have developed could then serve to measure that contribution. We have no way of knowing the degree to which the other subjects in the main body of our experiment made pursuit movements despite the fixation instructions and the fixation point. This auxilliary experiment shows that the Johansson effect cannot be explained solely as the cancellation of the stimulus motion by effects of pursuit eye movements.

A second substantive finding in these data is that, because of the stationary point *D*, there is no common vector greater than zero. Thus the results do not support an explanation of the Johansson effect in terms of an automatic vector extraction applied over the entire field of view. Perhaps the vector-extraction model must be phrased in more local terms (for example, beyond some distance, the points do not affect each other), or perhaps it must take the observer's intention into account.

Both findings call for quantitative measurement under a wider range of conditions before we can essay a more adequate theory. Our method should prove valuable for that purpose and for the more general problem of determining the stimulus and task factors responsible for the organization of motion perception.

JULIAN HOCHBERG
PETER FALLON

*Department of Psychology,
Columbia University,
New York 10027*

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2. ———, *Visual Motion Perception* (Psychology Laboratory Report, University of Uppsala, Uppsala, 1971).
3. G. Johansson, in *Perception: Essays in Honor of James J. Gibson*, R. MacLeod and H. Pick, Eds. (Cornell, Ithaca, 1974), p. 135.
4. A. Stoper, *Percept. Psychophys.* **13**, 201 (1973).
5. Display timing was controlled by a crystal clock (DEC Dk8-EC). A point-plot display unit (DEC VC8E) linked the CPU to the oscilloscope. The display was presented 850 times each second. Between any two successive display cycles, a point could move 0.012° of visual angle. The speed of spot motion was controlled by varying the number of display cycles between displacements.
6. An assembly language program was developed by P.F. to compute and control the display of moving dot patterns. The package provides relatively high speed and absolute control of presentation rate.
7. Three dots were used here, as they were more distinctive in peripheral vision than a single dot would have been. The horizontal extent of the line formed was 0.34° of visual angle.
8. The horizontal velocity component of the comparison stimulus was within the range of ± 9.57° visual angle per second.
9. The subject could not control the motion of *B* during its presentation. Except after a match was reported, the same motion would result if the potentiometer were left unchanged.
10. This instrument is a television analog computer system that calculates the direction of gaze by comparing the position of the center of the pupil of the left eye with the center of a corneal reflection in that eye. Accuracy is typically well within 1.5° of visual angle, and the device is relatively free from error introduced by small head movements. The working precision varies with subject and configuration; in this experiment, changes in horizontal eye direction of 0.36° could always be detected. An eye patch occluded the right eye. The stimulus field was no longer in complete darkness (as it was in the first experiment). Instead, the infrared illuminator of the eye movement monitor introduced a dim visible haze through which the stimulus dots appeared to move, which may have caused the slight decrease in that subject's Johansson effect (this decrease was not significant: $t = 1.14$, d.f. = 48, $P > .10$).
11. Supported by National Institute of Child Health and Human Development Grant R01-HD-06768-01A1 to J.H.

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Deep-Sea Macroplanktonic Sea Cucumbers: Suspended Sediment Feeders Captured from Deep Submergence Vehicle

Abstract. *Observations in situ confirm the swimming and feeding behavior in previously unreported dense assemblages of the holothurian* Peniagone diaphana, *at a depth of 2000 meters, off southern California. Proximate analysis of captured specimens indicates that this organism may represent a numerically significant, but low organic content member of many near-bottom deep-sea communities.*

Ever since Théel defined the deep-sea holothurian order Elasipoda (*1*), the bizarre variations in body form of these unusual animals have been of great interest to zoologists who study morphology (*1*, *2*). Indeed, one can hardly invoke a less appropriate term than "sea cucumber" to describe the translucent, vertically oriented, free-swimming forms (Fig. 1), which we saw in all directions from a deep sea submersible cruising near the sea floor, 2000 m deep off San Clemente Island. The real significance of being surrounded by living hordes of an organism known previously from only a handful of preserved specimens (*3*), is that we now have a record for the existence of a substantial population (*4*) of relatively large deep-sea organisms, living in close association with the sea floor, yet scarcely considered (*5*) in the various models of energy exchange proposed for the deep ocean (*6*). This oversight is undoubtedly due to the fact that deep-sea near-bottom communities (within 200 m of the bottom) have not been routinely or effectively sampled.

A series of dives in Deep Submer-

Fig. 1. A photograph in situ of *Peniagone diaphana* drifting above the sea floor at a depth of approximately 2000 m.

Table 1. Chemical composition of *Peniagone diaphana*. Analyses were made by means of standard methods (*21*). Caloric contents were estimated from lipid (9.3 kcal/g), carbohydrate (4.1 kcal/g), and protein (4.7 kcal/g) contents. The high values of carbon and nitrogen relative to carbohydrate, lipid, and protein suggests that there may be a substantial amount of small nitrogen-containing organic molecules, presumably amino acids.

Parameter measured	Animal number			
	1	2	3	Mean
Length (total, cm)	7.3	5.0	6.0	6.1
Wet weight (g)	35.7605	13.1056	12.4244	20.4302
Dry weight (g)	1.3771	0.5040	0.4526	0.07779
Ash weight (g)	1.0894	0.3902	0.3572	0.6123
Water (% wet weight)	96.15	96.15	96.36	96.22
Carbohydrate (% wet weight)	0.0093	0.0117	0.0065	0.0092
Lipid (% wet weight)	0.1173	0.0598	0.0957	0.0909
Protein (% wet weight)	0.0416	0.1397	0.0801	0.0871
Carbon (organic, % wet weight)	0.0732	0.1436	0.1192	0.1120
Nitrogen (organic, % wet weight)	0.0291	0.0534	0.0404	0.0410
Kilocalories per 100 g (wet weight)	1.32	1.26	1.39	1.32

gence Research Vessels (DSRV) *Turtle* and *Sea Cliff* (*7*) provided three of us (A.T.B., L.B.Q., J.J.C.) with the opportunity to observe, photograph (*8*), and capture (*9*) specimens of an elasipod holothurian (Figs. 1 and 2) encountered as dense aggregations (*4*) extending up to 70 m above the sea floor off Southern California. Subsequent examination of live and preserved specimens (*10*) revealed that all of them belong to the species *Peniagone diaphana* (Théel) (*11*).

The rotund body of *P. diaphana* is slightly compressed dorso-ventrally and constricted anteriorly prior to expanding into the sharply peaked prominence anterior and dorsal to the mouth (Fig. 2). The mouth itself is surrounded by a circlet of ten short tentacles, each of which ends in fine subdivisions. Posteriorly, the anus opens dorsally, just at the base of the flattened, paddlelike postanal fan, whose distal edge consists of eight fingerlike extensions of the body wall (Fig. 2).

In order to visualize accurately the behavior of *P. diaphana*, it is necessary to remember that we have described this animal as if it were a conventional "sea cucumber," that is with the mouth oriented ventrally and the body resting horizontally on interradii ABE. All of the hundreds of *Peniagone* viewed, 0.5 cm to > 15 cm long (*12*), held the long axis of their bodies vertically, swimming in the water column through an activity best described as slow, simultaneous stroking with oral tentacles and postanal fan. We found that regardless of size, active *P. diaphana* comb the water column at a steady 10 to 20 cycles per minute (*13*). This behavior was not altered when the submarine was motionless on the bottom or when the external viewing lights would suddenly be switched on after a period of "no light" observations. During more than 12 hours of combined bottom diving time (*14*), we never observed *Peniagone* with its body in a horizontal orientation, or in contact with the substrate. Moreover, since the most violent activity observed (tail-to-head flexures at ~ 2 seconds each) created barely sufficient thrust to propel a large specimen 2 meters from the approaching submarine, we emphasize that these organisms cannot be considered to be truly active swimmers (nekton), but rather macroplankton.

Appreciation of the fine interaction between oral tentacles and postanal fan may be gained most readily from Fig. 3, A to F (*15*). During the raising and exten-

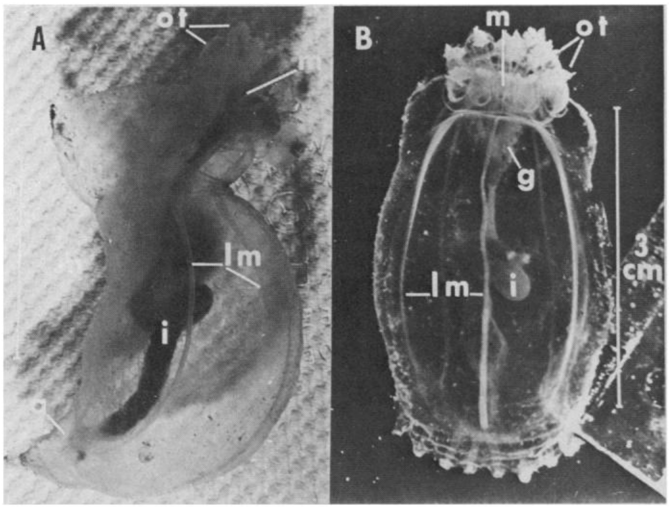

Fig. 2 (left). General anatomy of adult *Peniagone diaphana* from off Southern California. (A) Living, shipboard specimen viewed from right side. (B) Ventral view of live shipboard specimen of *P. diaphana*. Most prominent of the internal organs visible through the semitransparent body wall of living specimens are the five thin, diagnostic longitudinal muscle bands (*lm*), the conspicuously pigmented intestinal tract (*i*) with its characteristic loop midway between mouth (*m*) and anus (*a*), and in larger specimens, delicate pink branches of the reproductive system (*g*) clustered near the base of the oral tentacles (*ot*).

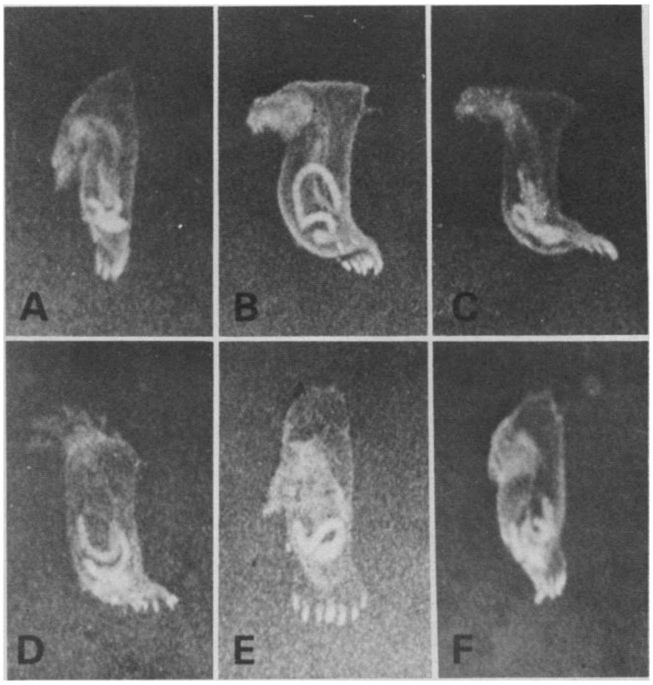

Fig. 3 (right). Photographic sequence of in situ swimming-feeding cycle characteristic of Southern California *Peniagone diaphana* (*15*). This cycle consists of slow, rhythmic, simultaneous raising, extending, and lateral expanding of oral tentacles and postanal fan (B to D) from vertical, downward pointing "rest" position (A and F). Time from rest position (A) to full expansion (D) was typically 5 to 6 seconds with the same time required for the return to "rest." The movement of the postanal fan presumably serves to counteract the shifting of the body axis which would result from activity of the oral tentacles alone.

sion stage, the oral tentacles not only shift position from vertical to horizontal (Fig. 3, B and C), but elongate and spread laterally, ultimately forming a thin horizontal fan (Fig. 3D). Parallel activity occurs in the slightly less extensible postanal fan, again with coincidence between maximum extension and lateral spreading. Simultaneous downstroke (Fig. 3E) then brings both the oral tentacles and postanal fan into the vertical plane (Fig. 3F) completing the cycle. Since virtually all active, undisturbed (*16*) specimens observed were in various stages of this same slow, rhythmic stroking, we assume this behavior must affect not only locomotion, but also facilitate respiration and generate whatever water currents are necessary for near-bottom (suspension) feeding. Those few inactive animals observed (*17*) were all in the terminal position (Fig. 3F) with oral tentacles and postanal fan down, but they still remained off the bottom in a vertical orientation.

Both the relatively delicate morphology and generally low level of activity seen in *P. diaphana* fit current concepts of energy conserving adaptations to such low-energy environments as the deep sea (*18*). Just how little energy may be required to maintain a population of a given deep-sea organism is demonstrated by the results of proximate analyses of three freshly frozen specimens of *P. diaphana* (Table 1). These results indicate the content of organic matter in *P. diaphana* is extremely low, and, presumably, the metabolism is also low.

The notion that *P. diaphana* survives on an extremely low energy budget seems inescapable—more problematic is the source of this low energy food. The guts of most animals viewed *in situ* were distended with material, which, on the basis of analysis (by D.L.P.), after capture was composed of sponge spicules, holothurian spicules, diatom frustules, foraminiferan shells, and unidentifiable material. Finding sponge and holothurian spicules in the gut material suggests that the food of *P. diaphana* is of benthic origin. Further evidence of the sedimentary nature of the food comes from both the low carbon content (5.45 percent, dry weight) and high ratio of C to N (10.9) of the intestinal contents (*19*). Having never encountered *P. diaphana* in contact with substrate, we must conclude that near-bottom water movements suspend sufficient bottom detritus to meet the dietary requirements of this unexpected, apparently widespread (*20*), population of deep-sea macroplanktonic "dirigibles."

ANTHONY T. BARNES
LANGDON B. QUETIN
JAMES J. CHILDRESS
Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara 93106
DAVID L. PAWSON
Curator, Echinoderms,
National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

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2. Théel (*1*) and L. Hyman, [*The Invertebrates: Echinodermata* (McGraw-Hill, New York, 1955), pp. 133, 203, 206, 208] provide excellent illustrations of the various elasipod floats, sails, tentacular and podial rings, and postanal keels, all interpreted as being, for the most part, adaptations for swimming or maintaining neutral buoyancy.
3. Since most of the Elasipod genera now recognized occur on or near the sea floor at depths of 100 to 6000 m, reliable correlation of their morphology with function has had to await development of requisite deep-sea photographic and submersible technology. Initially, lack of familiarity with such relatively inaccessible organisms led to the creation of multiple genera from fragmentary remains of single species. Most elasipod genera are now considered to have cosmopolitan distributions. Their wide distribution is discussed by B. Heezen and C. D. Hollister [*The Face of the Deep* (Oxford Univ. Press, London, 1971), pp. 71–85].
4. All observations of *Peniagone* were made at depths between 1900 to 2100 m (5700 to 6200 feet) in San Clemente basin, 32°29.0′N, 118°1.6′W. On each dive covering less than 1 km^2 per dive we encountered virtually hundreds of specimens. In regions of high density one *Peniagone* was seen approximately each 3 m along a given horizontal transect. Occasionally we passed suddenly from high density zones to areas virtually devoid of the animals, which however, seemed to have no preference for broken as opposed to open terrain, or obvious shifts in the turbidity of the seawater. We assume that this distribution may be typical for this depth and latitude in the eastern Pacific.
5. That the extent of man's knowledge regarding any environment is a function of both sampling techniques and accessibility of the environment was reinforced not only by our stumbling into this unexpected holothurian assemblage, but also by our consistent encounters with previously unreported high densities (3/100 m^3) of the primitive annelid *Peobius* at depths of approximately 780 m. Such observations underscore the unique role of deep-sea research vessels in the study of deep-sea biology.
6. H. L. Sanders and R. R. Hessler, *Science* **163**, 1419 (1969); P. K. Dayton and R. R. Hessler, *Deep-Sea Res.* **19**, 199 (1972).
7. Both DSRV *Turtle* and *Sea Cliff* are submersibles of the *Alvin* class, carrying two crew and one observer and supported by the U.S. Navy. These dives were part of a program aimed at examining in situ behavior of midwater organisms.
8. All in situ photographs were taken with a 70-mm Hydro Products deep-sea photographic camera incorporating a Leitz *f*/2.5 fully corrected water contact lens and two synchronized external strobes. The black-and-white photographs presented here are enlarged copies of sections of the original High Speed Ektachrome transparencies.
9. Living specimens of *Peniagone* were captured at depth by visually aligning an 18-inch-diameter plankton net (held by one DSRV manipulator) with the desired animal and running it down. This trial-and-error method yielded the investigators 22 specimens of *Peniagone*.
10. Two groups of *Peniagone* ($N = 7$, $N = 11$) were kept alive for 48 hours in containers of aerated, nonrecirculating, 4°C seawater. Specimens were preserved in 10 percent buffered formalin in seawater.
11. B. Hansen, [*Galathea Report* No. 13 (1975)] reports *Peniagone diaphana* from the Atlantic in depths of 2550 to 5600 m and from the Tasman Sea in depths of 4670 to 4732 m. The present record from off California represents a considerable range extension, both geographically and in terms of depth of occurrence. Hansen also noted that the species has the "ability to lead a pelagic life" (p. 155). Until now, *P. diaphana* has been known from a total of approximately ten specimens from six localities. It now seems likely that these specimens were "strays" from large populations living near the sea floor.
12. Larger specimens seemed darker in color, being a more noticeably orange-pink than the smaller animals.
13. These values are based on stopwatch records for time from full "down" to fully expanded position in ten different animals ranging in size from 1.5 to 10 cm in length.
14. We made bottom observations during three dives in October, 1974, one dive in November, 1974, and three dives in January, 1975. These dives typically included 3 hours bottom diving time each and took place during all times of the day. Nonetheless the same activity was seen in the *Peniagone* in all dives.
15. Figure 3, A to F is actually a composite reconstruction of photographs of three different animals, but one which best portrays behavior observed in active *Peniagone*.
16. We recognize the perturbation inherent in the operation of the submersible (such as lights, vibration, and turbulence); nonetheless, it was usually possible to approach within centimeters of most *Peniagone* without triggering any overt change in ongoing behavior.
17. The nearly black appearance of the gut and obvious lack of movement in a few very large animals raises the possibility that they may have in fact been neutrally buoyant, but dead *Peniagone*.
18. E. G. Barham, in *Proceedings of an International Symposium on Biological Sound Scattering in the Ocean* (Maury Center for Ocean Science, Washington, D.C., 1971), pp. 100–118.
19. The intestinal contents of five animals were separately analyzed for carbon, hydrogen, and nitrogen with the use of a Hewlett-Packard 185b C, H, and N analyzer. The carbon content was 5.49 ± 0.30 (standard error of the mean) percent of the dry weight. Hydrogen was 1.1 ± 0.03 percent of dry weight. Nitrogen was 0.50 ± 0.02 percent of dry weight. The ratio C/N is equal to 10.98. These values are within the range for sediments in the basins off Southern California [K. O. Emery, *The Sea off Southern California* (Wiley, New York, 1960)].
20. During dive No. 589 of DSRV *Alvin*, D. L. P. observed and photographed Atlantic *Scotoanassa*, recording activity strikingly similar to that observed off Southern California.
21. J. J. Childress and M. Nygaard, *Mar. Biol.* **27**, 225 (1974). Because of the losses of small amounts of inorganic material in our ashing technique, we regard any estimate of total organic matter (ash-free, dry weight) as being at best spurious when dealing with samples of such low organic content.
22. We thank the men of Submarine Development Group 2, the crews of DSRV's *Turtle* and *Sea Cliff*, the men of the *Maxine "D"* for their support, and Lt. "Sandy" Sanderson for having initially confronted A.T.B. with the existence of this deep-sea holothurian assemblage. Supported by ONR contract N-00014-75-C 0242 to James F. Case and NSF grant GA33 232 (to J.J.C.).

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