

Therefore, it appeared that only those steroids with biological glucocorticoid and/or mineralocorticoid activity were capable of stimulating growth hormone synthesis.

The results of these and previous studies (1) suggest that glucocorticoids at physiological levels have a direct effect on pituitary cells in culture, causing an increase in growth hormone synthesis. These findings are in contrast to the suppressive effect of pharmacological doses of cortisol on growth hormone release (8). The GH₁ cells provide a model system with which to study the mechanism of the cortisol-induced synthesis of a specific protein and the control of growth hormone production in vitro.

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Bivalve Mollusk Burrowing Aided by Discordant Shell Ornamentation

Abstract. Oblique and chevron-like ridges on the shell surfaces of certain burrowing bivalve mollusks grip the sediment during shell-rocking movements to aid in sediment penetration. These ridges (characterized by steep dorsal slopes and gentle ventral slopes) have evolved through convergence in several families in association with particular behavioral and ecological traits.

Analysis of mechanical functions of present-day skeletal features can provide important information for interpreting the evolution and paleoecology of fossil groups. Bivalve mollusks, because of their high ecologic and taxo-

nomic diversity in both modern and ancient seas, offer great potential for the functional morphologic approach. One of the most significant shell features of burrowing bivalves is the configuration of surface ornamentation.

Oblique and chevron-shaped ridges, especially, have aroused curiosity because they have evolved independently in fossil and living species of several families and because they represent departures from normal shell geometry (1). I have analyzed the function of such ridges for three living genera and found that they serve as mechanical aids to burrowing.

Most ridged ornamentation in bivalves follows simple concentric or radial patterns. Concentric ridges are secreted periodically during shell growth by the entire mantle edge (which underlies the shell margin). Radial ridges are the product of continuous secretion by discrete zones of the mantle margin. Unusual ridge patterns of the type considered here (discordant ridges) transect both concentric and radial structures and are secreted by migration of ridge-secreting zones along the mantle edge during growth. Secretion of chevron-shaped discordant ridges (Fig. 1) further requires periodic formation of new ridge-secreting zones at central positions, from which the zones divide and migrate in opposite directions.

In the four living species I have studied (*Tellina similis*, *Strigilla canaria*, and *Strigilla mirabilis* of the Tellinacea and *Divaricella quadrisulcata* of the Lucinacea) the ridges are asymmetrical, dorsal slopes being steeper than ventral slopes. Shells of the *Strigilla* and *Divaricella* species are nearly circular in outline, and the ridges form a chevron-like pattern. These species are restricted to clean sand substrata, where wave or current scour commonly necessitates downward movement for maintenance of normal burial depths. They are deep burrowers, living at sediment depths several times their shell lengths. Burrowing paths were studied by time-

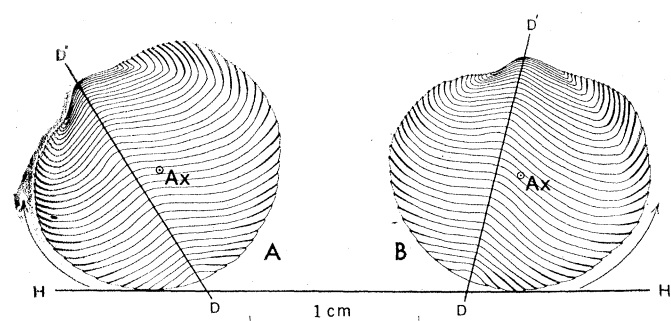


Fig. 1. Mechanism by which chevron-like ridges aid burrowing of *Divaricella quadrisulcata*. (A) Shell orientation at maximum forward rotation. (B) Shell orientation from which forward rotation begins. Ax, axis of rotation; D-D', demarcation line between anterior and posterior portions of ridges; H-H', horizontal line. Arrows indicate angle and direction of rotation from each position.

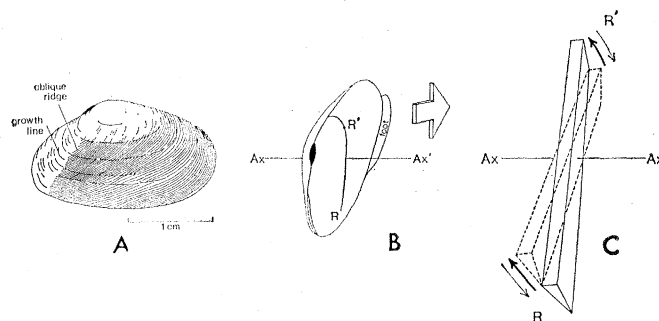


Fig. 2. Mechanism by which oblique ridges aid burrowing of *Tellina similis*. (A) Lateral view of shell. (B) Oblique dorsal view of burrowing animal (schematic), large arrow showing direction of sediment penetration. (C) Diagram of a single ridge of ornamentation, heavy and light arrows denoting rotation opposed by large and small frictional forces, respectively. Ax-Ax', axis of rotation; R-R', single ridge.

lapse x-radiography of animals permitted to burrow in narrow sediment-filled aquaria. Downward movement in all three species is nearly vertical (before assumption of normal feeding positions). Burial is achieved through a succession of distinct downward movements, each of which is accomplished by a well-patterned muscle contraction sequence. The sequence is nearly identical for the great majority of bivalve species and usually culminates in a forward-and-back rocking motion (2). In the three circular species under discussion, shell rotation is remarkably smooth, and the angle of rotation is relatively large (30° to 45°).

Mechanical operation of the asymmetrical chevron-shaped ridges is illustrated by *Divaricella* (Fig. 1). During forward rotation from position B, the steep dorsal ridge slopes posterior to the demarcation line (*D-D'*) grip the sediment in a rasp-like manner, carrying sediment upward and forcing the shell downward. The gentle ventral ridge slopes anterior to the demarcation line slip through the sediment with less friction. During backward rotation from position A, the frictional disparity is reversed, and the anterior parts of ridges aid in penetration. The anterior position of the demarcation line reflects the anterior direction of rocking movement from position B.

In *Tellina similis*, a more elongate species, the discordant ridges pass obliquely across the shell surface (Fig. 2A). The species lives in muddy sand and, being a deposit feeder, requires an efficient burrowing mechanism for lateral migration when it depletes local food supplies. Rocking movements are rapid and pass through a very small angle (less than 15°). Anterior and posterior portions of ridges alternately grip and slide through the sediment (Fig. 2C) to aid in substratum penetration. The ridges are oriented at approximately right angles to the direction of substratum penetration, which maximizes their effectiveness.

Asymmetrical discordant ridges are apparently restricted to sand-dwelling species. Most subtidal muds are too fluid to be gripped effectively. The ridges are also apparently restricted to species with some cause for periodic burrowing, such as need to offset sediment scour or to migrate during deposit feeding.

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Ontogeny of Adrenergic Arousal and Cholinergic Inhibitory Mechanisms in the Rat

Abstract. *With spontaneous activity as a measure of arousal, dose response curves were established for scopolamine and amphetamine administered to 10-, 15-, 20-, 25-, and 100-day-old rats. Amphetamine always increased activity, but scopolamine had no effect on younger rats, which suggests that adrenergic excitatory areas in the brainstem mature more rapidly than cholinergic inhibitory areas in the forebrain.*

Generalized excitatory and inhibitory systems in the brain regulate overall levels of arousal. The major excitatory center is thought to be the brainstem reticular formation. When activity in this area is destroyed by lesions, stupor results (1); when the area is activated by electrical stimulation, electrocortical and behavioral arousal occurs (2). Acting in opposition to this excitatory region are certain forebrain structures which serve to modulate reticular excitability. When these centers or their connections with the brainstem are impaired, the effects of reticular stimulants are greatly augmented (3). When this area is activated by electrical stimulation, arousal is depressed (4).

The biochemical substrates of the arousal areas in the hindbrain and inhibitory centers in the forebrain are distinct, with the former primarily adrenergic in nature and the latter predominantly cholinergic (5). Amphetamine, which mimics adrenergic transmission by release of norepinephrine (6), particularly in the brainstem (7), induces large increments in locomotor activity, while adrenolytic agents depress arousal and generally lead to sedation (8). The anticholinergic drug scopolamine, which blocks acetylcholine transmission by occupation of postsynaptic sites (9), produces marked increments in activity (10), while anticholinesterases (11) and cholinomimetic agents (12) depress arousal.

It is now generally accepted that the

development of the brain proceeds rostrally with phylogenetically primitive hindbrain structures maturing earlier than the younger forebrain systems (13). Thus neonatal animals should pass through a phase during which they are responsive to reticular stimulants and unaffected by cholinergic blocking agents because of the functional absence of forebrain inhibitory mechanisms. We now show that the neonatal rat is responsive to the reticular stimulant amphetamine, before it is responsive to scopolamine, an inhibitor of forebrain cholinergic activity.

Degree of behavioral arousal was measured in stabilimeter activity cages scaled to the size of the animal. The largest cages, those used for the adults (14) consisted of wire mesh cages, 17.5 by 20.0 by 37.5 cm, mounted on a central axle which permitted the cage to tip slightly and activate a sensitive switch as the rat moved from one end to the other. For 10-day-old rats the cage dimensions were scaled down to 6.3 by 7.5 by 13.7 cm, and for 15-, 20-, and 25-day-old rats the cage was 8.7 by 10.0 by 18.7 cm. The activity cages were housed in temperature-controlled cubicles maintained at 29°C for the 10-, 15-, 20-, and 25-day-old rats and at 22°C for the 100-day-old rats.

Dose response curves for both amphetamine and scopolamine were determined at five different ages: 10, 15, 20, 25, and 100 days. At each dose 10 to 16 rats were tested, and each rat was tested only once. A total of 772 Sprague-Dawley rats were used, half of which were male and half female.

Rats were removed from living cages in a central colony room, placed in the activity cages for a 30-minute habituation period, and then injected with one dose of either *d*-amphetamine sulfate (0.250, 0.50, 1.0, 2.0, 4.0, or 8.0 mg/kg, salt weight), scopolamine hydrochloride (0.125, 0.250, 0.50, 1.0, 2.0, or 4.0 mg/kg, salt weight) or an equivalent volume of the 0.9 percent saline vehicle. They were then returned to the cages for 2 hours; during this time the number of crossings was recorded on printing counters every half hour. In addition, methylscopolamine hydrobromide (0.125, 0.250, 0.50, 1.0, 2.0 or 4.0 mg/kg, adjusted for equivalent amounts of scopolamine), a drug which does not cross the blood-brain barrier in significant quantities (15), was administered to a group of 25-day-old rats for control of the possible peripheral effects produced by the sco-