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AUSTRALIAN NATIONAL ANTARCTIC RESEARCH EXPEDITIONS

# ANARE RESEARCH NOTES 1

A guide to the Euphausiacea of the Southern Ocean

John M Kirkwood

INFORMATION SERVICES SECTION  
ANTARCTIC DIVISION  
DEPARTMENT OF SCIENCE AND TECHNOLOGY

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A N A R E

R E S E A R C H

N O T E S

1

A guide to the Euphausiacea of the Southern Ocean

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## SOURCES OF ILLUSTRATIONS

The figures listed below have been modified after the indicated sources. Original figures are not included in this list, and the sources of maps and tables will be cited in the text.

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4, 5	Mauchline (1980b)
11	Boden (1954)
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26 to 32	Boden (1954)
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A GUIDE TO THE EUPHAUSIACEA OF THE SOUTHERN OCEAN

by

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ABSTRACT

A general guide to the Euphausiacea of the Southern Ocean is presented, with emphasis on the Antarctic species and in particular on Euphausia superba. Keys to the Euphausiacea on either side of the Antarctic Convergence are provided, and all species mentioned in the keys have their distributions mapped. Short descriptions of the biology of Euphausia superba, Euphausia crystallorophias, Euphausia frigida, Euphausia triacantha, Euphausia vallentini, Thysanoessa macrura, Thysanoessa vicina and Bentheuphausia amblyops are also given. The larval development of the five most common Antarctic species, Euphausia superba, Euphausia crystallorophias, Euphausia frigida, Euphausia triacantha and Thysanoessa macrura is outlined and compared. The sexual maturation of Euphausia superba is described, and a description of the various methods employed in measuring Euphausiaceans is provided. A glossary of technical terms has also been compiled.



## 1. INTRODUCTION

The aim of this handbook is to provide a general guide to the Euphausiacea of the Southern Ocean, with particular emphasis on Euphausia superba Dana (Antarctic krill). It is designed for use by non-specialists, and for this reason a glossary is provided and all important features mentioned in the keys and the text are illustrated.

For the purposes of this paper, the Southern Ocean is that body of water south of the southern continents (Australia, Africa and South America) and surrounding Antarctica. There are two major circumpolar surface water masses in the Southern Ocean, the boundary between them being the Antarctic Convergence. Few species of the Euphausiacea are found on both sides of this convergence, so separate keys have been prepared for the species on each side.

The Euphausiacea consists of two families, the Euphausiidae (85 species) and the Benth euphausiidae (one species). It is an entirely marine order of the Crustacea, being generally shrimp-like in appearance. The Euphausiacea was previously lumped together with the order Mysidacea in a discarded group known as the Schizopoda. This association is considered to be artificial, and these two orders are now placed in different super-orders. Table 1 and Figures 1, 2 and 3 illustrate some of the more obvious differences between the shrimps (Natantia), the Mysidacea and the Euphausiacea.

<u>FEATURE</u>	<u>ORDER MYSIDACEA</u> (Peracarida)	<u>ORDER EUPHAUSIACEA</u> (Eucarida)	<u>SUB-ORDER NATANTIA</u> (Eucarida:Decapoda)
Carapace	Free of last 4 thoracic segments	Fused to all thoracic segments	Fused to all thoracic segments
Gills	Enclosed by carapace	On bases of thoracic legs	Enclosed by Carapace
Maxillipeds	Thoracic legs I, or I and II	Absent	Thoracic legs I, II and III
Statocysts	On endopod of uropods	Absent	On antennular peduncle
Broodpouch	Present	Absent*	Absent
Heart	Elongate	Short sac	Short sac

\*Females of the genera Nyctiphanes, Nematobrachion, Nematoscelis and Stylocheiron carry their fertilised eggs in sacs held by the thoracic legs, but as these sacs are not ingrowths from a thoracic leg they are not true broodpouches.

Table 1. Comparison of the features of the orders of Mysidacea and Euphausiacea and the sub-order Natantia.

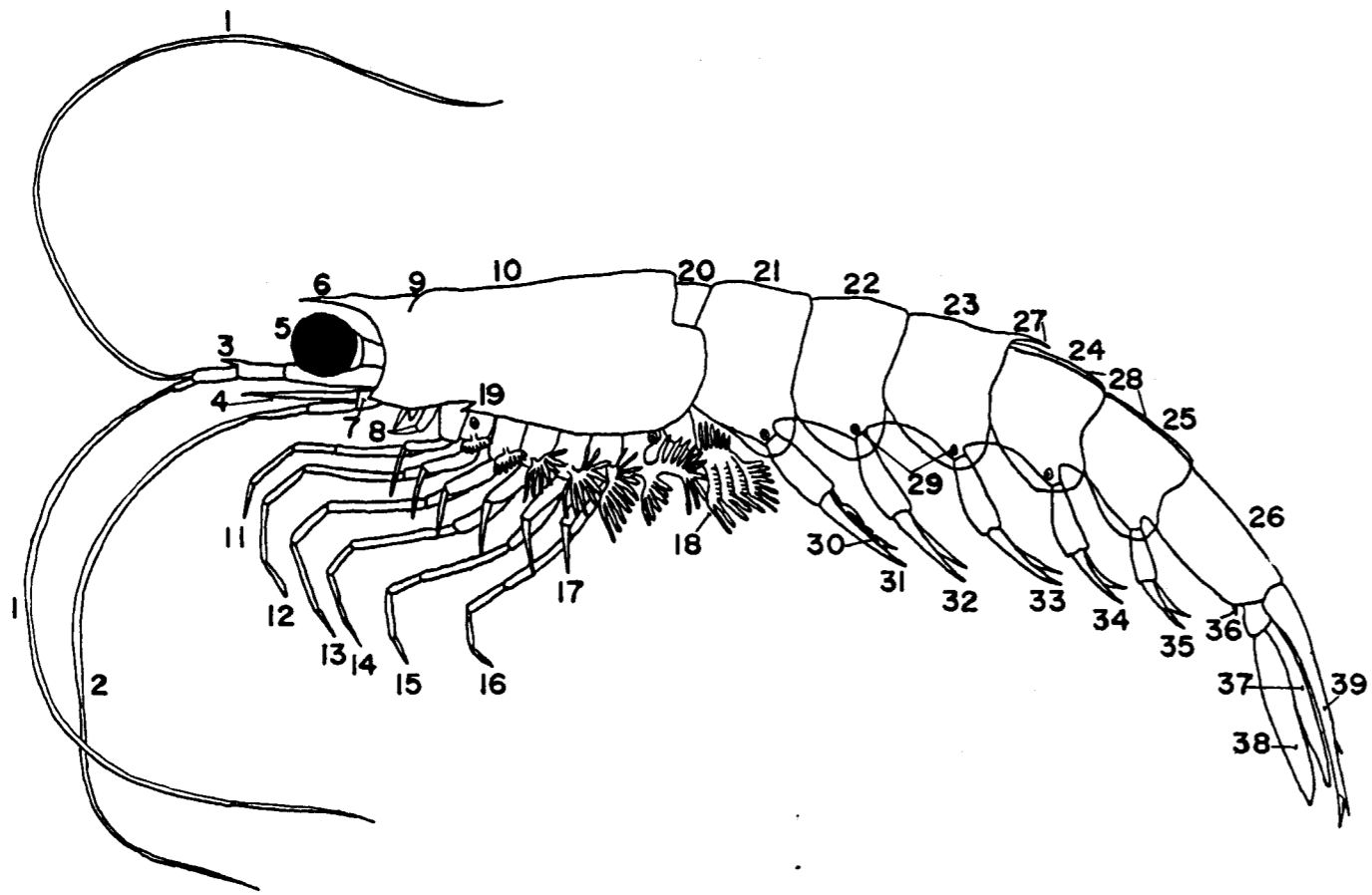


Figure 1. External morphology of an euphausiid (setae omitted). 1, flagellae of antennule; 2, flagellum of second antenna; 3, antennule lappet; 4, antennal scale (scaphocerite); 5, compound eye; 6, rostrum; 7, antennal peduncle; 8, mouthparts; 9, cervical groove; 10, carapace; 11-16, thoracic legs I-VI (endopods); 17, exopod of thoracic appendage VI; 18, gills (podobranchiae); 19, spine; 20, intermediate plate; 21-26, abdominal segments I-VI; 27, dorsal spine; 28, dorsal keels; 29, photophores (luminescent organs); 30, petasma (males only); 31-35, pleopods; 36, pre-anal spine; 37, endopod of uropod; 38, exopod of uropod; 39, telson.

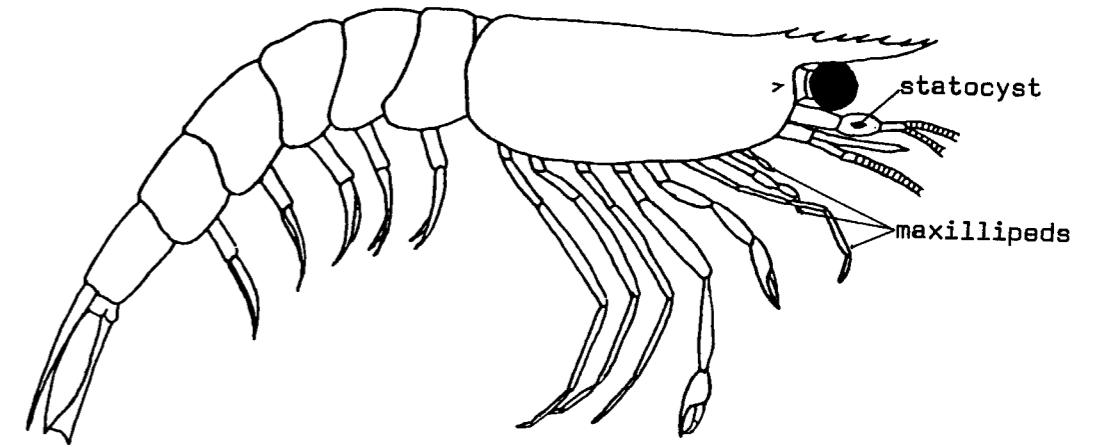


Figure 2. Natant Decapod

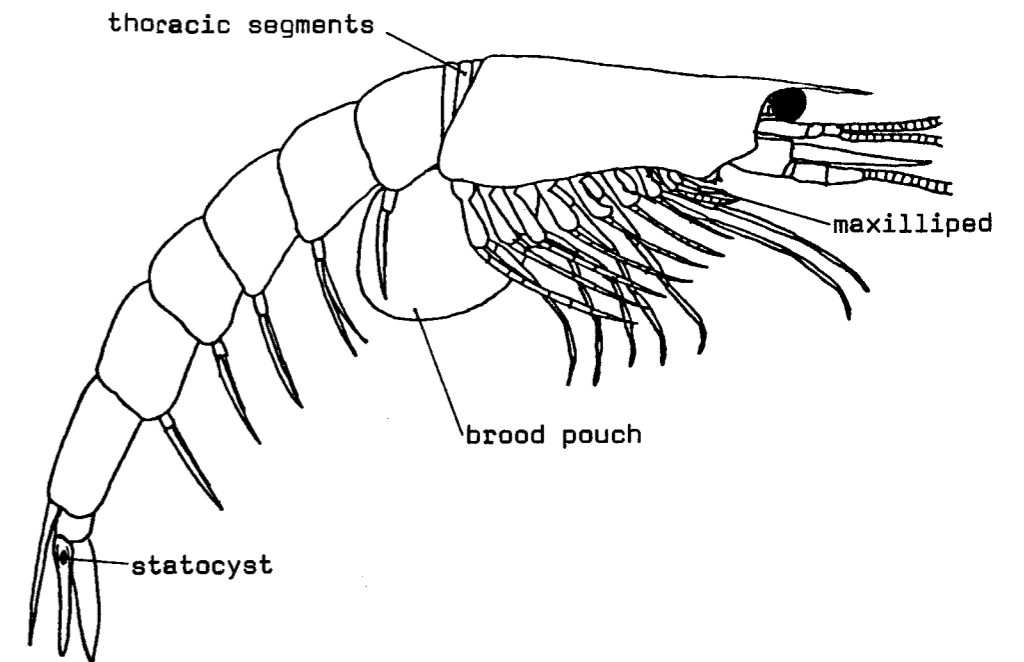
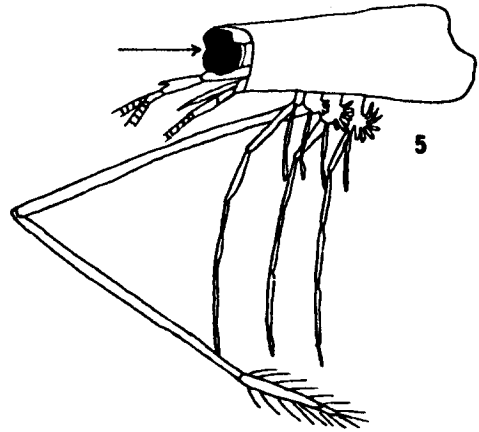
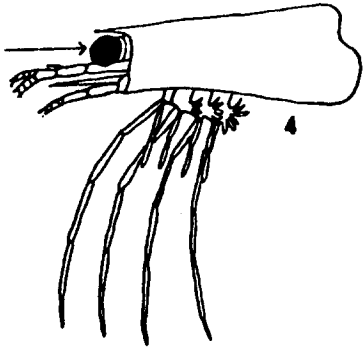


Figure 3. Mysid

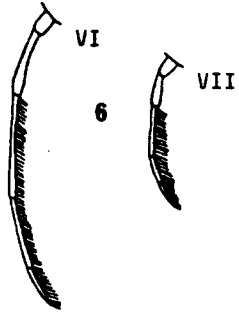
2. KEY TO THE EUPHAUSIACEA FOUND SOUTH OF THE SOUTHERN CONTINENTS  
BUT NORTH OF THE ANTARCTIC CONVERGENCE

Modified after Lomakina (1966), Mauchline and Fisher (1969).

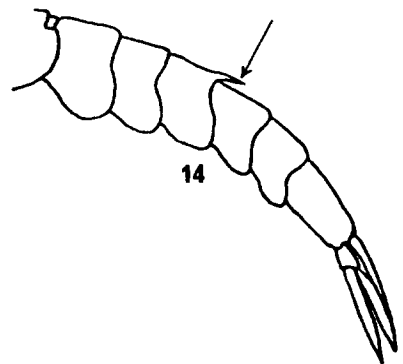
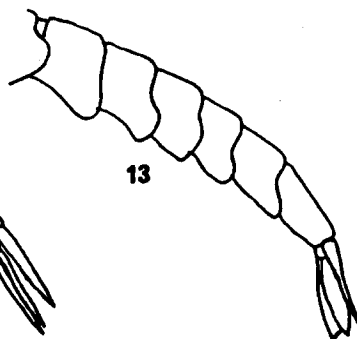
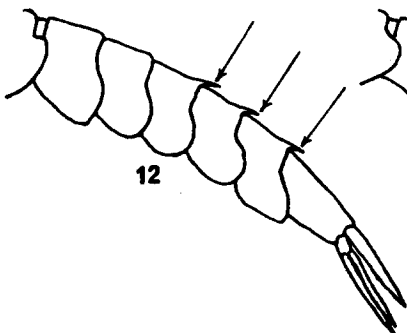
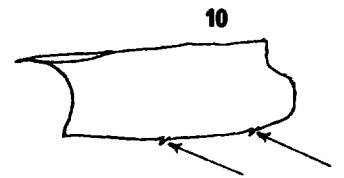
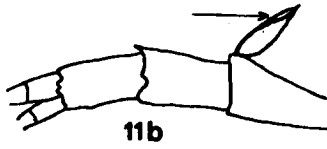
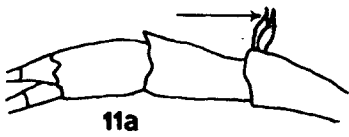
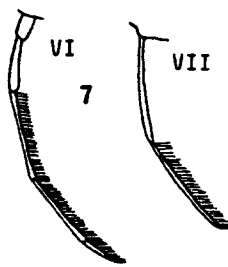
1. a) All thoracic legs well developed. Pleopods I and II of males without petasmas. Do not possess luminescent organs. Have a transverse suture on exopod of uropods. .... Family BENTHEUPHAUSIIDAE  
 .... Bentheuphausia amblyops G.O. Sars
- b) Thoracic legs VIII, and often VII, rudimentary. Pleopods I and II of males modified as petasmas. Possess luminescent organs. No transverse suture on exopod of uropods. .... Family EUPHAUSIIDAE .... 2
2. a) Eyes more or less round. No thoracic leg elongate and modified as a predatory leg (Figure 4). .... 3
- b) Eyes bilobed. Thoracic legs II or III elongate and modified as predatory legs (Figure 5). .... 13
3. a) Endopod of thoracic appendage VII developed and segmented (Figures 6 and 7). .... 3
- b) Endopod of thoracic appendage VII rudimentary and unsegmented.  
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4. a) Endopod of thoracic appendage VII made up of the usual five segments, but slightly shorter than other thoracic legs (Figure 6).  
 .... genus Thysanopoda .... 5
- b) Endopod of thoracic appendage VII made up of only two segments, but is equally as long as other thoracic legs (Figure 7).  
 .... Nyctiphanes australis G.O. Sars
5. a) Carapace with a distinct cervical groove (Figure 8). Sixth abdominal segment longer than the fifth. .... Thysanopoda egregia Hansen
- b) Carapace without a distinct cervical groove (Figure 9). Sixth abdominal segment shorter than the fifth.  
 .... Thysanopoda acutifrons Holt and Tattersall
6. a) Two pairs of spines on lower edge of carapace (Figure 10). Antennule lappet directed upwards in females (Figure 11a) and slightly recurved in males (Figure 11b). .... Euphausia recurva Hansen
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- b) Antennule lappet consisting of a single lobe. .... 11



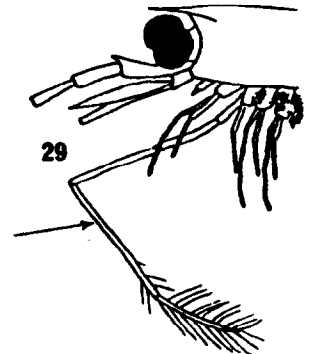
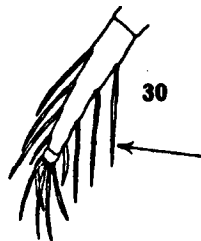
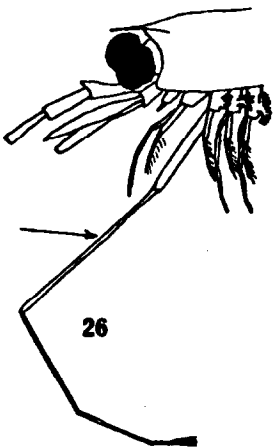
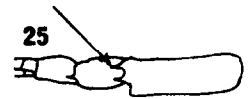
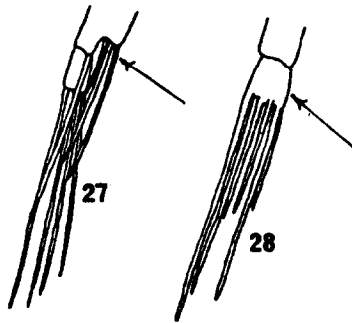
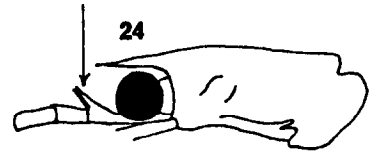
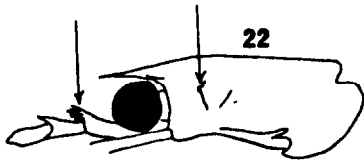
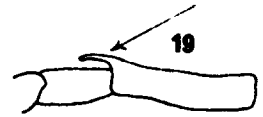
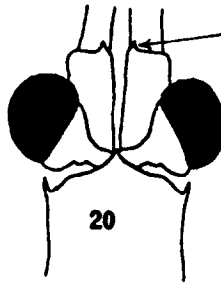
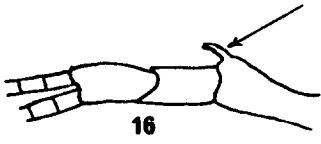
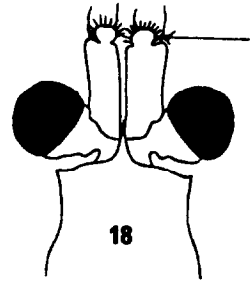
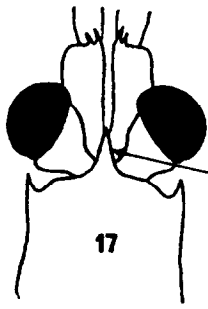
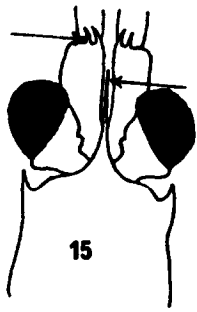
thoracic legs



thoracic legs



9. a) Posterior mid-dorsal spine on abdominal segment III. (Figure 14).  
       .... Euphausia similis v. armata Hansen
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       .... Euphausia similis v. crassirostris Hansen
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       .... Euphausia vallentini Stebbing
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       .... Euphausia lucens Hansen
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       Antennule lappet split into four to six processes (Figures 22 and 23).  
       .... Euphausia spinifera G.O. Sars
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       (Figure 27). Rostrum either curved downwards or absent. Upper part of  
       eye about equal in width to lower. (Figure 31).  
       .... Nematoscelis megalops G.O. Sars
- b) Setae on last segment only of predatory legs forming distal bundles.  
       (Figure 28). Rostrum straight. Upper part of eye narrower than lower.  
       (Figure 32). ..... Nematoscelis microps G.O. Sars



16. a) Abdominal segment VI shorter than the sum of the two preceding segments. Length of abdominal segment VI about twice its height. Petasma with terminal and proximal processes having triangular tips (Figure 33).

.... Thysanoessa gregaria G.O. Sars

b) Abdominal segment VI as long as the sum of the two preceding segments. Length of abdominal segment VI about three times its height. Petasma with terminal and proximal processes flattened distally (Figure 34).

.... Thysanoessa vicina Hansen

17. a) Predatory legs slender, naked but for a bundle of distal setae (Figure 26). Eyes large, upper part broader than lower (Figures 35 and 36).

.... genus Nematobranchion .... 18

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.... Nematobranchion flexipes Ortmann

b) Rostrum absent. No lateral denticle on lower edge of carapace (Figure 36). No dorsal spines on abdominal segments (Figure 43).

.... Nematobranchion boopis Calman

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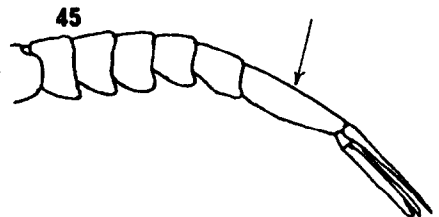
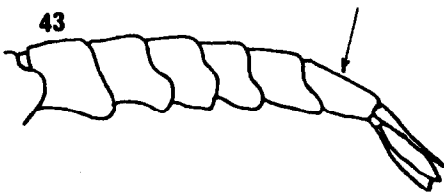
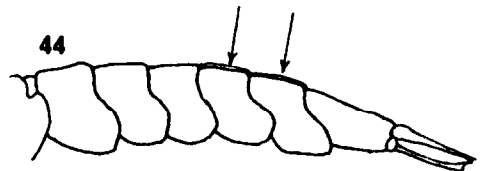
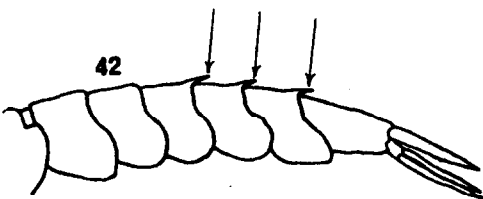
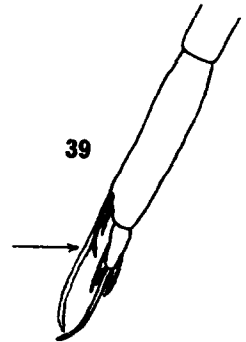
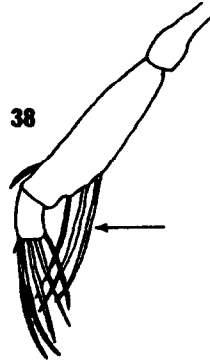
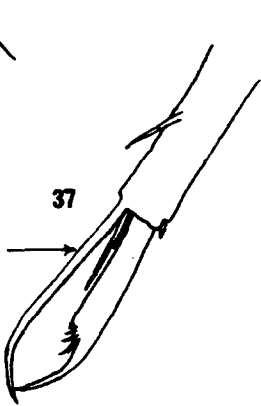
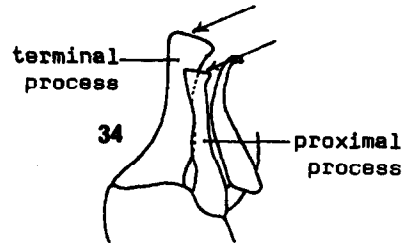
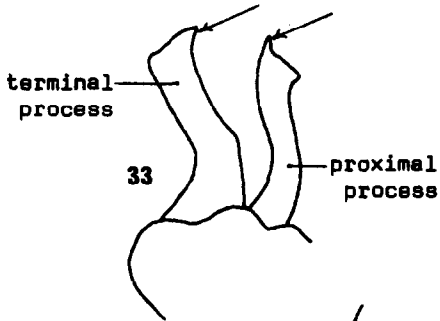
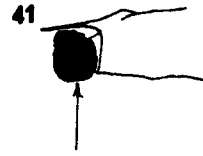
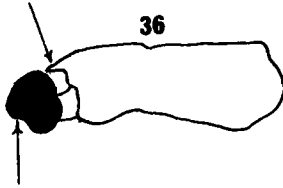
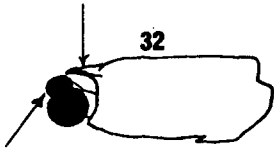
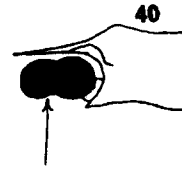
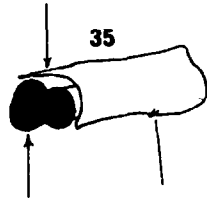
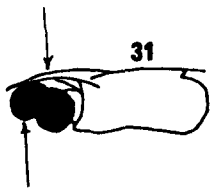
.... Stylocheiron maximum Hansen

21. a) Upper part of eye with four or five enlarged crystalline cones in a transverse row. .... Stylocheiron affine Hansen

b) Upper part of eye with at least seven enlarged crystalline cones in a transverse row. .... 22

22. a) Upper part of eye with seven or eight enlarged crystalline cones in a transverse row. .... Stylocheiron carinatum G.O. Sars

b) Upper part of eye with more than eight enlarged crystalline cones in a transverse row. .... 23





23. a) Abdominal segment VI nearly three times as long as V (Figure 45).

.... Stylocheiron elongatum G.O. Sars

b) Abdominal segment VI only marginally longer than V (Figure 43).

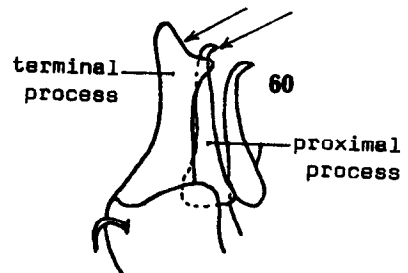
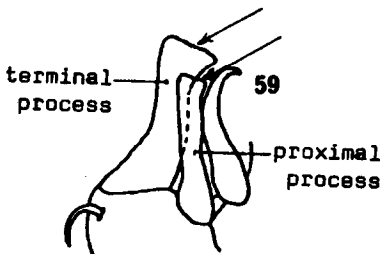
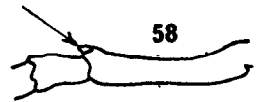
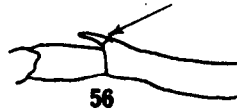
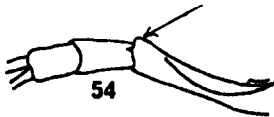
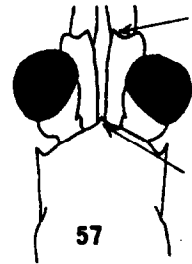
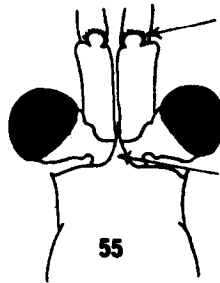
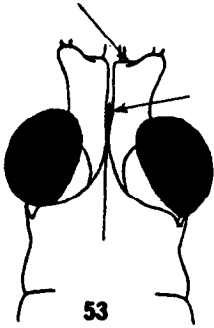
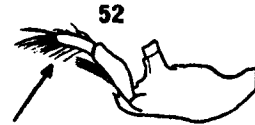
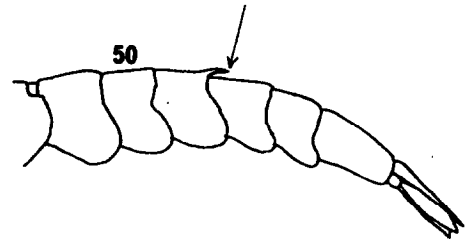
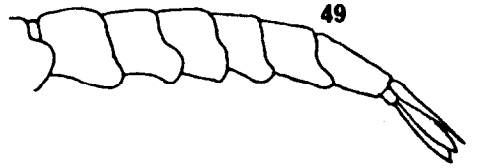
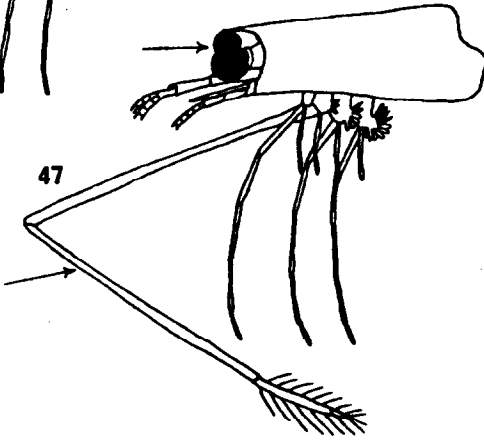
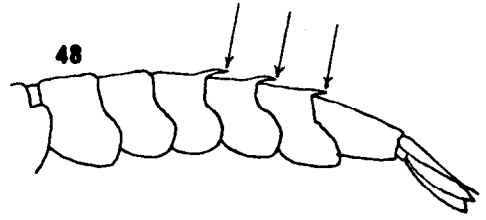
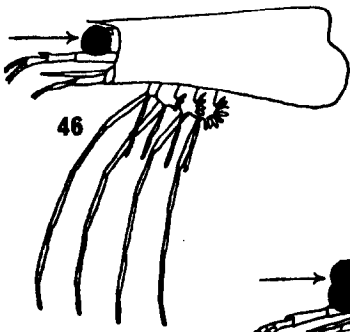
.... Stylocheiron longicorne G.O. Sars



3. KEY TO THE EUPHAUSIACEA FOUND SOUTH OF THE ANTARCTIC CONVERGENCE

Modified after Lomakina (1966), Mauchline and Fisher (1969), Mauchline (1980b).

1. a) All thoracic legs well developed. Pleopods I and II of males without petasmas. Do not possess luminescent organs. Have a transverse suture on exopod of uropods. .... Family BENTHEUPHAUSIIDAE  
.... Bentheuphausia amblyops G.O. Sars
- b) Thoracic legs VII and VIII rudimentary. Pleopods I and II of males modified as petasmas. Possess luminescent organs. No transverse suture on exopod of uropods. .... Family EUPHAUSIIDAE .... 2
2. a) Eyes more or less round. Thoracic legs II not modified as elongate predatory leg (Figure 46). .... genus Euphausia .... 3
- b) Eyes bilobed. Thoracic legs II modified as elongate predatory legs (Figure 47). .... genus Thysanoessa ... 7
3. a) Abdominal segments III, IV and V with posterior mid-dorsal spines (Figure 48). .... Euphausia triacantha Holt and Tattersall
- b) Spines absent from abdominal segments, or on segment III only (Figures 49 and 50). .... 4
4. a) Distal segment of mandibular palp long and slender, seven times as long as it is broad (Figure 51). .... Euphausia superba Dana
- b) Distal segment of mandibular palp short and broad, three times as long as it is broad (Figure 52). .... 5
5. a) Rostrum long and slender, reaching anterior edge of eyes. (Figure 53).  
Antennule lappet absent (Figure 54).  
.... Euphausia crystallorophias Holt and Tattersall
- b) Rostrum short, not reaching anterior edge of eyes (Figures 55 and 57).  
Antennule lappet present (Figures 56 and 58). .... 6
6. a) Antennule lappet protruding forward horizontally as a broad rounded lobe (Figures 55 and 56). Abdominal segment III usually with a posterior mid-dorsal spine (Figure 50).  
.... Euphausia vallentini Stebbing
- b) Antennule lappet very short, triangular (Figures 57 and 58). Abdominal segments without dorsal spines (Figure 49).  
.... Euphausia frigida Hansen
7. a) Adults shorter than 17 mm long. Petasma with terminal and proximal processes flattened distally (Figure 59).  
.... Thysanoessa vicina Hansen
- b) Adults usually longer than 18 mm, and up to 28 mm long. Petasma with terminal process having a broadened lobe distally, and proximal process having a curved tip (Figure 60). ... Thysanoessa macrura G.O. Sars



#### 4. NOTES ON ANTARCTIC EUPHAUSIIDS

##### 4.1 Euphausia superba Dana, 1850

- E. murrayi G.O. Sars, 1883
- E. antarctica G.O. Sars, 1883
- E. glacialis Hodgson, 1902
- E. australis Hodgson, 1902

E. superba is one of the largest species of euphausiid in the world, and easily the largest in the Southern Ocean, reaching a maximum length of 60 mm. This species has a circumpolar distribution south of the Antarctic Convergence, but its main area of abundance is south of 60°S where it forms a huge proportion of the total marine biomass. Gulland (1970) estimates that E. superba forms fifty per cent of the Antarctic zooplankton biomass.

Birds, fish, squid, baleen whales, many seals and several carnivorous zooplankton species all rely on E. superba as their staple food source. E. superba is the only euphausiid which feeds predominantly on phytoplankton (Everson, 1977), but it also takes protozoans, invertebrate larvae, small crustacea and possibly detritus (Mauchline and Fisher, 1969). It is obvious that the type of food taken alters markedly over winter, with the covering of the sea by ice greatly reducing phytoplankton abundance, but it is not known what E. superba eats at this time, if in fact it eats at all. Growth rates of this species over winter are certainly much less than in the summer (Bargmann, 1945).

E. superba spawn near the surface from late January to March, the eggs sinking through the water column whilst cleavage and embryonic development occurs (Marr, 1962). The newly hatched nauplii then swim towards the surface, and have usually developed about as far as the first calyptosis stage by the time they reach near surface waters. Individual age classes of E. superba show a very strong tendency to aggregate, and form swarms throughout all stages of development (Marr, 1962).

Swarms of adult E. superba can be found as deep as 150 m by day (although the vast majority occupy depths from ten to forty metres), but almost all rise to the top ten metres by night (Marr, 1962). This diurnal vertical migration enables E. superba to take advantage of the abundant phytoplankton in near surface waters by night, whilst making it less prone to predation from the predominantly surface-feeding predators by day. Rising to the surface by night may also enable separate swarms to inter-mingle for the purpose of mating, as swarms are frequently composed almost entirely of a single sex.

##### 4.2 Euphausia crystallorophias Holt and Tattersall, 1906

E. crystallorophias is restricted almost exclusively to the inshore waters of the Antarctic continental shelf, where it is the dominant euphausiid species (Baker, 1966). This species is quite similar to E. superba, but has a longer rostrum, larger eyes and a shorter mandibular palp and attains a maximum length of only thirty-five millimetres. It is a cold water stenothermic species, only being found in waters colder than 0°C (Lomakina, 1966). E. crystallorophias is usually found in the top 300 m of the water column. Like E. superba it has a strong tendency to form swarms, and forms a significant proportion of the food of inshore predators such as seals, penguins and fish (Mauchline and Fisher, 1969).

4.3 Euphausia frigida Hansen, 1911

E. splendens Calman, 1901

Euphausia sp. Tattersall, 1908

E. crystallorophias Illig, 1930 (in part)

This relatively small species attains a maximum length of only twenty-four millimetres (John, 1936). It undertakes a considerable vertical migration, rising from 250-500 m by day to around fifty metres by night (Mackintosh, 1934; Hardy and Gunther, 1935). E. frigida can be readily recognised by its conspicuous red mandibles and its short triangular rostrum. E. frigida does not form large swarms, and comprises only a very small proportion of the diet of higher level consumers (Lomakina, 1966). It is more common in waters warmer than 0°C, and has not been found under areas of pack ice (Lomakina, 1966).

4.4 Euphausia triacantha Holt and Tattersall, 1906

E. triacantha has a circumpolar distribution between the latitudes of 50°S and 60°S, occurring on both sides of the Antarctic Convergence but being considerably more common just south of it (Baker, 1966). It lives between 250 m and 750 m depth by day, rising above 250 m by night, and grows to a maximum length of thirty-two millimetres (Baker, 1959). E. triacantha does not form swarms, and has never been recorded from the stomachs of whales (Mauchline and Fisher, 1969). Amongst the Antarctic euphausiids, this species is easily recognisable by the prominent dorsal spines on abdominal segments three to five, and by the distinctive red colour of the anterior end of the cephalothorax.

4.5 Euphausia vallentini Stebbing, 1900

E. splendens Sars, 1885 (in part)

E. patachonica Colosi, 1917

E. vallentini has a circumpolar distribution on both sides of the Antarctic Convergence, with the majority being just north of the Convergence. This species tends to form quite large swarms which are most common from 100 m to 250 m by day, rising to near surface waters by night (Mauchline and Fisher, 1969). It can be readily distinguished from other euphausiids by the presence on most individuals of a dorsal spine on the third abdominal segment only and by its distinctive antennule lappet. The maximum length recorded for E. vallentini is twenty-eight millimetres (Mauchline and Fisher, 1969).

#### 4.6 Thysanoessa macrura G.O. Sars, 1883

T. macrura is a very common and widespread circumpolar Antarctic species, being second only to E. superba in total numbers. It is found in all Antarctic seas, from amongst pack ice over the continental shelf to the open oceans, and is also found north of the Antarctic Convergence adjacent to South America (Lomakina, 1966). It is apparent from the structure of its elongate second thoracic legs that T. macrura preys on smaller invertebrates, but it also filters large quantities of detritus and micro-organisms from the water (Mauchline and Fisher, 1969). In areas of low E. superba abundance, T. macrura probably replaces the former species as the major food source of predators of higher trophic levels. It forms very large swarms, and probably performs diurnal vertical migrations (Hardy and Gunther, 1935), although this has yet to be proven. T. macrura has a maximum length of 28.5 mm (Lomakina, 1966).

#### 4.7 Thysanoessa vicina Hansen, 1911

T. macrura Tattersall, 1908

Little is known of this small and quite rare species, possibly because its morphological similarity to T. macrura has led to it being overlooked by several workers. The only reliable difference between the two species is in the structure of the petasma of males. Also the maximum length recorded for T. vicina is seventeen millimetres (Lomakina, 1966), making it much smaller than the former species. It prefers slightly warmer waters than T. macrura, and is found on both sides of the Antarctic Convergence. T. vicina is most often observed in the top 250 m, but has been found as deep as 1000 m, and is thought to perform diurnal vertical migrations (Hardy and Gunther, 1935).

#### 4.8 Bentheuphausia amblyops G.O. Sars, 1885

Thysanopoda (?) amblyops G.O. Sars, 1883

B. amblyops is the only member of the family Bentheuphausiidae. As its name suggests it is a bathypelagic species, being widespread in waters deeper than 1000 m down to the greatest ocean depths (Mauchline and Fisher, 1969). At these depths the only food source available would be particulate detrital matter. Only a single specimen has been recorded from south of the Antarctic Convergence, at about 64°S, 162°E (Lomakina, 1966). B. amblyops is quite a large euphausiacean, attaining a length of up to fifty millimetres (Mauchline and Fisher, 1969). It is unique in the order in having no luminescent organs, reduced eyes and no petasmas on the males (Sars, 1885).





5. RANGES OF DISTRIBUTION OF SOUTHERN OCEAN EUPHAUSIACEA

The Euphausiacea, as an order, is cosmopolitan in the world's oceans, but the distribution of each species is restricted primarily by water temperature. Each species has its own particular range of temperature tolerance (Table 2), so that the decreasing surface water temperature in higher latitudes of the Southern Ocean tends to impose a definite latitudinal succession on euphausiid species (Figure 61).

<u>SPECIES</u>	<u>MINIMUM(°C)</u>	<u>MAXIMUM(°C)</u>	<u>SOURCE</u>
<u>E. spinifera</u>	6	19	Lomakina (1966)
<u>E. lucens</u>	5	18	Lomakina (1966)
<u>E. longirostris</u>	3.0	16	Lomakina (1966)
<u>E. vallentini</u>	2	10	Lomakina (1966)
<u>E. triacantha</u>	1.8	11.88	Baker (1959)
<u>E. frigida</u>	-0.7	5	Lomakina (1966), Rustad (1930)
<u>E. superba</u>	-1.89	3.9	Marr (1962), Lomakina (1966)
<u>E. crystallorophias</u>	-1.8	0	Lomakina (1966)
<u>T. gregaria</u>	3	24	Lomakina (1966)
<u>T. vicina</u>	0	8	Lomakina (1966)
<u>T. macrura</u>	-1.8	8	Lomakina (1966), Sheard (1953)

Table 2: Range of temperatures at which some common Southern Ocean euphausiids have been caught.

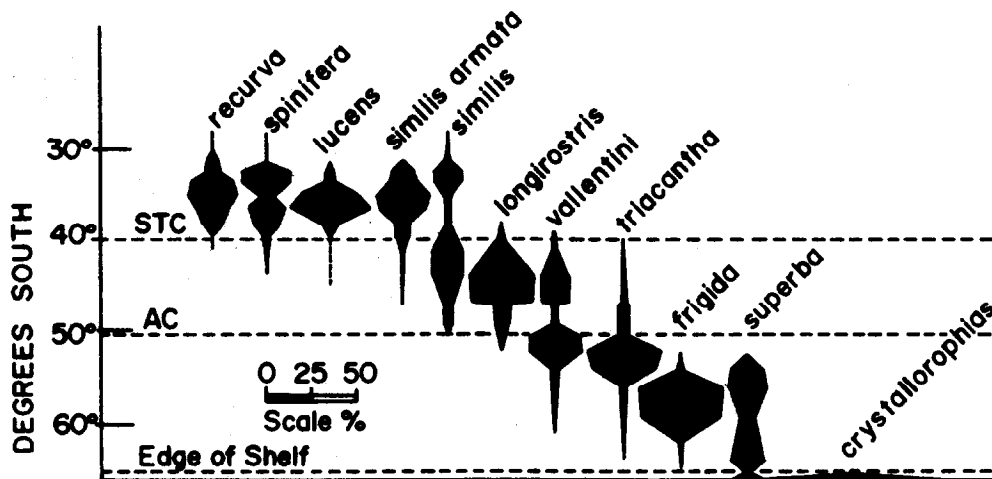
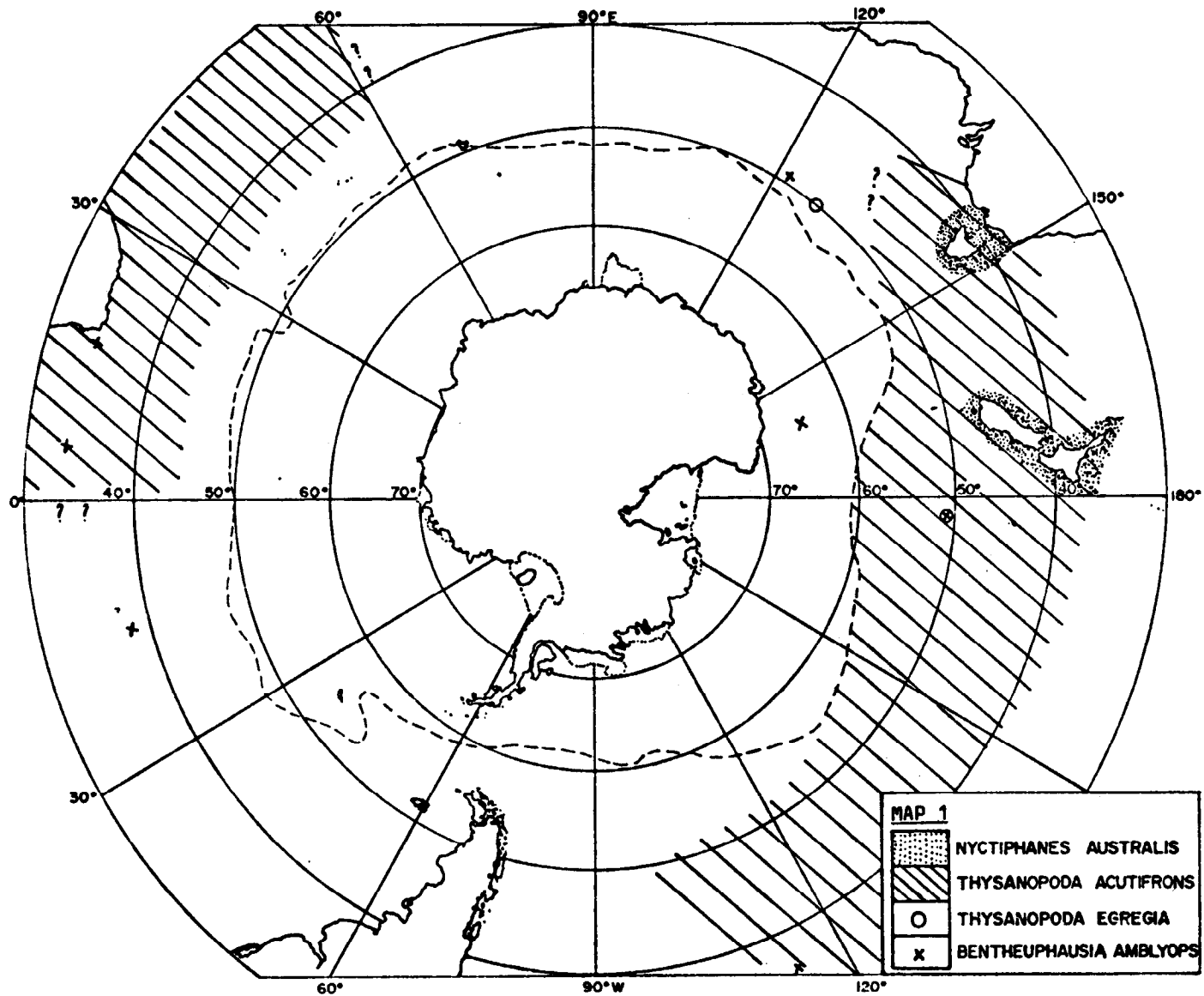
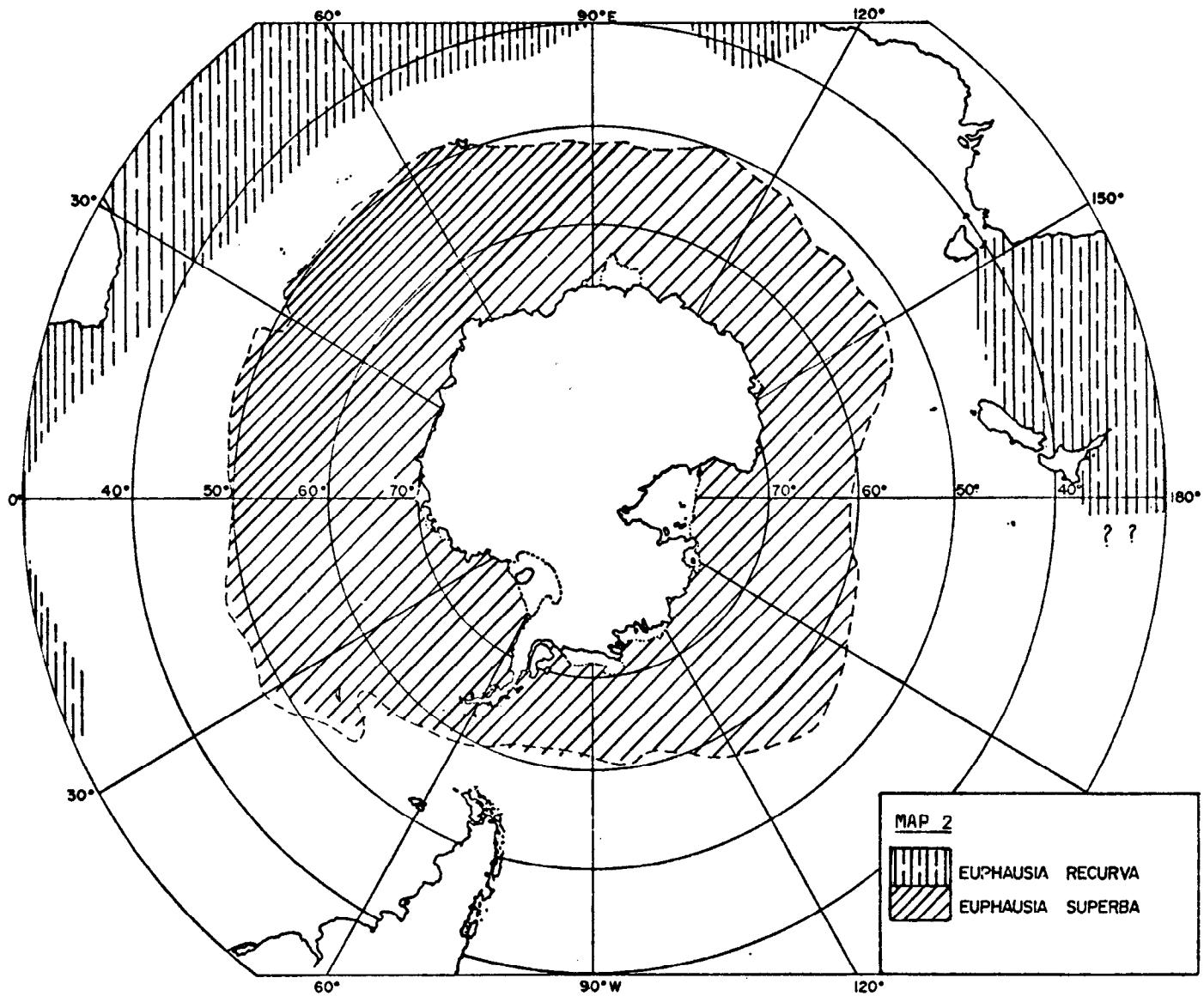


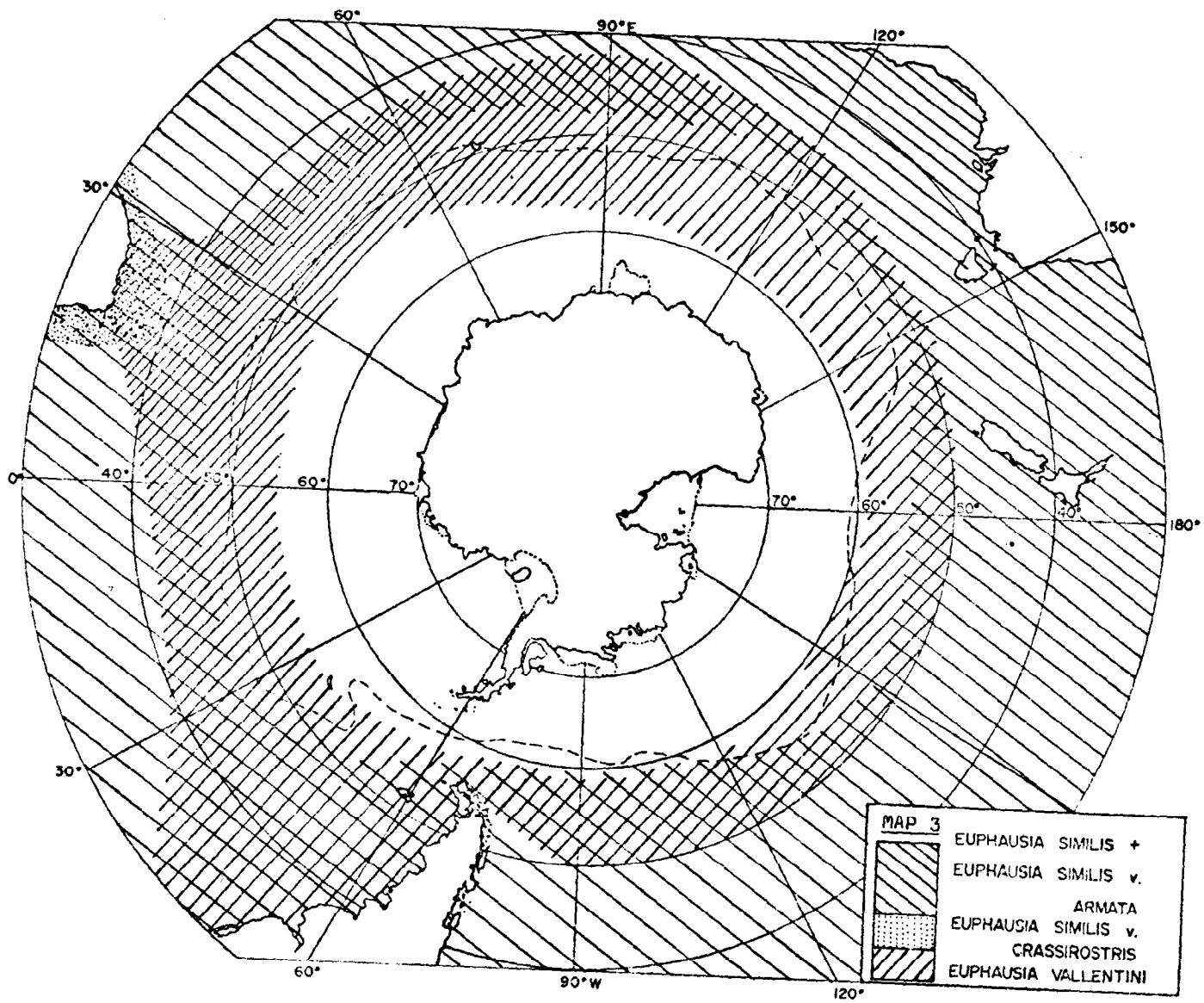
Figure 61: Latitudinal succession of species of Euphausia in the Indian Ocean (after Baker, 1966).

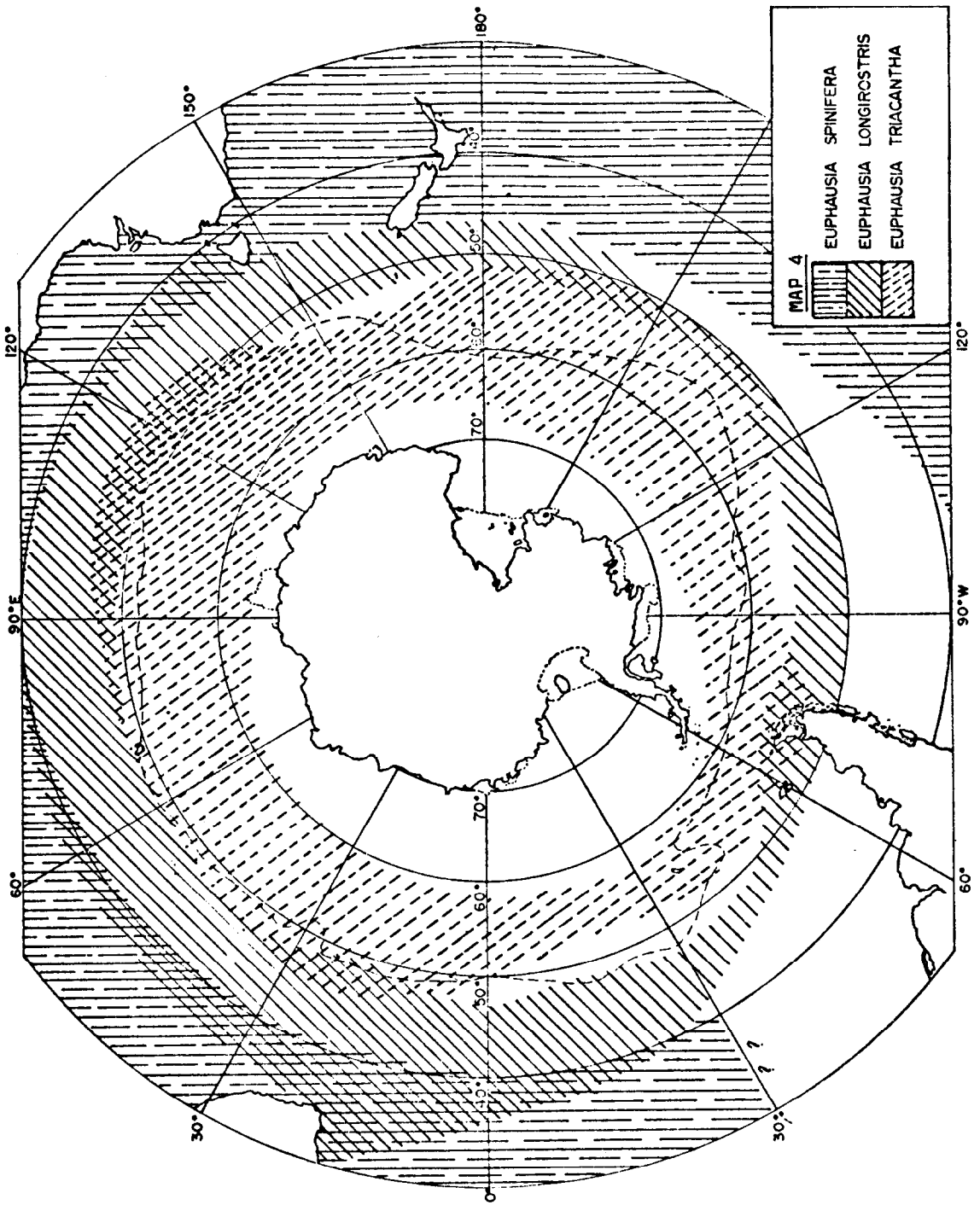
The following maps show the known ranges of species of Euphausiacea within the Southern Ocean. They are modified from similar maps presented in Lomakina (1966) and Mauchline and Fisher (1969). The mean position of the Antarctic Convergence, as determined by Mackintosh (1946), is shown in each map as a dotted line; thus:-

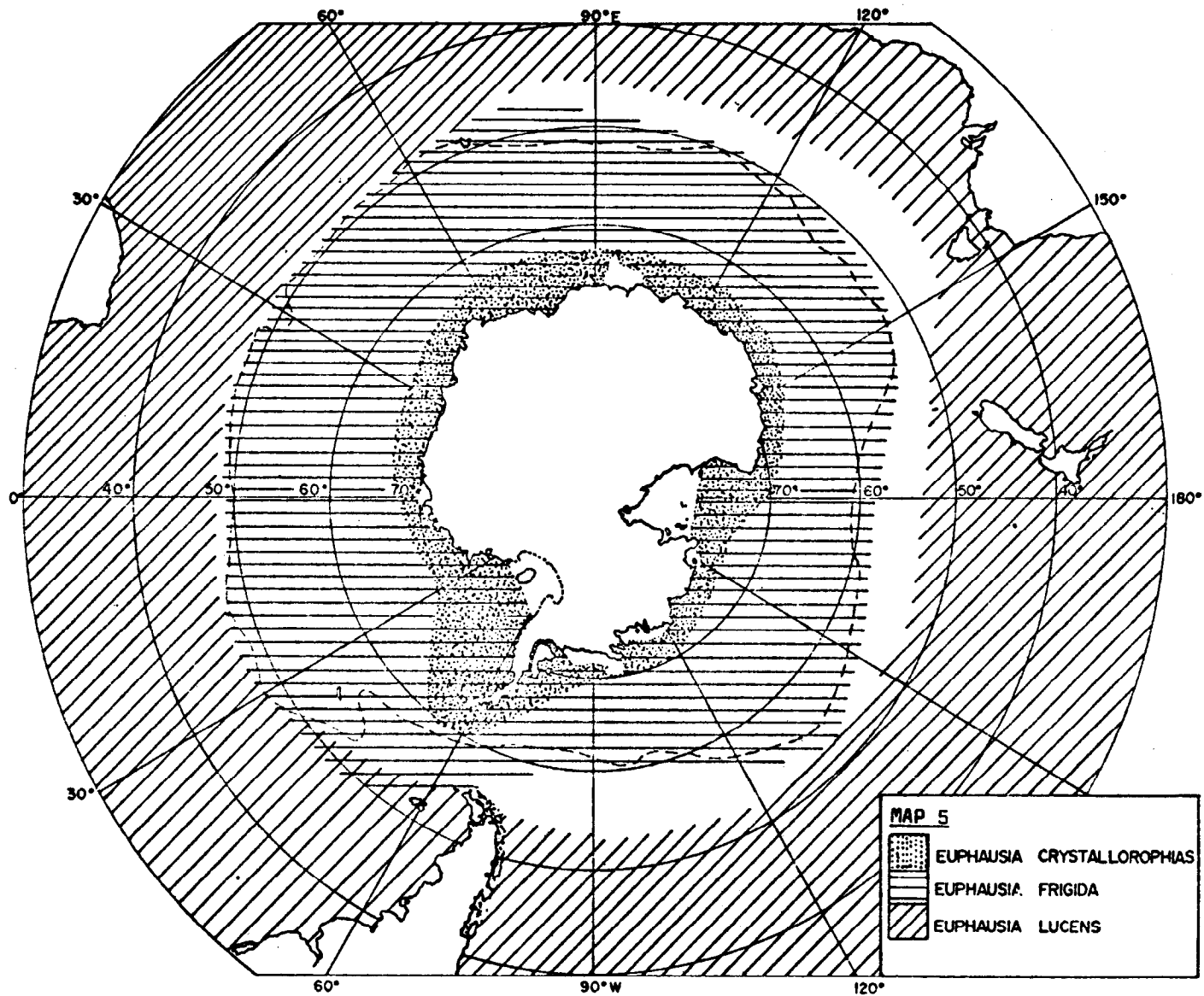


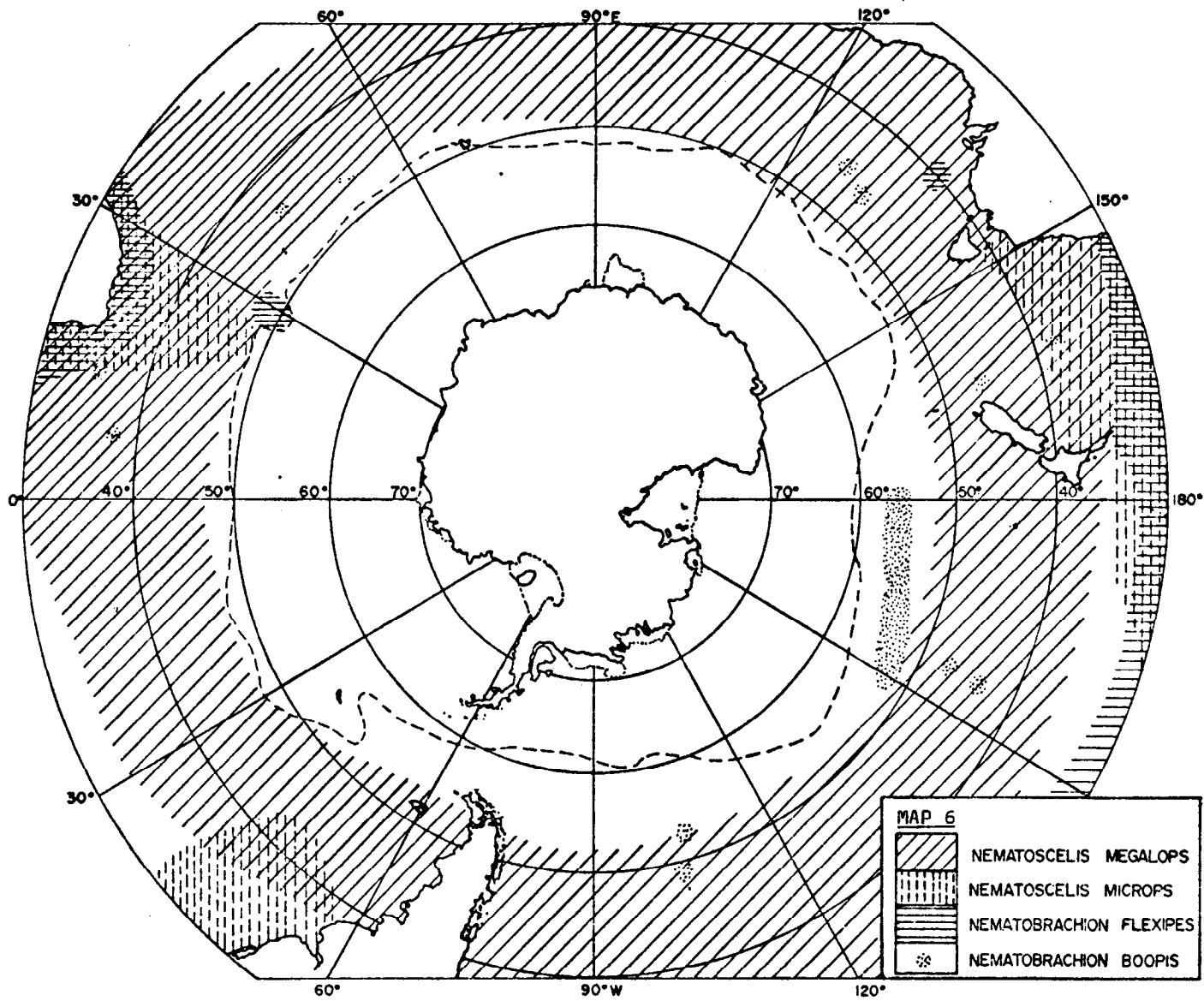


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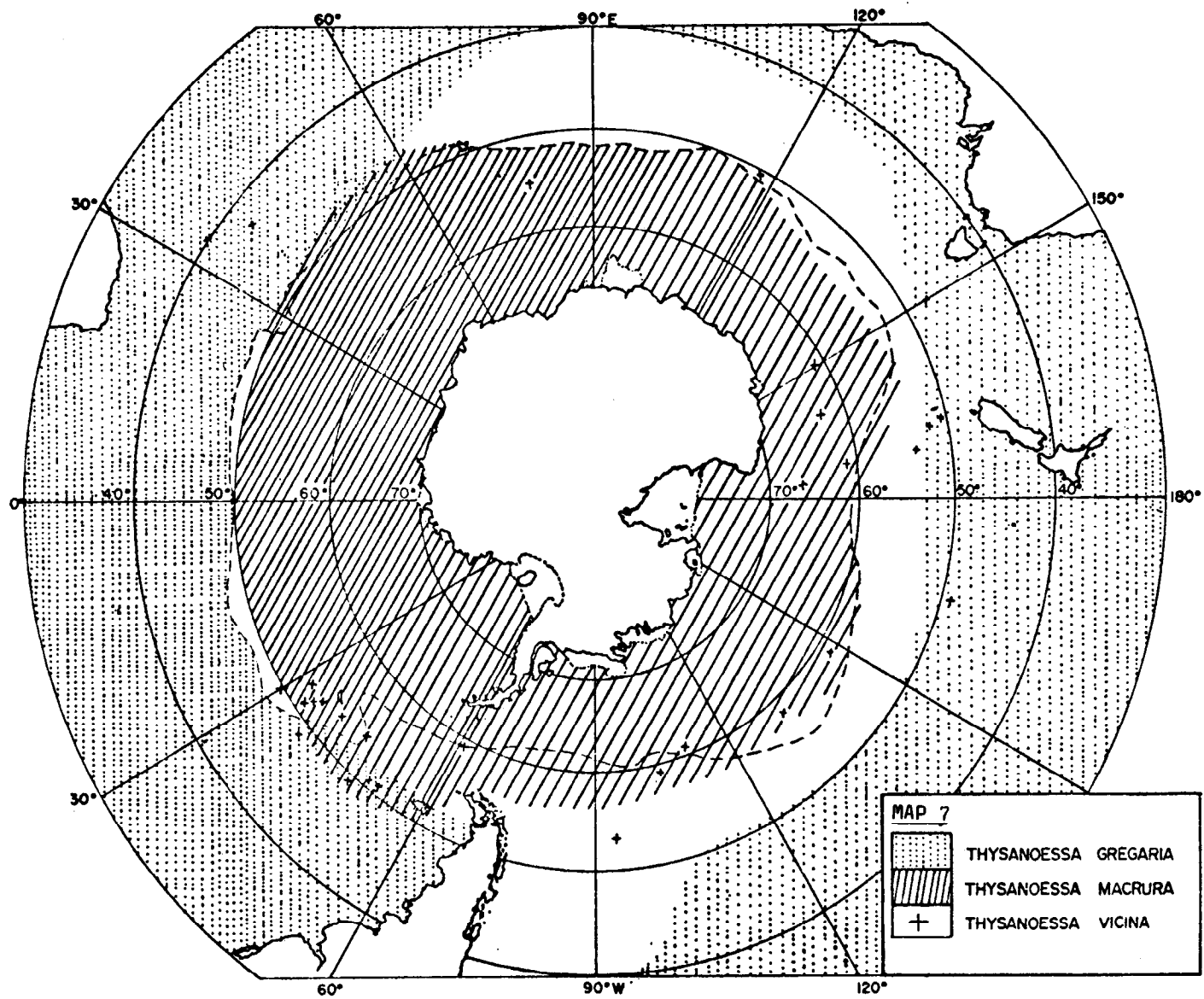


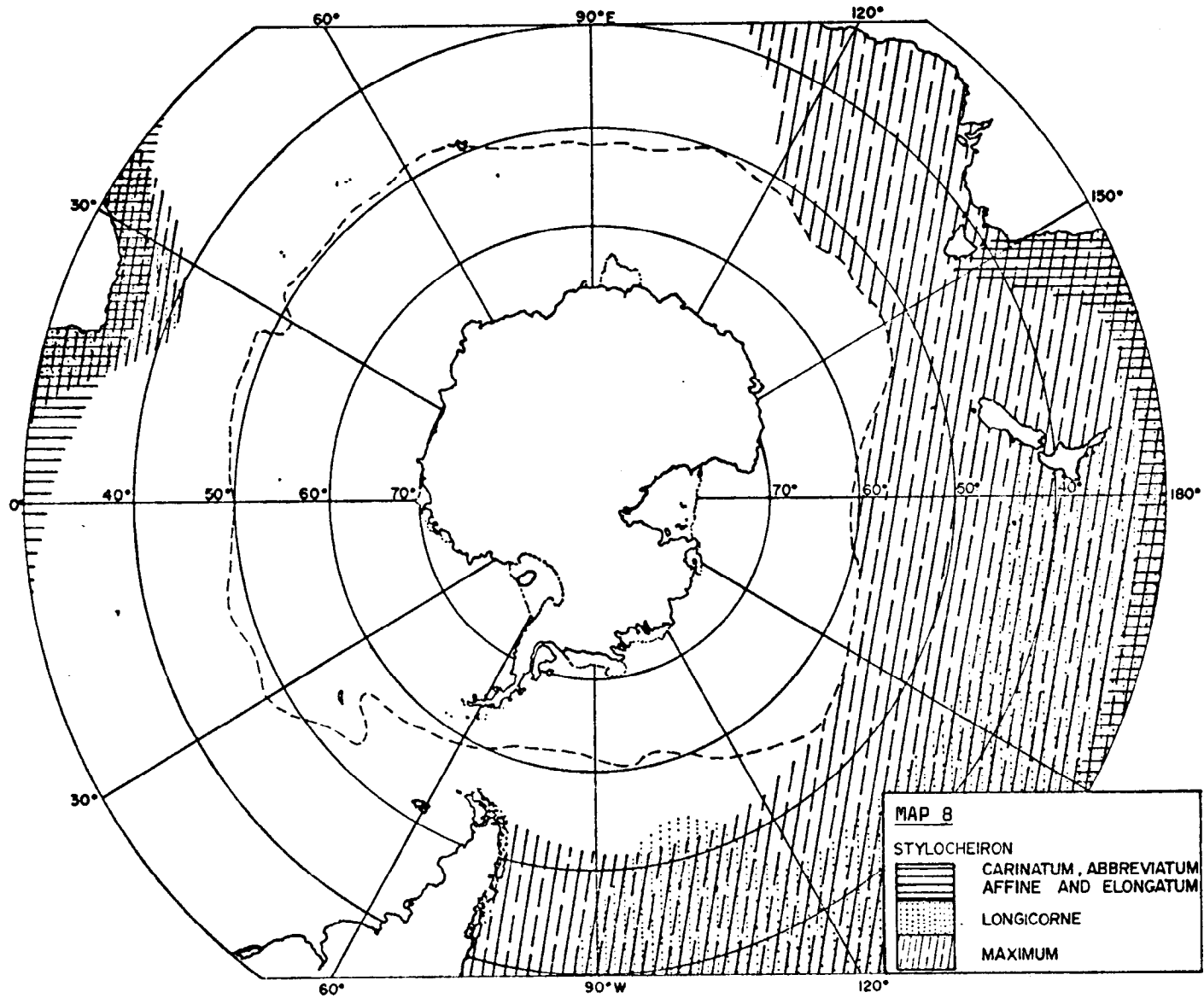












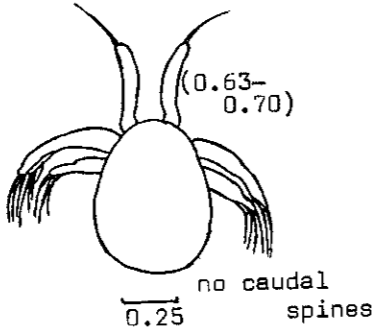
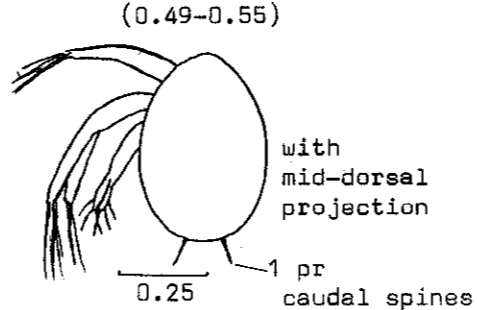
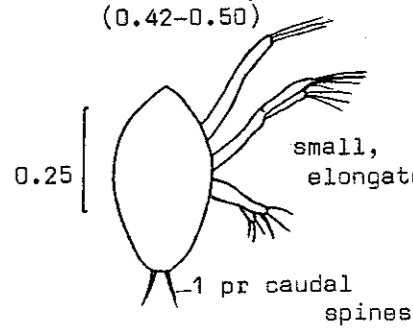
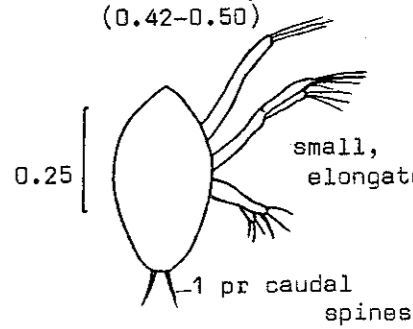
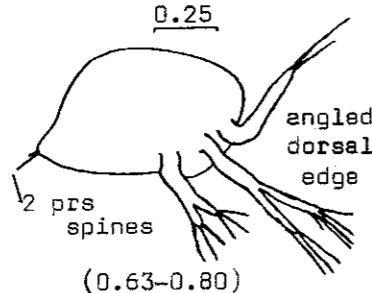
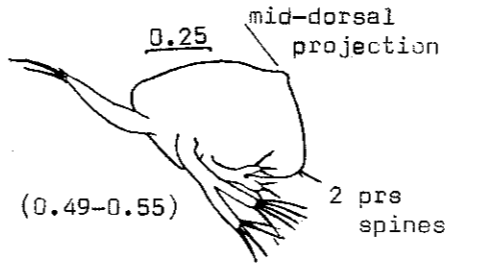
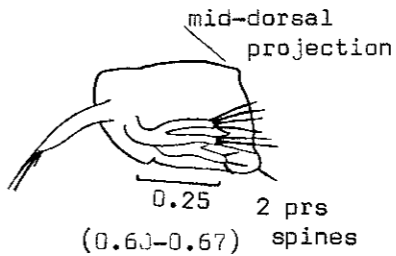
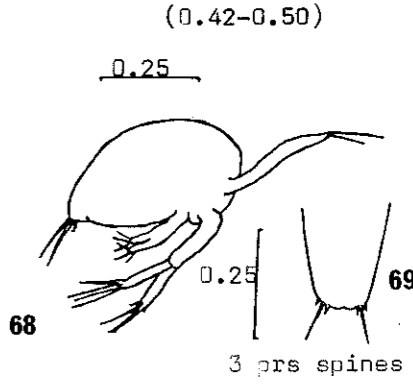
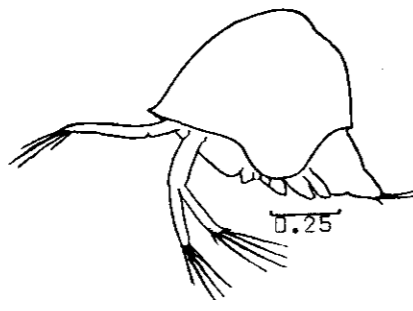
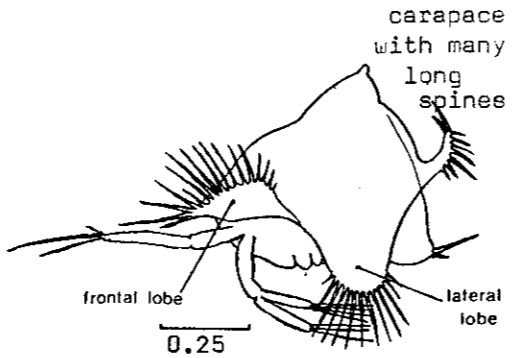
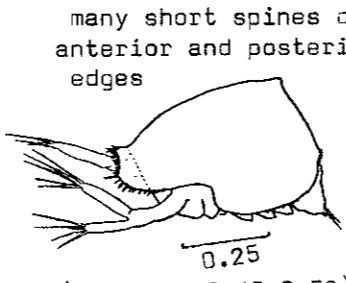
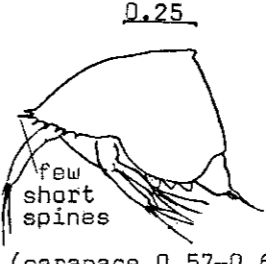
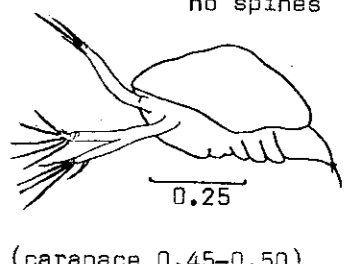
## 6. LARVAL DEVELOPMENT OF THE ANTARCTIC EUPHAUSIIDS

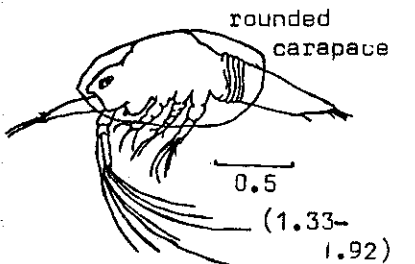
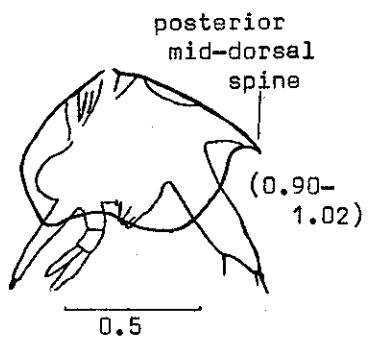
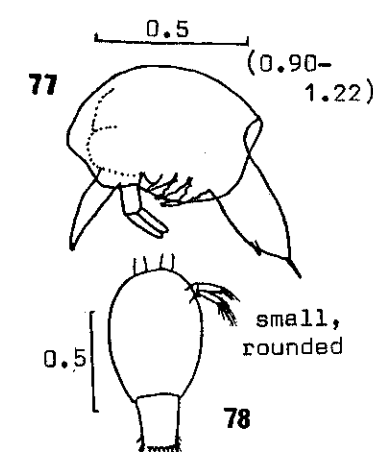
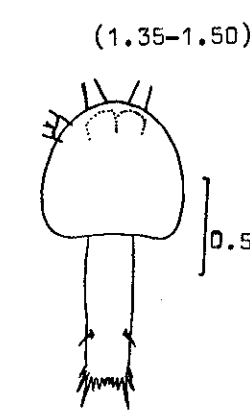
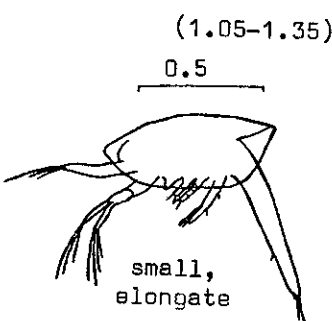
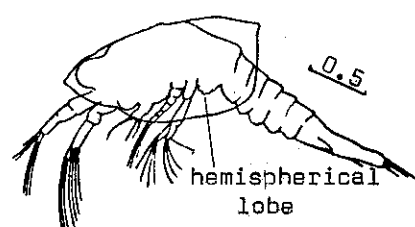
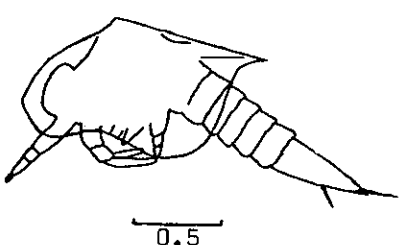
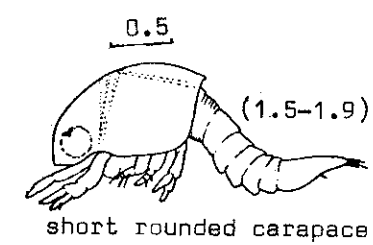
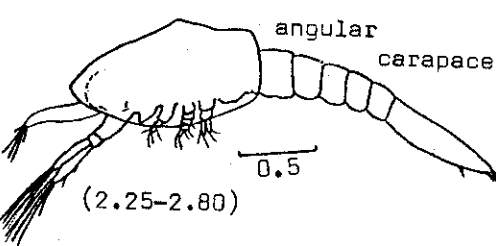
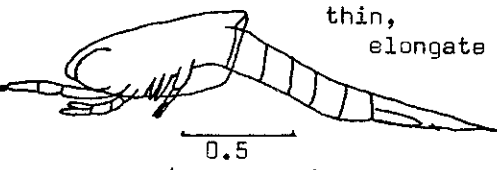
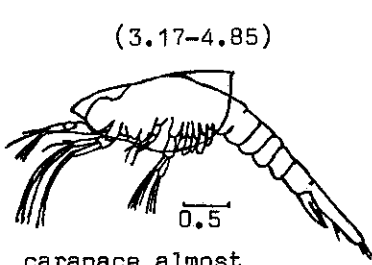
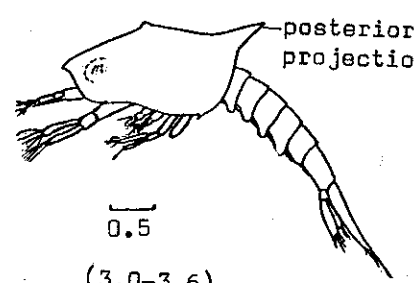
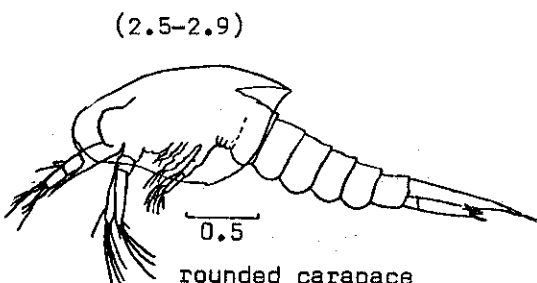
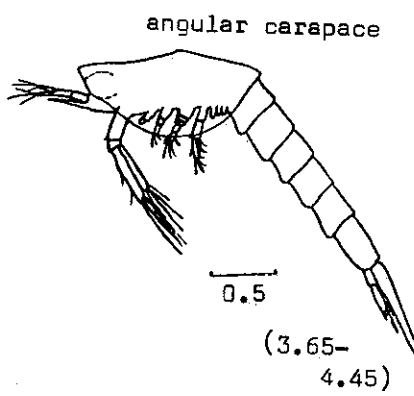
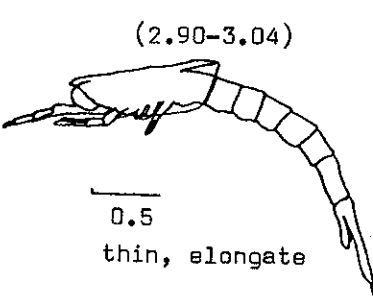
The development of euphausiids from hatching to the juvenile stage on can be divided into four distinct phases (nauplius, metanauplius, calyptopis and furcilia), which can be further subdivided into twelve stages. The features which characterise each stage, along with illustrated descriptions of larval development of the five most common Antarctic euphausiids, are presented on the following pages. The species described are Euphausia superba, Euphausia triacantha, Euphausia frigida, Euphausia crystallorophias and Thysanoessa macrura.

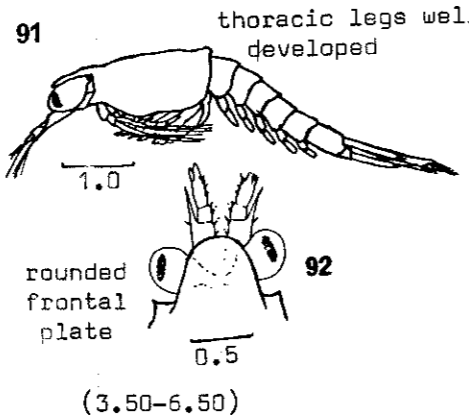
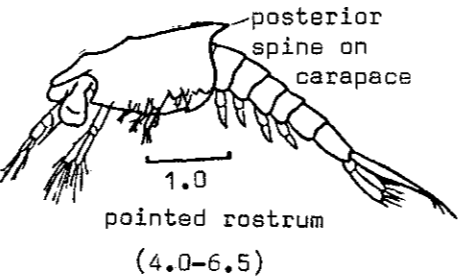
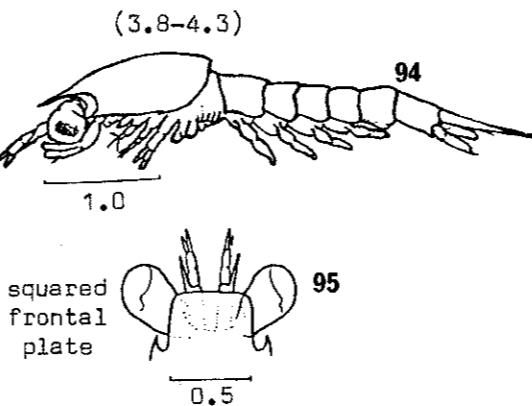
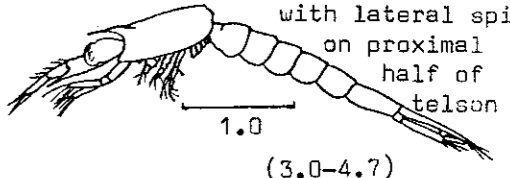
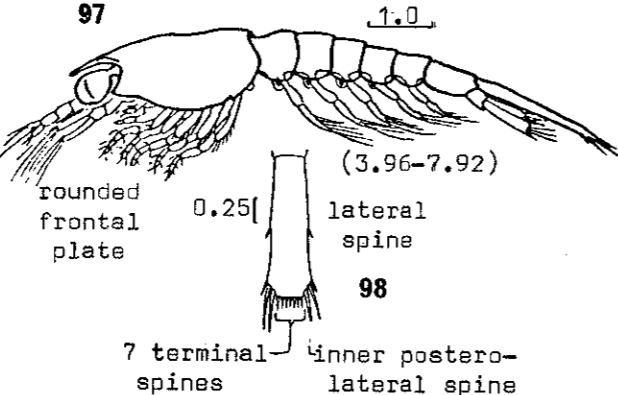
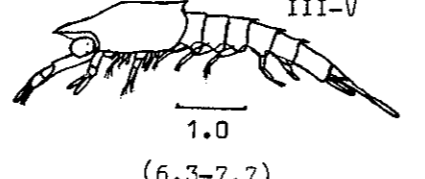
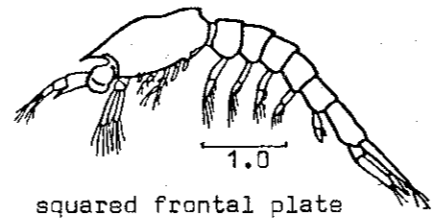
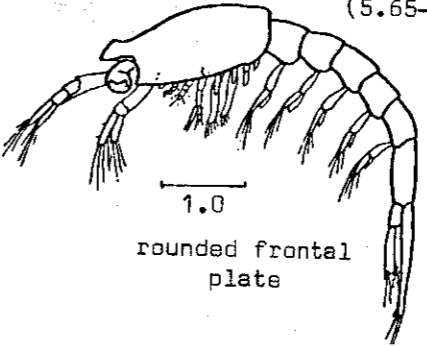
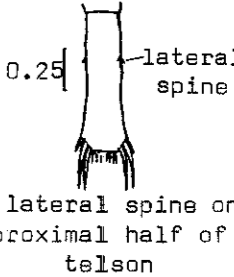
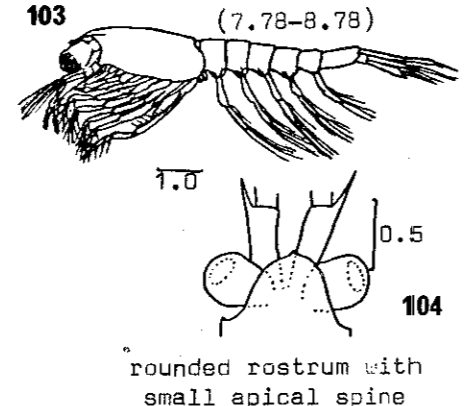
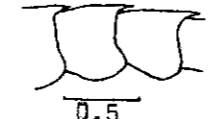
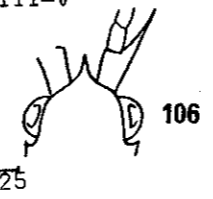
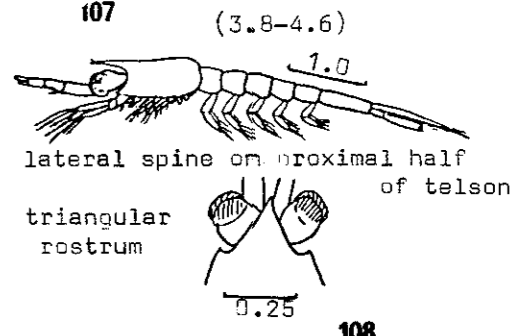
### CORRECTION

Please note that the following species have been misspelt in the figures on page 29 to 32:

T. macrura  
E. triacantha  
E. crystallorophias

<p><b>NAUPLIUS I</b></p> <ul style="list-style-type: none"> <li>•oval unsegmented body</li> <li>•no compound eyes</li> <li>•3 prs of appendages</li> <li>•usually with 1 pr of long caudal spines</li> </ul>	<p><u>E. superba</u></p>  <p>no caudal spines</p> <p>0.25</p> <p>(0.63-0.70)</p> <p>62</p>	<p><u>E. triacantha</u></p> <p>UNKNOWN</p>	<p><u>E. frigida</u></p>  <p>(0.49-0.55)</p> <p>with mid-dorsal projection</p> <p>0.25</p> <p>1 pr caudal spines</p> <p>63</p>	<p><u>E. crystallorophias</u></p>  <p>(0.60-0.67)</p> <p>•1 pr caudal spines</p> <p>•mid-dorsal projection</p> <p>0.25</p> <p>small, elongate</p> <p>1 pr caudal spines</p> <p>64</p>	<p><u>T. macrara</u></p>  <p>(0.42-0.50)</p> <p>0.25</p> <p>1 pr caudal spines</p> <p>64</p>
<p><b>NAUPLIUS II</b></p> <ul style="list-style-type: none"> <li>•oval unsegmented body</li> <li>•no compound eyes</li> <li>•3 prs of appendages</li> <li>•with at least 2 prs of caudal spines</li> </ul>	 <p>0.25</p> <p>angled dorsal edge</p> <p>2 prs spines</p> <p>(0.63-0.80)</p> <p>65</p>	<p>UNKNOWN</p>	 <p>0.25</p> <p>mid-dorsal projection</p> <p>(0.49-0.55)</p> <p>2 prs spines</p> <p>66</p>	 <p>mid-dorsal projection</p> <p>0.25</p> <p>2 prs spines</p> <p>(0.60-0.67)</p> <p>67</p>	 <p>(0.42-0.50)</p> <p>0.25</p> <p>3 prs spines</p> <p>68</p> <p>69</p>
<p><b>METANAUPLIUS</b></p> <ul style="list-style-type: none"> <li>•carapace with abdomen and 2 prs of appendages protruding</li> <li>•rudimentary eyes</li> <li>•mouthparts and 1st thoracic legs all present as buds</li> </ul>	<p>no spines on carapace</p>  <p>0.25</p> <p>(carapace 0.70-0.78)</p> <p>70</p>	<p>carapace with many long spines</p>  <p>frontal lobe</p> <p>0.25</p> <p>lateral lobe</p> <p>(carapace 0.67-0.73)</p> <p>71</p>	<p>many short spines on anterior and posterior edges</p>  <p>0.25</p> <p>(carapace 0.45-0.52)</p> <p>72</p>	 <p>0.25</p> <p>few short spines</p> <p>(carapace 0.57-0.67)</p> <p>73</p>	<p>no spines</p>  <p>0.25</p> <p>(carapace 0.45-0.50)</p> <p>74</p>

<p><b>CALYPTOPIS I</b></p> <ul style="list-style-type: none"> <li>• unsegmented abdomen distinct from cephalothorax</li> <li>• lateral spine on abdomen</li> <li>• mouthparts developed</li> </ul>	<p><u>E. superba</u></p>  <p>rounded carapace</p> <p>0.5</p> <p>(1.33-1.92)</p> <p>75</p>	<p><u>E. tracantha</u></p>  <p>posterior mid-dorsal spine</p> <p>0.5</p> <p>(0.90-1.02)</p> <p>76</p>	<p><u>E. frigida</u></p>  <p>0.5</p> <p>(0.90-1.22)</p> <p>77</p> <p>0.5</p> <p>small, rounded</p> <p>78</p>	<p><u>E. crystallorophias</u></p>  <p>(1.35-1.50)</p> <p>0.5</p> <p>angular carapace</p> <p>79</p>	<p><u>T. macrara</u></p>  <p>(1.05-1.35)</p> <p>0.5</p> <p>small, elongate</p> <p>80</p>
<p><b>CALYPTOPIS II</b></p> <ul style="list-style-type: none"> <li>• abdomen segmented, 6th segment not distinct from telson</li> <li>• uropods not distinct from telson</li> <li>• eyes enclosed by carapace</li> <li>• pleopods absent</li> </ul>	 <p>0.5</p> <p>hemispherical lobe</p> <p>long rounded carapace</p> <p>(2.13-3.33)</p> <p>81</p>	 <p>0.5</p> <p>carapace with posterior mid-dorsal projection</p> <p>(1.9-2.3)</p> <p>82</p>	 <p>0.5</p> <p>(1.5-1.9)</p> <p>short rounded carapace</p> <p>83</p>	 <p>angular carapace</p> <p>0.5</p> <p>(2.25-2.80)</p> <p>84</p>	 <p>thin, elongate</p> <p>0.5</p> <p>(1.75-2.80)</p> <p>85</p>
<p><b>CALYPTOPIS III</b></p> <ul style="list-style-type: none"> <li>• telson distinct from 6th abdominal segment</li> <li>• uropods distinct from telson</li> <li>• eyes enclosed by carapace</li> <li>• pleopods absent</li> </ul>	 <p>(3.17-4.85)</p> <p>0.5</p> <p>carapace almost straight</p> <p>86</p>	 <p>posterior projection</p> <p>0.5</p> <p>(3.0-3.6)</p> <p>87</p>	 <p>(2.5-2.9)</p> <p>0.5</p> <p>rounded carapace</p> <p>88</p>	 <p>angular carapace</p> <p>0.5</p> <p>(3.65-4.45)</p> <p>89</p>	 <p>(2.90-3.04)</p> <p>0.5</p> <p>thin, elongate</p> <p>90</p>

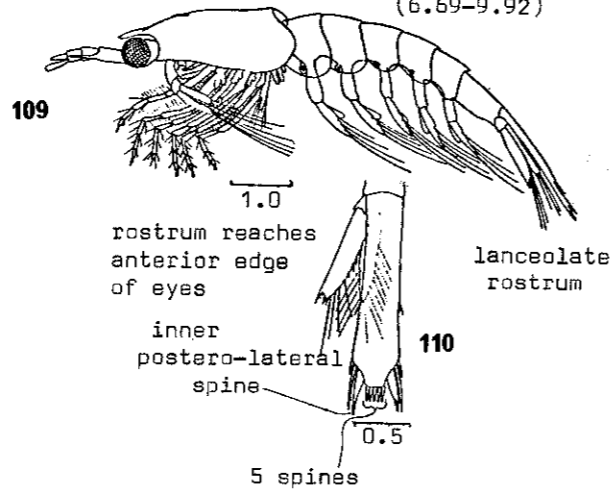
<p>FURCILIA I</p> <ul style="list-style-type: none"> <li>•eyes on mobile stalks, distinct from carapace</li> <li>•with 0 to 5 pleopods, all non-setose</li> <li>•telson with 7 terminal spines</li> </ul>	<p><u>E. superba</u></p> <p>91 thoracic legs well developed</p>  <p>92 rounded frontal plate</p> <p>(3.50-6.50)</p>	<p><u>E. triacantha</u></p>  <p>93 posterior spine on carapace</p> <p>pointed rostrum</p> <p>(4.0-6.5)</p>	<p><u>E. frigida</u></p> <p>(3.8-4.3)</p>  <p>94</p> <p>95 squared frontal plate</p>	<p><u>E. crytallorophias</u></p> <ul style="list-style-type: none"> <li>•rounded frontal plate</li> <li>•thoracic legs poorly developed</li> <li>•(5.00-6.25)</li> </ul>	<p><u>T. macrara</u></p> <p>triangular rostrum</p> <p>only species with lateral spine on proximal half of telson</p>  <p>96</p> <p>(3.0-4.7)</p>
<p>FURCILIA II</p> <ul style="list-style-type: none"> <li>•with 3 to 5 pleopods, at least 1 pr being setose</li> <li>•telson with 7 terminal spines</li> <li>•inner postero-lateral spine as wide as other telson spines</li> </ul>	<p>97</p>  <p>98 rounded frontal plate</p> <p>0.25 lateral spine</p> <p>7 terminal spines inner postero-lateral spine</p> <p>(3.96-7.92)</p>	<p>99</p>  <p>spines on abdominal segs. III-V</p> <p>(6.3-7.7)</p>	<p>100</p> <p>(4.7-5.7)</p>  <p>squared frontal plate</p>	<p>101</p> <p>(5.65-7.40)</p>  <p>rounded frontal plate</p>	<p>102</p> <p>(3.3-4.3)</p> <p>triangular rostrum</p>  <p>0.25 lateral spine</p> <p>lateral spine on proximal half of telson</p>
<p>FURCILIA III</p> <ul style="list-style-type: none"> <li>•inner postero-lateral spines with very wide bases</li> <li>•all 5 pleopods setose and natatory</li> <li>•telson with 7 terminal spines</li> </ul>	<p>103</p> <p>(7.78-8.78)</p>  <p>104 rounded rostrum with small apical spine</p>	<p>105</p> <p>(6.5-9.2)</p>  <p>spines on abdominal segments III-V</p> <p>lanceolate rostrum</p>  <p>106</p>	<p>107</p> <p>(5.5-6.7)</p> <ul style="list-style-type: none"> <li>•squared frontal plate</li> <li>•(5.5-6.7)</li> </ul>	<p>UNKNOWN</p>	<p>107</p> <p>(3.8-4.6)</p>  <p>108 lateral spine on proximal half of telson</p> <p>triangular rostrum</p>

FURCILIA IV

- inner postero-lateral spines with very wide bases
- telson with 5 terminal spines

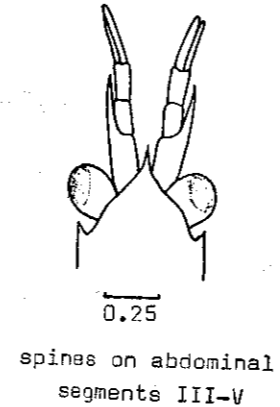
E. superba

(6.69-9.92)



E. triacantha

(7.5-10.2)

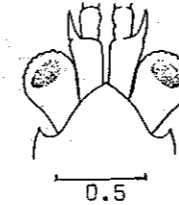


111

E. frigida

(6.5-7.7)

- rostrum not reaching anterior edge of eyes



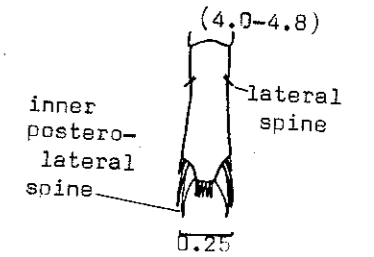
112

E. crystallorophias

UNKNOWN

T. macrara

(4.0-4.8)

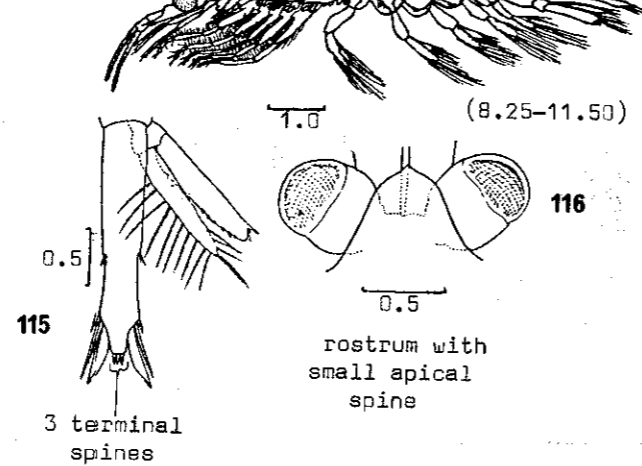


113

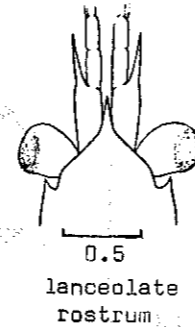
FURCILIA V

- telson with 3 terminal spines

114



(8.8-11.7)



117

- short rostrum, not reaching anterior edge of eyes
- (7.0-8.3)

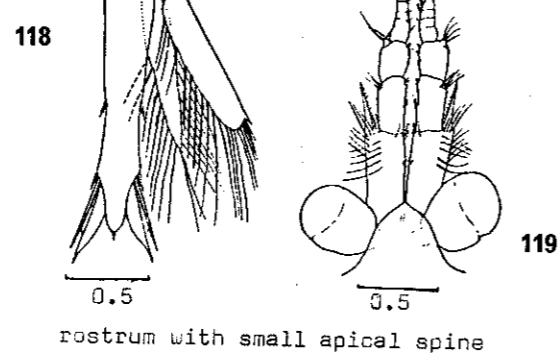
UNKNOWN

- lateral spine on proximal half of telson
- (4.6-5.9)

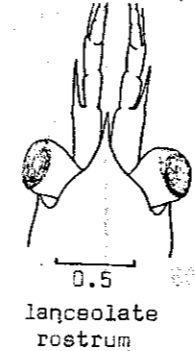
FURCILIA VI

- telson with a single terminal spine only

118



(8.5-11.4)



120

- rostrum very short
- (6.8-9.6)

UNKNOWN

- lateral spine on proximal half of telson
- (5.2-6.7)





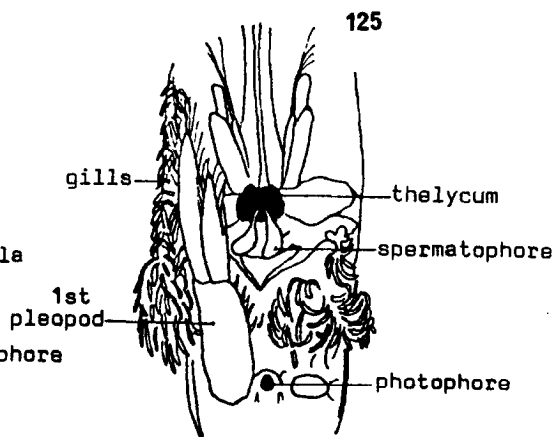
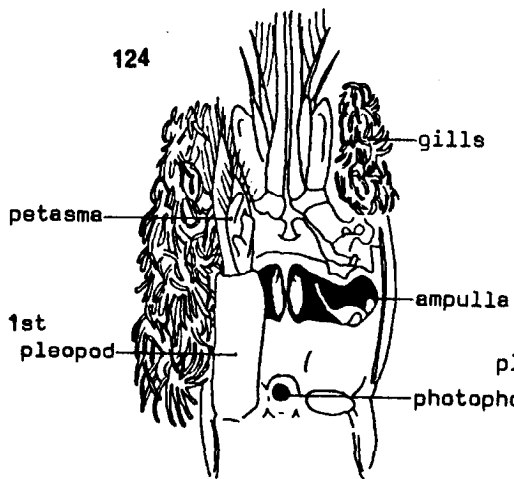
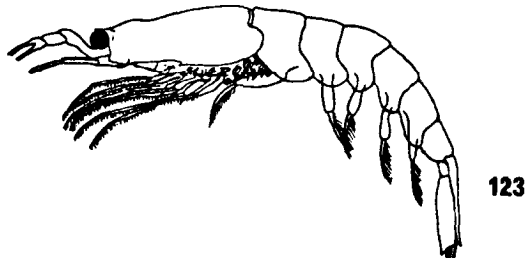
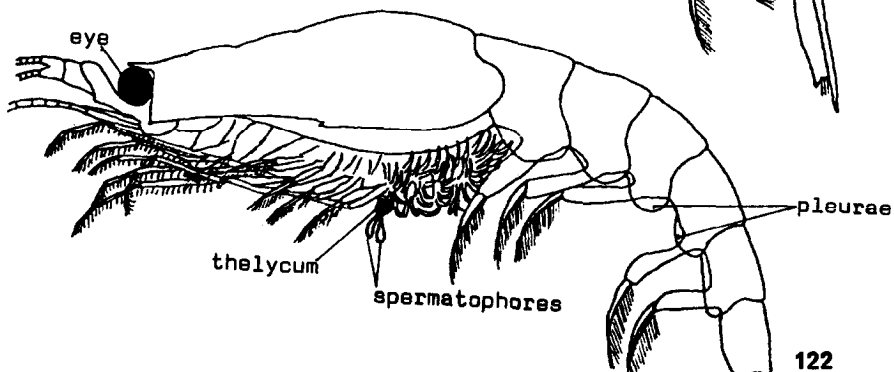
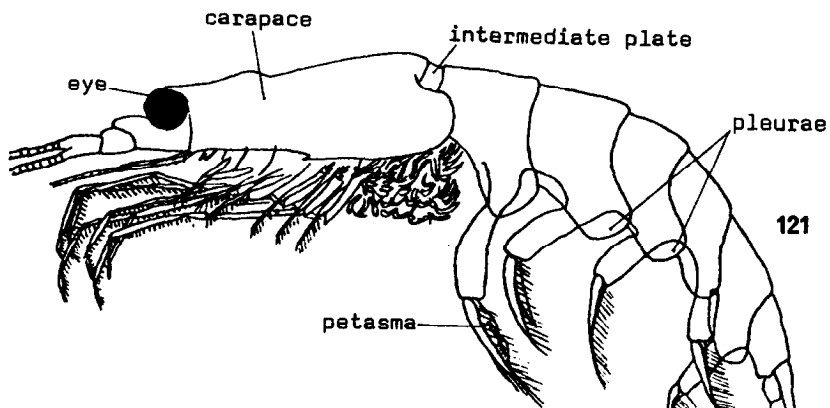
## 7. REPRODUCTION AND SEXUAL MATURATION OF *Euphausia superba*

The sex of adult *E. superba* can usually be determined simply by a short look at the general body form. When compared with adult females of similar size, adult male *E. superba* have larger eyes, a shorter carapace, longer pleopods, longer abdominal pleurae, a more obvious intermediate plate between carapace and abdomen, and are generally more red in colour. Figures 121 and 122 contrast some of the more apparent differences between the two sexes.

As juvenile euphausiids mature, they gradually acquire and develop gonads and external sexual features. This development can be separated into various stages as each new feature is acquired, and a classification of these sexual maturity stages has been developed by Makarov and Denys (1980).

In the male reproductive system, spermatozoa formed in the testes pass along the vas deferens, where a spermatophore sac is secreted around them (Mauchline and Fisher, 1969). These spermatophores are then stored in a ventral ampulla prior to ejaculation. Although the process of mating in euphausiids has not been observed, a good deal can be inferred from the structure of the external sexual apparatus. It appears that the male uses its second petasma to transfer these spermatophores from its ampulla to its first petasma (Brinton, 1978). The male then uses its first petasma to attach the spermatophores to the thelycum of a female. The spermatophores are then somehow emptied of their spermatozoa which pass up an oviduct to a large ovary, where internal fertilisation of the ova occurs (Bargmann, 1937). The ovary is subsequently grossly distended by developing ova, which are released to the water just prior to cleavage (Mauchline and Fisher, 1969).

Figures, facing page: 121. Adult male (X2.2); 122. Adult female (X2.2); 123. Juvenile (X2.2); 124. Ventral view of male (X3.0); 125. Ventral view of female (X3.0).



## 7.1 Sexual maturity stages of E. superba

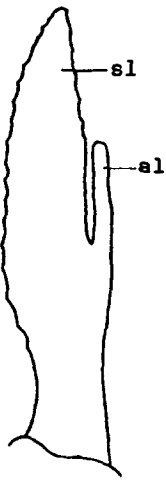
after Makarov and Denys (1980)

1. Juvenile: External sexual features (i.e. petasmas and ampullae in males, thelycum in females) not present. Individuals may be sexed by dissection, but as they are not in or approaching reproductive condition this is generally considered unnecessary.
  
2. Sub-Adult:  
Male: Developing petasmas visible. Ampullae small and pale.  
2AM: Petasmas single undivided lobes (Figure 126b).  
2BM: Petasmas bilobed, but have no wing (Figure 126c).  
2CM: Petasmas almost fully developed, with "wings" present (Figure 126d).  
(As it is difficult to distinguish these stages without a microscope, sub-adult males may simply be referred to as 2M).  
  
Female: Developing thelycum visible, its colour ranging from white to pale red.
  
3. Adult:  
Male: (Figure 121): Petasmas fully developed (Figure 126e). Ampullae usually bright red and clearly visible beneath the gills (Figure 124).  
3AM: Spermatophores not present in ampullae  
3BM: Spermatophores extruding from pore on ampullae, or present within and easily ejected by pressure on the ampullae.  
  
Female: (Figure 122): Thelycum bright red, fully developed, and clearly visible through the gills (Figure 125).  
3AF: Thelycum bears no spermatophores.  
3BF: Spermatophores attached to thelycum. Empty space between ovary and body wall.  
3CF: Spermatophores attached. Ovary fills thoracic space.  
3DF: Spermatophores attached. Carapace noticeably swollen by enlarged ovary. (Figure 122).  
3EF: Carapace swollen in contour, but with large hollow space owing to the recent spawning of eggs. The stress of capture frequently causes the carapace of 3E females to collapse.

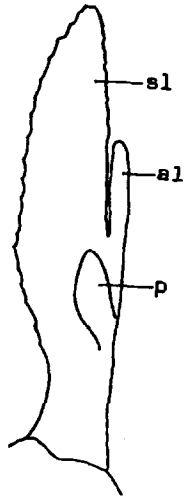
This system is basically the same as that proposed by Mauchline et. al. (1979). The only changes are in the division of sub-adult males into 2AM, 2BM and 2CM (which is not recommended for field use anyway) and the addition of a new stage (3EF) to denote post-spawn females. The numeration system has also been modified.

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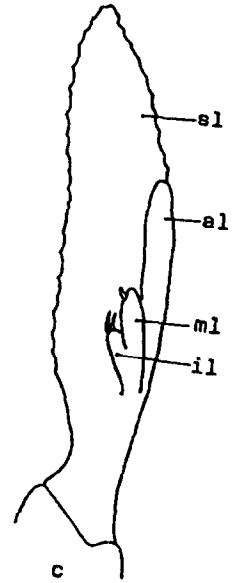
Facing page, Figure 126. The development of the first petasma of E. superba (X16). a, undifferentiated endopod of juvenile; b, petasma of 2A male; c, petasma of 2B male; d, petasma of 2C male; e, fully developed petasma of adult male. al, auxiliary lobe; il, inner lobe; ll, lateral lobe; ml, middle lobe; p, petasma; pa, additional process; pp, proximal process; pt, terminal process; sl, setigerous lobe; w, wing.



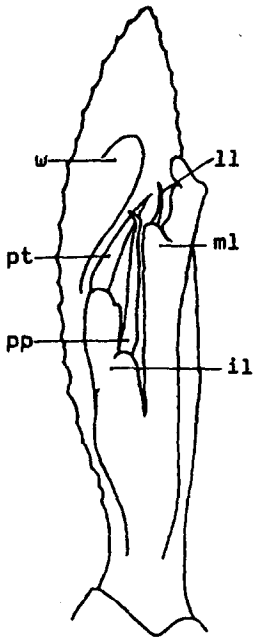
a



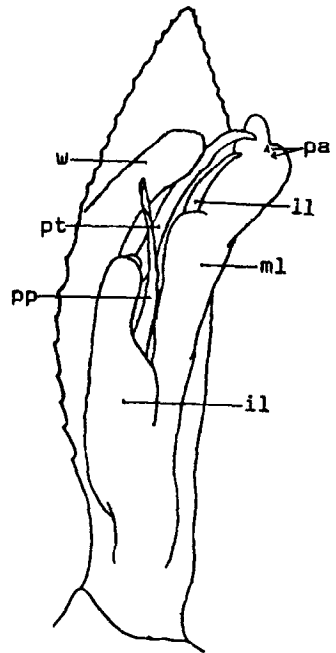
b



c



d



e

## 8. STANDARD MEASUREMENTS USED IN THE STUDY OF EUPHAUSIIDS

After Mauchline (1980a).

Reference Measurement: total body length from the anterior lateral edge of the carapace to the posterior tip of the uropod. This measurement ignores the rostrum, the length of which may vary considerably within and between species or which may be broken.

Standard 1: total length from the tip of the rostrum to the tip of the uropod. This measurement can be done quickly and accurately using a measuring board, providing the individual is large enough.

Standard 2: body length from the tip of the rostrum to the posterior edge of the sixth abdominal segment. This measurement ignores the telson, which is often damaged.

Standard 3: body length from the anterior lateral edge of the carapace to the posterior edge of the sixth abdominal segment. This measurement ignores both the rostrum and the telson.

Standard 4: carapace length from the tip of the rostrum to the mid-dorsal posterior edge of the carapace. This measurement is not affected by preservatives, which tend to cause shrinkage of soft parts such as between the abdominal segments.

Standard 5: carapace length from the anterior edge of the carapace to the mid-dorsal posterior edge of the carapace. This measurement ignores the rostrum and is not affected by preservatives.

Standard 6: carapace length from the anterior edge of the carapace to the posterior lateral edge of the carapace. This measurement ignores the rostrum and is not affected by preservatives.

Standard 7: uropod length from the origin of the tip of the uropod. This is the only reliable measurement which can be made on a cast exoskeleton.

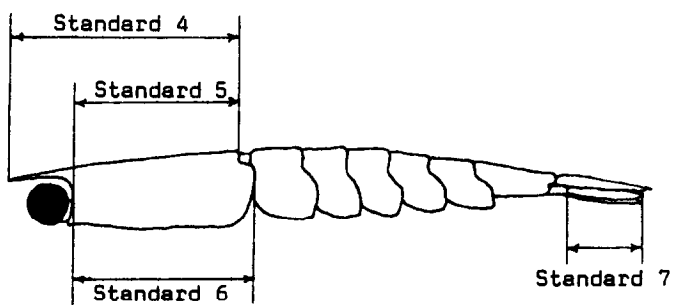
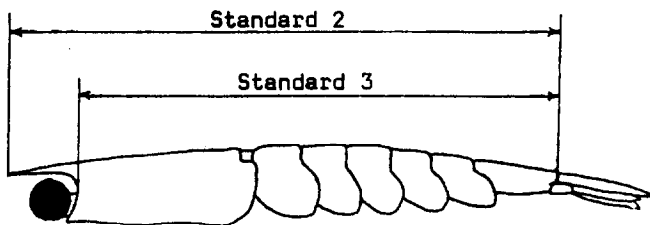
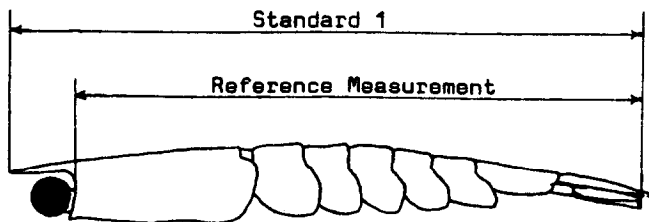


Figure 127. Measurements used in euphausiid studies.

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## GLOSSARY

- adult:** sexually mature individual
- ampulla:** distal region of ejaculatory duct, in which fully formed spermatophores are stored prior to ejaculation. Visible in adult males as red patches in the ventral integument, between the two 7th thoracic appendages.
- antenna:** (= 2nd antenna), paired 2nd head appendages, uniramous, jointed and whip-like in adult Euphausiacea (adj. antennal).
- antennule:** (= 1st antenna), paired 1st head appendages, biramous, jointed and whip-like in adult Euphausiacea (adj. antennular).
- antennular penduncle:** see penduncle.
- antennular lappet:** protuberance on dorsal side of antennular penduncle.
- basis:** (= basipodite), second basal segment of an appendage.
- bathypelagic:** refers to free swimming, deep water organisms.
- bifurcate:** (= biramous), consisting of two branches or rami.
- biomass:** total mass of living organisms.
- brood pouch:** ventral pouch arising from lateral ingrowths from the bases of thoracic appendages of mature female mysids, in which eggs are stored. Not present in Euphausiacea.
- calyptopis:** (= protozoa), larval stages IV to VI. Feature abdomen distinct from cephalothorax, immobile compound eyes enclosed by carapace, legs and pleopods not developed.
- carapace:** thin shield of exoskeleton covering cephalothorax. Fused to all thoracic segments in Euphausiacea.
- carpus:** third segment of endopod of thoracic appendage.
- caudal:** related to tail or posterior regions of the body.
- cephalothorax:** head and thorax combined.
- cervical groove:** transverse groove on dorsal side of carapace in cervical region (where head joins thorax).
- chela:** prehensile claw (adj. chelate).
- cleavage:** repeated subdivision of ovum in early stages of embryonic development.
- coxa:** (= coxopodite), first basal segment of an appendage.

crystalline cones: cone shaped structures in the ommatidia (facets) of compound eyes; function as lenses.

dactylus: fifth (usually distal) segment of endopod of thoracic appendage.

denticle: small spine or projection.

distal: furthest from the base or origin (cf. proximal).

ejaculatory duct: distal region of vas deferens.

embryonic: refers to the developmental stages of an animal from fertilisation of the ovum to birth or hatching.

endopod: (= endopodite), inner branch of an appendage.

epipod: (= epipodite), structure located on the outer side of the base of a thoracic appendage. Modified as gills in Euphausiacea.

eurythermic: able to exist over a wide range of temperatures (cf. stenothermic).

exopod: (= exopodite), outer branch of an appendage.

exoskeleton: (= cuticle), hard external covering of the body.

filiform: slender, thread-like.

flagellum: long, whip-like part of antenna or antennule.

foliaceous: leaf-like or leafy

furcilia: (= zoea), larval stages VII to XII. Feature compound eyes projecting beyond edge of carapace on stalks, legs and pleopods developing.

gill: feathery, thin-walled external respiratory surface. Arising from the coxae of the thoracic appendages in euphausiacea.

gravid: with ovary containing developing oocytes.

integument: outer covering

intermediate plate: small plate between carapace and abdomen on dorsal side.

ischium: first (proximal) segment of endopod of thoracic appendage.

juvenile: immature individual, not morphologically distinct from adult except for the external sexual features (i.e. petasma or thelycum), which are not present.

keel: (= carina), raised ridge of exoskeleton

labium: paired third mouthparts which act as a lower lip (adj. labial)

labrum: first mouthpart (actually formed from hinged plate of exoskeleton), which acts as an upper lip.

larva(e): immature individual, morphologically distinct from adult.

mandible: paired second mouthparts, used for biting and grinding (adj. mandibular).

maxilla(e): (2 pairs), fourth and fifth mouthparts, used for manipulating food.

maxillipeds: anterior thoracic appendages which have been modified to assist in the manipulation of food. Not present in Euphausiacea.

merus: second segment of endopod of thoracic appendage.

metanauplius: larval stage III. Feature mouthparts and first thoracic legs all present as rudimentary buds, antennae and antennules developed as natatory structures.

natatory: associated with or used for swimming.

nauplius: larval stages I and II. Feature three obvious pairs of appendages; uniramous antennules, biramous antennae and mandibles.

oocyte: developing egg, within the ovary of a female.

ovigerous: carrying oocytes.

palp: endopod of mandible or maxilla, used for cleaning mouthparts.

peduncle: base of antenna or antennule.

petasmas: copulatory organs present on the endopods of the first two pairs of pleopods of male euphausiids. Used to transfer spermatophores from the male to the female during mating.

photophores: luminescent organs. Most of the Euphausiacea have ten photophores: 1 on each eyestalk, 1 on the base of each of the second and seventh thoracic appendages, and 1 between each of the bases of the first four pairs of pleopods. Stylocheiron spp. have five photophores; on the eyestalks, bases of the seventh thoracic appendages and between the first pair of pleopods; and Bentheuphausia has none.

plankton: organisms which float or drift passively in aquatic environments.

pleopods: paired natatory appendages situated on the ventral sides of the first five abdominal segments.

pleura: that part of the lateral exoskeleton of the abdominal segments which extends beyond the ventral side of the abdomen.

podobranch(iae): gill arising from the coxa of an appendage (as in the Euphausiacea).

- predatory legs:** elongate second or third thoracic legs, modified for grasping prey.
- propodus:** (= propus), fourth segment of endopod of thoracic appendage.
- protopod:** (= protopodite), base of an appendage (coxa + basis)
- proximal:** nearest to the base or origin (cf. distal).
- rostrum:** mid-dorsal projection of the anterior edge of the carapace (adj. rostral).
- scaphocerite:** (= antennal scale), scale-like exopodite of antenna.
- segment:** major portion of body or appendage, usually separated by flexible joints.
- seta(e):** bristle or "hair" on integument (adj. setose).
- spermatophore:** packet of spermatozoa which is passed from a male's ampulla to a female's thelycum during mating.
- spine:** pointed protrusion of the exoskeleton.
- statocyst:** small round vesicle used for maintaining balance. Not present in Euphausiacea.
- stenothermic:** only able to survive in a restricted range of temperatures (cf. eurythermic).
- sub-adult:** immature individual, not morphologically distinct from adult except for the external sexual features (i.e. petasma or thelycum) which are only partially developed and are not functional.
- suture:** non-articulated line of junction between two adjacent plates of exoskeleton.
- telson:** terminal segment of abdomen.
- thelycum:** copulatory organ of female Euphausiacea; situated ventrally and medially on the sixth thoracic segment (between the two sixth thoracic legs).
- uniramous:** consisting of a single branch or ramus.
- uropod:** broad flattened appendage associated with the telson.
- vas deferens:** duct leading from the testes to the ampulla, along which fully developed spermatozoa pass prior to spermatophore formation.

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