

The nomenclature and diagnostic characters of four north-eastern Atlantic species of the genus *Munida* Leach: *M. rugosa* (Fabricius), *M. tenuimana* G. O. Sars, *M. intermedia* A. Milne Edwards and Bouvier, and *M. sarsi* Huus (Crustacea, Decapoda, Galatheidae)

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(Accepted 16 May 1985)

Within the genus *Munida* the names *M. rugosa* (Fabricius) and *M. bamffia* (Pennant) are at the centre of a long-standing and complex nomenclatural confusion. An examination of the literature and of extensive collections has permitted the confusion to be resolved and indicates that four species are involved, with overlapping but distinct geographical and bathymetric ranges within the north-eastern Atlantic. Three of the species occur also in the Mediterranean and appear to be undergoing speciation, but the distinctions between the Atlantic and Mediterranean populations are not sufficiently distinct to warrant sub-specific recognition.

Introduction

The north-eastern Atlantic and Mediterranean representatives of the galatheid genus *Munida* have been the subject of much nomenclatural and taxonomic controversy and confusion, particularly with regard to the specific epithets *rugosa* Fabricius and *bamffia* Pennant and a variety of additional names proposed for the same or closely related taxa. Consequently, although the species concerned are by no means uncommon and have been reported many times, there is still considerable uncertainty about how many species are involved and which names should be applied to them.

Zariquiey Alvarez (1952) summarized the history of the problem and, after an examination of extensive material, largely clarified the situation. However, his historical resumé is rather incomplete and his taxonomic interpretation led him subsequently (Zariquiey Alvarez 1958 a, 1968) to nomenclatural conclusions which, in working through our own material, we found confusing and unacceptable.

We hope in this work to resolve the confusion and to demonstrate that the following four species, with overlapping but generally increasing depth distributions, are involved in the north-east Atlantic: *M. rugosa* (Fabricius, 1775), *M. intermedia* A. Milne Edwards and Bouvier, 1899, *M. sarsi* Huus, 1935 and *M. tenuimana* G. O. Sars, 1872.

History

In the following chronological treatment, only those references which have affected the nomenclature of the species involved have generally been included.

The first post-Linnean description of a *Munida* species is that of Fabricius (1775, p. 412), who introduced the specific epithet *rugosus* (under *Pagurus*) as follows.

‘11. P. thorace rugoso, antice ciliato, spinoso, rostro tridente, manibus filiformibus. Habitat in mari mediterraneo. Affinitas summa praecedentis, cujus forte varietas. Loco rostri dentes tres acutissimi, intermedio majori. Ad basin dentes duo elevati, acuti. Margo thoracis anticus spinosus.’

The preceding species was *Pagurus (Galathea) strigosus*, so that Fabricius’ description clearly identified *rugosus* as belonging to the genus for which Leach (1818) subsequently proposed the name *Munida*. However, the description is insufficiently detailed to identify the species with certainty, and the specimen or specimens on which it was based have not been located and are probably lost (see Zimsen 1964).

Two years later, Pennant (1777: p. 17) described a *Munida* species (under *Astacus*) taken near Banff (mis-spelt Bamff) on the north-east coast of Scotland, and gave it the specific name *Bamffius*. Pennant’s description contains even fewer details than that of Fabricius, but it is accompanied by a figure. However, neither the description nor the illustration definitely identify the species, and it is not clear whether Pennant had actually seen a specimen since he says that the engraving was based on a drawing provided by the Reverend Mr Cordiner who ‘communicated’ the species to him. There are two dried specimens of *Munida* in the Pennant collection which came to the British Museum (Natural History) in about 1912 and which have been tentatively labelled as possible types of *Astacus Bamffius*. However, Pennant’s description seems to be based on a single specimen which was considerably larger than either of the extant specimens, so that it is not possible to accept them as his types. He refers to the claws as being ‘six inches and a half long’, whereas the largest of the dry specimens has a total length, including the rostrum, of about 42 mm, while its claws are only about 130 mm, or a little over five inches, long.

Thus, neither of the specific names principally involved in the subsequent confusion can be attached with certainty to a particular species on the basis of the published descriptions alone. Nor, indeed, is it clear whether these descriptions refer to a single species or to two distinct forms. Since the identity of the species to which these names apply is crucial to the problem, it is fortunate that there is strong circumstantial evidence for a solution. Although neither Fabricius nor Pennant give depths of collection for the specimens on which their descriptions were based, it is inconceivable that at that time either of them could have obtained material from deeper than a few tens of metres. Since only one of the possible candidates occurs shallower than about 100 m both in the Mediterranean and in the North Sea, both Fabricius and Pennant must have been referring to this shallow-living species to which the name *rugosa* must therefore apply.

Fabricius was himself convinced that Pennant’s species was the same as his own, for whereas in 1781 and 1787 he referred only to his earlier description of *Pagurus rugosus*, in 1793 and 1798 he included *Bamffius* as a synonym within the genus *Galathea* which he had established in the earlier of these works.

Herbst (1782) had referred only to Pennant’s account under the name *Cancer bamfficus*, a misspelling which seems to have been the source of the later widespread use of the epithet *bamffica*, while Leach (1814) reported the species as *Galathea Bamfia*.

Otherwise, however, the priority of Fabricius' name was generally recognized throughout the first half of the nineteenth century, with Leach (1815 a, b), Risso (1816, 1827), Lamarck (1818) and H. Milne Edwards (1837) all referring to it as *Galathea* (or *Galatea*) *rugosa*, while Leach (1818) placed *rugosa* in his newly established genus *Munida* and was followed in this by Desmarest (1825).

Bell (1847) confirmed the validity of the genus *Munida* and gave an illustration and description of a single species which is clearly *rugosa*. He included the names of both Fabricius and Pennant in the synonymy, but referred only to Fabricius' 1798 work, apparently not appreciating the priority of the 1775 account. This failure to recognize Fabricius' priority resulted in several later authors incorrectly using Pennant's name although they considered *rugosus* and *bamffius* to be synonyms. In any case, Bell proposed a new name, *Rondeletii*, for *rugosa* and justified this action because 'The discovery of a second species ... has rendered this necessary, as the latter is far more rugous in every part than the present species' (Bell 1847, p. 21). Under the present code of nomenclature, Bell's provision of such a new name for *rugosa* is not justified and falls as a junior synonym of the name that it was intended to replace. The second species to which Bell refers was apparently *M. gregaria* (Fabricius) which Darwin had collected during the voyage of the *Beagle* but which Bell had not realized had already been described by Fabricius in 1793 (see Chancellor *et al.*, in the press).

G. O. Sars (1872) described a new species, *M. tenuimana*, from near Utne (Hardangerfjord) at a depth of 500 fathoms. Sars also listed *M. rugosa*, saying that whereas this species was commonly encountered in Hardangerfjord at depths between 80 and 150 fathoms, *M. tenuimana* was not found shallower than 300 fathoms.

In 1883 Sars recognized, for the first time, the existence of three closely related *Munida* species in the North Sea, but listed only two of these, *Rondeletii* and *tenuimana*. However, he provided illustrations of the anterior part of the carapace and the eyes of all three species (Sars, 1883 table 1, figs 4, 5, 6) and wrote that *Rondeletii* can be readily distinguished from *rugosa* by its small eyes, lacking eyelashes (Børstekrands), and the complete absence of the two dorsal spines on the fourth† abdominal somite. These distinctions do, indeed, separate the shallowest species from the deeper living forms, but Sars had thus used a junior synonym of *rugosa* for the shallowest form and had applied the name *rugosa* to a species which at that time was still without a valid name.

Despite Sars' acumen in recognizing the existence of three distinct species, which many subsequent authors failed to do, this paper seems to have been at the root of much of the confusion which followed. For it represents the first published suggestion that *rugosa* and *bamffia* (= *Rondeletii*) might refer to distinct species, a mistake which was perpetuated by Ortmann (1892) and several later authors.

In their early work on *Munida*, A. Milne Edwards and Bouvier (1894 a) failed to distinguish between the *rugosa* group of species, reporting material from depths ranging from 20 to 1360 m under the name *bamffia*, while in their account of the *Hirondelle* collections made between 1886 and 1888 (A. Milne Edwards and Bouvier 1894 b) they specifically synonymized *rugosa*, *tenuimana* and *Rondeletii*.

Caullery (1896) similarly failed to distinguish separate species in the material collected from the *Caudan* between 180 and 1410 m in the Bay of Biscay, though he did notice differences, particularly in the spination of the posterior border of the carapace and of the abdominal tergites.

† In this paper, and in his 1872 description of *tenuimana*, Sars numbers the abdominal somites wrongly, calling this one the third. His intentions are, however, clear.

In their main works on *Munida*, A. Milne Edwards and Bouvier (1899, 1900) produced almost total confusion. First, they concluded that *Munida bamffica* (following Herbst's original erroneous spelling, see above) represented a single variable species within which they recognized five varieties or forms to which they applied the names *bamffica* (or 'forme typique') *tenuimana*, *rugosa*, *intermedia* and *gracilis*, the latter, they thought, perhaps being identical to *M. gracilis* Henderson, 1885, described from *Challenger* material collected in New Zealand waters (see Henderson 1888). An extensive account of the 'typical' form was provided, but the other varieties were distinguished only in a key (1899, p. 80). An examination of their material in Paris reveals that, quite apart from the nomenclatural error in separating the names *bamffica* and *rugosa*, much of the confusion resulted from their misconception of Sars' *tenuimana*.

Shortly after the early cruises of the *Travailleur* to the Bay of Biscay and the Mediterranean, A. Milne Edwards (1881 a, b, 1882 a, b) had published a series of more or less popular articles in which all of the *Munida* material collected was simply referred to as *tenuimana*. In a further paper (A. Milne Edwards 1883), an illustration (plate 11) was provided of a form for which A. Milne Edwards and Bouvier later (1894 a) introduced the name *perarmata* in their general review of the galatheids, without realizing the close similarity between this form and Sars' *tenuimana*.

When these authors subsequently undertook a detailed study of the decapods collected during the cruises of the *Travailleur*, *Talisman*, *Hirondelle* and *Princesse Alice*, they treated *tenuimana* as a variety of their *bamffica*, as noted above, and quite distinct from *perarmata*. Consequently, in 1899 they included A. Milne Edwards' early references to *tenuimana* within the synonymy of *bamffica*, but failed to note that they had used part of this 'tenuimana' material to establish *perarmata*. Similarly, in 1900 they listed the *Travailleur* catches of what they considered to be *perarmata*, but failed to refer to Milne Edwards' early publications and included typical Atlantic specimens of true *tenuimana* in the list of material examined. With this additional complication, the names used by A. Milne Edwards and Bouvier (1899, 1900) correspond to our interpretation approximately as follows: the 'typical' form (*bamffica*) = *rugosa*; '*rugosa*' = *sarsi*; '*tenuimana*' and '*gracilis*' = *intermedia*; '*perarmata*' = *tenuimana*.

Thus, the distinctions in A. Milne Edwards and Bouvier's (1899) key, based mainly on the presence or absence of spines on the fourth abdominal tergite and on various parts of the carapace, are largely invalid. However, in their first group of varieties (*bamffica*, *intermedia* and *gracilis*), distinguished from the second group (their *tenuimana* and *rugosa*) by the absence of spines on the fourth abdominal somite, Milne Edwards and Bouvier were certainly dealing with two species, one of which was at that time without a proper name. Within this group, '*bamffica*' was inadequately distinguished from *intermedia* and *gracilis* by the presence of one or two pairs of submarginal spines on the posterior branchial areas of the carapace. However, although not explicitly stated, the key and the accompanying text also implies that the eyes in *intermedia* and *gracilis* are larger and have longer corneal setae. This combination of an unarmed fourth abdominal somite, large eyes and long corneal setae would have generally separated the un-named form from the remaining species in the complex. Consequently, the name *intermedia* for this species must be considered as valid. In the original publication of the name *intermedia* (A. Milne Edwards and Bouvier 1899) the text contains no mention of any material attributed to this variety. However, plate IV, fig. 13 shows a specimen from *Travailleur* station 83 (south of Madeira, 400 m) which is labelled *intermedia*. Fig. 14 on the same plate is labelled 'var. *intermedia* . . . passant à la

var. *rugosa* (Travailleur, 1882, 512 m)', but this specimen was regarded as var. *rugosa* by A. Milne Edwards and Bouvier (1900) and, in fact, belongs to *sarsi*.

Although A. Milne Edwards and Bouvier (1899) did not provide a list of specimens examined, they had certainly used the material collected up to that time during the cruises of the Prince of Monaco and those of the *Travailleur* and *Talisman* expeditions. This material would have included the male specimen from *Travailleur* station 7 referred to as 'assez bon type de la var. *intermedia*'. This specimen (Paris Museum no. Ga 935) is in good condition but, while it undoubtedly belongs to *intermedia*, it has well-developed spines on the 4th abdominal tergite and therefore does not correspond to the original diagnosis. Consequently, the station 83 specimen (a small female, Paris Museum no. Ga 938) is the only representative of *intermedia* clearly identified as such in the original publication and is here designated as the lectotype of the species, although it is in rather poor condition.

Appellöf (1906) examined material only from the North Sea and therefore did not see *M. intermedia*. However, he clearly distinguished between *bamffica* Pennant (= *rugosa*) *rugosa* sensu Sars (= *sarsi*) and *tenuimana* Sars and provided good illustrations of the first two abdominal somites in the latter two species. He also pointed out that the species have quite different depth distributions, *rugosa* being found only at shallow depths, *sarsi* at 100–300 m and *tenuimana* at 350–400 m.

Hansen (1908) did not see Appellöf's paper until after his own account had been written (see his footnote, p. 33). He agreed with Appellöf in recognizing the validity of *tenuimana*, but specifically synonymized Sars' *rugosa* with *bamffia* (as *bamffica*). He pointed out, for the first time, the major differences in the ornamentation of the sternal plastron between *tenuimana* and what he took to be *bamffia*. However, his illustration of the thoracic sternum in this species (op. cit. plate II, fig. 3 a) is actually *M. sarsi* and, in view of the depths from which his samples came, it is probable that most of his material belonged to this species.

Kemp (1910) recorded as *M. bamffica* seven specimens collected by *HMS Huxley* from the neighbourhood of the Shamrock Canyon in 1906, noting that the 'scaly appearance of the thoracic sternum' clearly distinguished them from *M. tenuimana*. However, from the depth of collection (439–750 m) these specimens were almost certainly *M. sarsi*.

Selbie (1914) agreed with Hansen's interpretation and recognized only *tenuimana* and *bamffica* (with Sars' *rugosa* as a synonym) in his material from the *Helga* collections in Irish waters. However, like Hansen, his illustrations attributed to *bamffica* (plate XI, figs 13, 14) seem to be of *sarsi*, although this material, which was collected from depths between 37 and 670 m, probably also contained true *rugosa*.

Dons (1915) examined material from a variety of Norwegian localities and, like Appellöf, recognized three distinct species to which he applied the names *bamffica*, *rugosa* and *tenuimana*. Dons provided good illustrations of the sternal plastron, third maxilliped and basal segment of the antenna in the three forms and also figured the first post-larval stage of *rugosa* (= *sarsi*) collected from the plankton of Tromsø Sound.

Bouvier (1922) perpetuated his earlier errors with A. Milne Edwards, referring to Atlantic *tenuimana* as *M. perarmata* and dealing with two varieties of *M. bamffica*. Of the two specimens referred to the typical *bamffica*, one belongs to *sarsi* (Station 1052, 440 m, Norway) and the other to *intermedia* (Station 1190, 628 m, Cape Verdes). Those attributed to var. *rugosa* include two *sarsi* and one *tenuimana*.

Brinkmann (1936) examined abundant material of *Munida* from Norwegian waters in a study of the rhizocephalan parasites. He concluded that three species, with quite

different depth distributions, were represented, and clearly distinguished between them with a series of characters, principally concerned with the ornamentation of the sternal plastron and the spination of the merus of the third maxilliped. Brinkmann pointed out that the names *rugosus* of Fabricius and *Bamffius* of Pennant are synonyms (though he did not recognize the priority of Fabricius), and must refer to the shallowest species, using the same argument of the inaccessibility of the deeper fauna in the eighteenth century as that used here. Consequently, he proposed the name *M. sarsi* for the *M. rugosa* of Sars, since no other name was available. The name *Munida sarsi* was actually first used by Huus (1935) in a paper on the larval stages of the *Munida* species of the Norwegian fjords. In a footnote to his introduction, Huus clearly attributes the name to Brinkmann and refers to this author's work on the *Munida* species which he had apparently seen in manuscript. Moreover, *M. sarsi* is clearly identified in this footnote as a new name for the *rugosa* of Sars, but not of the *rugosus* of Fabricius. It is not clear from Huus' paper whether he actually hatched larvae from ovigerous females held in the laboratory or whether he maintained plankton-caught larvae until they moulted to an identifiable stage. Certainly there are no females clearly identified as having provided larvae among the Huus material deposited in the Bergen Museum, although it is possible that such species were lost when the Museum was evacuated during the war (E. Willassen, personal communication). In any case, since both Huus and Brinkmann were working in the same laboratory it is inconceivable that they applied the name *sarsi* to different species. Huus clearly distinguished between his larvae of *sarsi* and *tenuimana* and, with some difficulty, distinguished these species from *M. bamffia* (= *rugosa*) by comparing them with Lebour's (1930) description of the latter. Thus, although he obviously did not intend to describe a new species, Huus fulfilled all of the conditions required by the International Code of Zoological Nomenclature and *M. sarsi* must therefore carry the authorship Huus, 1935.

Stephensen (1939) adopted the name *M. sarsi* Brinkmann and indicated that the material reported by Hansen (1908) from the Faeroes all belonged to this species, as suggested above. Stephensen also identified as *sarsi* a specimen in the Copenhagen Museum labelled from Ajaccio in Corsica. This specimen, which is indeed *sarsi*, apparently came to Copenhagen from the Paris Museum in 1899 and is labelled Ajaccio 26 Met. "Travailleur" 15 Juli 1881'. A second specimen of *sarsi*, with the same locality details, was apparently sent from Paris to the British Museum (Natural History) also in 1899 (BM(NH) reg. no. 99.3.23). Both specimens had been identified by A. Milne Edwards and Bouvier as '*Munida bamffia* var. *rugosa* G. O. Sars', and these authors (1900) list 'trois exemplaires typiques de la variété *rugosa*' as 'Travailleur', 1881 au large d' Ajaccio?'. The question mark implies some doubt about this locality and, since *sarsi* has otherwise never been recorded from the Mediterranean and a depth of 26 m would be remarkably shallow for this species, or even for true *rugosa*, we believe that it represents a simple labelling error. The third specimen does not appear to be in the collections of the Paris Museum and was probably sent to another national institution at the same time.

Bouvier (1940) once again persisted in applying the interpretation of A. Milne Edwards and Bouvier (1899), recognizing the varieties *bamffia*, *intermedia*, *gracilis*, *tenuimana* and *rugosa* within a single variable species.

Zariquiey Alvarez (1946) went even further than A. Milne Edwards and Bouvier, recognizing only a single species in this complex in the Mediterranean, which he called *bamffia*, and within which he distinguished 10 forms or varieties including *perarmata* and *curvimana*!

Later, this same author (Zariquiey Alvarez 1952) carried out a careful and comprehensive review of the problem and changed his interpretation completely. He now acknowledged that *rugosa* was a senior synonym of *bamiffia* and also recognized the validity of the species *sarsi*, *tenuimana* and *perarmata*, pointing out the close similarity between the last two. Finally, he described a Mediterranean variety of *sarsi* under the name *M. sarsi* subsp. *meridionalis* which was distinguished rather unsatisfactorily from *sarsi* by the spination of the carapace and the abdominal tergites, the form of the carapace striae and the relative lengths of the dactyls and propods of the ambulatory legs. Curiously, although Zariquiey Alvarez illustrated the third maxilliped of several of the forms with which he dealt, including his new subspecies, and he used features of the merus to separate some species, he did not mention this appendage in his accounts of either *sarsi* or *sarsi meridionalis* and therefore missed one of the most obvious differences between them.

Later, Zariquiey Alvarez (1958 a) realized that his *meridionalis* was a synonym of *intermedia* var. *sarsi*, and in his account of the effects of bopyrid parasites on the identified in his earlier paper were simply geographically separated varieties of a single species which could not be consistently distinguished, the priority of the name *intermedia* demanded a nomenclatural change. Consequently, he suggested that his *M. sarsi meridionalis* should become *M. intermedia* while *M. sarsi* should become *M. intermedia* var. *sarsi*, and in his account of the effects of bopyrid parasites on the secondary sexual characters of *Munida* species (Zariquiey Alvarez 1958 b) he refers simply to *M. intermedia* without distinguishing between the varieties. This nomenclature was subsequently used in his general review of Iberian decapods which was published posthumously (Zariquiey Alvarez 1968). Since we disagree with this interpretation and consider *sarsi* and *intermedia* to be distinct and consistently separable species with overlapping geographical distributions, we propose that *meridionalis* is simply a junior synonym of *intermedia* (see below).

Identification

From a study of the published nomenclatural history summarized above and an examination of material in the collections of the Muséum national d'Histoire naturelle, Paris, the British Museum (Natural History), London, and the Institute of Oceanographic Sciences, Wormley, UK, we believe that the four species dealt with here can be distinguished in the following manner:

- 1 Eyes small, maximum corneal diameter about one-quarter length of anterior border of carapace between bases of anterolateral spines. Principal transverse striae on posterior part of carapace continuous, without interruptions in the cardiac region. Fourth abdominal tergites never armed with spines *rugosa*
- Eyes large, maximum corneal diameter at least one-third length of anterior border of carapace. Principal transverse striae on posterior part of carapace interrupted in the cardiac region. Fourth abdominal tergite with or without a pair of spines 2
- 2 A spine at the distal external angle of merus of third maxilliped, usually distinct. Fourth abdominal tergite with or without a pair of spines *intermedia*
- No spine at the distal external angle or merus of third maxilliped. Fourth abdominal tergite almost always with at least one pair of dorsal spines 3
- 3 Cardiac region never with spines. Numerous spinules on the hepatic and anterior branchial regions of carapace. Piliferous striae very dense on abdominal tergites. Sternal plastron with numerous, short striae. Ventral edge of merus of P1 unarmed. *sarsi*
- Cardiac region often with spines. A single spinule on the hepatic region, anterior branchial region unarmed (apart from the lateral spines). Few piliferous striae on abdominal tergites. Sternal plastron with few short striae. Ventral edge of merus of P1 with small spines throughout its length *tenuimana*

Synonymies, diagnostic features, geographical variations and distributions

In this section we provide extensive, but not exhaustive, synonymies of the taxa dealt with and summarize their main diagnostic features and morphological variations. Because of the nomenclatural confusion in the past, it is difficult to determine geographical and bathymetrical ranges with confidence. Those provided are therefore minimal, being based on literature records for which the identifications can be determined with certainty, together with the records from the collections which we have been able to examine.

***Munida rugosa* (Fabricius, 1775)**

(Figs 1 a, b; 2 a, e; 3 a, b)

- Pagurus rugosus* Fabricius, 1775: 412.
Astacus Bamffius Pennant, 1777: 17, plate 3, fig. 25.
Pagurus rugosus: Fabricius, 1781: 508.
Cancer Bamfficus: Herbst, 1782: 58, plate 27, fig. 3.
Pagurus rugosus: Fabricius, 1787: 328.
Cancer rugosus: Linnaeus, 1788: 2985.
Galathea rugosa: Fabricius, 1793: 472.
Galathea rugosa: Fabricius, 1798: 425.
Galathea longipeda: Lamarck, 1801: 158.
Galathea rugosa: Latreille, 1802: 198.
Galathea rugosa: Bosc, 1801–1802: 87.
Galatea Bamfia: Leach, 1814: 398.
Galatea rugosa: Leach, 1815 a: plate 19, figs 1–3.
Galathea rugosa: Leach, 1815 b: 341.
Galathea rugosa: Risso, 1816: 70.
Galathea rugosa: Lamarck, 1818: 214.
Munida rugosa: Leach, 1818: 52.
Munida rugosa: Desmarest, 1825: 191.
Galathea rugosa: Risso, 1827: 46.
Galathea rugosa: H. Milne Edwards, 1837: 274.
Galathea rugosa: Lucas, 1840: 172.
Galathea rugosa: Loven, 1853: 21.
Munida Rondeletii: Bell, 1847: 208.
Munida Rondeletii: Lilljeborg, 1852: 22.
Munida Rondeletii: Gordon, 1852: 3684.
Munida Bamffica: White, 1857: 89.
Munida rugosa: Stimpson, 1858: 238.
Munida Bamffica: Kinahan, 1862: 364.
Munida rugosa: Heller, 1863: 192, plate 6, figs 5, 6.
Galathea rugosa: Goës, 1863: 165.
Munida rugosa: Grube, 1864: 62.
Munida Bamffia: Norman, 1869: 265.
Munida rugosa: Stalio, 1877: 655.
Munida rugosa: Stossich, 1881: 204.
Munida Rondeletii: Sars, 1883: 43, pl. 1, fig. 4.
Munida rugosa: Carus, 1885: 489.
Munida bamfia: Henderson, 1886: 28.
Munida bamffia: Bonnier, 1888: 78 (part), plate 13, figs 7, 8.
Munida rugosa: Gourret, 1888: 31.
Munida bamffica: A. Milne Edwards and Bouvier, 1894 b: 83 (part), pl. 7, figs 1–7.
Munida Bamffica: Caullery, 1896: 389 (part).
Munida rugosa: Adensamer, 1898: 618.
Munida bamffica: A. Milne Edwards and Bouvier, 1899: 81 (part), pl. 4, figs 6, 7.
Munida bamffica var. *gracilis*: A. Milne Edwards and Bouvier, 1899: plate 4, fig. 7.
Munida bamffica: A. Milne Edwards and Bouvier, 1900: 299 (part).
Munida rugosa: Graeffe, 1902: 37.
Munida bamffica: Appellöf, 1906: 139.
Munida bamffica: Hansen, 1908: 32 (part ?).
Munida rugosa: Pesta, 1912: 108 (part).
Munida bamffica: Selbie, 1914: 73 (part).
Munida bamffica: Dons, 1915: 84, figs 25, 28, 31.
Munida rugosa: Blohm, 1915: 37.
Munida bamffica: Pesta, 1918: 262 (part ?), fig. 81.
Munida Rondeletii: Osorio, 1923: 8, pl. 16, fig. 3.
Munida bamffica: Lebour, 1930: 179 (larvae).
Munida bamffica: Nobre, 1931: 182 (part ?), figs 103, 104.
Munida bamffia: Huus, 1935: 15 (larvae).
Munida Bamffica: Nobre, 1936: 114 (part), figs 97, 98.
Munida bamffia: Brinkmann, 1936: 13, pl. 5, figs 13, 16.
Munida bamffica: Ingrand, 1937: 57.
Munida bamffia: Stephensen, 1939: 11.
Munida bamffia: Bouvier, 1940: 171 (part).
Munida bamffia: Zariquiey Alvarez, 1946: 130, plate 18 (part).
Munida rugosa: Zariquiey Alvarez, 1952: 147, 158, figs 3A, 3B.
Munida rugosa: Zariquiey Alvarez, 1958 b: 101, fig. 3.
Munida bamffia: O'Ceidigh, 1962: 162.
Munida rugosa: Bourdon, 1965: 22.
Munida rugosa: Zariquiey Alvarez, 1968: 285, fig. 101 a.
Munida rugosa: Stevcic, 1969: 129.

Munida bamffia: Pocock, 1889: 427.
Munida bamffica: Ortmann, 1892: 253.
Munida bamffia: A. Milne Edwards and
 Bouvier, 1894a: 256, 258, 319 (part).

Munida rugosa: Koukouras, 1973: 756.
Munida rugosa: Koukouras and Kattoulas,
 1975: 283.
Munida rugosa: Pastore, 1976: 111.

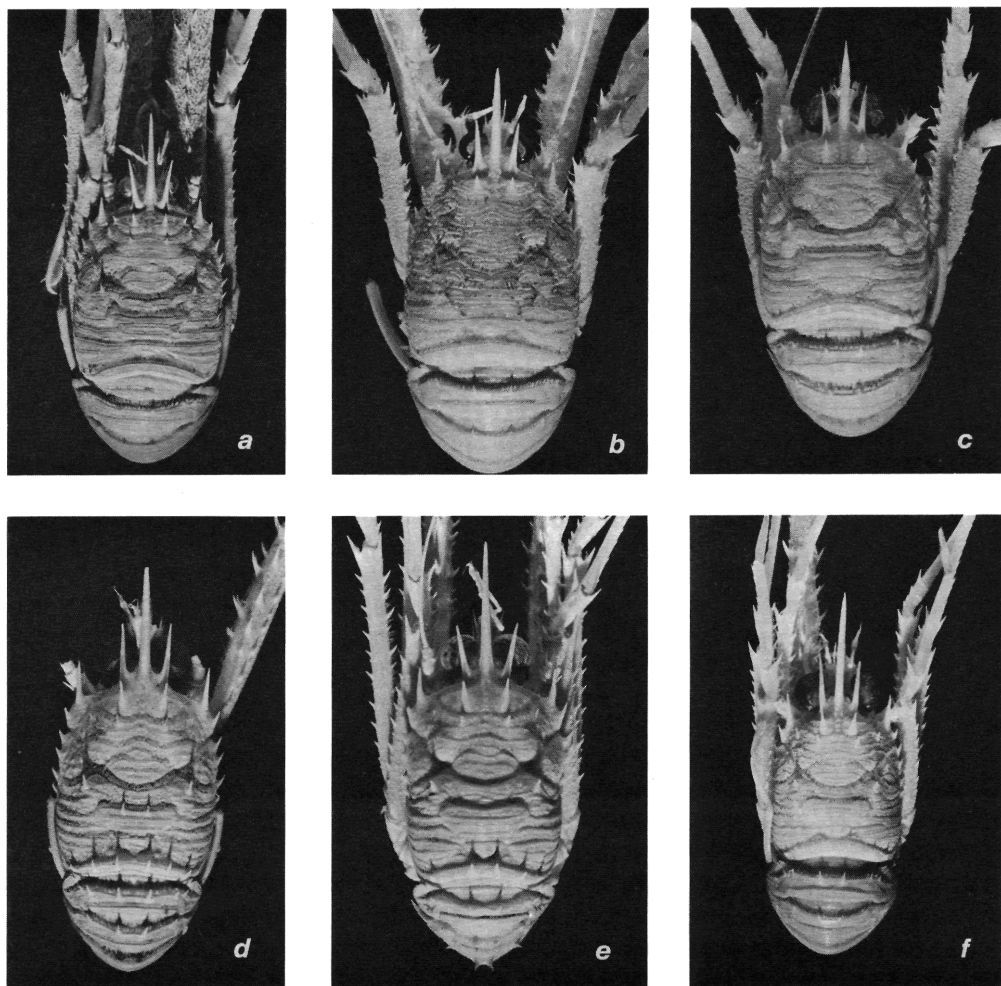


FIG. 1. Dorsal view of carapace and anterior abdominal somites; *a*, *Munida rugosa*, ♂ CL (total carapace length from the tip of the rostrum to the posterior carapace margin) 50.3 mm, Mediterranean, BM(NH) 1968.1.9.18–20; *b*, *M. rugosa*, ♂ CL 32.6 mm, Goban Spur; *c*, *M. sarsi*, ♂ CL 28.2 mm, Porcupine Seabight; *d*, *M. tenuimana*, ♂ CL 23.3 mm, Porcupine Seabight; *e*, *M. tenuimana*, ♂ CL 39.0 mm, Mediterranean (Polymed II CMO7); *f*, *M. intermedia*, ♀ CL 24.4 mm, Azores (Biacores, St. 41).

Remarks. *Munida rugosa* is distinguished from the other three species by its relatively small eyes, with the setae arising from the corneal margin all short and sub-equal in length, and by the presence of uninterrupted transverse striae on the posterior part of the carapace (fig. 1 a, b). The merus of the third maxilliped carries a strong spine at the distal external angle similar to that in *intermedia*, but significantly longer (fig. 2 a). The piliferous striae on the sternal plastron are longer and straighter than the much more numerous and curved striae in *sarsi*. Moreover, the fourth sternite and the medial regions of the third are usually devoid of striae in *rugosa* whereas these regions always have many striae in *sarsi* (fig. 3 a, b, c). The absence of spines on the fourth abdominal tergite consistently distinguishes *rugosa* from *sarsi* and *tenuimana* in which such spines are always present, although they may be minute in small specimens of *sarsi*. Although we are here suggesting that the Atlantic and Mediterranean populations of *rugosa* represent a single species, there are distinct geographical variations. Within the Atlantic populations there is a clear gradient from north to south, the more southerly specimens tending to be generally more spinose, having a higher density of piliferous setae on the abdomen and sternal plastron and having longer and more gracile pereopods. In these features specimens from the southern parts of the Atlantic range, and particularly those from the southern Bay of Biscay and the Atlantic coast of the Iberian Peninsula, approach the condition in the Mediterranean material. However, whereas the third pair of lateral branchial spines are always well-developed in Mediterranean specimens, they are lacking or reduced to very small spinules in Atlantic material. In living or freshly preserved material the cephalothorax is red-brown and much duller than in *sarsi*. The rostral spine is usually uniformly red, but the apex and the lateral surfaces are sometimes white. The supra-ocular and frontolateral spines are red basally with the distal one-third white. The dorso-anterior surface of the abdomen is the same red-brown colour as the carapace, but the flexed posterior portion is a very pale orange. Chelipeds are a dull beige base colour from which emerge vivid red spines with white tips. The large spine on the propodus, in front of the articulation with the dactyl, is a particularly intense and brilliant red. The fingers are irregularly marked with alternating red and white blotches or marbling. Legs 2–4 are a dull orange-red, with the dactyls and distal portions of the propods a dirty white in external view.

Distribution. Eastern Atlantic from Shetland and Sognefjord (Norway) in the north to Madeira in the south, Mediterranean at least as far east as the Adriatic. From about 30 to 300 m depth.

Munida sarsi Huus, 1935

(Figs 1 c, 2 c, 3 c, 4 a)

Munida rugosa: Sars, 1872: 283 (40).

Munida rugosa: Sars, 1883: plate 1, fig. 5.

Munida bamffia: Bonnier, 1888: 78 (part ?).

Munida bamffia: A. Milne Edwards and Bouvier, 1894 a: 257, 325 (part).

Munida bamffia: A. Milne Edwards and Bouvier, 1894 b: 83 (part).

Munida Bamffica: Caullery, 1896: 389 (part).

Munida bamffica: A. Milne Edwards and Bouvier, 1899: 75 (part).

Munida bamffica var. *rugosa*: A. Milne Edwards and Bouvier, 1899: 80 (part), plate 4, figs 12, 15, 16.

Munida bamffica: Kemp, 1910, 415.

Munida bamffica: Selbie, 1914: 73 (part), plate 11, figs 13, 14.

Munida rugosa: Dons, 1915: 72, figs 21, 22, 24, 26, 29, 32, plate 2, fig. 10.

Munida bamffica var. *rugosa*: Bouvier, 1922: 44 (part).

Munida sarsi Huus, 1935: 8 (larvae).

Munida Sarsi: Brinkmann, 1936: 13, plate 5, figs 14 a, 14 b, 17 b, 17 c.

Munida sarsi: Stephensen, 1939: 11 (part).

Munida bamffia: Bouvier, 1940: 172 (part).

Munida bamffia: Zariquiey Alvarez, 1946: 130 (part).

Munida bamffica var. *tenuimana*: A. Milne Edwards and Bouvier, 1899: 80 (part), plate 4, figs 8, 9.

Munida bamffica var. *intermedia* A. Milne Edwards and Bouvier, 1899: 80 (part), plate 4, fig. 14.

Munida bamffica: A. Milne Edwards and Bouvier, 1900: 299 (part).

Munida rugosa: Appellöf, 1906: 139, plate 2, fig. 1.

Munida bamffica: Hansen, 1908: 32 (part), plate 2, fig. 3 a.

Munida sarsi: Zariquiey Alvarez, 1952: 172, fig. 4.

Munida intermedia var. *sarsi*: Zariquiey Alvarez, 1958 a: 50.

Munida intermedia subsp. *sarsi*: Zariquiey Alvarez, 1968: 283 (key).

Munida intermedia var. *sarsi*: Zariquiey Alvarez, 1968: 286.

Remarks. *Munida sarsi* differs from *rugosa* in its large eyes, the interrupted transverse striae on the posterior region of the carapace (fig. 1 c), and the form and number of piliferous striae on the sternal plastron (fig. 3 c). In all of these features *sarsi* resembles *intermedia* from which, however, it is clearly distinguished by the absence of a spine at the distal external angle of the merus of the third maxilliped (fig. 2 c). While the fourth abdominal tergite always carries a pair of spines in adult *sarsi*, these may be very small or even absent in juveniles. This feature alone will therefore not consistently distinguish *sarsi* from *intermedia* together with which it often occurs in the southern part of its range. In all cases, however, *sarsi* is readily distinguished from *intermedia* in having many more intercalary striae on the abdominal tergites (fig. 4 a). In fresh material the striae on the cephalothorax and the anterior part of the abdomen are a quite brilliant orange, but the cervical groove and the anterior and posterior carapace margins are white and the flexed posterior part of the abdomen is a pale orange-red. The rostral spine is orange in the basal half, white distally and often with an orange tip. The supra-ocular spines and anterolateral carapace spines are uniformly orange-red. The chelipeds are generally a very pale and dull red-brown, but the distal parts of the merus and carpus are more intensely pigmented, giving a general impression of bars of colour. The mid-sections of the fingers also carry rather bright-red bands, sometimes rather irregular or marbled. The distal one-third of the fingers are always white. Most of the spines on the chelipeds are white, but those on the dorsal surfaces, and particularly on the propodus, are a more intense orange than the general background colour. The most intense colour on the animal is in small spots of brilliant scarlet on the arthrodistal membranes between the propodi and meri of the chelipeds. The eyes are an iridescent green. Like the chelipeds, the legs are generally a rather pale orange, but with more intense colour on the distal parts of the merus, carpus, propodus and dactyl.

Distribution. *Munida sarsi* is the most northerly of the species dealt with, having been recorded in the Atlantic from North Cape (Norway) and Greenland to the southern Bay of Biscay and northern coast of Spain. The species has not been recorded from the coast of Portugal or from the Mediterranean (but see p. 147). *Munida sarsi* has been recorded frequently at depths between about 200 and 800 m and occasionally to about 1000 m; it seems to be most abundant between about 250 and 400 m. In the upper part of its bathymetric range *sarsi* is frequently taken together with *rugosa*.

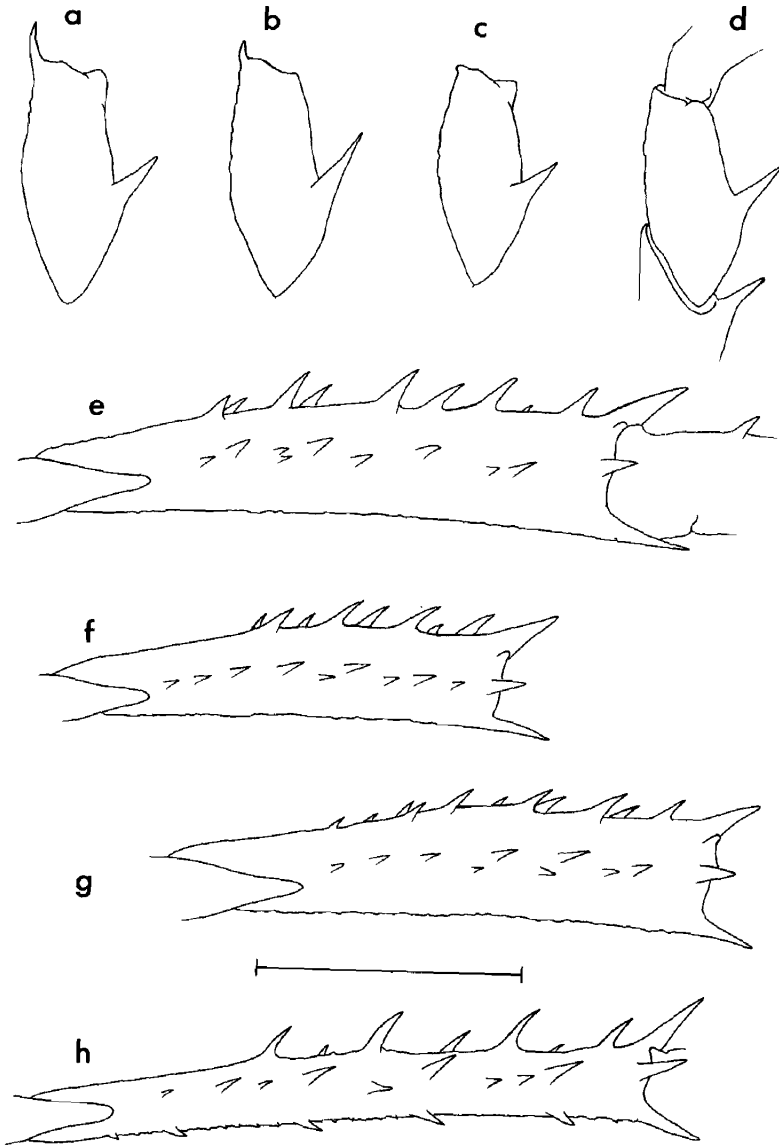


FIG. 2. Merus of third maxilliped (a-d) and left cheliped (e-h) in *Munida* species: a, *M. rugosa*, ♂ CL 33.0 mm, Porcupine Seabight; b, *M. intermedia*, ♀ CL 33.0 mm, Mediterranean, BM (NH) 1954.11.4.97-100; c, *M. sarsi*, ♂ CL 28.0 mm, Porcupine Seabight; d, *M. tenuimana*, ♀ CL 30.1 mm, Porcupine Seabight; e, *M. rugosa*, ♂ CL 27.0 mm, Porcupine Seabight; f, *M. intermedia*, ♀ CL 25.0 mm, Bay of Biscay; g, *M. sarsi*, ♂ CL 27.3 mm, Porcupine Seabight; h, *M. tenuimana*, ♀ CL 27.8 mm, Porcupine Seabight. Bar scale represents 5 mm for a-d, and 10 mm for e-h.

Munida intermedia A. Milne Edwards and Bouvier, 1899

(Figs 1 f, 2 b, f 3 d, 4 b)

Munida bamffia: Bonnier, 1888: 78 (part ?).
Munida bamffia: A. Milne Edwards and Bouvier, 1894 a: 257, 325 (part).

Munida bamffia: Bouvier, 1940: 171 (part).
Munida bamffia tenuimana: Bouvier, 1940: plate 5, fig. 3.

Munida Bamffica: Caullery, 1896: 389 (part ?).
Munida bamffica: A. Milne Edwards and Bouvier, 1894 b: 83 (part ?).
Munida bamffica: A. Milne Edwards and Bouvier, 1899: 80 (part).
Munida bamffica var. *intermedia* A. Milne Edwards and Bouvier, 1899: 80 (part), plate 4, fig. 13.
Munida bamffica var. *gracilis* A. Milne Edwards and Bouvier, 1899: 80 (part), plate 4, fig. 11.
Munida bamffica: A. Milne Edwards and Bouvier, 1900: 299 (part), plate 29, fig. 18.
Munida bamffica: Pesta, 1918: 262 (part ?).
Munida bamffica: Bouvier, 1922: 43 (part).

Munida bamffia: Zariquiey Alvarez, 1946: 13, plate 8 (part).
Munida sarsi subsp. *meridionalis* Zariquiey Alvarez, 1952: 181, fig. 5.
Munida intermedia: Zariquiey Alvarez, 1958 a: 50.
Munida intermedia: Forest, 1965: 349.
Munida intermedia: Zariquiey Alvarez, 1968: 286, figs 101 b, c.
Munida tenuimana: Miyake and Baba, 1970: 77, fig. 5.
Munida intermedia: Stevcic, 1976: 103.

Remarks. Like *M. sarsi*, *M. intermedia* is distinguished from *M. rugosa* by its large and dilated eyes, usually with a series of long hairs originating at the margin of the cornea and extending over the corneal surface, and by the absence of continuous transverse striae on the posterior region of the carapace, behind the cervical groove (fig. 1 f). On the other hand, *intermedia* resembles *rugosa* in having a prominent spine, albeit rather smaller, at the distal external angle of the merus of the third maxilliped (fig. 2 b). The hepatic regions of the carapace are much less rugose than in *sarsi*, while the piliferous striae on the abdominal somites are accentuated, but few in number. The piliferous striae on the sternal plastron are intermediate between the numerous short striae of *sarsi* and the less abundant and much longer ones of *rugosa* (fig. 3 d). The number and size of the hepatic and gastric spines, and the number of spines on the posterior border of the carapace, are variable in *intermedia*. Similarly, while the fourth abdominal tergite is unarmed in most individuals, as in *rugosa*, it may carry a pair of spines which are often unequal. Like the other species, *M. intermedia* exhibits considerable geographical variations. Thus, the spines on the fourth abdominal tergite are more often present in specimens from the southern parts of the range than from the north. On the other hand, the spine on the distal external angle of the merus of the third maxilliped, normally characteristic of this species, is very small or even scarcely discernible in some specimens from off southern Ireland which are otherwise clearly identifiable as *intermedia* by their colouration, by the absence of spines on the fourth abdominal tergite, and by the relative paucity of intercalary striae on the abdominal tergites (fig. 4 b). The cephalothorax and abdomen in fresh material are red-brown or orange, rather similar to *rugosa*. Also like *rugosa* the rostral spine is uniformly red, while the supra-orbital spines are red basally but with the distal one-quarter to one-third white. However, the orbital region in front of and beneath the frontal border, on either side of the insertion of the optical peduncle, is marked with bright-red patches; this region has no trace of colour in the other species. Chelipeds and legs coloured more or less as in *rugosa*, but the fingers of the chelipeds are quite bright orange proximally and whitish distally, while there is a brilliant-red spot surrounding the mesioproximal spine on the movable finger.

Distribution. Eastern Atlantic from the Goban Spur at about 50°N to approximately the latitude of Dakar, Azores; Mediterranean as far east as the Adriatic. From 120 to 800 m depth, although one record (*Travailleur* station 101), in the Bay of Biscay, is from 1360 m.

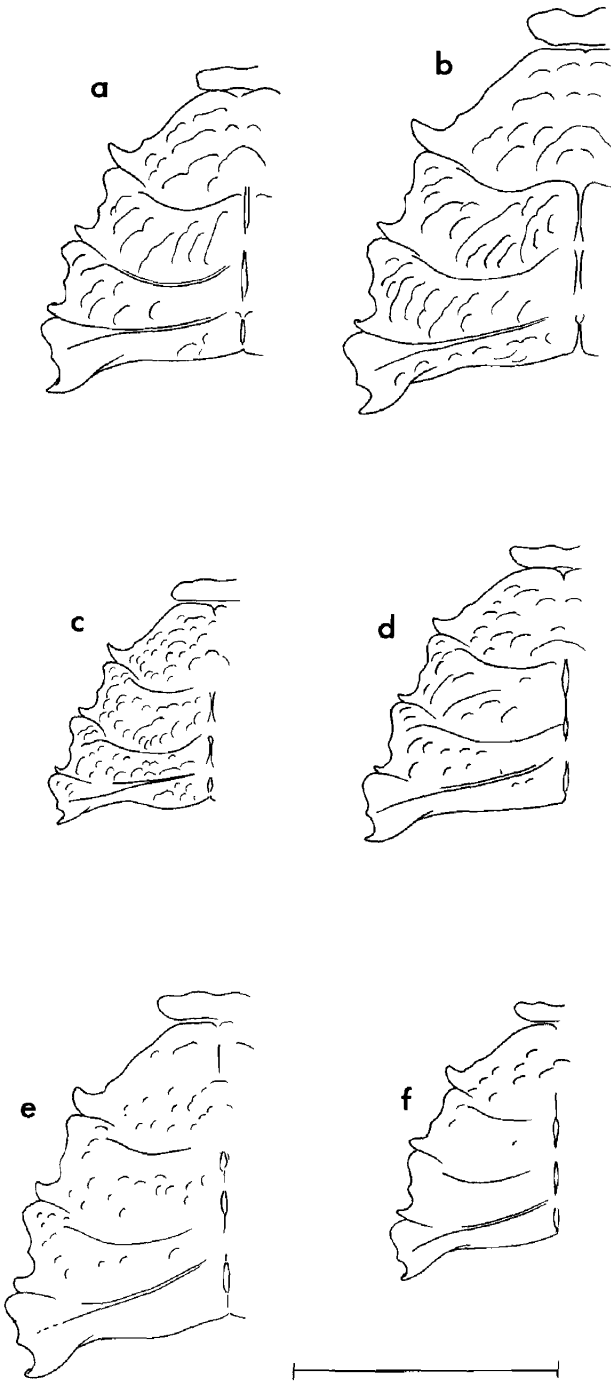


FIG. 3. Sternal plastron in four *Munida* species to show piliferous striae: a, *M. rugosa*, ♂ CL 33.0 mm, Porcupine Seabight; b, *M. rugosa*, ♂ CL 46.5 mm, east coast of Elba, BM (NH) 1968.1.9.18-20; c, *M. sarsi*, ♂ CL 28.0 mm, Porcupine Seabight; d, *M. intermedia*, ♀ CL 33.0 mm, Mediterranean, BM (NH) 1954.11.4.97-100; e, *M. tenuimana*, ♂ CL 39.00 mm, Mediterranean, Paris Museum, Polymed II, CMO7/140; f, *M. tenuimana*, ♀ CL 30.1 mm, Porcupine Seabight. Bar scale represents 10 mm.

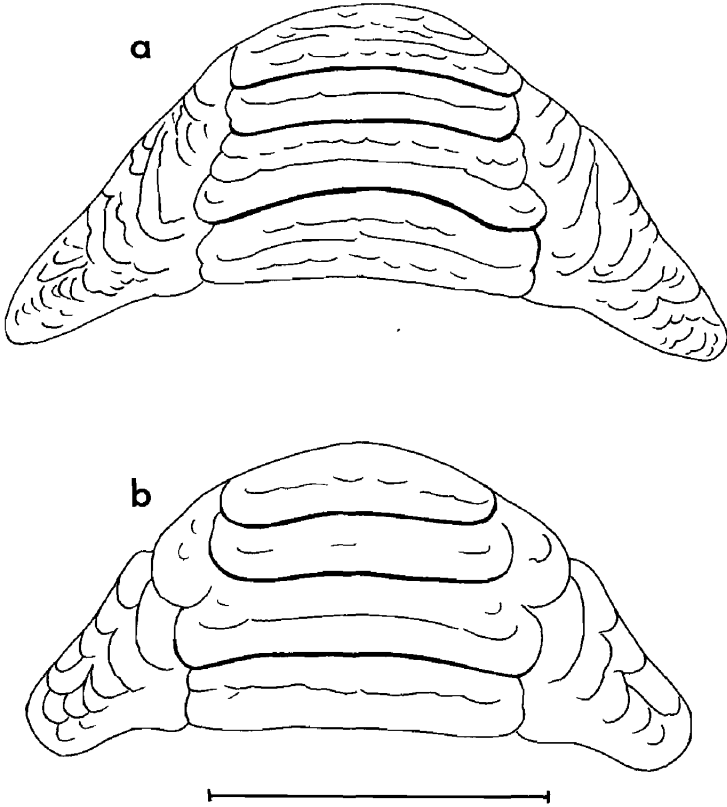


FIG. 4. Fifth abdominal tergite in a *Munida sarsi*, ♀ CL 21.5 mm, Porcupine Seabight, and b, *M. intermedia*, ♂ CL 22.2 mm, Azores (Biacores Station 41). Bar scale represents 5 mm.

***Munida tenuimana* G. O. Sars, 1872**

(Figs 1 d, e; 2 d, h; 3 e, f)

- Munida tenuimana* Sars, 1872: 257; 1877: 238.
Munida tenuimana: A. Milne Edwards, 1881 a: 879; 1881 b: 54; 1882 a: 89; 1882 b: 13, 37 (part).
Munida tenuimana: A. Milne Edwards, 1883: 31, plate 11.
Munida tenuimana: Sars, 1883: 44, plate 1, fig. 6.
Munida tenuimana: Perrier, 1886: 52 (part).
Munida tenuimana: Gourret, 1888: 31.
Munida tenuimana: Sars, 1889: 178 (larvae).
Munida perarmata: A. Milne Edwards and Bouvier, 1894 a: 257, 325; 1899: 81; 1900: 305, plate 30, fig. 1.
Munida tenuimana: Appellöf, 1906: 139, plate 2, fig. 2.
Munida tenuimana: Hansen, 1908: 34, plate 2, fig. 4 a, plate 3, fig. 1 a.
Munida tenuimana: Selbie, 1914: 77, plate 11, figs 15, 16.
Munida tenuimana: Dons, 1915: 84, figs 23, 27, 30, 33, plate 2, fig. 11.
Munida tenuimana: Pesta, 1918: 265, fig. 82.
Munida perarmata: Bouvier, 1922: 44.
Munida tenuimana: Huus, 1935: 8 (larvae).
Munida tenuimana: Brinkmann, 1936: 14, plate 5, fig. 18 b.
Munida tenuimana: Saemundsson, 1936: 13; 1937: 16.
Munida tenuimana: Stephensen, 1939: 12.
Munida perarmata: Bouvier, 1940: 173.
Munida tenuimana: Zariquiey Alvarez, 1952: 197, fig. 6.
Munida perarmata: Zariquiey Alvarez, 1952: 207, fig. 7; 1958 b: 101.
Munida perarmata: Forest, 1965: 348.
Munida perarmata: Zariquiey Alvarez, 1968: 288.
Munida perarmata: Stevcic, 1969: 129.

Remarks. *Munida tenuimana* is distinguished from the other species in having a row of spines along the ventral border of the merus of the chelipeds (fig. 2 h), and in having rather few short striae on the sternal plastron (fig. 3 e, f) compared with the much longer and more abundant striae in the other species. The eyes in *M. tenuimana* are large, as in *sarsi* and *intermedia*, but none of the setae arising from the proximal corneal margin are significantly elongated. Like *sarsi*, the merus of the third maxilliped has no spine at the distal external angle (fig. 2 d) and the fourth abdominal tergite always carries a pair of spines, at least in adult specimens. However, whereas *sarsi* always has a series of small spinules on the hepatic and anterior branchial regions of the carapace, *tenuimana* has only a single spinule on the hepatic region and none on the anterior branchial region. Cardiac spines are never present in *sarsi*, but are frequently present in *tenuimana*. The spines on the legs, carapace and abdomen, and particularly those on the posterior border of the carapace, are generally better developed than in the other species, giving *tenuimana* a more spinous overall appearance. *Munida tenuimana* was originally described from Norwegian material and was subsequently reported for a number of Atlantic localities. In 1894, A. Milne Edwards and Bouvier introduced the name *M. perarmata* for a Mediterranean specimen but later totally confused their use of the names *tenuimana* and *perarmata*, as noted above. The name *perarmata* then virtually disappeared until Zariquiey Alvarez (1952) resurrected it, concluding that *perarmata* was restricted to the Mediterranean and was specifically distinct from the Atlantic form, *tenuimana*. Zariquiey Alvarez thought the two species could be distinguished by the presence of spines on the cardiac region of the carapace in *perarmata* while such spines were never present in *tenuimana*, and the presence of numerous short piliferous striae on the segments of the sternal plastron in *perarmata* whereas these striae were much less numerous in *tenuimana* and were restricted to the anterior sternite. From an examination of a large series of specimens from the Atlantic and a smaller series from the Mediterranean, it is clear that these distinctions will differentiate between many specimens from the two areas, but that they are not consistent. Thus, whereas most Mediterranean specimens have two or three spines beside the mesocardiac groove and up to four spines beside the cervical groove, occasional individuals have no spines at all. On the other hand, about half of the Atlantic specimens examined have no cardiac spines, the remainder having one or two spines by the mesocardiac groove and occasionally a spine beside the cervical groove. Similarly, while most Mediterranean specimens have obvious striae on at least the first three segments of the sternal plastron, in some individuals they are reduced or absent, at least on the second and third segments. Atlantic specimens usually have the striae restricted to the anterior segment, but about one-third of the specimens examined have clear striae on the more posterior segments. Finally, the fifth abdominal somite of most Mediterranean specimens has intercalary striae, between the three main ones, which are absent from most Atlantic specimens; again, however, this distinction does not hold in all cases. Thus, although the Atlantic and Mediterranean populations of *tenuimana* seem to have diverged more than those of the other two species which occur in both areas, the resulting differences are not sufficiently consistent to warrant the recognition of even sub-specific status, so that the name *perarmata* is therefore considered simply as a synonym of *tenuimana*.

In living material the dorsal carapace surface is a very pale pink, almost white. The rostral spine is white proximally and pale-rose distally, while the supra-ocular spines are similar but a brilliant vermilion distally. The anterolateral carapace spines are vermilion throughout. The dactyls of the pereopods and the tips of both the movable and immovable finger of the chelipeds are very intense vermilion. The other segments of

all of the legs are pale pink dorsally and a more intense red ventrally. The dactyl and merus of the third maxillipeds and the cutting surfaces of the mandible are also a very intense red. Whereas the ventral surfaces of the cephalothorax and abdomen in the other species are scarcely pigmented, in *tenuimana* these regions are clearly coloured pale orange. Consequently, the overall appearance of *tenuimana*, with a pale upper surface and red-tipped spines and a generally orange under surface, with brilliant red tips to the legs in both views, is quite distinct.

Distribution. In the Atlantic from David Strait, Iceland and Vestfjorden (Norway) to the coasts of Spain and Portugal, and in the Mediterranean as far east as the Adriatic. Stephensen (1939) refers to several records in Icelandic waters at depths between 120 and 280 m, but *tenuimana* generally occurs much deeper. Sars recorded it from no shallower than 300 fathoms (550 m) in the Norwegian fjords, though Brinkmann (1936) gives its upper limit as 250–300 m. The deepest Atlantic record is that of Hansen (1908) at a depth of 799 fathoms (1460 m) to the south-west of Iceland, and it has frequently been taken at depths between about 700 and 1400 m in the Porcupine Seabight and the Bay of Biscay. In the Mediterranean the species has been recorded from 400 to 1775 m.

Conclusion

Four species within this nomenclaturally confused complex seem to be consistently and clearly separable and should bear the following names: *Munida rugosa* (Fabricius), *M. tenuimana* G. O. Sars, *M. intermedia* A. Milne Edwards and Bouvier, and *M. sarsi* Huus. Three of these species, *rugosa*, *intermedia* and *tenuimana*, occur in both the Atlantic and Mediterranean, while *sarsi* is apparently restricted to the Atlantic. All of the species exhibit significant geographical morphological variations and those occurring in both the Atlantic and the Mediterranean are probably undergoing speciation. This process seems to have proceeded farthest in *tenuimana* in which the Atlantic or Mediterranean origin of most individuals can be determined on morphological grounds. However, even in this case the distinctions do not seem to be sufficiently consistent to warrant the recognition of separate subspecies, at least on the basis of the available rather inadequate collections.

Acknowledgements

In our attempts to unravel this complex taxonomic and nomenclatural situation we have received help and/or advice from Dr M. E. Christiansen, University of Oslo, Dr J. Forest, Muséum national d'Histoire naturelle, Paris, Dr L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden, Dr R. W. Ingle, British Museum (Natural History), London, Dr E. Willassen, Zoological Museum, Bergen, Dr T. Wolff, Zoological Museum, Copenhagen and Dr R. V. Melville, Commission of Zoological Nomenclature. We are most grateful to each of these colleagues for their assistance, but the responsibility for any residual errors of interpretation or fact remains with ourselves.

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† Bosc's book is usually referred to as having been published in 1802. However, Dr L. B. Holthuis has pointed out that it was actually published between 23 September 1801 and 20 January 1802 (see Dupuis, 1975, *Bulletin of Zoological Nomenclature*, **32**, (1), 4).

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