

Gammarid amphipods (Crustacea) in Norway, with a key to the species

Wim Vader¹ and Anne Helene S. Tandberg²

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Thirteen species in the amphipod family Gammaridae have been reported from Norway. This paper gives a survey of the distribution and habitat of all 13 species of the family Gammaridae occurring or expected to occur in Norwegian waters: both marine, brackish and fresh, including Svalbard, in addition to four species found in close neighbouring waters. It also provides a short history of the study of Gammaridae in Norway, as well as an illustrated identification key to all species in the area.

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1. Tromsø Museum – Universitetsmuseet, Universitetet i Tromsø, NO-9037 Tromsø, Norway.

2. Universitetsmuseet i Bergen, avd for Naturhistorie, PO Box 7800, NO-5020 Bergen, Norway.

Corresponding author: Anne Helene S. Tandberg

E-mail: anne.helene.tandberg@uib.no

INTRODUCTION

The many similar-looking amphipod species in the family Gammaridae, collectively called ‘marflo’ in Norwegian, are both widespread and numerous in many places, in fresh water, brackish water, and on the sea shore. They are an important part of the various ecosystems, they are good indicators of water quality, and they are also often used in toxicology studies. To identify them to species, however, is not always easy. The usual identification method for amphipods we use in Norway, i.e. the combination of the always excellent illustrations in the old monograph by G.O.Sars (1890-95) with the keys and distribution data in the various papers by Stephensen (1928, 1929, 1935-42), fails dismally in this case: Sars (op. cit.) described only five species of *Gammarus*, three in sea water (*G. locusta*, *G. campylops*, *G. marinus*), one in brackish biotopes (*G. duebeni*) and one in fresh water (*G. pulex*). Now, however, we know 13 species in Norway (without, by the way, either *G. campylops* or *G. pulex*).

The aim of this paper is 1. To give a short historical overview of the study of *Gammarus* species s.l. in Norway, 2. To provide an illustrated identification key to the Norwegian Gammaridae species, including a few species that have not yet been found here, but may occur, 3. To give references to good descriptions and illustrations of all species, and 4. To give a

short review of the distribution and habitat of every species in Norway.

There are some further freshwater amphipods in Norway, that traditionally have been reckoned in the Gammaridae s.l. These are the so-called ‘glacial relicts’ *Gammaracanthus lacustris* (Sars, 1867) and *Pallasea quadrispinosa* (Sars, 1867), that occur in some deep lakes in SE Norway; *Pallasea* has recently also been discovered on Jæren (Spikkeland et al. 2012). A marine *Gammaracanthus* species also occurs in Arctic waters. These are now considered to belong to the families Gammaracanthidae and Pallaseidae, and are not dealt with here. A further, non-indigenous freshwater amphipod has very recently been found on Jæren, i.e. *Crangonyx pseudogracilis* Bousfield, 1958 (Spikkeland et al. 2016); this species belongs in the family Crangonyctidae, and is also excluded.

In recent years, many places in Europe, in both fresh and brackish waters, have had an influx of Ponto-Caspian species, especially in rivers and in the inner parts of the Baltic Sea. One of these is the ill-famous ‘killer amphipod’ *Dikerogammarus villosus* (Sowinsky, 1894). None of these species have hitherto been recorded in Norwegian waters and we have not included them in this paper, with the exception of the American immigrant *Gammarus tigrinus* Sexton, 1939.

History

The development of gammarid classification in northern Europe in the last 100–150 years seems to have happened in definite stages. In the first stage a number of species was described: *Gammarus krøyeri* Rathke, 1843, *G. poecilurus* Rathke, 1843, *G. duebeni* Liljeborg, 1852, *G. mutatus* Liljeborg, 1855, *G. batei* Boeck, 1861 and *G. lacustris* Sars, 1863. In most cases there was no type material conserved and the descriptions are so vague and incomplete that it is now often practically impossible to identify these species. In the next stage practically all these species were again viewed as junior synonyms of the three classic *Gammarus* species of the area: *Gammarus locusta*, *G. marinus* and *G. pulex*. Characteristic for this stage is e.g. that Liljeborg already in 1855 reduced his own *G. duebeni* to a synonym of *G. locusta*, while Sars in 1892 no longer saw his own *G. lacustris* as different from *G. pulex*; both, as we now know, incorrect decisions.

The third stage started with Sexton who, starting around 1910, over many years carried out a large number of rearing and crossing experiments with various *Gammarus* species in the Plymouth laboratory in England (see e.g. Sexton 1923, Sexton & Clark 1936). She found that the species were not at all so variable as everybody thought at the time: even when reared under quite different regimes, specimens at the same stage of development remained morphologically extremely similar. Sexton also described a few new species from brackish water, i.e. *Gammarus zaddachi* in 1912. She was clearly far ahead of her time, however, and it took more than 25 years for the leading European specialists (Chevreux, Schellenberg, Stephensen) to accept *G. zaddachi* as a valid species.

In the 1930's there was a change again, and new species were described regularly, usually without comparing them with the names from the first stage. In 1930 Gurjanova recognized Birula's *Gammarus wilkitzkii* as 'a good species'. In 1931 followed *Gammarus setosus* Dementieva and *Rivulogammarus scandinavicus* S. Karaman (= *G. lacustris*), in 1938 *G. finmarchicus* Dahl (in the same year also described from USA as *G. greenfieldi* Shoemaker), *G. obtusatus* Dahl and *G. stoerensis* Reid, in 1939 *G. tigrinus* Sexton, and in 1940 *Marinogammarus pirloti* Sexton & Spooner. In 1942 Sexton divided her *Gammarus zaddachi* into a 'freshwater' and a 'saline' form, in 1947 called *G. z. zaddachi* and *G. z. salinus* by Spooner. That same year Segerstråle (1947) described a third, more northern form as *G. z. oceanicus*, and all three forms were upgraded to species level by Kinne (1954). This almost completed the picture for NW Europe, except for the splitting of the *Gammarus locusta* group by Stock (1966, 1967), who i. a. showed that Sars's *G. campylops*, until then looked at as a synonym of *G. locusta*, in reality represented an independent species, which he named *G. inaequicauda* (Stock & Kant, 1966).

As we see, in this period also a few new genus names appear, besides the original *Gammarus*: *Rivulogammarus* S. Karaman, 1931 for freshwater species, *Marinogammarus*

Sexton & Spooner, 1940 for the species of the stony littoral, and *Lagunogammarus* Sket, 1971 for the greater *G. zaddachi* group. *Rivulogammarus* is not an available name, having the same type species as *Gammarus* (Stock 1969a), while *Lagunogammarus*, although taken in use in her monograph by Tzvetkova (1975) is also no longer in use (Hou & Sket 2016). As shown below, the situation for *Marinogammarus* is more complicated.

In this period several different classification and systematics models were taken in use in taxonomy: phenetics, cladistics, molecular classifications, and in our opinion a final classification of European gammarids has not yet been obtained. Stock (1968, 1969b, Pinkster & Stock 1970) worked on *Marinogammarus* (which he replaced by the older name *Chaetogammarus*, coined for a Black Sea species); he removed *M. obtusatus* to the Baikal genus *Eulimnogammarus* (a move no longer followed by anyone), and *M. finmarchicus* back to *Gammarus s. str.*, close to *G. duebenii*.

The latest revision is that by Hou and Sket (2016), and even though also that one has already drawn criticism and has not yet been followed by WoRMS (Horton et al. 2018), it is used here. They restored the genus *Marinogammarus* (still called *Echinogammarus* in WoRMS), but in a most interesting development these authors also declared *M. stoerensis* to be the probable sister group of all remaining gammarids and erected the genus *Relictogammarus* for this species (Hou & Sket 2016); also this species is accepted as *Echinogammarus* in WoRMS.

The present paper deals with the following 17 species, of which 4(*) have not yet been recorded from Norwegian waters, but may conceivably occur there:

- * *Gammarus crinicornis* Stock, 1966
- G. duebenii* Liljeborg, 1852
- G. inaequicauda* Stock, 1966
- G. lacustris* Sars, 1863
- G. locusta* (Linnaeus, 1758)
- G. oceanicus* Segerstråle, 1947
- * *G. pulex* (Linnaeus, 1758)
- G. salinus* Spooner, 1947
- G. setosus* Dementieva, 1931
- * *G. tigrinus* Sexton, 1939
- * *G. wilkitzkii* Birula, 1897
- G. zaddachi* Sexton, 1912
- Marinogammarus finmarchicus* (Dahl, 1938)
- M. marinus* (Leach, 1815)
- M. obtusatus* (Dahl, 1938)
- M. pirloti* Sexton & Spooner, 1940
- Relictogammarus stoerensis* (Reid, 1938)

Identification key

In the construction of this key we have, as always in such cases, based ourselves for a large part on earlier work by Sexton & Spooner (1940), Reid (1944), Kinne (1954), Hynes et al. (1960), Stock (1966, 1967), Bousfield (1969) and Lincoln (1979), but in a few cases we have chosen new criteria. The key will work for

adult and subadult specimens, but is not reliable for juveniles and small immatures. For illustrations to the key, see figs 1 and 2. All illustrations are based on drawings originally presented in Sars (1890-95), Sexton & Spooner (1940), Sexton (1942), Stephensen (1949), Barnard (1959), Økland (1969), Pinkster (1970), Bousfield (1973) and Lincoln (1979).

Key to the *Gammarus/Marinogammarus/Relictogammarus* in Scandinavian waters (Adult specimens)

1. a) U3 outer ramus with only 1 article. (Inner ramus 30-40% of outer ramus length. P7 basis posterodistally with only setae.)
..... *Marinogammarus finmarchicus* (Dahl, 1938)
- b) U3 outer ramus with 2 articles 2
2. a) U3 inner ramus more than half length of outer ramus first article (Figure 1) 3
- b) U3 inner ramus less than one third of outer ramus first article (Figure 1) 16
3. a) Eyes oval, not higher than 2x width (Figure 1) 4
- b) Eyes “long and narrow”, clearly higher than 2x width (Figure 1) 7
4. a) Ventral margin of mandible palp 3rd article: setae not of equal length - producing an uneven fringe. (Peduncle A1 art 2 and 3 subequal in length)
..... *Gammarus wilkitzkii* Birula, 1897
- b) Ventral margin of mandible palp 3rd article: setae of equal length - producing a comb-shaped structure 5
5. a) Several plumose setae on P5-7, urosome and telson. Large arctic marine species
..... *Gammarus setosus* Dementieva, 1931
- b) No plumose setae on P5-7, urosome and telson. Boreal fresh water species 6
- 6: a) Ep2 and 3 subequal in shape, hind corner acute. A2 flagellum in ♂ without brushes of sensory setae (Figure 1) *Gammarus lacustris* G. O. Sars, 1863
- b) Ep2 and 3 not alike in shape: lower hind corner acute in Ep 3, but not in Ep2. A2 flagellum in ♂ with brushes of sensory setae (Figure 1)
..... *Gammarus pulex* (L, 1758)
- 7: a) Ventral margin of mandibular palp art. 3: all setation of similar type, either forming an uneven fringe, or an even comb-like structure 8
- b) Ventral margin of mandibular palp art. 3: setae on inner part of margin uneven, on outer part of margin even. (All legs, antenna 2 and uropod 3 are heavily setose with long curled setae)
..... *Gammarus tigrinus* Sexton, 1939
- 8: a) Ventral margin of mandibular palp art. 3: setae not of equal length, forming an uneven fringe 9
- b) Ventral margin of mandibular palp art. 3: setae of equal length, forming a comb-shaped structure 11
- 9: a) A1 peduncle in ♂: 3rd article as long as 2nd article (>40 mm). Large arctic under-ice species (Figure 1) *Gammarus wilkitzkii* Birula, 1897
- b) A1 peduncle in ♂: 3rd article not longer than 50-60% of 2nd article (< 25 mm) (Figure 1) 10
- 10: a) P7 article 5: marginal setae obviously longer than spines (Figure 1) *Gammarus zaddachi* Sexton, 1912
- b) P7 article 5: marginal setae not longer than spines; most obviously shorter (Figure 1)
..... *Gammarus salinus* Spooner, 1947
- 11: a) P7 article 2: posterodistal margin with setae only (Figure 1) *Gammarus duebenii* Liljeborg, 1852
- b) P7 article 2: posterodistal margin with both setae and spines (Figure 1) 12
- 12: a) A1 peduncle: 3 setae groups on article 1, 4-5 setae groups on article 2. Mandibular palp ventral margin art. 3: all setae in the “comb” of equal length ..13
- b) A1 peduncle: 1-2 setae groups on article 1, 1-2 setae groups on article 2. Mandibular palp ventral margin art. 3: setae in “comb” become gradually longer towards tip of article 14
- 13: a) Several plumose setae on P5-7, urosome and telson. P7 basis posterior margin with several long setae. Setae on telson are 3x as long as the spines. (Figure 2) *Gammarus setosus* Dementieva, 1931
- b) No plumose setae on P5-7, urosome or telson. P7 basis posterior margin with few and short setae. Setae on telson 2x as long as the spines (Figure 2)
..... *Gammarus oceanicus* Segerstråle, 1947
- 14: a) Urosome segments with almost no visible “humps”. P7 basis 1.2 - 1.3 times longer than wide
..... *Gammarus crinicornis* Stock, 1966
- b) Urosome segments with clear “humps”. P7 basis more than 1.5x longer than wide 15
- 15: a) U3 inner ramus almost as long as outer ramus art. 1 (90-100%). Ep3 with several setae along hind margin. A2 in ♂ with calceoli (Figure 2)
..... *Gammarus locusta* (L, 1758)
- b) U3 inner ramus obviously shorter than outer ramus art. 1 (75-90%). Ep3 with 0-1 setae along hind margin. A2 in ♂ lacks calceoli (Figure 2)
..... *Gammarus inaequicauda* Stock, 1966

- 16: a) P7 article 2 posterodistal margin with setae only (adults < 10 mm). (U3 with almost only spines) (Figure 2) *Relictogammarus storerensis* (Reid, 1938)
 b) P7 article 2 posterodistal margin with both setae and spines (Figure 2) 17
- 17: a) A1 peduncle: article 2 as long as article 1. Ep 3 hind corner rounded. (In ♂, the “hand” (propodus & dactylus) is much larger in P1 than in P2. The antennae have long and stiff setae, in every group one of the setae is a lot longer than the rest) (Figure 2) *Marinogammarus obtusatus* (Dahl, 1938)
 b) A1 peduncle: article 2 much shorter than article 1. Ep 3 hind corner is rectangular or acute (Figure 2) . 18
- 18: a) Ep 3: hind corner very acute. A1 peduncle: article 1 shorter than articles 2+3. Spines on urosome form a continuous arc. U3: outer ramus in ♂ without plumose setae, in ♀ with plumose setae on inner margin (Figure 2)
 *Marinogammarus marinus* (Leach, 1815)
 b) Ep 3: hind corner rectangular. A1 peduncle: article 1 almost as long as articles 2+3. Spines on urosomal segment 1 do not form a continuous arc. U3: outer ramus in both ♂ and ♀ with plumose setae on inner margin (Figure 2)
 *Marinogammarus pirloti* Sexton & Spooner, 1940

A survey of gammarid species in Norway

The geographic distribution of gammarid species in Norway is not well known, as is the case for many other intertidal amphipods; most of the classical papers on Norwegian amphipods dealt mainly or exclusively with dredged material. In addition, older records can in general not be trusted, as the classification of gammarids has undergone vast changes in the last decades.

The data used in this survey stem from the compilation by Vader et al. (1979, brought up-to-date by Brattegard & Vader (2018, unpublished)), from our own field observations in western and northern Norway, as well as from papers by Sars (1890-95), Stephensen (1935-42), Dahl (1946), Segerstråle (1947,1954), Spooner (1947), Steen (1951), Oldevig (1959), Brattegard (1966), Dennert (1973), Ingolfsson (1977), Palerud et al (2004), and a series of papers on freshwater gammarids by Økland (1965, 1969, 1970, 2011a,b). For the ecological data we have relied mostly on data from Western Europe, the series of papers from Newfoundland by Steele & V. Steele (1969, 1970, 1972, 1975; V. Steele & Steele 1970, 1972), and the Oslofjord studies of Skadsheim (1982, 1983, 1984). There has been much research also in the Baltic, but the situation there, with a lowered, but more or less constant salinity, is quite different from the situation in the intertidal, estuaries and pollens in Norway with their very changeable salinity.

In this survey we have divided the gammarids of Norway into 8 groups. We have deviated from the traditional grouping on two points: we have joined *Gammarus oceanicus* (although originally described as a subspecies of *G. zaddachi*) with *G. setosus*, and also *G. duebenii* with *Marinogammarus finmarchicus*.

Gammarus oceanicus and *G. setosus* are both uniformly coloured species with a northerly and amphiatlantic distribution, while *G. zaddachi* and *G. salinus* are striped animals with a more southerly and purely eastern Atlantic distribution.

Similarly *G. duebenii* and *?M. finmarchicus* show many morphological and ecological similarities. The final taxonomic position of *finmarchicus* is still unclear, and many authors place it in *Gammarus*, close to *G. duebenii*.

A. *Gammarus locusta* group

In the older literature, in Norway, practically all fully marine *Gammarus* were called *G. locusta*, although Sars (1890-95) realized there was a different species, which he called *G. campylops*. In 1967 Stock revised the *Gammarus locusta* group, and i.e. described four species from northern Europe, two of which have been found also in Norwegian waters; *G. locusta* s. str. and *G. inaequicauda* (=Sars's *campylops*, but not *campylops* Leach), while a third, *G. crinicornis*, may still be found in the SW.

All the species in this group are mainly sublittoral boreal marine or brackish water forms.

1. *Gammarus locusta* (Linnaeus, 1758)

Descriptions and illustrations: Sexton 1942, pl. 3 figs 19-24; Spooner 1947, p. 7, figs 1, 2 A-B, 3; Kinne 1954, p. 409, figs 1-2pp, 4-6; Stock 1967, p. 11, fig. 1.

Ecology and habitat: A marine, mainly sublittoral species of the algal belt, tolerates some lowering of the salinity, but not much, unless it is stable, as in the Baltic. Not often found in the intertidal during ebb. A useful review is Costa & Costa (2000)

A very special case was the situation in Rauneforden near Bergen, where large amounts of kelp (mainly *Laminaria*) washed down to the bottom at 240 m. In this biotope *Gammarus locusta* was surprisingly common, and the animals grew very large (Vader, unpubl. obs.).

Distribution in Norway: Not really well known because of earlier confusion, mainly with *G. oceanicus*, and the fact that this species mainly lives on the outer coast and largely sublittorally. Occurs quite commonly along the entire South and West coast, much more sparingly east of the North Cape. It does not penetrate into the fjords much, and in the North it is restricted to the outer coast. Surprisingly, recent studies have found the species present in Kongsfjorden, Svalbard (Berge & Shunatova, pers. comm.)

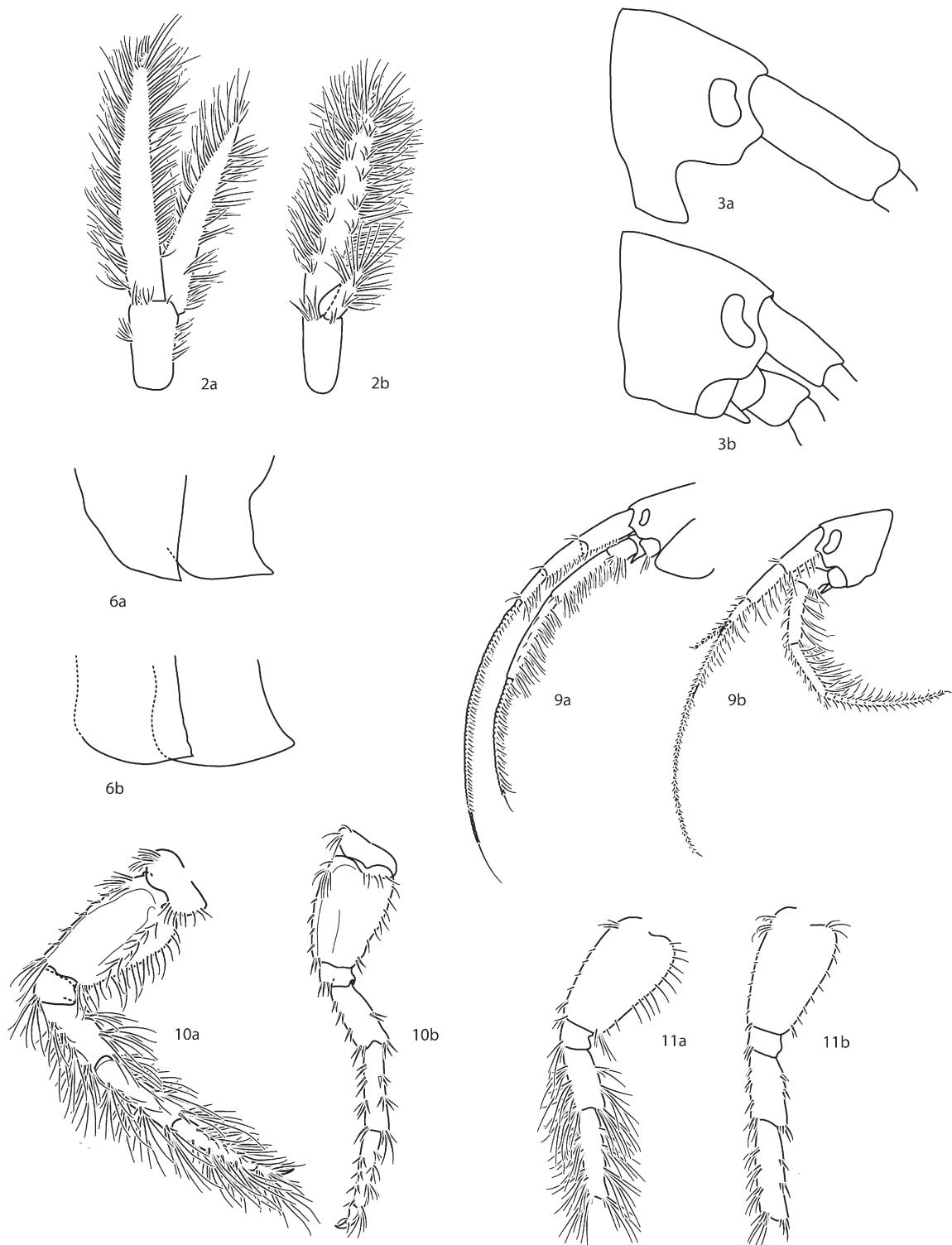


Figure 1. Illustrations to questions 2, 3, 6, 9, 10 and 11 from the key. 2a: *Marinogammarus marinus* illustration from Sexton & Spooner (1940). 2b: *Gammarus wilkitzkii* illustration from Barnard (1959). 3a: *Gammarus wilkitzkii* illustration from Barnard (1959). 3b: *Gammarus tigrinis* illustration from Lincoln (1979). 6a: *Gammarus lacustris* illustration from Økland (1969). 6b: *Gammarus pulex* illustration from Pinkster (1970). 9a: *Gammarus wilkitzkii* illustration from Barnard (1959). 9b: *Gammarus salinus* illustration from Lincoln (1979). 10a: *Gammarus zaddachi* illustration from Sexton (1942). 10b: *Gammarus salinus* illustration from Sexton (1942). 11a: *Gammarus duebenii* illustration from Lincoln (1979). 11b: *Gammarus oceanicus* illustration from Lincoln (1979).

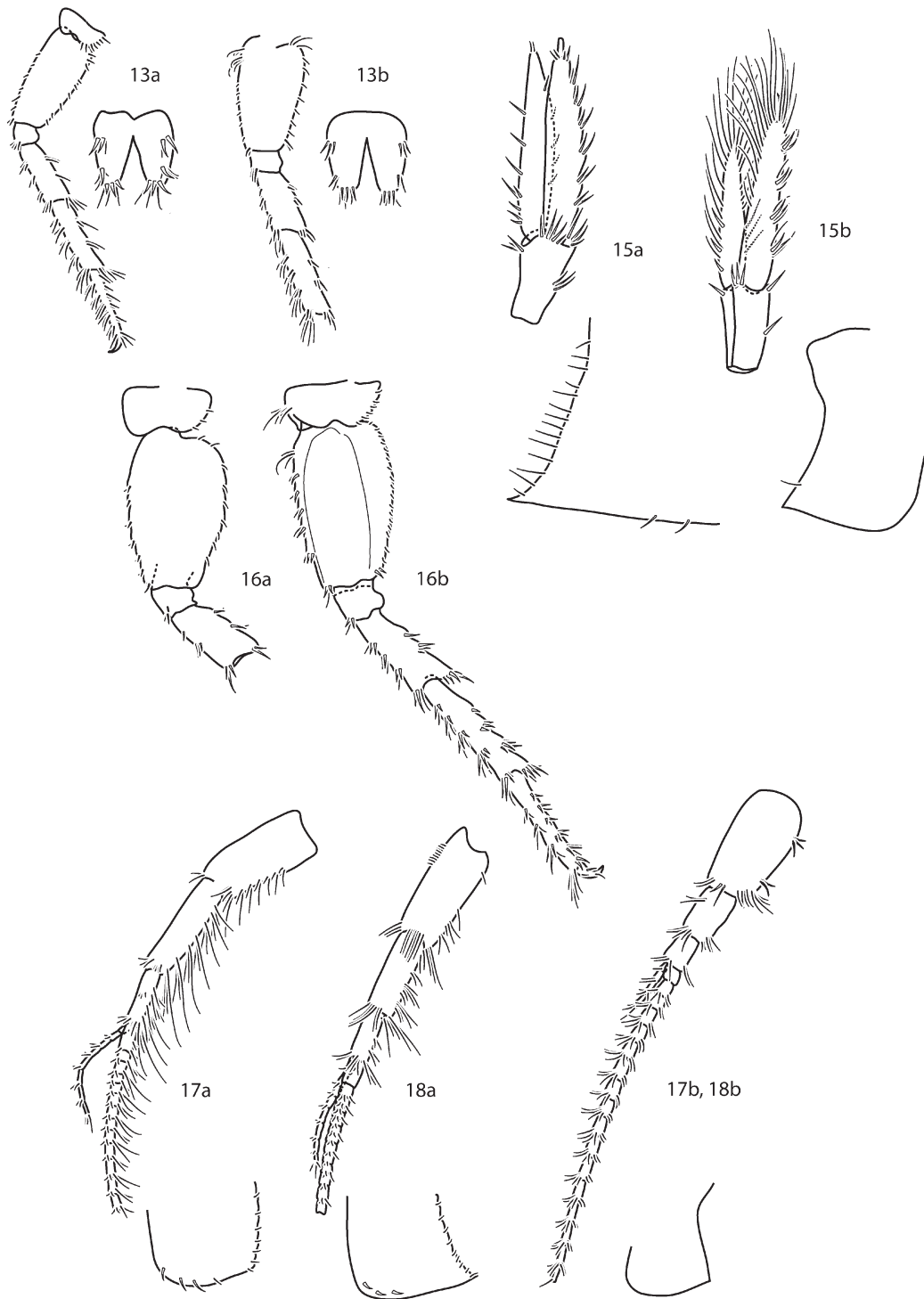


Figure 2. Illustrations to questions 13, 15, 16, 17 and 18 from the key. 13a: *Gammarus setosus* illustration from Bousfield (1973). 13b: *Gammarus oceanicus* illustration from Lincoln (1979). 15a: *Gammarus locusta* illustration from Lincoln (1979). 15b: *Gammarus inaequicauda* illustration from Sars (1890-95). 16a: *Relictogammarus stoerensis* illustration from Sexton & Spooner (1940). 16b: *Marinogammarus marinus* illustration from Sexton & Spooner (1940). 17a: *Marinogammarus obtusatus* illustration from Sexton & Spooner (1940). 18a: *Marinogammarus marinus* illustration from Sexton & Spooner (1940). 17b and 18b: *Marinogammarus pirloti* illustration from Sexton & Spooner (1940).

2. *Gammarus crinicornis* Stock, 1966

Synonyms: *Gammarus plumicornis* s. Pirlot (1939) and den Hartog (1964); non *G. plumicornis* Costa, 1853

Description and illustrations: Pirlot 1939, p. 54, figs 4-7 (as *G. plumicornis*); Stock 1967, p. 32, figs 14-16; Lincoln 1979, p. 263, fig 121.

Ecology and habitat: A marine, mainly sublittoral species, often from sandy bottoms with many loose algae. In the Netherlands often in the surf zone off sandy beaches (Vader, unpubl. obs.). Not found in brackish water.

Distribution: Not well known, not yet found in Norway. Occurs from W. Africa along the coasts to S. England and the Netherlands, also in the Mediterranean.

3. *Gammarus inaequicauda* Stock, 1966

Synonyms: *Gammarus campylops* s. Sars (1890-95); non *G. campylops* Leach, 1815. This species is very close to *G. insensibilis* Stock, 1966

Descriptions and illustrations: Sars 1890-95, p. 500, pl. 176-2 (as *G. campylops*); Stock & Kant 1966, pp 9-11, figs 1-2.; Stock 1967, p. 22, figs 7-8.

Ecology and habitat: In Norway, this is a species of the shallow subtidal in protected, often densely vegetated areas of somewhat varying salinity. The intertidal in these areas is generally occupied by other *Gammarus* species, often *G. salinus*.

Distribution in Norway: This species was originally described from Moss in the Oslo fjord. Its distribution is not yet fully known, but it seems to be quite widespread in the right biotopes along the south coast (Vader et al. 1984). Outside Norway, the only records still seem to be from Poland (Jazdzewski 1970)

B. *Gammarus oceanicus* group.

This is a group of quite large, unicoloured, basically marine *Gammarus* species, with a northerly and amphi-atlantic distribution. They are basically sublittoral, but are found more often intertidally than the species in group A, especially in the far north. Along the Norwegian coast they live primarily among algae, but in Arctic areas they are often found in *Marinogammarus*-like biotopes, intertidally below stones.

4. *Gammarus oceanicus* Segerstråle, 1947

Synonyms: *Gammarus zaddachi oceanicus* auct.; *Lagunogammarus oceanicus* auct.

Descriptions and illustrations: Segerstråle 1947, p. 226, fig. 3 a-g; Spooner 1951, p. 130; Dunbar 1954, p. 765, fig. 31; Kinne 1954, p. 414, figs 1-2, 4pp; Lincoln 1979, pp 243, 253, figs

100e, 111c, 119.

Biology: Along the south and west coast and in the large fjords of western Norway this is a species of the low intertidal and shallow subtidal, where it is primarily found in the algal belt of Fucaceae and is generally very common. In Northern Norway, and still more characteristically in Svalbard, this species is also very often found under stones in the lower intertidal, even on mudflats with occasional algae-covered large stones (Weslawski 1994).

Distribution in Norway: This is probably the most numerous *Gammarus* species on the Norwegian coast, where it also penetrates far into the fjords (Brattegard 1966, Vader 1977a). *G. oceanicus* is also common in Svalbard waters, but it is absent from the southern North Sea. It has recently been found further north than earlier in Svalbard waters, probably as a result of global warming (Węślawski et al. 2018)

5. *Gammarus setosus* Dementieva, 1931

Synonym: *Lagunogammarus setosus* auct.

Description and illustrations: Stephensen 1935-42, p. 321, fig. 41; Segerstråle 1947, p. 241, fig. 7; Christiansen 1965, fig. 3; Bousfield 1973, p. 50, pl. 1-2.

Biology: A mostly arctic marine, largely intertidal species. In the Arctic (Weslawski 1994), and also in Iceland (Ingolfsson 1977), this species is often found intertidally under stones, generally above the zone populated by *G. oceanicus*. In Newfoundland *G. setosus* is only found in the outlets of cool fresh-water streams in summer (V. Steele & Steele 1970), and this is precisely the biotope in which we have found this species in Finnmark, where it is found in the larger rivers, usually below the waterline.

Distribution in Norway: This is basically an Arctic species, and it has been reported from only a few places in Northern Norway (Malangen, Hammerfest, Tana) (Vader 1977b); a record from the Oslofjord (Stephensen 1935-42, p. 323) we consider doubtful. The species has an amphi-atlantic, high northern distribution, and is common on Svalbard.

C. The *Gammarus zaddachi* group

The three species *G. zaddachi*, *G. salinus* and *G. wilkitzkii* appear to be closely related morphologically, zoogeographically and ecologically; however, the 'under-ice high-arctic' *G. wilkitzkii* seems quite different from the other two, that are confined to a quite restricted area in northwestern Europe: south to western France (Bretagne). All three are basically brackish water species. *G. zaddachi* and *G. salinus* are easily recognized compared to the species in groups A and B because of their colour pattern; they have a clear pattern of transverse dark stripes on a light brown background.

6. *Gammarus zaddachi* Sexton, 1912 (s. Spooner, 1947)

Synonyms: *Gammarus zaddachi zaddachi* auct.; *G. setosus balticus* Dementieva, 1931; *G. sarsi* Reid, 1939; *G. ochlos* Reid, 1945; *Lagunogammarus zaddachi* auct.

Descriptions and illustrations: Sexton 1942, p. 593, pl. 1, figs 1-7, pl. 2, figs 10-14 (as *G. zaddachi*, freshwater form); Segerstråle 1947, p. 231, figs 3h-j, 5; Spooner 1947, p. 20, figs 4A-B, 5A-C; Kinne 1954, p. 417, figs 1-4pp; Dennert et al. 1969, p. 23; Lincoln 1979, pp 239, 243, 249, figs 110a, 111a-b, 114.

Ecology and habitat: *Gammarus zaddachi* is a brackish water amphipod, living subtidally or in the lower intertidal. It is quite common in the lower intertidal in the inner fjords (where *G. duebenii* occupies the upper intertidal), but on the outer coast it is generally confined to river mouths (Vader 1977a-b). Also there it lives mainly in the lower intertidal or shallow subtidal, while *G. duebenii* occupies the higher intertidal. Compared to areas further south (den Hartog 1964, Spooner 1947) *G. zaddachi* in Norway seems to occupy somewhat less saline waters. Migratory movements, quite conspicuous in French estuaries (Dennert et al. 1969, Stock 1966, Girisch et al. 1974), have not yet been studied in Norway.

Distribution in Norway: *Gammarus zaddachi* occurs all along the Norwegian coast, in the right biotopes (Brattegard 1966, Dennert 1973, Vader 1977a-b). On the open coast it is restricted to the outlet of minor streamlets, where it may penetrate quite far inland (Vader 1977b). In the inner parts of the large fjords, often meso- or even oligohaline, *G. zaddachi* becomes the dominant amphipod in the lower intertidal, often together with *G. oceanicus* (Brattegard 1966, Vader 1977a). The species is absent from Svalbard.

A very aberrant biotope was discovered by the Økland family (Økland et al. 2011): a population of *G. zaddachi* lives at 150 m depth in the freshwater lake Eikeren in inland southern Norway.

7. *Gammarus salinus* Spooner, 1947

Synonyms: *Gammarus zaddachi salinus* auct.; *Lagunogammarus salinus* auct.

Descriptions and illustrations: Sexton 1942, pl. 1, figs 8, 9, pl. 2, figs 15-18 (as *G. zaddachi*, saline form); Spooner 1947, p. 20, figs 4C, 5D-E; Kinne 1954, p. 416, figs 1-4pp; Dennert et al. 1969, p. 23; Lincoln 1979, pp 243, 251, figs 111f, 115.

Ecology and habitat: Elsewhere in Europe *Gammarus salinus* is known as the species concentrated in the areas with the largest oscillations in salinity (den Hartog 1964, Movaghar 1964, Meurs & Zauke 1988); this is in agreement with the situation in the inner Oslofjord (Skadsheim 1983). Here *G. salinus* lives in the lower intertidal, while the records from the south coast and the Bergen area mostly concern the shallow subtidal, as in the estuaries of Western Europe (Spooners 1947,

den Hartog 1964), although also there the species may occur intertidally under special circumstances, usually involving lowered salinity (Vader 1965).

Distribution in Norway: Not well known. The species is common in the inner part of the Oslofjord (Skadsheim 1983, 1984), and it has also been found along the south coast (Dennert 1973, Vader et al. 1984). In the Hardangerfjord Brattegard (1966) found *G. salinus* only in the side fjords, while the northernmost records hitherto are from the Bergen area (Vader 1972). Vader (1977a) did not find *G. salinus* at all in the Sognefjord. *G. salinus* is a southern species, occurring along European coasts south to N. Spain (van Maren 1975); it is absent from Iceland (Ingolfsson 1977).

8. *Gammarus wilkitzkii* Birula, 1897

Synonym: *Lagunogammarus wilkitzkii* auct.

Descriptions and illustrations: Sexton 1942, p. 601; Gurjanova 1951, p. 764, fig. 551; Barnard 1959, p. 120, pls 10-13.

Ecology and habitat: This large and slow-growing species occurs primarily in the pack ice (Weslawski 1994), where it is omnivorous (Arndt 2002). In areas with seasonal ice cover the animals may live benthically in the ice free periods (Arndt et al. 2005).

Distribution: This is a high-arctic species, occurring along the coasts of Siberia and northern Canada, as well as in the pack ice of the Polar Sea. It has never yet been found in Norwegian waters outside Svalbard. Svalbard distribution is mapped by Węśławski et al. (2018).

D. The *Gammarus tigrinus* group

9. *Gammarus tigrinus* Sexton, 1939

Description and illustrations: Sexton 1939, pp 545-548, pls IV-VI; Bousfield 1973, pp 51-52p. 50, pl. IV-14; Lincoln 1979, p. 254, fig. 117.

This species belongs to a group of primarily American brackish- and fresh-water *Gammarus* species, which in many ways parallel the *G. zaddachi* group in Europe, i.a. by their conspicuous 'tiger stripes' (cf e.g. Bousfield 1969). *G. tigrinus* has no doubt been imported to Europe by man, but when and where is unknown. It was first discovered in Britain in the 1930's and described as a new species by Sexton (1939). It was later recognized as identical to certain populations of the American freshwater species *G. fasciatus* Say, 1818 but this species was split by Bousfield (1958), with the brackish water populations retaining the name *G. tigrinus*. Later it was imported by fisheries people to both the Netherlands and Germany, in the hope that this would increase the food basis for freshwater fish; instead the species quickly developed into a problem (see i.e. Ruoff 1968). Its dispersal in the Netherlands

has been followed in detail over the years, and it is clear that *G. tigrinus* is completely dominant to the indigenous *Gammarus* species in many habitats; it is i.e. less sensitive to pollution (see e.g. Nijssen & Stock 1966, Gras 1971).

Ecology and habitat: In the USA *Gammarus tigrinus* is a species of oligohaline and mesohaline habitats in estuaries. In Europe it is found in similar biotopes, e.g. in the Baltic Sea, but also in stagnant oligohaline brackish and even in fresh water, where it often has ousted the local indigenous *Gammarus* species.

Distribution: In Europe hitherto found in Ireland, Britain, Holland, Germany and the Baltic Sea. *Gammarus tigrinus* has not yet been recorded from Norway.

E. The *Gammarus lacustris* group.

This group contains the pure freshwater species. Morphologically the group is characterized by short oval eyes, and a short inner ramus of uropod 3. The two Nordic species are probably not especially closely related. *G. lacustris* has a holarctic distribution, while *G. pulex* is exclusively palaeartic.

NB. The genus name *Rivulogammarus* S. Karaman, 1931, often used for this group, is unavailable (Stock, 1969a).

10. *Gammarus lacustris* Sars, 1863

Synonyms: *Rivulogammarus lacustris* auct.; *Gammarus pulex* sensu Sars (1890-95); non *Cancer pulex* Linnaeus, 1758; *Rivulogammarus scandinavicus* S. Karaman, 1931.

Description and illustrations: Sars 1890-95, p. 503, pl. 177-2 (as *G. pulex*); Økland 1969, p. 132, figs 16-23.

Ecology and habitat: Dealt with in detail by Økland (1969). *G. lacustris* lives in lakes, ponds and slow moving rivers at places where the water is not too acidic and too deficient in calcium.

Distribution: See Segerstråle (1954) and Økland (1969, fig.2). This species occurs in most of Norway, but has not been reported from Østfold and Agder, while there are no reports from Lofoten-Vesterålen either. Around Bergen *G. lacustris* has been recently discovered by Bjerknes (pers. comm.). Outside Norway, *G. lacustris* has a very wide holarctic distribution at northerly latitudes.

11. *Gammarus pulex* (Linnaeus, 1758)

Synonyms: *Rivulogammarus pulex* auct.; *Gammarus pulex pulex* auct.

Description and illustrations: Schellenberg 1942, pp 24-26, figs 6b, 7, 8 (as *G. p. pulex*); Pinkster 1970, pp 181, 183, 185, figs1 p. 179, figs 1-4.

Ecology and habitat: Character species of rivers with not too strong currents, but it can also live in stagnant ditches and

pools, and even in oligohaline brackish water.

Distribution: The Scandinavian distribution has been mapped by Segerstråle (1954). *Gammarus pulex* has in Sweden been found close to the border of Østfold in SE Norway, but as yet there are no Norwegian records.

F. The *Gammarus duebenii* group

Here we have combined *G. duebenii* and *Marinogammarus finmarchicus*, both somewhat odd man out in their genus, both morphologically and ecologically. Both are largely intertidal species, although *duebenii* has a much wider ecological tolerance, and both have an amphi-atlantic distribution. (Pinkster et al. (1970) split off the freshwater populations in Ireland and Brittany as *G. d. celticus*; this taxon is not considered here). In contradistinction to the species in the *zaddachi* and *tigrinus* groups, these species are not patterned, but unicoloured.

12. *Gammarus duebenii* Liljeborg, 1852

Synonyms: *Rivulogammarus duebenii* auct. (NB. The specific epithet is often written *duebeni*, and the author's name Liljeborg; both are incorrect).

Description and illustrations: Sars 1890-95, p. 507, pl. 177-1; Kinne 1954, p. 419, figs 1-4pp; Lincoln 1979, pp 243, 245, figs 111e, 112.

Ecology and habitat: *Gammarus duebenii* is a very euryoecious species, and generally one can say that it occurs everywhere where other *Gammarus* and *Marinogammarus* species do not thrive (see e.g. Forsman 1951, Kinne 1953, den Hartog 1964). In Norway the main biotope is supralittoral rockpools, the mouth of small and medium large streamlets (here they can ascend quite a bit upstream and live at least temporarily in pure freshwater), and intertidally, under stones and among algae in meso- and oligohaline brackish waters, as in the inner part of fjords (Brattgard 1966, Vader 1977a).

Gammarus duebenii has also several times been found in 'freshwater' lakes and pools in Norway (see Økland 1970, Kjærstad et al. 2016). As 'marflo' samples are often transported by fishermen between lakes and even from the shore to lakes, some of these occurrences may be not quite natural.

Distribution. Common along the whole coast of Norway, but absent from Svalbard waters. A few freshwater occurrences.

13. *Marinogammarus finmarchicus* (Dahl, 1938)

Synonyms: *Gammarus finmarchicus* auct.; *Chaetogammarus finmarchicus* auct.; *Gammarus greenfieldi* Shoemaker, 1938; *Echinogammarus finmarchicus* auct.

Description and illustrations: Dahl 1938, p. 125, figs 1-10 (*Gammarus f.*); Stephensen 1935-42, p. 344, figs 45-46 p.p.; Sexton & Spooner 1940, p. 656, figs 6,7; Bousfield 1973, p.

58, pl. 7; Lincoln 1979, pp 238, 243, 247, figs 110d, 111g, 113 (*Gammarus f.*)

Ecology and habitat: Under stones in the lower intertidal, preferably where some water remains at low tide. Penetrates to a certain distance in fjords: in Hardanger to indre Samlafjorden (Brattegard 1966), in the Sognefjord to Helle (Vader 1977a).

Distribution: Common along most of the Norwegian coast (not in Svalbard), but there are few records as yet from the Skagerrak coast.

G. The *Marinogammarus* group

All *Marinogammarus* species are marine and occur mostly intertidally, usually more under stones or in gravel than among algae. Even though one may find several species closely together, the species nevertheless differ in their specific demands. This may lead to a microsegregation, even when present below the same boulder. An example is shown by a study in the Netherlands (Vader 1965) from a sandy beach with scattered large stones and some freshwater flow. Here *Gammarus salinus* kept to the free water puddles, *Marinogammarus obtusatus* lived in clumps of *Mytilus* above the water, and *Relictogammarus stoerensis* in the gravel and sand; three species below the same boulder, but still in different habitats!

There are no *Marinogammarus* species on Svalbard. Their role in the intertidal is there taken over by *Gammarus setosus* and to a certain degree *G. oceanicus*. In mesohaline and oligohaline areas, and high in the intertidal, *G. duebenii* takes over the 'under stones' habitat.

14. *Marinogammarus marinus* (Leach, 1815)

Synonyms: *Gammarus marinus* auct.; *Chaetogammarus marinus* auct.; *Echinogammarus marinus* auct.

Description and illustrations: Stephensen 1935-42, p. 340, figs 45-46pp; Sexton & Spooner 1940, p. 638, figs 1-2; Lincoln 1979, pp 265, 267, figs 122a, 123 (*Chaetogammarus m.*).

Ecology and habitat: This is the most euryoecious of the *Marinogammarus* species. Usually it is to be found under stones in the upper half of the intertidal. In places with some freshwater flow, or where *M. obtusatus* and/or *?M. finmarchicus* for some reason are absent, it may occur lower down. *M. marinus* tolerates more sediment in the substrate than the other species, and it also occurs in brackish waters. In estuaries it occurs far into the mesohalinity (den Hartog 1964). In the fjords in W. Norway it penetrates very far: in Hardanger until Osafjorden (Brattegard 1966), in the Sognefjord far into the Lusterfjord (Vader 1977a).

Distribution in Norway: Very common everywhere in southern Norway. Its distribution is insufficiently known in northern Norway: it is not rare around Tromsø, but we know of no reliable records east of the North Cape.

15. *Marinogammarus obtusatus* (Dahl, 1938)

Synonyms: *Chaetogammarus obtusatus* auct.; *Eulimnogammarus obtusatus* auct.; *Echinogammarus obtusatus* auct.

Description and illustrations: Dahl 1938, p. 127 (*as Gammarus o.*), figs 11-21; Stephensen 1935-42, figs 45-46pp; Sexton & Spooner 1940, p. 650, fig.5; Pinkster & Stock 1970, p. 207, figs 2 a-g (*Eulimnogammarus o.*); Lincoln 1979, p. 273, fig. 126 (*Eulimnogammarus o.*).

Ecology and habitat: Under stones in the lower intertidal, preferably on a substrate of sand, gravel, or shells; occurs also on intertidal pebble beaches. Tolerates some freshwater flow, but not much fine sediment. Penetrates less far into fjords than *?M. finmarchicus*: in Hardanger to Samlafjorden (Brattegard 1966), in the Sognefjord to Lavik (Vader 1977a)

Distribution in Norway: Probably occurs along the entire Norwegian coast, but absent in Svalbard.

16. *Marinogammarus pirloti* Sexton & Spooner, 1940

Synonyms: *Chaetogammarus pirloti* auct.; *Echinogammarus pirloti* auct.

Description and illustrations: Sexton & Spooner 1940, p. 667, figs 9-10, pl. 4; Lincoln 1979, pp 265-269, figs 122b, 124 (*Chaetogammarus p.*).

Ecology and habitat: Intertidally, under stones and among algae (*Ascophyllum*, *Enteromorpha*) at places where freshwater flows out. Distribution very patchy, but may be numerous where occurring. Apparently confined to the outer coast.

Distribution in Norway: Not well known. Discovered in Norway by Tulkki (1963) in the outermost Hardangerfjord. Later once found in the Oslofjord (C. Christophersen, pers. comm.) and a few places between Hardanger and the outer Trondheimsfjord (Vader 1969), in all cases close to the open coast, as is also the case in Britain (Spooner 1957). Not yet found further north than the Trondheimsfjord, but may well occur there.

H. The *Relictogammarus* group

This consists of only the small species *R. stoerensis*, which according to the studies of Hou & Sket (2016) should be considered the sister group to all other Gammaridae.

17. *Relictogammarus stoerensis* (Reid, 1938)

Synonyms: *Gammarus stoerensis* Reid, 1938; *Marinogammarus stoerensis* auct.; *Chaetogammarus stoerensis* auct.; *Echinogammarus stoerensis* auct.

Description and illustrations: Stephensen 1935-42, p. 346, fig. 49 (*Marinogammarus st.*); Sexton & Spooner 1940, p. 662, fig. 8 (*Marinogammarus st.*); Lincoln 1979, p. 271, fig. 125

(*Chaetogammarus st.*).

Ecology and habitat: Intertidal, under stones and in gravel, coarse mud-intermixed sand or other mixed fine substrate, at places where lesser amounts of freshwater flow out. The vertical distribution covers almost the entire intertidal, down from MHWN; higher up it is often replaced by *Gammarus duebenii*. *R. stoerensis* tolerates much brackish water; in the Sognefjord the first author (Vader 1977a) found them at Dale in the Lusterfjord, where the fjord is ice-covered several months each winter. In the inner fjords *R. stoerensis* may be almost dominant some places (cf Skadsheim 1983) and it is there, where the salinity is very variable during the year, much less confined to freshwater trickles.

Distribution in Norway: Probably common along the entire Norwegian coast, but absent from Svalbard. There are as yet few records from N. Finnmark (Vader 1971), but the species also occurs in the Murmansk region (Segerstråle 1948).

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