4. M. Ewing, A. P. Crary, H. M. Rutherford, *ibid.* **48**, 753 (1937); S. Katz and M. Ewing, *ibid.* **67**, 475 (1956); B. C. Heezen, C. D. Hollister, W. F. Ruddiman, *Science* **152**, 502 (1966); B. C. Heezen, *Univ. Mo. Rolla J. V.H.M. McNutt Geol. Dep. Colloq. Ser. 1 No. 1* (1968), p. 5; J. I. Ewing, W. M. Ewing, R. Leyden, *Amer. Ass. Petrol. Geol. Bull.* **50**, 1948 (1966); R. E. Sheridan, C. L. Drake, J. E. Nafe, J. Hennion, *ibid.* **50**, 1972 (1966).
5. J. B. Hersey, E. T. Bunce, R. F. Wyrick, F. T. Dietz, *Bull. Geol. Soc. Amer.* **70**, 437 (1959).
6. G. G. Shor and R. W. Raitt, *Int. Geol. Congr. Mexico 20th Sect. 9* (1958), vol. 2, p. 243; E. L. Hamilton, *Bull. Geol. Soc. Amer.* **70**, 1399 (1959); K. O. Emery, *The Sea off California, a Modern Habitat of Petroleum* (Wiley, New York, 1960).
7. J. T. Wilson, *Sci. Amer.* **208**, No. 4, 86 (1963).
8. J. R. Heirtzler, G. O. Dickson, E. M. Herron, W. C. Pitman III, X. LePichon, *J. Geophys. Res.* **73**, 2119 (1968).
9. E. H. Bailey, W. P. Irwin, D. L. Jones, *Calif. Dep. Natur. Resour. Div. Mines Bull.* 183 (1964), p. 1.
10. V. H. Benioff, *Bull. Geol. Soc. Amer.* **65**, 385 (1954); *Geol. Soc. Amer. Spec. Pap.* **62**, 61 (1955); *Can. Dominion Observ. Publ.* **20**, 395 (1959).
11. A. Knopf, *Geol. Soc. Amer. Spec. Pap.* **62**, 694 (1955).
12. J. Gilluly, *Quart. J. Geol. Soc. London* **119**, 133 (1963).
13. ———, *Bull. Geol. Soc. Amer.*, in press.
14. This suggestion has been independently made by W. Hamilton, January 1969 (personal communication).
15. W. G. Ernst, *J. Wash. Acad. Sci.* **50**, 2 (1960); R. G. Coleman and D. E. Lee, *Amer. J. Sci.* **260**, 577 (1962); ———, *J. Petrol.* **4**, 260 (1963); W. G. Ernst, *ibid.*, p. 1.
16. R. G. Coleman, D. E. Lee, L. B. Beatty, W. W. Brannock, *Bull. Geol. Soc. Amer.* **76**, 483 (1965).
17. R. S. Dietz, *ibid.* **74**, 947 (1963); B. M. Page, *Calif. Dep. Natur. Resour. Div. Mines Bull. 190* (1966), p. 255.
18. K. J. Hsu, *Bull. Geol. Soc. Amer.* **79**, 1063 (1968).
19. B. Isaacs, J. Oliver, L. R. Sykes, *J. Geophys. Res.* **73**, 5855 (1968).
20. H. W. Menard, Jr., *Marine Geology of the Pacific* (McGraw-Hill, New York, 1964).
21. J. Ewing and M. Ewing, *Science* **156**, 1590 (1967).
22. E. Orowan, *ibid.* **146**, 1003 (1964).
23. L. C. Pakiser and J. S. Steinhardt, *Res. Geophys.* **2**, 123 (1964).
24. J. Gilluly, in *What's New on Earth* (Rutgers Univ. Press, New Brunswick, N.J., in press).
25. I thank P. Averitt, D. Lee, and P. Lipman for comment and discussion.

2 June 1969

Fossil Foraging Behavior: Computer Simulation

Abstract. *Meander patterns produced by ancient sediment feeders can be simulated by digital computer with x-y plotter output. Change in input constants (with a single program) produces variation comparable to genetically controlled behavioral differences between species and genera.*

Paleontology is usually confined to the description, distinction, and analysis of purely anatomical information. However, in explaining trails, burrows, and other trace fossils, it is possible to deal with the activities of organisms. Of the many activities (such as hunting, escaping, resting, and burrowing), sediment feeding in benthonic invertebrates produces the most regular patterns. Feeding patterns are best developed in deep-sea deposits (both Recent and ancient) because of the even distribution of food particles in most deep-sea sediments as opposed to the patchy distribution of food typical of shallow water environments (*1*). Uniform distribution of food favors compact grazing patterns that provide maximum coverage of a given area and minimum crossing of existing tracks. A compact pattern appears to be favored also because it reduces the chance of interference between individuals of a population of sediment feeders. These requirements have been met by a multitude of two- and three-dimensional trail and burrow patterns. However, meander systems are used most commonly—just as they are in human contour plowing and other agricultural activities.

Meanders forming in modern sediments are difficult to observe. The few examples known are either hidden within the sediment or restricted to deep-sea floors, beyond the reach of continued observation. The bulk of our knowledge thus comes from rocks of deep-sea origin, where the patterns are readily observed on bedding planes, particularly on the soles of turbidite beds.

Principles for the interpretation of fossil foraging behavior were developed by Richter (*1*). He pointed out that the animal that made the trace fossil known as *Helminthoidea labyrinthica* had its movements during feeding controlled by a set of basic reactions: (i) strophotaxis, that made the animal turn around 180° at intervals; (ii) phobotaxis, that kept it from crossing other tracks, including its own; and (iii) thigmotaxis, that made it keep close contact with former tracks. Richter's model was supplemented by Seilacher (*2*) who also suggested behavioral models for other types of meandering trace fossils, and pointed out that the phylogeny of certain behavioral patterns can be traced on this basis.

With these considerations, we have developed a digital computer program to simulate the foraging behavior. The program assumes that a hypothetical animal can sense its immediate surroundings and can convert the resulting information into behavioral instructions. The track itself is simulated as a sequence of points in a hypothetical two-dimensional space—each point being defined by a pair of coordinates in an x-y system. Each point represents a "step" taken by the animal. As the program is executed (that is, as new steps are generated) the points are plotted on an x-y plotter, and, because the plotter pen is held in the down position, a continuous line is produced.

The "animal" used for the simulation is assumed to be capable of four types of movement. It can move straight ahead, turn toward or away from a preexisting track, or make a full 180° turn. The choice of movements is determined by a search procedure simulating the presumed sensory system of the animal. Before each new x-y point is added to the track, the region of the x-y space in front of and to the side of the leading end of the track is searched for previously computed points. The information provided by this search is used to determine the direction of the step.

Examination of fossil meander patterns indicates that the 180° turns are made not only to avoid obstructions (such as a preexisting track), but also to confine foraging to a relatively small area. There is considerable variation in the frequency of such turns, which leads to variation in meander length; the variation in meander length is simulated in the program with the use of random number generation to determine the lengths of those meanders not terminated by obstructions.

The program provides for a starting configuration consisting of a straight track (of arbitrary length) ending in a 180° turn. The search procedure described above starts only after the initial turn is executed. If the length of the initial straight track is made very small, the simulation starts in effect with a turn. If no other turns are specified (or if meander length is made very long), the result will be an Archimedes spiral—a common pattern in trace fossils.

Several behavioral characteristics were varied from one simulation to the next. Principal among these are: (i) the turning radius for 180° turns; (ii) the mean distance between a developing track and preexisting tracks; (iii) the allowable deviation from this mean distance; (iv) the relative intensities of thigmotaxis and phobotaxis (expressed as the angle of turn made to move toward an existing track relative to that for movement away); (v) the mean length of meanders not terminated by obstructions; and (vi) the variability in the length of such meanders.

Running the program several times without changing the behavioral controls produced different output patterns (caused by the random selection of meander length). This variation is strikingly similar to differences between individual patterns within a single species of trace fossils. Changing behavioral controls from run to run causes more marked differences in pattern, these being comparable to differences actually observed between species and genera.

Figures 1, 2, and 3 show typical examples of computer output (right) and actual foraging patterns (left). The example in Fig. 2 calls for special consideration. This is a case where the animal's thigmotaxis is so weak that, after a 180° turn, close contact with the earlier track is restored only after about half the length of the meander. Beyond this point, the earlier track is followed closely until a new 180° turn is signaled. This pattern is presumably not as efficient as more compact meander patterns because large areas are left untouched. It suggests that thigmotaxis and phobotaxis may reasonably be considered as genetically distinct behavioral reactions.

The simulations demonstrate that it is possible to look upon a considerable variety of two-dimensional foraging patterns as resulting from one behavioral model. The examples differ only in elements controlled by chance and by the input controls (primarily the six listed above). What actually corresponds to our program in a given animal is not known, but it is clear that the genetic controls need not be more complicated than our model. The wide applicability of a single computer program suggests that the biological analog may not be very different.

Many more species patterns could be simulated by computer with little or no elaboration of the program. This would lead to a better understanding of the change of parameters necessary to transform one species or variant into another and would also have some effect on the classification of these trace fossils. But simulation becomes increasingly difficult as more complex behavioral patterns are tackled, and is probably impossible in many cases. The primary value of the simulation studies is not to be found on the level of factual results. The mere presence of the computer method encourages rigorous analysis of meander patterns in trace fossils. Each tentative model can be tested at will. In a sense, therefore, the simulation process has most value before it is successful.

DAVID M. RAUP
Department of Geological Sciences, University of Rochester, Rochester, New York 14627

ADOLF SEILACHER
Department of Geology, University of Tübingen, Germany

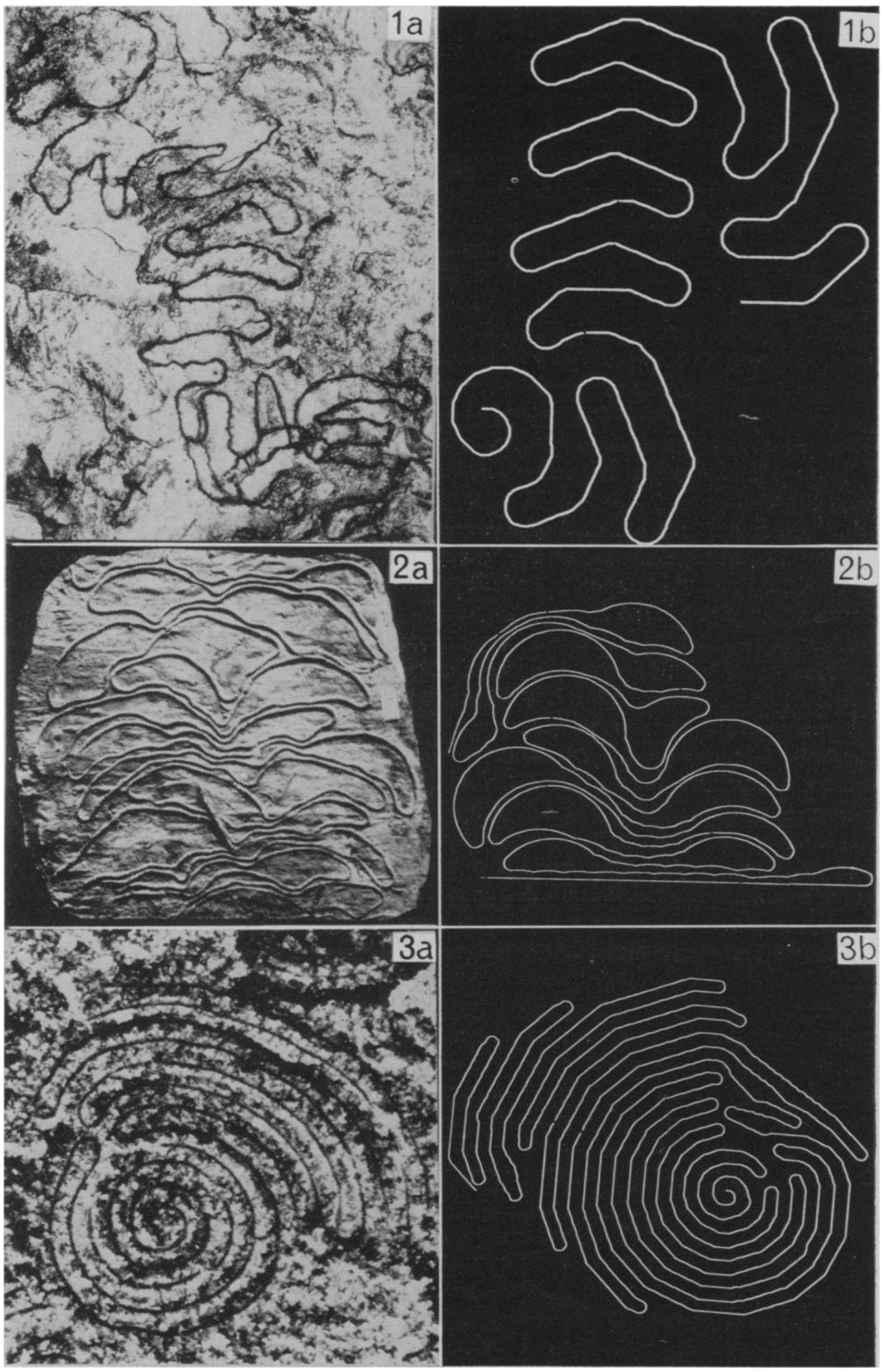

Fig. 1. (a) Loose meanders of *Dictyodora* (Ordovician flysch; Barrancos, Portugal; Tübingen catalog No. 1368/2; × 0.5) and (b) comparable computer output. Fig. 2. (a) A complex meander (Cretaceous flysch of Italy; × 0.3) and (b) its simulation (see text). Fig. 3. (a) Burrows of living beach worm *Paraonis fulgens* (natural size; photograph by H. Roeder) and (b) its simulation.

References and Notes

1. R. Richter, *Palaeobiologica* **1**, 226 (1928).
2. A. Seilacher, *Sci. Amer.* **217**, No. 2, 72 (1967).
3. Supported by the Petroleum Research Fund administered by the American Chemical Society.

27 March 1969