

A tubular protozoan predator: A burrow selectively filled with tubular agglutinated protozoans (Xenophyophorea, Foraminifera) in the abyssal South China Sea

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ABSTRACT

We report the occurrence of an unusual agglutinated protozoan-filled burrow recovered in a box core collected in 1998 from a depth of 2496 m in the South China Sea. The onion-shaped burrow occurring some 8 cm beneath the sediment surface was packed full with specimens of xenophyophoreans and foraminifera dominated by a single genus (*Aschemonella*) that had been living on the surface of the 1991 Mt. Pinatubo ash layer. This selective scavenging of epibenthic tubular agglutinated protozoans contributes to the patchiness of the benthic fauna on the sea floor. Because the tubular protozoans selectively agglutinate mafic mineral grains from the volcanic ash, two levels of biological scavenging are involved with the redistribution of these volcanic grains.

INTRODUCTION

The observation that benthic macrofaunal invertebrates prey upon benthic foraminifera is long established (Lipps & Valentine, 1970; Sliter, 1971). In the deep sea, benthic foraminiferans and other protozoans make up a significant proportion of the biomass, and serve as prey items for numerous macrofaunal organisms (Sokolova, 1997). Already in the last century the gut contents of holothurians collected during the HMS Challenger Expedition were found to contain large numbers of benthic foraminifera. More recently, Svavarsson *et al.* (1993) found benthic foraminifera in the gut contents of two species of isopod crustaceans (*Ilyarachna hirticeps* and *Eurycope inermis*) in the Norwegian Sea, Langer *et al.* (1995) found selective predation of foraminifera by the deep-sea scaphopod *Fissidentalium megathyris* off California, and Sokolova *et al.* (1995) found agglutinated foraminifera in the gut contents of four species of abyssal ophiurids collected from the Orkney Trench of the Southern Ocean. According to Sokolova (1997), agglutinated protozoans belonging to the group of xenophyophoreans and komokiacean foraminifera may constitute up to 40% of the gut contents in some abyssal macrobenthos. There is no doubt that deep-sea benthic foraminifera constitute a key link in the metazoan food chain.

A number of deep sea deposit feeders are known to non-selectively collect surface sediment and transfer this material to their burrows. For example Kotake (1991) reported the occurrence of a volcanic ash-filled *Zoophycos* burrow beneath a fossil ash layer in the Pliocene Shiramazu Formation of Japan. There is also evidence that abyssal sipunculid worms gather recently arrived phytoplankton detritus and sequester this organic-rich material at depth in their burrows (Jumars *et al.*, 1990), thereby creating a cache of food that can be utilised later.

However, the selective caching behaviour of benthic macrofauna is not commonly observed. A burrow

with concentrations of fish scales has been reported by Bromley (1996), but to our knowledge there have been no reports of burrows filled with tubular agglutinated protozoans in either the foraminiferal or trace-fossil literature. The purpose of this paper is to report the occurrence of an unusual onion-shaped burrow that provides evidence of selective predation upon tubular agglutinated protozoans belonging to the xenophyophorean genus *Aschemonella* and the foraminiferal genus *Rhabdammina*.

Study area

The studied cores were collected from the South China Sea during Cruises 132 & 140 of the R/V Sonne as part of a long-term investigation to study the particle flux and benthic ecology of the South China Sea (Wiesner *et al.*, 1998; Hess *et al.*, 2001). The area off the Philippine Island of Luzon is being periodically sampled as part of an ongoing program to study the recolonisation of the sea floor by benthic foraminifera following the 1991 Mt. Pinatubo volcanic eruption. The deposition of the ash from Mt Pinatubo volcano was a single, short-term event (Wiesner *et al.*, 1995) that took place on June 15-16th, 1991. The ash settled to the sea floor at sinking speeds in excess of 1670 m per day (M. Wiesner, personal communication, 1999), resulting in complete mass mortality of the benthic foraminiferal fauna in areas where the ash is several centimetres thick (Hess & Kuhnt, 1996).

The box core studied in detail here (R/V Sonne Cruise 132, Station 39) was collected from a depth of 2496 m at 14°18.713'N, 119°25.523'E in the South China Sea (Fig. 1). At this station the 1991 tephra layer is 2-3 cm thick and is comprised of fine grained andesitic ash (Plate 1). In general, the tephra layer is visibly graded, and larger mafic mineral grains are concentrated at the base of the layer. The tephra layer is underlain by 8-10 cm of soft, highly bioturbated dark yellowish brown clay with dusky yellowish brown manganese streaks that probably reflect the

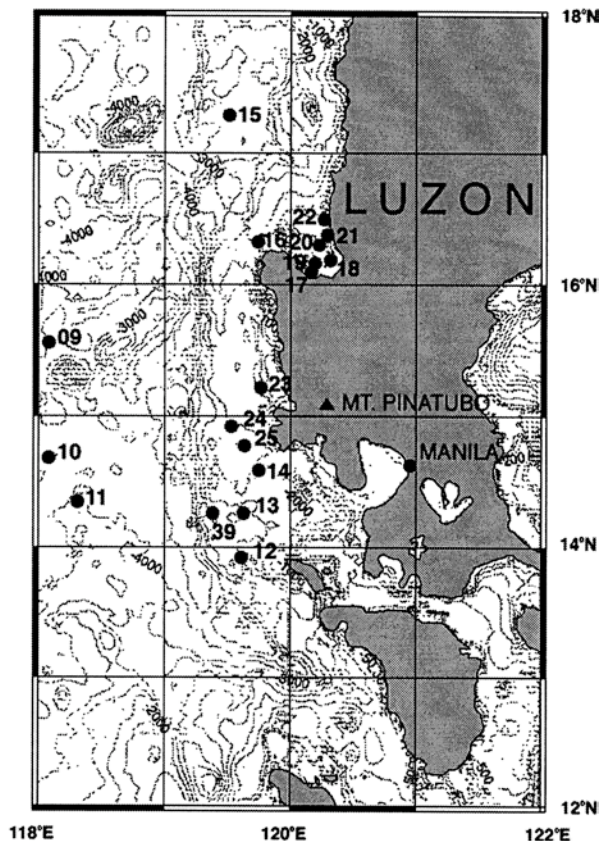


Figure 1. Location of the studied SO-132 boxcore stations off Luzon Island, South China Sea.

position of the pre-1991 redox boundary. The surface of the box core was undisturbed by coring, and displayed several mounds with open burrows, clusters of xenophyophoreans, and a small amount of brown fluff on top of the light grey volcanic ash (Plate 1). Shipboard visual examination of the core surface and subsequent scrutiny of the core photographs failed to reveal any obvious tubular agglutinated protozoans on the surface of the ash.

The burrow

The burrow was onion shaped, with an inclined entrance tube (0.5 cm diameter) that was open to the sea floor. The burrow was constructed in abyssal brown clay beneath the 1991 Mt. Pinatubo ash layer, which was 3.0–3.2 cm thick at this locality (Wiesner *et al.*, 1998). In the recovered box core, the burrow was exposed in a split subcore (Plate 2), and consequently we have no information about the three-dimensional geometry of the burrow in the missing part of the core. Because of this, we cannot be completely certain of the taxonomic affinity of the ichnofossil. The recovered part of the burrow is similar in overall morphology and dimensions to the burrows and feeding cavities created by maldivid polychaetes ("bamboo worms") found by Levin *et al.* (1997) on the Carolina slope. However, the lack of an agglutinated burrow lining suggests that a different animal constructed the burrow, possibly a crustacean (Lisa Levin, personal communication to MAK, 1999).

In the section of the core that was available to us, the agglutinated protozoan-filled part of the burrow

was observed about 8 cm beneath the sediment surface, and the chamber was 2.5 to 3 cm in diameter. A total of 83 specimens of *Aschemonella ramuliformis* and *Rhabdammina discreta* filled the chamber of the burrow completely (Plate 2). Only a few specimens of non-tubular agglutinated foraminifera were found, including one specimen each of *Ammodiscus* sp. and *Cyclammina cancellata*. The tubular tests appeared to be undamaged, up to 2.5 cm long, and in random orientation.

Two distinct types of tubular agglutinated protozoans were found in the burrow. A few of the specimens constructed their tests of aeolian quartz grains, and were therefore probably alive at the time of the 1991 eruption. However, the majority of specimens in the burrow were constructed of agglutinated dark grains of volcanic phenocrysts (mostly plagioclase and hornblende) and volcanic glass that were delivered to the sea floor by the Mt. Pinatubo volcanic eruption. Electron microprobe analysis (courtesy of Adrian P. Jones at UCL) of four dark-coloured specimens from the burrow confirmed that the dominant mineral phase in the test wall is volcanic glass. These specimens constituted part of the "recolonisation fauna" of agglutinated foraminifera and xenophyophoreans that is now establishing itself on top of the ash layer (Hess & Kuhnt, 1996; Hess *et al.*, 2001).

DISCUSSION

Biological implications

The burrow occupant must have made regular forays to the sea floor to search for prey items, bringing specimens back to its burrow, a behaviour known as "caching" (Jumars *et al.*, 1990). In our observations of box cores and multicores from the study area we have found numerous living specimens of *Rhabdammina* and other tubular agglutinated protozoans (up to 3 cm length) standing erect on the sediment surface. At this particular station, the population of living agglutinated protozoans visible on the surface of the box core was conspicuously low compared with neighbouring stations, and the sediment surface consisted mostly of fine ash (Plate 1). This implies that the foraging area of the animal was greater than ca. 0.25 m² (the surface area of the box core).

In our experience with live specimens of *Rhabdammina*, the organism appears to anchor itself in the substrate by means of its pseudopodia. Specimens recovered in box cores often stand erect, and need to be pulled out of the sediment with the aid of tweezers. The finding of large, mainly undamaged specimens within the burrow infilling implies that a predator with articulated appendages inhabited the burrow. Because the *Aschemonella* and *Rhabdammina* specimens are quite long and are unbroken, we suspect they did not pass through the gut of a benthic metazoan. Gut content studies have shown that deep sea scaphopods, ophiurids, and isopods have a preference for non-tubular agglutinated foraminifera (Svavarsson *et al.*, 1993; Langer *et al.*, 1995; Sokolova *et al.*, 1995). Instead, we assume that the predator may have sucked out the protoplasm from the tubular-shaped foraminiferal tests. Although we cannot be certain, we therefore believe that the organism was a small crustacean that occupied the burrow.

Because the specimens of agglutinated protozoans

within the burrow consisted of pre- and post-ash individuals, it is possible that this predator had substituted its preferred prey during the period of time following the deposition of the ash layer when no living agglutinated protozoans were available. This period of time may have been several years, because in 1994 populations of tubular foraminifera were still quite low compared with the pre-ash fauna (Hess & Kuhnt, 1996). However, by late 1996 tubular foraminifera were visibly present on the surface of the ash at most stations recovered during R/V Sonne Cruise 114. *Aschemonella* and *Rhabdammina* are among the largest tubular agglutinated protozoans in the South China Sea area. We further assume that some time was required for the agglutinated protozoans to grow to a size large enough that the predator would be able to find them.

The finding of a agglutinated protozoan-filled burrow has interesting implications for recolonisation studies of benthic foraminifera, which can obviously be biased by the presence of predators. If the specimens from the burrow were redistributed evenly on the sediment surface within the box core, a 100 cm² surface sample would contain several individuals, yet none were observed on the surface of the ash. Under normal circumstances, an agglutinated foraminiferal fauna with low numbers of tubular forms might be interpreted as a disturbed fauna that is in an early stage of faunal succession (Kaminski *et al.*, 1988).

A consequence of the presence of predators is the fact that their biasing effect on the abundance of prey species increases with decreasing prey density. At low prey concentrations, the predator's foraging area must be larger. If the density of predators is itself low and their foraging areas non-overlapping, the patchiness of surface-dwelling *Aschemonella* and *Rhabdammina* populations would increase.

An interesting implication is the fact that we are not aware of the population density of the agglutinated protozoan predators. We suspect their density in the area affected by the 1991 Mt. Pinatubo ash deposit is still low, because in our observations of 42 box cores on the R/V Sonne-132 cruise in 1998, we only observed one such burrow. A second (but degraded) burrow was observed in the same general area during R/V Sonne-140 cruise in 1999. Likewise, the presence of "pockets" of tubular agglutinated protozoans in deep-sea sediments to our knowledge have not been reported in the paleontological literature. However, the lack of evidence does not constitute evidence for the lack of a particular phenomenon. It is highly unlikely that only a single animal in the South China Sea preyed upon tubular agglutinated protozoans. We assume that this type of scavenging by burrowing macrofaunal invertebrates also exists in other geographical areas as well as in the geological record.

Sedimentological implications

Agglutinated benthic foraminifera often display grain selectivity. Heron-Allen (1915) pointed out examples of species of agglutinated foraminifera that have preferences for grains of a given size or composition. In the case of the post-eruption agglutinated protozoans recolonising the 1991 volcanic ash layer, there is a distinct preference for dark-coloured mafic mineral grains. Electron microprobe analysis of three specimens of *Aschemonella* from the burrow (kindly carried

out by Adrian Jones at UCL) revealed the presence of andesitic glass, plagioclase, hornblende, magnetite, and some barite (probably of biogenic origin). The predominance of dark mineral phases makes the specimens easy to observe on a background of light grey volcanic ash. Just as termites have been observed to pick up particular mineral grains and carry them to their mounds (A.P. Jones, personal communication), the epifaunal agglutinated foraminifera through their scavenging behaviour are effective in concentrating particular grains from the volcanic ash.

As the trophic structure of the benthic community in the area affected by the 1991 volcanic ash layer becomes re-established, we would expect to observe the beginnings of predator-prey relationships. Benthic foraminifera are at the base of the metazoan food chain in the deep sea, as they themselves consume bacteria and even dissolved organic matter. In turn, they serve as food items for metazoans. In this particular case, we observe two different levels (akin to trophic levels) of selective scavenging of mafic mineral grains from the 1991 volcanic ash layer. Firstly, these grains are taken up from the base of the volcanic ash layer by the agglutinated protozoans and brought to the sediment surface. Finally, these grains (now incorporated into the protozoan test) are subducted into the metazoan burrow and meet their final resting place some 8 cm below their point of origin. At some later stage the organic cement that the protozoan uses to bind the agglutinated grains usually disintegrates, and the grains are released into the sediment. The end result of these two levels of scavenging is the fractionation of the volcanic ash particles based on mineralogical composition and redistribution of these mafic mineral particles into the brown clay beneath the ash layer.

In a tracer experiment carried out at a 850 m deep station on the Carolina continental slope, maldanid polychaete worms were found to rapidly subduct freshly emplaced algal carbon and inorganic materials (sediment and glass beads) to depths of 10 cm or more (Levin *et al.*, 1997). After 1.5 days, the polychaetes had transferred a large amount of uningested tracer material from the sediment surface to the bottom of their burrows, indicating that these organisms may be responsible for a large proportion of organic matter subduction. However, the polychaetes studied by Levin *et al.* were nonselective in their choice of material that was subducted into their burrows, and transferred all the emplaced surface materials. The predator inhabiting the burrow in our study was probably not a maldanid polychaete, as it displayed a strong preference for selecting tubular agglutinated protozoans.

We now have evidence that this fractionation of the 1991 Mt. Pinatubo ash layer is taking place, albeit still on a very small scale. On Cruise 140 of the R/V Sonne, which took place in late April, 1999, we observed a "pocket" of dark mineral grains with a few pre-ash *Rhabdammina* specimens in a burrow at 10 cm depth in one of the multicores collected from a nearby station (14°35.04'N, 119°45.07'E, 2511 m water depth). The burrow was circular in cross-section, about 1 cm in diameter, and was clearly visible against the background of dark yellowish brown clay (Plate 3). Although the burrows of this type are still rarely encountered in the study area, we suspect that with the passage of time the scavenging of epifaunal tubular agglutinated protozoans and their subduction by metazoan predators will be an

important factor in the bioturbation process.

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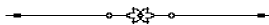




Plate 1. A. Lateral view of box core SO-132, station 39. Grey layer at surface is the 1991 Mt. Pinatubo ash layer. B. Surface of box core SO-132, station 39, showing the presence of burrow mounds and large xenophyophoreans. Photos courtesy of W. Kuhnt.



Plate 2. A. The burrow as it first appeared in a section from box core SO-132, station 39. B. Excavation of the entrance tube. Metric ruler for scale. C. Excavated burrow, showing open entrance tube. D. Detail of living chamber, filled with 83 black (post-1991) specimens of *Aschemonella ramuliformis*. Light brown specimens are pre-1991 individuals of *Rhabdammina discreta*. All photos taken by MAK with a Sony digital camera on board the R/V Sonne.



Plate 3. Views of a burrow filled with dark volcanic ash grains (degraded xenophyophoreans) and *Rhabdammina* recovered at 10 cm depth in a multicore tube (SO-140, station 14).