TRAIL-PRODUCING BEHAVIOR OF *OLIVA SAYANA* (GASTROPODA) IN THE LOWER FORESHORE AT BOGUE BANKS, NORTH CAROLINA

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ABSTRACT

Olive snails living on a very low-gradient, fine to medium sand substrate in the lower foreshore at Pine Knoll Shores produced two kinds of surface trail. Most olives made short, straight to slightly curved trails only a few 10's-of-cm's long, then dived below the surface pushing up a crescent-shaped pressure ridge of sand ahead of the shell. A few snails, however, including some that were experimentally exhumed, prolonged their surface exposure and produced elaborate trails > 100 cm in length. Prolonged exposure often was related to disturbance: exhumed snails wandered across the beach during low tides in an attempt to locate wet, soft sand for reburrowing, and sometimes "floundered" when suitable substrate could not be located. Trails made in this way have wide-looping sections followed by circling/meandering parts. Some snails may have been simply "dawdling", but none of the olives observed, during daylight at this location, seemed to be searching for food. Although interpretation of shapes of trails in plan view is problematic (as would be the resulting trace fossils), cross-sectional shape of the trails is clearly a result of water content and firmness of the sand substrate. Trails having V-shaped cross sections and indistinct marginal levees were produced in soupy sand; U-shaped cross sections having overarching upper limbs were made in wet, firm surfaces; and rectangular cross sections with discontinuous levees were produced by olives moving over dry, hard sand.

INTRODUCTION

We are accustomed to thinking of the phenotypic properties of invertebrate animals, including behavioral systems represented in trace fossils such as burrows and trails, as being wholly adaptive or efficient. If the behavior of organisms were not efficient, the expected results should include reduced fitness, competitive displacement, and exposure to predation. Behavioral aspects of phenotypes ought to be solutions to problems of staying alive in the short run, and ultimately a means of leveraging genes into subsequent generations. This is largely true, but certain activities of organisms do not appear to be efficient uses of energy or adaptively advantageous. Part of this apparent inefficiency results from organisms finding themselves in situations not accommodated by their behavioral programs, and part could be owing to the fact that not all behavior has an immediate, adaptive application. Using human-related metaphors, the former would be floundering, and the latter is a kind of dawdling.

In June, 1995, I observed the trail-producing behavior of *Oliva sayana* Ravenel, 1834, on the ocean beach at Pine Knoll Shores, approximately 15 km west of Beaufort Inlet on Bogue Banks (Fig. 1). The locality has been described by Miller (1995). Specifically, I photographed olives on a very low-gradient, fine to medium sand substrate, in the lower foreshore during a series of low tides (Fig. 2). I also induced the snails to produce traces by exhuming them. Olives appear to be confined to such low-gradient, relatively lower-energy sandflats in this area.

OLIVA SAYANA AT PINE KNOLL SHORES

Olive shells are a familiar component of shelly deposits on North Carolina beaches in the vicinity of Cape Lookout. Living specimens of *O. sayana* are found on exposed and protected sand beaches and intertidal flats (Pearse *et al.*, 1942; Abbott, 1968, 1974; Porter, 1974; Gosner, 1978; Dover and Kirby-Smith, 1979; Meyer, 1994; Abbott and Morris, 1995). Although the largest populations are located in lower intertidal to shallow subtidal environments, a few records have the species in deeper subtidal settings (see Porter, 1974; Dover and Kirby-Smith, 1979). The snail is a motile, shallow-burrowing predator/scavenger that often occurs in localized aggregations or patches (Olsson and Crovo, 1968; Dover and Kirby-Smith, 1979; Meyer, 1994). Maximum density of individuals at Pine Knoll Shores was in the order of 0.5 to 2 snails/m^2. Olives have a patchy distribution here, owing to patchiness of suitable substrate, but within patches individuals did not appear to be aggregated. *Donax variabilis* is extremely abundant at the study site and may be the main prey of olives here (Dover and Kirby-Smith, 1979, p. 21). *Oliva sayana* also is a well known component of nearshore Pleistocene deposits in coastal North Carolina (Richards, 1950, 1962; Du Bar *et al.*, 1974). Some of the empty shells on local beaches could be reworked, both from Pleistocene units and from relict Holocene deposits on the continental shelf (Mixon and Pilkey, 1976; Miller, 1995).

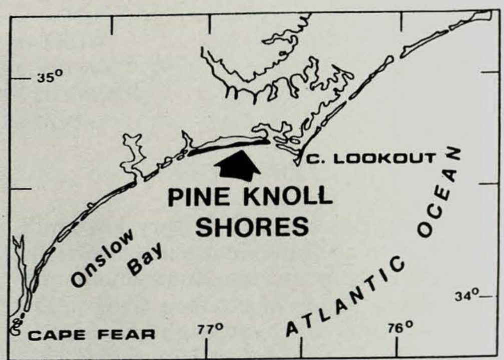

Figure 1. Map showing location of study site on Bogue Banks.

TRACE-PRODUCING BEHAVIOR

There have been few detailed studies of burrowing and trail-making behavior of *O. sayana*. Olsson and Crovo (1968) described behavior of aquarium specimens, emphasizing feeding and reproductive activities. Robert W. Frey and his co-workers mention trails and burrowing behavior of olives in coastal Georgia, as part of their characterizations of modern depositional environments (Frey and Howard, 1969, p. 428-429; Dörjes, 1972, figs. 3 and 4; Howard and Dörjes, 1972, figs. 11 and 14; Howard and Frey, 1980, fig. 21B). These studies documented *O. sayana* as a shallow-tier burrower in beach-related tidal flats and described the species commonly co-occurring with the olives (Frey and Howard, 1972; Howard and Dörjes, 1972). Actual trace-producing behavior was described only generally.

Probably the best description of burrowing was presented over fifty years ago by Pearse *et al.* (1942, p. 150, fig 6). They described the following style of burrowing:

> "Those [burrowing sandflat organisms] that have a very broad foot, secrete much slime, and plunge directly into wet sand (Polynices, Oliva, Olivella, Sinum). These have smooth shells more or less enveloped by the mantle...Oliva [*O. sayana*] has a shiny shell shaped like a torpedo...which readily penetrates sand...A speedy burrower [one specimen of *O. sayana*]...covered itself in 1 minute, 30 seconds..."

They recorded the stages of burrow initiation in a series of photographs taken at 15-second intervals.

Frey and Howard (1972 p. 175, fig. 4) used x-radiographs to show *O. sayana* producing a bioturbate texture in sand. They noted that "...bioturbation by many animals together [including *O. sayana* in the x-radiograph] produces streamy, ropy, or otherwise more irregular textures than those ordinarily seen in cores or other vertical exposures...". In the wet sand of ocean beaches and tidal flats, subsurface burrowing by *O. sayana*, then, is more likely to produce diffuse biodeformation structures than discrete burrows (see Bromley, 1996, p. 8 and 24-25 for description of "intrusion" burrowing causing eddy diffusion patterns and this kind of homogenization of the sediment).

Trail-producing behavior is seldom described in the literature, but is well known to shell collectors. Dover and Kirby-Smith (1979, p. 21) mention that "... olives are predaceous, nocturnal snails... As they move in search of food, they leave a furrowed trail." My observations suggest that feeding behavior is not the only behavioral system resulting in the generation of surface trails.

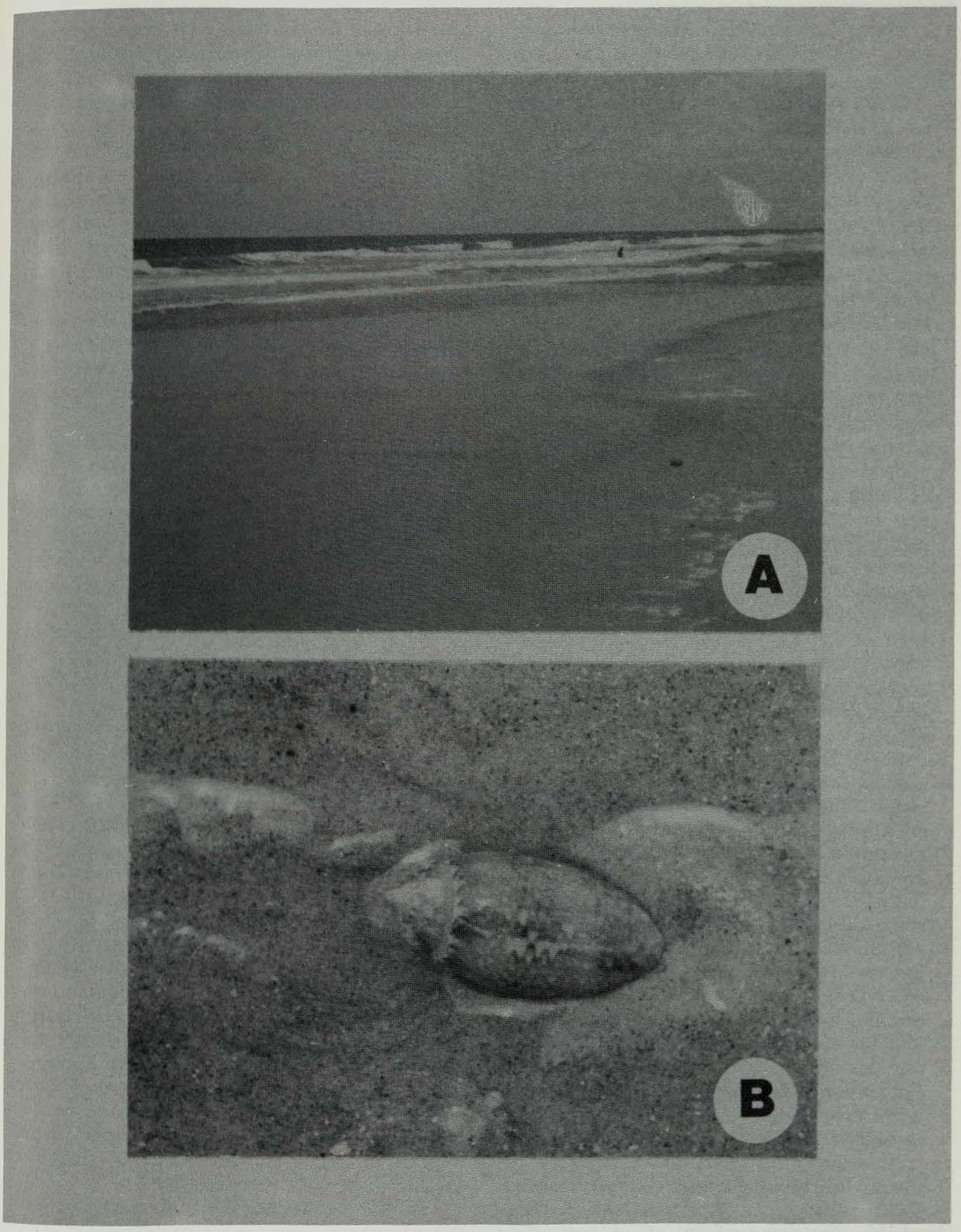

Figure 2. Study site. A, Very low-gradient stretch of beach showing the lower foreshore during a low tide in June, 1995. B, *Oliva sayana* initiating a burrow. Note the large amount of cloudy mucus in the vicinity of the shell and the pressure ridge formed in the sand by the snail diving below the surface. The shell in this photograph, and the shells in Figs. 3 and 4, are approximately 6 cm in length.

OLIVE TRAILS AT PINE KNOLL SHORES

Olive snails are easily located during low tide on nearly flat stretches of beach in the lower foreshore zone. Covered snails were found by locating "dimples" on the surface where olives had recently tunneled into the beach (Fig. 2B). The dimples were produced when snails dived below the surface, pushing up a crescent-shaped pressure ridge of sand ahead of the shell. Most snails dived at angles of 10°-40° relative to the surface and often produced a large quantity of mucus either just before or as burrowing was initiated. Some of the dimples were at the end of trails having varied cross-sectional shapes.

Trails produced in soupy sand were V-shaped in cross section and had indistinct levees (Fig. 3B). In firmer sand, U-shaped furrows were produced having overarching upper limbs (Fig. 3A). These are essentially shallow, horizontal burrows with part of the roof missing. On hard, dry sand, the trails were rectangular in cross section and had irregular, discontinuous levees (Fig. 3C). Water content of the substrate is the primary control of these shapes.

Most of the trails were short, straight to slightly curved structures a few 10's-of-cm's in length, but a few were curved to meandering traces > 100 cm long. At Pine Knoll Shores, during low tides and during daylight hours, most olives attempted to cover themselves without delay to prevent exposure on the sandflat. Presumably, prolonged exposure would increase the chances of encounter with predators (mainly birds at this location) and physiologic stress caused by high temperatures and desiccation. The tendency to reburrow immediately after exposure, however, was not ubiquitous. Some of the snails remained at the surface or were only partially concealed in sand for 10's-of-minutes, while moving across the lower beach. Because potential food such as *D. variabilis* was ignored by the wandering snails, olives apparently were not prolonging exposure to search for food, at least not while I watched them. Olives may have become exposed by localized scour accompanying the falling tide, but it is also possible that they emerge on their own in response to some form of environmental stimulus (indicating a self-initiated *action pattern* in the terminology of ethologists [Dawkins, 1986]).

I located several dimples, showing the position of recently covered olives, during three separate low tides, and dug up the snails to observe any trace-producing behavior in response to the exposure. After reorienting their bodies to bring the foot into full contact with the substrate, artificially disturbed olives either produced short trails and then suddenly plunged below the surface, or as described above, they wandered over the sandflat producing long, elaborate trails. Figure 4 shows the trail produced by an exhumed individual that wandered over the sandflat rather than reburrowing immediately. The consistency of the sand substrate was changing rapidly, from firm and wet to hard and dry, during the interval of the three photographs (30 - 40 minutes). The snail was exposed over 10 times longer than the individuals that reburrowed quickly, and produced a composite trail having an earlier wide-looping part (featuring U-shaped cross sections) and a later circling to tightly meandering part (having rectangular cross sections) centered at the middle of the trail system. The long axis of the wide-looping section was oriented more or less perpendicular to the trend of shoreline, suggesting that the snail was prolonging exposure and producing the long trail while trying to locate soft, wet sand for reburrowing. Not all of the long trails at the same location were oriented in this way. On essentially flat areas of the beach, disturbed olives may not be able to judge direction to the ocean and wetter substrates. As the substrate became dry and hard, the snail in Figure 4 produced the circling and meandering part of the trail. This pattern seems to record searching for wet sand, followed by an interval of "floundering" when suitable substrate had not been located.

Snails produced the elaborate surface trails when they were exposed for long periods of time, but it was not always clear why the snails postponed reburrowing in the first place. The long, complex trails are not necessarily related to feeding behavior. Such structures in certain

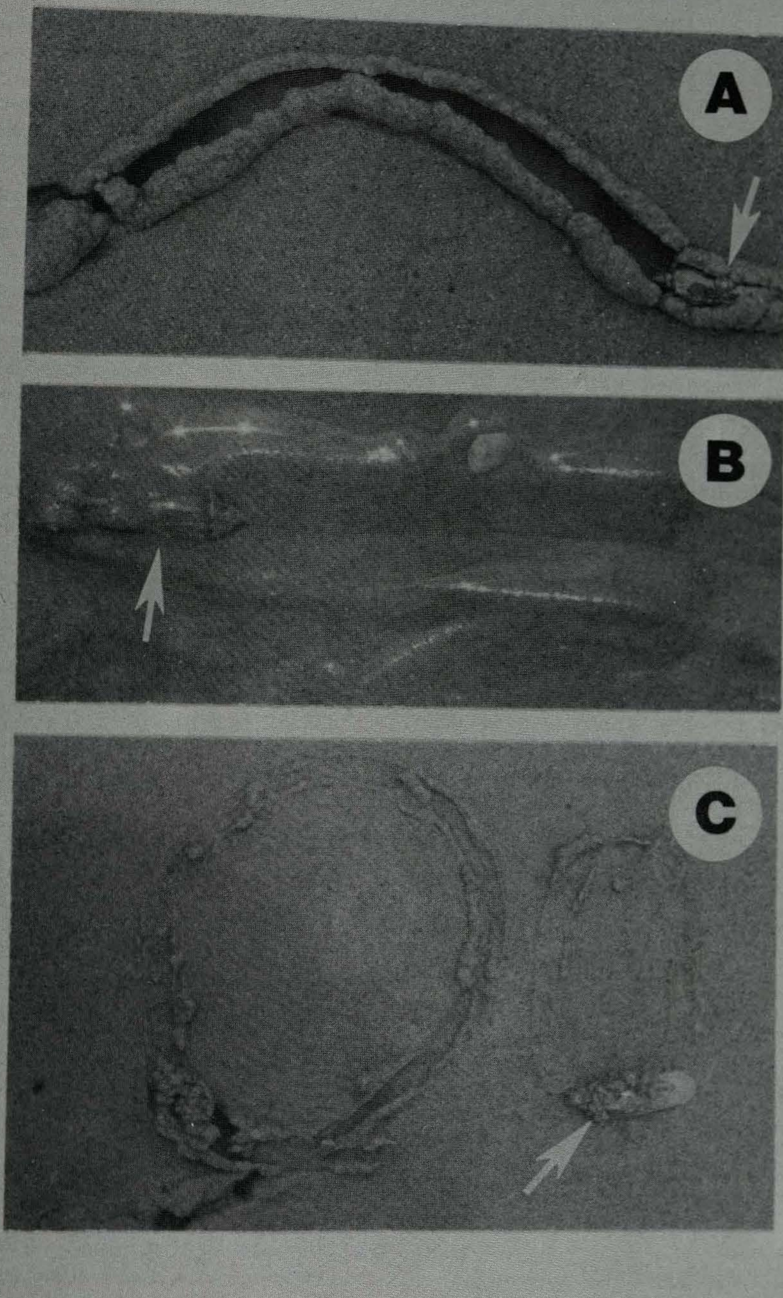

Figure 3. Substrate consistency controlling cross-sectional shapes of surface trails. A, U-shaped in wet, soft sand. B, V-shaped in soupy sand. C, Rectangular cross sections in dry, firm sand. Arrows indicate position of the olives.

cases seem to represent reaction to disturbance (being exposed at the surface) and a fruitless attempt to locate a suitable place to reburrow in wetter, softer sand (Figs. 3C and 4). Long trails produced in soft, wet sand, which were not made by snails searching for food, have no obvious function or purpose (Fig. 3A).

POTENTIAL TRACE FOSSILS

Surface trails like the ones made by *O. sayana* in the lower foreshore at Pine Knoll Shores are likely to be destroyed by erosion. Populations of the same species living on more protected sandflats in the same area, however, could produce preservable structures (see Dover and Kirby-Smith, 1979, p. 8-9). Ichnologists would identify such trails with ichnogenera such as *Archaeonassa* or possibly the all-inclusive *Scolicia* (see Buckman, 1994). From a paleoethologic point of view, wide-looping trails would suggest *repichnia* (locomotion) or *pascichnia* (grazing activity); circling or meandering trails would be interpreted as *pascichnia* or *praedichnia* (referring to predatory behavior). The olive trails that I observed apparently were neither ordinary repichnia nor were the trace producers searching for food, at this particular time and place. Although trail cross-sectional shapes would record water content and substrate consistency unambiguously, overall shape of trails in plan view could reflect reaction to disturbance or something akin to volition *as well as* ordinary movement and feeding activity.

ACKNOWLEDGMENTS

I thank Mr. and Mrs. Daniel Leitch, III, for their generous hospitality at Pine Knoll Shores. Rosemary Hawkins typed the manuscript. A special acknowledgment is due to Dr. Emily H. Vokes, my friend and mentor, for keeping this interesting, high quality journal alive and well for three decades.

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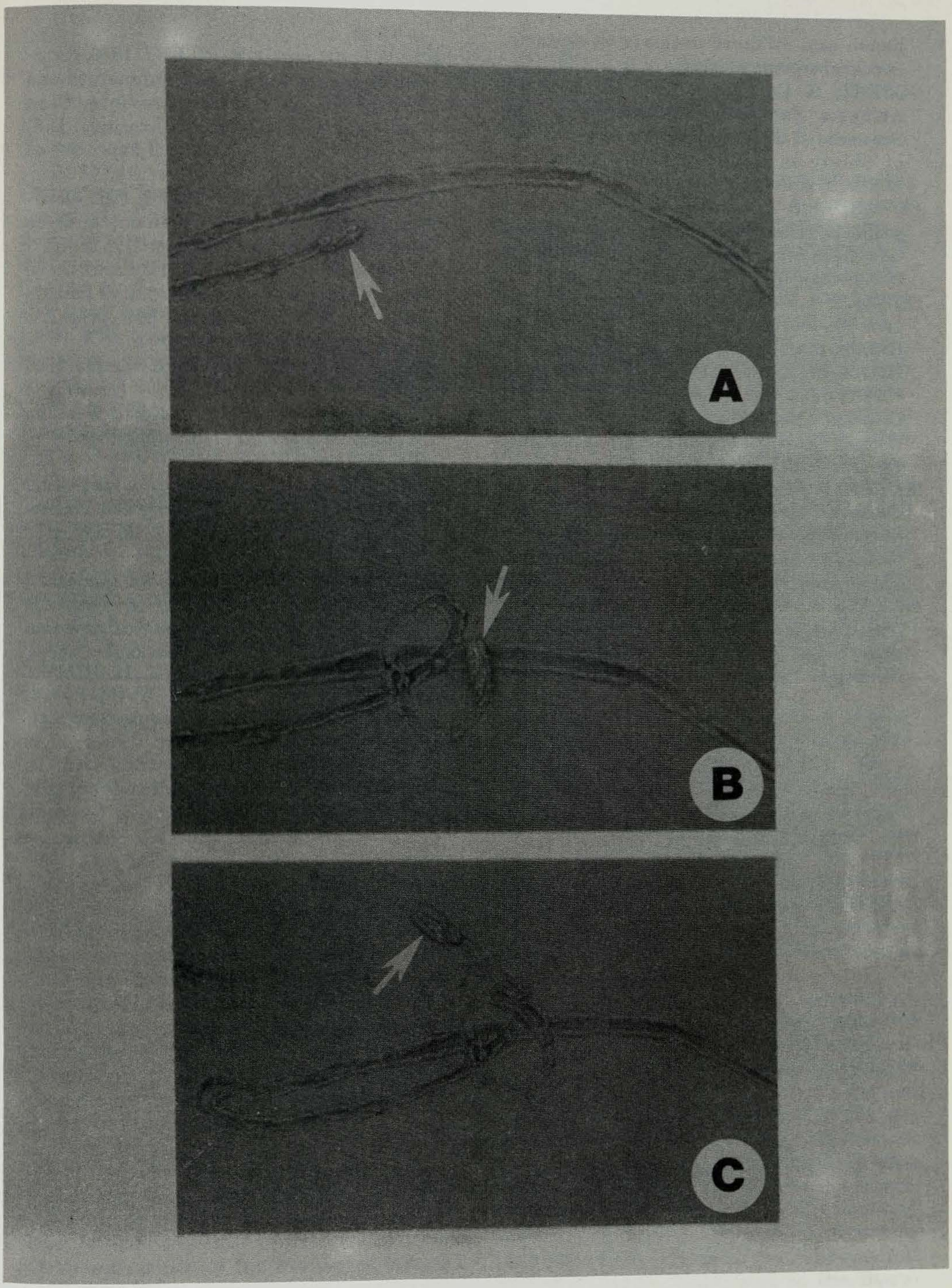
Figure 4. Olive exhumed during low tide producing a long, elaborate trail rather than reburrowing immediately. A, Generation of wide-looping trail. B, Initiation of circling/meandering pattern. C, Position of olive (arrow) at end of composite trail after 30 - 40 minutes of surface exposure.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August 27, 1997