

Recently, Gold (4) extended Hill's model to cover a range of speeds, arguing that if animals increase speed by increasing stride frequency, and if the work per gram per stride is constant over the entire range of speeds, this would explain the empirical relation between energetic cost of running and body size in mammals (1). We have found that stride frequency and stride length both increase with increasing speed, and that within a gallop speed is increased primarily by increasing stride length while frequency remains nearly constant. At comparable speeds (such as at the trot-gallop transition), however, Gold's argument remains valid for geometrically similar animals. McMahon (3) suggested a model based on elastic similarity whereby animals regularly thicken their proportions as body size increases. Herschman (5) extended Gold's argument to conform to an elastic similarity model and predicted that stride length will be proportional to  $W^{0.375}$ . McMahon (6) has also used his model to predict that running speed is proportional to  $W^{0.25}$  and stride frequency is proportional to  $W^{-0.125}$  at the trot-gallop transition (7). Both Herschman's and McMahon's predictions are in substantive agreement with the data reported here.

We propose that the speed at the trot-gallop transition point is a "physiologically similar speed" for animals of different size. It has the advantage over top speed that it can be easily measured. If one uses this transition point to construct new scaling models, however, it is important to understand why animals change gait at this point. It seems likely that at the transition to each gait additional elements of the body are recruited for storage of elastic energy, with little energy being stored in elastic elements during walking, energy being stored in the elastic elements of the limbs during trotting, and finally, the entire trunk being involved in elastic storage during galloping. This remains very speculative and much more work is needed before the reasons for changing gaits can be clearly defined.

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#### References and Notes

1. C. R. Taylor, K. Schmidt-Nielsen, J. Raab, *Am. J. Physiol.* **219**, 1104 (1970).
2. A. V. Hill, *Sci. Prog.* **38**, 209 (1950).
3. T. A. McMahon, *Science* **179**, 1201 (1973).
4. A. Gold, *ibid.* **181**, 275 (1973).
5. A. Herschman, *Am. J. Phys.* **42**, 778 (1974).
6. T. A. McMahon, in preparation.
7. As explained in (3), elastic similarity between animals of different body weight requires that the diameter ( $d$ ) of every element (bone, muscle, limb) be maintained proportional to the  $3/2$  power of the length ( $l$ ) of that element. Thus  $l$  increases as  $W^{1/3}$ , but  $d$  increases as  $W^{3/8}$ . Suppose a stimulated muscle and its tendon are thought of as a spring, and this

spring acts at each joint as a restoring force against forces produced by inertia. For a sufficiently large number of joints, we can model the skeleton and its musculature as a continuous beam, for which the group  $f^2 l^3 / d^2$ , where  $f$  is the natural frequency, is a constant (eigenvalue) in a given mode of vibration. Setting  $l \propto W^{1/3}$  and  $d \propto W^{3/8}$ ,  $f$  is proportional to  $W^{-1/8}$ . Galloping animals are thus seen as mass-spring-lever systems vibrating at their resonant frequencies. By fixing their stride length at the trot-gallop transition proportional to  $d$  and hence proportional to  $W^{3/8}$ , they fix their speed proportional to  $fd$  or  $W^{-1/8+3/8} = W^{1/4}$ .

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## Vermetid Gastropods and Intertidal Reefs in Israel and Bermuda

**Abstract.** *Small-rimmed intertidal reefs develop in the subtropical marine waters of Israel and Bermuda when erosion of exposed promontories is arrested by vermetid gastropods. The reefs in Bermuda are actively growing, wave-resistant biogenic structures, while those in Israel are limestone structures only encrusted by a relatively thin layer of vermetid shells cemented by coralline algae.*

Several species of vermetid gastropods are gregarious, and encrust intertidal bench-like ledges or form massive reefs (1). This report describes reefs in Shikmona, on the Mediterranean coast of Israel (32°49'N, 34°57'E), and in Bermuda, which is at the same latitude and has several similar physical marine conditions (2). In both cases vermetids have a significant role in reef development (3). The reefs are small intertidal formations 2 to 5 m in diameter resembling miniature atolls (Fig. 1) and are usually circular with raised, overhanging rims somewhat higher at the seaward side. They enclose a shallow basin with a flat bottom in Shikmona and a deep cup-shaped hollow in Bermuda.

The Shikmona reefs are made of limestone encrusted by vermetids. The limestone relief is leveled off and surrounded by an elevated rim about 10 cm high, covered by a crust of *Dendropoma petraeum* (Monterosato) 10 to 15 cm thick. The basin is covered by a crust of *Vermetus triquetrus* Bivona-Bernardi 2 to 4 cm thick. The rim is incessantly swept by the surf and is exposed to the air at low tide; the basin is protected from the full impact of the waves and from exposure to air by the water retained by the rim. Correspondingly, the short, rugged shell of *D. petraeum* is tightly sealed, with a wide operculum which protects the animal from predators, desiccation (4), and wave impact. The shell of *V. triquetrus* is longer and thinner, with a fragile, upturned terminal part, and the tiny operculum is nonfunctional, allowing the animal to withdraw deep into the shell (4).

Both species are plankton-feeders. *Vermetus* produces a mucus web, and agitation at the reef's rim would probably render its employment difficult. *Dendropoma petraeum* filter-feeds through a well-developed gill (5), and turbulence at the reef's rim ensures a food supply and facilitates water inhalation.

In Shikmona "microatolls" form on rocky promontories that have been chemically and biologically (6) eroded into basin-shaped depressions surrounded by slightly elevated rims. When erosion lowers the basin to fall within the narrow vertical range of the vermetids, the water-covered surface becomes colonized by *V. triquetrus*. The top of the seaward edge, which is exposed to the waves, becomes encrusted by *D. petraeum*. This cemented crust apparently stabilizes the substrate against further erosion. A small-rimmed ledge is thus established at the seaward side of the promontory. It is then progressively widened when solution basins located farther leeward are eroded to the level where *V. triquetrus* can flourish. The direction of the incident waves varies with the configuration of the shore. Reflected backwash from other rocky promontories initiates at the lee side the same processes that have previously taken place at the seaward side, until the promontory becomes surrounded by a rimmed edge from all sides. Eventually, when all rock remnants have been eroded to the level of effective vermetid growth, a miniature atoll is formed, whose rim and enclosed basin are preserved by the protective growth of *Dendropoma* and *Vermetus*, respectively (Fig 1). The upward growth of

the crust is limited by the contemporary sea level, and when the upper limit for optimal growth within the intertidal range is reached, the crust does not become any thicker, but a lateral outgrowth of *Dendropoma* takes place. Below the level of this rim the rocky surface is directly exposed to intensified erosion initiated by boring organisms that produce a deep undercut and an eventual collapse. Thus, the advancing sea destroys existing reefs and initiates new ones, and by the time younger reefs are being formed at the retreating shore, older ones have already been destroyed.

The Bermuda microatolls have been widely referred to as "serpulid reefs" (7), although the amount of serpulid tubes in them is insignificant and *Dendropoma irregulare* (Orbigny) provides the bulk of their crust (8). Since the rims of both the Shikmona and the Bermuda reefs are overgrown by a *Dendropoma*, it has been suggested that in Bermuda the rim surrounds a deep and not a shallow basin because no species of *Vermetus* is available in Bermudan waters to perform the protective role played by *V. triquetrus* in

Israel (9). However, I have found *D. irregulare* growing not only on the outer rim but all over the reef's surface, and discovered that a species of *Vermetus* occurs in the intertidal zone of Bermuda, although not on microatolls.

The Bermudan formations have been described as made of eolianite, with rims encrusted but not built by lime-secreting organisms (10). However, cross-sectional exposures of several reefs (11) showed that at least to the depth of 5 m the reefs are made of biogenic material. Thus, while the Israeli microatolls are rocks only encrusted and temporarily maintained by vermetids, the Bermudan ones are genuine organic reefs built by vermetids and coralline algae (Fig. 1). In Bermuda, older vermetid and algal material is removed because of destruction by borers below the actively growing surface, and the hollows are filled by a new growth of algae, foraminiferans, and serpulids, but not by vermetids. Many voids are also filled with sand-sized skeletal debris that is pumped into the internal crevices, where it becomes firmly cemented. Thus, although Bermudan microatolls are largely non-

vermetid, they were initiated and are perpetuated by vermetids and certain algae. These organisms are continually replaced by a secondary growth and deposition of other organisms and materials.

The initial stages of the formation of Bermudan and Israeli microatolls are similar: solution basins at the higher intertidal level of exposed Bermudan promontories are lowered to form bench-like ledges with pronounced seaward rims encrusted by *D. irregulare*. But in Bermuda *Dendropoma* also encrusts much of the ledges' surfaces, where *Vermetus* sp. (?) is rare. Also, the surfaces of fully mature microatolls and of younger, vermetid-encrusted ledges are at the same level in Israel, whereas in Bermuda the surface of microatolls is lower than that of ledges (Fig. 1). This is due to continuing erosion of the Bermudan ledges, even after they are encrusted with vermetids, by the boring activity of sea urchins, *Echinometra subangularis* (Leske). These densely inhabit the ledges, whereas in Israel the number of sea urchins is negligible. Thus, the surface of a Bermudan ledge is rapidly lowered to a level not inhabited by sea urchins, where growth of *D. irregulare* and coralline algae proceeds unhindered and is directed laterally to form overhanging edges. Borings in these edges presumably fill rapidly, and the outgrowth is consolidated into an enduring mass.

Transgression (12) has presumably provided an opportunity for the Bermudan vermetids and algae to grow upward and thus increase the thickness of the crust. The crust should be thickest and the eolianite core buried deepest in the older microatolls, which are now located far off the present Bermudan shore. Thus, the basins of the Israeli formations result from differential erosion, whereas those of the Bermudan microatolls result from differential growth. The rims of the Bermudan reefs, being at a lower level than the Shikmona rims, do not protect the basins from turbulence. Therefore, basins are not inhabited by *Vermetus* but by some *D. irregulare*.

In Shikmona live *D. petraeum* are confined to patches cleared of seaweeds by grapsid crabs. Presumably, the dense growth obstructs the flow of plankton-carrying water. In Bermuda grapsid crabs on microatolls are rare, and *D. irregulare* thrives under algal cover. I have found that this species utilizes mucus webs, although it uses ciliary

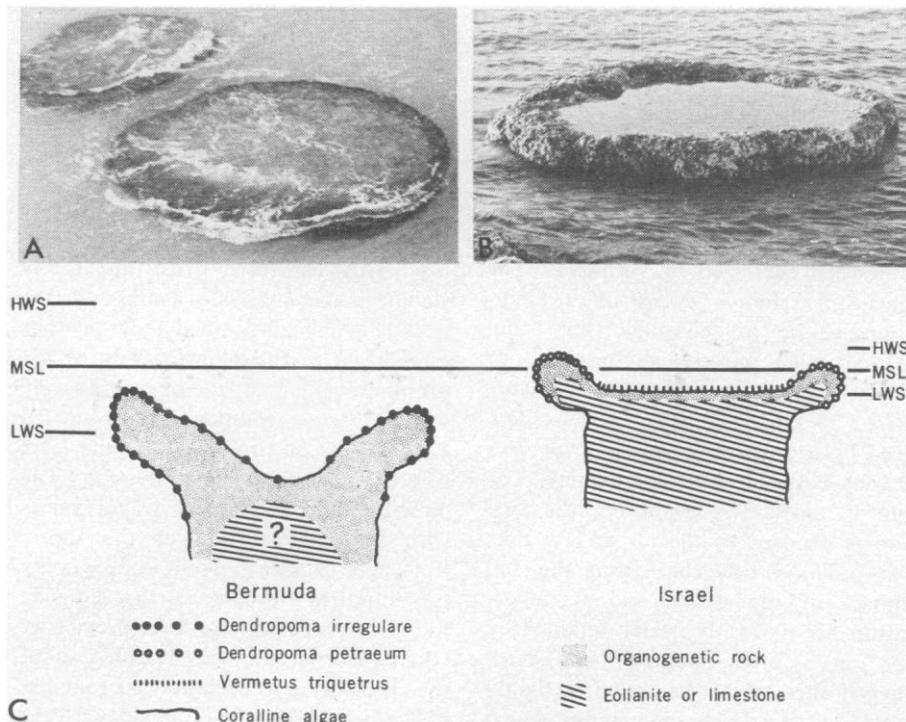


Fig. 1. Microatolls off (A) the south shore of Bermuda and (B) Shikmona, Israel. Their schematic profiles are shown in (C). The biogenic rock is made mainly of cemented empty shells and skeletons of the vermetids and coralline algae living on the surface. Coralline algae encrust all surfaces not covered by vermetids. The extension of the eolianite core in the Bermudan reef is uncertain and probably varies between reefs. The range between mean high water of spring tide (HWS) and mean low water of spring tide (LWS) in Bermuda is about 1 m. Both reefs are about 2 m in diameter; the photographs were taken at low tide; MSL, mean sea level.

feeding too (13). Thus, in the Israeli formations *Vermetus* and *Dendropoma* diverge in both habitat and feeding techniques, but in the Bermudan formations the local *Dendropoma* occupies both habitats and possibly utilizes both feeding methods.

Intertidal reefs with features similar to those in Israel and Bermuda are known from the Cape Verde Islands (14) and Fernando de Noronha Island (15). They should probably not be expected where fringing coral reefs occur: the habitat of vermetid reefs in subtropical waters is very close to that of fringing coral reefs in tropical waters. In Bermuda, where winter surface temperatures are higher than in Israel (16), coral reefs do occur, but they do not reach the surface, and microatolls are located at the seaward edge of these reefs, where one could have expected a fringing coral reef.

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#### References and Notes

- J. M. Pérès and J. Picard, *Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars.* 4, 2 (1952); *ibid.* 47, 5 (1964); R. Molinier and J. Picard, *Ann. Inst. Oceanogr. Monaco* 28, 163 (1953); M. Fevret and P. Sanlaville, *Mediterranee* 2, 113 (1965).
- Average sea-surface temperatures for the warmest month in Israel and Bermuda are 28°C. Average tides are about 30 cm in Israel and 100 cm in Bermuda.
- Studies were carried out during 1965 at Shikmona and in August and September 1968 in Bermuda. Observations were made by diving, and samples were taken with hammer and chisel.
- J. E. Morton, *Proc. R. Soc. N.Z.* 79, 43 (1951); *Bull. Br. Mus. (Nat. Hist.) Zool.* 2, 585 (1965).
- C. M. Yonge and E. J. Iles, *Ann. Mag. Nat. Hist.* 3, 536 (1939); C. M. Yonge, *Sci. Rep. Great Barrier Reef Exped.* 1, 259 (1932).
- K. O. Emery, *J. Geol.* 54, 209 (1946); R. Revelle and K. O. Emery, *U.S. Geol. Surv. Prof. Pap.* 260-T (1957), p. 699; J. Picard, *Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars.* 8, 55 (1954).
- S. Ekman, *Zoogeography of the Sea* (Sidgwick & Jackson, London, 1953), p. 54; R. Hesse, W. C. Allee, K. P. Schmidt, *Ecological Animal Geography* (Wiley, New York, 1951), p. 252. Other names used in the literature for the same reefs are "serpentine atolls" and "serpentine reefs."
- A. E. Verrill, *Trans. Conn. Acad. Arts Sci.* 11, 413 (1901-1902); H. Prat, *Bull. Inst. Oceanogr. Monaco No.* 705 (1936); T. A. Stephenson and A. Stephenson, *Endeavour* 13, 72 (1954).
- U. Safriel, *Proc. Malacol. Soc. Lond.* 37, 27 (1966).
- A. Agassiz [*Am. J. Sci.* 47, 411 (1894); *Bull. Mus. Comp. Zool. Harv. Coll.* 26, 209 (1895)] claimed that by hammering to a depth of not more than 45 cm he had exposed the eolianite core; the relation between it and the organogenic crust, as visualized by Agassiz, are clearly illustrated in A. E. Verrill, *Trans. Conn. Acad. Arts Sci.* 12, 45 (1907), p. 124, figure 29.
- R. N. Ginsburg, E. A. Shinn, J. H. Schroeder, *Program Annu. Meet. Geol. Soc. Am.* (1967), p. 78.
- L. S. Land, F. T. Mackenzie, S. J. Gould, *Geol. Soc. Am. Bull.* 78, 993 (1967).
- R. Robertson, thesis, Stanford University (1959); reported by Morton (4).
- C. Crossland, *Proc. Zool. Soc. Lond.* 1, 170 (1905). This is at 15°N, 25°W.
- M. Kempf and J. Laborel, *Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars.* 43, 9 (1968). This is at 3°51'S, 32°26'W.
- The average sea-surface temperature for the coldest month is 17°C in Israel and 19°C in Bermuda.
- Contribution No. 528 from the Bermuda Biological Station. Supported in part by NSF grant GB-6404 to the Bermuda Biological Station and in part by NSF grant GB-6230 to N. G. Hairston, University of Michigan, Ann Arbor. Thanks are due to R. N. Ginsburg for allowing me to collect samples from the exposures he made.

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## Radioimmunoassay for Human Procollagen

**Abstract.** Rabbit antisera were produced against the procollagen molecule secreted into the medium of cultured human skin fibroblasts. The isolated antigenic, amino terminal portion of the procollagen molecule was purified, labeled with iodine-125, and used in a radioimmunoassay which detected nanogram quantities of the same antigen. With the assay, immunologically identical molecules were detected in the culture medium of different strains of human fibroblasts and in normal human serums. Serums from human cord blood contained a 12-fold higher concentration of the antigen than serums from adults, while serums from other vertebrates gave reactions to incomplete cross-reactivity or non-reactivity.

Cultured human skin fibroblasts synthesize a procollagen molecule (molecular weight, 360,000) composed of three polypeptide chains (1, 2). The first 200 residues at the amino termini of each of the three chains (the propeptides) are in a globular conformation (3) stabilized by interchain disulfide bonds between half-cystine residues. The remainder of the molecule is in a triple-helical array stabilized by noncovalent interactions between the chains. An enzymatic excision of the amino terminal

globular sequences occurs after procollagen is secreted from the cell. One product of the excision is tropocollagen (molecular weight, 285,000), the triple-helical molecule which aggregates to form collagen fibers.

Procollagen accumulates in the medium of cultured human diploid skin fibroblasts because the enzymatic excision of the globular sequences occurs slowly and appears to be a rate-limiting step in this system (2). Rabbits injected with culture medium from these cells develop antibodies directed only against antigenic determinants in the

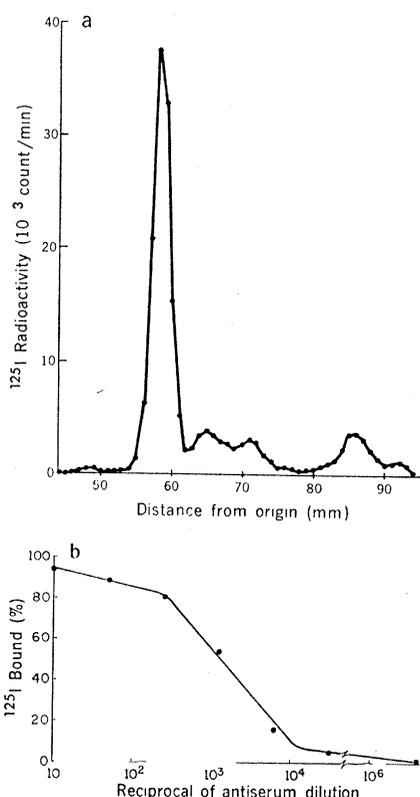


Fig. 1. (a) Electrophoresis of  $^{125}\text{I}$ -labeled antigen on polyacrylamide gel containing SDS and urea. The sample was dissolved in the running buffer for electrophoresis and denatured by heat; electrophoresis and measurement of radioactivity in gel slices were performed as described (1). (b) Titration of antiserum to iodinated antigen. All dilutions were made with a standard buffer containing 0.025M phosphate, pH 7.6, 0.1 percent ovalbumin, and 0.03 percent Triton X-100. Duplicate tubes contained dilutions of adsorbed rabbit antiserum (in 0.1 ml), 0.1 ml of  $^{125}\text{I}$ -labeled propeptide (50,000 count/min), 0.1 ml of 5 percent normal rabbit serum, and 0.2 ml of buffer. Tubes were incubated for 2 hours at 37°C and then for 24 hours at 4°C. Sheep antiserum to rabbit 7S globulin (0.075 ml), 0.1 ml of EDTA (0.1M in buffer), and buffer to a final volume of 1.0 ml were added. Tubes were incubated for 1 hour at 37°C and 4 hours at 4°C and then centrifuged at 5000g for 10 minutes. Supernatants were added to Aquasol (New England Nuclear), and the radioactivity was measured in a scintillation spectrometer. Rabbit antiserum was omitted from control tubes.