Preliminary account of the loriciferan fauna of the Faroe Bank (NE Atlantic)

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Abstract

Twelve new species included in six genera (*Nanaloricus*, *Armorloricus*, a new nanaloricid genus, *Pliciloricus*, *Rugiloricus* and a new genus of a new order) have been found on the Faroe Bank, southwest of the Faroe Islands. The highest species diversity is found on the slopes, where station 627 has the highest with six species including three genera. Subsequently, there are only a few species found on the plateau, where especially the two interstitial nanaloricid genera (*Armorloricus* and *Nanaloricus*) dominate.

The Faroe Bank material has given new valuable information about the different types of life cycles in Loricifera. In the genus *Rugiloricus* a new type of larva, a ghostlarva, has been found. The ghostlarva does not resemble any other kind of loriciferan larvae. This makes the life cycles of *Rugiloricus* much more complicated than first assumed. The life cycles of *Rugiloricus* consist of several loops or cycles, e.g., a sexual life cycle, a parthenogenetic life cycle with neotenous larvae and a sexual cycle with a reduction of the postlarva. The Faroe Bank study has also confirmed that the family Nanaloricidae only has a typical sexual life cycle, with a Higgins-larva, a postlarva and an adult. Another interesting result is found in the new order, which has a pedogenetic life cycle with a cyst-like ghostlarva.

Introduction

Loriciferans are microscopical bilaterally symmetrical metazoans ranging from 100 µm to 1 mm. They are marine animals inhabiting the interstitial spaces of shell gravel, oolytic sand or mud (Kristensen, 1983; Higgins and Kristensen, 1986). The morphology, terminology and reproduction of Loricifera have in recent years been fully described (Higgins and Kristensen, 1986; Kristensen, 1991; Kristensen and Brooke, 2002; Kristensen and Gad, 2004).

The phylum Loricifera was described in 1983 by Reinhardt M. Kristensen from shelly gravel off the coast of Roscoff, France (Kristensen, 1983). The description included a single species, the type species, *Nanaloricus mysticus* Kristensen, 1983 of the family Nanaloricidae. In 1986 Higgins and Kristensen described another family, Pliciloricidae, from coarse sand off the coast of North and South Carolina, USA (Higgins and Kristensen, 1986), including two genera, *Pliciloricus* and *Rugiloricus*, with five and three species respectively. An additional species, *Nanaloricus khaitatus* Todaro and Kristensen, 1998, was described from the Mediterranean Sea, Italy (Todaro and Kristensen, 1998). The first

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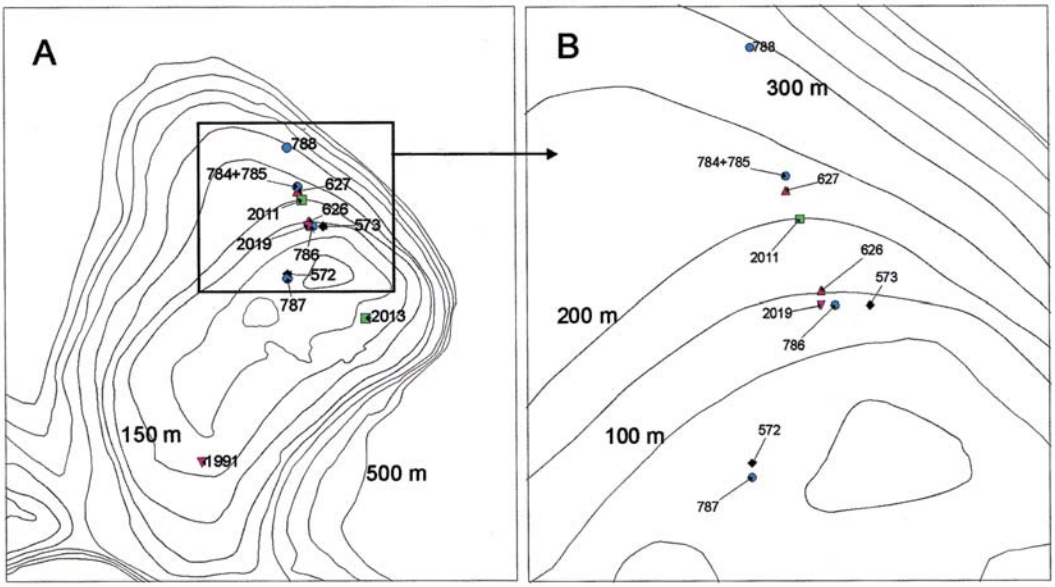


Fig 1. *A. Map of the Faroe Bank with all the stations. B. Close-up of the northern slopes.*

deep-sea loriciferan *Pliciloricus hadalis* Kristensen and Shirayama, 1988 was recorded in 1988 from the Izu-Ogasawara Trench, Western Pacific (Kristensen and Shirayama, 1988) and recently another deep-sea species *Phoeniciloricus simplidigitatus* Gad, 2004 has been described off Papua New Guinea (Gad, 2004). Most recently, a new nanaloricid genus including two species *Armorloricus elegans* Kristensen and Gad, 2004 and *A. davidi* Kristensen and Gad, 2004 has been described from Trezen ar Skoden near Roscoff, France (Kristensen and Gad, 2004).

The Faroe Bank is situated 75 km southwest of the Faroe Islands in the North Atlantic Ocean. The Faroe Bank rises from approximately 900 to around 100 meters depth on the plateau. The sediment around the bank to the plateau varies from muddy to finer carbonated sand and coarse shell sand (Hansen *et al*., 2001; Magnussen, 2002).

The purpose of this study was to describe the loriciferan fauna of the Faroe Bank especially with emphasis on the species diversity and the different types of life cycles.

Materials and methods

Loriciferans were recorded from 1989 to 2001, at thirteen stations on the Faroe Bank (Fig. 1A). Most of the stations are located on the northern slopes from around 150 to 271 meters (Fig. 1B). The samples were collected with three types of gear: meiofauna dredge, Plymouth anchor dredge and a large triangular dredge with a finer inner lining of approximately 100 µm. The sediment on the stations consists of shell gravel, shell sand and fine carbonated sand (silt)

mixed with basalt sand. For further information on station data, sampling gear, temperature and sediment see Nørrevang *et al*. (1994).

The samples were processed according to the usual procedures (Higgins and Kristensen, 1986). Prior to sorting the animals were stained with "Rose Bengal". Most of the extracted specimens were mounted on slides in glycerol and afterwards sealed with glyceel®. The rest of the specimens were prepared for scanning electron microscopy (SEM) according to usual procedures (Higgins and Kristensen, 1986). The animals on the slides were studied using a light microscope, Olympus BX51 with phase-contrast, Normarski technique and DIC (differential interference contrast) microscopy. Photos were taken with an Olympus C-3030 zoom digital camera. The SEM specimens were examined using a JEOL JSM-6335-F scanning electron microscope.

Table 1. *The species from the Faroe Bank*

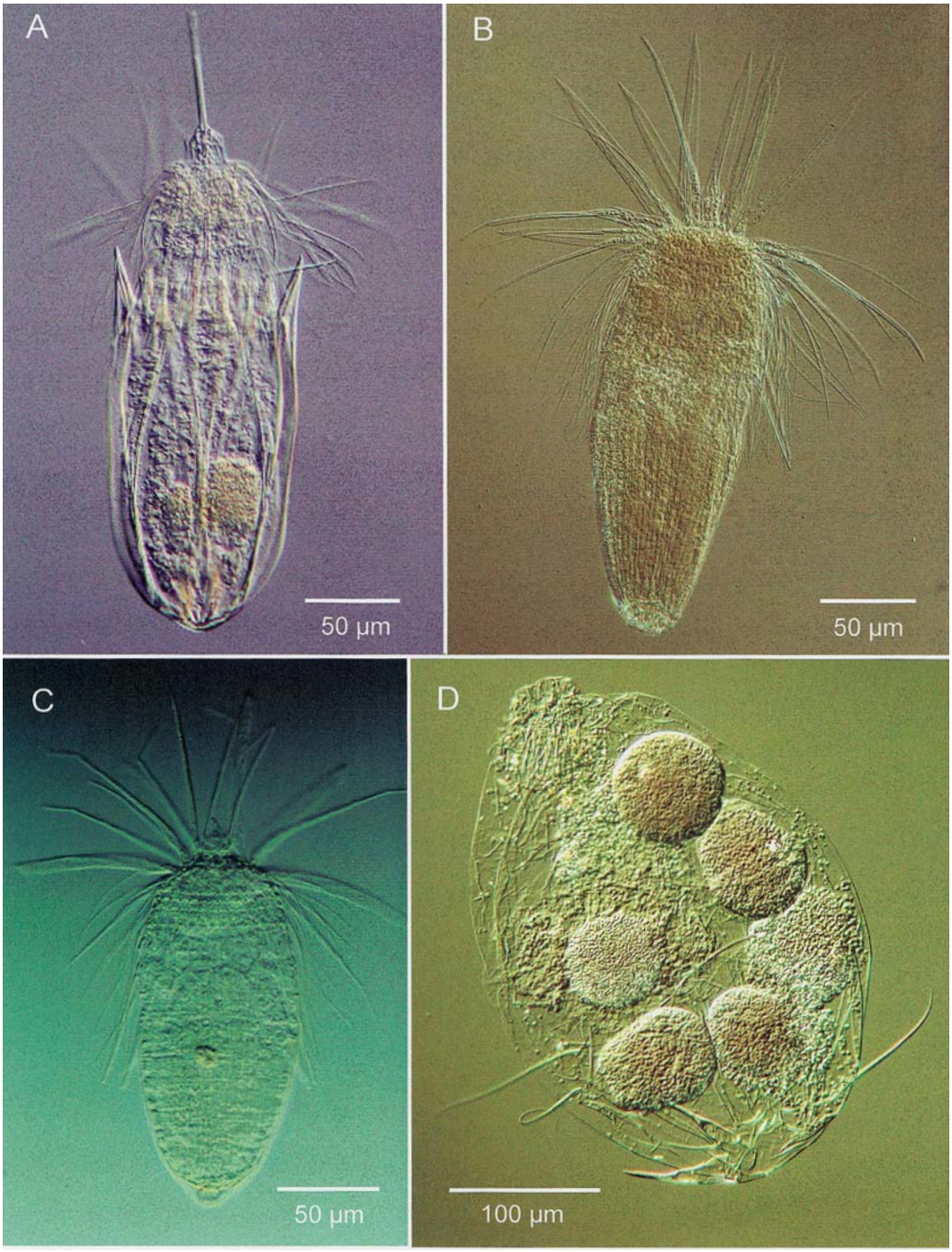
Nanaloricida
- Nanaloricidae
  - *Nanaloricus nov. sp*. 1
  - *Nanaloricus nov. sp*. 2
  - *Armorloricus Kristenseni*
  - *Armorloricus nov. sp*. 2
  - *Nov. gen. 1 et nov. sp*. 1
- Pliciloricidae
  - *Pliciloricus nov. sp*. 1
  - *Pliciloricus nov. sp*. 2
  - *Rugiloricus nov. sp*. 1 (*carolinensis*-type)
  - *Rugiloricus nov. sp*. 2 (*cauliculus*-type)
  - *Rugiloricus nov. sp*. 3 (*cauliculus*-type)
  - *Rugiloricus nov. sp*. 4 (*cauliculus*-type)

New order
- New family
  - Nov. gen 2 et nov. sp. 1

Results

A total of 364 loriciferan specimens were obtained from the thirteen stations on the Faroe Bank. These specimens include twelve new species distributed between six genera: *Nanaloricus*, *Armorloricus*, a new genus of Nanaloricidae (nov. gen. 1), *Pliciloricus*, *Rugiloricus* and a genus (nov. gen. 2) belonging to a new order (see Table 1). Five new species of the family Nanaloricidae have been recorded. This includes four new species of two previously described genera (*Nanaloricus* and *Armorloricus*), and additionally a new species of a new genus. One of the species, *Armorloricus kristenseni* (Heiner, 2004) (Fig. 2A), has been described. At least six species of the family Pliciloricidae have been recorded. There are probably more than four species in the genus *Rugiloricus*, since it has been impossible to link all the Higgins-larvae to any of the four species. The genus *Rugiloricus* can be divided into two types: *carolinensis*-type (Fig. 2B) and *cauliculus*-type (Fig. 2C). The genus is probably plesiomorphic, since the two types of adults are morphologically and reproductively very different from each other. Additionally in Pliciloricidae two species of the genus *Pliciloricus* have been recorded and both species are currently being described (Heiner and Kristensen, in press). Lastly a new order has been found on the Faroe Bank. The new order comprises one single species with several different types of larvae.

The results from the Faroe Bank have given a greater insight in the complex life cycles of Loricifera. The two genera


A
50 µm
B
50 µm
C
50 µm
D
100 µm

Nanaloricus and *Armorloricus* have a typical life cycle with sexual reproduction (Higgins-larva, postlarva and adults) as seen in all species of the family Nanaloricidae (Kristensen, 1991; Kristensen and Brooke, 2002). In the family Pliciloricidae there are two different types of life cycles, the *Rugiloricus cauliculus*-cycle and the *Rugiloricus carolinensis*-cycle, the later including *carolinensis*-type species and all *Pliciloricus* species. The *cauliculus*-cycle is a very complex cycle with many different loops. The first loop is a sexual reproductive cycle identical to the one in Nanaloricidae, except that the postlarva does not resemble the adults. Another loop in this life cycle is the asexual life cycle, where the Higgins-larva becomes neotenous and develops a mature ovary. Four to eight eggs mature inside the neotenous larva and the eggs hatch into typical Higgins-larvae. These larvae are produced parthenogenetically, that is without fertilization from male gametes (Kristensen, 2002; Kristensen and Brooke, 2002). Finally, the last loop in the *cauliculus*-cycle is the life cycle of the ghostlarva, which is formed inside a neotenous Higgins-larva in the same way as seen in the parthenogenetic cycle (Fig. 2D). The ghostlarva produces several eggs without fertilization, which are pushed out into the lumen of the exuvium of the Higgins-larva. Here the eggs mature into embryos and then into new Higgins-larvae (Kristensen *et al*., 2003). The *Rugiloricus carolinensis*-cycle is found in the species of the *Rugiloricus carolinensis*-type and in the genus *Pliciloricus*. The life cycle is strictly sexual where a reduction of the postlarval stage has occurred. The postlarval stage is not completely reduced, since the cuticle of the postlarva can be seen inside the Higgins-larva and around the adult (Kristensen, 2002; Kristensen and Brooke, 2002). Another interesting life cycle is the pedogenetic life cycle found in the new order from the Faroe Bank. Present in this life cycle is a cyst-like ghostlarva. In the beginning the ghostlarva is free-living with a thin cuticle and internally it has a single ovary. The ovary produces several oocytes (10-45) that mature into eggs. The ghostlarva first moults into a postlarva and then the postlarva moults into an adult female. Hence, first the female and then the cuticles of the postlarva and the ghostlarva surround the growing ovary. At some stage the ghostlarva becomes cyst-like and the eggs inside the ovary start to mature into embryos and then Higgins-larvae. During the maturation of the embryos the female and the postlarva are reabsorbed until only their cuticles are remaining inside the cyst. The Higgins-larvae come out of the cyst-like ghostlarva by penetrating the two internal cuticles and finally through a posterior opening. Inside the cyst several maturation stages can be seen simultaneously.

Fig 2. *Photos of: A. Female adult of* Armorloricus kristenseni. *B. Male adults of* Rugiloricus *nov. sp. 1 (*carolinensis-type*). C. Female adult of* Rugiloricus *nov. sp. 2 (*cauliculus-*type). D. Neotenous larva of* Rugiloricus *nov. sp. 4 (*cauliculus-*type) with ghostlarva and embryos inside.*

Discussion

The Faroe Bank has a highly diverse loriciferan fauna, with at least twelve species.

A similar high diversity has only been found off Roscoff, France (Kristensen, 1983; Kristensen and Gad, 2004) with seven species, off North Carolina, USA (Higgins and Kristensen, 1986) with seven species and on the Great Meteor Seamount (Gad, in press) with fourteen species. It is presumed that, as we begin investigating the deep-sea more intensively, higher species diversities will be found (Gad, 2003).

Station 785 has the highest number of specimens with 71.7 % of the total number, due to the fact that it is the only station where all the material has been sorted out. Additionally 95 % of the specimens from station 785 are Higgins-larvae of the genus *Rugiloricus*. The high percentage of Higgins-larvae is due to the parthenogenetic life cycle, which is dominant in spring and summer. Station 627 has the highest species diversity with six species (four species of *Rugiloricus*, one of *Pliciloricus* and one of the new order) (Kristensen, 1992; 1999). This correlates with the results from other groups of meiofauna, e.g., Tardigrada (Hansen *et al*., 2001). The high diversity is probably due to its location on the slope near an area of natural methane gas seep (Kristensen, 1992; 1999). The two nanaloricid genera, *Nanaloricus* and *Armorloricus*, are only found on the plateau, whereas the other genera are found both on the slopes and on the plateau.

The Faroe Bank study shows once again that all nanaloricid species have only one type of life cycle, a sexual reproductive cycle. Additionally the Faroe Bank material has revealed that the life cycle of the family Pliciloricidae is much more complex than first assumed, with the introduction of a new type of larva, the ghostlarva.

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