

AN ACCOUNT OF *MARINOGAMMARUS*
(SCHELLENBERG) GEN. NOV. [AMPHIPODA],
WITH A DESCRIPTION OF A NEW
SPECIES, *M. PIRLOTI*

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From the Plymouth Laboratory

(Plate IV, Text-figs. I-11)

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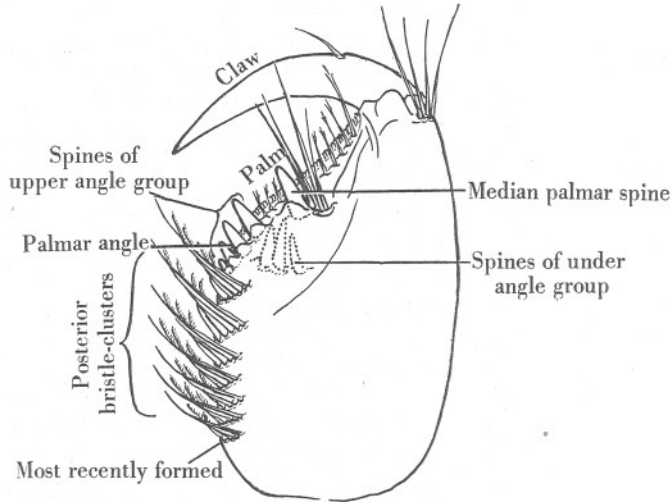
INTRODUCTION

The genus *Gammarus*, instituted by Fabricius in 1775, has come to include a large number of species—so many and so varied, in fact, that the necessity for a revision of the genus is well recognized. An extensive examination of the taxonomic literature has inevitably led to the conclusion that several more or less well-defined groups of species can be recognized among the total assemblage, and that some of these at least should be separated off as distinct genera.

In this present contribution we do not propose to discuss the dismemberment of *Gammarus* as a whole, but as a first step to treat one of the natural groups hitherto included within it. This group, here raised to generic status under the name of *Marinogammarus*, has been in special need of revision. It appears to have its headquarters in north-western Europe, and includes nearly half the British species of *Gammarus sens. lat.* Thus, from the point of view of our proposed aim of thoroughly revising the British species of this assemblage, an important part of the ground is here covered.

Karaman (1931) started the division of the genus, followed later by Schellenberg (1937*a*). The latter outlined and named several subgenera; but in the opinion of such well-known writers on Amphipoda as Prof. Jean-M. Pirlot and Prof. Louis Fage, these groups should be given full generic status, provided of course that they can be shown to possess distinct and constant characters. With this view we are in complete agreement. We have therefore taken one of the most clearly marked divisions, *Marinogammarus* (Schellenberg), giving its generic diagnosis, with descriptions and figures of all the six species which can be clearly recognized as belonging to it. It seems doubtful whether any other described species of palaeartic "*Gammarus*" not examined by us will prove to belong to this genus. Five of the six species are so far known to occur in Britain.

Our special thanks are due to Dr Isabella Gordon for her kind help in enabling us to have access to the collections preserved in the British Museum; to Prof. Louis Fage for having forwarded to us type specimens preserved in the Muséum National, Paris; to Prof. Jean-M. Pirlot, of the University of



Liège, for having placed at our disposal various material, including specimens, microscope mounts, and drawings; and to Mr G. I. Crawford for having sent us material (collected by himself) from wide-spread localities for the purpose of this work.

The whole work has also greatly benefited from the opportunities we have had for examining material sent to us for determination. From having seen samples from a number of different localities, we have been able to confirm the constancy of specific characters, to make a first step in defining the distribution of the different species, and to reduce considerably the probabilities

that still other overlooked species occur in Britain. Our grateful acknowledgements are due to the following zoologists: Mr R. Bassindale, Mr L. C. Beadle, Prof. A. D. Hobson, Mr R. MacDonald, Mr D. M. Reid, Hon. Miriam Rothschild, Dr K. Stephensen and Prof. C. M. Yonge. Records of material examined are listed under the separate species.

The terminology adopted throughout the paper is based on that of Stebbing (1906). The gnathopod armature, which has been found to show many interesting features, has been studied in greater detail than is perhaps customary: a diagram of a gnathopod hand is appended (p. 634) to make clear the designation of the structures referred to in the descriptions. The lateral plates of the first three pleon-segments are termed "epimera 1-3". The names used in describing certain types of setae are defined in a separate section at the end of the paper (pp. 676-81).

Measurements of length refer to the distance between the apex of the rostrum and the base of the telson, when the specimen is straightened out along a stage-micrometer. In the study of details of structure, specimens were dissected and their parts mounted for examination under the microscope. All drawings were made with the aid of a camera lucida. A set of permanent preparations, mounted in gum chloral solution, has been made for each species.

HISTORICAL

In north and west Europe, as well as in eastern North America, the species of the assemblage *Gammarus* comprise two very distinct types, recognized as long ago as 1815 by Leach. In his *Arrangement of the Crustacea* (1815, p. 359) Leach divided the species of *Gammarus* F. into two groups, according to the degree of development of the rami of uropod 3, characterized thus: "*cauda stylis geminatis superioribus stylo supero brevissimo*", with *G. aquaticus* (= *pulex*) and *G. marinus*; and "*cauda stylis geminatis superioribus stylis subaequalibus*", with *G. locusta* and *G. campylops*.

It must be noticed in passing that Leach's grouping contains an anomaly, which, as Walker (1911) has clearly shown, can only have been due to an unintentional error on the part of the author. Both *G. aquaticus* and *G. campylops* (see p. 673) had been placed in the wrong groups, and had doubtless been accidentally transposed. The necessity for this emendation must be accepted.

Of Leach's two divisions the second one should retain the generic name of *Gammarus*, with *locusta* (L.) as the type. The questions as to what other species are to be included in this segregate genus, and whether *pulex* and the freshwater forms which are grouped with it are to be given generic status, fall beyond the scope of the present work. It is only necessary to point out that *locusta* (L.), and the related species *duebenii* Liljeborg, *zaddachi* Sexton, and *chevreuxi* Sexton, are recognized as undisputed representatives of *Gammarus* in the restricted sense. These are relatively active free-swimming forms,

seeking the cover of weeds and vegetable debris rather than of stones, and with their optimum environment in permanent waters. Their most noticeable structural character is to be found in the long and well-developed inner ramus of uropod 3, both rami being fringed with long setae.

Leach's first division, for the inclusion of *marinus*, is the group which, as already stated, is here treated as a separate genus. It includes the genotype *marinus* (Leach) and five related species, of which four have only been recognized quite recently. The name *Marinogammarus* has to be used, as Schellenberg (1937*a*) has already formed a subgenus of this designation, with *marinus* as the only certain representative known to him. The species are essentially bottom-living forms, inhabiting the intertidal zone, and living amongst stones and shingle. The most distinctive character which separates them from *Gammarus sens. str.* is the short inner ramus of uropod 3—almost scale-like in most species; but this character is also shared by diverse groups of species, inhabiting south-eastern Europe and western Asia, which clearly cannot be placed in *Marinogammarus*. For an adequate diagnosis of the latter a combination of characters has to be taken into consideration. The best brief description that can be devised is "*Gammarus*-like species, with short inner ramus, almost or completely lacking setae on hind peraeopods and on the urosome dorsally, with elongate eyes, and adapted for life in stony intertidal habitats."

GENUS *Marinogammarus* (Schell.)

Gammarus in part Leach, 1815, p. 359; Sars, 1894, p. 496; Stebbing, 1906, p. 460.
Gammarus subg. *Marinogammarus* Schellenberg, 1937*a*, p. 270.

Body smooth and rounded. Pleon-segments 4-6 (or urosome) at most with slight dorsal elevations, never strongly produced; with four groups of spines, median and lateral, the two median groups remaining more or less separated in the mid-dorsal line; no setae present among these spines. Sideplates 1-4 not very deep, margins rounded and almost glabrous; 4 about as broad as deep, smoothly rounded on distal margin. Epimera of pleon-segments 2 and 3 never greatly produced posteriorly, the postero-distal angle from slightly acute to strongly obtuse.

Head without conspicuous rostrum; lateral lobes rounded. Eyes large, elongate, sometimes notably long and narrow, usually in adult slightly constricted in middle. Antenna 1 longer than antenna 2; basal joint of peduncle always long; accessory flagellum of medium length, with from 4 to 9 joints. Antenna 2 with flagellum usually slightly shorter than peduncle, occasionally equal to it in length, sometimes bearing calceoli.

Oral parts. Upper lip a little wider than deep, slightly emarginate at apex; lower lip without inner lobes. Mandible normal, with strongly dentate cutting-edge, accessory plate, spine-row, molar, and 3-jointed palp; the right mandible bearing a long stiff feathered bristle behind the molar. Maxilla 1 with inner plate bearing long feathered setae, and outer provided with stout

serrate spines; palp of the right maxilla with spine-teeth on the apex, that of the left with setiform spines. Maxilla 2 with rows of long serrated bristles on both inner and outer plates. Maxillipeds with inner plate armed distally with large spine-teeth; outer plate with long curved serrated spines and spine-teeth; palp well developed.

Gnathopods 1 and 2 subchelate, stronger in male than in female; hands in male usually not markedly different in size, occasionally 1 larger than 2; palmar median spine rounded, never truncate.

Peraeopods 1 and 2 sometimes more densely setose in female than in male. Peraeopods 3-5 armed with clusters of strong spines, setae rarely present; basal joint expanded, postero-distal corner of peraeopod 3 always free; claw strongly recurved.

Uropod 3 with outer ramus long and broad; inner ramus small, typically almost scale-like. Telson cleft to the base, each lobe at least twice as long as broad, with one lateral and one apical cluster of spines.

Male sensory setae usually with more or less abruptly narrowed apices; not developed on peraeopod 1.

Habitat essentially littoral, intertidal, sometimes further restricted to places subjected to freshwater influence. Structure and habits of species adapted for living under cover of stones.

Distribution: North Atlantic, temperate and boreal, coasts of west and north Europe and north-east America, range extending into adjoining seas.

Genotype: *Gammarus marinus* Leach, 1815.

Six species belonging to this genus are described below: *marinus* (Leach, 1815), *olivii* (Milne-Edwards, 1830), *obtusatus* (Dahl, 1938), *finmarchicus* (Dahl, 1938), *stoerensis* (Reid, 1938), and a new species, which we have called *pirloti* in honour of Prof. Pirlot of Liège.

A species of hitherto doubtful status, *Gammarus locustoides* Brandt 1851, has sometimes been provisionally grouped as a close relative of *marinus*, to which it bears a superficial resemblance. This species inhabits the coasts of the North Pacific, where the other marine *Gammarus* forms belong to *Anisogammarus*, a genus separated on the possession of thin processes attached to the gills. A re-examination of *G. locustoides* has shown it to possess this character; hence it is to be placed in that genus, and is not a *Marinogammarus*.

Marinogammarus marinus (Leach)Text-figs. 1*a-i*, 2*a-j*, 11*k, l*.

The principal references to the species are:

1815 *Gammarus marinus* Leach, *Trans. Linn. Soc.*, Vol. xi, p. 359.

1894 *Gammarus marinus* Sars, *Crust. Norway*, Vol. I, p. 497, Pl. 175.

1906 *Gammarus marinus* Stebbing, *Das Tierreich*, Vol. xxi, p. 472.

1925 *Gammarus marinus* Chevreux & Fage, *Faune de France*, Vol. ix, pp. 250-1, fig. 260.

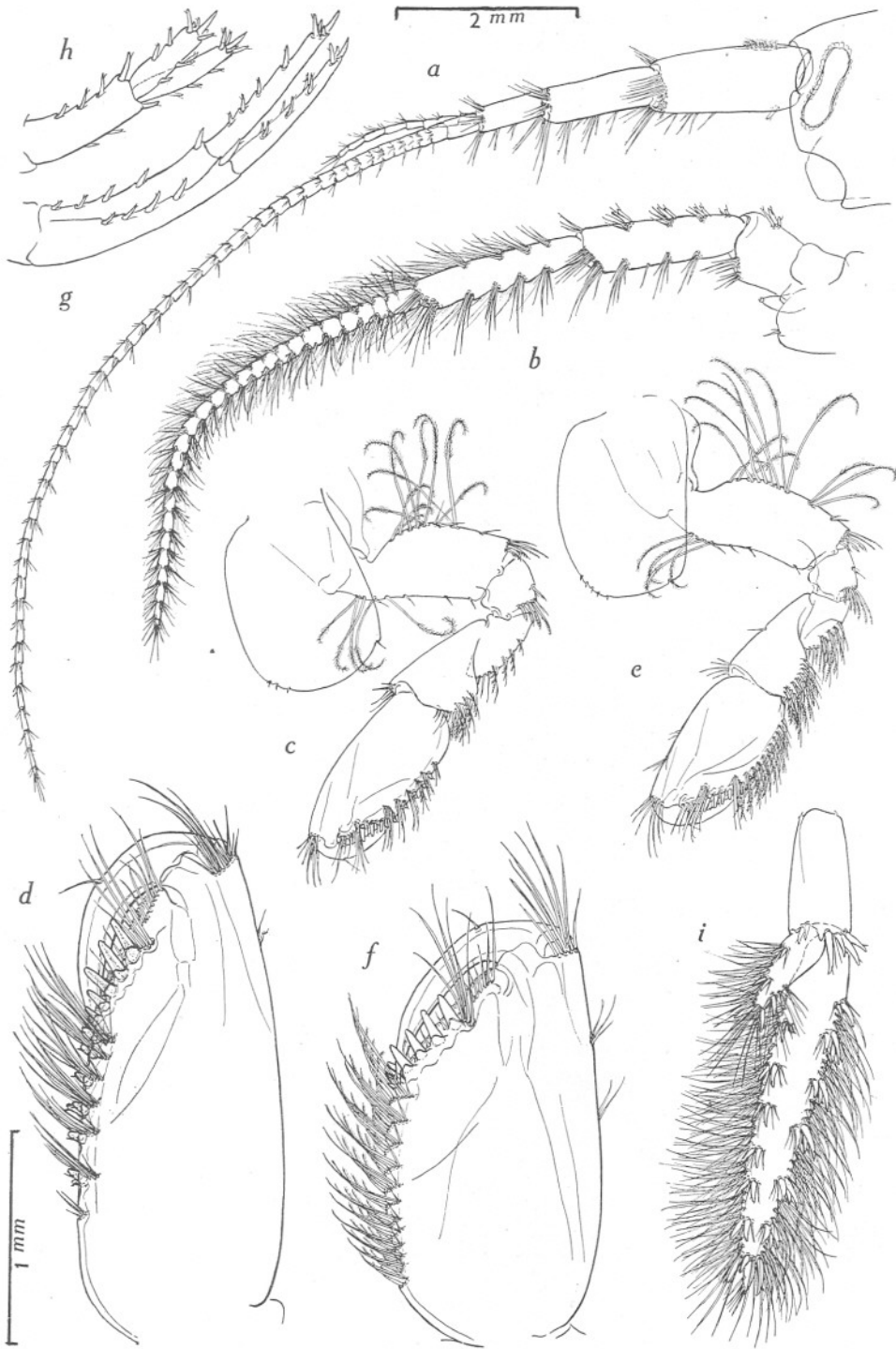
This species was instituted by Leach in 1815, but since then many other and quite distinct species have been frequently recorded as *marinus*, so that a great deal of confusion has been caused in the records of its distribution. For example, collections of "*marinus*" from the British coasts, Shetland, and the East Murmansk coast, have proved to be *obtusatus* Dahl; from Naples, *olivii* M.-Edw.; from Durham, *stoerensis* Reid, and so on. Many of the earlier writers classed *marinus* Leach as a variety of *locusta*. Spence Bate (1862, p. 215) recognized it as distinct, but included in its synonymy Milne-Edwards' *G. olivii* and *G. affinis*, as well as Rathke's *G. gracilis*, *G. poecilurus* and *G. kröyeri*. Stebbing (1906) follows him in this with the addition of *G. locustoides* Brandt. *Gammarus olivii*, however, has been proved a distinct species by Chevreux & Fage (1925), who examined and redescribed Milne-Edwards' types (see p. 645). The other species mentioned were not sufficiently defined or figured to be identified with any certainty.

Sars (1894) was the first to give a good definition and figures of *marinus*. We have refigured it here in order to draw attention to various details, particularly those which have diagnostic value in separating the species from others of the genus. These characters include the presence of a row of short spines (curvate in male, acute in female) on the posterior margin of the hand of gnathopod 1 (Text-fig. 1*d*), and the form and arrangement of setae on uropod 3 (Text-fig. 1*i*).

ADULT MALE.

Body slender and compressed. Pleon-segments 4-6 with dorsal spines more numerous than in the other species, the number increasing with age; each segment carrying two upward converging rows of 6-9 spines on each side, these four groups tending to merge into a continuous curved row. Sideplates 1-4 not very deep; 4 (Text-figs. 2*b* and 2*c*) about as broad as deep, distal expansion rather shallow, posterior expansion obliquely rounded. Epimera 2 and 3 (Text-fig. 2*g*), postero-distal corner of 2 subquadrate, of

Text-fig. 1. *Marinogammarus marinus* (Leach), male. Figures drawn from an adult male, captured Plymouth district (Tamar Estuary, Thorn Point, 10. xii. 37), compared with specimens from other localities, Great Britain, Northern Ireland, Denmark and Norway. Magnification $\times 13$, except *d* and *f* $\times 28$. *a*, head and antenna 1, outer surface left side; *b*, antenna 2, outer surface left side; *c*, gnathopod 1, left side; *d*, gnathopod 1, left side, hand enlarged; *e*, gnathopod 2, left side; *f*, gnathopod 2, left side, hand enlarged; *g*, uropod 1, left side; *h*, uropod 2, left side; *i*, uropod 3, showing the inner ramus.



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3 somewhat acute and more produced than in the other species; posterior margins inset with numerous upward-pointing setules.

Head (Text-fig. 1*a*) not quite as long as peraeon-segments 1 and 2 combined; with lateral lobes vertically truncate, distal margin rounded, sinus rather deep. Eyes notably long and narrow, slightly constricted in the middle, the elongation evident from a very early age; pigment black. Antenna 1 (Text-fig. 1*a*) with joint 1 of peduncle clearly longer than joint 2, but somewhat shorter than 2 and 3 combined, joint 2 approaching twice length of joint 3; flagellum about $2\frac{1}{2}$ times as long as the peduncle, the number of joints reaching at least 47; accessory flagellum about half the length of the peduncle, 8-jointed in large specimens. Antenna 2 (Text-fig. 1*b*) considerably shorter than antenna 1; flagellum about as long as peduncle, 26–29-jointed in large specimens; dense tufts of male sensory hairs (p. 680 and Text-fig. 11*d*) developed on joints 4 and 5 of the peduncle, and on the flagellum; calceoli lacking. An occasional seta on peduncle of antenna 1 with bifurcate apex.

Gnathopods (Text-figs. 1*c–f*). Hand of gnathopod 1 (Text-fig. 1*d*) appreciably longer than that of gnathopod 2; elongate; palm oblique; median palmar spine not separated from the angle spines; the most distal of posterior bristle-clusters situated at the level of the palmar angle: this hand showing an important diagnostic character—the posterior margin being provided with a series of short curvate spines arising in connexion with the bristle-clusters, all the bristle-clusters, except the most proximal (i.e. the most recently formed), having 1 or 2 of these spines inset closely beside it on the extreme edge of the margin. Hand of gnathopod 2 (Text-fig. 1*f*) with the palm nearly transverse, and palmar angle well-defined; median spine, as in gnathopod 1, not separated from angle spines; normal with respect to position of the most distal posterior bristle-cluster and to absence of curvate spines along posterior margin. Joint 5 subequal in length to that of gnathopod 1. Bifurcate setae on both gnathopods, except hand of gnathopod 1.

Peraeopods 1 and 2 (Text-fig. 2*a, b*) sparsely setose, lacking both male sensory and bifurcate setae. Basal joint of peraeopod 3 (Text-fig. 2*d*), with posterior distal angle free, subangulate; those of peraeopods 4 and 5 (Text-fig. 2*e, f*) narrowed distally, with the angle “closed”, inset with a group of 2 or 3 spines; posterior expansions in all three with numerous marginal setules. Peraeopod 4 with joint 4 over twice as long as distal width; peraeopods 4 and 5 with joint 5 rather longer than joint 6.

Uropod 1 (Text-fig. 1*g, h*) reaching beyond uropod 2. Uropod 3 (Text-fig. 1*i*) with outer ramus long, bearing dense clusters of spines and setae around both margins, the setae mainly of the male sensory type, and none plumose; second joint short, spiniform, with a tuft of setae at tip (in the newly hatched young this joint more than half the length of joint 1; Text-fig. 2*i*); inner ramus very narrow, about one-quarter length of outer, nearly surrounded by a dense fringe of hairs and spines. Telson (Text-fig. 2*j*) rather small, lobes distally divergent, each with a lateral cluster of spines near base, and a cluster of 3 on the truncate apex.

ADULT FEMALE.

Differences from adult male as follows.

Both antennae with bifurcate setae well distributed.

Gnathopods. Joint 5 longer in gnathopod 2 than in gnathopod 1. Hand of gnathopod 1 much smaller and very different in form from that of male, the palm not at all oblique; spines present, as in male, between the more distal of the posterior seta-clusters, these spines acute and not curvate. Hand of gnathopod 2 smaller than in male, elongate. Bifurcate setae well distributed on both gnathopods.

Peraeopods 1 and 2 (Text-fig. 2c) much more setose. Brood-plates comparatively large, anterior pair (attached to gnathopod 2) with hairs of anterior margin forming a continuous dense row.

Uropod 3 (Text-fig. 2h) with outer ramus bearing plumose hairs amongst the setal fringe on the inner margin; spines on inner margin long and slender; inner ramus very sparsely setose.

Eggs dark brownish when newly laid, changing to dull yellow as embryos develop; produced in batches of between 30 and 50; size rather smaller than in some of related species (average dimensions of one batch of 11 recently laid: 0.49×0.59 mm.). Young 2-2 $\frac{1}{4}$ mm. at extrusion.

SIZE AND COLOUR.

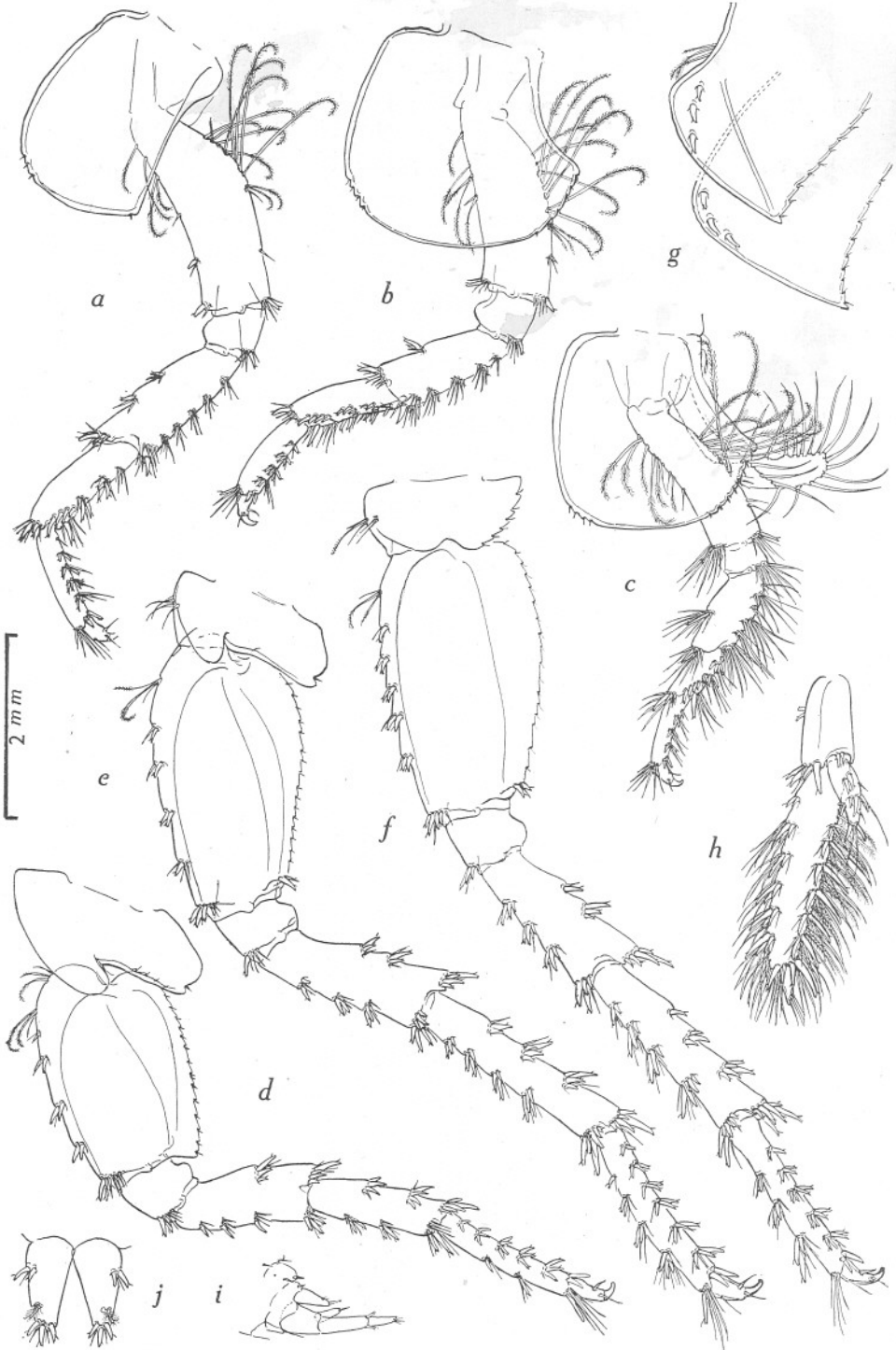
Length of male 15-25 mm.; female on average smaller, to about 20 mm. Colour dark green, sometimes suffused with reddish or yellowish brown, body pigment of adult typically denser than in related species; pleon-segments at most with diffuse patches of pink, never with clearly defined orange patches.

HABITAT.

A littoral species, distributed along the sea-coast, and penetrating estuaries for some distance; strictly intertidal, its optimum being between high-water neaps and about mid-tide level; seeking cover of stones, clusters of fucoids, and other objects lying on the ground; on gravels, mixed grounds, and even soft mud, but scarce or absent on cleaner sands or shingle.

MATERIAL EXAMINED.

England. SOUTH DEVON AND EAST CORNWALL: many samples, both from the coast near Plymouth and from the shores of estuaries from the River Lynher to the River Axe, including among others, the following: Plymouth Sound, shore of Sutton Pool, Rum Bay, Drake's Island, etc., less numerous in general than *M. obtusatus*; Plymouth district, seventy-five specimens out of 700 *Marinogammarus* preserved in the Laboratory stock bottles. Rivers Tamar, Lynher, and Tavy estuaries, in many samples from various points of the estuarine area, mainly in upper half of tidal zone under weeds and stones, reaching to



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North Hooe, Maristow Quay, Sconner Creek, head of Tamerton Lake, etc. (see Hartley & Spooner, 1938, Pl. XVIII), material recorded by Crawford (1937, p. 650) confirmed; the only species of *Marinogammarus* known from this area. River Plym estuary in fifteen samples, ranging up to Marsh Mills Railway Bridge; River Yealm estuary, in samples from near mouth and middle reaches; River Erme estuary, in four samples from near seaward end; River Avon estuary, plentiful intertidally under weeds and stones up to half a mile below Aveton Gifford; Kingsbridge estuary, under weeds, upper part of tidal zone in Blank's Mill Creek; River Exe estuary, intertidally opposite Woodbury Road Station and at Topsham; River Axe estuary, intertidally in two stations above Axmouth.

NORTH DEVON: River Taw estuary, Caen River, in two samples recorded by Crawford (1937, pp. 653-4), identity confirmed. NORTH SOMERSET AND WEST GLOUCESTER: Severn estuary: plentiful in many samples, mainly from upper tidal levels and about mid-tide, from Kilve to Sheperdine, March to August 1939; also one ♀ Sharpness, 16. iv. 39 (identified for Mr R. Bassindale).

LINCS: River Welland near Holbeach, pool on banks near sea-wall, 30. vii. 39 (Miriam Rothschild), 2 imm. NORTH-EAST YORKS AND DURHAM: River Tees: among specimens in tube labelled "*G. marinus* Leach", Tees Survey Investigations (material deposited at the Plymouth Laboratory), confirming that the species is at least included in the records given under this name by Alexander *et al.* (1935, p. 55). NORTHUMBERLAND coast: Howick, 2. vi. 39, sample containing many adults, but sizes small, showing evident signs of stunted growth (identified for Mr L. C. Beadle); Blyth, ditch from salt pans, 4. vii. 34, 7 large ♂♂, 8 large ♀♀, 1 imm. (identified for Prof. A. D. Hobson). ISLE OF MAN: Castletown, 7. ix. 38, 11 adults (coll. G. I. Crawford).

Scotland. EAST LOTHIAN: near Reed Point, under stones just below high-water mark, 1. v. 32, 1 ♂ and 1 ♀; Port Seton, under stones near high-water mark, 7. iii. 32, 1 ♂ and 2 ♀♀ (identified for Prof. A. D. Hobson). FIRTH OF TAY: samples from Tees Survey Investigations preserved in the Plymouth Laboratory as follows: Section XI of river, high-tide level, 3 examples, mid-tide level, numerous, low-tide level, many; Section X, low-tide level, a number; Section IX, high-tide level, one example, low-tide level, a number; Section VIII, tidal zone, 2 ♂♂ and 1 ♀: thus confirming the distribution of *G. marinus* given by Alexander *et al.* (1935, p. 55) (note, however, that a few *M. finmarchicus* were mixed with this species, see p. 661).

Text-fig. 2. *Marinogammarus marinus* (Leach), male and female. Figures drawn from same adult male as in Text-fig. 1, and a large female from same sample which hatched 49 young. Magnification $\times 13$, except *i* $\times 45$. *a*, peraeopod 1 of ♂, left side; *b*, peraeopod 2 of ♂, left side; *c*, peraeopod 2 of ♀, with brood-plate shown, left side; *d*, *e* and *f*, peraeopods 3, 4 and 5 respectively, of ♂, left side; *g*, epimera of pleon-segments 2 and 3 of ♂, left side; *h*, uropod 3 of ♀, left side; *i*, uropod 3 of one of this female's newly hatched young, taken from the incubatory pouch, showing the different proportions of the joints of outer ramus at birth, left side, $\times 45$; *j*, telson of ♂.

ARGYLLSHIRE: Clachan Strand, 2. vi. 35, "under weed", 5 ♂♂, 9 ♀♀, 2 imm. (identified for Prof. A. D. Hobson). INNER HEBRIDES: Isle of Muck, August 1938 and 1939, in three samples, 1 ♂ and 6 imm.; Raasay, August 1937, in three samples, 4 ♂♂, 6 ♀♀, and 15 imm.; South Rona, August 1937, in thirteen samples, 50 ♂♂, 39 ♀♀, 73 imm. (identified for Prof. A. D. Hobson). WEST SUTHERLAND: Bay of Stoer, 14. iv. 39 (D. M. Reid), large ♂ and ♀ (confirmed by Dr K. Stephensen). ORKNEYS: Hoy, Quoyness, rocky shore near high water, 20 ♂♂, 5 ♀♀ and 8 imm. (coll. K. M. G. Fleming).

Ireland. ANTRIM: Whitehouse, 11. i. 36 (coll. R. MacDonald). WEST CORK: Glengarriff, shore, in *Fucus spiralis* and *Pelvetia canaliculata*, 23. vii. 38, five examples. SOUTH KERRY: Kenmare, shore, among *Ascophyllum*, etc., 23. vii. 39, twenty-five examples, adults and well-grown imm.; Kenmare, small brackish stream (with *G. zaddachi*), 23. vii. 38, 1 imm. (coll. G. I. Crawford).

Continental. DENMARK: ♂ and ♀ ovigerous, determined and dissected by Prof. J. Pirlot, "conforme aux figures de Sars". NORTH NORWAY: Svolvær, Lofoten Islands, marine, sheltered, mid-tide, 26. vi. 39, 11 ♂♂ and 9 ♀♀ (coll. G. I. Crawford).

DISTRIBUTION.

In view of the fact that any of the species of *Marinogammarus* may in the past have been recorded as "*marinus*" (and several notable instances of this have actually been found), the data on the distribution of this species will have to be reviewed afresh. At present it can be said that the species is widely distributed in the British Isles, and is probably the most abundant of the genus owing to its tolerance of estuarine as well as of marine conditions. Its presence along the western and northern coast of Scandinavia is also established.

This may be accepted as at least the main species referred to by Chevreux & Fage (1925, p. 251) as occurring along the Channel and Atlantic coasts. It may be noted that these authors give no instances of its occurrence on the Mediterranean coast of France, where it seems to be entirely replaced by *M. olivii*, and in the writings of Schäferna and Karaman no records for south-east Europe are given. In view of this, and in view, furthermore, of the fact that Stebbing's specimens of "*marinus*" from Naples were found to be *olivii* (see p. 649) extreme doubt may be expressed as to whether the species ranges into the Mediterranean Sea at all. Older records from this area, such as those quoted by Sars (1894, p. 498) must be taken to refer to *olivii* or some other species.

Marinogammarus olivii (Milne-Edwards)Text-figs. 3*a-l*, 4*a-o* and 11*f*.

1830. *Gammarus olivii* Milne-Edwards, *Ann. Sci. Nat.*, Vol. xx, pp. 367, 372, Pl. X, figs. 9, 10.
1862. *Gammarus marinus in part.* Spence Bate, *Cat. Amphip. Brit. Mus.*, p. 215, Pl. XXXVIII, fig. 4.
1894. *Gammarus marinus in part.* Sars, *Crust. Norway*, Vol. I, p. 498.
1906. *Gammarus marinus in part.* Stebbing, *Das Tierreich*, Vol. xxi, p. 472.
1925. *Gammarus olivii* Chevreux & Fage, *Faune de France*, Vol. ix, pp. 251-2, fig. 262.

This is the only species of *Marinogammarus* as here defined which has not yet been recorded from Britain, but as it has been found in Morbihan, Brittany (Chevreux & Fage, p. 252), it may well occur also on this side of the Channel.

G. olivii was first described by Milne-Edwards from specimens taken at Naples. He considered it to resemble *G. locusta* except for several characters, such as the shape of the eyes, gnathopod hands, unequal rami of third uropods, etc. In 1862 Spence Bate included the species under *G. marinus* Leach, and was followed in this by Sars and Stebbing. Later Chevreux & Fage re-examined Milne-Edwards' type specimens preserved in the Paris Museum, and were thus enabled to give the excellent description and figures which placed the distinction of the species beyond question.

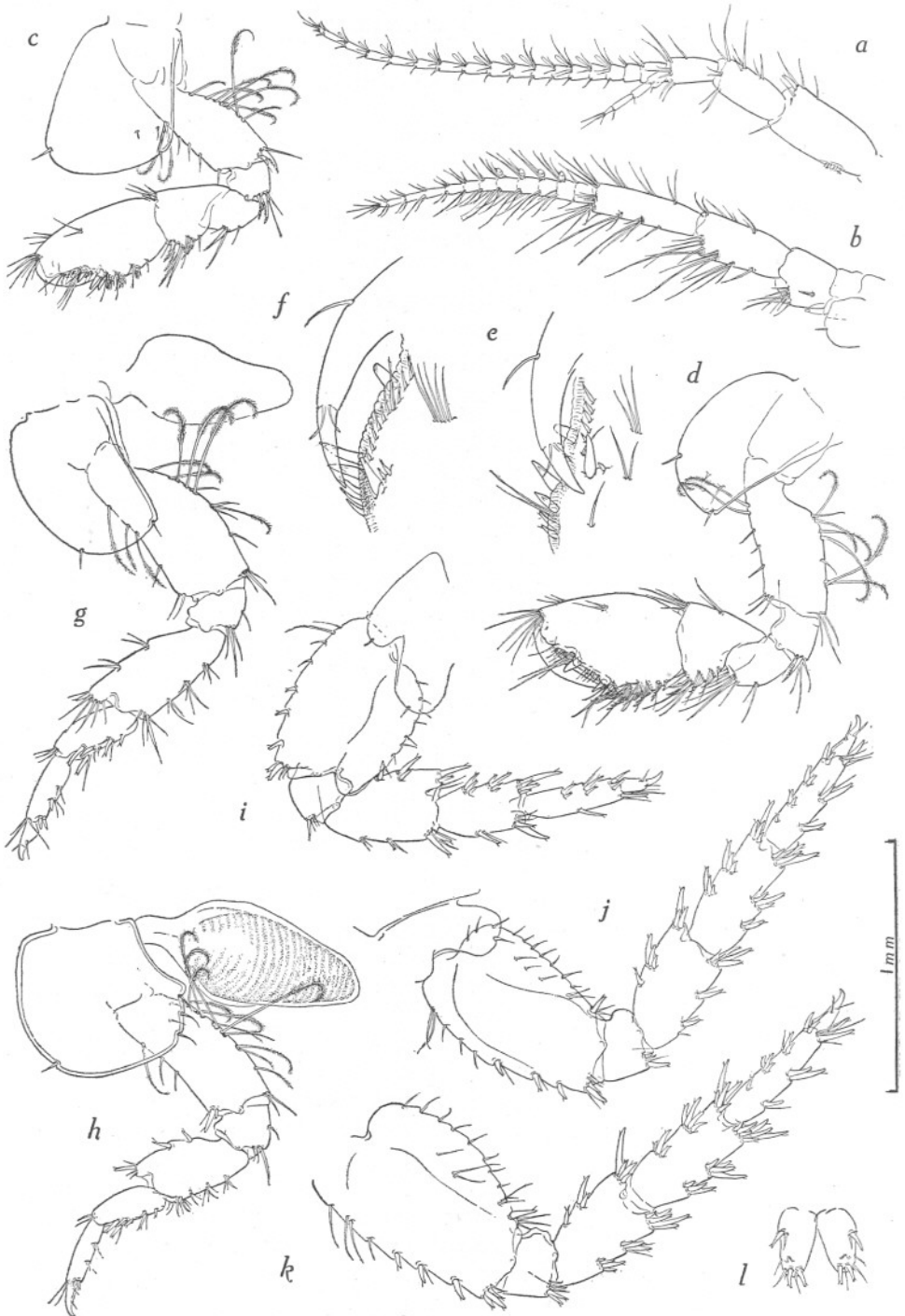
Through the courtesy of Professor Louis Fage we have had the opportunity of examining Milne-Edwards' types. We have also seen specimens, kindly forwarded by Dr Isabella Gordon, which are preserved in the British Museum. The latter include examples in Stebbing's collection, labelled "*Gammarus marinus*", from Naples: from one of these, a young male, most of the figures given here have been drawn.

It will be seen that *olivii* is clearly related to *marinus*, and not, as some recent authors have suggested, to *Gammarus pungens* Milne-Edwards.

ADULT MALE.

Pleon-segments 4-6 produced in rounded humps, spines short, armature very sparse and different from *marinus*; formula in specimens examined being 2 : 1 : 1 : 2 on each of the three segments. Sideplates 1-4 deeper than corresponding segments; 4 about as wide as deep, with 3-4 setae inset on the posterior expansion. Epimeron 2 (Text-fig. 4*a*) with posterior margin somewhat rounded, and distal angle subobtuse; epimeron 3 (Text-fig. 4*b*) with margin straight, and angle rectangular; margins with several small setae inset. Setose armature on body and limbs in general longer than in other species of genus.

Head (Text-fig. 4*k*) with lateral lobes truncate, and lightly concave, lower angle obtuse, sinus rather deep. Eyes relatively large, broader and more reniform in shape than in *marinus*; somewhat constricted in middle; described



E.W.S. del.

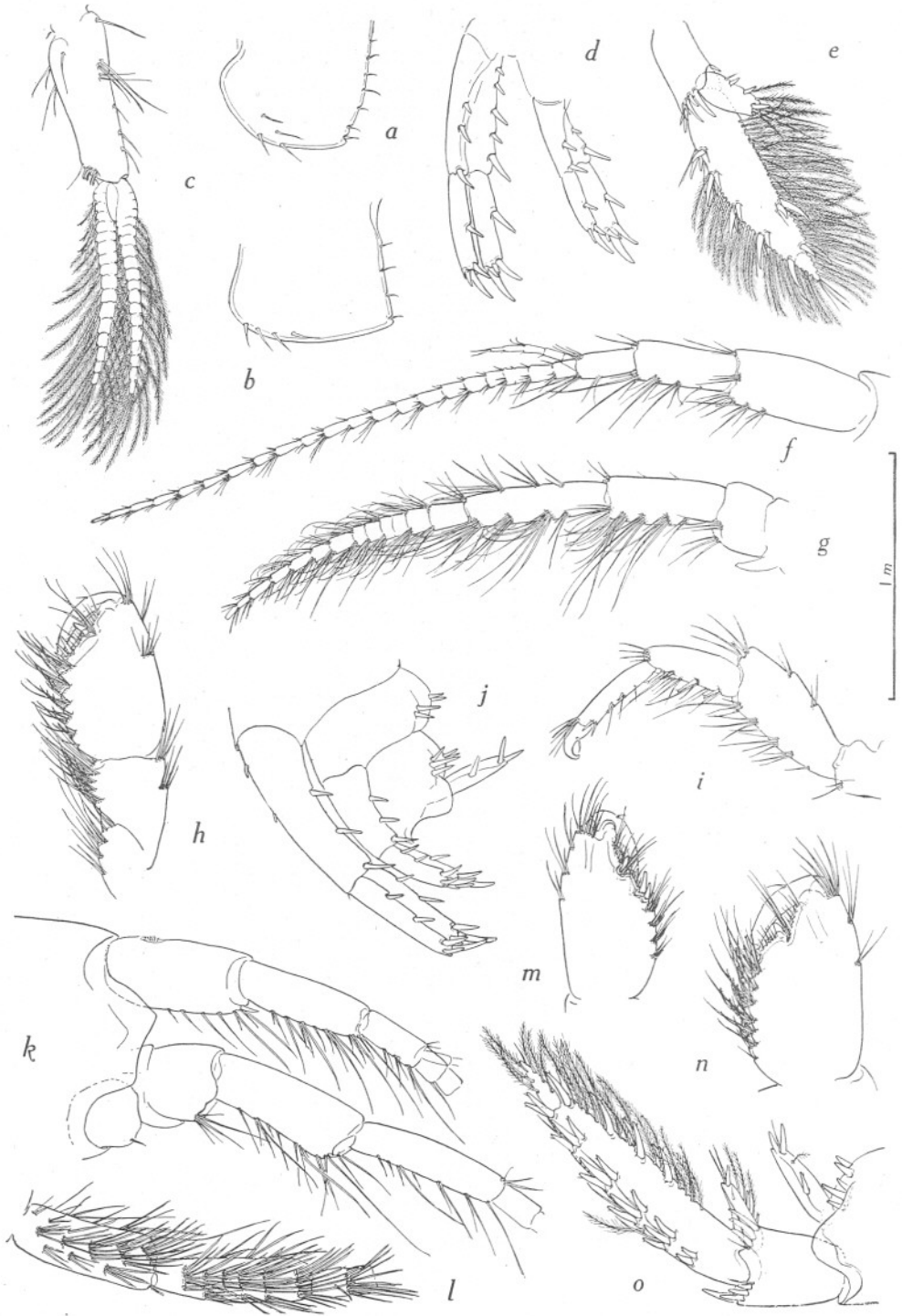
by Milne-Edwards as "plus lunulés que chez la Crevette locuste"; pigment brown, apparently soluble in alcohol. Antennae with setae relatively longer than in the other species of the genus. Antenna 1 (Text-figs. 3*a*, 4*f*, 4*k*), peduncle with joint 1 large and stout, longer than joint 2 but not as long as 2 and 3 combined; flagellum rather less than twice the length of the peduncle, possessing 22 joints in the largest specimen examined; accessory flagellum with about 5 joints. Antenna 2 (Text-figs 3*b*, 4*g*, 4*k*, 4*l*) not much shorter than antenna 1; flagellum shorter than peduncle, possessing about 14 joints in larger specimens, bearing calceoli on four proximal joints, and provided with rows of male sensory hairs (p. 680 and Text-fig. 11*f*) on under surface. Bifurcate setae apparently absent on both antennae.

Gnathopods (Text-figs. 3*c-f*, 4*h*, 4*m*, 4*n*). Hand of gnathopod 1 of distinctive shape, narrowed distally, palm very oblique, concave, irregularly undulate; palmar angle roundly produced; median spine separated from palmar angle-row by a wide gap; claw much curved, closing down over the under surface just behind the median spine (Text-fig. 3*e*). Hand of gnathopod 2 larger than that of gnathopod 1, palm rather oblique, slightly concave; median spine separated as in gnathopod 1; palmar angle rounded, well defined; tip of claw fitting into a tuberculated groove on under surface of palmar angle; posterior margin somewhat longer than palm. Both gnathopods bearing scattered bifurcate setae on the hands and some of the proximal joints, these setae less conspicuous than usual owing to their shorter apices.

Peraeopods (Text-figs. 3*g-k*, 4*i*) short and strongly built, especially the 3 hinder ones, joint 4 exceptionally broad in all. Peraeopods 1 and 2 sparsely setose, lacking both male sensory and bifurcate setae, joint 4 produced forward at anterior angle. Peraeopods 3-5 with numerous spine-clusters. Basal joint in peraeopod 3 with posterior distal angle free and well rounded; in peraeopods 4 and 5 basal joint abruptly narrowed behind, the angle "closed" and bearing one large spine; posterior expansions crenulate, with long and slender setules inset in the indentations.

Uropod 1 extending slightly further than uropod 2 (Text-figs. 4*d* and *j*). Uropod 3 (Text-figs. 4*e* and *o*), outer ramus long and broad, 2-jointed, carrying groups of spines, and densely fringed on both margins with long plumose setae: inner ramus very small and narrow, bearing feathered setae apically. Telson (Text-figs. 3*l* and 4*j*) extending to the length of peduncle of uropod 3;

Text-fig. 3. *Marinogammarus olivii* (Milne-Edwards), male. Figures drawn from a young male captured at Naples (Stebbing coll., in coll. Brit. Mus.); compared in detail with Milne-Edwards' type specimens, also from Naples (in coll. Mus. National, Paris), and with a specimen from Cap d'Antibes (in coll. Brit. Mus.). Magnification $\times 36$, except *e* $\times 112$. *a*, antenna 1, inner surface, right side, showing aesthetascs; *b*, antenna 2, outer surface, left side; *c*, gnathopod 1, left side; *d*, gnathopod 2, left side; *e*, gnathopod 1, under surface, right side, showing the palmar margin of hand, with the spine-clusters at the palmar angle, and the position of the claw when closed, $\times 112$; *f*, gnathopod 2, under surface, as above; *g*, peraeopod 1, left side, with gill in outline; *h*, peraeopod 2, left side, with gill attached; *i*, *j*, *k*, peraeopods 3, 4, and 5 respectively, left side; *l*, telson.



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each lobe with lateral group of 1-2 spines, an apical group of 2 spines and 2 setae, and a pair of sensory plumose hairs inset in sockets below the apex.

Size: rather small, about 7-10 mm. in length, apparently of same range as *pirloiti*. *Colour*: green (Milne-Edwards): translucent yellowish grey; eggs olive-green (Chevreux & Fage).

Habitat: Marine littoral, under stones (Chevreux & Fage).

MATERIAL EXAMINED.

Continental. ITALY: Naples, 2 ♂♂, Milne-Edwards' types of *Gammarus olivii* preserved in the Paris National Museum (sent by Prof. L. Fage) (Text-figs. 4*f-j*): Naples, three examples, including one young ♂ figured (Text-figs. 3*a-l*, 4*a-e*), Stebbing coll., preserved in coll. Brit. Mus. [1928-12-1], labelled "*Gammarus marinus*" (presumably original identification). SOUTHERN FRANCE: Cap d'Antibes, 1 ♂, A. O. Walker coll., in coll. Brit. Mus. [1925-9-8, 1167-76], det. Schellenberg as "*Gammarus (Echinogammarus) olivi* M. Edw." (Text-figs. 4*k-o*).

DISTRIBUTION.

The records for this species are summarized by Chevreux & Fage (1925, p. 252). It is evident that the species has its headquarters in the western Mediterranean, seven localities along the Riviera coast of France and one in Corsica being given, and the species recorded as very common. Naples (the type locality), Tunisia, and Algeria are also quoted. Along the Atlantic seaboard localities include the Canary Islands and the Brittany coast at Etel, Morbihan. The species does not figure in lists of amphipod records from south-east Europe given by Schäferna and Karaman, and would thus appear not to extend into the eastern Mediterranean.

Text-fig. 4. *Marinogammarus olivii* (Milne-Edwards), male. Figs. *a-e* drawn from the same young male as in Text-fig. 3; Figs. *f-j* drawn *in situ* from older males, Milne-Edwards' type specimens (in coll. Mus. National, Paris); and Figs. *k-o* drawn *in situ* from another older male, captured at Cap d'Antibes (in coll. Brit. Mus.). Magnification $\times 36$.
a, epimeron 2, left side; *b*, epimeron 3, left side; *c*, pleopod, showing coupling-spines on peduncle, and cleft spines of inner ramus; *d*, uropods 1 and 2, left side; *e*, uropod 3; *f*, antenna 1 (flagellum broken at tip), left side; *g*, antenna 2 (flagellum broken at tip), left side; *h*, gnathopod 2, terminal joints, left side; *i*, pereopod 1, joints 4 to 7, left side; *j*, pleon-segments 5 and 6, with uropods 1 and 2 and telson; *k*, head and peduncle joints of antennae; *l*, antenna 2, peduncle joints 4 and 5, showing the sensory male hairs on under surface; *m*, hand of gnathopod 1, right side; *n*, hand of gnathopod 2, left side; *o*, uropod 3 (the plumose hairs of the outer margin have been broken off, but their sockets can be plainly seen between the spine clusters).

Marinogammarus obtusatus (Dahl)

Text-figs. 5a-n, 11c, o.

1938. *Gammarus obtusatus* Dahl, *Kong. Norske Vidensk. Selsk. Forhandl.*, Vol. x, no. 34, pp. 125-8, figs. 11-21.

This species was found many years ago in Plymouth Sound by one of the authors (E. W. S.) and used in breeding experiments in the Laboratory. It is the "littoral species not yet named" referred to in the paper on "Moulting and Growth-Stages, etc." (Sexton, 1924, pp. 342-4); but although it was recognized as new to science and its characters noted for the work, no diagnosis was published. A brief recapitulation of its breeding habits, as then studied, is given on pp. 655-6.

More recently it was discovered in Belgium by Prof. J.-M. Pirlot, to whose courtesy we are indebted for material and information. Prof. Pirlot had a full description and series of drawings prepared when Dahl's publication appeared in 1938. Dahl's description was taken from material collected by the *Gunnerus* Expedition to Finmark under Mr Carl Dons in 1937.

In the meantime it had been ascertained that the species was plentiful at Plymouth and was actually being collected in greater number than *marinus*. In 1938 Reid pointed out the occurrence of Dahl's *obtusatus* in Britain, giving some widely separated localities, and indicating, as has since been amply confirmed, that the species is widespread and common. In collections examined we have found it quite as frequently as *marinus*, from which it differs in several conspicuous characters, yet under which name it has repeatedly passed. That it should have been so confused seems remarkable.

The only published description, that of Dahl, requires amplification in many particulars, and a more complete and detailed set of illustrations has been considered necessary. The species is readily recognized by the elongated peduncle joint 2 of antenna 1, by the long graduated outstanding setae of both antennae, by the small male gnathopod 2 contrasting with the large gnathopod 1, by the obtusely rounded posterior angles of the epimera (a character which is only shared by *stoerensis*), and by the prominence of the spines amongst the sparse setae of uropod 3.

ADULT MALE.

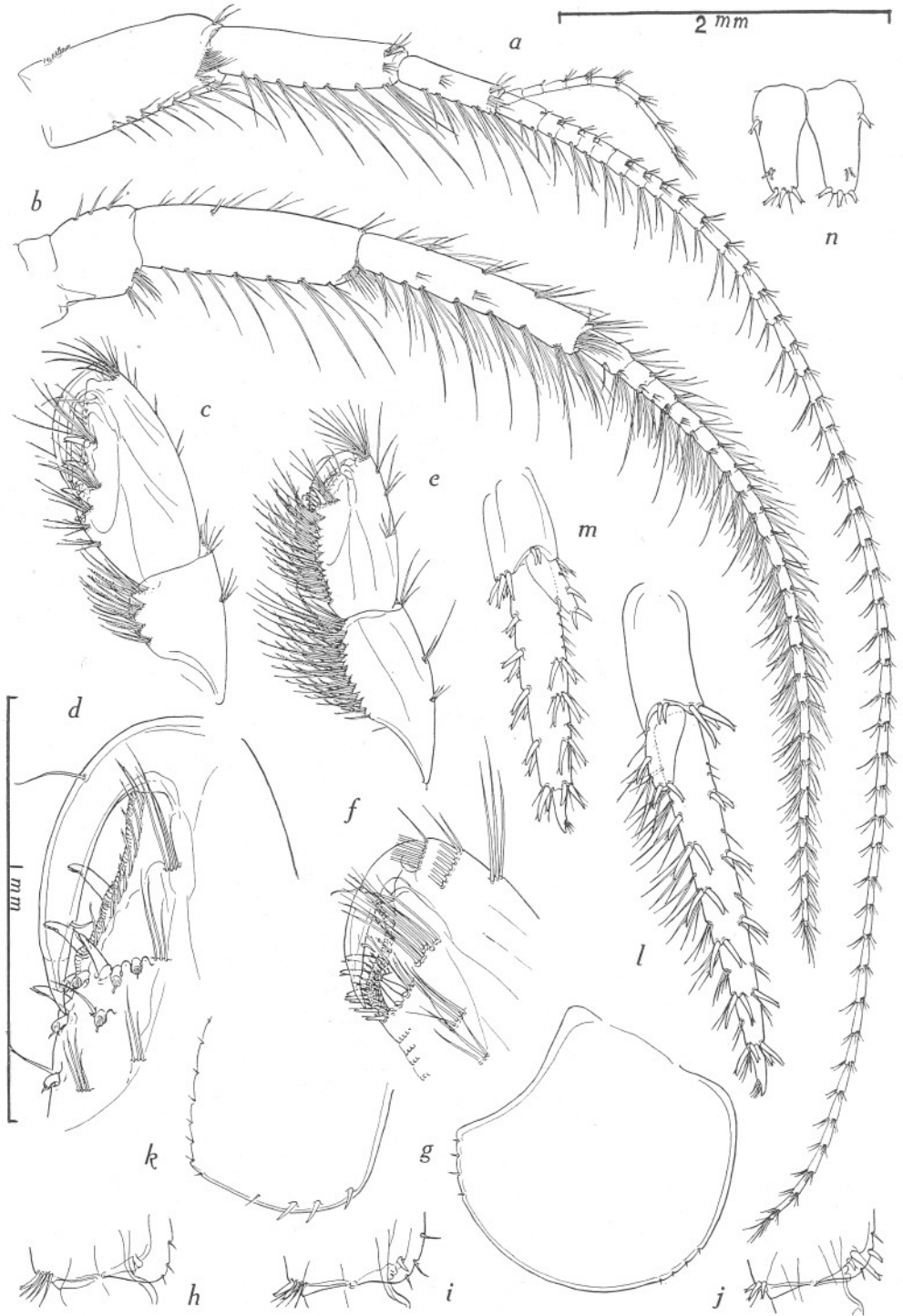
Body compressed and slender, as in *marinus*. Pleon-segments 4-6 a little produced dorsally; spinose armature rather like that of *marinus* in the largest specimens; spines long, becoming numerous, each lateral group forming an upward curve, with the spines outstanding and divergent; the median groups set in a straight line across the distal margins; the lateral groups seen dorsally forming a series embracing also the outstanding spine-group on the peduncle of uropod 3; spine formula in large males: 5:3:3:5-4 or 5:2:2:4 or 5-4:1:1:4. Sideplate 4 (Text-fig. 5g) about as broad as deep, of distinctive form, distal expansion very shallow thus bringing the posterior point of its

greatest width unusually low, and giving the point an almost triangulate outline. Epimera 2 and 3 (Text-fig. 5*k*) resembling *stoerensis*; distal and posterior margins rounded, angle obtuse (hence the name of *obtusatus*); setules inset on posterior margin.

Head lateral lobes rounded; sinus not deep. Eye shorter than in *marinus* in early stages, but becoming increasingly elongate with age; in adults often clearly constricted in middle, sometimes sinuous in shape; pigment purplish black. Antennae (Text-fig. 5*a, b*) long; 1 longer than 2; peduncles longer in proportion than those of other species. In both antennae joints of peduncles and flagella showing a diagnostic feature—viz. each seta-cluster containing one long stiff outstanding seta, these outstanding setae forming a graded series on each joint (almost as in *Gammarus zaddachi* Sexton); flagella with the fourth outstanding seta the longest, the others decreasing in length towards the apex. Antenna 1 peduncle with joint 1 long and stout, joint 2 slender, fully equalling 1 in length. Primary flagellum with about 46 joints in large specimens; accessory flagellum with 7–9. Antenna 2 with flagellum of about 23–24 joints, subequal in length to the peduncle; male sensory hairs (p. 680 and Text-fig. 11*c*) rather sparse; calceoli lacking. Both antennae bearing numerous well-formed bifurcate setae (Text-fig. 11*o*).

Gnathopods (Text-fig. 5*c-f*). Hand of gnathopod 1 much larger than that of gnathopod 2; of distinctive structure, though on the same lines as that of *marinus*, differing in the greater obliquity of the palm, in the smaller number and the wider spacing of the angle-spines, and in the smaller number of the posterior bristle-clusters; palm undulate, very oblique, merging into the posterior margin of the hand without a defined angle; its margin bearing at equal intervals 3 long stout spines, the median and two of the angle-group, with the peculiar male curvate spines, as in *marinus*, on both sides of the angle, a single pair below it (Text-fig. 5*d*); posterior bristle-clusters few in number, the most distal arising, as in *marinus*, at the level of the angle-group. Gnathopod 2 with joint 5 subequal in length to 6, longer in proportion than in gnathopod 1. Hand of gnathopod 2 much smaller, and of very different structure from that of gnathopod 1; narrow, elongate, the posterior margin about twice length of palm; palm nearly transverse, concave, with palmar angle rounded, and spines not separated as in gnathopod 1; median spine adjacent to angle-group, but situated slightly in front of it, and almost as far down the palm as in *stoerensis*; posterior bristle-clusters numerous. Both gnathopods bearing numerous well-developed bifurcate setae.

Peraeopods 1 and 2 with setae and spines sparse. Peraeopod 3 (Text-fig. 5*h*) basal joint with postero-lateral angle free and rounded. This angle in peraeopods 4 and 5 (Text-fig. 5*i, j*) bearing spines inset on the under surface, but not completely “closed” and representing an interesting intermediate condition between *marinus* (closed) and *finmarchicus* (free). Peraeopods 4 and 5 relatively elongate, joint 4 about three times as long as broad, joints 5 and 6 subequal in length.



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Uropod 1 extending a little beyond uropod 2, bearing a long curved spine on peduncle. Uropod 3 (Text-fig. 5*l*) outer ramus 2-jointed; with clusters of long spines and of fine setae bordering the inner margin, and with spines and some small setae on outer side; much more sparsely setose than in *marinus*; plumose setae lacking: inner ramus very small, about 20% length of outer, bearing spines and setae on inner margin. Telson (Text-fig. 5*n*) as long as peduncle of uropod 3; lobes about twice as long as broad, each with one spine in lateral group, three spines with one stout seta in apical group, and a pair of plumose sensory hairs below the apex.

ADULT FEMALE.

Differences from adult male as follows.

Antenna 1 not longer than twice length of peduncle. Antenna 2 with gland-cone long and narrow.

Gnathopods: hands of somewhat similar size, very setose. Hand of gnathopod 1 much smaller than in ♂; posterior margin, as in ♂, developing a single pair of spines situated between the two most distal of the posterior bristle-clusters—these spines pointed, not curvate. Hand of gnathopod 2 narrow and elongate.

Peraeopods 1 and 2 sparsely setose, but setae on average longer and somewhat more numerous in each cluster than in male.

Brood-plates. Anterior brood-plate with setae along anterior margin numerous, but not so dense as in *marinus*.

Uropod 3 (Text-fig. 5*m*) with outer ramus relatively shorter and inner ramus longer than in ♂; rami with clusters of elongate spines along margins, but setae very few and short, giving the limb an almost glabrous appearance.

Eggs deep purple when newly laid; size relatively large, 0.60 × 0.70 mm.; and number in a brood relatively small (for further data see below). Young about 2½ mm. long at extrusion, larger than in *marinus*.

SIZE AND COLOUR.

Size range of adults a little less than that of *M. marinus*. Colour, pale brown to olive green, often with a distinct purple or pinkish tinge, occasionally individuals quite rich pink; no orange patches on pleon-segments 1-3.

Text-fig. 5. *Marinogammarus obtusatus* (Dahl). All figures except *f* and *m*, drawn from a large male, captured Steepholm Island, Bristol Channel; fig. *f* drawn from a male, 13 mm. long, and *m* from a large female, 12 mm. long (11 young in pouch), both captured Plymouth Sound, shore adjoining bathing-place, Feb. 1940. Magnification × 22.4, except *d* and *f* × 62. *a*, antenna 1 of ♂, outer surface, right side; *b*, antenna 2 of ♂, outer surface, right side; *c*, gnathopod 1 of ♂, terminal joints 5-7, left side; *d*, gnathopod 1 of ♂, under surface of distal portion of hand, right side, showing the spine-clusters at the palmar angle; *e*, gnathopod 2 of ♂, terminal joints 5-7, left side; *f*, gnathopod 2 of ♂, under surface of distal portion of hand, showing the spine-clusters and tuberculate surface of the palmar angle; *g*, sideplate 4, right side; *h*, peraeopod 3, left side, postero-distal angle of basal joint; *i*, peraeopod 4, left side, postero-distal angle of basal joint; *j*, peraeopod 5, left side, postero-distal angle of basal joint; *k*, epimeron 3, right side; *l*, uropod 3 of ♂; *m*, uropod 3 of ♀; *n*, telson.

HABITAT.

A littoral species, distributed along sea coast, but penetrating only a short distance into estuaries; essentially intertidal, but with optimum zone lower down the shore than *marinus*—about mid-tide level to low-water neaps. Like *marinus*, seeking cover of stones and seaweed, but typically associated with the less muddy and more stony grounds, and capable of existing amongst comparatively clean pebbles.

MATERIAL EXAMINED.

England. SOUTH DEVON: Plymouth Sound, various collections from shore below the Marine Biological Laboratory, Drake's Island, and Rum Bay: including preserved specimens of original material collected in 1913, and fresh collections in 1938 and 1939: abundant, taken in greater numbers than related species. Plymouth Breakwater, 2. viii. 89, one in the Laboratory museum, labelled "*Gammarus marinus*". Plymouth district: 473 specimens out of 700 *Marinogammarus* preserved in the Laboratory stock bottles; by far the most numerous species. Wembury, under stones at mid-tide level, 17. iii. 39. NORTH SOMERSET: Severn Estuary: Steepholm Island, 2 ♂♂ and 1 ♀ (identified for Prof. C. M. Yonge): Kilve, mid-tide level, May and August 1939, considerable samples; Weston-super-Mare, Birnbeck Island, April and August 1939, considerable samples, but none in samples from higher up estuary (identified for Mr R. Bassindale). ISLE OF MAN: Port Erin, 30. viii. 38, 5 ♂♂, 3 ♀♀, 10 imm. and young; Port St Mary, rock crevices near high water, 12. ix. 38, 5 ♂♂, 4 ♀♀, 1 imm.; Bay na Carrickey, 9. ix. 38, 6 ♂♂ and 2 ♀♀ (all above sent by Mr G. I. Crawford). NORTHUMBERLAND: Cullercoats, 22. iii. 32, 3 ♂♂ and 1 (?) ♀ (sent by Mr G. I. Crawford); from north and south side of Bay, 14. x. 39, considerable samples of rather small average size (identified for Mr L. C. Beadle).

Scotland. BERWICKS: Burnmouth, under stones near high water, 8. v. 32, 6 ♂♂, 5 ♀♀, 2 imm.; EAST LOTHIAN, Port Seton, under stones near high water, 6 ♂♂, 6 ♀♀, 1 imm. (identified for Prof. A. D. Hobson). INNER HEBRIDES: Isle of Muck, Camas Mor, 23. viii. 38, 5 ♂♂, 9 ♀♀, 5 imm.; Raasay, August 1937, samples from four localities, including 18 ♂♂, 11 ♀♀ and 3 imm.; South Rona, August, 1937, samples from two stations, including 8 ♂♂, 7 ♀♀ and 4 imm. (identified for Prof. A. D. Hobson). ORKNEYS: Hoy, Quoyness, rocky shore, 7 ♂♂, 5 ♀♀, 2 imm. (coll. K. M. G. Fleming). SHETLANDS: large ♂ and two smaller, in Norman coll., Brit. Mus. [1911-11-8], labelled *Gammarus marinus*.

Ireland. COUNTY DOWN: Garrahan Isle, near Groomspoint, 20. ix. 39, 3 ♂♂ from a number collected under stones (determined and sent by Mr R. MacDonald, confirmed E. W. S.).

Continental. BELGIUM: Blankenberghe, March 1935 and 1936, and April 1938 (various specimens, slides and drawings lent by Prof. J.-M. Pirlot).

NORTH NORWAY: Porsanger Fjord, Suogalina, 6. vii. 39, between mid-tide and low-water neaps, 17 ♂♂, 6 ♀♀, 10 imm.; Rimabukt, 10. vii. 39, between mid-tide and low water, under stones, 26 ♂♂, 19 ♀♀, 2 imm.; Rørwik, near Trondhjem, 24. vi. 39, mid-tide, ♂ and ♀ (coll. G. I. Crawford). EAST MURMANSK: shore of Barents Sea (det. *Gammarus marinus* Leach by Mme E. Gurjanova), 2 large ♂♂, in coll. Brit. Mus. [1936. 3. 8].

DISTRIBUTION.

Dahl (1938) described the species from specimens collected in localities in West Finmark (Type locality: Hasvik, Sørøy), and East Finmark. Further localities for the north and west coast of Norway are given above. Reid (1939) records *obtusatus* as plentiful in the Scilly Islands, at Plymouth, and on the north and west coasts of Sutherland. From the additional records given, it is evident that the species is distributed along the whole west coast of Great Britain, including outlying islands, and down the east coast at least as far south as Newcastle. From its discovery by Prof. Pirlot in Belgium, it may be expected to occur all round the shores of the North Sea in suitable localities, though probably more localized owing to the character of the shore. The species is often numerous where it occurs, and may entirely replace *marinus*, under which name it has often been recorded in the past.

BREEDING HABITS.

Numbers of the species were kept in the Laboratory for some years to study their life history particularly in regard to the growth-stages from birth to maturity. The results given here were obtained in laboratory conditions, it being impossible to make any observations in their natural habitat. The moulting and oviposition of the female were watched on several occasions, and were practically the same as observed and described for *G. chevreuxi* (Sexton, 1924, p. 344). The gonads show very clearly in life as dark purplish bands against the translucent greenish colour of the animal's body, and the eggs could be seen during oviposition passing down the oviducts as a continuous bright coloured line. The eggs when laid into the pouch are a rich reddish purple shade, large, and few in number, usually from 8 to 12 in a batch. In summer they take from 12 to 14 days to hatch, but the time of the young leaving the pouch varies considerably. Sometimes the female lets them all out in about 4-5 days, sometimes she keeps them until they all have had their first moults and then extrudes them and the cast skins together, or she may let them out 1 or 2 at a time over a period of several days. In one case observed the female kept some for 13 days, and, in another, one young was retained for 17 days and then was only let free by keeping the female on a slide until she opened her pouch. It is thus very difficult to know how many days to count as a moulting period as two or more moults may take place before extrusion. One young, extruded at 5 days, moulted afterwards at intervals of 8, 8, 9, 8, 10 and 12 days; and another of the same brood at 8, 9, 10, 9, 9

and 9 days. None reached maturity, partly owing to the difficulty of finding suitable food, and partly to the impossibility of providing surroundings sufficiently like their natural habitat to keep them healthy. They live normally under fucoids and small stones on the beach between tide-marks, but seaweed could not be used in the culture-pots because of its rotting and fouling the water.

The moulting period of the female is from 24 to 28 days in summer. In the experiments mentioned the females of the other species, viz. *Gammarus locusta*, *chevreuxi* and *pulex* extruded the young soon after hatching and moulted within a very short time; in *obtusatus*, twice the length of time appeared to be taken, an "incubatory" period of about 12-14 days till the eggs hatched, and a second period of the same length of time during which the young remained in the pouch for one or more growth stages.

Recent measurements of the eggs are as follows: average of batch of 8, newly laid, 0.60×0.69 mm.; and of another of 7 with embryos formed, 0.61×0.73 mm.

Marinogammarus finmarchicus (Dahl)

Text-figs. 6a-h, 7a-f, 11b, j, p.

1938. *Gammarus finmarchicus* Dahl, *Kong. Norske Vidensk. Selsk. Forhandl.*, Vol. x, no. 34, pp. 125-8, figs. 1-10.
 1938. *Gammarus (Marinogammarus) greenfieldi* Shoemaker, *Journ. Washington Acad. Sci.*, Vol. xxviii, no. 7, pp. 329-32, fig. 2.

In 1937, one of the authors (G. M. S.), when revising amphipod material originally collected during the Tees Survey Investigations (see Alexander *et al.* 1935) and deposited in the Museum of the Plymouth Laboratory, discovered some specimens which clearly belonged to an undescribed species of *Gammarus*. They came from the estuary of the River Tay, East Scotland. Not long afterwards they were identified with a species which had just been independently described by Dahl (Jan. 1938) and Shoemaker (July 1938). In the meantime the presence of the species in the Plymouth district was discovered and living material examined. Dahl's name, *finmarchicus*, holds priority. Shoemaker's description is the more complete and his illustrations the more detailed. These descriptions are recapitulated below, with some details and figures added, for the sake of full comparison with the other species of the genus described here.

Three characters peculiar to *finmarchicus* distinguish it at a glance from the others, viz. in all the basal joints of the three hinder pereopods the posterior distal angle is clearly free; the second joint of the outer ramus of uropod 3 is completely lacking; and the inner ramus of the same uropod is of appreciable length, attaining in the adult about 40% of that of the outer ramus. The somewhat fan-shaped arrangement of the tufts of setae on uropod 3 provides another character readily noticed in sorting specimens from mixed samples.

ADULT MALE.

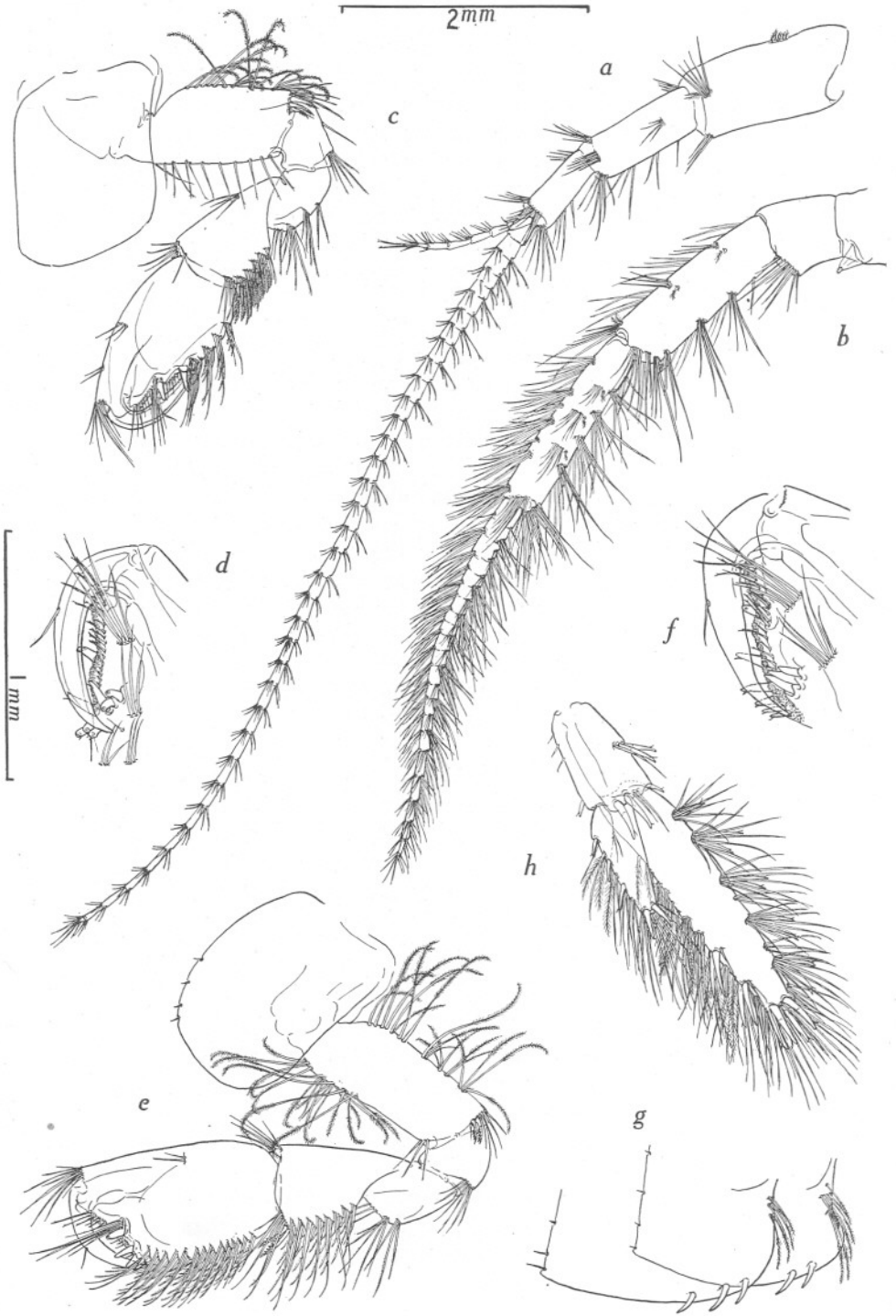
Body resembling *marinus*, a little less elongate than in *obtusatus*. Pleon-segments 4 and 5 very slightly raised dorsally, the spines in segments 4-6 arranged in four groups, the usual formula being 3 : 2 : 2 : 3—3 : 2 : 2 : 3—2 : 1 : 1 : 2. Sideplates 1-4 a little deeper than the corresponding segments, with distal margins rounded; sideplate 4 (Text-fig. 7*b*) as broad as deep, distal expansion shallow, with about 5 setules inset on the posterior expansion. Epimera 2 and 3 (Text-fig. 6*g*) with posterior margin straight, inset with a few setules, anterior margin carrying clusters of feathered setae; distal margin somewhat rounded, bearing 2-3 strong spines anteriorly; postero-distal angle subrectangular, not produced.

Head with lateral lobes broadly rounded; sinus rather deep. Eye subreniform in younger stages, elongate and narrow in larger animals; black. Antenna 1 (Text-fig. 6*a*) longer than antenna 2; joint 1 of peduncle stout and about a fourth as long again as joint 2; flagellum considerably more than twice the length of the peduncle, possessing about 40 joints in large specimens; accessory flagellum with 6-7 joints. Antenna 2 (Text-fig. 6*b*) peduncle with joint 4 stouter and slightly shorter than 5; flagellum possessing about 22 joints, somewhat shorter than peduncle; both peduncle and flagellum joints furnished with fan-shaped clusters of outstanding setae, a few small plumose sensory hairs, and numerous clusters of male sensory hairs (p. 680 and Text-fig. 11*b*); calceoli lacking. Bifurcate setae sparsely distributed on antenna 1. Mouth parts normal, agreeing with generic diagnosis; described and figured by Shoemaker (1938, p. 330).

Gnathopod 1 (Text-fig. 6*c, d*) with hand decidedly smaller than that of gnathopod 2, a little shorter and much narrower; palm very oblique, undulate, merging into the posterior margin, palmar angle, however, defined on each side by a long spine and groups of the small curvate male spines; tip of claw closing down between the latter on under surface of palm. Median spine in both gnathopod hands separated from spines of angle-group by a wide gap. Gnathopod 2 (Text-fig. 6*e, f*) with hand widest distally; palm nearly transverse, its angle well defined and marked by four graduated spines; posterior margin distinctly longer than palm, bearing numerous bristle-clusters.

Peraeopods (Text-fig. 7*a-e*) 1 and 2 with clusters of setae on posterior margin of joint 4, and of setae and spines on that margin of joints 5 and 6. Peraeopods 3-5 stout and armed with clusters of long spines and setae; basal joints more expanded than in other species of genus, with posterior expansion not narrowed distally, thus leaving the postero-distal angle almost as clearly free in peraeopods 4 and 5 as in peraeopod 3; this angle rounded in peraeopod 3, less so in peraeopod 4, and subangulate in peraeopod 5, each with a seta inset. Peraeopod 4 with joint 4 two and a half times as long as wide at apex; joints 5 and 6 subequal.

Uropod 1 extending a little beyond uropod 2; its peduncle with a prominent spine on lower margin. Uropod 3 (Text-fig. 6*h*) with outer ramus long and broad ending in a cluster of four long spines at apex, joint 2 completely



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lacking; outstanding fan-shaped groups of long slender spines and setae situated on both margins and apex, but spines lacking on proximal two-thirds of inner margin: inner ramus attaining about 40% the length of the outer, bearing spines and setae only on the inner margin and at the apex: long plumose setae distributed along inner margins of both rami. Telson (Text-fig. 7f) with each lobe about twice as long as broad, bearing three long spines and some setae in lateral cluster, three spines and several setae in apical cluster, and two short plumose sensory hairs in sockets below the apex.

ADULT FEMALE.

Differences from adult male as follows.

Antenna 1 with flagellum about twice length of peduncle. Bifurcate setae well distributed on antennae, especially on antenna 2.

Gnathopods. Hands smaller than in male, nearly equal in size; gnathopod 1 with palm of hand less oblique; gnathopod 2 with hand more elongate, the posterior margin fully twice as long as palm. (Peraeopods 1 and 2 with armature as in male.)

Brood-plates much as in *marinus*, but row of setae on anterior margin of first brood-plate only moderately dense.

Uropod 3 with armature of spines and setae much as in male, but setae sparser.

Eggs large (average size 0.55×0.65 mm. when newly extruded), and relatively few in number (10 to 30 in a batch).

Young extruded at comparatively large size, $2\frac{1}{2}$ mm. in length; eyes black; at once distinguished by the long spiniform setae on uropod 3, and by the absence of joint 2 of that limb.

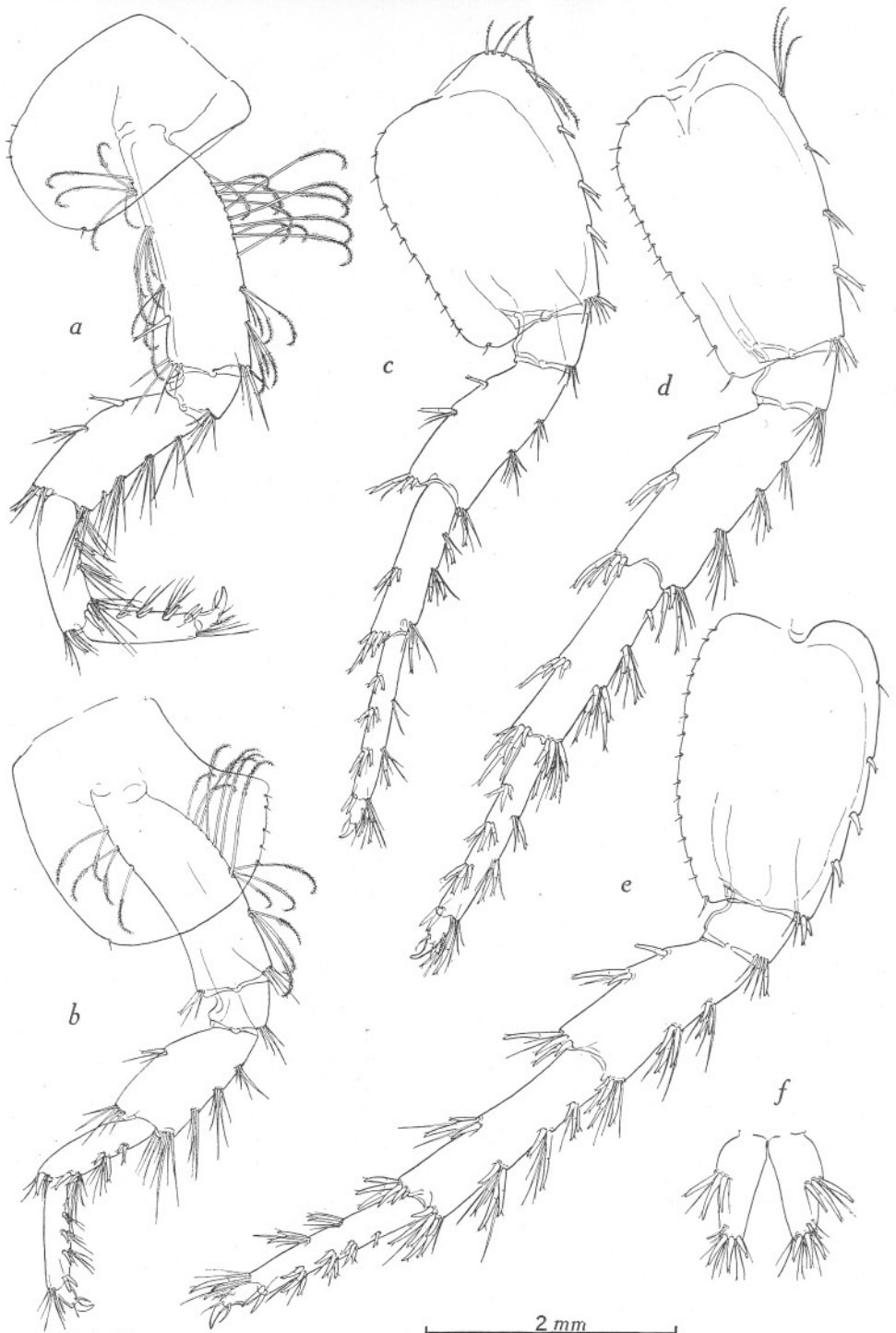
SIZE AND COLOUR.

Size range comparable with that of *obtusatus*, only somewhat less than in *marinus*; male 15–20 mm., female on average smaller. Colour uniformly pale brown or yellowish, with at most slight infuscation on the posterior borders of some segments, often suffused with a brighter yellow, sometimes very deeply; no orange-red patches on sides of pleon.

HABITAT.

A marine littoral species, occurring intertidally along the sea coast, and for a short distance up estuaries. Frequenting stony ground, often in company with *obtusatus*, but generally scarcer and more local than that species.

Text-fig. 6. *Marinogammarus finmarchicus* (Dahl), male. Figures drawn from a male, taken on shore of River Tay estuary, East Scotland (Tees Survey collections). Magnification $\times 18$, except *d* and *f* $\times 36$. *a*, antenna 1, left side; *b*, antenna 2, left side; *c*, gnathopod 1, left side; *d*, gnathopod 1, right side, distal portion of hand from under surface, showing armature of palm and palmar angle; *e*, gnathopod 2, left side; *f*, gnathopod 2, right side as in *d*; *g*, epimera 2 and 3, right side; *h*, uropod.



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Text-fig. 7. *Marinogammarus finmarchicus* (Dahl), male (cont.). Drawings from same male as in Text-fig. 6, $\times 18$. a, pereopod 1; b, pereopod 2; c, pereopod 3; d, pereopod 4; e, pereopod 5; f, telson.

MATERIAL EXAMINED.

England. SOUTH DEVON. Plymouth Sound, shore adjoining the bathing place below the Marine Biological Laboratory, 10. viii. 38, plentiful, both sexes and young stages under stones on concrete, in company with *M. obtusatus*. Plymouth district: 57 specimens out of 700 *Marinogammarus* preserved in the Laboratory stock bottles. Revelstoke beach, under pebbles, 4. v. 40; both sexes.

NORTHUMBERLAND: Cullercoats, north of bay, 4. x. 39, 4 ♂♂ and 1 ♀ (mixed with a number of *M. obtusatus*) (identified for Mr L. C. Beadle): Cullercoats, south side of bay, 26. iii. 35, 1 ♂ and 1 ♀; Blyth, ditch from Salt Pans, 4. vii. 34, 1 imm. with other *Marinogammarus* specimens (identified for Prof. A. D. Hobson).

Scotland. EAST LOTHIAN: Port Seton, 7. iii. 32, under stones near high water, 1 ♂, 2 ♀♀ (identified for Prof. A. D. Hobson). FIRTH OF TAY: Section XI (see Alexander *et al.* 1935), high-tide level, 1 ♀, mid-tide level, 1 ♂, low-tide level, 2 ♂♂ and 2 ♀♀, all mixed with numerous *M. marinus* (Tees Survey collections, deposited in Plymouth Laboratory museum). INNER HEBRIDES: Raasay, in samples from two stations, August 1937, including 2 ♂♂, 3 ♀♀, 12 imm. South Rona, August 1937, in samples from two stations, including 1 ♂ and 2 imm. (identified for Prof. A. D. Hobson).

Ireland. COUNTY DOWN: south side, Great Copeland Island, 13. v. 39, "slightly brackish pool", large ♀ (sent and determined by Mr R. MacDonald, confirmed E. W. S.).

Continental. NORTH NORWAY: Porsanger Fjord, Honningsvåg, 5. vii. 39, just above mid-tide, 2 ♀♀, 1 imm.; Suogalina, 6. vii. 39, in brackish splash pools near high water, 9 ♂♂, 5 ♀♀, large size, lower half of tidal zone, 1 ♂; Rimabukt, 10. vii. 39, between mid-tide and low water, under stones, 3 ♂♂ and 1 ♀; Tromsø, Telegraph bugd, 30. vi. 39, swimming at half-tide, 4 ♂♂, 5 ♀♀ (coll. G. I. Crawford).

DISTRIBUTION.

The species was previously known from West and East Finmark (type locality: Hasvik, Søroy) (Dahl, 1938), and the Atlantic coasts of North America (Shoemaker, 1938). Additional localities for north Norway are given above. This is the first occasion on which *M. finmarchicus* has been recorded from Britain, and the records given above show that it is present on the south-west and north-east coasts of England, east and west coasts of Scotland, and north-west coast of Ireland. The species is evidently much scarcer and more localized than *obtusatus*, but our present knowledge of its range is insufficient to indicate whether it is as widely distributed.

Marinogammarus stoerensis (Reid)

Text-figs. 8a-o, 11a.

1938. *Gammarus marinus* Leach, var. *stoerensis* Reid, *Ann. Mag. Nat. Hist.*, ser. 11, Vol. 1, pp. 287-9, figs. a-e; ♀.
1938. *Gammarus* (*Marinogammarus*) *stoerensis* Stephensen, *Kong. Norske Vidensk. Selsk. Forhandl.*, Vol. XI, no. 36, pp. 143-6 (with figs.); ♂, ♀.

In 1932 females of a small species of *Gammarus*, recognized as undescribed, were collected by one of the authors (G. M. S.) near the mouth of the River Avon, South Devon. They were kept for some time in the Laboratory, attention being mainly given to the retarded development of the dark pigment in the eyes of the young. A few specimens of an unknown species, collected by Mr G. I. Crawford near the mouth of the River Yealm, South Devon, in 1936, were later discovered to be the same. These, furthermore, appeared to correspond with a form briefly described by Reid in 1938 as a variety of *marinus*, from females collected in Stoer Bay, West Sutherland, Scotland. This identification was confirmed by the examination of an immature female specimen kindly forwarded to us by Mr Reid, and was placed beyond doubt when a fuller description and figures by Dr Stephensen (1938) appeared shortly afterwards. Dr Stephensen established *stoerensis* as a distinct species, pointing out the differences from *marinus*. The species was collected about this time in additional localities in the Plymouth district.

Marinogammarus stoerensis differs from other species of the genus in several respects. The size is small, not exceeding 7 or 8 mm., the contrast being particularly evident in the males which are apparently of even smaller average size than the females; the brood-plates of the female, especially the two anterior pairs are abnormally broad, and at the same time relatively long, so that in life the full brood-pouch protrudes well below the level of the distal margins of the sideplates; the hands of the two gnathopods in the male are more alike than in related species; the 6th joints of pereopods 4 and 5 are distinctly longer than the 5th joints; the eyes of the young at extrusion are red, gradually darkening during the earlier growth stages; and, finally, the cuticle is microscopically striate. Another striking character is the position of the median palmar spine on the hands of the male gnathopods. This spine, as in *marinus* (Text-fig. 1d, f) and *obtusatus* (Text-fig. 5f), appears to form one of a continuous row with the spines of the angle-group, but in this species is set unusually far back, and produces the appearance of a "quite naked palm" in the words of Stephensen (1938, p. 145).

The following amplified description is given for convenience of comparison with the other species described here.

ADULT MALE.

Body elongate, laterally compressed. Pleon-segments 4-6 not produced dorsally; the dorsal spines in four groups, with the spines short and few in number, the formula in the adult being: 1 : 1 : 1 : 1—2 : 1 : 1 : 2—1 : 0 : 0 : 1.

Sideplate 1 (Text-fig. 8c) parallel-sided; sideplate 4 (Text-fig. 8h) a little longer than greatest width; distal expansion rather deep and evenly rounded, with 2 setules inset posteriorly. Epimera 2 and 3 (Text-fig. 8l) with distal margins rounded, bearing 3 spines anteriorly; posterior distal angles obtuse, or obtusely quadrate.

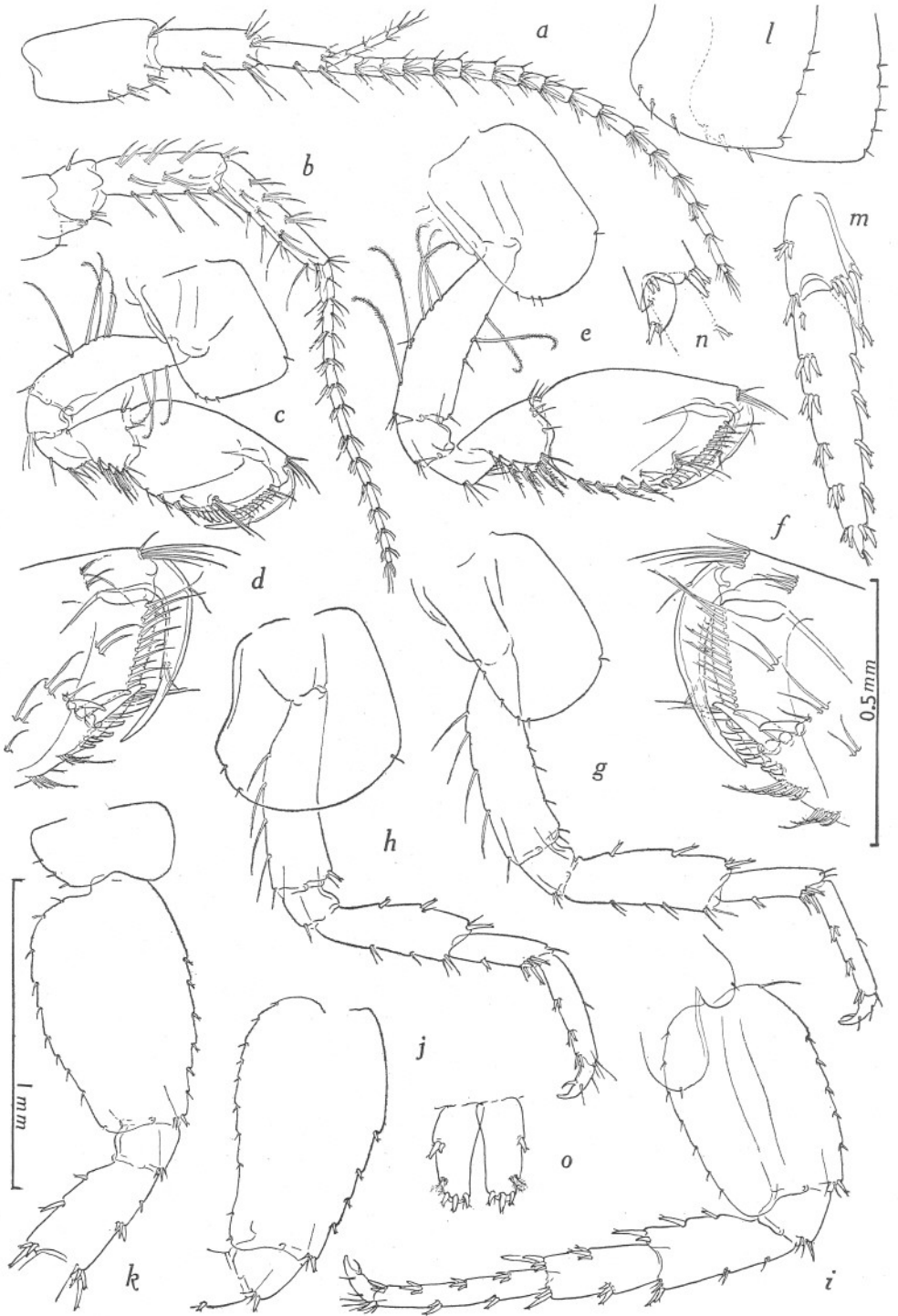
Head with lateral lobes rounded. Eye relatively large, often slightly constricted in middle. Antennae short with few joints, 1 rather longer than 2. Antenna 1 (Text-fig. 8a) peduncle with joint 2 long, but distinctly shorter than joint 1; flagellum less than twice length of peduncle, possessing about 17 joints; aesthetascs unusually long; accessory flagellum with about 4 joints. Antenna 2 (Text-fig. 8b) with joint 4 of peduncle broad, and about equal to joint 5 in length; flagellum about 13-jointed, slightly shorter than peduncle; setae sparse, the male sensory hairs (p. 680 and Text-fig. 11a) very few in number; calceoli lacking. Bifurcate setae only on basal joints of antennae 2.

Gnathopods (Text-fig. 8c-f) relatively large and more strongly-built than in the other species here described. Hand of gnathopod 1 shorter than that of gnathopod 2 but more similar in structure than in related species; palm less oblique than in related species, but still forming a continuous curve with posterior margin. Hand of gnathopod 2 with palm nearly transverse, palmar angle rounded, posterior margin a little longer than palm. Both gnathopod hands with median spine separated from base of claw by an unusually wide gap, this spine with its accompanying seta-cluster set close up against the angle spine row (Text-fig. 8c, e); spines of lower angle-group unusually long (Text-fig. 8d, f); claw with tip unusually long and slender.

Peraeopods 1 and 2 (Text-fig. 8g, h) very sparsely setose, lacking both bifurcate and male sensory setae. Peraeopods 3-5 (Text-fig. 8i-k) relatively elongate, furnished with short spines; basal joint in peraeopod 3 moderately expanded, with posterior distal angle free and well rounded; those of peraeopods 4 and 5 with posterior expansion much narrower distally but with the angles distinctly free and devoid of spines (condition intermediate between *obtusatus* and *finmarchicus*): joint 6 considerably longer than joint 5. Peraeopod 4 with joint 4 about twice length of apical width.

Uropod 1 scarcely extending beyond uropod 2, the apices of the rami of both, and of the telson, in line with the distal margin of peduncle of uropod 3. Uropod 3 (Text-fig. 8m) with outer ramus 2-jointed, broad and stout, bearing clusters of short spines, completely devoid of setae; inner ramus small and scale-like, with 1 small seta on inner margin, and 1 spine and 1 small seta apically. Telson (Text-fig. 8o) lobes about twice as long as wide; each with 1-2 spines in lateral cluster, a pair of plumose sensory hairs below the apex, and three spines in apical cluster.

Cuticle microscopically striated over almost the whole of the body, the striated effect being due to minute plications producing patterns resembling human finger-prints; the plications, under high magnification, apparently longitudinally serrate.



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ADULT FEMALE.

Differences from adult male as follows.

Antennae bearing numerous well-formed bifurcate setae.

Gnathopod hands smaller than in male. Peraeopods 1 and 2 not more setose than in male, but bearing some bifurcate setae, situated on joints 2 and 3 of peraeopod 1 and joint 2 of peraeopod 2.

Brood-plates, especially the two anterior pairs, attached to gnathopod 2 and peraeopod 1, abnormally large, being long and exceptionally broad; the two posterior, attached to peraeopods 2 and 3, clavate and broader than in other species; in life full brood-pouch visible well below the level of the margins of the sideplates and even protruding below the basal joints of the limbs.

Telson with 4 spines in each apical cluster.

Eggs relatively large for size of animal; number in one brood also relatively large, typically between 20 and 30; colour dark green when newly laid, the embryos becoming bright orange.

IMMATURE.

Eyes of young at extrusion containing very little dark pigment, appearing more or less bright red, the dark pigment accumulating during first few weeks of life, until eye-colour more or less black.

Uropod 3 outer ramus: stoutness, and shortness of spines, apparent at early age.

Cuticle not evidently microscopically striate in younger stages.

SIZE AND COLOUR.

Length of adult male abnormally small, $4\frac{1}{2}$ –7 mm.; that of female on average somewhat larger, 5–8 mm.; young on average 1.3 mm. at extrusion. Colour translucent, pale slate-blue to greenish grey; at most, obscure diffuse patches of pink on hinder pleon-segments, well-defined orange patches not developed; bright orange of embryos very conspicuous in females with incubating brood.

HABITAT.

A marine littoral species, strictly intertidal, inhabiting the zone between high- and low-water neaps, characteristically where freshwater streams or

Text-fig. 8. *Marinogammarus stoerensis* (Reid), male. Figures (except *n*) drawn from a male, 6 mm. long, taken at Kilve, shore of Bristol Channel, 7. v. 39 (R. Bassindale); compared with specimens from Plymouth district. Magnification $\times 45$, except *d* and *f* $\times 77.5$. *a*, antenna 1, left side, inner surface, showing the large aesthetascs; *b*, antenna 2, left side, inner surface, showing the male sensory hairs on the peduncle; *c*, gnathopod 1, right side; *d*, gnathopod 1, left side, distal portion of hand, from under surface, showing spine-cluster at palmar angle; *e*, gnathopod 2, right side; *f*, gnathopod 2, right side, as in *d*; *g*, *h*, peraeopods 1 and 2 respectively, right side; *i*, peraeopod 3, right side; *j*, peraeopod 4, right side, basal joint; *k*, peraeopod 5, right side, proximal joints 1–4; *l*, epimera 2 and 3, left side; *m*, uropod 3; *n*, uropod 3 of a female, inner ramus; *o*, telson.

seepage flow over the tidal zone; under flat stones with *Procerodes ulvae*, *Melita palmata*, etc.; penetrating for only a short distance into estuaries.

MATERIAL EXAMINED.

England. SOUTH DEVON AND EAST CORNWALL: Plymouth Sound: between Cawsand and Penlee Point, 5. viii. 38, numerous under stones in a small freshwater stream flowing over rocks of tidal zone, ♀♀ and immature; Bovisand Bay, 10. viii. 38, intertidally under stones, ground influenced by freshwater seepage, one ♀ ovigerous, 5 young ♂♂ and many young ♀♀, immature numerous, collected with *Procerodes ulvae*, etc.; Crownhill Bay, Bovisand, 11. x. 38, under stones about mid-tide level, in freshwater seepage 20 immature amongst numerous *M. pirloti*, with *Procerodes ulvae*. Plymouth district: Drake's Island, tidal zone, 24. i. 39, 1 ♂, 13. ii. 39, 1 ♀ and 1 imm. Three specimens (♀♀) out of 700 *Marinogammarus* preserved in the Laboratory stock bottles. South Devon coast: Wembury, Church beach, 12. viii. 38, under flat stones, etc., about mid-tide level, where freshwater stream flows over shore, young of both sexes and immature plentiful, no breeding adults; River Yealm estuary, near mouth, 18. iii. 34, under stones and *Fucus serratus* on sandy ground, 1 ♂ and 4 ♀♀ (G. I. Crawford); Revelstoke beach, 4. v. 40, very numerous in freshwater stream flowing over tidal zone, sheltering under pebbles and eating a green alga, ♀♀ with broods and immature plentiful, but no ♂♂; River Erme estuary, near mouth, 5. iii. 39, 1 ♂; River Avon estuary, near mouth, 22. iv. 32, one ♂ and several ♀♀, young reared in laboratory; Thurlestone, 15. x. 38, plentifully under stones at outflow of freshwater drain over reef of rocks, 3 young ♂♂, several young ♀♀, numerous imm.

NORTH SOMERSET: Severn estuary: Kilve, 7. v. 39, stream flowing over tidal zone, 4 ♂♂, 3 ♀♀, 1 imm. (identified for Mr R. Bassindale). DURHAM: 1 ♀ and another, in coll. Brit. Mus. [1911. 11. 8], labelled "*Gammarus marinus*" Leach.

Scotland. EAST LOTHIAN: Port Seton, under stones near high water, 7. iii. 32, one advanced imm., amongst other *Marinogammarus* spp. (identified for Prof. A. D. Hobson). WEST SUTHERLAND: Bay of Stoer (type locality), 1 maturing ♀ (sent by Mr D. M. Reid). INNER HEBRIDES: Isle of Muck, 3. viii. 38, in two stations, 4 ♀♀ and 2 imm. (identified for Prof. A. D. Hobson).

Continental. NORTH NORWAY: Hammerfest, Skaervoy, 2. vii. 39, mid-tide level, streamlet, 1 ♂ and 3 ♀♀ (coll. G. I. Crawford).

DISTRIBUTION.

So far *M. stoerensis* has only been recognized from Scotland, England and Norway. The localities for the latter country given by Stephensen (1938) with the additional one given above show that the species is well distributed along the west and north Norwegian coast. To the single previously known British locality of Stoer Bay (Reid, 1938), others are recorded above, and these, though few in number, indicate that the species is well distributed. If specially

looked for the species will probably be found plentiful in many places, as it has proved to be in the Plymouth district. In ordinary collecting it is apt to escape notice owing to its small size and its localization to confined areas where there is freshwater influence.

Marinogammarus pirloti sp. nov.

Plate IV, figs. 1-17; text-figs. 9a-f, 10a-e and 11e, g-i, m, n.

The species here described was first noted from the Plymouth district in 1913, when it was recognized as new to science. It was kept at the Laboratory and used in the hybridizing experiments of 1913-14 (referred to as "another brackish water species at Cawsand within the tidal zone" Sexton, 1928, p. 52).

The first specimens, taken in August and September 1913, were from Cawsand Bay on the west side of Plymouth Sound, where a freshwater trickle falls into a tidal pool on the beach. The animals were present in numbers amongst the shingle, clinging to the under surface of flat stones. Later in the same year, the species was found at Wembury beach, in a similar habitat.

A fresh search in 1938 and 1939 revealed that the species was present in several localities in Plymouth Sound, e.g. Drake's Island, Bovisand Bay, Crownhill Bay near Bovisand, Wembury Point, as well as at Wembury Church beach, and Revelstoke, particularly abundant where there are freshwater trickles over the tidal zone. It is especially numerous at Wembury Point, from which the type specimens have been taken, under pebbles and flat stones in the upper part of the beach where the stony area borders on the reefs of rock, and where there is a good deal of infiltration of drainage water from the land. Here and in other places, it is often collected in company with *Procerodes (Gunda) ulvae*.

Specimens have also been taken from the following localities: Isle of Man, Niarbyl Bay, 18. ix. 38, collected by Mr G. I. Crawford, from a freshwater stream flowing over the beach; West Sutherland, Stoer Bay, 16. iv. 39, collected by Mr D. M. Reid from under stones, about half-tide mark, and noted as common. It thus seems probable that the species is widely distributed on rocky shores in the west of the British Isles, favouring stony beaches where there is freshwater influence. It is not, however, as yet known to penetrate into estuaries.

DESCRIPTION

ADULT MALE.

Body decidedly stout in appearance, with all its parts rounded. Pleon-segments 4-6 produced dorsally in rounded humps each carrying the four spine groups usual in the genus, the spine formula as follows: 2 : 1 : 1 : 2—3 : 1 : 1 : 3—2 : 1 : 1 : 2. Sideplates 1-4 rather deeper than the corresponding segments, convex, with the anterior distal angles much rounded; 3 and 4 of the same length, 3 narrow, 4 distally expanded, its length equal to the width across the expansion. Epimera of pleon-segments 1-3 (Pl. IV, fig. 13) with

anterior margins rounded; posterior margin of 1 rounded, of 2 and 3 straight with two or three setae inset; postero-distal angle of 2 subobtuse, of 3 rectangular, both angles with a small acute projection.

Head measured along the dorsal line much longer than the 1st peraeon-segment, about five-sixths the length of the 1st and 2nd combined; rostrum not much produced; lateral lobes obliquely truncate, upper angle rounded and sloping gradually up to the insertion of antenna 1, lower angle obtuse, sinus below rather deep, with the post-antennal corner produced to a subacute angle.

Eye large and long, wide at both ends, somewhat narrowed towards the middle; retinal pigment black, occasionally rather dilute, the ommatidia separated by a reticulation of white pigment. Antenna 1 (Pl. IV, fig. 1) only a little longer than antenna 2; joint 1 of peduncle unusually large and stout, equal to combined length of joints 2 and 3, bearing 4 plumose hairs in the sensory groove; joint 2 barely one and a half times length of joint 3; primary flagellum about twice as long as the peduncle (with about 23 joints in larger specimens); accessory flagellum about 5-jointed. Whole antenna sparsely setose, the setae mainly of the bifurcate type; aesthetascs (Text-fig. 11g) present on all joints of primary flagellum except the first, inset on the under surface. Antenna 2 (Pl. IV, fig. 2) peduncle with joints 4 and 5 subequal in length, 4 stouter than 5; flagellum stout, subequal to the last three joints of peduncle, about 14-jointed, bearing calceoli (Pl. IV, fig. 3) on joints 2-7; dense fan-shaped clusters of male sensory setae developed all along inner surface from distal end of peduncle joint 4, the dense hair fringe so formed being conspicuous when animal viewed from above, the sensory setae themselves hyaline, flattened, and abruptly narrowed towards the apex (p. 680 and Text-fig. 11e); some of the setae on peduncle joints, usually the longest of each cluster, of bifurcate type (p. 677 and Text-fig. 11n.).

Mouth-parts normal (see Text-fig. 9 for details).

Gnathopods 1 and 2 of heavy build, not greatly dissimilar in size, hand of 2 broader but not longer than that of 1; basal joints unusually broad; median palmar spines rounded, not truncate; claw impinging on under surface owing to slight torsion of palm at the angle. Hand of gnathopod 1 (Pl. IV, figs. 4, 5) about the length of basal joint, elongate oval; palm very oblique, almost continuous with posterior margin; median palmar spine rounded and ridged on the tip, separate from spines of angle-group; claw closing between the two spine groups at the palmar angle, each group containing 1 spine like the median spine, and 2 of the small curvate type. Hand of gnathopod 2 (Pl. IV, figs. 6, 7) with palm not nearly so oblique as that of 1; palmar margin as in gnathopod 1, coarsely crenulate, with small deeply bifurcated setae along its inner edge, and longer ones on its outer side; ending, with a slight torsion on the under surface at the palmar angle in a groove or indentation minutely tuberculate; tip of claw fitting into groove between the angle-spine groups (Pl. IV, fig. 7); posterior margin slightly longer than palm. Bifurcate setae distributed on both gnathopods except hand of gnathopod 1.



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Text-fig. 9. *Marinogammarus pirloti*, sp.n. Mouth-parts of the adult male figured in Pl. IV, $\times 77.5$; a, upper lip; b, lower lip; c, maxilla 1; d, maxilla 2; e, mandibles; f, maxilliped.

Peraeopods all with unusually broad 4th joints, and strongly recurved claws. Peraeopods 1 and 2 (Pl. IV, figs. 8, 9) sparsely setose, joints 5 and 6 armed with strong sensory spines of a special type; a few bifurcate setae present on joint 2 distally. Peraeopods 3-5 (Pl. IV, figs. 10-12) armed with clusters of short stout spines, setae present only in terminal clusters of joint 6. Basal joint of peraeopod 3 nearly as wide as long; its posterior distal angle produced to a rounded lobe; those of peraeopods 4 and 5 with this angle not free, the posterior expansion narrowing distally and ending in a group of 2 or 3 spines. Joint 4 of peraeopods 4 and 5 scarcely more than $1\frac{1}{2}$ times as long as wide distally; joints 5 and 6 subequal.

Gills well developed, ovate, stalked; carried on peraeon segments 2-7 (see Pl. IV, fig. 6); the second (attached to peraeopod 1) the longest, extending to about the distal end of 2nd (= basal) joint of the limb.

Pleopods comparatively short. Peduncles carrying a row of coupling spines, and strong setiform spines near the inner distal angle; coupling spines long, curved, with five hooks on the upper side, and two larger hooks underneath near apex; three coupling spines and two setiform on pleopod 1; two and two respectively on pleopod 2, and two and three on pleopod 3. Rami subequal, about $1\frac{1}{2}$ times length of peduncle, each with a large basal joint, and 16 to 18 small joints. Feathered swimming setae on all the joints; and cleft spines present on basal joints of inner rami, three on the first, two on the second, and two on the third; each spine with a strong feathered shaft, and a deeply cleft apex.

Uropod 1 (Pl. IV, fig. 14) extending beyond uropod 2 (Pl. IV, fig. 15), their peduncles reaching the level of the distal margin of pleon-segment 6. Uropod 3 (Pl. IV, fig. 16) outer ramus 2-jointed, joint 2 minute and bearing long setae, joint 1 long and broad, carrying groups of spines and a dense setal fringe on each margin, setal fringe of inner margin longer, composed mainly of plumose setae, that of outer margin composed of slender hyaline setae, none plumose. Telson (Pl. IV, fig. 17) cleft to the base; each lobe with an apical group of three spines, a lateral group of two spines, and a pair of short plumose sensory hairs inset in sockets on the upper surface between the two spine-groups.

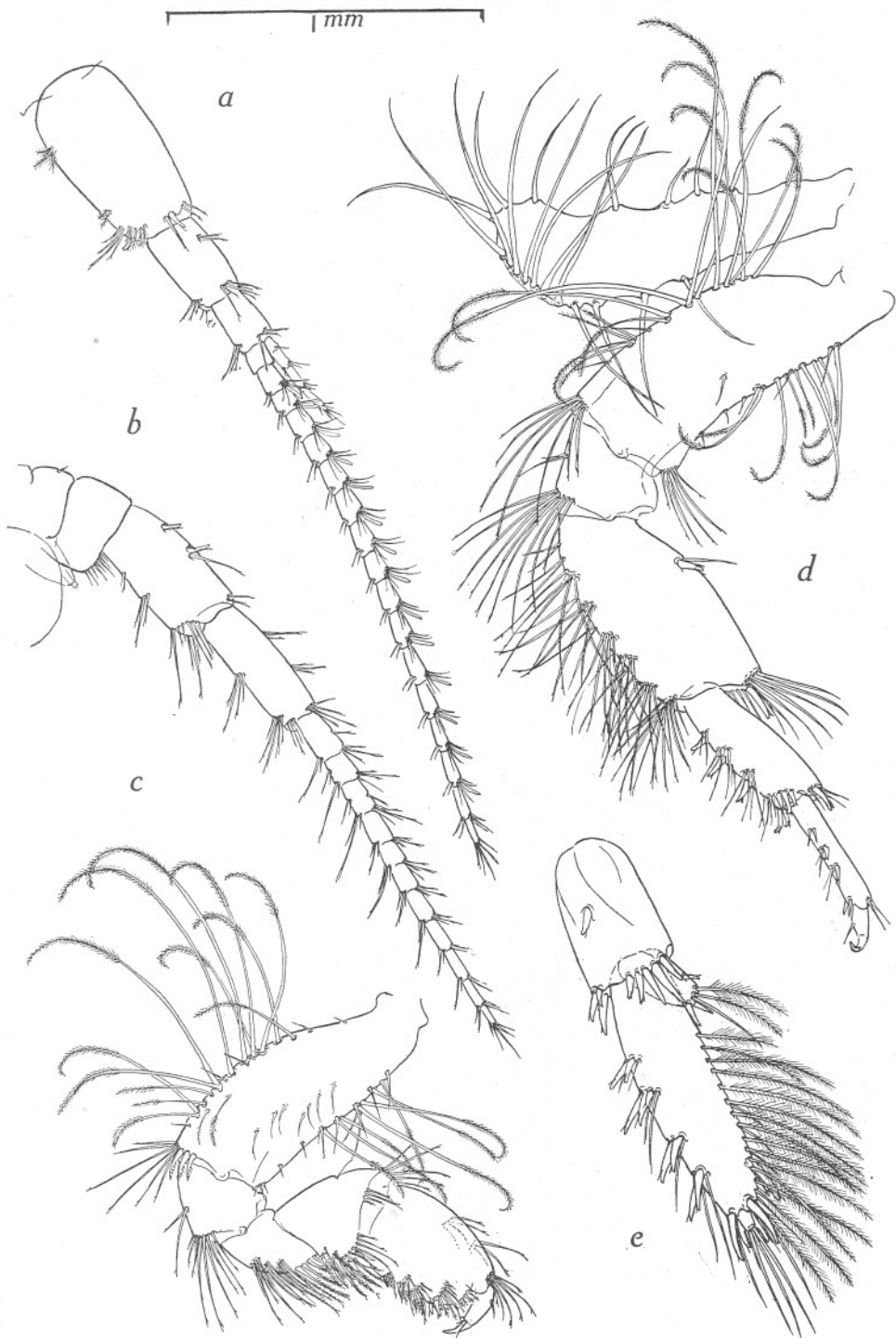
ADULT FEMALE (Text-fig. 10).

Differences from adult male as follows.

Antenna 1 (Text-fig. 10a) joint 1 of peduncle even more robust than in male, longer than combined length of joints 2 and 3. Antenna 2 (Text-fig. 10b) sparsely setose, but with more numerous bifurcate setae.

Gnathopods (Text-fig. 10c) with smaller hands, bifurcate setae well distributed and present on hand of gnathopod 1.

Peraeopods 1 and 2 (Text-fig. 10d) much more setose than in the male; joint 4 bearing clusters of long setae posteriorly, and a dense tuft at the anterior distal angle.



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Text-fig. 10. *Marinogammarus pirloti* sp.n., adult female. Figures drawn from a female taken in the same sample as the male figured in Pl. IV (Wembury Point, south Devon), $\times 36$. a, antenna 1, left side, under surface; b, antenna 2, right side; c, gnathopod 1; d, pereopod 1; e, uropod 3.

Brood-plates, situated on gnathopod 2 and pereopods 1-3, narrow; that on gnathopod 2 clavate; those on pereopods 2 and 3 linear. The fringing hairs numbering successively on the right side 36, 18, 11 and 7; on the left side 34, 16, 10 and 7.

Uropod 3 (Text-fig. 10e) outer ramus with outer margin bearing groups of spines but very few setae, inner margin bearing only two distal groups of spines and a fringing row of long plumose setae.

Eggs very dark grey, almost black, when newly laid, changing to dull yellow as embryos develop; laid in rather small batches (17 in pouch of the female figured); relatively large (average size of one batch measured 0.54×0.69 mm.).

IMMATURE.

Eye black from time of extrusion. The characteristic large first joint of peduncle of antenna 1 distinguishable at an early age. Orange pigment patches present (see below).

SIZE AND COLOUR.

Size moderately small, male length to 14 mm., female to 11 mm.

Colour, pale green, often suffused with tinges of brown, pink or blue; irregular bright orange patches (clusters of "oil-globules") on sides of all pleon-segments, and small orange spots at the base of pereopods 3-5.

DISTINGUISHING CHARACTERS.

The main diagnostic character of *M. pirloti* is the excessive disproportion in size between the large 1st joint and the short 2nd and 3rd joints of antenna 1, the former being fully equal in length to the two latter combined. Though a larger species than *stoerensis*, it is considerably smaller than *marinus*, *obtusatus*, or *finmarchicus*. Unlike any of these four species, it develops clearly defined patches of orange pigment on the sides of the pleon-segments.

The chief differences from *M. marinus* (p. 638) are as follows. In antenna 1, joint 1 equals 2 + 3 in length instead of being somewhat shorter, and joint 2 is not nearly twice the length of joint 3; the male sensory setae of antenna 2 are arranged in denser tufts and form a conspicuous fringe along the inner margin of the limb; calceoli are present on antenna 2; sideplate 4 has an appreciably deeper distal expansion; the joints of the pereopods are in general broader, especially joints 4 and 5 of the three hinder; uropod 3 in the male has a dense fringe of plumose setae along the inner margin (this fringe in *marinus* consisting of slender straight setae with modified apices), and in both sexes the spines are stouter; the eye is never strikingly narrow relative to its length; orange pigment spots are developed; the size is smaller; and the body considerably stouter.

The diagnostic characters of *obtusatus* (p. 650), *finmarchicus* (p. 656) and *stoerensis* (p. 662) at once distinguish those species, and it only remains to refer to *olivii* (p. 645). To this latter species *pirloti* is evidently related. The size,

form and general proportion of the limbs are very similar in the two species, except that *olivii* is rather more slender in build. In both species calceoli are present on the male antenna 2, and uropod 3 on its inner margin possesses a dense setal fringe of plumose hairs. There are, however, important differences, which may be summarized as follows. In *olivii* the setae and setules are in general notably longer than in other species of the genus, whereas, if anything, the reverse tendency is shown in *pirloti*; in *olivii* the relative lengths of the peduncle joints of antenna 1 are not abnormal, joint 1 being shorter than 2 and 3 combined, and the peduncles of both antennae are more setose; the male gnathopod 1 differs in the two species, that of *olivii* having somewhat more specialized features (see pp. 647 and 668 and compare Text-fig. 3c, e with Pl. IV, figs. 4, 5); the setal fringe of male uropod 3 contains plumose hairs on both margins in *olivii*, on the inner only in *pirloti*; in the male *olivii* there are only a few scattered bifurcate setae on the gnathopods, whereas in male *pirloti* they are distributed on both antennae and joint 2 of pereopods 1 and 2; and in pereopod 1 of *olivii* the antero-distal angle of joint 4 is more produced.

INDETERMINATE SPECIES.

Gammarus cam[p]ylops Leach.

- 1814 *Gammarus camylops* Leach, *Edinburgh Encycl.*, 1813-14, Vol. VII, p. 403
(written "*camylops*" in Appendix).
 1815 *Gammarus campylops* Leach, *Trans. Linn. Soc.*, Vol. XI, p. 360.
 1830 *Gammarus camphylops* Milne-Edwards, *Ann. Sci. Nat.*, Vol. XX, p. 367.
 1862 *Gammarus camptolops* Spence Bate, *Amph. Crust. Brit. Mus.*, p. 209,
Pl. XXXVII, fig. 3.
 1863 *Gammarus campylops* Spence Bate & Westwood, *Brit. Sessile-eyed Crust.*
Vol. I, pp. 375-7.
 non 1894 *Gammarus campylops* Sars, *Crust. Norway*, Vol. I, pp. 500-2, Pl. CLXXVI,
fig. 2.
 non 1906 *Gammarus camylops* Stebbing, *Das Tierreich*, Vol. XXI, pp. 476-7.
 1911 *Gammarus marinus* var. Walker, *Ann. Mag. Nat. Hist.*, ser. 8, Vol. VII,
pp. 397-9.
 non 1922 *Gammarus locusta* var. *campylops* Schliez, *Zool. Anz.*, Vol. LIV, pp. 215-17.

The status of this species, introduced by Leach (1814, 1815), has been the source of much confusion and controversy. Leach's descriptions were extremely meagre, the possession of a sinuous eye ("*oculis flexuosis*") being the only really diagnostic character given. However, his two type specimens—from Loch Ranza, Isle of Arran—were preserved in the British Museum, where they have been re-examined on two occasions. Spence Bate (1862, 1863) figured and drew up a short description of the species on the strength of the characters he found in these types, and in additional material which he assigned to the same species. He figures (1862, Pl. XXXVII) the inner ramus of uropod 3 as about 30% of the outer ramus. Other characters to which he calls attention include the produced infero-posterior angle of epimeron 3 (a character here shown to distinguish *marinus* from other related species), the

“disc-shaped” basal segments of the hind peraeopods, the subequal gnathopods, etc. As to the shape of the eye, he figures it (1862) as elongate and constricted in the middle, but in his description he says it is “occasionally shaped like the letter S.” He adds that the shape of the eye is not to be depended on as a specific character, as among a considerable number of specimens in his material he found as many, if not more, had eyes of a linear form. In the second description (1863, p. 375) his figure shows the eye definitely sigmoid. Unfortunately Spence Bate’s descriptions are inadequate for critical purposes, and there is furthermore some doubt how far the few details he gives can be relied on.

More recently, however, Walker (1911) made a special re-examination of the types, with the help of Dr Calman; their report has to be considered the final word on the subject, as we have been informed that the specimens are no longer in existence. Mr Walker and Dr Calman found the specimens in a good state of preservation: they confirmed that the length of the inner ramus was correctly figured by Spence Bate, and in their opinion the specimens showed no definite character to separate them from *marinus* apart from the sigmoid eye. But they agreed that this character has no certain taxonomic value, and concluded that the types of *G. campylops* Leach could only be variants of *G. marinus*.

The significant point confirmed by Walker was that Leach’s *campylops* had a short inner ramus and closely resembled *marinus*—or, as we should now put it, the species at least belonged to genus *Marinogammarus*. Further important points were made by Walker. Thus he points out the anomaly in Leach (1815), referred to on p. 635, and gives valid reasons for supposing that *aquaticus* (with long inner ramus) and *campylops* (with short inner ramus) had been unintentionally transposed in the original grouping of the four species of *Gammarus* known at that time. Walker was also in a position to call attention to the fact that *Gammarus campylops* Sars 1894 could not possibly be the same as Leach’s species, and recognized, as can be readily confirmed from Sars’s descriptions and drawings, that this species is an ally of *G. locusta* (L.), and may in fact only represent young forms of that species. This conclusion applies also to the *Gammarus camylops* of Stebbing (1906), whose description is simply a repetition of that of the species described and figured by Sars.

One further use of the name *campylops* remains to be mentioned. Schliez (1922), accepting Walker’s verdict that Sars’s *campylops* was nothing to do with Leach’s species, went further and attempted to identify Sars’s species with *Gammarus zaddachi* Sexton 1912. Disregarding the question whether the name *campylops* could justifiably be used at all, and holding the erroneous view that *zaddachi* Sexton was only a variety of *G. locusta*, he was led to give *zaddachi* the name of *G. locusta* var. *campylops*! More recent German writers, however, have apparently discarded the view that *campylops* is synonymous with *zaddachi*.

In arriving at their own conclusions the present writers have to take con-

sideration of the facts that distinct species allied to *marinus* are now known to exist, and that determinations of "*marinus*" made in the past may refer to any of these species. The conclusions are as follows. (i) The short original descriptions by Leach are inadequate to indicate with any certainty even to what group of species his *campylops* belonged. (ii) The supplementary descriptions by Spence Bate cannot be relied on for correctness of detail, and it is only through Walker's re-examination that the fact can be accepted that Leach's specimens possessed *marinus*-like characters. (iii) Walker's verdict to the effect that the types probably belonged to *marinus* has to be emended, in the light of our present knowledge, to the effect that they belonged to *marinus* or one of the other species of *Marinogammarus*. (iv) Since the types are no longer available for examination, the species remains indeterminate, and the name *camylops* or *campylops* Leach has to be relegated as a doubtful synonym of one of the species of *Marinogammarus*.

We may add that we entirely agree that Sars's *campylops* is not Leach's species. If this form proves indeed to be a valid species, it will require a new name (International Rules of Nomenclature, Article 35). While it may perhaps represent only a young stage (as Walker suggested), or a stunted population of *G. locusta*, the possibility that it is a form of *G. zaddachi* seems out of the question.

MATERIAL EXAMINED. A tube of seven specimens of queried *Gammarus campylops* from A. O. Walker's collection, preserved in the British Museum [1925. 9. 8: 1160-66] has been examined. The original label, in Walker's hand-writing, reads: "Argo: Killiebegs, 9. viii. 90, W.A.H.: *Gammarus campylops* Leach (or *locusta* juv.?)." The specimens have been re-determined as young stages of *G. locusta* (L.), the largest being a female which had just reached maturity.

KEY TO SPECIES OF *MARINOGAMMARUS*

- a. Posterior angle of epimera 2 and 3 obtusely rounded; uropod 3 devoid of setae, or else antenna 1 with joints 1 and 2 equal in length.
(Body relatively elongate; never dense fringe of setae on uropod 3; pereopods 1 and 2 only sparsely setose, even in adult female.)
- b. Size relatively large (adults above 10 mm.); antenna 1 with joint 2 of peduncle as long as joint 1; hand of male gnathopod 1 considerably larger than that of gnathopod 2, brood-plates of female normal; spines on urosome and uropods acute and prominent; uropod 3 of normal shape, bearing setae in adult male; cuticle microscopically smooth *obtusatus* (Dahl)
- bb. Size exceptionally small (adults below 8 mm.); antenna 1 with joint 2 of peduncle shorter than joint 1; hand of male gnathopod 1 not larger, actually rather smaller, than that of gnathopod 2; brood-plates of female abnormally large, especially in respect to breadth; spines on urosome dorsally few and short; uropod 3 more robust, completely lacking setae, and with short inconspicuous spines; cuticle microscopically striate *stoerensis* (Reid)
- aa. Posterior angles of epimera 2 and 3 subrectangular or acute; uropod 3 bearing setae; antenna 1 with joint 2 of peduncle clearly shorter than joint 1.

- b. Inner ramus of uropod 3 of one-third to two-fifths length of outer ramus; outer ramus of uropod 3 with joint 2 completely lacking; basal joints of pereopods 4 and 5 with posterior distal angle clearly free and lacking group of spines. (Setae on uropod 3 arranged in rather conspicuous spreading tufts; epimera 2 and 3 subrectangular posteriorly; telson lobes with three spines in lateral group *finmarchicus* (Dahl))
- bb. Inner ramus of uropod 3 less than one-third length of outer ramus; outer ramus with joint 2 present; basal joints of pereopods 4 and 5 with posterior distal angle not free and bearing a group of spines. (Pereopods 1 and 2 more densely setose in female.)
- c. Larger species; epimeron 3 with posterior distal angle distinctly produced, acute; urosome spines numerous, the groups tending to coalesce into a single curved row; hand of male gnathopod 1 somewhat larger than that of gnathopod 2; median palmar spine of both male gnathopods adjacent to spines of palmar angle; pereopods 4 and 5 rather more elongate, joint 4 three times as long as broad distally; uropod 3 lacking plumose setae; side-plate 4 with shallower distal expansion; male antenna 2 lacking calceoli *marinus* (Leach)
- cc. Smaller species; angle of epimeron 3 subrectangular; urosome spines few in number, the groups remaining separated; hand of male gnathopod 1 smaller than that of gnathopod 2; median palmar spine of both male gnathopods separated from spines of palmar angle by a distinct gap; uropod 3 bearing a fringe of plumose setae (dense in male) at least on inner margin; pereopods 4 and 5 stouter, joint 4 only twice as long as broad; sideplate 4 with rather deep distal expansion; calceoli present.
- d. Antenna 1 with joint 1 robust, at least as long as 2 + 3 combined; peduncles of antennae less setose; hand of male gnathopod 1 of normal type; uropod 3 with setal fringe composed of plumose setae on inner margin only; setae in general shorter, setules normal. (Bifurcate setae present on both antennae and basal joints of pereopods 1 and 2 in either sex) *piriloti* n.sp.
- dd. Antenna 1 with joint 1 longer than 2, but clearly shorter than 2 + 3; peduncles of antennae more setose; hand of male gnathopod 1 with palmar angle roundly produced; uropod 3 with setal fringe composed of plumose setae on both outer and inner margins; setae and setules, in most places where they occur, relatively longer than in other species of genus. (Bifurcate setae absent on antennae and pereopods of male; male sensory setae lacking on uropod 3) *olivii* (Milne-Edwards)

ON TYPES OF SETAE FOUND IN *MARINOGAMMARUS*

Species of this genus are relatively glabrous compared with other *Gammarus*-forms, and on the whole not richly supplied with setae. In some, however, antenna 2, the gnathopods distally, and uropod 3 may have dense fringes, and a moderate or sparse number of setae regularly occur along antenna 1 and pereopods 1 and 2. The setae themselves are usually of more or less specialized types, possessing modified apices. Some marked specific distinctions have been discovered in the structure of certain of these types, as well as in their distribution or relative abundance. In this section it is proposed to give an outline of the main types of setae which occur, and to indicate the features which are usefully studied in their taxonomic bearing.

Examinations of setae have been made on parts mounted in gum chloral solution, under the magnification of a $\frac{1}{12}$ objective (oil immersion).

SIMPLE FORMS OF SETAE. Simple, unspecialized, setae taper gradually throughout their length towards the apex, are circular in cross section, and are devoid of any processes arising from their shaft. They possess the general feature common to all setae: the existence of a minute pore at the extreme apex, connecting with the hollow interior. This pore is clearly visible under high magnification; and when a seta from a fresh animal is examined, minute drops of fluid can be seen emerging from it when light pressure is exerted on the cover-slip. The distribution of simple forms of setae calls for no special discussion.

SETAE WITH FLANGED OR GROOVED APICES. In species of *Marinogammarus* the majority of the setae are not simple. Those which are not specialized in other respects usually possess modified apices. The modification consists either in the development of a flange or flattened groove at the apical end of the main shaft, or a subsidiary process arises near the apex so that this appears to be cleft, or both. Unbranched setae with flanged or grooved apices are perhaps the most generally distributed in all species. The setae thus modified may be short or long. The structure of the apex is most readily observed in short, relatively broad, setae, such as may be observed on antenna 1 of *M. marinus* female (Text-fig. 11e). The illustration shows how part of the shaft is compressed to form a thin flange, the thickened part being much narrowed. There appears to be a groove between the flange and the main portion of the shaft, at least at its base. The course of the central cavity passing upwards to the apical pore is clearly visible. Numerous setae in both sexes of *marinus* have essentially this type of apex. Text-fig. 11k illustrates the apex of a long seta from antenna 2 of the male.

Corresponding setae in other species have a similar general form, but show specific variations in pattern. Thus the flanged apices in *pirloiti* (Text-fig. 11m) are often broad, show clearer indications of a groove, and can almost be termed narrowly spatulate. Minute striations can sometimes be seen on the flange, as in the seta illustrated. The most readily distinguished specific type is that found in *finmarchicus*, in which the apices have the appearance of one shown in Text-fig. 11j.

SETAE WITH BIFURCATE APICES. Sometimes the shaft of the seta is divided near its apex into two branches, producing an effect which is here termed "bifurcate" (Text-fig. 11g, n, o). The two branches are not symmetrical. In all types which have been studied the internal cavity passes up through only one of the branches, which carries the apical pore at its extremity, and which is here referred to here as the main branch. The second branch appears to be devoid of an internal cavity and apical pore. It is almost invariably shorter, sometimes considerably, and often narrower than the main branch: it is also typically sharper and less flexible. The main branch may be narrowly flanged

just like the apex of an unbranched seta. The bifurcate setae of *pirloiti* (Text-fig. 11*n*) are typically so flanged.

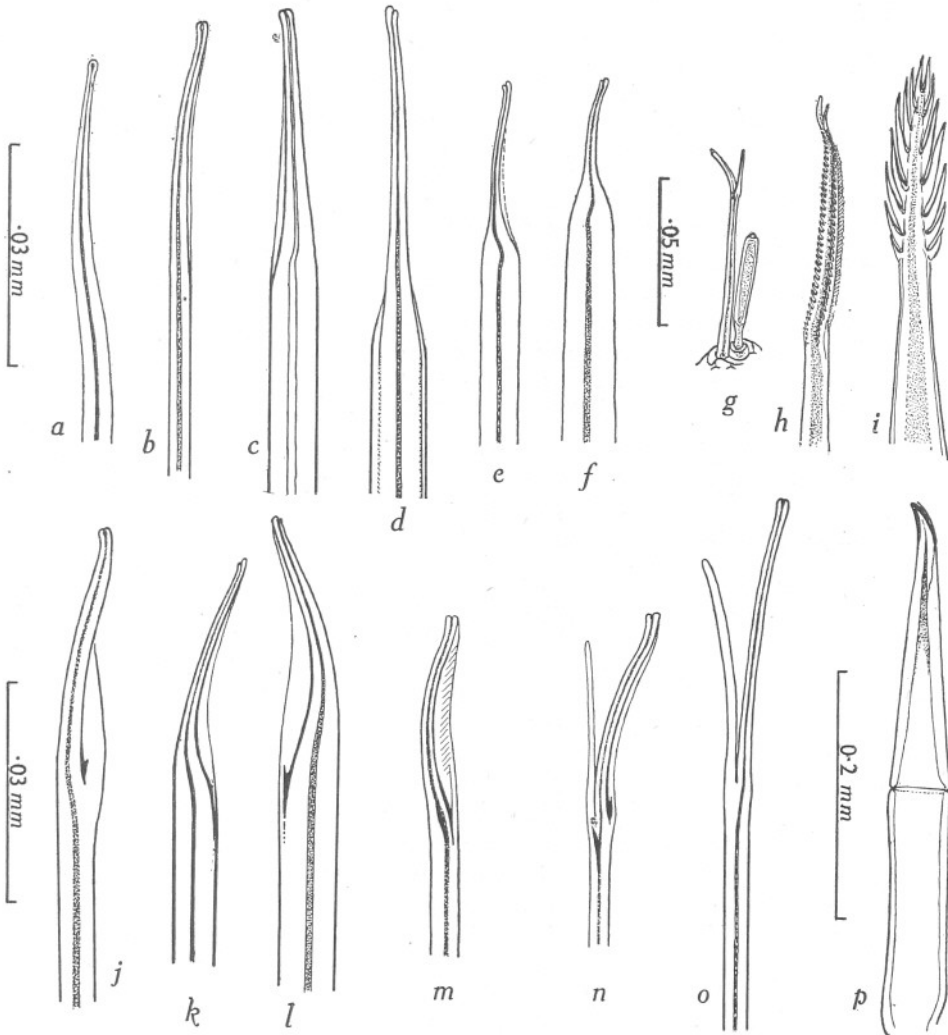
Specific differences in the form and dimensions of bifurcate setae occur. Thus in *obtusatus* (Text-fig. 11*o*) both branches are long and slender, the main branch being apparently without a flange. The few bifurcate setae present in male *olivii* have very short apices.

The frequency and distribution of bifurcate setae vary considerably in different forms. In the first place they are in general less abundant and more restricted in their distribution in the male sex than in the female of the same species. This difference is sometimes very marked, and is at least apparent in all species investigated. Two contrasting examples may be given. The females of both *pirloiti* and *stoerensis* possess conspicuous bifurcate setae distributed on the following limbs: antenna 1 and 2, gnathopod 1 and 2, peraeopod 1, joints 2 and 3, peraeopod 2, joint 2. In the male *pirloiti* the distribution is very similar, except that there are none on the hand of gnathopod 1 or on peraeopod 2, joint 2, and they are much sparser on antenna 2. In the male *stoerensis* they are almost entirely confined to the two gnathopods. When bifurcate setae are sparse, it is usually found that setae showing this condition are restricted to the longest one in a cluster.

Secondly there are specific differences. These are more apparent in the male. In *obtusatus* and *pirloiti* the setae are well distributed on the anterior limbs, whereas in *marinus*, *olivii* and *stoerensis* they are confined to certain joints of the gnathopods, or almost so. In *olivii* they are particularly sparse, and provide an interesting contrast with the related *pirloiti*. Usually there are none on the hand of male gnathopod 1; but some are present on the posterior margin in *stoerensis*. In the female, *marinus* completely, and *finmarchicus* almost, lacks these setae on peraeopods 1 and 2.

Apparently no bifurcate setae ever occur on uropod 3. It may also be noted that the specialized serrated setae (Text-fig. 11*h*) which are characteristic of the clusters on the posterior margins of gnathopod 1, joint 5 and gnathopod 2, joints 5 and 6, are typically bifurcate at the apex.

MALE SENSORY SETAE. The setae which fall in this category are developed in the male at sexual maturity as secondary sexual structures. Among Gammarids in general they may assume various forms: thus in *G. chevreuxi* they are slender, soft and curled. In *Marinogammarus* they are always straight, though typically more flexible and less strongly chitinized than other setae. Usually in this genus they are appreciably narrowed at the apex, sometimes very abruptly. Another characteristic feature is that these hairs occur in relatively few positions. It is in fact only on antenna 2 that they are always fully developed. They may also occur sparsely on the hand of gnathopod 2, and among the hair fringes of uropod 3, though in these positions they are less differentiated and should perhaps not be classed with the antennal setae at all. No special male setae of any sort are developed on any of the peraeopods.



G. M. S. del.

Text-fig 11. *Marinogammarus*, dermal armature. Figures drawn under $\frac{1}{2}$ objective. Magnification: *a-f* and *j-o* $\times 967$, *g-i* $\times 384$, *p* $\times 163$. *a*, apex of male sensory seta from antenna 2 of *M. stoerensis* ♂; *b*, apex of male sensory seta from antenna 2 of *M. finnarchicus*; *c*, apex of male sensory seta from antenna 2 of *M. obtusatus*; *d*, apex of male sensory seta from antenna 2 of *M. marinus*; *e*, apex of male sensory seta from antenna 2 of *M. pirloti*; *f*, apex of male sensory seta from antenna 2 of *M. olivii*; *g*, *M. pirloti* ♂, aesthetasc and small bifurcate seta from antenna 1, under surface of flagellum joint 1; *h*, *M. pirloti* ♂, serrated falciform bristle from proximal bristle-cluster on gnathopod 2 hand; *i*, *M. pirloti* ♂, flat dentate spine from gnathopod 2, joint 5 (second spine in group of three on posterior margin distally); *j*, *M. finnarchicus* ♂, apex of long seta from uropod 3; *k*, *M. marinus* ♂, apex of long seta from peduncle of antenna 2; *l*, *M. marinus* ♀, apex of short seta from cluster on distal end of peduncle joint 2 of antenna 1; *m*, *M. pirloti* ♂, apex of long seta from palmar margin of gnathopod 2 hand (similar form on uropod 3, etc.); *n*, *M. pirloti* ♂, apex of long bifurcate seta from antenna 2 flagellum; *o*, *M. obtusatus* ♂, apex of long bifurcate seta from antenna 2 flagellum; *p*, *M. finnarchicus* ♂, spine from pereopod 5, joint 4 apex.

The brief account and illustrations (Text-fig. 11a-f) here given refer specifically to the setae developed in clusters along the inner border of antenna 2. These have a constant form in each species. The differences between the species are more apparent than may be suggested by the outline drawings.

In *stoerensis* (Text-fig. 11a) they are relatively short, being somewhat broad at the base and tapering gradually towards the apex. The apical pore is conspicuous and the extremity is distinctly minutely bulbous. More flexible than the other setae on the limb, they often assume a curved or sinuous shape in microscope mounts. Their form is thus simple, and proves to be the least specialized of the six species. They are also developed in fewer numbers than in the other species. A few apparently similar setae occur on the gnathopod hands, but none on uropod 3 (which is glabrous).

The male sensory seta of *finmarchicus* (Text-fig. 11b) is elongate and narrow, relatively simple in form, except that the apex, which tapers gradually, possesses a distinct, but very narrow, flange. These hairs are not so obviously distinguishable from certain other setae of antenna 2, but they are distinctly more flexible. They are developed in quite dense clusters. Setae which resemble them occur among the fringes of uropod 3.

In *obtusatus* (Text-fig. 11c) the setae are not so greatly differentiated from other types, possessing a distinct flange on their gradually tapering apex. They are long, with stout shafts, and are developed in moderate numbers. Some similar setae occur on the relatively sparsely haired uropod 3.

The setae in *marinus* (Text-fig. 11d) show a more distinctly narrowed apex, though the narrowing is not very abrupt. The shafts are rather broad, but not flattened. The setae are long, and arise in fairly dense clusters. Setae of a very similar type form a dense fringe along the inner border of uropod 3.

A still greater contrast between the male sensory setae and other types is found in *pirloiti*. The former (Text-fig. 11e), besides being less strongly chitinized and more flexible, have flattened shafts and are appreciably broader (compare Text-fig. 11e, n). At the apex the seta narrows abruptly, and a fine narrow flange is visible at the base of the attenuated apical portion. These setae arise in dense clusters. Similar setae, but narrower and less differentiated, occur in a few clusters on the hand of gnathopod 2, and plentifully on uropod 3, especially along the outer margin.

In *olivii* (Text-fig. 11f) these setae have a form resembling the above, except that the shafts are even broader, and the apices shorter. The similarity of the male sensory setae in *pirloiti* and *olivii* provides striking confirmation of the view that these two species are nearly related. In *olivii*, too, they are developed in dense tufts; but setae which in any way resemble them are lacking on uropod 3.

PLUMOSE SETAE. Long setae with feather-like processes are often developed on uropod 3, where they may (as in other *Gammarus*-forms) form the main

elements of the setal fringes. The extent to which they are developed in the different species is as follows.

In *marinus* none occur in the male, the relatively dense hair fringes being composed of setae of other types, but a few occur along the inner margin of the outer ramus in the female. In *obtusatus* (fringes sparse) and *stoerensis* (fringes altogether absent) they are lacking in both sexes. In *finmarchicus* a sparse row of plumose setae occurs along the inner margin of the outer ramus, each seta being associated with a separate cluster of non-plumose setae. In the two remaining species, *piriloti* and *olivii*, plumose setae form dense fringes, and occur on the short inner ramus as well as on the outer. In the former species, however, the fringe of plumose setae is situated only along the inner margin, whereas in the latter it extends around both margins.

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EXPLANATION OF PLATE IV.

Marinogammarus pirloti sp.n., adult male. Figures drawn from an adult male captured at Wembury Point, near Plymouth, 18. iii. 39. All figures, except fig. 3, reproduced at the same magnification of $\times 36$.

Fig. 1, antenna 1; fig. 2, antenna 2; fig. 3, calceolus and bifurcate seta from joint 3 of antenna 2 flagellum, $\times 62$; fig. 4, gnathopod 1; fig. 5, gnathopod 1, under surface of hand, showing the palmar margin and angle spines; fig. 6, gnathopod 2, with gill attached; fig. 7, gnathopod 2, under surface, showing the palmar margin and angle spines; fig. 8, peraeopod 1; fig. 9, peraeopod 2, with gill outlined; fig. 10, peraeopod 3; fig. 11, peraeopod 4; fig. 12, peraeopod 5; fig. 13, epimera of pleon-segments 1-3; fig. 14, uropod 1; fig. 15, uropod 2; fig. 16, uropod 3; fig. 17, telson, dorsal view.

POSTSCRIPT. For observations on the powers of osmotic regulation in *Marinogammarus obtusatus*, see Beadle and Cragg (1940). The same authors are publishing in the *Journal of Animal Ecology* further observations relating to some of their collections which we have determined and recorded under "material examined". Prof. A. D. Hobson is in possession of additional data on the habitats of examined material, some of which was collected by Dr E. A. T. Nicol.

