

REMARKS ON *GAMMARUS LACUSTRIS* G. O. SARS, 1863,
WITH DESCRIPTION OF *GAMMARUS VARSOVIENSIS* N. SP.
(CRUSTACEA, AMPHIPODA)

by

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ABSTRACT

On the ground of the examination of a large material from Poland and from other countries, the variability of *Gammarus lacustris* G. O. Sars, 1863, is discussed. *Gammarus wigrensis* Micherdziński, 1959, is in the author's opinion an immature *G. lacustris*.

A detailed description of *Gammarus varsoviensis* n. sp. is given. Some ecological and biological data on both species are discussed, as well as their distribution in Poland.

INTRODUCTION

Gammarus lacustris G. O. Sars, 1863, is regarded by the majority of the European authors as a monotypic species (Segerstråle, 1954; Micherdziński, 1959; Økland, 1969; Roux, 1972; Pinkster, 1972). In North America, however, Bousfield (1958) recognized two subspecies, *G. l. lacustris* and *G. l. limnaeus* Smith, 1874. Schellenberg (1937) pointed out the differences in some morphological features between various Eurasian populations, belonging in his opinion to *G. lacustris*. He regarded *Rivulogammarus scandinavicus*, *R. stoliczkae* and *R. bolkayi* of S. Karaman (1931, 1934a, 1934b) as well as *Gammarus pulex extensus* Martynov, 1931, as synonyms of *G. lacustris*. On the other hand, in his 1942 monograph, Schellenberg suggested that this diversity could not simply be regarded as variability within a species, but as closely related forms: "Nahestehende Formen sind über Eurasien weit verbreitet" (: 33). Segerstråle (1954) and Pljakić (1963) noticed some morphological differences among various *G. lacustris* populations in Scandinavia and in Yugoslavia, but did not recognize any new taxa.

Abbreviations. —

IZPAN W-wa = Zoological Institute, Polish Academy of Sciences, Warsaw; MZUWr = Zoological Museum,

University of Wrocław; ZZOUŁ = Department of General Zoology, University of Łódź; ZMA = Zoological Museum, University of Amsterdam.

A = antenna; P = pereopod; U = uropod.

MORPHOLOGICAL REMARKS

The following morphological details have been used in distinguishing *G. lacustris*: length of the antennae and number of their flagellum segments, eye size, setosity of P3 and P4, shape of the P7 basis, shape and armature of the epimeral plates, urosomal armature, mutual proportions of the third uropod rami and the armature of its exopodite outer margin. All these features may be of importance provided that the population variability, associated with sex, age and season, are considered and the dimensions of the morphological features are given quantitatively.

The confusion concerning *G. lacustris* may, in the author's opinion, originate from the lack of a careful study of its life cycle. In Poland the largest specimens of this species are found in spring (males up to 24, females up to 20 mm). This wintering generation, after the breeding period, dies in June and July. In summer mostly young animals are collected. In early autumn, owing to rapid growth in the hot months, animals up to 14 mm are available, though these are, in general, subadult specimens. They have initial or at most medium-sized oöstegites in females and only a few (0—5) calceoli in males.

In connection with these observations the results of Menon (1969) are worth mentioning. After examination of a large material he proved, that in a *G. lacustris* population, inhabiting a Canadian lake near Edmonton (Alberta), in August and September only 1 or 2% of the total population

were adult, the remaining being juveniles and immatures. It is to be noted that the area of Menon's investigations lies at the same latitude as northern Poland, about 54° N.

These large but not entirely full-grown gammarids can be mistaken for mature ones, but in comparison with adult, vernal *G. lacustris* specimens, they have different body proportions and are less spiny and setose. In the author's opinion the description of *Gammarus wigrensis* by Micherdziński (1959) is based on such specimens.

Micherdziński (1959) distinguished *G. wigrensis* from *G. lacustris* on the basis of the smaller eye, more slender dactyli and less dense armature of the U3 exopodal outer margin in the former. The present author was fortunate enough to be able to examine the type-material of *G. wigrensis* as well as about 40 paratypes and other specimens identified by Micherdziński as this species. All these specimens are considered young or subadult stages of typical *G. lacustris*, collected in late August and early September. The type specimen, a young male 13 mm long, has only 2 calceoli. The feminine appearance of its gnathopods, also used to some extent as a distinguishing feature of *G. wigrensis*, is normal for young males of many gammarid species. All females in the material examined had small, initial oöstegites and the number of calceoli in males did not exceed 5 (one exception: 8 calceoli in a male of 14 mm long) and ranged from 1 to 3 in animals up to 12 mm in length.

Micherdziński (1959) regarded the comparatively sparse setation of the outer margin of the U3 exopodite as the most important distinguishing feature and reported that in *G. wigrensis* the total number of setae does not exceed 12, feathered setae do not exceed 7, whereas in *G. lacustris* their number reaches 40 and 20, respectively.

In Poland, however, the present author has found certain populations of *G. lacustris*, with adults of 16—20 mm in length, that have richly setose third uropods, with over 50 setae on the exopodal outer margin; about half of these setae is feathered (viz. in a lake in Mosina, Poznań prov.; in peat-bog tarns in Błonie, Łęczyca district, Łódź prov.). In other populations of *G. lacustris*, on the other hand, the largest specimens have corresponding numbers of these setae that rarely exceed 30 and 15, respectively (Gieret Lake, Sejny district, Białystok prov.; Żarnowieckie Lake near Gdańsk; Huczwa River near Werbkowice, Lublin prov.). Consequently, in populations of the first group, smaller and younger subadult specimens,

measuring 10—14 mm, already have a "lacustris-like" setation of the U3 exopodite, with some 20 setae, among which about 10 are feathered, while those of the second group have a "wigrensis-like" setation, with about 10 setae, of which 5 plumose, as mean values. All adult specimens of *G. lacustris* from more than 30 samples collected in the Suwalskie Lakes area, and also from the type locality of *G. wigrensis*, Wigry Lake, exhibited this second type of setation.

The author was also able to examine 11 gammarid samples from Zoölogisch Museum, University of Amsterdam, containing some 300 specimens collected by Mr. J. D. van Mansvelt in the summer of 1971 in northeastern Poland and identified as *G. wigrensis* (coll. nrs. ZMA Amph. 103420 to 103430). All these samples consist of young or subadult *G. lacustris* only, except sample no. 103425 (Necko Lake), in which *G. lacustris* is mixed with a new species, to be described below. The author found in this Amsterdam material only one female specimen (about 13 mm in length) with brood pouch. Its U3 first exopodal segment had about 30 setae on the outer margin; half of these setae were feathered, as is typical for *G. lacustris*. Some of the largest male specimens in these samples, about 12—14 mm long, possess a few calceoli. The majority of male specimens up to about 12 mm in length have none or only 1 to 3 calceoli.

A biometrical analysis of Polish material of "*G. wigrensis*" is presented in table I. As expected, the amount of U3 setation increases gradually with size. As all these animals were collected at the beginning of autumn (26.VIII—2.IX.1935, coll. S. Feliksiak), large specimens with denser setation are lacking. Such specimens may be present in October-November; these would fill the gap between summer "*G. wigrensis*" and spring *G. lacustris*.

It is worth while to bear in mind, that Micherdziński himself (1959: 576), when describing "*G. wigrensis*", has stressed the need of further investigations in the light of the variability range of *G. lacustris*.

The above mentioned diversity in *G. lacustris* populations, as shown by the setation of the U3, should be considered in further detailed investigations of the *G. lacustris*-group. Up to now the author has not observed any correlation between this feature and the habitat. Both densely and sparingly setose populations were found in stagnant as well as in running waters. It should be borne in mind as well, that interbreeding experiments be-

Table I. Variability of some morphological features of "*Gammarus wigrensis*". Paratypes from the Wigry Lake, Białystok prov., Poland, and other specimens from nearby localities; all collected from 26.VIII. to 2.IX.1935, identified by W. Micherdziński. The number of specimens examined has been parenthesized.

Length class (mm)		7—9	9—11	11—13	>13
Number of calceoli (♂♂)	range	0	0—3	0—5	5; 8
	mean	0 (4)	0.6 (8)	2.0 (15)	—
Eye: length/width ratio	range	1.4—1.8	1.4—1.8	1.5—1.9	1.5; 1.8
	mean	1.6 (6)	1.6 (14)	1.6 (15)	—
P7 dactylus: length/max. width ratio	range	3.4—4.5	3.4—4.7	3.5—4.6	4.0; 4.1
	mean	4.0 (6)	3.9 (14)	4.3 (15)	—
U3 exopodite I outer margin: N of all setae	range	3—10	5—14	3—16	15 19
	mean	5.7	9.3	10.3	—; —
N of feathered setae	range	0—4	1—5	1—7	5 4
	mean	— (6)	— (13)	— (12)	—
U3 rami proportions: endopodite / exopodite I × 100	range	77—84	80—89	80—89	86; 91
	mean	82.0 (6)	84.6 (13)	84.8 (12)	—

tween the two Canadian subspecies of *G. lacustris*, one from a lake (*G. l. lacustris*), the other from a stream (*G. l. limnaeus*) gave positive results (Hynes & Harper, 1972), showing the lack of genetic barriers between morphologically and ecologically different populations.

Eye and dactyli proportions, when not exactly measured, are of little taxonomic value. The author investigated these features in some *G. lacustris* populations, using the length/width ratio. The indices for the eye ranged from 1.4 to 1.7, whereas those for the P7 dactylus ranged from 4.0 to 5.5, usually from 4.0 to 4.5. It is possible that the ratio eye length/head length would be more useful, but it should be mentioned that Segerstråle (1954) supposed an influence of temperature and of nutritive conditions on the eye size in *G. lacustris*.

Garbini (1895) recorded *Gammarus fluviatilis zachariasi* from the Lake of Plön (Germany); Straškraba (1967) presumes this to be identical with *G. wigrensis*. Schellenberg (1934) recorded both *G. lacustris* and *Gammarus pulex* (Linnaeus, 1758) from this lake, while Ehrenberg (1957) recorded *G. pulex* only. The present author found indeed in Ehrenberg's material (10 samples) merely *G. pulex*. Most likely both species living in this lake occupy somewhat different habitats, and thus may not always be found together. *G. fluviatilis zachariasi* Garbini, 1895, probably is based on immature specimens of *G. lacustris*.

The differences between *G. l. lacustris* and *G. l.*

limnaeus, as given by Bousfield (1958: 60), deserve some discussion. According to Bousfield (loc. cit.) *G. l. lacustris* has the epimera 2 and 3 "... weakly acute, not produced posteriorly...", while in *G. l. limnaeus* they are "... acute, produced posteriorly, ...". In practice it is very difficult to evaluate to what extent the epimeral plate is produced. Pinkster (1972: 166) in the diagnosis of European *G. lacustris*, which according to Bousfield belongs to the nominal subspecies, states: "The posterodistal corner(s) ... of the second and third (plates) are always sharply pointed.". Cole (1970), in discussing the shape and armature of the epimeral plates in North American gammarids has also expressed some doubts, describing second epimera of both subspecies of *G. lacustris* as "... remarkably produced" (: 342, 345, figs. 23, 26).

The differences in eye shape, both in diagnosis, key and figures of Bousfield (1958) are not sufficiently marked to separate reliably the subspecies in question. The difference in the total number of urosome spines seems to be the most useful, since the ranges given by Bousfield do not overlap (10—14 for *G. l. lacustris* and 14—24 in *G. l. limnaeus*). In the majority of populations of *G. lacustris* from Poland the total number of urosome spines range from 8 to 16 in about 95 % of the animals. The most common formula of urosome spines is 1 : 2 : 1, 1 : 2 : 1 and 1 : 0 : 1. In a lake in Mosina (Poznań prov.), however, a rather spiny population was encountered, in which the most

common formula is 2 : 2 : 2, 2 : 2 : 2 and 2 : 0 : 2. Occasionally, the present author has found in Poland large specimens of *G. lacustris* with urosome spines adding up to 20.

The armature of the lower portion of the epimeral plates (Cole's, 1970, facial and submarginal ventral armature) also deserves attention. This feature, among others, was used by S. Karaman (1931) when describing *Rivulogammarus scandinavicus*. I investigated this feature in *G. lacustris* in many samples from Poland and in several samples from other countries (Canada, Great Britain, Finland, U.S.S.R.). The armature of the lower portion of the 2nd epimeral plate, which is most often considered, consisted usually of spines and rather long setae, but in various proportions — in some populations numerous setae (up to 10) prevailed, in other populations spines were predominant. Moreover, sometimes one can find in the same population specimens rather dissimilarly armed in this respect. Characteristic of a great majority of *G. lacustris* examined, even young specimens, is a minimum of one rather long seta on the anterior part of the submarginal ventral portion of epimeron 2 (fig. 2E). This feature is also clearly illustrated in Schellenberg's drawings (1937: 492, fig. 3) of the epimera of various European *G. lacustris* populations.

The rather wide range of the number of A1 flagellum segments in *G. lacustris* should be stressed here, whereas, in a particular population, this number is dependent on sex and size. The results of the examination of several specimens from various populations are given in table II. Pinkster (1972) reports for males of *G. lacustris* a

range from 18 to 25 segments. In *G. lacustris* populations from the Yugoslavian mountain lakes, Pljakić (1963) has found higher numbers, reaching even distinctly more than 30. Similarly, Schellenberg (1937) reports a number of A1 flagellum segments in *G. lacustris* from the Bodensee of over 30.

Stable characters of *G. lacustris* seem to be: (1) A2 peduncle segments IV and V sparsely setose (2—3 tufts of rather short setae); flagellum in males with calceoli but without a brush of setae; (2) slender dactyli (P7 dactylus length/width ratio in adults usually at least 4.0, often nearly 5.0); (3) posterodistal corner of P7 basis without spines and usually with 2 or 3 short setules; (4) second epimeral plate rather strongly or strongly produced posteriorly; its anterior ventral portion usually with at least one rather long or long seta; (5) 3rd uropod endopodite long, at least 4/5 of the length of the 1st exopodal segment; outer margin of the exopodite with smooth and feathered setae, the latter numbering from several to 20 and even more.

The populations of *G. lacustris*, examined by the author, illustrate the wide variation in many morphological features. *G. lacustris* has a wide geographic range, being found in most of the northern holarctic area, probably as a result of its ecological potency. Despite this wide distribution, there appears to be in general little indication of speciation, implying that gene flow is probably maintained between various populations within the entire geographic range. Segerstråle (1954) has suggested that this communication can be due to bird transport.

Table II. Range of the number of A1 flagellum segments in various *Gammarus lacustris* populations. The number of specimens examined has been parenthesized.

Locality	♂♂		♀♀	
	Specimen size (mm)	Number of segments	Specimen size (mm)	Number of segments
Lake near Mosina, Poznań prov., Poland	14—18	26—35 (7)	12—14	23—27 (7)
Outflow from the Modła Lake, Koszalin prov., Poland	15—20	24—31 (7)	12—16	23—28 (5)
Lake on Anglesey, Great Britain	12—15	23—28 (7)	10—12	21—26 (6)
Kevojärvi Lake, Utsjöki, Finland	15—20	26—31 (7)	12—14	21—26 (7)
Stream near Mimosa, Ontario, Canada (ssp. <i>limnaeus</i>)	12—16	18—24 (9)	10—13	16—22 (6)

In Poland, however, the author believes he has found a good species, allied to *G. lacustris*. This new species, described below, has been named in

honour of Poland's capital, Warsaw (in Latin: Varsovia).

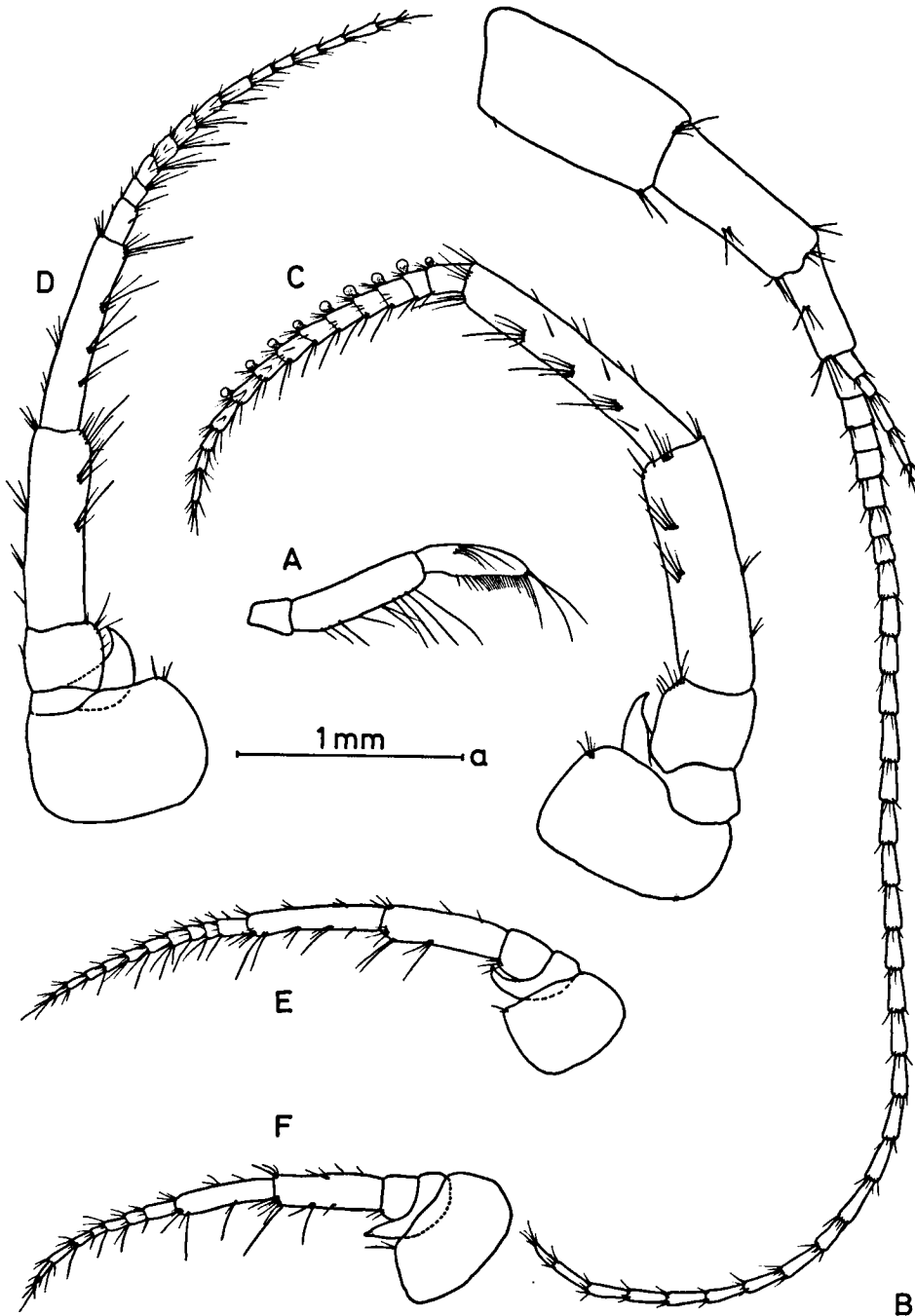


Fig. 1. A—E, *Gammarus varsoviensis* n. sp., ♂, paratype, 15 mm, from the old bed of the Vistula River in Secymin Nowy, Warsaw prov., Poland: A, mandible palp, B, first antenna, C, second antennna; ♀ (ovigerous), paratype, 15 mm, the same locality: D, second antenna; juv.,

paratype, 7.5 mm, the same locality: E, second antenna. F, *Gammarus lacustris* G. O. Sars, juv., 7.5 mm, from the Pomorze Lake, Białystok prov., Poland, second antenna. All scale a.

DESCRIPTION OF A NEW SPECIES

Gammarus varsoviensis n. sp.

Gammarus lacustris; Micherdziński, 1959: 570—573, partim; Jażdżewski, 1970: 50—51, partim, but majority of the material, fig. 2 (juv.).

Material examined. —

Poland:

1) Several old beds of the Vistula River in Secymin Nowy, Nowy Dwór Maz. district, Warsaw prov. (large cross in fig. 7; a map and many biological data on this locality can be found in the papers by Kordakow, 1969, and Krajewski, 1975): 8 samples with about 100 specimens. Type locality: old bed of the Vistula River, 200 × 50 m, situated at the beginning of the village of Secymin Nowy, some 50 m from the bank of the Vistula. Depth up to 1 m, sand, mud, detritus; *Nuphar* sp., *Potamogeton* sp., *Ceratophyllum* sp., 22.VIII.1969, coll. S. Krajewski, 10 ♂♂, 16 ♀♀ (mostly ovigerous), 9 juv. Holotype ♂ 15 mm, allotype ♀ (ovigerous) 12 mm, paratypes: 2 ♂♂, 2 ♀♀, 2 juv. (ZMA, no. Amph. 105001 a, b, and c, respectively). Paratypes: 5 ♂♂, 9 ♀♀, 5 juv. (ZZOUL, sample no. 292, 3 microscopical slides); 1 ♂, 2 ♀♀, 1 juv. (IZPAN W-wa); 1 ♂, 2 ♀♀, 1 juv. (MZUWr). Remaining samples in ZZOUL.

2) Vistula River in Warsaw, Saska Kępa; 1 sample, 9 specimens; according to Micherdziński (1959: 573) together with *Chaetogammarus ischnus sowinskyi* (Behning, 1914) and *Corophium curvispinum* G. O. Sars, 1895 (IZPAN W-wa, no. 62/34).

3) Biebrza River system (see Jażdżewski, 1970): 43 samples with about 850 specimens; in 4 samples together with *G. lacustris*, in 1 sample with *Gammarus fossarum* Koch, 1836, in 1 sample with both *G. fossarum* and *G. lacustris*. Among others the sample in ZMA, no. Amph. 103418, identified as *G. lacustris*. Remaining samples in ZZOUL.

4) Narew River and its affluents: 9 samples, about 200 specimens; in 1 sample with *G. lacustris*, in 1 sample with *G. fossarum*. Among others samples in ZMA, no. Amph. 103414 and 103415, identified as *G. lacustris*; remaining samples in ZZOUL.

5) Bug River and its affluent Krzna River: 4 samples, 40 specimens (ZZOUL).

6) Święta River, Nowy Dwór Gd. district, Gdańsk prov.: 1 sample, 7 specimens (IZPAN W-wa, no. 1504).

7) Noteć River, Chodzież district, Poznań prov.: 1 sample, 17 specimens; together with *Gammarus roeseli* Gervais, 1835 (ZZOUL).

8) Marycha River, Sejny district, Białystok prov.: 1 sample, 6 specimens (ZMA, no. Amph. 103433, identified as *G. lacustris*).

9) Augustowski Canal: 3 samples, about 60 specimens; 1 sample in ZMA, no. Amph. 103417, identified as *G. lacustris*; remaining samples in ZZOUL.

10) Necko Lake near Augustów, Białystok prov.: 2 samples: ZMA, no. Amph. 103425, identified as *G. wigrensis*, in fact 7 *G. varsoviensis* and 5 *G. lacustris*, and ZMA, no. Amph. 103435, about 50 specimens, identified as *G. lacustris*.

11) Rospuda Lake near Augustów, Białystok prov.: 1 sample, 9 specimens, together with *G. lacustris* (ZZOUL).

U. S. S. R.:

12) Starucha River near Pińsk (one of the Pripet' River arms), Belorussian S.S.R.: 1 sample, 2 specimens; together with *G. lacustris* (ZZOUL).

13) Zajeleńskie Lake (old bed of the Niemen River), Mosty, near Grodno, Belorussian S.S.R.: 1 sample, 1 specimen (IZPAN W-wa, no. 85/31).

Berlin (West):

14) Berlin (West), Neuer See, Tiergarten, 29.X.1898, coll. W. Hartwig: 1 sample (Zool. Mus. Humboldt Univ. Berlin, no. 14502).

Description. —

Maximal size observed in both sexes 20 mm, but adults usually have a length of 10—13 mm (♀♀) and 12—16 mm (♂♂).

The head (fig. 2A) has rather characteristic interantennal lobes; their lower, rounded corner is somewhat produced forwards, whereas the upper "corner" is weakly marked, so the anterior lobe margin is oblique. Sinus deep. The eyes are large, kidney-shaped, their length/width ratio is usually almost 2.

The first antenna (fig. 1B) slightly more than $\frac{1}{3}$ (♀) or $\frac{1}{2}$ (♂) of the total body length. Peduncle segments I to III bear 0—1, 1—2, and 0—1 groups of ventral setules, respectively. The flagellum in adult males (with a body length of more than 12 mm) consists of 30 to 35 segments, the accessory flagellum has 4 to 5 segments. The respective numbers for adult females (length > 10 mm) are 26 to 31 and 3 to 4. The second antenna (figs. 1C, D) in females is less than $\frac{1}{3}$ and in males more than $\frac{1}{3}$ of the body length. Fourth peduncle segment usually with 2 (1—3), fifth segment usually with 3 (2—4) groups of ventral setae; calceoli present in males, up to 12 in number in largest specimens. The smallest male observed with calceoli was 8 mm long. The flagellum of A2 in adult males 13- to 17-segmented, in females 10- to 13-segmented.

Gland cone of a very characteristic shape (figs. 1C, D, E) more or less curved upwards, its tip very often nearly touches the lower surface of the third antennal peduncle segment. The cone is rather short, only $\frac{1}{2}$ — $\frac{2}{3}$ of the length of the third peduncle segment in large animals, and hardly reaching the end of this segment in younger, smaller specimens (compare figs. 1F and 2D).

The mandible palp (fig. 1A) lacks setae on its first segment; the setules on the inferior margin of the third segment are arranged in a comb-like row.

The palms of both gnathopods (figs. 3A and B)

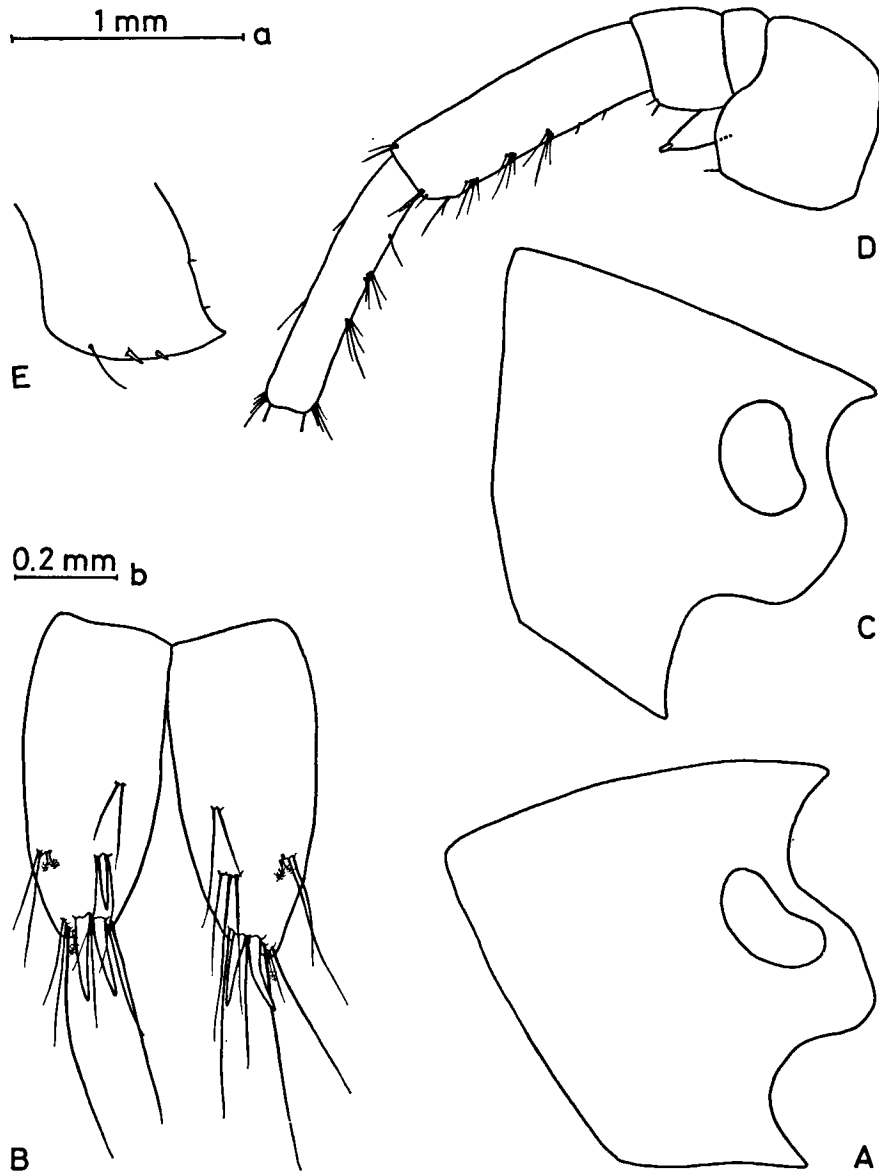


Fig. 2. A—B, *Gammarus varsoviensis* n. sp., ♂, paratype, the same specimen as in fig. 1: A, head (scale a), B, telson (b). C—E, *Gammarus lacustris* G. O. Sars, ♂, 15 mm, from the Żarnowieckie Lake, Gdańsk prov.,

Poland: C, head (a), D, peduncle of the second antenna (a); juv., 7.5 mm, from the Pomorze Lake, Białystok prov., Poland: E, second epimeral plate (a).

are similar to those in *G. pulex* and *G. lacustris*.

The setation of the third leg in males is dense and long (fig. 4A); some setae of merus, carpus and propus are longer than the length of the propus. In larger males these setae are curved distally but not curled. P3 in females somewhat less setose. The fourth leg (fig. 4B) is also rather densely setose. The legs 5, 6, and 7 (figs. 5A, B, C) are in general armed as in *G. pulex* or *G. lacustris*. The basis of P7 is not especially slender, its length/max. width ratio ranging from 1.4 to

1.7. The posterodistal corner of the basis of P7 is usually more pronounced in comparison to that in *G. pulex* or *G. fossarum* and always devoid of a spine on its inner surface. Instead of a spine there are usually 1 to 3 short setules in this place (fig. 4C). *G. varsoviensis* has this feature in common with *G. lacustris*. The dactylus of P7 shows a length/max. width ratio of usually about 4.0 or less.

The posterior margin of the metasome tergites, especially of the third one, are bordered with

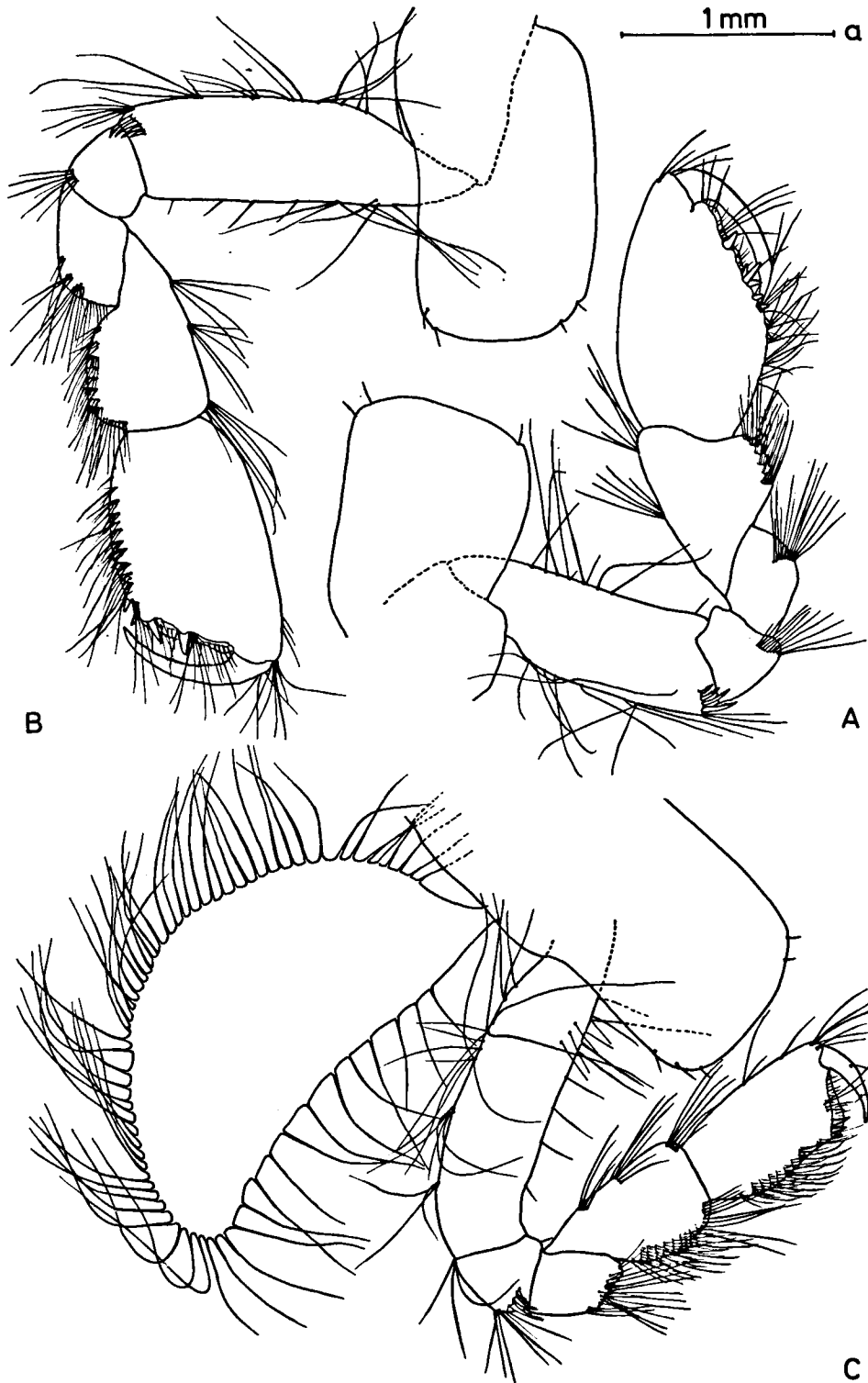


Fig. 3. A—C, *Gammarus varsoviensis* n. sp., ♂, paratype, the same specimen as in fig. 1: A, first gnathopod, B, second gnathopod; ♀ (ovigerous), paratype, the same specimen as in fig. 1: C, second gnathopod. All scale a.

several fine, rather long setules (fig. 6A) reaching even beyond the half of the following abdominal segment in young animals. In adult specimens these setules are proportionally shorter, but usually they are conspicuous.

The pleopodal retinacula usually consist of 4 to 5 spines, of which two are hooked and remaining are simple with fine hairs at the tip (fig. 6E).

The second epimeral plate (fig. 6C) is acute

but not exceedingly produced. In the lower anterior portion of the plate setae are never observed, thus the ventral submarginal armature consists of spines only, usually 4 to 6 in adults. The spines may occasionally be accompanied by very short setules, which are shorter than the spines.

The urosomal spine formula most often is 1 : 2 : 1, 1 : 2 : 1 and 1 : 0 : 1; sometimes two

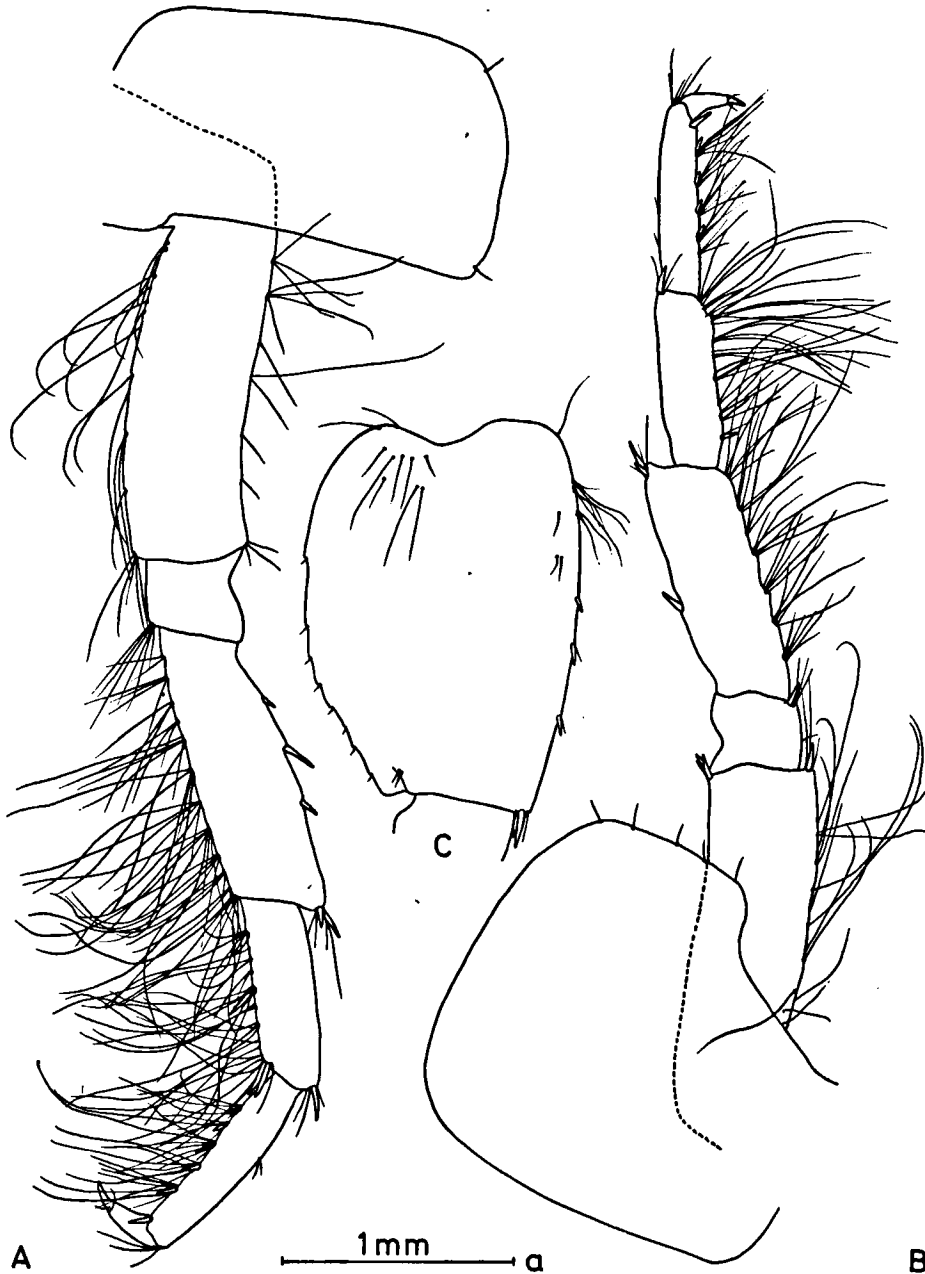


Fig. 4. A—C, *Gammarus varsoviensis* n. sp., ♂, paratype, the same specimen as in fig. 1: A, third leg, B,

fourth leg; ♀ (ovigerous), paratype, the same specimen as in fig. 1: C, basis of the seventh leg, inner side. All scale a.

spines are encountered in lateral groups. In addition to these spines there are several setae both in the medial and the lateral groups, some of which are very long; in adult specimens, their length may attain twice or more that of the spines (fig. 6A); in younger animals the setae are of about the same length as the spines or somewhat longer.

The third uropod (figs. 6F, G) has rather slender rami, usually of somewhat sabre-like shape. Exopodal outer margin rich in setae, about half of which feathered (table III). These setae are long, their length surpasses twice the width of the uropod rami. The ratio endopodite/exopodite I \times 100 is usually below or near 80 % (table III).

Telson (fig. 2B) with 1 or 2 apical spines and several (4 to 6) apical setae; in young animals (less than 7 mm long) some of the apical setae are of about the same length as the spines, in medium sized subadults (7–12 mm) they are about 1.5–2 times as long as the spines, and in adult specimens (>12 mm) they may even be 2.5 times as long. The subbasal and subapical telson armature consists usually of setae only, which are often also very long. Occasionally a single subbasal or subapical spine is also encountered.

The females exhibit in general the normal sexual dimorphism, viz. lack of calceoli, shorter antennae, smaller gnathopod propodus, more robust P7 basis

and shorter and less setose third uropods (figs. 1D, 3C, 4C, table III).

The following morphological features are of special importance in distinguishing *G. varsoviensis* from *G. lacustris*:

1. The eye length/max. width ratio is larger in *G. varsoviensis*: a mean of 1.9 opposed to 1.6 for *G. lacustris*. (There is some overlap of ranges.)
2. The antennal gland cone of *G. lacustris* is straight, i.e. both the upper and lower edges are slightly convex (figs. 1F, 2D). In all *G. lacustris* examined the tip of the cone is located at some distance of the antennal peduncle and is directed obliquely downward. The end of the gland cone in young *G. lacustris* extends beyond the end of the third antennal peduncle segment (fig. 1F); in medium sized specimens it reaches or overreaches the end of this segment (fig. 2D), whereas in the largest specimens it reaches to about 4/5–3/4 of the length of this segment. In *G. varsoviensis* the gland cone is distinctly shorter and curved upwards, its upper edge is concave, its lower one convex (figs. 1C, D, E).
3. The number of flagellum segments of both antennae is somewhat higher in *G. varsoviensis*; on the average the specimens of this species have some 2 to 4 segments more in the A1 flagellum, and some 1 to 2 segments more in the A2 flagel-

Table III. Variability of some morphological features in *Gammarus varsoviensis* n. sp. The number of specimens examined has been parenthesized.

Length class (mm)		5–7	7–9	9–11	11–13	13–15
Number of calceoli ($\delta \delta$)	range	0	0–6	3–7	5–7	7–11
	mean	0 (2)	2.4 (9)	5.5 (14)	6.3 (3)	9.4 (5)
Eye: length/width ratio	range	—	—	1.6–2.1	—	—
	mean	—	—	1.9 (30)	—	—
P7 basis: length/max. width ratio	range	1.4–1.6	$\delta \delta$ 1.5–1.6 $\text{♀} \text{♀}$ 1.4–1.5	$\delta \delta$ 1.4–1.6 $\text{♀} \text{♀}$ 1.4–1.6	$\delta \delta$ 1.6 $\text{♀} \text{♀}$ 1.4–1.7	$\delta \delta$ 1.5–1.7 $\text{♀} \text{♀}$ 1.4–1.6
	mean	1.5 (9)	1.53 (7) 1.44 (10)	1.51 (14) 1.47 (11)	1.6 (3) 1.5 (8)	1.64 (5) 1.5 (7)
U3 exopodite I outer margin:	range	6–13	$\delta \delta$ 13–23 $\text{♀} \text{♀}$ 10–24	$\delta \delta$ 19–40 $\text{♀} \text{♀}$ 13–27	$\delta \delta$ 42–50 $\text{♀} \text{♀}$ 22–50	$\delta \delta$ 40–70 $\text{♀} \text{♀}$ 30–52
	mean	8	16.9 15.1	25.5 18.8	45.0 38.1	58.6 42.7
N of all setae	mean	8 (7)	(8)–(10)	(13)–(10)	(3)–(9)	(5)–(7)
N of feathered setae	mean	3.3	6.3 5.9	10.0 8.8	19.0 15.2	21.8 16.6
U3 rami proportions: endopodite \times 100	range	62–74	67–80	71–84	74–87	74–87
exopodite I	mean	69.1 (7)	74.7 (18)	77.9 (23)	78.7 (11)	79.8 (11)

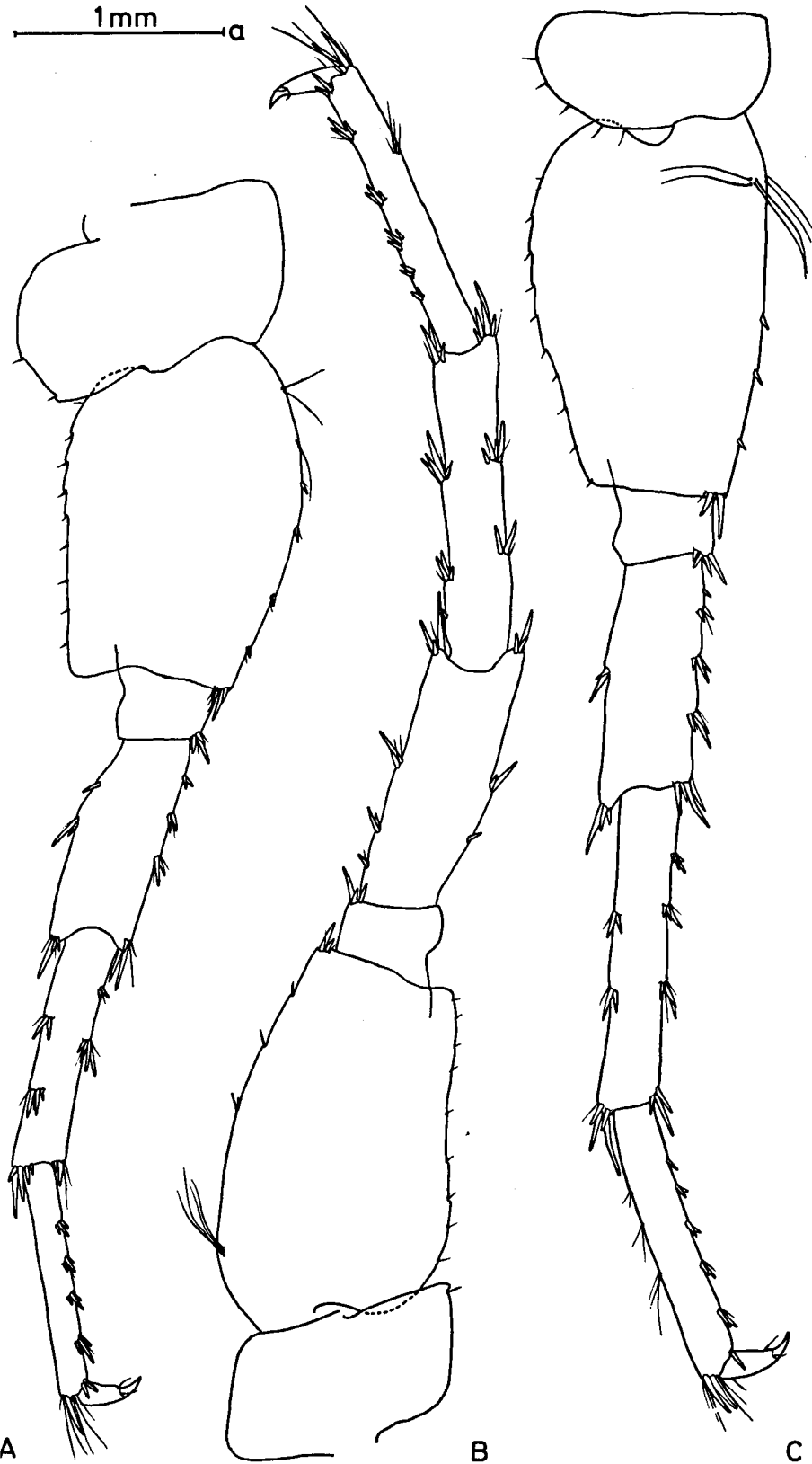


Fig. 5. A—C, *Gammarus varsoviensis* n. sp., ♂, para-type, the same specimen as in fig. 1: A, fifth leg, B, sixth leg, C, seventh leg. All scale a.

lum than in specimens of *G. lacustris* of the corresponding sex and size. Similarly, the accessory flagellum has usually 3 to 5 segments in the former species and 2 to 4 segments in the latter.

4. *G. lacustris* usually has more slender dactyli. Normally, in adults the length/max. width ratio of the P7 dactylus exceeds in this species 4.0, reaching even 5.0 and more, while in *G. varsoviensis* this ratio hardly ever exceeds 4.0.

5. Delicate, but comparatively long setules, ornamenting the hind margins of the metasome tergites are probably a characteristic feature of all *lacustris*-related gammarid species. These setules are usually prominent in juvenile specimens (up to 7 mm) of both species in question, but they are longer and more conspicuous in *G. varsoviensis*. In adults setules become proportionally shorter and less prominent, but in *G. varsoviensis* they are still rather long and conspicuous (fig. 6A), whereas in large *G. lacustris* they are hardly noticeable.

6. Ventral submarginal armature of the second epimeral plate in *G. varsoviensis* consists of spines only, while in *G. lacustris* there are usually some long setae in front of or mixed with the spines. In prevailing majority of the Polish *G. lacustris* samples, as well as in the samples from Canada (4 samples), Great Britain (1), Finland (2) and the U.S.S.R. (4), the author has found always at least one such seta (fig. 2E). In *G. varsoviensis* such setae were never found.

7. Setosity of urosome and telson is not prominent in *G. lacustris*, for the setae accompanying spines are usually shorter than the spines or of equal length; they rarely are somewhat longer, and then only in the largest specimens. In *G. varsoviensis*, even in young specimens, the setae attain or surpass the length of the spines; in adult animals the setae may be twice as long or longer. This difference between these two species is somewhat comparable to the situation in *Gammarus salinus* Spooner, 1947 and *G. zaddachi* Sexton, 1912.

The new species exhibits some similarities to the North American *Gammarus pseudolimnaeus* Bousfield, 1958, a species inhabiting also mainly rivers and streams. Compared with Bousfield's (1958) description and drawings, both species seem to have the following features in common: large reniform eye, short gland cone, armature of the peduncles of the antennae, comparatively conspicuous setules on the metasome tergites hind margins, rather long setae in the dorsal pleon armature, and the proportions of the third uropod rami.

The differences consist mainly in the armature

of legs 3 and 4, which are densely setose in *G. varsoviensis* and sparingly setose in *G. pseudolimnaeus*, in the setation of the basis of P7 (several setae on the inner surface and some 10 to 15 short setules bordering the hind margin in *G. varsoviensis* versus rich setation of the inner surface and over 20 comparatively long setae, lining the hind margin in *G. pseudolimnaeus*), in the ventral armature of the epimeral plates 2 and 3 (spines only in *G. varsoviensis*, many setae in *G. pseudolimnaeus* — see also Cole, 1970), and in the setation of the telson and of the U3 exopodal outer margin (rich and long in *G. varsoviensis*, sparse and shorter in *G. pseudolimnaeus*).

ECOLOGICAL AND BIOLOGICAL REMARKS

The majority of all available samples consisted purely of *G. lacustris* or only of *G. varsoviensis*. In 113 samples examined, *G. lacustris* occurred together with *G. varsoviensis* in 9 samples, with *G. fossarum* in 1 sample, with *G. pulex* in 4 samples, with *G. zaddachi* in 1 sample, with *Pallasea quadrispinosa* G. O. Sars, 1867 in 7 samples, with *Synurella ambulans* (F. Müller, 1846) in 6 samples, and with *Crangonyx* sp. in one sample from Canada (ssp. *limnaeus*). In 77 samples examined, *G. varsoviensis* occurred together with *G. fossarum* in 3 samples, with *G. roeseli* in 1 sample, with *G. lacustris* in 9 samples, and with *Chaetogammarus ischnus sowinskyi* and *Corophium curvispinum* in one sample.

The co-occurrence of *G. lacustris* and *G. varsoviensis* gives further support to the presumption that *G. varsoviensis* is a good species.

Both species discussed are generally encountered in the northeastern part of Poland (fig. 7). The only site in Poland for *G. varsoviensis* outside the Vistula drainage system is the Noteć River which, however, is connected with the Vistula River by the canal Vistula-Noteć.

The occurrence of *G. varsoviensis* in two haphazard samples from the systems of the Niemen and Pripet' Rivers (vicinity of Grodno and Pińsk, respectively) suggests its possible common presence at least in the area of the neighbouring Belorussian S.S.R., where the marshy landscape with a dense river net is similar to the Polish areas (viz. the Bug and Narew Rivers drainage systems), where *G. varsoviensis* is frequent.

G. varsoviensis generally inhabits moderately flowing lowland streams and rivers. It was found,

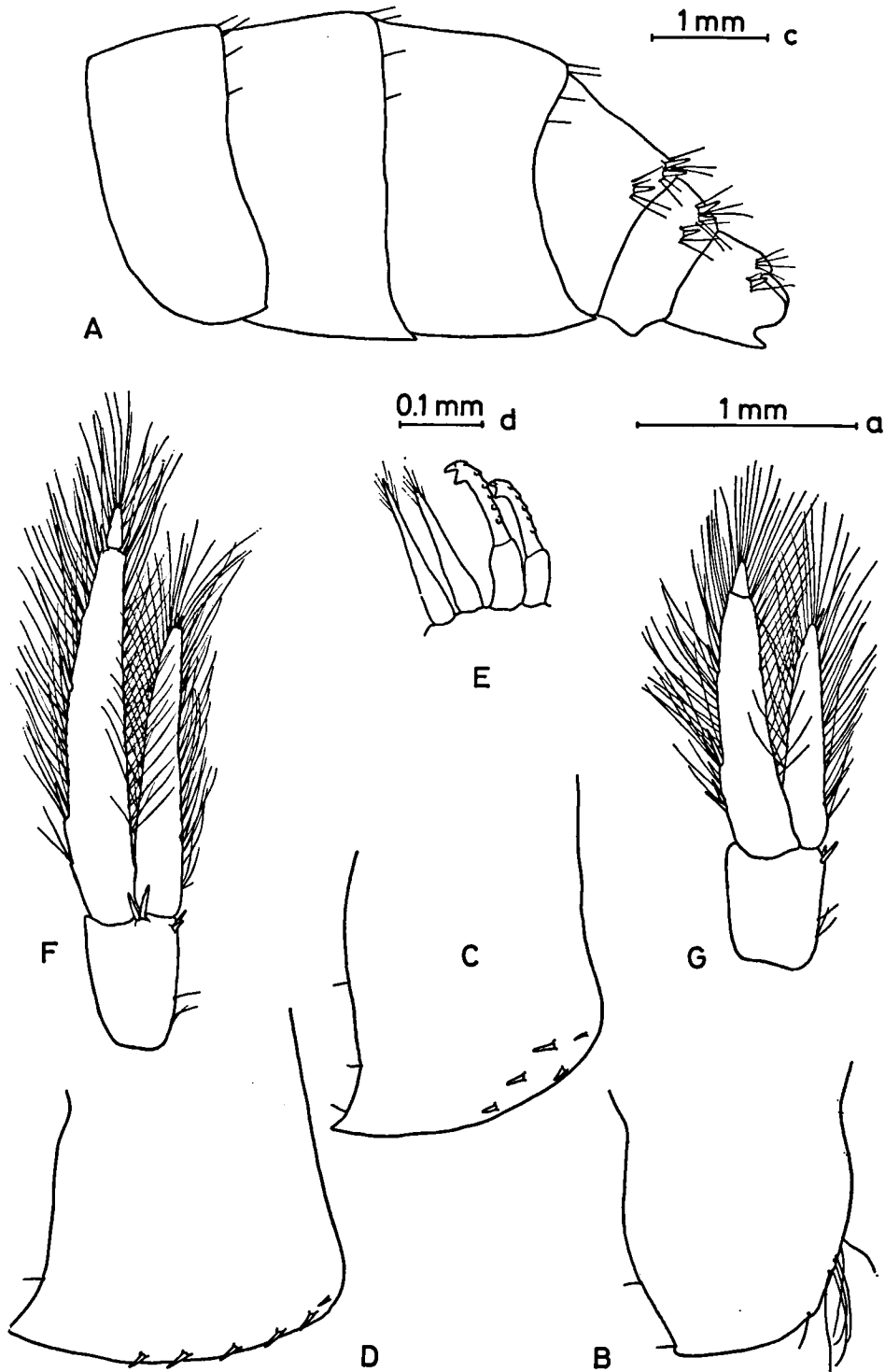


Fig. 6. A—G, *Gammarus varsoviensis* n. sp., ♂, paratype, the same specimen as in fig. 1: A, abdomen (scale c), B, C, D, first, second and third epimeral plates (a), E, pleopodal retinacula (d), F, third uropod (a); ♀

(ovigerous), paratype, the same specimen as in fig. 1: G, third uropod (a). For the sake of clarity in the third uropods all setae are drawn as simple; in fact about half of them are feathered on the outer exopodal margin.

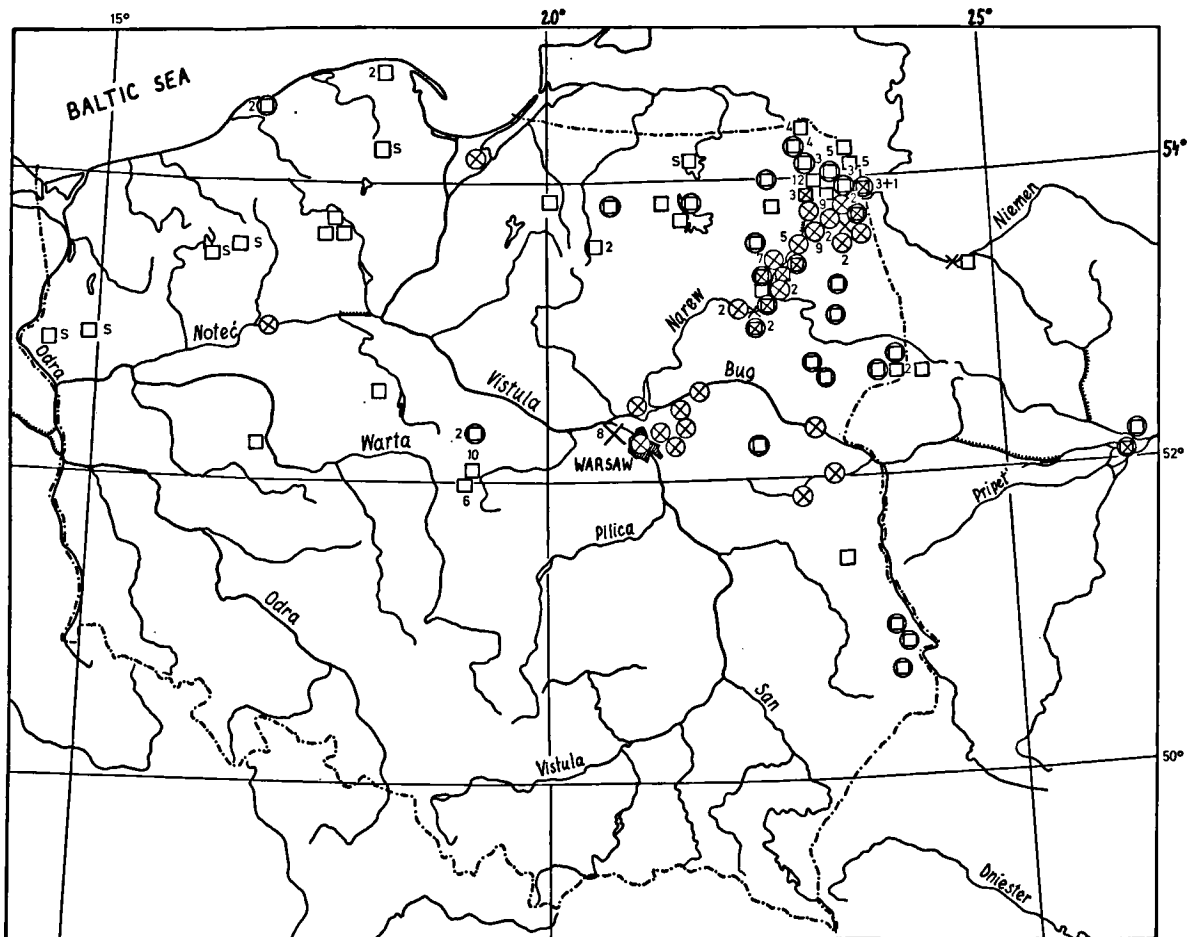


Fig. 7. The distribution of *Gammarus varsoviensis* n. sp. and *Gammarus lacustris* G. O. Sars in Poland and in western Belorussian S.S.R. Cross = *G. varsoviensis*; square = *G. lacustris*; encircled symbols = occurrence in running water; symbols without circle = occurrence

in stagnant water. The numeral at the symbol denotes the number of samples taken in the same or nearby localities. The larger cross indicates the type-locality of *G. varsoviensis*. S = data based on Schellenberg (1934), remaining data based on the present material.

in some few localities, also in lakes with exchange of water by inflow and outflow along rivers as, for example, the Rospuda and Necko Lakes, Augustów district, Białystok prov., and the Zajeleńskie Lake in Mosty, Grodno district, Belorussian S.S.R. (for a description of this locality, see Wolski, 1932), or in temporary flooded meadows and in old riverbeds, nearly every year connected with a river, e.g. in old beds of the Vistula River in Secymin Nowy (type locality).

G. lacustris is generally regarded as an inhabitant of stagnant waters. Hynes et al. (1969), Økland (1969) and Pinkster (1972) attributed the few occurrences of *G. lacustris* in running waters to passive drift. In Poland *G. lacustris* locally occurs in some rather fast flowing streams and rivers, that are not connected in their upper reaches with a lake. Engelhardt (1957) reports similar

occurrence of this species in Swedish Lapland. It seems, however, that the lakes, ponds and tarns represent the main habitat of *G. lacustris*.

G. lacustris tolerates low oxygen and high ion concentrations. Decksbach (1952) reports, that in central Russia *G. lacustris* inhabits lakes the water of which contains 9 grams of dry residue per liter. In Poland near Błonie (Łęczycza district, Łódź prov.) this species lives in brackish peat-bog tarns, where the chloride content alone is more than 3 grams per liter.

The life cycles of *G. lacustris* and of *G. varsoviensis* are not exactly known in our area. The life cycle of *G. lacustris* in Poland may be similar to that in Great Britain (Hynes, 1955), where the new generation of *G. lacustris*, hatched in species begins to breed in winter and the young generation hatches in April and May. In Poland

spring, apparently does not breed in late summer or autumn of that year. It is possible that the breeding period of this species in our country, in comparison to that in the British Isles, has somewhat shifted in time, owing to more severe winters, but precise observations are lacking. It may be stressed that Økland (1969) has found breeding females of *G. lacustris* as late as in September in Norway.

Hynes (1955) reports for *G. lacustris* from Great Britain a one-year life cycle; Hynes & Harper (1972), on the other hand, describe a two-year life cycle of ssp. *limnaeus* from Canadian streams in which the most intense breeding takes place in May, June and July. This difference in life cycle may be due to the considerably lower temperatures of these streams throughout the year (always less than 13° C).

There is some indication that *G. varsoviensis* differs from *G. lacustris* also in its reproductive cycle. In late spring (May, June) the largest speci-

mens of *G. varsoviensis* are found (up to 20 mm in length), the females having embryos or empty brood pouches; then, at the end of August one encounters smaller specimens (up to 15 mm), being, however, also in the reproductive stage (females with embryos). Thus it seems to be possible that two generations per year are produced, one in spring, offspring of the overwintering adults, the second in late summer and autumn, when this spring generation breeds.

As it is indicated above, nearly the whole material, identified in an earlier paper (Jażdżewski, 1970) as *G. lacustris*, belongs in fact to *G. varsoviensis* n. sp. The data in that paper concerning the fecundity of "*G. lacustris*" refer in reality to the latter. Based on a rather scarce material it was found that the females had from 17 (♀ 11 mm) to 57 (♀ 15 mm) eggs per clutch. The mean for 5 females in the length class of 12—13 mm was 28, the same for 5 females in the length class of 13—14 mm was 35.

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