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THE PRESENT POSITION OF *GAMMARUS TIGRINUS* SEXTON, 1939, IN THE NETHERLANDS, WITH
THE DESCRIPTION OF A NEWLY DISCOVERED AMPHIPOD SPECIES, *CRANGONYX PSEUDOGRACILIS*
BOUSFIELD, 1958 (CRUSTACEA, AMPHIPODA)

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ABSTRACT

Since its first discovery in the Netherlands in 1964, *Gammarus tigrinus* has rapidly spread over inland waters in the western and north-eastern parts of the Netherlands. It appeared that at the end of 1976, *G. tigrinus* had replaced the local *Gammarus* species in most of the newly invaded waters. Surveys carried out in 1978 and 1979 showed a different and rather confusing pattern i.e. that *G. tigrinus* is still extending its range in the delta region of the Netherlands and in the province of Zuid-Holland but that its spreading has come to a stand still in the rest of the country. It has even disappeared from a great number of formerly inhabited waters. In some of these waters indigenous species like *G. d. duebeni* and *G. p. pulex* reappeared after an absence of many years. The severe cold during the winter of 1978/1979 is considered to be one of the main causes of this decline of the *G. tigrinus* population.

During the 1979 survey in the north-eastern part of the Netherlands, another, originally American, amphipod species, *Crangonyx pseudogracilis* Bousfield, 1958, was found. A description of this new faunal element is given.

INTRODUCTION

After its introduction into the Netherlands (probably in 1964) *Gammarus tigrinus* has rapidly invaded nearly all oligohaline waters in the

country as was shown in a series of sampling surveys (see Dieleman & Pinkster, 1977, and fig. 1). In the first years after its introduction *G. tigrinus* was often found together with one or more of the local species *G. d. duebeni* Liljeborg,

1852, *G. zaddachi* Sexton, 1912, and *G. p. pulex* (Linnaeus, 1758), but gradually the impression was gathered that the local species had disappeared from areas in which they used to be very common in former days. Smit (1974) in his 1973 survey paid special attention to the position of these original inhabitants and came to the astonishing result that they had almost completely disappeared from the waters inhabited by *G. tigrinus*. Pinkster et al. (1977) tried to give an answer to the question how this newly introduced species could compete so successfully with the original inhabitants. Possible answers to these questions have been sought in differences in (a) salinity tolerance, (b) salinity preference, (c) life cycle, (d) egg incubation time and (e) time to reach sexual maturity. It was found that in oligohaline waters *G. tigrinus* has a much greater reproductive capacity than any of the three indigenous species, chiefly because of three reasons. In the first place its reproductive cycle, which has a resting stage in the cold winter months and a reproductive stage in the summer months. The two local brackish water species *G. duebeni* and *G. zaddachi* can reproduce only during the colder winter months (in oligohaline waters). Secondly its shorter incubation time which enables the species to produce many (theoretically sixteen) generations during one season. The local forms can only produce one to four generations. Thirdly, its very short time to reach sexual maturity.

Since the last survey in 1976 (Dieleman & Pinkster, 1977) some interesting phenomena occurred, viz., the very cold spring of 1978, causing very low watertemperatures during the period that the overwintering population of *G. tigrinus* usually starts to reproduce, and the long and very cold winter and spring of 1978/1979 resulting in freezing of nearly all surface waters during many months, especially in the northern parts of the country. Since *G. tigrinus* is not able to reproduce at temperatures below 5.0°C, whereas on the contrary the local species *G. zaddachi* and *G. d. duebeni* rather reproduce at low temperatures we were anxious to see if these low temperatures actually had influenced the position of *G. tigrinus* as compared to the local species.

Another interesting feature was the recording of *G. tigrinus* (most probably from the German

population) from localities in the drainage basin of the river Ems, some of them quite close to the Dutch/German border (Herhaus, 1978).

These facts were the stimulus for a new survey along the boundaries of the distributional area as established in 1976, along the eastern border of the Netherlands, as well as in those areas which were covered with ice during many months. The total area investigated during the present survey is indicated in fig. 2.

THE POSITION OF *G. TIGRINUS* AT THE END OF 1979

Unlike the situation found in previous surveys, the overall picture obtained was not easy to explain. On the one hand a range extension was found in the delta region and in the province of Zuid-Holland, but on the other hand *G. tigrinus* had disappeared from extensive areas in the north-eastern parts of the country and in the province of Noord-Holland. The present results, together with the situation found by Dieleman & Pinkster (1977) are illustrated in fig. 1. Table I summarizes the exact localities, dates and chlorinities of the new samples containing *G. tigrinus*.

Notable is the range extension in the southwest, on the islands of Hoeksche Waard and Goeree Overflakkee as well as in the Hollandsch Diep. All these localities, except one, had no gammarid fauna during the previous survey.

In the province of Zuid-Holland the species is gradually invading the central part both from the north and the south; all new localities are deeper waters, often strongly influenced by man (Rotte, Rotte-Lakes (= recreation lake), Grecht, etc.).

In the northern provinces the situation appeared to be completely different. *G. tigrinus* could not be found in many formerly inhabited waters while in other localities it could hardly be retraced because of the reduced population density. There seems to be a correlation between the depth and chlorinity of the water and the presence or absence of *G. tigrinus*. It appeared that in the provinces of Groningen and Friesland *G. tigrinus* had disappeared from nearly all shallower waters (ditches and lakes like the Schildmeer and Tjeukemeer) but that it was still present in the deeper

waterways like the Eemskanaal, the Van Starckenborghkanaal and the Van Harinxmakanaal. Likewise in some waters with a relatively high chlorinity, as can be found behind the dikes of the Waddenzee, the species is still present, although less numerous.

In the central part of the Netherlands the localities just inside the dikes of the former Zuiderzee, inhabited by *G. tigrinus* in 1976, have been abandoned.

In the province of Noord-Holland the situation is more or less comparable with what was found in the northern provinces: *G. tigrinus* is scarce or absent. To illustrate the decline of this recently so successful species we may mention that during the summer of 1979 we were not able to collect enough specimens of *G. tigrinus* for our laboratory experiments, even not within a week, whereas it took us only five minutes in the years up to 1977 ! It must be noticed here that in the neighbourhood of Amsterdam this decline in population density already started in 1978.

Intensive sampling along the Dutch/German border revealed, that no invasion had taken place from any of the populations recently introduced into West Germany.

THE POSITION OF THE INDIGENOUS SPECIES IN THE INVESTIGATED AREA

Gammarus p. pulex (Linnaeus, 1758)

Although *G. tigrinus* won some ground in the central part of the province of Zuid-Holland, *G. p. pulex* is still the dominant species there (fig. 2), with the exception of some lakes in which *G. tigrinus* is the only gammarid. As already discussed by Dieleman & Pinkster (1977), this area is characterized by the presence of many oligohaline, relatively unpolluted ditches with a well-developed and diverse flora and fauna. Verbeek (1977) found *G. p. pulex* to be characteristic for relatively small unpolluted clear waters together with Ephemeroptera and larvae of Odonata. In these habitats *G. tigrinus* was hardly ever found. In lakes and canals *G. p. pulex* was usually absent or found together with *G. tigrinus*.

In the provinces of Friesland and Groningen *G. p. pulex* has maintained its position in the fresh and oligohaline waters on sandy bottoms. In the Tjeukemeer, where *G. tigrinus* used to occur in massive numbers during the last ten years, a small population of *G. p. pulex* has returned after the disappearance of *G. tigrinus*. Likewise *G. p. pulex* won some ground on the Kamper-eiland, near the mouth of the river IJssel, in the province of Overijssel.

In the province of Noord-Holland *G. p. pulex* is more frequently found than in the previous years.

Gammarus d. duebeni Liljeborg, 1852

In the province of Groningen and Friesland *G. d. duebeni* so far did not benefit on a large scale from the disappearance of *G. tigrinus*. In the province of Noord-Holland *G. d. duebeni* is found more frequently than in the previous years, sometimes in rather dense populations, although it certainly did not yet take over the position of *G. tigrinus*. In the province of Zuid-Holland the sudden replacement of this species by *G. tigrinus* in one locality in the Hoeksche Waard (the Wijde Sande near Goudswaard), where it was very abundant in 1976, was remarkable. Now not a single specimen was found among the numerous *G. tigrinus*.

Gammarus zaddachi Sexton, 1912

The position of *G. zaddachi* did not change since the last survey in 1976. It did not take advantage of the disappearance of *G. tigrinus* to re-invade the once abandoned localities. The limited tolerance for low salinities restricts the distribution of this species.

DISCUSSION

A possible explanation for the decline of *G. tigrinus* may be found in the low water temperatures in the spring of 1978 and the subsequent long and very cold winter of 1978/1979. As Pinkster et al. (1977) explained *G. tigrinus* is not able to reproduce at temperatures below 5°C. So in spring

1978 the overwintering females were not able to reproduce because of the low temperatures and many of them must have died before producing offspring. Most probably the first batches of eggs in the brood-pouch never developed into juveniles. In many localities in Noord-Holland it lasted till the end of the summer until a small population had build up again. During the following severe winter of 1978/1979 many shallow waters, especially in the northern provinces, have been frozen to the bottom, a condition which must have been fatal for a large part of the *Gammarus* population. Furthermore, extreme snow-fall prevented light to penetrate into the water beneath the ice, thus creating oxygen depletion as an additional stress. Even if some part of the population did survive, it probably was not able to reproduce in the following spring since water temperatures stayed at a low level till the middle of May. In deeper waters and in waters with a relatively high chlorinity the influence of the frost has been less severe. In those waters *G. tigrinus* could survive in the bottom layers of about 4°C and raise a new generation at the end of the summer of 1979. Locally, thermal pollution may act favourably (e.g. Berumermeer, Van Starckenborghkanaal).

In the southwestern part of the country the influence of the winter has been shorter and less severe than in the northern part, which may explain the differences found.

Most probably the severe winter did not affect the populations of *G. p. pulex* and it even looks as if this species took advantage of the decline of *G. tigrinus* to return to formerly inhabited localities.

As could be expected *G. d. duebeni* and *G. zaddachi* did not suffer much from the severe winter and *G. d. duebeni* could even take some advantage of it in its competition with *G. tigrinus*. Likewise it is clear that because of the unfavourable reproduction time and consequently low reproductive capacity (in oligohaline waters) they were not able to rapidly repopulate the localities deserted by *G. tigrinus*. It will be very interesting to follow the future developments and the long term effects of the variations in the climatic conditions on the position of *G. tigrinus* and the indigenous species.

FIRST RECORD OF *CRANGONYX PSEUDOGRACILIS*
Bousfield, 1958, IN THE NETHERLANDS

During the present survey we unexpectedly came across another amphipod species, so far unknown to the Dutch fauna, which was identified as *Crangonyx pseudogracilis* Bousfield, 1958. Like *G. tigrinus* this originally North American species was recently introduced into England and has become common in central and southern England and Wales, extending towards Yorkshire, with isolated records from Northumberland, Grangemouth, the Lake district and the Norfolk Broads. It inhabits rivers, canals, ponds, lakes and reservoirs (Gledhill, Suttcliffe & Williams, 1976). Recently it has also been recorded from a pond in Dublin, Ireland (Holmes, 1975). It can tolerate saline and polluted waters.

During the present survey it was found for the first time in a moderately polluted canal near Boerakker in the province of Groningen. Since then intensive sampling has been carried out in the many water systems connected with this first locality. It appeared to be present in six other localities, up to 15 km from the first (see fig. 3 and Table II). All these localities, except one, are moderately polluted larger waterways.

So far little is known about the biology of the species in these newly invaded habitats. In a future publication we shall try to give more details on these aspects and on the range extension of this species in the Netherlands. It will be clear that the presence of this new invader offers an interesting possibility to study the mechanism of dispersal and the competition with other species.

Since *C. pseudogracilis* is new to the Dutch fauna, a complete description of both sexes is given.

Diagnosis.-

A small to medium size species from surface waters. It can be easily distinguished from other epigeal forms in western Europe because of its smooth unarmed dorsal surface (fig. 4A); outer margin of uropod 3 armed with marginal spines only; telson cleft to about the middle; pereopod 6 always longer than pereopod 7.

Description.-

Male: Much smaller than the female; maximum length observed 4 mm. Metasome and urosome segments rather flat, the dorsal armature being completely absent (fig. 4A).

The lateral cephalic lobes rounded. Eyes well-developed, reniform, up to twice as long as wide, their upper margin widely separated from the middorsal line.

First antenna (fig. 4B) less than half as long as the body length. Third peduncle segment about half as long as each of the other two. The number of segments in flagellum and accessory flagellum is 14 to 18 and 2 respectively. The armature is poorly developed. Some of the flagellar segments bear club-shaped aesthetascs.

Flagellum of second antenna (fig. 4C) poorly developed. Usually no more than five segments, gradually decreasing in length can be found. Characteristic spirally wound club-shaped aesthetascs are found on peduncle segments 4 and 5 and on some of the flagellar segments (figs. 1C and C').

Mouth parts: Mandibles (fig. 6A) subequal; they have strongly dentate cutting edges, a row of five feathered setae and a well-developed molar. First segment of mandibular palpa unarmed, second segment with 8 to 12 setae along the inferior margin; third segment armed with one A-seta, an irregular row of 12 to 14 D-setae, 5 E-setae and 2 long C-setae (for terminology see Karman, 1971). Inner lobe of the first maxilla (fig. 6B) armed with 8 apical plumose setae; the palp with 7 or 8 slender spines (or stiff setae). Inner plate of maxilla 2 (fig. 6C) with a row of 5 plumose setae implanted on the inner surface. Inner plates of the maxillipeds (figs. 6D, D') armed distally with a series of strong spine teeth. The palp is well-developed. The lower lip (fig. 6E) has small inner lobes. For further details of the mouth parts see figs. 6A-E.

Propodus of gnathopod 1 (fig. 4D) smaller than that of gnathopod 2 (fig. 4E). The palm is set with a double row of spine teeth (fig. 4D'); the strongest of them implanted near the palmar angle. The moderately slender dactylus hardly reaches the palmar angle.

Propodus of gnathopod 2 (fig. 4E) more elongate than in gnathopod 1. Palm likewise set with a double row of spine teeth (fig. 4E'). The

dactylus almost reaches the palmar angle. For the remainder the armature of both gnathopods is poorly developed.

Coxal plates of gnathopods 1 and 2 and pereopod 3 longer than broad, each set with some setae. Coxal plate 4 about as broad as long. Armature of pereopods 3 and 4 (figs. 4F, G) very poor. Dactyli slender.

Pereopods 5 to 7 also poorly armed. Dactyli relatively slender (fig. 5F). Basal segments (figs. 5F-H) strongly serrate. Pereopod 6 always longer than pereopod 7.

Basipodite of uropod 1 strongly developed. Endopodite about $3/4$ as long as exopodite; both are armed with numerous spines (fig. 4H). The endopodite of uropod 2 is likewise about $3/4$ as long as the exopodite; it is distally armed with a characteristic comb-like row of short spines (fig. 4I). Uropod 3 (fig. 5I) weakly developed; endopodite very short, unarmed; exopodite 1.5 to 2 times as long as the basipodite, armed with spines only.

The posteroinferior corners of epimeres 1 to 3 are always more or less acute (fig. 4A, 5E), poorly armed with a few spinules only.

Telson (fig. 4I) cleft to about the middle, its lobes distally armed with 2 or 3 spines.

Female: Much larger than the male; maximum length observed 9 mm. Marked sexual dimorphism exists in almost every appendage and is summarized as follows: (1) The absence of the characteristic aesthetascs in the first and second antennae (figs. 6F, G); the somewhat denser and longer setation of antenna 2. (2) The relatively weak propodus of gnathopod 1 as compared to that of gnathopod 2; the absence of the characteristic double row of spine teeth on the palms of both gnathopods; the better developed setation of the gnathopods (figs. 5A, B). (3) The higher number of spines and setae on pereopods 3 to 7. (4) The absence of the comb-like row of spines on the endopodite of uropod 2.

Variability.-

So far no important variability has been observed, except in the number of spines and setae on the appendages. This was hardly to be expected since all material was collected during a short period within a restricted area. In the future monthly samples will be taken which may

give us more information about the possible seasonal variability of morphological characters.

Remarks.-

This species, which is new to the Dutch fauna, can be easily recognized in the field because of its different locomotory behaviour. Unlike all other indigenous aquatic amphipod species it does not crawl on its side but it "walks" upright like talitroid species.

Considering the present distributional area and the number of specimens found, the introduction of this species must have taken place already some time ago. It may have occurred some time between autumn 1976, when no *Crangonyx* was found in the present distributional area, and 1979.

So far two *Crangonyx* species are known from western Europe, viz. *C. subterraneus* Bate, 1859, and *C. paxi* Schellenberg, 1935. These species can be easily separated from *G. pseudogracilis* since they lack eye pigments. They both live in subterranean waters (Schellenberg, 1942).

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Table I

NEW RECORDS OF *GAMMARUS TIGRINUS* IN THE NETHERLANDS SINCE AUTUMN 1976

Locality	Municipality	Accompanying <i>Gammarus</i> species	Date	mg Cl/1
Province of Zuid-Holland				
Dinsdagsche Wetering, E of Noordwijk-Buiten	Noordwijk		28-VI-1978	-----
Haarlemmer Trekvaart, near Voorhout	Voorhout		28-VI-1978	-----
Noordwijksche Vaart, 1 km N of Rijnsburg	Rijnsburg		28-VI-1978	-----
Oegstgeester Kanaal	Oegstgeest		28-VI-1978	-----
Rotte, near Zevenhuizen	Zevenhuizen		23-VI-1978	-----
Upper course of Rotte, 1 km W of Moerkapelle	Moerkapelle	<i>G. p. pulex</i>	23-VI-1978	
Rotte at Oud Verlaat	Zevenhuizen		21-IX-1979	239
Newly dug pool E of Oud Verlaat	Zevenhuizen		21-IX-1979	234
Logger Vliet, 3 km NE of Numansdorp	Numansdorp		8- X-1979	235
Kreek, at Zuidzijde	Nieuw Beyerland		8- X-1979	255
Kleine Gat, 2 km N of Z. Beyerland	Zuid Beyerland		8- X-1979	293
Ditch in Eendrachtspolder, 2 km W of Nieuwendijk	Goudswaard		8- X-1979	810
Oude Wijde Sandee, 0.5 km SE of Goudswaard	Goudswaard		8- X-1979	1488
Zuiderdiep, 2 km N of Dirksland	Dirksland		8- X-1979	413
Ditch in polder Kraaijenisse, 1 km NE of Melissant	Dirksland		8- X-1979	373
Binnenhaven at Stellendam	Goedereede		8- X-1979	384
Wilnise Zuw, 2 km S of Wilnis	Wilnis	<i>G. p. pulex</i>	22-VI-1978	347
Grecht, 1.5 km S of Woerdense Verlaat	Nieuwkoop	<i>G. p. pulex</i>	21-VI-1978	-----
Ditch, directly NE of Kockengen	Kockengen		22-VI-1978	-----
Province of Noord-Brabant				
Hollandsch Diep, 1 km W of Willemstad	Willemstad		14-IX-1978	-----

Table II

RECORDS OF *CRANGONYX PSEUDOGRACILIS* IN THE NETHERLANDS

Locality	Municipality	Accompanying <i>Gammarus</i> species	Date	mg Cl/1
Matsloot at Boerakker, NW of Leek	Leek		8-VIII-1979	51.4
Wold- or Langsdiep at Sebaldeburen	Zuidhorn		8-VIII-1979	91.9
Wold- or Langsdiep 0.5 km S of Gaarkeuken	Grijpskerk		26- X -1979	
Wold- or Langsdiep between Ooster- and Westerzand	Grootegast		1- X - 1979	
Schipsloot at Hamrik	Marum		1- X -1979	56
Oude Dwarsdiep near Lucaswold	Marum		1- X -1979	79
Letterbretterdiep at Enumatil	Leek	<i>G. p. pulex</i>	10- X -1979	
Hunze, SW of Adorp	Sauwerd	<i>G. tigrinus</i>	10- X -1979	

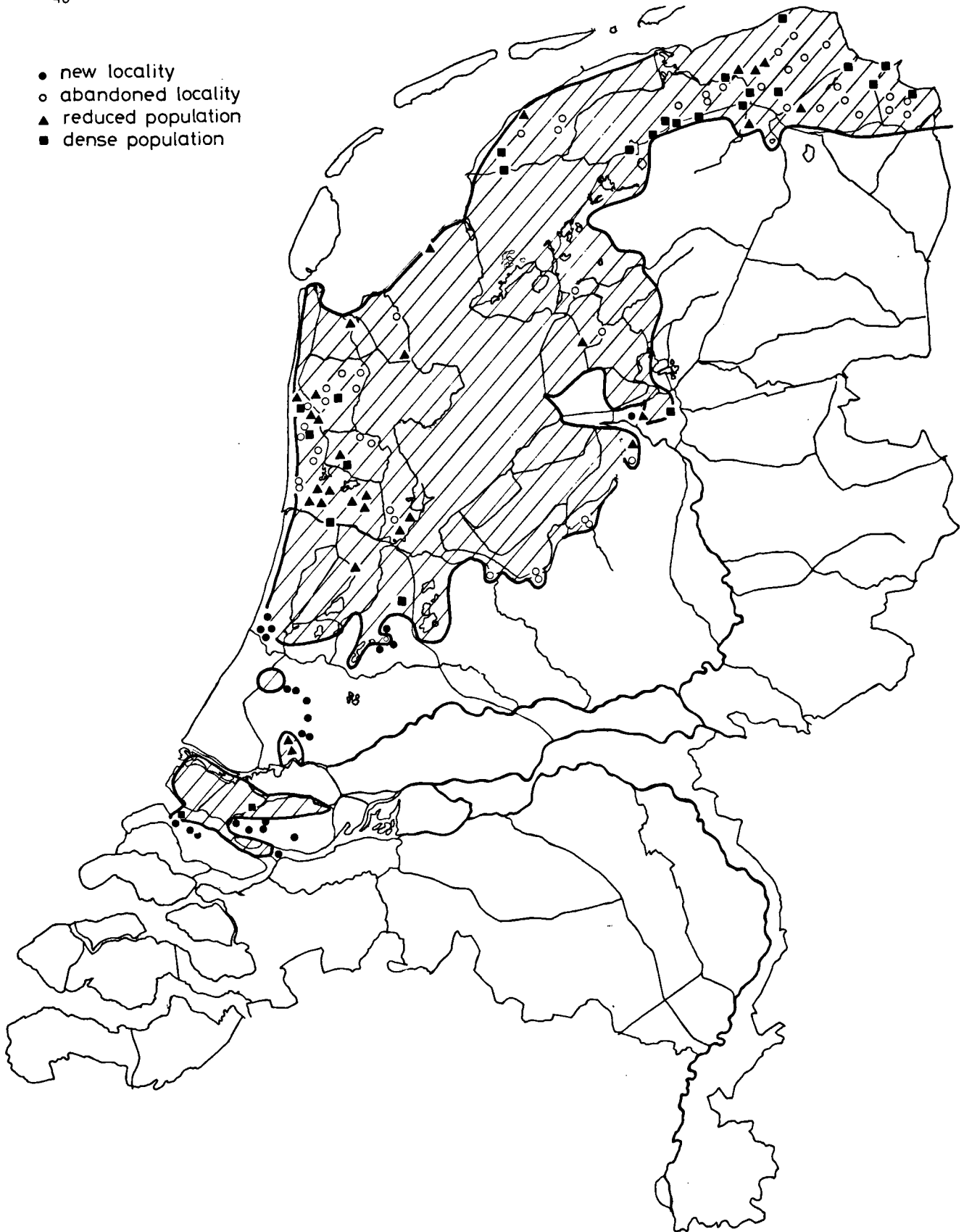


Fig. 1. Records of *Gammarus tigrinus* in the Netherlands at the end of 1979. ● new locality (or group of proximate localities); ○ formerly inhabited, now abandoned localities; ■ old locality with healthy, dense population; ▲ old locality with very reduced population. The minimal area occupied by the species at the end of 1976 is hatched.

- ▲ *G. zaddachi*
- *G. duebeni*
- *G. pulex*

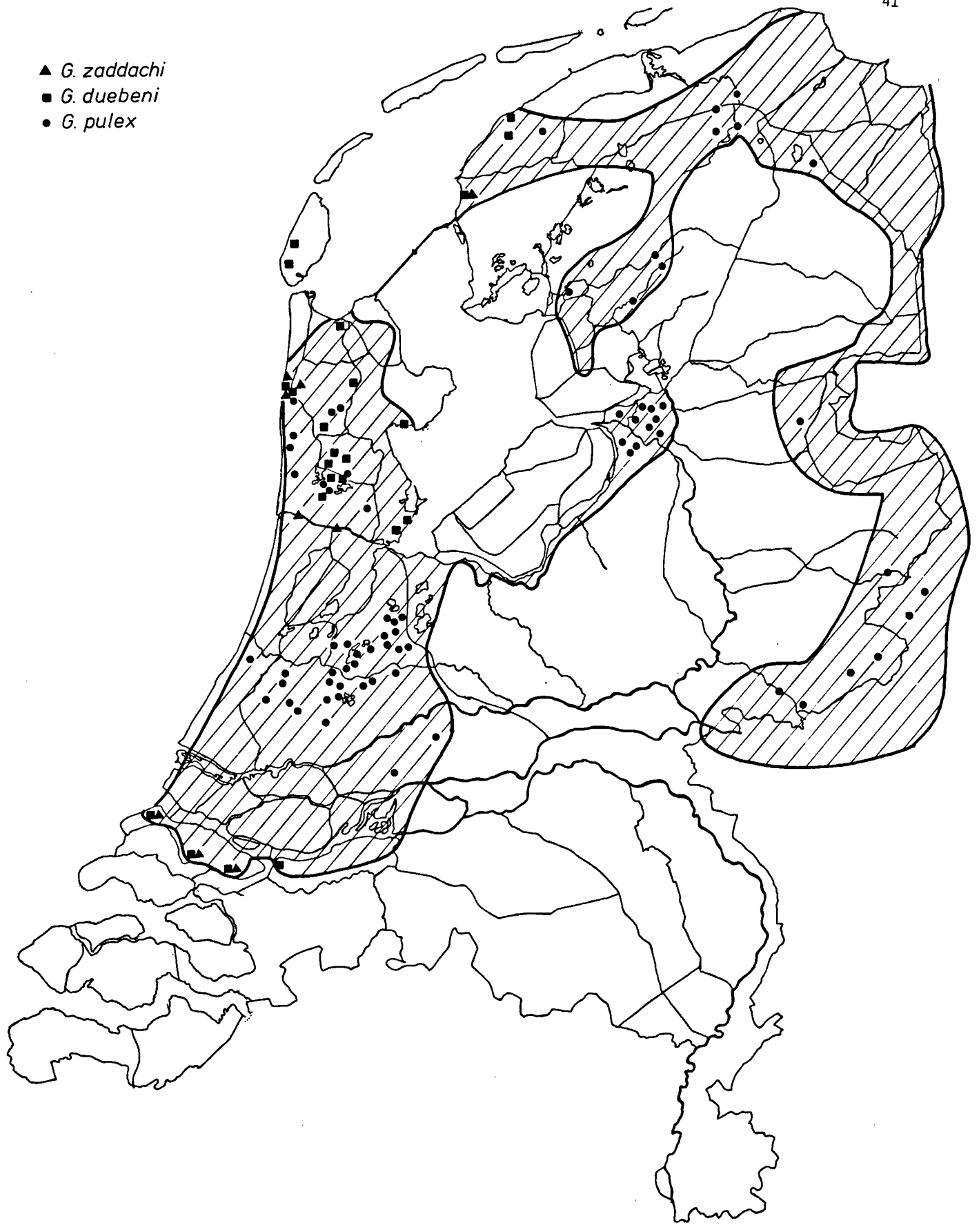


Fig. 2. Records of indigenous *Gammarus* species in the area investigated (hatched). ● *Gammarus p. pulex*; ■ *Gammarus d. duebeni*; ▲ *Gammarus zaddachi*.

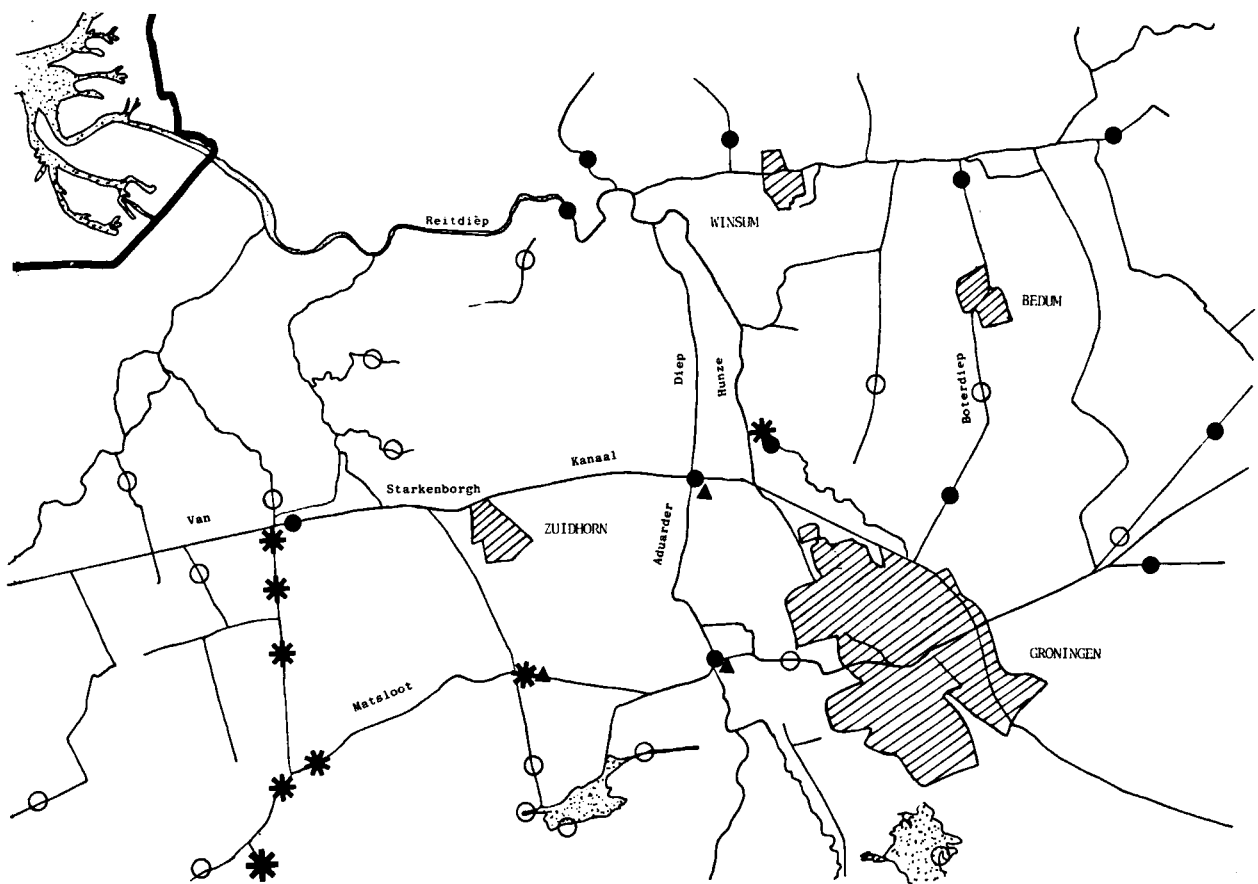


Fig. 3. Distribution of *Crangonyx pseudogracilis* and other aquatic amphipod species at the end of 1979. * *C. pseudogracilis*; ▲ *G. p. pulex*; ● *G. tigrinus*; ○ negative sample.

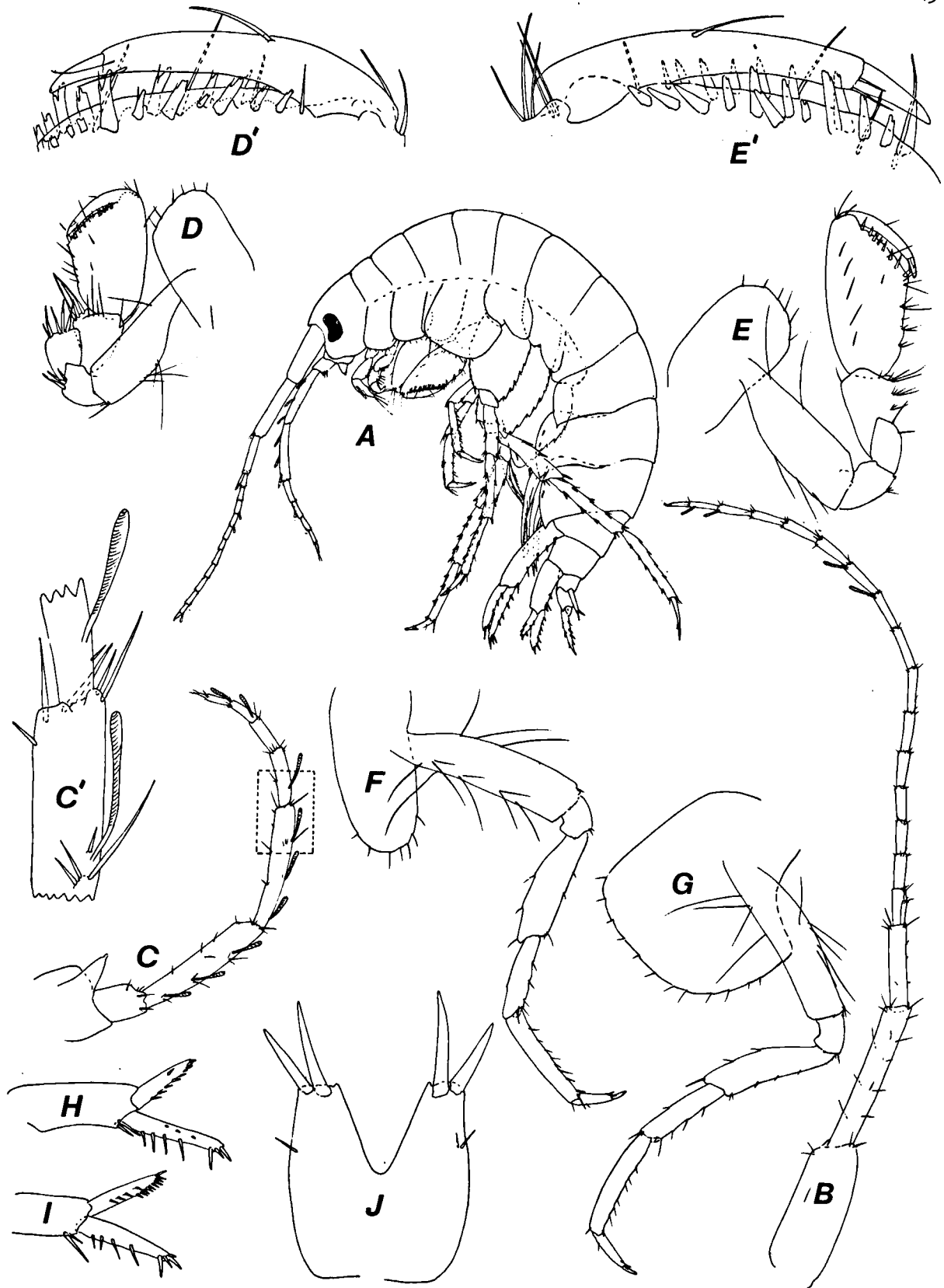


Fig. 4. *Crangonyx pseudogracilis* Bousfield, 1958, ♂ from Boerakker, province of Groningen, the Netherlands. A, habitus (scale I); B, first antenna (III); C, second antenna (III); C', detail of second antenna (V); D, first gnathopod (III); D', detail of first gnathopod (V); E, second gnathopod (III); E', detail of second gnathopod (V); F, third pereiopod (III); G, fourth pereiopod (III); H, first uropod (III); I, second uropod (III); J, telson (V).

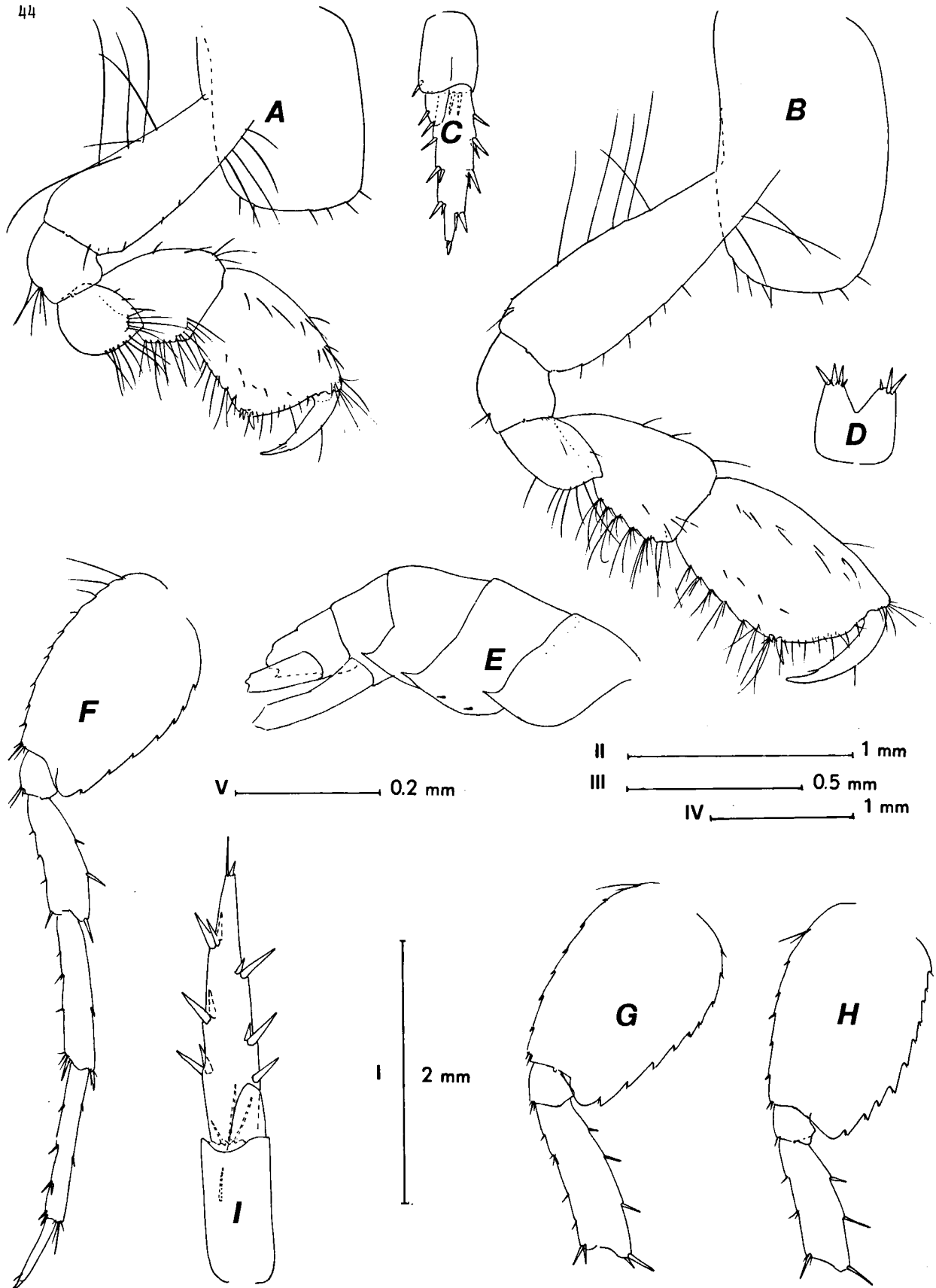


Fig. 5. *Crangonyx pseudogracilis* Bousfield, 1958, A-E ♀, F-I ♂, from Boerakker, province of Groningen, the Netherlands. A, first gnathopod (scale III); B, second gnathopod (III); C, third uropod (III); D, telson (III); E, pleosome (I); F, fifth pereopod (III); G, sixth pereopod (III); H, seventh pereopod (III); I, third uropod (V).

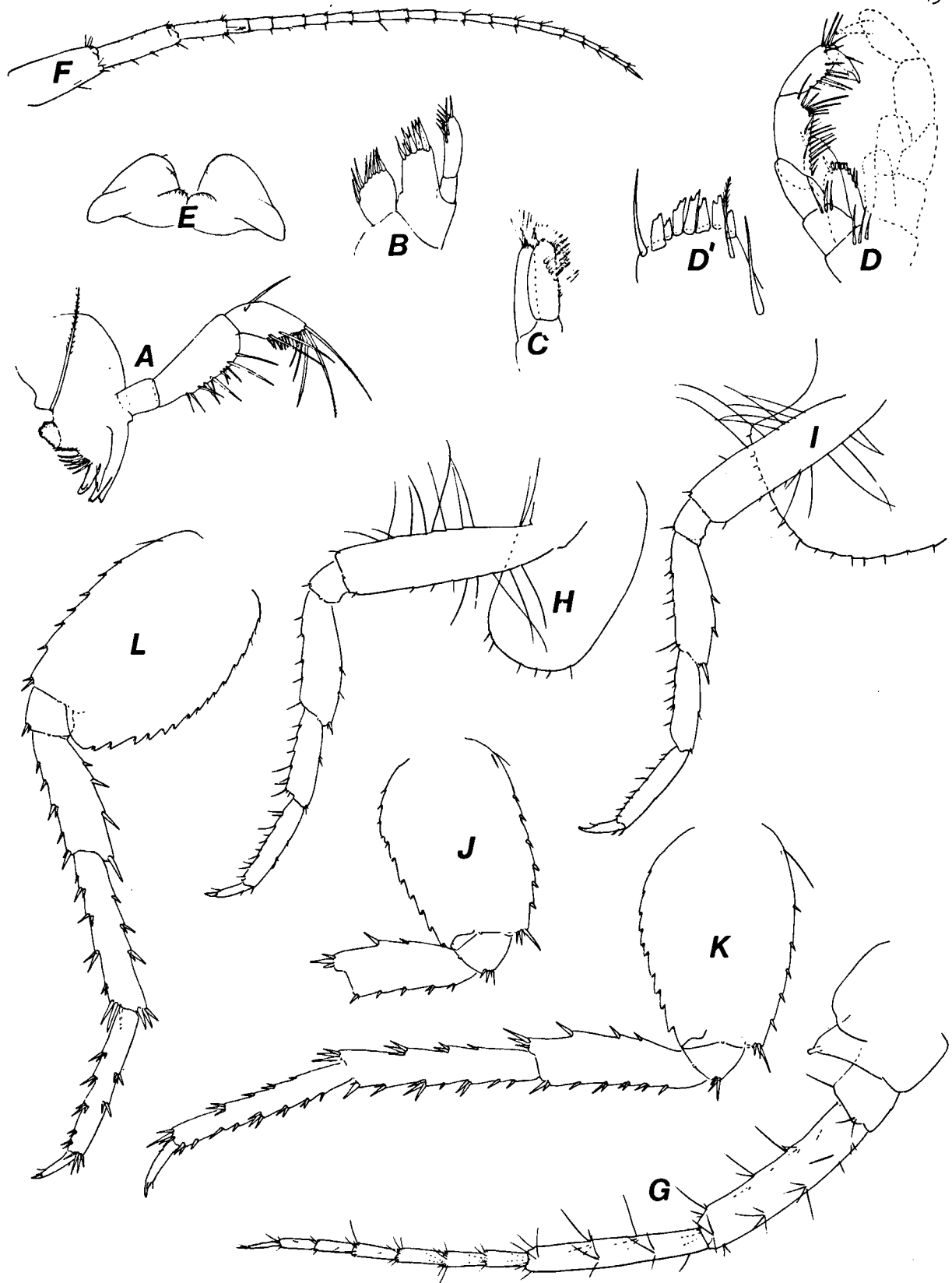


Fig. 6. *Crangonyx pseudogracilis* Bousfield, 1958, ♀ from Boerakker, province of Groningen, the Netherlands. A, mandible (scale III); B, first maxilla (III); C, second maxilla (III); D, maxilliped (III); D', detail of maxilliped (V); E, lower lip (III); F, first antenna (III); G, second antenna (III); H, third pereopod (II); I, fourth pereopod (II); J, fifth pereopod (II); K, sixth pereopod (II); L, seventh pereopod (II).