Uiblein, F., Ott, J., Stachowisch, M. (Eds), 1996: Deep-sea and extreme shallow-water habitats: affinities and adaptations. - Biosystematics and Ecology Sereies 11: 221-231.

Morphological and reproductive adaptations in Antarctic meso- to bathypelagic Mysidacea, with description of *Mysifaun erigens* n.g. n.sp.

K. J. WITTMANN

Abstract: Among Mysidacea that frequently occur in 100-700 m depths in high-Antarctic regions, one finds special morphological adaptations in both sexes such as modified inner branches of the antennae, extremely large penes, or even glandiform structures. A species with erectile penes, previously unknown for the entire group of animals, is described as *Mysifaun erigens* n.g. n.sp. Females show no obvious peculiarities in primary sexual characteristics. High oil content and "large" size of the body are evident and interpreted as adaptive under conditions of strong seasonality in food supply. However, the Antarctic species appear to be in the lower size range when compared with a worldwide relation between body size and temperature. Extrapolations based on summer data suggest that the breeding cycle of a *Mysidetes* species corresponds to "cold-season breeding" as defined by WITTMANN (1984). The sexual morphological peculiarities are interpreted as being adaptive for males. They may have the chance to reproduce only once in their lifetime during a very short period. While it may be advantageous to bear highly efficient giant penes for mating, this may be inconvenient for normal activities such as swimming.

Introduction

A highly diverse marine fauna is found in and above the (deep) shelf in high-Antarctic regions in the Weddell Sea. Animals are adapted to extremely low temperatures with very small annual variations of -2 to 0°C. Mysid shrimps (Mysidacea) are among many groups of organisms very poorly known in the high-Antarctic benthos. Therefore, the primary objective of this study was to provide basic data for the monographic series "Antarctic Benthos" in the frame of the Antarctic Survey of the German Science Foundation. It was no surprise that many species new to science were found using specially adapted sampling methods (WITTMANN 1995a) in remote sea areas covered by ice most of the year. On the other hand, it was unexpected that a variety of special morphological adaptations were found, in part new to science, that are rare or even absent in warmer climates (WITTMANN 1995b). Therefore, besides the contribution to knowledge of biodiversity and benthic ecology, this study also deepens our insights in kryobiology, sexual biology, and general morphology of life under stenokryophilic and deep-water conditions.

Material and Methods

Materials were sampled in the Weddell Sea (Antarctica) during "Polarstern" expedition ANT VIII/5 in 1989/90 at depths of 80-1050 m. Methods of collection and first results on board are available in WITTMANN (1991, 1995a), sampling stations and their characteristics in EMSCHERMANN et al. (1991), methods of shipboard microphotography in SVOBODA (1992). Sampling stations for the animals in Fig. 1 are st. 16-421 for Fig. 1C; st. 16-423 for Figs 1A, B, D, F; st. 16-456 for Figs 1G, H; st. 16-489 for Fig. 1E.

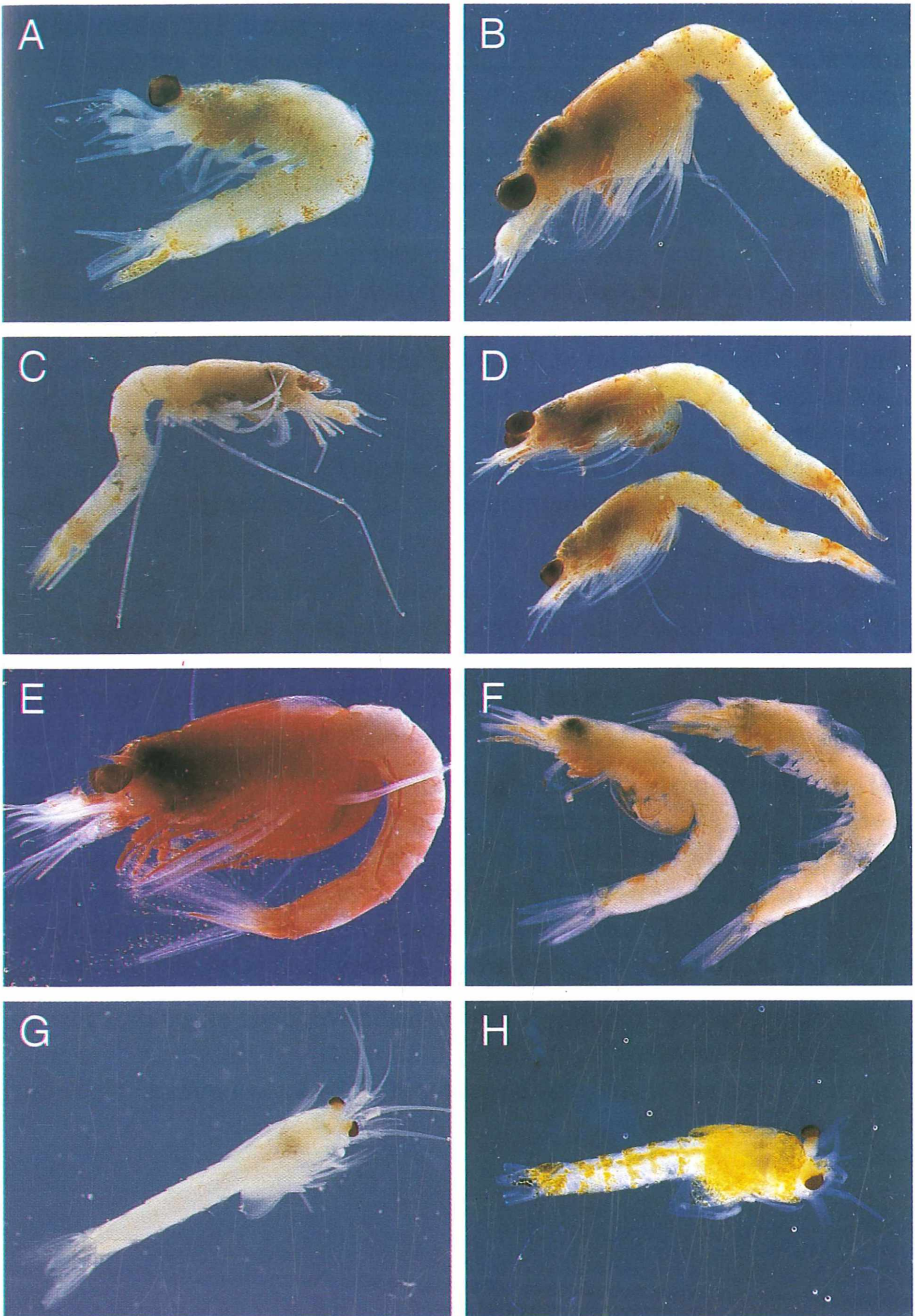
Larval stages in the marsupium are distinguished according to WITTMANN (1981). Body size was measured from tip of rostrum to terminal end of telson, without spines. Dissected materials were mounted in SWAN-medium on slides.

Results

Morphology of Antarctic mysid species

At first glance, among the 35 mysid species so far determined in materials from "Polarstern" collections, the large body size is a striking peculiarity of the Antarctic fauna in the Weddell Sea. Adult sizes range between 4.4 mm (only one indiv.) for a *Mysidella* species and a mean of 58 mm (n = 50) for *Antarctomysis ohlinii* HANSEN (c.f. sizes indicated in Fig. 1 and by WITTMANN 1990). These sizes are in the lower range of a linear relationship between inverse ambient temperature and log body length of mysid species, compared on a worldwide basis (c.f. Fig. 5 in WITTMANN 1984).

Fig. 1: Shipboard photomicrographs of freshly fixed Weddell Sea Mysidacea. A: Holotype of *Mysifaun erigens* n.g. n.sp. male with body length 12 mm. B: Form near *Mysidetes* with modified inner ramus of antenna, male 24 mm. C: *Mysidetes* sp. B with extremely long penes, male 17 mm; the individual was heavily damaged during sampling, but both long and thin penes extending far beyond the cephalothorax remained intact. D: *Mysidetes* sp. A, two females measuring 13 and 14 mm in length. E: *Boreomysis brucei* W.M. TATTERSALL, female 36 mm, a typical mesopelagic form of the southern ocean. F: *Paramblyops brevirostris* O.S. TATTERSALL, a blind representative of meso- to bathypelagic waters, female 15 mm, male 16 mm. G: *Heteromysis* sp., representative of a coastal and strictly benthic genus with maximum number of species in (sub)tropical seas, female 12 mm. H. *Mysidella* sp., a dwarf among Antarctic mysids, also with benthic habit, female 4.4 mm.


A
B
C
D
E
F
G
H

In thisrespect, Antarctic mysids are unexpectedly small. The reason for this is the absence of large oceanic Lophogastrida, especially of the giant genus *Gnathophausia*, which is completely absent in extremely cold marine waters.

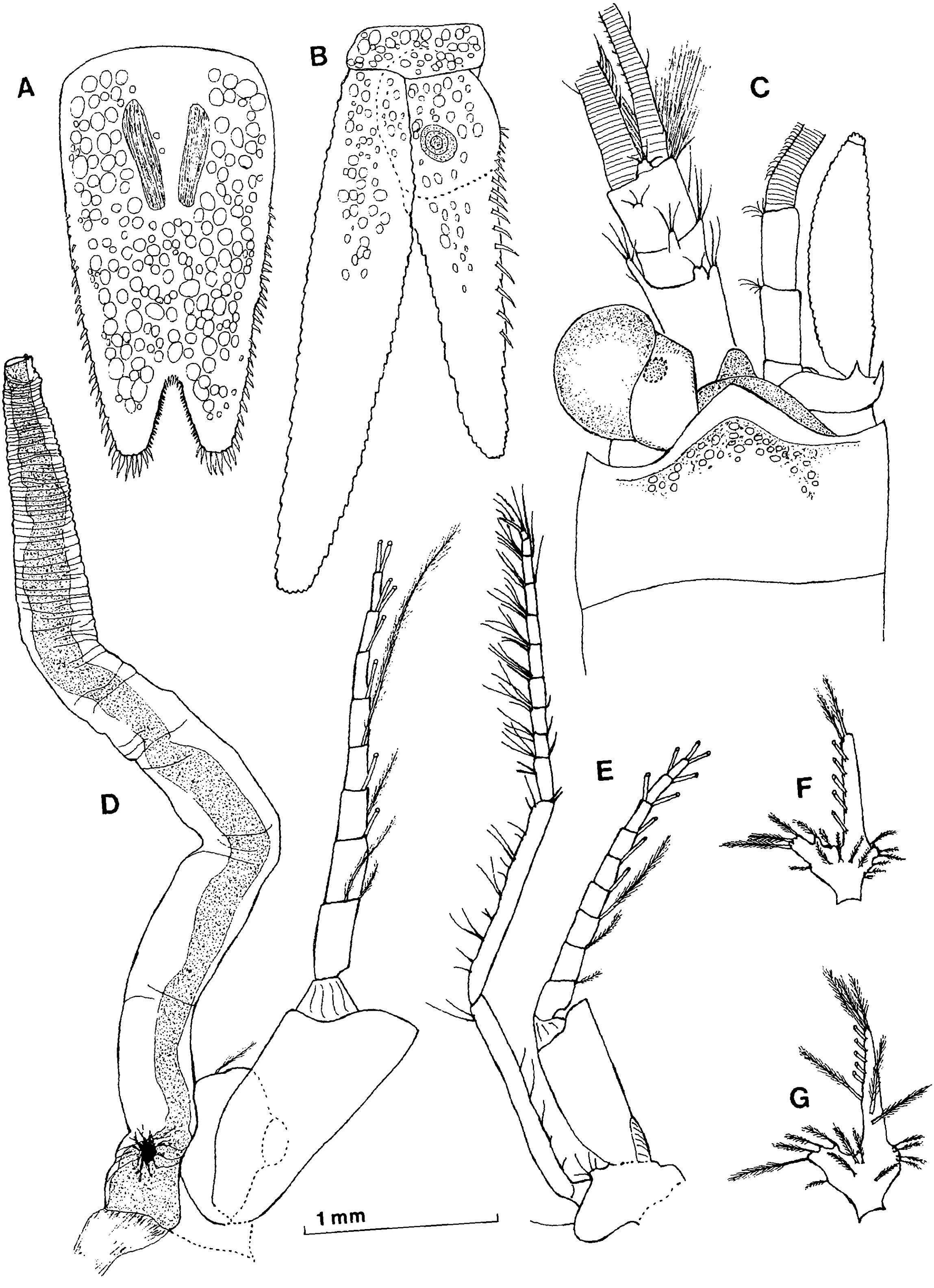
Sampling took place in summer, when biological production was high. Accordingly, all species studied had a high fat content, visible in the form of numerous oil globules (Figs 1A, H, 2A-C) under the microscope. There is a clear inverse relation between body size and oil content. The dwarf among Antarctic mysids, the above-mentioned *Mysidella*, is completely interspersed with oil globules. Even the colour of this animal is dominated by its fat content (Fig. 1H). The three species of the new genus described below are of small to intermediate size, and all showed a high oil content. Less oil was observed in larger species (Figs 1B, E), at least by microscopical examination. Fat is usually stored in specific organs: all observed (14) species of *Mysidetes* and related genera showed maximum numbers of oil globules in the telson (Figs 1A, 2A).

Modified basal segments of the antennal flagellum were found in two species of *Amblyops,* with less strong modification also in five species of *Mysidetes* (Fig. 1B). Modifications involve rich setation patterns, large size, and form of basal segments (see Fig. 1A in WITTMANN 1995b). In addition, the antennulae (Fig. 2C) are modified in males, as usual in the family Mysidae.

The males of many *Mysidetes* and related species showed large to giant penes that were even larger than the cephalothorax (Fig. 1C). Several species new to science showed a variety of characteristic morphological features in glandiform structures (Fig. 1B in WITTMANN 1995b) and/or penes with erectile tissue (Fig. 2D), previously unknown for the entire order Mysidacea. Females (Fig. 1D) in this group showed no obvious special adaptations.

The rich sample of morphotypes found in the Weddell Sea requires a larger, more comprehensive treatment that will be published elsewhere. Nevertheless, the present arguments may be exemplified by a most remarkable animal described in the following:

Fig. 2: Camera lucida drawings of *Mysifaun erigens* n.g. n.sp. from the Weddell Sea; male 12 mm, female 12 mm, subad. fem. 9 mm. A. Telson of male in dorsal view. B. Uropods of male in ventral view. C. Cephalic region of male, dorsal aspect. D. Left penis with eighth thoracic exopod. E. Fifth thoracic appendages of subad. female. F. Fourth pleopod of adult female. G. Fourth pleopod of male. For size comparison, all drawings are on same scale.


A
B
C
D
E
F
G
1 mm

Mysifaun, new genus

Beyond type species, the following definition anticipates the results on two further undescribed species found during expedition ANT VIII/5 in the Weddell Sea:

Definition: Mysidae with most characters as in *Mysidetes* HOLT and TATTERSALL (1906). Eyes and carapace normal. All three segments of antennular peduncle produced into several setose lobes (Fig. 2C). Antennal scale setose all around, with a small terminal joint; inner branch of antena not modified. Mouthparts, thoracopods, pleopods, and uropods as in *Mysidetes*. Tarsus (i.e. carpopropodus plus dactylus) of pereiopods multisegmented (Fig. 2E). Pleopods reduced to simple setose plates, practically identical in both sexes (c.f. Figs 2F, G). Telson bifid, ending in two well-rounded lobes (Fig. 2A).

Males. Terminal segment of antennular peduncle with a small appendix masculina in ventral position, representing rather a dense brush of bristles emerging from a bilobate emargination than a well-formed appendix. Penes extremely thick, large to giant in length; provided with erectile capability due to a variously folded cuticle (Fig. 2D) that allows for observed strong modifications in thickness, length, and form. Males of this genus are immediately recognizable by this unique feature in the order Mysidacea.

Females. Two pairs of brood lamellae and all remaining maior sexual characteristics as in *Mysidetes*. Details of telson development allow distinction from most but not all species of *Mysidetes*.

Type species: *Mysifaun erigens* n. sp.

Derivatio nominis: the monstrous genital appendages give the animal the appearance of a small mysid faun. Grammatical sex is defined as male. Name of type species is participium praesens of the Latin verb "erigere" = erect.

Mysifaun erigens, new species (Figs 1A, 2)

Material: Antarctica, Weddell Sea, "Polarstern" expedition ANT VIII/5, Hol 14, station 16-423, coor. 74.85°S/27.64° W, 17.1.1990, epibenthic sledge, mud flat with sponges in 470 m depth; holotype male 12 mm, paratypes 3 males 9-12 mm, 1 female 12 mm, 5 subadults 7-10 mm; deposited at Naturhistorisches Museum Wien, reg. nos 12969, 12970.

Description (males 9-12 mm, female 12 mm): Body proportions as in Fig. 1A. Masses of oil globules are visible, in decreasing order, in telson (Fig. 2A), uropods (Fig. 2B), pleon, and cephalothorax (Fig. 2C). Eyes with large cornea, eyestalks with minute scales (Fig. 2C) along outer and inner margin; no ocular papillae present. Rostrum well developed, subtriangular, emarginate, less than half the length of eyestalks.

Antennular peduncle massive in both sexes, with setose lobes as in Fig. 2C, where the largest lobe is distally on the outer border of the basal segment. Antennal scale extends to about same height as antennular peduncle. Minute terminal segment of scale separated from basis by a very subtle suture, terminal segment with five setae; antennal sympod anteriorly produced into a dorsal and an additional lateral spiniform process (Fig. 2C).

Mouthparts as usual for *Mysidetes* species. Labrum rounded. Left mandibula: pars incisiva with three teeth, lacinia mobilis with four teeth, pars centralis with four serrate spines. Right mandibula: pars incisiva with 3-4 teeth, lacinia mobilis resembling a moveable desk with numerous small teeth, pars centralis with a dense brush of bristles, one separate and six compound large teeth. Pars molaris representing a strong rasp in both mandibles. According to MAUCHLINE (1980), a large pars molaris is associated with herbivorous filter feeding in mysids, the hard diatom frustules being ground by this region. Stomach (i.e., prestomach) with rich armature of bristles and serrate spines. Stomachs were found almost empty; a few diatoms and foraminiferans could be identified. This and the morphology of the mouthparts suggest that the animal is mainly a filter feeder.

Basis of first thoracic endopod with a large hairy endite; first thoracic epipod leaf-like, with one large seta. Tarsus of pereiopods 10- to 13-segmented; dactylus with minute claw (Fig. 2E). First and eighth thoracic exopod 9-segmented (Fig. 2D), second to seventh 10-segmented (Fig. 2E). Penes variable in size, extending up to tip of antennular peduncle or only to mandibles; maximum thickness observed is that illustrated in Fig. 2D, minimum is about half that size (Fig. 1A). Pleopods of both sexes as in Figs 2F, G, with size continuously increasing from first to fifth pleopod.

Endopods of uropods (Fig. 2B) slightly longer than last abdominal somite, endopod extending slightly beyond telson; with 16-19 regularly arranged spines on inner margin; terminal 30 % of endopod without spines. Statoliths small (Fig. 2B), of fluorite type.

Telson with 22-26 spines on lateral margins and 5-7 larger, subequal spines in terminal position on each lobe. Spines showing continuous increase in size along outer margins, i.e., not arranged in groups of alternating size; basal 35-40 % of telson without spines. Cleft is only about 20 % of telson length, lateral borders with 16-20 small spines, bottom of cleft with 5-7 distinctly larger, spiniform laminar processes.

Colour of freshly formalin-fixed individuals (Fig. 1A): Cornea brown, body yellowish orange. The yellowish complexion comes not from pigment but from the rieh oil content, especially in the pleon and tail fan. Tergites of pleon, carapace, and mouthparts from labrum to first maxilleped show a more intense red-orange pigmentation. Stomach appears transparent.

Bionomic observations on a *Mysidetes* species

Sampling data are available only for summer months, from December to February. With a total of 1810 individuals, *Mysidetes* sp. A (Fig. 1D; similar to *Mysidetes antarctica* O.S. TATTERSALL, but with smaller and differently formed penes) was the most abundant species. From December to February, freshly hatched postmarsupial stages were completely absent and adult males were rare (3 %). In contrast, juveniles (28 %), subadults (51 %), and females with empty brood pouch (12 %) were very frequent. Among females which carried young (6 %, n= 105), most had embryonated eggs (67 %). Those with nauplioid larvae were rarer (24 %), but still more frequent than those with postnauplioid larvae (9 %). Towards the end of summer, a slight increase in the relative proportions of adults was observed in both sexes.

Discussion

Winter samples of high-Antarctic animals are extremely difficult and expensive to obtain. Therefore, such materials are rare and one should rest content with small data bases and only fragments of life cycles. Available data may be used as parts of a puzzle where data from other sources, especially data on Arctic species, may be integrated:

The above observations on *Mysidetes* sp. A suggest that the reproductive cycle proceeds similarlly to that in the Arctic (as observed by LASENBY and LANGFORD, 1972, on Arctic populations of *Mysis relicta*); at least there are no traces of contradictory data. The animals accumulate storage materials during summer and gain sexual maturity in early autumn. Presumably in March and April the eggs are deposited in the brood pouch and copulation takes place. Shortly afterwards the adult males die. The larvae develop in the brood pouch during autumn and winter. After about eight months of development they are liberated from the brood pouch in early summer, when they can profit from the plankton boom for fast individual growth. Thus the animals should represent "cold-season breeders" as defined by WITTMANN (1984).

Observed "large" body sizes and high oil contents are also in line with considerations on the difficult trophic situation of Antarctic (deep-water) animals: a very short favourable season with plenty of food and a long season with food scarcity or even starvation. The literature has long since proven that food availability and not temperature is the main problem for life under high Antarctic conditions.

The antennal modifications observed in both sexes, at least as far as larger numbers of setae are concerned, may also possibly serve to more efficiently detect food. However, the detection of mating partners may also be difficult for both sexes under conditions of low population densities, especially in deep waters. Findings of giant specimens of bathypelagic *Gnathophausia* species far away from the normal distribution range (FAGE 1941, NOUVEL 1943) may be indicative of a delayed (or repeated?) maturation moult due to failure in finding a mating partner, although alternative explanations are possible as well.

Most mysids sampled in the Antarctic came on board already in moribund condition. Therefore, no one has ever observed mating behaviour in these species. Females do not show obvious special morphological adaptations of primary or secondary sexual characteristics. This leads to the assumption that copulation and fertilization proceed in a manner similar to that known from species in warmer climates, where the eggs are fertilized in the brood pouch (NOUVEL 1940, WITTMANN 1982).

Giant penes are normally found only in sedentary animals such as cirripeds (KLEPAL et al. 1972). Enormous sexual organs in vagile males, especially in perfect swimmers such as mysids, are a quite outstanding feature and thus seek explanation. Among mysids, giant penes are known from *Mysidetes antarcitca, M. farrani* (HOLT and TATTERSALL), *M. halope* (O'BRIEN), *M. kerguelensis* (ILLIG), *M. peruana* BACESUCU, *Mysifan erigens* n.g. n.sp., *Mysidella tanakai* II, and *M. typhlops* G.O. SARS. All these species inhabit temperate to arctic climates. Large, but rarely giant, penes are common in the genera *Mysidetes* and *Mysidella*, more rarely also in *Heteromysis*. These genera, belonging to different tribes or subfamilies of the family Mysidae, have in common that the male pleopods are reduced as in females. In "normal" Mysidae, fourth and/or third male pleopods are modified and may have some function for copulation (MAUCHLINE 1980, WITTMANN 1982). Thus, the lack of modified pleopods may favour the evolution of large penes; nevertheless, small penes are found in a few species of *Mysidetes* and many species of *Heteromysis*. During copulation, males of *Heteromysis armoricana* introduce their large, but not giant, penes into the brrod pouch where fertilization of freshly deposited eggs takes place (NOUVEL 1940).

The sexual morphological peculiarities of certain mysids in the Antarctic are interpreted as being adaptive for males. They possibly have a chance to reproduce only once in their lifetime during a very short period. If copulation proceeds as rapidly as in species of temperate climates (NOUVEL 1940, WITTMANN 1982), it would be crucial for males to use their modified antennulae to detect females ready for mating and to introduce their penes into the brood pouch as fast as possible. Here, the giant penes may be useful to gain precedence in mating, or may even favour higher precision in the transfer of gametes. In order to transfer the genes to the next generation, fitness for survival may be less important than fitness for reproduction. In this sense, it would be advantageous to bear a pair of highly efficient giant penes for mating, even though this may be inconvenient for normal activities such as swimming.

Acknowledgements

The German Science Foundation and the Alfred-Wegener-Institut für Polar- und Meeresforschung (Bremerhaven) are greatly acknowledged for their invitation and support during Antarctic expedition "Polarstern" ANT VIII/5. Great thanks to A. SVOBODA (Bochum) for facilities and collegial assistence with shipboard microphotography.

References

EMSCHERMANN, P., KLEPAL, W., KRAPP, F., STEINER, S., SVOBODA, A., WITTMANN, K. J., 1991: Systematische und faunistische Bestandsaufnahme des Benthos des Weddellmeeres. - Ber. Polarforsch. (Rep. Polar Res.) **86**: 30-31.

FAGE, L., 1941: Mysidacea Lophogastrida I. - Dana Report **19**: 52 pp.

HOLT, E. W. L., TATTERSALL, W. M., 1906: Preliminary notice of the Schizopoda collected by H.M.S. "Discovery" in the Antarctic Region. - Ann. Mag. nat. Hist. Ser. 7, **17**:1-11.

KLEPAL, W., BARNES, H., MUNN, E. A., 1972: The morphology and histology of the cirripede penis. - J. Exp. Mar. Biol. Ecol. **10**: 243-265.

LASENBY, D. C., LANGFORD, R. R., 1972: Growth, life history and respiration of *Mysis relicta* in an Arctic and temperate lake. - J. Fish. Res. Board Can. **29**: 1701-1708.

MAUCHLINE, J., 1980: The biology of mysids and euphausiids. - Adv. Mar. Biol. **18**: 1-681.

NOUVEL, H., 1940: Observation sur la sexualité d'un mysidacé, *Heteromysis armoricana* n. sp. - Bull. Inst. Océanogr. **789**: 1184-1186.

NOUVEL, H., 1943: Mysidacés provenant des campagnes du Prince Albert Ier de Monaco. - In RICHARD, M. J., (Ed.): Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier, Fasc. **105**:1-128 + 5 pls. - Imprimerie de Monaco.

SVOBODA, A., 1992: Close-up photography of marine life on board of research vessels. - Sci. Mar. **56**: 239-244.

WITTMANN, K. J., 1981: Comparative biology and morphology of marsupial development in *Leptomysis* and other Mediterranean Mysidacea (Crustacea). - J. Exp. Mar. Biol. Ecol. **52**: 243-270.

WITTMANN, K. J., 1982: Untersuchungen zur Sexualbiologie einer mediterranen Mysidacee (Crustacea), *Leptomysis lingvura* G.O. Sars. - Zool. Anz. **209**: 362-375.

WITTMANN, K. J., 1984: Ecophysiology of marsupial development and reproduction in Mysidacea (Crustacea). - Oceanogr. Mar. Biol. ann. Rev. **22**: 393-428.

WITTMANN, K. J., 1990: Mysidacea. - In SIEG, J., WÄGELE, J. W., (Eds.): Fauna der Antarktis, pp. 130-133. - Berlin: Parey.

WITTMANN, K. J., 1991: Systematisch-faunistische und biomineralogische Untersuchungen an Mysidacea (Crustacea) des Weddellmeeres. - Ber. Polarforsch. (Rep. Polar Res.) **86**: 37-40.

WITTMANN, K. J., 1995a: Wie man ein engmaschiges Netz über felsigen Grund zieht: Erfahrungen mit dem Epibenthosschlitten am Grunde des Weddellmeeres. - Ber. Polarforsch. (Rep. Polar Res.) **155**: 92-93.

WITTMANN, K. J., 1995b: Sexuelle Hypertrophien bei Mysidaceen (Crustacea) als polare Anpassungen der Reproduktionsbiologie und ihre Bedeutung für die Biodiversität in antarktischen Gewässern. - Ber. Polarforsch. (Rep. Polar Res.) **155**: 94-97.

Address of the author:

Karl J. WITTMANN, Institut für Allgemeine Biologie der Universität Wien, Schwarzspanierstr. 17, A-1090 Wien, Austria.
email: karl.wittmann@univie.ac.at

Zeitschrift/Journal: Biosystematics and Ecology

Jahr/Year: 1996

Band/Volume: 11

Autor(en)/Author(s): Wittmann Karl J.

Artikel/Article: II. Temperature. Morphological and reproductive adaptions in Antarctic meso- to bathypelagic Mysidacea, with description of Mysifaun erigens n.g. n.sp. In: Deep Sea and Extreme Shallow-water Habitats: Affinities and Adaptations. 221-231