

OBTUSOECIA (HALOCYPRIDA: MYODOCOPA: OSTRACODA) A BIPOLAR PLANKTONIC OCEANIC GENUS. TAXONOMY, BATHYMETRY AND ZOOGEOGRAPHICAL DISTRIBUTION

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Abstract.— Full detailed descriptions of the two species of *Obtusoecia*, one of two planktonic halocyprid ostracod genera that are bipolar, demonstrate that the taxonomic separation of these two forms formerly considered to be conspecific, is valid. The segregation of the genus from *Porroecia* is also validated. The value of characters of limbs other than the first and second antennae particularly in defining halocyprid genera is emphasised. Zoogeographical distributions of the two species based on comprehensive compilations of both published and unpublished data show that *O. obtusata* is confined to the North Atlantic, whereas *O. antarctica* has an Antarctic circumpolar distribution. Detailed bathymetric profiles show that *O. obtusata* is a shallow mesopelagic species that is overwhelmingly dominant at depths of 50–200 m in subpolar seas, and shows limited ability to submerge at lower depths, so that it is restricted to seas that have a marked seasonal cycle of turn-over and stratification. It is postulated that the bathymetric distributions of the two species are similar, also that *O. antarctica* is more likely to be ancestral to *O. obtusata* than vice versa.



Key words.— *Obtusoecia*, halocyprid ostracods, taxonomy, bathymetry, zoogeography, bipolarity.

INTRODUCTION

The genus *Obtusoecia* was established by Martens (1979a,b) to include two closely related species, *O. obtusata* (Sars, 1865) from the North Atlantic and *O. antarctica* (Martens, 1979) from the Southern Ocean, designating *O. obtusata* as the type species for the genus. These two species had initially been placed in the genus *Conchoecia* by Müller (1906a, 1912), and was later attributed to a genus *Spinoecia* by Poulsen (1973). However, Martens (1979a) demonstrated that this genus was heterogeneous and split it into *Obtusoecia* and *Porroecia*.

Obtusoecia obtusata (Sars, 1865) was one of the earliest species to be described, and has been frequently reported from the North Atlantic (Angel and Fasham

1975, Apstein 1911, Aurivillius 1898, 1899, Brady and Norman 1896, Chavtur, 1991, 1992, Cleve 1903, Cleve and Pettersson 1903, Davidson 1924, Ellis 1985, Elofson 1941, Grainger 1965, Gran 1902, Granata and Caporiacco 1949, Hulings 1967, Huntley et al. 1983, Kielhorn 1952, Müller 1901, 1931, Damas and Koefoed 1907, Paulsen 1909, Sars 1865, 1890, 1922–28, Shih and Laubitz 1978, Skogsberg 1920, Stephensen 1938, Vanhoffen 1897, Vavra 1906, Wiborg 1954, 1955, Williams 1975). Müller (1906a) reported a very similar form from the Southern Ocean to which he gave sub-specific status, *Conchoecia obtusata antarctica*. This species has also been widely reported both with and without the sub-specific epithet (Müller 1906b, 1908, Deevey 1974, 1976, 1978, Hillman 1967, 1968, 1969, Iles 1953, Ramirez and Mogulivsky 1971).

Poulsen (1973) placed both forms in his new genus *Spinoecia*, but only had a single specimen that he attributed to *Spinoecia obtusata antarctica* Dana station 3624 (28°18'S, 177°01'E). However, on the basis of the zoogeographical information given below the identity of this specimen must be regarded as dubious. Martens (1979a) not only demonstrated that the two forms are distinct species, but also placed them in a new genus *Obtusoecia*. He raised *O. antarctica* to full specific status, and erected a new genus *Porroecia*, to accommodate the other species of Poulsen's genus *Spinoecia*. Subsequently the Southern Ocean species has been widely reported (Angel 1981, Benassi et al. 1992, 1994, Blachowiak-Samolyk 1999, 2001, Blachowiak-Samolyk and Zmijewska, 1995, 1997, Chavtur and Kruk 2003, Deevey 1982, Drapun 1982, 1983, 2003, 2005, Drapun et al. 1991, Gollasch 1997, Hopkins 1985, Hopkins and Torres 1988, Jazdzewski et al. 1982, Kock 1992, Kruk and Chavtur 2003, see also the website on Southern Ocean planktonic ostracods recently developed by Blachowiak-Samolyk and Angel (2004).

There are some doubtful reports of *O. obtusata* from the Mediterranean (Furnstein 1960, Kimor and Berdugo 1967, Kimor and Wood 1975), which, if confirmed, would indicate the species is a glacial relict. *O. obtusata antarctica* is also included in Chen and Lin's book on Ostracoda of Chinese Seas along with other Southern Ocean species (Chen and Lin 1995).

Until recently most systematic and taxonomic treatments of halocyprid ostracods have concentrated on the characteristics of the carapace and first and second antennae. However, Chavtur and Stovbun (2003) in substantially revising the systematics of *Archiconchoecia*, and Chavtur (2003) in describing new species of *Metaconchoecia* and have demonstrated the value of characteristics of the other limbs in the systematics of the group. As a contribution to the re-assessments of the various genera, and as part of our continuing studies of high latitude halocyprids we provide the first fully detailed descriptions of the two species of *Obtusoecia*, and summarise the current knowledge of their zoogeographical and bathymetric ranges. In the taxonomic descriptions we use the nomenclature for the setae is that was developed by Skogsberg (1920) and described by Iles (1953). The nomenclature is also illustrated in Angel (1993) and on the website by Blachowiak-Samolyk and Angel (2004).

MATERIALS AND METHODS

The materials for this study have mainly been derived from sampling programmes undertaken in the pre-second World War era by Discovery Investigations and the Post-War sampling programmes of the National Institute of Oceanography (which became the Institute of Oceanography Sciences and more recently moved to the Southampton Oceanography Centre).

Zoogeographical data have been compiled from the data base held at Southampton Oceanography Centre (now available generally via OBIS) published literature (see Blachowiak-Samolyk and Angel, 2004) and substantially supplemented with unpublished data from a numbers of sources (See Acknowledgements).

Post-war Discovery samples were collected with RMT1 samplers (0.32 mm mesh), which are semi-quantitative and sorted under stereo-microscopes. Whenever practical total samples were sorted and analysed. Whole animals were measured at $\times 50$ magnification using a Wild M5 stereomicroscope, and of dissected animals mostly at $\times 100$ magnification using a Wild M20 microscope. Drawings were made using a camera lucida, adding scales with a micrometer slide. These drawings were scanned and traced using Illustrator 7 to generate digital images.

The specimens that were dissected and stained in lignin pink, have been permanently mounted on slides and deposited in the Natural History Museum London. The bulk of the material examined is still held at the National Oceanography Centre Southampton, but will eventually likewise be deposited at the Natural History Museum, London.

SYSTEMATICS

Obtusoecia Martens, 1979

Type species. *O. obtusata* (Sars, 1865)

Type material. Permanent preparations of the dissected specimens used to prepare the illustrations in this paper have been deposited at the Natural History Museum, London registration numbers:

O. obtusata female — 2005.2021

O. obtusata male — 2005.2022

O. antarctica female — 2005.2023

O. antarctica male — 2005.2024

Diagnosis. A genus of Conchoecinae. Both dorsal and ventral corner are. Males are of 25% smaller in size than females. Frontal organ ends in a long sharp point. Female first antenna carries a long dorsal seta. The hook on the male's left endopodite of the second antenna is buckle-shaped and approximately 13% of carapace length, whereas the hook on right endopodite is short and straight.

Description. This definition is based on measurements of the carapaces, frontal organs, and first and second antennae shown in Table 1, and the tabulation of the characteristics of the other limbs, which are illustrated in the figures and tabulated in Appendix 1. Table 1 also includes data for *Porroecia porrecta* that is the type species for the genus *Porroecia* to enable comparisons to be made between the two genera.

Table 1. Meristic measurements of specimens of male (8) and female (9) of *Obtusoecia antarctica* mostly from Discovery stations 2024 (30 March 1937, 45°01'18"S, 33° 42'00"E), but two of the females were from station 1772 (23 May 1936, 36°01'48"S, 0° 04' 18"E), and of male (10) and female (6) *O. obtusata* all from Discovery station 7709#58 (1 May 1971, 60° 04' 06"N, 19° 38' 42"W). Compared with similar data for the type species of *Porroecia* (Angel, 1969). The carapace length data are based solely on the individual specimens whose limbs were measured and, therefore, differ slightly from the more comprehensive length data listed in Table 2. The values for the various setae and limb segments are given as the mean percentages of the carapace length of each individual. (n/a = not applicable).

| | <i>Obtusoecia obtusata</i> | | <i>Obtusoecia antarctica</i> | | <i>Porroecia porrecta</i> | |
|-------------------------|------------------------------|--------------|------------------------------|--------------|------------------------------|-------------|
| | Male | Female | Male | Female | Male | Female |
| Carapace | | | | | | |
| Length | 1.21 ± 0.030 | 1.75 ± 0.039 | 1.26 ± 0.039 | 1.65 ± 0.067 | 1.42 ± 0.019 | 1.70 ± 0.03 |
| Height (as % of length) | 47.9 ± 1.26% | 42.9 ± 1.11 | 47.8 ± 1.04 | 45.1 ± 0.40 | 44.0 ± 0.84 | 42.3 ± 0.68 |
| Breadth | 39.5 ± 1.34% | 34.1 ± 1.14 | 39.1 ± 0.45 | 33.2 ± 0.99 | 44.4 ± 0.94 | 36.5 ± 0.81 |
| Frontal organ | | | | | | |
| Stalk | 28.8 ± 1.03% | 23.9 ± 1.27 | 34.5 ± 0.81 | 32.3 ± 0.99 | 34.2 ± 0.53 | 25.9 ± 0.74 |
| Capitulum | 9.6 ± 0.66% | | 13.6 ± 0.75 | | 12.6 ± 0.41 | |
| First antenna | | | | | | |
| Segment 1 | 15.5 ± 0.69% | Fused | 17.6 ± 0.60 | Fused | 15.8 ± 0.25 | Fused |
| Segment 2 | 14.5 ± 0.60% | | 17.3 ± 0.71 | | 16.0 ± 0.34 | |
| Total | 31.5 ± 0.68 | 15.8 ± 1.15 | 35.3 ± 0.57 | 17.4 ± 0.46 | 33.5 ± 0.54 | 16.8 ± 0.62 |
| seta a | 16.0 ± 1.19% | 12.8 ± 0.74 | 19.4 ± 0.90 | 12.23 ± 0.49 | 16.4 ± 0.57 | 10.4 ± 0.37 |
| seta b | 39.1 ± 1.27 | | 43.8 ± 0.95 | | 41.6 ± 0.84 | |
| seta c | 11.4 ± 0.57 | | 13.1 ± 0.83 | | 4.7 ± 0.24 | |
| seta d | 39.3 ± 1.45 | | 43.4 ± 0.86 | | 42.4 ± 0.96 | |
| seta e | 42.9 ± 1.08 | 33.6 ± 0.66 | 47.9 ± 1.51 | 35.7 ± 0.76 | 44.8 ± 0.87 | 25.7 ± 0.77 |
| e seta armature | 8–10 pairs + ~24 alternating | n/a | 8–9 pairs + ~16 alternating | n/a | 15 pairs + 27–31 alternating | n/a |
| dorsal seta | n/a | 12.2 ± 0.78 | n/a | 11.6 ± 0.62 | n/a | absent |
| Second antenna | | | | | | |
| Protopodite | 44.8 ± 1.01% | 36.6 ± 0.65 | 49.2 ± 0.89 | 40.2 ± 1.01 | 44.2 ± 0.57 | 35.1 ± 0.55 |
| Exopodite segment 1 | 18.8 ± 0.42% | 14.6 ± 0.15 | 20.9 ± 0.54 | 18.2 ± 0.49 | 13.5 ± 0.33 | 11.5 ± 0.23 |
| Exopodite segments 2–8 | 8.6 ± 0.27% | 6.1 ± 0.21 | 9.2 ± 0.18 | 6.90 ± 0.21 | 6.6 ± 0.09 | 5.5 ± 0.14 |
| Longest swimming seta | 43.0 ± 1.47% | 35.3 ± 1.19 | 47.5 ± 0.87 | 39.8 ± 1.29 | 34.0 ± 0.69 | 26.5 ± 0.47 |
| Seta f | 34.9 ± 1.98% | 24.6 ± 0.57 | 38.3 ± 1.23 | 25.0 ± 0.47 | 40.1 ± 0.73 | 16.7 ± 0.49 |
| Seta g | 28.1 ± 1.16% | 19.6 ± 0.94 | 29.7 ± 0.58 | 19.4 ± 0.98 | 30.1 ± 1.04 | 12.3 ± 0.29 |
| Setae h, i, j | 22.9 ± 1.13% | | 21.7 ± 0.93 | | 16.6 ± 0.41 | 11.0 ± 0.44 |

Carapace (Fig. 1). Lacks both surface sculpturing and spines. Posterior corner rounded and the posterior margin arcs smoothly into the ventral surface. The asymmetrical gland on the right valve opens just anterior to the posterior hinge and the one on the left valve opens on the curve of the posterior ventral corner. Both species are of medium length (♀ 1.5–2.0 mm; ♂ 1.1–1.3 mm). There is marked sexual dimorphism in carapace length between the two sexes, males being ~ 30% shorter than the females. Males are shorter and broader in the majority of halocyprids but such a marked disparity in size is unusual but not exceptional (e.g. *Orthoconchoecia haddoni*). The rostrum small; in ventral aspect almost obscured; the visible length contributes only 5–7% of the ventral aspect of the carapace length. The carapace is slim – the maximum width being 32.5–36% of the length in males and 37–40% in females. Similarly the

maximum height is small relative to many other genera (41–45% in males and 46–50% in females).

Frontal organ (Fig. 2). In males the shaft extends to level with the end of the first antenna. There is a clear suture separating the stem from the capitulum, which is down-turned by ~30° and has either a rounded or a pointed tip. In females the frontal organ is fused into a single unit and is straight or slightly down-turned and ends in a point.

First antenna (Fig. 2). Clearly segmented in males but obscurely segmented in females. In males the a-seta is S-shaped and longer than the second segment of the limb, and the c-seta is almost as long. The b- and d-setae are sub-equal and only slightly shorter than the e-seta. The armature on the male e-seta consists of short basally pointing spines that distally are paired and then become alternate proximally. In females the a-d setae are less

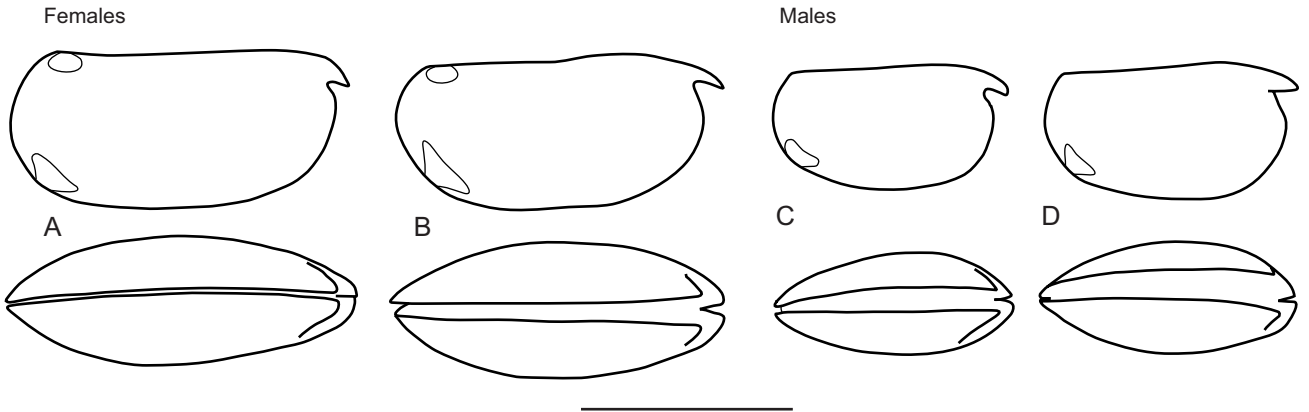


Figure 1. Carapaces of female (A) and male (B) *O. obtusata* and female (C) and male (D) *O. antarctica* in lateral and ventral aspect.

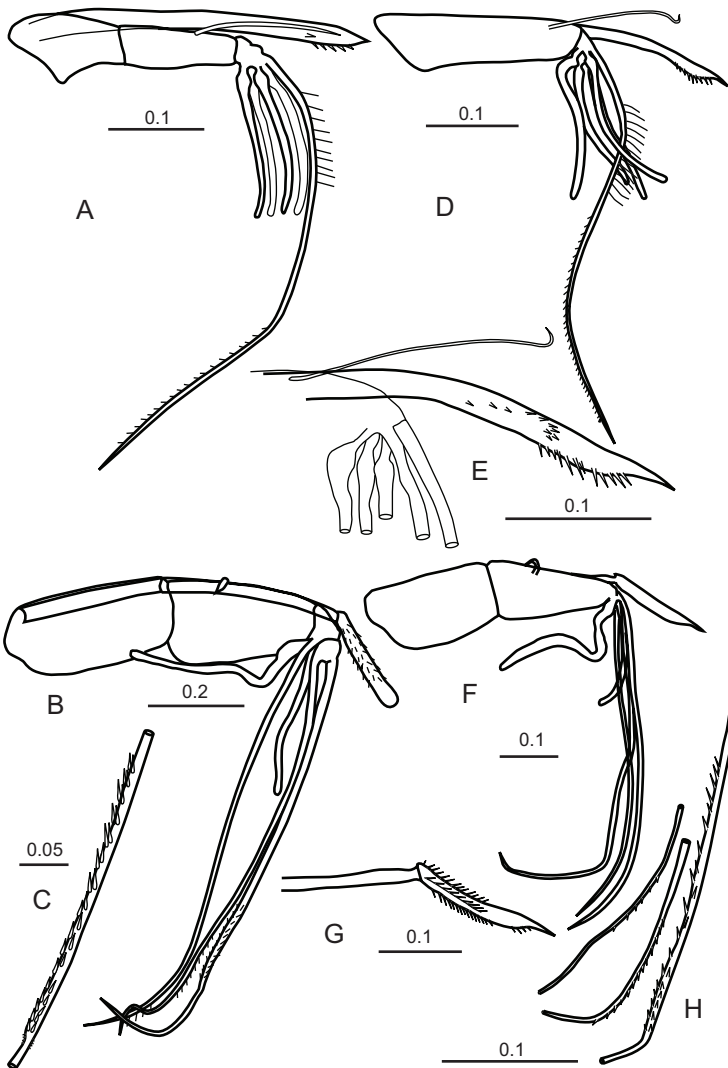


Figure 2. Frontal organs and first antennae. (A–C) *O. obtusata*; (D–H) *O. antarctica*. (A, D) female; (B, F) male; (C) armature of e-seta of male; (E) detail of female frontal organ capitulum; (G) detail of male frontal organ capitulum; (H) armature of d-, b- and e-setae of male.

than half the length of the e-seta. The e-seta carries fine long hairs on the basal third of its leading edge, character that is shared only with the genera – *Porroecia* and *Macroconchoecia* and some *Paraconchoecia* species. There is a long dorsal seta.

Second antenna (Fig. 3). In females the protopodite is 35–40% of the carapace length. The exopodite is a little over half the length of the protopodite. The longest swimming setae are almost the same length as the protopodite. On the endopodite the processus mamillaris is tall and pyramidal. The a- and b-setae are bare; the inner a-seta is half the length of the b-seta. On the second endopodite segment the c-, d- and e-setae are absent. The longest of the terminal seta, g-, is bare and about quarter the carapace length. The remaining setae are subequal and only a little shorter than the g-seta.

In males the protopodite is proportionally longer and is nearly half the carapace length. The exopodite is also relatively longer than in the female but is still not much more than half the protopodite length. The swimming setae are much the same length as the protopodite. The a- and b-setae on the first segment of the endopodite are curved, and the longer b-seta carries long hairs. On the second segment the c- and d-setae are relatively long, slim and bare. The small, curved e-seta is inserted at the base of the f-seta. The g-seta is just over a third the carapace length, the f-seta is only slightly shorter, the h-j setae are about a fifth the carapace length. The hook appendage on the right endopodite is very large and elaborate. The basal shank is long and straight with the h-j setae inserted at about a third the length. The hook is then angled about 135° and there is another straight section before a further angle

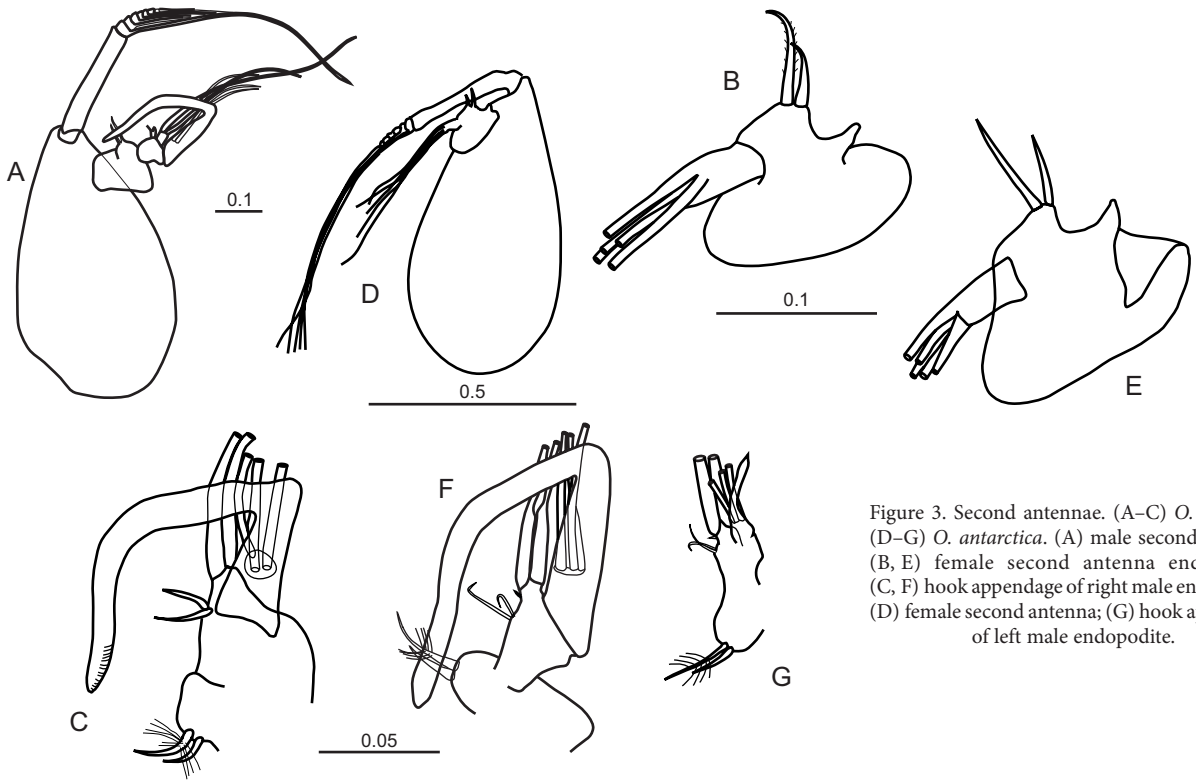


Figure 3. Second antennae. (A–C) *O. obtusata*; (D–G) *O. antarctica*. (A) male second antenna; (B, E) female second antenna endopodite; (C, F) hook appendage of right male endopodite; (D) female second antenna; (G) hook appendage of left male endopodite.

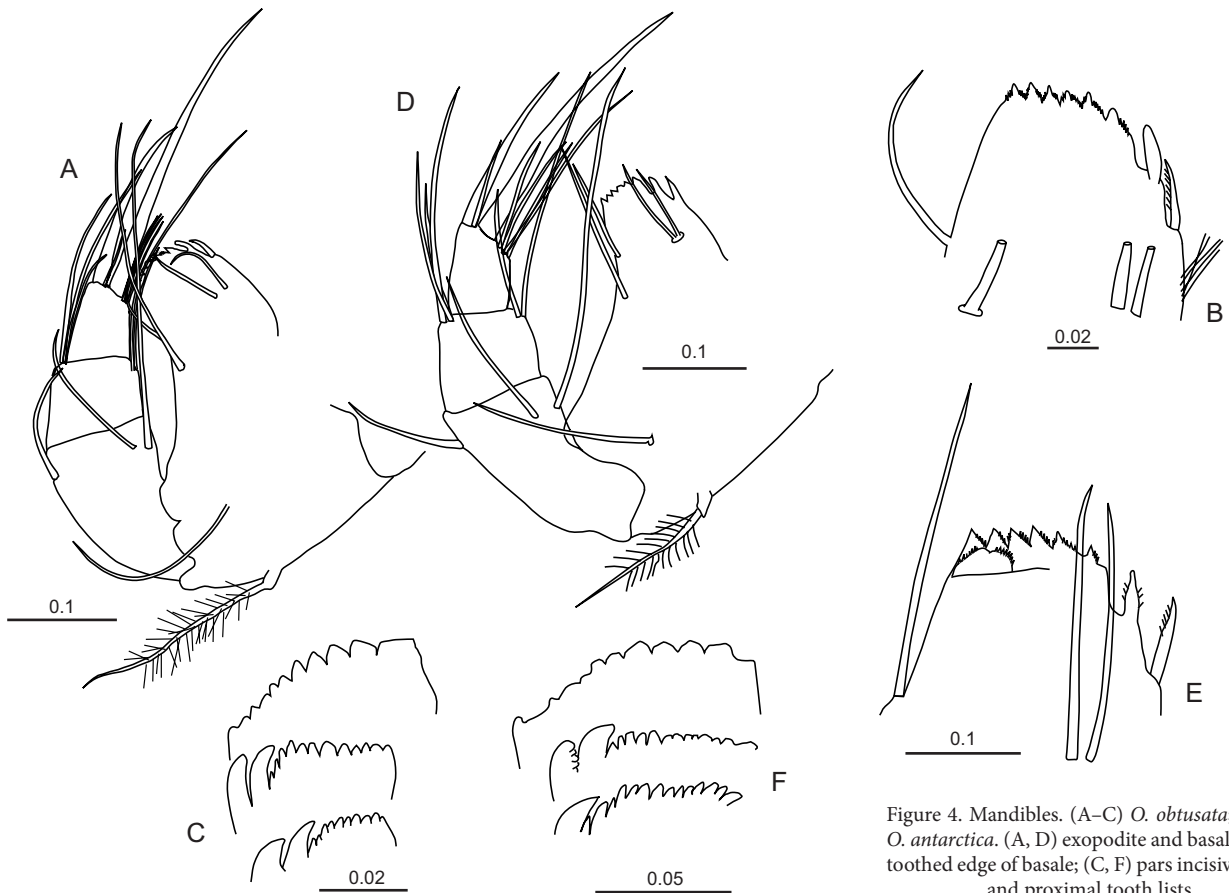


Figure 4. Mandibles. (A–C) *O. obtusata*; (D–F) *O. antarctica*. (A, D) exopodite and basale; (B, E) toothed edge of basale; (C, F) pars incisiva, distal and proximal tooth lists.

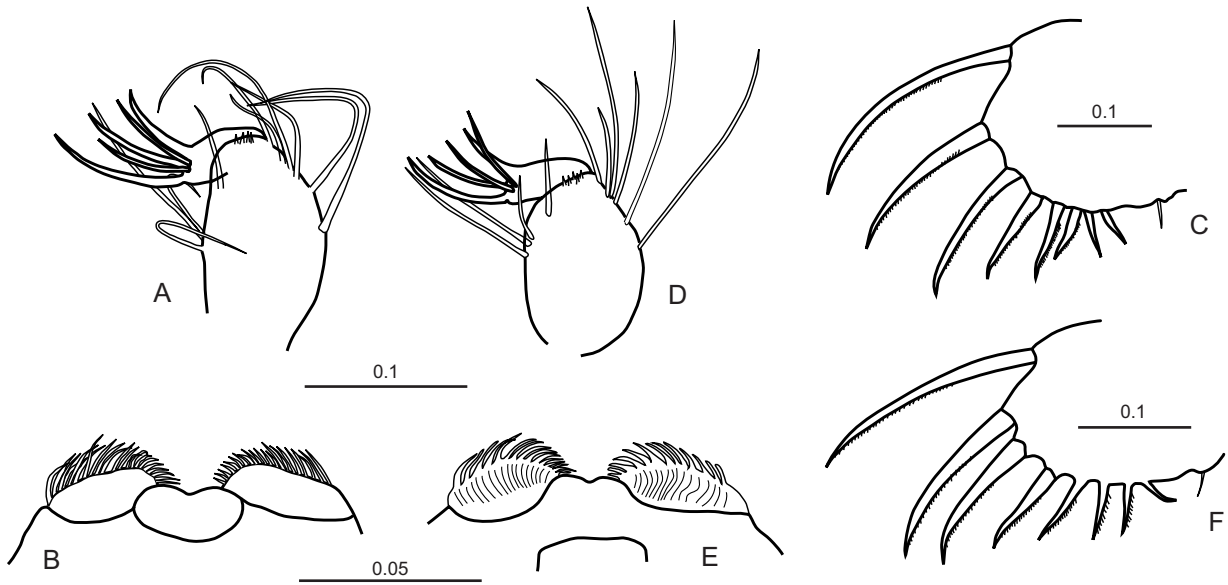


Figure 5. Maxilla endopodite, labrum, and caudal furcae. (A–C) *O. obtusata*; (D–F) *O. antarctica*. (A, D) maxilla; (B, E) labrum; (C, F) furca.

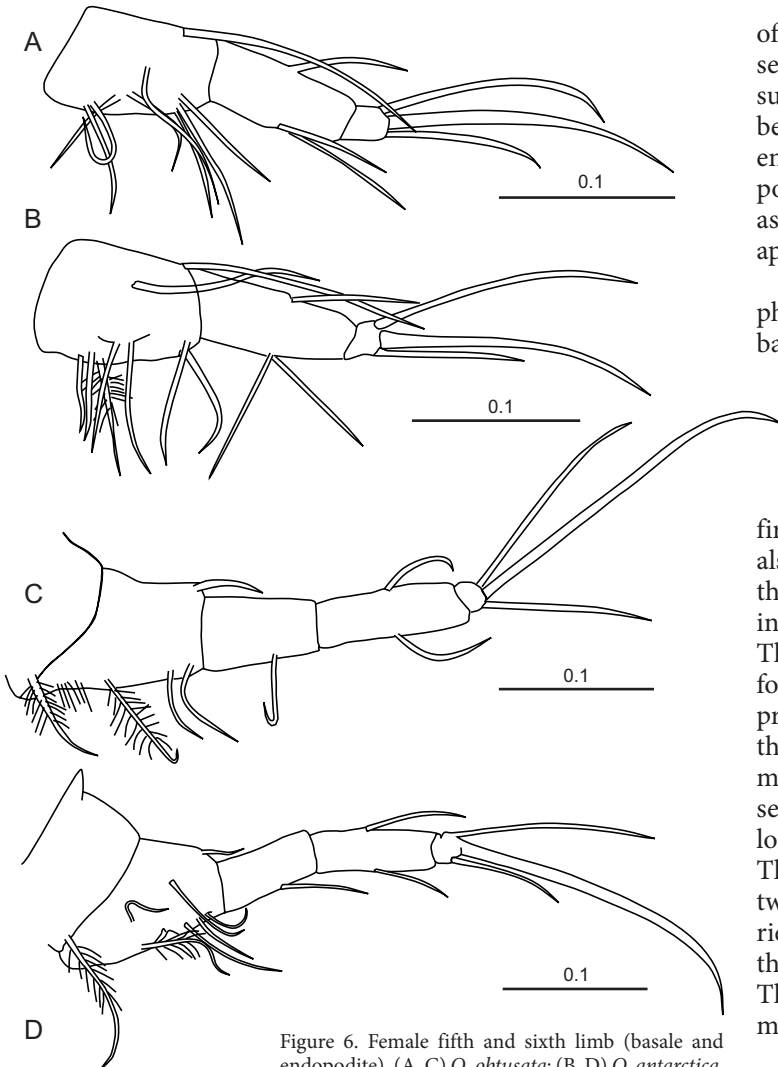


Figure 6. Female fifth and sixth limb (basale and endopodite). (A, C) *O. obtusata*; (B, D) *O. antarctica*. (A, B) fifth limb; (C, D) sixth limb.

of about 45°. There is then a slightly curved section leading to a blunt point with extensive subterminal ridging. The tip is angle back well beyond the base. The hook appendage on the left endopodite is reduced to a short straight bluntly pointed peg. This genus shows the most marked asymmetry in the development of the hook appendages of all the Conchoecinae.

Mandible (Fig. 4). Shows no sexual dimorphism. The exopodite is a small knob on the basale that carries a plumose seta. In addition the basale has a long lateral seta. The outer edge of the toothed edge of the basale has two spine teeth, the first sharp pointed the second with a bluntly rounded tip. There are six subserrate, triangular, inner teeth the first of which is offset from the others. There is also a blunt outer broad tooth, which overlaps the inner 2–3 inner triangular teeth. The pars incisa is a curved row of 11–14 triangular teeth. The distal tooth list consists of two large teeth followed by 12–15 much smaller peg teeth. The proximal list has a large tooth followed by a further 11 to 14 unevenly sized teeth. The first segment of the endopodite carries a distal plumose seta on its outer dorsal edge and two setae, one long the other moderately long on its inner side. The second segment has three dorsal setae and two ventral setae. The third terminal seta carries two long claw setae with a slim seta between them and then ventrally a further four slim setae. The length of the longest claw seta is 70% or more of the dorsal edge of the limb.

Maxilla (Fig. 5). The basal segment of the exopodite has three anterior, one lateral and six

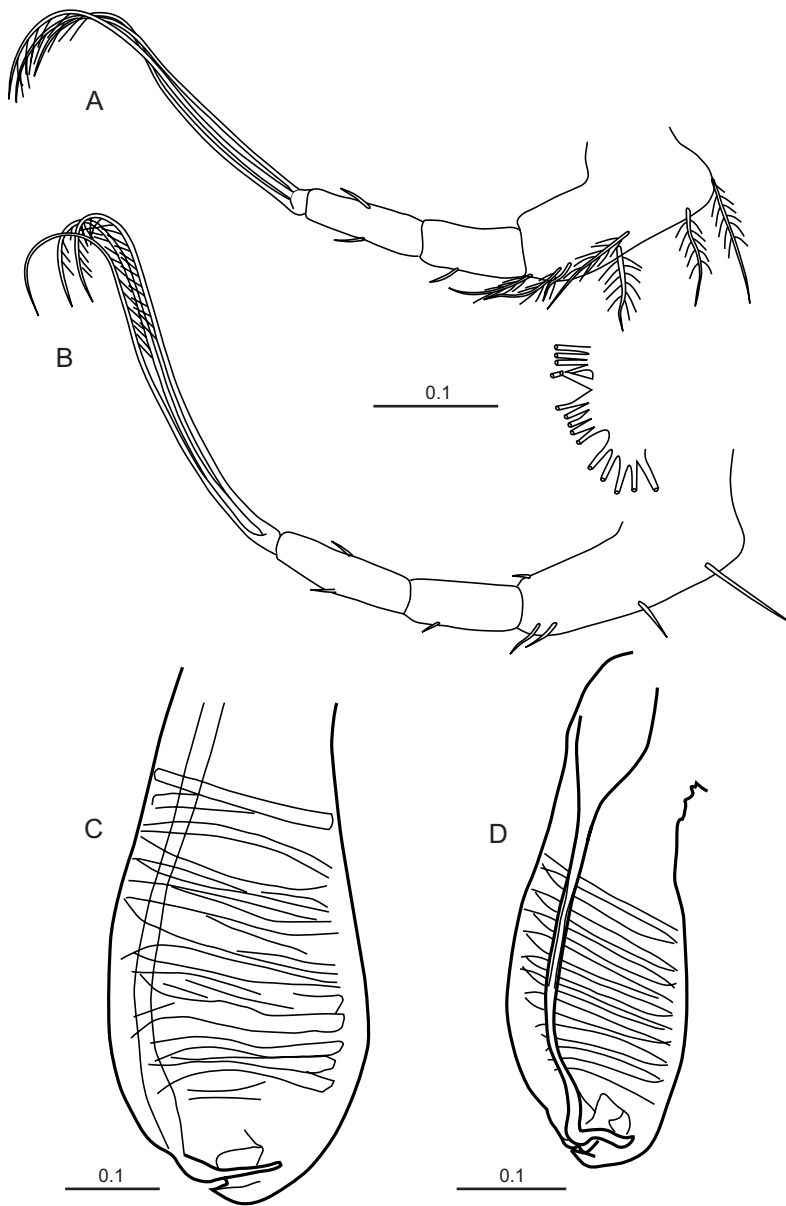


Figure 7. Male sixth limb (basale and endopodite) and intromittent organs. (A, C) *O. obtusata*; (B, D) *O. antarctica*. (A, B) sixth limb; (C, D) intromittent organ.

posterior setae. On the outer distal edge there is also a patch of short pointed spines. The terminal segment has three terminal claw setae and two subterminal setae, a pattern common to most Halocyprinae (some species of *Bathyconchoecia* have four terminal claw setae).

Labrum (Fig. 5). It has a smoothly rounded shallow notch, which is flanked by 14–15 filaments.

Fifth limb (Fig. 6). No sexual dimorphism. The epipodial setae are in groups of 5, 5 and 4 or 5; in the living animal these setae together with those on the sixth limb beat continually, driving a respiratory flow of water through the carapace. Following Boxshall (1998) and Kornicker (2003) the dorsal setae are interpreted as being remnants

of the exopodite so the main limb is the endopodite, which implies the podomere on which it is mounted is the basale. The basale carries laterally three groups of setae consisting of four plumose, two bare and three (one plumose) setae. There are two lateral setae and in one species a plumose seta. Dorsally there is a medial plumose seta and a long bare distal setae (the remnant of the endopodite) that extends well beyond the end of the limb. The 'first' segment has medially two ventral setae and one dorsal seta. The second segment has three curved terminal claw setae. The middle claw seta is the longest (>80% the length of the limb), but the dorsal seta is only a little shorter but slimmer, whereas ventral seta is half the length of the central seta. Variations in the ratios between the lengths of these claw setae may prove useful generic characters.

Sixth limb (Figs 6–7). The epipodial formula is 7+5+5. There is marked sexual dimorphism in the morphology of this limb. In females the setae on the first three endopodite segments are longer than in the male. Ventrally the first segment has a medial plumose seta and more distally three bare setae. There are either no or two lateral setae, and there is a very short dorsal seta. The second segment has only a single medial ventral seta, and the third segment has both a dorsal and a ventral medial seta. The end segment has three terminal curved claw setae. The central longest claw seta is almost as long as the limb and nearly twice as long as the dorsal seta.

In males the first endopodite segment has ventrally one plus one plus two bare setae, no lateral setae and a tiny dorsal seta (not shown in Fig. 7A). As in the female, the second segment has a single ventral seta, and the third a dorsal and ventral seta. The end segment carries three unequal arching setae that are longer than the limb. The ventral seta is slightly shorter than the other two and is bare, whereas the other two carry long filaments along their distal halves. In other genera these setae can range between all being equal and plumose to marked differences in the lengths (particularly the ventral most seta) and whether they are plumose or not.

Caudal furca (Fig. 5). The eight claw setae diminish evenly in size and there is an unpaired seta. The first seven pairs of claw setae are lined with secondary spinules, but the last pair is bare.

Intromittent organ (Fig. 7). The male copulatory appendage is exceptional large. Its length and breadth

is ~25% and ~12.5% of the carapace length respectively and there are unusually high numbers of oblique muscles (10–12).

ZOOGEOGRAPHICAL DISTRIBUTIONS

We have reviewed most accessible published records of these species and compiled a database of all records that we consider to be reliable and can be geopositioned. Some earlier published records have had to be discarded because they include no positional data. These published records have been substantially supplemented with numerous unpublished data from *Discovery Investigations* (Angel, unpublished), the identification of more recent plankton surveys (e.g. Polish/Norwegian investigations around Svalbard and *Hudson* surveys in the Labrador Sea) and records provided by Dr Vladimir Chavtur (Vladivostok) from the many Russian expeditions in the Arctic and North Atlantic. In total there are 516 records for *O. obtusata* and 244 for *O. antarctica*. These have been plotted to show the zoogeographical ranges of the two species (Figs 8 and 9).

The distribution of *O. obtusata* (Fig. 8) shows that it is restricted to the North Atlantic. Its absence from the North Pacific has been confirmed (Chavtur, personal communication; Angel, unpublished data). Within the North Atlantic the records are almost entirely restricted

to the regions where there is some seasonal stratification of the upper water column. Its occurrence in the Arctic is probably associated with the inflow of Atlantic water, and changes its future presence/absence there could prove useful as an indicator of climate change. Its abundance was low in an intensive series of samples collected at 40°N 20°W, just to the north of the Azores, which is probably close to the southern limit of its range. It was absent from intensive series of samples collected both at 30°N 23°W, in a series of oblique hauls taken along 30°N from Northwest Africa to Bermuda, and in the vicinity of Bermuda (Deevey 1968, Angel 1979).

We consider the records from the Mediterranean (Granata and Caporiacco, 1949; Furnestin, 1960) to be of dubious validity, but have no objective reasons to reject these records. We have recently examined some samples collected in the Alboran Sea (January 1997), and found no specimens either in the Atlantic inflow water or in the underlying Mediterranean Water (unpublished data). So if these records are confirmed, the Mediterranean population is probably a glacial relict and should be critically examined to see if it has diverged from the parental stock. The three records from south of the equator were all by Vavra (1906). Many of Vavra's identifications have been called into question (e.g. Skogsberg 1920), and there have been no recent reports of this species this far south despite substantial sampling. Unfortunately none of Vavra's material appears to be extant and so cannot be checked.

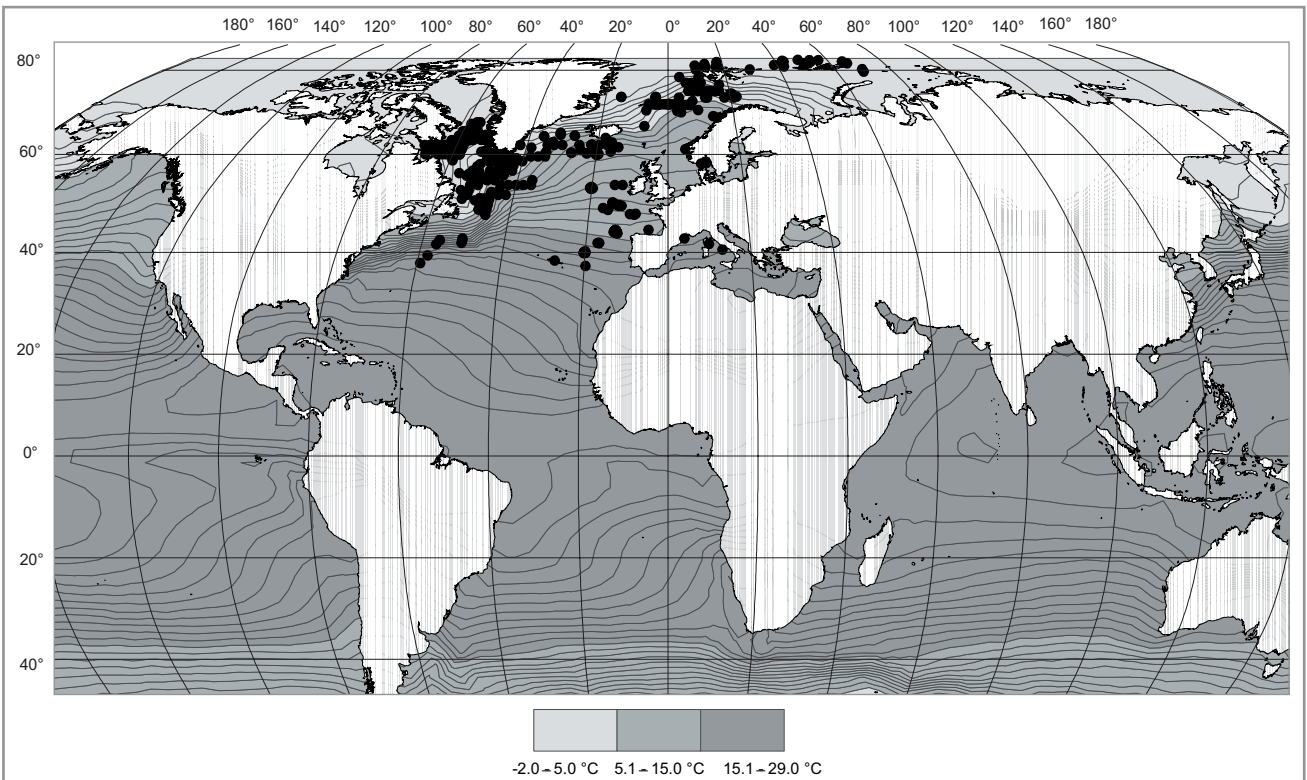


Figure 8. Global distribution of *O. obtusata* showing that it is confined to the North Atlantic.

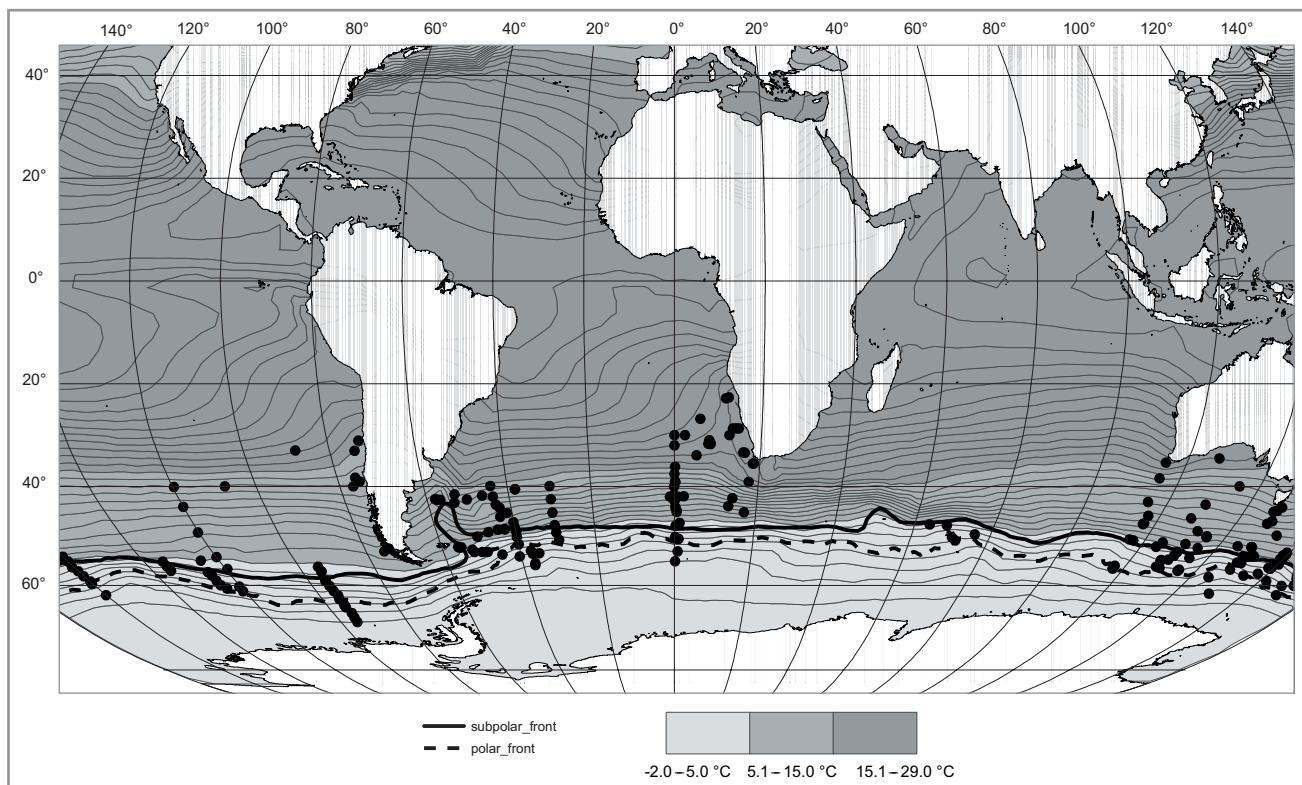


Figure 9. Global distribution of *O. antarctica* showing that it is confined to the Southern Hemisphere.

The zoogeographical range of *O. antarctica* is likewise mainly restricted to temperate and subpolar waters in the Southern Ocean. There are sufficient reliable records of this species to the north of the subpolar front to be confident that it can survive to the north of it. While some of these records are from upwelling regions (e.g. Iles 1953, Martens 1979b) and were probably associated with the cool upwelled waters. The species is undoubtedly rare at such low latitudes; one possible explanation is that these records were associated with cold-core mesoscale eddies that had transported normally temperate populations equatorwards.

BATHYMETRIC RANGES

There are good data for the bathymetric range of *O. obtusata* in the Northeast Atlantic. Detailed day and night vertical sampling was conducted at 60°N 20°W, 53°N 20°W (Angel and Fasham 1975) and 44°N 13°W (Angel 1977). Figure 10 shows the profiles expressed both as percentages of the total population in the water column (histograms) and proportions of the total ostracod population at each sampling horizon. Estimates of the total numbers (per m²) in each series in the water column sampled, of adult females: males: juvenile instars are shown for each profile. All the profiles were observed in spring (April 1971, 60°N; May 1971 53°N;

early April 44°N). Even so seasonality may have been a factor contributing to some of the differences seen between the profiles, as the onset of stratification and the spring bloom migrates northwards. For example at 60°N in pre-spring bloom conditions, males greatly outnumbered adult females and juvenile instars were extremely abundant, whereas at 53°N during the bloom there were hardly any juveniles and females outnumbered males by 2:1.

At 60°N the majority of the population was concentrated at the 25–100 m where it contributed 80–100% of the specimens sampled. Few specimens were sampled from >400 m. There was little evidence of ontogenetic migration apart from the 10% of the population by day and by night containing a relatively greater proportion of adults. At 53°N the population was concentrated a little deeper at 100–300 m by day and 50–300 m at night, indicating a slight upward drift in the population at night, but no clear diel migration. The species was numerically dominant at 50–200 m contributing nearly 50% to the total halocyprid population. Once again few specimens were sampled at depths >400 m. The sharp reduction in juveniles compared to 60°N suggests that there is a generation that overwinters as juveniles and matures in early spring. If males mature earlier than the females, it would explain the switch in the sex ratios between the 60°N and 53°N samples; as the season progresses males may become outnumbered by the

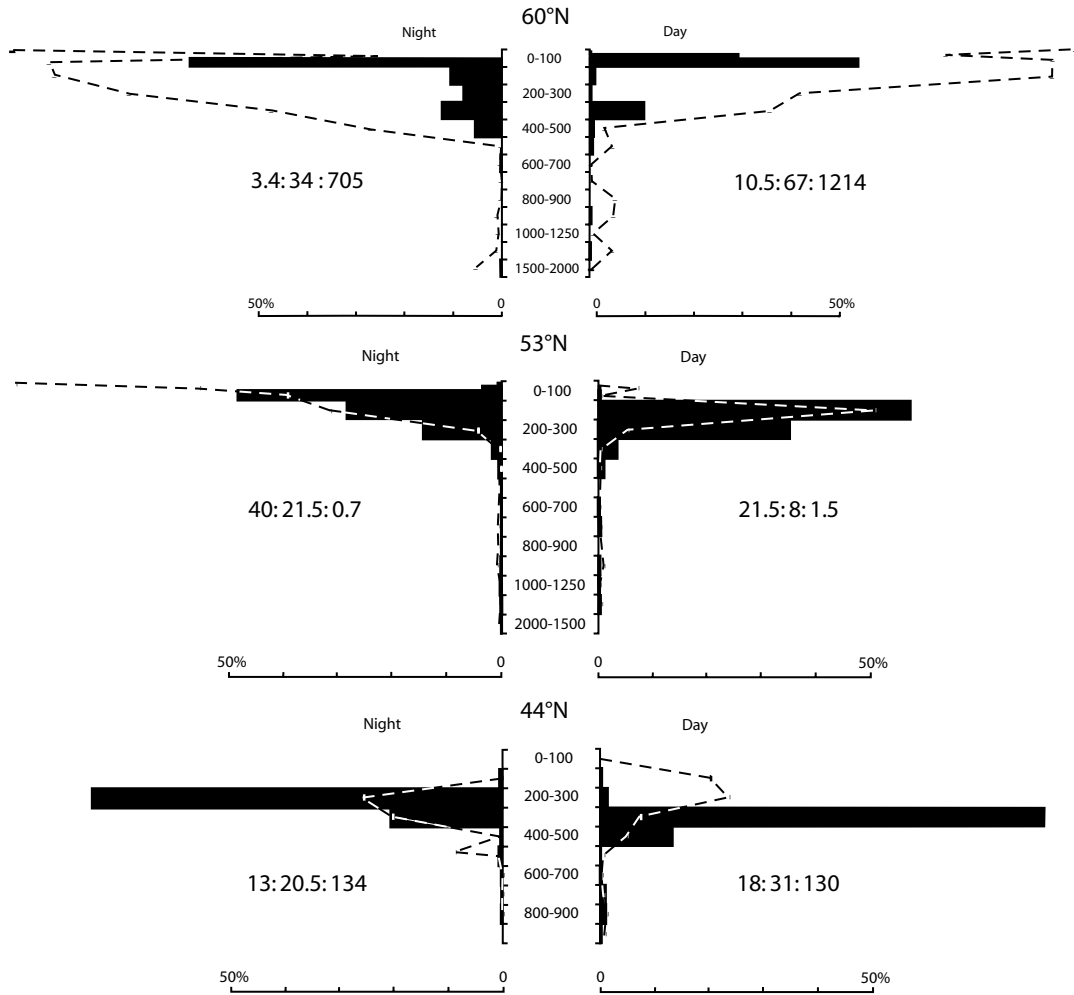


Figure 10. Day and night bathymetric profiles of *O. obtusata* at three positions in the Northeast Atlantic: Upper – 60°N 20°W (Discovery Station 7709; April 1971); Middle – 53°N 20°W (Discovery station 7711, May 1971); Lower – 44°N 13°W (Discovery station 8507, April 1973). The histograms show the percentage of the species's total water column population sampled within each depth horizon, and the dashed lines indicate the species's percentage contribution to the total halocyprid population sampled within each horizon. For each profiles the estimated total water column abundances (numbers m⁻²) are shown for adult females: males: juveniles. Note that the sampling at 60°N and 53°N extended down to depths of 2000 m, but that at 44°N only to 1000 m, and there are unexplained disparities in the estimated abundances between the day and night profiles.

females. At 44°N there was again a hint of an upwards drift at night with the main bulk of the population inhabiting depths of 300–500 m by day and 200–400 m at night. However, here the species's contribution to the total halocyprid populations was always <30%. It also occurred in sparse numbers at 40°N 20°W (Angel and Fasham 1975), and most abundantly at 200–300 m.

Drapun (2005) shows the bathymetric range of *O. antarctica* is 25–500 m in the region of the Falklands Current with the bulk of the population at 200–300 m, and there is slight upward movement at night. In the West Wind Drift the range is 100–500 m by day, again with the bulk of the population at 200–300 m, but the centre of the range moves up at night to 100–200 m. Otherwise most samples have come from vertical hauls to the surface, and the species has been encountered more frequently and more abundantly in samples collected from the upper 200

m. The niche occupied and dominated by *O. obtusata* in the North Atlantic seems to be occupied, at least in part, by *Pseudoconchoecia serrulata*.

DISCUSSION

The genus is clearly distinguished from all the other genera in the subfamily Conchoecinae. Table 1 gives comparable meristic data for the two *Obtusocia* species and the type species for the most similar genus *Porroecia*, *P. porrecta*, which had been placed in the same genus *Spinocia* by Poulsen (1973). It reveals substantial differences notably in females, the absence of the dorsal seta on the first antenna and the relative lengths of the other setae on the first as well as the second antenna. In males there are clear differences in the length of the c-seta and

armature of the e-seta of the first antenna, and the setae on the second antenna. There are substantive differences in the morphologies of the other limbs, which we have not listed herein. So we agree with Martens's (1979a) decision to split Poulsen's genus.

Within the genus *Obtusoecia*, the two species are similar in appearance, but show several small but consistent differences. These are listed in Appendix 1, but detailed comparison between *O. obtusata* and *O. antarctica* is given below.

All the main features of the two species are illustrated except for the 7th limbs. The drawings are used to compare and contrast the species and the text highlights the interspecific differences. To facilitate the interspecific comparisons each limb of the two species are illustrated together (those of *O. obtusata* are either on the left, or above, those of *O. antarctica*).

Carapaces. There are some subtle differences in the carapace outlines (Fig. 1). Carapace lengths are listed in Table 2 for all stages of the species sampled in nets with mesh sizes of 320 μm , but some of the material was collected in finer 200 μm mesh nets. The data for *O. obtusata* have been divided into broad latitudinal regions, and show there is a trend for carapace length sizes to diminish with decreasing latitude. However, there are some unresolved problems in these data as regards the juvenile instars. The marked size disparity between adult male and females is also likely to be reflected in the sizes of the penultimate maturation stage (A-1). Thus our separation of specimens into stage A-1 and A-2 juveniles at 53–60°N may be erroneous and the Labrador Sea juveniles may all be A-1, the larger being A-1 females and the smaller being A-1 males. Similarly there are three juvenile specimens of *O. antarctica* that are anomalous in size. They were clearly immature, but were larger than adult males and seemed rather too large to be normal females. There would seem to be a number possible explanations:

1. There may be some cryptic species that we have confused;
2. There are seasonal, regional or bathymetric shifts in size;
3. The measurements of these specimens were inaccurate.

Frontal organs. There are clear differences between the two species in the frontal organs in both sexes (Fig. 2). In *O. antarctica* the female frontal organ is longer, more spinose, more pointed and slightly downturned, and in males the capitulum is pointed compared with rounded in *O. obtusata*.

First antennae (Fig. 2). There are minor differences in the lengths of the limb and the setae relative to the carapace length, and also in the armature of the setae (Table 1). The lengths of the setae relative to each other are very similar (e.g. the length of the convoluted a-seta and the c-seta being subequal with the second segment), as is seen within other genera.

Table 2. Carapace lengths of adult and juvenile stages of *O. obtusata* from three locations in the North Atlantic 53 to 60°N, 20°W and 44°N, 13°W and in the Labrador Sea (55–60°N and 45–53°W) and *O. antarctica* specimens from a range of pre-war *Discovery* Stations. Measurements were made using a micrometer eyepiece Wild M5 stereomicroscope at $\times 50$ magnification, with a precision of 0.02mm.

Obtusoecia obtusata

Northeast Atlantic 53–60°N 20°W (n = 2690)

| | n | mean | range (mm) |
|-----|------|------------------|------------|
| ♀ | 72 | 1.75 \pm 0.053 | 1.58–1.86 |
| ♂ | 270 | 1.21 \pm 0.030 | 1.14–1.30 |
| A-1 | 582 | 1.16 \pm 0.068 | 1.04–1.34 |
| A-2 | 648 | 0.90 \pm 0.043 | 0.82–1.02 |
| A-3 | 1118 | 0.70 \pm 0.050 | 0.56–0.80 |

Labrador Sea 50–60°N, 44–53°W (n = 454)

| | n | mean | range (mm) |
|-----|-----|------------------|------------|
| ♀ | 206 | 1.81 \pm 0.060 | 1.62–2.02 |
| ♂ | 120 | 1.19 \pm 0.036 | 1.10–1.26 |
| A-1 | 78 | 1.14 \pm 0.048 | 1.02–1.22 |
| A-2 | 31 | 0.71 \pm 0.054 | 0.60–0.80 |
| A-3 | 19 | 0.43 \pm 0.024 | 0.40–0.50 |

Northeast Atlantic 44°N 13°W (n = 138)

| | n | mean | range (mm) |
|-----|----|------------------|------------|
| ♀ | 13 | 1.55 \pm 0.056 | 1.44–1.64 |
| ♂ | 19 | 1.15 \pm 0.027 | 1.12–1.20 |
| A-1 | 12 | 1.00 \pm 0.036 | 0.94–1.06 |
| A-2 | 42 | 0.85 \pm 0.035 | 0.74–0.90 |
| A-3 | 52 | 0.62 \pm 0.030 | 0.56–0.68 |

Obtusoecia antarctica (n = 251)

| | n | mean | range (mm) |
|------|----|------------------|------------|
| ♀ | 94 | 1.65 \pm 0.067 | 1.48–1.78 |
| ♂ | 88 | 1.26 \pm 0.039 | 1.16–1.34 |
| A-1? | 3 | 1.39 | 1.36–1.44 |
| A-2 | 55 | 1.04 \pm 0.034 | 0.94–1.16 |
| A-3 | 11 | 0.75 \pm 0.027 | 0.70–0.80 |

Second antennae (Fig. 3). Once again there are minor differences in the ratio of the lengths of the segments to the carapace lengths, while these differences are just significant they are too variable to enable reliable identification. The marked disparity between the left and right hook appendages, the right being massively developed vis-à-vis the left being reduced to a simple peg, is a character unique to this genus.

Mandibles (Fig. 4). There are no interspecific differences that can reliably be used to distinguish the species. The minor differences that appear in the diagrams are mostly artefacts caused by damage during dissection or the orientation of the limbs on the slides.

Maxillae (Fig. 5). No interspecific differences.

Fifth limbs (Fig. 6). The difference in the epipodial formula given in Appendix 1, may be a dissection arte-

fact. Similarly the minor differences in the numbers of setae on the various segments are neither reliable nor easy to check in individual specimens. However, the differences in the ratios of the lengths of the dorsal and central terminal setae are reliable and easy to check.

Sixth limbs (Figs 6 and 7). These limbs are very similar between the two species, but the difference in the ratios of the lengths of the terminal setae in the females are a good distinguishing character.

Caudal furcae (Fig. 5). The furcae are very similar. The only difference of possible significance being the lack to secondary spination on the seventh pair of claw spines in *O. obtusata* whereas in *O. antarctica* these claw spines are spinose.

Intromittent organs (Fig. 7). The large length and breadth of these organs relative to the carapace length is a character shared with very few other halocyprid species (e.g. *Mikroconchoecia echinulata*). The large numbers of oblique muscles (10–12) is a unique generic character.

Generally we agree with Martens's (1979a) division of the original bipolar species *O. obtusata* into separate species found the Northern and Southern Hemispheres respectively. None of the interspecific differences are substantive enough to lead us to the conclusion that their similarity results from evolutionary convergence (e.g. the marked similarity in all the characteristics of their mandibular structures and much of the setation of the fifth and sixth limbs are consistent with them having a common ancestry). Thus the genus is bipolar, and one of the species is likely to be ancestral to the other. The absence of *O. obtusata* or a sibling species from the North Pacific slightly favours the speculation that *O. antarctica* rather than *O. obtusata* is the ancestral species. During the glaciations the narrowness of the Atlantic and the greater dynamism of the ocean's circulation may have allowed the advection of viable populations via mesoscale eddies from the Southern to the Northern Hemisphere, where they would have found an unoccupied niche in the upper water column. The absence of a sibling species in the North Pacific is perhaps because the size of the Pacific resulted in the trans-hemispheric advection being too slow for the populations to remain viable. Knowledge of halocyprids in the Central and North Pacific remains totally inadequate. The only other 'bipolar' halocyprid genus is *Boroecia*. This genus is being revised (Angel and Blachowiak-Samołyk in preparation) and it shows some interesting differences. There are two North Atlantic/Arctic species, but just one Southern Ocean species. A novel species occurs in the North Pacific and another, formerly attributed to the Southern Ocean species occurs in the equatorial Pacific. The difference in the zoogeography of the two genera may be linked to *Boroecia* species living at greater depths, which enabled them to submerge and survive at bathypelagic depths at low latitudes.

The bathymetric distribution of *O. obtusata* shows that it occupies shallower depths in temperate and sub-

polar seas than other halocyprid species and it drifts upwards at night rather than actively migrates. These data come from a single season, spring, and may not reflect the species's behaviour during other seasons. There is also the suggestion in the data that the species may have a life cycle that is seasonal, and that there may be minor shifts in carapace size between generations developing in different seasons.

The value of plotting zoogeographical data is partly in providing good information about the geographical ranges of species, but it also highlights data that are anomalous and hence possibly erroneous. It raises questions about what criteria can be used to make objective judgements as to when such data should be discarded. Another future use of such plots will be to detect any shifts in the distributions that may result from climate shifts. It is also possible that some species may be sufficiently faithful to specific environmental characteristics, such as an envelop of water temperatures or seasonality of primary production, the species can then be used as indicators. Thus a latitudinal asymmetry may result from the large-scale gyral circulation patterns of the oceans, or the anomalous occurrence of subpolar species at low latitudes may indicate the influence of mesoscale eddies. But this will require routine analyses and archiving of data sets that are currently not undertaken.

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Appendix 1. Tabulation of characters of carapaces and limbs of the two species of *Obtusoecia* that can be used as a basis for improving generic descriptions for the other halocyprid genera.

Abbreviations: PDV – post dorsal corner, PVC – post ventral corner, LAG – left asymmetrical gland, RAG – right asymmetrical gland.

| ♂ Male | <i>O. antarctica</i> | <i>O. obtusata</i> |
|------------------------------|---|--|
| Carapace | | |
| opening of left gland | 0.1mm anterior of hinge at PDC | almost adjacent to PDC |
| opening of right gland | on rounded PVC | slightly posterior to PVC |
| Special characters | clear large group of male glands just below PDC on right valve, but smaller group on left | no male glands evident |
| | abundant edge glands along posterior two-thirds of ventral margin | abundant edge glands along central 1/3rd ventral margin |
| Frontal organ | | |
| Capitulum and stem | separate | separate |
| Capitulum shape | down-turned, broadest at base tapers distally and spinose, then curves slightly anteriorly and becomes bare and ends in a long sharp point | rounded end with fine spinules in central region of ventral surface |
| length relative to antenna 1 | stem slightly shorter than limb | stem distinctly shorter than limb |
| Antenna 1 | | |
| a-seta | S-shaped with short basal shank | S-shaped with short basal shank |
| b-seta armature | 2–3 fine spinules | bare |
| d-seta armature | 8–10 distally pointing fine spinules level with distal region of e seta armature | none evident |
| e-seta | angled beyond armature | angled beyond armature |
| e-seta armature | ~33 short sharp spines, initially arranged as 8–9 pairs with a further 16–17 spines that become alternating and then tend to become paired again proximally | ~42 short sharp spines, initially arranged as 8–10 pairs then with a further 20–26 alternating fine spines |
| Antenna 2 | | |
| Endopodite | | |
| Segment 1 | | |
| processus mamillaris | broad triangle fine point bent over | bluntly pointed |
| a-seta | bare, curved 2/3s b | curved bare, 5/6s b |
| b-seta | curved with 5–6 long hairs | curved towards end, large patch (>6) of hairs at midpoint |
| Segment 2 | | |
| c- and d-setae | slim, bare, longer than width of segment | slim, bare, longer than width of segment |
| e-seta | minute | ?none |
| g-seta | bare, swollen at base | bare, swelling near base abruptly narrows |
| f-seta | bare, swollen at base | bare, swelling near base abruptly narrows |
| right hook appendage | exceptionally large, long base on which h-j setae are inserted, 135° angle then straight before 45° angle then slightly curved to pointed end with extensive sub-terminal ridging | similar to <i>O. antarctica</i> |
| left hook appendage | only straight shank pointed at end, carrying h-j setae | similar to <i>O. antarctica</i> |
| h-, i-, j-setae | inserted on shank of hook | similar to <i>O. antarctica</i> |
| Labrum | very shallow rounded notch flanked by 14–15 setae | similar to <i>O. antarctica</i> |
| Mandible | | |
| Endopodite | | |
| Segment 1 | | |
| dorsal setae | 1 distal plumose | 1 distal plumose |
| ventral setae | 1 long, 1 moderate | 1 long, 1 medium |
| Segment 2 | | |
| dorsal setae | 3 | 3 |
| ventral setae | 2 | 2 |
| Segment 3 | | |
| terminal setae | 2 claw + 5 setae, longest 70% of limb | 2 claw + 5 setae, longest 82% of limb |
| Basal endite, teeth | 6 triangular (1 slightly offset) + 1 blunt + 1 sharp spinose, lateral tooth overlaps 2 triangular teeth | similar to <i>O. antarctica</i> except lateral tooth overlaps 3 triangular teeth |

| ♂ Male | <i>O. antarctica</i> | <i>O. obtusata</i> |
|---------------------------|---|---|
| pars incisa | ~14 | ~11 |
| distal tooth list | 2 large + 13-15 | 2 large + 12 |
| proximal list | 3 large + ~12 smaller | 1 + 1 + 1 + 9 |
| lateral setae on endite | 2 | 2 |
| Exopodite | small knob carrying plumose seta | similar to <i>O. antarctica</i> |
| Comment | long lateral seta on basale | similar to <i>O. antarctica</i> |
| Maxilla | | |
| Basal segment | | |
| anterior setae | 3 | 3 |
| lateral setae | 1 | 1 |
| posterior seta | 6 | 6 |
| terminal spines | 4 | 3-4 |
| Distal segment | | |
| claw seta | 3 | 3 |
| normal setae | 2 | 2 |
| Fifth limb | | |
| Epipodial setae | 5 + 5 + 4 | 5 + 5 + 5 |
| Basale | | |
| ventral setae | 4 (plumose) + 2 + 3 (1 plumose) | similar to <i>O. antarctica</i> |
| lateral setae | 2 | 2 + 1 plumose |
| dorsal setae | 1 plumose + 1 very long (reaches beyond end of limb) | 1 long reaches beyond end of limb |
| Endopodite segment 1 | | |
| ventral setae | 2 | 2 |
| dorsal setae | 1 | 1 |
| height/length % | 45% | 41% |
| Endopodite segment 2 | | |
| terminal setal ratios | 97:100:53 | 87:100:52 |
| longest seta:endopodite % | 82% | 86% |
| Sixth limb | | |
| Epipodial setae | 7 + 5 + 5 | 7 + 5 + 5 |
| Basale | | |
| dorsal setae | 1 + 2 | ? |
| ventral setae | 0 | 0 |
| lateral setae | 1 tiny | ? |
| dorsal setae* | 1 | 1 |
| Endopodite segment 1 | | |
| ventral setae | 0 | 0 |
| dorsal setae | 1 | 1 |
| Endopodite segment 2 | | |
| ventral setae | 1 | 1 |
| dorsal setae | 1 | 1 |
| height/length% | 29% | 30% |
| Endopodite segment 3 | | |
| terminal setae | ventral seta bare slimmer and slightly shorter than other two | ventral seta bare slimmer and slightly shorter than other two |
| terminal setae:endopodite | ~145% | 114% |
| Caudal furca | | |
| Paired claws | 8 (last pair bare), evenly diminishing with size | similar to <i>O. antarctica</i> |
| unpaired dorsal seta | present smaller than last paired claws | present, longer than last paired claws |
| Intromittent Organ | | |
| | very broad, 10 oblique muscles, length ~30% carapace length | very broad, 12 oblique muscles, length ~30% carapace length |
| | 0.36 x 0.165mm | 0.347x 0.15mm |

| ♂ Female | <i>O. antarctica</i> | <i>O. obtusata</i> |
|--|--|--|
| Carapace | | |
| opening of LAG | 0.1mm anterior of hinge at PDC | 0.06mm anterior of hinge at PDC |
| opening of RAG | on rounded PVC, slightly above PVC | on rounded PVC, slightly above PVC |
| Special characters | posterior margin curves smoothly into ventral margin but angle of curvature changes abruptly at mid-height | posterior margin smoothly curved with out change at midheight |
| Frontal organ | | |
| Capitulum and stem | fused | fused |
| Shape | angled down ~10° spinose distally, hirsute proximally, similar breadth to stem, ends in long fine point | almost straight, inflated towards end which is a long fine point, few coarse spines on ventral side, |
| Length relative to antenna 1 | stem projects clear of limb | Projects beyond end of limb but shorter |
| Antenna 1 | | |
| Segments | fused | fused |
| a-d setae | third length of e seta | similar to <i>O. antarctica</i> |
| e-seta | third length of carapace length | similar to <i>O. antarctica</i> |
| e-seta armature | ~10 hairs on basal quarter of leading edge, distally sparse fine spinules on trailing edge | fine hairs along basal quarter, spinules along trailing edge distal to ends of the a-d setae |
| Antenna 2 | | |
| Protopodite % of carapace L | 42.50% | 36.6%L |
| Exopodite 1 as % L | 18.0% | relatively shorter |
| Exopodite 2-9 | ~2/5's first segment | ~2/5's first segment |
| Endopodite segt 1 | | |
| processus mamillaris | tall pointed pyramidal | similar to <i>O. antarctica</i> |
| a- and b-setae | bare, curved, a half length of b | similar to <i>O. antarctica</i> |
| Endopodite segt 2 | | |
| c-setae | absent | absent |
| g-seta | ¼ carapace length, bare | similar to <i>O. antarctica</i> |
| f-j setae | f slightly longer but others subequal | subequal |
| sixth limb | | |
| Epipodial setae | 7 + 5 + 5 | 7 + 5 + 5 |
| Endopodite | | |
| Segment 1 ventral setae | 1 plumose + 3 bare | 2 + 2 bare |
| lateral setae | 1 + 1 | none evident |
| dorsal setae | 1 bare short distal | 1 bare shortish |
| Segment 2 ventral setae | 1 | 1 |
| dorsal setae | 0 | 0 |
| Segment 3 ventral setae | 1 | 1 |
| dorsal setae | 1 | 1 |
| height/length ratio | about 33% | similar to <i>O. antarctica</i> |
| Segment 4 Terminal seta | | |
| dorsal:median:ventral | 55:100:35 | 60:100:48 |
| Longest setae: 3 rd segment | 230% | 230% |
| Longest setae: endopodite | 98% | 92% |