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LOBSTER-KRILL

ANOMURAN CRUSTACEA THAT ARE THE FOOD OF WHALES

By

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CONTENTS

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(Plate IV; text-fig. 1)

Two species of the genus *Munida*, *M. subrugosa* (White) and *M. gregaria* (Fabricius), are closely allied and very similar in general characters. They are often found together in the same localities, and occur in both the South Atlantic and Pacific Oceans. They are of particular interest to the Discovery investigations as *M. gregaria*, probably with a third allied species, *Pleuroncodes planipes* (Stimpson) from the Pacific coast of Mexico, form an important food of some species of whale.

M. gregaria has a pelagic post-larval stage which differs in appearance from the adult, while in *M. subrugosa* the corresponding stage is bottom-living and similar to the adult. Considerable confusion as to the relation of the pelagic post-larval stage of *M. gregaria* to the adult exists in the literature relating to the species. This post-larval stage was originally named as a separate species, *Grimothea gregaria*, and the name *Grimothea* is used in this paper as a convenient label for this stage of the species. The hybrid English-Norwegian term, "lobster-krill",[1] is adopted as more descriptive than the corresponding New Zealand name, "whale-feed", which in that country refers only to the *Grimothea* stage of *M. gregaria*.

MATERIAL EXAMINED

The Discovery collections contain a long series of both species and their post-larval stages.

St. 51. 4. v. 26. Off Eddystone Rock, East Falkland Islands. Large otter trawl, 105–115 m.
M. subrugosa. 19 specimens, 7 ♂, 12 ♀, 16·5–38·0 mm., 3 with Bopyrid parasites on the gills.
M. gregaria. 45 specimens, 28 ♂, 17 ♀, 13·0–38·0 mm., 1 with Bopyrid parasite on gills.
Fine nets on trawl, 105–115 m.
M. subrugosa. 12 specimens, 5 ♂, 7 ♀, 12·0–20·0 mm.; 81 specimens, post-larval, 3·5–8·5 mm.
M. gregaria. 39 specimens, post-larval (*Grimothea*), 8·0–12·0 mm.

St. 67. 23. v. 26. 47° 18′ 00″ S, 51° 52′ 00″ W. 4000 m. 1-metre horizontal tow-net, 90 (–0) m.
M. gregaria. 27 specimens, post-larval (*Grimothea*), 9·0–11·0 mm.

St. 223. 27. iv. 27. St Francis' Bay, Cape Horn. 55° 51′ 15″ S, 67° 29′ 30″ W. Rectangular bottom net, 63 m.
M. subrugosa. 35 specimens, 21 ♂, 13 ♀, 20·0–35·0 mm.
M. gregaria. 60 specimens, 30 ♂, 30 ♀, 20·0–34·0 mm.

St. WS 100. 23. iv. 27. 50° 53′ 00″ S, 61° 26′ 00″ W. 132 m. 1-metre horizontal tow-net, 61 m.
M. gregaria. 276 specimens, post-larval (*Grimothea*), 7·5–9·0 mm.

[1] "Krill" is a Norwegian word meaning "whale-food".

St. WS 576. 17. iv. 31. Berkeley Sound, East Falkland Islands. 51° 35′ 00″ S, 57° 49′ 45″ W. Large otter trawl, 34–24 m.

M. subrugosa. 4 specimens, all ♀, 29·0–34·0 mm.

M. gregaria. 20 specimens, 10 ♂, 10 ♀, 28·0–37·0 mm.

S.S. 'Ernesto Tornquist.' Gulf of St George, Patagonia. 45°–47° S, 66°–68° W. All *M. gregaria*.

23. iii. 29. Surface. 13 specimens, 4 ♂, 9 ♀, 21·0–31·0 mm.

27. iii. 29. Surface. 15 specimens, 5 ♂, 9 ♀, 1 damaged, 18·0–29·0 mm.

29. iii. 29. Surface. 20 specimens, 8 ♂, 12 ♀, 20·0–28·0 mm.

2. iv. 29. Surface. 18 specimens, 7 ♂, 11 ♀, 20·0–32·0 mm.

5. iv. 29. Surface. 21 specimens, 6 ♂, 14 ♀, 1 damaged, 20·0–33·0 mm.

6. iv. 29. Surface. 14 specimens, 6 ♂, 8 ♀, 19·0–31·0 mm.

The measurements of the specimens refer to the length of the carapace from its posterior border to the tip of the rostrum.

DISTRIBUTION

Both *Munida subrugosa* and *M. gregaria* are restricted to the southern hemisphere, and their distribution, so far as our present knowledge goes, appears to be sharply discontinuous. They have been found in abundance in the waters of New Zealand and its sub-Antarctic islands, and in Bass Strait. In the South Atlantic they occur in plenty at the Falkland Islands, Tierra del Fuego, the Magellan Straits and Patagonia. *M. gregaria* has been recorded from the west coast of South America as far north as latitude 41° 30′ S and on the east coast as far north as latitude 51° S. The corresponding latitudes for *M. subrugosa* are 50° S on the west coast and 35° S on the east coast.

The two species evidently inhabit comparatively warm water. They are found near the Falklands and at Cape Horn, where surface temperatures vary between 5·5° and 9·0° C., but are entirely absent from the much colder waters of the South Shetlands, South Georgia and Bouvet Island. At Tristan da Cunha and Gough Island, where temperatures are higher than at the Falklands, neither species has been found, and there are no records from the Kerguelen area.

The vertical distribution of *M. subrugosa* extends from the shore to a recorded depth of 600 fathoms (Henderson, 1888), and of *M. gregaria* from the shore to a recorded depth of 60 fathoms (Young, 1925).

SWARMING

Both *M. subrugosa* and *M. gregaria* frequently occur in enormous shoals, the adults usually on the bottom, while the *Grimothea* stage of *M. gregaria* has been on occasion so plentiful at the surface as to colour the sea bright red over large areas. The adult *M. gregaria* is also sometimes found in swarms at the surface.

At St. 51 (4. v. 26, off Eddystone Rock, East Falkland Islands) the *Grimothea* stage of *M. gregaria* was found to be swarming at the surface, and at the same time large numbers of the adults of *M. gregaria* and adults and young of *M. subrugosa* were taken in the trawl on the bottom at a depth of 105–115 m. So great was the catch of these Crustacea that after preserving a long series of specimens the remainder was sent to the cook and was much appreciated in the wardroom and on the mess-deck. At St. 223

(27. iv. 27, St Francis' Bay, Cape Horn) 95 adults of both species were taken on the bottom at 63 m. in a haul of only 7 min. duration. Similarly at St. WS 576 (17. iv. 31, Berkeley Sound, East Falkland Islands) numbers of adults of both species were taken on the bottom at a depth of 34–24 m. Thomson (1898, p. 194) has recorded of the adult *M. subrugosa* that in New Zealand "occasionally it comes up Otago Harbour in countless swarms, creeping up to the steps of the jetties and on to the submerged stones of the piers. It always appears to keep near the bottom and is rather slow and sluggish in its movements till pursued, when it jerks itself rapidly backwards".

There are many records of swarms of the *Grimothea* stage of *M. gregaria* being seen at the surface in South American seas. Some of the earlier records are quoted below (p. 479). From New Zealand waters Young (1925, p. 318) records, "*Munida gregaria* in its swimming stage visits Otago Harbour in large numbers during the warmer months of the year. The shoals are so large that the water appears to be quite red with the thousands of individuals which are clustered together. The smaller shoals often take a circular shape like a swarm of bees, and the incessant motion of each individual tends to heighten this illusion". The occurrence of swarms in other parts of the New Zealand seas is noted below (pp. 481–482) in discussing the relations of other animals to these Crustacea. On the other hand, that the swarms of the *Grimothea* stage are not always found at the surface is shown by the specimens in the Discovery collections from 105–115 m. (St. 51) and 61 m. (St. WS 100). It is of interest to note in this connection that Cheever (1850, p. 48),[1] speaking of the food of the Southern Right Whale, states, "the living of this vast animal is thought to be upon a substance which I hear universally called by whalemen 'right whale feed'. It appears in the water as a red-coloured insect. ...It is, in fact, a little red shrimp, sometimes seen floating on the surface of these seas alive, oftener dead, when it has the appearance at a distance of patches or clots of blood, only yellower....This 'feed' is supposed to lie generally rather deep under water in these southern seas, as whales are often taken in greatest numbers where none of it is to be seen on the surface".

Information and specimens kindly supplied by Captain S. Fagerli of the S.S. 'Ernesto Tornquist' show that the adult *M. gregaria* also swarms at the surface of the sea at times on the Patagonian coast. Captain Fagerli was whaling off the coast of Patagonia in the seasons 1927–8 and 1928–9, and states that enormous shoals of adult *M. gregaria* were observed at the surface of the sea all the way down the Patagonian coast from Bustamente Bay in the Gulf of St George to south of Santa Cruz (latitude 45° to 50° S). After high water with the wind on shore great numbers were seen washed up on the beaches. Shoals of the *Grimothea* stage were also seen; the swarms of adults and of the *Grimothea* stage were observed from the shore out as far as 70 fathoms of water. Captain Fagerli has presented to the Discovery collections specimens from Bustamente Bay, caught at the surface in a small net alongside his ship as she lay at anchor. All the specimens, 101 in number, are adult *M. gregaria*, and were taken between March 23 and April 6, 1929.

[1] Cheever, Rev. H. T., *The Whaleman's Adventures in the Southern Ocean*. Ed. by the Rev. W. Scoresby. London, 1850.

In 1926 Captain Fagerli was whaling in Magdalena Bay on the Pacific coast of Mexico, and here also he observed at the surface shoals of adult *Munida* that appeared to be identical with those seen off Patagonia. Here also, after an on-shore wind, the beach at high-water mark was found covered with *Munida* to a depth of several inches. As Captain Fagerli had no specimens from Mexico an enquiry was sent to Dr Waldo L. Schmitt of the Smithsonian Institution, and his reply to Dr Kemp states that the U.S. National Museum has no specimens of *M. gregaria* from the west coast of America in its collections. He states: "I am without information on the score of pelagic swarms of post-larval *Munidas*. There is, however, a common pelagic form on the west coast of Mexico which is considered a good species and genus, *Pleuroncodes planipes*, Stimpson. Its abundance has been commented upon from time to time. In our *Mexico and Central America Coast Pilot* (*West Coast*), Hydrographic Office (Publ.) No. 84, sixth edit., p. 79, under Magdalena Bay, 'Phenomenon', appears the following:

"'A remarkable phenomenon, said to occur frequently in the bay, is the appearance of vast numbers of crustacea, resembling the shrimp, but not edible. They are from 1 to 2 inches long, giving the water a crimson color. The receding tide leaves the shore covered with thick layers, on which the sea birds feed, and the stench arising from their decomposition fills the air.'

"I first saw this or a similar note in an earlier edition when I was down there with the 'Albatross' in 1911, and though we got no specimens of them at that place, we have since received a number from Magdalena Bay from the late C. R. Orcutt, a veteran shell collector and former good friend of the Museum. I feel certain that this is the species referred to in the coast pilot, not only because it is found at Magdalena Bay, but because it is a well-known pelagic form along the west coast. Regarding its abundance, Stimpson, at the end of his original description, says:

"'This species lives in the open ocean, and is sometimes found in vast quantities in the Pacific off the American Coast. It was taken by Mr. Grayson in N. lat. 24°, W. long. 130°. In March, 1859, it was thrown ashore in considerable numbers at Monterey, California, from which place specimens were forwarded to us by Alex. S. Taylor, Esq.'

"From a letter from Mr G. E. MacGinitie of the Hopkins Marine Station at Pacific Grove, we learn of 'great quantities washed ashore on January 12, 1931, at the isthmus, Catalina Island'. In 1911 we got about two quarts in our dredge net in the course of a haul, made in 491 fathoms however, off Cape San Lucas, Lower California.... You may be interested to know, on the other hand, that upwards of 300 specimens of *M. quadrispina* were taken at one time by the Albatross in 238 to 310 fathoms, off Santa Barbara Island, April 12, 1904".

There is thus reason to believe that *Pleuroncodes planipes* (Plate IV, fig. 7) was the species seen by Captain Fagerli off the Mexican coast. Perhaps also it was this species that was recorded from Callao Harbour in 1830 by Guérin Méneville (below p. 476).

Swarms of the *Grimothea* stage of *M. gregaria* have been recorded from South American waters in all months from November to May inclusive, but appear to have been seen most frequently in the early months of the year. Young (1925, p. 319) gives

a table showing the recorded occurrences of shoals of *Grimothea* in Otago Harbour, New Zealand, by months from 1898 to 1924 inclusive, from which it appears that they occur throughout the year, but are most frequent during the southern summer. He says, "It will be seen that they are practically always present during December, January and February, but the extent of the shoals varies considerably from year to year. They have been exceedingly plentiful during 1923 and 1924. When the spring shoals make their first appearance the individuals are nearly transparent, the eyes and a red spot on the carapace being the most prominent features; but they grow very rapidly, and the colouring becomes a more intense red as time goes on. By the beginning of December the whole of the body is a brilliant red, with a very much darker spot on the carapace".

Most of the specimens of *M. subrugosa* and *M. gregaria* in the Discovery collections were taken during the third quarter of the moon (21 to 0 days of age); but no lunar period of swarming is indicated, as the specimens from St. 67 were taken when the moon was 12 days old, while Captain Fagerli says that the shoals of *Grimothea* and also of adult *M. gregaria* off the coast of Patagonia were seen practically daily from January to May.

CHARACTERS SEPARATING *MUNIDA SUBRUGOSA* AND *M. GREGARIA*, AND THEIR POST-LARVAL STAGES

M. subrugosa and *M. gregaria* are distinguished from each other by a number of characters which were clearly defined by Lagerberg (1906, p. 6). They are—the shape and direction of the rostral spine; the shape of the carapace and degree of development of the spines at the antero-lateral corners of it; the length of the eyestalk and shape of the cornea; the shape and spinulation of the merus of the chelae; the form of the endopodite of the external maxilliped; and the shape of the abdomen in cross-section, and its spinulation. These differences are not particularized here as they are given in detail in parallel columns by Lagerberg, but figures illustrating them are appended (Fig. 1). The most obvious distinction between the two species is, however, in the form of the eyes, and by this character alone they can be readily distinguished. In *M. subrugosa* they are directed forwards and are short, but with a large cornea, and in dorsal view with a strongly concave dividing line between cornea and stalk (Fig. 1 *c*). In *M. gregaria* they are directed outwards and the whole eye is distinctly longer, but the cornea is smaller and the line of junction between cornea and stalk is nearly straight (Fig. 1 *c'*). Dr Kemp records the following note on the colour of the species (St. 51): "In *M. subrugosa* the carapace is pale reddish brown throughout, with the transverse ridges slightly darker. The central rostral spine is reddish, but the two lateral spines white. The eyes are directed forwards in life, with the upper surface of the eyestalks white. The chelipeds have a conspicuous dark brown patch at the base of the fingers, the finger tips and the dactyli of all the walking legs being white. The large spines are everywhere white at the tip and very dark brown at the base. *M. gregaria* is very dark brown throughout, often with a bluish tinge on the back of the carapace and chelipeds, and entirely without the diversity of colouring seen in *M. subrugosa*. In life the eyes are directed outwards".

The characteristic direction of the eyes persists in most of the preserved specimens. Dr Kemp's note continues: "The early post-larval stages of the two species differ widely. In *M. subrugosa* they live on the bottom and closely resemble the adult in colour. In *M. gregaria* they are pelagic, often found at the surface; in colour they are a clear red,

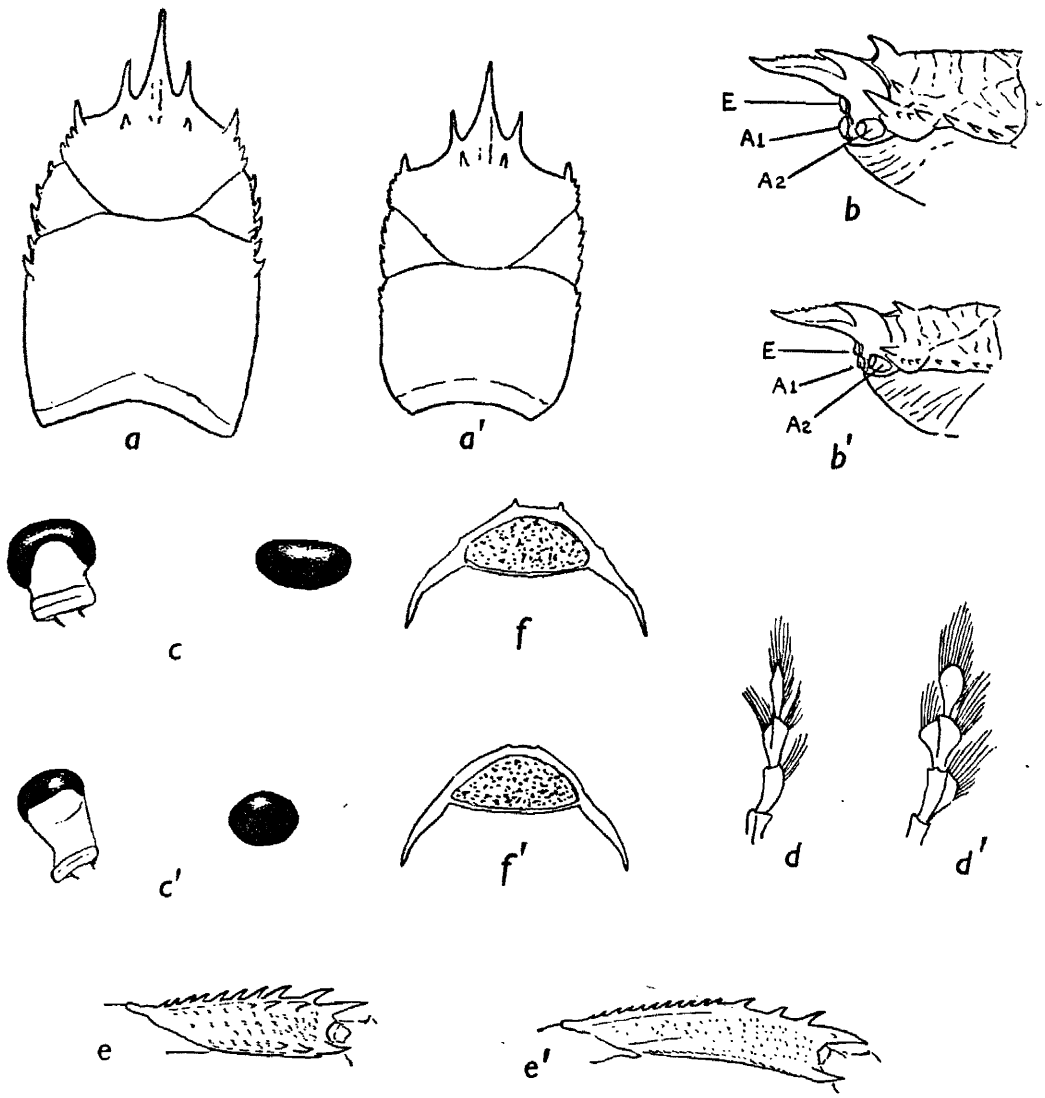

Fig. 1. *Munida subrugosa* (*a–f*) and *M. gregaria* (*a'–f'*).

a. Outline of carapace in dorsal view: × 1½.
b. Anterior part of carapace in side view: × 1½. *E*, insertion of eye; *A* 1, *A* 2, insertions of 1st and 2nd antennae.
c. Eye in dorsal and end views: × 3.
d. Terminal segments of third maxilliped: × 1½.
e. Internal surface of merus of chela: × 1½.
f. Cross-section of abdomen at 2nd abdominal segment: × 1½.

of great brilliance and transparency, with the stomach visible as a black mass. The food of this pelagic stage, in part at any rate, is diatoms, and individuals kept alive in a glass dish showed a strong positive heliotropism".

I am unable to find any important difference in structure between the early post-larval stage of *M. subrugosa* and the adult (Plate IV, figs. 1, 4).

The early post-larval *Grimothea* stage of *M. gregaria* (Plate IV, fig. 5) differs from the adult in addition to the above-mentioned characters, in size, being about 7–12 mm. in length of carapace as against the 20–38 mm. of the adult. The exoskeleton is much softer and less calcified. The spines and imbricating scales of the carapace, of the abdominal segments and of the limbs are more feebly developed than in the adult. The breadth of the carapace between the antero-lateral spines is relatively greater. The chelae and endopodites of the external maxillipeds are longer in proportion and there is a greater development of setae upon them (Plate IV, fig. 5). The Rev. T. R. R. Stebbing (1919, p. 330) records and figures an early larval stage of *M. gregaria* 2 mm. in length. I am unable to find any other description or figure of the larval stages of either *M. gregaria* or *M. subrugosa*, though Young (1925, p. 319) records from MSS. at the Otago Fish Hatchery that Anderton hatched out larvae of *M. gregaria* on September 28, 1908 and October 4, 1914.

The stage in the life history when the *Grimothea* of *M. gregaria* assumes the adult characters and takes to the bottom appears to vary. The largest *Grimothea* in the Discovery collections measures 12 mm. in length of carapace (St. 51), while the smallest *M. gregaria* with adult characters measures 13 mm. (Plate IV, fig. 6) in length of carapace (St. 51). On the other hand, the specimens taken from swarms at the surface off the Patagonian coast vary in carapace length from 18 mm. (S.S. 'Ernesto Tornquist', 27. iii. 29) to 33 mm. (S.S. 'Ernesto Tornquist', 5. iv. 29) (Plate IV, fig. 3). These appear to be adult, but all have a number of *Grimothea* characters, so that they are almost intermediate between the *Grimothea* stage and the bottom-living adult. Allowing for the fact that the specimens are preserved in formalin, whilst the remainder of the collection, with the exception of the *Grimothea* specimens from St. WS 100, are preserved in spirit, they nevertheless appear to have been less heavily calcified than specimens taken on the bottom. In addition they have a smaller development of spines, particularly those on the antero-lateral corners of the carapace, the chelae are longer and more slender and have a greater development of setae, as also do the external maxillipeds, which are longer in proportion to the total body length (cf. Plate IV, figs. 2 and 3).

This confirms in part the views of Chilton (1909, p. 612, see below, p. 479). He argues that the *Grimothea* stage may remain pelagic for a longer or shorter time, depending on the abundance of food at the surface and the availability or otherwise of a suitable bottom to which the *Grimothea* may descend and become adult. He thinks that the *Grimothea* may become bottom-living at an early age or, alternatively, may continue pelagic and become sexually mature and breed at or near the surface. The small specimen with adult characters from the bottom, and the large ones with *Grimothea* characters from the surface, recorded above, support this view. They do not, however, uphold Chilton's contention that *M. subrugosa* and *M. gregaria* are one and the same species. The abundance of the large surface-living form off the coast of Patagonia is probably due to a plentiful food supply, but what other biological or physical factors determine whether the *Grimothea* shall continue pelagic or take to the bottom are unknown. Off the Patagonian coast the swarms do not remain pelagic because there is no suitable

bottom available, as the sea off this coast is very shallow up to 100 miles off shore, and the swarms were seen from the shore line out to water 70 fathoms deep. It is noteworthy in this connection that the allied anomuran species *Pleuroncodes planipes* is pelagic when adult and occurs in similar enormous swarms, as detailed above (p. 472).

NOTE ON THE HISTORY OF THE SPECIES

I place here a summary of the somewhat involved literature relating to the specific distinctions of *M. subrugosa* and *M. gregaria* and its *Grimothea* stage.

In 1793 Fabricius described the specimens of the immature pelagic form taken by Banks in the South Atlantic (latitude 37° 30′) during Cook's first voyage. These he named *Galathea gregaria*. In 1820 Leach placed the species in a new genus which he named *Grimothea*, its chief distinguishing character being the foliaceous external maxilliped. In this he was followed by Desmarest in 1825. In 1830 Guérin Méneville, in his report on the results of the voyage round the world of 'La Coquille', recorded and figured specimens from Callao Harbour. Milne Edwards, in 1837, thought he could distinguish the specimen figured by Guérin Méneville from the typical *Grimothea gregaria* by the small size of the telson and proposed the name *Grimothea Duperreii* for Guérin Méneville's specimens. This is only a synonym.

In 1843 the Erebus and Terror Expedition brought back from the Auckland Islands specimens of an adult bottom-living form with cylindrical external maxillipeds. These were named *Galathea subrugosa*, but not described, by White in 1847, in his list of Crustacea in the British Museum. The plates for the report on the Crustacea of the expedition, including figures of the species, were at that time engraved, but they were not published until 1874 (Miers, 1874, Plate 3). Dana, in 1852, in his *Crustacea of the United States Exploring Expedition* described a specimen from Tierra del Fuego and referred it with doubt to White's *M. subrugosa*. He had apparently seen the unpublished plates of the Erebus and Terror report to which he makes reference. He also recorded abundant specimens of *Grimothea gregaria* from Tierra del Fuego. He described and figured both forms. During the voyage of H.M.S. 'Nassau', 1866–9, R. O. Cunningham (1871) found *Galathea subrugosa* common in the Straits of Magellan and off the west coast of Patagonia. He also recorded *Grimothea gregaria* from the Falkland Islands and from between the Magellan Straits and the Falkland Islands.

In 1874 the report on the Crustacea of the Erebus and Terror Expedition was published, and in it Miers briefly described *Munida subrugosa*. He stated that in his opinion the specimens figured by Dana were specifically distinct as they differed in the number and arrangement of the spines on the carapace and in the shape of the hands. No mention is made of *Grimothea gregaria*, though Cunningham in 1871 had stated that he had seen a sketch of the species by Dr Hooker done from a specimen taken at the south of Tierra del Fuego during the Erebus and Terror Expedition. Filhol in 1874 recorded a large series of specimens of *Munida subrugosa* from Campbell Island and stated that they were identical with specimens from Port Famine (Straits of Magellan). He also recorded the immature form from Stewart Island and Cook Strait, and dis-

tinguished it from *Grimothea gregaria* by the slightly longer external maxillipeds (foliaceous in both forms) and named it *Grimothea novae-zelandiae*. This distinction, however, is not valid. He did not consider it to be the young of *M. subrugosa* from which it is distinguished by the foliaceous external maxillipeds. Miers, in the catalogue of New Zealand Crustacea, 1876, described *M. subrugosa* and added: "I think it quite possible that the *Grimothea gregaria*, Leach, very common at the Falklands, and in the Straits of Magellan, is the immature condition of *M. subrugosa*. The only difference of any importance between them consists in the elongated foliaceous external maxillipeds of *G. gregaria* on which Leach established the genus *Grimothea*, and it is also a much smaller species. But in a large series of specimens in the National Collection named, I think rightly, by Dr Cunningham *M. subrugosa*, and obtained at various points at the southern extremity of the American continent, there is considerable variation in the length of the external maxillipeds. On the other hand, specimens agreeing with *G. gregaria* in all respects have just been received by the British Museum from New Zealand. I have not, however, been able to observe a *complete* gradation between the two species. The hands in *G. gregaria* are granulous, in *M. subrugosa* they are usually spinulous".

Targione Tozzetti in 1877 described and figured specimens of *M. subrugosa* from western Patagonia. His specimens conformed with Dana's description and figure. In 1878 Hutton recorded specimens of *M. subrugosa* from the Auckland Islands and he evidently thought that they were a distinct species from *Grimothea gregaria* for he said, "The young specimen is quite as small or smaller than *Grimothea gregaria*, so abundant round the South Island in March, and yet it does not show the slightest approach to the foliaceous maxillipeds of *Grimothea*. The habits of the two species are also quite different. *Grimothea* is pelagic and floats on the surface of the sea, while *Munida* lives at the bottom". However, in 1881 Miers received further specimens from the Straits of Magellan taken during the survey of H.M.S. 'Alert', and in discussing these he stated that the British Museum had received specimens from New Zealand identical with those from Patagonia, though the type specimens (from New Zealand) differed slightly. From this he concluded that Dana's *M. subrugosa* was identical with that of White and of Cunningham. He also considered *Grimothea gregaria* to be only the young form of *M. subrugosa*, for which he adopted the name *Munida gregaria*.

Henderson's Challenger Report in 1888 recorded specimens of *M. subrugosa* from Patagonia, Falkland Islands, off Montevideo and Bass Strait. No specimens of *Grimothea gregaria* were taken by the 'Challenger', but two specimens were received from Wellington Museum (New Zealand). The Challenger specimens did not support the view that *Grimothea gregaria* was the young stage of *M. subrugosa*, as there were some that were not more than one-third of the size of ordinary specimens of *Grimothea*, which yet had all the characters of the adult *M. subrugosa* and were taken on the bottom along with them. Henderson, however, pointed out that the general appearance of *Grimothea* favours the theory of immaturity and that the only essential difference between *Grimothea* and *M. subrugosa* is the length and foliaceous character of the external maxilliped, which

is doubtless an adaptation to pelagic life; and he admitted that it may "be possible that some of the newly hatched young pass to the surface and exist for a longer or shorter period in the *Grimothea* state". Henderson named his specimens from Bass Strait *M. subrugosa* var. *australiensis*; he distinguished them by the large development of spines and stated "in other respects this variety cannot be distinguished from the typical form of *M. subrugosa*; indeed on examining a series of the latter nearly all the above-mentioned spinules can be made out in different specimens, though I have failed to see any in which so many were present at the same time".

A. Milne Edwards, in 1891, in the report of the "Mission Scientifique du Cap Horn", gave a full description of *M. gregaria* and stated that *M. subrugosa* was a distinct species, basing his separation on several characters which depend on the size and sex of the individual, and on the foliaceous external maxilliped of *M. gregaria*.

G. M. Thomson in 1898 fully discussed the question as to whether *Grimothea gregaria* is the young stage of *M. subrugosa*. He said, "*Munida* has the exoskeleton rather hard, and exhibiting considerable complexity of imbricating scales and of spines on its surface, but, with the exception of its softer and thinner texture, *Grimothea* has the same spines and markings. The difference in the length and development of the external maxillipeds, on which Leach founded the latter genus, and on which Miers and Henderson lay so much stress, is after all a comparative one. In several large males of *Munida* the joints all show the flattened and foliaceous form characteristic of *Grimothea*, as well as the densely fringing setae, while in one large female the joints are completely foliaceous. To show the relative lengths of the parts in the two forms, I append a table of measurements of a few individuals taken at random.... The relative length of the body to that of the external maxilliped is about 5 to 2 in *Munida* and 5 to less than 3 in *Grimothea*. The sexes are usually present in about equal proportions in shoals of *Grimothea*.... Out of a large number of specimens of *Grimothea* all had the pair of spines at the side of the median line of the second, third and fourth abdominal segments, said by Miers to be characteristic of *Munida*. On the other hand, several male specimens of the latter wanted the characteristic 'spine on either side of the middle of the gastric region', while in some females they were but slightly developed. Until, then, the life history of these crustaceans is worked out I am inclined to treat *Grimothea gregaria* as merely a stage in the development of *Munida subrugosa*". The specimens that he identified as *M. subrugosa* (adult) were undoubtedly *M. gregaria*, hence the confusion.

In 1902 Lenz recorded specimens of *M. gregaria* from the Patagonian region and stated that he regarded *M. gregaria* and *M. subrugosa* as different species. In the same year Hodgson recorded examples of *M. subrugosa* from Auckland and Campbell Islands and said that "general opinion" did not support the view that *Grimothea gregaria* was the young stage of *M. subrugosa*, though the only good character separating them was the form of the external maxilliped. Benedict in 1903 stated that *Grimothea gregaria* was the young stage of the bottom-living form which he called *M. gregaria*. But he was not satisfied that the bottom-living form from the Cape Horn region was identical with that from New Zealand waters, which he consequently listed as *M. subrugosa*. He did not,

however, state whether he regarded the *Grimothea* of New Zealand waters as the young of *M. gregaria* or of *M. subrugosa*. Previous authors nevertheless have stated that they had specimens in every way identical from both localities.

In 1906 Lagerberg, working on the plentiful material of the Swedish South Polar Expedition, gave a comparative account of the species *M. gregaria* and *M. subrugosa*, showing that they differ in the form of the rostrum, the shape and spinulation of the carapace, the shape of the abdomen, the shape of the eyes and eyestalks, in the shape and spinulation of the chelae, and in the form of the external maxilliped.

Chilton in 1909 discussed the relationship between *Grimothea gregaria* and *M. subrugosa* and came to the conclusion that there was one species only. He said, "It is of course only natural that the immature form should be pelagic in habit, while the mature form inhabits the bottom of the sea; and it seems likely that in this case, just as in some other well-known animals, the immature stage may under certain circumstances be prolonged, and even become sexually mature without completely losing its immature characters. I consider then that the foliaceous maxillipeds of *G. gregaria* are associated with its pelagic habit, and that in the absence of favourable circumstances (e.g. a suitable sea bottom at moderate depth) it may continue pelagic, increase in size, and even become sexually mature without losing its foliaceous maxillipeds; but if it reaches a suitable locality it adopts a more sedentary life on the bottom of the sea and in its subsequent moults the external maxillipeds tend to become shorter and less foliaceous and are infolded instead of being kept extended as in the pelagic form". This opinion appears to be arrived at through confusing the adult *M. gregaria* and *M. subrugosa*, and in ignorance of Lagerberg's earlier paper.

In 1911 Ortmann recorded specimens of both species from Patagonia and verified the differences recorded by A. Milne Edwards. The Rev. T. R. R. Stebbing in 1914 recorded specimens of both species from the Falkland Islands, but noted Chilton's view, and pointed out that the generic name *Grimothea* appears to have precedence over *Munida*. In 1919 the same author recorded a very early zoea stage from the Falkland Islands.

EARLY RECORDS OF SHOALS OF THE *GRIMOTHEA* STAGE OF *M. GREGARIA*

Shoals of the pelagic *Grimothea* stage of *M. gregaria* have been noticed and recorded by navigators from as early as the sixteenth century.

In 1594 Sir Richard Hawkins ran into a cove in the Straits of Magellan of which he says, "They sounded a cove some sixteene leagues from the mouth of the Straite, which after we called Crabby Cove. It brooked its name well for two causes; the one for that all the water was full of a small kind of red crabbes; the other, for the crabbed mountains which overtopped it; a third, we might adde, for the crabbed entertainment it gave us".[1]

In 1598 when Simon de Cordes, Sebald de Wert and Dirk Gherritz were sailing south on March 12, "having passed Rio de la Plata, the sea appeared as red as blood. The water was full of little red worms which, when taken up, jumped from the hand like

[1] Hawkins, Sir Richard, *Observations in his voyage into the South Sea*, 1593. London, 1622.

fleas. Some were of the opinion that at certain seasons of the year the whales shake these worms off from their bodies, but of this they have no certainty".[1]

The chronicler of the voyage of Schouten and Le Maire in 1615 says, "towards 35½° [south] we saw those insects of which Sebald de Werd had spoken to us, and which made the sea quite red", while L'Heremite, when sailing for the coast of Brazil from Annobon which he had left on November 11, 1623, "on the 19th and 20th of January 1624 observed the sea discoloured with an infinite number of small shrimps".[2] On January 30 he made Cape de Penas, Tierra del Fuego.

Captain John Narborough, commanding H.M.S. 'Sweepstakes', in 1670, records, "Tuesday February 1st. Foggy weather; several beds of sea weeds floating in the water and sea fowls striking about them for small fish. It fell calm in the afternoon; we had many small shrimps about the ship and eight young seals came close to us. This evening I sounded but had no ground at 130 fathoms....February 5th. We were this day in latitude 41° S and longitude west from the Lizard 52° 50'".[3]

Dampier says, in the account of his voyage round the world, under January 28, 1683, "The day that we made these islands [the 'Sibbel de Wards', now called the Jason Islands, off the north west point of the Falkland Islands] we saw great Sholes of small Lobsters, which coloured the Sea red in spots, for a mile in compass, and we drew some of them out of the Sea in our Water-buckets. They were no bigger than the top of a Man's little Finger, yet all their Claws, both great and small like a Lobster. I never saw any of this sort of Fish naturally red but here; for ours on the *English* Coast, which are black naturally, are not red till they are boiled: neither did I ever anywhere else meet with any Fish of the Lobster-shape so small as these; unless, it may be, Shrimps or Prawns: Capt. *Swan* and Capt. *Eaton* met also with Sholes of this Fish in much the same Latitude and Longitude".[4] Cowley, who sailed with Dampier, also records the occurrence of the red lobsters.

In 1696 De Gennes, sailing down the Patagonian coast at the end of January, found "the sea so covered with little lobsters that one could say the sea was red with them. We took up more than ten thousand of them in baskets".[5]

Le Hen-Brignon records that on March 7, 1747, in 42° 22′ S, off the coast of Patagonia, "at 6 in the evening we saw an enormous number of little red fish, of the size and shape of a small lobster. They had two fairly long pincers at the front of the head".[5]

Commodore Byron says that on November 14, 1764, "the sea appeared as red as blood, being covered with a small shell fish of that colour, somewhat resembling our crayfish, but less, of which we took up great quantities in baskets".[6] The following day his position was 45° 21′ S, 63° 2′ W.

[1] Translated from Des Brosses, *Histoire des Navigations aux Terres Australes*. Paris, 1756.

[2] Prior, S., *All the voyages round the world*. London, 1820.

[3] Burney, J. A., *Chronological History of Voyages and Discoveries in the South Seas*. London, 1803–17.

[4] Dampier, W. A., *New Voyage Round the World*. 7th edition, London, 1717.

[5] Translated from Des Brosses, *Histoire des Navigations aux Terres Australes*. Paris, 1756.

[6] Hawkesworth, *Account of the Voyages undertaken by order of His present Majesty for making Discoveries in the Southern Hemisphere*. London, 1773.

Captain Wallis, commanding H.M.S. 'Dolphin', says that when in 48° 56′ S, 65° 6′ W, on December 9, 1766, "this day we saw such a quantity of red shrimps about the ship that the sea was coloured with them".[1]

Sir Joseph Banks during Cook's first voyage found *Grimothea* off the coast of Patagonia. He says,[2] "2nd January 1769. Met with some small shoals of red lobsters, which have been seen by almost everyone passing through these seas; they were, however, so far from colouring the sea red, as Dampier and Cowley say they do, that I may affirm that we never saw more than a few hundreds of them at a time. We called them *Cancer gregarius*". On his return he sent his specimens to Fabricius who first described the species scientifically and named it "*Galathea gregaria*".

It is apparent from most of the above accounts that the animals referred to are the pelagic *Grimothea* stage of *M. gregaria*.

LOBSTER-KRILL THE FOOD OF BIRDS AND FISHES

As would be expected, the abundant shoals of the *Grimothea* stage of *M. gregaria* are eagerly preyed upon by other animals. Thomson, 1898, records that "*Grimothea* occurs in our [New Zealand] seas, especially in the summer months, in enormous shoals, which frequently colour large areas bright red. These shoals consist often of immense numbers of individuals, of which such masses are thrown up on the beaches as at times to create a stench.... They constitute a very common article of food for both fishes and sea birds. Even in midwinter when none have been seen swimming about, I have got them in hundreds in the stomachs of red- and blue-cod and hapuku". Anderton, 1906, says, "During the season that the 'whale feed' is in the ocean and the bay the stomachs of almost all fish, including flat fish, have been found to contain large numbers of them, and it is certain that they constitute one of the most important fish foods, and no doubt play a considerable part in the migration of many fish".

E. R. Waite, 1909, speaking of the Auckland Island Shag says, "One of the most striking features of the voyage was presented during our passage down the Auckland coast. In the offing the sea was black in patches with shags, and by the aid of a glass or when sufficiently near to such a body we noted that considerable commotion was taking place. The birds were evidently feeding; their food, whatever its nature, being scattered over wide areas, but evidently closely packed where it occurred. At the time I considered the birds were catching fish, but later changed my views. It is quite impossible to convey any idea of the number of birds thus engaged. In passing from the shore to their feeding grounds, or in the reverse direction, their flight behind, over and in front of the vessel was a constant stream, and this continued for many miles. The birds returning to the shore were noticed to be heavy with food; their bodies were fully distended and the flight in consequence distinctly laboured....A flat stretch of rock below our camp at the Auckland Islands proved to be a favourite assembling ground for shags and we had no trouble in observing them....I examined the stomachs of others

[1] See note 6 on p. 480.

[2] Banks, Sir J., *Journal during Captain Cook's first voyage*. Ed. Sir J. Hooker. London, 1896.

and found them to be crowded with small crustaceans resembling *Munida*: one contained small fish bones in addition.... I examined the stomachs of our captures and in every case found them to contain the reddish mass which I have above attributed to partially digested *Munida*. Since the foregoing was written Prof. Benham writes to me, 'the Shags that were opened had the stomach filled with the crustacean *Munida subrugosa*'".

Young (1925) says, "When the shoals are on the surface [of Otago Harbour] the stomachs of most of the fish caught are found to be crammed with whale feed".

LOBSTER-KRILL AS WHALE FOOD

M. gregaria is the species to which the term "lobster-krill" is mainly applied, though, as is shown above, *Pleuroncodes planipes* is also probably included under this name. In New Zealand the *Grimothea* stage of *M. gregaria* is known as "whale-feed". Chilton in 1904 appears to be the first to print this name, and Anderton in 1906 and Young in 1925 use the same expression.

In 1926 Sir Sidney Harmer received from the New Zealand Government Offices in London a series of photographs of whaling in New Zealand waters. Copies of seven of the photographs are now in the British Museum. These show phases of the chase and capture of Humpback whales from motor launches in the waters of Cook Strait. The most interesting photograph, however, is of ten specimens of the *Grimothea* stage of *M. gregaria*. This photograph is labelled "Euphausians or Plankton. Alive whale's feed on a plate (so called), like small lobsters and red. The sea is red for acres and humpback whale open their mouths and swim through". The photograph shows quite clearly and unmistakably that the whale-feed is the *Grimothea* stage of *M. gregaria*. Mr Drew, Publicity Officer at the New Zealand Government Offices, kindly informed the writer that the whaling station at which these photographs were taken is known as Te Awite and is situated in the South Island on the shore of Tory Channel which connects Queen Charlotte Sound with Cook Strait. He has himself seen the sea coloured red by "whale-feed" over large areas in Cook Strait, and he understands that similar shoals are met with on the whaling grounds off Cape Brett, Bay of Isles, on the east coast of the North Island.

It is clear, then, that the *Grimothea* stage of *M. gregaria* forms the food of the Humpback whale in New Zealand waters, at least on occasion. From the great abundance of the shoals of "whale-feed" it appears to be probable that their occurrence may have an important bearing on the migrations of the Humpback whale in the New Zealand seas.

I am able to record that other species of whale also feed upon the shoals of *M. gregaria*, both in the adult and *Grimothea* stages. A whaling station operated from 1908 to 1916 at New Island in the Falkland Islands, where *Grimothea* is known to be plentiful at times. The *Grimothea* has features so distinctive that it needs no scientific training to recognize it as different from the usual Euphausian krill eaten by whales, and consequently the writer sought information on the point. However, as the station at New

Island was closed sixteen years ago, it is difficult now to trace anyone who worked there or who would be able to give reliable information on the question. Herr Sigurd Risting, of Sandefjord, Norway, is likewise unable to trace anyone at this distance of time. Dr Kemp adds that he has made many enquiries without result. The information received from Captain Fagerli, however, shows that on the Patagonian coast *M. gregaria* and its *Grimothea* stage form the food of the Sei whale. During the seasons 1927–8 and 1928–9 between 1300 and 1400 Sei whales were taken, all of which were feeding on lobster-krill. Both adult *M. gregaria* and the *Grimothea* stage were found in the whales; nearly always the stomachs contained either adults or *Grimothea*, rarely both. Many whales were taken feeding at or near the surface, but there is no evidence indicating that any were feeding on adult *M. gregaria* at the bottom. The same lobster-krill was also found in Humpback and Right whales, two of the former and three of the latter having been taken. Three Blue whales were taken, but none had this krill in the stomach. In 1926 at Magdalena Bay on the Pacific coast of Mexico where similar shoals, presumably of *Pleuroncodes planipes*, were seen, the Sei, Humpback and Pacific Grey, but not the Blue whales, were found to be feeding on these crustacea.

Captain Fagerli noticed that the blubber oil obtained from Sei whales on the Patagonian and Mexican coasts was always of a definitely yellowish colour, quite unlike that obtained from this species elsewhere. He believes that the difference in colour is produced by feeding on lobster-krill.

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PLATE IV

Fig. 1. *Munida subrugosa*. ♂ from St. 51, 37 mm. in length of carapace. Note forwardly directed eyes and characters of endopodite of third maxilliped.

Fig. 2. *Munida gregaria*. ♂ from St. 51, 38 mm. in length of carapace. Note outwardly directed eyes and characters of endopodite of third maxilliped.

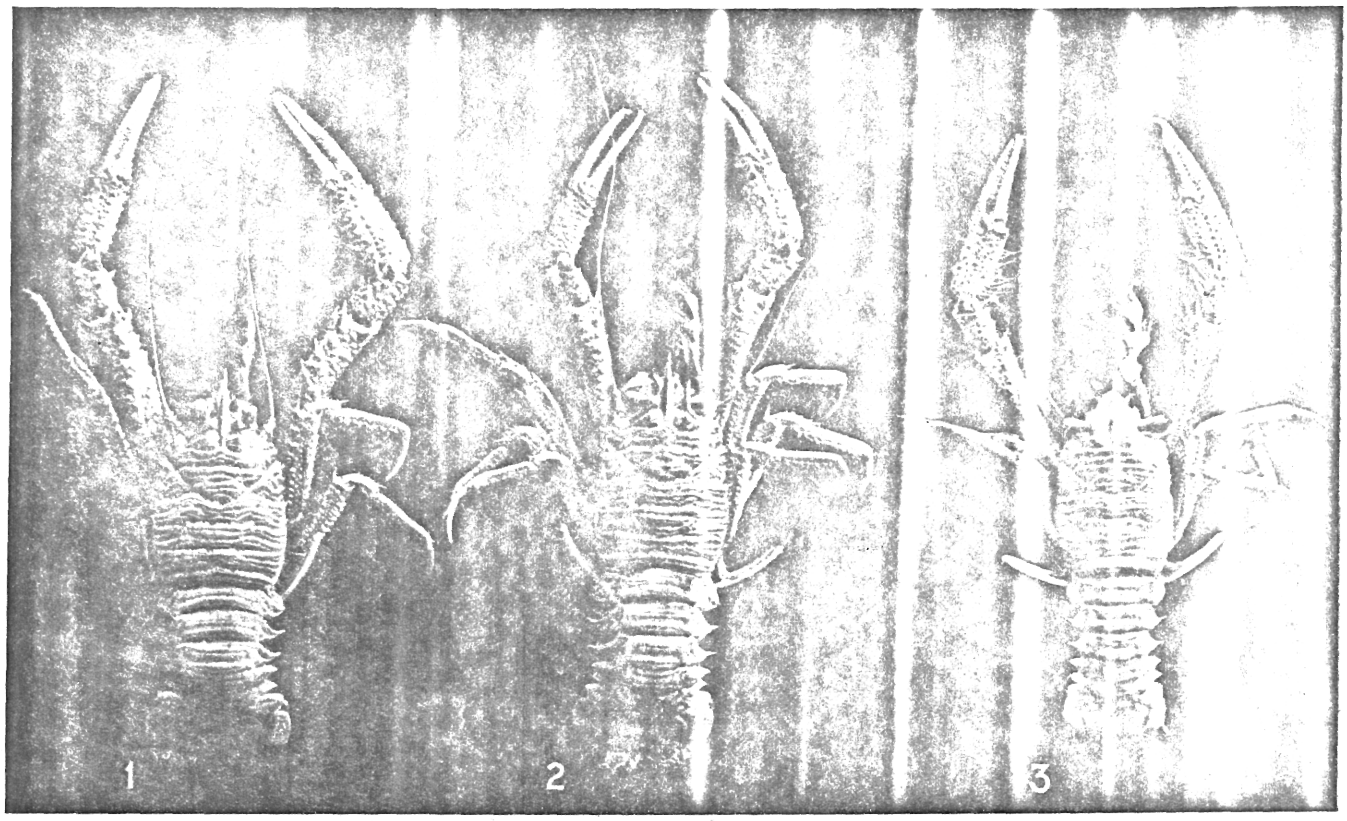
Fig. 3. *Munida gregaria*. ♂ collected by the S.S. 'Ernesto Tornquist', 33 mm. in length of carapace. Note broadly foliaceous endopodites of third maxilliped and slender merus of chelae.

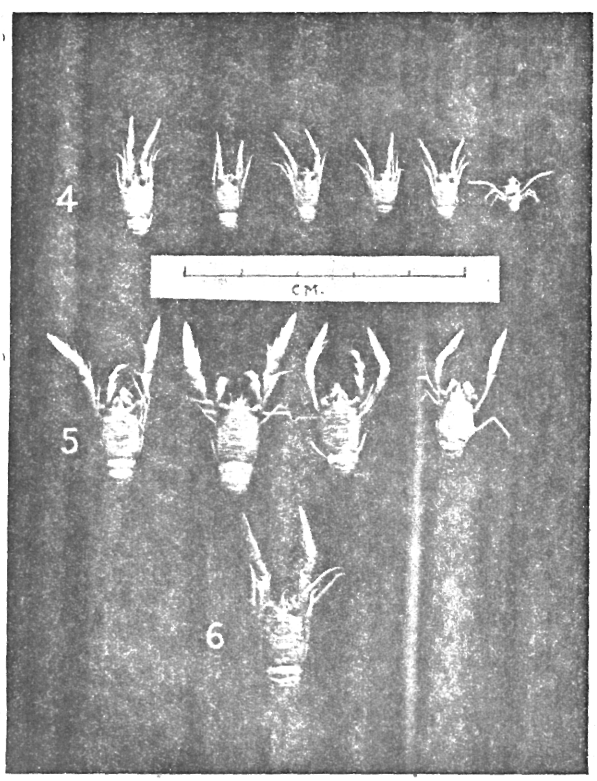
Fig. 4. *Munida subrugosa*. Post-larval young from the bottom: St. 51.

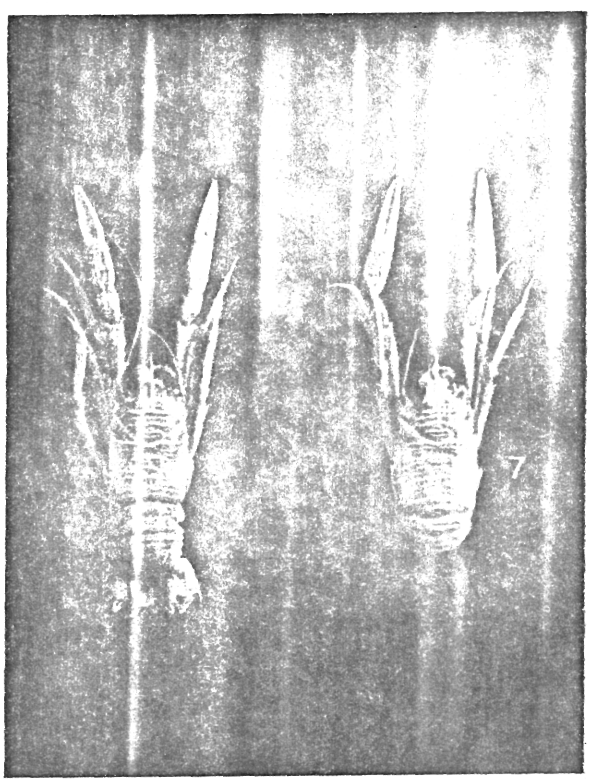
Fig. 5. *Munida gregaria*. Post-larval pelagic young (*Grimothea* stage): St. 67.

Fig. 6. *Munida gregaria*. The smallest specimen with adult characters in the collection. Length of carapace 13 mm.: St. 51.

Fig. 7. *Pleuroncodes planipes*. ♂ (left) and ♀ (right) from Magdalena Bay, Lower California, kindly supplied by Dr Waldo L. Schmitt.







LOBSTER-KRILL: *MUNIDA* AND *PLEURONCODES*