

Polymorphism and Distribution of *Ceratoserolis trilobitoides* (Eights, 1833) (Crustacea, Isopoda) in the Weddell Sea and Synonymy with *C. cornuta* (Studer, 1879)

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Summary. A rich collection of *Ceratoserolis trilobitoides* from the Antarctic Peninsula and the western and southern Weddell Sea is evaluated to describe the polymorphism and variations of the pigmentation. The species is very variable, though local populations show a relatively homogenous morphology. Transitional forms connect different morphotypes. Presumably the relative immobility of these animals, together with low fecundity and geographical or hydrographical barriers are responsible for the evolution of local races. *C. cornuta* and the "colour-species" of Cals (1977) are synonymized with *C. trilobitoides*.

Introduction

During the expeditions 1982/83 and 1984/85 of *RV Polarstern* among the soft-bottom benthic crustaceans of the Weddell Sea the conspicuous serolid isopods could be collected in large numbers. These are carnivorous animals which live, often half buried, on the sandy or muddy sea-floor. The biggest species, *Ceratoserolis trilobitoides*, a disc-shaped animal, has an obvious variation of colour pattern, which has been described already by Cals (1976, 1977), who erected four new species on the base of pigments and cuticular scales. To estimate the validity of these species a study of polymorphism based on a large number of specimens became necessary. In the present study the morphotypes of populations from the Weddell Sea and the Antarctic Peninsula are described and causes for the variations and the systematic consequences are discussed.

Material and Methods

Samples of benthos were collected from *RV Polarstern* during the expeditions 1982/83 and 1984/85 by means of an Agassiztrawl. Invertebrates were sorted out on deck by hand, sediment was washed through a 1 mm-sieve. During the last expedition living specimens were immediately placed in aquaria, wherein they were transported to

Bremerhaven in a temperature-controlled container. To study pigmentation and behaviour living specimens were photographed on board.

Drawings were prepared with a stereomicroscope "Wild M5" and a camera lucida.

Several hundred specimens of *C. trilobitoides* were caught, in 43% of all samples (between 20 and 1,145 m depth) this species was present (for distribution see Fig. 1). The sampling method allows no further quantitative analysis.

For comparison of morphological variations populations from the following stations were studied:

62°38.81'S 55°45.20'W, depth 277 m (north of Joinville Island, Bransfield Strait), 62°8.84'S 58°0.46'W, depth 449 m (entrance of Admiralty Bay, King George Island), 60°42.40'S 45°33.07'W, depth 86 m (off Signy Island), 72°30.35'S 17°29.88'W, depth 240–254 m (Vestkapp), 74°39.25'S 25°18.86'W, depth 605–610 m (northeast of Halley Bay), 77°42.25'S 36°48.09'W, depth 1,145 m (Filchner-depression), 77°31.67'S 42°12.42'W, depth 592–630 m (Gould Bay).

For comparison the following material, previously described by Studer (1879, "Gazelle"-collection) and Sheppard (1933, "Discovery"-collection) was used:

"*Serolis cornuta*": specimens from Kerguelen, 47°52'S 66°41'E, "Gazelle"-collection (Zoologisches Museum Berlin, Kat. Nr. 4601); "Discovery" station 363 (B.M.N.H. 1934. 10. 16.: 809–810) and "Discovery" station 164 (B.M.N.H. 1934. 10. 16.: 811–814).

"*Serolis trilobitoides*": "Discovery station 170 (B. M. N. H. 1934. 10. 16.: 845–846), "Discovery" station 172 (B.M.N.H. 1934. 10. 16.: 847–850).

Results

A) Distribution

Figure 1 shows the new localities. *C. trilobitoides* has previously been found at the Antarctic Peninsula, the South Shetlands and South Orkneys, but not in the Weddell Sea. Figure 2 shows the places from which the species is known so far. It colonizes an enormous area, from the subantarctic Crozet-Islands (Studer 1879) to the sea floor under the Ross Ice Shelf (Lipps et al. 1979); it has a circumpolar distribution. The Patagonian localities (Eights 1833) are dubious, possibly other serolids were taken for *C. trilobitoides*. New discoveries from this area

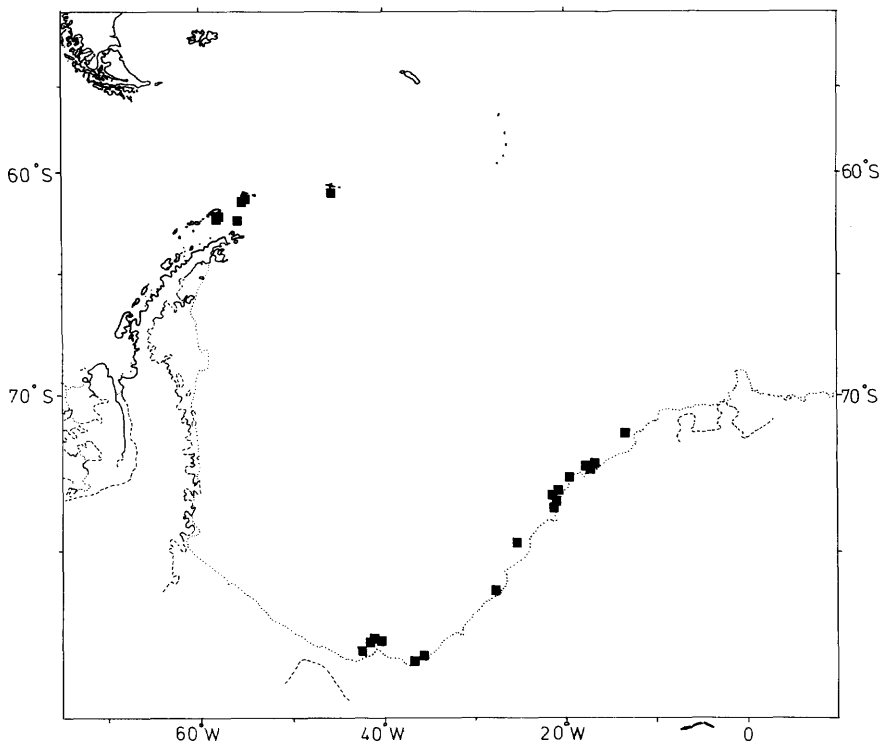


Fig. 1. The new localities where *C. trilobitoides* was found (Antarctic Peninsula and Weddell Sea)

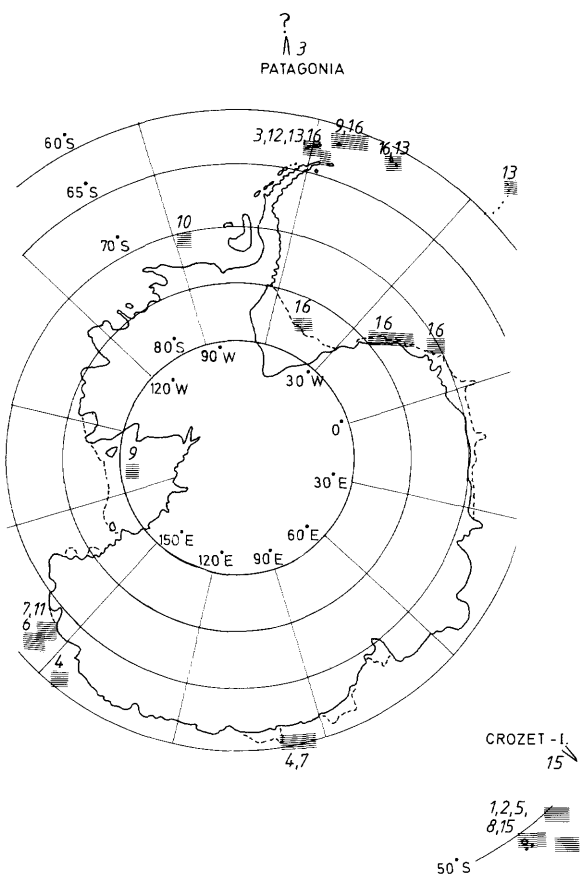


Fig. 2. Authors mentioning the occurrence of *C. trilobitoides*: 1 Cals 1977; 2 Cléret 1973; 3 Eights 1833; 4 Hale 1937; 5 Hale 1952; 6 Hodgson 1910; 7 Kussakin 1967; 8 Kussakin and Vasina 1982; 9 Lipps et al. 1979; 10 Monod 1926; 11 Nierstrasz 1931; 12 Richardson 1913; 13 Sheppard 1933; 14 Sheppard 1957; 15 Studer 1879; 16 present paper

are not known, though some authors have followed the earlier statements (e.g. Nordenstam 1933).

C. trilobitoides is obviously a species which prefers soft bottom and therefore is not present on some shallow littoral areas. It has been found in depths between 24 and 950 m (see Kussakin 1967, 1982). In the *Polarstern* collections it was present in the area of the Antarctic Peninsula at depths between 86 and 449 m (shallowest station: 20 m, Admiralty Bay, King George Island; no station deeper than 449 m), in the Weddell Sea between 198 and 1,145 m (no deeper station).

So the species is eurybath; we do not know to which maximal depth it penetrates the bathyal continental slope.

B) Polymorphism

Polymorphism was studied in populations from the Antarctic Peninsula to the southern Weddell Sea. A statistical comparison of the animal's size is not very instructive, for this purpose the samples are too small. Nevertheless it seems that in some localities distinct differences exist: near Signy Island (South Orkneys) adult males measured 50 to 63 mm length, ovigerous females 52 to 62 mm; equivalent sizes from Admiralty Bay (King George Island, South Shetlands) are 60–67 mm and 66–73 mm, in the Gould Bay (southern Weddell Sea) 57–78 mm and 60–78 mm. Comparing the quotient length: width, no clear trend was discernible, variations within the samples are too great (examples for the quotient length/width: Signy Island: in males from 0.94 to 0.98, in ovigerous females from 1.04 to 1.11; Admiralty Bay: in males 1.09–1.12, in ovigerous

females 1.04–1.10; Gould Bay: in males 1.08–1.18, in ovigerous females 1.16–1.38). Generally animals are slightly longer than wide, some specimens from Signy Island are slightly wider than long.

Those features used by Sheppard (1933) and Carvacho (1977) to describe the differences between *C. cornuta* and *C. trilobitoides* show an important variability. The pleotelsonic mediadorsal spines and the structure of the two dorsal lobes of the cephalothorax, which adorn the area between the eyes, have within a single population a relatively uniform appearance. Figures 3 to 9 show for each locality these details from a selected adult male and a mature female.

A striking feature is the sexual dimorphism of the cephalothoracic lobes in the population from Admiralty Bay (King George Island), where the male specimens have a relatively smooth caudal surface of these lobes, while some deep notches are present in females. This dimorphism was also noted, though less pronounced, in specimens from Signy Island. While in the populations from the western shelf of the Weddell Sea the lobes of both sexes are relatively smooth, the lobes of specimens from Filchner depression, Gould Bay and Bransfield Strait (north of Joinville Island) have deep posterior notches.

The features of the pleotelson show similar regional trends: at the more northern sites the mediadorsal keel bears only few and large spines, especially around Signy Island; the pleotelsonic apex has clearly a longer point than in specimens from the southwestern and southern Weddell Sea (in Table 1: quotient (length of pleotelson minus caudal point)/(length of caudal point)). In the southern localities the number of lateral and mediadorsal spines increases, the spines are smaller.

The animals from the Bransfield Strait (Fig. 3) bear a singular feature: a pair of dorsal spines is present on both sides of the pleotelsonic keel. In no other locality could this structure be found.

The diagonal ridges on the anterior pleotelson show an increased number of small tubercles in specimens from the southern Weddell Sea.

Some features of the figured specimens are summarized in Table 1.

In general terms, the populations from the more northern localities have similar features, some of these are accentuated in the animals from Signy Island (number of spines); the other extreme to the latter morphotype is found in the Filchner-depression, with related morphotypes east and west of it. The population from Vestkapp has an intermediate position. But not only both extremes

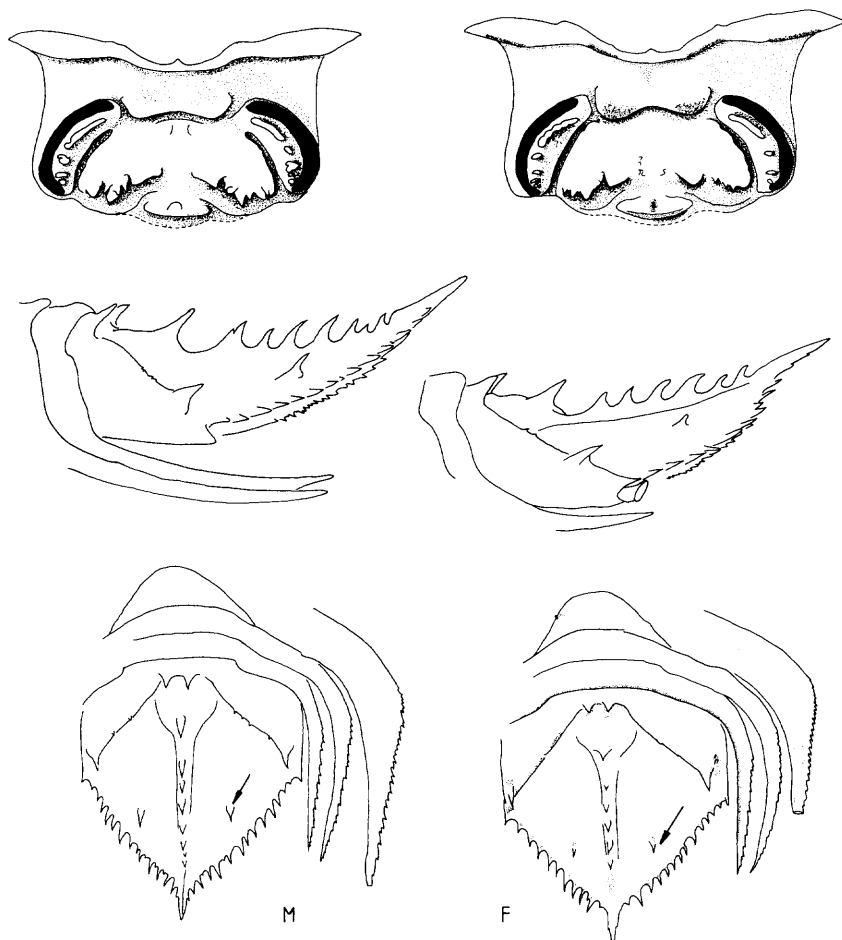


Fig. 3. Features of *C. trilobitoides*. *Left side:* male (M), *right side:* ovigerous female (F). *Above:* cephalothorax in dorsal view; *center:* pleotelson in lateral view; *below:* pleotelson and first 3 pleonites in dorsal view. Locality: Bransfield Strait

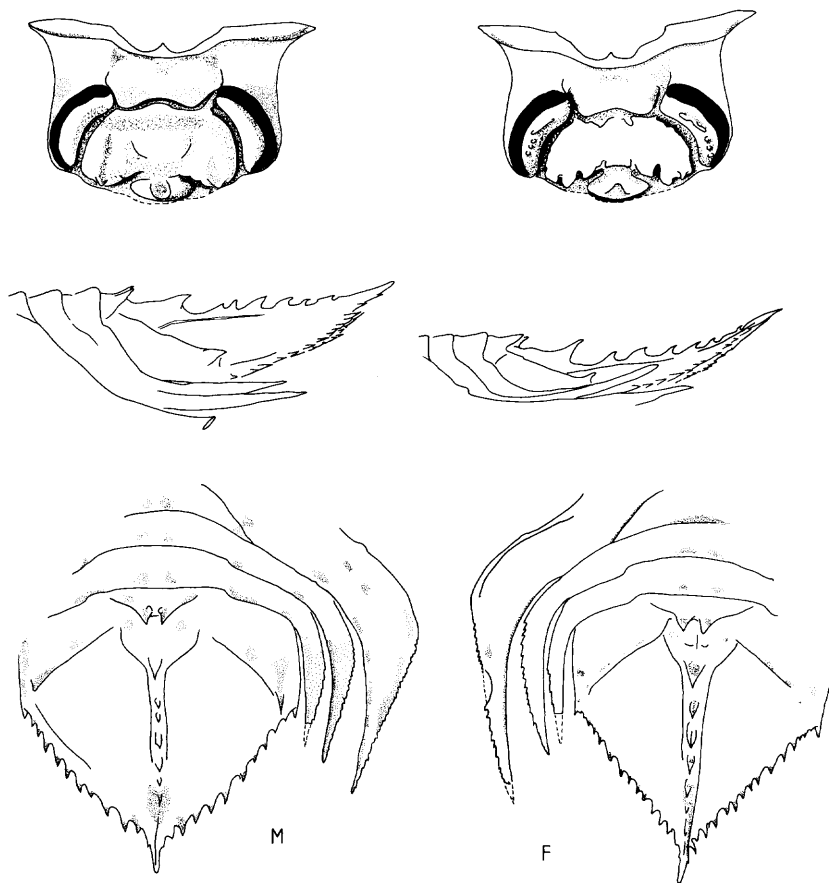


Fig. 4. Features of *C. trilobitoides* (arrangement as in Fig. 3). Locality: Admirality Bay, King George Island

have very characteristic peculiarities, as already mentioned for the pair of telsonic spines in the population from Bransfield Strait.

Searching for further features the subchelate male pereopod 2 has been compared. Figure 10 shows, in addition to material from the localities already discussed, the pereopod 2 of a male from Zadovski Island (South Sandwich Islands) (Fig. 10: B), and for comparison the subchela of *C. pasternaki*, the second, considerably smaller species of the genus *Ceratoserolis*.

The propodus bears 2 rows of composite spines, one of which is longer (hatched in Fig. 10); distally between both rows a single spine is present (marked with "x" in Fig. 10). Groups of similar morphotypes cannot be defined, but there are clear differences between *C. pasternaki* (Fig. 10 A) and *C. trilobitoides*. *C. pasternaki* has considerably fewer spines, the distal concavity of the propodal palm is longer, the medial spine between the two rows is lacking. This comparison is important to gain an idea of the variations that occur at the species level.

Table 1. Comparison of morphological features of *C. trilobitoides* from different localities

Locality	Bransfield Strait	Admirality Bay	Signy Island	Vestkapp	N.E. of Halley	Filchner-depression	Gould Bay
Cephalothoracic lobes	notched	sex. dimorphic, smooth	sex. dimorphic, smooth	relatively smooth	notched	notched	notched
Chephalothoracic lobes	notched	sex. dimorphic, smooth	sex. dimorphic, smooth	relatively smooth	notched	notched	notched
No. of mediodorsal spines of pleotelson	7–8	7	4–7	8–10	9–12	10–11	10–14
No. of lateral spines of pleotelson	13–17	12–18	10–11	11–16	17–20	19–27	18–21
Quotient (length of pleotelson)/ (length of terminal spine)	9.3	7.5	5.3	9.7	15.3	32.8	16.4

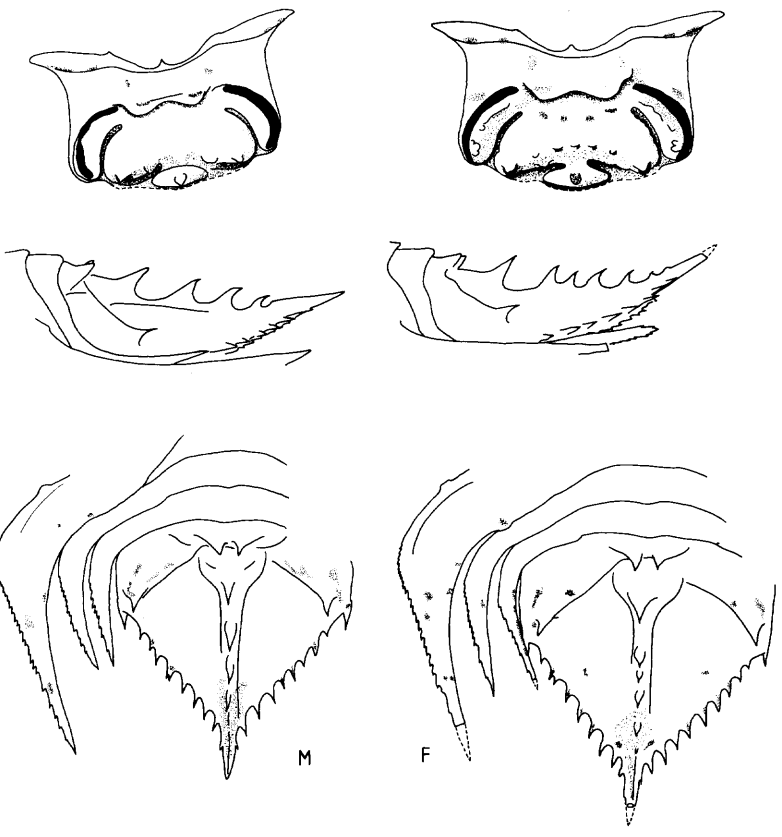


Fig. 5. Features of *C. trilobitoides* (arrangement as in Fig. 3). Locality: off Signy Island

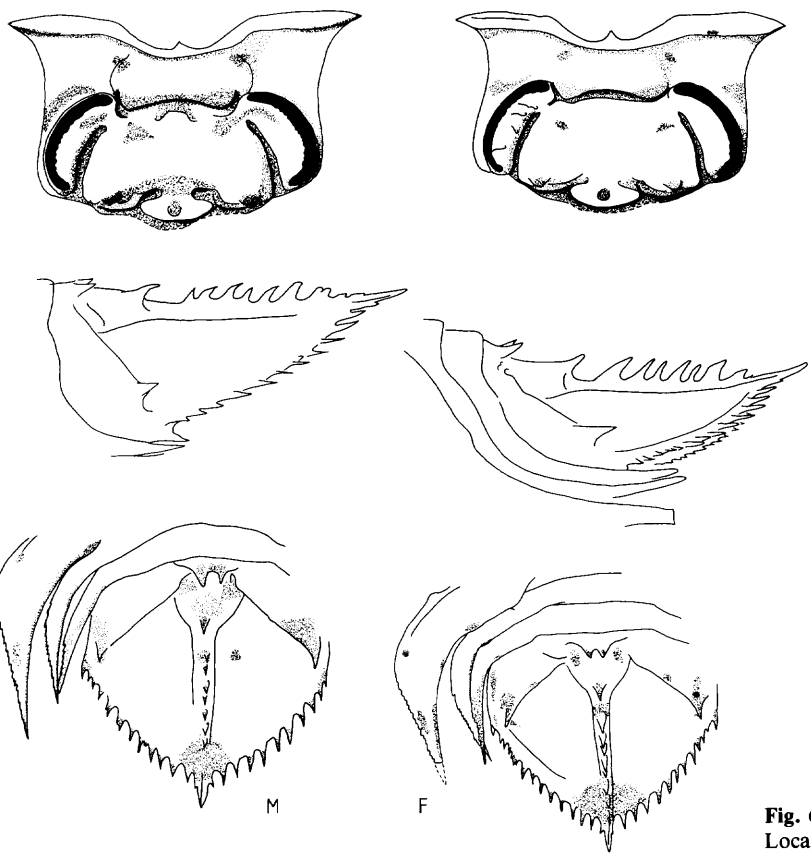


Fig. 6. Features of *C. trilobitoides* (arrangement as in Fig. 3). Locality: Vestkapp, eastern Weddell Sea

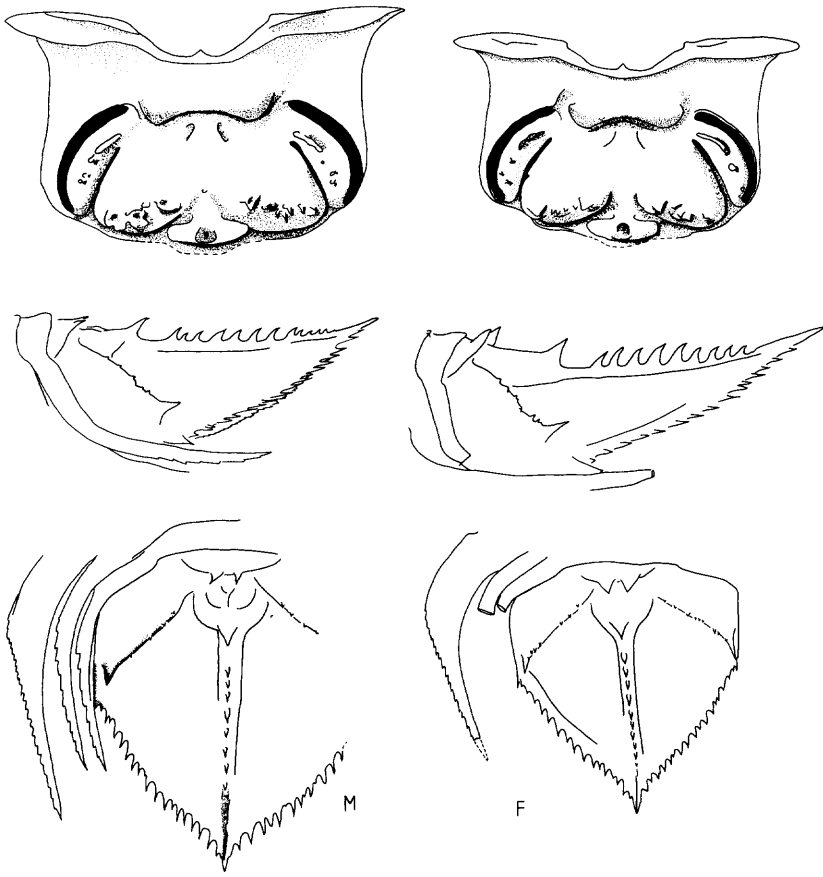


Fig. 7. Features of *C. trilobitoides* (arrangement as in Fig. 3). Locality: NE of Halley Bay

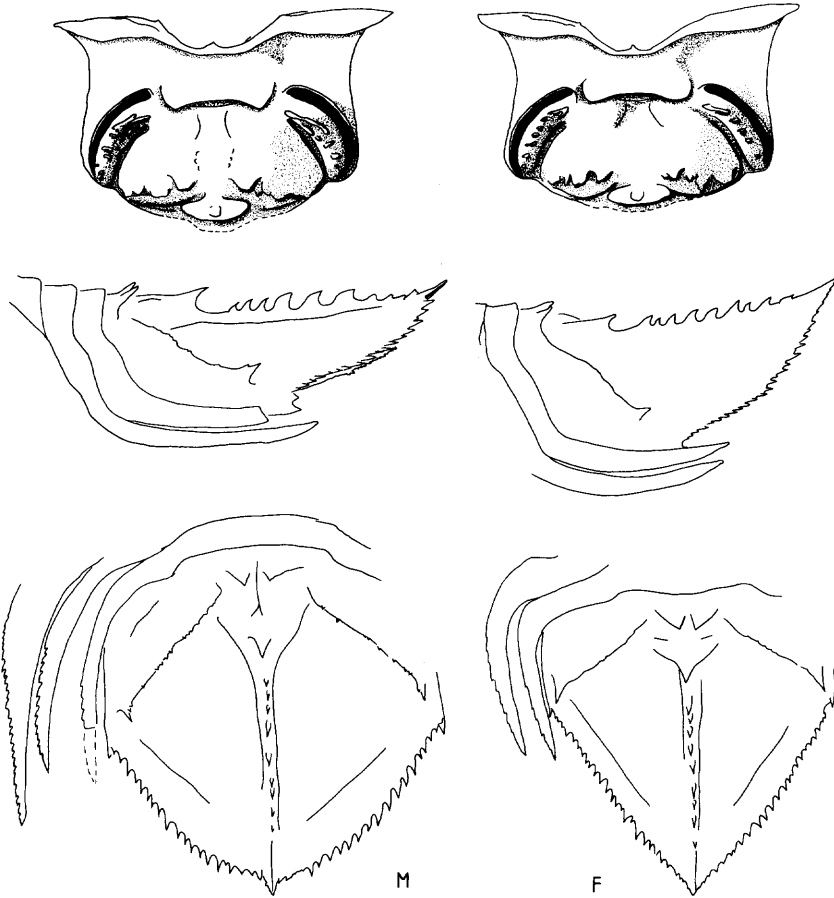


Fig. 8. Features of *C. trilobitoides* (arrangement as in Fig. 3). Locality: Filchner-depression

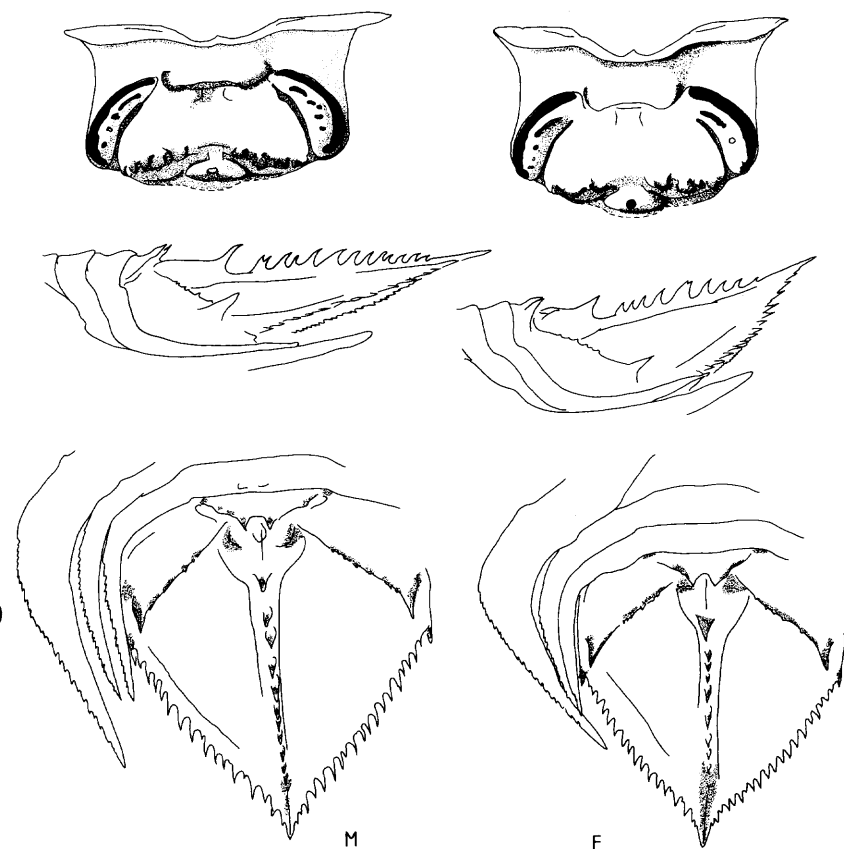


Fig. 9. Features of *C. trilobitoides* (arrangement as in Fig. 3). Locality: Gould Bay

C) Pigment Patterns

Figure 11 shows some typical dorsal pigment patterns from the area studied. The colour is produced by a grey-yellow tinge of the integument, in transparent specimens the inner organs shine through, many small, dark grey or brown chromatophores determine the general colour, accumulations of larger brown chromatophores are responsible for the patches. Though the arrangement of the brown patches varies individually within the populations, e.g. individuals from Admiralty Bay (Fig. 11: 1) may have smaller patches than in the figured specimen, it is possible to define a basic pattern for each population. Several small patches, often occurring in single central rows on the coxal plates, together with a light integument are typical for most animals from the northern localities. Specimens from Bransfield Strait have a slightly darker integument. A pair of anterolateral and a terminal brown patch are present on the pleonelson of specimens from Admiralty Bay, Vestkapp and Gould Bay. No brown patches can be seen in the population from Filchner-depression, where the general colour is a bluish dark grey. In the Gould Bay very dark as well as lighter specimens occur together with intermediate forms.

D) Physiological Races

It is probable that the genetic variability described will not be restricted to the phenotypes but will also show in

physiological adaptations. Though the Southern Polar Ocean is relatively homogeneous in comparison with other oceans we must assume, that for the stenoecic antarctic invertebrates, which live at the lower limit of the temperature range near the freezing point, already small variations of the environmental conditions will have important effects. While the upper sublittoral water of Admiralty Bay has temperatures of near -2.0°C to $+2.5^{\circ}\text{C}$ (measured 1977/1978: Presler 1980), we find in the Filchner-depression on the bottom a supercooled water (-2.2°C -2.3°C : Gammelsrød and Slotsvik 1981) of high salinity (probably throughout the year). Possibly physiological differences can be measured when populations of both areas are compared. An indication for differences in the tolerance for small variations of temperature and salinity is the mortality we observed while keeping specimens in aquaria. Though it was intended to keep temperature constantly at -1°C and salinity at 33.3‰, due to technical problems some variations occurred (temperature up to $+3^{\circ}\text{C}$, salinity around 34.5‰). These changes are stress-factors and probably caused several animals to die (physiological mechanisms are not known). Specimens from Filchner-depression lived only for 2–3 weeks. Figure 12 shows that the specimens from Signy Island survived cultivation best while those from Gould Bay seem to be very delicate. But as we do not know what effect the change in pressure during capture has, we must be careful with the interpretation of Fig. 12.

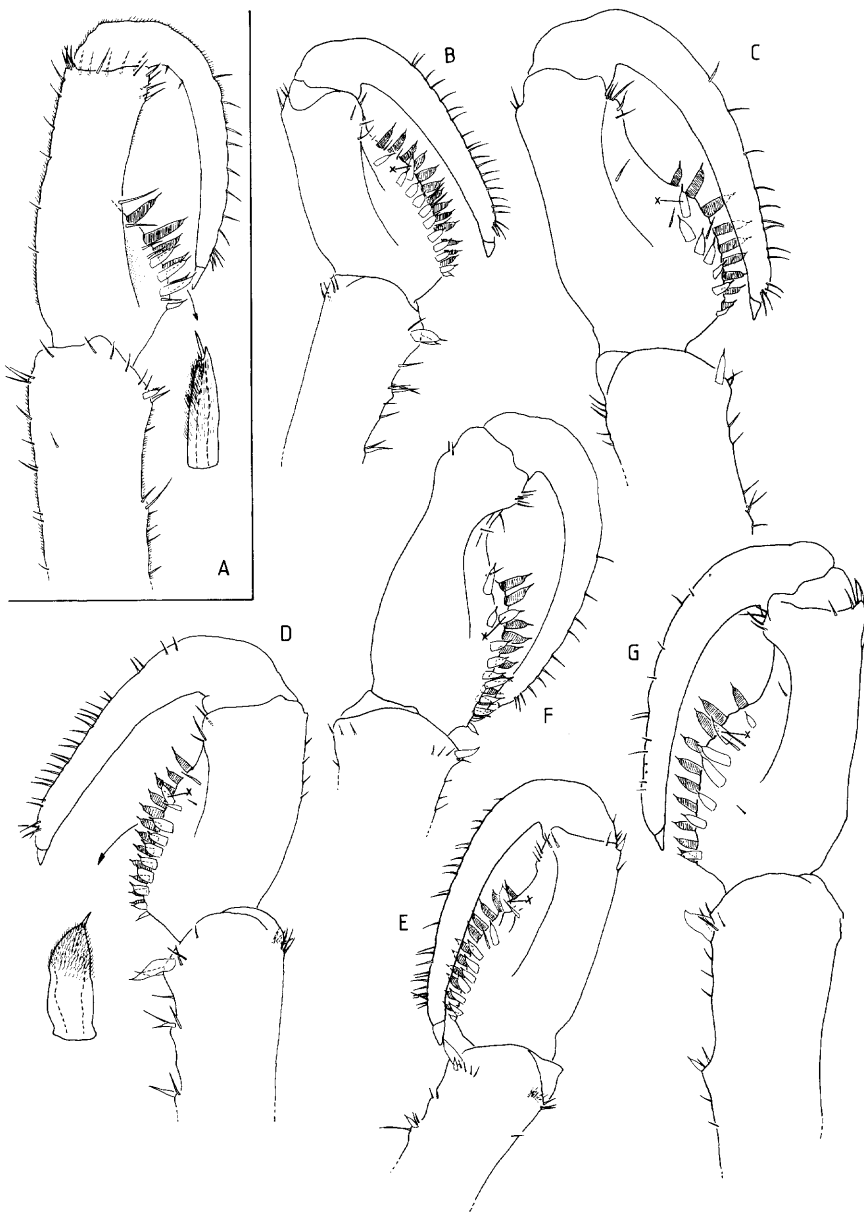


Fig. 10. Subchela of male pereopod 2. *A*: *C. pasternaki*, specimen of 31 mm length, from 72°31.64' S 17°34.97' W. *B–G*: *C. trilobitoides*. *B*: Specimen of 49 mm length, from SE of Zadorovski Island (South Sandwiches), "Discovery" Station 363 (B.M.N.H.). *C*: Specimen of 63 mm from Bransfield Strait. *D*: Specimen of 53 mm from off Signy Island. *E*: Specimen of 64 mm from Vestkapp. *F*: Specimen of 79 mm from NE of Halley Bay. *G*: Specimen of 62 mm from Gould Bay. Longer spine row of propodus hatched, medial composite spine of propodal palm marked with "x"

E) Systematics: Synonymy with C. cornuta (Studer, 1879)

A comparison of the type material of *C. cornuta* and specimens designated by Sheppard as *C. cornuta* and *C. trilobitoides* with the present collection was necessary to clarify the confusion about these two species. Among the material of the present study the variety from Signy Island is a typical "*cornuta*"-form, which is distributed in several more northern antarctic places (Crozet Islands, South Orkneys, South Sandwich Islands: Sheppard 1933). Sheppard (1933) discusses the following features:

1) "... The shape of *S. cornuta*,..., is almost circular, whilst that of *S. trilobitoides* is broadly ovate...". It has already been mentioned that the quotient length/width varies within populations and no striking differences could be found when comparing specimens from different localities.

2) "... that (= the terminal segment) of *S. cornuta* is longer than broad with a much more acute posterior extremity and with a longer terminal spine...". Figures 3–9 show the variability of this feature, no exact boundary can be drawn between morphotypes. The same is true for the remaining features: 3) mediodorsal spines of pleotelson, 4) length of coxal plates of the seventh thoracic somite, 5) the colour.

Carvacho (1977) emphasized another feature: "... chez *S. cornuta* elle (= l'ornementation située derrière chaque oeil) prend la forme d'un cône; tandis que chez *S. trilobitoides* il s'agit d'une structure trilobulée...". This feature is dimorphic in some populations; smooth lobes also appear in other populations, which have a morphology of Sheppard's *trilobitoides*.

We must conclude that *C. cornuta* (Studer 1879) is a junior synonym of *C. trilobitoides* (Eights 1833) and that

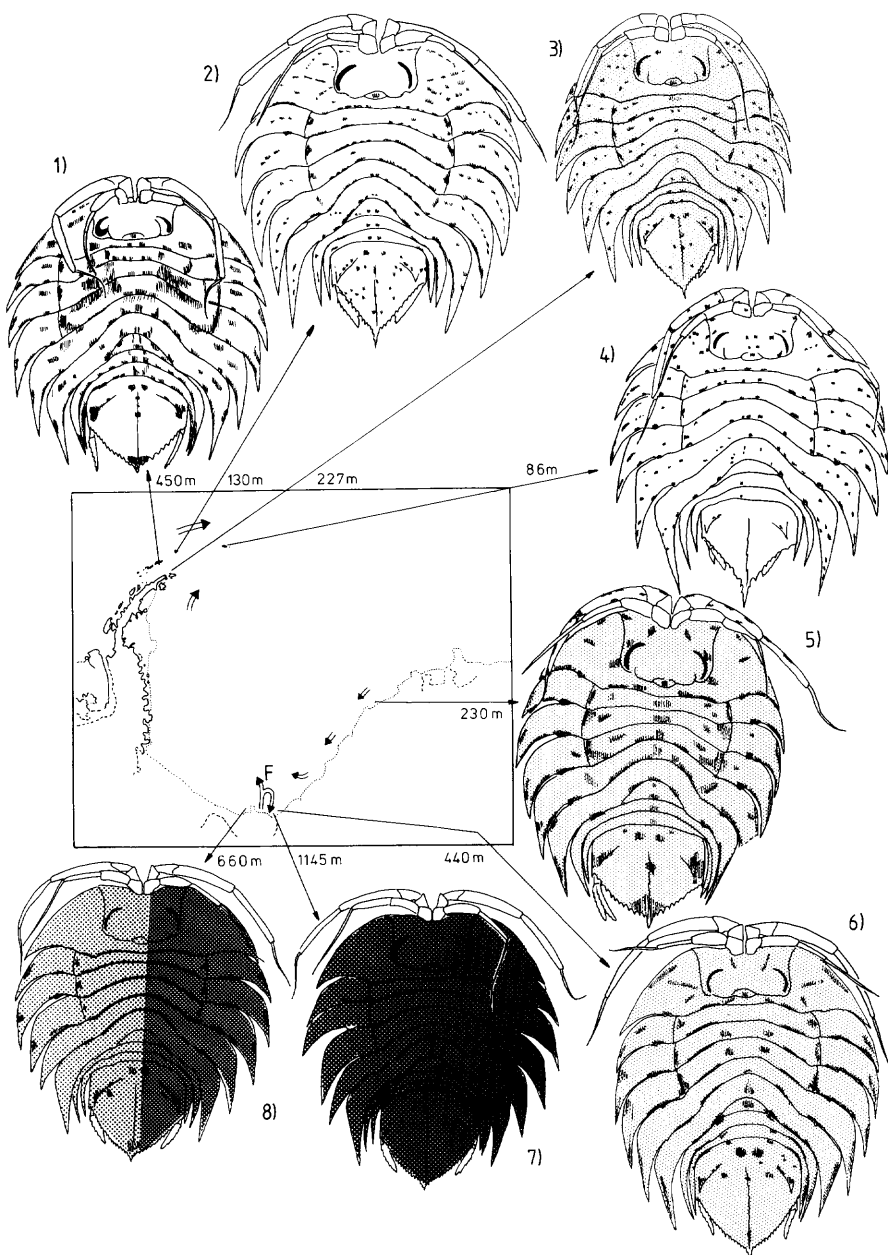


Fig. 11. Variation of colour pattern in populations of *C. trilobitoides* (drawn after photographs of living specimens). The map shows the Weddell Sea with important currents (arrows; F: area of Filchner-depression). The depth of the localities is indicated. Localities: 1 King George Island, 2 Elephant Island, 3 off Joinville Island ($62^{\circ}39'S$ $55^{\circ}45'W$), 4 Coronation Island, 5 Vestkapp ($72^{\circ}25'S$ $16^{\circ}27'W$), 6 eastern side of Filchner-depression, 7 Filchner-depression, 8 Gould Bay ($72^{\circ}18'S$ $41^{\circ}26'W$); the population from Gould Bay consisted of darker and less dark specimens

the "cornuta" morphotype is only one of several local varieties of a widely distributed species. This synonymy was first suggested by Hodgson (1910), with our richer material it can be confirmed.

Discussion

The question whether phenotypical differences indicate the presence of several species or not cannot always be solved. The crucial point is if a reproductive isolation is probable or not. As soon as indications for gene flow are found, we must suppose that we are dealing with a single biospecies (see Willmann 1985). Then *C. trilobitoides* should be considered as a widely distributed, very variable biospecies, which because of a reduced panmixis is in the process of speciation, which resulted until now in races that still can exchange genes. This is suggested by

the distribution of pigment patterns and the many intermediate features that connect different morphotypes. To separate two morphospecies would be a subjective act and yield artificial taxa.

The 'colour-species' proposed by Cals (1977: *C. maculatovirgata*, *C. albohirsuta*, *C. griseostrigosa*, *C. lineatocostata*), superficially described and without designated type material, have not to be discussed seriously in the light of the present results.

Intraspecific variability of serolids was discussed by Holdich and Harrison (1980). The Australian species *Serolis minuta* shows differences which do not justify the separation of species. *S. minuta* also has an area of distribution which includes important climatic differences (from about $26^{\circ}S$ to $37^{\circ}S$). To decide whether a variation is a new species or not Holdich & Harrison recom-

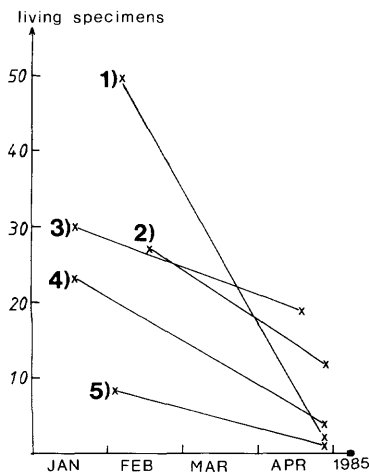


Fig. 12. Survival of *C. trilobitoides* kept in aquaria at about -1°C and a salinity of 33.3‰. The specimens were collected at the following localities: 1 Gould Bay (depth 660 m), 2 Signy Island (depth 86 m), 3 Vestkapp (230 m), 4 Admiralty Bay, King George Island (450 m), 5 NE of Halley Bay (200 m)

mend to compare a large number of specimens from different samples.

Considering the variability of these isopods we must ask if the genus *Ceratoserolis* really can be separated from *Serolis*, as proposed by Cals (1977) for the species *S. trilobitoides*, *S. cornuta* and *S. pasternaki* (without naming a type species, which should be *S. trilobitoides*, as this species was principally discussed by Cals).

It is obvious that "*Serolis*" in its present state is a polyphyletic genus containing species of varying morphology, as those oval animals without protruding coxal plates (e.g. *S. ovata*, *S. latifrons*, *S. elliptica*) or the species with long coxal plates and mediodorsal spines on cephalothorax and tergites (e.g. *S. johnstoni*, *S. geraldchei*, *S. spinosa*) or species with a shortened thorax (e.g. *S. tropica*, *S. carinata*, *S. mgrayi*). To define genera from monophyletic groups of species is very useful, especially in course of a revision, which for serolids is still lacking. Therefore the author feels that the genus *Ceratoserolis* should not be rejected. *Ceratoserolis* can be recognized by its nearly circular shape, the protruding, caudally directed coxal plates, the long epimera of pleonites 2 and 3, which nearly reach or surpass the apex of the last coxal plate, the sculptured cuticle between the eyes, the visible suture lines of coxal plates 2 to 4, the typical pleotelson, the absence of dorsal spines on cephalothorax or tergites. The similarities between *C. pasternaki* and *C. trilobitoides* have been noted by Kusakin (1967) as well as the differences, of which the size of the sexually mature animals and the form of the male P2 are the most conspicuous. These differences are not within the range of the polymorphism of *C. trilobitoides*, *C. pasternaki* really is a separated species, no hybrids have been found until now.

The different pigment patterns of *C. trilobitoides* possibly are an adaptation to the colour of the sediment,

exact studies on this subject are lacking. It is difficult to explain why the populations living in the aphotic zone on the bottom of the deep Filchner depression have such a dark coloration. This adaptation might have occurred in the shallower Gould Bay. Cryptic coloration and active (physiological) colour change of serolids have been described by Moreira (1974). Physiological changes of pigmentation have not been observed in *C. trilobitoides*, though many specimens were kept for several months on different sediments in aquaria.

The patterns are fixed by the arrangement, size and colour of chromatophores.

Another aspect of the present findings is important for discussions on antarctic ecology: This species shows through its local races how immobile it is and how few possibilities for the colonization of unpopulated areas these animals have. The existence of these races is possibly an indication for the low tolerance of disturbances of some benthic invertebrates. It is not known how many offspring this species can produce per unit of time (the specimens possibly live 6 years, a female can produce about 100 eggs: Luxmoore 1982; embryonal development lasts about 2 years: Wägele, in press), but it seems very probable that productivity is as low as in other polar invertebrates (see Clarke 1982). This phenomenon, combined with immobility and the lack of swimming stages results in genetically stable populations which have only few contacts with their closest neighbours. This is most conspicuous in the southern Weddell Sea, where between $77^{\circ}39.63'S$ $35^{\circ}23.91'W$ and $77^{\circ}42.25'S$ $36^{\circ}48.09'W$ a sharp separation of pigment patterns has been found (Fig. 11: 6 and 7). In this area hydrographical conditions might form a barrier for migrations. As already mentioned the Filchner-depression has at its bottom one of the coldest water bodies, which flows from under the Shelf Ice to the north and is partly led back south, where it disappears again under the Filchner Ice Shelf (Carmack and Foster 1975). The Filchner population possibly has special adaptations to very low temperatures; it seems to have contacts to the more western population of the Gould Bay, where dark pigmentation is also frequent.

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