

ent study ranged from 23 to 63 nm. Thus, both the rhabdosomes and chrysotile fibrils are within the range of outer diameters (10 to 100 nm) reported in the literature for single fibers of chrysotile from Quebec (5, 6).

Both rhabdosomes and chrysotile also may show telescopic morphology with one tube nesting into another tube (5-7). However, under high magnification the rhabdosomes occasionally demonstrate a "braided" or spiral appearance. Such braiding has not been observed in chrysotile asbestos, stained or unstained.

In any event it was evident that the similarity of chrysotile asbestos and negatively stained rhabdosomes is too great to permit reliable identifications to be made simply from electron micrographs of negatively stained specimens. Unequivocal results can, however, be obtained rather easily with the use of the standard electron microscope. The technique is based on the fundamental differences in the chemistry and the molecular structures of proteinaceous and silicate fibers. After the samples had been mounted in the usual way on Formvar-coated graphite substrates, micrographs were taken of stained and unstained specimens with an electron microscope (Philips 200). We observed that negative staining with 1 percent uranyl acetate greatly enhanced the rhabdosome images (Fig. 2a). In fact, without such staining the rhabdosomes appeared as completely unstructured bodies (Fig. 2b). However, staining of asbestos microfibrils revealed no increased clarity of the image and no enhancement of structural detail. In fact, a single asbestos microfibril which was studied without staining was reexamined after staining and the two micrographs were indistinguishable. This diagnostically useful result is doubtless due to the low atomic scattering amplitudes of the components of the organic material as compared to those of the chrysotile asbestos $[(OH)_8Mg_6Si_4O_{10}]$.

Another diagnostic tool can be applied if the microscope is used for electron diffraction. We found that the chrysotile fibers give their characteristic diffraction patterns (8), but that no equivalent patterns could be obtained from the rhabdosomes even at voltages as low as 10 percent of normal.

Confusion is not likely to arise in cases involving types of asbestos other than chrysotile, for example, crocidolite and amosite, which are not tubular. It is conceivable that halloysite [endellite, $(OH)_8Al_4Si_4O_{10} \cdot 4H_2O$], which can have a tubular morphology (9) with diameters

ranging over those found in rhabdosomes and chrysotile, might, without the techniques discussed in this report, be confused with organic microtubes. However, this mineral does not have the widespread industrial use of asbestos.

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Chemosensory Grazing by Marine Calanoid Copepods (Arthropoda: Crustacea)

Abstract. *In laboratory experiments, mixed populations of two marine copepods (Acartia clausi and Eurytemora herdmanni) when fed artificial food particles consisting of microcapsules that were either enriched with an encapsulated homogenate of naturally occurring phytoplankton or nonenriched preferentially ingested the enriched capsules. Beads or nonenriched capsules were either seldom ingested or not ingested at all. The observations demonstrate that filter-feeding in these species is a behavioral process, under sensory control, and that the copepods are able to discriminate between enriched and nonenriched food particles.*

A number of recent hypotheses concerning the mechanisms of feeding by calanoid copepods suggest that these copepods are able to select particles on the basis of size only and that selection is not behaviorally determined (1). It has been claimed that the filtering structure has a variable retention efficiency for natural

or artificial particles of different sizes with large particles being more efficiently retained than smaller ones (1). By contrast, in other feeding studies performed with naturally occurring particles (2) it has been demonstrated that copepods preferentially feed on the sizes of food particles that are most abundant in the

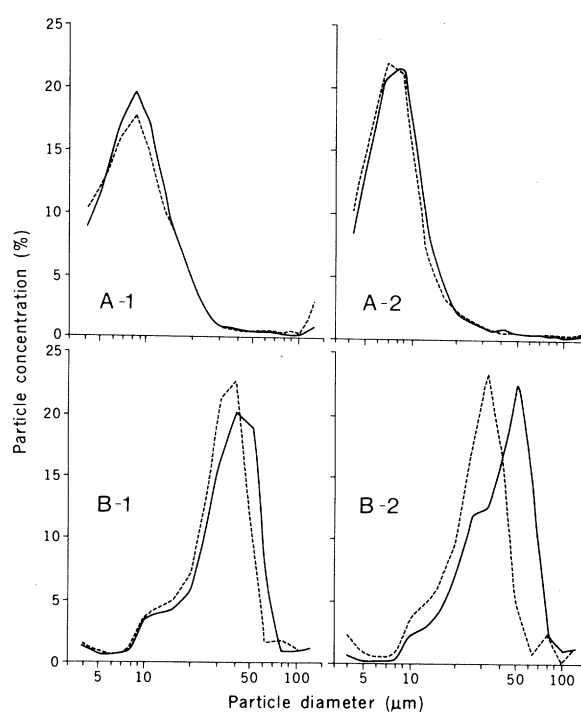


Fig. 1. Feeding activity of copepods measured by comparing unimodal particle size distributions of microcapsules in control (without animals, —) and in experimental (with animals, ----) bottles. Each curve represents the average of 9 or 15 replicate counts. Experiments A-1 and A-2 were performed, respectively, with small enriched and small nonenriched microcapsules; experiments B-1 and B-2, with large enriched and large nonenriched capsules.

Table 1. Feeding by marine copepods on enriched microcapsules (containing an encapsulated homogenate of phytoplankton) or nonenriched microcapsules. Values in columns 3, 5, and 6 represent the mean value $\pm$ the standard deviation; N is the number of experiments, and n is the number of replicate measurements. Experiments A-1 and A-2, and B-1 and B-2, were conducted simultaneously; experiments C and D were conducted at two different times.

Experiment	Size mode (μm)	Number of copepods in experiment	Experiment time (hours)	Concentration (particles per liter)	Ingestion rate per copepod (particles per liter per hour)	Particle debris production (%)	Consumption (%) in the range	
							< 15 μm	> 40 μm
A-1	8*	646 $\pm$ 52 ($N = 3$)	4	$11.6 \times 10^6 \pm 3.1 \times 10^5$ ($n = 9$)	334 $\pm$ 19 ($n = 9$)	3.10	100	
A-2	8†	671 $\pm$ 32 ($N = 3$)	4	$10.3 \times 10^6 \pm 1.4 \times 10^5$ ($n = 9$)	107 $\pm$ 20 ($n = 9$)	5.40	100	
B-1	50*	640 $\pm$ 54 ($N = 5$)	4	$12.1 \times 10^6 \pm 2.7 \times 10^5$ ($n = 15$)	59 $\pm$ 19 ($n = 15$)	12.95		100
B-2	50†	642 $\pm$ 141 ($N = 5$)	4	$12.1 \times 10^6 \pm 3.1 \times 10^5$ ($n = 15$)	0 ($n = 15$)	28.15		0
C	8†, 50*	329 $\pm$ 22 ($N = 2$)	3	$17.2 \times 10^6 \pm 3.4 \times 10^5$ ($n = 6$)	467 $\pm$ 26 ($n = 6$)	2.80	20	80
D	8*, 50†	266 $\pm$ 34 ($N = 6$)	3	$5.4 \times 10^6 \pm 9.2 \times 10^4$ ($n = 18$)	229 $\pm$ 10 ($n = 18$)	4.42	100	0

*Experiments with enriched microcapsules.

†Experiments with nonenriched microcapsules.

biomass and that they shift their grazing pressure according to the variations in the standing stock and particle size spectrum occurring with time.

Such opportunistic feeding behavior as well as the shifting responses demonstrated for both adult and young copepods (3) argue for a sensory mechanism, either mechanical reception (4) or chemical perception, in the copepod's feeding process. However, chemical perception seems more likely, provided that the copepods are able to first grasp and then reject particles that are held in the mouthparts and moved about as if being "tasted" (5). It has been suggested that the sensilla in the mandibles and the labrum aid the copepods in selective filter-feeding (6). Chemoreceptors have been described for several crustaceans (6, 7); however, no direct evidence for chemosensory feeding has been provided for herbivorous copepods, although several planktonic and bathypelagic crustaceans have been shown to respond to certain chemical substances (8). The fact that plankton search for food and females (3, 9) strongly suggests that chemical perception is a basic sensory mechanism that is found in many free-swimming organisms. In this report we show that chemoreception occurs in copepods and present evidence that chemical perception is used by copepods to make feeding decisions.

Copepods were collected with plankton nets (202- μm mesh size) towed at the surface in the St. Lawrence estuary near Rimouski, Quebec, Canada. A natural population of mixed adult and young copepods was used in the experiments, and, depending on the time within the 3-month sampling period, it was dominated by either *Acartia clausi* (Giesbrecht) or *Eurytemora herdmanni* (Thompson and Scott). At least 300 individual copepods (Table 1) were placed in each of a series of 500-ml glass bottles

filled with particle-free natural seawater which had been collected at the surface just prior to the plankton tows and filtered twice through 0.8- μm Millipore filters; the copepods spent at least 12 hours in the bottles before the grazing experi-

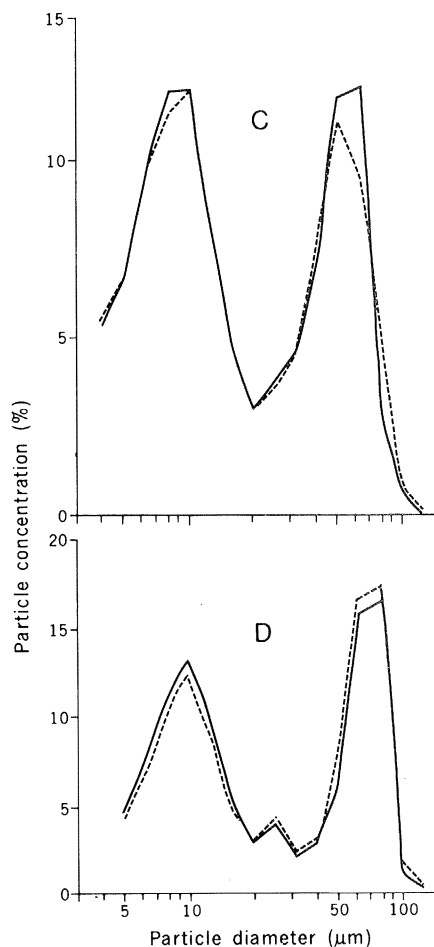


Fig. 2. Feeding activity of copepods measured by comparing bimodal particle size distributions of microcapsules in control (without animals, —) and experimental (with animals, ----) bottles. Each bimodal size distribution curve represents the average of 6 or 18 replicate counts. Experiment C is for enriched microcapsules in the large size range; experiment D is for enriched microcapsules in the small size range.

ments started. Then they were allowed to feed on microcapsules (particles consisting of thin semipermeable polymer membranes around aqueous microdroplets of proteins or cell homogenate) except in one experiment in which beads (Sephadex G-75) were used. Short-term experiments (Table 1) were conducted in a darkened room at temperatures near in situ (8° to 10°C). The bottles were subjected to continuous gentle motion to prevent particle sedimentation.

We prepared the microcapsules with nylon-protein walls permeable to small molecules, using a modification of earlier methods (10). Artificial food particles are known to be acceptable to a wide range of filter feeders (4, 11). We produced satisfactory microcapsules with peak concentrations in the sizes ~ 8 and $\sim 50 \mu\text{m}$ by stirring protein emulsions at speeds of 2500 and 1000 rev/min, respectively. "Enriched" capsules were produced just before the start of the grazing experiments with encapsulated homogenate consisting of a freeze-dried water-soluble fraction of a concentrate (400 mg/ml) of naturally occurring particles collected during a phytoplankton bloom mixed with albumin (400 mg/ml in water). As this material was permeable to small molecules [pore size, $\sim 18 \text{ \AA}$ (10)], we assumed that the enriched capsules would let small molecules, originating from the homogenate, diffuse and thus stimulate the feeding. "Nonenriched" capsules were produced from albumin, individual molecules of which were too large ($\sim 100 \text{ \AA}$) to escape, and dialyzed in 2.8 percent NaCl for 24 hours to remove any permeable products. We estimated particle size distributions and concentrations of microcapsules before experiments with an electronic counter (Coulter model TA), using a tube with an aperture of 280 μm . We measured ingestion rates at the end of each experiment by comparing Coulter counts of the mi-

crocapsule suspensions in bottles containing copepods with control bottles containing no animals. Each set of experiments (including those with enriched and nonenriched microcapsules) were carried out simultaneously to ensure identical environmental conditions for all bottles.

When the copepods were fed with large microcapsules, net ingestion could be measured only for the enriched capsules (Table 1, experiment B-1) even though debris particles of smaller size were produced (Fig. 1, experiment B-1). There was little or no net ingestion of the unenriched particles but very intense production of particle debris (Table 1; Fig. 1, experiment B-2); in this case, there was considerable modification of the particle size distribution as shown by the experimental curve appearing at the left of the control curve. This was presumably a result of mastication followed by rejection (5, 7). The ingestion rate of experiment B-1 was significantly different from that of experiment B-2 (*t*-test, $P < .05$).

The particle size distributions in nature are not as simple as those shown in Fig. 1. Generally particle size distributions in seawater are bi- or polymodal, and thus copepods are able to choose particles from among several sizes (3). We created this condition artificially in a second series of experiments in which bimodal particle size distributions with peaks of approximately equal concentration alternately contained the enriched particles of either the large size (Fig. 2, experiment C) or the small size (Fig. 2, experiment D). In experiment C, ingestion occurred in both particle size peaks but it was four times higher for large enriched particles than for large nonenriched particles. Moreover, the production of particle debris was negligible (Table 1). Because of the large production of small-sized particle debris in type D experiments which always masked the feeding responses of copepods to particles smaller than 20 μm , the net ingestion rates of small capsules could never be measured. We then replaced the large-sized microcapsules with beads of similar sizes (Sephadex G-75) in order to reduce the production of debris. We assumed that this substitution did not affect the feeding mechanisms, provided that copepods can ingest hard plastic beads within this size range (4). Moreover, if the copepods select only on the basis of size, beads should be ingested about as readily as microcapsules (4). The production of debris was then negligible (Table 1, experiment D), and preferential feeding could be observed in the

size range corresponding to the small enriched particles (Fig. 2, experiment D).

In experiments A, B, C, and D, copepods always preferentially consumed microcapsules that were enriched with homogenate of naturally occurring phytoplankton. Feeding on large particles, whether enriched or not, corresponds to raptorial behavior (5). This behavior was particularly intense with nonenriched capsules, judging from both the greater production of particle debris and the low or even zero rate of ingestion. Small particles are easily ingested by the copepods; large particles have to be broken up by the copepods first, and their ability to do this presumably depends on the size of the mouth aperture. Copepods are able to distinguish between "good" food and "nonfood," by "tasting" either the outside (before mastication) or the inside (after mastication) of the particles (Fig. 1, experiments A and B). The copepods discriminated between two types of particles on the basis of their chemical "scent," independent of their size. Therefore, filter-feeding by copepods is a sensory-determined behavioral process.

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Copulatory Vocalizations of *Chacma* Baboons (*Papio ursinus*), Gibbons (*Hylobates hoolock*), and Humans

Abstract. *The copulatory vocalizations of female baboons (Papio ursinus) are more complex than those of female gibbons (Hylobates hoolock) or human females. Adult males of all these species begin calling later than the female, but subordinate baboon males do not call. Copulatory vocalizations may serve to mutually stimulate the mating partners or to incite male competition.*

Vocalizations during copulation are widespread among primate species, from prosimians (1) to the apes (2, 3) and man (4-9), yet their significance is seldom discussed. Before now no sonographic analyses of human copulatory sounds have been available. When compared with the extensive details of the physical and physiological features of human coitus (7), this omission seems surprising. Either the clinical circumstances required for observations of some aspects of coitus (7) inhibited vocalizations or they were simply not reported. Interpretations based upon the concepts of orgasm and pleasure intrude into the human-oriented literature, providing little insight into the meaning of these sounds. Here we contrast copulatory vocalizations by humans, monogamous gibbons (*Hylobates hoolock*), and promiscuous

troop-dwelling baboons (*Papio ursinus*) and evaluate their possible significance relative to their social setting.

Sexual arousal and orgasm in humans may be communicated by verbal or non-verbal sounds (or both), including changes in respiratory rate (7), moans, and gasps (4-9). Some individuals sob or laugh uncontrollably during orgasm (6, 9). Individually or culturally improvised verbalizations may also accompany coitus and orgasm (5, 6, 9).

Individuals may suppress all copulatory vocalizations, usually from fear of being overheard (9). Humans may also vocalize to mimic orgasm (8).

Sonagrams of human copulatory vocalizations (Fig. 1) obtained from films and a tape (10) show that female sounds gradually intensified as orgasm approached and at orgasm assumed a rap-