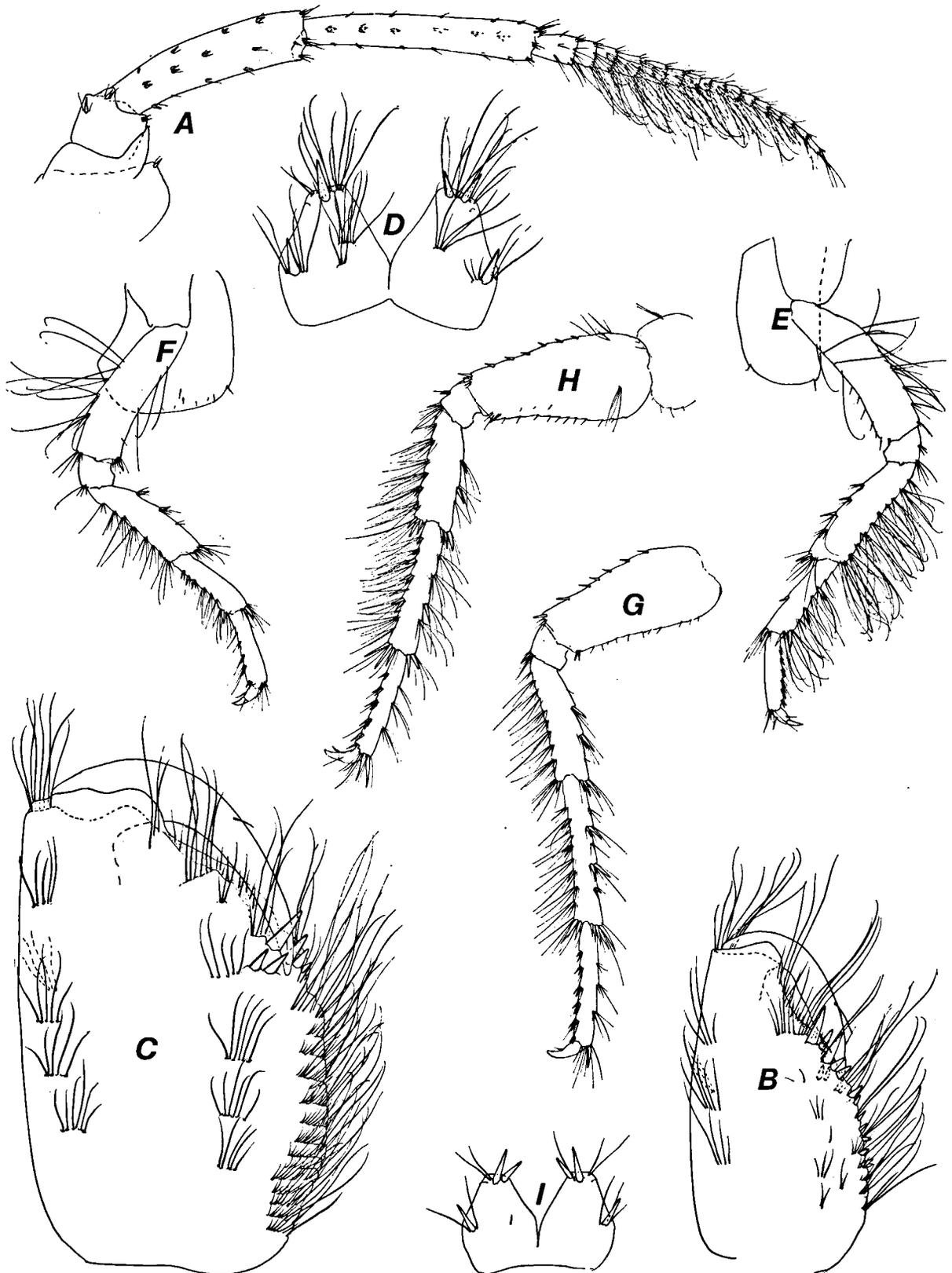


Fig. 6 A—D. *Echinogammarus aquilifer* Pinkster, 1969, ♂, from the type-locality. A, second antenna (scale II); B, hand of first leg (III); C, hand of second leg (III); D, telson (III).

E—I. *Echinogammarus meridionalis* n. sp., ♂ from the type-locality. E, third leg (II); F, fourth leg (II); G, sixth leg (II); H, seventh leg (II); I, telson (III).

Echinogammarus meridionalis n. sp.

Figs. 5, 6 E-I

Material examined. —

Portugal

prov. Leiria:

- Río Alcaide, on road N 243, near Alcaria, S. of Batalha, 25-VI-1970, slowly running, slightly polluted stream with gravel bottom, 5—30 cm deep, 10—200 cm wide, temp. 17°C, pH 6.0, Cl 15 mg/l, Ca 81 mg/l, many specimens, many of them in pre-copulation. Male holotype and many paratypes have been deposited in the Zoölogisch Museum Amsterdam (ZMA Amph. 103.027).
- Small brooklet near Valado, E. of Nazara, 25-VI-1970, slowly running, slightly polluted stream with sandy bottom, 20 cm deep, 2—3 m wide, temp. 17.5°C, pH 6.0, Cl 52 mg/l, Ca 13 mg/l, 2 specimens (ZMA).

Description. —

Male: A very characteristic species, a little smaller than *E. berilloni*. The largest male in the material examined measured 16 mm.

Head (fig. 5A) with truncate lateral lobes, and obtuse angles. The eyes are relatively large, with a deep dark colour in live specimens.

The first antenna (fig. 5B) resembles that of *E. berilloni*. Its accessory and main flagellum have 5 to 6 and 30 to 36 elements, respectively.

The extremely setose second antenna (fig. 5C) is by far the most characteristic feature of the animal, and makes the species clearly recognizable within this group. It is a little shorter than the first antenna. The flagellum is shorter than the slender peduncle, possessing 19 (18 to 20) segments in larger specimens. The distal half of the 4th and the entire 5th peduncle segments, both segments almost equal in length, are covered with transverse rows of long, slightly curved setae. The flagellum is likewise armed with densely implanted setae, diminishing in length towards the end. As a whole this setation makes the impression of a flag along the entire ventral margin of the antenna.

The mandible palp (fig. 5D) differs only from the one found in *E. berilloni* in having 6 long terminal setae on the third segment, instead of 4 to 5.

The elongate coxal plates 1 to 4 have rounded inferior corners, and bear very few setules along the lower margin. The hand of the first gnathopod (figs. 5E, F) has an oblique palm. Except for the normal groups of setae the armature consists of a transverse row of spines near the palmar angle and some smaller so-called "Stiftstacheln" only. The medial palmar spine is always absent. The

hand of the second gnathopod (figs. 5G, H) is stronger than that of the first. Its palm is less oblique than in *E. berilloni*. Like in the first leg, the medial palmar spine is always absent; a group of 5 spines is found near the palmar angle. The setae on the lateral surface of the propodus are short. The third and fourth legs are slender (figs. 6E, F), the setation on the third being longer than that on the fourth.

The basal segment of leg 5 (fig. 5I) has a backward protruding lobe. It is sparsely armed with some small spinules along the anterior and small setules near the posterior margin. The other segments bear few groups of spines and setae only, being rather short in comparison with other members of the *E. berilloni*-group. The sixth and seventh legs have a slender, elongate basal segment, likewise very poorly armed (figs. 6G, H). The setation of the distal segments is a little longer than in P5.

The uropods closely resemble those of *E. berilloni* (fig. 5J). The telson lobes are only little longer than wide. Each lobe bears a lateral group of 1 spine and some setae, and an apical group of 1 to 3 spines and 2 to 4 setae (fig. 6I).

As in *E. calvus*, the segments of the metasome and urosome are armed with some small spines and a small number of setules (fig. 5K) only. The first urosome segment shows a dorsal concavity ("saddle").

The epimeral plates are characterized by the absence of setation, and sharp postero-inferior corners (fig. 5K).

Female: Even more than in other species within this group, the female resembles the male. Although the flag-like setation of A2 is less developed than in the male, it still remains very characteristic.

Ecology and distribution. — Since the species was found in two localities only (map III), both in the province of Leiria, Portugal, we cannot give other information on its ecology than that mentioned under material.

Echinogammarus longisetosus n. sp.

Figs. 7-9

Material examined. —

Spain

prov. Navarra:

- Río Arga, 0.5 km upstream of Urtasun (= N.N.W. of Pamplona), 14-VII-1969, moderately fast running

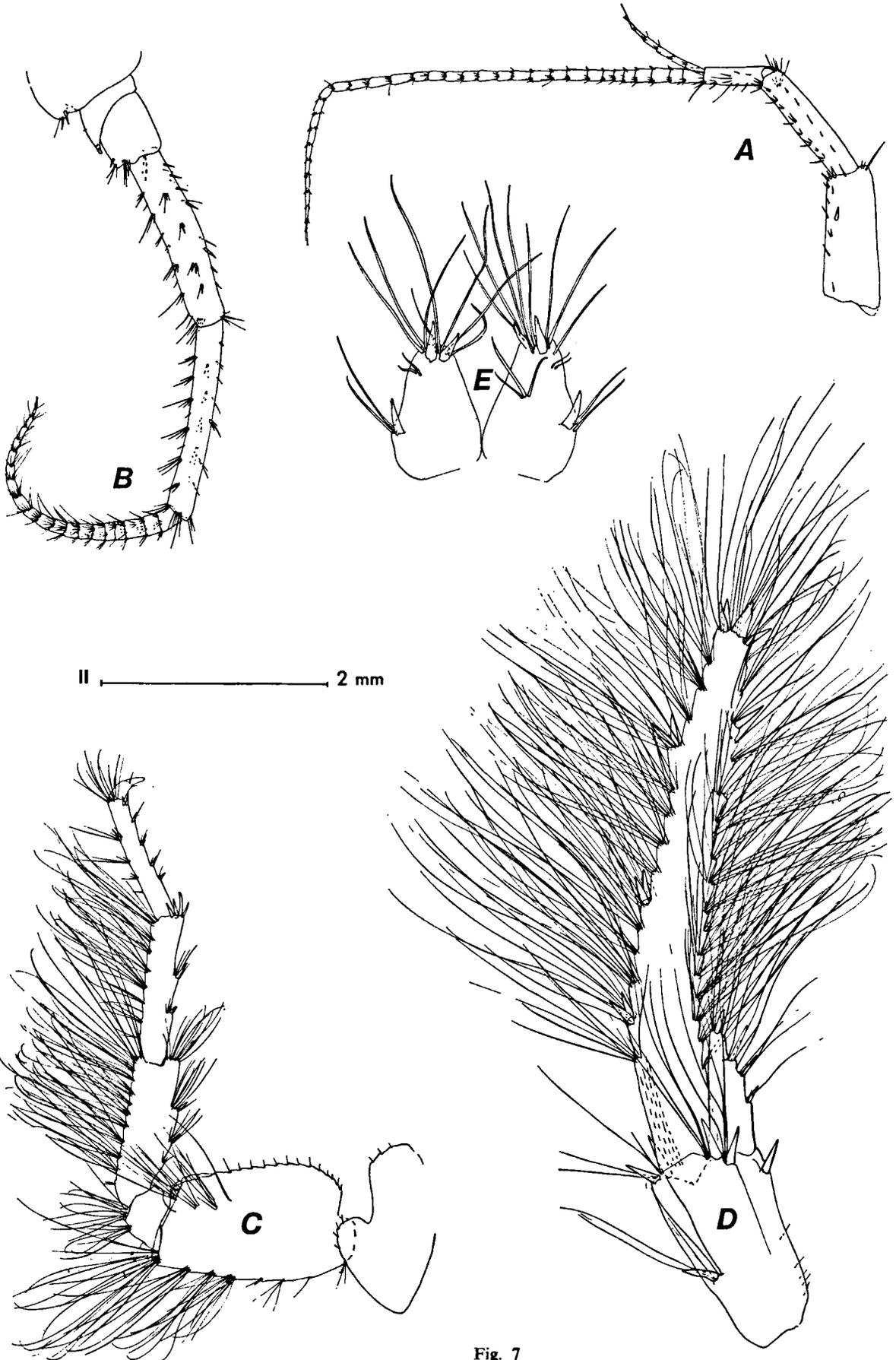


Fig. 7

- stream, gravel bottom, Cl 16 mg/l, Ca 56 mg/l, many specimens, many of them in precopulation. (The ♂ holotype, ♀ allotype, and many paratypes have been deposited in the Zoölogisch Museum Amsterdam, under cat. no. ZMA Amph. 103.025). Accompanying species: *E. berilloni*.
- Río Irati, near village Arrive, 14-VII-1969, polluted, moderately fast running stream, Cl 4 mg/l, Ca 54 mg/l, 4 juveniles (ZMA).
 - Erreca-Beltz alongside road N 121, about 21 km N. of Pamplona, 14-VII-1969, clear, moderately fast running stream, with stony bottom, 3 m wide, Cl 9 mg/l, many specimens (ZMA).
 - Río Ibur, near village Irurita, 15-VII-1969, clear, slowly running stream, with gravel bottom, Cl 16 mg/l, Ca 32 mg/l, 20 specimens (ZMA).
 - Río Leoz, on road N 121, about 3 km N. of Berasain, near Tafalla, 19-VI-1970, clear, fast running stream with stony bottom, temp. 16°C, pH 6.5, 20 to 30 cm deep, 1 m wide, Cl 20 mg/l, Ca 77 mg/l, many specimens, many of them in precopulation (ZMA).
 - Río Leoz, on road N 121, 1 km N. of Tafalla, 19-VI-1970, fast running, strongly polluted stream, with bottom of clay and stones, temp. 18°C, pH 6.5—7, Cl 18 mg/l, Ca 127 mg/l, 2 specimens (ZMA).
 - Río Alhama, 1 km N. of Cintruenigo, 19-VI-1970, slightly polluted, moderately fast running stream, with stony bottom, temp. 20°C, pH 6.6, Cl 300 mg/l, Ca 222 mg/l, 20 to 40 cm deep, 4 to 10 m wide, many specimens (ZMA).
 - Tributary of Río Araquil, about 4 km N. of Irurzun, on road N 240, 25-VIII-1968, 30 specimens (ZMA).
 - Confluent of Arroyo Artesiaga, S. of Irurita, 15-VII-1969, clear, fast running stream, with gravel bottom, 5 cm deep, 50 cm wide, Cl 9 mg/l, Ca 38 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. aquilifer*.
 - Tributary of Río Arga, about 10 km N.W. of Pamplona, on road N 240, 25-VIII-1968, Cl 17 mg/l, many specimens, many of them in precopulation (ZMA).
 - Río Arga, on road C 135 near Zubiri, 25-VIII-1968, Cl 6 mg/l, 15 specimens (ZMA).
 - Small brook, about 2 km W. of Aburrea Baja, 14-VII-1969, 1 to 1.5 m wide, stony bottom, Cl 4 mg/l, Ca 54 mg/l, many specimens, many of them in precopulation (ZMA).
 - Small brook between Aburrea Alta and Aburrea Baja, N.E. of Pamplona, 14-VII-1969, Cl 11 mg/l, Ca 100 mg/l, many specimens (ZMA).
 - Tributary of Río Salazar, about 2 km W. of Escaroz (about 28 km E. of Burguete), 14-VII-1969, about 1 m wide, stony bottom, Cl 5 mg/l, Ca 88 mg/l, 15 juveniles (ZMA).
- prov. San Sebastian:
- Tributary of Río Deva, upstream of village Mendaro, 4-VII-1969, polluted stream with stony bottom, Cl 11 mg/l, Ca 50 mg/l, many specimens (ZMA). Accompanying species: *E. berilloni*.
- Río Ursurian, near village Ursurian, 15-VII-1969, polluted stream, with stony bottom, about 1.5 m wide, Cl 11 mg/l, Ca 68 mg/l, 8 specimens (ZMA).
- prov. Alava:
- Río Bayas, S. of Subljana, 4-VII-1969, Cl 9 mg/l, Ca 72 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. calvus*.
 - Small brook near Tuesta, 4-VII-1969, about 1 m wide, with stony bottom, Cl 10 mg/l, Ca 74 mg/l, many specimens, many of them in precopulation (ZMA).
- prov. Burgos:
- Small brook, on road Pancorbo-Oña, W.N.W. of Fuenta, 5-VII-1969, 1 m wide, Cl 8 mg/l, Ca 84 mg/l, many specimens, many of them in precopulation (ZMA).
 - Río Oca, near Terminon, S.W. of Oña, 5-VII-1969, moderately fast running stream with clay bottom, 5 to 10 m wide, Cl 93 mg/l, Ca 154 mg/l, many specimens, many of them in precopulation (ZMA).
- prov. Zaragoza:
- Tributary of Río Piédra, 0.5 km N. of Monasterio de Piédra, 15 km S.E. of Alhama de Aragon, 13-VII-1969, clear, fast running stream, clay bottom, about 1 m wide, Cl 15 mg/l, Ca 98 mg/l, many specimens, many of them in precopulation (ZMA).
 - Tributary of Río Piédra, E. of Nuevalos, 13-VII-1969, clear fast running stream, with gravel bottom, about 1.5 m wide, pH 6.5, Cl 1 mg/l, Ca 182 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. echinosetosus*.
 - Tributary of Río Gallégo, near Zuera, 13-VII-1969, clear, fast running stream, gravel bottom, 5 cm deep, 30 cm wide, Cl 1 mg/l, Ca 128 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. berilloni*.
 - Tributary of Río Aragon, on road N 240, near Asoberal, 36 km W. of Jaca, 14-VII-1969, clear, moderately fast running stream, with gravel bottom, Cl 90 mg/l, Ca 102 mg/l, many specimens (ZMA).
 - Río Martín, near Escatron, 84 km E. of Zaragoza, 14-IV-1967, many specimens (MSNV).
 - Río Gallégo, near Zuera, 15-V-1967, many specimens (MSNV).
 - Small brook, about 7 km S.W. of Huesca, on road N 123, 13-VII-1969, clear, fast running stream with gravel bottom, about 10 cm deep, 80 cm wide, Cl 23 mg/l, Ca 92 mg/l, many specimens, many of them in precopulation (ZMA).
- prov. Rincón de Ademuz:
- Tributary of Río Turia, near village Las Santos, near crossing of roads N 420 and N 330, 38 km S. of Teruel, 11-VII-1969, clear, moderately fast running stream, with stony bottom, Cl 13 mg/l, Ca 80 mg/l, many specimens (ZMA).
- prov. Teruel:
- Río Guadalope, about 8 km S. of Alcañiz, near village Castelseras, 12-VII-1969, slightly polluted, moderately fast running stream, about 10 m wide, Cl 18 mg/l, Ca 52 mg/l, 12 specimens (ZMA).
 - Río Guadalopillo, about 24 km S.W. of Alcañiz,

Fig. 7. *Echinogammarus longisetosus* n. sp., ♂, from the type-locality. A, first antenna (scale II); B, second an-

tenna (II); C, fifth leg (II); D, third uropod (III); E, telson (III).

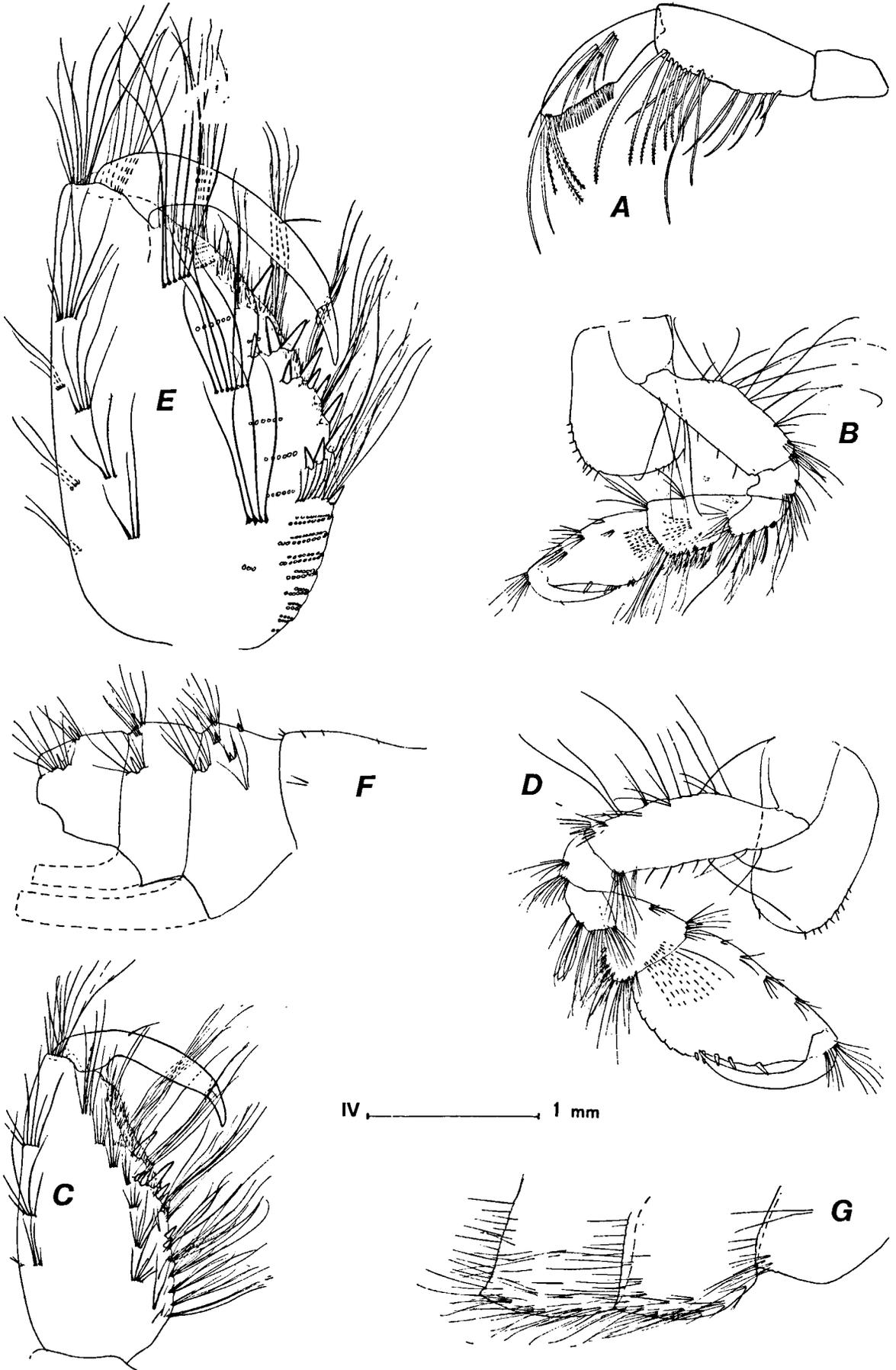


Fig. 8

- 12-VII-1969, rather fast running stream, with stony bottom, about 2 m wide, Cl 47 mg/l, Ca 208 mg/l, many juveniles (ZMA).
- Río Guadalopillo, 32 km S.W. of Alcañiz, 2 km S.W. of village Alcoriza, 12-VII-1969, rather fast running stream, with stony bottom, about 1.5 m wide, Cl 23 mg/l, Ca 110 mg/l, many specimens (ZMA).
 - Tributary of Río Esteruel, alongside road N 211 near village La Zoma, alt. 1100 m, about 14 km E. of Montalban, 12-VII-1969, clear, fast running stream with stony bottom, Cl 5 mg/l, Ca 60 mg/l, many specimens, many of them in precopulation (ZMA).
 - Río de Cabra, near village Castel de Cabra, 11 km E. of Montalban, 12-VII-1969, slightly polluted, moderately fast running stream, Cl 9 mg/l, Ca 98 mg/l, many specimens, many of them in precopulation (ZMA).
 - Tributary of Río Turia, S. of Libros, about 25 km S. of Teruel, 11-VII-1969, 1—2 m wide, gravel bottom, Cl 34 mg/l, Ca 84 mg/l, many specimens (ZMA). Accompanying species: *E. margalefi*.
 - Río Jiloca, near Caminreal, 12-VII-1969, clear, fast running stream, about 2.5 m wide, more than 2 m deep, pH 6.5, Cl 34 mg/l, Ca 110 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. echinosetosus*.
 - Río Mijares, near Mora de Rubielos, 7-V-1969, alt. 700 m, many specimens (MSNV).
 - Río Mijares, near Mora de Rubielos, 8-V-1967, many specimens (MSNV).
- prov. Barcelona:
- Ribeira Pontóns, 500 m E. of Pontóns, W. of Villafraanca del Panades, 16-IV-1971, slightly polluted, moderately fast running stream with stony bottom, 20 to 40 cm deep, 3 to 4 m wide, temp. 15.0°C, pH 5.0, Cl 85.7 mg/l, Ca 59.2 mg/l, many specimens, many of them in precopulation (ZMA).
 - Small brook in Sierra de Montsény, near Santa Fé de Montsény, alt. 1500 m, 3-V-1967, many specimens (MSNV).
 - Another small brook in Sierra de Montsény, near Santa Fé de Montsény, alt. 1500 m, 2-V-1967, many specimens (MSNV).
 - Small brook in Sierra de Montsény, alt. 1300 m, 3-V-1967, many specimens (MSNV).
- prov. Tarragona:
- Cemented well near Santa Creus, N.E. of Valls, 15-IV-1971, slightly polluted, moderately fast running, about 10 cm deep, temp. 14.4°C, pH 5.0, Cl 25 mg/l, Ca 104 mg/l, many specimens, many of them in precopulation (ZMA).
 - Río Gaya, 500 m S. of Aguamurcia, N.E. of Valls, 15-IV-1971, clear, moderately fast running stream with stony bottom, 50 cm deep, 2—4 m wide, temp. 17.4°C, pH 5.0, Cl 6 mg/l, Ca 104 mg/l, many specimens, many of them in precopulation (ZMA).
- prov. Gerona:
- Tributary of Río Fluvia, N. of Crespia, S. of Figueras, 18-IV-1971, clear, moderately fast running stream with gravel bottom, about 50 cm deep, 2—3 m wide, temp. 13.8°C, pH 5.0, Cl 22 mg/l, Ca 102 mg/l, 1 specimen (ZMA).
 - Río Fluvia, under bridge near Esponella, N.E. of Bañolas, 18-IV-1971, slightly polluted, fast running stream with stony bottom, 0.5 to 2 m deep, more than 10 m wide, temp. 16.2°C, pH 6.0, Cl 100 mg/l, Ca 138 mg/l, many specimens, many of them in precopulation (ZMA).
- prov. Lerida:
- Río Farfaña, at Castello de Farfaña, W. of Balaguer, 19-IV-1971, moderately polluted, moderately fast running stream with stony bottom, 50 cm deep, 1 m wide, temp. 16.2°C, pH 6.5, Cl 270 mg/l, Ca 198 mg/l, 20 specimens (ZMA).
 - Río Llobregos, at Pons, N.E. of Balaguer, 19-IV-1971, clear, moderately fast running stream with clay bottom, more than 1 m deep, 2 to 3 m wide, temp. 14.2°C, pH 6.0, Cl 93 mg/l, Ca 148 mg/l, many specimens, many of them in precopulation (ZMA).
 - Fontana de la Bargasses, well alongside road C 147, 4 km S. of Selles, S. of Tremp, 14-IV-1971, clear, moderately fast running stream with gravel bottom, about 5 cm deep, temp. 12.4°C, pH 6.0, Cl 6 mg/l, Ca 80.3 mg/l, many specimens, many of them in precopulation (ZMA).
 - Ribeira Noguera Ribagorzana, near Alfarras, N. of Lerida, 19-IV-1971, slightly polluted, slowly running stream with stony bottom, 50 cm deep, 4 to 5 m wide, temp. 15.1°C, pH 6.0, Cl 35 mg/l, Ca 95.9 mg/l, many specimens, many of them in precopulation (ZMA).

Description. —

Male: A medium large species; the maximum length observed after examination of 45 samples is 15 mm. In general the body is slender and resembles that of *E. berilloni*, although the arrangement of the setae is completely different.

The head (fig. 9A) has broadly rounded lateral lobes; sinus rather shallow. The eyes are subreniform in juveniles, elongate and narrow in older animals.

The first antenna has no striking differences as compared to that of *E. berilloni* (fig. 7A).

The flagellum of the second antenna (fig. 7B) is short, compared to the peduncle segments. The second peduncle segment bears the short gland cone. Peduncle segment 4 is a little shorter than segment 5. The setae along the ventral margin of segments 4 and 5 are to some extent variable in length.

The propodus of the first leg is a little longer than the carpus, elongate, pyriform; armed with a medial palmar spine and with some spines near the palmar angle. Moreover, the merus, carpus, of second leg (II); F, urosome (II); G, epimeral plates (II).

Fig. 8. *Echinogammarus longisetosus* n. sp., ♂, from the type-locality. A, mandible palp (scale III); B, first leg (II); C, hand of first leg (III); D, second leg (II); E, hand

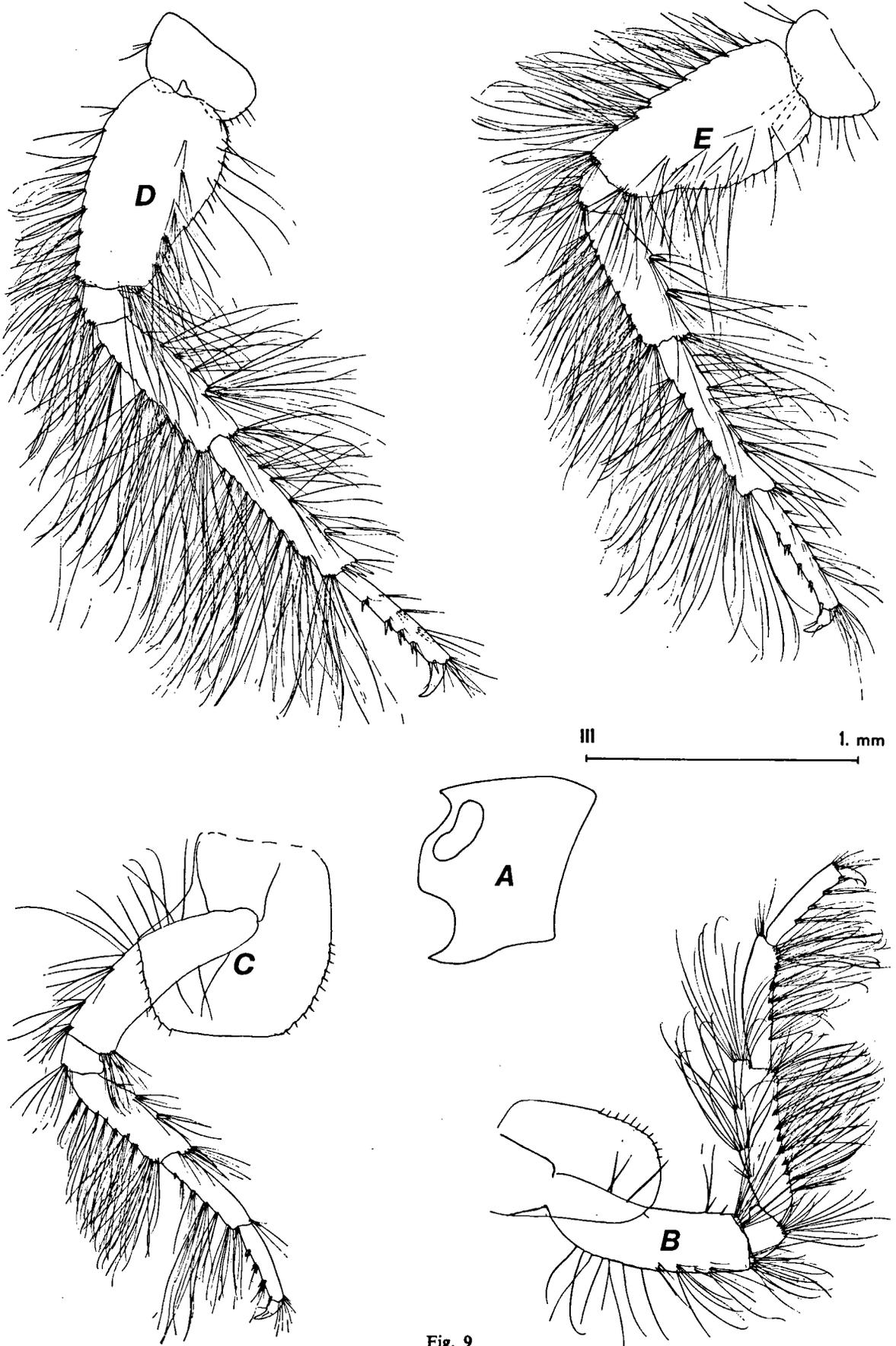


Fig. 9

and propodus of this leg are provided with tufts of very long setae as illustrated in figs. 8B and C.

The hand of the second gnathopod (figs. 8D, E) is relatively short, always less than twice as long as wide. In comparison with *E. berilloni*, the palm is less oblique while the medial palmar spine has moved a little towards the articulation with the dactylus. Near the palmar angle two transverse rows of spines are implanted. The lateral surface and the posterior margin are covered with many groups of very long setae (most of them have been omitted in the figures).

The merus and carpus of P3 and P4 (figs. 9B, C) are provided with dense brushes of very long setae along the anterior margin. In addition, the merus of P3 bears groups of long setae along the posterior margin. The coxal plates are relatively short with rounded inferior corners bearing short setules.

The basal segment of the fifth leg has a backward protruding lobe. The basis, merus, and carpus of this leg are provided with clusters of very long setae along the anterior margin (fig. 7C). The 6th and 7th leg have elongate basal segments. Their setation is even more characteristic than that of P5, since the bundles of long setae do not only occur along the anterior, but likewise along the posterior margin of merus and carpus (figs. 9D and E). Some long setae, increasing in number from P5 to P7, are implanted on the lateral surface of the basal segments.

Uropods 1 and 2 are identical to those in *E. berilloni*. The elongate outer ramus of uropod 3 is armed with many tufts of very long setae on both the inner and outer margins (fig. 7D).

The telson lobes are about 1.5 times as long as wide, each bearing 1 to 3 apical spines and one lateral spine. The spines are accompanied by a varying number of very long setae. Sometimes some long setae are found on the dorsal surface of the lobes as well (fig. 7E).

The metasome is sparsely armed with very small spines and setules. Generally the urosome segments are armed with a middorsal group of one spine and some long setae, and some lateral groups. There are no obvious elevations or excavations (see fig. 8F).

The back corners of the second and third epimeral plates vary from almost rectangular to slightly pointed. They are set with rather long

setae, both along the margins and on the lateral surface (fig. 8G).

The colour of live specimens varies from milky-white to greenish with orange dots on the metasome segments. The antennae always have an orange coloration. The proposed specific name, *longisetosus*, alludes to the clusters of very long setae on the gnathopods, pereopods, and uropods.

Female: In this species, as in several others, the female differs from the male in the gnathopods, which lack a medial palmar spine, and in the setation, which is better developed on the antennae, but is rather poor on the legs. Nevertheless females of this species make a more "hairy" impression than females of other members in the *berilloni*-group.

Variability. — In some populations from the north-eastern parts of Spain, the setae on the peduncle segments of the second antenna are longer, than in certain populations from the north-western part of the Iberian peninsula.

Ecology and distribution. — This is a species from the moderately fast running middle courses of freshwater streams. It seems to prefer high concentrations of Ca-ions. Since it is a species with a rather large range (see map III) in the northern half of Spain, it can be found sympatrically with various other species, such as *E. aquilifer* in the western Pyrenees, *E. berilloni* and *E. calvus* in the upper course of the Rio Ebro, and *E. echinosetosus* and *E. margalefi* in the south-eastern part of its distribution area. Data on interspecific competition are not available (see table I). Like *E. berilloni*, it can stand a rather high degree of pollution.

Echinogammarus tarragonensis n. sp.

Figs. 10A-D

Material examined. —

Spain

prov. Tarragona: Tributary of the Río Ciurana, 4.5 km S. of Curnudella, W. of Reus, 14-IV-1971, clear, moderately fast running stream with gravel bottom, temp. 12.4°C, pH 6.0, Cl 12 mg/l, Ca 59 mg/l, many specimens, many of them in precopulation. The ♂ holotype and many paratypes have been deposited in the Zoölogisch Museum Amsterdam under nr. ZMA Amph. 103.029.

Description. —

This species is very similar to *E. longisetosus*,

fourth leg (II); D, sixth leg (II); E, seventh leg (II).

Fig. 9. *Echinogammarus longisetosus* n. sp., ♂, from the type-locality. A, head (scale II); B, third leg (II); C,

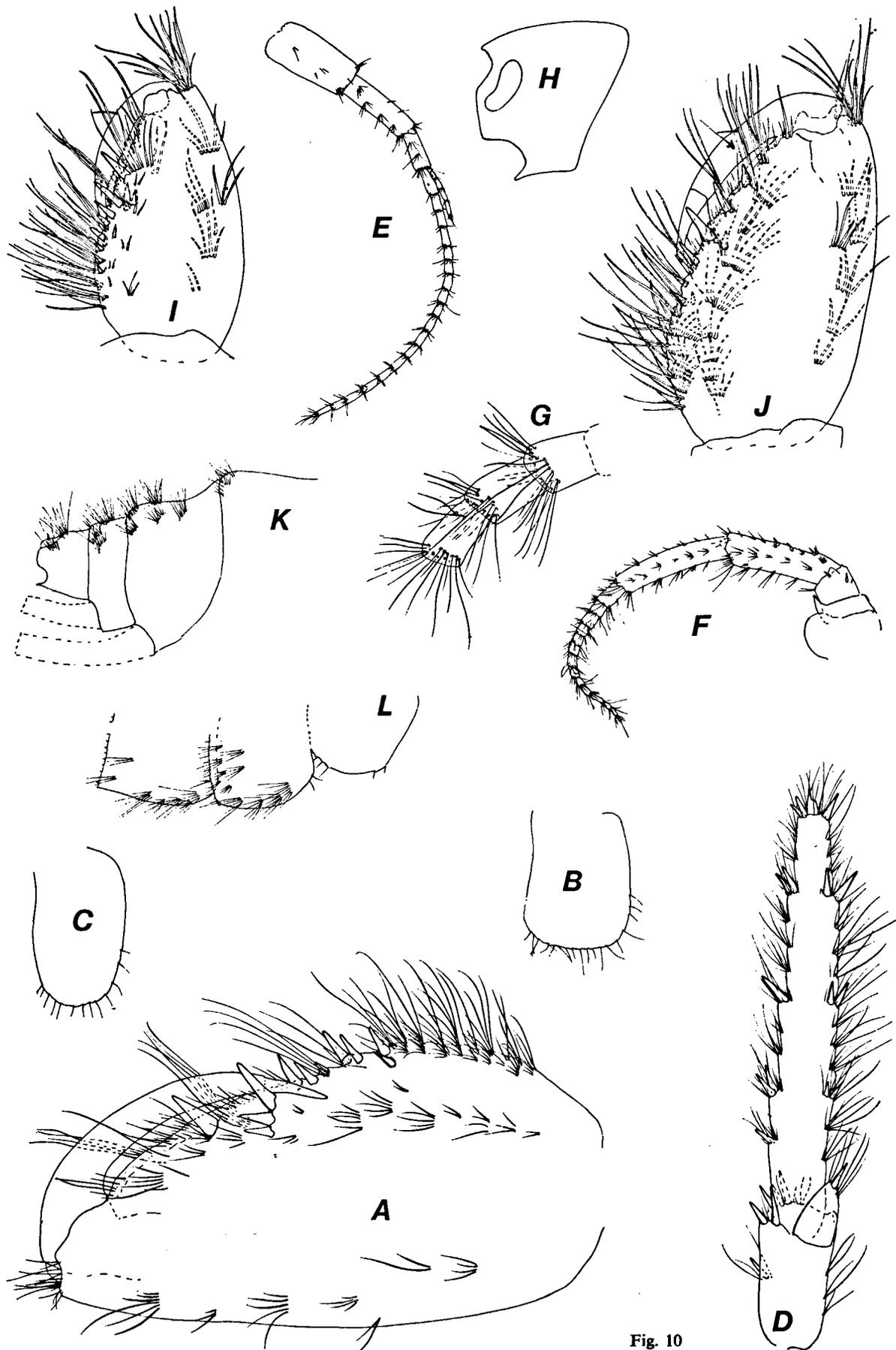


Fig. 10

described before. It differs from this species in the following characters (based on ♂):

- (1) The setae on the peduncle segments of A2 are shorter.
- (2) The setae implanted on the hands of the first and second gnathopods (fig. 10A) are very short against very long in *E. longisetosus*. The number of spines near the palmar angle of P2 is reduced.
- (3) The coxal plates of P1 and P2 bear long setae along the ventral margin (see figs. 10B and C).
- (4) The setae along the margins of uropod 3 (fig. 10D), very long in *E. longisetosus*, are short in this species.

The other characters, such as the very long setation of the legs, the structure of the mandible palp, and the armature of the dorsal surface and telson, are identical to those in *E. longisetosus*.

Since the species is found in one locality only (see Map III), no other data on its ecology can be given, than those mentioned under "Material examined".

Remarks. — This species has many characters in common with *E. longisetosus*. However, the differences mentioned in the preceding lines are stable within this sample. They all fall outside the range of variability observed in the 45 samples available of *E. longisetosus*. Since this sample was collected within the distribution area of *E. longisetosus* we believe that this form must be considered a valid species. As the only locality known at present is situated in the province Tarragona, the specific name *tarragonensis* is proposed.

Echinogammarus aquilifer Pinkster, 1969.

Figs. 6A-D

E. aquilifer Pinkster, 1969: 140—142, figs. 1, 3—8; Pinkster & Stock, 1971: 48.

Material examined. —

France

dépt. Basses-Pyrénées:

- Spring zone of the river Laxa, on Mont Mondarrain, alt. 625 m, 15-VII-1969, clear, fast running stream, about 30 cm wide, 5—10 cm deep, Cl 11 mg/l, Ca 8 mg/l, many specimens, many of them in precopulation (ZMA).
- River Laxa, on Mont Mondarrain, alt. 350 m, 15-VII-1969, clear, fast running stream, about 2 m

wide, Cl 11 mg/l, Ca 9 mg/l, many specimens, many of them in precopulation. Accompanying species: *Echinogammarus berilloni* (Catta) (ZMA).

- River Laxa, S. of Espelette, 15-VII-1969, clear, fast running stream, with stony bottom, about 1.5 m wide, Cl 10 mg/l, Ca 46 mg/l, 10 specimens (ZMA) Accompanying species: *E. berilloni*.
 - River Ouhabia, on road from St. Pée to Arbonne, 15-VII-1969, slightly polluted, slowly flowing stream, with some pebbles on sandy bottom, about 1.5 m wide, Cl 21 mg/l, Ca 40 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. berilloni*.
- dépt. Landes:
- Small brook, 2 km N.E. of St. Martin de Seignanx (= N.E. of Arbonne), 7-V-1970, temp. 11.8°C, pH 5, Cl 23 mg/l, Ca 45 mg/l, many specimens, many of them in precopulation (ZMA).

Spain

prov. Navarra:

- River Petite Nive, about 5 km S. of Valcarlos, 25-VIII-1968, clear, fast running stream, about 50 cm wide, stony bottom, Cl 27 mg/l. (The ♂ holotype, ♀ allotype and 27 paratypes have been deposited in the Zoölogisch Museum Amsterdam under cat. no. ZMA Amph. 102.126, 102.127 and 102.128).
- Small brook, just S. of village Almandoz (= S.W. of Elizondo), 15-VII-1969, slightly polluted, moderately fast running stream, with stony bottom, Cl 10 mg/l, Ca 48 mg/l, many specimens, many of them in precopulation (ZMA).
- Río Baztan, N. of Elizondo, 15-VII-1969, clear, fast running stream, with stony bottom, 4 m wide, Cl 8 mg/l, Ca 32 mg/l, 1 specimen (ZMA). Accompanying species: *E. berilloni*.
- Confluent of Arroyo Artesiaga, S. of Irurita, 15-VII-1969, clear, fast running stream, with gravel bottom, 5 cm deep, 50 cm wide, Cl 9 mg/l, Ca 38 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. longisetosus*.

Description. —

The descriptions and illustrations given by Pinkster (1969) form a good basis for the recognition of the species. For the sake of completeness, the most important characters, along with some illustrations are repeated.

Male: A relatively small species, maximum length observed being 12 mm.

The lateral lobes of the head have rounded corners, the sinus is shallow; the eyes are elongate.

The third segment of the first antenna is short, less than half as long as the second.

The second antenna (fig. 6A) has slender peduncle segments 4 and 5 armed with 3 rows of

Fig. 10 A—D. *Echinogammarus tarragonensis* n. sp., ♂, from the type-locality. A, hand of second leg (scale III); B, first coxal plate (II); C, second coxal plate (II); D, third uropod (IV).

E—L. *Echinogammarus margalefi* n. sp., ♂, from the type-locality. E, first antenna (II); F, second antenna (II); G, detail of second antenna (III); H, head (II); I, hand of first leg (III); J, hand of second leg (III); K, urosome (II); L, epimeral plates (II).

spines and setae. The armature of the flagellum is absolutely distinctive, because of the flag-like brush of setae along the inferior margin, which is reminiscent of the situation found in *G. pulex*.

The hand of the first gnathopod has a very oblique palm (fig. 6B). A medial palmar spine is present, but unlike in *E. berilloni* it is not separated from the palmar angle spines by a wide gap.

The hand of the second gnathopod (fig. 6C) is relatively short, 1.5 times as wide as long. A medial palmar spine is never found. The coxal plates of the first two legs are almost rectangular, while those in legs 3 and 4 are rounded.

The basal segment of legs 5, 6 and 7 is relatively wide, subrectangular. In leg 5 it is hardly longer than wide. The posterior margin of the basis is finely creuulated and set with short setae. Only few groups of setae are implanted on the lateral surface of the basal segments. For the remainder these legs are less setose than in *E. berilloni* and resemble those of *E. calvus*.

The third uropod is more strongly developed than in *E. berilloni*. The length of their setation is intermediate between *E. berilloni* and *E. longisetosus*.

The telson lobes are broad, little longer than wide (fig. 6D). Apart from the apical and lateral groups of elements, which are usually found in this species group, clusters of long setae are implanted on the upper surface as well.

The metasome and urosome segments have no dorsal elevations or excavations. They are armed with small tufts of short, slightly curved setae.

The posterior corner of the third epimere is a little sharper than that of the second. The epimeral armature is rather scanty.

The setation of the second antenna, of P5 through P7, and of the telson resemble that found in *E. zebrinus*, but nevertheless the species can easily be distinguished through the absence of a medial palmar spine in P2 and the different armature of the dorsum.

Female: As in other species, the female is less characteristic than the male. Nevertheless, females from this species can be easily identified, because of the flag-like brush of setae on the second antenna.

Ecology and distribution. —

Intensive sampling has proved that the species inhabits a very small area only in the south-western part of France, and in the north-western part of

Spain, on the foot-hills of the Pyrenees (see Map III). It is found under stones in narrow, clear, and rather fast running upper reaches of mountain streams, a biotope somewhat similar to that of *Gammarus fossarum* in the French Alps. When the stream gets wider the species is gradually outnumbered by *E. berilloni* or *Gammarus pulex*.

Echinogammarus zebrinus Pinkster & Stock, 1971.

Fig. 11

E. zebrinus Pinkster & Stock, 1971: 43—51, figs. 4—7.

Material examined. — see Pinkster & Stock, 1971.

Description. —

The recent description of this species may serve as a good basis for its recognition.

Male: It is a large species (males up to 19 mm long have been observed) and it is the only one within this group that can be distinguished in the field with the naked eye, because of its typical colouration. Like a zebra, it has lighter and darker (almost black) vertical stripes on each body segment.

As in *E. aquilifer*, the flagellum of the second antenna bears a flag-like brush of setae, the individual setae are a little shorter, however. On the other hand, the setae on the fifth peduncle segment are longer than in the other species (figs. 11A, B).

The hands of both the first and second gnathopods have oblique palms, always provided with a pointed medial palmar spine. A group of spines is always found near the palmar angle. The coxal plates of legs 1 through 4 have rounded corners and generally long setae along the inferior margin; legs 5, 6, and 7, and the third uropod are almost identical to those in *E. berilloni*.

As in *E. aquilifer*, the telson lobes bear one or two dorsal groups of setae, in addition to the normal groups of elements (fig. 11C). Very characteristic is the conspicuous armature of the dorsal surface of the body (fig. 11D), with its numerous small curved spines. In addition there are some tufts of setae, very short on the first segment of the metasome, but increasing in length and number towards the third urosome segment.

Female: Although most of the characteristic features (such as the "flag" on the second antenna) of the male are absent or less developed in the females, this sex can still easily be recognized by the striped colouration and the armature of the dorsum.

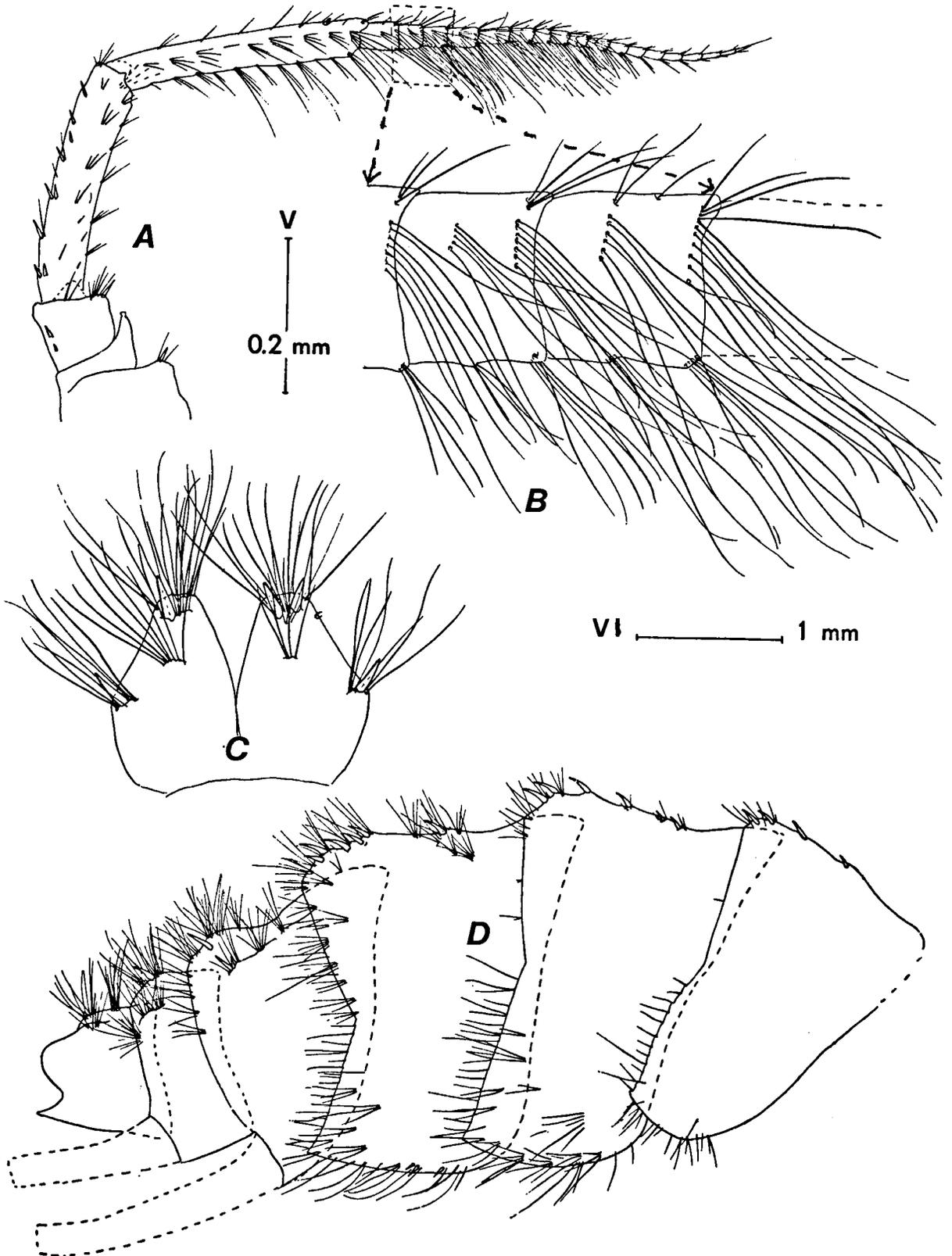


Fig. 11. *Echinogammarus zebrinus* Pinkster & Stock, 1971, ♂, from the type-locality. A, second antenna (scale VI);

B, detail of second antenna (V); C, telson (III); D, pleosome and urosome (II).

Variability. — Except for the "normal" variability, this species shows some variability in the length of the endopod of uropod 3. It can vary from less than 10% to more than 20% of the length of the exopod (see Pinkster & Stock, 1971).

Ecology and distribution. — In spite of intensive sampling, the species was found only in a very limited area around Mont-de-Marsan in southwestern France (see map in Pinkster & Stock, 1971). In this region it inhabits a wide range of biotopes not only fluctuating in the chemical composition of the water (e.g., the amount of Ca-ions varied from 3.3 mg/l to 69.8 mg/l), but also in the bottom composition (mud, sand, stones) and vegetation. Therefore, it is a little astonishing that a species of such adaptability could never be traced beyond its very restricted area. The species coexists with both *E. berilloni* and *E. pacaudi* (see table I).

Remarks. — Within the *berilloni*-group, *E. meridionalis*, *E. aquilifer*, and *E. zebrinus* occupy a special place since they possess a flag-like brush of setae on the second antenna. They form a series in which *E. zebrinus* is still closely related to *E. berilloni*, while in *E. meridianus* the relation is hard to see. In this series there seems to exist a certain regularity, in that along with the presence of a flag-like brush on the second antenna there is a tendency towards the loss of the medial palmar spines (and part of the armature of the dorsum). So, in *E. meridianus* which has a brush on both the flagellum and peduncle segments of A2, the medial palmar spines are absent in both gnathopods; in *E. zebrinus* which has a less developed "flag", these spines are still present, while *E. aquilifer* is intermediate. These tendencies strike me, since both the gnathopods and the second antenna play such an important role during the first stages of the precopulation.

Echinogammarus feminatus n. sp.

Figs. 12-13

Material examined. —

France

dépt. Basses-Pyrénées:

- River le Landistou, on road D35, S.W. of Bruges, about 20 km W. of Lourdes, 24-VIII-1968, Cl 7 mg/l, 40 specimens, some of them in precopulation. (The ♂ holotype, ♀ allotype, and 38 paratypes have been deposited in the collection of the Zoölogisch Museum Amsterdam, under cat. nr. ZMA Amph. 103.026).

dépt. Hautes-Pyrénées:

- River l'Arros, 2 km S.E. of St. Stevens, near Tarbes, 14-III-1972, clear, moderately fast running stream, with stony bottom, about 2 m wide, 10 to 60 cm deep, pH 7.9, many specimens (ZMA). Accompanying species: *Echinogammarus pacaudi*, *E. berilloni*.
- River la Bouès, 3 km E. of Autin, near Tarbes, 14-III-1972, clear, moderately fast running stream, with stony bottom, about 1 m wide, 10–40 cm deep, pH 8.2, many specimens (ZMA). Accompanying species: *Echinogammarus pacaudi*.

Description. —

Male: Maximal length observed 16 mm. The head and the shape of the eyes are identical to those in *E. berilloni*.

The first antenna (fig. 12A) is longer than half the body length. Its third peduncle segment is more than half as long as the second. The flagellum and accessory flagellum have 26 to 30 and 5 to 6 segments, respectively. The second antenna (fig. 13A) has slender peduncle segments and an 18- to 23-segmented flagellum. As in the first antenna, the last two peduncle segments are ventrally armed with groups of 1 to 3 rather long setae (longer than the diameter of the segments on which they are implanted). Because of these antennae, which resemble those of female *E. berilloni*, the species is called *feminatus*, latin for effeminate.

Within the *berilloni*-group, *E. feminatus* is the only species with a more or less irregular row of setules on the third segment of the mandible palp (fig. 13B), the setae in the proximal part being distinctly shorter than those in the terminal part. Five plumose terminal setae and two groups of setae on both the inner and outer surface complete the armature of this segment.

The hand of the first gnathopod (figs. 12B, 13C) has an oblique palm and a medial palmar spine. For the remainder P1 shows no particularities.

The hand of the second gnathopod (figs. 13D, 12C) is more than twice as long as wide. A transverse row of spines is implanted near the palmar angle. In comparison to *E. berilloni*, the pointed medial palmar spine has moved towards the articulation with the dactylus. In between this spine and the palmar angle group, another strong pointed spine can be found. The coxal plates of the first four legs have rounded inferior corners, and bear only few setae along the margins.

The setation in P3 is longer than in P4 (figs. 12D, E). These legs, as well as the posterior three

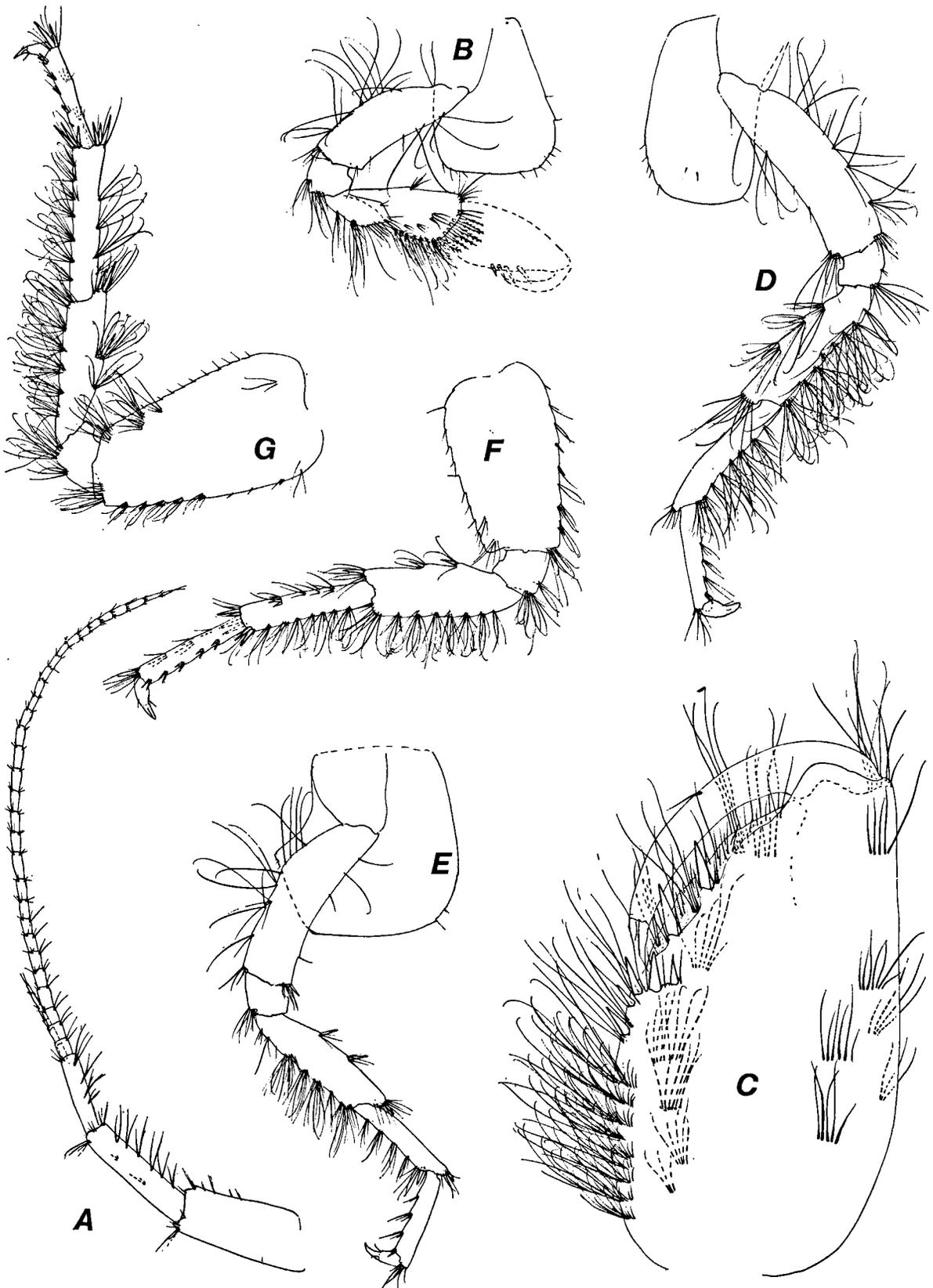


Fig. 12. *Echinogammarus feminatus* n. sp., ♂, from the type-locality. A, first antenna (scale II); B, first leg (II);

C, hand of second leg (III); D, third leg (II); E, fourth leg (II); F, fifth leg (II); G, seventh leg (II).

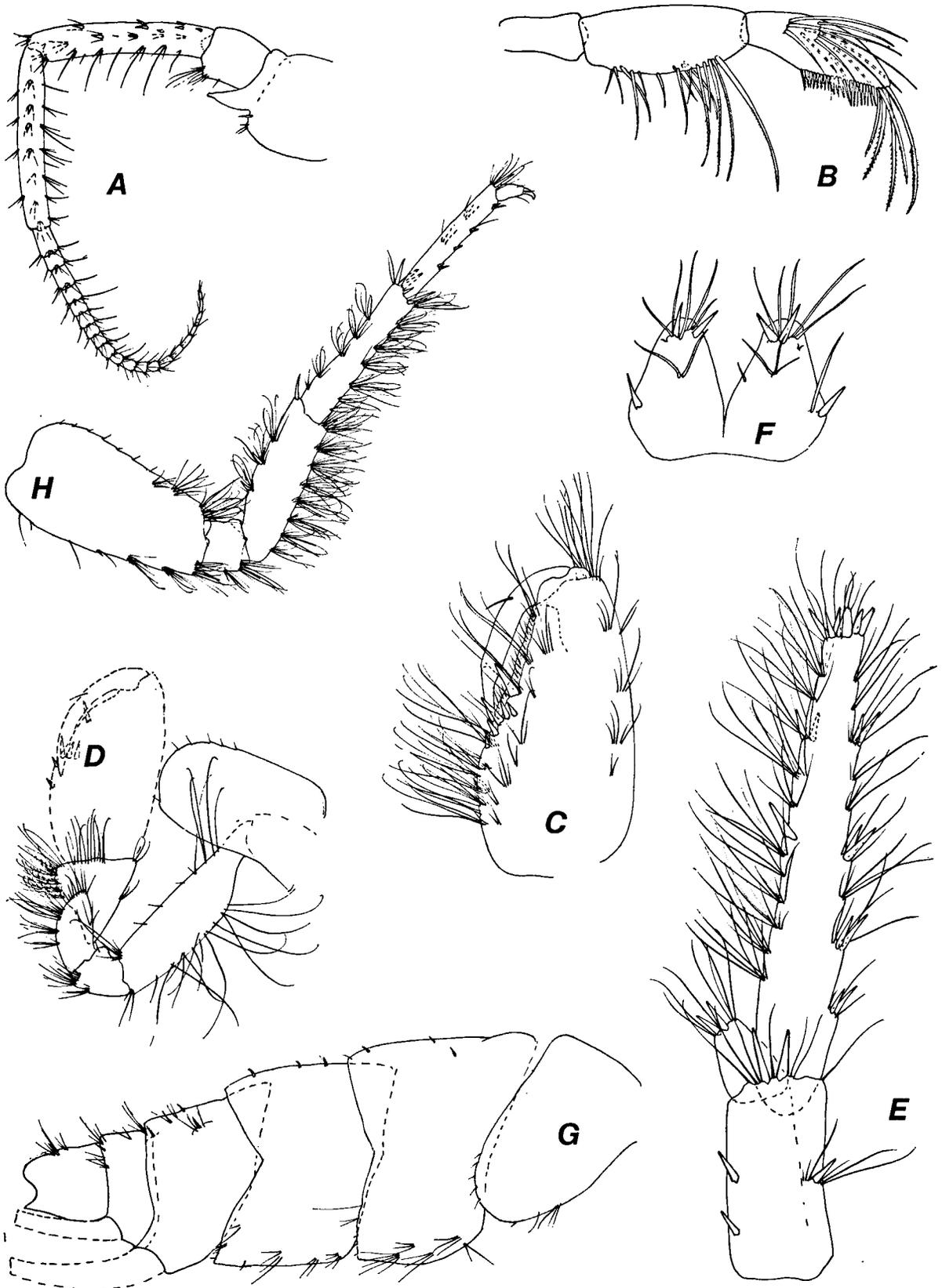


Fig. 13. *Echinogammarus feminatus* n. sp., ♂, from the type-locality. A, second antenna (scale II); B, mandible palp (III); C, hand of first leg (III); D, second leg (II);

E, third uropod (III); F, telson (III); G, pleosome and urosome (II); H, sixth leg (II).

pereiopods, almost resemble those of *E. calvus* (see figs. 12F, G, 13H).

The third uropod (fig. 13 E) is relatively short. Its armature is rather poor for the *berilloni*-group.

Except for the usual armature, the telson (fig. 13F) bears a few setae on the dorsal surface of the lobes.

The metasome and urosome segments have no dorsal elevations or excavations and attract attention because of the poor setation only. The third epimeral plate is more sharply pointed than the second; both bear a few groups of short setae on the lateral surface (fig. 13G). This "baldness", in combination with the setation pattern of the antennae, make this species look like females of *E. berilloni*. Nevertheless it can be easily recognized by the structure of the hand of the gnathopods.

Female: It is very hard to distinguish females of this species from those of *E. berilloni*.

Ecology and distribution. — So far this species has only been found in three localities in the central part of the Pyrenees. Ecological data, other than those already mentioned under "material examined" are not available.

Echinogammarus echinosetosus n. sp.

Figs. 14-15

Material examined. —

Spain

prov. Zaragoza:

- Tributary of Río Piédra, E. of Nuevalos, 13-VII-1969, clear, fast running stream, with gravel bottom, about 1.5 m wide, pH 6.5, Cl 1 mg/l, Ca 182 mg/l, many specimens, many of them in precopulation. (The ♂ holotype, ♀ allotype, and many paratypes have been deposited in the Zoölogisch Museum Amsterdam, under cat. nr. ZMA Amph. 103.030). Accompanying species: *E. longisetosus*.
- Río Piédra, 200 m upstream of the Monasterio de Piedra, 13-VII-1969, clear, fast running stream with stony bottom, about 10 m wide, pH 6.5—7, Cl 13 mg/l, Ca 80 mg/l, many specimens, many of them in precopulation (ZMA).
- Río Jiloca, near village Morata de Jiloca, 13 km S.E. of Calatayud, 12-VII-1969, moderately polluted stream with clay bottom, about 5 m wide, Cl 45 mg/l, Ca 148 mg/l, many specimens, many of them in precopulation (ZMA).

prov. Teruel:

- Río Jiloca, near Caminreal, 12-VII-1969, clear, fast running stream, about 2.5 m wide, more than 2 m deep, pH 6.5, Cl 34 mg/l, Ca 110 mg/l, many specimens, many of them in precopulation (ZMA). Accompanying species: *E. longisetosus*.
- Upper reaches of Río Martín, alongside road N 211, near Vivel del Río Martín (= 12 km W. of

Montalban), 12-VII-1969, slightly polluted, moderately fast running stream with gravel bottom, about 1 m wide, 50 cm deep, Cl 17 mg/l, Ca 84 mg/l, many specimens, many of them in precopulation (ZMA).

- Río Pancrudo on road N 234, about 5 km N. of Cala Mocha, 12-VII-1969, clear, moderately fast running stream, about 2 m wide, gravel bottom, Cl 36 mg/l, Ca 276 mg/l, many specimens, many of them in precopulation (ZMA).

- Río Jiloca near Burbaguena, alongside road N 234, 12-VII-1969, polluted fast running water, about 3.5 m wide, Cl 32 mg/l, Ca 160 mg/l, many specimens (ZMA).

prov. Guadalajara:

- Río Jálon, on road N 11, near Medinacelli, 27-VII-1970, clear, fast running stream with sandy bottom, 20 cm deep, 2 m wide, 17°C, pH 6, Cl 4 mg/l, Ca 90 mg/l, many specimens, many of them in precopulation (ZMA).

prov. Soria:

- Río Jálon, near Sta. Maria de Huerta, 31-V-1970, many specimens, many of them in precopulation (ZMA).

prov. Castellon:

- Cemented irrigation ditch, alongside road N 340, 600 m N. of Chilches, 35 km N. of Valencia, 19-V-1971, many specimens, many of them in precopulation (RMNH). Accompanying species: *Echinogammarus pacaudi*.

Description. —

Male: Maximum length 14 mm; in general smaller.

Head with rounded lateral lobes (fig. 14A), eyes reniform, more than twice as long as wide.

The peduncle of A1 (fig. 14B) is very short in comparison to the 33- to 40-segmented flagellum. Peduncle segments 4 and 5 of A2 (fig. 14C) are long and slender, set with groups of short setae (shorter than the diameter of the segments on which they are implanted). The segments of the 19- to 23-segmented flagellum are relatively short and bear many short setae near their distal end.

The comb of setae along the ventral margin of the third segment of the mandible palp differs from most other members in the group in having a few longer setae intermixed with the elements of the normal regular row (fig. 14D).

The hand of the first gnathopod (figs. 14E, 15A) is piriform and has a very oblique palm, so that there is no obvious palmar angle. Compared with *E. berilloni*, the medial palmar spine has moved towards the articulation with the dactylus. Likewise on the palm, but widely separated from this spine, a group of strong, graduated spines can be found towards the basis of the hand.

The basal portion of the enormous propodus of P2 is swollen (figs. 14F, 15B). The very long dactylus, the characteristic implantation of the

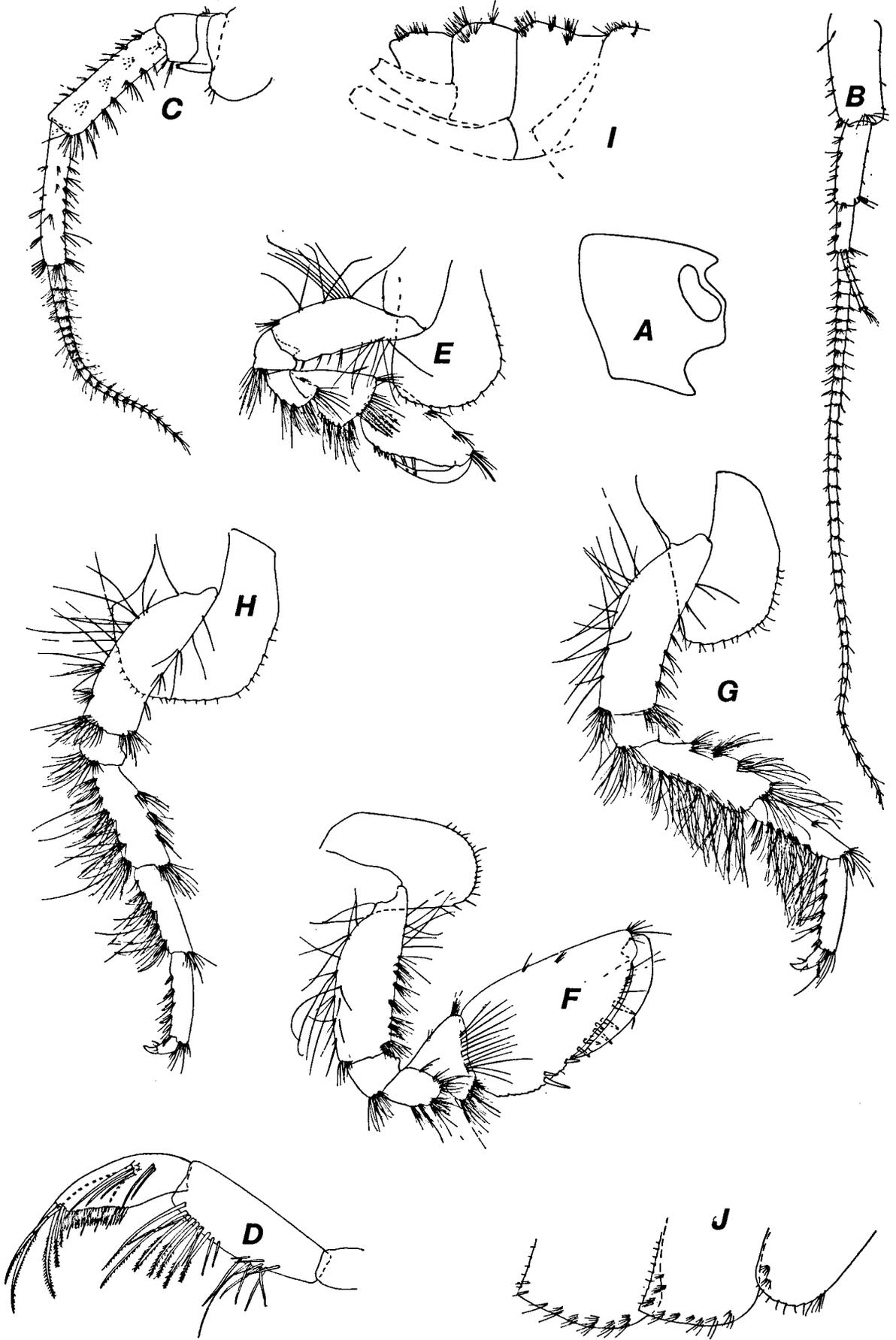


Fig. 14

many spines along the palm, and the transverse row of spines on the wide basal portion make this hand most characteristic within the *berilloni*-group. The setae along the palm of both hands often bear plumosities. P3 and P4 are not very characteristic; their coxal plates, like those of the gnathopods, have rounded inferior corners, and many short setae along the inferior margin (figs. 14G, 14H).

The basal segment of P5 is hardly more than 1.5 times as long as wide and has a backward protruding lobe (fig. 15C). In P6 and P7 (figs. 15D, 15E), where the basal segment is more elongate, this lobe is less pronounced. The armature of these legs is characteristic, not on account of the position of the groups of elements, but because of the very short almost spine-like setae in these groups.

The inner ramus of the well-developed third uropod (fig. 15F) sometimes is a little longer than in most other species in the group; it can attain about 25% of the exopodal length. The setation is rather short.

The telson (fig. 15G) has some groups of setae implanted on the dorsal surface of the lobes.

The first urosome segment has a dorsal excavation ("saddle") (fig. 14I). The metasome, the urosome, as well as the epimeral plates (fig. 14J) are set with the same spine-like setae that can be found on the legs (the proposed specific name *echinosetosus* alludes to this feature).

The short spine-like setation, along with the enormous gnathopods, and the characteristic mandible palp, make this species readily identifiable.

Female: Can be distinguished from females of other species by the structure of the mandible palp only.

Variability. — In addition to the "normal" unstable characters, the hand of P1 shows variability in the number of spines participating in the row along the palm. The relative length of the endopod, in Ur3, varies from 0.1 to 0.25 times the length of the exopod.

Ecology and distribution. — As far as we can judge at the moment, the species seems to prefer rather fast running middle courses of streams, with a high amount of Ca-ions. Neither the structure of

the bottom, nor the presence or absence of vegetation, seem to have any influence on its distribution, which is restricted to a rather small area in Spain, draining into the Mediterranean (see Map III). Twice it has been found together with *E. longisetosus*, another member of the *berilloni*-group, and once together with *Echinogammarus pacaudi* (see table I).

Echinogammarus margalefi n. sp.

Figs. 10 E—L, 16.

Material examined. —

Spain

prov. Teruel:

— Río Guadalajara near Albaracin, 6-V-1967, alt. 1150 m, many specimens (MSNV).

— Frias de Albaracin, Monte Universali, 6-V-1967, alt. 1600 m, many specimens (MSNV).

— Tributary of Río Turia, S. of Libros, about 25 km S. of Teruel, 11-VII-1969, 1—2 m wide, gravel bottom, many specimens, Cl 34 mg/l, Ca 84 mg/l. (The ♂ holotype, ♀ allotype, and many paratypes have been deposited in the Zoölogisch Museum, Amsterdam, under no. ZMA Amph. 103.024.) Accompanying species: *E. longisetosus*.

— Río Moron on border of prov. Teruel and prov. Castellon, 11-VII-1969, shallow, stony bottom, Cl 14 mg/l, Ca 76 mg/l, 12 specimens (ZMA).

prov. Cuenca:

— Río Riánsares, on road N 400, about 12 km E. of Tarancón, 10-VII-1969, about 1.5 m wide, stony bottom, Cl 14 mg/l, Ca 440 mg/l, many specimens (ZMA).

— Nameless tributary of Río Teja, near N 420 at Boniches, 11-VII-1969, limestone, Cl 29 mg/l, Ca 82 mg/l, many specimens (ZMA).

— Río Teja, tributary of Río Gabriel, on road N 420 near Boniches (87 km S.W. of Teruel), 11-VII-1969, clear, fast running stream with stony bottom, about 5 m wide, Cl 33 mg/l, Ca 74 mg/l, many specimens (ZMA).

— Río Teja, on road N 420, near Huerquina, 11-VII-1969, about 2.5 m wide, stony bottom, Cl 24 mg/l, Ca 84 mg/l, many specimens, many of them in precopulation (ZMA).

— Upper reaches of Río Gabriel, on road N 420, near Salvacanete, 11-VII-1969, about 3 m wide, shallow, stony bottom, Cl 8 mg/l, Ca 80 mg/l, many specimens, many of them in precopulation (ZMA).

prov. Rincon de Ademuz:

— Río Turia near Torre Alta, 11-VII-1969, moderately polluted, fast running stream, stony bottom, about 4 m wide, Cl 29 mg/l, Ca 132 mg/l, many specimens (ZMA).

prov. Ciudad Real:

— Río Guadiana, about 10 km S.W. of Ciudad Real,

Fig. 14. *Echinogammarus echinosetosus* n. sp., ♂, from the type locality. A, head (scale II); B, first antenna (II); C, second antenna (II); D, mandible palp (III); E, first

leg (II); F, second leg (II); G, third leg (II); H, fourth leg (II); I, urosome (II); J, epimeral plates (II).

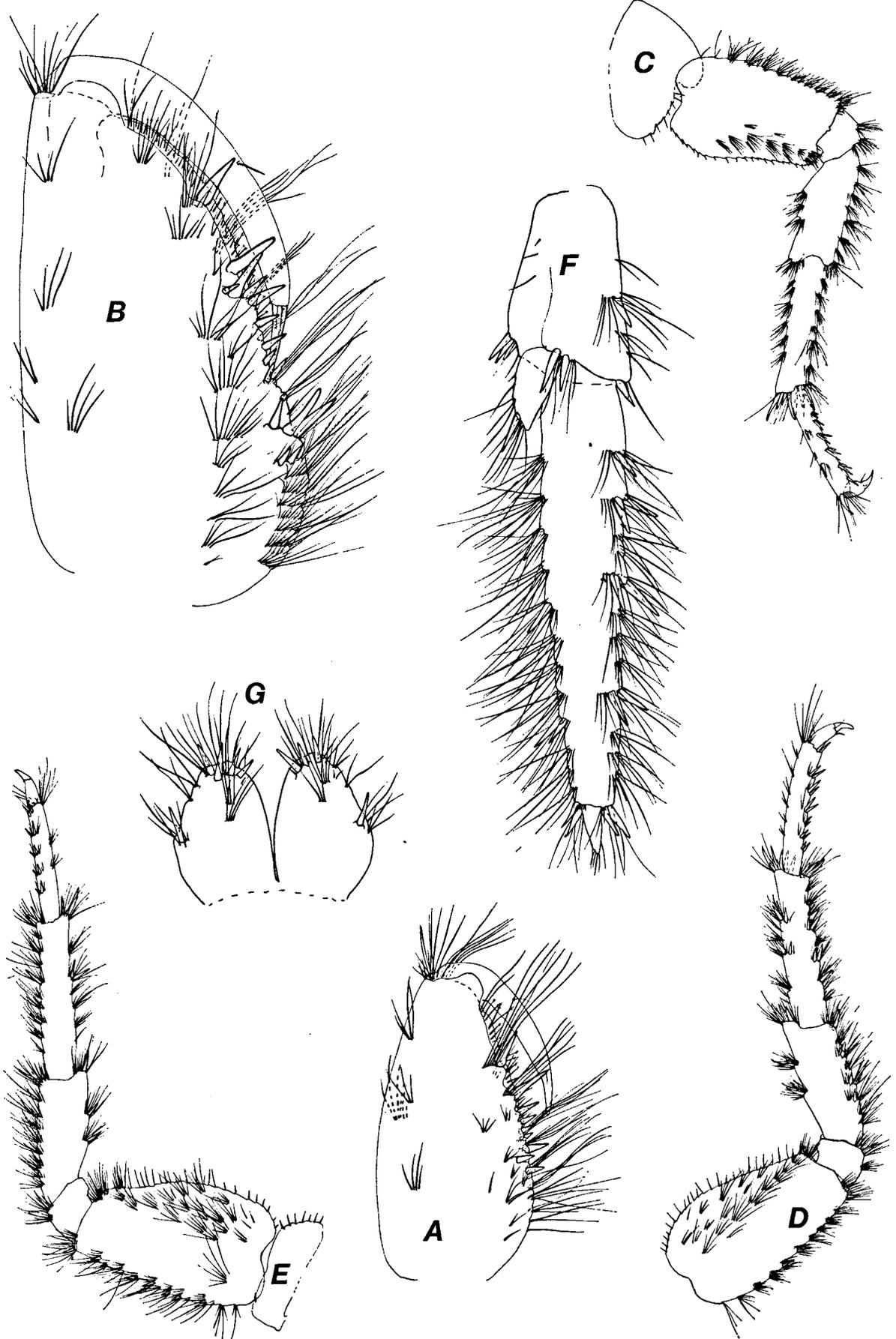


Fig. 15

on road N 430, 7-IX-1970, slightly polluted, slowly running stream, stony bottom, more than 1 m deep, more than 10 m wide, temp. 25.5°C, pH 6, Cl 86 mg/l, Ca 168 mg/l, many specimens (ZMA).

- Río Guadiana, about 10 km S.E. of Malagón, 7-IX-1970, slightly polluted, moderately fast running, sandy and stony bottom, 20—60 cm deep, 5 m wide, temp. 25.2°C, pH 6.0, many specimens, some of them in precopulation (ZMA).

prov. Toledo:

- Río Tajo, near Aranguez, on road N IV, about 40 km S. of Madrid, 26-VII-1970, moderately fast running, slightly polluted, more than 2 m deep, about 20 m wide, pH 6—6.5, many specimens, many of them in precopulation (ZMA).

prov. Valencia:

- Río Turia, S. of Liria, on road C 3322, near Liria, 9-IX-1970, moderately fast running, clear, stony and clayish bottom, 1 m deep, 5 m wide, temp. 23.2°C, pH 6, Cl 78 mg/l, Ca 132 mg/l, many specimens (ZMA).

Description. —

Male: The smallest species within the *E. berilloni*-group; the maximum length observed was 11 mm. The lobes of the head have rounded corners; the eyes are relatively small, no more than twice as long as wide. The sinus is rather deep (fig. 10H).

The first antenna (fig. 10E) has a short flagellum, with at most 20 segments. The armature is very poor.

Peduncle segments 4 and 5 of A2 (figs. 10F, G) are armed with 3 rows of short elements. The setae of the short flagellum are little longer than the diameter of the segments on which they are implanted.

The mandible palp is in so far particular that it bears some setae on the inner surface of the second segment (fig. 16A).

In comparison with other members of this group, the hand of both gnathopods 1 and 2 (figs. 10 I, J) are small and have a very oblique palm. In both, the medial palmar spine has moved towards the articulation with the dactylus. Very often another, smaller spine (indicated by an arrow in fig. 10 J) can be found in P2. The inner and outer surface of the hands are set with many groups of setae.

The coxal plates 1—4 have rounded inferior corners, set with some short setules (figs. 16 B, C, D and E).

Legs 5, 6, and 7 (figs. 16 F, G, H) are relatively short and armed with smaller spines and short setae.

The third uropod is short, without particularities

(fig. 16 I). A limited number of setae is found on the dorsal surface of the rather short telson lobes (fig. 16 J). A saddle is present on the first urosome segment (fig. 10 K). The setation of the dorsal surface of the urosome and epimeral plates is a little longer than in *E. echinosetosus* (figs. 10 K, L).

Except for the armature of the hands of the gnathopods, this species very much resembles juvenile *E. berilloni* or *E. echinosetosus*. Since only sexually adult specimens were used for the present morphological studies, there can be no confusion. In this species precopulation occurs at a body size far smaller than ever observed in *E. berilloni* or *E. echinosetosus*.

Female: Very small, without outstanding characters.

Ecology and distribution. — The species is found in the upper and middle courses of streams, draining both into the Mediterranean and into the Atlantic (see map III). All these waters have in common, that they are highly mineralized, and particularly rich in Ca-ions. The bottom always consists of stones, gravel or other hard material. Vegetation was found in a few instances only. It seems that the species has a very wide temperature tolerance, since it was found in lowland waters at 25.5°C, but also at an altitude of 1600 m, in waters where in summer the temperature did not exceed 11°C.

This species is dedicated to Dr. R. Margalef, of Barcelona, in recognition of his excellent ecological work and in particular for his contribution to the knowledge of Spanish amphipods.

Species inserta sedis

In two localities, both in Spain, somewhat outside the main distribution area of the *berilloni*-group, animals have been found which certainly are closely related to *E. berilloni*. However, they could not be identified since only females or juveniles were available. Intensive search, in two successive years, for more material from these localities or in waters belonging to the same drainage system, completely failed, because of pollution (in the Río Duero) or because of man-made water works which had completely changed or destroyed the old localities.

These localities are:

- Prov. Caceres: Abadia, 5-V-1960, 7 specimens (RMNH) (these specimens were erroneously record-

Fig. 15. *Echinogammarus echinosetosus* n. sp., ♂, from the type locality. A, hand of first leg (scale III); B, hand

of second leg (III); C, fifth leg (II); D, sixth leg (II); E, seventh leg (II); F, third uropod (III); G, telson (III).

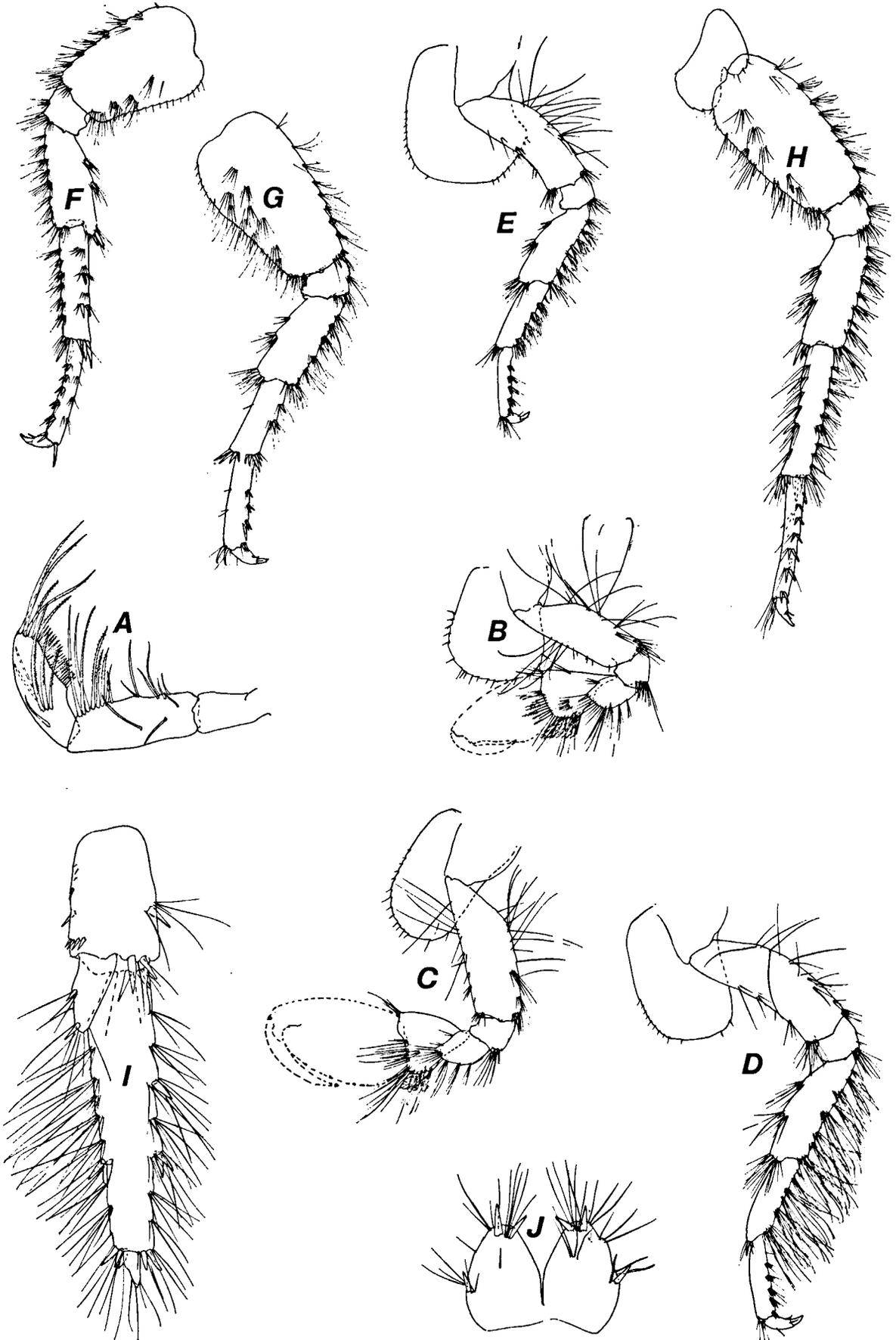


Fig. 16

ed as *E. lusitanus* by Stock, 1968 : 52).

- Prov. Zamora: Auxiliary bed of the Rio Duero, 500 m W. of the bridge at Zamora, 10-VII-1969, moderately fast running, very polluted stream, about 100 m wide, Cl 30 mg/l, Ca 70 mg/l, 3 specimens (ZMA).

DISCUSSION

When reviewing the distribution of freshwater gammarids in the Iberian peninsula (see also Pinkster, 1971 and in press, and Pinkster & Stock, 1970 and 1972) it soon becomes clear that two main distribution areas can be distinguished: (a) a southern one, inhabited by members of the *Echinogammarus simoni*-group, and (b) a northern one with members of the *Echinogammarus berilloni*-group. Both species-groups show only a narrow zone of overlap; the only exception being *E. lusitanus* (a member of the *simoni*-group) which is distributed in very soft waters in the extreme north-western corner of the Iberian peninsula, entirely disjunct from the main range of the *simoni*-group, and surrounded by an area in which members of the *E. berilloni*-group are the only freshwater amphipods.

Apart from these two species-groups, both inhabiting a more or less demarcated area, members of two other groups of freshwater amphipods have been found, all in more or less isolated relic-like localities. These are members of the *Gammarus pulex*-group on the one hand, members of the genus *Eulimnogammarus* on the other. The nature of the biotopes in which populations of these two species-groups use to live, and their present degree of isolation against geneflow seem to indicate that we have to do with the relics of formerly more widely distributed forms. The extreme morphological variability found within various populations of these species (see Pinkster, 1971, for *Gammarus gauthieri* and Pinkster, in press, for members of the genus *Eulimnogammarus*), are an indication that we have to do with small, isolated populations, being so little numerous that the total gene pool is reduced and that homeostasis (through suppressor genes) is weakened. Pinkster, in press, pointed out that these Spanish *Eulimnogammarus*-species, as well as their relatives in Lake Baikal, are descendants of the same old limnic fauna, that occurred

in the entire Euro-Asiatic region during the Tertiary period. This idea is supported by Basikalova, 1945, who assumed that the genus *Eulimnogammarus* is one of the five old, primitive genera of amphipods from which all other gammarids are descendants. She considers the genus *Gammarus* (meaning in reality the *Gammarus pulex*-group, in the context of Bazikalova's work) to be one of the other basic groups from which most of the other freshwater gammarids have been derived. This idea is not at all astonishing since members of this *Gammarus pulex*-group can be found in the whole Euro-Asiatic region, in Northern Africa and even in North America. The same holds true for the genus *Eulimnogammarus*, since members of this genus can be found not only in Lake Baikal, as was previously assumed, but also in coastal waters in the Arctic, Western Europe, and North America, and moreover in many freshwater localities in the Iberian peninsula and in the Pyrenees (see Pinkster, in press).

The *E. berilloni*- and *E. simoni*-species-groups must be considered more recent invaders, the latter coming from the South, the former coming from the North. This corresponds well with the fact, that the *Echinogammarus simoni*-group has its main distribution area in northern Africa, which area was in contact with Eurasia during many periods of its geological history. The close relationship demonstrated between North African and Iberian forms of certain fresh-water gammarids, has been found in many other groups of organisms as well, e.g., in several groups of phanerogams, and vertebrates, but also in aquatic invertebrates such as the subterranean amphipod genus *Pseudoniphargus*, and the isopod genus *Sphaerobathytropa* (see Brehm, 1947; de Lattin, 1967).

It is almost sure that in the case of the *E. simoni*-group, there has not been a single invasion only, but more likely a series of successive invasions or may be faunistic exchanges during the different periods during which connections between the African and European continents did exist. This also explains the special position of *E. lusitanus* in the N.W. part of the Iberian peninsula. This species was probably the first member of the group that invaded the peninsula and lost contact with its relatives because of the formation of a sea-arm

Fig. 16. *Echinogammarus margalefi* n. sp., ♂, from the type locality. A, mandible palp (scale III); B, first leg (II); C, second leg (II); D, third leg (II); E, fourth leg

(II); F, fifth leg (II); G, sixth leg (II); H, seventh leg (II); I, third uropod (III); J, telson (III).

between N. Africa and Spain in the valley of the present Guadalquivir as happened for instance during the Burdigalien (Sollaud, 1939; Mélenlez, 1965). Once it was isolated, it could develop into a highly specialized species, that could successfully invade and maintain itself in the very poorly mineralized and acid waters in the north-western part of the peninsula, a region that did not change since palaeozoic times. Regarding the distribution pattern of the *Echinogammarus berilloni*-group, it appears that the western parts of the Pyrenees and the adjacent parts of Spain and France form the centre from where most species within this group originated.

Since *E. berilloni* can live without ill-effects in 80% sea-water (Vincent, 1971) and since it can be found in estuaries and even on the open beach, on the condition that competing species are absent (present work, own observation) we must assume that in this case we have to do with invaders from the sea.

Most probably, when regarding the distribution pattern of the various species within this group, there has not been one single invasion, but a series of subsequent invasions. The occurrence of *E. berilloni* s.str. in the lower stretches of the river systems are an indication that this species is the most recent invader. This is supported by the distribution pattern in the western Pyrenees, a region where several species, belonging to this group are found, and where *E. berilloni* inhabits always the more downstream parts of the river systems, while other species as *E. aquilifer*, *E.*

calvus, or *E. longisetosus* occur in the faster running, upper courses of these systems. Such a series of subsequent invasions and successive isolations thus created favorable conditions for the developing of numerous species within this group, all of them with their own, more or less restricted distribution area.

In some regions, especially in the western Pyrenees, where many different types of biotopes can be found, and where climatological conditions are not too extreme, this finally resulted in a distribution pattern which is almost similar to that encountered in the *Gammarus pulex*-group in other parts of Europe, including the typical ecological zonation throughout the river system.

In areas with more severe climatological conditions, e.g. the interior of the peninsula with very hot summers causing the desiccation of the lower stretches, and with very cold winters during which the most upstream stretches of the river freeze, a clearly developed zonation is usually absent and the number of species found within one system is usually reduced to one only.

A problem which is still unsolved is the recent discovery of *E. pacaudi* in a temporary irrigation ditch, near Chilches in the province of Castellon. As yet, this species was known from a rather restricted area (from the northern slopes of the Pyrenees to the river Garonne) only. In spite of intensive sampling, the species never has been found in between these two widely separated areas. Maybe, further and more intensive sampling will provide the answer to this new question.

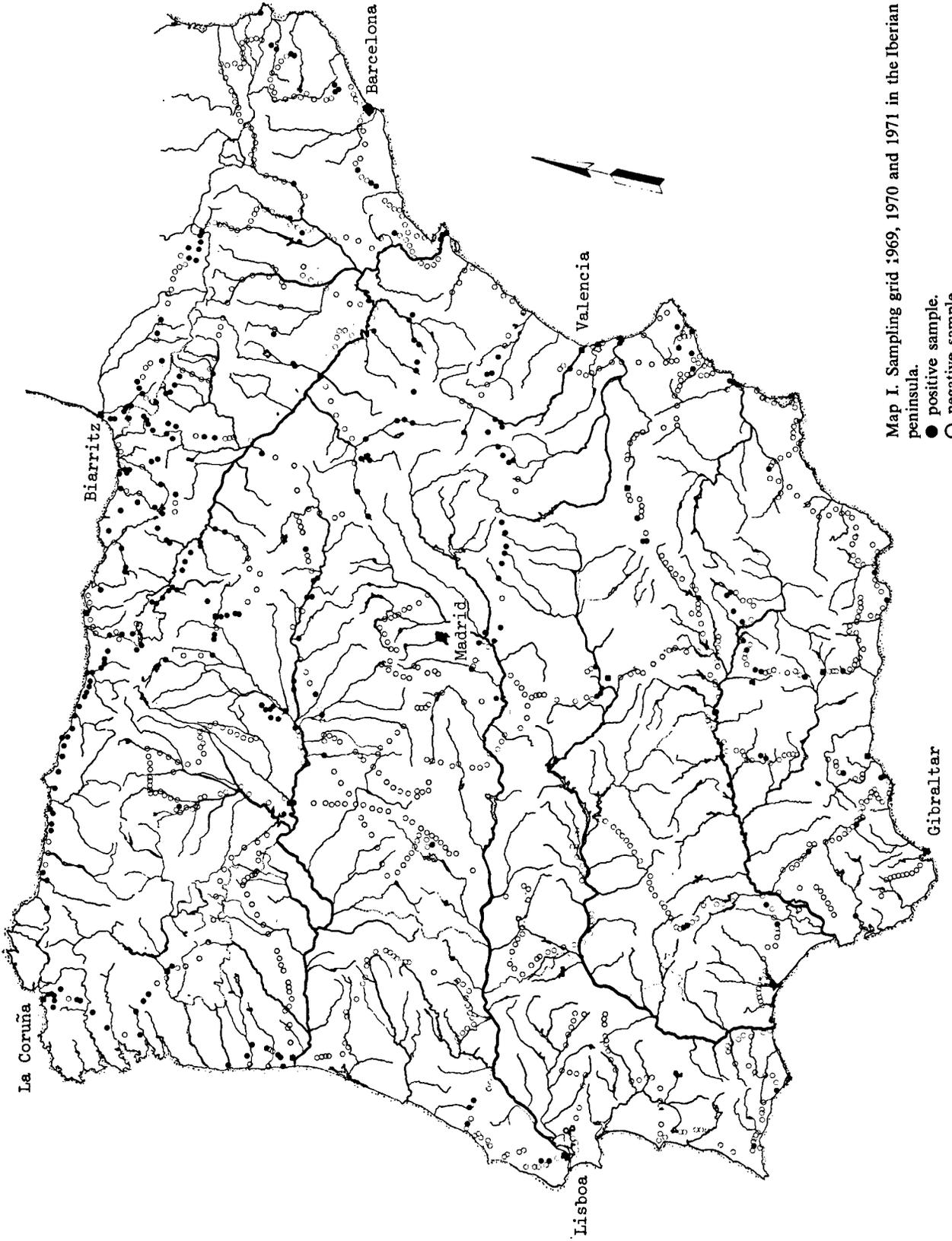
Table I
Sympatric occurrence of members of the *E. berilloni*-group

species	found in 1 sample with	found in the same stream system with
<i>E. berilloni</i>	<i>E. aquilifer</i> <i>E. longisetosus</i> <i>E. zebrinus</i> (<i>E. pacaudi</i>) <i>E. feminatus</i>	<i>E. aquilifer</i> <i>E. longisetosus</i> <i>E. zebrinus</i> (<i>E. pacaudi</i>) <i>E. calvus</i> <i>E. feminatus</i>
<i>E. calvus</i>	<i>E. longisetosus</i>	<i>E. longisetosus</i> <i>E. berilloni</i>
<i>E. margalefi</i>	<i>E. longisetosus</i>	<i>E. longisetosus</i>
<i>E. longisetosus</i>	<i>E. berilloni</i> <i>E. echinosetosus</i> <i>E. aquilifer</i> <i>E. margalefi</i> <i>E. calvus</i>	<i>E. berilloni</i> <i>E. echinosetosus</i> <i>E. aquilifer</i> <i>E. margalefi</i> <i>E. calvus</i>
<i>E. echinosetosus</i>	<i>E. longisetosus</i> (<i>E. pacaudi</i>)	<i>E. longisetosus</i> (<i>E. pacaudi</i>)
<i>E. feminatus</i>	<i>E. berilloni</i> (<i>E. pacaudi</i>)	<i>E. berilloni</i> (<i>E. pacaudi</i>)
<i>E. zebrinus</i>	<i>E. berilloni</i> (<i>E. pacaudi</i>)	<i>E. berilloni</i> (<i>E. pacaudi</i>)

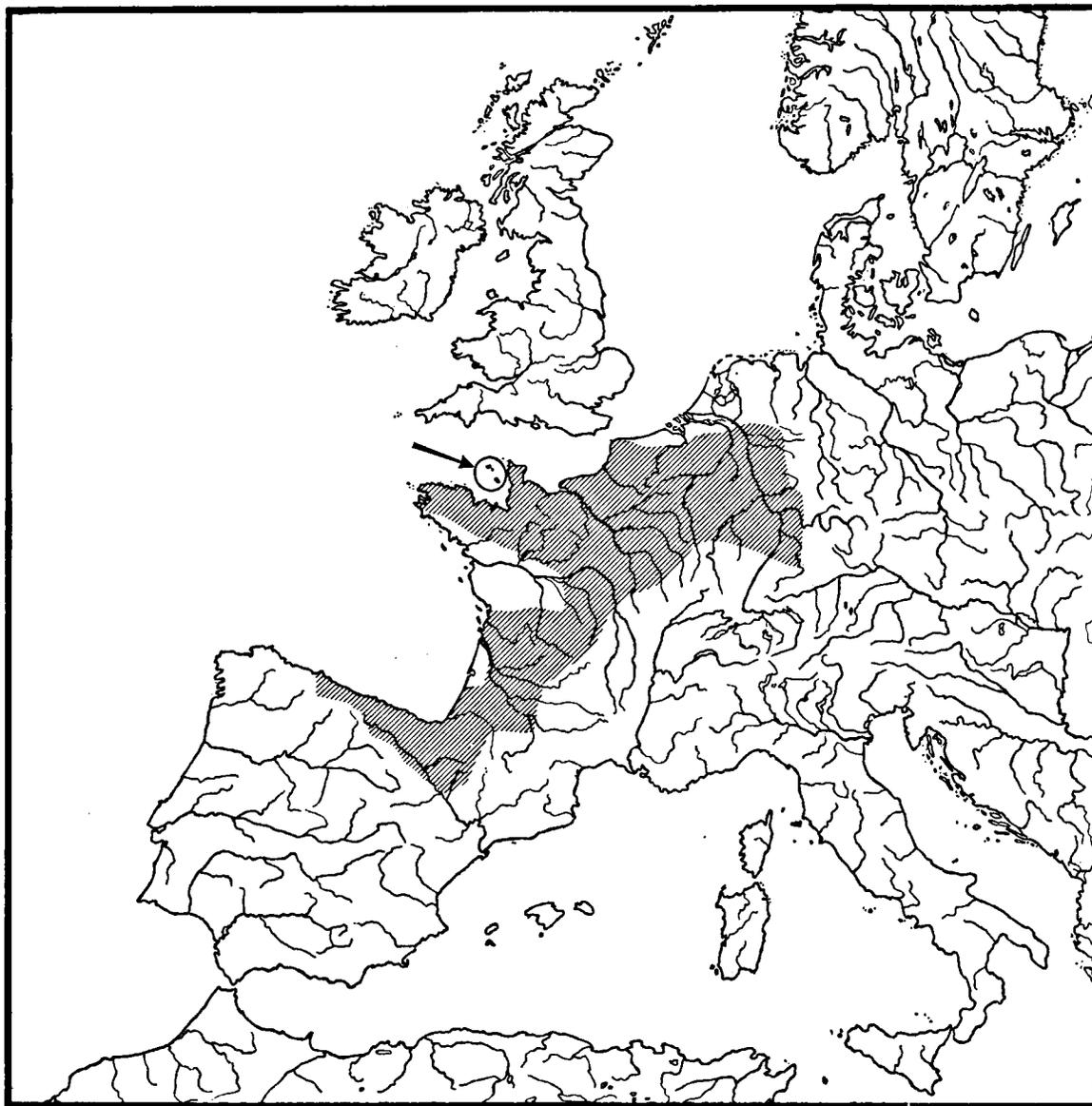
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Map I. Sampling grid 1969, 1970 and 1971 in the Iberian peninsula.
● positive sample.
○ negative sample.



Map II. The distribution of *Echinogammarus berilloni* (Catta) in Western Europe (hatched area plus the encircled Channel Islands).