

The genus *Bathyporeia* Lindström, 1855, in western Europe (Crustacea: Amphipoda: Pontoporeiidae)

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The amphipod genus *Bathyporeia* Lindström, 1855, on the European Atlantic coasts is revised and new identification keys are provided. The importance of new characters such as the morphology of the first uropod is stressed. The following species are fully redescribed and illustrated: *B. elegans* Watkin, 1938, *B. gracilis* G.O. Sars, 1891, *B. guilliamsoniana* (Bate, 1857), *B. nana* Toulmond, 1966, *B. pelagica* (Bate, 1857), *B. pilosa* Lindström, 1855, *B. sarsi* Watkin, 1938, and *B. tenuipes* Meinert, 1877. *B. elegans* exhibits unusual variation, of which the taxonomical significance is still unclear. It has been observed for the first time that all species of the genus exhibit an unusual sexual dimorphism on the mandibular palp: in the adult males, the ventral border of the terminal article has a comb of stiff setae which is lacking in females and immature males. Furthermore, a locking system holding together the inner plates of the maxilliped is described and illustrated. A previously overlooked vestigial dactylus on the second and the fifth pereopod is described.

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1. Introduction

In his well-known monograph, Lincoln (1979) expressed the feeling that in the North East Atlantic area, there was scarcely a single amphipod species that was adequately described and defined at that time. Today, his statement remains largely true, although the difficulties with identification vary considerably from group to group. In this context, the genus *Bathyporeia* Lindström, 1855, of which a typical representative is illustrated on fig. 1, is certainly one of the most problematic taxa. This genus comprises many species, very closely related to each other, that exhibit considerable sexual dimorphism, allometric variation, and sometimes significant intraspecific variation. *B. nana* Toulmond, 1966 is the only species, that has been fully described and illustrated. Other species are known incompletely, by short descriptions and by semi-diagrammatic illustrations of some parts only. This situation is particularly deplorable since many species are common or even abundant, and therefore often present in the samples of ecologists working on the benthos of soft bottoms. Several benthos specialists, such as Junoy & Viéitez (1990), Cattrijse et al. (1993) and Ysebaert et al. (1998) report serious difficulties in identification. Misidentifications are probably not uncommon, as is the case for the material of Dörjes & Reineck (1977), that has been re-examined during the present study.

In the present paper, all species found in western Europe, from the North Cape to southern Spain are redescribed. This is the first paper in a world-scale revision of the genus *Bathyporeia*. Adult specimens are fully illustrated for the first time and new identification keys are provided. It is hoped that this work will facilitate their identification considerably, although *Bathyporeia* will undoubtedly remain a difficult genus. Unfortunately, some questions remain open concerning *B. elegans* Watkin, 1938, which exhibits considerable geographic variation.

2. Historical review

The history of the genus *Bathyporeia* is rather complicated, especially with regard to the period before Watkin's (1938) revision. For this reason, a detailed historical account is given here, the first part of it being largely a re-transcription of Watkin's excellent review.

The genus *Bathyporeia* was created by Lindström (1855) with the description of the type species of the genus: *Bathyporeia pilosa* Lindström, 1855, from specimens from the Baltic Sea.

Bate (1856; 1857a) described two further species, for which he erected a new genus, *Thersites* Bate, 1856: *Thersites pelagica* Bate, 1856 and *Thersites Guilliansoniana* Bate, 1857. Later, Bate (1857b) discovered he had overlooked Lindström's (1855) paper. He subsequently adopted the genus proposed by the Swedish naturalist (misspelling it as *Bathyporea*) but erroneously considered his species *Guilliansoniana* (spelled this time

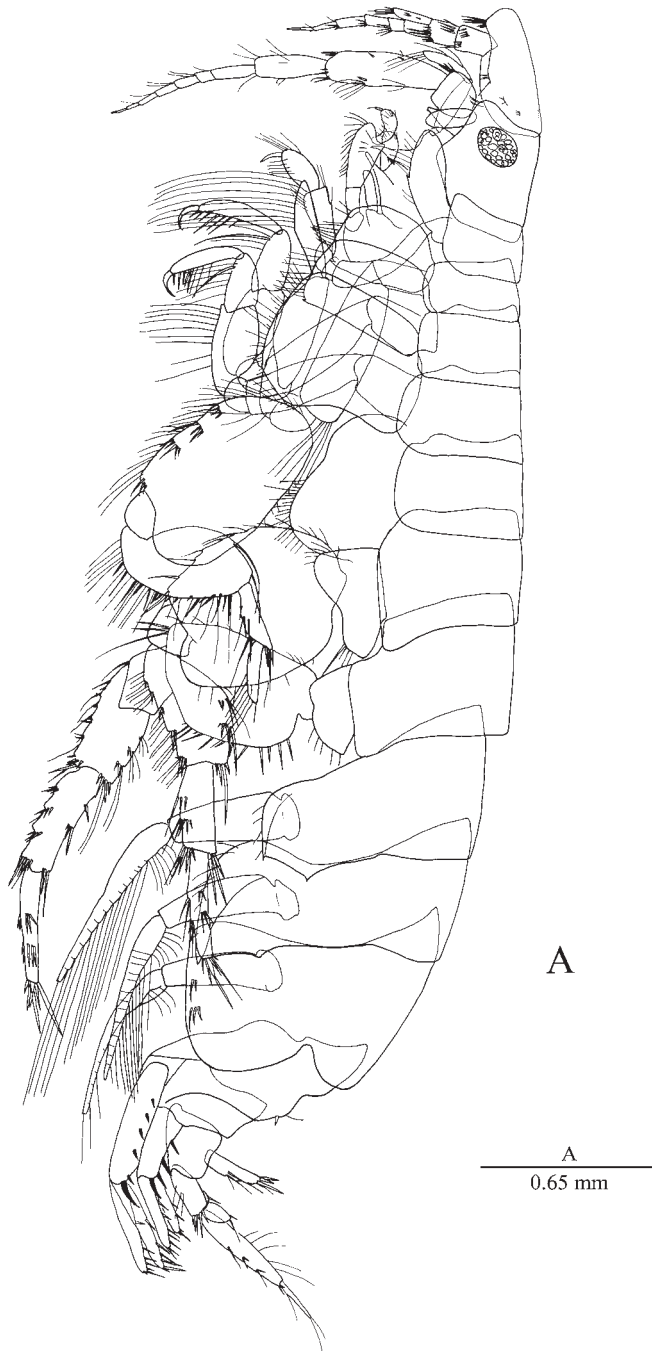


Fig. 1. *Bathyporeia elegans* Watkins, 1938 forma A, female, Grindøen, 23.viii.1884, TMU 1395. Complete animal. Composite drawing; mostly after an exuvium, except eye and third uropod: after another female mounted on the same slide.

as *Guilliamsonia*) a junior synonym of *B. pilosa*. Bate (1862) gave more detailed descriptions of his '*B. pilosa*' and *B. pelagica*, and described a further species, *B. Robertsonii*. His illustrations however are crude, inaccurate and very difficult to interpret. It should be noted that *Thersites* Bate, 1857 is a junior homonym of a mollusc genus. Bate and Westwood (1863) treated the three species *B. pelagica*, '*B. pilosa*' and *B. Robertsonii* again in their monograph of British sessile-eyed crustaceans.

Marcusen (1867: 359) described a new species from the Black Sea, *B. pontica*, in a minimalist diagnosis: "ähnlich der *B. Robertsonii* Sp. Bate, mit calceola am unteren Fühler, aber auch einer calceola am oberen."

Stebbing (1875) placed all West European species in synonymy, only recognizing the nominal species *B. pilosa* as a valid species. Meinert (1877) accepted Stebbing's point of view but described one further species: *B. tenuipes* Meinert, 1877. Blanc (1884) too accepted Stebbing's point of view. Later, Chevreux (1887) resurrected *B. Robertsonii* but suspected that *B. pilosa* and *B. pelagica* would indeed be identical.

Robertson (1888) considered *B. Robertsonii* a junior synonym of *B. pilosa*, but was inclined to believe that *B. pelagica* was a valid species. It is however doubtful that "his" *B. pelagica* specimens actually belong to that species, since his specimens were all subtidal.

Bonnier (1890) considered *B. pelagica* and *B. Robertsonii* as junior synonyms of *B. pilosa*.

In his famous 'Account of the Crustacea of Norway', G.O. Sars (1891) described and accurately illustrated five species occurring in Scandinavia, for which he used the following names: *B. gracilis* G.O. Sars, 1891, *B. norvegica* G.O. Sars, 1891, *B. pelagica*, *B. pilosa* and *B. Robertsonii*. He considered *B. tenuipes* a junior synonym of *B. pelagica*. Della Valle (1893) accepted *B. norvegica* as valid, but considered *B. pelagica*, *B. Robertsonii* and *B. gracilis* junior synonyms of *B. pilosa*. On the other hand, Scott (1893) recognized three species as occurring in the Firth of Forth: *B. norvegica*, *B. pelagica* and *B. robertsonii*, providing some illustrations of them. Walker (1895a) examined the material present in the British Museum, which presumably had been identified by Spence Bate. He made the following comments:

"*Bathyporeia pilosa* (Lindström).

Two tubes so labelled. Of these no. 50 contains two females of *B. norvegica* (Sars); the other (no. 85) contains eleven specimens, all of which have dark eyes; some have dorsal spines on the fourth pleon-segment, others have not; one (a large female) had a rudimentary tooth slightly in front of the rounded hind margin of the third pleon-segment.

Bathyporeia pelagica (Bate). One adult male, 5 millim. long.

This agrees with the form described by Sars under the above name. The eye is large and dark, but it is impossible to say what colour it was when fresh, as red eyes sometimes fade entirely in spirit and sometimes turn dark. It must be confessed that, of the five species of *Bathyporeia* given by Sars, only *B. norvegica* (Sars) seems to be distinct, owing to its having the hinder angle of the third pleon-segment produced to a point, instead of being rounded, as in the other species."

In a further paper, Walker (1895b) considered *B. pelagica*, *B. Robertsonii* and *B. gracilis* as junior synonyms of *B. pilosa*.

Hansen (1897: 120) considered that amongst the species recognized by G.O. Sars (1891), *B. norvegica* and *B. gracilis* were definitely good species, whilst he suspected

that *B. pelagica* and *B. Robertsonii* could be junior synonyms of *B. pilosa*. However he provisionally retained the species as valid.

As concerns *B. gracilis*, *B. norvegica*, *B. pelagica* and *B. Robertsoni*, Norman (1900) stated that he could not regard them as valid species. Norman (1905) considered *B. norvegica* a junior synonym of *B. guilliamsoniana* (for which he used the incorrect spelling *Guilliamsonii*). In the list of species in that paper, he kept *B. Robertsoni* and *B. pelagica* distinct from *B. Guilliamsonii* without comment.

Reibisch (1905) recognized 4 species, of which he gave a good descriptive and illustrated account: *B. norvegica* (actually *B. guilliamsoniana*), *B. pelagica* (actually *Bathyporeia elegans*), *B. gracilis* (actually *B. tenuipes*) and *B. pilosa*. He expressed doubts whether *B. pilosa* and *B. Robertsoni* are actually distinct species, but his drawing of a P5 of *B. pilosa* seems to be really based on that species. Reibisch (1905) suspected that *B. tenuipes*, then only known by a rudimentary description, could be a synonym of *B. pelagica*. The valuable paper of Reibisch (1905) has been largely ignored, even by Watkin (1938).

Stebbing (1906) recognized six species: *B. gracilis*, *B. norvegica*, *B. pelagica*, *B. pilosa*, *B. Robertsonii* and *B. lindströmi* Stebbing, 1906. Of the latter species, he had never seen specimens but based his description on Della Valle's (1893) account on Mediterranean '*B. pilosa*'.

Chevreur (1911) described a new species from Algeria, on the basis of males only: *Bathyporeia megalops*.

Chevreur & Fage (1925) recorded three species occurring along the coasts of France: *B. Guilliamsoniana*, *B. pelagica* and *B. Robertsoni*. The present re-examination of Chevreur's collection showed that many specimens were misidentified. Chevreur & Fage (1925) recorded *B. guilliamsoniana* in the Mediterranean for the first time. They also recorded *B. pelagica* from the Canary Islands and Dakar. These southern records of *B. pelagica*, which are also cited in Chevreur (1925), seem to be highly questionable, since I found no *B. pelagica* in the African *Bathyporeia* of the Chevreur's collection.

In his 'Danmarks Fauna', Stephensen (1928) recognized four species: *B. guilliamsoniana*, *B. pelagica*, *B. pilosa* and *B. robertsoni*.

As a lapsus, Crawford (1937) introduced the name *Bathyporeia elegans*, as "*Bathyporeia elegans* Sars", with brief morphological notes, for a species which he believed to be *B. gracilis* G.O. Sars, 1891, mixing the author's name of *B. gracilis* G.O. Sars, 1891 with the specific (and then unpublished) name of *B. elegans* Watkin, 1938. This thorny nomenclatural problem will be discussed in the present account of *B. elegans* Watkin, 1938.

Watkin (1938) largely clarified the previous taxonomic chaos, recognizing 7 species: *B. elegans*, *B. gracilis*, *B. guilliamsonian*, *B. pelagica*, *B. pilosa*, *B. sarsi* and *B. tenuipes*. He questioned the validity of *B. gracilis* and considered *B. lindstromi* a problematic species, since he had no suitable material of that species at his disposition. Finally, he overlooked *B. megalops*.

Watkin (1938) accepted Walker's (1895a) opinion that *B. norvegica* is a junior synonym of *B. guilliamsoniana* and stated that it was impossible to be certain if the two female specimens in tube no. 50 of Bate's collection are the type specimens. He re-examined the holotype of *B. pelagica* (Bate, 1856), and based the redescription of that species on it, "as far as possible without dissection".

He established a new species for the '*B. pelagica*' of G.O. Sars (1891), naming it *Bathy-*

poreia elegans Watkin, 1938. The syntypes were collected from the Ognebugt off Jæderen, southwestern Norway. He also recorded specimens from Denmark and the British Isles, which he identified as belonging to this new species. He considered "*Bathyporeia elegans* Sars" of Crawford (1937) to be a junior synonym of *B. tenuipes* Meinert, 1877. However, it is not clear if he has actually seen Crawford's specimens.

He re-examined the holotype of *B. tenuipes* Meinert, 1877. The description of the species by Meinert is poor and without illustrations. Watkin showed that *B. tenuipes* is a clearly distinct species.

Of the two syntypes of *B. gracilis* G.O. Sars, 1891, Watkin re-examined the male, but was unable to find the female, which is presumably lost. He pointed out the affinities of this rare species with *B. tenuipes*, and even considered that both species could possibly be identical.

He indicated that the holotype of *B. pilosa*, which was collected in the Baltic sea, was no longer extant, however, he had the opportunity to examine fresh Baltic specimens, as well as specimens from the British Isles. He also stated that the poorly described type material of *B. Robertsonii* Bate, 1862 was no longer extant (which is actually incorrect) but he made extensive collections at Bate's type station, the Isle of Cumbrae. He found *B. pilosa* in large numbers around this island, while he failed to find any *B. sarsi* there. Therefore, he concluded that *B. Robertsonii* should be considered a junior synonym of *B. pilosa*.

He described a new species, *Bathyporeia sarsi* after G.O. Sars' (1891) material of *B. Robertsonii*, which proved to be erroneously identified. As concerns the type material of his new species, he made the following statement: "Type specimens, three adult males, two of which are extant, in the Zoological Museum, Oslo, Locality (Sars, 1891, p. 132) Sorvaer [sic], west coast of Finmark, northern Norway." Watkin (1938) also recorded this species from various localities in Northwest Europe.

Today most of the taxonomical and nomenclatural statements of Watkin (1938) are still correct. However, his descriptions are very incomplete and his illustrations are small and very schematic, and they concern only a very limited number of appendages. Many important characters have been overlooked, and the intraspecific variability has scarcely been examined.

Schellenberg (1942) and Gurjanova (1951) accepted the views of Watkin (1938) and reprinted part of his figures.

The genus *Bathyporeia* was only known from the northeastern Atlantic, the Mediterranean and the Black Sea, until Shoemaker (1949) described a highly characteristic species from the Atlantic coast of North America: *B. quoddyensis*.

K.H. Barnard (1951) recorded *Bathyporeia gracilis* in a list of additions to the South African amphipod fauna, without any description or comment.

Toulmond (1966) gave a good description accompanied by excellent figures of an additional northwestern European species, *Bathyporeia nana*. That species has probably been overlooked by previous carcinologists due to its very small size and perhaps its similarity with *B. elegans*.

Vader (1970) examined a few additional specimens of *B. gracilis* and was able to confirm the validity of that species. He gave a new descriptive account of that species. The species appears to be quite rare. He also stated that a study of a number of samples of South African *Bathyporeia*, including the material recorded by K.H. Barnard (1951),

had shown that this material does not belong to *B. gracilis*, but to a species close to, though probably not identical with *B. tenuipes*. So far, that species has not been named.

Bousfield (1973) described a second Western Atlantic species, which occurs along the East coast of the USA: *B. parkeri*. That species shares several unusual characters with *B. quoddyensis*, which was also studied by Bousfield (1973).

Bellan-Santini (1973) described two new species from the Mediterranean coasts of France: *B. phaiophthalma* and *B. leucophthalma*.

Griffiths (1974a, 1974b, 1975, 1976) briefly recorded again the undescribed South African *Bathyporeia* referred to by Vader (1970), as *Bathyporeia* sp.

In his monograph of British marine amphipods, Lincoln (1979) briefly described *B. elegans*, *B. gracilis*, *B. guilliamsoniana*, *B. nana*, *B. pelagica*, *B. pilosa*, *B. sarsi*, and *B. tenuipes*. He gave figures for each species, but only a few appendages and other bodyparts of each species were illustrated. His figures are original, except those for *B. gracilis*, which were copied from G.O. Sars (1891).

Barclay (1982) re-examined the syntypes of *B. Robertsonii* Bate, 1862, which had been deposited in the British Museum (Natural History), but had lain unregistered until 1952. He confirmed Watkin's (1938) opinion (who did not have the opportunity to examine them and believed them to be lost) that it was indeed a junior synonym of *B. pilosa*.

Bellan-Santini & Vader (1988) described four new species from the Mediterranean Sea: *B. pseudopelagica*, *B. sardoa*, *B. sophiae* and *B. sunnivae*. They also claimed to have found the following species in the Mediterranean: *B. guilliamsoniana*, *B. leucophthalma*, *B. lindstromi*, *B. megalops*, *B. nana*, and *B. phaiophthalma*.

Finally, Bellan-Santini (1989) redescribed and illustrated all the Mediterranean species known so far, for which she used the following names: *B. guilliamsoniana*, *B. leucophthalma*, *B. lindstromi*, *B. megalops*, *B. nana*, *B. phaiophthalma*, *B. pseudopelagica*, *B. sardoa*, *B. sophiae* and *B. sunnivae*.

3. Ecology and biology

Although this paper is devoted to the systematics of the genus *Bathyporeia*, it seems useful to give a brief review of their ecology and biology, which have been the object of detailed studies.

All the species of the genus are burrowing animals confined to sandy bottoms (Toulmond, 1964). According to Toulmond, they have a definitive preference for very fine well-sorted sands, with an unimodal curve with a maximum between 90 and 200 μ , which can sometimes be fairly muddy and occasionally reductive, but always with a high percentage of carbonate particles. According to Vader (1965) however, they can be found in slightly coarser sediments, and are not found in sediments with a silt content of more than 5-10%, with the exception of *B. pilosa* which has been recorded in sediment with as much as 25% silt. About 90% of the specimens are found in the first 5 centimetres of the sand, and they have not been recorded deeper than 12 centimetres in the sediment (Salvat, 1967).

Bathyporeia spp. exhibit a well marked zonation pattern (Watkin, 1942; Colman & Segrove, 1955a; Toulmond, 1964; Vader, 1965, 1966; Salvat, 1967), which is related to

the physiological resistance of the different species (McGrorty, 1971). On an exposed sandy beach, *B. pilosa* is found on the highest part of the shore. It is gradually replaced by *B. sarsi* which is itself replaced by *B. pelagica*. On the lowest parts of the shore, *B. pelagica* is replaced by *B. elegans*, *B. nana* and *B. guilliamsoniana*. *B. elegans* and *B. guilliamsoniana* are predominantly subtidal species extending their distribution to the lowest part of the shore (Colman & Segrove, 1955a). These six species are not always found together on every shore. Considerable variation in the zonation pattern has been recorded, depending on the granulometry, the salinity conditions, the exposure of the shore (Vader, 1965, 1966; Fish & Preece, 1970a), and of course the geographical distribution of the species. Furthermore, some up- and down-shore migrations have been observed during the year (Ladle, 1975). *B. tenuipes* has been recorded on the shore only once (Faure, 1969), whilst the rare *B. gracilis* has been recorded below tide marks only. *B. pilosa* and *B. sarsi*, which are restricted to the shore on open coasts, also occur subtidally in estuarine conditions.

All species may be found in completely marine habitats, but only *B. pelagica*, *B. elegans*, *B. sarsi* and *B. pilosa* exhibit a certain rate of euryhalinity, with *B. pelagica* tolerating seawater of moderately low salinity and *B. pilosa* thriving in truly brackish waters (Vader, 1965, 1966).

Nicolaisen & Kanneworff (1969) have published a detailed account, with excellent figures, on the burrowing behaviour of *Bathyporeia sarsi* and *B. pilosa* and their position at rest in the sand. It is worthwhile to cite their description of that position, since it helps to understand why these organisms have such an unusual and modified morphology. "The animal is lying upside down in a small cavity, the roof of which it supports by means of the second pereopods and the first and second uropods [which are then anteriorly directed]. The only connection to the water above the sand is through the interstices as no tube is made. The apex of each second pereopod is surrounded by a whorl of long bristles and at their posterior margins the merus and carpus carry long bristles which assist in supporting the roof. The abdomen is bent upwards and somewhat forwards and the first and second uropods are directed forwards so as almost to reach the bristle whorls of the second pereopods. The first and second uropods are supplied with movable spines (...) along their margins. The spines are spread out [upwards] when the uropods are pressed against the roof of the burrow. The third uropods, which are used in swimming only, are directed backwards [at 180° from the first two pairs of uropods]. The sides of the cavity are guarded by the limbs and the coxal and epimeral plates." In their figure 2, they also show the last four articles of P3-P4 to be laterally directed.

The Danish authors indicate that the spines on the pereopods play a major role in the movements of the animal in the sediment. Friction against sand grains causes the spines to rise when the limbs move backwards, whilst they are pressed against the limb during the forward movement. Spines and bristles with this function both aid in carrying sand grains backwards and in pushing the body forwards. Nicolaisen & Kanneworff (1969) also give a detailed account of the digging and feeding process of the animals, and indicate that they are eating particles adhering on sand grains but not the ciliates moving in the sand interstices. They observed that stomach contents consist of unidentifiable matter and crushed diatom frustules. Wolff (1973) concludes that they should be considered as selective deposit-feeders.

The *Bathyporeia*, and mainly the adults (especially the adult males), are known for swimming at night in the water column (Watkin, 1939b; Colman & Segrove, 1955b; Preece, 1971b; Dauvin & Zouhiri, 1996). During this swimming stage, their zonation pattern remains unaltered (Watkin, 1939b, 1941; Colman & Segrove, 1955b). In tidal waters, the swimming rhythm exhibits a semi-lunar periodicity (Preece, 1971b), swimming specimens being much more frequently observed just before the full and the new moon, i.e. close to spring tides (Watkin, 1939b). This periodicity is correlated with the embryonic development that often takes about 15 days in summer, the advanced embryonic stages having their maximum frequency at about the time of spring tide (Fish, 1975). However, such a regular periodicity is not observed in all populations (Mettam, 1989). Unlike *Haustorius arenarius* (Slabber, 1769), *Bathyporeia* specimens swim in a normal position with their back upwards (Watkin, 1939a).

Each female lays several successive egg clutches and has several fertile intermoult, which in some species can be interrupted by a period of sexual rest. In this period the oostegites lose their setae (Salvat, 1967). The mature males of most *Bathyporeia* species have much longer antennae than females and immature males. This is however not the case in *B. gracilis* and in the Northwest Atlantic species *B. parkeri*, where the antennae have a similar size in the adults of both sexes (personal observation). It is apparently not known whether the mature males of the species with long antennae have one or several successive fertile intermoult. Bonnier (1890) suspected that the males with long antennae could regress to their previous condition with short antennae after the reproduction period, since there is a considerable overlap in size of males with short and long antennae. This however is speculation, as it has never been demonstrated experimentally. Testicles with ripe spermatozooids are only present in males with long antennae and in those males that are at the very end of the intermoult preceding that stage (Bonnier, 1890). On the other hand, an original observation is available for one species with short-antennated males: *B. parkeri*. A male of that species examined by the present author and which was already mature (it had calceoli on antennae) was obviously preparing an extra moult. Indeed the new inner and outer plates of the maxilliped with well developed spines and setae could be observed by transparency inside the old one. So, in *B. parkeri*, the males continue to moult after maturity, at least in some cases. Maybe both sexes continue to moult after maturity in species with short-antennated males, whilst post-puberal moults are restricted to females in species with long-antennated males.

In the Straits of Dover, there are two generations per year, at least for *B. pelagica*, *B. pilosa* and *B. sarsi* (see Salvat, 1967), while there is often only one generation per year farther north (Ladle, 1975; Köhn & Sammour, 1990; Persson, 1982). In *B. pelagica*, the minimal and average size of ovigerous females exhibits some variation around the year but this is not very important (Salvat, 1967). On the other hand, the same author indicates that at equal size, there is considerable temporal variation in the average number of eggs per egg batch in that species, the number of eggs per batch being twice as high in May as in February.

Bathyporeia spp. are occasionally parasitized by the nicothoid (previously choniostomatid) copepod *Sphaeronella paradoxa* Hansen, 1897, *B. pelagica* and *B. sarsi* being the most commonly infested species (Hamond, 1973). The parasites look like little spherules and are found in the marsupium of the females (Hansen, 1897; Scott, 1904; Hamond,

1967, 1973; Costello & Myers, 1989; Gotto, 1993). Normally, *S. paradoxa* seems to inhibit the host from producing eggs or embryos, although a female *B. sarsi* with both her own eggs and a *S. paradoxa* in the brood pouch has been recorded (Hamond, 1973). Laboratory observations indicate that the newly hatched copepodites of *S. paradoxa* immediately swim to *Bathyporeia sarsi* and cling to their gills (Hamond, 1973). The same author thinks that infection of new hosts takes place when *B. sarsi* come out of the sand in swarms shortly after it has been flooded by the rising tide.

Ramified colonies of peritrich ciliates are often observed on the appendages of *Bathyporeia* species, sometimes in large number (personal observations), the nature of this association however, is not yet known. Associations with ciliates have apparently previously been unrecorded, since Fernandez-Leborans & Tato-Porto (2000a, 2000b) and Fernandez-Leborans (2001) do not record the genus *Bathyporeia* in their lists of crustaceans with epibiont ciliates.

4. Material and methods

4.1. Dissection, microscopical preparations, illustrations and descriptions

So far, most species of the genus *Bathyporeia* have never been properly described and illustrated, therefore causing considerable problems for benthos ecologists, who regularly have to identify them. As a cladistic analysis of the genus will probably be carried out in the near future, great care has been taken to detect previously overlooked characters, and the descriptions have been made as precise as possible. For each species, all parts of the adult female have been illustrated, as well as some parts of the male, especially those characters that are sexually dimorphic. In some species, figures of immature or not fully grown animals have been added. In descriptions, if not stated otherwise, the ratios of appendages and the number of setae on coxae only concern mature females. Males are usually slightly more slender and less setose than females.

Examination in toto.— Complete animals in glycerine were examined under a Leitz Dialux microscope, in a hollow microscopic slide of 76 × 26 mm. Drawings of the anterior part of the head with the eye and the posterior part of the body were carried out with a Reichert camera lucida mounted on the microscope. Special care has been given to the illustrations of the dorsal and the ventrolateral part of the first urosomite and the outer dorsal spines of the peduncle of the first uropod. In a few cases shrinkage of pereopods occurred when specimens were transferred directly from alcohol to glycerine. It is advisable to put specimens in a mixture of alcohol and glycerine first, before transferring them to pure glycerine.

Dissection.— Dissection has been carried out in glycerine with fine forceps and mounted needles under an Aus Iena Technival II dissecting microscope using direct and transmitted light. The abdomen is separated from the thorax. The somites bearing the epimeral plates are first dissected: they are disarticulated, the pleopods (unimportant) are removed, and eventually the right and left epimeral plates are separated (a rather delicate operation). Then the dorsal part of the first urosomite is carefully excised, since it comprises important features. Afterwards, the third uropods are removed; they are always very easy to separate and are already lost in many animals.

Then the telson is removed together with the third urosomite. These two elements should not be separated from each other. Finally, the second urosomite and the first urosomite (previously deprived of its dorsal part) are separated from each other. Great care should be taken in order to let the first and second uropods stay attached to the remains of their respective urosomites. This way the left and right uropods attached to the remains of the urosomite form a V-shaped structure, which normally keeps a stable and adequate position when put between slide and cover slide. It is then possible to carry out accurate standardized drawings in dorsal view of these very important appendages, which so far have not attracted enough attention from carcinologists. For the dissection of the pereopods, it is easiest to disarticulate their whole somite first, rather than immediately dissecting them (the risk of damage to the gills and oostegites is reduced this way). The thoracic somites can be discarded after dissection as they don't contain specific characters. The dissection of the first thoracic somite and pereopod is more delicate due to their small size and can be delayed until the head is dissected. As concerns the head, the antennae are first removed taking care in avoiding contact with the fragile mandibular palps situated between the antennae. The mouthparts are removed one by one. The left and right half of the maxilliped should not be separated. The proper removal of the lips is fairly difficult. It is impossible to prevent the loss of eyes during the dissection of the cephalic appendages.

Mounting of the slides.— The appendages are first examined (and illustrated) in glycerine on microscopic slides of 76×35 mm. On such wide slides, the risk of glycerine seeping out of the slide is reduced. Then the pieces are permanently mounted in Faure's liquid (Reyne, 1949) on classical 76×26 mm microscopic slides.

Drawings.— The antennae are always shown from the outer side (this is not always the case in drawings in the literature). It has not been possible to show the mandible itself in a standardized orientation since the structure is inflexible. This however, has no negative consequences, since its morphology is quite constant in European species. The mandibular palp however, should be shown in a flattened position to depict the actual width differences of its second article, avoiding orientation artefacts. It has not been possible to show the palp of the first maxilla in a standardized way and the apparent differences between the drawings are artefactual.

As concerns the palp of the maxilliped, the terminal crown of setae of the third article is not shown on the detailed illustrations. Similarly, the apical and marginal setae of the second article of the palp have been omitted. Only the important setae are illustrated in a standardized and precise manner this way.

The pereopods and the coxal plates are shown from their outer side. The mesial side of the basis and ischium of P7 too is illustrated, since it exhibits some interesting features. Note that the surface setae of the coxae 1-4 always arise from the mesial side (many illustration in the literature erroneously suggest the contrary). Similarly, in many previously published figures, a row of setae is shown on the surface of the basis of P6. Such a row indeed exists but it is present on the mesial side, and is therefore not illustrated here. Note that the upper border of the coxal plates (where they articulate with the carapace) is difficult to see and that the drawings of that connective area are not always perfectly accurate.

As it has not been possible to draw the mesial ornamentation in a precise and standardized way, only the spines/setae of the outer side of the propodus P3-P4 have been

illustrated. In order to simplify the drawing, only one carpal structure, a special long robust spine which is here named the 'carpal fang' (see next section), has been illustrated. Great care has been given to illustrate the uropods in a standardized dorsal view, since these appendages are often illustrated in inadequate orientations in literature.

The logical succession of the appendages on the plates has not always been respected, in order to optimise the place available.

Descriptive process.— Complete illustrations based on the examination of a limited number of animals only has been carried out first (59 plates). Afterwards, a preliminary description has been written for each species on the basis of these illustrations. Then, the variations in each species have been scrutinized by the examination of all specimens available, 17 further plates have been drawn and the descriptions expanded.

4.2. Terminology and abbreviations

The general terminology of amphipod morphology can be found in various handbooks, such as Lincoln (1979) and Bellan-Santini (1999) and will not be repeated here.

For the definition of setae, setules, spines and teeth, a strictly practical terminology has been used in the descriptions. The term 'tooth' is used for non-articulate acute protrusions of coxae and epimeral plates. The terms spines and setae are used to designate articulate ornamentations of the body and appendages, the robust ones being called spines, the slender ones setae. Actually, the concept of 'spine' in the present paper corresponds to those of 'cuspidate and conate setae' of Watling (1989). On the dorsal distal part of the merus of P5 and on the posterior border of the basis of P7, the same homologous structure is sometimes called seta and sometimes spine, depending on its robustness. The term 'setulose setae' is used for setae with lateral ornamentations (setules), the term 'plumose setae' for those setae which are really feather-shaped, and the term 'pappose setae' for those setae with setules arranged in various planes. The term 'setulose setae' is more general, especially applying to setae with few setules. The term 'plumodenticulate setae' is used for the posterodistal seta(e) of the merus of P5, which are proximally setulose and distally denticulate. The term 'setule' is used in three cases: 1) for the lateral ornamentation of plumose, pappose or setulose setae, 2) for the upper branch of the tip of the carpal fang, and 3) for some very short setae. In the mouthparts, the following kinds of spines are recognized: nodular spines (broad and more or less elliptic articulate structures), 'fang-shaped' spines (long, slightly flattened, slightly curved, acute-tipped articulate structures), curved conical spines (curved conical articulate structures) and comb-like cuspidate spines (strong articulate structures with a very strong, comb-like denticulation).

The 'pseudorostrum' is the first article of the peduncle of the first antenna, which is overdeveloped in the genus *Bathyporeia*. It exhibits various groups of spines and setae of which two terms are used in the descriptions: the 'proximoventral plumose setae' and the 'apical spines'. The proximoventral plumose setae are arranged in a longitudinal row arising from the proximal part of the ventral side of the pseudorostrum; this row is occasionally reduced to a unique seta. The apical spines are a group of long and strong spines on the ventral side of the tip of the pseudorostrum.

The nomenclature of Lowry & Stoddart (1992) and Berge (2001) has been adopted

for the spines on the outer plate of the first maxilla. These authors recognized two rows of 'spine-teeth' (ST) in a crown arrangement.

The anterior setae of coxa 1 are the marginal setae of the ventrodistal border of the first coxal plate. This border has an oblique orientation and is anterior to the ventral tooth or notch of the coxal plate, when present.

The 'carpal fang' is a distinctive, long and very robust spine arising from the posterior border of the carpus of the third and fourth pereopods. Under the light microscope, its tip may appear as entire or bifid, depending on the species. Actually, it probably always consists of 2 distal elements, but these can be completely or nearly fused.

On the large and elliptic posterior border of the fifth pereopod two groups of setae are situated (each can be reduced to a single seta), the 'posteromedian seta group' on the middle of the border, and the 'posterodistal seta group' distally.

In the genus *Bathyporeia*, the posterior part of the body is very complex and could be a source of confusion. Its morphology is therefore illustrated in figure 2, with detailed explanations.

Most measurements taken to calculate the ratios of the appendages are illustrated on fig. 3. These ratios should be considered approximations only, as they are dependent on the orientation of the appendages on the microscopical preparations, which is never exactly the same.

Abbreviations

A1:	first antenna (antennula)
A2:	second antenna (antenna)
Coxa 1-7:	coxal plates of the first to seventh pereopods
Ep1-Ep3:	first to third epimeral plates
Md:	mandible
Mx1:	first maxilla (maxillula)
Mx2:	second maxilla (maxilla)
Mxp:	maxilliped
P1:	first pereopod (first gnathopod)
P2:	second pereopod (second gnathopod)
P3-P7:	third to seventh pereopods
U1-U3:	first to third uropods
Ur1:	dorsal part of the first urosomite (fourth pleosomite)
BM:	The Natural History Museum, London (previously British Museum Natural History))
DM:	Dublin Museum
MNHN:	Muséum National d'Histoire Naturelle, Paris
NIOO-KNAW (CEMO):	Netherlands Institute of Ecology, Centre for Estuarine and Marine Ecology, Yerseke
NMWZ:	National Museum of Wales, Cardiff
OUMNH:	Oxford University Museum of Natural History
RMNH:	Naturalis - Nationaal Natuurhistorisch Museum, Leiden (previously Rijksmuseum van Natuurlijke Historie, Leiden)
RUG:	Rijksuniversiteit, Gent

TMU: Tromsø Museum
 ZMA: Zoölogisch Museum, Amsterdam
 ZMO: Zoologisk Museum, Oslo

4.3. Practical recommendations for preservation and identification

First of all, the specimens should be properly fixed, if possible in ethanol 70% (or preferably 96-100% for DNA sequencing) and care should be given to avoid the introduction of dirt in the vials. Identifications becomes considerably more difficult and time consuming when specimens are distorted or when particles of dirt are glued on them. Distortion not only makes some characters impossible to observe, but often induce artefacts in the shape of the pseudorostrum. Formaline fixed specimens are not suitable for DNA sequencing.

In most cases, identification is possible by careful examination of the whole animal using a dissecting microscope under a magnification of 50 ×, with both direct and transmitted light. In the case of small-sized animals (especially for specimens thought to belong to *B. nana*), examination in glycerine in a hollow slide under a high power microscope should be carried out.

Two or more species often co-occur in the same sample. The sex and the stage of the animals should be noticed, since sexual dimorphism and allometric variations are considerable. Note that in some species, adulthood may be reached in a fairly wide range of sizes, and females may spawn during several successive intermoult. Females can be easily recognized by the occurrence of oostegites and by the spines on the major flagellum of the first antenna (lacking in the males) and fewer articles of this flagellum than in males. In most species, the second antennae in males have many more articles than in the females, and in adult males, the second antennae are usually much longer than in females. The ultimate article of the mandibular palp, usually visible without dissection, is also sexually dimorphic in adults: it has a ventral comb of stiff setae in the adult male, which is lacking in the female. Spines of the exopod of the first uropod restricted to the distal part of the exopod a clear sign that the specimen is not fully grown. In immature males, the first articles of the flagellum of the second antennae are much broader than long (often discoid), whilst they are as long as, or longer than broad in adult males.

The ratios and the number of spines and setae indicated in this paper should not be considered absolute as a limited number of specimens has been examined or measured. The numbers given should be considered indicative of the usual range of variation. Number of spines and setae dramatically increase with size. The descriptions are based on adults only if not stated otherwise. The identification of immature specimens however, should not be too problematic.

Too much importance has been attributed to the shape of the tip of the first article of the peduncle of the first antenna (pseudorostrum) in previous literature. Although the shape has some taxonomical value, individual variations can be substantial in some species. Furthermore, in a few species, such as *B. sarsi*, the structure exhibits significant sexual dimorphism. Finally, as stated above, if specimens have not been properly fixed, the pseudorostrum can exhibit misleading distortions.

It should be realized that some structures may be rubbed off, including the dorsal ornamentation of the first urosomite.

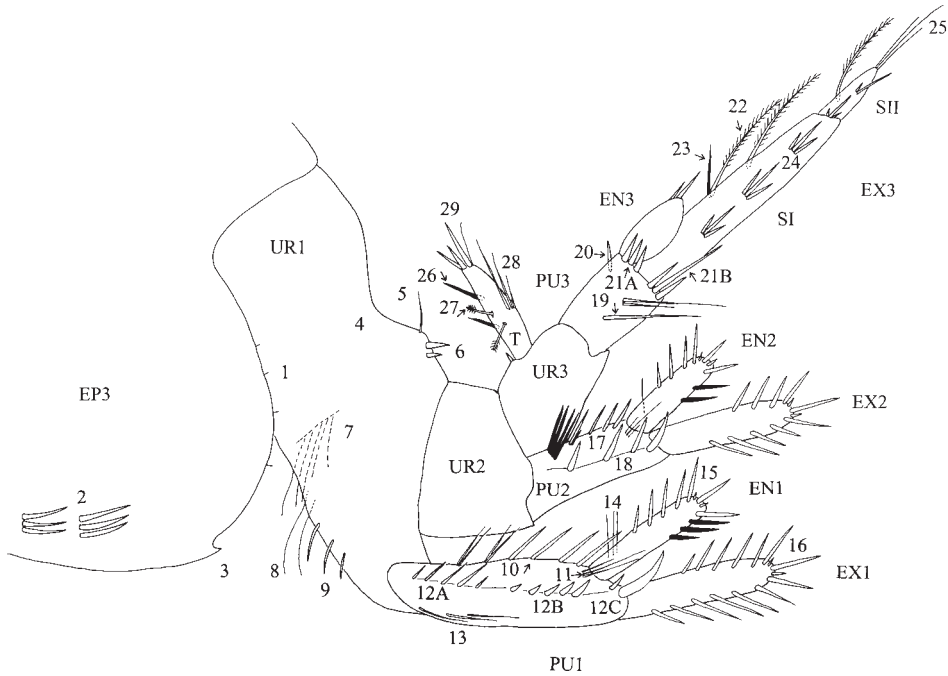


Fig. 2. *Bathyporeia* species. Schematic view of the posterior part of body. In real specimens, some parts overlap, and the orientation of the first two uropods is somewhat different (the endopod and the exopod of the first two uropods have here been twisted to show their dorsal side). EP3, third epimeral plate: 1, posterior setules; 2, transverse rows of spines; 3, posterior tooth (not always present). UR1, first urosomite: 4, dorsal depression of urosomite; 5, anteriorly directed dorsal seta (always present); 6, posteriorly directed dorsal spines (not always present); 7, sternal transverse row of setae, seen by transparency; 8, slender ventrolateral setae arising from the mesial side; 9, strong ventrolateral setae arising from outer side (not always present). PU1, peduncle of first uropod: 10, dorso-mesial spines/setae; 11, central group of long setae; 12A-C, outer dorsal spines: 12A, proximal slender spines (not always present); 12B, strong spines (may be present all along the peduncle when the proximal slender spines are absent); 12C, small and large strong distal spines; 13, ventrolateral strong setae. EN1, Endopod of first uropod.- 14, ventromesial setae; 15, dorsal spines (those in black not always present). EX1, Exopod of first uropod: 16, dorsal spines (often all or almost all aggregated near the tip in immatures). UR2, second urosomite. PU2, peduncle of second uropod: 17, dorso-mesial spines/setae (may be either in transverse rows: in black or in groups of 1 or 2); 18, outer dorsal spines. EN2, endopod of second uropod (idem as EN1). EX2, exopod of second uropod (idem as EX1). UR3, third urosomite (with one or several dorsal distal spinules). PU3, peduncle of third uropod: 19, outer setae; 20, mesial spine(s); 21A, dorsal distal spines; 21B, ventral distal spines (the dorsal and the ventral groups can merge in some species). EN3, endopod of third uropod. EX3, exopod of third uropod: SI, first article; SII, second article:- 22, mesial setae (laterally directed, usually but not always plumose); 23, accessory spines, in black (obliquely pointing upwards; not always present); 24, groups of outer spines; 25, distal setae. T, Telson: 26, mesial spines, in black (so far only known in the American species *B. quoddyensis*); 27, dorsal setae; 28, outer spines/setae; 29 distal spines/setae.

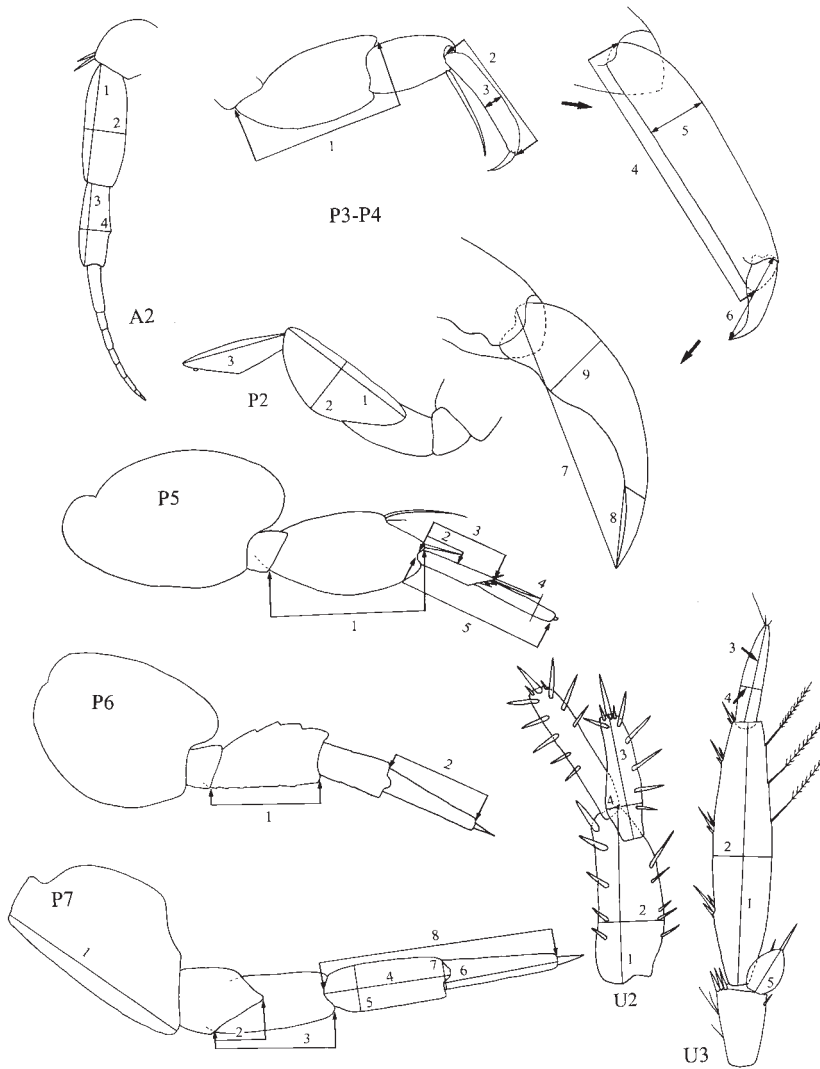


Fig. 3. *Bathyporeia* species. Most important lengths and widths used for the ratios of appendages. A2, second antenna: 1, length of fourth article; 2, width of fourth article; 3, length of fifth article; 4, width of fifth article. P2, second pereopod: 1, length of carpus; 2, width of carpus; 3, length of propodus. P3-P4, third and fourth pereopods: 1, length of merus; 2, length of propodus; 3, width of propodus; 4, length of propodus; 5, width of propodus; 6, 7, length of dactylus; 8, length of unguis; 9, width of dactylus. P5, fifth pereopod: 1, length of merus; 2, extension of dorsal distal spine/seta of merus; 3, length of carpus; 4, relationship between length of longest dorsal carpal spine / length of propodus; 5, length of carpus + propodus. P6, sixth pereopod: 1, anterior length of merus; 2, length of propodus. P7, seventh pereopod: 1, length of basis; 2, extension of ischium on merus; 3, length of merus; 4, length of carpus; 5, width of carpus; 6, length of propodus; 7, width of propodus; 8, length of carpus + propodus. U2, second uropod: 1, length of peduncle; 2, width of peduncle; 3, length of endopod; 4, width of endopod. U3, third uropod: 1, length of second article of exopod; 2, width of second article; 3, length of first article; 4, width of first article; 5, length of endopod.

5. Systematic account

5.1. Genus *Bathyporeia* Lindström, 1855

Bathyporeia Lindström, 1855: 59; Bruzelius, 1859: 90; Bate, 1862: 172; Bate & Westwood, 1862: 302; Boeck, 1876: 208; Blanc, 1884: 61; Stebbing, 1888: 286; G.O. Sars, 1891: 127; Della Valle, 1893: 751; Stebbing, 1906: 119; Chevreux & Fage, 1925: 91; Stephensen, 1928: 129; Stephensen, 1929: 82; Watkin, 1938: 214; Gurjanova, 1951: 335; J.L. Barnard, 1969: 254; Bousfield, 1973: 104; Lincoln, 1979: 314; J.L. Barnard & C.M. Barnard, 1983: 98, 567; Bellan-Santini, 1989: 365; Withers, 1990: 445.

Thersites Bate, 1856: 59 (nomen nudum); Bate, 1857a: 146 (Non *Thersites* L. Pfeiffer, 1855 = Mollusca).

Bathyporeia Bate 1857b: 271 (lapsus for *Bathyporeia*).

Systematic position.— Order Amphipoda Latreille, 1816, suborder Gammaridea Latreille, 1802, family Pontoporeiidae Dana, 1853.

Type species.— *Bathyporeia pilosa* Lindström, 1855.

Description.— Rostrum obsolete. Anterior border of head weakly concave. Lateral lobes of head obsolete; postantennal sinus replaced by a faint concavity; ventral part of head weakly concave.

Ommatidia usually present; if absent, outline of eye remaining distinct. Eye more or less elliptic, sometimes vaguely reniform, much bigger in male than in female.

First article of peduncle of A1 (pseudorostrum) considerably expanded in vertical axis, subrectangular to subelliptic, with different kinds of spines and setae. Dorsoproximal row of tiny spinules or papillae in shallow longitudinal groove. Ventroapical group of opaque long robust spines (apical spines). Outer row of long narrow acute-tipped opaque and usually non-setulose spiniform setae (anteroventral spiniform setae) proximal to articulation with second article. One fairly short blunt-tipped transparent pappose seta present at anterior part of that row; similar transparent pappose setae of different sizes occurring more ventrally in unordered disposition (anteroventral blunt setae). Longitudinal row of long plumose setae ventroproximally, sometimes reduced to a single seta (proximoventral plumose setae). Two longitudinal rows of about 3 tiny robust setae (anterior and posterior short setae) above proximoventral plumose setae. Anterior short setae all transparent. Posterior short setae normally include 2 transparent and one opaque setae.

Second article of A1 peduncle articulated with ventral part of first article (geniculate articulation). Second and third articles of A1 peduncle robust, similar-sized, with distal long spines. Major flagellum with similar spines only in female, with many aesthetascs in male (and calceoli in mature males); number of articles higher in males than in females. Accessory flagellum 2-articulate; first article spinose, much longer than second.

A2 longer than A1. Peduncle slightly longer than flagellum in females, shorter than flagellum in males of most species (subequal in *B. gracilis* and some non-European species such as *B. parkeri*). Fourth article longer than fifth. Flagellum with calceoli in adult males. Flagellum usually with much higher number of articles in male than in female; articles in immature males very narrow, especially in proximal part of flagellum, often discoid rather than cylindrical; articles longer in adult males, becoming cylindrical. This development pattern probably only concerns the species with long antennae in adult males. Upper lip semicircular, distally slightly trilobed. Lower lip with outer and mandibular lobes rounded, with anterior lobes rounded but distally narrowed.

Mandible with large 3-articulate palp; first article short, second article usually elongate, sometimes ovate, third article elongate; first << third < second; first article glabrous; second article with several unordered setae on ventral border, with dorsal border glabrous or with group of 1-2 setae; third article with 1-3 groups of 1-3 setae on dorsal border, with group of over eight terminal setae, with ventral border devoid of setae in females, without or with one seta in immature males, with comb of short stiff setae in adult males. Incisor process well-developed: long and distally truncate, without teeth. Lacinia mobilis well-developed, elongate, following axis of incisor process, without crenulations but with distal notch on one side (at least in some European species), or even deeply cleft on one side (American species). Row of erected coalescent fang-shaped spines on distal half of space between incisor and molar process: almost always two on one side and three on other side; two much smaller, non-erected nodular spines more proximally. Molar process well-developed, circular, with fairly even surface, with one posterior setulose strong seta.

First maxilla with palp setose; outer plate with comb-like cuspidate spines in 6/3 crown arrangement; inner plate subtriangular, bearing row of about ten strong setae on straight mesial border, with few usually shorter setae on distal part of anterior border.

Second maxilla elliptic. Mesial border of upper plate with row of strong setae dorsally, and another row ventrally; additional setae present in between; anterodistal part of ventral surface with three strong setae: one short and two long. Mesial border of inner plate with row of strong setae dorsally, and another row ventrally; distal 0.3 of posterior border with row of fairly strong marginal setae; posterior part of ventral surface with longer oblique row of stronger setae, converging proximally towards posterior border.

Maxillipedal palp 4-articulate; first article short and broad; second article large, flattened, terminated in rounded lobe, with many slender setae on mesial border, with longitudinal row of strong setae on dorsal surface; third article well-developed, with or without longitudinal row of strong setae, more distally with two small transverse groups of strong setae (one dorsal and one subventral), with crown of terminal setae; fourth article short and narrow with one long terminal seta, and occasionally with 1-2 short accessory setae. Outer plate semicircular, with one distal short, strong, setulose seta. Mesial part of ventral surface with row of strong nodular spines overreaching mesial border, with strong setae, either single or in groups of two. Inner plate semicircular, with small distal notch; several distal strong setae, three strong nodular distal spines arising from the ventral side more mesially; mesial border with one subdistal conical and curved spine arising from ventral side interlocking with that of its opposite inner plate and forming locking system holding both inner plates together; mesial border with row of strong setae.

Coxal plates (coxae) as long or slightly longer than their somite, with ventral border setose; coxae 1-3 with or without small posterior tooth; coxa 4 with setae on posterior border, some setae more robust than ventral ones; coxa 1 elongate; coxae 2-3 subrectangular to trapezoidal; coxa 3 longer than coxa 2; coxa 4 rounded and postero-ventrally somewhat expanded; coxae 5-7 bilobed; coxae 6-7 quite small.

Gills present on P2-P6, elliptic, much shorter on P6 than on other pereopods, somewhat asymmetrical on P5. Oostegites slender, on P3-P5.

P1 < P2 ≈ P3 ≈ P4 < P5 < P6 ≈ P7.

P1 very small but of fairly basal morphology; basis slightly concave anteriorly; ischium and merus very short; carpus elongate, regularly broadening from proximal to distal part; propodus regularly rounded, with many setae, without spines; dactylus curved, finger-like.

Basis of P2 with group of strong and very long pappose setae on posterodistal angle. Merus and carpus with strong and long setae on posterior border. Anterior border of carpus with several groups of short setae. Propodus strongly modified: elongate, with anterior border straight or nearly so; posterior border divided into two more or less straight parts, separated by obtuse angular discontinuity: proximal part glabrous, distal part with considerable number of strong, very long setae; outer surface above distal part with smaller row of shorter setae. Dactylus, bud-shaped, with one distal seta, truly vestigial, distinct only at highest magnification under light microscope (fig. 72D).

P3-P4 very similar (coxae excepted). Basis elongate. Ischium very short. Merus long but very broad, with transverse row of short setae at distal 0.8 of anterior border; ventrally setose. Carpus broad and fairly short, posteriorly setose; in addition to 'normal' setae of posterior border, one subdistal long and very strong spine, here named the 'carpal fang', present. Propodus elongate (slightly shorter in P4 than in P3) with spines and strong setae on posterior border. Dactylus of fairly basal morphology but of variable size and proportions.

Basis of P5 broadly elliptic with protruding posterodistal rounded lobe, with transverse combs of spines on anterior border. Ischium broad and short with distal transverse comb of spines. Merus elliptic; one strong seta at 0.6 of posterior margin, usually accompanied by one or more accessory setae (posteromedian seta group); another strong seta, or group of strong setae (strongly sexually dimorphic in some species) often accompanied by one or more setules (strong seta(e) together with setules named posterodistal seta group) on posterodistal tip; anterior border of merus with row of irregular-sized spines, with row of long setae more mesially; most, sometimes all, of these setae plumose over entire length, distalmost setae usually proximally plumose and distally serrate (plumodenticulate setae). Carpus and propodus cylindrical, fairly short and similar-sized; posterior border of carpus overlapping propodus; carpus with distal transverse row of strong spines; anterior border with several groups of strong spines, usually accompanied by few setae. Propodus with regularly spaced single setae on anterior border, with group of terminal setae including one or two short styliform spines. Dactylus bud-shaped, truly vestigial, only distinguishable with highest magnifications under light microscope (fig. 73B).

Basis of P6 broadly elliptic, with posterodistal lobe, with longitudinal row of setae on mesial surface (not illustrated in present paper). Ischium broad and short. Merus posteriorly convex with at least three transverse groups of strong spines; anteriorly straight, with transverse groups of spines and, in more mesial position, with sublongitudinal groups of spiniform setae. Carpus and propodus well-developed, cylindrical, with several transverse groups of strong spines. Dactylus reduced and narrowly conical, more or less hidden by terminal crown of propodal spines. Carpus and propodus somewhat more slender in males than in females.

Basis of P7 subrectangular, with posterior spines or strong setae, depending on species, with anterior short setae, with longitudinal row of very thin setae on outer

surface, with many strong pappose setae on posterior 0.3 of mesial surface, with row of spines or spinules on proximal part of anterior 0.3 in females of several species. Ischium pentagonal. Carpus and propodus well-developed, cylindrical, with several transverse groups of strong spines. Dactylus reduced and narrowly conical, more or less hidden by terminal crown of propodal spines. Carpus and propodus somewhat more slender in males than in females.

Ep1 fairly small, with row of long spines on ventral border. Posterior part of ventral border terminated by tooth; tooth followed by curved groove, running along surface of epimeral plate. Posterior border with marked angular discontinuity, usually with regularly spaced setules.

Ep2 well-developed. Ventral part of outer surface with strong curved pappose setae. Posterior part of ventral border terminated by tooth; tooth followed by curved groove, running along surface of epimeral plate. Posterior border with marked angular discontinuity, usually with regularly spaced setules.

Ep3 well-developed. Ventral part of outer surface with strong but fairly short spines, usually disposed in transverse rows. Posteroventral border either with tooth, with trace of tooth, or regularly rounded. Posterior border slightly curved and usually with regularly spaced setules.

Pleopods ordinary.

Urosomite 1 dorsally with median transverse depression, deeper in male than in female. Posterior elevation with pair of anteriorly directed setae, longer in male than in female. Additionally, in many species, one or more pairs of posteriorly directed small conical spines behind these setae. Ventrolateral prolongation with or without short and strong outer setae.

Urosomite 3 usually with one or more median spinules on posterodorsal border.

Uropods well-developed.

Peduncle of uropod 1 dorsally flattened or slightly concave, with outer dorsal row of spines (distal spine strongest), with mesial dorsal row of (groups of) spines/setae, with outer ventral row of short and strong setae. Exopod and endopod well-developed, subcylindrical, with marginal upwards-directed spines; small conical spine on each side of long terminal spine. Proximal part of endopod with short longitudinal ventromesial row of long setae.

Uropod 2 very similar to, but shorter than, uropod 1, without outer ventral longitudinal row of setae on peduncle.

Peduncle of uropod 3 short, with at least two single setae or at least one group of setae on outer border, with one subdistal small spine or group of two spines on mesial border, with distal transverse row of strong spines on distal dorsal and ventral borders (both distal groups can merge together). Exopod consisting of long proximal and short distal article, with several groups of slender spines on outer border, with several to many, usually plumose, setae on mesial border; setae either single or forming pair with shorter non-setulose spiniform seta pointing obliquely upwards (accessory seta); average number of mesial setae slightly higher in males, however, range found in both sexes usually widely overlapping. Endopod very short, more or less elliptic, with few well-developed marginal spines.

Telson cleft along almost entire length; each lobe with mediolateral notch from which group of long spines arises; with broad tip from which terminal row of spines

and setae arises, with two dorsal transparent setulose setae.

Sexual dimorphism and allometric variations.— As indicated in the description, various characters are sexually dimorphic. The eyes are bigger in males, especially in adults (fig. 34A-B), than in females (fig. 26A). In some species, the pseudorostrum may have a different shape (fig. 69B versus 61B, 67A-B). Both antennae have more articles in the males than in females and their ornamentation is different in both sexes. Calceoli are present in the adult male only, and in females the major flagellum of A1 has spines that are lacking in the male (fig. 57B-C versus 51B-C). The mandible has a comb of setae on the ventral border of the ultimate article in the adult male (fig. 34F) that is absent in the female (fig. 26G) and the immature male. In the male, the number of setae is reduced on some parts of the pereopods, especially on the coxal plates of P2-4, the basis of P5-P7 (fig. 35B versus 32A). The shape of these setae is sometimes considerably different. The posterodistal seta of the merus of P5 may be significantly shorter in the adult male of some species like *B. guilliamsoniana* (fig. 35A), than in the female (fig. 31C) and the immature male. The posterior spines/setae of the basis of P7 are more slender (and often less numerous) in the males than in the females (fig. 69F versus 65B), but the importance of that dimorphism is more pronounced in some species than others. The carpus and the propodus of P6-P7 are somewhat longer in the males than in the females. Of course, the oostegites are present in the female only. The dorsal depression of the first urosomite is deeper (fig. 59F-G), and the pair of anteriorly directed setae is longer in the male than in the female (fig. 59E). The third uropod is slightly longer, and has often more setae on its mesial side in the male than in the female. These setae are often somewhat longer in males (fig. 76I) than in females (fig. 75D).

There are considerable changes during the growth of the animal. The number of antennal and antennular articles, and the number of setae, spines and groups of setae increases with size, these differences can be spectacular (compare the figures of a young female *B. sarsi* (fig. 67-68) with those of adults (fig. 60-66)). The eye may be weakly developed in small immatures, with a small diameter and a reduced number of ommatidia. In immature males of most species, the articles of the flagellum of the second antenna are very short, especially the proximal ones, being often discoid rather than cylindrical (fig. 34E). At maturity, these articles lengthen considerably and become proximally cylindrical and distally narrowly cylindrical (Fig. 34D). The metamorphosis of the antennae in males was already described by Bonnier (1890).

The peduncle of the first uropod has less dorsal outer spines in small than in large specimens. Finally, it is important to point out that on the exopod of the first and second uropods of not fully grown specimens, the spines are restricted to, or more numerous on, the distal 0.2 of the appendages (fig. 67H), whilst they are spread along a large part of its length in adults (fig. 66D).

5.2. Diagnostic importance of characters

As this paper is the first detailed comparative study on species of *Bathyporeia*, a review of the importance of the characters in the genus has been considered as essential. A thorough discussion of their diagnostic value is given hereafter.

Eye development.— The shape and size of the eyes exhibits minor interspecific differences, but they are fairly variable and should not be considered an important

diagnostic character. There is one case which needs special considerations. In the adult males of *B. megalops*, the eyes are dorsally fused. This is normally not the case in other species. There is however two remarkable exceptions in the material examined: one adult, but not very large, Irish male of *B. guilliamsoniana* and one normal-sized male of *B. guilliamsoniana* from the French part of the English Channel exhibit exactly the same disposition as in *B. megalops*. It should be pointed out that *B. megalops* is very close to *B. guilliamsoniana*. The structural organization of the eye is of specific value: the ommatidia are well-developed in all known species except *Bathyporeia gracilis*, where they are either vestigial or absent. In West Atlantic species the ommatidia are few in number and not coalescent (as in small juvenile of European species).

First antenna.— The tip of the first article of the peduncle of A1 (pseudorostrum) exhibits significant differences between species, as already pointed out by Watkin (1938). However, too much importance has been attributed to that character, probably because it is easy to see, and many misidentifications have resulted from this. Indeed, in some species, the pseudorostrum exhibits fairly important individual variations, and distortion artefacts are not uncommon in specimens that have been fixed with insufficient care. Furthermore, in some cases, it can exhibit some sexual dimorphism. So, when mixed samples of *B. pilosa* and *B. sarsi* have to be sorted out, the shape of the pseudorostrum can be used as a reliable and easy discriminative character for female specimens, but much less for the males which require a more careful examination.

The average number of proximoventral plumose setae on the pseudorostrum shows some differences between species. However, that character always exhibits some individual variations, and the number of these setae increases with the size of the animal, maturity being not always achieved at the same size. The other setae and spines of the pseudorostrum exhibit very little interspecific variation. Only in *B. tenuipes* the apical spines are less numerous and less developed than in other species.

The number of articles on the major flagellum of A1 (which is sexually dimorphic) is never constant within a species, but its range exhibits moderate interspecific differences. The length of the major flagellum is sometimes of some specific value, being longer in the male *B. pilosa* than in those of other species. The average number of lateral spine groups on the first article of the accessory flagellum also shows minor differences between some species. The size of the second article has sometimes been considered as taxonomically important (Watkin, 1938; Vader, 1970). However, during the present study, considerable individual variation in that character has been observed, sometimes even in the same specimen (fig. 20B-C), its value should thus be considered questionable.

Second antenna.— In most species examined so far, the third article of the peduncle of A2 has a single anterior group of spines and setae in distal position, the occurrence of a second group in a more proximal position is however not uncommon. In *B. gracilis* there are always 2-3 groups and in *B. tenuipes* 3-4.

The ornamentation pattern on the fourth article of the peduncle of A2 shows minor interspecific differences, but individual variations are not negligible. In some cases, the robustness of the fourth and fifth article is of specific value. In *B. tenuipes*, they are more slender than in other species for example.

In the females, the number of articles on the flagellum of A2 exhibits only minor specific differences. In adult males however, the number of articles differs markedly

between species. In adult males, the relationship between the length of A2 and the body length is of considerable importance too. Note that some previous authors use the relative lengths of the flagellum and body, not the complete length of A2 as given here.

Mouthparts.— The mouthparts exhibit very little differences between the species. The penultimate article of the mandibular palp is slender in all northwestern European species except *B. pilosa*, in which it is ventrally expanded. The drawing of Bousfield (1973: 235) suggests that the ultimate article of the mandibular palp is dorsally slightly sigmoid in the northwestern Atlantic species *B. parkeri* Bousfield, 1973, whilst it is regularly convex in other species.

The number of strong setae on the dorsal surface of the second article of the maxillipedal palp shows minor differences between species. On the third article, a longitudinal row of setae is present in the adults of most species except for *B. gracilis*, *B. nana*, *B. tenuipes* and apparently the American species *B. parkeri* and *B. quoddyensis* (see Bousfield, 1973: 235). Its absence in *B. nana* could result from the small size of the species, but that explanation does not hold for the other species. The number of spines on the inner side of the outer plate exhibits minor interspecific differences, but it also exhibits some individual variations and the number increases with the size of the specimen.

Coxal plates.— The presence/absence of a posterior tooth on the three first coxal plates is of great importance. Three patterns have been recorded: no tooth on any coxa; a tooth on coxae 2-3 only (eventually with a trace of a tooth on coxa 1); a tooth on all the three coxae. The tooth of coxae 2-3 can be separated from the coxa either by a deep notch in species such as *B. elegans* or by a shallow notch as in *B. pelagica*. In the species without posterior tooth on coxa 1, the junction between the ventral and the posterior border can be rounded (*B. pilosa* and *B. sarsi*) or angular (*B. nana*). The tip of coxa 1 can be more or less rounded or acute (note that the microscopical preparation should be made properly, to prevent misleading orientation artefacts). The anterior and posterior borders of coxa 2 can be ventrally diverging (as in *B. tenuipes*), converging (as in *B. pilosa*), or more or less parallel (as in *B. guilliamsoniana*). The anterior and posterior borders of coxa 3 can be ventrally converging (as in *B. pilosa*) or more or less parallel (as in *B. sarsi*), but this difference is not very important. The shape of coxa 4 exhibits minor specific differences in proportions, which are difficult to quantify. The number, the slenderness, and the size regularity of marginal setae on coxae 1-4 show moderate specific differences. Note however that the number of setae increases dramatically with the size of the animal and that it is higher in females than in males. On coxa 1 of *B. nana*, there is a very short apical seta (apical setule), which is not present in any other western European species. In *B. gracilis* and *B. tenuipes*, the distalmost normal setae of coxa 1 are closer to the tip than in other species. The number of setae on the mesial surface of the coxae 2-3 also exhibits some specific variations, being especially numerous in *B. tenuipes*.

First pereopod.— P1 shows very few differences, except that the propodus is slightly more elongate in *B. elegans*, *B. nana* and apparently *B. parkeri* (see Bousfield, 1973: 235) than in other species.

Second pereopod.— In the western European species, P2 exhibits very little variation, although the carpus and propodus proportions exhibit minor interspecific differences. The drawings of Bousfield (1973) and Bellan-Santini (1989) suggest more

important variations concerning the carpus and the propodus shape and proportions in extralimital species.

Third and fourth pereopods.— P3 and P4 are very similar and are therefore treated together. The characteristics of the tip of the carpal fang (blunt or acute, with or without apical setule, length of apical setule) are very important; its length also has some importance. The robustness of the propodus and its relative length to that of the merus are fairly important; their setation/spination pattern is of minor importance, although it is more developed in *B. guilliamsoniana* than in any other species. The size, shape and robustness of the dactylus and the size of the unguis are of major specific value.

Fifth pereopod.— In P5, the shape and the ornamentation of the basis exhibits very minor differences among the western European species. It looks markedly different however, in the Mediterranean *B. sophiae* Bellan-Santini & Vader, 1988, in which the anterior border is very distinctly concave and scarcely setose (Bellan-Santini, 1989). The merus of P5 exhibits moderate differences in shape, proportions and ornamentation of the anterior border. Characteristics of the two groups of setae of its posterior border (posteromedian and posterodistal groups) are of essential importance. The characteristics of the accessory seta(e) of the posteromedian seta group are important to separate *B. pilosa* and *B. sarsi*. Even more important is the length of the major seta of the posterodistal group. It can be short in both sexes (*B. tenuipes*), short in the male and long in the female (*B. guilliamsoniana* and *B. pelagica*) or long in both sexes (in the remaining western European species); in those cases, some sexual dimorphism persists but the size differences are very minor. The ratio between the combined length of carpus + propodus and merus length exhibits small but significant differences between species. Finally, the relationship between the average length of the longest posterior spine of the carpus and the tip of the propodus varies between the different populations of *B. elegans*.

Sixth pereopod.— In P6, the shape and the ornamentation of the basis exhibits minor specific differences (the seta pattern is also sexually dimorphic and varies allometrically). Although it is not of absolute discriminative value, the number of spine/seta groups on the posterior border of merus is very important in separating *B. guilliamsoniana* from other species, since this character is easy to see (this difference is not valid for all populations of *B. guilliamsoniana*). Furthermore, the ornamentation of the anterior border of the merus exhibits minor interspecific differences. The length and the proportions of the carpus and propodus are often very important. The presence/absence of one or several groups of spines on the posterior border of P6 (in addition to the distal group) is of prime importance. In *B. tenuipes*, the spines of the carpus and propodus are more slender than in any other species.

Seventh pereopod.— In P7, the posterior ornamentation of the basis (number, length and robustness of spines/setae) is often highly characteristic for a species, but it must be kept in mind that it is often markedly sexually dimorphic. This important marginal ornamentation should not be confused with the thin glabrous setae of the outer surface and the strong pappose setae of the mesial surface, both being of no specific value. In the females of several species, there is, in addition to those pappose setae, a more anterior row of glabrous spines on the mesial side. In the two American *Bathyporeia* species, *B. quoddyensis* Shoemaker, 1949 and *B. parkeri* Bousfield, 1973, the posterior border of the basis exhibits a well-developed protrusion, that is absent or

indistinct in European species (see Bousfield, 1973: 235). The shape and length of the ischium exhibits significant differences between the species (note that its outer and mesial sides can be morphologically different). Just like in P6, the length and proportions of the carpus and propodus are often very important, and in *B. tenuipes*, the spines of the carpus and propodus are more slender than in other species.

First and second epimeral plates.— The acuity of the median angle of the posterior border of the first and second epimeral plates exhibits minor differences between some western European species. More pronounced differences have been observed in northeastern American species (Bousfield, 1973).

Third epimeral plate.— The shape of the third epimeral plate and especially its posterior border is very important. The presence/absence of a small posterior tooth is of specific value, although it may exhibit some sexual dimorphism. Note that the posterior protrusion found in young *B. nana* is possibly not homologous to the posterior tooth. The number of transverse rows of spines is important in some species, but it is by no means constant, and it is size-dependent. In some extralimital species, those spines are never in rows. The number of setules on the posterior border is of minor importance.

Urosomites.— On the dorsal border of the first urosomite, the presence/absence, the number, and sometimes the size of the posteriorly directed conical spines is extremely important. The presence/absence of strong setae arising from the outer side of the ventrolateral border is important too.

First uropod.— In U1, the outer dorsal border (the two apical spines excluded) consists either of a proximal row of long slender spines followed by a row of short more robust spines (*B. gracilis* and *B. tenuipes*) or a single row of short robust spines (other western European species). The total number of spines on the outer dorsal border too exhibits significant differences between species. The length and slenderness of the exopod and endopod, as well as those of their spines, exhibit moderate specific differences. In most species, the endopod has a single (subdistal) spine on the border facing the exopod, but in *B. guilliamsoniana* (and the Mediterranean *B. megalops* and *B. sunnivae*) there are several spines on that border. This is perhaps the most useful character to distinguish *B. guilliamsoniana* from its relatives.

Second uropod.— In U2, the number of spines on the outer dorsal border exhibits minor differences between species. In adult *B. tenuipes*, the dorsomesial ornamentation of the proximal half is quite distinctive, consisting of transverse rows of strong setae or slender spines, whilst in other species the setae are single or in pairs. The length and slenderness of peduncle, exopod and endopod, as well as those of their spines, exhibit moderate interspecific differences. In most species, the endopod has a single (subdistal) spine on the border facing the exopod, but in *B. guilliamsoniana* (and the Mediterranean *B. megalops* and *B. sunnivae*), there are several spines on that border, just as in U1.

Third uropod.— On the outer border of the peduncle, the setation pattern shows some differences between species, and the number and the size of the spines on its dorsal and ventral distal borders are sometimes of some specific value. Especially in *B. pilosa*, the distal spines are quite short and few in number. The first article of the exopod can be broad with a short second article (*B. pilosa* and *B. sarsi*) or slender with a longer second article (other species). On the outer side, the number of spine groups, the aver-

age number of spines per group, and the average length of the spines in each group is of some specific value. These spine groups are especially numerous in *B. guilliamsoniana*, and especially well developed in *B. gracilis* and *B. tenuipes*. The number and length of the major (usually plumose) setae of the mesial side are also of some importance. These setae are shorter in female *B. gracilis*, *B. tenuipes* and *B. nana* than in other species, and they are less numerous in females and immature males of *B. nana*. The presence/absence, size, and sometimes the slenderness of the accessory spiniform setae of the mesial side, are of great specific value. The first article of the exopod always has setae on both sides. In some cases, such as in *B. guilliamsoniana*, the seta pattern of the second article is identical to that of the first. In some other cases, only the mesial side has or may have setae, and in *B. gracilis*, the second article has no lateral setae at all (at least in the few specimens recorded so far). The shape of the endopod exhibits minor differences between the species. Its spine number is of some specific value, but it should be borne in mind that it may be sexually dimorphic, especially in *Bathyporeia pilosa*.

The telson exhibits no significant differences between the European species. In the northeastern American species *B. quoddyensis* however, there are spiniform setae on the mesial side of the telson lobes (Bousfield, 1973), which have not been recorded in any other species. The position of the outer group of spines exhibits specific differences in the American species too, while it is fairly constant in European species.

Colour.— The life colour of the body, eggs, eyes (Watkin, 1938) and viscera (Nicolaisen & Kanneworff, 1983: 238) is of some taxonomical value. In species with dark red eyes, some ophthalmic pigmentation sometimes persists for years in preserved specimens.

5.3. Keys to species

5.3.1. Simplified key

1. First urosomite usually without posteriorly directed spines; first article of U3 exopod very broad, second article of U3 exopod shorter than width of first 2
- First urosomite with at least one pair of posteriorly directed spines; first article of U3 slender, second article of U3 exopod longer than width of first 3
2. Apex of pseudorostrum regularly rounded and very narrow; tip of coxa 1 fairly narrow; subdistal setule of carpal fang about as long as tip of fang; merus of P5 with posteromedian group of setae consisting of one major glabrous seta and one long very plumose accessory seta; basis of P7 with narrow setae on posterior border in females; ventrolateral part of first urosomite never with strong outer setae
 *B. pilosa* Lindström, 1855
- Apex of pseudorostrum subrectangular and broad in females, more rounded and fairly narrow (i.e. much less characteristic) in males; tip of coxa 1 broadly rounded; subdistal setule of carpal fang much longer than tip of fang; merus of P5 with posteromedian group of setae consisting of one major glabrous seta and 1-2 very short setae which are sparsely setulose or appear as non-setulose in microscopical preparations; basis of P7 with spines on posterior border in females; ventrolateral part of first urosomite often with one or several short strong outer setae
 *B. sarsi* Watkin, 1938

3. Endopod of uropod 1-2 with one long spine only, in subdistal position, on the border facing the exopod; merus of P6 most commonly with four or more dorsal groups of spines/setae (distal group included) 4
 - Endopod of uropod 1-2 with several long spines on the border facing the exopod; merus of P6 normally with three dorsal groups of spines (sometimes with four) [females and often males with posterior tooth on Ep3] *B. guilliamsoniana* (Bate, 1857)
4. P6 carpus with 1-3 groups of spines on posterior border (in addition to distal group); ventrolateral border of first urosomite with several strong outer setae; most commonly two or more posteriorly directed similar-sized pairs of dorsal spines on first urosomite; dorsolateral spines of U1 peduncle proximally long and narrow, more distally short, but fairly narrow, distal spine long and robust 5
 - Dorsal ornamentation of carpus of P6 consisting of one distal group of spines only; ventrolateral border of first urosomite without strong outer setae; most commonly one posteriorly directed pair of dorsal spines on first urosomite (rarely two); dorsolateral spines of U1 peduncle all robust and similar-sized (or gradually increasing in size) except for larger distal spine 6
5. Dorsoapical part of pseudorostrum not or slightly overhanging; posterodistal seta of merus of P5 long and slender, reaching more than 0.6 of carpus length in both sexes; anterior and posterior border of coxa 2 parallel *B. gracilis* G.O. Sars, 1891
 - Dorsoapical part of pseudorostrum moderately to strongly overhanging; posterodistal seta of merus of P5 short and spiniform, reaching less than 0.4 of carpus length in both sexes; anterior and posterior border of coxa 2 strongly diverging downwards *B. tenuipes* Meinert, 1877
6. Total body length of adults > 3 mm; coxa 1 without apical setule 7
 - Total body length of adults normally < 3 mm; coxa 1 with apical setule *B. nana* Toulmond, 1966
7. Pseudorostrum usually fairly rounded, overhanging or not; dactylus of P3-P4 with posterior border distinctly curved, unguis well-developed; coxa 1 with tooth; coxae 2-3 with acute tooth separated from coxa by deep notch; carpal fang of P3-P4 with tip entire; posterodistal seta of merus of P5 long and slender in both sexes (reaching more than 0.65 of carpus in males); Ep3 toothless *B. elegans* Watkin, 1938
 - Pseudorostrum distinctly subquadrate, especially in females, with dorsoapical part overhanging; dactylus of P3-P4 with posterior border straight, unguis very short; coxa 1 without tooth; coxae 2-3 with posterior tooth broadly triangular and separated from coxa by very shallow notch; carpal fang of P3-4 with bifid tip; posterodistal seta of merus of P5 short and spiniform in adult males (reaching about 0.3 of carpus), long and slender in females and immature males; Ep3 always with small tooth in females, with or without small tooth in males *B. pelagica* (Bate, 1856)

5.3.2. Diagnostic key

1. Species very robust. First urosomite usually without posteriorly directed spines (posteriorly directed spines rarely present in *B. pilosa*, less infrequently in males);

- P3-P4 dactylus short and robust and with convexity (swelling) on posterior border, unguis short; first article of U3 exopod very broad, second article of U3 exopod shorter than width of first article [coxae 1-3 without tooth; endopod of uropod 1-2 with only distal and subdistal spines on the border facing the exopod] 2
- Species slender to moderately robust. First urosomite with at least one pair of posteriorly directed spines; P3-P4 dactylus not especially robust, with posterior border straight or regularly concave, unguis long except in *B. pelagica*; first article of U3 slender, second article of U3 exopod longer than width of first article 3
2. Apex of pseudorostrum regularly rounded and very narrow; flagellum of A1 of males very long (combined length of major flagellum and last two articles of peduncle sometimes more than twice length of pseudorostrum); A2 of adult males 0.8 times as long as body or longer than body; penultimate article of mandibular palp very broad; tip of coxa 1 fairly narrow; subdistal setule of carpal fang about as long as tip of fang; posteromedian group of setae on merus of P5 consisting of one major glabrous seta and one (rarely two) long, very plumose, accessory seta; carpus of P6 with or without median group of spines/setae on posterior border; basis of P7 with narrow setae on posterior border in females; surface of Ep3 most commonly with 1-3 groups of spines in adult specimens; dorsal part of first urosomite rarely with pair of posteriorly directed spines; ventrolateral part of first urosomite never with strong outer setae; U1 peduncle with 2-5 outer dorsal spines; endopod of U3 with two spines in adult females *B. pilosa* Lindström, 1855
 - Apex pseudorostrum subrectangular and always broad in females, more rounded and fairly narrow (i.e. much less characteristic) in males; flagellum of A1 of males not especially long (combined length of major flagellum and last two articles of peduncle always much less than two times length of pseudorostrum); A2 of adult males about 0.6 times as long as body; penultimate article of mandibular palp not especially broad; tip of coxa 1 broadly rounded; subdistal setule of carpal fang much longer than tip of fang; posteromedian group of setae of merus of P5 consisting of one major glabrous seta and 1-2 very short setae, sparsely setulose or appearing non-setulose in microscopical preparations; carpus of P6 never with median group of spines/setae on its posterior border; basis of P7 with spines on posterior border in females; surface of Ep3 most commonly with 4-6 groups of spines in adult specimens; dorsal part of first urosomite never with posteriorly directed spines; ventrolateral part of first urosomite often with one or several short strong outer setae; U1 peduncle with 6-7 outer dorsal spines; endopod of U3 with 3-5 spines in adult females *B. sarsi* Watkin, 1938
 3. Endopod of uropod 1-2 with a single long spine in subdistal position on border facing exopod; mesial border of endopod of U3 usually with two setae in some seta groups (usually one long plumose seta and one shorter glabrous spiniform seta pointing obliquely upwards); merus of P6 frequently with four or more dorsal groups of spines/setae (distal group included); tip of coxa 1 moderately narrow to broad 4
 - Endopod of uropod 1-2 with several long spines on border facing exopod; mesial border of endopod of U3 with only one (plumose) seta per seta group (except the last seta group of the first article, where there are sometimes one plumose seta and one short seta); merus of P6 normally with three dorsal groups of spines (some-

times four); tip of coxa 1 very narrow [large species; coxae 1-3 with tooth; dactylus of P3-P4 long, with long unguis; posterodistal angle of merus of P5 with short spiniform seta in adult males, with one long slender seta or spiniform seta in females and immature males; basis of P7 with long setae on posterior border; Ep3 with one well-developed tooth in females, with or without tooth in males; ventrolateral border of first urosomite without strong outer setae; outer dorsal spines of U1 peduncle all fairly robust, slightly increasing in size towards tip, distal spine largest] *B. guilliamsoniana* (Bate, 1857)

- 4. Anterior part of third article of peduncle of A2 often with spines or strong setae in two or more different positions; carpus of P6 with 1-3 groups of spines on posterior border (in addition to distal group); propodus of P6 very narrow and slightly longer than anterior length of merus; ventrolateral border of first urosomite with several strong outer setae; most commonly two or more posteriorly directed similar-sized dorsal spines on first urosomite; dorsolateral spines of peduncle of U1 proximally long and narrow, more distally short but fairly narrow, distal spine long and robust [penultimate article of Mxp without longitudinal row of setae on inner side; coxa 1 without tooth or with trace of tooth; coxae 2-3 with well-developed tooth; dactylus of P3-P4 with well-developed unguis; posterior border of basis of P7 with slender or fairly slender ornamentation in females; Ep3 without tooth] 5
- Anterior part of third article of peduncle of A2 most commonly with only one group of spines/setae in subdistal position (second group, usually with slender setae only, sometimes occurs behind it); dorsal ornamentation of carpus of P6 consisting of distal group of spines only; propodus of P6 not especially narrow and shorter than anterior length of merus; ventrolateral border of first urosomite without strong outer setae; most commonly only one posteriorly directed pair of dorsal spine on first urosomite (rarely two); dorsolateral spines of peduncle of U1 all robust and similar-sized (or gradually increasing in size), except distal one which is larger 6
- 5. Dorsoapical part of pseudorostrum not or slightly overhanging; eye with imperfectly developed ommatidia; A2 much shorter than body in both sexes, with about 12 articles in mature males; posterodistal seta of merus of P5 long and slender, reaching more than 0.6 of carpus length in both sexes; anterior and posterior border of coxa 2 parallel; P6-P7 carpus not especially elongate; carpus of P6 about 0.7 times as long as propodus; small species *B. gracilis* G.O. Sars, 1891
- Dorsoapical part of pseudorostrum moderately to strongly overhanging; eye normally developed; A2 shorter than body in females and longer than body, with 39 to 42 articles, in mature males; posterodistal seta of merus of P5 in both sexes (both in adults and immatures) short and spiniform, reaching less than 0.4 of carpus length; anterior and posterior border of coxa 2 strongly diverging downwards; P6-P7 carpus extremely elongate; carpus of P6 about 0.9 times as long as propodus; large species *B. tenuipes* Meinert, 1877
- 6. Pseudorostrum variable (but usually fairly rounded in *B. elegans*, regularly rounded in *B. nana*); P3-P4 dactylus with posterior border distinctly curved, with unguis well-developed, at least 0.22 times as long as total length of dactylus, usually longer; coxae 2-3 either without tooth (*B. nana*) or with acute tooth separated from coxa by deep notch (*B. elegans*); carpal fang of P3-P4 with tip entire; posterodistal

- seta of carpus of P5 long and slender in both sexes (reaching more than 0.65 of carpus in males); ischium of P7 reaching 0.37 to 0.41 of outer side of merus in females. [Ep3 toothless in *B. elegans*, with obtuse protrusion in juvenile *B. nana*; peduncle of U1 with up to 14 dorsal outer spines in *B. elegans*] 7
- Pseudorostrum with dorsoapical part overhanging and distinctly subquadrate, especially in females; dactylus of P3-P4 with posterior border straight, with unguis very short, at most 0.15 as long as total length of dactylus, usually shorter; coxae 2-3 with broadly triangular posterior tooth, separated from coxa by very shallow notch; carpal fang of P3-4 with tip bifid; posterodistal seta of merus of P5 short and spini-form in adult males (reaching about 0.3 of carpus length), long and slender in females and immature males; ischium of P7 reaching 0.44 to 0.47 of outer side of merus in females. [Coxa 1 without tooth; coxae 2-4 with setae not very irregularly sized; coxae 2-3 usually with about 7-15 setae in mature females (i.e. a low number); coxa 4 usually with less than 30 setae in mature females; Ep3 with small tooth in females, with tooth or rounded in males; peduncle of U1 with at most 10 outer dorsal spines] *B. pelagica* (Bate, 1856)
 - 7. Coxae 1-3 with tooth; coxa 1 without apical setule and with several anterior setae; coxae 2-4 with very irregular-sized setae; basis of P7 with at least five spines in juveniles (many more in adults), spread along posterior border; tip of pseudorostrum regularly rounded or overhanging; pseudorostrum with at least one proximoventral plumose seta in small juveniles (always several in adult and large juveniles); Ep3 with at least one transverse row of spines in small juveniles, always with several rows in adults and large juveniles; posteroventral border of Ep3 regularly rounded and toothless; mesial border of exopod of U3 with several long plumose setae in both sexes; outer setae of peduncle and exopod of U3 not especially long and robust in females; adults usually longer than 3 mm *B. elegans* Watkin, 1938
 - Coxae 1-3 toothless; coxa 1 with one (rarely two) apical setule(s) and one single but long anterior seta; coxae 2-4 with setae of less varying size; basis of P7 with 2-4 spines on proximal half of posterior border; pseudorostrum regularly rounded (not overhanging); pseudorostrum with only one proximoventral plumose seta; Ep3 with one single transverse row of spines; Ep3 with posterior tooth in juveniles (gradually disappearing with growth); mesial border of exopod of U3 with several long plumose setae in males but with only one or two (groups of) short non-plumose setae in females; outer setae of peduncle and exopod of U3 very long and robust in females; adults at most 3.5 mm long, usually smaller *B. nana* Toulmond, 1966

5.4. Descriptions of species

5.4.1. *Bathyporeia elegans* Watkin, 1938 (figs. 1, 4-18)

Bathyporeia pelagica; G.O. Sars, 1891: 129, pl. 44 fig. 1; Scott, 1893: 213, pl. 5 fig. 23-25; Reibisch, 1905: 158, pl. 4 fig. 7-8; Tesch, 1916: 324; Chevreux & Fage, 1925: 93 (in part); Stephensen, 1929: 83, fig. 20.94 (after Stephensen, 1928); Stephensen, 1938: 141 (key); Shoemaker, 1949: 389 (in part; discussion).

Bathyporeia pelágica; Stephensen, 1928: 131, fig. 25.8.

Bathyporeia elegans Watkin, 1938: 222, fig. 3; Schellenberg, 1942: 167, fig. 136 (after Watkin); Yashnov,

1948: 282, pl. 72 fig. 4 (after G.O. Sars); Gurjanova, 1951: 338, fig. 198 (after Watkin); Toulmond, 1966: 229 (discussion), 231 (key); Bellan-Santini, 1973: 101, table II; Lincoln, 1979: 314, 318, fig. 149a-e; Enckell, 1980: 519, fig. 2391 (after Watkin); Köhn & Gosselck, 1989: 72, pl. 22 fig. 3; Withers, 1990: 445, fig. 9.30 (after Lincoln); Faasse & Stikvoort, 2002: 62 (colour description).

Not *Bathyporeia elegans* Sars sensu Crawford, 1937: 639 (= *Bathyporeia gracilis* G.O. Sars, 1891 or *Bathyporeia tenuipes* Meinert, 1877).

Types.— See material examined. Type locality: Southern Norway, Ognebugt, Jæderen, 58°31'N 05°45'E.

Material.— **Forma A. Norway:** TMU 8582: 1 ovigerous female, Finnmark, Loppa, MLWS, vii.1976, leg. W. Vader. TMU 2922: 1 immature male, Vannø, 4 m, 06.vi.1924, leg. T. Soot-Ryen (originally identified as *B. pelagica* Sp. Bate). TMU 1394: 18 specimens (incl. adults of both sexes), Skatøren, 69°42'N 19°02'E, 1881 (originally identified as *B. pelagica* Sp. Bate). TMU 1395: 26 specimens (incl. adults of both sexes), Grindøen, 69°38'N 18°52'E, 23.viii.1884 (originally identified as *B. pelagica* Sp. Bate). TMU 2919: 3 specimens in poor condition, Loppa, st. 3, 10-35 m, 24.vii.1931 (originally identified as *B. pelagica* Sp. Bate). TMU 2924: 1 adult female, Tromsø area, Gibostad, 69°21'N 18°04'E, station I b, 0.5-3 m, 19.vii.1917, leg. C. Dons. TMU 2930: 1 adult female, Tromsø, no more information (originally identified as *B. pelagica* Sp. Bate). TMU 2940: over 50 specimens (incl. adults of both sexes), Tromsø area, Ramfjorden, IXa, 69°32'N 19°03'E, about 15 m depth, 24.viii.1921, leg. T. Soot-Ryen (originally identified as *B. pelagica* Sp. Bate). TMU 11 875: 15 specimens including 1 ovigerous female, Tromsø area, Kvaløya, north coast, 1 km east of Sommarøy bridge, 69°37'N 18°05'E, 0.5 m depth, fine clean sand, exposed shore, kitchen sieve, 25.v.2002, leg. C. d'Udekem d'Acoz. TMU 9388: about 20 specimens, Tromsø area, Kvaløya, north coast, 1 km east of Sommarøy bridge, 69°37'N 18°05'E, 0.5 m depth, fine clean sand, exposed shore, kitchen sieve, 11.viii.2002, leg. C. d'Udekem d'Acoz. RMNH A: 10 specimens, Tromsø area, Kvaløya, north coast, 1 km east of Sommarøy bridge, 69°37'N 18°05'E, 0.5 m depth, fine clean sand, exposed shore, kitchen sieve, 11.viii.2002, leg. C. d'Udekem d'Acoz. TMU 7479: 10 specimens, idem, in absolute alcohol. TMU 9389: 3 females and exuvium of female, Tromsø area, Kvaløya, north coast, 1 km east of Sommarøy bridge, 69°37'N 18°05'E, intertidal, same level as *Fucus evanescens*, fine clean sand, exposed shore, kitchen sieve, 11.viii.2002, leg. C. d'Udekem d'Acoz. TMU 2927: 20 specimens, Narvik area, Ofoten, sta. 28, 1.5 m depth, 30.viii.1930. TMU 2928: 1 specimen, Nordland, Folden, station VIIIb, grab, 9.vii.1923, clay with sand, 21 m, leg. T. Soot-Ryen (originally identified as *B. pelagica* Sp. Bate). ZMO F2656: 50 specimens previously designated as **syntypes** of *Bathyporeia elegans* by Watkins, Southern Norway, Ognebugt, Jæderen [current name = Jæren (Jæren area), Ognabukta (bay of Ognå)]; approximate coordinates: 58°31'N 05°45'E], no date, previously identified as *B. pelagica* Sp. Bate by G.O. Sars; amongst these 50 specimens of *B. elegans*, 1 female, 3.2 mm long in curved position, fully dissected and mounted in Faure's liquid, is here designated as **lectotype**, and 2 detached third uropods mounted in Faure's liquid as well as the 49 remaining specimens are here designated as **paralectotypes**; special sub-numbers have been given for each slide and the remaining **syntypes**: F2656a, 49 specimens, **paralectotypes**, ethanol; F2656b, detached right U3, sex unknown, **paralectotype**, slide; F2656c, ovigerous female, P4-7 (except one P7), **lectotype**, slide; F2656d, ovigerous female, Md, Mx1, Mx2, head carcass, **lectotype**, slide; F2656e, ovigerous female, P1-A1-A2, **lectotype**, slide; F2656f, ovigerous female, P2-3, isolated gill, **lectotype**, slide; F2656g, ovigerous female, uropods 2-3, telson, dorsal part of urosomite 1, **lectotype**, slide; F2656h, ovigerous female, EP1-3, **lectotype**, slide; F2656i, ovigerous female, pleopods with eggs, **lectotype**, slide; F2656j, ovigerous female, Mxp, **lectotype**, slide. **Probably belonging to forma B. Denmark:** TMU 2920: 5 specimens in poor condition, Kattegat, Hauch St. 486 Jæt V, Jegens Odde [label difficult to decipher], 2.5-6 m, sand. **Forma B. Germany:** TMU 1117: 1 immature male and 18 fine females (2 dissected and mounted), Aussen Jade, st. 2, 15.vii.1968, leg. J. Dörjes. TMU 1119: 4 specimens, Jade, station C1, 19/03/1971, leg. J. Dörjes. TMU 1122: 5 specimens, Aussen Jade, st. 4, 15.vii.1968, leg. J. Dörjes. TMU 1952: 3 specimens, Jade, station 33, 03.iv.1975, leg. J. Dörjes. TMU 1123: 3 females, Aussen Jade, st. 504, 14.iv.1967, leg. J. Dörjes. TMU 1120: 1 immature male, Jade, station 506, 14.ii.1967, leg. J. Dörjes. TMU 4911: 1 adult male, Jade, station C27/9, 27.ix.1972, leg. J. Dörjes. TMU 1951: 1 female, Mellum, 53°44'N 08°06'E, sta-

tion MB 4/72, 07.vi.1972, leg. J. Dörjes. TMU 1124: 1 ovigerous female, Mellum, 53°44'N 08°06'E, station MB 5/72, 07.vi.1972, leg. J. Dörjes. TMU 2451: 1 small female, Mellum, 53°44'N 08°06'E, station MB 6/72, 07.06.1972, leg. J. Dörjes. TMU 1961: 3 specimens, Mellum, 53°44'N 08°06'E, station MB 8/72, 07.ii.1972, leg. J. Dörjes. TMU 1115: 1 female, Mellum, 53°44'N 08°06'E, station MB 9/72, 07.ii.1972, leg. J. Dörjes. TMU 1121: 3 specimens, Mellum, 53°44'N 08°06'E, station MB 70/82, 26.vii.1972, leg. J. Dörjes. TMU 1116: 1 adult female, Mellum, 53°44'N 08°06'E, station MB 24/32, 20.vii.1972, leg. J. Dörjes. TMU 1118: 2 females, Norderney, station Ney 102, 53°42'N 07°09'E, viii.1971, leg. J. Dörjes. **The Netherlands:** TMU 9435: over 200 adult specimens (both sexes but mostly males), The Netherlands without precise locality. ZMA, Crust. Amph 200259: 1 adult male and 2 females, North Sea, 10 km west of Texel, st. 9, vi.1992, leg. D. Platvoet (previously identified as *B. guilliamsoniana* by D. Platvoet). RMNH A 4920: 1 very large and 1 young female, North Sea, 51°36'58"N 02°54'12"E, 21-60 m, grab 1493, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4921: 7 small specimens, North Sea, 51°36'10"N 02°56'58"E, 30.60 m, grab 1495, 01.vii.1966. RMNH A 4922: 1 ovigerous female, North Sea, 51°33'27"N 03°05'18"E, 27 m, grab 1501, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4923: 7 specimens including a very large female, North Sea, 51°47'06"N 02°56'26"E, 30.60 m, grab 1480, 01.vii.1966, leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4924: 14 specimens including very large females, North Sea, 51°32'10"N 03°09'20"E, 19.80 m, grab 1504, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4925: 16 specimens including adult females, North Sea, 51°30'14"N 03°15'00"E, 6.30 m, grab 1508, 01.vii.1965; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4926: 8 specimens including very large females, North Sea, 51°33'50"N 03°04'00"E, 18.00 m, grab 1500, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4927: 1 adult male and adult female, North Sea, 51°31'38"N 03°10'54"E, 18.00 m, grab 1505, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4928: 12 specimens including large females, North Sea, 51°35'42"N 02°58'20"E, 34.20 m, grab 1496, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4929: 1 adult male and 1 young female, North Sea, 51°41'04"N 02°41'48"E, 35.10 m, grab 1484, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4930: 1 large adult female, North Sea, 51°34'48"N 02°01'10"E, 35.60 m, grab 1498, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4931: 6 specimens including a very large female, North Sea, 51°36'30"N 02°55'36"E, 32.40 m, grab 1494, 01.vii.1966; leg. W.J. Wolff, W.R., J.N., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4932: 1 adult male, Oosterschelde, grab 1733, 7 m, 06.x.1966; leg. Wim Vader, W.J. Wolff, Lein de Wolf, A.S., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4933: 5 specimens, province of Zeeland, Krabbegat, trap Westenschouwen, 2 m; 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, A.S., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4934: 1 large adult female, province of Zeeland, Krabbegat, trap Westenschouwen, 4 m, 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, A.S., don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH, previously A 4935: 1 adult male (previously identified as and mixed together with *B. pelagica*), North Sea, 51°38'51"N 03°30'15"E, 10.8 m, grab 1457, 01.vii.1966, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH, previously A 4936: 2 adults (previously identified and mixed with *B. pelagica*), mouth of Oosterschelde, Krabbegat, trap Westerschouwen, 4.0 m, grab 1715, 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. **Belgium:** RUG: 3 specimens including an adult male, western half of the Belgian coast (western coastal sandbanks), less than 5 km offshore (previously together with *Bathyporeia guilliamsoniana* and *Urothoe poseidonis*), station HA 9910036, years 1999-2000, S. Degraer coll. RUG: 9 specimens, western half of the Belgian coast (western coastal sandbanks), less than 5 km offshore (previously together with *Bathyporeia guilliamsoniana* and *Pontocrates arenarius*), years 1999-2000, station HH 9910046, S. Degraer coll. RUG: about 20 specimens, western half of the Belgian coast (western coastal sandbanks), less than 5 km offshore, no station number, years 1999-2000, S. Degraer coll. **Ireland:** OUMNH: 1 female and 11 immatures, "sample V", Valencia, no exact coordinates, depth <15m, sandy bottom, 1990-2000, S. De Grave leg. OUMNH: about 15 specimens,

sample VF 14, Co Kerry, Valencia sound, 51°56'45"N 10°17'18"W, sand, 10 m depth, 1990-2000, S. De Grave leg. TMU 12 170: about 10 specimens, Portrance, years 1990-2000, S. De Grave leg. **France:** TMU 12 280: 1 specimen, English Channel, Saint-Michel-en-Grève, 48°41'N 03°35'W, sheltered shore, lower part of the shore, fine sand, 17.iv.2003, fixed alive in absolute alcohol, leg. C. d'Udekem d'Acoz. TMU 12 267: 6 specimens, English Channel, Saint-Efflam, 48°41'N 03°37'W, sheltered shore, lower part of the shore, fine slightly muddy sand, 20.iv.2003, fixed in 95% alcohol, leg. C. d'Udekem d'Acoz. TMU 12 268: 5 specimens, same sample, fixed in 95% alcohol. TMU 12 269: 10 specimens, same sample, in alcohol 70%. TMU 12 270: 10 specimens, same sample, in 70% alcohol. TMU 12 294: 1 ovigerous female, English Channel, Saint-Jean-du-Doigt, 48°42'N 03°47'W, exposed shore, sand, lower part of the shore, 19.iv.2003, fixed in 95% alcohol, leg. C. d'Udekem d'Acoz. MNHN, previously Am 2565: 1 specimen (previously identified as *B. guilliamsoniana* and mixed with *B. guilliamsoniana*, *B. pelagica* and *B. tenuipes*), Bay of Biscay, Le Croisic, 47°18'N 02°31'W, Stations 55, 75, 87, collection Ed. Chevreux. MNHN, previously Am 5244: 7 ex. (previously identified as *B. pelagica* but mixed together with *B. tenuipes* and *B. pelagica*), Bay of Biscay, 'baie du Croisic', collection Ed. Chevreux. MNHN Am 5243: 21 ex. (previously identified as *B. pelagica*), Bay of Biscay, Arcachon, banc du Bernet, lower shore, stn. 763, 11.ix.1912, collection Ed. Chevreux, MNHN previously Am 2571: several specimens (previously identified and mixed together *B. guilliamsoniana*) France, Bay of Biscay, Arcachon, Station 760, viii.1912, collection Ed. Chevreux.

Description.— Species of normal robustness. Eye with well-developed ommatidia in adults. Pseudorostrum with rounded to fairly angular tip, of normal height, not overhanging to strongly overhanging, with 2-5 proximoventral plumose setae in adults; development and number of apical spines normal. Major flagellum of A1 with 5-7 articles in females, 8-13 in males; first article of accessory flagellum with two to three non-apical groups of spines. Flagellum of A1 in males of normal length (combined length of major flagellum and distal two articles of peduncle always much shorter than twice length of pseudorostrum). Anterior border of third article of peduncle of A2 usually with one group of spinules and setae in apical position only; fourth article with lateral and apical spinules; flagellum with 7-10 articles in females, 28-47 in males (highest numbers observed in largest specimens); A2 of adult males as long as, to distinctly longer than, body length. In females, ratio between length and width of fourth article of A2: 3.0 to 3.5, of fifth article: 3.0.

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with 4-6 strong setae on dorsal surface, all or all but one in one row; third article with longitudinal row of setae on dorsal side (in addition to two transversal groups of anterior setae); outer plate with 5-8 nodular spines (most commonly six).

Coxa 1 not especially elongate, with tip narrowly rounded, with ventral tooth (with one seta associated with this tooth), with 3-14 anterior setae in mature females, without apical setule.

Coxa 2 with posterior tooth; tooth separated from coxa by deep notch; transition between anterior and ventral border fairly to perfectly gradual, with or without slight angular discontinuity; anterior border straight to convex; anterior and posterior border almost parallel (faintly converging downwards); ventral border with 16-40 irregular- to very irregular-sized setae in adult females, of normal width or thickness, longest setae of normal length (the number of setae increases with body-size); mesial setae variable in number (5-17).

Coxa 3 with posterior tooth; tooth separated from coxa by deep notch; anterior

and posterior border slightly converging downwards; ventral border with 17-34 irregular-sized setae in adult females, of normal width, longest setae of normal length (number of setae increases with body-size); mesial setae variable in number (5-15).

Coxa 4 with 32-84 irregular-sized setae in adult females, of normal width, longest setae of normal length (number of setae increases with body-size); posterior setae not setulose.

Propodus of P1 rather elongate.

Length/width ratio of carpus of P2: 3.0-3.5; ratio between propodus length and carpus length: 0.80-0.85.

P3 with carpal fang nearly reaching tip of propodus or overreaching it, distally styliform, without accessory setule; propodus slender; outer spines/setae of propodus 'normal' in number (7-12), size and shape; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly concave. Ratio between propodus length and merus length of P3 in adult females: 1.0. Ratio between dactylus length and propodus length of P3 in adult females: 0.25-0.35. Ratio between dactylus length and merus length of P3 in adult females: 0.25-0.35. Ratio between length and width of propodus of P3 in adult females: 5.5-7.5. Ratio between length and width of dactylus of P3 in adult females: 4.0-4.5 (sometimes 3.5). Ratio between unguis length and total length of dactylus of P3 in adult females: 0.25-0.35. Ratio between unguis length and dactylus width in P3 of adult females: 1.0-1.5.

P4 with carpal fang nearly reaching tip of propodus or overreaching it, distally styliform, without accessory setule; propodus slender; outer spines/setae of propodus 'normal' in number (7-11), size and shape; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly concave. Ratio between propodus length and merus length of P4 in adult females: 0.75-0.85. Ratio between dactylus length and propodus length of P4 in adult females: 0.30-0.40. Ratio between dactylus length and merus length of P4 in adult females: 0.25-0.35. Ratio between length and width of propodus of P4 in adult females: 4.5-6.0. Ratio between length and width of dactylus of P4 in adult females: 4.0-5.0. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.20-0.40. Ratio between unguis length and dactylus width in P3 of adult females: 1.0 to 1.5.

Median part of anterior border of basis of P5 nearly straight (very faintly concave) or with distinct concavity; posteromedian seta group of merus with one long and strong curved major seta and 0-1 (very rarely 2) non-setulose accessory setae, usually, but not always, long; posterodistal seta group with one long and strong curved or straight seta (reaching at least 0.65 of carpus and occasionally overreaching it in females), and 1-3 setules (no important sexual dimorphism); anterodistal area always with plumodenticulate setae; longest posterior spine of carpus reaching or overreaching tip of propodus; ratio between carpus + propodus length and merus length in adult females: 0.80-0.90.

Posterodistal lobe of basis of P6 protruding and wide; anterior border strongly and regularly convex; posterior border strongly convex in its proximal 0.25, moderately convex on its distal 0.75; in females, anterior border with succession of several narrow non-setulose setae (or appearing as such in light microscopy), several strong plumose spines/setae, several strong non-setulose spines/setae. Merus of P6 with 3-6 (usually 4-5) posterior groups of spines/setae (proximal group often reduced to single seta)

and 6-8 (sometimes nine) anterior groups; longest seta of each anterior seta group of significantly increasing size towards distal part of merus; carpus without posterior spines (distal group not considered) (tens of specimens have been examined); propodus with 1-3 posterolateral, and 2-4 anteromesial groups of spines (terminal crown of spines not considered). Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 0.85-0.90.

Posterior border of basis of P7 with robust ornamentation (spines); spines slightly irregular in size, shortest average size in middle of border, 10-38 spines in adult females, 6-17 in adult males (highest number in largest animals; number also population dependent); mesial side usually with spines in females. Ischium moderately elongate, reaching 0.37 to 0.41 of outer side of merus (five specimens measured); anterodistal border faintly concave on outer side, moderately concave on mesial side; posterodistal border faintly concave both on outer and mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 2.5-3.0, of propodus: 6.0-7.5, ratio between length of carpus and length of propodus: 0.90-0.95, ratio between length of propodus + carpus and length of basis: 1.5.

Middle of posterior border of Ep1 and Ep2 angular and produced in tooth.

Ep3 with posteroventral border regularly rounded, without posteroventral tooth, with 2-5 transverse groups of spines in adults, or with one transverse group of spines anteriorly followed by four single spines, with 0-3 setules on posterior border (i.e. low number).

Urosomite 1 with one pair of anteriorly directed setae, and one pair of posteriorly directed spines (sometimes two pairs, at least in Forma B) dorsally; ventrolateral border without strong setae arising from outer side.

Peduncle of uropod 1: outer dorsal border with 6-14 spines consisting of following succession: 1) 4-12 regularly spaced short robust spines, of slightly and gradually increasing size towards tip, 2) larger space followed by penultimate short robust spine, 3) very short space followed by very strong ultimate spine; dorsomesial border with styliform spines, mostly single but some in groups of two (5-11 groups). Endopod and exopod of normal length and robustness; endopod with border facing exopod, with only one long spine in subdistal position. Spines on endopod and exopod of normal robustness. Dorsal ratio between length of endopod and length of peduncle about 0.85 (one female measured). Dorsal ratio between length and width of endopod 6.5 (one female measured).

Peduncle of uropod 2: of normal proportions (dorsal ratio between length and width in mature female 2.6), outer dorsal border with 4-9 short and robust spines; dorsomesial border with 2-5 single, robust spines. Endopod and exopod of normal length and robustness; endopod with border facing exopod with only one long spine in subdistal position. Spines on endopod and exopod of normal robustness. Dorsal ratio between length and width of endopod 4.5.

Setation of uropod 3 without strong sexual dimorphism. Peduncle of uropod 3 with distal spines in normal number, longest spines about as long as endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with 2-4 groups of 1-6 thin and slender, not very long setae. Endopod elliptic, with 2-3 spines. Exopod with first article narrow, second article long. Second article of exopod with 1-4 (sometimes 0) lateral setae on mesial side and 0-2 on outer side. Mesial side of exopod (first

and second articles together) with 8-18 long plumose setae of normal morphology, and 3-10 well-developed accessory spiniform non-setulose setae, all (except one or two proximalmost) plumose setae much longer than longest setae on outer side (in both sexes). Outer side of exopod (first and second article together) with 4-9 groups of 1-3 spiniform setae, slightly shorter than, or about as long as, exopod width. Ratio between length and width of second article of exopod: 4.0-5.5. Ratio between length of second article and length of first article: 0.35-0.40 (sometimes 0.30). Ratio between length of second article and width of first article: 1.6-2.1 (sometimes 1.4). Ratio between length of second article of exopod and length of endopod: 1.3-2.1.

Lobes of telson without mesial setae.

Colour pattern.— Appearance with naked eye: usually pale greyish, sometimes orange; under dissecting microscope whitish, usually with green longitudinal line in viscera, with bright red eyes; extruded eggs and filled ovaries pinkish purple. In specimens freshly fixed in alcohol, eye usually white, but grey in some specimens (original colour description after shore specimens from Tromsø area, northern Norway). Faasse & Stikvoort (2002) give a similar colour description for Norwegian specimens, describing them as yellowish brown. White, eyes bright red; viscera yellowish; eggs whitish (original colour description after specimens from the shores of Saint-Efflam and Saint-Jean-du-Doigt, France). Watkin (1938) gives the following colour description, presumably based on specimens from Kames Bay, southwestern Scotland: "Eyes with bright red pigment. The body of both male and female is translucent with practically no pigment. The colour of the eggs is yellowish."

Size.— Up to 6 mm (Watkin, 1938).

Ecology.— From the lower part of the shore (Watkin, 1939b, 1942; Colman & Segrove, 1955a), as high as the level of *Fucus serratus* Linnaeus, 1753 in northwestern Europe (see Toulmond & Truchot, 1964), down to 69 m depth (Reibisch, 1905 as *B. pelagica*). Recorded on fine or muddy sand (Lincoln, 1979). Community of sand sediments with *Abra alba* (W. Wood, 1802) and *Corbula gibba* (Olivi, 1792): sandy facies with *Aponuphis bilineata* (Baird, 1870) (as *Hyalinoecia bilineata*), where it can be quite common (Cabioch, 1968: 634). Usually not very abundant in the intertidal zone (Watkin, 1939b, 1942), although it may locally be the dominant species (Toulmond, 1964; Toulmond & Truchot, 1964). In the southern North Sea, it is the commonest subtidal *Bathyporeia* species (Tesch, 1916 as *B. pelagica*). Most abundant in fine sand mixed with shell; also on very fine, medium and coarse sands mixed with shell or gravel; low densities when organic matter, *Echinocardium* or worm tubes, are present (Fincham, 1969). According to Vader (1965), less tolerant to mud than *B. guilliamsoniana* and *B. pilosa*. Euryhaline species found both on open coasts and in estuarine habitats (Vader, 1966). Occasionally parasitized by the nicothoid copepod *Sphaeronella paradoxa* Hansen, 1897 (Hansen, 1897 as *Bathyporeia pelagica*; Toulmond & Truchot, 1964; Gotto, 1983).

Biological references.— Zonation pattern: Watkin (1939b, 1942), Stock & de Vos (1960), Toulmond (1964), Toulmond & Truchot (1964), Howells (1964), Colman & Segrove (1955a, 1955b), Fincham (1971). Granulometry preference: Spooner (1957), Stock & de Vos (1960), Vader (1966), Withers & Thorp (1978). Burrowing behaviour: Watkin (1939a). Swimming behaviour: Watkin, (1939a, 1939b), Colman & Segrove (1955b), Bossanyi (1957). Dynamics of populations: Dauvin (1987). Long-term variations in population density: Rachor & Gerlach (1978), Dauvin (1987). Pollution sensitivity: Dauvin

(1987). Fish predation: Poxton et al. (1983), Beare & Moore (1997). Parasites: Hansen (1897, as *B. pelagica*), Toulmond (1964), Toulmond & Truchot (1964), Gotto (1993).

Distribution.— Eastern Atlantic: all the coasts of Norway (Brattegard & Holthe, 1997); as far north as Vardø 70°22'N 31°06'E (Schneider, 1926 as *B. pelagica*); Sweden [Bohuslän] (Oldevig, 1959); Denmark (Schellenberg, 1942); Germany (Schellenberg, 1942; Stock & de Vos, 1960; Gosselck et al., 1993; Kröncke et al., 2001); Doggerbank (Kröncke, 1991); The Netherlands (Vader, 1965, 1966; Faasse & Stikvoort, 2002); Belgium (Leloup & Konietzko, 1956; Ysebaert et al., 2000); all the coasts of the British Isles (Watkin, 1938; Lincoln, 1979); French part of the English Channel (Toulmond & Truchot, 1964; Dauvin, 1999; Dauvin & Bellan-Santini, 2002); all the French coasts of the Bay of Biscay (Salvat, 1964; Lagardère, 1966; Faure, 1969; de Montaudouin & Sauriau, 2000); Spanish coasts of the Bay of Biscay (Lastra et al., 1990); northwestern Spain (Currás & Mora, 1991); southwestern Portugal (Rodrigues & Dauvin, 1985; Marques & Bellan-Santini, 1985, 1991). There are records from Morocco (Elkaïm, 1976a; Menioui & Bayed, 1986), "North Africa", Madeira and Canary Islands (Lincoln, 1979), which require confirmation.

Taxonomical remarks.—Vader (1966) already pointed out that *B. elegans* is a very variable species. The size of the specimens considerably varies from population to population, and small adult *B. elegans* can be difficult to separate from *B. nana* (see section on that species). However, *B. elegans* also exhibits significant geographical variations and two "forms" are recognized here: a northern morphologically homogeneous typical Forma A, found along the coasts of Norway, and a more variable Forma B of more southern occurrence (British Isles, Germany, The Netherlands, Belgium, France). As a rule, for any given size, Forma B is more spiny and setose than Forma A. Both forms have been illustrated in detail and the differences between them are listed below.

Shape of tip of pseudorostrum.— Forma A: rounded, not or slightly overhanging; Forma B: rounded to bluntly angular, faintly to strongly overhanging.

Number of proximoventral setae on pseudorostrum.— Forma A: 2 in adults (sometimes 1 in large immatures); Forma B: 2-5 (usually 3- 4).

Number of anterior setae on coxa 1 in mature females.— Forma A: 3-4; Forma B: 6-14.

Number of ventral setae on coxa 2 in mature females.— Forma A: 16-25; Forma B: 16-40.

Number of mesial setae on coxa 2 in mature females.— Forma A: 5-9; Forma B: 9-17.

Number of ventral setae on coxa 3 in mature females.— Forma A: 17-25; Forma B: 17-34.

Number of mesial setae on coxa 3 in mature females.— Forma A: 5-7; Forma B: 6-15.

Number of marginal setae on coxa 4 in mature females.— Forma A: 32-45; forma B: 40-84.

Relationship in P5 between length of longest posterior spine of carpus and length of propodus.— Forma A: spine never reaching tip of propodus and often far from reaching tip; Forma B: usually overreaching tip of propodus (occasionally a little shorter).

Number of posterior spines on basis of P7 in mature females.— Forma A: 10-17; Forma B: 14-38.

Number of outer dorsal spines on peduncle of uropod 1.— Forma A: 6-9; Forma B: 8-14 (usually 9-13).

Number of outer dorsal spines on peduncle of uropod 2.— Forma A: 4-5; Forma B: 5-9 (most commonly 6-7).

Number of setae on mesial side of uropod 3 exopod.— Forma A: 8-13; Forma B: 10-18.

Number of spine groups on outer side of uropod 3 exopod.— Forma B: 4-5; Forma B: 5-8 (sometimes 9).

Ornamentation of mesial border of second article of exopod in uropod 3.— Forma A: 0-2 setae (tens of specimens have been checked); Forma B: 1-4 setae.

Ornamentation of outer border of second article of exopod in uropod 3.— Forma A: always devoid of setae (tens of specimens have been checked); Forma B: 0-2 setae (most commonly 1-2 setae).

Egg colour.— Forma A: pinkish purple (present examination of specimens from Tromsø area); Forma B: yellowish (Watkin, 1938) or whitish (present examination of specimens from France).

Size.— Forma A: up to 4.5 mm; Forma B: up to 5.5 mm.

The significance of these small differences is currently unknown. I have spent a considerable time on their examination, but the situation remains unclear and puzzling. More extensive studies, eventually with a molecular approach, are necessary to clear the taxonomic value of the differences observed between populations.

Interestingly, when examining their French material of "*Bathyporeia pelagica*" (actually a mixture of *B. elegans* and *B. pelagica*), Chevreux & Fage (1925: 94) already detected some differences between northern and southern specimens, since they state: "diffère de la forme norvégienne par ses périop.[périopodes] plus épineux et par la présence de soies au 2e [deuxième] art.[article] de la branche ext.[externe] des urop.[uropodes] III" [They differ from the Norwegian form by their more spiny pereopods, and by the occurrence of setae on the second article of the exopod of the third uropod].

Nomenclatural remarks.— It was Crawford (1937: 639), who first introduced the name *Bathyporeia elegans*, in very singular circumstances. His account runs as follows: "*Bathyporeia elegans* Sars is a name applied to a slender form of *B. pelagica* with less well-developed eyes. The specimens of this genus [*Bathyporeia*] from the finer sand of Cawsand Bay were of this form, but it is doubtful if it is a distinct species."

One year later, Watkin (1938) published a "normal" description of a *Bathyporeia elegans*, as "*B. elegans*, nom. nov.", the term "nom. nov." alluding to the fact that the name *Bathyporeia pelagica* Bate, 1857 had long been erroneously applied to Watkin's species. Watkin (1938: 222, footnote) referred to Crawford's paper, as follows: "Mr. G. I. Crawford desires me to state that his reference to *B. elegans*, this *Journal* Vol. XXI, p. 639, line 4, is an error and should be read *B. gracilis*."

Actually, Crawford (1937) obviously had knowledge of the -then unpublished-name *Bathyporeia elegans* Watkin, intended to write *Bathyporeia gracilis* Sars, but in a surprising lapsus used the name *elegans* instead of *gracilis*, resulting in the abnormal combination '*Bathyporeia elegans* Sars'. That mistake could have serious nomenclatural implications, since the account of '*Bathyporeia elegans* Sars' by Crawford (1937) includes descriptive information, i.e. it is not a nomen nudum.

The International Code of Zoological Nomenclature (fourth edition), article 13.1 states that to be available, every new name published after 1930 must satisfy the provisions of Article 11 [effective publication of a name properly constructed] and must

13.1.1 be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon. Crawford's (1937) account fulfills these conditions, despite the fact that he clearly did not intend to create a new species. Therefore, on these bases, *Bathyporeia elegans* Watkin, 1938 could be considered as a junior homonym of *Bathyporeia elegans* Crawford, 1937. If that homonymy status is admitted, then Article 52.2 states that: "When two or more names are homonymous, only the senior, as determined by the Principle of Priority (see Article 52.3), may be used as a valid name; for exceptions see Articles 23.2 and 23.9 (unused senior homonyms) (...)." The article 23.9 on the reversal of precedence states: "In accordance with the purpose of the Principle of Priority [Art. 23.2], its application is moderated as follows: 23.9.1. prevailing usage must be maintained when the following conditions are both met: 23.9.1.1. the senior synonym or homonym has not been used as a valid name after 1899, and 23.9.1.2. the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least ten authors in the immediately preceding 50 years and encompassing a span of not less than ten years." In the present case, the article 23.9.1.2 is respected but not the article 23.9.1.1, since the name has first been introduced in 1937. So, according to the articles 23.9.1.1 and 23.9.1.2, a replacement name should be introduced.

However, the introduction of a substitution name would be far from desirable, since Watkin's name has been consistently used for that species in a considerable number of papers (mostly benthos studies) for over 60 years. Furthermore, the introduction of the name "*Bathyporeia elegans* Sars" by Crawford (1937) has been made in very unorthodox conditions, being a lapsus for "*Bathyporeia gracilis* Sars".

I have submitted this thorny problem to Prof. Sandro Minelli (University of Padova), who has been kind enough to examine it carefully. He proposed to me an artful solution to preserve Watkin's name:

"Your case, very unusual and apparently puzzling, does not seem to me, indeed, to be too difficult or 'risky'.

As far as I can understand, there is no doubt that Crawford did not intend to establish a new species. There is no need to wait for Watkin's note ["Mr. G.I. Crawford desires me to state etc.] to be certain of this circumstance, as Crawford (1937) specified an author's name (Sars) after the specific name '*elegans*'.

In my opinion, this case may be treated as an exceptional case of incorrect subsequent spelling. A case, to be sure, where the change in respect to the original spelling is not an orthographic variant but, as you have explained, a "subconscious contamination" from a still unpublished name circulated in private correspondence. A bad lapsus memoriae, rather than a lapsus calami. Nevertheless, something I would treat under Art. 33.3. That amounts as to regard "*Bathyporeia elegans* Crawford, 1937" as unavailable and, therefore, simply not existing from the point of view of nomenclature, but for listing in the bibliography/synonymy of *B. elegans*.

No harm, by consequence, in continuing to use Watkins's name. (...) I hope this short discussion may help you taking a decision, although I can easily understand that many zoologists may arrive at a conclusion other than the one sketched here."

For the sake of nomenclature stability, I think that it is preferable to follow the recommendations of Prof. Minelli, and the name *Bathyporeia elegans* Watkin, 1938, is therefore maintained in the present paper. However, as requested by Dr Hans Georg

Andres (in litt.), the case will be submitted to the International Commission for Zoological Nomenclature, in order to suppress Crawford's name.

The real identity of *Bathyporeia elegans* Crawford, 1937 is not clear, although it is definitely not *B. elegans* Watkin, 1938. In a footnote, page 222, Watkin (1938) wrote: "Mr. G. I. Crawford desires me to state that his reference to *B. elegans*, this Journal Vol. xxi, p. 639, line 4, is an error and should be read *B. gracilis*." However, Watkin (1938) apparently did not accept Crawford's identification, since on page 225, he indicates "*B. elegans* Crawford, 1937 a, p. 639" in the synonymy of *Bathyporeia tenuipes* Meinert, 1877, and gave no comments in his account of *B. gracilis* G.O. Sars, 1891. The morphological account of Crawford is poor but it indicates that it is a slender species with eyes less developed than in *B. pelagica*. This combination of characters agrees better with *B. gracilis* than with *B. tenuipes*. Indeed, while both species are slender (especially *B. tenuipes*), the eyes of *B. tenuipes* are well-developed and those of *B. gracilis* vestigial. However, he may have found either of those species. No type has been designated for *B. elegans* Crawford, 1937 and it is doubtful that any material has been preserved.

5.4.2. *Bathyporeia gracilis* G.O. Sars, 1891 (figs. 19-25)

Bathyporeia gracilis G.O. Sars, 1891: 132, pl. 45 fig. 1; Stebbing, 1906: 121; Watkin, 1938: 227, fig. 1h-m; Stephensen, 1929: 83, in part, fig. 20.95 (after G.O. Sars); Gurjanova, 1951: 344, fig. 203 (after G.O. Sars); Toulmond, 1966: 229 (discussion), 231, (key); Vader, 1970: 155, fig. 1-5; Bellan-Santini, 1973: 101, table II; Lincoln, 1979: 314, 322, fig. 151h-l (after G.O. Sars); Enckell, 1980: 519, fig. 2394 (after Watkin).

? *Bathyporeia elegans* Crawford, 1937: 639 (not *Bathyporeia elegans* Watkin, 1938).

Not *Bathyporeia gracilis*; Norman, 1900: 331, no morphological account (= *Bathyporeia tenuipes* Meinert, 1877, see Lincoln, 1979: 318); K.H. Barnard, 1951: 704 (probably an undescribed species); Day, 1959: 528 (ibid.).

Types.— G.O. Sars (1891) states that: "Only two specimens, male and female, have hitherto come under my notice. They were both taken, a long time ago, off the west coast of Norway, from rather deep water, the exact locality not stated." Watkin (1938) states that the male only is extant. Vader (1970) states that of Sars' type-material, the female specimen has apparently been dissected and lost, but that the male is still present in the collections of the Zoologisk Museum, Oslo. He indicated that the male syntype of *Bathyporeia gracilis* (Zoologisk Museum, Oslo, reg. no. F 2130) is labelled "*Bathyporeia gracilis* G. O. Sars, Norv. Occident., GOS and that this specimen was examined in toto, after clearing in lactic acid. See also the section 'material examined'.

Material.— **Norway:** ZMO F2130: 1 adult male, syntype, Western Norway [original Sars' label: "*Bathyporeia gracilis*, GO Sars Norv. occident. GOS"]. TMU 4926: 1 adult female, North Sea, Odin, 60°08'N 02°17'E, 106 m depth, St. 10-1, leg. Akvaplan, 08/vi/1991 [ommatidia poorly developed]. **Ireland:** TMU 4923: 1 adult female (fully dissected and mounted in Faure's liquid), Valencia, no exact coordinates, depth <15m, sandy bottom, 1990-2001, S. De Grave coll., [ommatidia absent; a lot of colonial peritrich ciliates on appendages]. NMWZ 1997.052: 1 female with 1 egg, Amphipoda Irish Sea, Swiss Stn. 98A, leg. D. McGrath [ommatidia scarcely distinct].

Description.— Species of normal robustness to fairly slender. Eye with incompletely developed ommatidia or no ommatidia in adults. Pseudorostrum with more or less rounded tip, of normal height, not or very slightly overhanging, with 2-3 proximoventral plumose setae in adults; development and number of apical spines normal. Major flagellum of A1 with 5-6 articles in females, eight in male syntype; first article of accessory flagellum with 2-3 non-apical groups of spines in females examined, apparently none on female illustrated by Vader (1970), three in male syntype. Flagellum of A1 of male of normal length (combined length of major flagellum and two distal articles of peduncle much shorter than twice length of pseudorostrum). Anterior border of article 3 of peduncle of A2 with one group of distal spinules and 1-2 single strong setae in more proximal position; fourth article with lateral and apical spinules; flagellum with 7-8 articles in females examined, and 12 in male syntype, A2 of adult male much shorter than body length. In females, ratio between length and width of fourth article of A2: 3.5, of fifth article: 3.5 (2 females measured).

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with about four strong setae on dorsal surface, all but one in one row; third article without longitudinal row of setae on dorsal side (only transversally-rowed anterior setae present); outer plate with seven nodular spines, in dissected female.

Coxa 1 fairly elongate, with tip narrowly rounded, without ventral tooth but with more or less distinct notch (with one seta associated with this notch), with 10-11 anterior setae in dissected female [7 setae on figure of Vader (1970)], without apical setule.

Coxa 2 with posterior tooth; that tooth separated from coxa by deep notch; transition between anterior and ventral border fairly gradual, with slight angular discontinuity; anterior border straight; anterior and posterior border parallel; females with ventral border with 21-28 very irregular-sized narrow setae in females examined [17 on figure of Vader (1970)], longest setae not especially long; mesial setae not in unusually high number: seven in dissected female and three on figure of Vader (1970).

Coxa 3 with posterior tooth; that tooth separated from coxa by deep notch; anterior and posterior border parallel; females with ventral border with 18-33 very irregular-sized narrow setae, longest setae not especially long; mesial setae not in unusually high number: five in dissected female and eight on figure of Vader (1970).

Coxa 4 with 39-60 very irregular-sized narrow setae, of normal width, longest setae not especially long; posterior setae not setulose.

Propodus of P1 of normal proportions.

Length/width ratio of carpus of P2: 3.0; ratio between propodus length and carpus length: 0.90.

P3 with carpal fang reaching about tip of propodus, distally styliform and without accessory setule; propodus slender; outer spines/setae of propodus 'normal' in number (7-8), normal in size, long setae normal in shape, short setae slender; dactylus slender, with well-developed unguis, with posterior border straight to faintly concave. Ratio between propodus length and merus length of P3 in adult females: 0.90. Ratio between dactylus length and propodus length of P3 in adult females: 0.30-0.35. Ratio between dactylus length and merus length of P3 in adult females: 0.25. Ratio between length and width of propodus of P3 in adult females: 5.5-6.5. Ratio between length

and width of dactylus of P3 in adult females: 4.5-5.0. Ratio between unguis length and total length of dactylus of P3 in adult females: 0.25. Ratio between unguis length and dactylus width in P3 of adult females: 1.0-1.5.

P4 with carpal fang nearly reaching tip of propodus or distinctly shorter, distally styliform, without accessory setule, or fairly blunt with accessory setule slightly longer than tip; propodus slender; outer spines/setae of propodus 'normal' in number (7-9), size and shape; dactylus slender, with well-developed unguis, with posterior border straight to faintly concave. Ratio between propodus length and merus length of P4 in adult females: 0.80. Ratio between dactylus length and propodus length of P4 in adult females: 0.30. Ratio between dactylus length and merus length of P4 in adult females: 0.25. Ratio between length and width of propodus of P4 in adult females: 4.5-5.0. Ratio between length and width of dactylus of P4 in adult females: 4.0. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.25-0.30. Ratio between unguis length and dactylus width in P4 of adult females: 0.95-1.0.

Median part of anterior border of basis of P5 straight to inconspicuously convex; posteromedian seta group of merus with one long, strong curved seta, and one non-setulose short or very short accessory seta; posterodistal seta group with one long, strong, slightly curved seta (reaching 0.85-0.95 of carpus in females, about 0.65 in male syntype), and one or two setules (only slight sexual dimorphism in posterodistal seta group); anterodistal area with plumodenticulate setae; longest posterior spine of carpus overreaching or not reaching tip of propodus; ratio between carpus + propodus length and merus length in adult females: 0.95.

Posterodistal lobe of basis of P6 weakly protruding and very wide; anterior border strongly and regularly convex; posterior border moderately convex on largest part of its length; in females, anterior border with succession of several narrow non-setulose setae (or appearing as such in light microscopy), several strong plumose spines/setae, one distal strong non-setulose spine/seta. Merus of P6 with 4-5 posterior groups of spines/setae (proximal two setae poorly developed) and six anterior groups; longest seta of each anterior seta group of slightly increasing size from proximal towards distal part of merus; carpus with group of posterior spines (in addition to distal group); propodus with three posterolateral and three anteromesial groups of spines (terminal crown of spines not considered) in specimen dissected [two posterolateral and three anteromesial groups in figure of Vader (1970)]. Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 1.1.

Posterior border of basis of P7 with fairly robust ornamentation (spines), shortest average size of spines on middle of border, this median shortening weak and with little variation in individual size of spines; number: 13-17 in adult females, number unknown in adult males but probably less; mesial side without spines in dissected female. Ischium distinctly elongate, reaching 0.50 of outer side of merus; anterodistal border slightly concave both on outer and mesial side [more concave on the figure of Vader (1970) than in female dissected]; posterodistal border straight on outer and mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 3.5, of propodus: 6.0, ratio between length of carpus and length of propodus: 1.2, ratio between length of propodus + carpus and length of basis: 1.5.

Middle of posterior border of Ep1 and Ep2 angular but not produced in tooth.

Ep3 with posteroventral border regularly rounded, without posteroventral tooth, with 3-6 transverse groups of spines, with 4-6 setules on posterior border.

Urosomite 1 with one pair of anteriorly directed setae, and three pairs of posteriorly directed and similar-sized spines [according to G.O. Sars (1891), there were only two pairs of spines in now lost female syntype] dorsally; ventrolateral border with 2-3 long strong setae arising from outer side.

Peduncle of uropod 1: outer dorsal border with 7-8 spines consisting of following succession: 1) 3-4 regularly spaced slender spines (the two proximalmost fairly long), 2) 1-2 regularly spaced, short, fairly robust spines, 3) larger space followed by one penultimate, fairly short, robust spine, 4) very short space followed by one very strong, ultimate spine; dorsomesial border with styliform (nearly setiform) spines, single or in groups of two (6-8 groups). Endopod and exopod of normal length and robustness; endopod with border facing exopod, with only one long spine, in subdistal position. Spines on endopod and exopod of normal robustness, except for fairly long and slender mesial spines of endopod. Dorsal ratio between length of endopod and length of peduncle: about 0.80. Dorsal ratio between length and width of endopod: 6.5.

Peduncle of uropod 2: of normal proportions (dorsal ratio between length and width in mature female = 2.8), outer dorsal border with five fairly short to fairly long, and fairly slender to markedly slender spines; dorsomesial border with four groups of 1-2 styliform to setiform spines. Endopod and exopod of normal length and robustness; endopod with border facing exopod, with only one long spine in subdistal position. Endopod and exopod spines of normal robustness, except for very long and very slender mesial spines of endopod. Dorsal ratio between length and width of endopod: 6.0.

Peduncle of uropod 3 with distal spines in normal number, longest spine distinctly overreaching endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with 3-4 groups of one to three thin and fairly long setae in dissected female [three groups on Vader's (1970) drawing]. Endopod elliptic, with 3-4 spines of fairly similar size in dissected female [five spines on Vader's (1970) drawing]. Exopod with first article narrow, second long. Second article of exopod without lateral setae. Mesial border of exopod with seven non-long, non-plumose setae, 2-4 being associated with one well-developed, accessory, spiniform, non-setulose seta, none of mesial setae significantly longer than longest setae of outer side. Outer side of exopod with 4-5 groups of 3-4 (sometimes 2) spiniform setae, each group including two setae longer than exopod width. Ratio between length and width of second article of exopod: 5.0. Ratio between length of second article and length of first article: 0.35. Ratio between length of second article and width of first article: 1.8. Ratio between length of second article of exopod and length of endopod: 1.5.

Lobes of telson without mesial setae.

Colour pattern.— Unknown. Eye colourless in alcohol.

Size.— 6 mm (Lincoln, 1979).

Ecology.— In coarse sand or gravel, between 11 and 35 m (Jones, 1948, 1963), and down to 106 m depth (present material).

Distribution.— Western Norway [no further detail] (G.O. Sars, 1891); Odin (present data), Helgoland (Harms, 1993; Kühne & Rachor, 1996); Valencia in Ireland (present data); Isle of Man (Jones, 1948, 1963; Lincoln, 1979); Roscoff (Dauvin, 1981, 1988); south-western Portugal (Marques & Bellan-Santini, 1991, 1993).

Remarks.— On the basis of the examination of very limited material, Vader (1970) considered that the proportions of the second article of the accessory flagellum of A1 were probably a diagnostic character in *B. gracilis*. However, that article exhibits considerable size differences on left and right sides in the present dissected female. So, that character should not be retained as of diagnostic value. In other species too, it exhibits considerable individual variations. On the other hand, Vader (1970) suspected that the incomplete development of the eyes, as stated by G.O. Sars (1891), could be an artefact due to long preservation in alcohol. However, at least the four specimens examined, which were in good condition, had indeed imperfect eyes. The variability of that character should be carefully examined when more specimens will become available.

Watkin (1938) considered *B. gracilis* and *B. tenuipes* as closely related, and indeed, they have many characters in common: anterior part of third article of A2 often with spines/setae at three different positions (or even more); penultimate article of maxilliped palp without a longitudinal row of setae on the inner side; shape of coxa 1; well-developed tooth on coxa 2 and 3, but not on coxa 1; presence of at least one group of spines on the posterior border of the carpus of P6 (in addition to the distal group); propodus of P6 very narrow and slightly longer than anterior length of merus; third epimeral plate without posterior tooth; ventrolateral border of first urosomite with several strong outer setae; most commonly two or more posteriorly directed similar-sized dorsal spines on first urosomite; peduncle of first uropod with two kinds of outer dorsal spines.

B. gracilis is by far the most rarely recorded *Bathyporeia* species from western Europe. Its imperfect eyes are perhaps an indication that it lives deeper and more permanently in the sediment than other species, the loss of eyes being a frequent evolutionary trend in fossorial amphipods (Thurston & Bett, 1993: 866). The reduction of the flagellum of the second antenna in males (probably important for the detection of females in the pelagic migration in other species) could indicate that it remains permanently concealed in the sediment. This speculated deep-burrowing behaviour of *B. gracilis* could partly explain the scarcity of records of that species.

5.4.3. *Bathyporeia guilliamsoniana* (Bate, 1857) (figs. 26-36)

Thersites Guilliamsonia Bate, 1856: 59 (nomen nudum).

Thersites Guilliamsoniana Bate, 1857a: 146; White, 1857: 187 (discussion).

Bathyporeia Guilliamsonia; Bate, 1857b: 271.

Bathyporeia pilosa; Bate, 1857b: 271 (in part).

Bathyporeia pilosa; White, 1857: 188; Bate, 1862: 172, pl. 31 fig. 4; Bate & Westwood, 1862: 304, unnumbered fig. (after Bate, 1862); Boeck, 1872: pl. 7 fig. 3; Boeck, 1876: 209; Stebbing, 1875: 75, in part, ? pl. 3.

? *Bathyporeia pontica* Marcusen, 1867: 359.

Bathyporeia norvegica G.O. Sars, 1891: 128, pl. 43; Della Valle, 1893: 752 (key), 754 [no Mediterranean record]; Scott, 1893: 213, pl. 5 fig. 22; Walker, 1895a: 470; Walker, 1895b: 295; Reibisch, 1905: 157, pl. 4 fig. 2-6.

Thersites Guilliamsonii; Norman, 1900: 330 (erroneous spelling under the discussion on *Bathyporeia norvegica*).

Bathyporeia Guilliamsonia; Norman, 1905: 82, erroneous spelling, no morphological discussion.

Bathyporeia guilliamsoniana Stebbing, 1906: 120, fig. 30; Stephensen, 1929: 83, fig. 20.93 (after Sars); Watkin, 1938: 216, fig. 1a-g; Watkin, 1939a: 460, fig. 2; Schellenberg, 1942: 166, fig. 134 (partly original, partly after G.O. Sars and Watkin); Yashnov, 1948: 283; Gurjanova, 1951: 337, fig. 197 (after Watkin); Toulmond, 1966: 229 (discussion), 231, (key); J.L. Barnard, 1969: 255, fig. 100b; Bellan-Santini, 1973: 101, table II; Lincoln, 1979: 315, 316, figs. 146b, 147a-g, 148a-f; J.L. Barnard & C.M. Barnard, 1983: 230, fig. 28b; Bellan-Santini & Vader, 1988: 239; Köhn & Gosselck, 1989: 72, pl. 22 fig. 1 (after Lincoln); Enckell, 1980: 519, fig. 2388 (after Watkin); Withers, 1990: 445, fig. 9.30 (after Lincoln); Faasse & Stikvoort, 2002: 63, fig. 7.

? *Bathyporeia megalops* Chevreux, 1911: 184, fig. 6, pl. 10 fig. 1-11; Bellan-Santini, 1989: 371, fig. 248.

Bathyporeia guilliamsoniana; Chevreux & Fage, 1925: 92, fig. 84-85.

Bathyporeia guilliamsoniana; Stephensen, 1928: 130, fig. 25.1-7 (after Sars).

? *Bathyporeia guilliamsoniana*; Greze, 1985: 29, fig. 7-8; Bellan-Santini, 1989: 366, fig. 244-245.

Types.— Bate gives the type locality as Weymouth “on a fine sandy bottom”, and Tenby. One tube, labelled No. 50, from Bate’s collection and now preserved in the British Museum contains two females of *B. guilliamsoniana* (see Walker, 1895a as *B. norvegica*). Approximate coordinates of Weymouth: 50°37'N 02°30'W, and of Tenby: 51°40'N 04°41'W. According to Watkin (1938), “It is now impossible to be certain if the two female specimens in tube no. 50 of the Spence Bate collection are the type specimens.”

Material.— **Denmark:** TMU 2931: 2 adult males and 1 immature male, Denmark, no further data. **The Netherlands:** Netherlands Institute of Ecology (NIOO-KNAW), Centre for Estuarine and Marine Ecology (CEMO), Yerseke: 1 specimen, The Netherlands, no more information, M. Rietveld coll. TMU 9434: 1 immature male, 4.5 km from light ship Texel, Ephyra station 257, 0215-0515, 23 m, 22.ix.1966. TMU 9424: over 100 adult specimens (mainly males); The Netherlands, no precise locality, probably collected between 1960 and 1970. RMNH A 4982: 3 adult males, 8 adult females, 37 juveniles, North Sea, 51°35'42"N 02°58'20"E; 34.2 m, grab 1496; 01.vii.1966, leg. W.J. Wolff, WR, JN; det. W. Vader 1966; don. Hydrobiologisch Instituut, afdeling Delatonderzoek. RMNH A 4983: 8 adult females (1 ovigerous) and 15 juveniles (mixed with mysids), North Sea, 51°35'30"N 02°55'36"E, 32.4 m depth; grab 1494; 01.vii.1966, leg. W.J. Wolff, WR, JN; det. W. Vader 1966; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4984: 1 adult female and 1 juvenile, North Sea, 51°30'48"N 02°13'36"E, 9 m depth; grab 1507; 01.vii.1966; leg. W.J. Wolff, WR, JN; det. W. Vader; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. **Belgium:** RUG: 1 large immature male and 1 female; western half of the Belgian coast (western coastal sandbanks), less than 5 km offshore, HA 9910036, 1999-2000, S. Degraer coll. RUG: 3 large immature males and 5 females; western half of the Belgian coast (western coastal sandbanks), less than 5 km offshore, HH 9910046, 1999-2000, S. Degraer coll. **Ireland:** TMU 12 171: 1 adult male, 2 immature males (1 large and 1 small), 1 female (large immature male with four dorsal groups of spines on merus of P6; mature male rather small and with eyes dorsally fused), “BV”, SW Ireland, Bunavalla, small and shallow inlet along the Kerry Coast, fairly sandy environment, depth not known, but shallow, 1990-2000, S. De Grave coll. OUMNH: 3 females and 5 immature males, “BK”, SW coast of Ireland in Co. Kerry (about 20 km from Bunavalla), Ballinskelligs Harbour, 51°49'N 10°16.5'W, a shallow inlet in Ballinskelligs Bay, sheltered to the south by a relatively large island (Horse Island); the area has a relatively large seagrass bed, though this is patchily distributed; depth not known, but shallow, 1990-2000, S. De Grave coll. OUMNH: 1 adult and 1 immature female, “sample V”, Valencia, no exact coordinates, depth <15 m, sandy bottom, 1990-2000, S. De Grave coll. **France:** TMU 12 274: 1 adult male with eyes dorsally fused, English Channel, Saint-Jean-du-Doigt, 48°42'N 03°47'W, exposed shore, sand, extreme lower shore, 19.iv.2003, fixed in absolute alcohol, leg. C. d'Udekem d'Acoz. MNHN Am. 2580: 3 females (one with four dorsal groups of spines/setae on P6), English Channel, Roscoff, 48°43'N 03°59'W, lower shore, previously identified by E. Chevreux as *B. norvegica*, in 1903. MNHN Am. 2565: 1 adult male in poor condition, 1 immature male, 8 females

(merus of P6 with three groups of dorsal spines/setae in all specimens) (previously mixed with *B. pelagica*, *B. elegans* and *B. tenuipes*), Bay of Biscay, Le Croisic, 47°18'N 02°31'W, st. 55,75,87, collection Ed. Chevreux. MNHN Am 2571: 2 specimens (previously identified as *B. guilliamsoniana* but mixed together with *B. elegans*), Bay of Biscay, Arcachon, st. 760, viii.1912, collection Ed. Chevreux. **Spain:** TMU 9746: 1 adult female, Ria Pontevedra, 42°26'N 08°41'W, station N-13, coll. W. Vader. **Portugal:** TMU 9393: 2 females, Northern tip of Tróia peninsula, mouth of Sado estuary, 38°29'N 08°55'W, low spring tide, coarse sand with extremely low levels of organic matter, 12.vii.1999; cylindrical sediment corer, sample T8 IL2, Adelaide Ferreira coll. TMU 9394: 1 ovigerous female, Northern tip of Tróia peninsula, mouth of Sado estuary, 38°29'N 08°55'W, low spring tide, coarse sand with extremely low levels of organic matter, 19.03.2000; cylindrical sediment corer, sample 511, Adelaide Ferreira coll. **Unknown origin:** TMU 4912: 1 adult male, station D658.

Description.— Species of normal robustness. Eye with well-developed ommatidia in adults. Pseudorostrum with weakly subquadrate, nearly rounded tip, of normal height, not or scarcely overhanging, with 4-5 (rarely three) proximoventral plumose setae in adults; development and number of apical spines normal. Major flagellum of A1 with 6-9 articles in females, 12-14 in males; accessory flagellum with 3-4 non-apical groups of spines. Flagellum of A1 of males of normal length (combined length of major flagellum and two distal articles of peduncle always much shorter than twice length of pseudorostrum). Anterior border of article 3 of peduncle of A2 usually with only one group of spinules and setae in apical position (second group in more proximal position sometimes present); fourth article with lateral and apical spinules; flagellum with 8-12 articles in females, 48-57 in males; A2 of adult male longer than body. In females, ratio between length and width of fourth article of A2: 3.0, of fifth article: 4.0.

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with 7-8 strong setae on dorsal surface, all but one in one row (sometimes all in one row); third article with longitudinal row of setae on dorsal side (in addition to two transversal groups of anterior setae); outer plate with six (rarely five) nodular spines.

Coxa 1 not especially elongate, with tip acute or fairly acute, with ventral tooth (with one seta associated with this tooth), with 6-8 anterior setae decreasing in size towards tip, without apical setule.

Coxa 2 with posterior tooth; tooth separated from coxa by deep notch; transition between anterior and ventral border with pronounced angular discontinuity; anterior border straight; anterior and posterior border parallel or nearly parallel (very faintly diverging downwards); ventral border of females with 17-26 moderately irregular-sized and fairly slender setae, longest setae of normal length to fairly long; mesial setae not in unusually high number (4-9).

Coxa 3 with posterior tooth; tooth separated from coxa by deep notch; anterior and posterior border more or less parallel (inconspicuously converging downwards); ventral border with 18-25 moderately irregular-sized and fairly slender setae in adult females, longest setae fairly long; mesial setae not in unusually high number (2-11).

Coxa 4 with 46-56 irregular-sized, slender setae in adult females, longest setae of normal length to fairly long; posterior setae not setulose.

Propodus of P1 of normal proportions.

Ratio between length and width of carpus of P2: 2.5; ratio between propodus length and carpus length 0.75.

P3 with carpal fang reaching about tip of propodus, distally styliiform and without accessory setule; propodus very slender; outer spines/setae of propodus high in number (11-16), long and slender; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly concave. Ratio between propodus length and merus length of P3 in adult females: 0.90-0.95. Ratio between dactylus length and propodus length of P3 in adult females: 0.20-0.25. Ratio between dactylus length and merus length of P3 in adult females: 0.20-0.25. Ratio between length and width of propodus of P3 in adult females: 7.0-8.0. Ratio between length and width of dactylus of P3 in adult females: 4.0-4.5. Ratio between unguis length and total length of dactylus of P3 in adult females: 0.30-0.35. Ratio between unguis length and dactylus width in P3 of adult females: 1.5.

P4 with carpal fang reaching about tip of propodus, distally styliiform and without accessory setule; propodus slender; outer spines/setae of propodus high in number (12-15), long and slender; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly concave. Ratio between propodus length and merus length of P4 in adult females: 0.80-0.85. Ratio between dactylus length and propodus length of P4 in adult females: 0.25-0.30. Ratio between dactylus length and merus length of P4 in adult females: 0.20-0.25. Ratio between length and width of propodus of P4 in adult females: 6.0-6.5. Ratio between length and width of dactylus of P4 in adult females: 4.0-4.5. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.35-0.40. Ratio between unguis length and dactylus width in P3 of adult females: 1.5.

Median part of anterior border of basis of P5 nearly straight (inconspicuously concave); posteromedian seta group of merus with one major long, strong, curved seta and 1-3 shorter, and more slender, non-setulose or slightly plumose accessory setae; posterodistal seta group with one long and strong straight seta (reaching 0.70-0.85 of carpus) in females and immature males, with one short spine in adult males (reaching 0.30 of carpus) [very important sexual dimorphism!], and 3-4 setules; anterodistal area always with plumodenticulate setae; longest posterior spine of carpus usually not reaching (rarely overreaching) tip of propodus; ratio between carpus + propodus length and merus length in adult females: 0.75.

Posterodistal lobe of basis of P6 protruding and narrow; anterior and posterior borders strongly and similarly convex; in females, anterior border with succession of several fairly narrow setulose setae and several strong, non-setulose spines/setae. Merus of P6 most commonly with three posterior groups of spines/setae (three groups in all our specimens from the North Sea, but four in one French and one Irish specimen examined), 9-11 anterior groups in southern North Sea specimens (may be as few as seven in French and Portuguese specimens); longest seta of each anterior seta group increasing in size considerably towards distal part of merus; carpus without posterior spines (distal group not considered); propodus with 3-4 posterolateral and four anteromesial groups of spines (terminal crown of spines not considered). Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 0.85-0.90.

Posterior border of basis of P7 with slender ornamentation (strong setae: more slender in males than in females; setae in females sometimes slightly stronger than in illustrated specimen), distal setae longest, individual and average length of setae

remaining otherwise quite constant; number: 18-26 in adult females, 15-23 in adult males; mesial side without spines in females examined. Ischium fairly elongate, reaching 0.49-0.53 of outer side of merus (seven specimens measured); anterodistal border moderately concave on outer side, strongly concave on mesial side; posterodistal border straight or nearly straight (very faintly concave) both on outer and mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 2.5-3.0, of propodus: 3.5-5.0, ratio between length of carpus and length of propodus: 1.0, ratio between length of propodus + carpus length and length of basis: 1.5.

Middle of posterior border of Ep1 and Ep2 angular but not produced in tooth.

Ep3 with posteroventral border more or less angular, always with tooth in female, with tooth or with distinct angular discontinuity in males, with 3-9 transverse groups of spines in adults (when many spine groups present, anterior groups consisting of only one fairly small spine), with 4-7 setules on posterior border (i.e. normal to fairly high number).

Urosomite 1, dorsally with one pair of anteriorly directed setae and 1-2, sometimes three, pairs of posteriorly directed spine(s) (spines of uppermost pair much bigger than others); ventrolateral border without strong setae arising from outer side.

Peduncle of uropod 1: outer dorsal border with 6-9 (most commonly 7-8) spines consisting of following succession: 1) 4-6 regularly spaced, fairly short (but longer than in species like *B. elegans*) and fairly robust spines, of slightly and gradually increasing size towards tip, 2) larger space followed by one penultimate, short, robust spine, 3) very short space followed by very long and fairly robust ultimate spine; dorsomesial border with styliform spines (not in transverse rows) on distal part, and strong setae on proximal part (most in transverse groups of two, sometimes in groups of three) [difference between spines and setae not clear-cut and rather gradual], 6-8 dorsomesial groups of spines or setae. Endopod and exopod of normal length and robustness; endopod with border facing exopod with 4-5 (less in juveniles) long, regularly and widely spaced spines. Endopod and exopod spines of normal robustness. Dorsal ratio between length of endopod and length of peduncle: about 0.80. Dorsal ratio between length and width of endopod: 6.5.

Peduncle of uropod 2: of normal proportions (dorsal ratio between length and width in mature female = 2.6); outer dorsal border with 4-6 fairly long and robust spines; dorsomesial border with about three single, robust spines, and more proximally one group of 1-3 setae. Endopod and exopod fairly long and slender; endopod with border facing exopod, with four (less in juveniles) long, regularly and widely spaced spines. Endopod and exopod spines of normal robustness. Dorsal ratio between length and width of endopod: 4.5.

Peduncle of uropod 3 with distal spines in normal number or numerous, longest seta(e) reaching about length of endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with 3-4 groups of 1-4 fairly strong and fairly long setae. Endopod elliptic, with four (sometimes three) spines (one much longer than others). Exopod with first article narrow, second article long. Second article of exopod with lateral setae on both sides (in fairly high number). Mesial side of exopod with 12-16 long plumose setae of normal morphology in females (18-23 in males), without accessory spiniform non-setulose setae (except sometimes on the last seta group of the first

article), all (except proximalmost setae) plumose setae much longer than longest setae of outer side. Outer side of exopod with eight to twelve groups of 2-3 (rarely 4) spini-form setae, several being slightly longer than exopod width. Ratio between length and width of second article of exopod: 3.5, sometimes up to 4.5. Ratio between length of second article and length of first article: 0.35-0.40, sometimes as little as 0.20. Ratio between length of second article and width of first article: 1.3-1.7, sometimes as little as 1.1. Ratio between length of second article of exopod and length of endopod: 0.85-1.0, sometimes as little as 0.65.

Lobes of telson without mesial setae.

Colour pattern.— White; eyes red and fairly dark; viscera yellowish (original colour description after an adult male from the shore of Saint-Jean-du-Doigt, France). "It is translucent without any trace of pigment apart from the eyes which are bright red. Eggs with a yellowish tinge" (Watkin, 1938).

Size.— Up to 8 mm (Watkin, 1938).

Ecology.— On fine or muddy sand, from lower shore (Jones, 1948) to 75 m (Raitt, 1937). Most abundant in fine sand; also in very fine, medium and coarse sand mixed with shell, small gravel and worm tubes; low densities when organic matter is present (Fincham, 1969). In *Synapta* and *Leiochone* sands (Toulmond & Truchot, 1964). Community of sand sediments with *Abra alba* (W. Wood, 1802) and *Corbula gibba* (Olivi, 1792): sandy facies with *Aponuphis bilineata* (Baird, 1870) (as *Hyalinoecia bilineata*) (see Cabioch, 1968: 628). Normally not very abundant on the shore (Watkin, 1939b, 1942). In the intertidal zone, it is found on the lowest part of the shore, where the sand remains saturated in seawater (Salvat, 1967), and especially where there is some current in that interstitial water (Faure, 1972). It is however a predominantly subtidal species (Colman & Segrove, 1955a), although its maximum density is often in very shallow water (Clark & Milne, 1955). Avoids waters with a reduced salinity (Vader, 1966). The maximum recorded density is 1 550 individuals/m² (Fincham, 1971). On the shores of the Isle of Man, ovigerous females have been found year round, except in November, and with a peak in May (Fincham, 1971). The breeding period would be shorter in the subtidal zone (ibid.). Occasionally parasitized by the nicothoid copepods *Sphaeronella paradoxa* Hansen, 1897 (Hansen, 1897 as *Bathyporeia norvegica*; Gotto, 1993) and *Sphaeronella* sp. (Costello & Myers, 1989).

Biological references.— Zonation pattern: Watkin (1939b, 1942), Colman & Segrove (1955a, 1955b), Clark & Milne (1955), Toulmond (1964), Salvat (1967), Fincham (1971). Granulometry preference: Vader (1966), Withers & Thorp (1978). Burrowing behaviour: Watkin (1939a). Swimming behaviour: Watkin (1939a, 1939b), Colman & Segrove (1955b), Bossanyi (1957). Dynamics of populations: Salvat (1967), Fincham (1971), Bamber (1993). Long-term variations in population density: Rachor & Gerlach (1978), Bamber (1993), Armonies et al. (2001), Kröncke et al. (2001). Fish predation: Poxton et al. (1983), Beare & Moore (1997). Parasites: Hansen (1897 as *B. norvegica*), Gotto (1993). Ecophysiology: McGrorothy (1971).

Distribution.— Sweden [Bohuslän: Gullmarfjord] (Oldevig, 1959); southern Norway up to Rogaland county (Brattegard & Holthe, 1997); Shetland, all British coasts, North Sea (Lincoln, 1979); Danish part of the Baltic Sea (Köhn & Gosselck, 1989); western Germany (Ziegelmeier, 1978; Gosselck et al., 1993; Stecher & Dörjes, 1993; Kröncke et al., 2001); Doggerbank (Kröncke, 1991); The Netherlands (Vader, 1965, 1966; Faasse &

Stikvoort, 2002); Belgium (present material); French part of the English Channel (Salvat, 1967; Toulmond & Truchot, 1964; Dauvin, 1999); French part of the Bay of Biscay (Faure, 1969; Salvat, 1964, 1967; Sorbe, 1982; de Montaudouin & Sauriau, 2000); northwestern Spain (present material); western Portugal (Marques, 1981; Marques & Bellan-Santini, 1985); southwestern Portugal (Dexter, 1988; Marques & Bellan-Santini, 1985, 1991); and southern Portugal (Rodrigues & Dauvin, 1987). It has also been recorded in the whole Mediterranean (Bellan-Santini, 1989). These Mediterranean records are probably correct but need confirmation. The species has also been recorded in the Black sea (Müller, 1964; Greze, 1985).

Remarks.— Reibisch (1905, as *B. norvegica*) and Watkin (1938) already pointed out that, whilst the third epimeral plate has always a posterior tooth in females and immature males, that tooth may be replaced by a very obsolete protrusion in adult males. Reibisch (1905) gave excellent illustrations of the variations in that epimeral plate. On the other hand, the spine disposition on the endopod of the first two uropods, which is unique amongst western European *Bathyporeia* species and an easy diagnostic character, has not been used by previous investigators.

Bathyporeia megalops Chevreux, 1911, a species originally described after two males from Algeria (Chevreux, 1911) is very close to *B. guilliamsoniana* (Bate, 1857), and even possibly identical. The Mediterranean *Bathyporeia* of the group *guilliamsoniana* will be studied elsewhere.

5.4.4. *Bathyporeia nana* Toulmond, 1966 (figs. 37-42)

Bathyporeia nana Toulmond, 1966: 219, fig. 1-5; Fincham, 1967: 79; Bellan-Santini, 1973: 101, table II; Lincoln, 1979: 316, 322, fig. 151a-g; Barclay, 1982: 229; Withers, 1990: 445, fig. 9.30 (after Lincoln).
? Not *Bathyporeia nana*; Bellan-Santini, 1989: 371, fig. 249 (see remarks).

Types.— Type locality: southwestern part of the English Channel, France, East of the bay of Morlaix, Térénez; type deposition: holotype: an adult male deposited at the Station Biologique de Roscoff; paratypes deposited at the Muséum National d'Histoire Naturelle de Paris and at the Station Biologique de Roscoff, according to Toulmond (1966). See also section 'material examined'. Coordinates of Térénez: 48°41'N 03°51'W.

Material.— **Ireland:** NMWZ 1997.052: 1 adult male and 2 adult females (1 ovigerous with 3 eggs in marsupium), Amphipoda Irish Sea, Swiss Stn. 108A, 1997, leg. D. McGrath. NMWZ. 1997.052: 1 adult male, 3 large immature males and 8 females (1 ovigerous with 5 eggs), Amphipoda Irish Sea, Swiss Stn. 108B, 1997, leg. D. McGrath. NMWZ 1997.052: 1 small immature male, Amphipoda Irish Sea, Swiss Stn. 113B, 1997, leg. D. McGrath. NMWZ 1997.052: 1 large immature male, Amphipoda Irish Sea, Swiss Stn. 114B, 1997, leg. D. McGrath. TMU 12 172: about 10 specimens, Portrance, years 1990-2000 S. De Grave leg. **France:** TMU 4925: 2 males (the biggest partly illustrated but not dissected), 1 adult female (fully dissected and mounted in Faure's liquid), 1 complete immature female, 1 immature female without head (? paratypes), English Channel, bay of Morlaix, creek of Térénez (type locality), 48°41'N 03°51'W, iii.1965.

Description.— Species of normal robustness. Eye with well-developed ommatidia in adults. Pseudorostrum with very rounded tip, of normal height, not overhanging, with one proximoventral plumose seta; development and number of apical spines

normal. Major flagellum of A1 with 5-6 articles in females, eight in males; first article of accessory flagellum with two non-apical groups of spines. Flagellum of A1 of males of normal length (combined length of major flagellum and two distal articles of peduncle always much shorter than twice length of pseudorostrum). Anterior border of article 3 of peduncle of A2 usually with only one group of spinules and setae, in apical position [sometimes two, cf. drawing of Toulmond (1966)]; fourth article with lateral and apical spinules; flagellum with 5-8 articles in females, 26-29 in males; A2 of adult male longer than body length. In females, ratio between length and width of fourth article of A2: 3.5, of fifth article: 3.5.

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with about three strong setae on dorsal surface; third article without longitudinal row of setae on dorsal side (in addition to two transversal groups of anterior setae); outer plate with four nodular spines.

Coxa 1 not especially elongate, with tip well-rounded, without ventral tooth, with only one anterior seta, with one apical setule [sometimes two apical setules according to Lincoln (1979)].

Coxa 2 without posterior tooth; transition between anterior and ventral border very gradual, without angular discontinuity; anterior border rounded; anterior and posterior border converging downwards; dissected female with ventral border with 9-10 regular-sized, strong and long setae; one mesial seta in dissected female.

Coxa 3 without posterior tooth; anterior and posterior border slightly converging downwards; ventral border with 9-12 fairly regular-sized, strong and long setae; no mesial setae in dissected female.

Coxa 4 with 11-18 fairly regular-sized long and strong setae in dissected female; posterior setae not setulose.

Propodus of P1 rather elongate.

Ratio between length and width of carpus of P2: 3.0; ratio between propodus length and carpus length: 0.90.

P3 with carpal fang reaching about tip of propodus, distally styliform and without accessory setule; propodus fairly slender; outer spines/setae of propodus few in number: 6 in dissected specimen, normal in size and shape; dactylus slender, with well-developed unguis, with posterior border moderately, but distinctly and regularly concave. Ratio between propodus length and merus length of P3: 0.90. Ratio between dactylus length and propodus length of P3: 0.35. Ratio between dactylus length and merus length of P3: 0.30. Ratio between length and width of propodus of P3: 5.5. Ratio between length and width of dactylus of P3: 5.0. Ratio between unguis length and total length of dactylus of P3: 0.25. Ratio between unguis length and dactylus width in P3: 1.5.

P4 with carpal fang reaching about tip of propodus, distally styliform and without accessory setule; propodus fairly robust; outer spines/setae of propodus few in number: six in dissected specimen, normal in size and shape; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly concave. Ratio between propodus length and merus length of P4: 0.75. Ratio between dactylus length and propodus length of P4: 0.35. Ratio between dactylus length and merus length of P4: 0.20. Ratio between length and width of propodus of P4: 4.0. Ratio between length and width of dactylus of P4: 4.0. Ratio between unguis length and total length of

dactylus of P4: 0.20. Ratio between unguis length and dactylus width in P3: 0.95 (one adult female measured).

Median part of anterior border of basis of P5 straight; posteromedian seta group of merus with one long and strong, curved, major seta and one shorter, and much more slender, setulose accessory seta; posterodistal seta group with one long and strong, nearly straight seta (slightly overreaching tip of carpus in female, nearly reaching tip in male) and one setule (no important sexual dimorphism); anterodistal area with one plumodenticulate seta; longest posterior spine of carpus reaching or overreaching tip of propodus; ratio between carpus + propodus length and merus length in adult females: 0.80.

Posterodistal lobe of basis of P6 protruding and wide; anterior border strongly and regularly convex; posterior border weakly convex on largest part of its length; in female examined, anterior border with succession of several narrow non-setulose setae (or appearing as such in light microscopy), several strong plumose spines/setae, 1-2 strong non-setulose spines/setae. Merus of P6 with 3-4 posterior groups of spines/setae and 6-8 anterior groups; longest seta of each anterior seta group of slightly increasing size from proximal towards distal part of merus; carpus without posterior spines (distal group not considered); propodus with 1-2 posterolateral and two anteromesial groups of spines (terminal crown of spines not considered). Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 0.75.

Posterior border of basis of P7 with robust ornamentation (spines), restricted to proximal half, number: 2-4 (no sexual dimorphism); mesial side without spines in dissected female. Ischium fairly short, reaching 0.37 of outer side of merus (one specimen measured); anterodistal border nearly straight (inconspicuously concave) on outer side, faintly concave on mesial side; posterodistal border straight both on outer and mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 3.0, of propodus: 5.0-5.5, ratio between length of carpus and length of propodus: 1.0, ratio between length of propodus + carpus length and length of basis: 1.5.

Middle of posterior border of Ep1 and Ep2 angular but not produced in tooth.

Ep3 with posteroventral border more or less angular, with or without obtuse posteroventral protrusion in adults, with an obtuse protrusion in juvenile females, with only one transverse group of spines, with one setule on posterior border.

Urosomite 1, dorsally with one pair of anteriorly directed setae and one pair of posteriorly directed spine; ventrolateral border without strong setae arising from outer side.

Peduncle of uropod 1: outer dorsal border with 5-6 spines consisting of following succession: 1) 3-4 regularly spaced short robust spines, of slightly and gradually increasing size towards tip, 2) larger space followed by penultimate short robust spine, 3) very short space followed by very strong ultimate spine; dorsomesial border with 4-5 single styliform spines (proximal ones more slender). Endopod and exopod of normal length and robustness; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines of normal robustness, those of tip quite long. Dorsal ratio between length of endopod and length of peduncle: about 0.75. Dorsal ratio between length and width of endopod: 6.0.

Peduncle of uropod 2: of normal proportions (dorsal ratio between length and width in one mature female = 2.6), outer dorsal border with four short and robust spines; dorsomesial border with two single, fairly slender spines. Endopod and exopod of normal length and robustness; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines of normal robustness, those of endopod quite long. Dorsal ratio between length and width of endopod: 4.0.

Peduncle of uropod 3 with distal spines in reduced number (three dorsal and three ventral in dissected female), longest spines reaching about length of endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with three very long, very strong, single setae. Endopod ovate, with 1-2 spines. Exopod with first article narrow, second article long. Second article of exopod without lateral setae in female, with one seta (on mesial side) in male. Mesial side of exopod with only 1-2 short, non-setulose setae in females; with 11 to 12 long plumose setae of normal morphology and 3-4, well-developed, accessory, spiniform, non-setulose setae [two in male illustrated by Toulmond (1966)], plumose setae (except sometimes most proximal one) much longer than setae of outer side (sexual dimorphism considerably more important than in any other species). Outer side of exopod with 4-5 groups of 1-2 spiniform setae, some much longer than width of exopod in females, longest seta about same width in males. Ratio between length and width of second article of exopod: 4.0. Ratio between length of second article and length of first article: 0.30. Ratio between length of second article and width of first article: 1.7. Ratio between length of second article of exopod and length of endopod: 1.1.

Lobes of telson without mesial setae.

Colour pattern.— Living animals: body greenish and translucent, eyes bright red; in alcohol the animals become white and opaque and the eyes colourless (Toulmond, 1966).

Size.— Up to 3.0 mm (Toulmond, 1966; Lincoln, 1979), rarely up to 3.5 mm (Barclay, 1982).

Ecology.— Intertidal, from the level of mid low water neap-tide (Fincham, 1967), down to about 11 m depth (Fincham, 1969). Pure fine sand; reddish sand; sandy pools in seagrass meadows (Toulmond, 1966). Most abundant in very fine sand mixed with shell, or fine sand; also in medium and coarse sands mixed with shell and gravel (Fincham, 1969). At Port Erin Bay, the maximum density of 3 330 individuals/m² is reached in the finest grade sand (56% between 125-250 μ) (Fincham, 1967).

Biological references.— Zonation pattern: Fincham (1971). Granulometry: Toulmond (1966), Fincham (1969). Long-term variations in population density: Dauvin (1987). Pollution sensitivity: Dauvin (1987).

Distribution.— Eastern Atlantic: eastern and western coast of the British Isles (Fincham, 1967, 1973; Lincoln, 1979); as far north as Wigtown Bay, 56°29.5'N, in Western Scotland (Barclay, 1982); Bay of Morlaix, southwestern part of the English Channel (Toulmond, 1966).

Remarks.— This species is the smallest of the genus recorded in western Europe. Interestingly, it is present and even common in Kames bay (Barclay, 1982), the shore extensively studied by Watkin (1938, 1939a, 1939b, 1941, 1942), who overlooked it. The species has been recorded in the Mediterranean (Bellan-Santini, 1989). However, the drawings of the first uropod given by that author do not agree with topotypical

specimens, thus the identity of Mediterranean specimens needs confirmation.

In many respects, *Bathyporeia nana* looks very similar to *B. elegans*. A large part of the apparent differences between them results from the size difference (*B. nana* is smaller than *B. elegans*). Illustrations of juvenile *B. elegans* are given in figures 17 and 18 for comparison purposes. Small differences are observed. The coxa 1 of young *B. elegans* exhibits no distal setule as in *B. nana* (actually that is the most important difference). A small tooth remains present on the coxae 2-3 of young *B. elegans*, whilst there are none in *B. nana*. There are more posterior spines on the basis of P7 in young *B. elegans* than in *B. nana*. The seta pattern of U3 looks different in both taxa. On the basis of those observations, *B. nana* has to be retained as a valid species for the time being, but the examination of more extensive collections is highly desirable.

5.4.5. *Bathyporeia pelagica* (Bate, 1857) (figs. 43-50)

Thersites pelagica Bate, 1856: 59 (nomen nudum); Bate, 1857a: 146 (published in February 1857); White, 1857: 188 (published in July 1857, see Clark & Presswell, 2001: 166).

Bathyporeia pelagica; Bate, 1862: 174, pl. 31 fig. 6; Bate & Westwood, 1862: 309, unnumbered fig.; Stebbing, 1906: 120, in part; Chevreux & Fage, 1925: 93, fig. 86 (in part); Watkin, 1938: 219, fig. 2; Schellenberg, 1942: 167, fig. 135 (after Watkin); Shoemaker, 1949: 389, in part (discussion); Gurjanova, 1951: 342, fig. 201 (after Watkin); Toulmond, 1966: 229 (discussion), 231, (key); Bellan-Santini, 1973: 101, table II; Lincoln, 1979: 316, fig. 148g-l; Enckell, 1980: 519, fig. 2389 (after Watkin); Bellan-Santini & Vader, 1988: 232; Köhn & Gosselck, 1989: 72, pl. 22 fig. 2 (after Lincoln); Withers, 1990: 445, fig. 9.30 (after Lincoln); Faasse & Stikvoort, 2002: 63 (colour description).

Not *Bathyporeia pelagica*; G.O. Sars, 1891: 129, pl. 44 fig. 1; Scott, 1893: 213, pl. 5 fig. 23-25; Reibisch, 1905: 158, pl. 4 fig. 7-8; Tesch, 1916: 324; Stephensen, 1929: 83, fig. 20.94 (after Stephensen, 1928); Stephensen, 1938: 141 (= *B. elegans* Watkin, 1938).

Not *Bathyporeia pelagica*; Stephensen, 1928: 131, fig. 25.8 (= *B. elegans* Watkin, 1938).

Types.— Bate (1857) indicates the type locality as “Moray Frith [sic], Rev. G. Gordon” and Bate (1862) “Moray Forth [sic]” without further details. Bate & Westwood (1862) gives a little more information: “We have seen only a single imperfect specimen of this species, taken in the Moray Frith [sic], by Rev. Geo. Gordon in a considerable depth of water.” Watkin (1938) said: “Type specimen, a male, 5 mm. Long, in the Spence Bate collection, British Museum, tube no. 86. Locality, Bate (1863, p. 309), Moray Firth.” Thurston and Allen (1969) indicated that the registration number of that specimen that they refer as the holotype is: Reg. No. 1952 : 5 : 7 : 182. Approximate coordinates of Moray Firth: 57°39'N 03°57'W. I have re-examined that specimen and it is the species that it was supposed to be; it is an adult male in not so bad condition. See also the section ‘material examined’.

Material.— **United Kingdom:** BM 1452.5.7.182: 1 adult male, holotype, Moray Firth, 57°39'N 03°57'W. TMU 8665: 3 adult females, Scotland, Aberdeen beach, 57°08'N 02°05'W, 1960, leg. McIntire. TMU 7066: 1 adult male, Jersey, station 13; 21.viii.1968, leg. Wim Vader. **Germany:** TMU 9392: 1 adult male, Aussen Jade 2; 15.vii.1968, leg. J. Dörjes. TMU 4910: 1 specimen, Jade, station 33, 03.iv.1975, leg. J. Dörjes. TMU 4918: 7 specimens, Jade, station 506, 14.ii.1967, leg. J. Dörjes. TMU 4908: 3 specimens, Mellum, 53°44'N 08°06'E, station MB 24/32, 20.vii.1972, leg. J. Dörjes. TMU 4919: 1 female, Mellum-B, 53°44'N 08°06'E, station MB 16, leg. J. Dörjes. TMU 4917: 1 adult female, Mellum, 53°44'N 08°06'E, station MB 8/72, 07.ii.1972, leg. J. Dörjes. TMU 4921: 1 female, Mellum, 53°44'N 08°06'E, station MB 9/72, 07.ii.1972, leg. J.

Dörjes. TMU 9432: 2 specimens, Mellum, 53°44'N 08°06'E, station MB 23/72, 20.vii.1972, leg. J. Dörjes. TMU 4920: 1 female and 1 young, Mellum, 53°44'N 08°06'E, station MB 7, leg. J. Dörjes. **The Netherlands:** ZMA Amph. 104.532: 1 immature male and 3 females, Waddenzee, Meetpunt, 11 m depth, leg. Zoöl. St. Den Helder, 18.viii.1937, det. K. Schijfsma. RMNH A 4935: 15 specimens (previously mixed together with 1 adult male of the spiny form of *B. elegans*); North Sea, 51°38'51"N 03°30'15"E, 10.8 m, grab 1457, 01.vii.1966, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4936: 18 specimens (females and immature males) (previously mixed with 2 specimens of the spiny form of *B. elegans*), mouth of Oosterschelde, Krabbengat, trap Westerschouwen, 4.0 m, grab 1715, 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4937: 11 specimens, mouth of Oosterschelde, Oude Roompot direction Petroleumbol; grab 1725, 4 m, 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. **France:** RMNH A 4947: over 100 specimens, Strait of Dover, Wissant, 50°53'N 01°39'E, sample 2-6, 10-14 & 16-24, 13.x.1966, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4948: 18 specimens (1 female fully dissected, mounted in Faure's liquid and illustrated), English Channel, Ambleteuse, 50°49'N 01°36'E, sample 3 & 4, 12.x.1966, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling Delta onderzoek. RMNH A 4949: 25 specimens (including 2 adult males) (1 female fully dissected, mounted in Faure's liquid and illustrated), English Channel, Ambleteuse, 50°49'N 01°36'E, sample 5-7, 12.x.1966, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling Delta onderzoek. RMNH A 4950: 2 females, English Channel, Pointe aux Oies (north of Wimereux), 50°47'N 01°36'E, sample 4, 2.x.1964, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. TMU 12 238: many specimens, English Channel, Saint-Jean-du-Doigt, 48°42'N 03°47'W, exposed shore, coarse sand, middle of the shore, 18.iv.2003, fixed in 70% alcohol, leg. C. d'Udekem d'Acoz. TMU 12 347: 10 specimens, same locality, 19.iv.2003, fixed in absolute alcohol, leg. C. d'Udekem d'Acoz. TMU 12 296: many specimens, same sample, fixed in 70% alcohol. TMU 12 332: 5 specimens, same sample, fixed in 70% alcohol. MNHN previously Am. 2565: 3 specimens (previously identified as *B. guilliamsoniana* and mixed with *B. guilliamsoniana*, the spiny form of *B. elegans* and *B. tenuipes*); Bay of Biscay, Le Croisic, 47°18'N 02°31'W, Stas. 55,75,87, collection Ed. Chevreux. MNHN Am. 5244: 8 specimens (previously identified as *B. pelagica* but mixed together with *B. elegans* forma B and 8 *B. tenuipes*), Bay of Biscay, 'baie du Croisic', 47°18'N 02°31'W, collection Ed. Chevreux.

Description.— Species of normal robustness. Eye with well-developed ommatidia in adults. Pseudorostrum with angular tip, of normal height, overhanging, with 3-4, proximoventral, plumose setae in adults (sometimes only two in large immatures); development and number of apical spines normal. Major flagellum of A1 with 5-6 articles in adult females (sometimes only four in immatures), 8-10 in males; first article of accessory flagellum with 2-4 non-apical groups of spines. Flagellum of A1 of males of normal length (combined length of major flagellum and two distal articles of peduncle always much shorter than twice length of pseudorostrum). Anterior border of article 3 of peduncle of A2 usually with only one group of spinules and setae in apical position, sometimes with accessory group more proximally; fourth article with lateral and apical spinules; flagellum with 7-11 (usually 8-9) articles in females, 33-39 in males; A2 of adult male much longer than body length. In females, ratio between length and width of fourth article of A2: 2.5, of fifth article: 2.5.

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with about nine strong setae on dorsal surface, all but one in row; third article with longitudinal row of setae on dorsal side (in addition to two transverse groups of anterior setae); outer plate with 5-6 nodular spines.

Coxa 1 not especially elongate, with tip broadly rounded, devoid of ventral tooth and notch (but with one seta which seems to correspond to the tooth-associated seta of toothed species), with 4-5 anterior setae, without apical setule.

Coxa 2 with posterior tooth; tooth small and separated from coxa by very shallow notch; transition between anterior and ventral border very gradual, without angular discontinuity; anterior border well-rounded; anterior and posterior border not parallel (slightly converging downwards due to strong convexity of anterior border); ventral border in adult females with 7-13 fairly regular-sized, strong setae of normal length; mesial setae not in unusually high number (7-9 in two dissected females).

Coxa 3 with posterior tooth; tooth small and separated from coxa by very shallow notch; anterior and posterior border nearly parallel (inconspicuously converging downwards); ventral border with 9-15 fairly regular-sized strong setae in adult females, longest setae of normal length; mesial setae not in unusually high number (7-9 in two dissected females).

Coxa 4 with 15-29 fairly regular-sized narrow setae in adult females, longest setae of normal length; posterior setae not setulose.

Propodus of P1 of normal proportions.

Ratio between length and width of carpus of P2: 2.0; ratio between propodus length and carpus length: 0.90.

P3 with carpal fang reaching tip of propodus, distally styliiform and with bifid tip (anterior fork branch longer and stronger); propodus rather robust; outer spines/setae of propodus rather numerous (10-13), normal in size and shape; dactylus rather slender but short, with very reduced unguis, with posterior border straight. Ratio between propodus length and merus length of P3 in adult females: about 0.80. Ratio between dactylus length and propodus length of P3 in adult females: 0.20-0.25. Ratio between dactylus length and merus length of P3 in adult females: 0.15-0.20. Ratio between length and width of propodus of P3 in adult females: 5.5. Ratio between length and width of dactylus of P3 in adult females: 3.5-4.0. Ratio between unguis length and total length of dactylus of P3 in adult females: 0.085-0.10. Ratio between unguis length and dactylus width in P3 of adult females: 0.35-0.45.

P4 with carpal fang reaching tip of propodus, distally styliiform and bifid (anterior fork branch longer and stronger); propodus rather robust; outer spines/setae of propodus rather numerous (8-11), normal in size and rather robust; dactylus rather slender but short, with very reduced unguis, with posterior border straight. Ratio between propodus length and merus length of P4 in adult females: 0.65-0.70. Ratio between dactylus length and propodus length of P4 in adult females: 0.25. Ratio between dactylus length and merus length of P4 in adult females: 0.15-0.20. Ratio between length and width of propodus of P4 in adult females: 4.0-4.5. Ratio between length and width of dactylus of P4 in adult females: 3.5. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.10-0.15. Ratio between unguis length and dactylus width in P3 of adult females: 0.35-0.50.

Median part of anterior border of basis of P5 nearly straight (inconspicuously concave); posteromedian seta group of merus with one long and strong curved major seta and one long non-setulose accessory seta; posterodistal seta group with 1-2 setules, and one long and strong straight seta (reaching tip of carpus or nearly so) in females and immature males, with one strong and short spine reaching about 0.30 of carpus in adult males (i.e. important sexual dimorphism); anterodistal area always with plumodenticulate setae; longest posterior spine of carpus reaching or overreaching tip of propodus; ratio between carpus + propodus length and merus length in adult females: 0.75.

Posterodistal lobe of basis of P6 fairly protruding, and wide; anterior border strongly and regularly convex; posterior border weakly convex over largest part of its length; in females, anterior border with succession of several plumose setae of increasing length, and several strong non-setulose spines. Merus of P6 with four posterior groups of spines/setae (most proximal sometimes reduced) and 6-7 (sometimes 8) anterior groups in adults; longest seta of each anterior seta group of significantly increasing size from proximal towards distal part of merus; carpus without posterior spines (distal group not considered); propodus with 2-3 posterolateral and 2-3 anteromesial groups of spines (terminal crown of spines not considered). Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 0.80-0.85.

In females, posterior border of basis of P7 with robust ornamentation (strong spines); most spines short and regular-sized (very slightly decreasing in size towards tip), 1-2 most distal spines quite long, number: 10-13; in males, posterior border of basis of P7 with slender spines, median spines very slightly shorter, but otherwise regular-sized, number: 10-12; mesial side normally with spines in females. Ischium rather elongate, reaching 0.44-0.47 of outer side of merus (two females measured); anterodistal border slightly concave on outer side, strongly concave on mesial side; posterodistal border slightly concave both on outer and mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 2.0-2.5, of propodus: 6.0-7.0, ratio between length of carpus and length of propodus: 0.90, ratio between length of propodus + carpus length and length of basis: 1.5.

Middle of posterior border of Ep1 and Ep2 angular but not produced in tooth.

Ep3 with posteroventral border with more or less distinct angular discontinuity, with small posteroventral tooth in females, with or without small posteroventral tooth in males, usually with three transverse groups of spines in adults, with 2-5 setules on posterior border (i.e. normal number).

Urosomite 1, dorsally with one pair of anteriorly directed setae and one pair of posteriorly directed spines; ventrolateral border without strong setae arising from outer side.

Peduncle of uropod 1: dorso-lateral border with 7-10 spines consisting of following succession: 1) 6-7 short robust spines of slightly and gradually increasing size towards tip [regularly spaced except most proximal one(s)], 2) larger space followed by short, penultimate, robust, spine, 3) very short space followed by very strong, ultimate spine; dorsomesial border with styliform spines, distalmost spines single and stronger, others usually paired (4-6 groups). Endopod and exopod of normal length and robustness; endopod with border facing exopod, with only one long spine in subdistal position. Endopod and exopod spines of normal robustness. Dorsal ratio between length of endopod and length of peduncle: about 0.75 (1 female measured). Dorsal ratio between length and width of endopod: 5.0 (1 female measured).

Peduncle of uropod 2: of normal proportions (dorsal ratio between length and width in one mature female = 2.6), dorso-lateral border with five (sometimes six) spines that are short and robust; dorsomesial border with 4-5 spines, proximal spines slender (single or paired), distal spines robust (and always single). Endopod and exopod of normal length and robustness; endopod with border facing exopod, with

only one long spine in subdistal position. Endopod and exopod spines of normal robustness. Dorsal ratio between length and width of endopod: 3.5.

Peduncle of uropod 3 with distal spines in normal to fairly low number, longest spines reaching at least 0.8 of endopod length (endopodal spines excluded) and often overreaching it; outer border of peduncle of uropod 3 with one or three groups of 1-3 thin and not so long setae. Endopod subquadrate to asymmetrically elliptic, with 2-3 spines (up to 4 in males). Exopod with first article narrow, second article long. Second article of exopod with lateral setae on both sides in adults (1-2 on outer side; 2-3, sometimes four on mesial side in females; 3-4 on mesial side in males). Mesial side of exopod with 11-16 (in females), 15-20 (in males) long plumose setae of normal morphology and 2-7 well-developed, accessory, spiniform, non-setulose setae, all (except proximalmost) plumose setae much longer than longest setae of outer side. Outer side of exopod with 5-7 groups of 2-3 spiniform setae, some as long as or slightly longer than exopod width. Ratio between length and width of second article of exopod: 4.5. Ratio between length of second article and length of first article: 0.40-0.45. Ratio between length of second article and width of first article: 2.1-2.3. Ratio between length of second article of exopod and length of endopod: 1.5-2.0.

Lobes of telson without mesial setae.

Colour pattern.— White, in some specimens with a tinge of red on P6-P7, on urosome and on uropods; eyes red and fairly dark; eggs blue (original colour description after specimens from the shore of Saint-Jean-du-Doigt, France). "Eyes with dark red pigment. The body pigment is abundant, particularly in the pleon and its appendages, but it is variable in specimens from various localities. Eggs deep blue in colour" (Watkin, 1938).

Size.— Up to 6.8 mm (Salvat, 1967).

Ecology.— Usually found intertidally just below level of high water neap-tide (Lincoln, 1979) or just above mid-tide level (Salvat, 1967). Locally found below tide-mark (Vader, 1966), down to 11 m depth (present material). Movaghar (1964) records *B. pelagica* between 5 and 20 m in the estuary of the Elbe river, but a misidentification is not totally ruled out here. Prefers coarse, clean sand with at least 50% of the sediment coarser than 210 μ , and without admixture of mud and organic matter (Vader, 1965, 1966). As a consequence, in estuarine conditions, it is only found on exposed shores and sandy banks (Vader, 1966). In Wales, it disappears in summer from the estuarine environments (Fish & Preece, 1970a; Fish & Fish, 1978). It breeds year round all along the coasts of France (Salvat, 1967). In Wales, ovigerous females have only been reported from March to October, with a first maximum in the spring and a second in summer, and there would be two yearly generations (Fish & Preece, 1970a). Population densities up to 1 260 individuals/m² (Salvat, 1967). May be parasitized by the nicothoid copepod *Sphaeronella paradoxa* Hansen, 1897 (Stock & de Vos, 1960; Gotto, 1993), locally with a high rate of infestation (Hamond, 1967).

Biological references.— Zonation pattern: Watkin (1939b, 1942), Colman & Segrove (1955a, 1955b), Stock & de Vos (1960), Toulmond (1964), Howells (1964), Vader (1965, 1966), Salvat (1967), Fish & Preece (1970a). Granulometry preference: Spooner (1957), Vader (1965, 1966), Withers & Thorp (1978). Burrowing behaviour: Watkin (1939a). Swimming behaviour: Watkin (1939a, 1939b), Colman & Segrove,

1955b. Tidal rhythm: Fincham (1970b). Annual upshore and downshore changes of density: Fincham (1971). Migrations in estuarine conditions: Fish & Preece (1970a), Fish & Fish (1978). Embryonic development: Fish (1975). Dynamics of populations: Salvat (1967), Fincham (1970a), Fish & Preece (1970a), Fish (1975). Fish predation: Poxton et al. (1983), Beare & Moore (1997). Bird predation: Pienkowski (1983). Parasites: Stock & de Vos (1960), Hamond (1967, 1973), Gotto (1993). Ecophysiology: Fish & Preece (1970b), Preece (1970, 1971a).

Distribution.— Eastern Atlantic: Norway, as far north as the Trondheimfjord (Brattegard & Holthe, 1997); all British coasts, from Shetland to Channel Isles (Lincoln, 1979); western Germany (Stock & de Vos, 1960; Gosselck et al., 1993; Stecher & Dörjes, 1993; Kröncke et al., 2001); The Netherlands (Vader, 1965, 1966; Faasse & Stikvoort, 2002); Strait of Dover (present material); French part of the English Channel (Salvat, 1967; Toulmond & Truchot, 1964; Dauvin, 1999); along the French coasts of the Bay of Biscay (Lagardère, 1966; Faure, 1969; Salvat, 1967; Sorbe, 1978; de Montaudouin & Sauriau, 2000); northwestern Spain (Acuña Castroviejo & Mora Bermúdez, 1979; Viéitez, 1981; Laborda Navia, 1983; Mazé & Laborda, 1986; Mazé et al., 1990; Junoy & Viéitez, 1990); northern Portugal (Marques & Bellan-Santini, 1985); western Portugal (Marques, 1981; Marques & Bellan-Santini, 1985); southwestern Portugal (Marques & Bellan-Santini, 1987, 1991; Dexter, 1988); southern Portugal (Marques & Bellan-Santini, 1985); ? Morocco (Menioui & Bayed, 1986); ? Canary Islands, ? Senegal (Chevreux, 1925; Chevreux & Fage, 1925).

Remarks.— *Bathyporeia pelagica* is very similar to *B. elegans*, and sorting out mixed samples of both species may be fairly tedious, especially when the material is not in good condition. In such situations, the distinct morphology of the dactylus of P3-P4, a previously overlooked character, may prove to be very helpful. If the specimens are examined alive, the egg and ovary colour too may be useful.

It should be pointed out that *B. pelagica* shares two unusual characters with *B. guillemsoniana*: the important sexual dimorphism on the posterodistal seta of merus of P5 and the presence of a tooth (or a trace of tooth) on the posteroventral angle of the third epimeral plate. The eventual evolutionary significance of these shared characters is currently unknown.

5.4.6. *Bathyporeia pilosa* Lindström, 1855 (figs. 51-59)

Bathyporeia pilosa Lindström, 1855: 59, pl. 2 fig. 1-11; Bruzelius, 1859: 90 (? in part); Robertson, 1888: 46; Bonnier, 1890: 988 (in part); G.O. Sars, 1891: 133, pl. 45 fig. 2; Reibisch, 1905: 160, pl. 4 fig. 13; Stebbing, 1906: 121; ? Stephensen, 1929: 83, fig. 20.96; Stephensen, 1938: 141 (key); Watkin, 1938: 228, fig. 5; Schellenberg, 1942: 169, fig. 138 (after Watkin); Dahl, 1944: 8 (variability); Gurjanova, 1951: 341, fig. 200 (after Watkin); Toulmond, 1966: 229 (discussion), 231 (key); Bellan-Santini, 1973: 96, table I; Lincoln, 1979: 316, 320, fig. 150a-e; Enckell, 1980: 523, fig. 2395-2396 (after Watkin); Barclay, 1982: 230; Nicolaisen & Kanneworff, 1983: 238 (colour description); Bellan-Santini & Vader, 1988: 236; Köhn & Gosselck, 1989: 74, pl. 22 fig. 5; Withers, 1990: 445, fig. 9.31 (after Lincoln); Faasse & Stikvoort, 2002: 65 (colour description).

Bathyporeia robertsoni Bate, 1862: 173, pl. 31 fig. 5; Bate & Westwood, 1862: 307, unnumbered fig.; Robertson, 1888: 48.

Bathyporeia pilosa; ? Stephensen, 1928: 132, fig. 25.11-12.

? *Bathyporeia robertsoni*; J.L. Barnard & C.M. Barnard, 1983: 230, fig. 28D.

Not *Bathyporeia pilosa*; Bate, 1862: 172; Bate & Westwood, 1862: 304 (= *B. guilliamsoniana* (Bate, 1856)).

Not *Bathyporeia pilosa*; Della Valle, 1893: 752 (= *B. lindstromi* Stebbing, 1906).

Not *Bathyporeia robertsonii*; G.O. Sars, 1891: 131, pl. 44 fig. 2; Stebbing, 1906: 121 (= *Bathyporeia sarsi* Watkin, 1938).

Not *Bathyporeia robertsoni*; Chevreux & Fage, 1925: 94, fig. 87 (= *Bathyporeia sarsi* Watkin, 1938).

Not *Bathyporeia robertsoni*; Scott, 1893: 213, pl. 5 fig. 26-29; Stebbing, 1906: 121 (= *Bathyporeia sarsi* Watkin, 1938).

Types.— As concerns the types of *B. pilosa* Lindström, 1855, Watkin (1938) said: "Type specimen, a female, not extant. Locality, off the island of Gottland, Baltic." The exact locality is Visby, i.e. about 57°39'N 18°18'E, Lindström (1855: 63) giving the following indications: "Af denna nya form har jag hittills endast funnit några få exemplar på sandbotten med 18-24 famnars djup utanför Wisby [So far, I have only found a few specimens of that new form, at a depth of 18-24 fathoms, on sandy bottom, off Visby]." As concerns its junior synonym *B. robertsoni* Bate, 1862, Bate (1862) indicates: "Cumbrae, near Glasgow, in the month of February, in sand-pools near low-water mark; numerous, darting hither and thither (Robertson). It is named in compliment to the discoverer". Bate & Westwood (1862) gave a very similar account. As concerns the syntypes of *B. robertsoni*, Thurston & Allen (1969) indicated that two specimens in alcohol are in the British Museum, locality: Cumbrae, Firth of Clyde, Scotland, Bate's collection, reg. no. 1952 : 5 : 7 : 183-184. Barclay (1982) added: "There was some doubts (Watkin, 1938) whether specimens collected by David Robertson, the Cumbrae naturalist, and later named *B. robertsoni* by Bate (1862), was a new species. Sars (1895) had identified Norwegian specimens as *B. robertsoni* using Bate's description of the Isle of Cumbrae animals. However, the Norwegian specimens were later renamed *B. sarsi* (Watkin, 1938) and Watkin was of the opinion that the Cumbrae *B. robertsoni* were probably *B. pilosa* Lindström. Syntypes of *B. robertsoni* deposited in the British Museum, Natural History, had lain unregistered until 1952 (Miss J. Ellis, personal communication) and Watkin did not have the opportunity to examine them. I have now examined these syntypes and all are *B. pilosa*. This confirms Watkin's opinion and removes any doubts about the species mistakenly named and described by Bate as *B. robertsoni*." The approximate coordinates of the Isle of Cumbrae are 55°45'N 04°55'W.

Material.— **Denmark:** TMU 2946: 1 female, North Sjælland, Hornbæk, 56°05'N 12°27'E, sandy shore, 06.viii.1921, leg. Dr Th. Mortensen (initially identified as *B. robertsoni* and mixed together with 3 *B. sarsi*). **United Kingdom:** TMU 4922: over 200 young and small mature specimens (some dissected and mounted on slides), Jersey, station 13, 21.viii.1968, leg. Wim Vader. **The Netherlands:** ZMA Amph 100.01: 6 adult males, 2 immature males (1 with a single dorsal spine on first urosomite), 2 immature females, Eems estuary, stat. 165, 1954. ZMA Amph 100.704: 1 female, Eems estuary, stat. 212, 1954. ZMA Amph 100.706: 2 immature males and 1 female, Eems estuary, stat. 217, 1954. ZMA Amph 100.707: 1 immature male, 1 female, 1 juvenile, Eems estuary, stat. 218, 1954. ZMA Amph 100.708: 1 immature female, Eems estuary, stat. 245, 1954. ZMA, Amph 100.709: 1 immature male and 4 females, Eems estuary, stat. 254, 1954. ZMA Amph 100.710: 6 females, Eems estuary, stat. 255, 1954. ZMA Amph 100.716: 5 females, Eems estuary, stat. 304, 1954. ZMA Amph 100.717: 1 ovigerous female, Eems estuary, stat. 315, 1954. ZMA, previously Amph 100.952: 1 young female, Eems estuary, stat. 363, 1956 (previously identified as and mixed with *Bathyporeia sarsi*). NIOO-KNAW (CEMO): 1 specimen, The Netherlands, no more information, M. Rietveld coll. NIOO-KNAW (CEMO): 1 immature male, The Netherlands, station UJ98 552-01, M. Rietveld coll. NIOO-KNAW (CEMO): 1 adult male with a pair of spines on the first urosome, The Netherlands, station UJ98 552-15, M. Rietveld coll. NIOO-KNAW

(CEMO): 2 immature males (but close to maturity) with a pair of dorsal spines on the first urosomite, The Netherlands, station UJ98 552-04, M. Rietveld coll. RMNH A 4961: 12 specimens (1 female fully dissected and mounted in Faure's liquid), Westerschelde [Western Scheldt], between ton 50 and 59, grab 1239; 02.iv.1965; leg. CHB, JN, AS; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4962: 1 adult male (with a pair of dorsal spines on first urosomite), 3 adult females, 4 smaller females, Westerschelde [Western Scheldt], between 50 and 59, grab 1240; 27.iv.1965; leg. CHB, JN, AS; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4966: 26 females (mostly immatures), Westerschelde [Western Scheldt], 900 m E of grab 1228, grab 1229, leg. CHB, JN, AS; 27.iv.1965; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek [includes one female with 1 unpaired dorsal spine on first urosomite]. TMU 12 240: 15 specimens, Wemeldinge (western side), 51°32'N 03°59'E, sheltered shore, higher and middle of the shore, sand, 29.iv.2003, fixed in 95% alcohol, leg. C. d'Udekem d'Acoz. TMU 12 241: many specimens, same sample, fixed in 70% alcohol. **Belgium:** RMNH A 4964: 1 adult male and 4 females, de Haan, 51°16'N 03°02'E, beach, 05.x.1965, leg. WW, LdW, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. **France:** MNHN, previously Am 2575: 48 specimens, English Channel, Malo-les-Bains, 51°03'N 02°24'E, high tide, Stn 739, collection E. Chevreux (previously identified as *B. Robertsoni* and mixed together with *B. sarsi*). RMNH A 4965: 13 females (adults and young; 1 adult fully dissected and mounted in Faure's liquid), Strait of Dover, Wissant, 50°53'N 01°39'E; sample 1-3, 9; 13.x.1966, leg. Wim Vader, LdW, AS; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. TMU 9391: 16 specimens (both sexes, mostly adults), English Channel, Saint-Germain-sur-Ay, 49°14'N 01°39'W, shore, 02.iii.2002, leg. Francis Kerckhof. MNHN, previously Am. 2576: 6 specimens, English Channel, Saint Lunaire, 48°38'N 02°07'W, vi.[18]85, leg. Dolffus (previously identified as *B. Robertsoni*). TMU 12 278: 9 specimens, English Channel, Saint-Michel-en-Grève, 48°41'N 03°35'W, sheltered shore, highest part of the shore, fine sand, 17.iv.2003, fixed alive in absolute alcohol, leg. C. d'Udekem d'Acoz. TMU 12 306: over 500 specimens, English Channel, Saint-Efflam, 48°40'N 03°36'W, sheltered shore, highest part of the shore (above the level of maximum density of *B. sarsi*), fine sand, 20.iv.2003, fixed in 70% alcohol, leg. C. d'Udekem d'Acoz.

Description.— Very robust species. Eye rather small, with well-developed ommatidia in adults. Pseudorostrum with rounded and very narrow tip, not overhanging, with 2-3 proximoventral plumose setae in adults; development and number of apical spines normal. Major flagellum of A1 with 6-8 articles in females (there may be only five in immature females), 10-14 in males; first article of accessory flagellum with two non-apical groups of spines. Flagellum of A1 of males very long (combined length of major flagellum and two distal articles of peduncle often twice as long as pseudorostrum or even longer). Anterior border of article 3 of peduncle of A2 usually with only one group of spinules in apical position, but sometimes with accessory group proximally; fourth article with apical spines, with or without lateral spinules; flagellum with 7-11 articles in adult females, 23-37 in adult males; A2 of adult male almost as long as body length (at least 0.8 times as long as body) or longer than body. In females, ratio between length and width of fourth article of A2: 3.0, of fifth article: 2.5.

Penultimate article of mandible distinctly broadened on proximal 0.3.

Second article of maxillipedal palp with 7-9 strong setae on dorsal surface, all in one row or all but one in one row; third article with longitudinal row of setae on dorsal side (in addition to two transversal groups of anterior setae); outer plate with 5-6 nodular spines.

Coxa 1 not especially elongate, with tip narrowly rounded, without ventral tooth, with or without distinct notch, with 3-7 anterior setae, without apical setule.

Coxa 2 without posterior tooth; transition between anterior and ventral border perfectly gradual, without any angular discontinuity; anterior border strongly convex;

anterior and posterior border converging downwards; females with ventral border with 9-14, moderately irregular-sized, strong setae in adult females, longest setae fairly long; 0-5 mesial setae.

Coxa 3 without posterior tooth; anterior and posterior border converging downwards; ventral border with 13-19, moderately irregular-sized, strong setae in adult females, longest setae fairly long; mesial setae not in unusually high number (1-4).

Coxa 4 with 25-38 irregular-sized setae in adult females, of normal width, longest setae fairly long (number of setae increasing with size). Posterior setae setulose (unlike other species).

Propodus of P1 of normal proportions.

Ratio between length and width of carpus of P2: 2.5; ratio between propodus length and carpus length: 0.80 (one female measured).

P3 with carpal fang much shorter than propodus, distally very blunt and with accessory setule reaching tip of fang; propodus robust; outer spines/setae of propodus 'normal' in number (7-12), size, and shape; dactylus very robust, with fairly short unguis, with posterior border with distinct convexity. Ratio between propodus length and merus length of P3 in adult females: 0.70-0.90. Ratio between dactylus length and propodus length of P3 in adult females: 0.20. Ratio between dactylus length and merus length of P3 in adult females: 0.10-0.20. Ratio between length and width of propodus of P3 in adult females: 5.0-6.0. Ratio between length and width of dactylus of P3 in adult females: 3.0-4.0. Ratio between unguis length and total length of dactylus of P3 in adult females: 0.20-0.30. Ratio between unguis length and dactylus width in P3 of adult females: 0.50-1.0. (estuarine specimens more slender than those from open shores).

P4 with carpal fang much shorter than propodus, distally very blunt and with accessory setule reaching tip of fang; propodus robust; outer spines/setae of propodus 'normal' in number (8-10), size, and shape; dactylus very robust, with fairly short unguis, with posterior border with distinct convexity. Ratio between propodus length and merus length of P4 in adult females: 0.60-0.75. Ratio between dactylus length and propodus length of P4 in adult females: 0.20-0.25. Ratio between dactylus length and merus length of P4 in adult females: 0.10-0.15. Ratio between length and width of propodus of P4 in adult females: 4.0-5.0. Ratio between length and width of dactylus of P4 in adult females: 2.0-3.0. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.20-0.40. Ratio between unguis length and dactylus width in P3 of adult females: 0.40-1.0. (estuarine specimens more slender than those from open shores).

Median part of anterior border of basis of P5 straight; posteromedian seta group of merus with one long and strong curved major seta and one (rarely two) long, fairly slender, strongly plumose accessory seta(e); posterodistal seta group with one long strong straight or faintly curved seta (reaching tip of carpus) and 1-3 setules (no important sexual dimorphism); anterodistal area most commonly without plumodenticulate setae; longest posterior spine of carpus not reaching or overreaching tip of propodus; ratio between carpus + propodus length and merus length in females: 0.65-0.70.

Posterodistal lobe of basis of P6 not protruding but wide in open shore specimens (Jersey, Saint-Germain-sur-Ay, Blankenberge), lobe more pronounced in estuarine specimens (Westererschelde); anterior border strongly and regularly convex; posterior

border almost straight (faintly convex) on largest part of its length; in adult females, anterior border with setulose setae only, or with 1-4 non-setulose distal setae following more proximal plumose setae. Merus of P6 with 3-4 posterior groups of spines/ setae and 6-7 anterior groups; longest seta of each anterior seta group of significantly increasing size from proximal towards distal part of merus; carpus with or without posterior group of spines (distal group not considered); propodus with 2-3 posterolateral and 2-3 anteromesial groups of spines (terminal crown of spines not considered). Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 0.65-0.70 (open shores) or 0.85-0.90 (estuarine specimens).

Posterior border of basis of P7 with slender ornamentation (spiniform setae): in adult females, several fairly short setae on proximal 0.5 of basis, followed by longer space without setae, often much longer seta which is more or less setulose distally (that seta may be absent); total number of setae in adult females: 5-12; in adult males: 3-6 setae [only one in one large immature male examined], all short and on proximal 0.5 of basis; mesial side may have tiny spinules in females. Ischium very short, reaching 0.40-0.45 of outer side of merus; anterodistal border faintly concave on outer side, slightly more on mesial side; posterodistal border straight both on outer and mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 2.0-6.0; ratio between length of carpus and length of propodus: 1.0; ratio between length of propodus + carpus length and length of basis: 1.0-1.3.

Middle of posterior border of Ep1 and Ep2 bluntly angular and not produced in tooth.

Ep3 with posteroventral border regularly rounded, without posteroventral tooth, with 2-3 (rarely 4) groups of spines in adults (not always in regular transverse rows), with 0-4 setules on posterior border (i.e. a normal number).

Urosomite 1, dorsally with one pair of anteriorly directed setae and no posteriorly directed spine in open shore specimens examined; one spine or pair of spines (which can be very well-developed) sometimes present in estuarine specimens (from the Westerschelde and the Eems); ventrolateral border without outer strong setae (1-3 long slender setae or groups of two long slender setae arising from inner side may be present; such setae are not homologous to outer strong setae found in some other species).

Peduncle of uropod 1: outer dorsal border with 2-5 spines consisting of the following succession: 1) 0-3 short robust spines (regularly spaced if there are three spines), of slightly and gradually increasing size towards tip (first spine on 0.3 of peduncle if three spines; first spine on 0.5 if two spines; first spine on 0.6 if three spines), 2) larger space followed by penultimate short robust spine, 3) very short space followed by very strong ultimate spine; dorsomesial border with styliform spines, mostly single but occasionally in groups of two (4-5 groups). Endopod and exopod short and robust; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines fairly robust. Dorsal ratio between length of endopod and length of peduncle: about 0.60 (one female measured and one male measured). Dorsal ratio between length and width of endopod: 4.0 (1 female measured).

Peduncle of uropod 2: robust (dorsal ratio between length and width in a mature female = 2.2), outer dorsal border with 4-5 spines, which are fairly long and robust;

dorsomesial border with one robust spine and, more proximally, 1-2 groups of 1-2 strong setae or robust spines. Endopod and exopod short and robust; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines fairly robust. Dorsal ratio between length and width of endopod: 3.0 (one female measured).

Peduncle of uropod 3 with very few distal spines: about 2-4 (up to 5 in males) on dorsal side; 2-5 on ventral side (up to 9 in males), dorsal and ventral group of spines separated by distinct gap; all those spines very short, longest spines reaching 0.25-0.70 of length of endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with two (sometimes three) groups of 1-3 thin and not so long setae. Endopod mammiform (mesial side less convex than side facing exopod), with two spines in adult females (may be only one in small immatures), 2-6 spines in adult males. Exopod with first article broad and second short. Second article of exopod with one (sometimes 0 or 2) lateral seta(e) (if present on mesial side only). Mesial side of exopod with 8-12 (in adult females) and 13-19 (in adult males) long plumose setae of normal morphology and 0-4, well-developed, accessory, spiniform, non-setulose setae, all (except most proximal one) plumose setae much longer than longest setae of outer side. Outer side of exopod of females with 4-5 (sometimes 3 in not fully grown specimens) groups of 1-3 spiniform setae which may be as long as exopod width; 5-6 groups in males. Ratio between length and width of second article of exopod: 3.0-4.0. Ratio between length of second article and length of first article: 0.20. Ratio between length of second article and width of first article: 0.75-1.0. Ratio between length of second article of exopod and length of endopod: 0.80-0.90.

Lobes of telson without mesial setae.

Colour pattern.— White; eyes red and very dark (darker than in *B. sarsi*); viscera green; eggs blue (original colour description after specimens from the shores of Saint-Michel-en-Grève and Saint-Efflam, France). White; urosome often tinged with pink; eyes red and very dark (almost black); viscera dark green; eggs and ovaries blue (original colour description after specimens from the shore of Wemeldinge, The Netherlands). "Eye with dark red pigment. Eggs blue. Colour of body variable; in the reddish sands of Kames Bay the amount of red pigment in the pleon is considerable, in the lighter coloured sands of the Welsh coast pigment is much less" (Watkin, 1938). The body of Dutch specimens is more or less unpigmented (Faasse & Stikvoort, 2002). Nicolaisen & Kannevorff (1983) indicate that Danish *B. pilosa* and *B. sarsi* can easily be distinguished by their colour pattern: "...the colour of the contents of the hepatopancreatic caeca which was clearly visible through the cuticle of both living and newly killed animals. In *B. pilosa* the colour was brownish whereas it was bright green in *B. sarsi*. In addition, *B. pilosa* has a red pigmentation on the abdomen which is not present in *B. sarsi*."

Size.— Up to 6.8 mm (Salvat, 1967). There are considerable size differences between populations (personal observations).

Ecology.— Sandy beaches; may occur in area of reduced salinity (Lincoln, 1979). High water neap-tide level (Lincoln, 1979) to 42 m depth (Dahl, 1944). In open habitats, restricted to the highest part of the shore (Watkin, 1939b; Toulmond, 1964), but may be found subtidally in estuarine and brackish-water conditions (Lindström, 1855; Dahl, 1944; Vader, 1966; Persson, 1982; Köhn & Gosselck, 1989). On open coasts, it is

observed in the zone of water retention and the higher part of the zone of water resurgence, not in the zone of water saturation (Salvat, 1962, 1964), and it is more common on sheltered than on exposed shores (Salvat, 1962). This species is very euryhaline (Movaghar, 1964). It has actually a preference for brackish environments and has its maximal population densities in subtidal poly- and mesohaline waters (Vader, 1966). In Sweden it has been found at salinities as low as 6–8‰ (Dahl, 1944) and in the Gulf of Finland, as low as 4.5‰ (Segerstråle, 1944). Actually, as pointed out by Vader (1965), the conditions of the sediment on the upper part of the shore, even on open coasts, may be considered as brackish, since there are considerable fluctuations in the salinity of the ground water. Therefore, *B. pilosa* may be considered, to a certain extent, a brackish-water species. In optimal conditions, this species may have densities as high as 10 000 individuals/m² (Vader, 1966), and even sometimes 19 120 individuals/m² (Persson, 1982). No other *Bathyporeia* species lives in such high densities. It avoids too coarse sediments and prefers fine, somewhat muddy sand with at least 70% of the substrate finer than 210 μ (Vader, 1965, 1966). It is more tolerant to fine particles in the sediments than other species, and densities of 5 000 animals/m² have been found in sediments with up to 25% silt (i.e. particles with a diameter < 105 μ) (Vader, 1965). It feeds on epipsammic flora, and especially diatoms of the genus *Cocconeis* (see Sundbäck & Persson, 1981). In intertidal populations, ovigerous females are found year round in France and in Wales, but with considerable variation in number during the year; there would be two annual generations and those populations should be considered as bivoltine (Salvat, 1967; Fish & Preece, 1970a). Interestingly, in the Severn estuary, Wales, the life cycle is different up- and downstream. While the downstream population has the normal bivoltine cycle, the upstream population, which lives under an important ecological stress, is strictly univoltine, breeding only in mid-summer (Mettam, 1989). The species does not breed in December and January in the western Baltic, where the life span is about one year (i.e. the species is there univoltine), but with three distinct cohorts (Köhn & Sammour, 1990). In southeastern Baltic, the breeding period begins only in May (Jażdżewski, 1970). Persson (1982) too records an univoltine life cycle in the Baltic, and Powell & Moore (1991) made the same observation in southwestern Scotland, where ovigerous females are found from mid-March to mid-October, and where the population presumably consists of six cohorts. At equal size, the number of eggs per egg batch in *B. pilosa* is much smaller than in *B. pelagica* and *B. sarsi* (see Salvat, 1967), and Fish (1975) notes that *B. pilosa* has bigger eggs than *B. pelagica*. Furthermore, the average number of eggs is smaller in ecologically unfavourable conditions (Mettam, 1989). *B. pilosa* may be parasitized by the nicothoid copepod *Sphaeronella paradoxa* Hansen, 1897 (Hansen, 1897 as *Bathyporeia Robertsonii*; Gotto, 1893).

Biological references.— Zonation pattern: Watkin (1939b, 1942), Stock & de Vos (1960), Toulmond (1964), Howells (1964), Vader (1965, 1966), Salvat (1962, 1964, 1967), Fish & Preece (1970a). Annual upshore and downshore changes of density: Salvat (1967), Fish & Preece (1970a), Persson (1982), Nicolaisen & Kannevorff (1983). Granulometry preference: Stock & de Vos (1960), Movaghar (1964), Howells (1964), Vader (1965, 1966), Withers & Thorp (1978), Khayrallah & Jones (1980a, 1980b). Burrowing behaviour: Watkin (1939a), Nicolaisen & Kannevorff (1969). Swimming behaviour: Watkin (1939a, 1939b), Preece (1971b). Feeding behaviour: Nicolaisen & Kannevorff

(1969). Embryonic development: Fish (1975), Mettam (1989). Dynamics of populations: Howells (1964), Movaghar (1964), Salvat (1967), Jażdżewski (1970), Fish & Preece (1970a), Fish (1975), Persson (1982), Jagzdins & Soule (1984), Mettam (1989), Köhn & Sammour (1990), Powell & Moore (1991). Parasites: Hansen (1897, as *B. Robertsonii*), Gotto (1893). Pollution sensitivity: Cabioch et al. (1980), Khayrallah (1985). Ecophysiology: Fish & Preece (1970b), Preece (1970, 1971a), McGroarty (1971), Khayrallah (1985).

Distribution.— Eastern Atlantic: Western and Eastern coasts of British Isles; North Sea, Denmark (Lincoln, 1979); Norway [Oslo area only] (Brattegard & Holthe, 1997); Baltic as far north as Gottland [Visby] (Oldevig, 1959); Poland (Jażdżewski & Konopacka, 1993) and the gulf of Finland (Segerstråle, 1944); Western Germany (Stock & de Vos, 1960; Gosselck et al., 1993, Stecher & Dörjes, 1993; Kröncke et al., 2001); The Netherlands (Vader, 1965, 1966; Faasse & Stikvoort, 2002); Belgium (Leloup & Konietzko, 1956; Ysebaert et al., 2000); French part of the English Channel (Salvat, 1967; Toulmond & Truchot, 1964; Dauvin, 1999); French part of the Bay of Biscay, as far south as Arcachon (Salvat, 1962, 1964, 1969). There are also records from Morocco (Elkaïm, 1972a, 1972b, 1974, 1976a, 1976b; Menioui & Bayed, 1986), but the present examination of some specimens collected by Elkaïm proves that they do not belong to that species. They will be studied in a further paper. There is also a probably erroneous record from the northwestern Mediterranean (Massé, 1972).

Remarks.— As pointed out by Dahl (1944), the ornamentation of the third epimeral plate in *B. pilosa* is somewhat more variable than indicated by Watkin (1938) and should not be considered as an absolute character.

Bathyporeia pilosa and *B. sarsi* have many characters in common: absence of a tooth on coxae 1-3, very robust appendages (especially the dactylus of P3-P4), short and robust carpal fang with a slender setule, normally no posteriorly directed spine on the first urosomite, highly distinctive third uropod with a broad first and a very short second article. The robust appearance could merely be an adaptation to the life on the higher level of the shore, but the other common characters could possibly indicate a phylogenetic relationship between them. In the same context, it should be pointed out that some specimens of *B. pilosa* have a posterior group of spines on the carpus of P6, one or several such groups of spines being always present in *B. gracilis* and *B. tenuipes*.

In previous literature, *B. pilosa* has been described as devoid of posteriorly directed spines on the first urosomite. Certainly, it is the case in a large majority of specimens. However, during the present study, a small number of specimens examined, all from estuarine habitats and mostly males, had such spines. Estuarine specimens are slightly more slender than the specimens living on open shores, and the distal lobe of the merus of P6 is more developed in estuarine specimens. These differences are however minor and the recognition of two taxa is not justified on the basis of the data currently available.

5.4.7. *Bathyporeia sarsi* Watkin, 1938 (figs. 60-69)

Bathyporeia Robertsonii; ? Chevreux, 1887: 9; Chevreux & Fage, 1925: 94, fig. 83, 87 (at least in part).
Bathyporeia Robertsonii; G.O. Sars, 1891: 131, pl. 44 fig. 2; Stebbing, 1906: 121.

Bathyporeia robertsoni; Scott, 1893: 213, pl. 5 fig. 26-29; Stebbing, 1906: 121; ? Stephensen, 1929: 83, fig. 20.97 (after Stephensen, 1928).

Bathyporeia Robertsónii; ? Stephensen, 1928: 132, fig. 25.9-10.

Bathyporeia sarsi Watkin, 1938: 231, fig. 6; Schellenberg, 1942: 170, fig. 139 (after Watkin); Yashnov, 1948: 283, pl. 72 fig. 5 (after G.O. Sars); Gurjanova, 1951: 339, fig. 1999 (after Watkin); Toulmond, 1966: 229 (discussion), 231 (key); Nicolaisen & Kannevorff, 1969: 231, fig. 1-5, 7; Bellan-Santini, 1973: 96, table I; Lincoln, 1979: 320, fig. 150f-j; Enckell, 1980: 523, fig. 2397-2398 (after Watkin); Barclay, 1982: 230; Nicolaisen & Kannevorff, 1983: 238 (colour description); Bellan-Santini & Vader, 1988: 236; Köhn & Gosselck, 1989: 74, pl. 22 fig. 4 (after Lincoln); Withers, 1990: 446, fig. 9.31 (after Lincoln); Faasse & Stikvoort, 2002: 65 (colour description).

Types.— Zool. Mus. Oslo, nr F 1978: 2 adult males, previously syntypes, Northern Norway, Finnmark, Sørvær [original Sars' label: "*Bathyporeia Robertsoni*, Sp Bate Sørvær, Finnm. GOS'"]. The coordinates of Sørvær are 70°38'N 22°01'E. The male illustrated here is designated as the lectotype, the other as paralectotype. In the lectotype, the right third uropod is still present. In the paralectotype, both third uropods are missing.

Material.— **Norway:** ZMO F 1978: 2 adult males (lectotype and paralectotype), Northern Norway, Finnmark, Sørvær, 70°38'N 22°01'E [original Sars' label: "*Bathyporeia Robertsoni*, Sp Bate Sørvær, Finnm. GOS'"]. **Denmark:** TMU 12165: 3 specimens, North Sjælland, Hornbæk, 56°05'N 12°27'E, sandy shore, 06.viii.1921, leg. Dr Th. Mortensen (initially identified as *B. robertsoni* and mixed together with 1 *B. pilosa*, under the reg. nr. 2946). **United Kingdom:** TMU 4924: over 10 small specimens (some dissected and mounted on slides), Jersey, 21.viii.1968, st. 13, coll. W. Vader. **Germany:** TMU 9431: 2 specimens, Jade, station 33, 19.xi.1974, leg. J. Dörjes. TMU 1950: 1 female, Jade, station 38, 16.iv.1967, leg. J. Dörjes. TMU 4916: 1 specimen, Mellum, 53°44'N 08°06'E, station MB 2, leg. J. Dörjes. TMU 4909: 3 specimens, Mellum, 53°44'N 08°06'E, station MB 3, leg. J. Dörjes. TMU 4915: 1 female, Mellum, 53°44'N 08°06'E, station MB 6, leg. J. Dörjes. TMU 4914: 2 females, Mellum, 53°44'N 08°06'E, station MB 7, leg. J. Dörjes. TMU 4913: 1 juvenile male and 1 adult female, Mellum, 53°44'N 08°06'E, station MB 25/72, 20.vii.1972, leg. J. Dörjes. **The Netherlands:** ZMA Amph 100.947: >20 specimens (young and adults, poor condition), Eems estuary, stat. 364, 1956, det. J.H. Stock. ZMA Amph 100.949: 4 specimens, Eems-Dollard estuary, stat. 367, 1956, det. J.H. Stock. ZMA Amph 100.950: 22 specimens, Eems estuary, stat. 358, 1956, det. J.H. Stock. ZMA Amph 100.952: 14 specimens (young and adults, both sexes), Eems estuary, stat. 363, 1956, det. J.H. Stock (previously mixed with 1 *Bathyporeia pilosa*). ZMA Amph 100.953: 19 specimens (young and adults), Eems estuary, stat. 357, 1956, det. J.H. Stock. ZMA Amph 100.955: >20 specimens (young and adult specimens, both sexes), Eems estuary, stat. 359, 1956, det. J.H. Stock. ZMA Amph 100.956: >30 specimens (mostly young, not in very good condition), Eems estuary, stat. 365, 1956, det. J.H. Stock. ZMA Amph 100.958: 6 specimens, Eems estuary, stat. 360, 1956, det. J.H. Stock. NIOO-KNAW (CEMO): 1 specimen, The Netherlands, no more information, M. Rietveld coll. RMNH A 4968: 27 specimens (mostly adults, both sexes), Oosterschelde, between E.v.-S.v.K. and B.v. 5; grab 1730, 3 m depth, 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, AS; don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4969: 37 specimens (mostly adults, both sexes), Oosterschelde, grab 1735, 2 m depth, 06.x.1966, leg. Wim Vader, W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH A 4971: 36 adults (both sexes), W Zeeuws Vlaanderen, Verdronken Zwarte Polder, 05.x.1965, leg. W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. **Belgium:** RMNH A 4974: 55 specimens, almost all adults, between Zeebrugge and Blankenberge, 51°19'N 03°09'E, 05.x.1966, leg. W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. RMNH, previously A 4964: 1 adult male (identified as and mixed with 5 *Bathyporeia pilosa*), de Haan, 51°16'N 03°02'E, beach, 05.x.1966, leg. W.J. Wolff, Lein de Wolf, AS, don. Hydrobiologisch Instituut, afdeling Deltaonderzoek. **France:** RMNH A 4981: 66 specimens (adults and young), English Channel, Pointe aux Oies, 50°47'N 01°36'E, samples 1-3, 5, 6, 10, 14; 13.x.1966, leg. Wim Vader, don. Hydrobiologisch Instituut, afdeling

Deltaonderzoek. MNHN previously Am 2575: about 100 specimens (previously identified as *B. Robertsoni* and mixed together with *B. pilosa*), English Channel, Malo-les-Bains, 51°03'N 02°24'E, high tide, Stn 739, collection E. Chevreux. TMU 9390: over 40 specimens, English Channel, Saint-Germain-sur-Ay, 49°14'N 01°39'W, shore, 02.iii.2002, leg. Francis Kerckhof. MNHN previously Am 2576: 33 specimens (previously identified as *B. Robertsoni*), English Channel, St Lunaire, 48°38'N 02°07'W, vi.[18]85, leg. Dolffus. TMU 12 246: many specimens, English Channel, Saint-Michel-en-Grève, 48°41'N 03°35'W, sheltered shore, higher part of the shore, fine sand, 17.iv.2003, fixed alive in 70% alcohol, leg. C. d'Udekem d'Acoz. TMU 12 335: 15 specimens, English Channel, Saint-Efflam, 48°40'N 03°36'W, sheltered shore, higher part of the shore, fine sand, 20.iv.2003, fixed in 70% alcohol, leg. C. d'Udekem d'Acoz. TMU 12 279: 12 specimens, same sample, fixed alive in absolute alcohol. TMU 12 239: many specimens, English Channel, Saint-Jean-du-Doigt, 48°42'N 03°47'W, exposed shore, coarse sand, higher part of the shore, 18.iv.2003, leg. C. d'Udekem d'Acoz. TMU 12 333: 30 specimens, same locality, 19/04/2003, fixed in 95% alcohol **Spain**: TMU 9747: 1 adult female, Ria Pontevedra, 42°26'N 08°41'W, station 99. TMU 9745: 1 subadult female (partly dissected and mounted in polyvinyl lactophenol), 1 ovigerous female, 1 immature male, Ria Pontevedra, 42°26'N 08°41'W, station N-13 (previously identified as *Bathyporeia pelagica*).

Description.— Very robust species. Eye with well-developed ommatidia in adults. Pseudorostrum with tip subquadrate in females (more rounded in males), fairly high in females (less high in males than in females), scarcely to strongly overhanging, with 2-4 proximoventral plumose setae in adults; development and number of apical spines normal. Major flagellum of A1 with 5-7 (sometimes 8) articles in adult females, 8-11 in males; first article of accessory flagellum with 2-3 non-apical groups of spines. Flagellum of A1 of males of normal length (combined length of major flagellum and two distal articles of peduncle always much shorter than twice length of pseudorostrum). Anterior border of article 3 of peduncle of A2 usually with only one group of spinules and setae in apical position (rarely with small accessory group proximally); fourth article with apical spinules, with or without lateral spinules (few if present); flagellum with 8-10 articles in adult females, 15-21 in adult males; A2 of adult male much shorter than body length (about 0.6 as long as body length). In females, ratio between length and width of fourth article of A2: 2.5-3.0, of fifth article: 2.5-3.0.

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with about five strong setae on dorsal surface [may be only two in young specimens], all in one row, or all but one in one row; third article of adults with longitudinal row of setae on dorsal side (in addition to two transversal groups of anterior setae) [the longitudinal row may be lacking in immatures]; outer plate with 5-6 nodular spines.

Coxa 1 not especially elongate, with tip very broadly rounded, without ventral tooth or distinct notch, with about 6-8 anterior setae, without apical setule.

Coxa 2 without posterior tooth; transition between anterior and ventral border with distinct angular discontinuity; anterior border distinctly but moderately convex; anterior and posterior border subparallel (faintly diverging downwards on their upper 0.6); females with ventral border with 12-18 moderately irregular-sized, strong setae in adult females, longest setae fairly short; 0-2 mesial setae.

Coxa 3 without posterior tooth; anterior and posterior border parallel; ventral border with 12-21 moderately irregular-sized, strong setae in adult females, longest setae of normal length; mesial setae not in unusually high number (3-6).

Coxa 4 with 25-33 moderately irregular-sized, fairly short setae in adult females; posterior setae not setulose.

Propodus of P1 of normal proportions.

Ratio between length and width of carpus of P2: 2.5; ratio between propodus length and carpus length: 0.75.

P3 with carpal fang much shorter than propodus, distally very blunt and with accessory setule considerably overreaching tip of fang; propodus robust; outer spines/setae of propodus 'normal' in number (9-12), size and shape; dactylus robust, with fairly short unguis, with posterior border distinctly convex. Ratio between propodus length and merus length of P3 in adult females: 0.75-0.85. Ratio between dactylus length and propodus length of P3 in adult females: 0.20. Ratio between dactylus length and merus length of P3 in adult females: 0.15. Ratio between length and width of propodus of P3 in adult females: 5.5-6.0. Ratio between length and width of dactylus of P3 in adult females: 3.0-3.5. Ratio between unguis length and total length of dactylus of P3 in adult females: 0.20. Ratio between unguis length and dactylus width in P3 of adult females: 0.60-0.70.

P4 with carpal fang much shorter than propodus, distally very blunt and with accessory setule considerably overreaching tip of fang; propodus robust; outer spines/setae of propodus 'normal' in number (9-11), size and shape; dactylus robust, with fairly short unguis, with posterior border distinctly convex. Ratio between propodus length and merus length of P4 in adult females: 0.65-0.75. Ratio between dactylus length and propodus length of P4 in adult females: 0.20. Ratio between dactylus length and merus length of P4 in adult females: 0.15. Ratio between length and width of propodus of P4 in adult females: 4.5. Ratio between length and width of dactylus of P4 in adult females: 2.5. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.20. Ratio between unguis length and dactylus width in P3 of adult females: 0.45-0.50.

Median part of anterior border of basis of P5 faintly convex; posteromedian seta group of merus with one long and strong curved major seta and 0-2 short and slender, scarcely setulose or non-setulose accessory setae; posterodistal seta group with one long strong straight seta (nearly reaching tip of carpus) and 0-3 setules (no important sexual dimorphism); anterodistal area with 2-5 plumodenticulate setae; longest posterior spine of carpus not reaching or overreaching tip of propodus; ratio between carpus + propodus and merus length in adult females: 0.75.

Posterodistal lobe of basis of P6 protruding and wide; anterior border strongly and regularly convex; posterior border almost straight (faintly convex) on largest part of its length; in females, anterior border with succession of many plumose setae and plumose spines of increasing robustness, and few strong non-setulose spines. Merus of P6 most commonly with 4-5 posterior groups of spines/setae (often only 3 in young specimens) and 6-8 (usually 7) anterior groups; longest seta of each anterior seta group of significantly increasing size from proximal towards distal part of merus; carpus without posterior spines (distal group not considered); propodus with 2-4 posterolateral and 2-3 anteromesial groups of spines (terminal crown of spines not considered) in adults (one dorsolateral and one anteromesial groups in young specimens). Spines of carpus and merus robust and long. Ratio between length of propodus and anterior length of merus in P6: 0.85.

In females, posterior border of basis of P7 proximally with robust ornamentation (short and usually fairly regular-sized spines), distally with long robust setae, num-

ber: 13-18 in adults (5-6 in young specimens); in males, posterior border of basis of P7 with slender ornamentation on all its length (moderately short and regular-sized setae, except for longer distal seta), number: 7-12; mesial side with spinules in females. Ischium moderately elongate, reaching 0.37-0.39 of outer side of merus; anterodistal border weakly concave on outer side, slightly more on mesial side; posterodistal border straight on outer side, weakly concave on mesial side. Spines of carpus and merus robust and long. In females, ratio between length and width of carpus: 2.5, of propodus: 5.0, ratio between length of carpus and length of propodus: 0.95-1.0, ratio between length of propodus + carpus length and length of basis: 1.1.

Middle of posterior border of Ep1 and Ep2 bluntly angular and not produced in tooth.

Ep3 with posteroventral border regularly rounded, without posteroventral tooth, usually with 4-5 transverse groups of spines in adults (sometimes only 2), with 3-4 setules on posterior border (i.e. normal number).

Urosomite 1, dorsally with one pair of anteriorly directed setae and no posteriorly directed spine; ventrolateral border with 0-3 short strong setae arising from outer side. Peduncle of uropod 1: outer dorsal border with 5-7 spines consisting of following succession: 1) 3-5 regularly spaced short robust spines of slightly and gradually increasing size towards tip, 2) larger space followed by penultimate short robust spine, 3) very short space followed by very strong ultimate spine; dorsomesial border with single styliform spines on distal part, and setae (usually in groups of two) on proximal part (5-7 groups of spines and setae). Endopod and exopod fairly short and robust; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines of normal robustness. Dorsal ratio between length of endopod and length of peduncle: about 0.75 (one female measured). Dorsal ratio between length and width of endopod: 5.5 (one female measured).

Peduncle of uropod 2: robust (dorsal ratio between length and width in a mature female = 2.1), outer dorsal border with 4-5 (sometimes 6) fairly long and robust spines; dorsomesial border with 4-5 single long slender spines. Endopod and exopod fairly short and robust; endopod with border facing exopod, with only one long spine in subdistal position. Endopod and exopod spines of normal robustness but fairly long. Dorsal ratio between length and width of endopod: 3.5 (one female measured).

Peduncle of uropod 3 with distal spines in normal number (dorsal and ventral spines forming more or less continuous series, not two well separated groups), longest spines usually reaching 0.8 (sometimes only 0.5) of length of endopod or overreaching endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with two, rarely three groups of 1-2 slender and not so long setae. Endopod elliptic but distally fairly broad, with 3-5 spines in both sexes (one may be distinctly but not considerably longer than others). Exopod with first article broad and second short. Second article of exopod most commonly with one lateral seta, sometimes with two or three lateral setae (when lateral setae present, then on mesial side only), second articles without lateral setae not uncommon. Mesial side of exopod with 11-15 long plumose setae of normal morphology in females (13-20 in males) and 2-4 short to extremely short, accessory, spiniform, non-setulose setae (actually spinules and not setae), almost all plumose setae much longer than longest setae of outer side. Outer side of exopod with 4-5 (rarely 6) groups of 2-4 spiniform setae, longest slightly shorter

than exopod width. Ratio between length and width of second article of exopod: 3.5-4.5. Ratio between length of second article and length of first article: 0.20-0.25. Ratio between length of second article and width of first article: 0.85-1.2. Ratio between length of second article of exopod and length of endopod: 0.80-0.90.

Lobes of telson without mesial setae.

Colour pattern.— White; eyes red and dark; viscera green to yellowish; eggs and ripe ovaries blue (original colour description after specimens from the shores of Saint-Efflam and Saint-Jean-du-Doigt, France). Nicolaisen & Kannevorff (1983) indicate that Danish *B. pilosa* and *B. sarsi* can easily be distinguished by their colour pattern: "...the colour of the contents of the hepatopancreatic caeca which was clearly visible through the cuticle of both living and newly killed animals. In *B. pilosa* the colour was brownish whereas it was bright green in *B. sarsi*. In addition, *B. pilosa* has a red pigmentation on the abdomen which is not present in *B. sarsi*." The body of Dutch *B. sarsi* is more or less unpigmented (Faasse & Stikvoort, 2002). Eggs dark blue (Rasmussen, 1973). Eyes dark in alcohol (present material).

Size.— Up to 7.3 mm (Salvat, 1967), and exceptionally 8.0 mm (Rasmussen, 1973).

Ecology.— Intertidal to about 20 m (Vader, 1965). *B. sarsi* occupies an intermediate position on the shore between those of *B. pelagica* and *B. pilosa* in localities where the three species occur together (Salvat, 1967). However, in such localities, there can be a wide overlap between the distribution of *B. sarsi* and *B. pelagica* (ibid.). In open or fairly open habitats, *B. sarsi* is strictly intertidal (Toulmond, 1964; Vader, 1965). In such habitats it can be observed between high water marks of neap-tide and low water marks of spring-tide (but not low water marks of extreme spring-tide), and the maximum density occurs slightly above mid-tide level (Toulmond, 1964). On the other hand, in estuarine conditions, it may be found below low tide marks, locally down to 20 m (Vader, 1965). It is a fairly euryhaline species able to live in polyhaline conditions but not recorded in mesohaline waters (Vader, 1965). *B. sarsi* has been found at a fairly large range of granulometry, although it prefers somewhat coarser sediments than *B. pilosa* and finer ones than *B. pelagica* (see Vader, 1965). The population densities are always much lower than those of *B. pilosa*, almost never exceeding 1 000 individuals/m² (Vader, 1965), although densities of 1 105 individuals/m² have been recorded by Salvat (1967). *B. sarsi* breeds all year round on the northeastern coasts of France, with a spring and a summer peak, and there would be two yearly generations in that area (Salvat, 1967). Further south, in Arcachon, where the species is much more rare, the same author has not been able to establish a clear outline of the biological cycle of the species. Further north, in Northumberland, the life cycle of the species would be annual (Ladle, 1975). *B. sarsi* is occasionally parasitized by the nicothoid copepod *Sphaeronella paradoxa* Hansen, 1897 (Hamond, 1967; Gotto, 1993).

Biological references.— Zonation pattern: Stock & de Vos (1960), Toulmond (1964), Howells (1964), Colman & Segrove (1955a, 1955b), Vader (1965, 1966), Salvat (1967), Fish & Preece (1970a). Annual upshore and downshore changes of density: Ladle (1975), Nicolaisen & Kannevorff (1983). Burrowing behaviour: Schellenberg (1929 as *Bathyporeia robertsoni*), Nicolaisen & Kannevorff (1969). Granulometry preferences: Stock & de Vos (1960), Vader (1965, 1966), Withers & Thorp (1978). Swimming behaviour: Colman & Segrove (1955). Dynamics of populations: Howells (1964), Salvat (1967), Ladle (1975), Bamber (1993). Long-term variations in population density: Bamber

(1993). Feeding behaviour: Nicolaisen & Kannevorff (1969). Stomach morphology: Kannevorff & Nicolaisen (1969). Parasites: Hamond (1967, 1973), Gotto (1993). Eco-physiology: McGrorothy (1971).

Distribution.— Eastern Atlantic: Oslo area, Norway (Brattegard & Holthe, 1997); southern half of the British Isles (Lincoln, 1979); northeastern Scotland (Eleftheriou & Robertson, 1988); apparently absent in the past in western Scotland (Watkin, 1942) but now occurring there, including at Kames Bay, the station extensively studied by Watkin (Barclay, 1982); western Germany (Stock & de Vos, 1960; Gosselck et al., 1993; Stecher & Dörjes, 1993); western Baltic Sea [Kieler Bucht] (Köhn & Gosselck, 1989); The Netherlands (Vader, 1965, 1966; Faasse & Stikvoort, 2002); Belgium (present material); French part of the English Channel (Toulmond & Truchot, 1964; Salvat, 1967; Dauvin, 1999); French part of the Bay of Biscay (Salvat, 1967; Faure, 1969; Sorbe, 1982; de Montaudouin & Sauriau, 2000); northwestern Spain (Planas et al., 1984; Viéitez & Baz, 1988); western Portugal (Marques & Bellan-Santini, 1985); southwestern Portugal (Marques & Bellan-Santini, 1985, 1991); southern Portugal (Rodrigues & Dauvin, 1987).

Remarks.— I have re-examined the type material of *Bathyporeia sarsi* (previously identified as *B. Robertsonii* by G.O. Sars (1891)) and it indeed proved to belong to the species that it was supposed to be. However, I wonder if the type locality is correct. According to G.O. Sars (1891), Watkin (1938), and the labels of the type specimens, it would be Sørvær in West Finnmark, i.e. a very northern locality, far beyond the normal range of the species. Brattegard & Holthe (1997) indicate that in Norway, *B. sarsi* is present in the Oslo area, absent from all the west coast, and they indicate two very northern records, without precisions. One is evidently based on the types of *B. sarsi*. Nothing is known as concerns the other record, but it may well be based on a misidentification. Furthermore, I have found a small exposed sandy creek very favourable for *Bathyporeia* spp. in northern Norway (Tromsø area, Northern coast of Kvaløya, less than 1 km east of Sommarøy bridge). There, at 0.4 m below tide marks, *Bathyporeia elegans* (i.e. the normal species for very northern shores) was found in large numbers. Higher, on the lower third of the shore, in fine clean sand not saturated in water (at the same level as a belt of *Fucus evanescens*), I found again *B. elegans*, but at a very low density (only 3 specimens collected). On the higher third of the shore, the most favourable part for *B. sarsi*, which is essentially an intertidal species, I found no *Bathyporeia* at all. The granulometry of the sand looked the same on the whole shore. Although not conclusive, that single observation supports the present suggestion, i.e. that the type locality of *B. sarsi* is incorrect and that *B. sarsi* does not occur in Northern Norway.

Lincoln (1979) considers that the *Bathyporeia pilosa* of Elmhirst (1931) is probably *B. sarsi*. He could well be right but it cannot be demonstrated with certainty, since Elmhirst gave no morphological account of his specimens. Actually, there is obviously major confusion between species in Elmhirst's paper as he has evidently lumped different species together.

As pointed out by Salvat (1967), the number of groups of spines on the third epimeral plates is not an absolute differential character between *B. pilosa* and *B. sarsi*, as emphasized by Watkin (1938). Female *B. sarsi* have a pseudorostrum very different from that of *B. pilosa*: very broad and distinctly subquadrate, versus very narrow and

rounded. Females of those species can be easily separated on the basis of that character only. On the other hand, the pseudorostrum of male *B. sarsi* is more rounded and not as broad as in the female, and the differences of the pseudorostrum between *B. sarsi* and *B. pilosa* are not so pronounced. Therefore, a reliable identification of males requires a more careful examination than that of females.

Interestingly, *B. sarsi* has very often one or more short strong setae arising from the outer side of the outer ventral border of its first urosomite. The only other western European *Bathyporeia* with that character are *B. gracilis* and *B. tenuipes*.

5.4.8. *Bathyporeia tenuipes* Meinert, 1877 (figs. 70-76)

Bathyporeia Tenuipes Meinert, 1877: 101.

Bathyporeia tenuipes; Meinert, 1890: 158 (no morphological account); Watkin, 1938: 225, fig. 4; Schellenberg, 1942: 168, fig. 137 (after Watkin); Gurjanova, 1951: 343, fig. 202 (after Watkin); Toulmond, 1966: 229 (discussion), 231 (key); Bellan-Santini, 1973: 101, table II; Lincoln, 1979: 314, 318, fig. 149f-j; Withers, 1990: 446, fig. 9.31 (after Lincoln).

Bathyporeia gracilis; Norman, 1900: 326 (no morphological account); Reibisch, 1905: 158, pl. 4 fig. 9-12 (not *Bathyporeia gracilis* G.O. Sars, 1891).

? *Bathyporeia elegans* Crawford, 1937: 639 (not *Bathyporeia elegans* Watkin, 1938).

Bathyporeia tenuis; Köhn & Gosselck, 1989: 71, erroneous spelling for *B. tenuipes* (no morphological account).

Types.— Watkin (1938) indicated: "Type specimen, an adult male in the Zoological Museum, Copenhagen. Locality given on label in tube as Anholt, Kattegat". Watkin (1938) gave a re-description of that specimen, which leaves no doubt as concerns its identity. According to Dr Jørgen Olesen (pers. comm.), its registration number is ZMUC CRU8359. The approximate coordinates of Anholt are 56°42'N 11°32.5'E.

Material.— **Denmark:** TMU 9428: 1 adult male and 1 adult female in not so good condition, Hauch "St. 226, Hirsholmenes Fyrtaarn I St Ø1/2Ø, 5.5Kv mil, sand, 12 m depth, "(Meinert determ : Bestemm. Revid. Af E.E. Watkin, Aberystwyth, 1938)". TMU 9430: 2 adult females in poor condition, Hauch "St. 312. Nordre Rønner I VSG, 6 Kv.mil, 16 m, sand, sten., (Meinert determ; Bestem. Revid. Af E.E. Watkin, Aberystwyth, 1938)". **United Kingdom:** TMU 9427: 5 immature males (one partly dissected and mounted), 2 mature females (one dissected, mounted and fully illustrated), 3 immature females (one dissected and mounted), "Gorey-Jersey-boat", 20.viii.1952. **Ireland:** TMU 12 166: 1 mature male, 6 large immature males, 5 mature females (including 1 ovigerous), Galway Bay, GB4, Decca coordinates R.E.12/G.A.45, sand, 70 m depth, 25.vi.1974, Dave McGrath leg. TMU 12 167: 1 mature male (fully dissected and mounted), Galway Bay, GB4, Decca coordinates R.E.12/G.A.45, sand, 70 m depth, 25.vi.1974, Dave McGrath leg. DM: 8 mature females including 2 ovigerous, Galway Bay, GB 14, Decca coordinates R.D.22/G.A.45, shell debris, sand, 33 m depth, 26.vi.1974, Dave McGrath leg. DM: 1 large immature male, 2 mature females, Galway Bay, GB 47, Decca coordinates R.E.12/G.A.44, sand, 73 m depth, Dave McGrath leg. TMU 12 168: 1 large immature male and 7 mature females, Galway Bay, GB48, Decca coordinates R.E.14/G.A.44, sand, 78 m depth, Dave McGrath leg. TMU 12 169: 1 mature female (partly dissected and mounted), Galway Bay, GB48, Decca coordinates R.E.14/G.A.44, sand, 78 m depth, Dave McGrath leg. DM: 5 adult females, Galway Bay, GB 49, Decca coordinates R.E.16/G.A.44, sand, 77 m depth, Dave McGrath leg. **France:** TMU 12 272: 6 specimens, English Channel, Bay of Morlaix, "La Pierre Noire", sand, 10-20 m depth, ship Mysis, Picard's dredge, 15.iv.2003, fixed alive in absolute alcohol, leg. C. d'Udekem d'Acoz. TMU 12 328: 1 specimen, same sample, fixed in 70% alcohol. MNHN, previously Am. 2565: 1 female (previously identified as *B. guilliamsoniana* and mixed with *B.*

pelagica, *B. guilliamsoniana*, and the spiny form of *B. elegans*), Bay of Biscay, Le Croisic, 47°18'N 02°31'W, Stas. 55, 75, 87, collection Ed. Chevreux. MNHN, previously Am. 5244: 8 specimens including an adult male (previously identified as *B. pelagica*; actually *B. tenuipes* mixed together with *B. pelagica* and *B. elegans* forma B), Bay of Biscay, 'baie du Croisic', 47°18'N 02°31'W, collection Ed. Chevreux. **Unknown origin:** TMU 9429: 2 adult females and the posterior half of a third specimen, "St. 40" [no further indication].

Description.— Very slender species. Eye with well-developed ommatidia in adults. Pseudorostrum with angular to fairly rounded tip, of normal height, strongly overhanging, with 4-7 proximoventral plumose setae in adults (sometimes only 3 in immatures); apical spines small, spaced, and reduced in number (most commonly 4-5). Major flagellum of A1 with six articles in females, 11-12 in males; first article of accessory flagellum with 2-3 non-apical groups of spines. Flagellum of A1 of males of normal length (combined length of major flagellum and two distal articles of peduncle always much shorter than twice length of pseudorostrum). Anterior border of article 3 of peduncle of A2 usually with 3-4 groups of spinules and setae; fourth article with lateral and apical spinules; flagellum with 8-10 articles in adult females (may be only 6 in immature females), 39-42 in adult males; A2 of adult male distinctly but not considerably longer than body length. In females, ratio between length and width of fourth article of A2: 3.5-4.0, of fifth article: 4.0-5.0.

Penultimate article of mandibular palp elongate.

Second article of maxillipedal palp with about 4-6 strong setae on dorsal surface, all in one row or all but one in one row; third article without longitudinal row of setae on dorsal side (only anterior setae in transverse row present); outer plate usually with seven spines.

Coxa 1, fairly elongate, with tip narrowly rounded, without ventral tooth but with more or less distinct notch (one seta associated with that notch), with five anterior setae in dissected female, without apical setule.

Coxa 2 with posterior tooth; tooth separated from coxa by deep notch; transition between anterior and ventral border very abrupt, with strong angular discontinuity; anterior border straight; anterior and posterior border strongly diverging downwards (coxa more or less trapezoidal or triangular); females with ventral border with 30-36 irregular-sized setae in adult females, of variable width (some slender, some quite broad), longest setae short; mesial setae in very high number (18 in dissected female).

Coxa 3 with posterior tooth; tooth separated from coxa by deep notch; anterior and posterior border faintly diverging downwards; ventral border with 31-36 irregular-sized setae in adult females, of variable width (some slender, some quite broad), longest setae short; mesial setae in very high number (21 in dissected female).

Coxa 4 with 57-66 irregular-sized setae in adult females, of normal width, longest setae of normal length; posterior setae not setulose.

Propodus of P1 of normal proportions.

Ratio between length and width of carpus of P2: 3.0; ratio between propodus length and carpus length: 0.90 (one female measured).

P3 with carpal fang distinctly shorter than propodus, distally styliform and without accessory setule; propodus slender; outer spines/setae of propodus 'normal' in number (nine in dissected female), short, proximal setae slender, distal setae robust; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly

concave. Ratio between propodus length and merus length of P3 in adult females: 0.85-0.90. Ratio between dactylus length and propodus length of P3 in adult females: 0.30-0.40. Ratio between dactylus length and merus length of P3 in adult females: 0.25-0.35. Ratio between length and width of propodus of P3 in adult females: 5.5-6.0. Ratio between length and width of dactylus of P3 in adult females: 3.0-4.5. Ratio between unguis length and total length of dactylus of P3 in adult females: 0.20-0.35. Ratio between unguis length and dactylus width in P3 of adult females: 0.60-1.5.

P4 with carpal fang reaching about tip of propodus, distally styliiform and without accessory setule; propodus slender; outer spines/setae of propodus 'normal' in number (7-10), size and shape; dactylus slender, with well-developed unguis, with posterior border distinctly and regularly concave. Ratio between propodus length and merus length of P4 in adult females: 0.70-0.80. Ratio between dactylus length and propodus length of P4 in adult females: 0.40-0.45. Ratio between dactylus length and merus length of P4 in adult females: 0.25-0.35. Ratio between length and width of propodus of P4 in adult females: 4.5-5.5. Ratio between length and width of dactylus of P4 in adult females: 3.5. Ratio between unguis length and total length of dactylus of P4 in adult females: 0.25-0.40. Ratio between unguis length and dactylus width in P4 of adult females: 0.90-1.5.

Median part of anterior border of basis of P5 regularly convex; posteromedian seta group of merus with one long and slender curved major seta and 1-2 long, accessory setae (one may be setulose); posterodistal seta group with one short spine in both sexes (straight or weakly curved, and reaching 0.40 of carpus) and with 0-1 setule (no important sexual dimorphism); anterodistal area always with plumodenticulate setae; longest posterior spine of carpus not reaching tip of propodus; ratio between carpus + propodus length and merus length in adult females: 0.95.

Posterodistal lobe of basis of P6 protruding and wide; anterior border strongly and regularly convex; posterior border strongly convex on all its length (with slight proximal angular discontinuity), but less convex than anterior border; in females, anterior border with succession of several narrow non-setulose setae (or appearing as such in light microscopy), several slender (but stronger) plumose spines/setae, one strong non-setulose spine. Merus of P6 with 5-6 posterior groups of spines/setae and 6-7 anterior groups; longest seta of each anterior seta group of scarcely increasing size from proximal towards distal part of merus; carpus with 1-3 (most commonly 3) groups of posterior spines (in addition to distal group); propodus with 4-5 posterolateral and 4 anteromesial groups of spines (terminal crown of spines not considered). Spines of carpus and merus slender and fairly short. Ratio between length of propodus and anterior length of merus in P6: 1.1-1.2.

Posterior border of basis of P7 with slender ornamentation (fairly long, slender spines or strong setae in females, slender setae in males), spines/setae of very regular length, most distal slightly longer; number: 19-25 in adult females, 13-18 in adult males; mesial side without spines. Ischium very elongate, reaching 0.46 of outer side of merus (one specimen measured); anterodistal border weakly but distinctly concave on outer and mesial sides; posterodistal border straight on outer side, slightly concave on mesial side. Spines of carpus and merus slender and fairly short. In females, ratio between length and width of carpus: 6.5, of propodus: 7.0, ratio between length of carpus and length of propodus: 1.0, ratio between length of propodus + carpus length and length of basis: 2.0.

Middle of posterior border of Ep1 and Ep2 angular but not produced in tooth.

Ep3 trapezoidal, with posteroventral border fairly angular or rounded (posterior border very straight), without posteroventral tooth, with 5-10 transverse groups of spines in adults, with 1-8 setules on posterior border (i.e. sometimes high number).

Urosomite 1, dorsally with one pair of anteriorly directed setae and 1-4 pairs of similar-sized, posteriorly directed spines; ventrolateral border with 4-6 (sometimes only one) long strong setae arising from outer side.

Peduncle of uropod 1: outer dorsal border with 9-12 spines consisting of the following succession: 1) 4-6 regularly spaced long slender spines, of more or less decreasing size towards tip, 2) 3-5 regularly spaced, short, fairly robust spines, 3) larger space followed by one very short, robust, penultimate spine, 4) very short space followed by very long and fairly robust ultimate spine; dorsomesial border with styliform (nearly setiform) spines, single on distal part or in groups of two on proximal part (8-9 groups). Endopod and exopod very long and very slender; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines of normal robustness, except for long and very slender mesial spines of endopod. Dorsal ratio between length of endopod and length of peduncle: about 0.90. Dorsal ratio between length and width of endopod: 7.0.

Peduncle of uropod 2: of normal proportions (dorsal ratio between length and width in one mature female = 2.7), outer dorsal border with 5-6 fairly short and fairly slender spines; dorsomesial border with three single styliform spines on distal part, and three transverse rows of 2-4 long and robust setae in adults and large immatures. Endopod and exopod very long and very slender; endopod with border facing exopod, with only one long spine, in subdistal position. Endopod and exopod spines long and very slender. Dorsal ratio between length and width of endopod: 5.5.

Peduncle of uropod 3 with distal spines in normal number, longest spine twice as long as endopod (endopodal spines excluded); outer border of peduncle of uropod 3 with 3-4 groups of 1-3 robust and long setae. Endopod elliptic, usually with 3-4 spines. Exopod with first article narrow, second article long. Second article of exopod with lateral setae on both sides. Mesial side of exopod with 10-14 not so long, scarcely plumose setae (distinctly shorter in females than in males), and 7-9 very short and very thin (non-spiniform) accessory non-setulose setae, longest plumose setae only slightly longer than longest setae of outer side in females. Outer side of exopod with 9-11 groups of 1-5 long and strong and more or less spiniform setae, more developed in females than in males, several being longer than exopod width in females. Ratio between length and width of second article of exopod: 4.5 Ratio between length of second article and length of first article: 0.40 Ratio between length of second article and width of first article: 2.0 Ratio between length of second article of exopod and length of endopod: 2.0.

Lobes of telson without mesial setae.

Colour pattern.— White; eyes bright red (original colour description after subtidal specimens from "La Pierre Noire", bay of Morlaix, France). Eye colourless in alcohol.

Size.— 7 mm (Meinert, 1877).

Ecology.— On very fine sand mixed with shell (Fincham, 1969) and on fine sands (Toulmond & Truchot, 1964). Community of sand sediments with *Abra alba* (W. Wood, 1802) and *Corbula gibba* (Olivi, 1792): sandy facies with *Aponuphis bilineata*

(Baird, 1870) (as *Hyalinoecia bilineata*) (see Cabioch, 1968: 628). Rarely intertidal (Faure, 1969) to 78 m (present material). Lincoln (1979) indicates: "Depth range about 0-400 m", without further comments. In the North Sea, the species is never found close to the coasts (Reibisch, 1905 as *B. gracilis*).

Biological references.— Granulometry preferences: Fincham (1969), Dauvin (1987), Dauvin & Vallet (1997). Swimming behaviour: Dauvin & Zouhiri (1996). Long-term variations in population density: Dauvin (1987). Pollution sensitivity: Dauvin (1987).

Distribution.— Eastern Atlantic: central part of the North Sea (Reibisch, 1905 as *B. gracilis*); Denmark (Meinert, 1877, 1890); Sweden [Bohuslän: Gullmarfjord] (Oldevig, 1959); western Germany (Kröncke et al., 2001); Doggerbank (Kröncke, 1991); Channel Isles, West Channel, Scilly Isles, Bristol Channel, Solway, Belfast (Lincoln, 1979); Galway bay (present material); French part of the English Channel (Toulmond & Truchot, 1964; Dauvin, 1987, 1999; Dauvin & Vallet, 1997; Dauvin & Zouhiri, 1996); French part of the Bay of Biscay (Faure, 1969; de Montaudouin & Sauriau, 2000); Portugal (Marques & Bellan-Santini, 1991, 1993).

Remarks.— An essentially subtidal species, which has been rather infrequently recorded, although it is obviously not rare, and may even prove to be locally common (Dauvin, 1987). The shape of the pseudorostrum is more variable than suggested by literature data and is not always as acute as it is supposed to be. *B. tenuipes* is considerably more slender than any other *Bathyporeia* species from western Europe, and it shares several characters with *B. gracilis* (see account on that species).

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7. References

The figures and plates are indicated only if they have a separate pagination.

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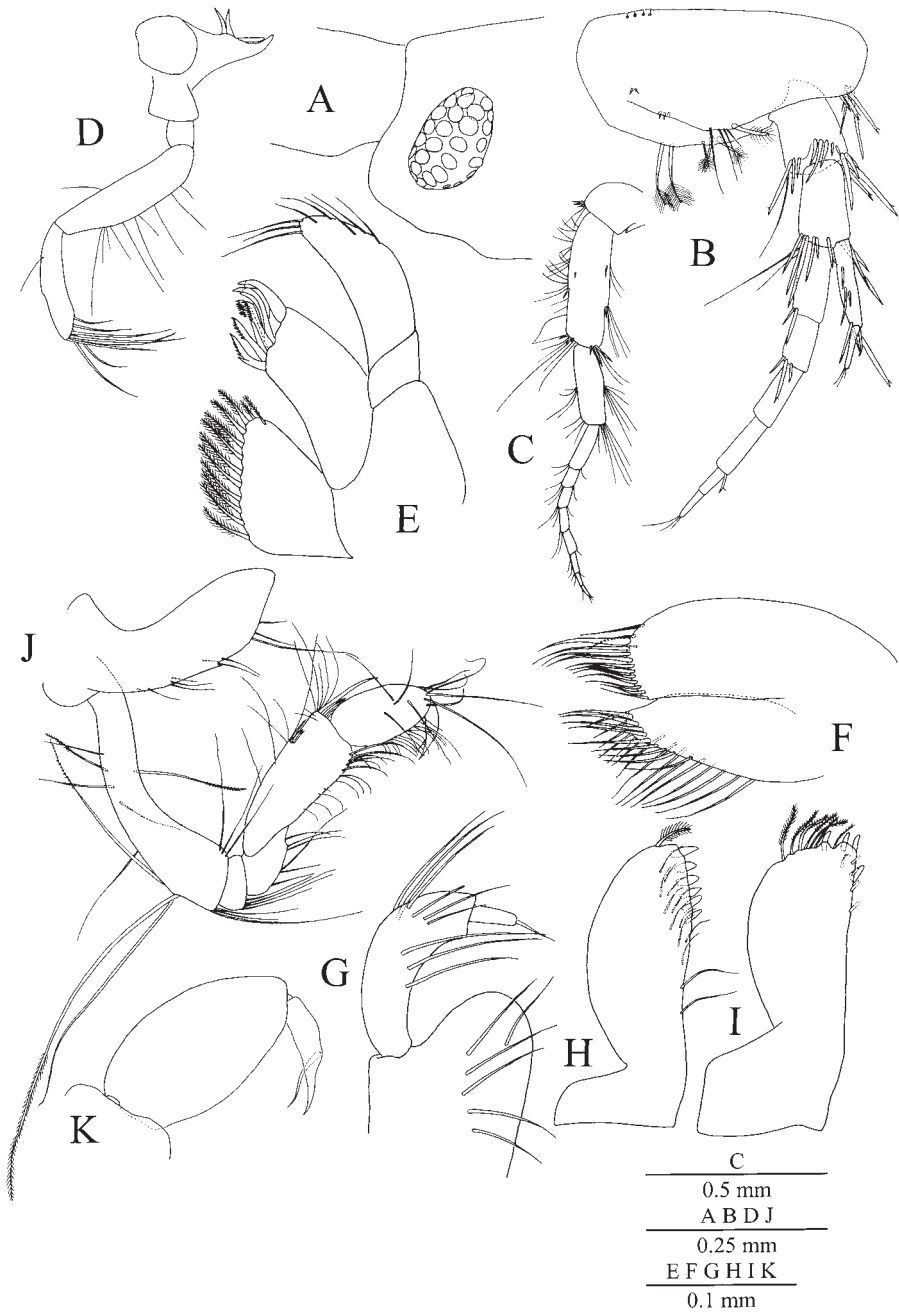


Fig. 4. *Bathyporeia elegans* Watkin, 1938, lectotype, female, forma A, southern Norway, Jæderen, Ognebuk, ZMO F2656. A, anterior part of the head; B, right A1; C, left A2; D, right Md; E, Mx1; F, left Mx2; G, left Mxp palp; H, left Mxp outer plate; I, left Mxp inner plate; J, right P1; K, anterior part of right P1.

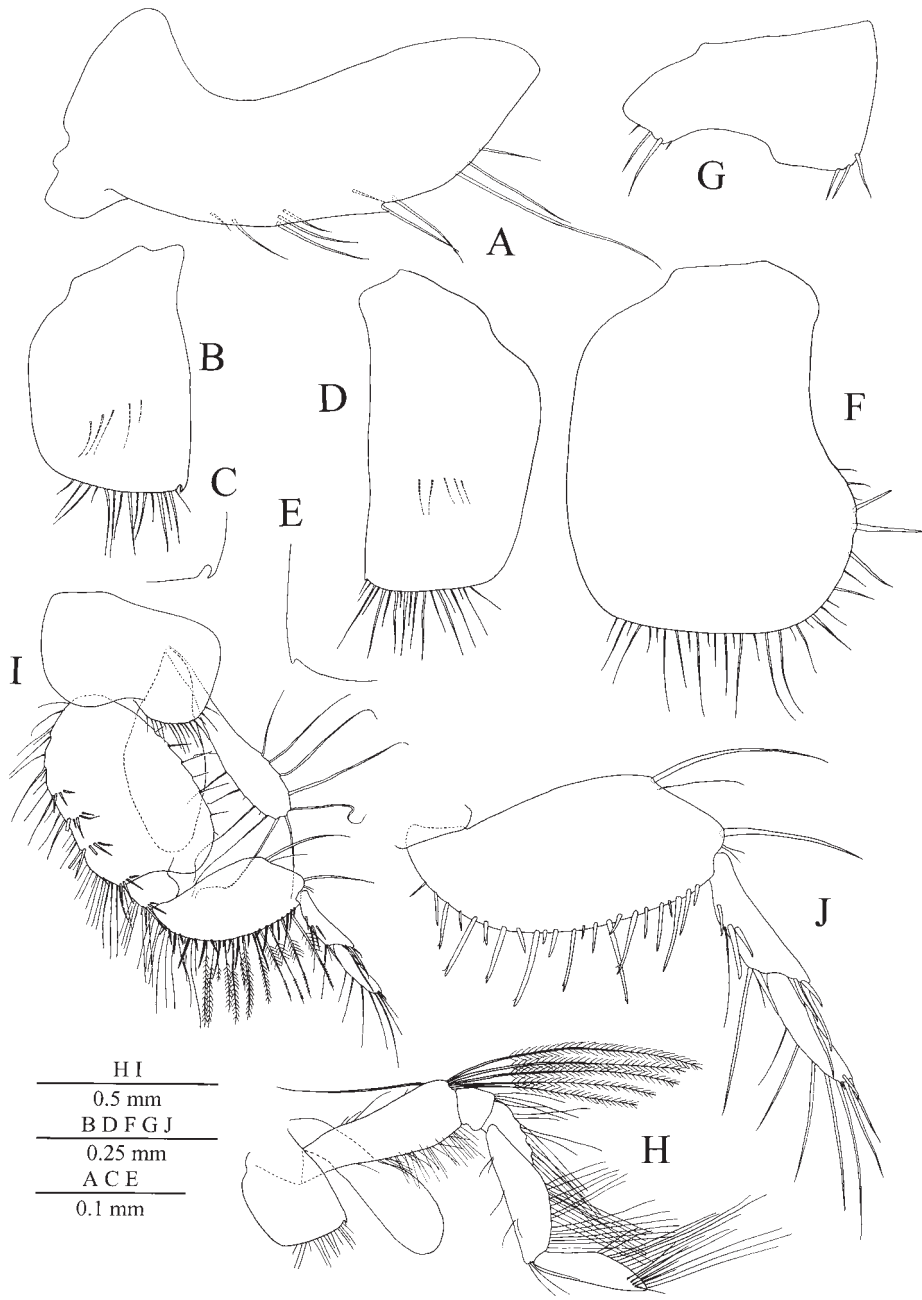


Fig. 5. *Bathyporeia elegans* Watkin, 1938, lectotype, female, forma A, southern Norway, Jæderen, Ognbukta, ZMO F2656. A, right coxa 1; B, left coxa 2; C, posteroventral corner of left coxa 2; D, right coxa 3; E, posteroventral corner of left coxa 3; F, left coxa 4; G, right coxa 6; H, left P2; I, left P5; J, left P5 distal part (meral ventral setae not shown).

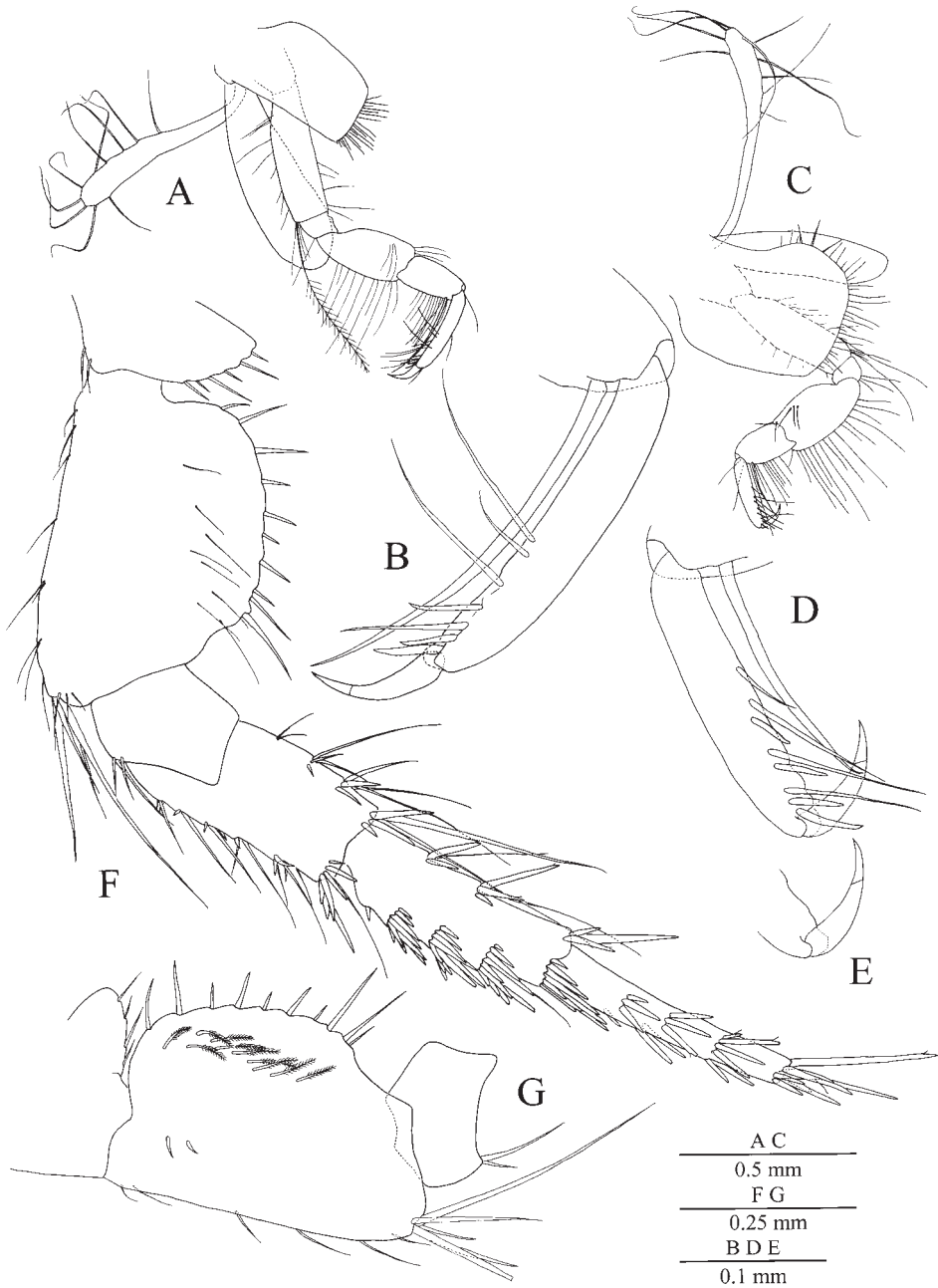


Fig. 6. *Bathyporeia elegans* Watkin, 1938, lectotype, female, forma A, southern Norway, Jæderen, Ognebukt, ZMO F2656. A, right P3; B, anterior part of right P3 (mesial spines/setae of propodus not shown); C, left P4; D, anterior part of left P4 (mesial spines/setae of propodus not shown); E, dactylus of left P4; F, left P7; G, right P7 proximal part (mesial side).

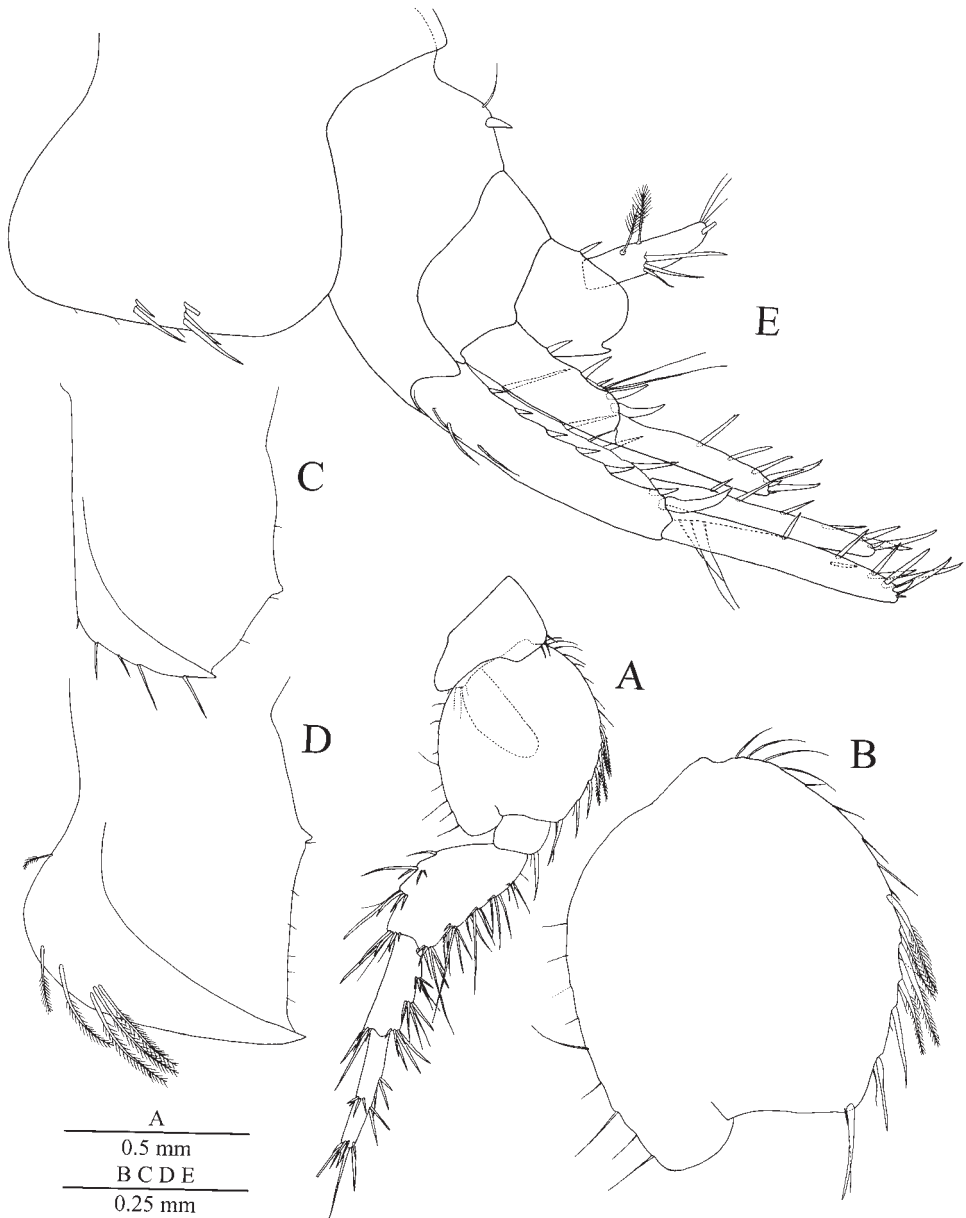


Fig. 7. *Bathyporeia elegans* Watkin, 1938, lectotype, female, forma A, southern Norway, Jæderen, Ognebukta, ZMO F2656. A, right P6; B, basis of right P6; C, left Ep1; D, left Ep2; E, left Ep3 and posterior part of body.

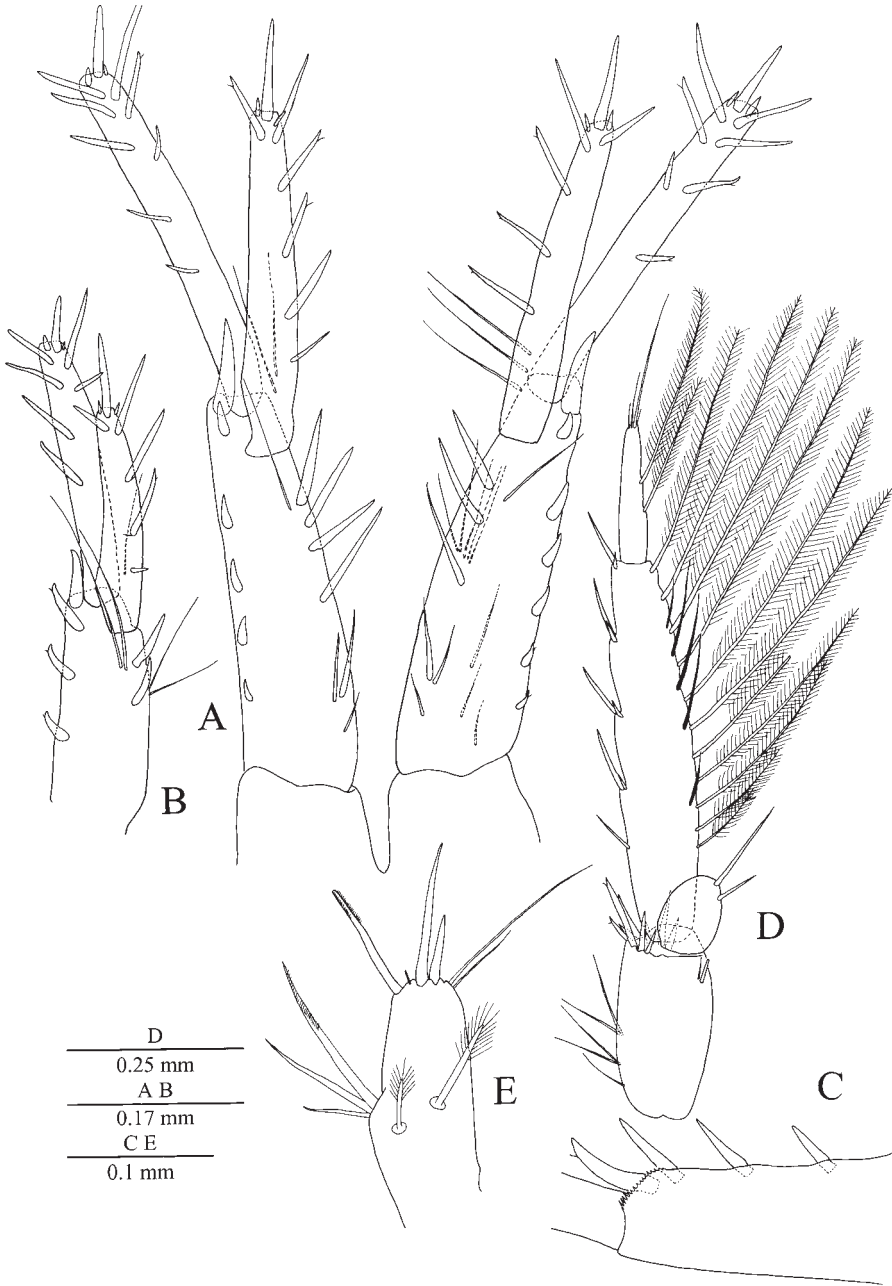


Fig. 8. *Bathyporeia elegans* Watkin, 1938, lectotype, female, forma A, southern Norway, Jæderen, Ognebukt, ZMO F2656. A, B, C, E, female, lectotype; D, sex unknown (detached appendage), paralectotype. A, right and left U1 (dorsal view); B, right U2 (dorsal view); C, right U2 peduncle (lateral outer view); D, left U3, E, right part of telson.

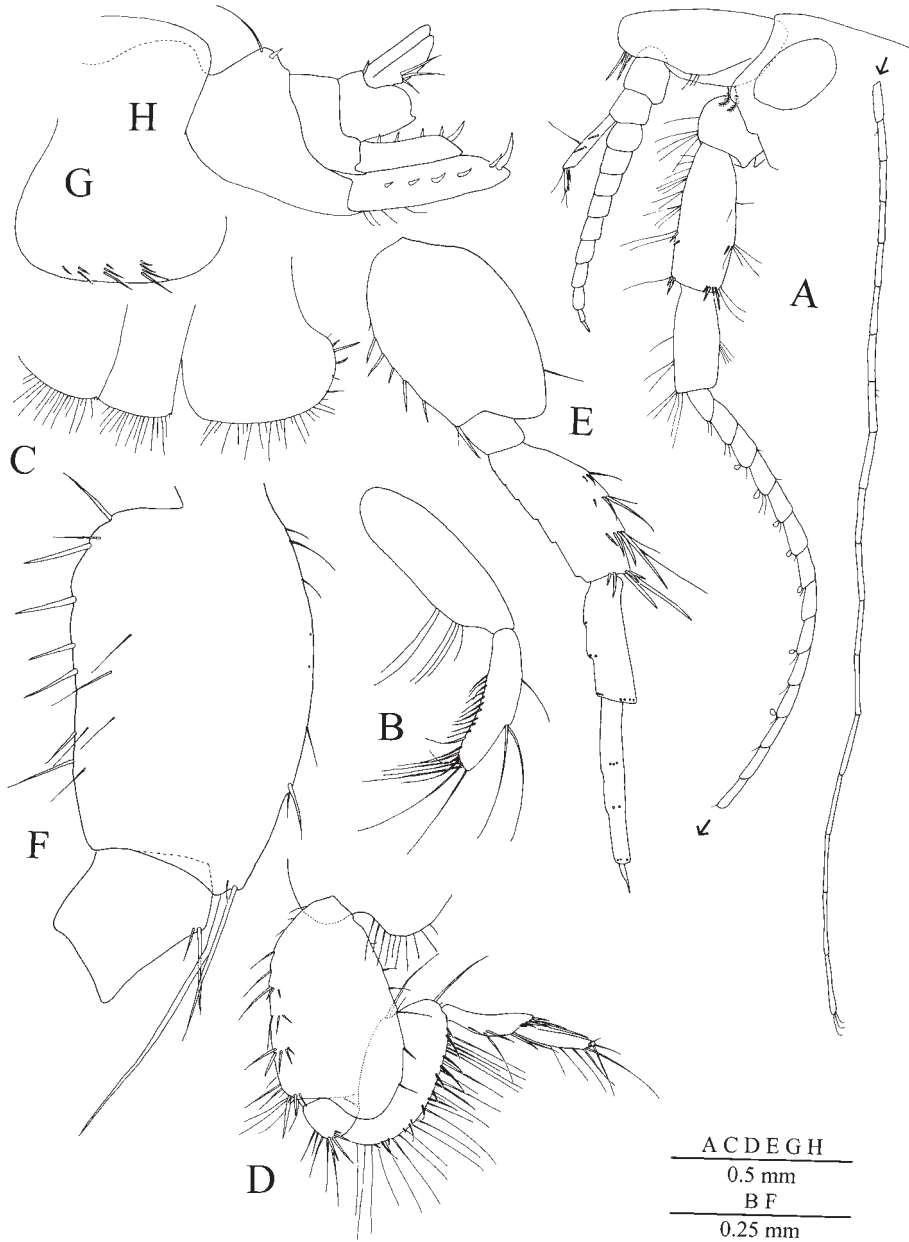


Fig. 9. *Bathyporeia elegans* Watkin, 1938, paralectotypes, males, forma A, southern Norway, Jæderen, Ognebuk, ZMO F2656. F, male paralectotype nr 1; B, nr 2; A, C, E, G, H, nr 3; D, nr 5. A, anterior part of head with left antennae (A2 flagellum drawn in two parts); B, left mandibular palp; C, left coxae 2-3-4; D, left P5; E, left P6; F, right P7; G, left Ep3; H, posterior part of body (apical setae of telson not shown).

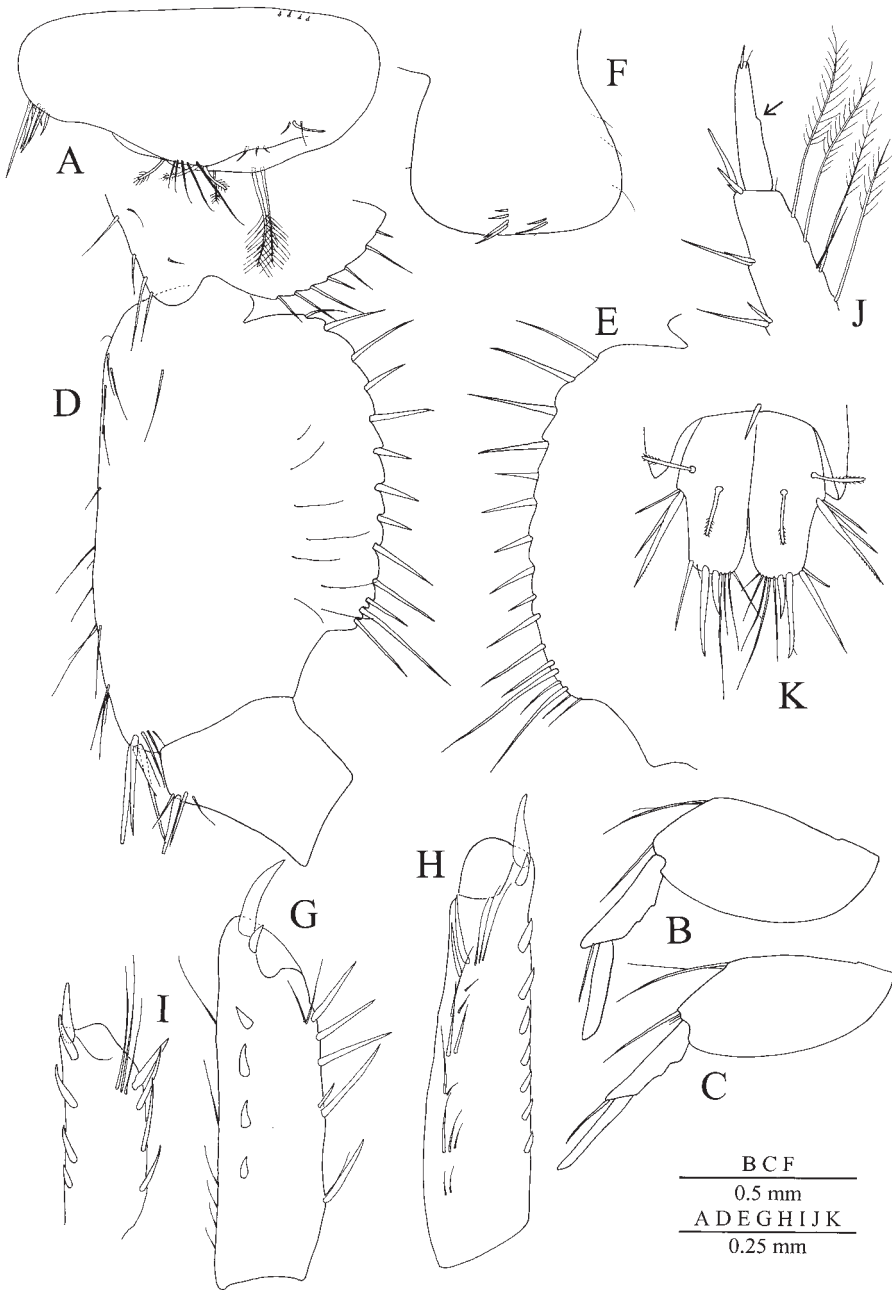


Fig. 10. *Bathyporeia elegans* Watkin, 1938, forma A, females, northern Norway, Tromsø area, Ramfjord, TMU 2490. A, first article of left A1; B, C, distal part of right P5 (with longest dorsal distal seta of carpus); D, proximal part of left P7; E, posterior border of basis of right P7; F, right Ep3; G, peduncle of right U1; H, peduncle of left U1; I, peduncle of right U2; J, tip of right U3; K, telson.

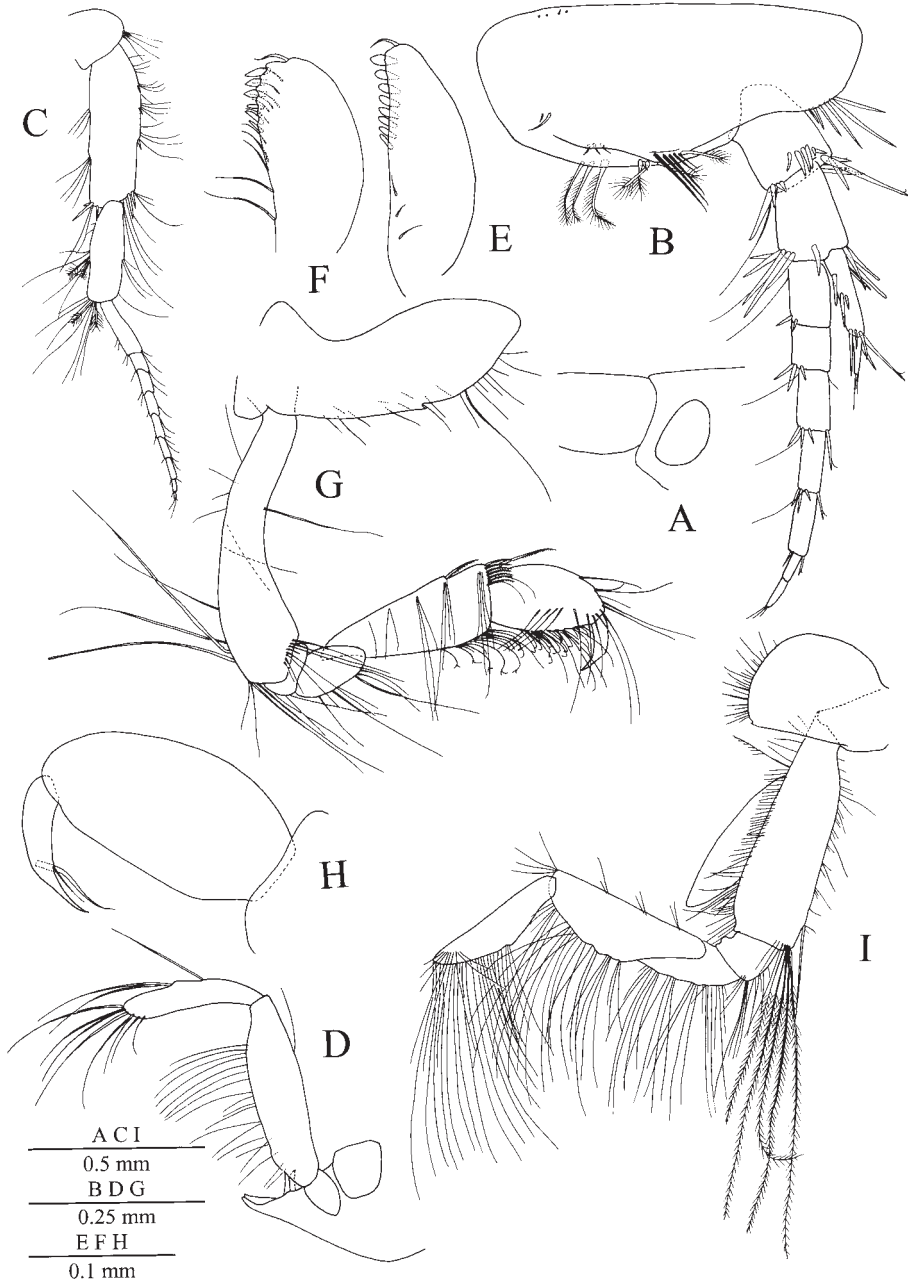


Fig. 11. *Bathyporeia elegans* Watkin, 1938, forma B, adults females, Germany, aussen Jade, station 2, TMU 1117. A-E, G, I, specimen 1; F, specimen 3; H, specimen 13. A, anterior part of head; B, right A1; C, right A2; D, left Md; E, F, outer palp of right Mxp; G, right P1; H, tip of left P1; I, left P2.

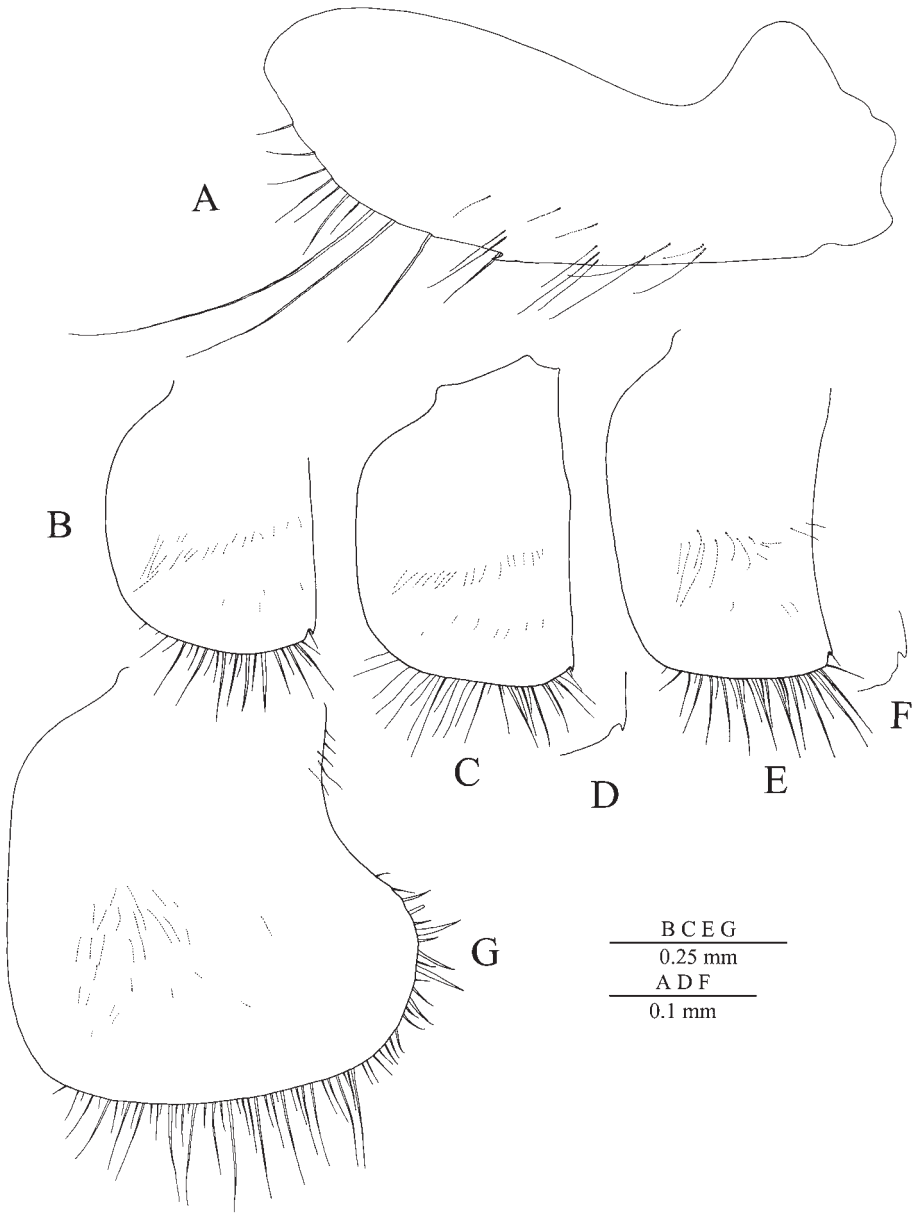


Fig. 12. *Bathyporeia elegans* Watkin, 1938, forma B, adult females, Germany, aussen Jade, station 2, TMU 1117. A, B, E, F, G, specimen 1; C, D, specimen 13. A, left coxa 1; B, C, left coxa 2; D, posteroventral angle of left coxa 2; E, left coxa 3; F, posteroventral angle of left coxa 3; G, left coxa 4.

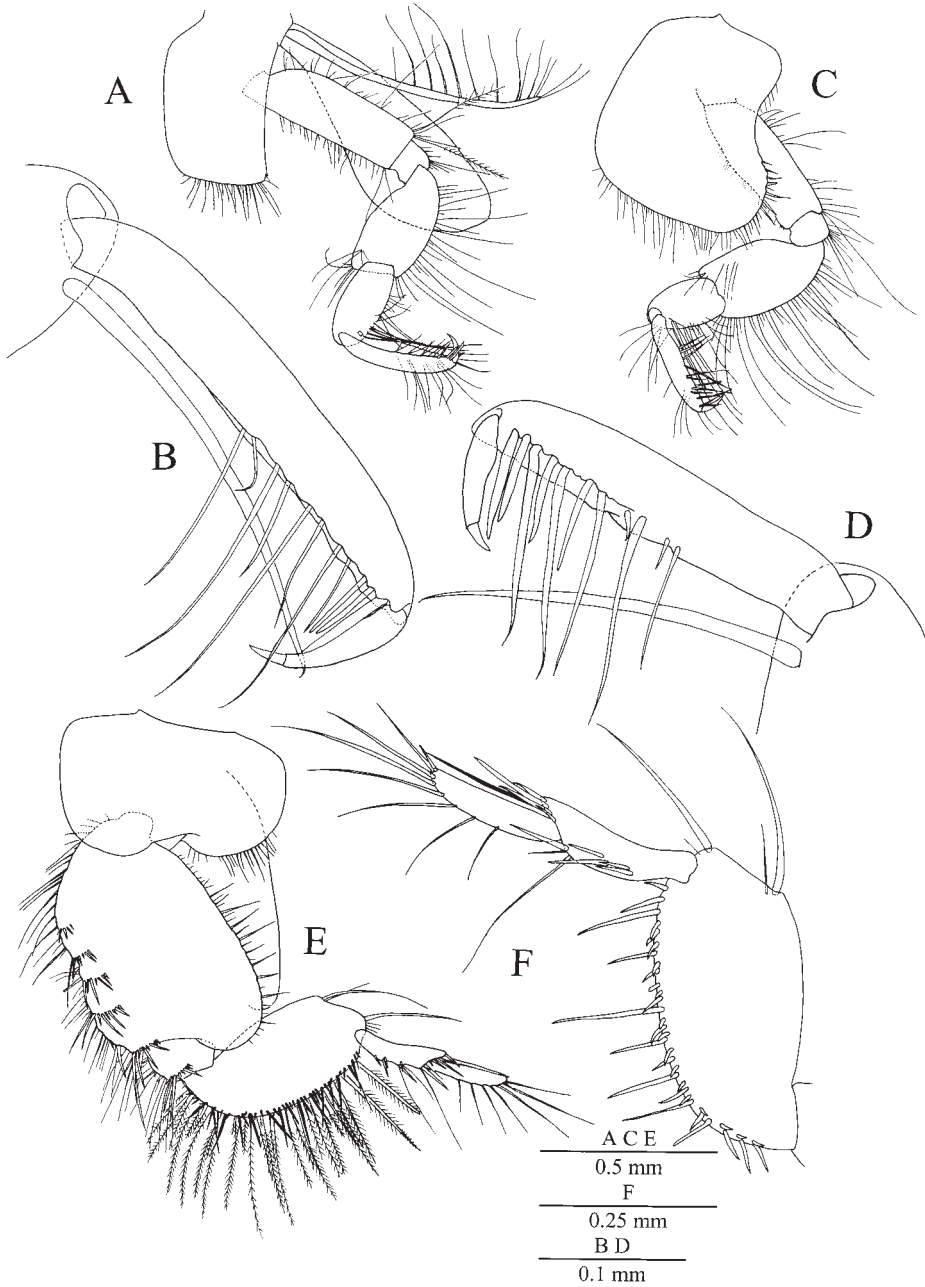


Fig. 13. *Bathyporeia elegans* Watkin, 1938, forma B, adult females, Germany, aussen Jade, station 2, TMU 1117. A, C, E, specimen 1; F, specimen 3; B, D, specimen 13. A, left P3; B, anterior part of right P3 (mesial spines/setae of propodus not shown); C, left P4; D, anterior part of left P4 (mesial spines/setae of propodus not shown); E, left P5; F, distal part of right P5 (setae of posterior border of merus not shown).

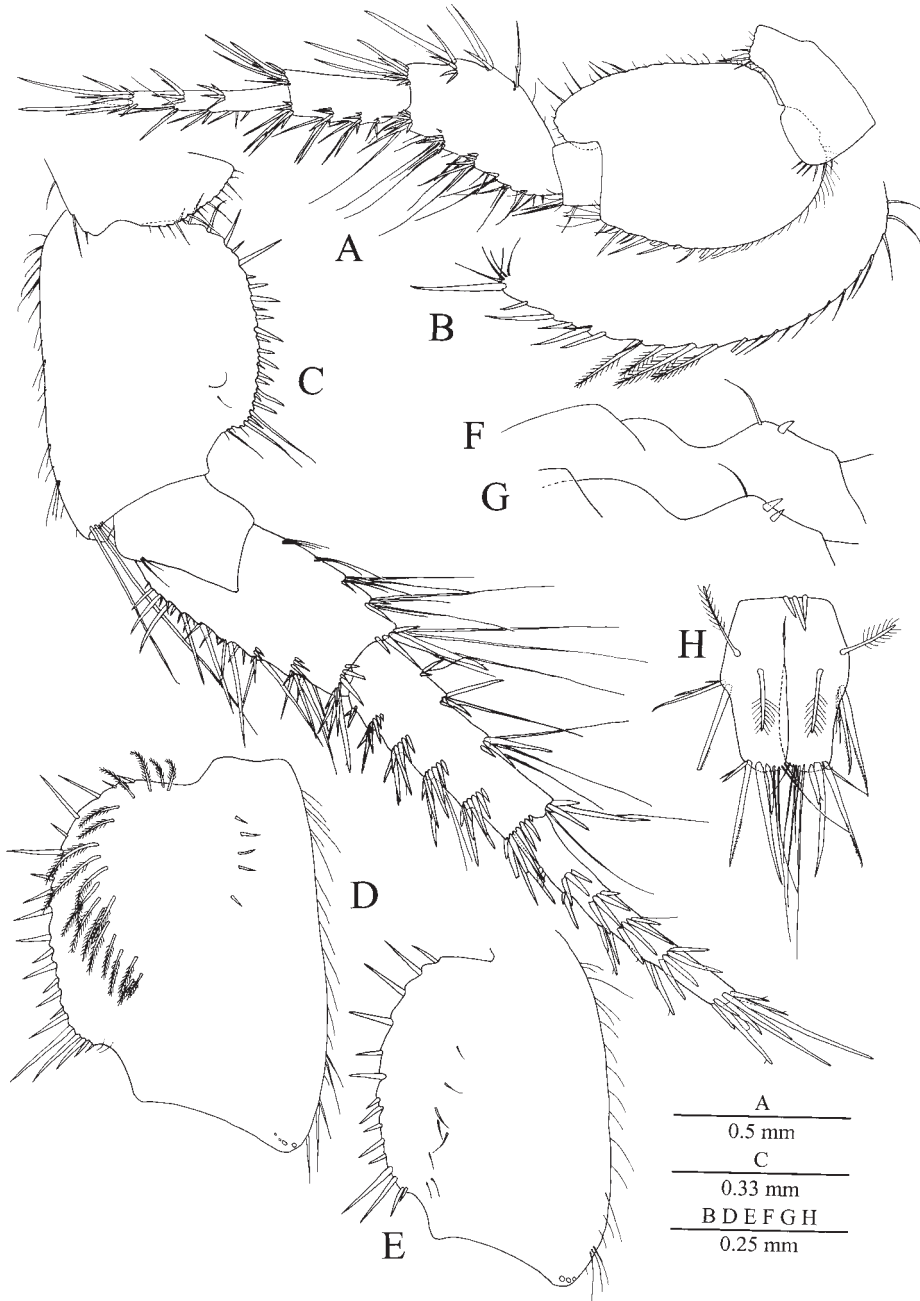


Fig. 14. *Bathyporeia elegans* Watkin, 1938, forma B, adult females, Germany, aussen Jade, station 2, TMU 1117. A, C, F, H, specimen 1; B, E, specimen 3; D, specimen 12; G, unnumbered specimen. A, right P6; B, anterior border of P6 basis; C, left P7; D, left basis of P7 (mesial side); E, left basis of P7 (outer side); F, G, urosomite 1 (left side); H, telson.

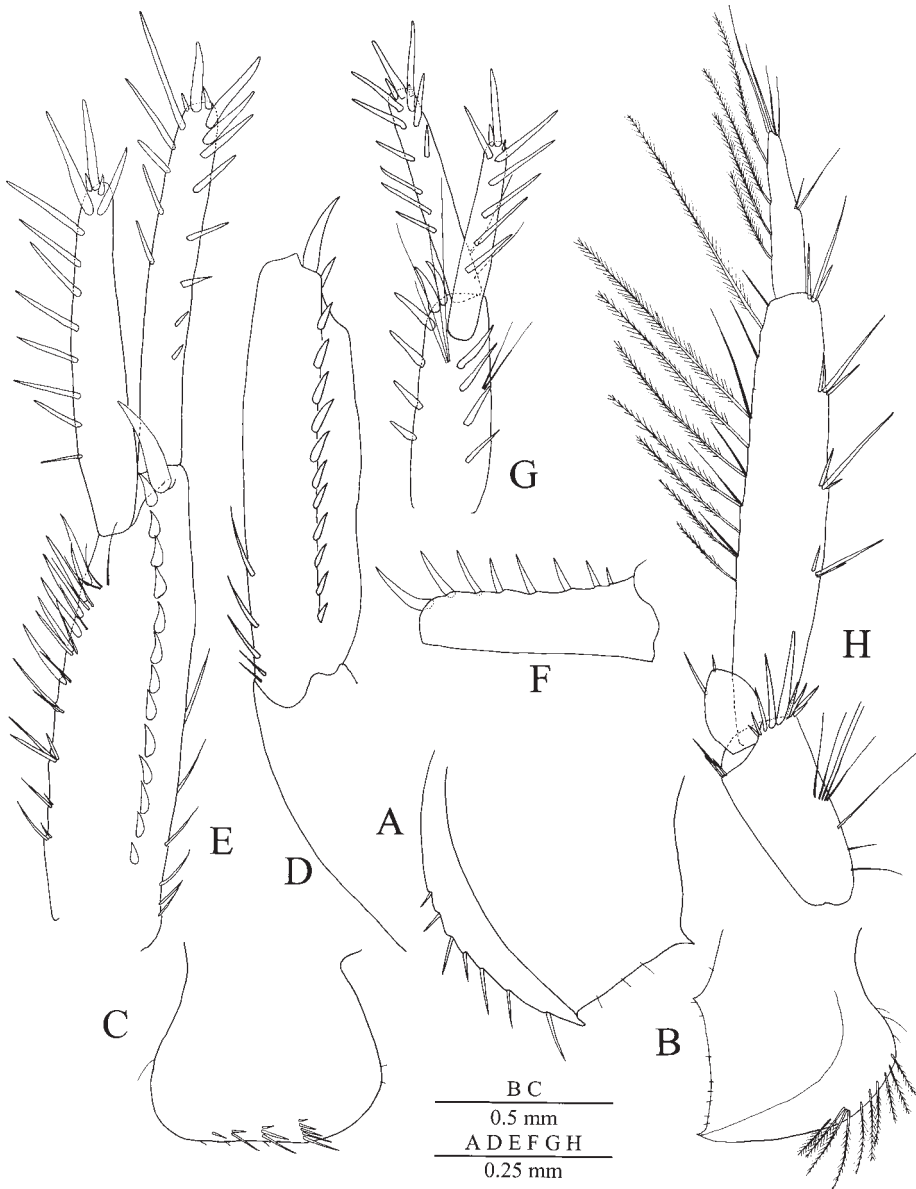


Fig. 15. *Bathyporeia elegans* Watkin, 1938, forma B, adult females, A-C, F-H, Germany, aussen Jade, station 2, TMU 1117: A-C, specimen 5; F, unnumbered specimen; G, specimen 1; H, specimen 13. D, E, The Netherlands, RMNH A 4931. A, Ep1; B, Ep2; C, Ep3; D, right U1 peduncle in lateral view (mesial ornamentation not shown); E, left U1 in dorsal view; F, U2 peduncle in lateral view (mesial ornamentation not shown); G, right U2 in dorsal view; H, right U3.

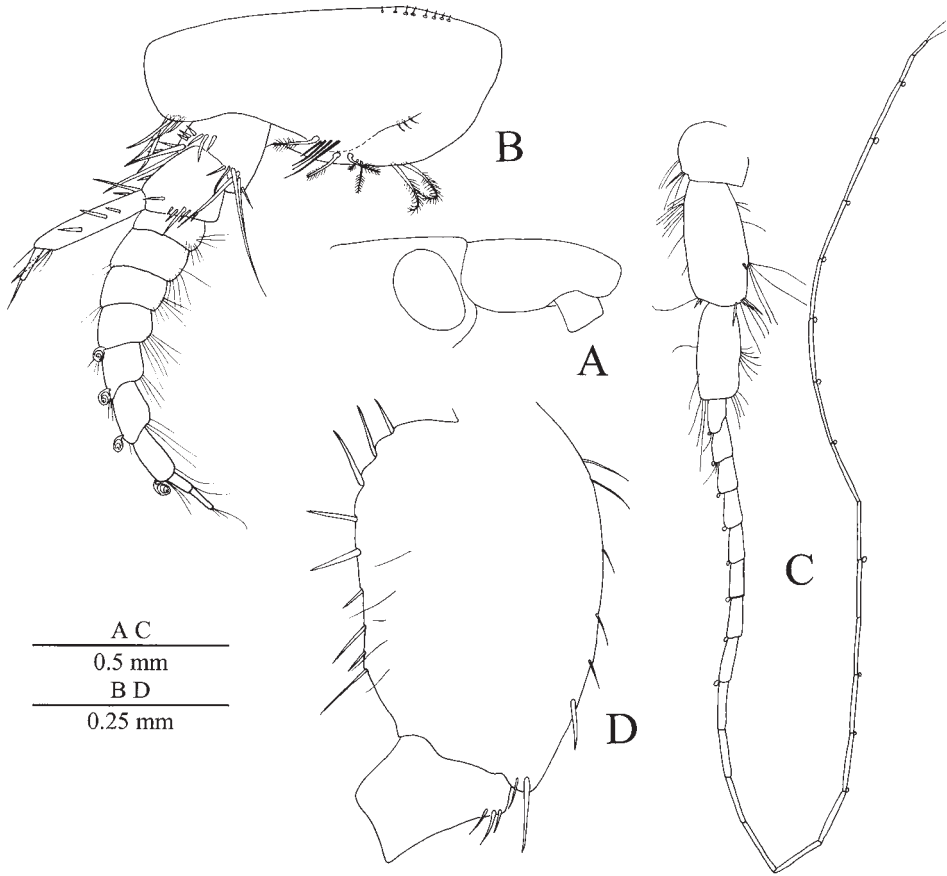


Fig. 16. *Bathyporeia elegans* Watkin, 1938, forma B, adult male (specimen 6), Germany, aussen Jade, station 2, TMU 1117. A, anterior part of head; B, left A1; C, left A2; D, basis and ischium of right P7 (outer side).

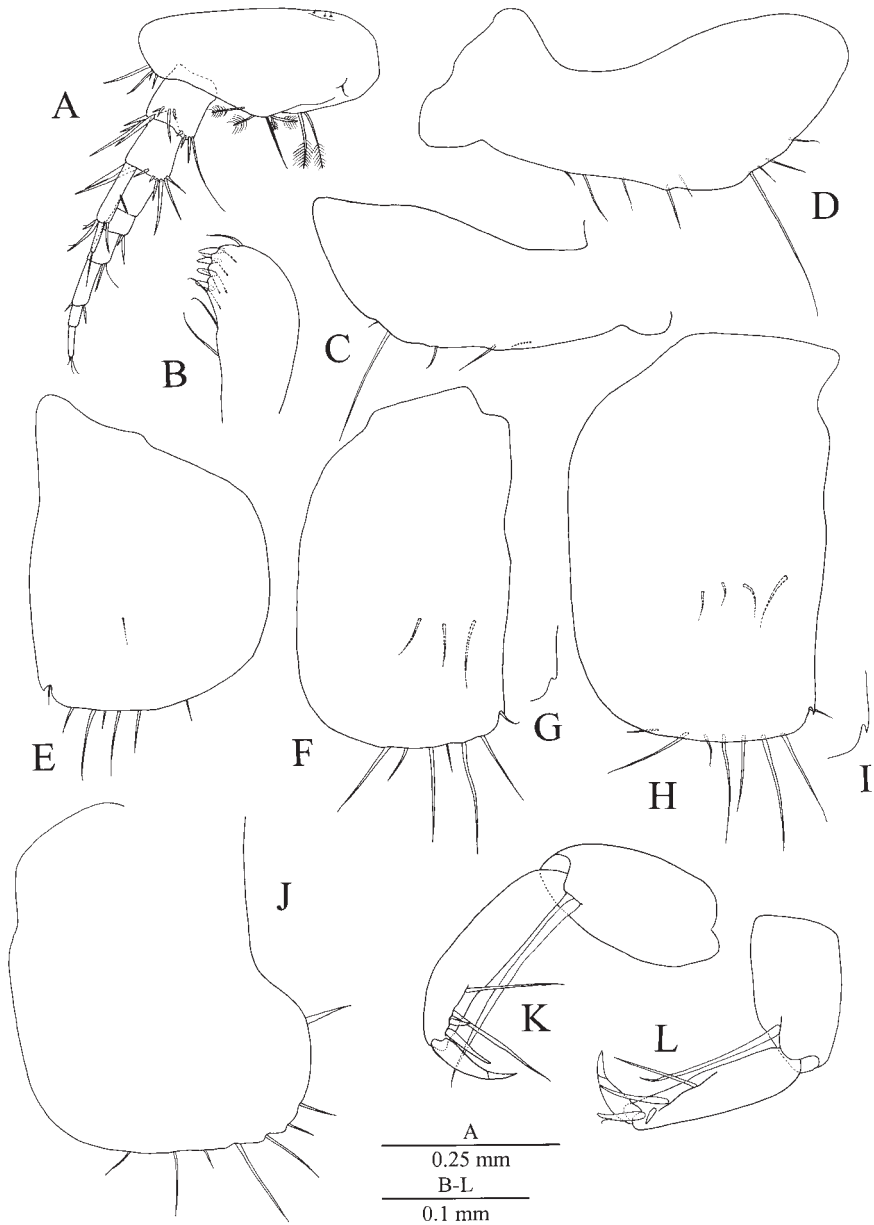


Fig. 17. *Bathyporeia elegans* Watkin, 1938, forma B, juvenile females, Ireland, Valencia sound, station VF 14, OUMNH. B, C, E, F, G, J, K, L: juvenile 1; A, D, H, I: juvenile 2. A, left A1; B, outer plate of right Mxp; C, left coxa 1; D, right coxa 1; E, right coxa 2; F, left coxa 3; G, posteroventral angle of left coxa 3; H, left coxa 3; I, posteroventral angle of left coxa 3; J, left coxa 4; K, last 3 articles of left P3; L, last 3 articles of right P4.

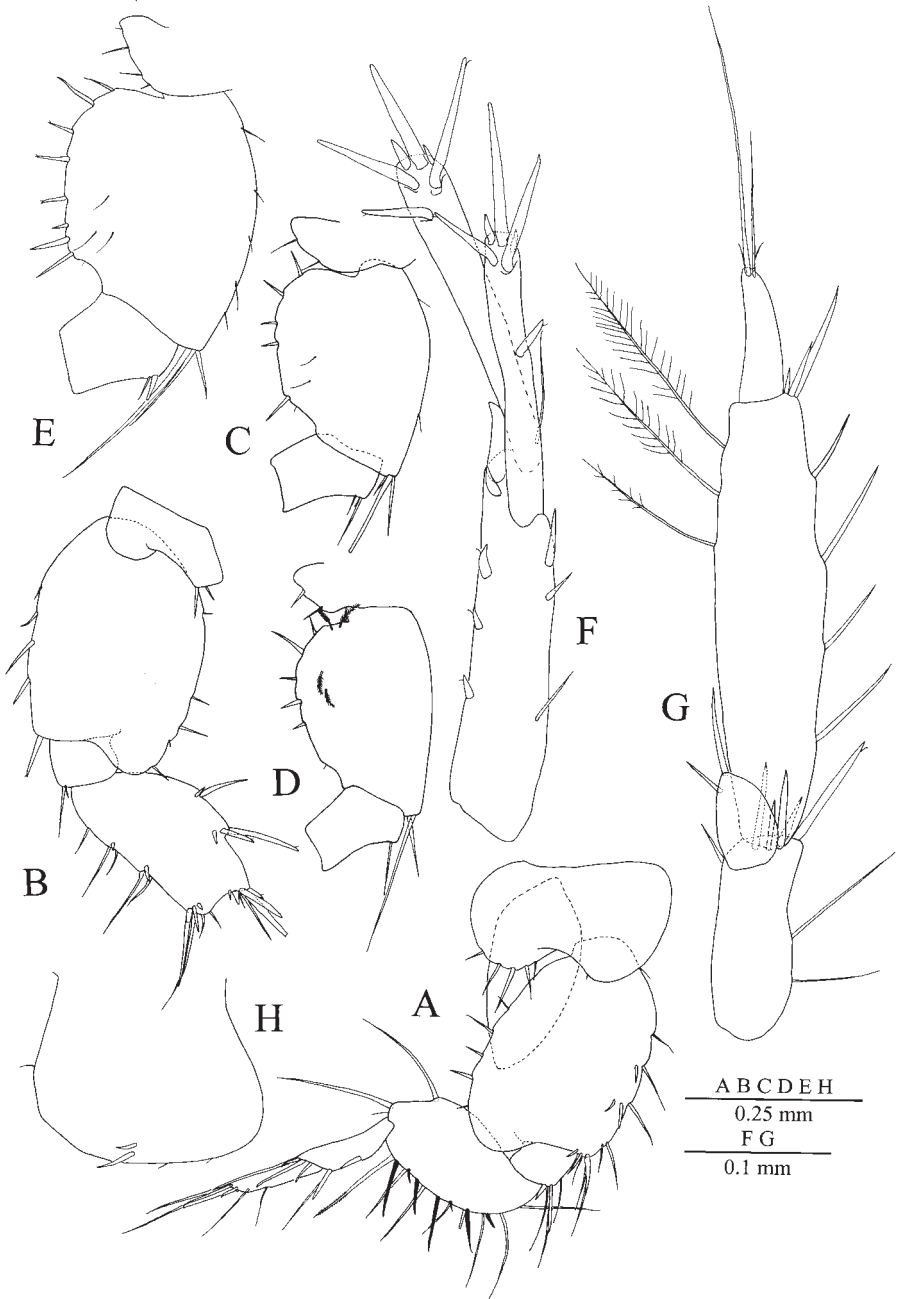


Fig. 18. *Bathyporeia elegans* Watkin, 1938, forma B, juvenile females, Ireland, Valencia sound, station VF 14, Oxford Natural History Museum. All after juvenile 1, except E: after juvenile 2. A, right P5; B, left P6; C, right P7 (outer side); D, left P7 (mesial side); E, right P7 (outer side); F, right U1; G, left U2; H, right Ep3.

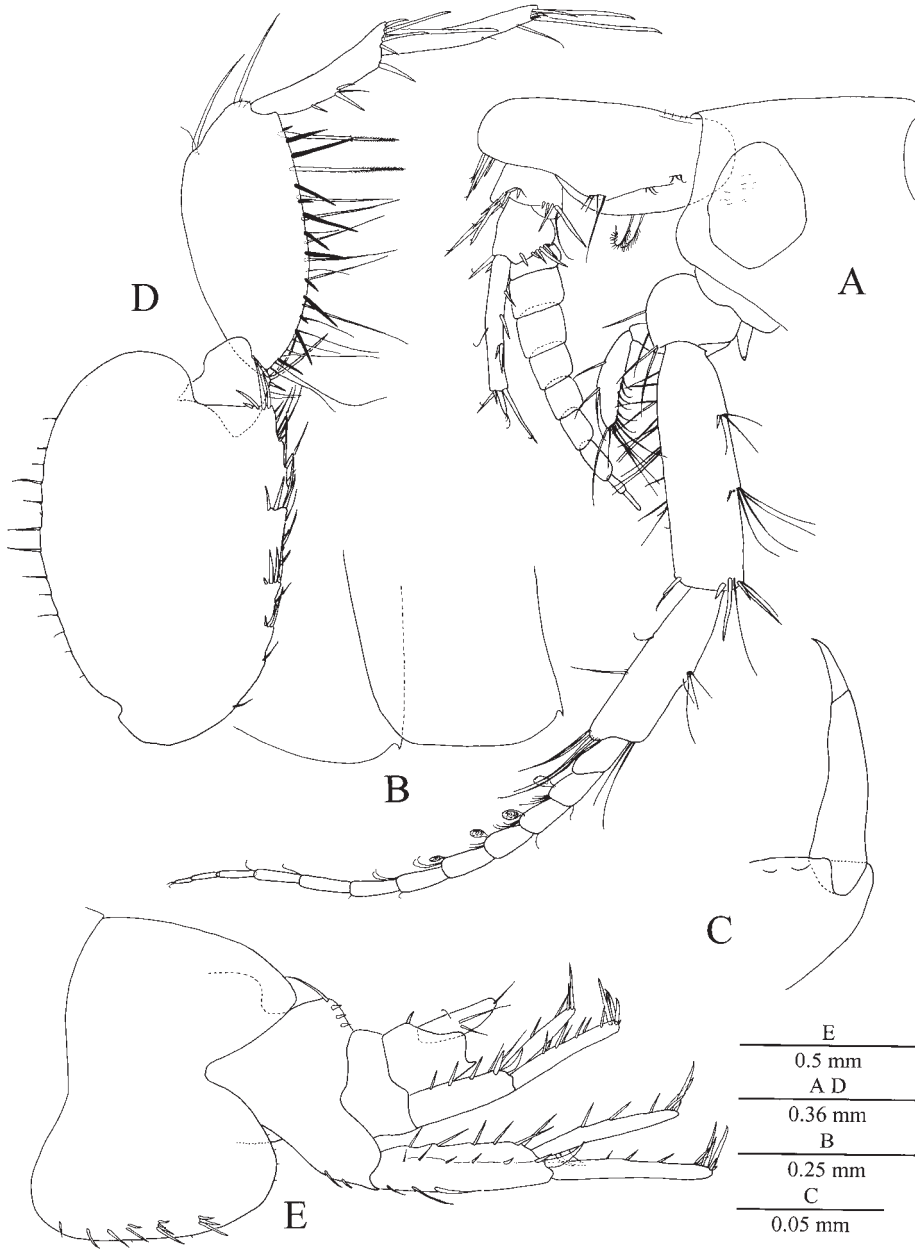


Fig. 19. *Bathyporeia gracilis* G.O. Sars, 1891, adult male, syntype, western Norway, ZMO F 2130. A, head, A1, A2 and mandibular palp; B, left coxa 2 to 3 (setae not shown); C, dactylus of P4; D, left P5; E, posterior part of body.

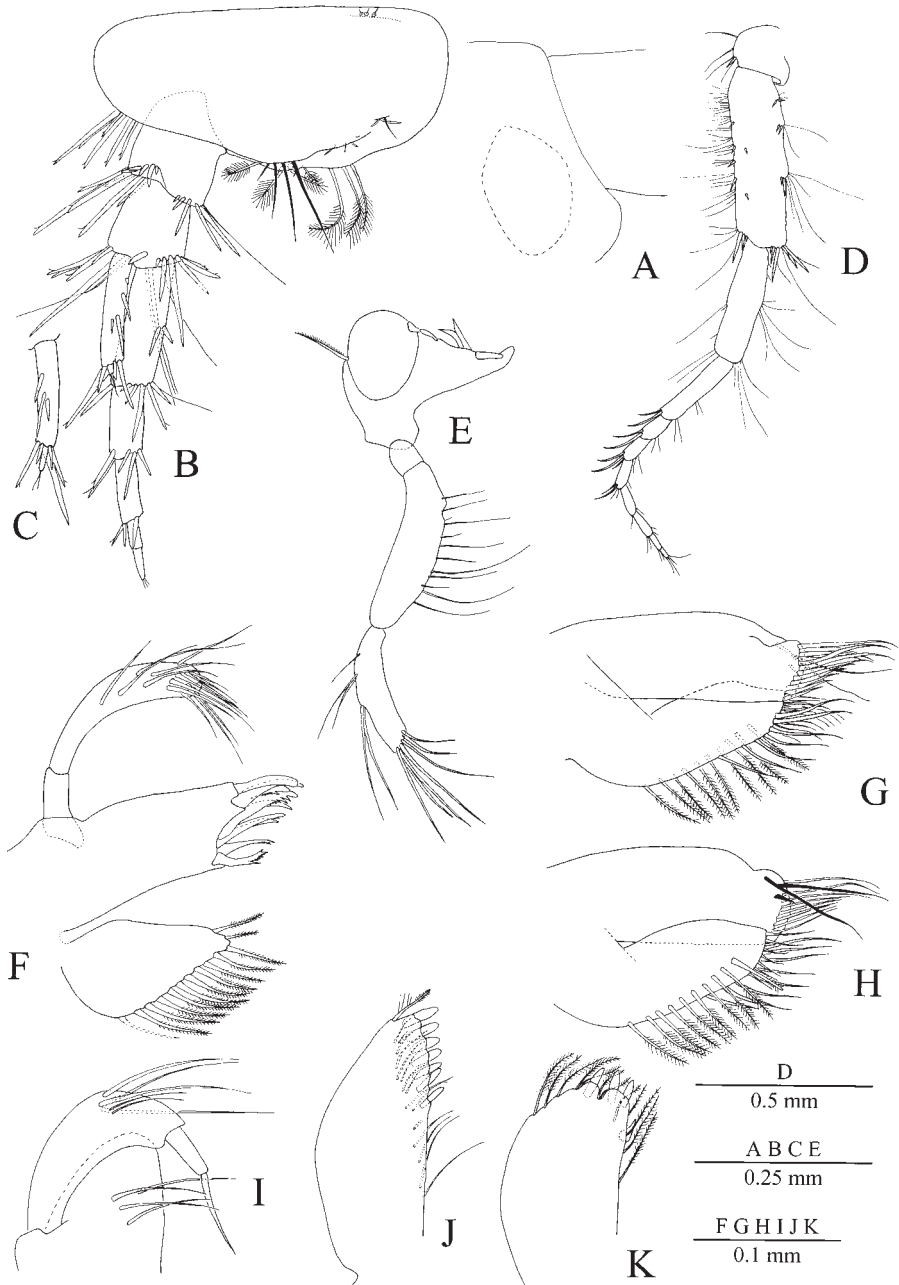


Fig. 20. *Bathyporeia gracilis* G.O. Sars, 1891, female, Ireland, Valencia, TMU 4923. A, anterior part of head; B, left A1; C, accessory flagellum of right A1; D, left A2; E, right Md; F, Mx1; G, left Mx2; H, right Mx2; I, left Mxp palp; J, left Mxp outer plate; K, left Mxp inner plate.

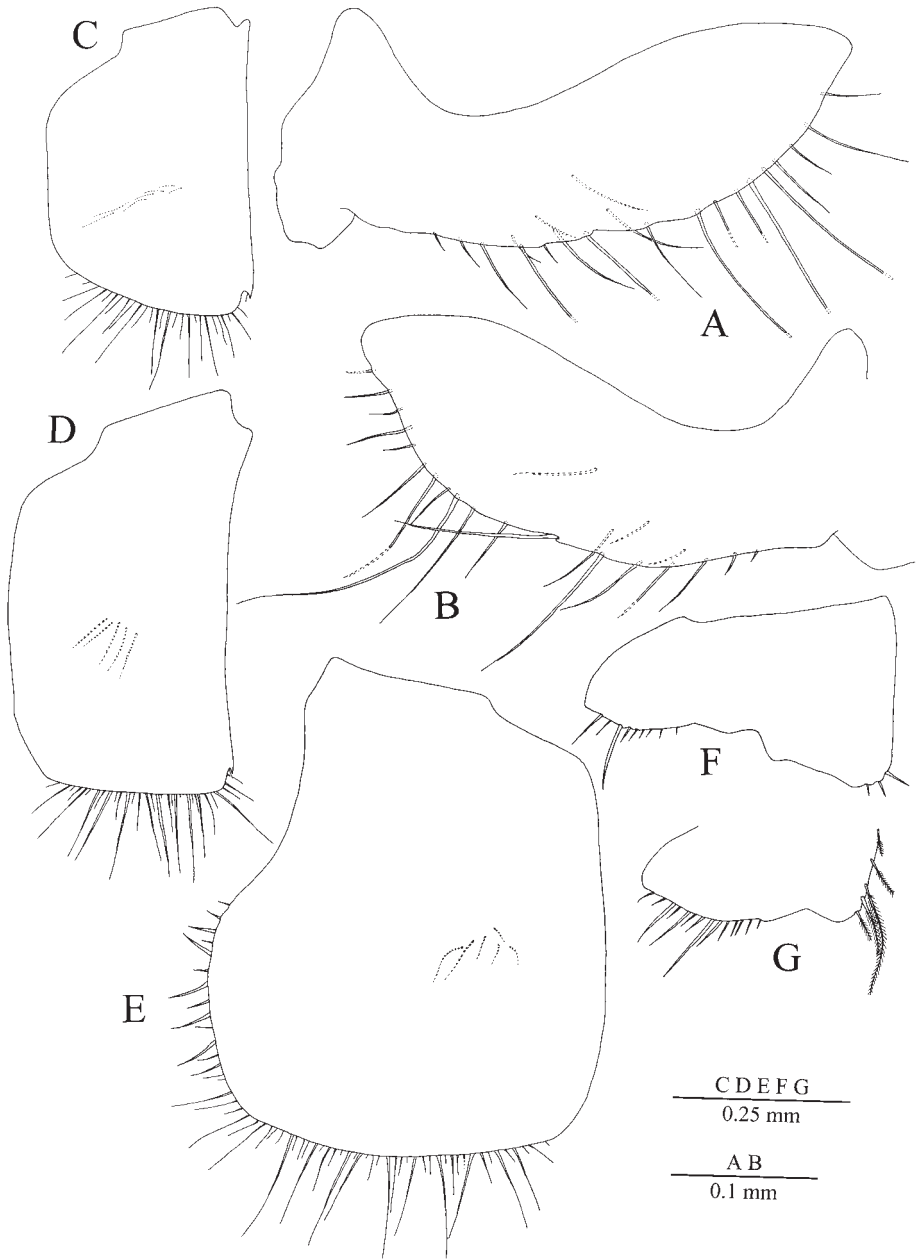


Fig. 21. *Bathyporeia gracilis* G.O. Sars, 1891, female, Ireland, Valencia, TMU 4923. A, right coxa 1; B, left coxa 1; C, left coxa 2; D, left coxa 3; E, right coxa 4; F, right coxa 6; G, right coxa 7.

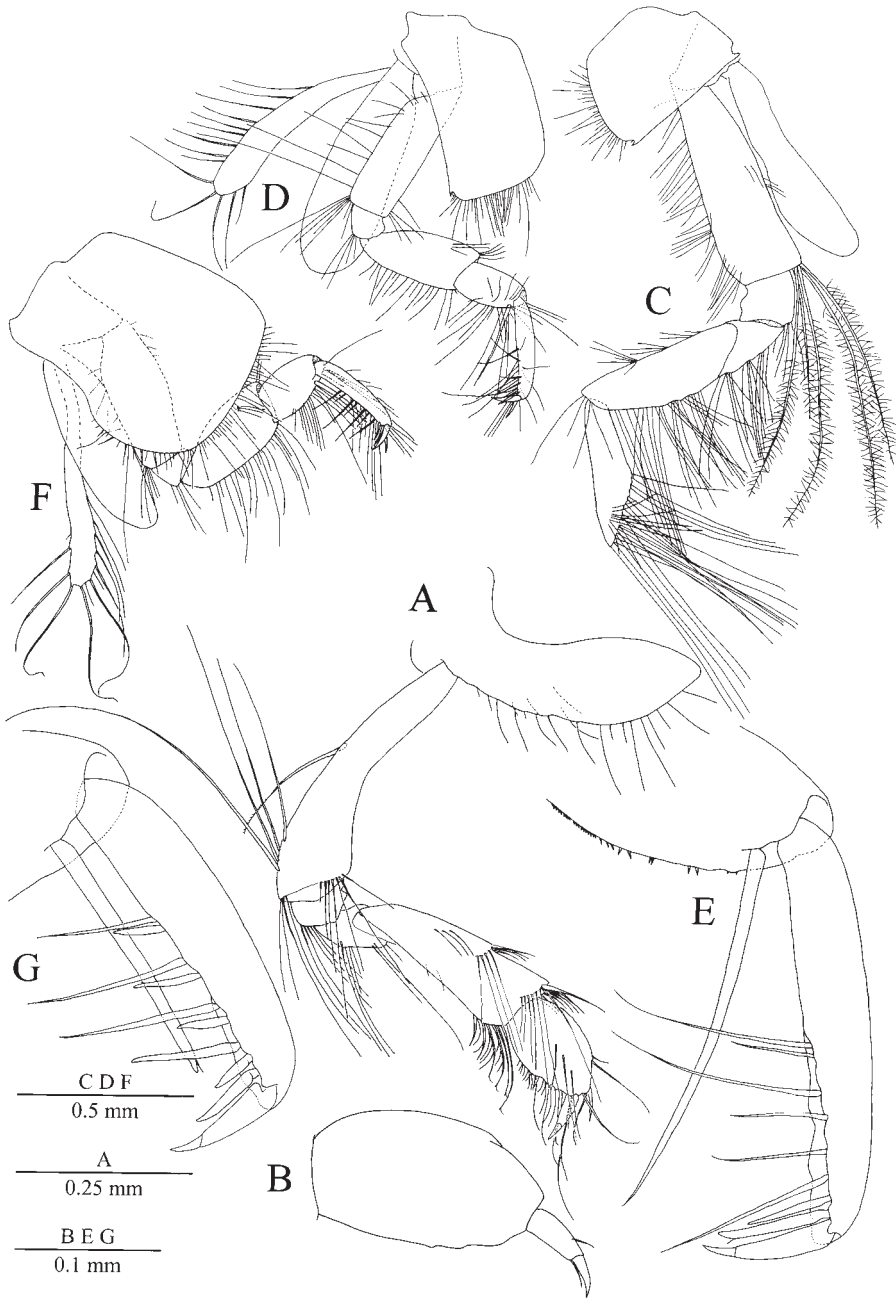


Fig. 22. *Bathyporeia gracilis* G.O. Sars, female, 1891, Ireland: A, C-F, Valencia, TMU 4923; B, Irish Sea station 98A, NMWZ 1997.052. A, right P1; B, anterior part of right P1; C, left P2; D, right P3; E, anterior part of right P3 (mesial spines/setae of propodus not shown); F, right P4; G, anterior part of right P4 (mesial spines/setae of propodus not shown).

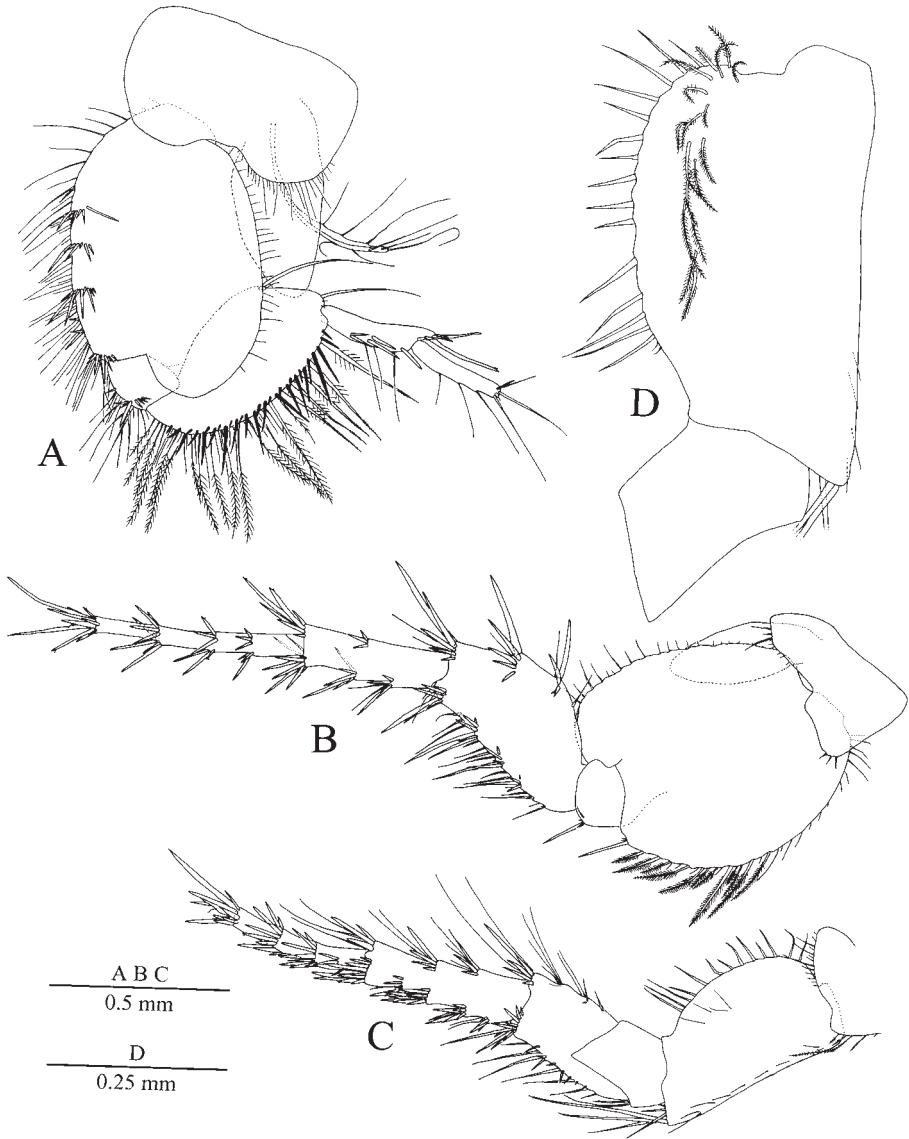


Fig. 23. *Bathyporeia gracilis* G.O. Sars, 1891, female, Ireland, Valencia, TMU 4923. A, left P5; B, right P6; C, right P7; D, basis and ischium of left P7 (mesial side).

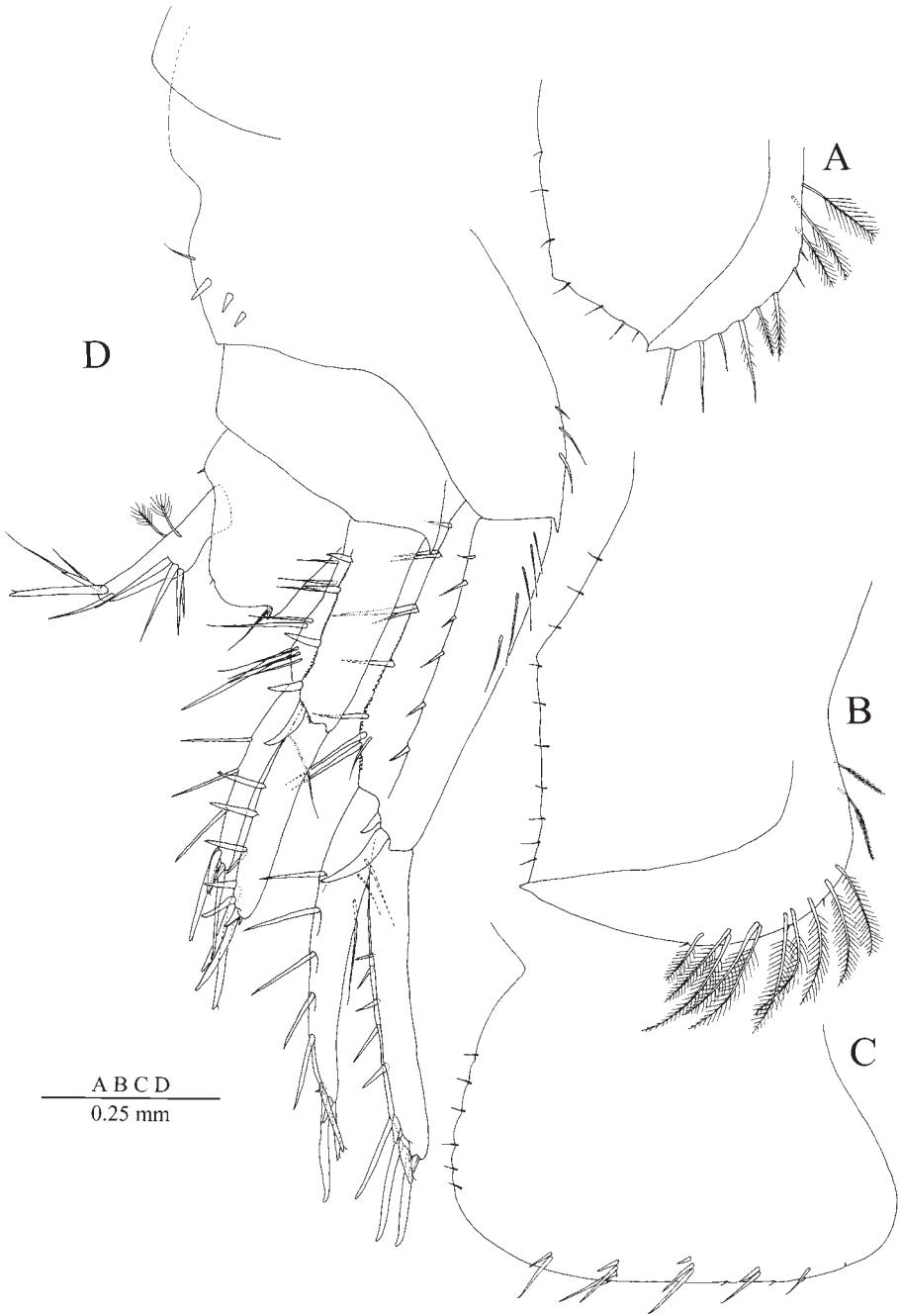


Fig. 24. *Bathyporeia gracilis* G.O. Sars, 1891, female, Ireland, Valencia, TMU 4923. A, Ep1; B, right Ep2; C, right Ep3; D, posterior part of body, right side in lateral view.

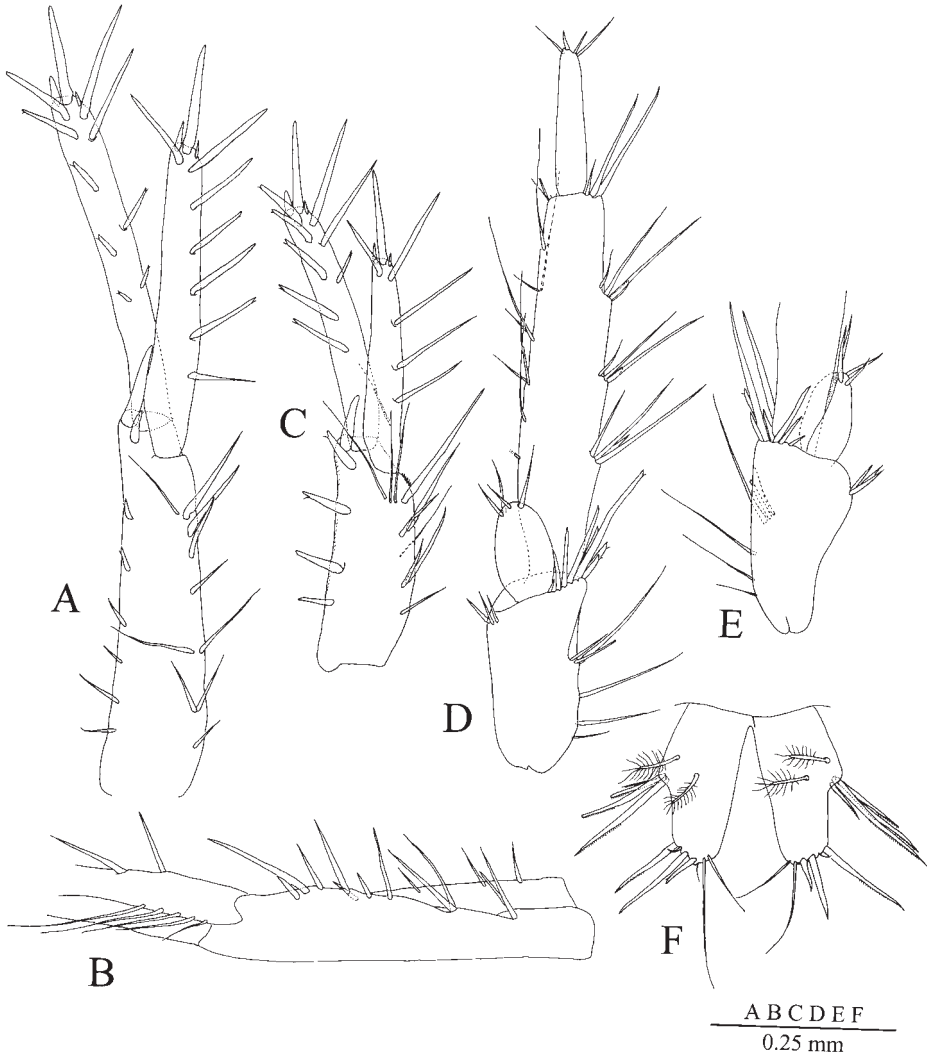


Fig. 25. *Bathyporeia gracilis* G.O. Sars, 1891, female, Ireland, Valencia, TMU 4923. A, right U1 (dorsal view); B, left U1 (lateral mesial view); C, right U2 (dorsal view); D, left U3 (dorsal view); E, left U3, proximal part (ventral view); F, telson.

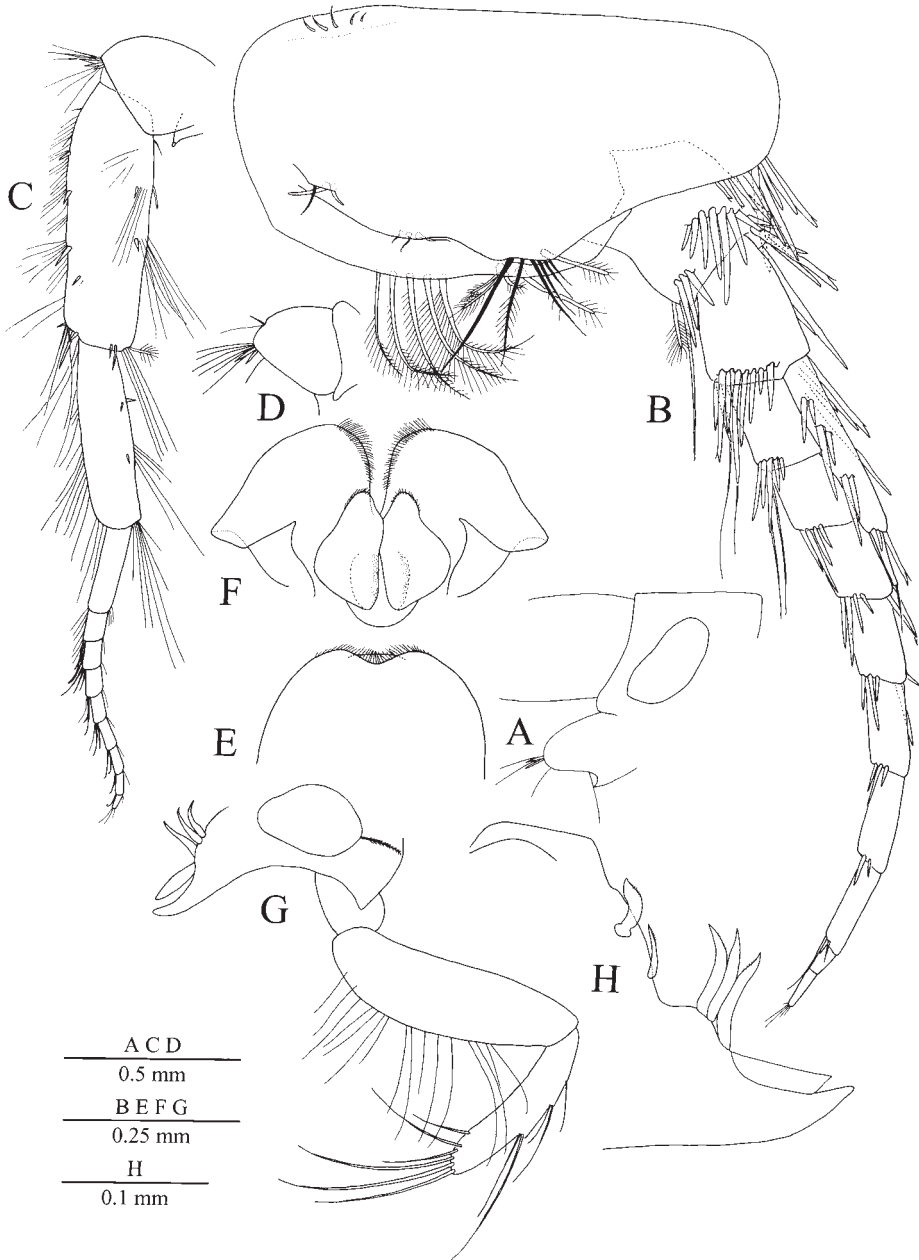


Fig. 26. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands TMU 9424 (A, D, specimen 2; G, spec. 3; E, F, H, spec. 4; B, C, spec. 16). A, anterior part of head; B, right A1; C, left A2; D, left A2 proximal part (less frequent disposition); E, upper lip; F, lower lip; G, left Md; H, Md (detail).

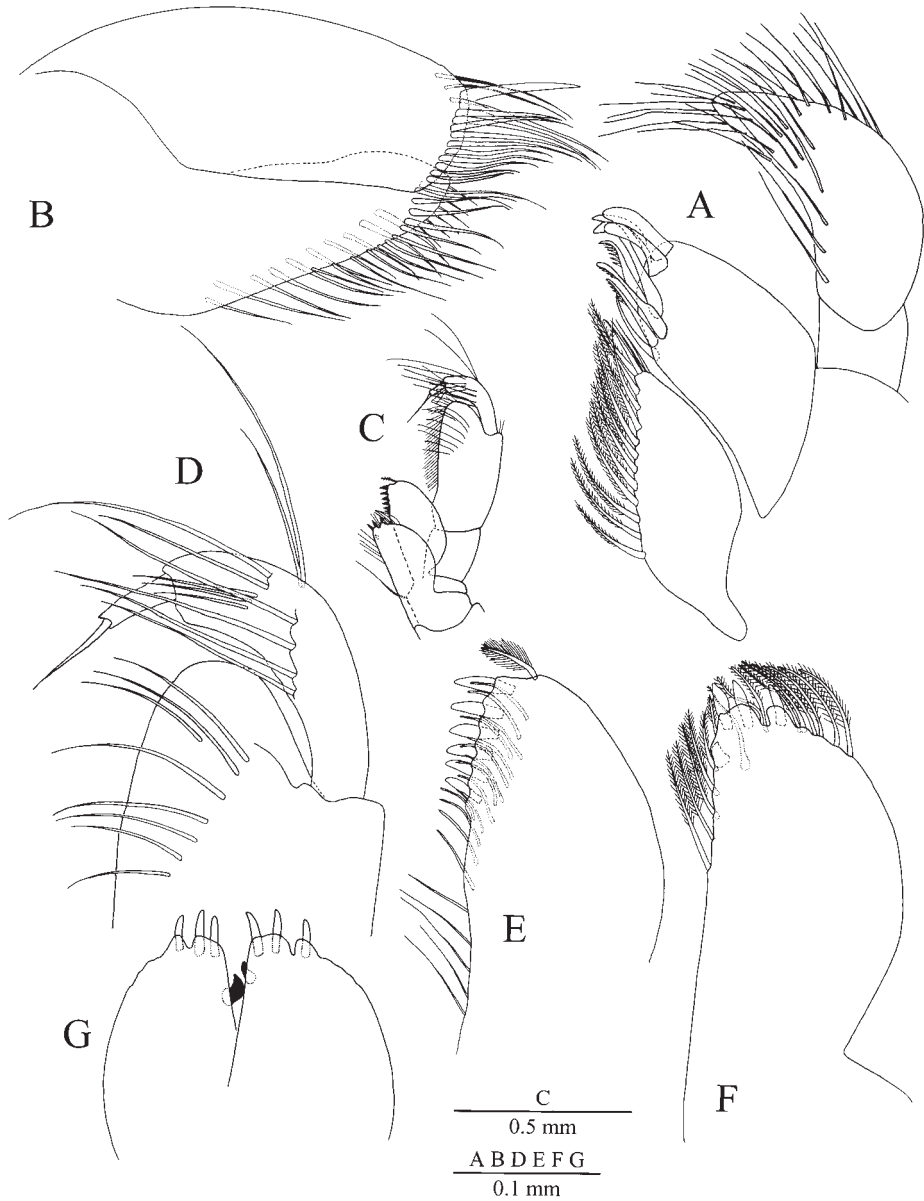


Fig. 27. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands TMU 9424 (B, specimen 2; A, spec. 3; G, spec. 5; C, D, E, F, spec. 16). A, Mx1; B, left Mx2; C, right Mxp; D, right Mxp palp; E, right Mxp outer plate; F, right Mxp inner plate; G, Mxp inner plates with locking system open (setae not shown).

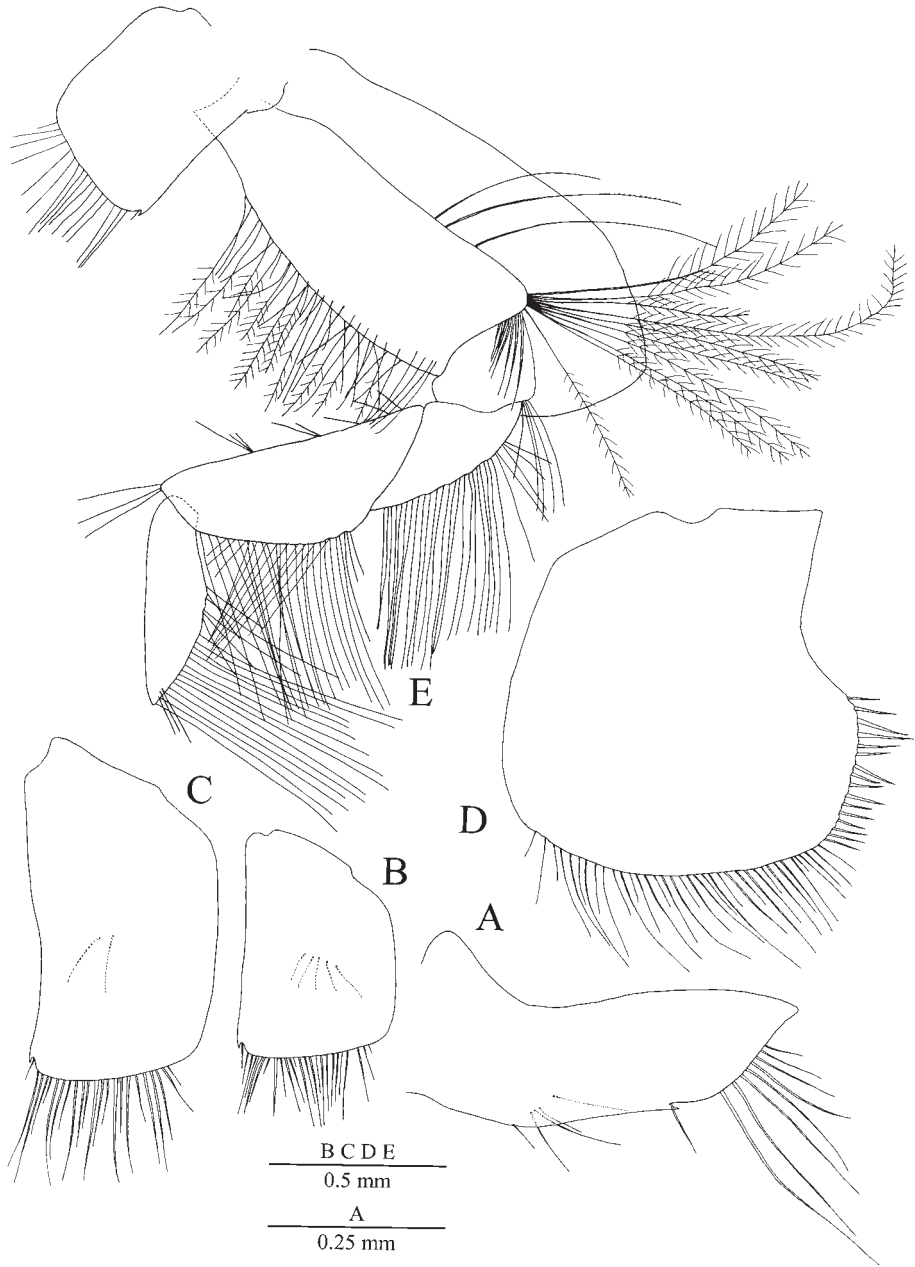


Fig. 28. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands TMU 9424 (A, E, specimen 2; C, D, spec. 16; B, spec. 17). A, right coxa 1; B, right coxa 2; C, right coxa 3; D, left coxa 4; E, left P2.

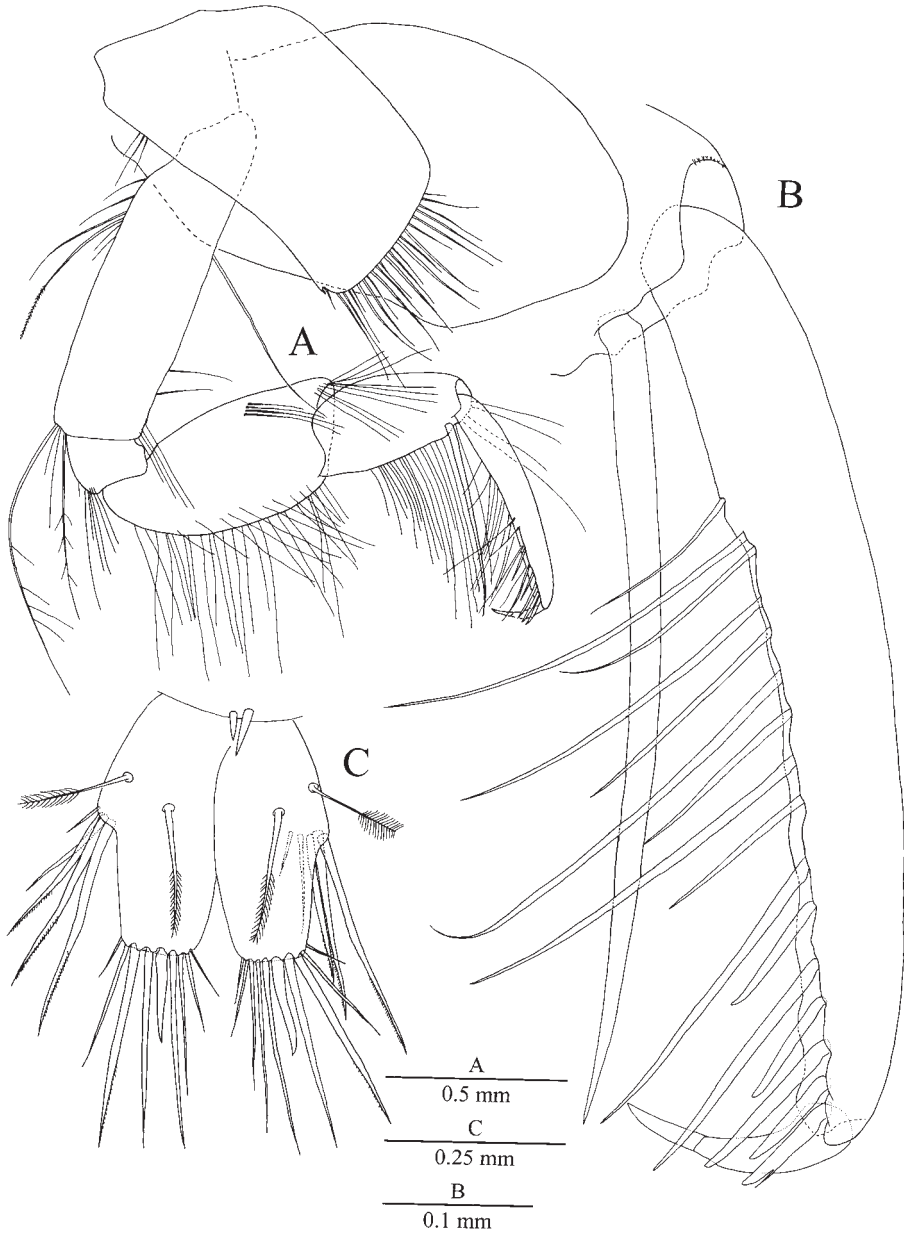


Fig. 29. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands, TMU 9424 (C, specimen 2; A, B, spec. 16). A, right P3; B, anterior part of right P3 (mesial spines/setae of propodus not shown); C, telson.

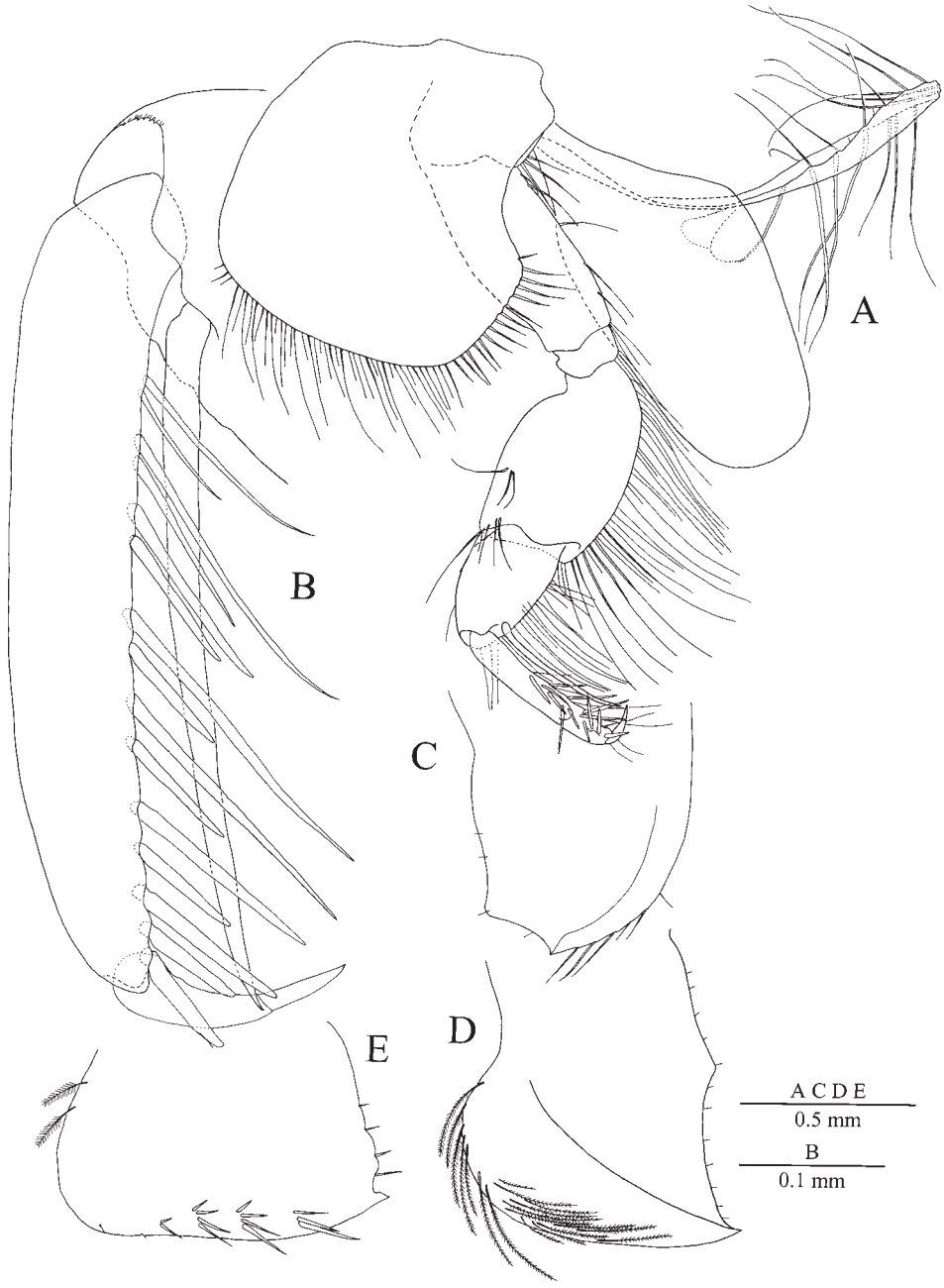


Fig. 30. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands, TMU 9424 (E, specimen 2; D, spec. 3; B, C, spec. 16; A, spec. 17). A, left P4; B, anterior part of left P4 (mesial spines/setae of propodus not shown); C, left Ep1; D, left Ep2; E, left Ep3.

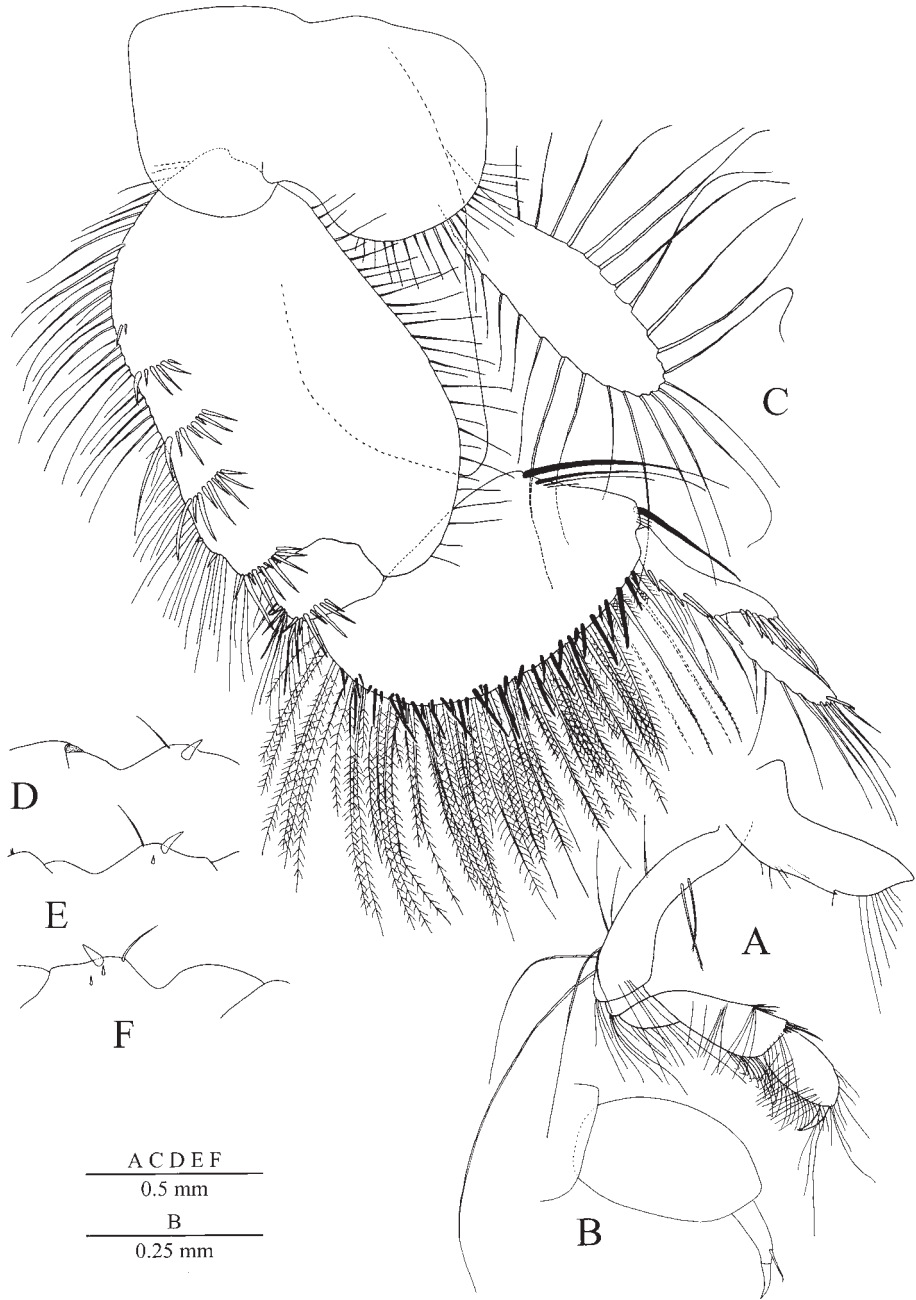


Fig. 31. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands, TMU 9424 (A, C, D, specimen 2; E, spec. 11; F, spec. 14; B, spec. 16). A, right P1; B, anterior part of right P1; C, left P5; D, Ur1; E, Ur1; F, Ur1 (less frequent disposition).

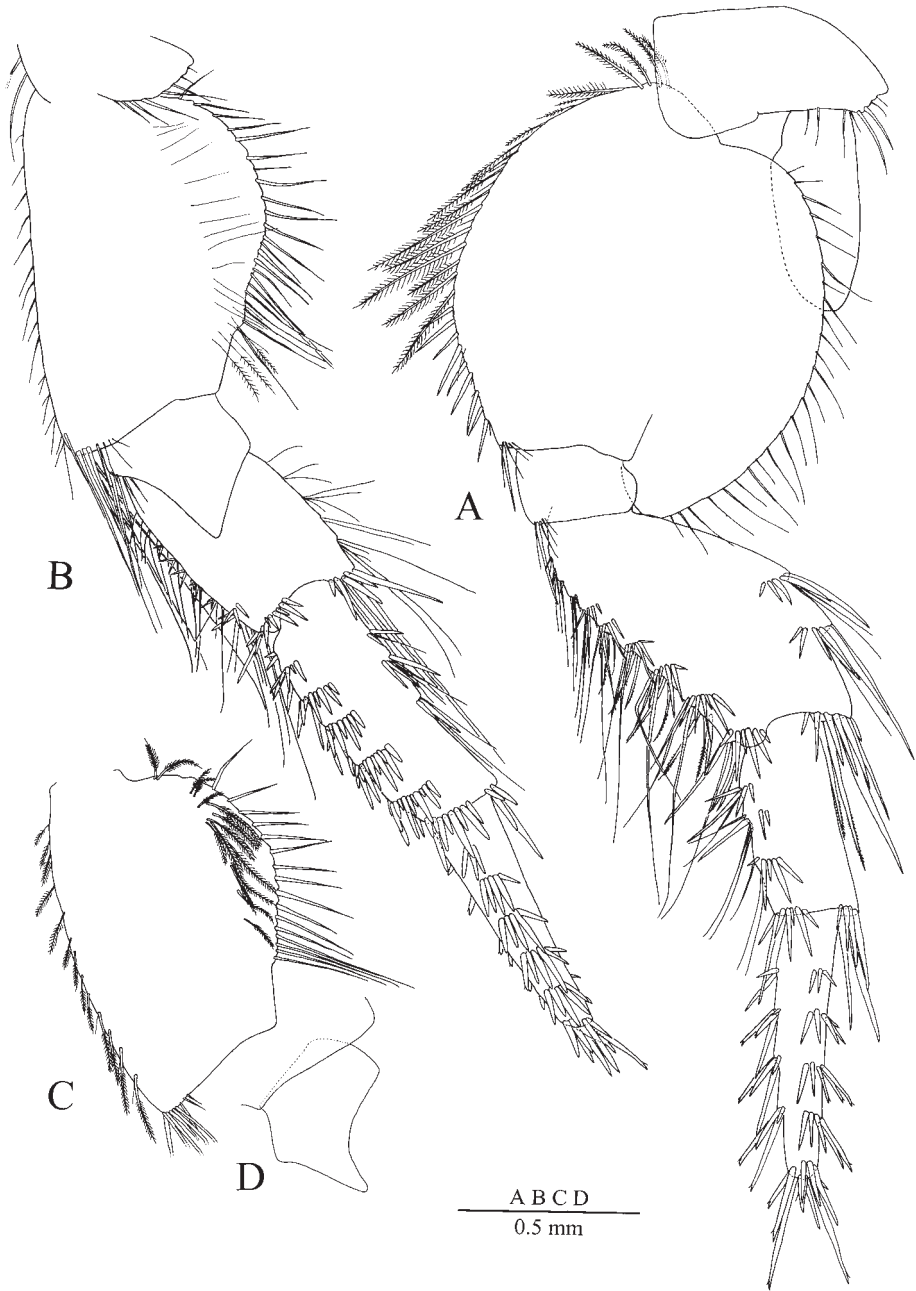


Fig. 32. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands, TMU 9424 (A, B, specimen 2; C, spec. 13; D, spec. 17). A, left P6; B, left P7; C, Right basis of P7 (mesial side); D, left P7 ischium (mesial side).

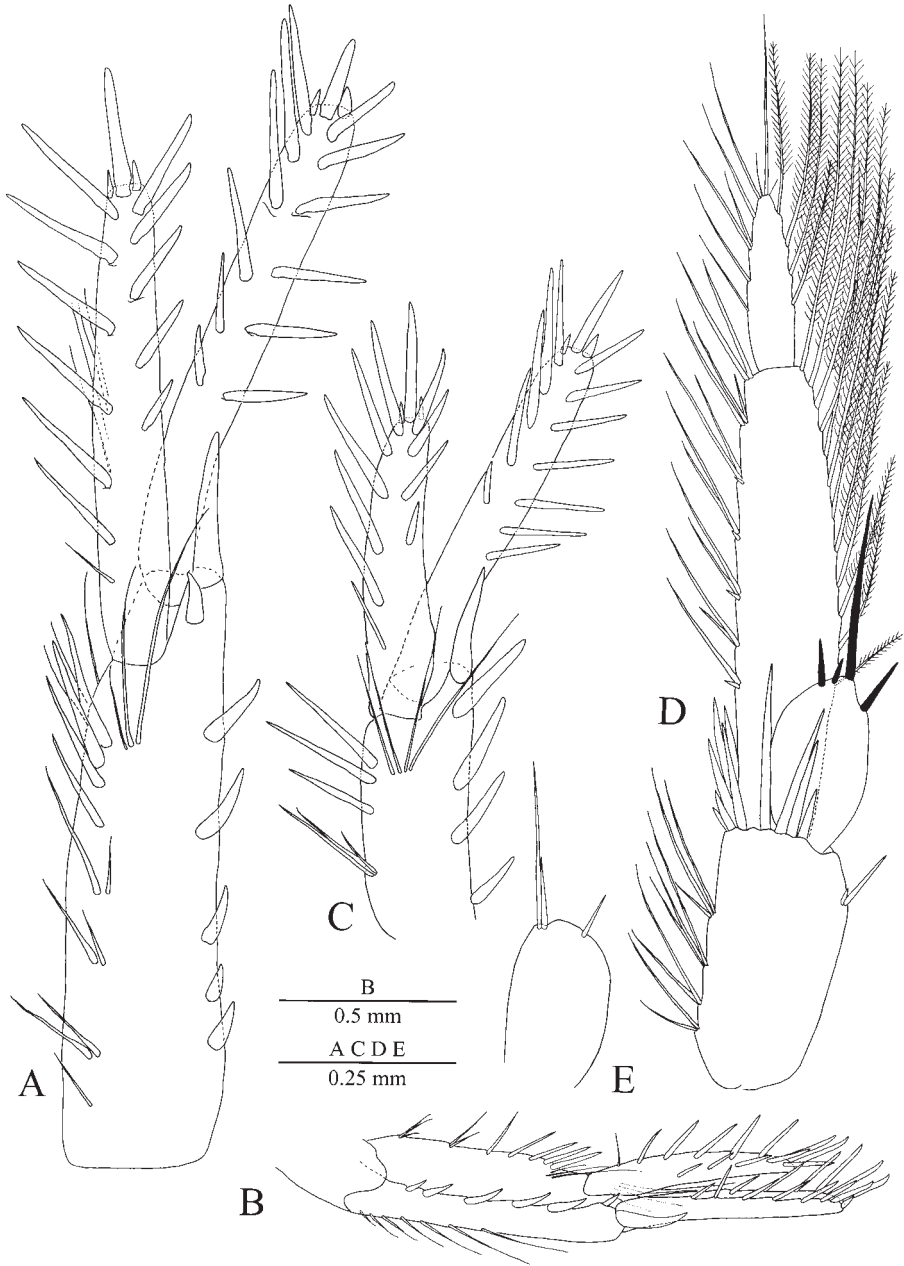


Fig. 33. *Bathyporeia guilliamsoniana* (Bate, 1857), females, Netherlands, TMU 9424 (B, C, D, specimen 2; E, spec. 4; A, spec. 16). A, left U1 (dorsal view); B, left U1 (lateral outer view); C, left U2 (dorsal view); D, right U3 (dorsal view); E, left U3 endopod (dorsal view), unusual ornamentation.

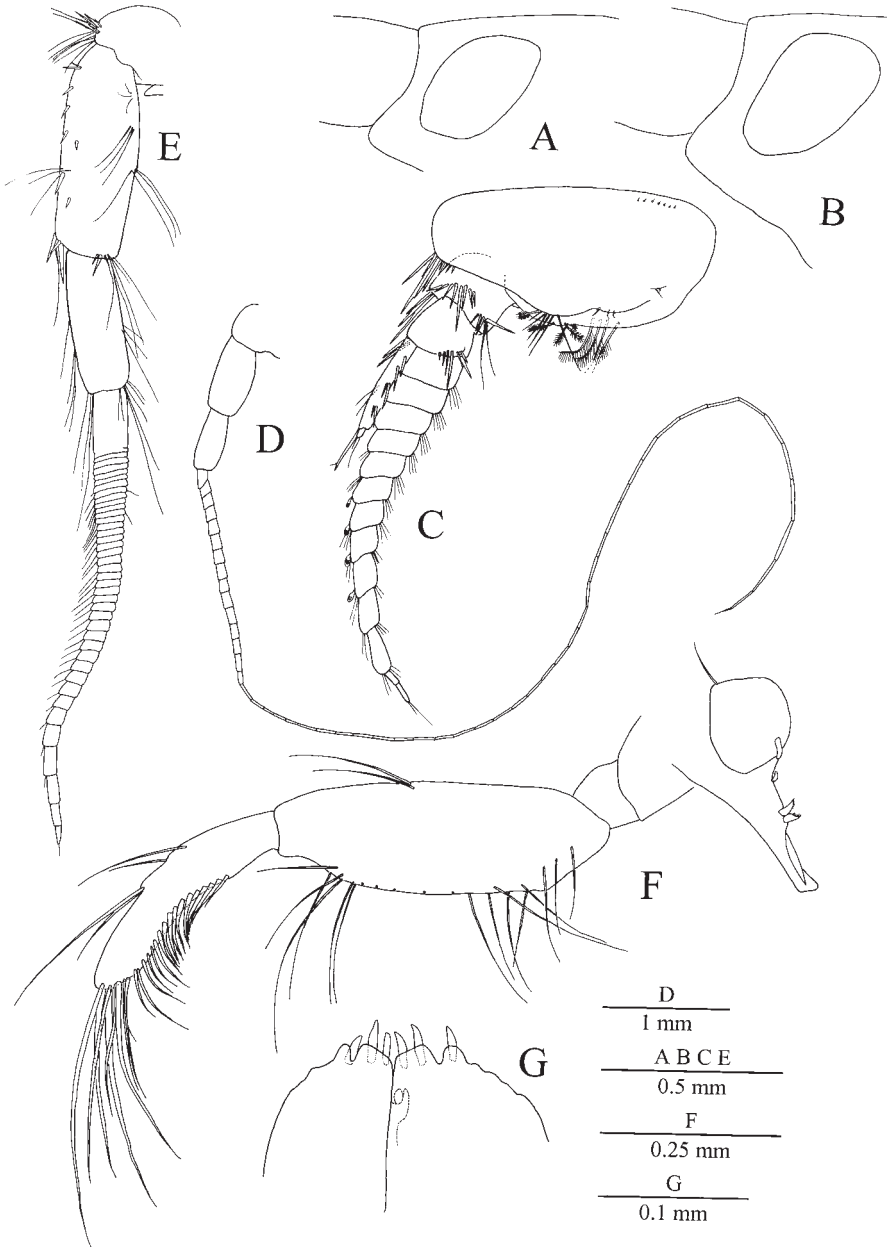


Fig. 34. *Bathyporeia guilliamsoniana* (Bate, 1857), males, Netherlands, TMU 9424 (E, specimen 1 (immature); A, C, D, F, G, spec. 6 (adult); B, spec. 7 (adult)). A-B, anterior part of head; C, left A1; D, left A2 of adult (spines/setae not shown); E, left A2 of immature; F, right Md; G, Mxp inner plates with locking system closed (setae not shown).

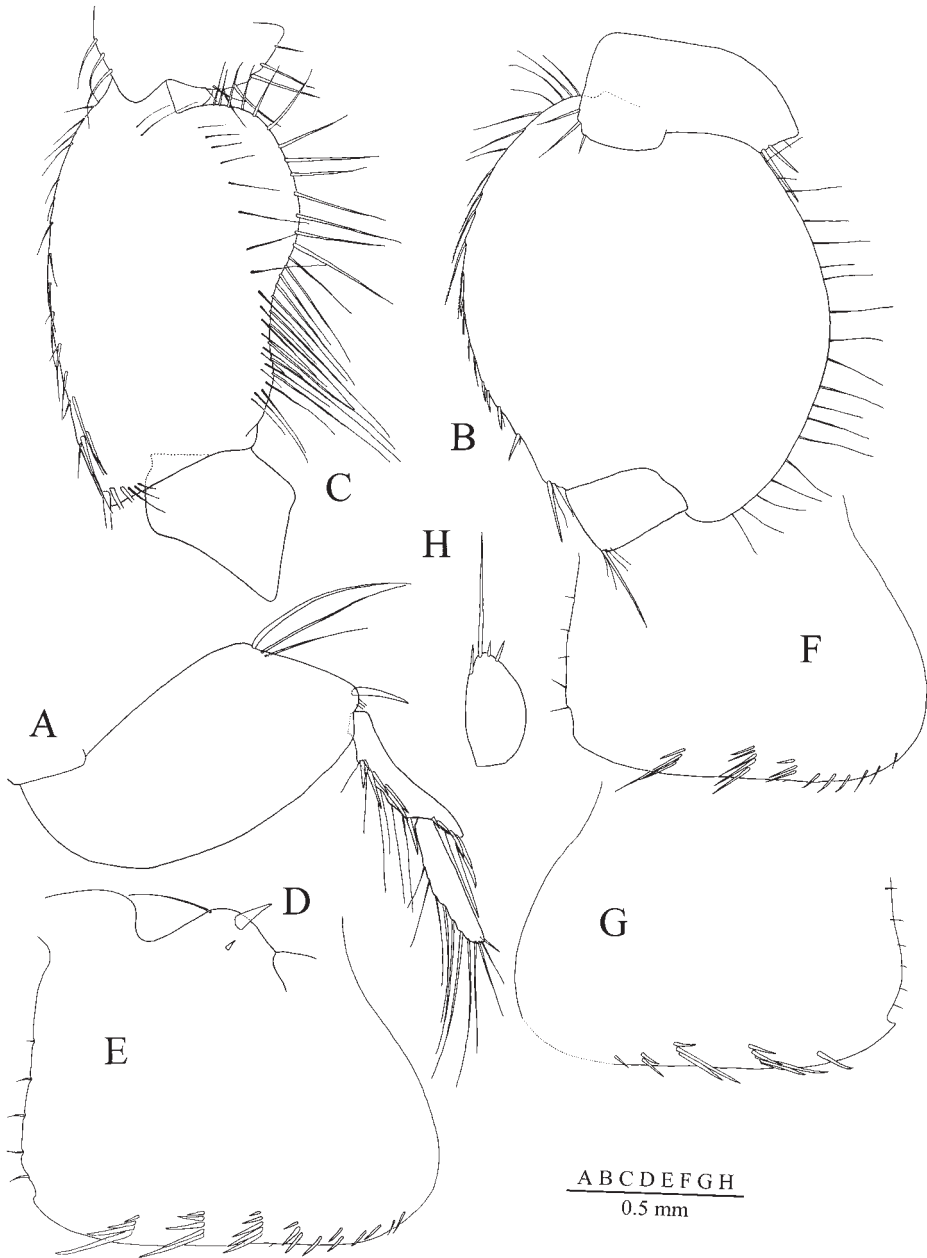


Fig. 35. *Bathyporeia guilliamsoniana* (Bate, 1857), males, Netherlands, TMU 9424 (A, B, D, F, G, specimen 6; C, E, H, spec. 7). A, left P5 distal part (meral ventral spines/setae not shown); B, left P6 proximal part; C, left P7 proximal part (outer view); D, Ur1; E, right Ep3; F, right Ep3; G, left Ep3 (same specimen as F); H, left U3 endopod (dorsal view).

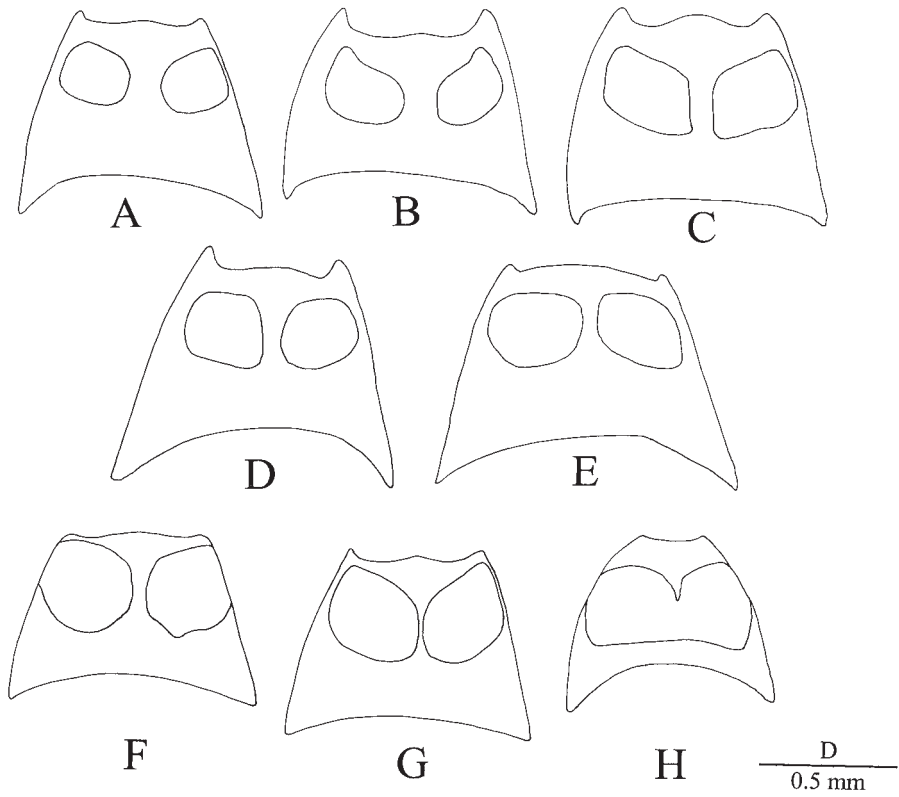


Fig. 36. *Bathyporeia guilliamsoniana* (Bate, 1857), males, A-G, Netherlands, TMU 9424; H, Ireland, Kerry coast, Bunavalla, TMU 12 171. Head in dorsal view.

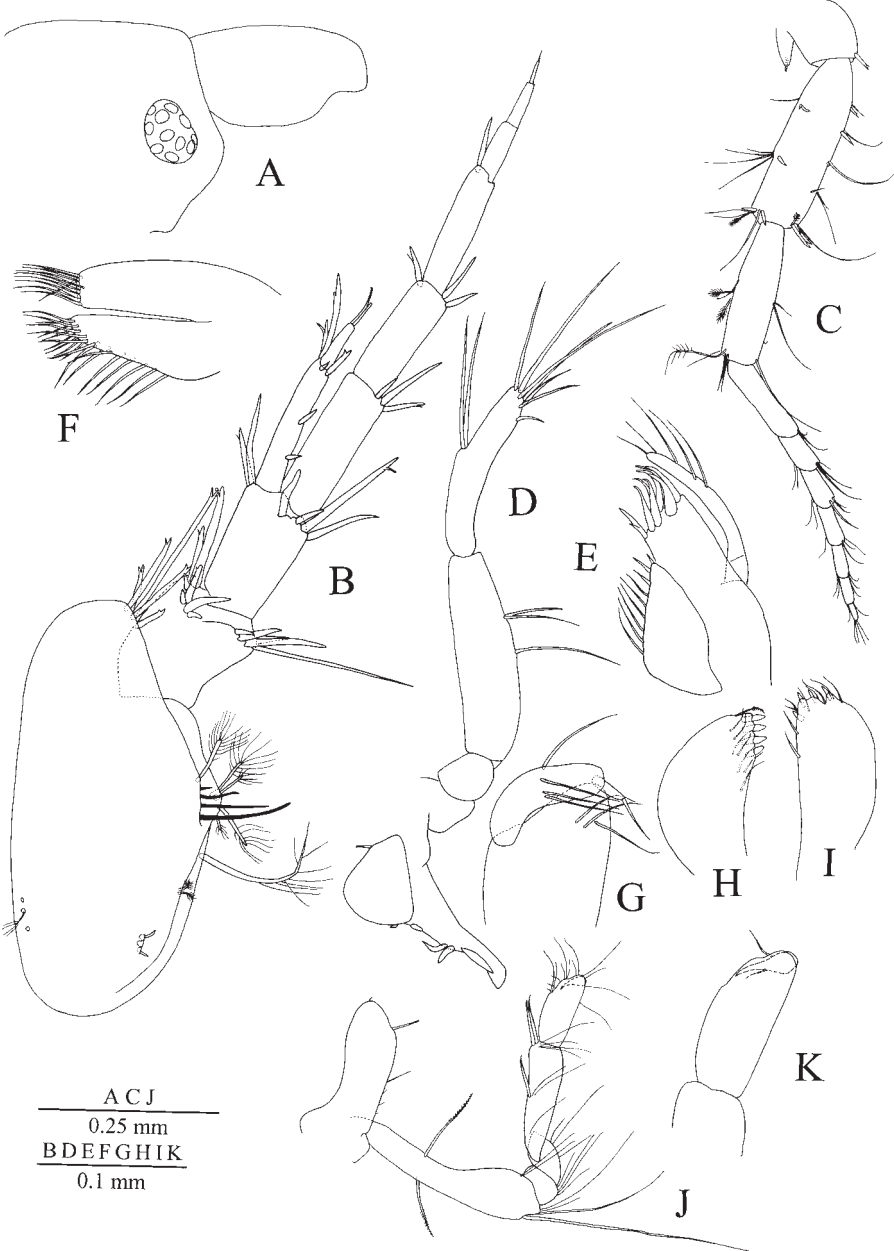


Fig. 37. *Bathyporeia nana* Toulmond, 1966, topotypical female, NW France, Térénez, TMU 4925. A, anterior part of body; B, right A1; C, right A2; D, left Md; E, right Mx1; F, Mx2; G, left Mxp palp; H, left outer plate; I, right outer plate; J, right P1; K, anterior part of right P1.

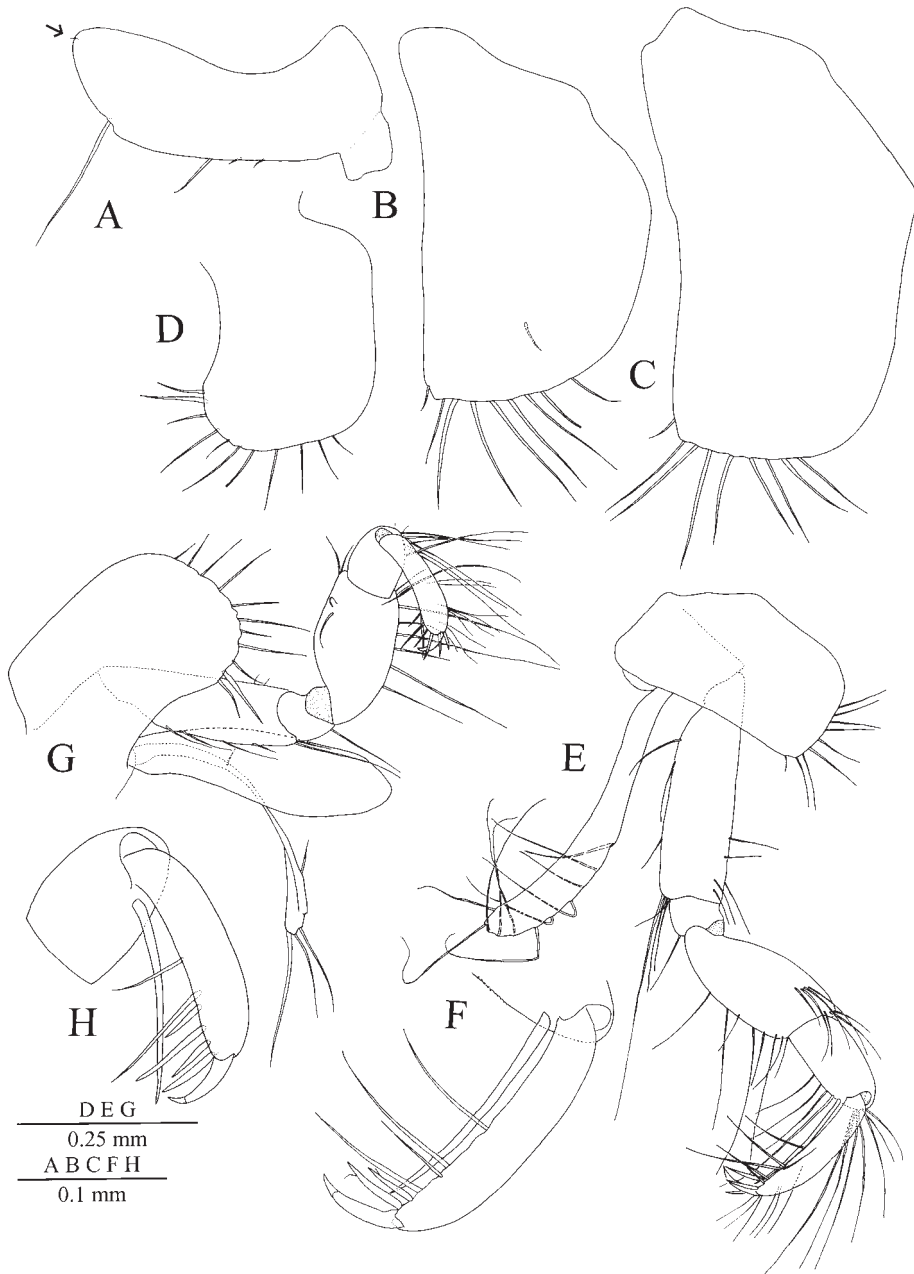


Fig. 38. *Bathyporeia nana* Toulmond, 1966, topotypical female, NW France, Térénez, TMU 4925. A, left coxa 1; B, right coxa 2; C, right coxa 3; D, right coxa 4; E, right P3; F, anterior part of right P3 (mesial spines/setae of propodus not shown); G, right P4; H, anterior part of right P4 (mesial spines/setae of propodus not shown).

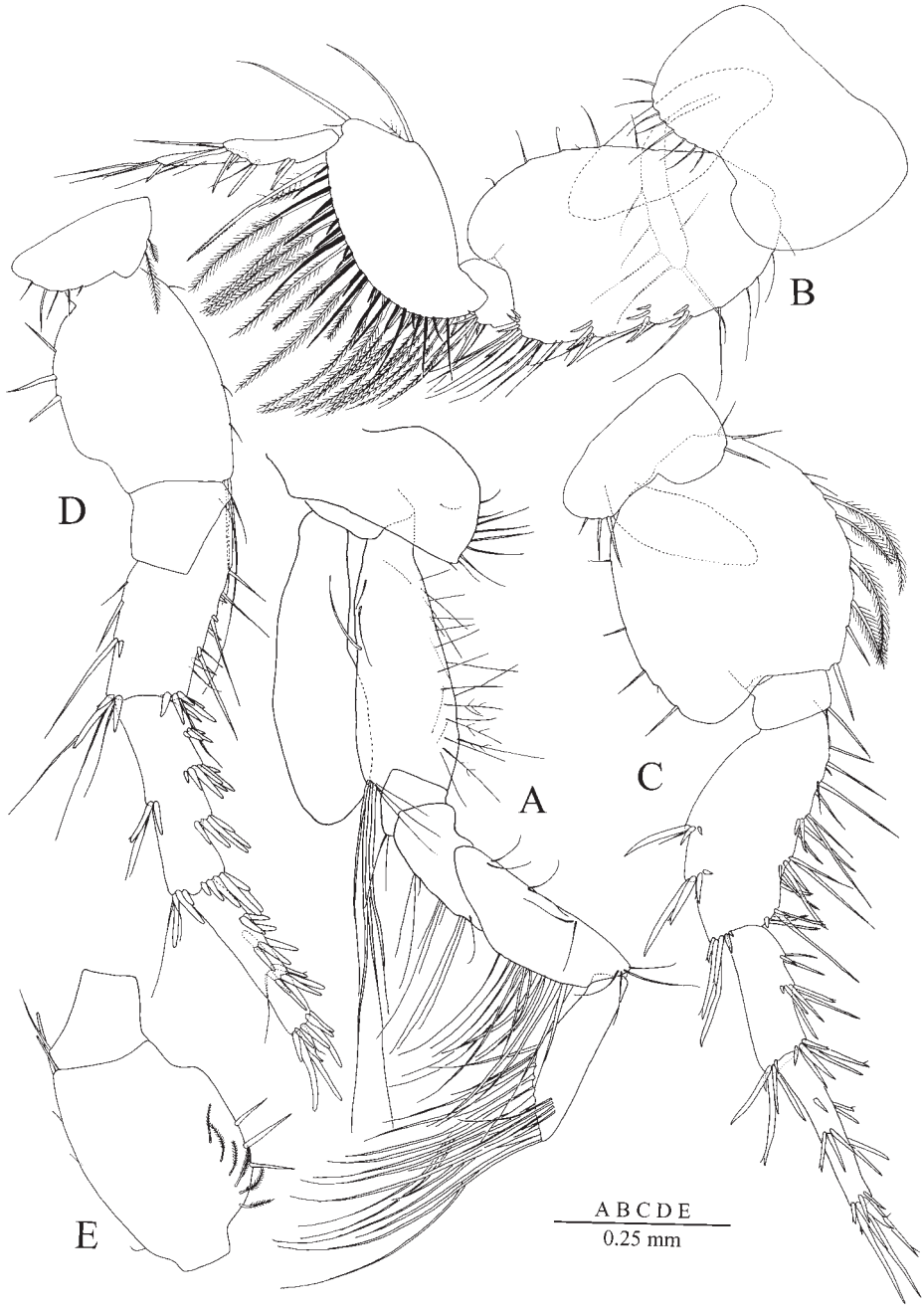


Fig. 39. *Bathyporeia nana* Toulmond, 1966, topotypical female, NW France, Térénez, TMU 4925. A, right P2; B, right P5; C, right P6; D, right P7; E basis and ischium of left P7 (mesial side).

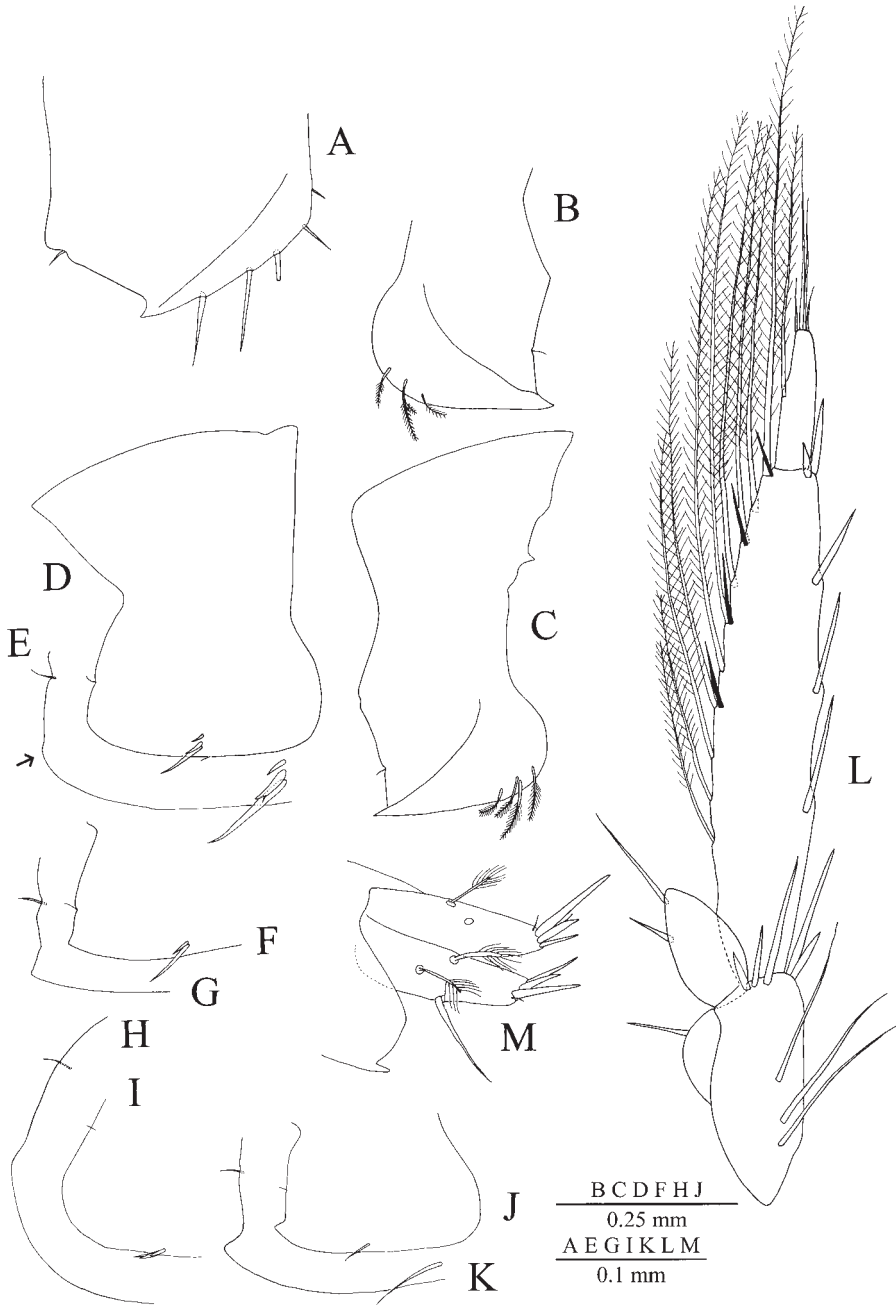


Fig. 40. *Bathyporeia nana* Toulmond, 1966, A-E, M, totypical female, NW France, Térénez, TMU 4925; F, G, immature female, Irish Sea station 108A, NMWZ 1997.052; H, I, L, adult male, Irish Sea station 108A, NMWZ 1997.052; J, K, juvenile male, Irish Sea station 113B, NMWZ 1997.052. A, right Ep1; B, left Ep2; C, right Ep2; D-K, Ep3 and its posteroventral angle; L, left U3 of male; M, telson in oblique view.

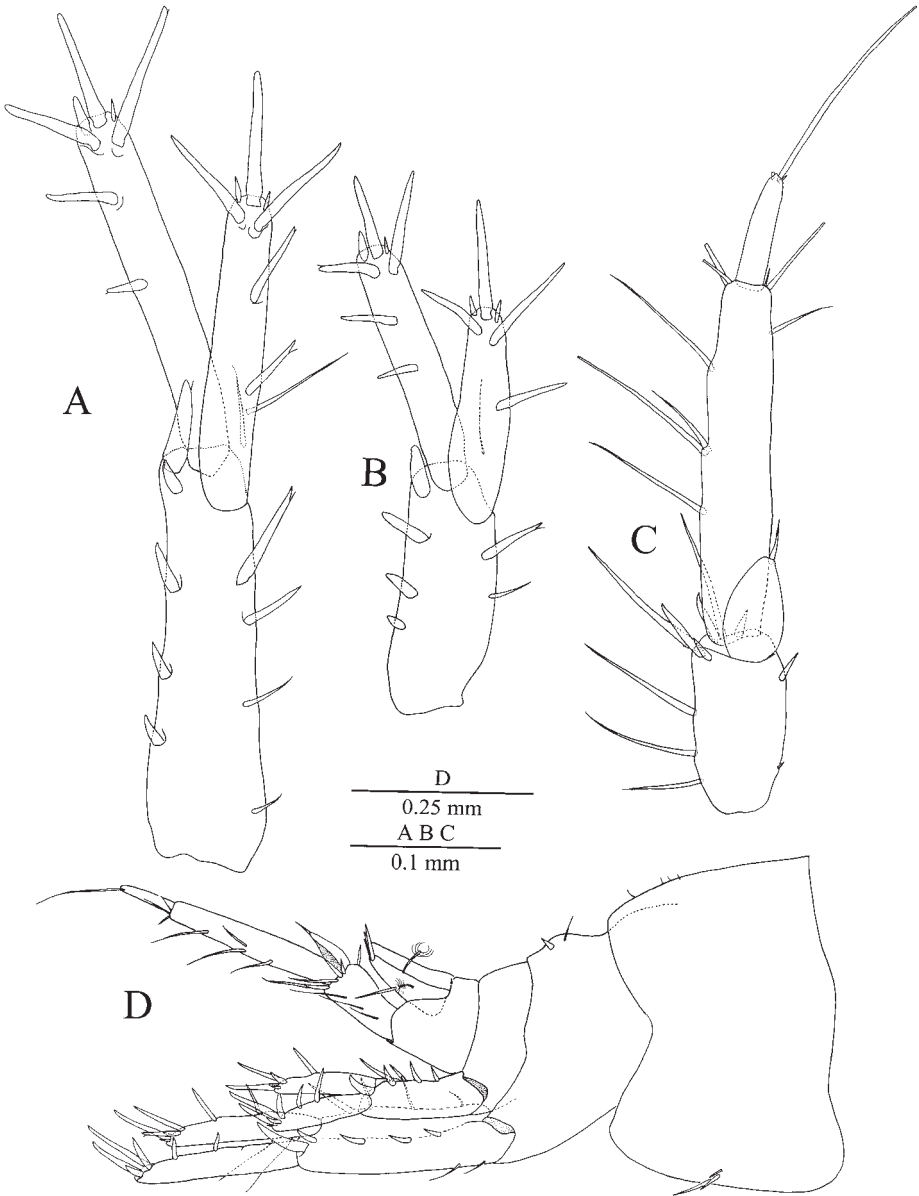


Fig. 41. *Bathyporeia nana* Toulmond, 1966, toptypical female, NW France, Térénez, TMU 4925. A, right U1 (dorsal view); B, right U2 (dorsal view); C, right U3 (dorsal view); D, posterior part of body.

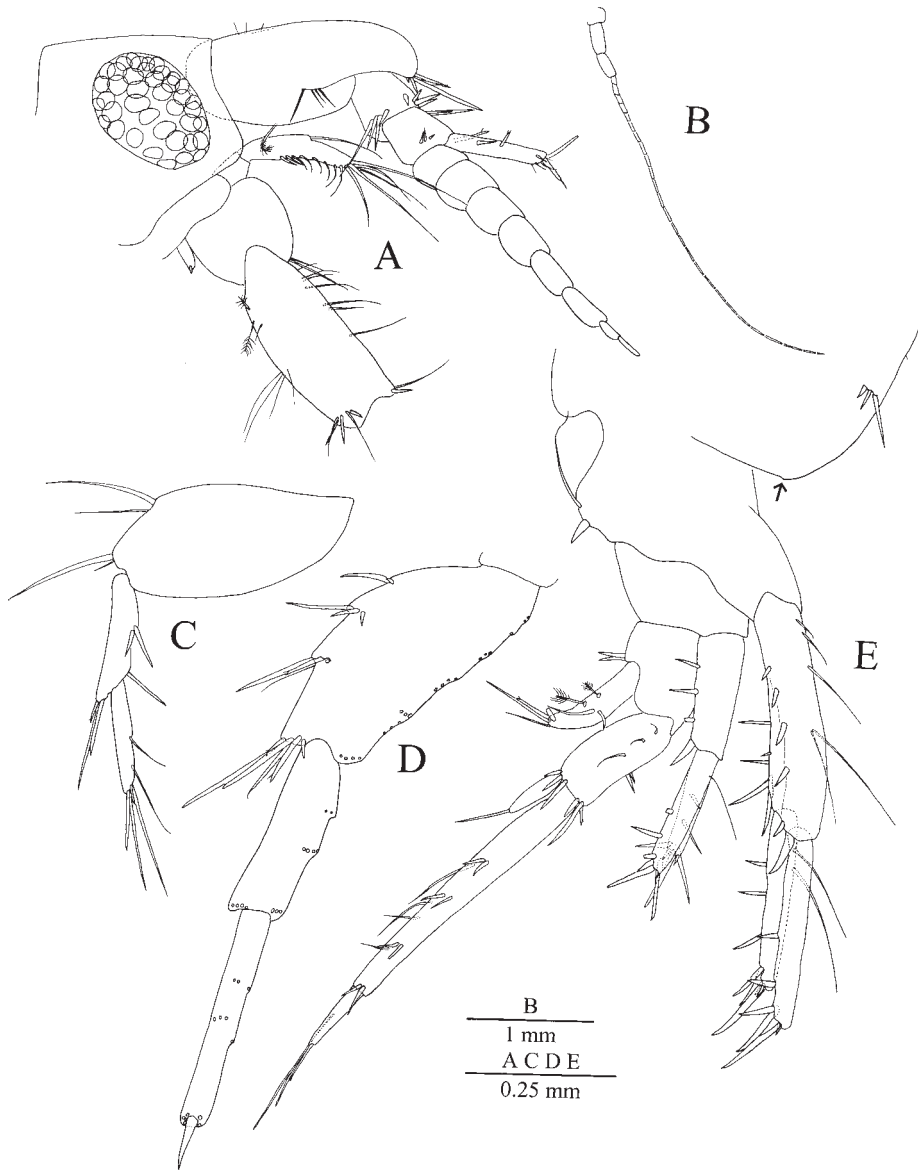


Fig. 42. *Bathyporeia nana* Toulmond, 1966, topotypical male, NW France, Térénez, TMU 4925. A, right side of head and cephalic appendages; B, right A2 (spines/setae not shown); C, right P5 distal part (meral ventral spines/setae not shown); D, right P6 distal part; E, posterior part of body.

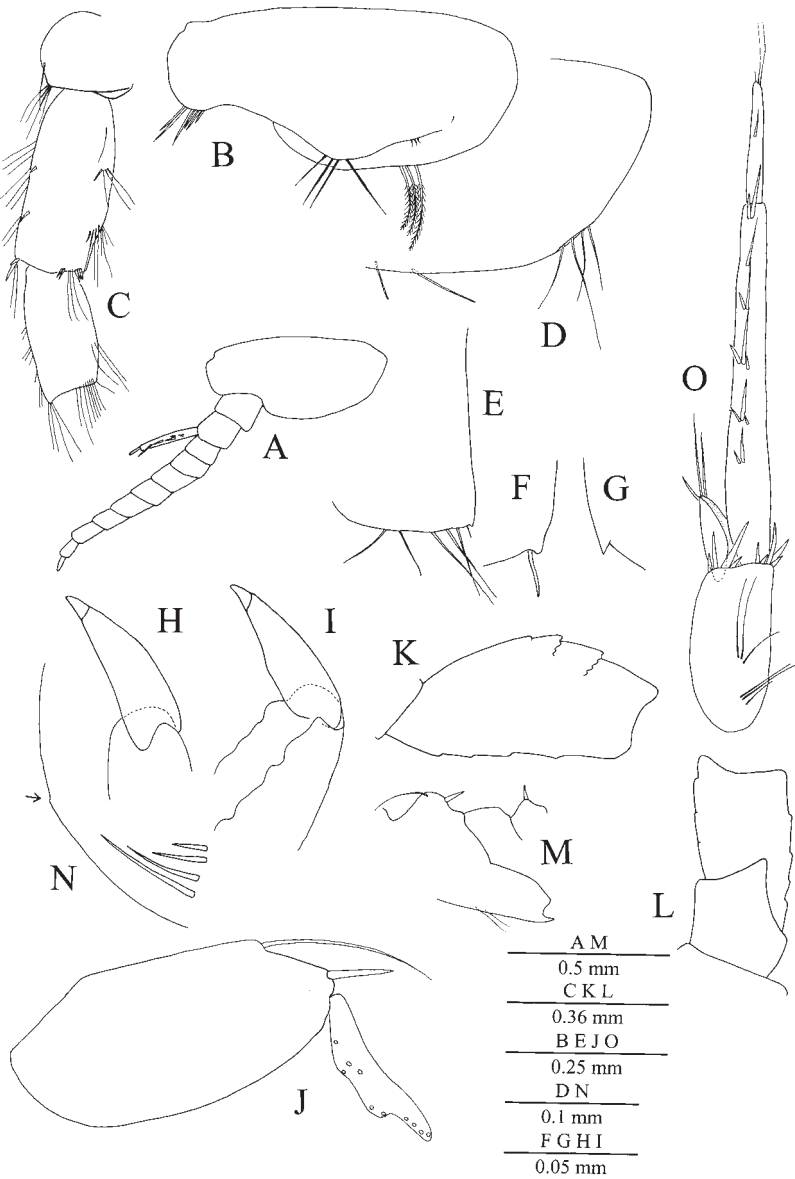


Fig. 43. *Bathyporeia pelagica* (Bate, 1857), adult male, holotype, United Kingdom, Moray Firth, BM 1452.5.7.182. A, left A1; B, first article of left A1; C, peduncle of left A2 (flagellum incomplete; 31 articles are remaining); D, right coxa 1; E, left coxa 3; F, posteroventral angle of right coxa 3; G, posteroventral angle of left coxa 3; H, dactylus of right P3; I, dactylus of right P4; J, merus and carpus of left P5; K, merus of left P6; L, ischium and merus of left P7 (outer side); M, urosomite 1 and dorsal part of urosomites 2 and 3 (on the urosomite 1, the long ventral setae arising from the mesial side are very thin; they have nothing to do with the short and strong setae of the outer side found in some other species); N, tip of right Ep3; O, left U3 in lateral view.

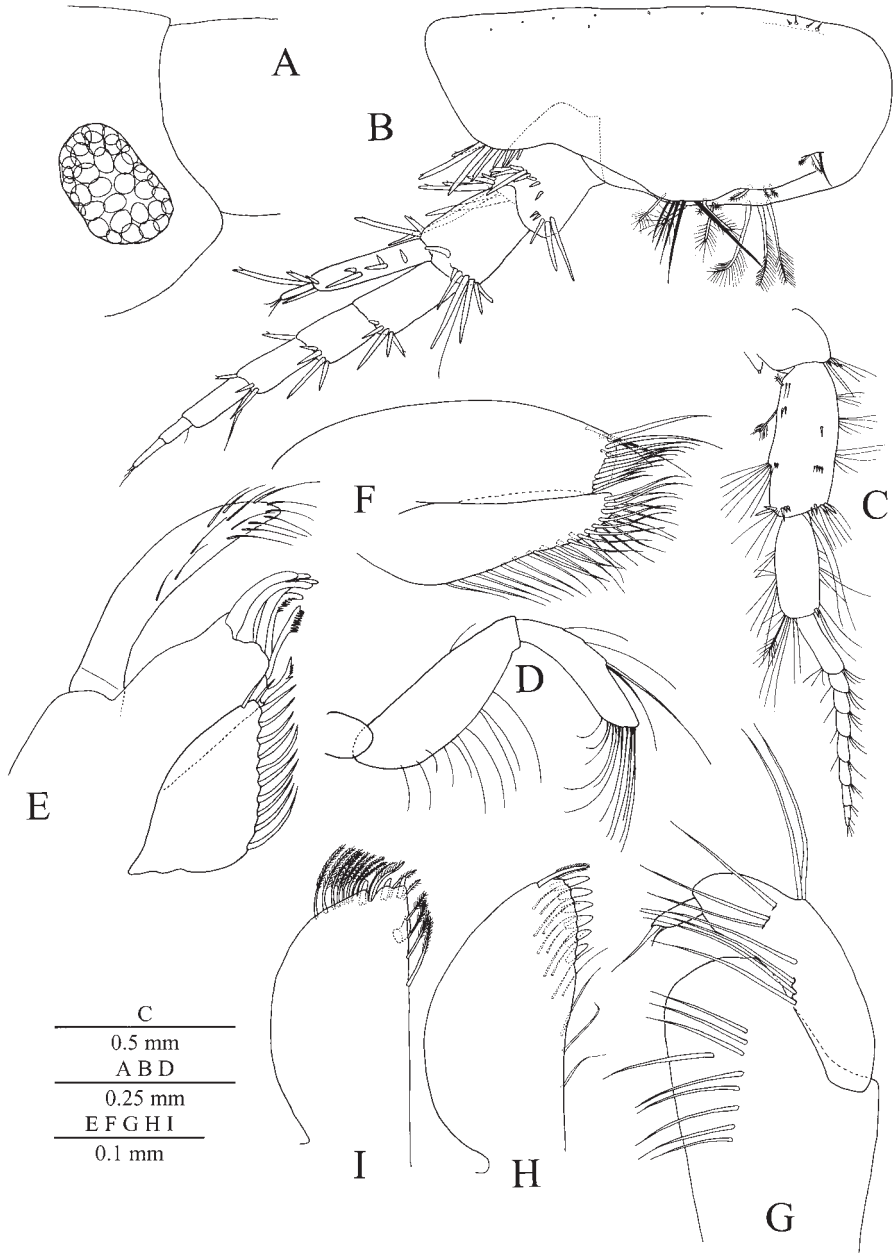


Fig. 44. *Bathyporeia pelagica* (Bate, 1857), female, NE France, Ambleteuse, RMNH A 4948. A, anterior part of the head; B, left A1; C, right A2; D, mandibular palp; E, left Mx1; F, Mx2; G, right Mxp palp; H, left Mxp outer plate; I, left Mxp inner plate.

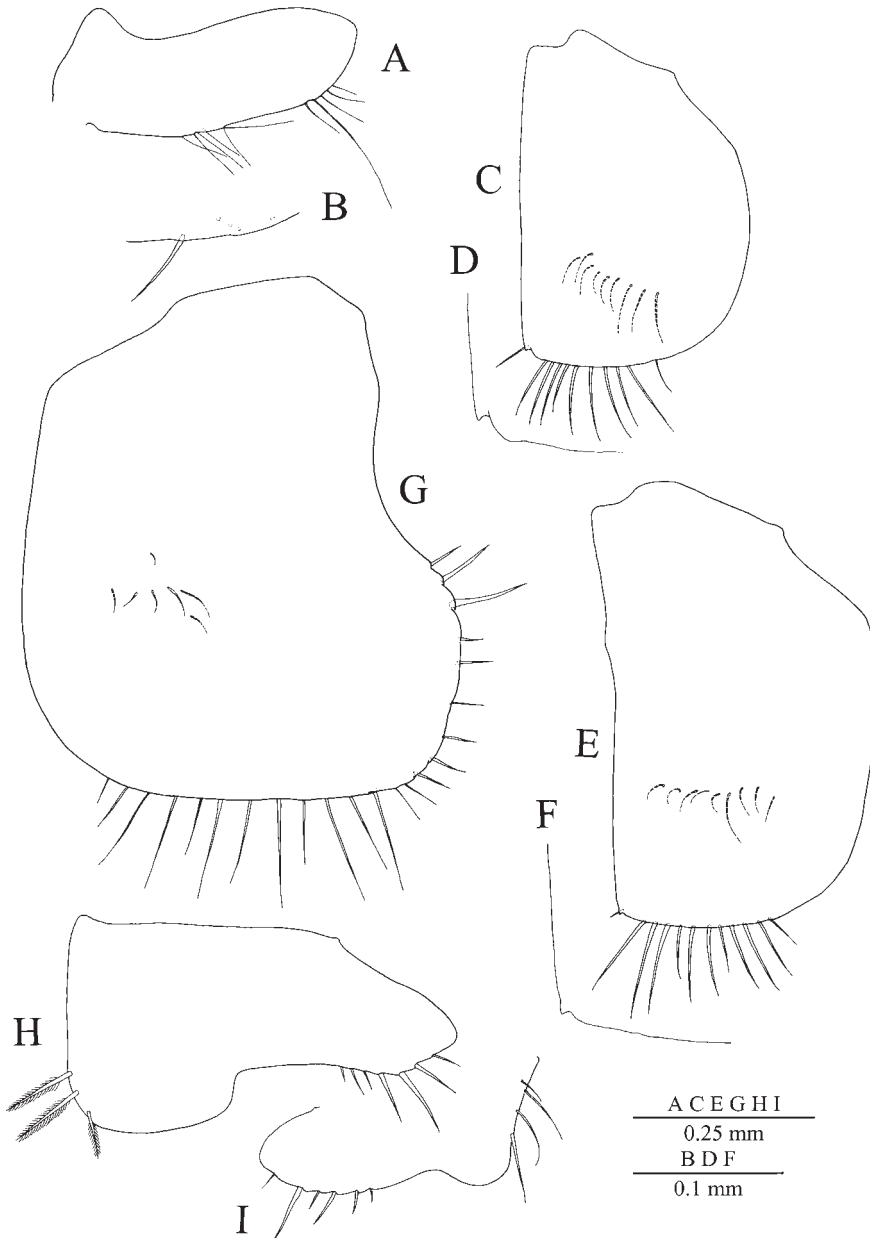


Fig. 45. *Bathyporeia pelagica* (Bate, 1857), female, NE France, Ambleteuse, RMNH A 4948. A, right coxa 1; B, ventral border of left coxa 1 (the four posterior setae are only indicated by their insertion point); C, right coxa 2; D, posteroventral angle of right coxa 2; E, right coxa 3; F, posteroventral angle of right coxa 3; G, left coxa 4; H, left coxa 6; I, right coxa 7.

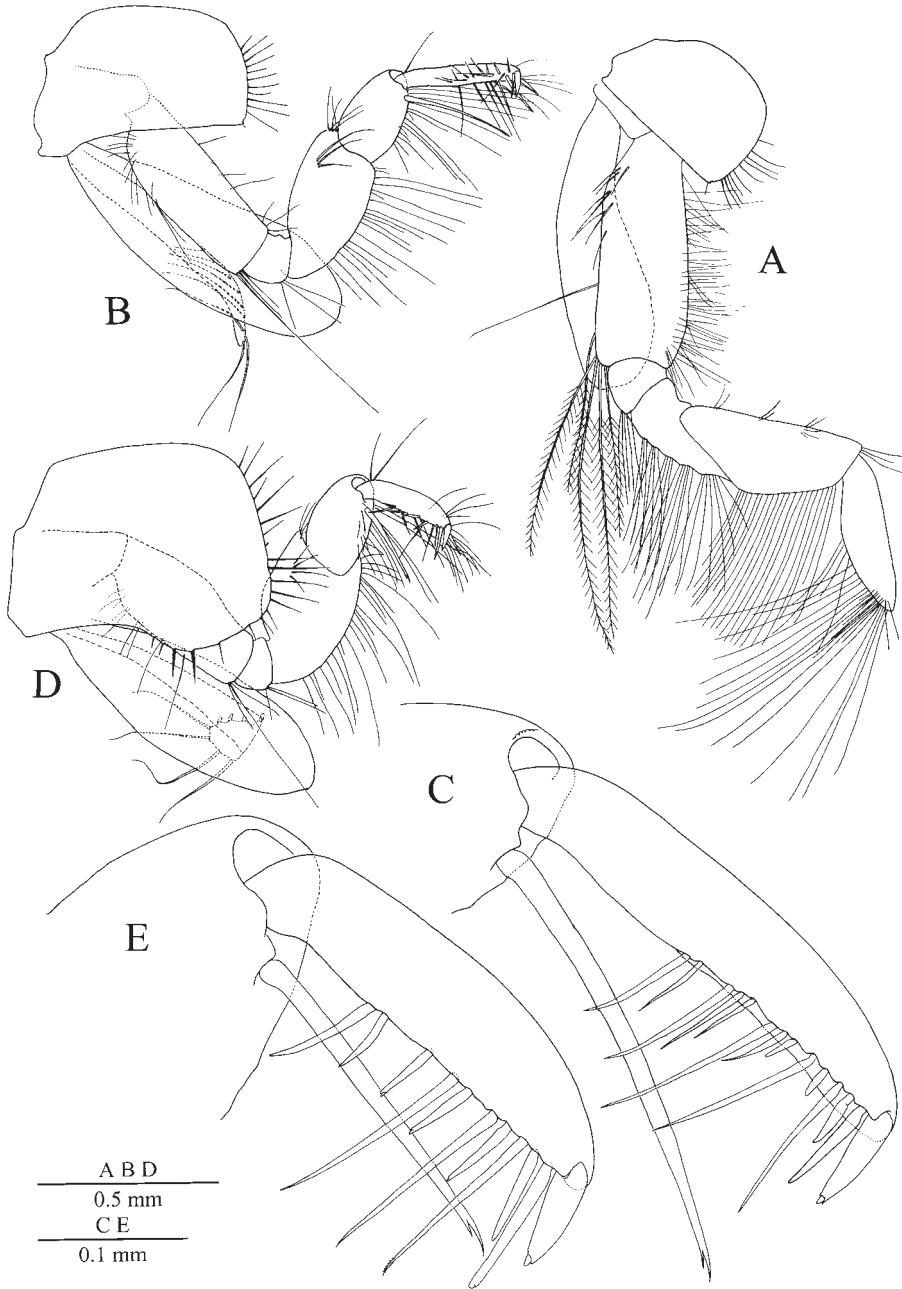


Fig. 46. *Bathyporeia pelagica* (Bate, 1857), female, NE France, Ambleteuse, RMNH A 4948. A, right P2; B, right P3; C, anterior part of right P3 (mesial spines/setae of propodus not shown); D, right P4; E, anterior part of right P4 (mesial spines/setae of propodus not shown).

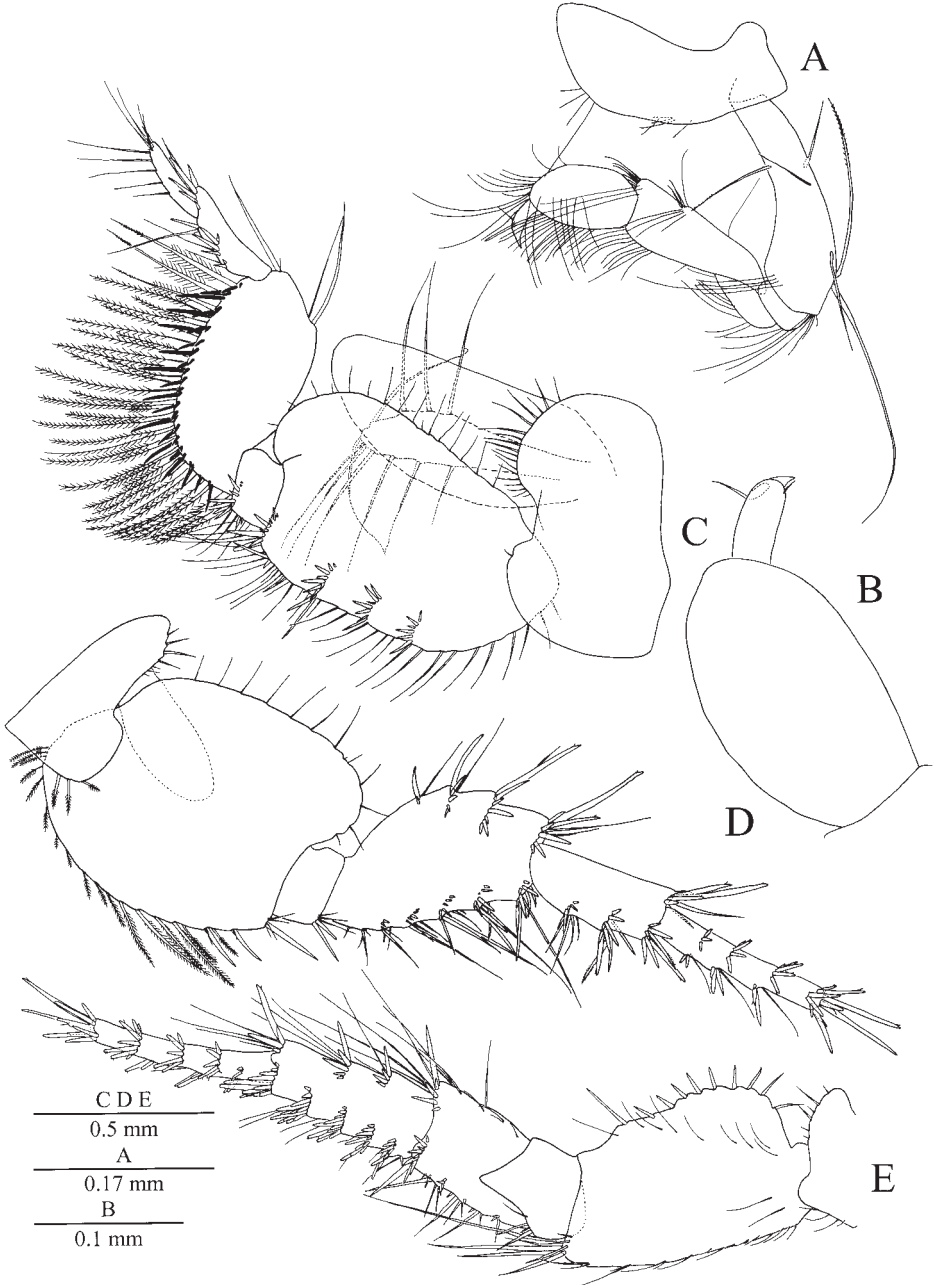


Fig. 47. *Bathyporeia pelagica* (Bate, 1857), female, NE France, Ambleteuse, RMNH A 4948. A, left P1; B, anterior part of right P1; C, right P5; D, left P6; E, left P7.

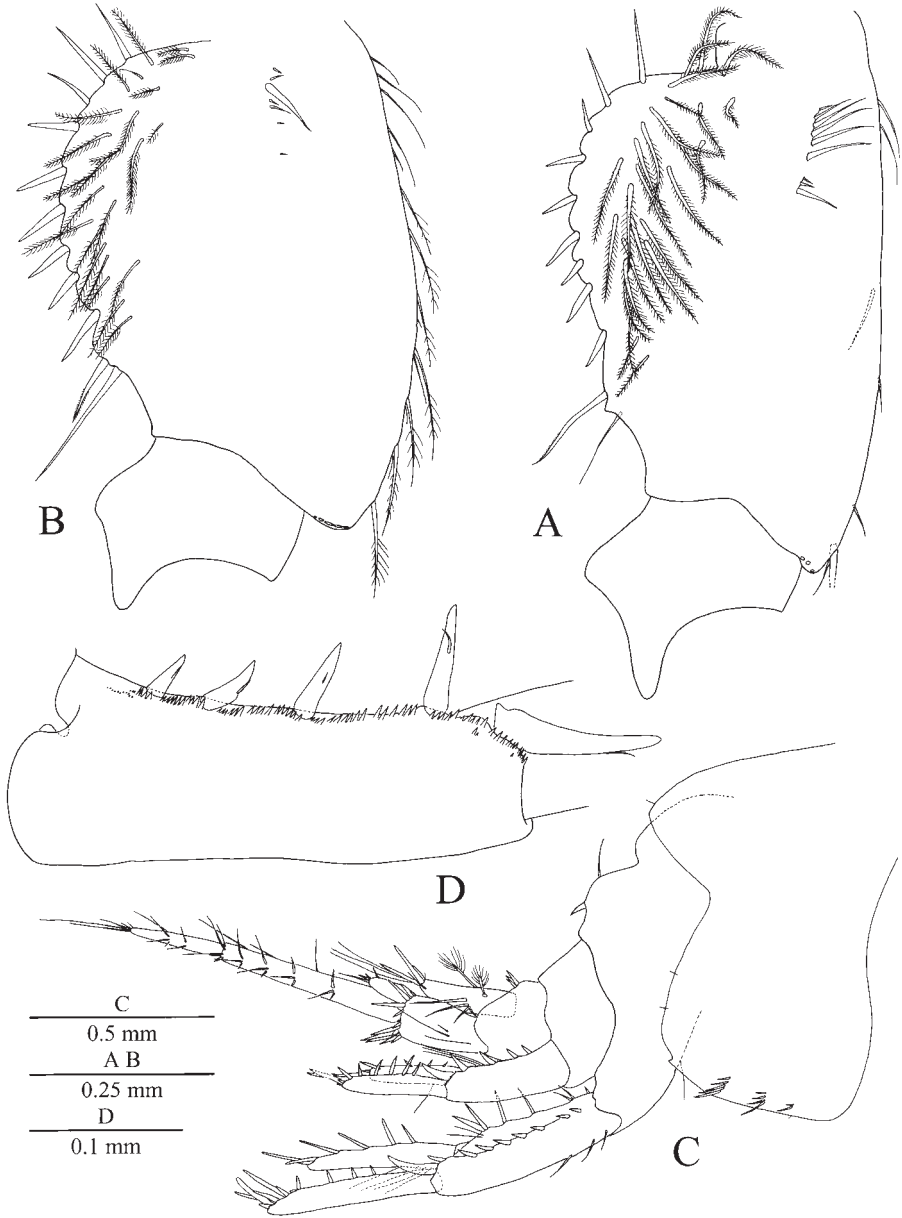


Fig. 48. *Bathyporeia pelagica* (Bate, 1857), females, NE France; B, Wissant, RMNH A 4947; A, C, D, Ambleteuse, RMNH A 4948. A, B, left basis and ischium of P7 (mesial side); C, posterior part of body; D, peduncle of left U2 (lateral view).

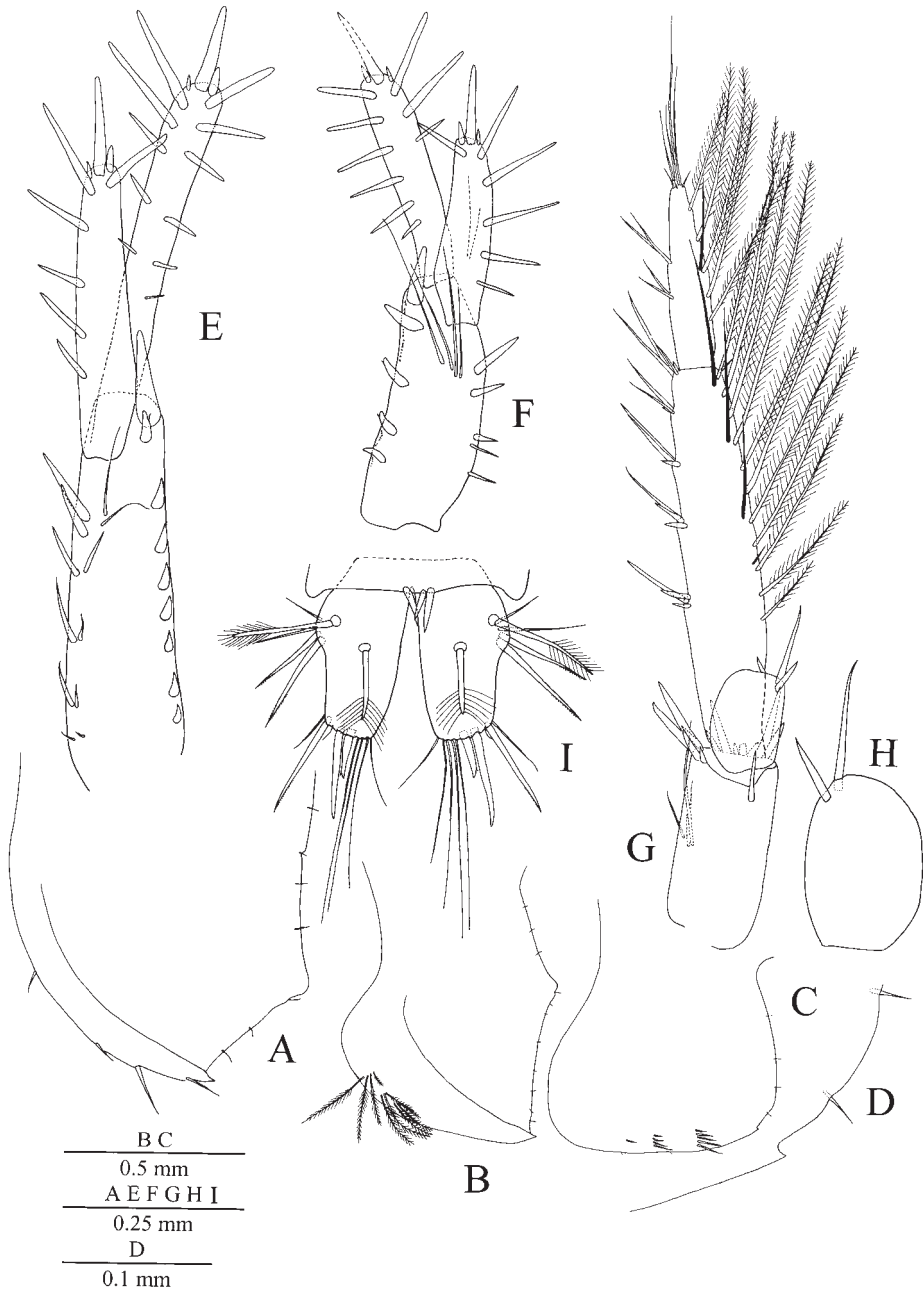


Fig. 49. *Bathyporeia pelagica* (Bate, 1857), female, NE France, Ambleteuse, RMNH A 4948, except H: female, Netherlands, Oosterschelde, Oude Roompot, RMNH A 4937. A, left Ep1; B, left Ep2; C, left Ep3; D, left Ep3 posteroventral angle; E, left U1 (dorsal view); F, right U2 (dorsal view); G, left U3 (dorsal view); H, endopod of right U3 (not the commonest morphology); I, telson.

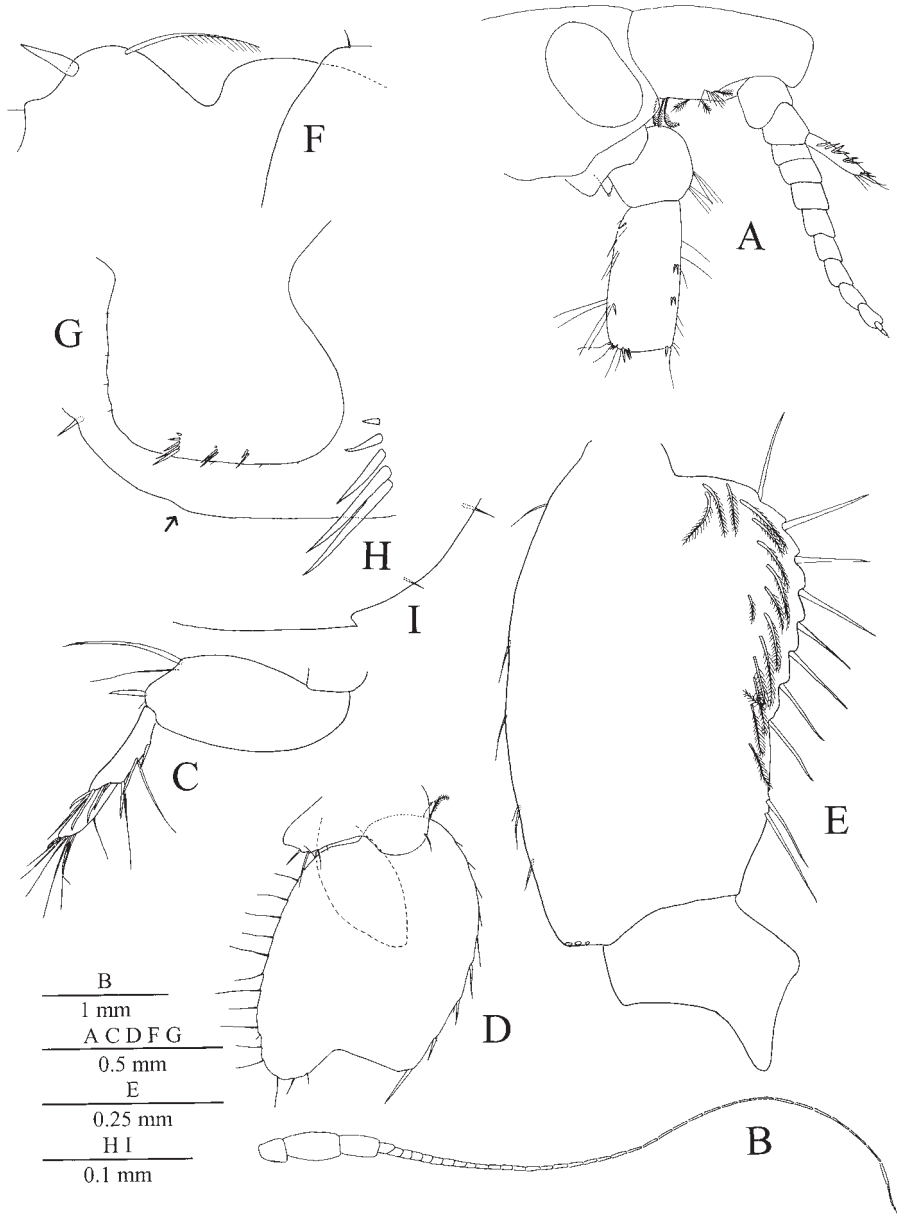


Fig. 50. *Bathyporeia pelagica* (Bate, 1857), males, NE France, Wissant, RMNH A 4947. A, male 1 (adult); B-H, male 2 (adult); I, male 3 (immature). A, head, A1, proximal part of A2 (some spines not shown); B, right A2; C, left P5 distal part (meral ventral spines/setae not shown); D, right P6 proximal part; E, right basis and ischium of P7 (mesial side); F, Ur1; G, right Ep3; H, right Ep3 posteroventral angle; I, left Ep3 posteroventral angle.

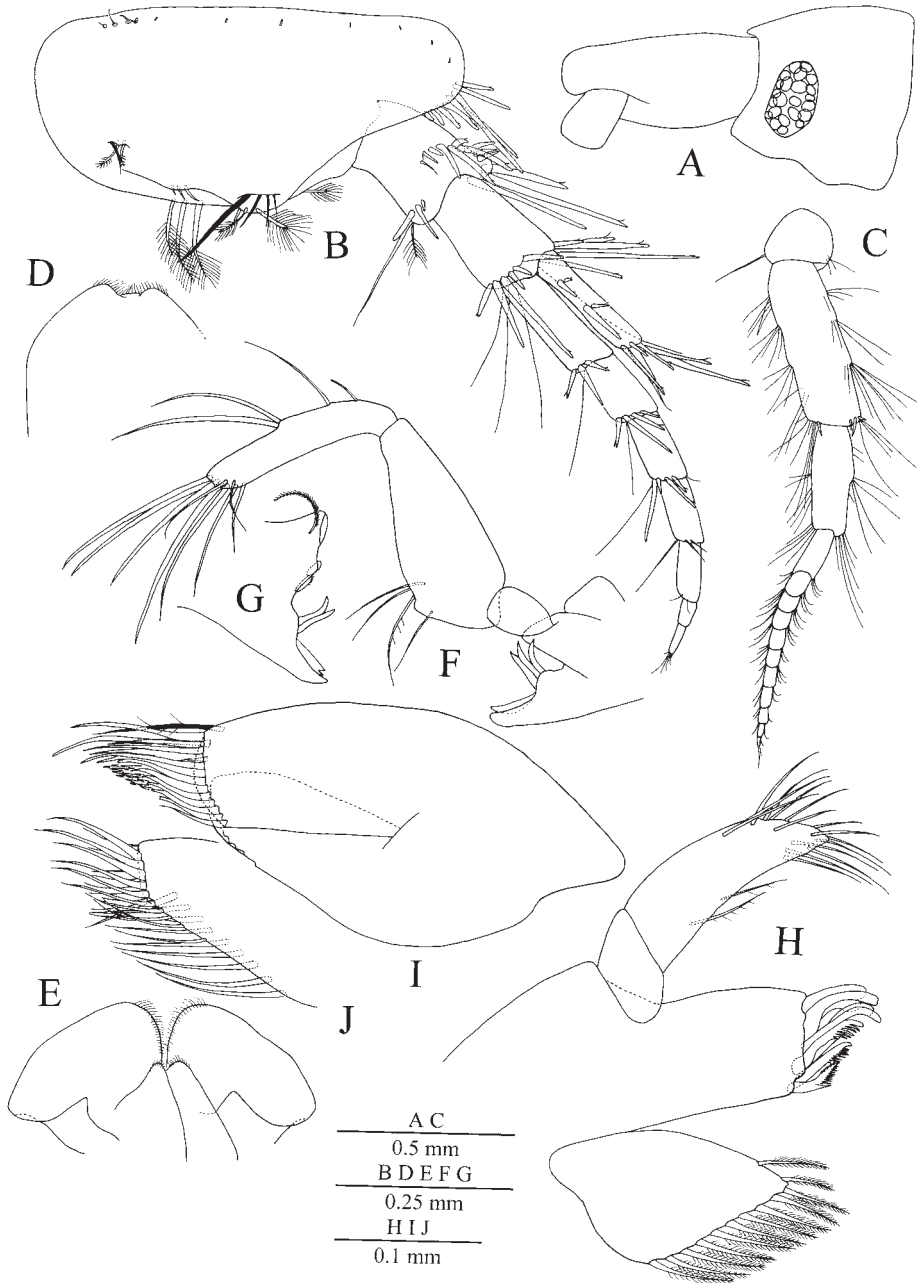


Fig. 51. *Bathyporeia pilosa* Lindström, 1855, adult female, NE France, Wissant, RMNH A 4965. A, anterior part of body; B, right A1; C, left A2; D, upper lip; E, lower lip; F, left Md; G, right Md (palp not shown); H, Mx1; I, left Mx2; J, inner plate of left Mx2.

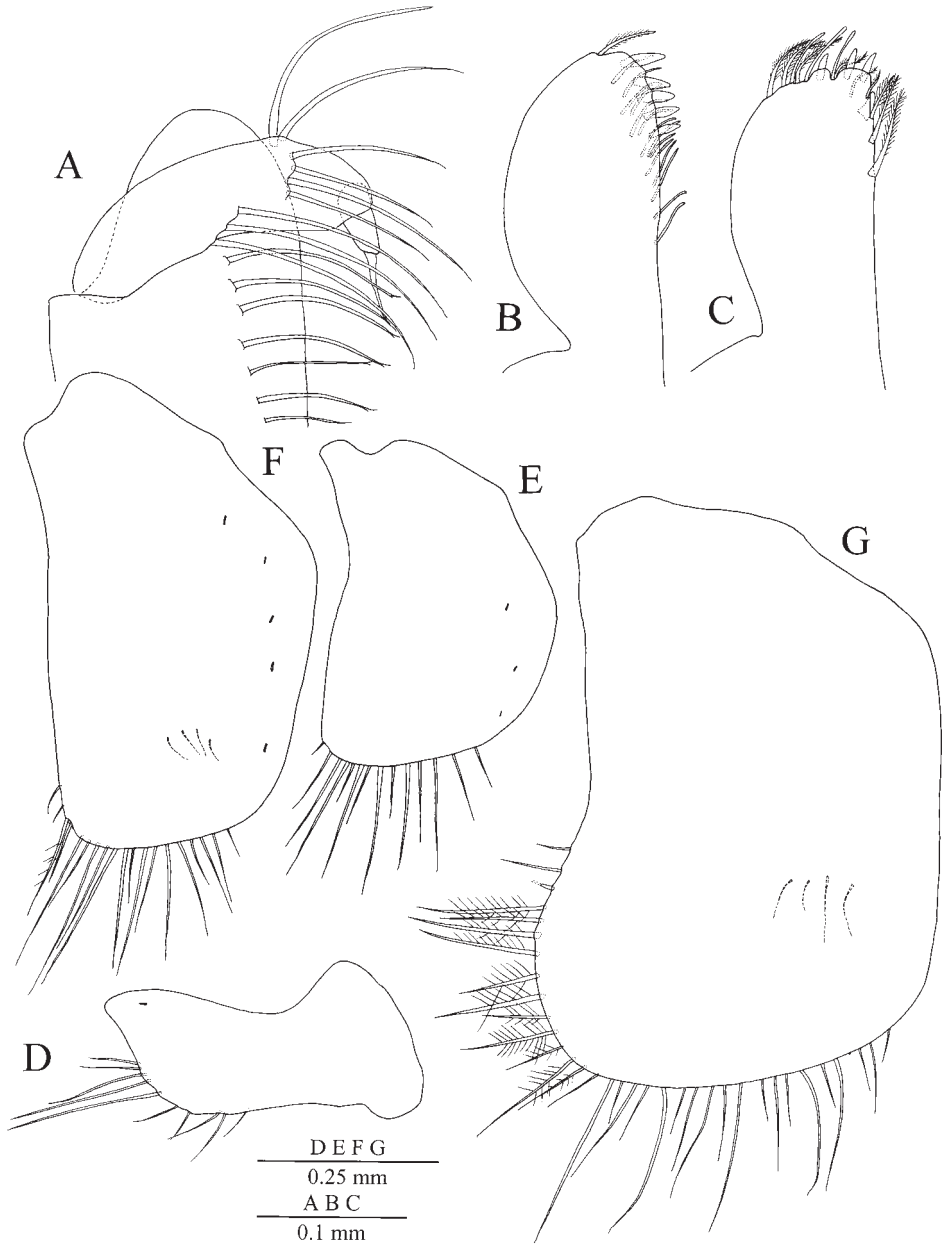


Fig. 52. *Bathyporeia pilosa* Lindström, 1855, adult female, NE France, Wissant, RMNH A 4965. A, left Mxp palp, B, left Mxp outer plate; C, left Mxp inner plate; D, left coxa 1, E, right Coxa 2; F, right coxa 3; G, right coxa 4.

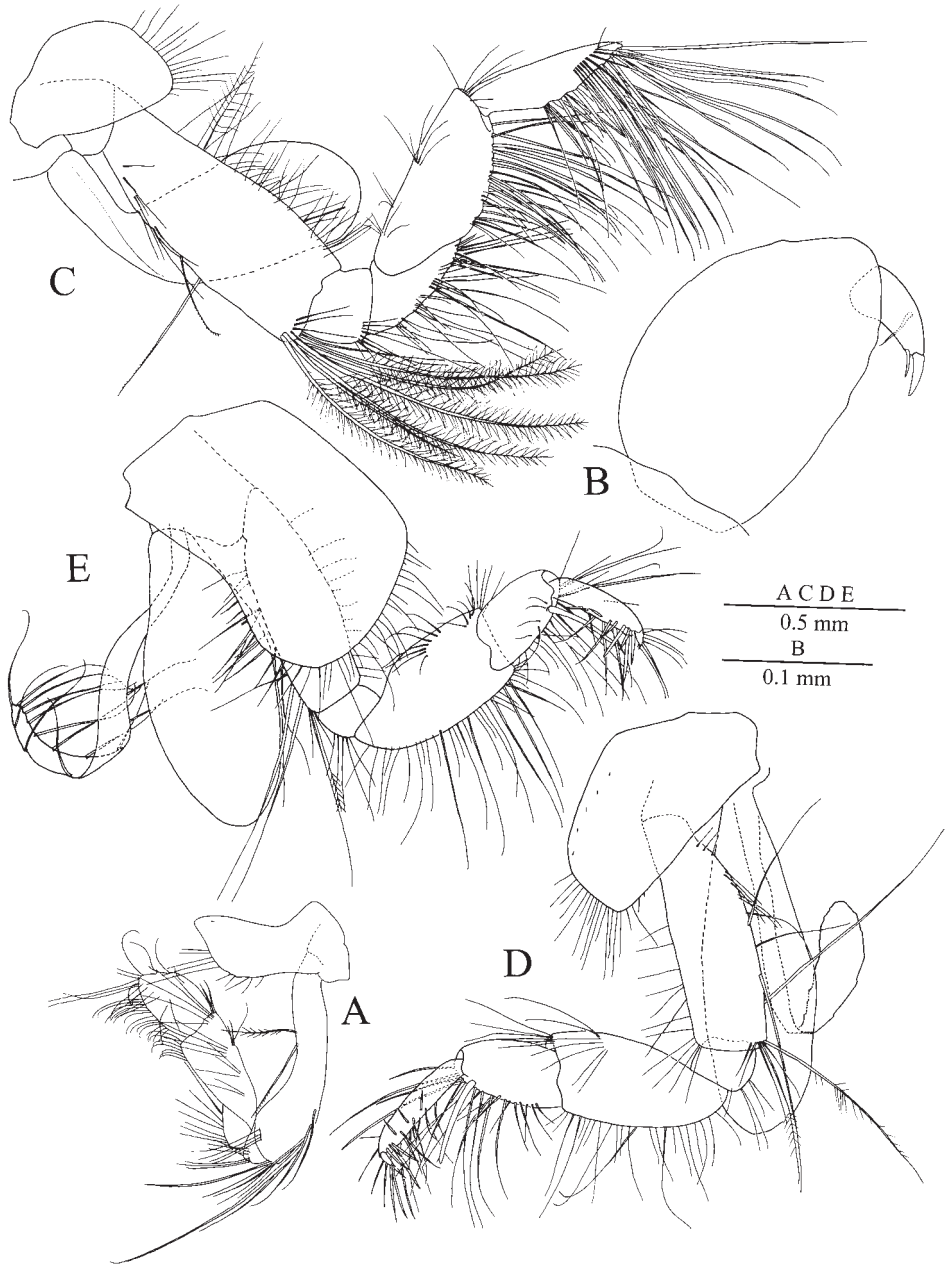


Fig. 53. *Bathyporeia pilosa* Lindström, 1855, adult female, NE France, Wissant, RMNH A 4965. A, left P1; B, tip of right P1; C, right P2; D, left P3; E, right P4.

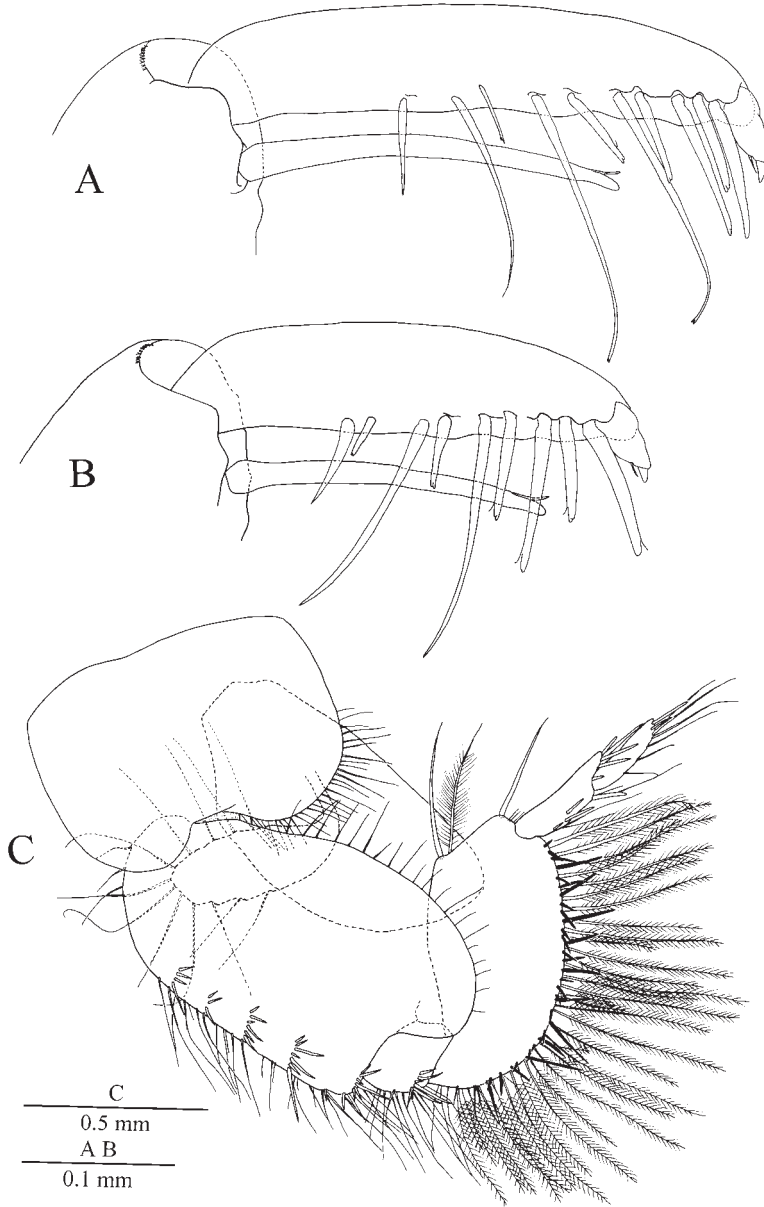


Fig. 54. *Bathyporeia pilosa* Lindström, 1855, adult female, NE France, Wissant, RMNH A 4965. A, anterior part of right P3 (mesial spines/setae of propodus not shown); B, anterior part of right P4 (mesial spines/setae of propodus not shown); C, left P5.

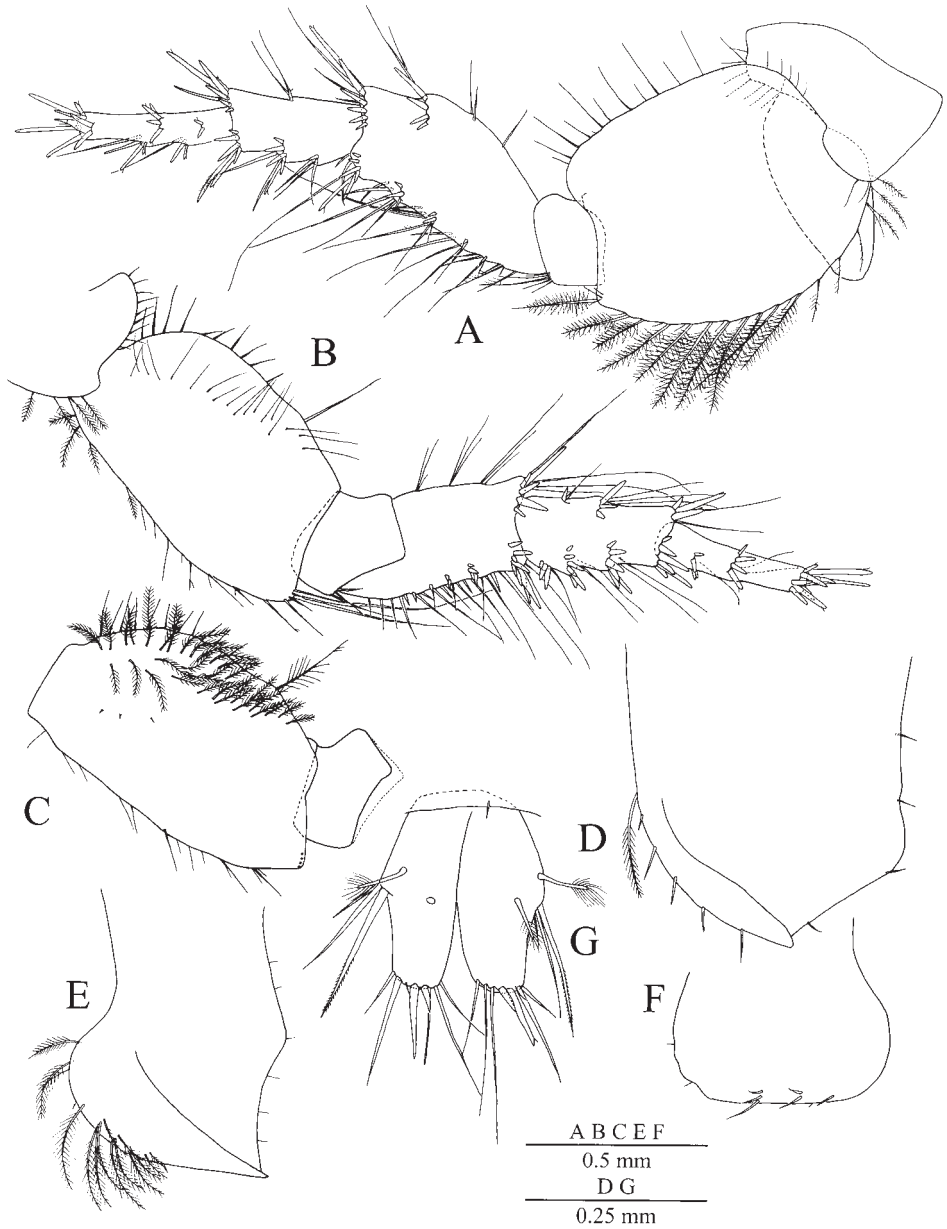


Fig. 55. *Bathyporeia pilosa* Lindström, 1855, adult female, NE France, Wissant, RMNH A 4965. A, right P6; B, left P7; C, right basis and ischium of P7 (mesial side) [right dotted line = outer side of ischium seen by transparency]; D, left Ep1; E, left Ep2; F, right Ep3; G, telson.

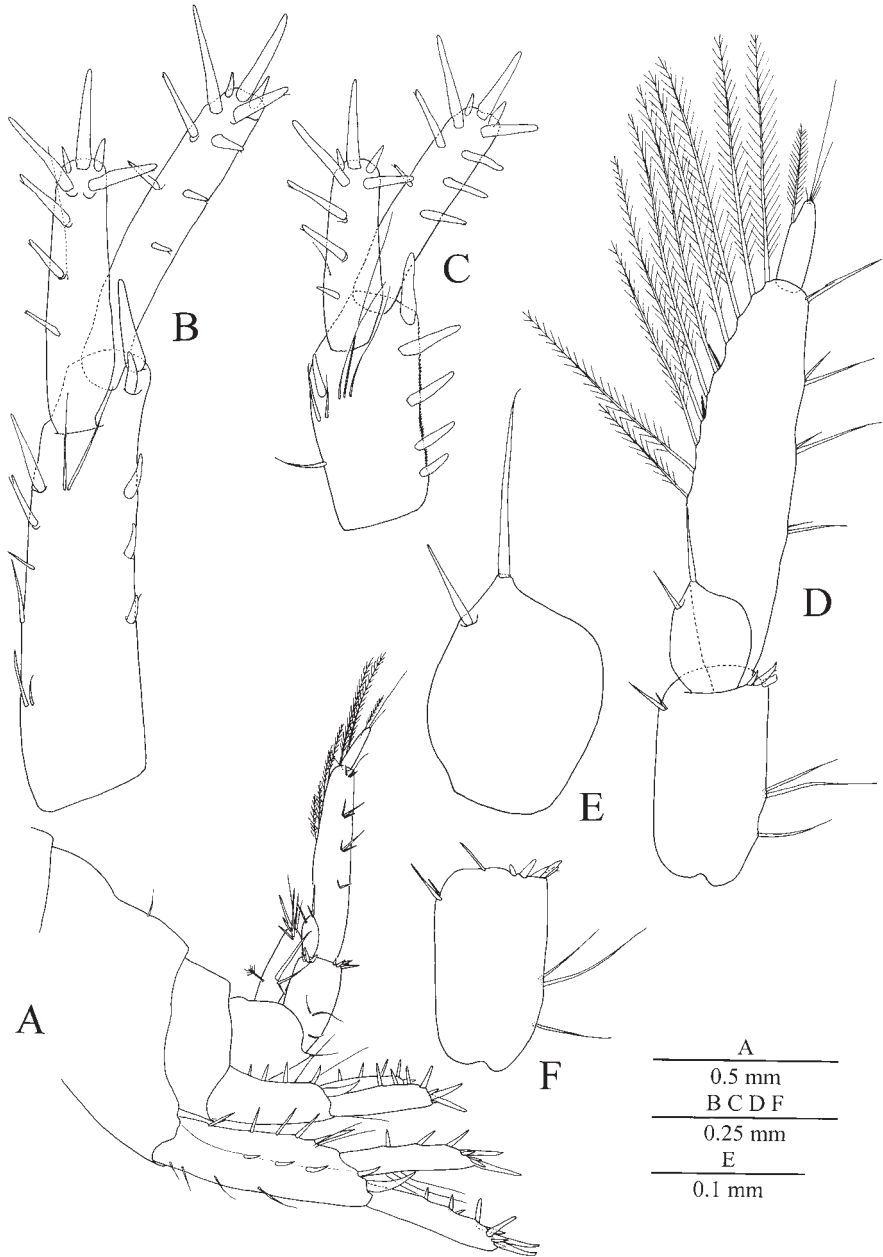


Fig. 56. *Bathyporeia pilosa* Lindström, 1855, adult female, NE France, Wissant, RMNH A 4965. A, posterior part of body; B, left U1; C, left U2; D, left U3; E, endopod of left U3; F, peduncle of right U3 (ventral view).

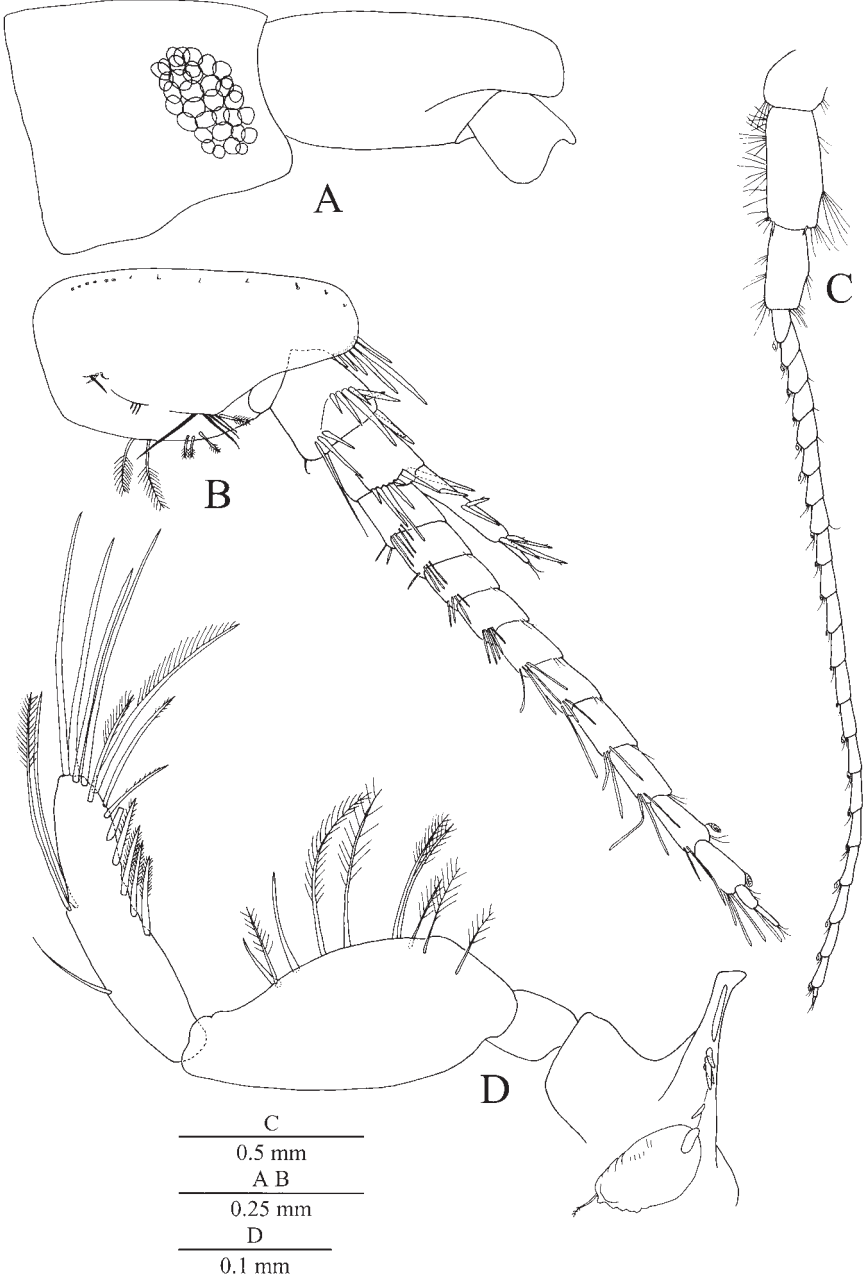


Fig. 57. *Bathyporeia pilosa* Lindström, 1855, adult male, Jersey, TMU 4922. A, anterior part of body; B, right A1; C, right A2; D, left Md.

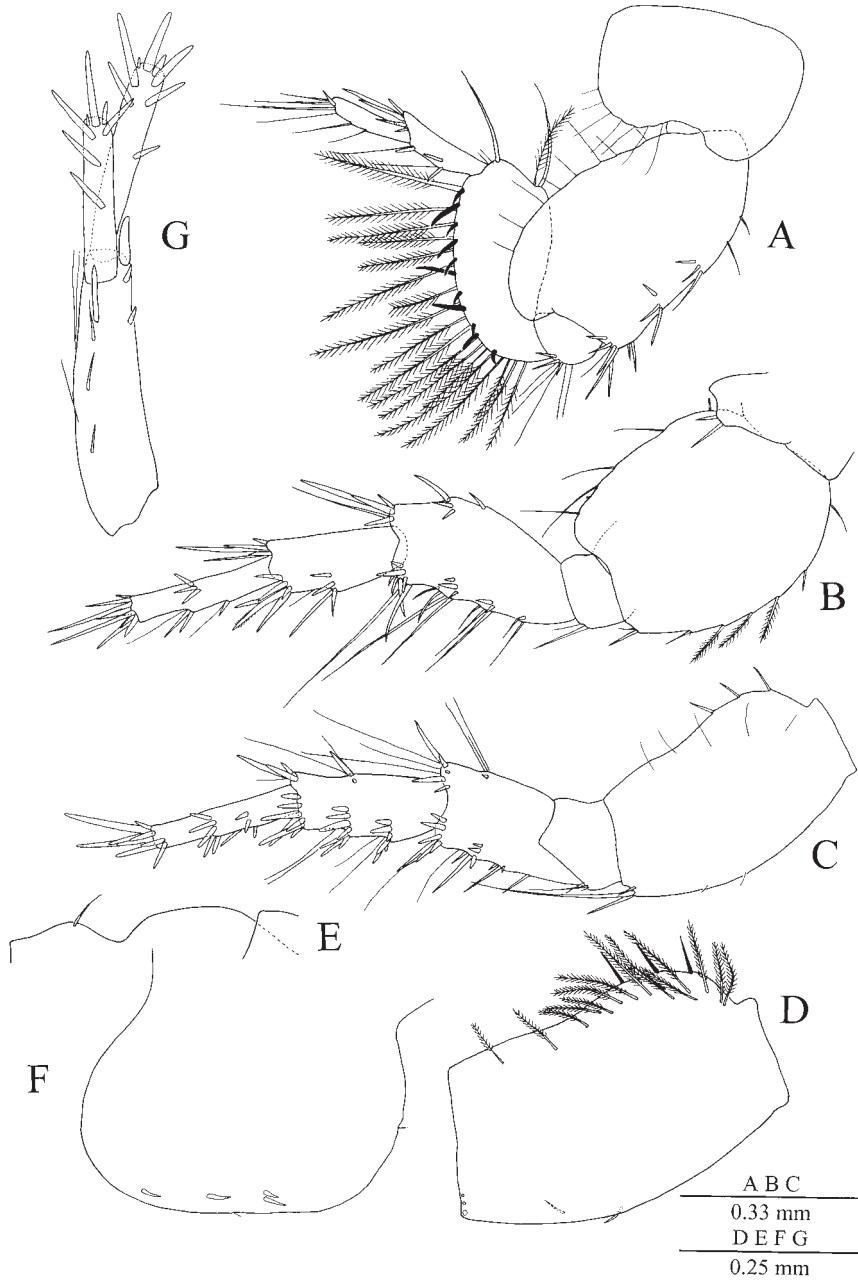


Fig. 58. *Bathyporeia pilosa* Lindström, 1855, adult male, Jersey, TMU 4922. A, right P5; B, right P6; C, right P7; D, left basis of P7 (mesial side); E, Ur1; F, Ep3; G, U1.

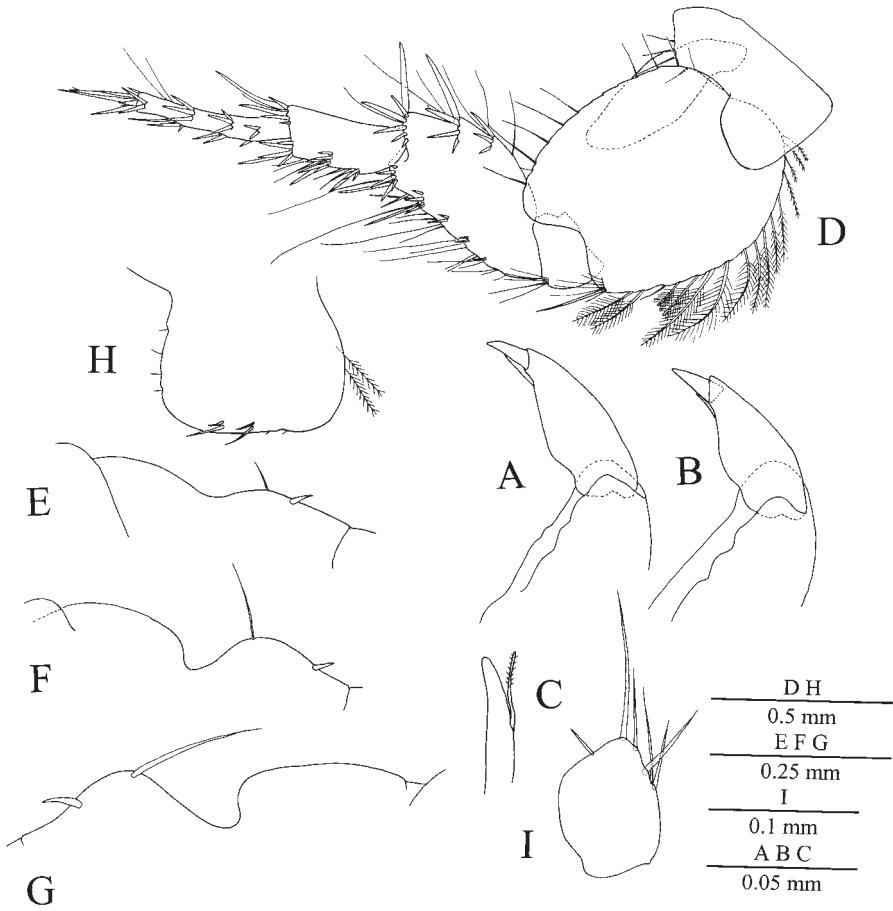


Fig. 59. *Bathyporeia pilosa* Lindström, 1855. A-D, H, females, The Netherlands, Westerschelde, RMNH A 4961; E, idem, RMNH A 4966; F, male, Eems estuary, ZMA 100 701; G, male, The Netherlands, Westerschelde, RMNH 4962; I, male, Normandy, Saint-Germain-sur-Ay, TMU 9391. A, dactylus of left P3; B, dactylus of left P4; C, tip of carpal fang of left P4; D, right P6; E, F, G, urosomite 1 (unusual ornamentation); H, right Ep3; I, endopod of right U3.

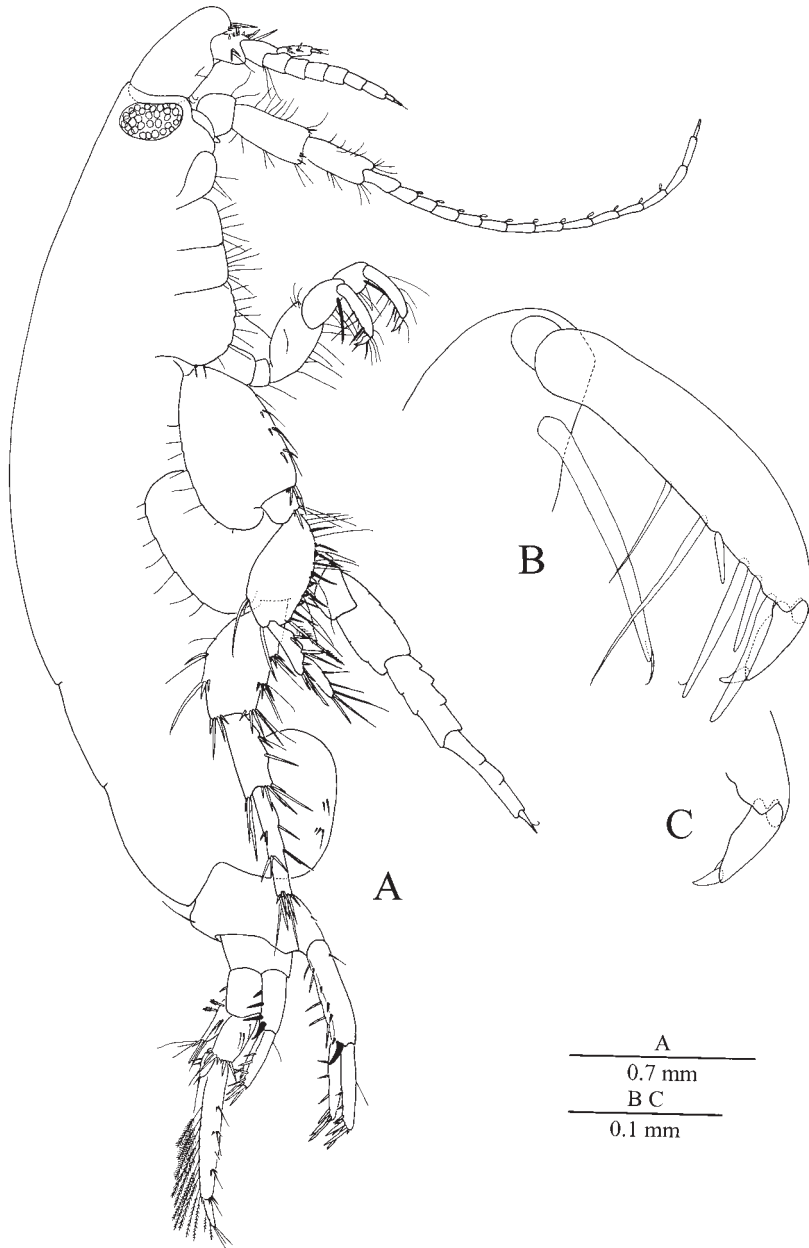


Fig. 60. *Bathyporeia sarsi* Watkin, 1938, adult male, lectotype, Norway, Finnmark, Sørvær, ZMO F 1978. A, specimen in lateral view; B, anterior part of right P4 (mesial spines/setae of propodus not shown); C, dactylus of right P4.

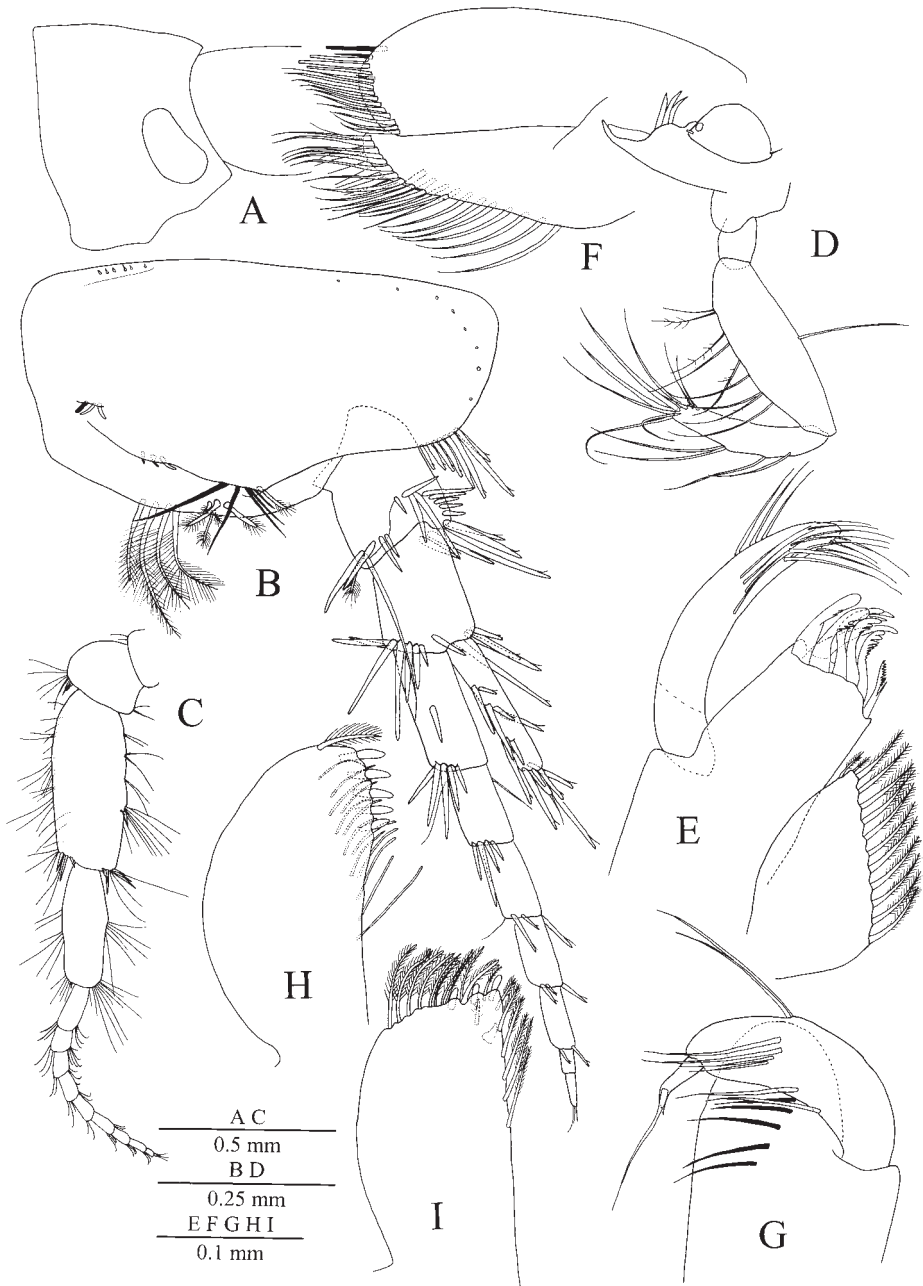


Fig. 61. *Bathyporeia sarsi* Watkin, 1938, adult female, Belgium, between Blankenberge and Zeebrugge, RMNH A 4974. A, anterior part of head; B, right A1; C, left A2; D, left Md; E, Mx1; F, left Mx2; G, right Mxp palp; H, left Mxp outer plate; I, left Mxp inner plate.

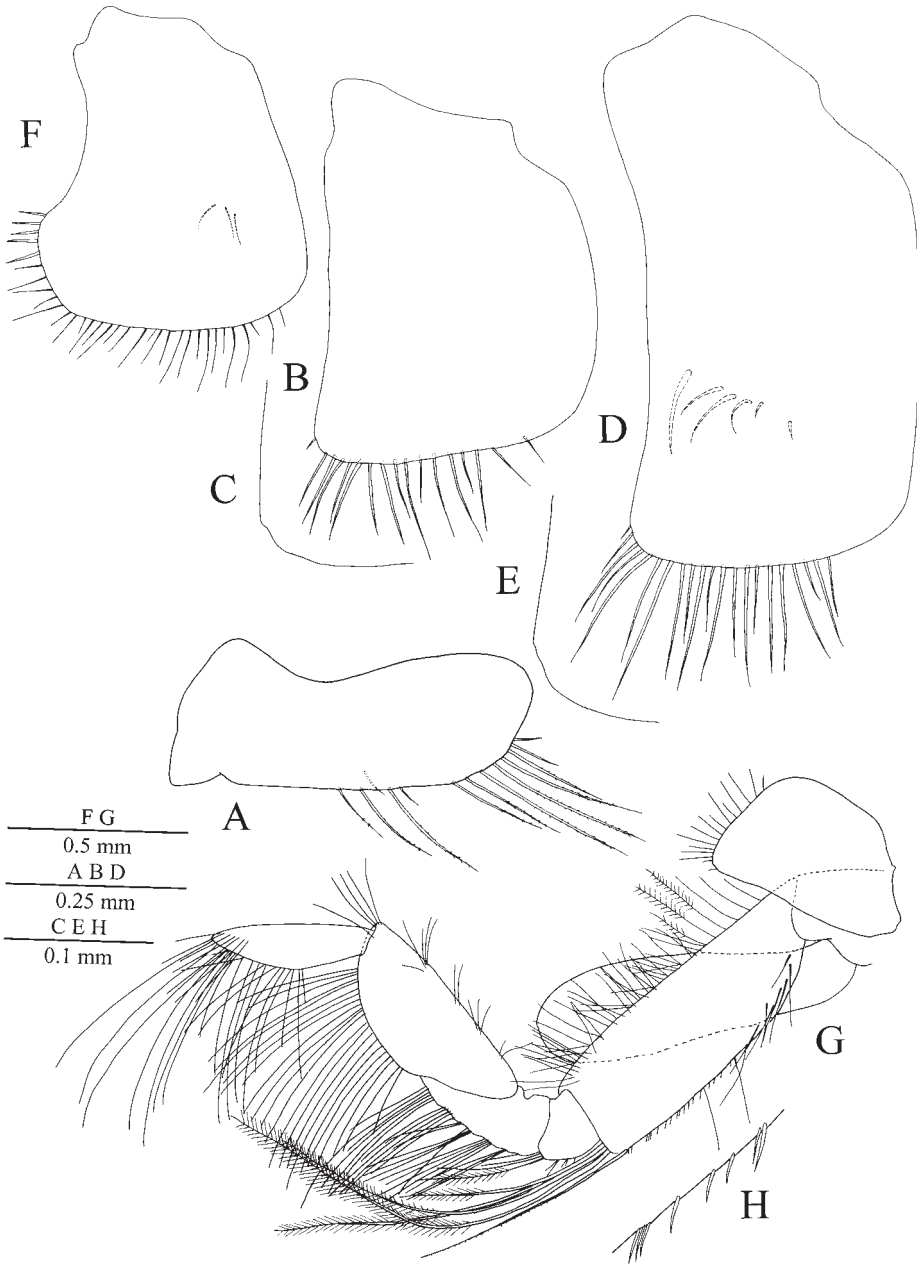


Fig. 62. *Bathyporeia sarsi* Watkin, 1938, adult female, Belgium, between Blankenberge and Zeebrugge, RMNH A 4974. A, right coxa 1; B, right coxa 2; C, posteroventral angle of right coxa 2; D, right coxa 3; E, posteroventral angle of right coxa 3; F, right coxa 4; G, left P2; H, posterior margin of left P2 basis.

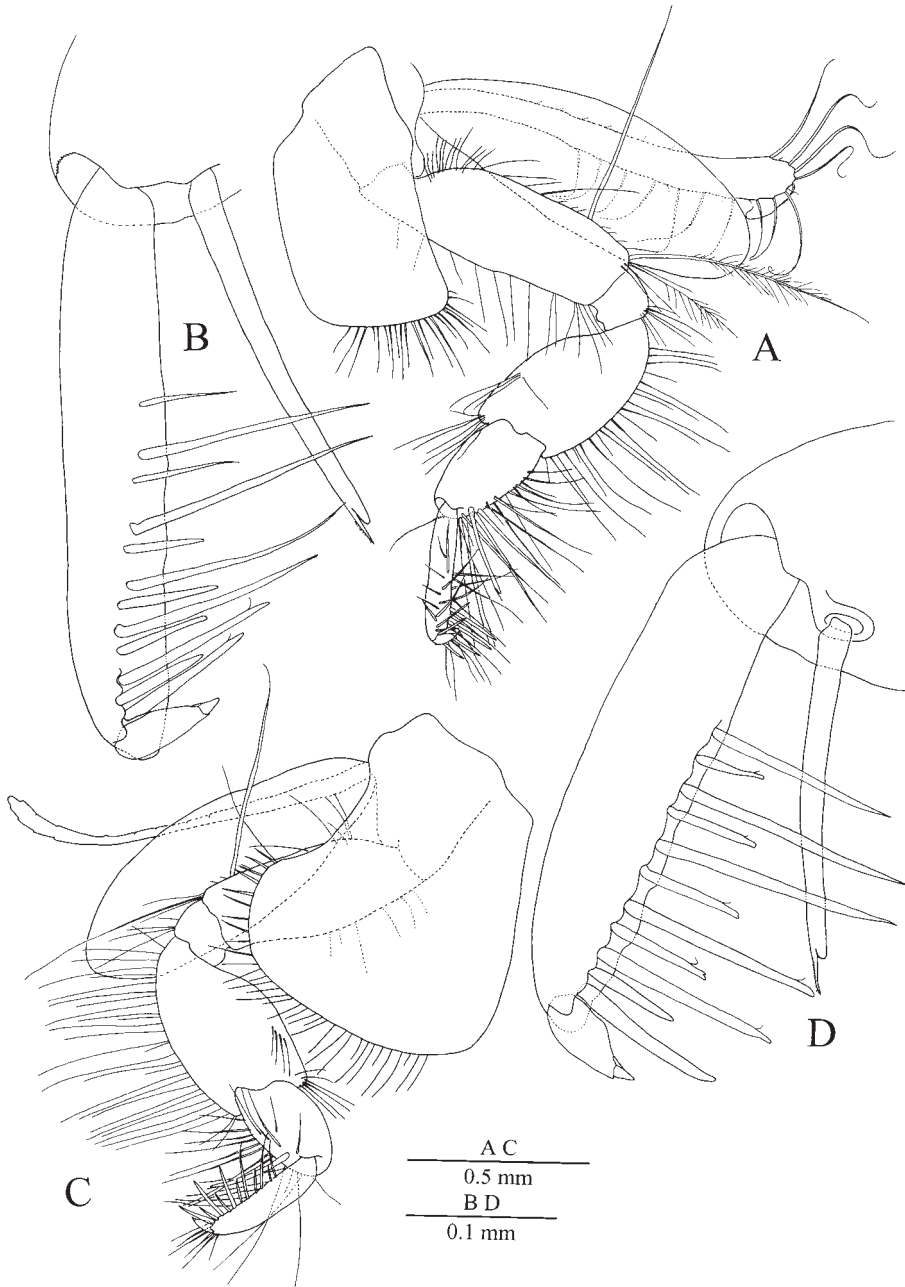


Fig. 63. *Bathyporeia sarsi* Watkin, 1938, adult female, Belgium, between Blankenberge and Zeebrugge, RMNH A 4974. A, left P3; B, anterior part of left P3 (mesial spines/setae of propodus not shown); C, right P4; D, anterior part of left P4 (mesial spines/setae of propodus not shown).

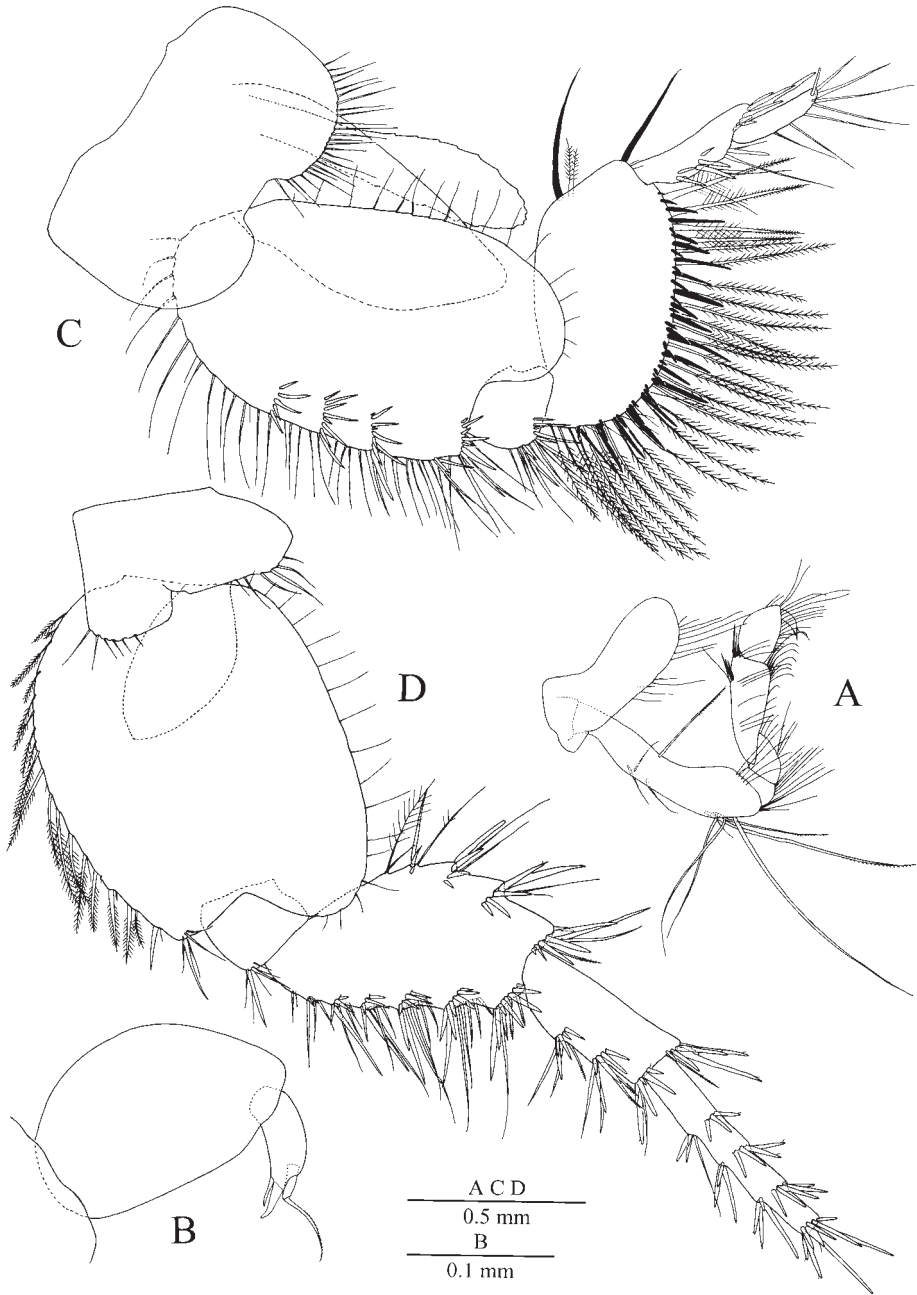


Fig. 64. *Bathyporeia sarsi* Watkin, 1938, adult female, Belgium, between Blankenberge and Zeebrugge, RMNH A 4974. A, right P1; B, anterior part of right P1; C, left P5; D, left P6.

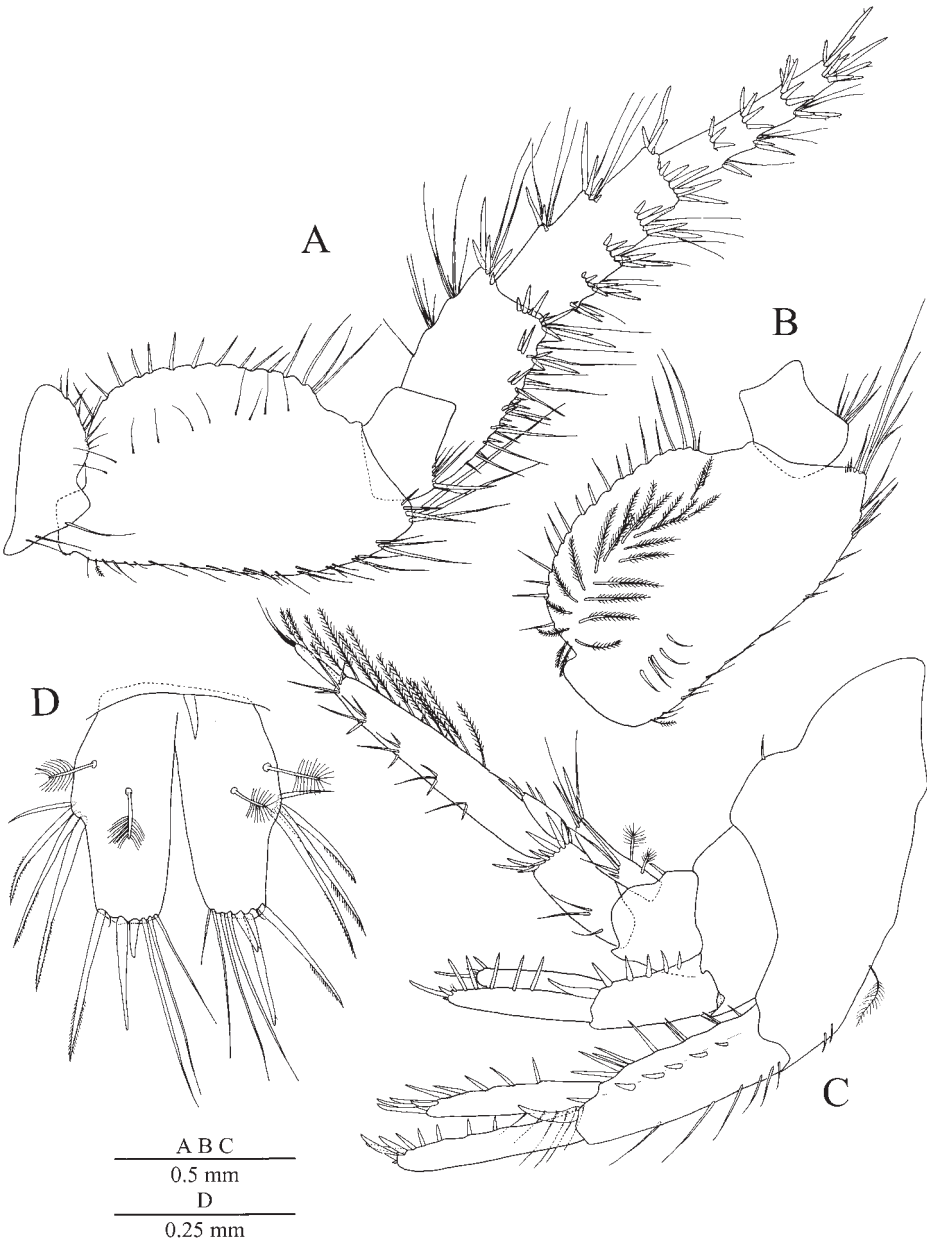


Fig. 65. *Bathyporeia sarsi* Watkin, 1938, adult female, Belgium, between Blankenberge and Zeebrugge, RMNH A 4974. A, left P7; B, basis and ischium of left P7 (mesial side); C, posterior part of the body; D, telson.

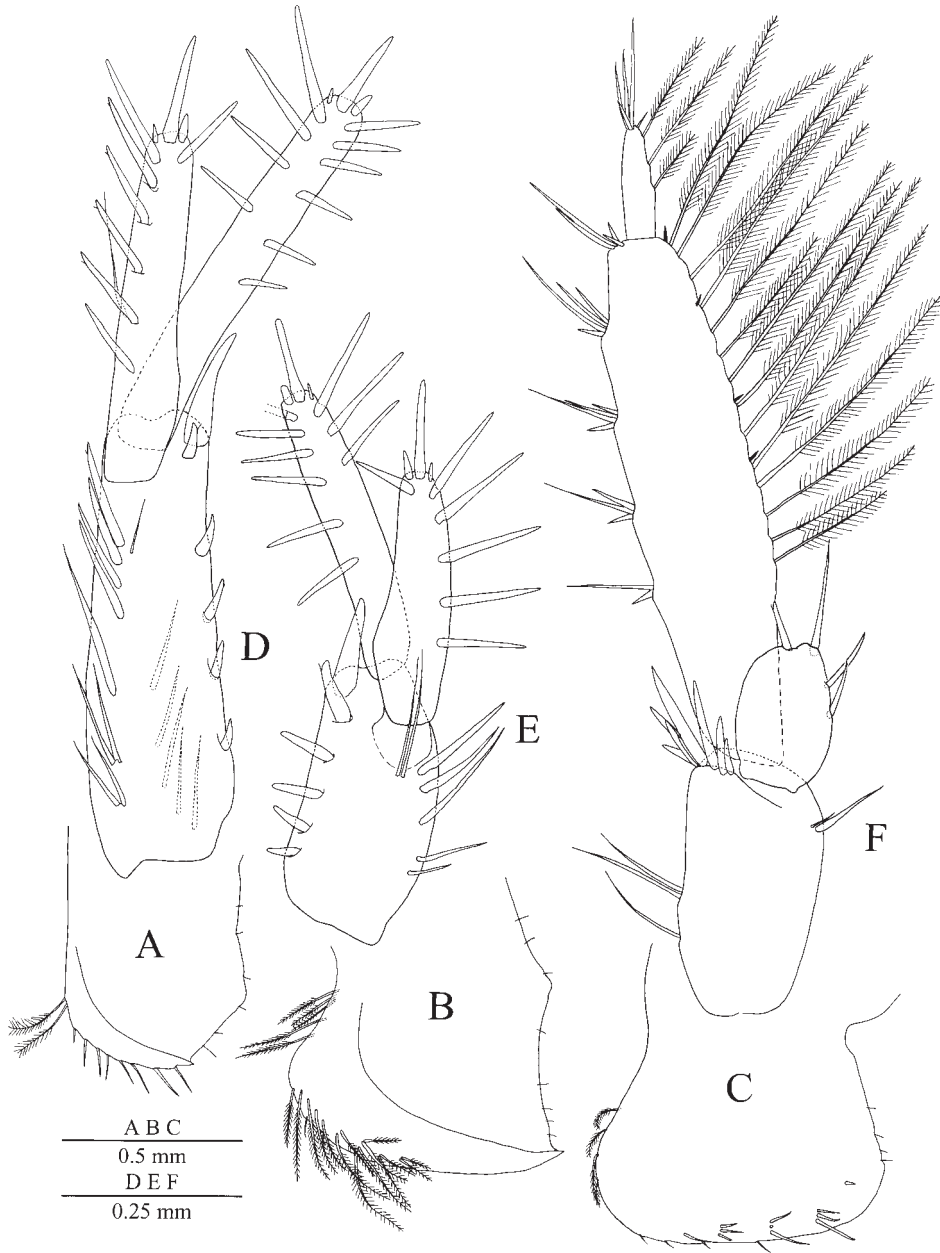


Fig. 66. *Bathyporeia sarsi* Watkin, 1938, adult female, Belgium, between Blankenberge and Zeebrugge, RMNH A 4974. A, left Ep1; B, left Ep2; C, left Ep3; D, left U1; E, right U2; F, right U3.

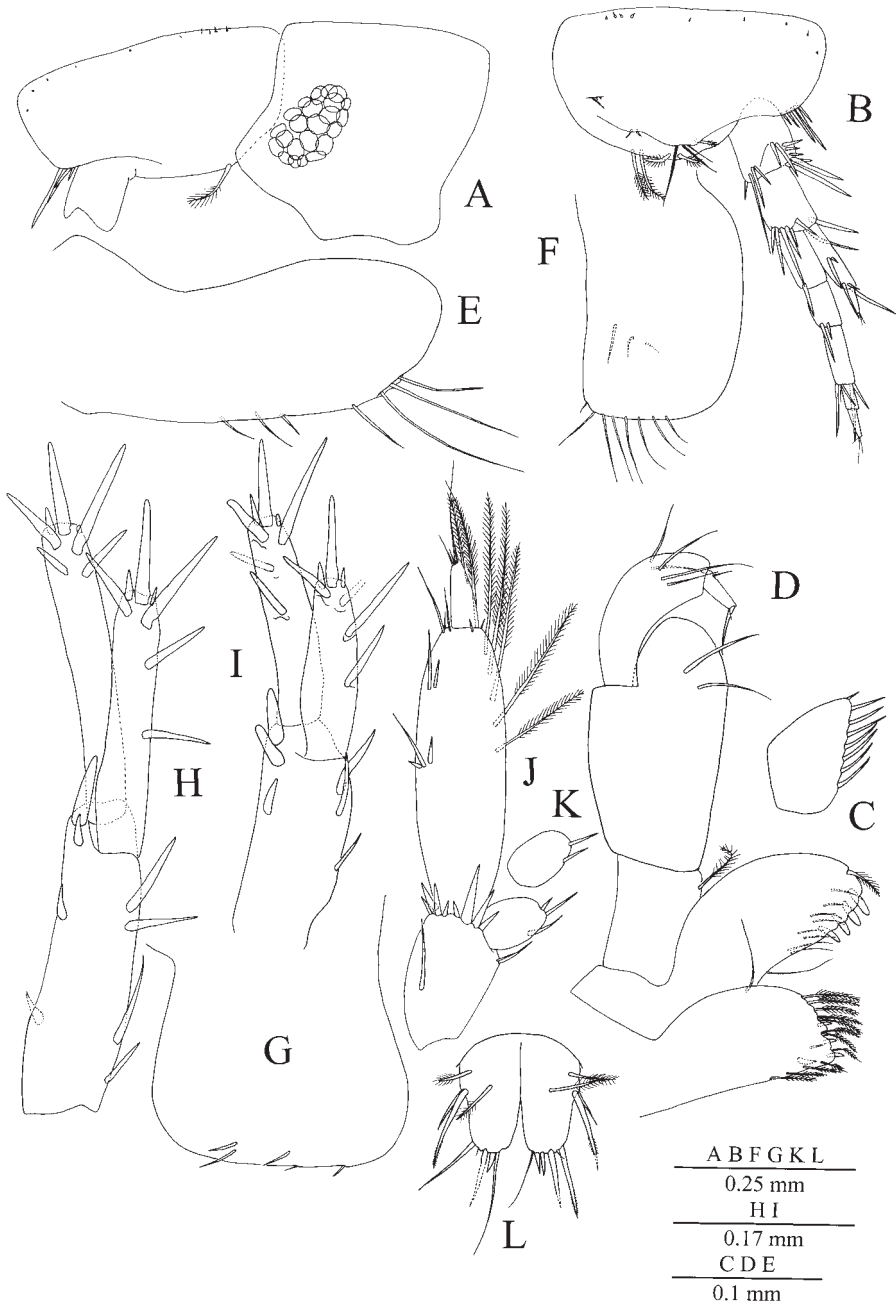


Fig. 67. *Bathyporeia sarsi* Watkin, 1938, young females, Jersey, TMU 4924 (A, E, F, G, H, I, specimen 2; J, L, specimen 3; B, C, D, K, specimen 4). A, head and first article of antennular peduncle; B, right A1; C, Mx1 inner plate; D, left Mxp; E, right coxa 1; F, right coxa 3; G, right Ep3; H, right U1; I, right U2; J, left U3; K, endopod of left U3; L, telson.

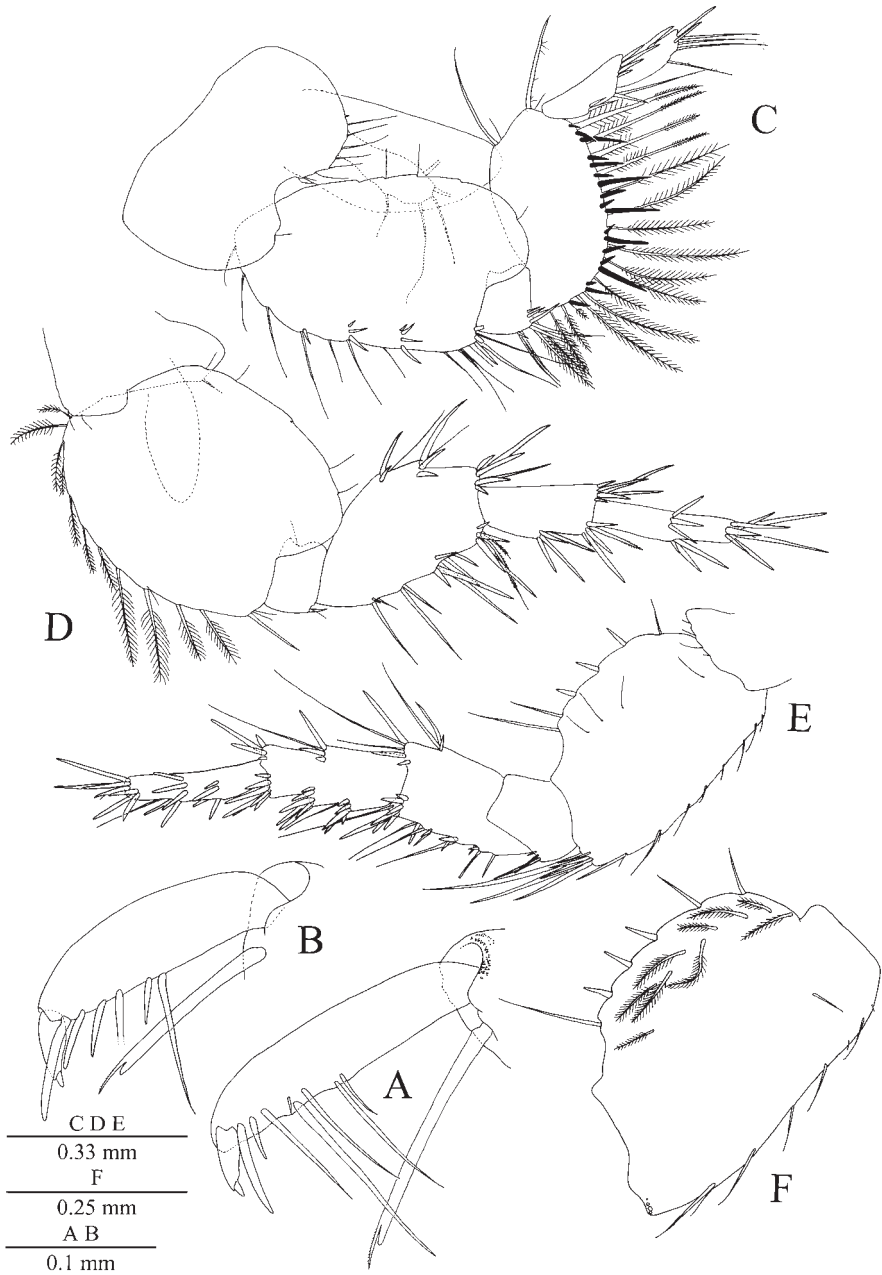


Fig. 68. *Bathyporeia sarsi* Watkin, 1938, young female, Jersey, TMU 4924 (all figures after specimen 2). A, anterior part of left P3 (mesial spines/setae of propodus not shown); B, anterior part of left P4 (mesial spines/setae of propodus not shown); C, left P5; D, left P6; E, right P7; F, left basis of P7 (mesial view).

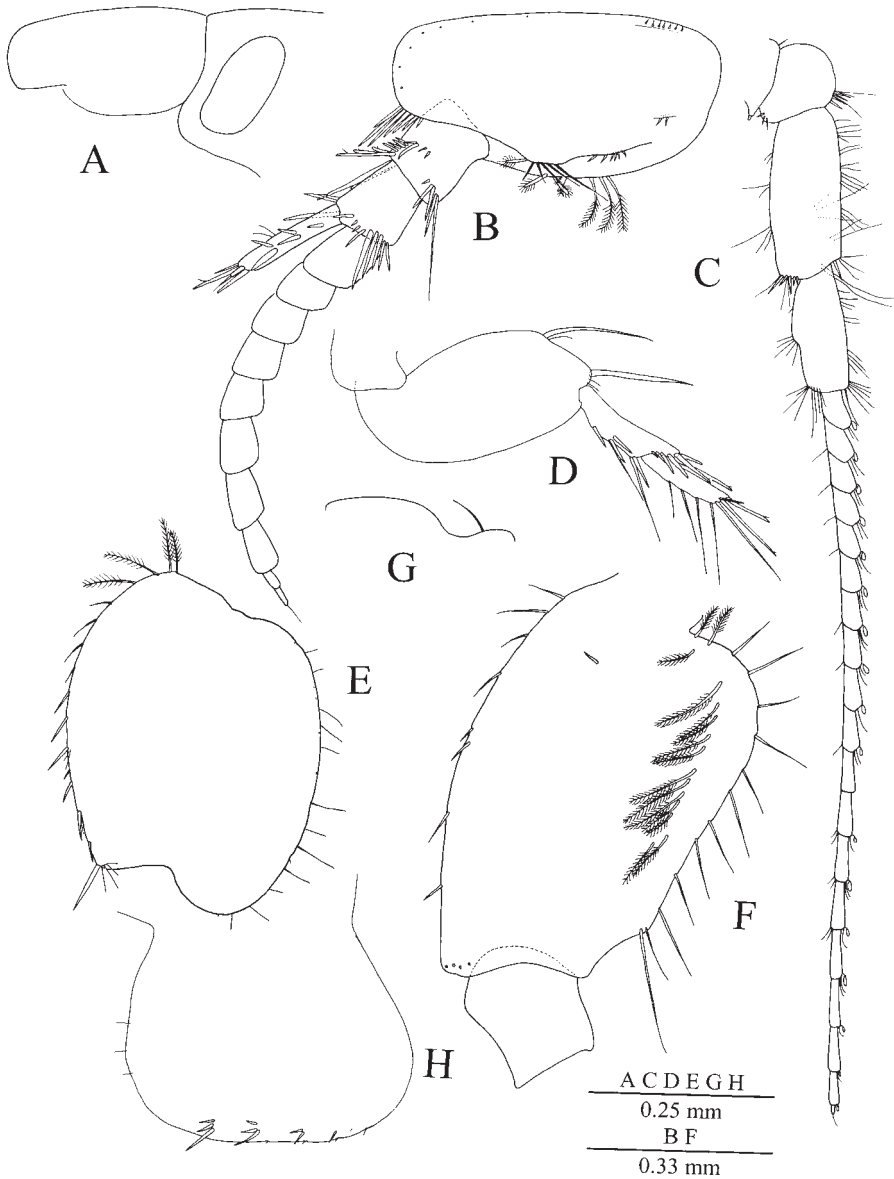


Fig. 69. *Bathyporeia sarsi* Watkin, 1938, adult male, Belgium between Blankenberge and Zeebrugge, RMNH A 4974. A, anterior part of head and first article of antennular peduncle; B, left A1; C, right A2; D, tip of left P5 (meral ventral spines/setae not shown); E, basis of left P6; F, basis and ischium of right P7 (mesial side); G, Ur1; H, right Ep3.

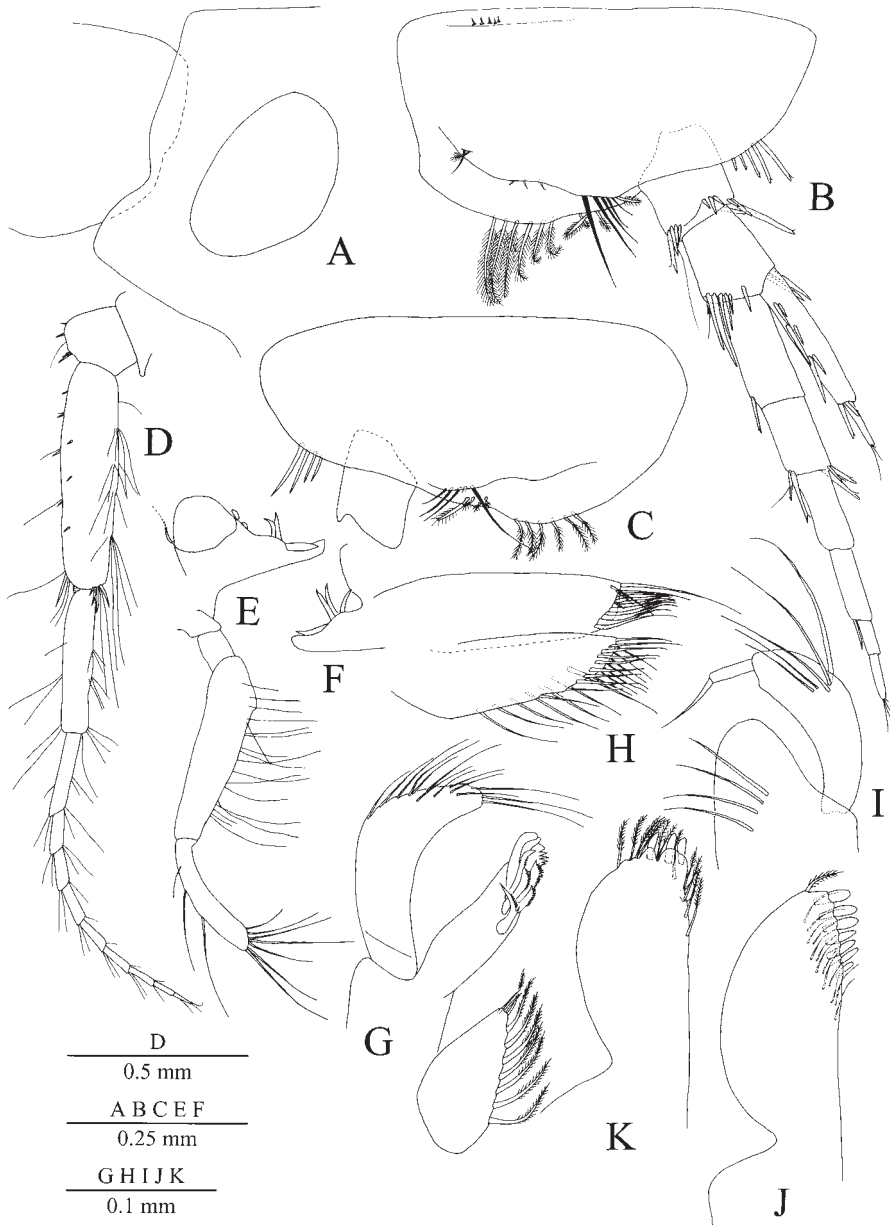


Fig. 70. *Bathyporeia tenuipes* Meinert, 1877, females. A, D-K, Jersey, Gorey, TMU 9427; B, Galway Bay, GB48, TMU 12 169; C, Hirsholmenes Fyrtaarn, st. 226, TMU 9428. A, anterior part of head; B, right A1; C, left A1 (tiniest setae rubbed off); D, left A2; E, right Md; F, left Md (palp not shown); G, left Mx1; H, Mx2; I, right Mxp palp; J, left Mxp outer plate; K, left Mxp inner plate.

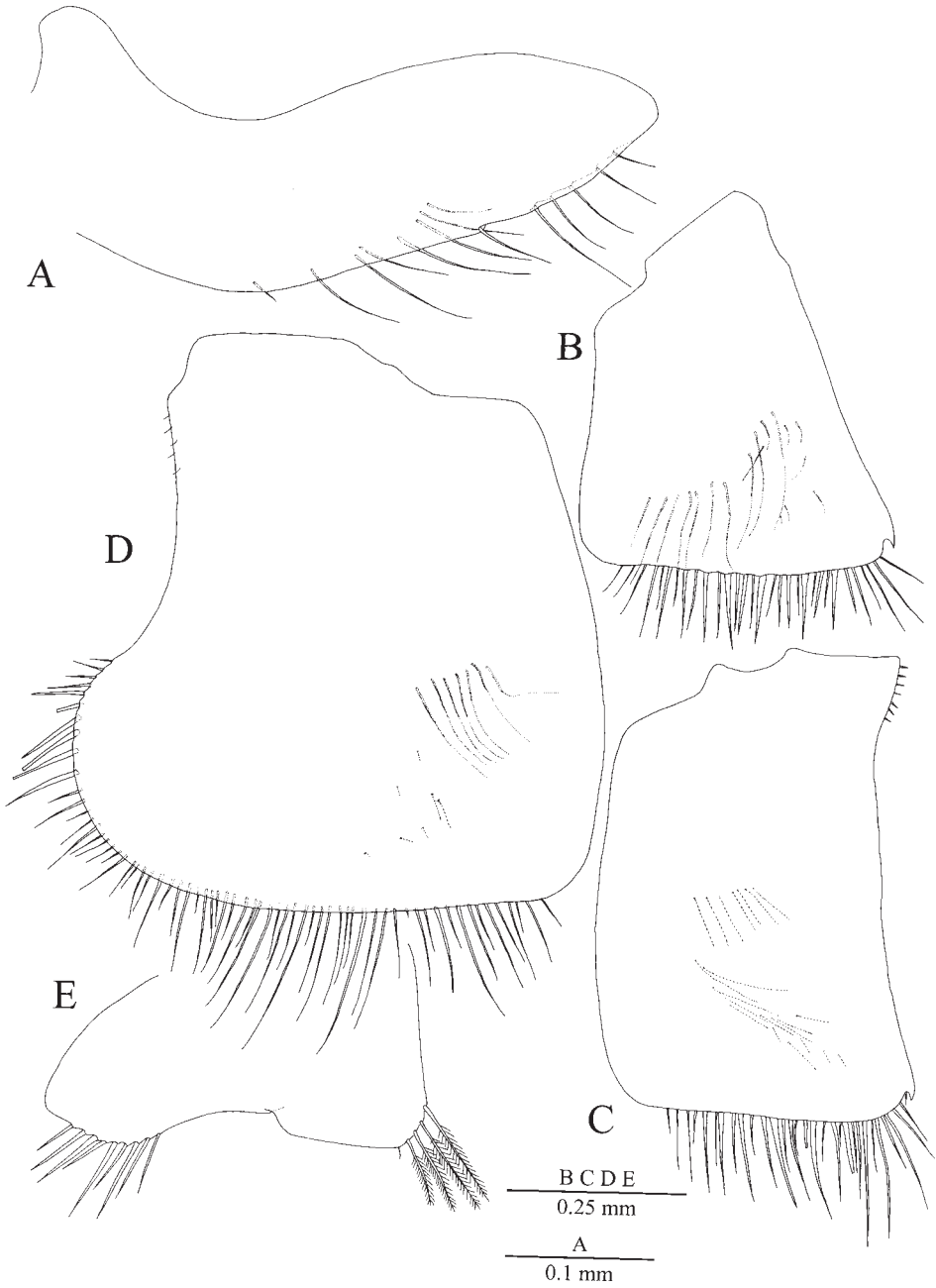


Fig. 71. *Bathyporeia tenuipes* Meinert, 1877, female, Jersey, Gorey. TMU 9427. A, right coxa 1; B, left coxa 2; C, left coxa 3; D, right coxa 4; E, right coxa 6.

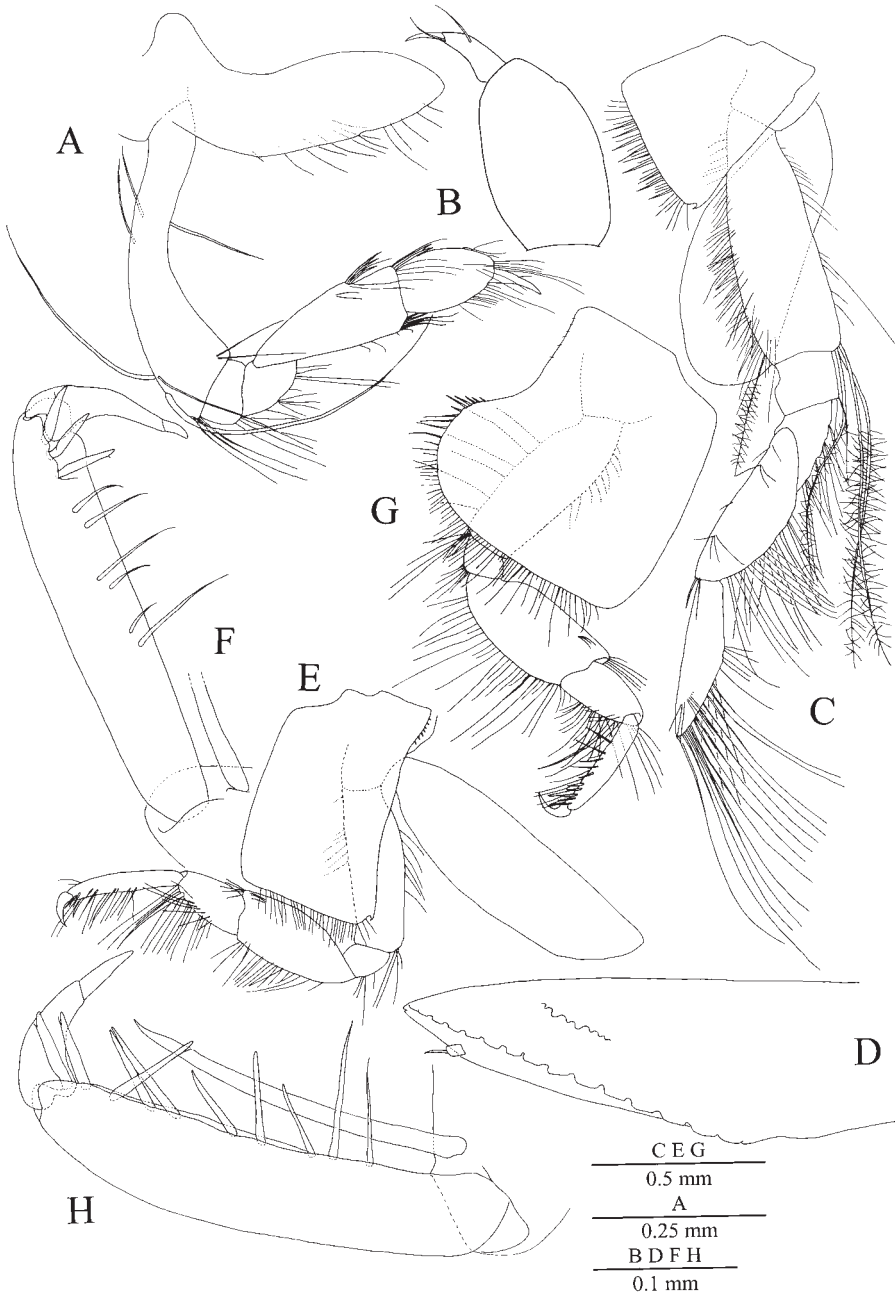


Fig. 72. *Bathyporeia tenuipes* Meinert, 1877, females. A, C, D, E, G, Jersey, Gorey, TMU 9427; B, Galway Bay GB14, Dublin Museum; F, H, Galway Bay, GB48, TMU 12 169. A, right P1; B, anterior part of right P1; C, left P2; D, anterior part of left P2, showing vestigial dactylus; E, left P3; F, anterior part of right P3 (mesial spines/setae of propodus not shown) [unguis usually longer than in illustrated specimen]; G, right P4; H, anterior part of right P4 (mesial spines/setae of propodus not shown).

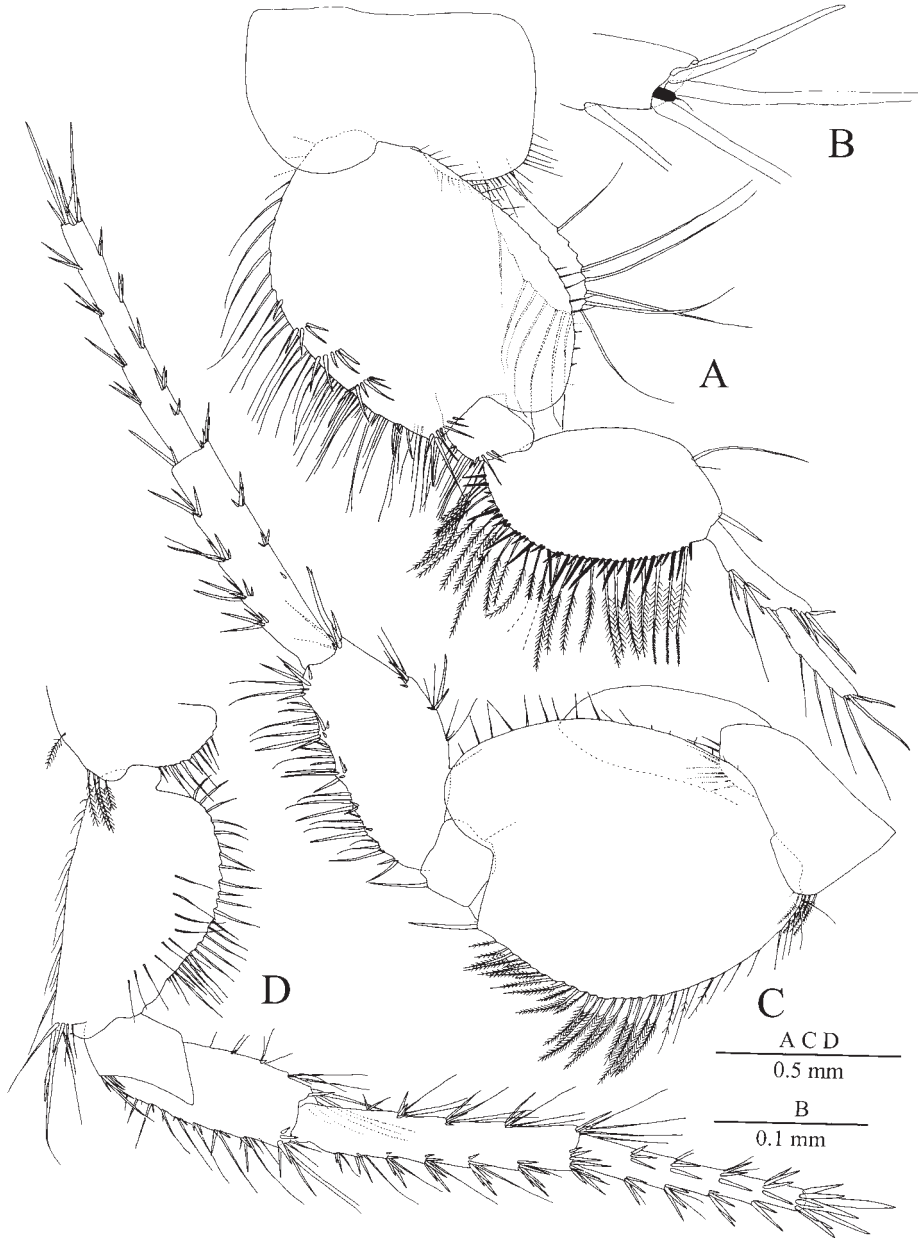


Fig. 73. *Bathyporeia tenuipes* Meinert, 1877, female, Jersey, Gorey, TMU 9427. A, left P5; B, tip of left P5, showing vestigial dactylus (in black); C, right P6; D, left P7.

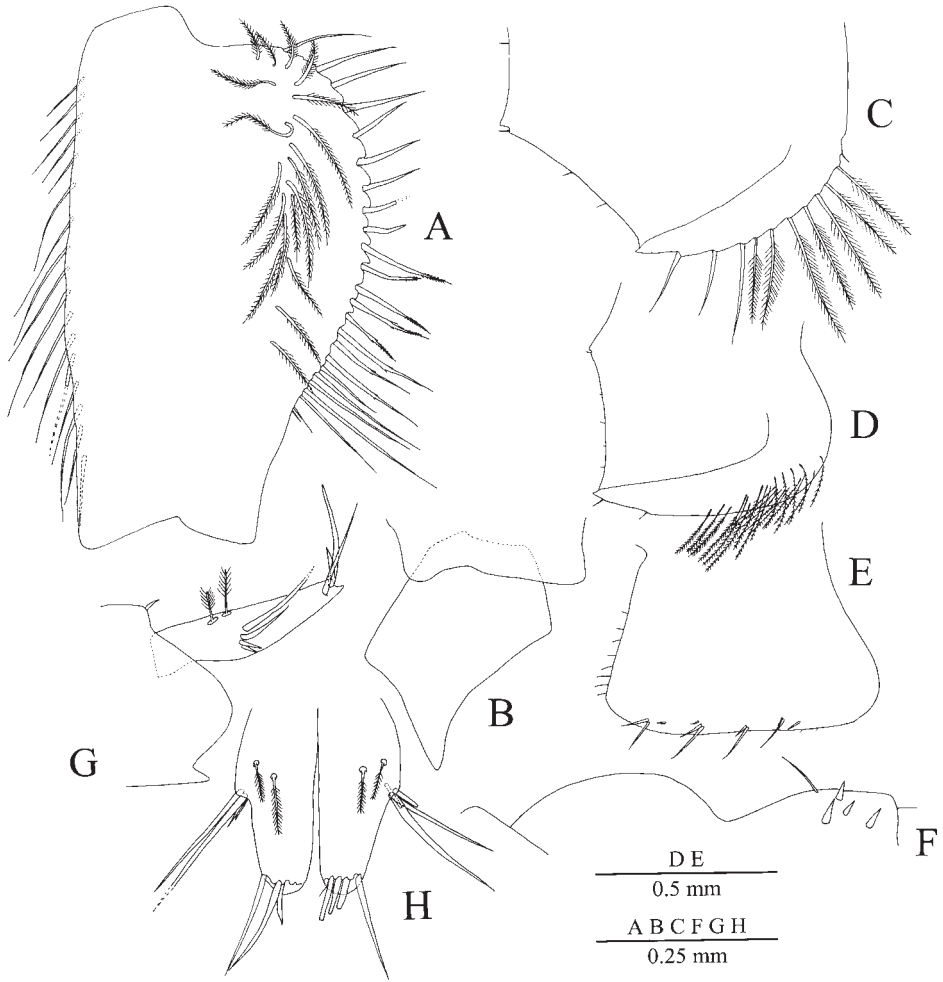


Fig. 74. *Bathyporeia tenuipes* Meinert, 1877, female, Jersey, Gorey, TMU 9427. A, right basis (mesial side); B, left P7 ischium (mesial side); C, right Ep1; D, right Ep2; E, right Ep3; F, Ur1; G, telson in lateral view; H, telson in dorsal view.

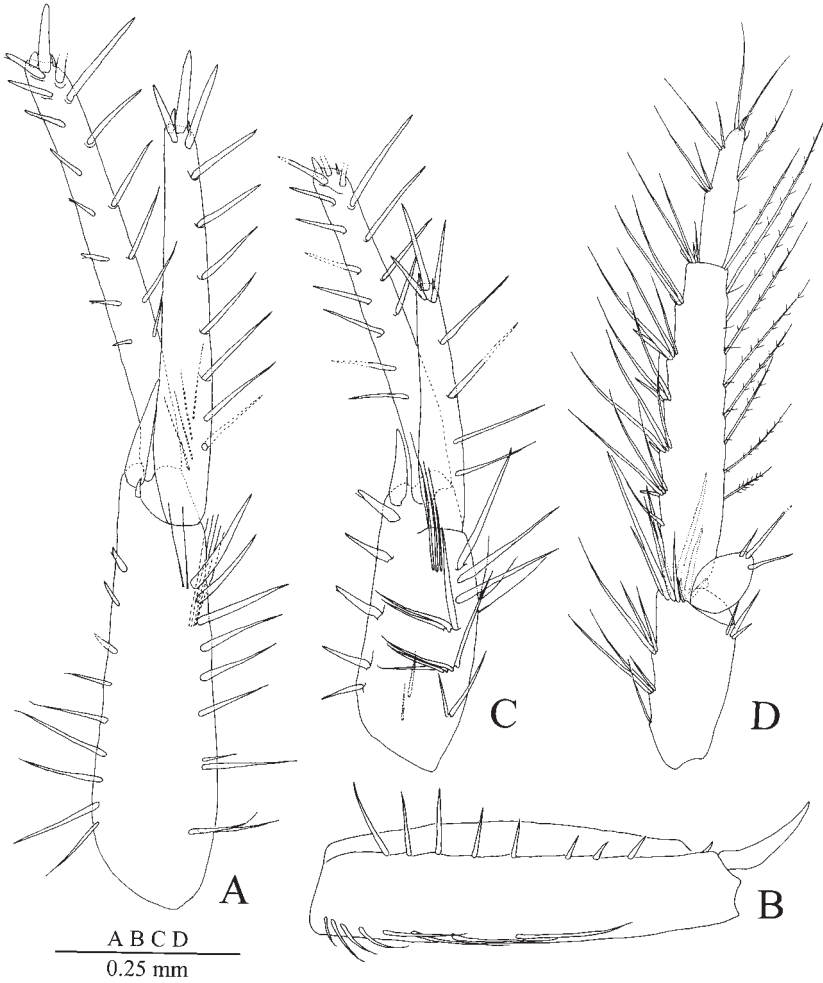


Fig. 75. *Bathyporeia tenuipes* Meinert, 1877, female, Jersey, Gorey, TMU 9427. A, right U1 (dorsal view); B, left U1 peduncle in lateral outer view (mesial spines/setae not shown); C, U2 (dorsal view); D, U3 (dorsal view).

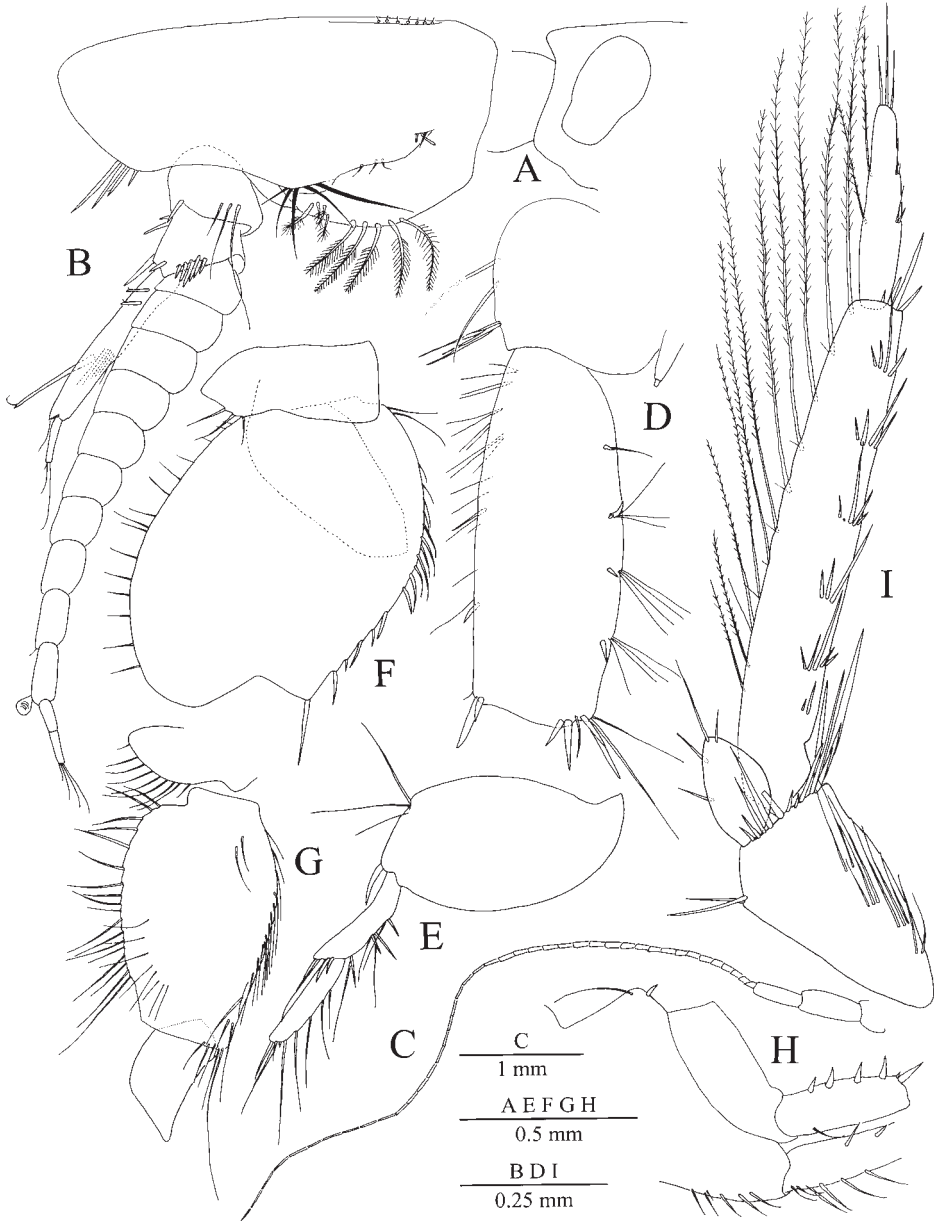


Fig. 76. *Bathyporeia tenuipes* Meinert, 1877, male. A, D, H, Hirsholmenes Fyrtaarn, st. 226, TMU 9428; B, C, E, F, G, I, Galway bay, GB4, TMU 12 167. A, anterior part of head; B, left A1; C, right A2 (spines/setae not shown); D, left A1 proximal part; E, right P5 distal part (meral ventral spines/setae not shown); F, right P6 proximal part; G, right P7, proximal part; H, Ur1-2 with proximal part of U1-2; I, left U3 (dorsal view).

8. Systematic index
(Genera in bold)

Abra	51	<i>paradoxa</i> , <i>Sphaeronella</i>	38, 51, 60, 67, 73
<i>alba</i> , <i>Abra</i>	51, 78	<i>parkeri</i> , <i>Bathyporeia</i>	9
Aponuphis	38	<i>pelagica</i> , <i>Bathyporeia</i>	56
<i>arenarius</i> , <i>Pontocrates</i>	34	<i>pelagica</i> , <i>Thersites</i>	4, 56
Bathyporeia	19	<i>pelágica</i> , <i>Bathyporeia</i>	32
<i>bilineata</i> , <i>Aponuphis</i>	38, 51, 78	<i>phaioophthalma</i> , <i>Bathyporeia</i>	9
<i>bilineata</i> , <i>Hyalinoecia</i>	38, 51, 78	<i>pseudopelagica</i> , <i>Bathyporeia</i>	9
Corbula	38	<i>pilosa</i> , <i>Bathyporeia</i>	4, 61
Echinocardium	38	<i>pilósa</i> , <i>Bathyporeia</i>	61
<i>elegans</i> , <i>Bathyporeia</i>	8, 9, 32	<i>pontica</i> , <i>Bathyporeia</i>	46
<i>evanescens</i> , <i>Fucus</i>	74	Pontocrates	34
Fucus	74	<i>quoddyensis</i> , <i>Bathyporeia</i>	8, 9
<i>gibba</i> , <i>Corbula</i>	51, 78	<i>robertsoni</i> , <i>Bathyporeia</i>	61, 69
<i>gracilis</i> , <i>Bathyporeia</i>	42, 75	<i>Robertsoni</i> , <i>Bathyporeia</i>	68
<i>Guilliamsonia</i> , <i>Thersites</i>	46	<i>Robertsonii</i> , <i>Bathyporeia</i>	68
<i>Guilliamsonia</i> , <i>Bathyporeia</i>	47	<i>Robertsónii</i> , <i>Bathyporeia</i>	69
<i>Guilliamsonia</i> , <i>Bathyporeia</i>	46	<i>sardoa</i> , <i>Bathyporeia</i>	9
<i>guilliamsoniana</i> , <i>Bathyporeia</i>	46	<i>sarsi</i> , <i>Bathyporeia</i>	8, 69
<i>guilliamsoniána</i> , <i>Bathyporeia</i>	47	<i>serratus</i> , <i>Fucus</i>	38
<i>Guilliamsoniana</i> , <i>Bathyporeia</i>	46	<i>sophiae</i> , <i>Bathyporeia</i>	9
<i>Guilliamsoniana</i> , <i>Thersites</i>	46	Sphaeronella	38, 51, 60, 67, 73
<i>Guilliamsonii</i> , <i>Thersites</i>	46	<i>sunniavae</i> , <i>Bathyporeia</i>	9
Leiochone	51	Synapta	51
<i>leucophthalma</i> , <i>Bathyporeia</i>	9	<i>tenuipes</i> , <i>Bathyporeia</i>	75
<i>lindstromi</i> , <i>Bathyporeia</i>	7, 9	<i>Tenuipes</i> , <i>Bathyporeia</i>	75
<i>megalops</i> , <i>Bathyporeia</i>	9	<i>tenuis</i> , <i>Bathyporeia</i>	75
<i>nana</i> , <i>Bathyporeia</i>	8, 9, 52	Thersites	4, 19
<i>norvegica</i> , <i>Bathyporeia</i>	6, 7, 46, 47, 51, 52		