

K⁺ on inhibiting the rate of ouabain binding to Na⁺,K⁺-ATPase is well known (1). Similar effects of [K]_o on the binding of cardiac glycoside to intact cells has also been discussed by several authors (1) who used reconstituted red blood cell ghosts and by Anderson *et al.* (5) who used canine Purkinje fibers. Although it has been demonstrated that E_{rev} of Purkinje fibers is altered by ouabain or a change in [K]_o, or both, it remains to be shown that this same phenomenon occurs in the atrial or ventricular myocytes which are the major components generating the positive inotropic state in heart. It is possible that Purkinje tissue is qualitatively different from contracting myocytes with respect to Na⁺,K⁺-ATPase. For instance, Kübler *et al.* (14) reported that cardiac conducting tissue and ventricular muscles differ both in amount of Na⁺,K⁺-ATPase and in sensitivity to ouabain; however, Palfi *et al.* (15) found no such ouabain sensitivity distinction. Uptake of [³H]labeled digoxin by sheep ventricle was 27.5 percent greater than by bundle of His and Purkinje fibers as reported by Hammerman *et al.* (16).

Our purified Na⁺,K⁺-ATPase hydrolytic activity was not stimulated by any concentration of ouabain, and positive inotropy of cat papillary muscles prevailed at concentrations below $5 \times 10^{-7}M$. Thus, it would be difficult to attribute the negative change in E_{rev} , reported by other authors who used low concentrations of ouabain ($10^{-8}M$), to a stimulation of Na⁺,K⁺-ATPase. Neither E_{rev} nor isolated Na⁺,K⁺-ATPase are entirely reflective of the exchange pump in the whole cell. The enzymatic mechanism, however, is generally accepted as the Na⁺,K⁺-exchange pump from the cell membrane (1). We recognize, however, that the isolated enzyme may behave differently from the enzyme in situ. It is clear that the important issue of "pump stimulation" deserves further work.

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Deep-Sea Foraging Behavior:

Its Bathymetric Potential in the Fossil Record

Abstract. *Spiral and meander foraging traces in the deep sea are not distributed in proportion to assumed food availability. Data collected by means of deep-sea photography failed to reveal a bathymetric gradient in behavioral complexity or sensitivity. The foraging paradigm developed by numerous trace fossil studies does not adequately predict the modern environment.*

In this report, a rigorous analysis is presented of modern spiral and meander foraging patterns on the ocean floor; the presence of such patterns in ancient strata has been interpreted to indicate bathyal to abyssal depths. Because of the difficulties of study in the deep sea, a paucity of traces have been identified in modern environments. Spiral and meander foraging patterns produced in modern sediments represent trace fossil counterparts that could possibly be used as direct standards for depth. If trace fossil theory predicts modern deep-sea trace morphology, diversity, or density (or all), its bathymetric potential will be substantiated.

Seilacher (1-3) suggested that trace fossils occur in depth-controlled communities. He postulated that in nutrient-enriched shallow marine systems, sediment ingesters need not conserve energy and therefore may forage inefficiently. Recurrent crossings of older traces and encounters between individuals are common. Conversely, in nutrient-limited deep-sea systems, sediment grazers must maximize areal coverage while minimizing energy output. Complex spiral and meander patterns that avoid recrossings and encounters between individuals are common. Subsequent studies (4) indicated the bathyal to abyssal *Ne-reites* community is closely depth-controlled. Its component grazing traces reflect highly organized foraging strategy.

Seilacher (2) argued against direct

comparison with data from the modern seafloor because organisms responsible for many trace fossils remain unknown in terms of taxonomic affinity and body structure. However, optimal foraging strategy is a behavioral principle (5) that has been elevated to the status of paradigm in a recent paper by Seilacher (6). Its bathymetric potential should represent an adaptive response to an increasingly limited resource, independent of organism identity.

A digital simulation model for two-dimensional feeding patterns preserved on bedding planes of ancient flysch deposits was developed by Raup and Seilacher (7). Their work demonstrated that what paleontologists viewed as highly variable and complex feeding traces could be precisely simulated by 1 to 4 behavioral commands. The simplest command produced a scribble; four commands produced a meander. Spirals were of intermediate complexity. More recently, computer evolutionary experiments by Papentin (8) demonstrated that selection for avoidance of crossing will result in both spiral and meander foraging strategies.

We hypothesized that corroboration of trace fossil theory required these data from a modern analog: (i) a bathymetric gradient in increased sensitivity to behavioral commands; hence, an increased organization with depth; (ii) a bathymetric gradient in behavioral complexity from scribbles to spirals to meanders;

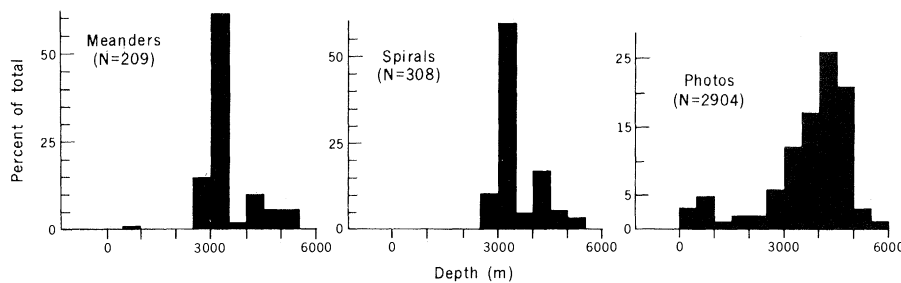


Fig. 1. Depth-frequency distributions of spiral and meander foraging patterns observed in deep-sea photographs.

(iii) spiral or meander (or both) presence in bathyal-abyssal zone and absence of same in littoral zone; and (iv) a high species diversity within a given habitat.

Heezen and Hollister (9) reported that spiral foraging patterns occurred most frequently in deep-sea stations in the high southern latitudes. We consequently selected for analysis 2904 bottom photos from 241 R/V *Eltanin* stations, cruises 5 to 55, in the South Pacific, Bellingshausen Sea, and Scotia Sea. Depths ranged from 100 to 6500 m.

Morphometric data were collected from undisturbed spirals and meanders (10). Length, radius, number of revolutions, ratio of length to radius, ratio of revolutions to length, and direction of coiling were calculated for each spiral. Length, number of 180° turns, maximum distance between turns, mean distance between meanders, and ratio of turns to length were calculated for each meander. We assumed that parameters affected by camera angle were randomly biased and independent of depth.

Peak occurrence of both spirals and meanders was at depths of 3000 to 3500 m (Fig. 1). Chi-square analyses of distribution data indicated significant ($P <$

.01) differences between the depth distribution of photos compared to that of spirals and meanders (indicating that we are not examining a sampling bias), but no difference ($P < .01$) between the depth distribution of spirals and that of meanders. Other surface traces observed in photographs from depths of 100 to 6500 m did not similarly peak at 3000 to 3500 m. We, therefore, infer that shear strength of the sediment, current effects, and bioturbation effects do not reach optimum values for trace preservation on the ocean floor at this depth.

Spirals are present at depths greater than 2500 m or less than 5500 m. The presence of meanders is less conclusively bounded because of a single occurrence at 594 m. Meanders did not occur at depths in excess of 5500 m. Analysis of 2500 bottom photos taken at depths of 1000 to 4500 m in the Arctic (11) yielded no spiral or meander patterns. A shallow-water deposition might previously have been attributed to a flysch or another purported deep-water sequence lacking meanders or spirals. In fact, the absence of these traces offers no conclusive evidence of bathymetry.

Regression analysis of the measured

and calculated dependent variables outlined above showed no significant correlation with depth (12). The expected morphological sequence was not observed: loosely coiled short spirals with low revolution to radius ratios were not replaced at depth by tightly coiled long spirals with high revolution to radius ratios. Similarly, we did not observe a depth-correlative trend from loosely patterned meanders with variable lengths, number of 180° turns, and low turn to length ratios to tight meanders of uniform length and turns with high turn to length ratios.

Five foraging patterns were apparent and can be compared with fossil analogs characteristic of the *Nereites* community (Fig. 2). The coiled meander had not previously been reported from the deep-sea floor, although fossil *Nereites* meanders are occasionally spiraled (13). A single meander enclosed in a spiral and grading into a meander compares with the surface expression of *Dictyodora*, a three-dimensional spreiten structure (3). The simple spiral resembles the ichnogenus form *Spirodesmos* (14). Very regular and closely spaced meanders compare with those of *Helminthoida*; loosely meandering traces most closely resemble those of *Helminthopsis* (15). A continuous trace from spiral to meander comprises many of the patterns, the meander forming the distal portion of the grazing trace, resembling the ichnogenus *Taphrhelminthopsis* (16). In the fossil record, spirals display similar dimensions, but the ancient meanders are generally smaller in maximum dimension than their modern counterparts.

A bathymetric gradient from scribbles to spirals to meanders is not apparent. Simple spirals did not give way to double spirals. Simple meanders were not replaced by coiled meanders. The grazing patterns were mixed and did not reflect a change in species diversity with depth.

Analysis of foraging behavior with known depth did not result in refinement of the bathymetric potential of foraging behavior. Spiral and meander foraging patterns are depth indicators only at intermediate depths and are not absolute indicators of the bathyal to abyssal environment. There are several possible explanations. Spiral and meander foraging strategy may represent a primitive behavior that is not plastic enough to respond to a gradient in nutrient supply. Presence or absence of the trace may be due to ecological interactions (such as predation and competition) which dictate abundance and distribution patterns that are not solely caused by autecological properties of the organisms which pro-

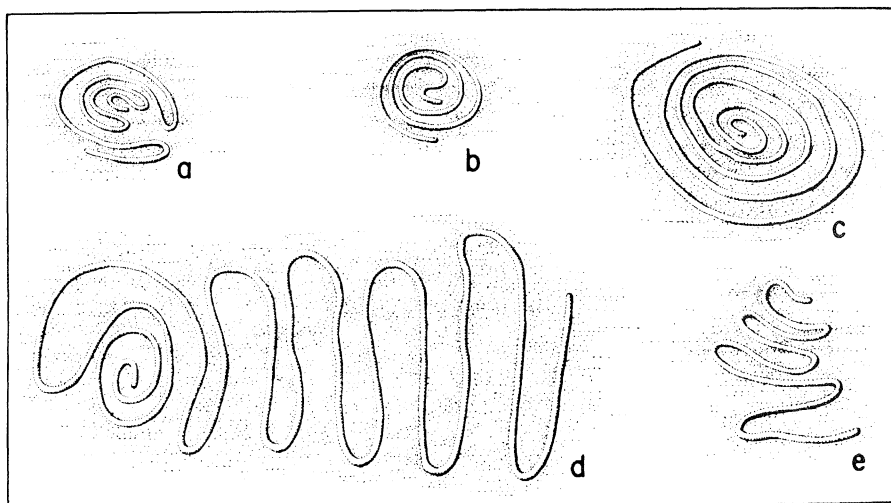


Fig. 2. Observed spiral and meander foraging types: (a) the coiled meander, *Eltanin* 14-4-1-6, 4152 m; (b) meander within spiral, *Eltanin* 15-28-29-19, 3550 m; (c) spiral, *Eltanin* 10-10-4-19, 4172 m; (d) spiral-meander, *Eltanin* 27-33-20-13, 3514 m; and (e) meander, *Eltanin* 27-33-20-7, 3514 m.

duce them, or may be affected by physical properties of the ingested sediment, such as particle size. Finally, the lack of behavioral response with depth may indicate a poor understanding of benthic trophic structure. Depth and food availability in deep-sea sediments may not correspond in a simple inverse proportionality as was recently suggested (17).

Spiral and meander traces in the deep sea are not distributed in proportion to assumed food availability. Although the depth stratification of ecologic interactions may in fact represent a gradient in trophic exchange processes, the presence and abundance of foraging traces is species-specific and not depth-correlative. Spiral and meander traces are relatively depth-specific and abundant in Antarctic waters but absent at similar depths in the Arctic. The presence or absence of a trace type may not be taken as a definitive depth indicator. However, because it is unlikely that deep-sea organisms will be studied experimentally, continued use of remote sensing photographic techniques can allow inferences with regard to paleobiologic relations.

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Human Lateralization from Head to Foot: Sex-Related Factors

Abstract. Sex differences in the pattern and maturation of lateral asymmetries of the human brain have been recently found by a number of investigators, suggesting that sex-related factors may differentially affect the two sides of the body. In this study, asymmetries in the size of the two feet were strongly related to sex and handedness, right-handed males having larger right feet and right-handed females having larger left feet, the reverse being seen in non-right-handed individuals. Since these differences were apparent even in children younger than 6 years, the fetal sex steroids may be critical in governing the maturation of both cerebral and pedal asymmetries.

A number of studies have reported functional differences in the patterns and maturation of cerebral lateralization in males and females (1). Witelson (2) found that right hemisphere functions mature considerably earlier in boys than in girls, and Reid (3) observed that in 5-year-olds the left hemisphere of girls and the right hemisphere of boys was more developed than that of the opposite half of the brain. This sex difference was found not only in right-handed children with language functions specialized to the left hemisphere and visuo-spatial functions to the right, but also in a subset of left-handed children with a reversed pattern of lateralization. Thus, relative hemispheric development as a function of sex was independent of the specializations of the two hemispheres, and the difference in boys and girls cannot, therefore, be attributed to sociocultural factors that might encourage different abilities in male and female children.

Since the differences in the sexes are apparent well before puberty, it seems reasonable to suggest that the fetal sex steroids may play a critical role in determining relative maturational rates of the

two half-brains and, possibly, of other bodily regions as well. Specifically, high concentrations of fetal sex hormones, present in the male, may asymmetrically enhance development of the right side of the body, while low concentrations of fetal sex hormones, present in the female, may asymmetrically enhance development of the left side of the body.

In this study we compared the sizes of the left and right feet of 150 individuals, 98 female of whom 18 were under age 6, and 52 male of whom 17 were under age 6. All data were collected by J.M.L. from customers in the shoe department of his clothing store located in a small Alabama town (Demopolis) in the western part of the state. Foot asymmetry was rated on a seven-point scale, ± 3 being assigned if one foot was larger than the other by a half shoe size or greater, ± 2 being assigned if one foot was larger than the other by less than half a shoe size, but by a readily obvious degree (approximately a quarter to a half shoe size), ± 1 being assigned when one foot was slightly (less than a quarter shoe size), but definitely, larger than the other, and 0 being assigned when either the feet were equal in size or when, though one foot appeared possibly larger than the other, the observer could not definitely rule out equality (4). Negative numbers were given if the left foot was larger than the right and positive numbers if the right foot was larger than the left. Handedness data were also obtained in an interview with the customer or, if a child, the parent. If an individual preferentially used the left hand for any skilled unimanual activity, he was placed into the nondextral group. When parents were uncertain of a young child's hand

Table 1. Distribution of right-handed and non-right-handed male and female subjects with respect to relative foot size.

Relative foot size	Right-handed		Non-right-handed	
	Males	Females	Males	Females
Left > right	2	55	6	0
Equal	10	18	6	2
Right > left	28	14	0	9
Total	40	87	12	11