

TAXONOMY AND BIOLOGY
OF *PELOSINA ARBORESCENS* WITH COMPARATIVE
NOTES ON *ASTRORHIZA LIMICOLA*
(FORAMINIFERIDA)

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ABSTRACT

The diagnosis of *Pelosina arborescens* Pearcey, 1914 is amended: only the Scottish specimens of the original description are now included in the species. Factors like water current, aquarium conditions, bioturbation and rough sampling and handling may cause a wide morphological variation which earlier caused uncertainty about the identity of the species. It was studied on the Swedish west coast, where it may reach 60 mm in length. It occurs below the halocline on bottoms with little bioturbation. It is a suspension feeder. The granuloreticulopodia are extended in the water, where they collect planktonic algae and detritus. It adapts its form according to the prevailing water current. The erect form allows it to penetrate the viscous sublayer and reach the turbulent boundary layer, where food is more plentiful. Studies of the functional biology of *P. arborescens* suggest that the shape and size of the test are adaptations that also protect against bioturbation and predation but may restrict the respiratory surface. Field observations and laboratory experiments under anoxic conditions show that *P. arborescens* can live anaerobically. Histological analysis of the protoplasm revealed large amounts of glycogen which may be used during anoxic periods. Some aspects of the biology are compared with *Astrorhiza limicola*.

INTRODUCTION

Pearcey (1914) based the description of *Pelosina arborescens* on specimens from the west coast of Scotland and from Antarctica. Lindroth (1935), Höglund (1947) and Christiansen (1958) reported *P. arborescens* from the Skagerrak. Apart from some general information (Christiansen 1971, Lipps 1983) and some observations on the spatial distribution (Gamitso et al. 1988, Levin et al. 1991), very little information exists on the biology of *P. arborescens*.

This paper describes the morphology of specimens collected at the Swedish west coast, investigates growth forms as a consequence of water flow and presents experimental evidence for anaerobic metabolism. The taxonomic relationship between the specimens collected along the Swedish coast and previously collected material is discussed.

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MATERIAL

Sediment samples were collected mainly in the Kosterfjorden (59°52.4'N; 11°6.5'E) at 10-240 m depths during 1980-1990 with epibenthic sledge, Ockelmann sledge, Van Veen grab, Haps, box corer and core sampler. Also, specimens were collected in the Gullmarsfjorden (58°17'N; 11°30'E) at 30-70 m depths and in various scattered localities in the Skagerrak. Höglund's (1947) material of *P. arborescens* was placed at my disposal for comparative morphological studies.

METHODS

Observations in aquarium

At Tjärnö Marine Biological Laboratory on the west coast of Sweden, *P. arborescens* were kept in unfiltered salt water pumped from 36 m depth in Kosterfjorden, i.e., from their natural habitat. Long-term observations were accomplished in an aquarium with a bottom surface of about 1 m² and exposed to a slow horizontal flow. Fresh bottom sediment, consisting of clay mixed with silt, together with its contents of living organisms, was collected from 80-60 m depth south of Yttre Vattenholmen in the Kosterfjorden. The studies lasted from August 1986 to September 1988. The temperature in the aquarium system was normally 10-12°C but during the last week of June 1988, it increased to 18-20°C for one to two days, and then dropped to 15°C during the following days before returning to its normal range. The salinity was 33⁰/00.

Behaviour in flowing water

In order to study the effect of water flow on the growth form, flume experiments were carried out in aquaria with a speed adjustable, unidirectional current. The areas of the aquaria were 50 × 80 cm and the water depths 2-10 cm. The water was introduced through a pipe with 40 small holes, placed in a depression in the sediment along the shorter end of the aquarium. A movable stereomicroscope was mounted above the aquaria allowing for observations of the entire surface of the sediment. The foraminiferans were also observed through the glass walls of the aquaria with a similar stereomicroscope, mounted horizontally.

Survival in anoxic environment

Effects of anaerobic conditions were studied during ten days with specimens adapted to 3°C and 12°C, respectively. The aquarium was covered by plastic foil to prevent oxygenation of the water. Dissolved oxygen was driven out by gaseous nitrogen through a wash bottle with alkaline pyrogallol. Detectable oxygen disappeared after about ten hours. The absence of oxygen was tested with an oxygen electrode.

Histological examination

Unstained slides with the entire protoplasm and sections of whole *P. arborescens* were studied with an interference contrast microscope (Leitz Orthoplan). Seven μm cross sections were stained with Ehrlich's hematoxylin-eosin or carmalum (Romeis 1968) and studied under a compound microscope. The occurrence of glycogen in the protoplasm was investigated with Best's carmine (Romeis 1968). A 20 mm long specimen was cut into 7 μm paraffin sections, mounted on 32 glass slides. Every fifth slide was treated with salivary amylase to remove glycogen. *Astrorhiza limicola* Sandahl, 1857 was studied in the same way. Pseudopodia were studied in a tubular plankton chamber, 10 mm high, with an inverted microscope.

RESULTS AND DISCUSSION

Taxonomy

Pearcey (1914) based the description of *Pelosina arborescens* on specimens from Scotland. He also figured some specimens of a slightly different shape from Antarctica. Unfortunately, Pearcey's type specimens held at the Royal Scottish Museum in Edinburgh are lost (Earland 1936, Smaldon et al. 1976). Höglund (1947) was uncertain about the identity of the Swedish specimens but wrote that Heron-Allen ('in litt.') said that he was sure that they were identical with Pearcey's species. Christiansen (1958) stated that specimens from the Oslofjord were identical with Höglund's (1947) material and referred to Höglund's uncertainty regarding the identity but presented no other opinion. Höglund pointed out some morphological characters which he did not find in the Swedish specimens. He stated: "The swelling at the base of the branches mentioned by Pearcey, does not occur in the Swedish specimens" and: "The transverse section in his [Pearcey's] figure shows a very wide chamber cavity, which does not agree with my specimens either." Furthermore, Höglund states: "I have never seen any specimens at all entirely coinciding with Pearcey's figures."

The growth form described by Pearcey was occasionally found in my Swedish

material. The complete specimen on which Pearcey based his description, was sampled with "trawl" and kept in an aquarium for five months. The specimen might have grown and regenerated wounded parts during this time. Its pseudopodia are very much extended in the water, without holding any detritus (his pl. I, fig. 1). I have never observed this behaviour and I interpret it as a reaction caused by inappropriate or insufficient food. I have seen specimens develop to a shape resembling Pearcey's entire specimen if they are kept in an aquarium without sediment. Pearcey (1914) described cross sections of two different specimens. One of them (his pl. I, figs. 4-5) has a considerably wider "chamber cavity" than any specimen found by me in Sweden. This specimen originates from the Weddell Sea (2620 fathoms) and I regard it as an undescribed species not identical with *P. arborescens* sensu Pearcey (1914: pl. I, figs. 1-3) (see below). However, the other cross section, which originates from a Scottish specimen, is not disproportionately wide when compared with the diameter of the narrowest part of the 'neck' of the largest specimens in my material. Regarding the variation in my Swedish material and the morphological adaptability of the species, I am of the opinion that the differences between this and Pearcey's material are so small that it does not motivate any taxonomic separation.

I assume Pearcey's material to represent two separate species. Therefore, I base the definition of *Pelosina arborescens* on Pearcey's figured specimen (pl. I, figs. 1-3) from Scotland, and exclude his specimen collected off Antarctica (pl. I, figs. 4-5) from *P. arborescens*.

Morphology

The general morphology of *P. arborescens* usually corresponds to the descriptions by Pearcey (1914) and Höglund (1947). Both stated that the open ends of the branches observed were apertures. I consider these holes to be artifacts, because the tips of the branches usually break off during handling. The outer ends of the branches gradually pass into the lumps of detritus kept by the pseudopodia around the upper part of the test. The morphology of *P. arborescens* will also be affected by water flow and bioturbation as described below.

The lower part of the test, which is buried in the sediment, it expanded to a lump which may exceed 10 mm diameter (see Fig. 5) in the largest specimens (40-60 mm long). The protoplasm occupies the central part of the test as a thin string-like structure (see Höglund 1947: pl. 6, fig. 4). Only the test wall is thickened, not the central protoplasm, but branches projecting from the string penetrate the test wall. No pseudopodia or protoplasmic protuberances were observed outside the test wall in living specimens, except those described below, which extended from the upper part of the test. The central protoplasmic string, dissected out from formalin fixed specimens, contained a single, centrally located, spherical to oval nucleus with a diameter of 600-800 μm .

The granuloreticulopodia in *P. arborescens* and *Pelosina variabilis sphaeriloculum* Höglund, 1947, projected through the tips and sides of the smallest branches in the uppermost part of the test and resembled those in *A. limicola* (cf. Cedhagen 1988, fig. 4). The density of the granules was slightly lower and the pseudopodial movements slightly slower in *Pelosina* spp. than in *A. limicola* at the same temperature.

Rough sampling and handling may cause morphological abnormalities in *P. arborescens*. Occasionally, specimens got caught between coarse particles like stones, shells etc., when bottom samples were sieved and left for some days. Within a few days *P. arborescens* adapted to these conditions by changing their tests into a distorted and abnormal shape.

Habitat and position in the sediment

Pelosina arborescens occur on the Swedish west coast, usually below 25 m depth. Lindroth (1935) found the species in the inner part of the Gullmarsfjorden at 18 m depths.

The species occurs on: (1) Soft bottoms which sometimes may be anaerobic (first observed by Mr. Stefan Persson, pers. comm.). (2) Rocky bottoms where they occur in crevices filled with soft sediment. (3) Soft bottoms with numerous tubicolous polychaetes, particularly Terebellida and Sabellida. (4) Clay bottoms with a high content of sand or silt, and a sparse burrowing macrofauna. (5) Soft bottoms with numerous coral fragments (*Lophelia pertusa* (Linnaeus, 1758)). The last two types are affected by fairly strong currents. The population densities of *P. arborescens* may be very high, with several thousand specimens per m², particularly on soft bottoms with much silt or sand. One common factor, characterizing the bottoms where *P. arborescens* occurs in larger numbers, is the low degree of bioturbation. Interestingly, *P. arborescens* in a few cases were found together with high densities of the brittle-star *Amphiura filiformis* (O. F. Müller, 1776), which causes heavy bioturbation (see below). A possible explanation of this could be that the occurrence of large amounts of shells and other mechanical obstructions in the sediment, locally restrain bioturbation.

Pelosina arborescens lives partly buried in the sediment (Fig. 1) with $\frac{1}{2}$ to $\frac{3}{4}$ of the test above the surface. Long, thin and flexible branches or 'roots' (sediment-covered protoplasmic strings) project from the lower part (Fig. 2). When a specimen is carefully loosened from the bottom a great deal of sediment adheres to the lower part (Fig. 2). Uprooted specimens of *P. arborescens* placed on the sediment surface raised and oriented themselves into their natural position within 2-14 days. This behaviour took place at a slower rate at lower temperatures (3-5°C). Erect *P. arborescens* in aquaria showed no signs of movements and remained in the same position for almost two years.

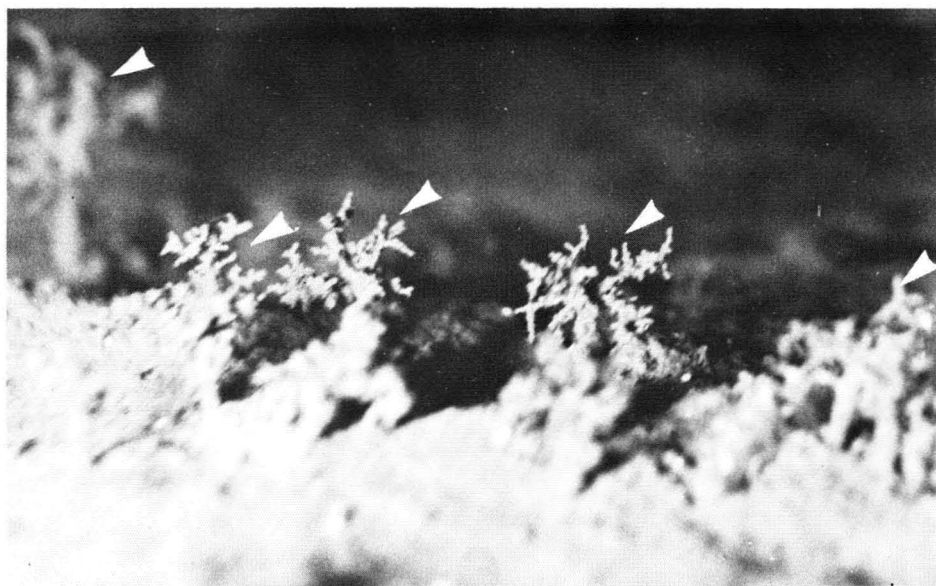
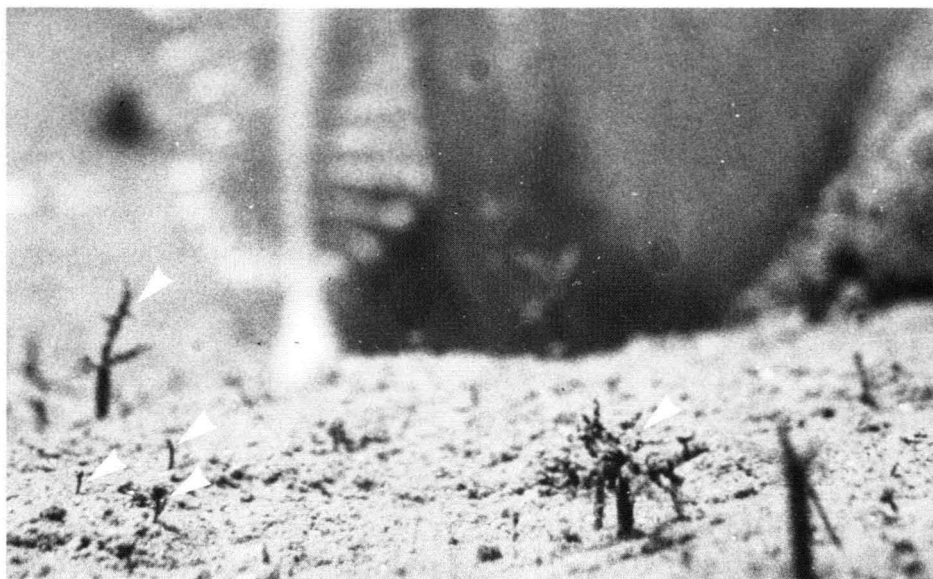


Fig. 1. *Pelosina arborescens* sitting in natural position in the aquarium used for long-time observations. The photograph was taken in winter when only a little detritus was attached to the foraminiferan.

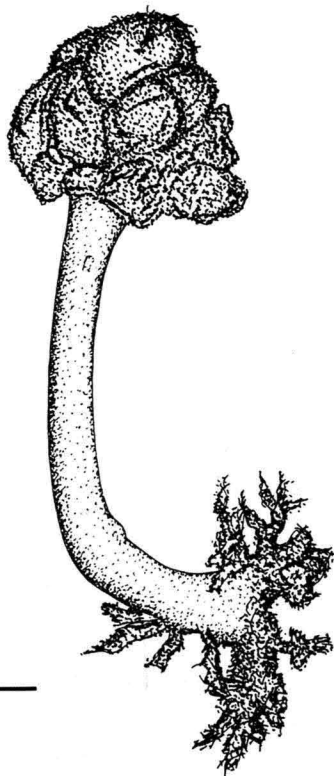


Fig. 2. Sediment accumulated to a specimen of *Pelosina arborescens* which has not been taken out of the water. Scale bar = 2 mm.

Gamitso et al. (1988) kept large amounts of natural sediment in their aquaria ('mesocosms') and observed *P. arborescens* for about one year. After a statistical analysis they concluded that their distribution in the aquarium was patchy, and presented the hypothesis that reproduction by division could explain this. The time span of the study by Gamitso et al. was shorter than my study during which specimens had grown slowly and had been stationary. Therefore I believe that division is rare and even if it occurs (see below), it is of little or no importance as an explanation of patchy distribution.

Feeding and food

The pseudopodia, extending from the branches, capture planktonic algae and detritus in the water. The adhering material accumulates into large lumps (Fig. 2) which fall apart as a result of the surface tension of the water when a specimen is picked. This explains why this structure has been overlooked in previous works. Many of the accumulated algae were ingested and could be observed in thousands within the protoplasm. The algal species composition in the ingested food was generally the same as that in the pelagial as in the case of *A. limicola* (Cedhagen

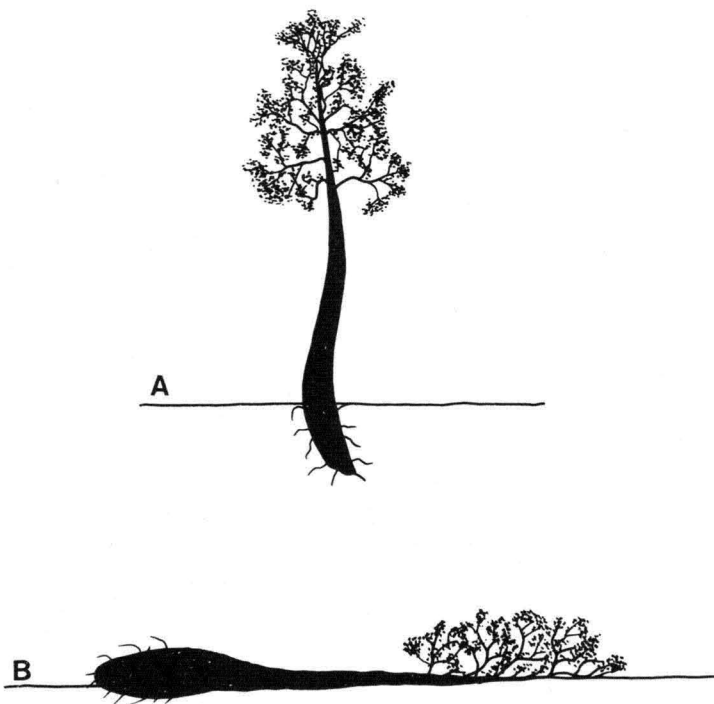


Fig. 3. Two drawings of the same *Pelosina arborescens* specimen in an aquarium with stagnant water (A) and with strong water current (B).

1988). On some occasions *P. arborescens* was collected during massive blooms of dinoflagellates, and the protoplasm of some of these specimens contained thousands of, e.g., *Prorocentrum minimum* (Pavillard, 1916), an alga which in large concentrations is toxic to many marine organisms. Other *P. arborescens* from the same sample were kept in an aquarium and the algae seemed not to have affected them negatively.

Pelosina arborescens, *A. limicola* and various other suspension-feeding foraminifera observed both in aquarium and in nature, do not collect any food during the coldest part of the winter, i.e., before the spring bloom, when the protoplasm is free from foreign particles (see also Cedhagen 1988 and 1991). The same condition is found in *Nonionellina labradorica* Dawson, 1860 collected on the same sea bottom (see Cedhagen 1991). The feeding activity (accumulation of detritus) started again in the middle or end of March. However, *P. arborescens* and *A. limicola* remained in their normal position in aquaria during this time.

Influence of water flow on the morphology

Specimens sampled in different seasons were kept in aquaria subjected to the fol-

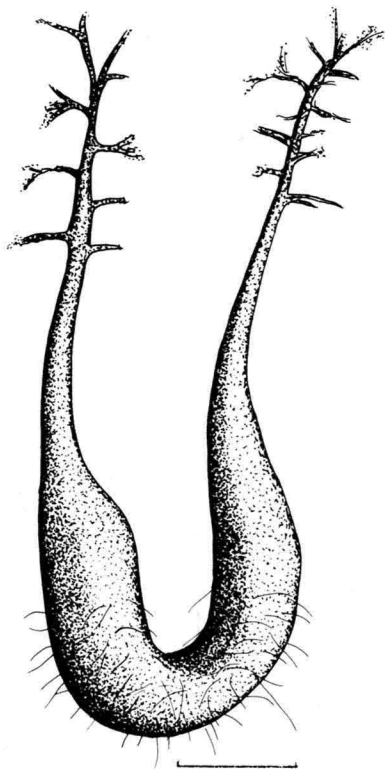


Fig. 4. A specimen of *Pelosina arborescens* with two fore-ends, probably caused by bioturbation or trawling. Scale bar = 5 mm.

lowing water flow conditions: (1) stagnant to near stagnant, (2) weak current and (3) strong current (c. 5-10 cm/s). Within a few days to a couple of weeks (depending on the temperature) the specimens in stagnant water assumed their erect natural position, extending 2-4 cm above the sediment surface (Fig. 3). Specimens exposed to strong currents remained flat on the bottom and collected detritus around the branches in this position (Fig. 3). Intermediary reactions were observed in the specimens in weak current.

One of the most important factors determining the amount of food available to a suspension feeder is the volume of water that can be filtered per unit time. The hydrodynamic conditions within the benthic boundary-layer are therefore important. These factors are described theoretically by Vogel (1981) and Wimbush & Munk (1970) and are summarized in Fig. 8. When a bottom surface is exposed to water flow, a laminar viscous sublayer develops close to the bottom (Fig. 8, A). Its thickness, on marine bottoms is some mm and rarely exceeds 1 cm. The turbulent boundary-layer (Fig. 8, B) develops above the viscous sublayer. Its velocity increases logarithmically with increasing distance from the bottom. The water volume that can be filtered passively, and consequently the available food, increases enormously in this layer. Thus, it is an advantage for a suspension feeder



Fig. 5. An adult specimen of *P. arborescens* during division, collected by H. Höglund at Smörkullen (Gullmarsfjorden), on July 23, 1926. Scale bar = 5 mm.

to grow sufficiently tall to reach the turbulent boundary-layer thereby allowing it to filter a volume 10-100 times larger than in the viscous sublayer.

The flume experiments indicate that there may be an advantage for erect growth forms due to the vertical flux of food close to the bottom. Another possible example is provided by the closely related *Pelosina variabilis sphaeriloculum*, which in its earliest stage develops only a pseudopodial network penetrating the sediment. When it reaches a length of some mm and enters the turbulent boundary-layer, it starts developing pseudopodia directed upwards. Several hundred specimens of *P. v. sphaeriloculum* were collected from a silty clay bottom at a depth of 35 m in the Kosterfjorden on November 6, 1984 and were adapted to the same hydrodynamic conditions as *P. arborescens*. Two of the specimens are shown in Fig. 6. Their orientation in the sediment is principally the same as that of *P. arborescens*. One specimen developed pseudopodia at both ends growing upwards and downwards respectively. The other specimen developed its pseudopodial network only from the lower end. Intermediary test forms were found in specimens of the same size. All smaller specimens were without pseudopodia or branches directed upwards but these structures developed with increasing size. This shows that *P. v. sphaeriloculum* first feeds on bottom material and grows to a certain size before it de-

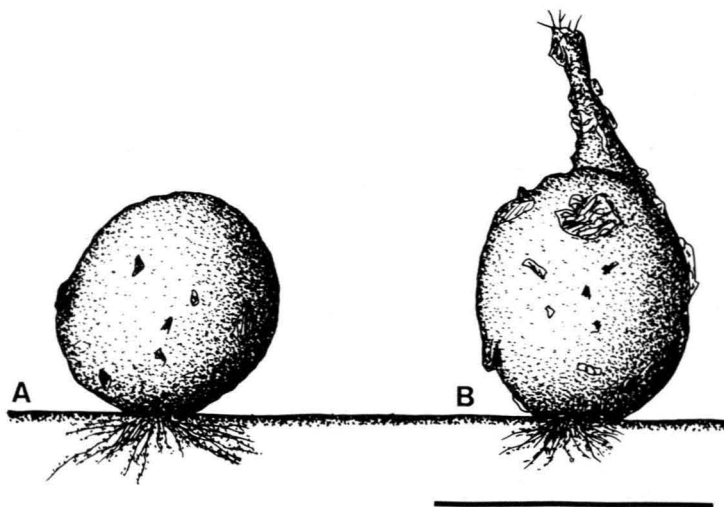


Fig. 6. *Pelosina variabilis spheriloculum*. Specimens up to this size were without an upper branch with pseudopodia (A) and most specimens above this size had such branches with pseudopodia (B). Intermediary forms were found among specimens of this size. Scale bar = 1 mm.

velops the upper branches and pseudopodia for suspension-feeding. The same end structure is found in many other large suspension-feeding foraminiferans with a vertical position on the sediment surface, e.g., *Bathysiphon* spp. (Nyholm 1957, Christiansen 1971, Menzies et al. 1973, Gooday 1983), *Marsipella arenaria* (Christiansen 1958), *Notodendrodes antarctikos* ((Delaca et al. 1980), *Haliphysema tumanowiczii* (Hedley 1958, Hedley & Wakefield 1967), *Dendrophrya erecta* (Christiansen 1958, Cedhagen unpubl.), *Jaculella obtusa* (Christiansen 1958), *Saccodendron heronalleni* (Höglund 1947), *Rupertina stabilis* (Lutze & Altenbach 1988), *Astrorhiza limicola* (Cedhagen 1988), *Astrorhiza arenaria* (Tendal & Thomsen 1988), and *Saccorhiza ramosa* (Altenbach et al. 1988), see Lipps (1983) for further references. Other suspension-feeding foraminiferans of small size often occur on elevated microhabitats which probably increase exposure to turbulent flow, (e.g., *Cibicidoides wuellerstorfi* and *Planulina ariminensis* (Lutze & Thiel 1989) as well as *Cibicides lobatulus* (Walker & Jacob, 1798) (Nyholm 1961), *C. refulgens* Montfort, 1808 and *Paromalina coronata* (Parker & Jones, 1857) (Cedhagen unpubl.). Erect growth form and elevated positions are also characteristic of many metazoan suspension feeders, and indicate a general selection for exposure to turbulent flow, (e.g., Sabellidae (Fauchald & Jumars 1979)) and amphipods (e.g., *Haploops tubicola* (Thorson et al. 1979) and *Dyopedos* spp. (Mettson & Cedhagen 1989)).

An increase in length coupled with an increased exposure to fast, turbulent flow, increases the risk of breakage or tilting. This risk is counteracted as the lower part of the test, which is burrowed in the sediment, usually expands into a large swelling, with many 'roots' in large specimens.

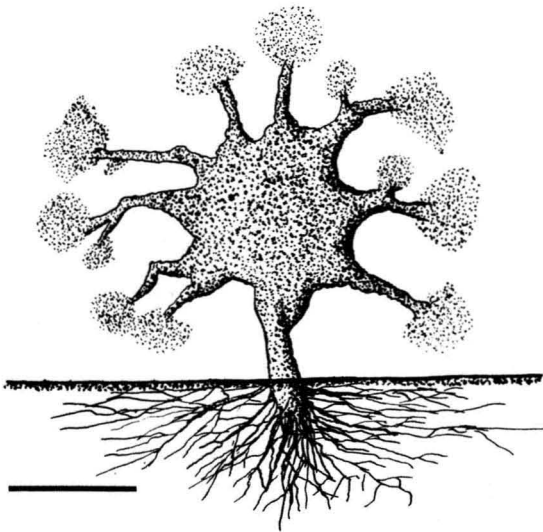


Fig. 7. *Astrorhiza limicola* sitting vertically in the sediment on one single arm in almost stagnant water. Scale bar = 2 mm.

Cedhagen (1988) described how *A. limicola* orient the test in an erect position perpendicular to the water flow direction. In the present study, I observed that when *A. limicola* was exposed to very slow current velocity for a longer period (1 month-1 year) the entire test often projected above the bottom surface. In these cases it was anchored by a single branch directed straight downwards (Fig. 7). This branch was more strongly built than others, and the pseudopodial network was very well-developed and attached to large amounts of coarser material and detritus. Specimens with the same general morphology were often found in samples from nature. The phenomenon has not been described earlier in literature but is illustrated by Höglund (1947: pl. 30, figs. 4-6 and 7) and by Cedhagen & Tendal (1989: fig. 1, Nr. G, N and O).

Astrorhiza limicola usually lives on sand and gravel in higher current velocities than *P. arborescens*. A viscous sublayer probably does not always develop on these rougher bottoms and, *A. limicola* therefore can filter effectively close to the bottom, a behaviour also observed for specimens of *P. arborescens* kept in strong water currents. However, when *A. limicola* occurs on soft bottoms exposed to slow currents, it positions its test in a more vertical position. In extreme cases (stagnant water) it is anchored by a single branch, apparently to raise itself to its maximum extent above the bottom (Fig. 7).

Epizoans

Normally, *P. arborescens* is without epizoans but on its "neck" one adult specimen of *Pyrgo williamsoni* (Silvestri, 1923) (Foraminifera: Miliolidae) was found within a secondary test made of detritus. Also suctoria (Protozoa: Ciliophora) occasionally occur in a similar position.

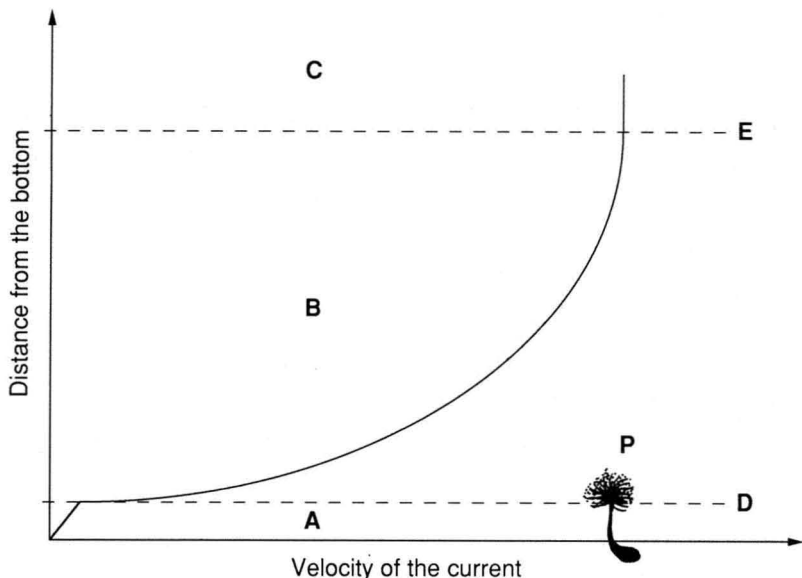


Fig. 8. The current regimes above the sea bottom, A = viscous sublayer, B = turbulent boundary layer; C = the free current. D, E = theoretical boundaries between flow regimes. *Pelosina arborescens* (P) is adapted to penetrate the viscous sublayer in order to reach the turbulent boundary layer.

Reproduction and longevity

Reproduction by division was not observed, but a few specimens out of several thousands had two parallel "necks", which projected from the common basal part (Fig. 5). This may result from damage by trawling and macrofauna, or as a result of somatic division.

Within 3-4 weeks (Sept. 1986) of the introduction of the sediment, two size classes of *P. arborescens* covered the entire bottom of the aquarium. The large specimens extended 10-20 mm above the sediment surface. Presumably they were adults surviving the transport into the aquarium. Thousands of juveniles had probably just settled and were 2-4 mm in length when first observed. I could follow their growth during almost two years until the sudden temperature rise killed them at the end of June, 1988. Although recruitment stock was presumed absent from the aquarium, I observed a few scattered newly settled specimens of *P. arborescens* during the first days of September, 1988. Possibly a few reproductive specimens survived in the afferent water pipe, which was not affected by the increased temperature. Consequently, *P. arborescens* may live for at least two years.

Temperature tolerance

Pelosina arborescens has a lower tolerance to high temperatures than *A. limicola*. *Pelo-*

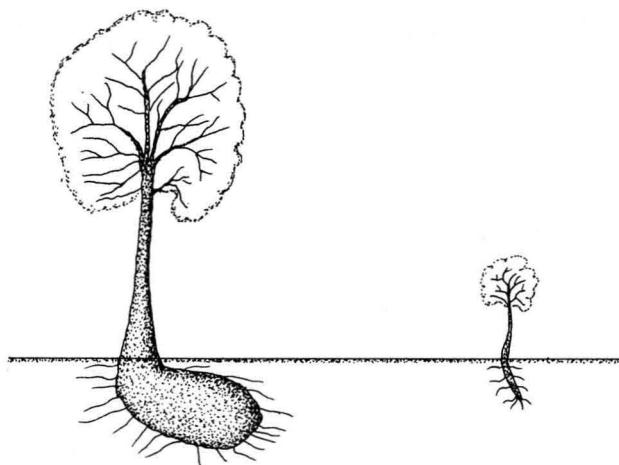


Fig. 9. Comparison between a large and a small specimen of *P. arborescens*. The enlarged basal part of the large specimen improves the holding in the sediment.

sina arborescens died but *A. limicola* survived during the before-mentioned temperature increase. Simultaneously, some 50-100 adults of each species survived in an aquarium with a low turnover of the same water in a constant temperature room (app. 12°C). Other specimens of *P. arborescens* and *A. limicola* were kept in an aquarium where the temperature was allowed to increase slowly to 23°C. The water was saturated with oxygen. *Astrorhiza limicola* tended to escape from the test on the first day and then showed no signs of life, but *P. arborescens* died without showing similar tendencies.

The main gaseous exchange between a foraminiferan and its environment probably takes place through the highly branched pseudopodia, containing large numbers of granules (= mitochondria). Therefore, the test may under certain conditions restrict respiration. Consequently, the sarcode of *A. limicola* may increase its surface area by leaving the test and survive as a naked amoeba at relatively high temperatures and low oxygen levels (Cedhagen & Tendal 1989). Specimens that had begun to leave their tests usually retracted their protoplasm if they were put in a refrigerator or if cold sea water was added. *Milliammina fusca* (Brady, 1870) and *Quinqueloculina seminulum* (Linnaeus, 1758) (Cedhagen unpubl.) can under similar circumstances partly leave their tests and retract the protoplasm. These species show high population densities on shallow bottoms (less than 25 m depths) where oxygen deficiency or an increased metabolic activity caused by high temperature may occur. The ability to leave the test to increase the respiratory surface may be interpreted as a survival adaptation. In contrast, I have never seen the sarcode of *P. arborescens* leave the test. It dies at high temperatures regardless of the rate of increase. One reason for not being able to leave the test may be that the protoplasm is more integrated with the test wall than it is in e.g., *A. limicola*.

Pelosina arborescens lives, in its natural state, below the thermocline where the

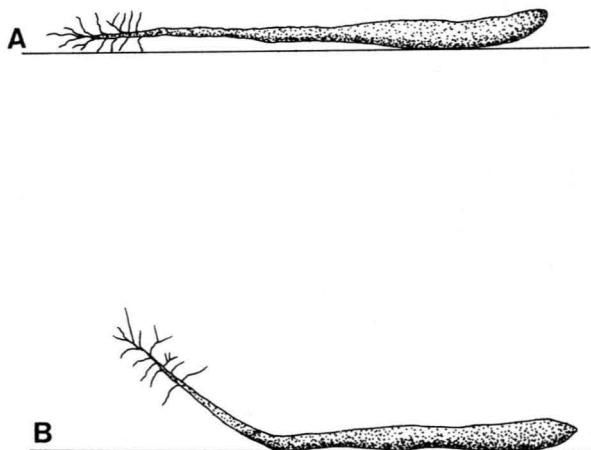


Fig. 10. *Pelosina arborescens*. Change of position during anaerobiosis, A = initial position, B = position after 4 days.

metabolic rate is probably low. Therefore, I regard the temperature as an important factor that restricts the upper bathymetric distribution of *P. arborescens* along the Swedish coast.

Anaerobiosis

The occurrence of *P. arborescens* on anoxic bottoms motivated me to study its ability to survive under such conditions. Five adults each of *P. arborescens* and *A. limicola* were kept under anoxic conditions at different temperatures. These experiments were repeated with a new set of foraminiferans.

After 4 days at 3°C, all *P. arborescens* had responded by bending one third of the fore-end of the test upwards at an angle of about 30° to the bottom (Fig. 10). This position was maintained during the rest of the 10-day experiment. During the same time, *A. limicola* showed no visible activity apart from extending a few pseudopodia along the bottom of the aquarium. The experiment under anoxic conditions was terminated by removing all specimens to an aquarium with well oxygenated water, at 12°C. Within 2-7 days all specimens resumed their normal, vertical position and began to collect detritus. The same experiment was carried out at 12°C. Here, *P. arborescens* showed the same reactions as it did at 3°C, but *A. limicola* showed a tendency to leave its test.

Histological investigations with Best's carmine showed that *P. arborescens* has relatively large amounts of glycogen, particularly in the protoplasm which penetrates the test wall. Slides treated with salivary amylase before staining with Best's carmine remained unaffected. Glycogen could not be found in *A. limicola*.

The anaerobiosis in *P. arborescens* and *A. limicola* is facultative and is possibly an adaptation to the seasonal variations in their environments where conditions of oxygen deficiency may prevail. Large amounts of organic material sediment e.g., during the spring- and autumn-blooms of planktonic algae. This could locally

cause oxygen deficiency. Facultative anaerobiosis would permit survival under these conditions.

The experiments mentioned above, and the distribution of the species in nature show that *P. arborescens* is adapted to survive extremely low concentrations of oxygen, but at low temperatures. Anaerobic metabolism produces less energy than aerobic metabolism and the metabolic rate is slower in larger organisms than it is in small (Krogh 1941). These conditions, the unfavourable surface-volume ratio of the protoplasm, and the long and slow intracellular transportation distances, makes *P. arborescens* less capable to survive in high temperatures at low oxygen levels.

In many organisms a key factor in surviving under anoxic conditions, is the ability to store glycogen for the anaerobic metabolism (the glycolysis) (Hochachka 1980). *Pelosina arborescens* is probably adapted to anaerobiosis as it shows normal reactions under anoxic conditions and also accumulates large amounts of glycogen. In *A. limicola* the ability to survive anaerobically, at least for longer periods of time, is less developed. Anaerobiosis may be a common phenomenon among foraminiferans. It probably occurs also in *Bulimina fusiformis* Williamson, 1858, and in *Eggerella scabra* (Williamson, 1858) since they sometimes occur in stagnant water which may even contain H₂S. Anaerobic metabolism was well-developed already in early geological periods since the presence of oxygen was a later event in the history of life (Berkner & Marshall 1965, Schopf 1978). Fossil communities from anaerobic and dysaerobic environments in Phanerozoic time are also well documented (Rhoads & Morse 1971, Schopf 1978). Bernhard (1986) and Tosk & Andersson (1988) described fossil and Bernhard (1989, 1992) recent communities of foraminiferans from anoxic environments. Today, anaerobiosis occurs in many higher organisms (Hochachka 1980, Tunnicliffe 1981) and microorganisms including Protozoa (Fenchel 1969, Sieburth 1979, Farmer 1980).

Influence of bioturbation

Most of the numerous *P. arborescens* specimens used for long-time studies in the aquarium were gradually destroyed by the introduced epibenthic macrofauna (the holothurians *Mesothuria intestinalis* (Ascanius, 1805) and *Parastichopus tremulus* (Gunnerus, 1767) and the decapods *Galathea strigosa* (Linnaeus, 1761) and *Munida* spp.). Some 40 specimens survived and grew to a size which apparently was sufficient to resist macrofaunal activity. In a few cases I observed how *M. intestinalis*, when encountering a small cluster of *P. arborescens*, changed direction, as though it was inconvenient to move across the adult foraminiferans. Since some clusters consisted of different size classes this demonstrates how adult foraminiferans can function as a mechanical protection for newly settled specimens. All *P. arborescens* specimens in this aquarium died as a result of the temperature rise in June 1988.

A few newly settled specimens observed later that summer were gradually destroyed by the movements of the macrofauna in 1-2 months.

Very few large foraminifera are found on homogeneous bottoms where the brittle-star *Amphiura filiformis* is common. Three of five Van Veen grab samples from a bottom at 15 m depth in the harbour of Strömstad on the Swedish west coast contained a clayey sediment with several hundred *A. filiformis*, but few or no *Astrorhiza limicola*. The remaining two samples contained a clay sediment with much sand and large numbers of *A. limicola* but only a few small *A. filiformis*. I found that this inverse relationship between *A. limicola* or *P. arborescens* and *A. filiformis*, is typical in the Skagerrak and the Gullmarsfjorden.

In aquaria *A. filiformis* caused a powerful bioturbation deep in the sediment as well as on the surface. I observed the effect of this bioturbation when all *A. filiformis* were picked out from acclimatized box core samples kept in an aquarium. The thickness of the oxic layer decreased from between 3 and 5 cm to about 5 mm within a few days. This bioturbation was particularly intense when the amount of sedimented nutrients increased on the sediment surface. In nature, this may occur after the spring and autumn phytoplankton blooms. An adult *P. arborescens* may resist this bioturbation, but the juveniles, which settle in the late summer before the autumn bloom, may not survive.

My hypothesis is that the foraminiferans can not survive intense bioturbation and consequently are restricted to bottoms unsuitable for the brittle-stars. The bottoms where suspension feeders like *P. arborescens* and *A. limicola* live are very often silty or sandy because of the water movements and are therefore very compact. This obstructs digging, and may restrict the occurrence of *A. filiformis*.

Scattered adult specimens of *P. arborescens* were occasionally sampled on trawled soft bottoms in the Skagerrak. The proportion of irregular or abnormal specimens was found to be higher here, than on untrawled locations or areas with less bioturbation. A special growth form encountered on these sea bottoms is represented by specimens having two upper parts, with pseudopodia directed upwards (Fig. 4).

Several *P. arborescens* adults were positioned upside-down in an aquarium in order to find out if this mode of growth might be caused by trawling or bioturbation. If only the tip of the upper part was buried in the sediment, the foraminiferans turned over and regained their natural position. However, they remained in the upside-down position if more than half of the test was buried. New branches of pseudopodia developed growing upwards from the lower part (previously buried in the sediment). This shows that they are able to reverse the polarity of their tests, and probably also the polarity of the sarcodae, as this is firmly integrated with the test wall. When such specimens were placed on the sediment surface, both ends usually turned upwards and simultaneously functioned as upper ends. The curved middle part of the test in these cases functioned as the lower end.

Protection against predation

Pelosina arborescens has a low nutritional content per unit volume because of the large amount of detritus and inorganic material in the test wall (see Höglund 1947: pl. 6, fig. 4). Levin et al. (1991) showed that the protoplasm comprises < 2% of the test volume in *P. cf. arborescens* from the deep-sea off California. Consequently, *P. arborescens* should be less attractive to predators. Mattson (1991 and pers. comm.) investigated the stomach contents of 2579 specimens of 22 fish species, which were trawled in the Gullmarfjorden, where *P. arborescens* is common. *Pelosina arborescens* was not found in any of the stomachs. This species was not overlooked because all clay structures and tubes in the fish stomachs were opened and the investigator was well acquainted with the appearance of *P. arborescens* (Mattson, pers. comm.). The absence of predation and the parallel to *Dyopedos* (see below) show that the food value of *P. arborescens* is too low to be of interest for fishes, a result that may also apply to other potential larger predators.

Most fish species are very attentive to the nutritional quality of the food and avoid objects with low or no nutritional content (Mattson 1991 and pers. comm.). Mattson & Cedhagen (1989) found that the amphipod *Dyopedos* probably defends itself against attacking fish by clinging firmly to a self-made clay structure, to be less attractive as a prey. The clay structure which the fish would have to swallow together with the amphipod is completely devoid of nutritional contents. Consequently, the entire mouthful would offer a low nutritive value.

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