

# Gnathostomulida Abundant Alongside Polychaete Burrows\*

K. Reise

2. Zoologisches Institut der Universität Göttingen, D-3400 Göttingen, Federal Republic of Germany  
and  
Biologische Anstalt Helgoland, Litoralstation, D-2282 List, Federal Republic of Germany

**ABSTRACT:** Since their first description in 1956, Gnathostomulida have been regarded as one of the rarest taxa in marine benthos. On tidal flats in the North Sea, however, they live alongside permanent polychaete burrows with up to 29 individuals and 5 species in 1 cm<sup>3</sup> of sediment. Near burrows of *Arenicola marina* and *Nereis virens*, all species show a high degree of spatial overlap, indicating a narrow niche for the entire taxon. As a key factor to gnathostomulid distribution the activity of sulfur bacteria is proposed.

## INTRODUCTION

Since Ax reported on the first 2 Gnathostomulida in 1956, 51 species belonging to 10 families have been described. Adults are worm-shaped and range from 300 to 3500 µm in length. A monoclialated epidermis and a muscular pharynx with a pair of jaws and a basal plate are characteristic for this group. Today, Gnathostomulida are interpreted phylogenetically as a sister group to the Platyhelminthes (Ax and Ehlers, pers. comm.). They move slowly by ciliary gliding through the interstices of marine sediments and probably feed on bacteria. Most Gnathostomulida have been extracted from sand by the method of 'deteriorating climate', but numbers obtained were rather low and there are no data on absolute abundance (Riedl, 1969; Sterrer, 1971a). Typical biotopes are the deeper and mostly H<sub>2</sub>S-rich sand layers with much detritus (Sterrer, 1971b); Riedl (1969) reported maximum density of the gnathostomulid population at the discontinuity layer between aerobic surface and anaerobic subsurface sediment. In the present paper I suggest a more specific place to look for Gnathostomulida, namely the vicinity of polychaete burrows.

## MATERIAL AND METHODS

### Habitat

Sampling was done on tidal flats at the eastern coast of the North Sea, close to the island of Sylt. Local tidal range is 1.7 m and salinity remains close to 31 ‰ S. The flats are part of the northern Wadden Sea and are populated by a rich endobenthic macrofauna dominated by the lugworm *Arenicola marina* L. Close to low tide level, lugworms give way to dense populations of the polychaetes *Nereis virens* Sars and *Lanice conchilega* (Pallas). The sediment is relatively coarse-grained (particles 250 to 1000 µm comprise 85 % of total dry weight; median, 456 µm; sorting coefficient, s<sub>0</sub> = 1.5) and the amount of detritus varies considerably on a micro scale. Further informations on physical factors and faunal composition of the area are outlined in Wohlenberg (1937), Reise (1978), and Reise and Ax (1979).

Burrows of *Arenicola marina* consist of a permanent, vertical tail shaft with 5 mm inner diameter, a horizontal gallery at 15 to 20 cm depth, and – as a temporary structure – a vertical head shaft through which surface sediment slides downward to become ingested by the lugworms (Rijken, 1979). Oxygenated water is pumped into the burrow via the opening of the tail shaft (Baumfalk, 1979). *Nereis virens* dwells in a burrow system shaped like a dendrogram, with several openings at the sediment surface. Only some of the branches are

\* This work was supported by the Deutsche Forschungsgemeinschaft (DFG)

irrigated with water from the surface, and these have been investigated with respect to the distribution of Gnathostomulida. Sediments of tidal flats are brownish and oxic in the upper 1 to 2 cm and turn black and oxygen deficient underneath. Burrows running through the black layer are surrounded by a brownish halo (2–4 mm), in turn giving way to a light grey coloured zone of varying extent which merges in the black sediment.

### Sampling

Samples have been taken with plexiglass tubes of 1 or 2 cm<sup>2</sup> cross section. To obtain microfauna alongside tail shafts of *Arenicola marina*, a 2 cm<sup>2</sup>-corer was placed upon sediment with the opening of a shaft right at center of the corer, then pressed downward to a depth of 8 cm, closed with the thumb and pulled out again. About every other time, the tail shaft happened to remain at the center of the corer for its entire length. This being the case, I let the sediment core slide out of the tube and cut it into 1 cm intervals.

Alternatively, I dug up burrows with a spade, removed the adjacent sediment until the brownish sand of the burrow lining became visible along its vertical axis, and then dissected the burrow with a knife into 1 cm segments and obtained samples with a 1 cm<sup>2</sup>-corer. In a similar way, 1 cm<sup>3</sup> samples have been taken from burrows of *Nereis virens*, *N. diversicolor* O. F. Müller and *Lanice conchilega*.

In the laboratory, the 1 or 2 cm<sup>3</sup> samples were washed in a beaker and decanted into sets of 8 to 12 Petri dishes, including the residual fraction. By moderately shaking the beaker, Gnathostomulida usually showed up in the first 1 to 4 Petri dishes. Neither sieves nor narcotics were used.

### Data Analysis

The degree of coexistence between species was measured with Jaccard's coefficient (number of joint occurrences divided by the sum of all separate and joint occurrences, while common absences are disregarded); levels of significance were checked with a table provided by Baroni Urbani (1980). Niche breadth and diversity are described with the simplest expression  $(\sum p_i^2)^{-1}$ , where  $p_i$  = proportion of a species occupying the  $i$ -th habitat fraction, or proportion of individuals belonging to the  $i$ -th species. Patchiness was measured with Lloyd's index  $\dot{m}/m$ , and significant deviation from apparent randomness was detected by consulting a  $\chi^2$ -table (Lloyd, 1967; Reise, 1979).

## RESULTS

### Preference to Polychaete Burrows

On tidal flats off the island of Sylt, 10 species of Gnathostomulida were recorded (Müller and Ax, 1971; Reise and Ax, 1979; this study). In the following list, species found outside burrows are characterized by 'O', alongside burrows of *Arenicola marina* by 'A', alongside burrows of *Nereis virens* or *N. diversicolor* by 'N', alongside tubes of *Lanice conchilega* by 'L':

*Haplognathia simplex* (Sterrer, 1966) O, A, N  
*Haplognathia filum* (Sterrer, 1966) O  
*Haplognathia rubromaculata* (Sterrer, 1969) O, A, N  
*Haplognathia rosea* (Sterrer, 1969) O, A, N  
*Haplognathia gubbarnorum* (Sterrer, 1969) O, A, N  
*Pterognathia swedmarki* (Sterrer, 1966) O, A, L  
*Pterognathia atrox* (Sterrer, 1969) O, A, N  
*Pterognathia sorex* (Sterrer, 1969) O, A, N  
*Mesognatharia remanei* (Sterrer, 1966) A  
*Gnathostomula paradoxa* (Ax, 1956) O, A, N, L

With the exception of *Haplognathia filum*, found only 3 times by Müller and Ax (1971), all species occurred near polychaete burrows.

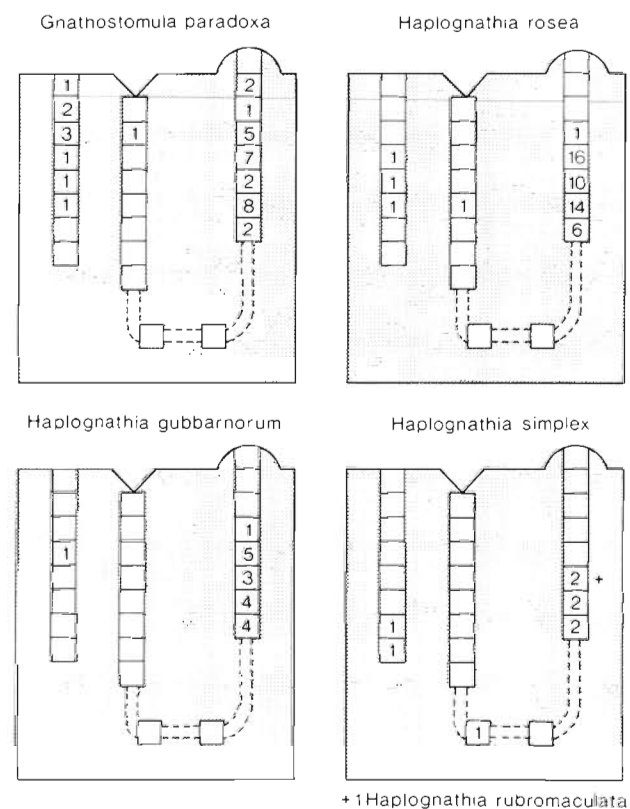


Fig. 1 Gnathostomulida alongside U-shaped burrows of *Arenicola marina* and away from burrows (left column). Squares: 1-cm intervals; numbers: individuals in 10 parallel samples (10 × 2 cm<sup>3</sup>). Tidal flat at Sylt in June 1980

On lugworm flats there is a clear preference of Gnathostomulida to the tail shaft region of burrows maintained by *Arenicola marina* (Fig. 1). On an adjacent flat at low tide level, populated by *Nereis virens*, 10 samples of 1 cm<sup>3</sup> have been taken from its burrows at depth of 10 cm, together with 10 controls a few cm away from burrows. While the latter contained only 1 specimen of *Pterognathia sorex*, the burrow samples comprised 34 individuals belonging to 6 species of Gnathostomulida. Nematoda were the only Metazoa being more abundant. A comparison between tail shafts of *A. marina* and burrows of *N. virens* shows a much higher abundance and diversity of Gnathostomulida near the latter (Table 1).

Table 1. Gnathostomulida alongside tail shafts of *Arenicola marina* (10 cores of 2 cm<sup>2</sup>, depth 3–8 cm, June 1980) and burrows of *Nereis virens* (10 cores of 1 cm<sup>3</sup>, depth 10 cm, August 1980); individuals 10 cm<sup>-3</sup>

Species	<i>A. marina</i>	<i>N. virens</i>
<i>Haplognathia simplex</i>	0.6	2
<i>Haplognathia rubromaculata</i>	0.1	+
<i>Haplognathia gubbarnorum</i>	1.7	8
<i>Haplognathia rosea</i>	4.7	9
<i>Pterognathia sorex</i>	0	9
<i>Pterognathia atrox</i>	0	1
<i>Gnathostomula paradoxa</i>	2.2	5
Sum of individuals	9.3	34
Species density in 10 cm <sup>3</sup>	2.8	6
Species diversity ( $\sum p_i^2$ ) <sup>-1</sup>	2.9	4.5

While most species remain rare or modest in numbers, *Gnathostomula paradoxa* occasionally exhibits mass occurrences. In September 1978 a set of 30 parallel samples (1 cm<sup>2</sup>, 0–5 cm depth) taken from the normal sediment contained 30 individuals. At the same time, on the same flat, 122 individuals were counted near a single tail shaft of *Arenicola marina* sampled with 1 cm<sup>2</sup> cross section (Fig. 2 D). Maximum density in 1 cm<sup>3</sup> was as high as 29. In subsequent years, *G. paradoxa* was an order of magnitude less abundant on this flat: 3 individuals below 40 cm<sup>2</sup> in October 1979, and 1 below 10 cm<sup>2</sup> in July 1980.

### Fine-Scale Distribution

In the normal sediment, *Gnathostomula paradoxa* prefers the transition zone between oxic and oxygen-deficient sediments, positioned 1 to 2 cm underneath the surface (see Fig. 2 in Reise and Ax, 1979). No *G. paradoxa* occurred below a depth of 5 cm. Alongside lugworm burrows their depth range extended to 12 cm (Fig. 2). Fine-scale sampling, done out in the field to avoid transport-related dislocations, are a matter of patience and repeated trials in these soft sediments, and cannot be done with deliberate repetitions. Four examples suggest that Gnathostomulida do not dwell directly at the inner burrow lining, but prefer the location where the sediment changes in colour from light grey to dark shade, usually some mm away from shafts (Fig. 3).

### Spatial Associations Between Species

Alongside lugworm burrows, all Gnathostomulida occupied about the same region at the tail shaft (Fig. 1). Computation of Jaccard's coefficient, measuring the degree of coexistence between species reveals significant positive associations. With respect to position in the sediment (squares in Fig. 1), significance was attained for the pairs *Gnathostomula paradoxa* x *Haplognathia rosea* and *H. rosea* x *H. gubbarnorum*. With respect to actual coexistence, calculated from the set of 30 parallel samples (2 cm<sup>2</sup>, depth 0–8 cm; see Fig. 1) taken in June 1980, pairs of *G. paradoxa* x *H. rosea*, *G. paradoxa* x *H. gubbarnorum*, *H. rosea* x *H. gubbarnorum*, and *G. paradoxa* x all local *Haplognathia* species combined, showed significant positive associations. Thus, there is a high degree of spatial overlap indicating very similar habitat preferences.

Using Levins measure of niche breadth,  $B = (\sum p_i^2)^{-1}$ , to estimate the range of habitats occupied on the *Arenicola marina* flat in June 1980 (Fig. 1), the order of species according to increasing habitat range is

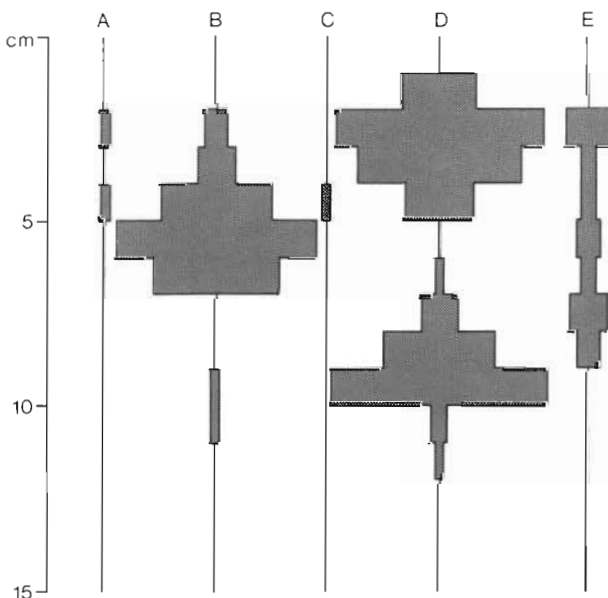


Fig. 2. *Gnathostomula paradoxa* alongside 6 tail shafts (1 cm<sup>2</sup>, depth 0–15 cm) of *Arenicola marina* in June (A, C), July (B), September (D), and October (E) 1978 on a tidal flat at Sylt

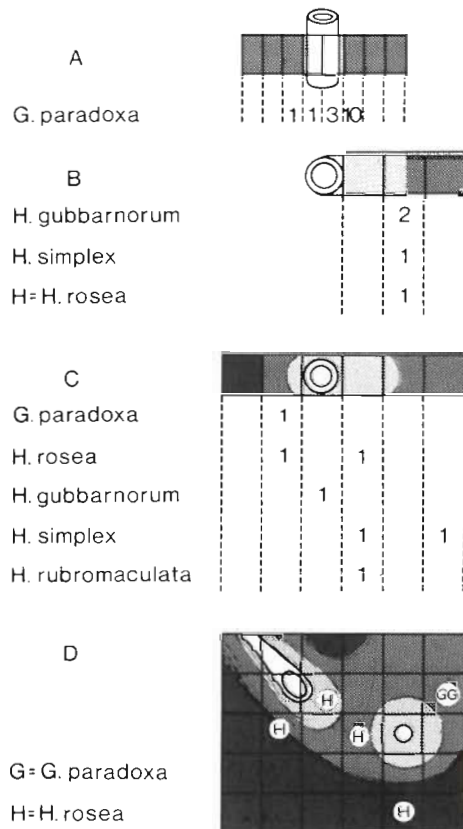


Fig. 3. Gnathostomulida close to burrows of *Arenicola marina* (A) and *Nereis virens* (B, C, D). Shading corresponds to natural colour of sediment, the immediate halo of burrows is brownish. A: horizontal transect through tail shaft at 5–6 cm depth, rectangles represent 0.5 cm<sup>3</sup>, breadth 0.5 cm, October 1980; B: horizontal transect at 5–6 cm, burrow and squares represent 0.5 cm<sup>3</sup>, side of square 1 cm, August 1980; C: horizontal transect at 7–8 cm, squares represent 1 cm<sup>3</sup>, side of squares 1 cm, August 1980; D: horizontal grid of 30 contiguous 1 cm<sup>3</sup>-cubes, one burrow cut oblique (left), the other branch without brownish halo, September 1980

*Haplognathia rosea* (B = 4.4) < *H. gubbarnorum* < *H. simplex* < *Gnathostomula paradoxa* (B = 8.1). The last-mentioned species is the least specific one with regard to habitat choice.

In Petri dishes, *Gnathostomula paradoxa* showed conspicuous gregariousness, and numbers per tail shaft of *Arenicola marina* varied considerably (Fig. 2). Between tail shafts there was a high degree of patchiness (measured with Lloyd's  $\dot{m}/m$ ), with the sum of Gnathostomulida being more clumped ( $m = 9.7$ ,  $\dot{m}/m = 1.4$ ,  $p < 0.001$ ) than each species separately. The same situation was observed between samples taken from 10 burrows of *Nereis virens* ( $m = 3.4$ ,  $\dot{m}/m = 1.9$ ,  $p < 0.001$ ). The encounter of 1 gnathostomulid in a sample increases the chance to find others. Consequently, species packing and species diversity are high. In the burrow of *N. virens* I found up to 5 species among 10 individuals in 1 cm<sup>3</sup> of sediment.

## DISCUSSION

What attracts Gnathostomulida to polychaete burrows? The tail shaft of *Arenicola marina* and the burrow of *Nereis virens* are both permanent structures, lined with mucus, and water is pumped in for respiration. This periodic irrigation (1) extends the aerobic zone far beyond the sediment surface, (2) transports dissolved nutrients into the bottom, and (3) flushes out metabolites from the surrounding sediment (Aller and Yingst, 1978; Yingst and Rhoads, 1980). In this way, polychaetes generate an aerobic/anaerobic interface with presumably much higher rates of transfer than is accomplished by mere molecular diffusion across the corresponding interface underneath the sediment surface. To small Metazoa the immediate vicinity of polychaete burrows constitutes a stable microenvironment, free from physical and predatory hazards as compared to the sediment surface, contains oxygen, and is a rich garden of bacteria to feed upon.

The food of Gnathostomulida is not definitely known; however, scraping off microorganisms from sand grains is the most probable way of feeding (Sterrer, 1971a). Distinct structures in the gut are rare but some bacteria, cyanobacteria and fungal hyphae have been observed (Riedl, 1969; Sterrer, 1971a; Kristensen and Nørrevang, 1977, 1978).

Analysis of fine-scale distribution in normal sediment and alongside polychaete burrows further suggests that it is the interface between aerobic and anaerobic sediments which is the key factor to gnathostomulid distribution. The interface, also called the redox potential discontinuity (RPD)-layer, is a site of high bacterial activity which mainly involves sulfide oxidation, sulfate reduction and fermentation (Jørgensen, 1977; Aller and Yingst, 1978; Kepkay and Novitsky, 1980; Yingst and Rhoads, 1980). In good agreement with this supposition is the remarkable observation of a faunal assemblage dominated by Gnathostomulida which was found beneath a white mat of sulfur bacteria close to a brine seep at 72 m depth in the Gulf of Mexico (Powell and Bright, in press).

A striking phenomenon is the narrow niche of the entire taxon of the Gnathostomulida. Alongside tail shafts of *Arenicola marina* all species show a high degree of spatial overlap, with regard to position and actual co-occurrence. Spatial niches are narrowest in the relatively primitive Haplognathiidae and broader in the advanced Gnathostomulidae. *Gnathostomula paradoxa*, a member of the latter family, occurs higher up in the sediment than the others, shows mass occurrences and is gregarious. A perfect ecological equivalent was described by Riedl (1969): *G. jenneri* Riedl 1971 from the Atlantic coast of North America.

Considering the abundance of permanent polychaete burrows in marine sediments, the Gnathostomulida probably can no longer be regarded as a rare component of the benthic fauna. In addition, other sites dominated by sulfur bacteria promise to be populated by a rich gnathostomulid fauna.

*Acknowledgements.* The hospitality of the Biologische Anstalt Helgoland, Litoralstation List is kindly acknowledged. I am indebted to P. Ax, E. Powell and two unknown advisors for improving this paper by critical comments. Thanks are due to R. von Sivers who skillfully prepared the art work.

#### LITERATURE CITED

- Aller, R. C., Yingst, J. Y. (1978). Biogeochemistry of tubedwelling: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). *J. mar. Res.* 36: 201–254
- Ax, P. (1956). Die Gnathostomulida, eine rätselhafte Wurmgruppe aus dem Meeressand. *Abh. math.-naturw. Kl. Akad. Wiss. Mainz* 8: 1–32
- Baroni Urbani, C. (1980). A statistical table for the degree of coexistence between two species. *Oecologia* 44: 287–289
- Baumfalk, Y. A. (1979). On the pumping activity of *Arenicola marina*. *Neth. J. Sea Res.* 13: 422–427
- Jørgensen, B. B. (1977). The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark). *Limnol. Oceanogr.* 22: 814–832
- Kepkay, P. E., Novitsky, J. A. (1980). Microbial control of organic carbon in marine sediments: Coupled chemoautotrophy and heterotrophy. *Mar. Biol.* 55: 261–266
- Kristensen, R., Møbjerg, Nørrevang, A. (1977). On the fine structure of *Rastrognathia macrostoma* gen. et sp. n. placed in Rastrognathiidae fam. n. (Gnathostomulida). *Zool. Scr.* 6: 27–41
- Kristensen, R., Møbjerg, Nørrevang, A. (1978). On the fine structure of *Valvognathia pogonostoma* gen. et sp. n. (Gnathostomulida, Onychognathiidae) with special reference to the jaw apparatus. *Zool. Scr.* 7: 179–186
- Lloyd, M. (1967). 'Mean crowding'. *J. Anim. Ecol.* 36: 1–30
- Müller, U., Ax, P. (1971). Gnathostomulida von der Nordseeinsel Sylt mit Beobachtungen zur Lebensweise und Entwicklung von *Gnathostomaula paradoxa* Ax. *Mikrofauna Meeresbod.* 9: 1–41
- Powell, E. N., Bright, T. J. (1981). A thiobios does exist—gnathostomulid domination of the canyon community at the East Flower Garden brine seep. *Int. Revue ges. Hydrobiol.* (in press)
- Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. *Helgoländer wiss. Meeresunters.* 31: 55–101
- Reise, K. (1979). Spatial configurations generated by motile benthic polychaetes. *Helgoländer wiss. Meeresunters.* 32: 55–72
- Reise, K., Ax, P. (1979). A meiofaunal 'thiobios' limited to the anaerobic sulfide system of marine sand does not exist. *Mar. Biol.* 54: 225–237
- Riedl, R. (1969). Gnathostomulida from America. First record of the new phylum from North America shores. *Science*, N. Y. 163: 445–452
- Rijken, M. (1979). Food and food uptake in *Arenicola marina*. *Neth. J. Sea Res.* 13: 406–421
- Sterrer, W. (1971a). On the biology of Gnathostomulida. *Vie et Milieu* 22 (Suppl.): 493–508
- Sterrer, W. (1971b). Gnathostomulida: Problems and procedures. In: Hulings, N. C. (ed.) *Proceedings of the first international conference on meiofauna. Smithsonian contributions to Zoology.* 76: 9–15
- Wohlenberg, E. (1937). Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. *Helgoländer wiss. Meeresunters.* 1: 1–92
- Yingst, J. Y., Rhoads, D. C. (1980). The role of bioturbation in the enhancement of bacterial growth rates in marine sediments. In: Tenore, K. R., Coull, B. C. (eds.) *Marine benthic dynamics.* Univ. South Carolina Press, Columbia, S. C., pp. 407–421

This paper was submitted to the editor; it was accepted for printing on August 16, 1981