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7. The leaf bases are inserted upon the erect distal end of the branch unit at 50° to 60° from the vertical. However, the leaf blade bends downward to present most of the leaf surface at 75° to 95°.
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12. A. L. Loeb, *Space Structures* (Addison-Wesley, Reading, Mass., 1976), p. 111.
13. The calculations were carried out by an electronic digital microcomputer with a disk memory (P652 and DAS 604, Olivetti). Simulations were drawn by an x-y plotter (WX535, Watanabe Sokuki, Tokyo).
14. The signs of θ_1 and θ_2 of the first bifurcation are reversed in each sequential lateral branch of the tier. All later bifurcations, however, follow the rules of the *Terminalia* simulation (*10*). The change in initial symmetry occurs in nature. We are presently investigating the effects of such natural symmetry changes.
15. The following are the means and standard deviations calculated for 65 bifurcations observed in nature: $\theta_1 = 24.4°$, $s_1 = 5.94°$; $\theta_2 = -36.9°$, $s_2 = 6.92°$; $|\theta_1| + |\theta_2| = 61.3°$, $s_{1+2} = 7.30°$. The previously published values for θ_1 and θ_2, 27° and $-35°$, respectively, were based on a more limited sample of bifurcations (*8, 10*).
16. We thank J. E. Eckenwalder and P. F. Stevens for reading the manuscript. Supported in part by NSF grant DEB77-13953.

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Brachiopods: Biomechanical Interdependences Governing Their Origin and Phylogeny

Abstract. *The adaptive advantage of epibenthic articulate brachiopods over inarticulate forms resulted from a modification of the mechanics of shell opening from an indirect hydraulic system to a direct muscular one. As a consequence, the articulate brachiopods were able to reduce the complex muscular system of the ancestral inarticulates, freeing two-thirds of the space within the shell for enlargement of the feeding apparatus. The original hydraulic mechanism of the inarticulate brachiopods most likely evolved from the hydrostatic skeleton of metameric lower invertebrates, probably polychaete-like annelids, as shown by a biomechanical analysis. The transitional stages between such annelids and inarticulate brachiopods are presented and explained as adaptive improvements in body construction.*

The vast majority of brachiopods, or lamp shells, are epibenthic, sessile, suspension feeders. This relatively uniform way of life permits an easier comprehension of the structure and function of their morphology than of that in many other groups of organisms. Moreover, they are well suited for analysis of the biomechanics of each morphological feature and the interaction or interdependence of the individual parts of the apparatus comprising such biological systems as shell opening and feeding. A more detailed understanding of the biomechanics of these systems is fundamental for a better comprehension of the evolutionary history of the brachiopods, including their origin from lower invertebrates and the major phylogenetic changes within the group.

The major evolutionary advance within the lamp shells is expressed by the two major subgroups, namely, the primitive Inarticulata (brachiopods with valves not rigidly hinged to one another) and the advanced Articulata (those having a hinge of interlocking teeth and sockets between the valves). A comparison of the muscular systems and the lophophores (food gathering and respiratory apparatus) of typical representatives from both groups (Fig. 1) shows that in the Inarticulata most of the space within the shell is occupied by muscles and coelomic cavities, while in the Articulata the anterior two-thirds of the shell interior is occupied by the lophophore. Two questions come to mind immediately. Why do these differences exist, and how can the direction of evolutionary change be ascertained within the lamp shells?

The answer to both questions lies in the mechanism of shell opening in the two groups and in the consequences of the modification of this mechanism for the rest of the morphology of the brachiopods. The muscular system that opens the shell in the Articulata has been described and is understood clearly, but little has been written about the morphology and function of the shell-opening mechanism in the Inarticulata. An examination of the anatomy of the latter revealed that they open their valves by an indirect hydraulic system. They lack directly acting opening muscles such as those of the Articulata. Instead, the Inarticulata possess a set of longitudinal muscles that run obliquely through the body and have one end attached to the posterior end of the ventral valve and the other end inserting into the soft body of the animal (Fig. 2). On contraction, these muscles pull the body into the posterior part of the shell. Because of the constant volume of the fluid-filled coelom, the body swells in other directions. Lateral swelling is prevented by two partitions (the gastroparietal and ileoparietal "bands") in association with the laterally positioned longitudinal muscles; consequently, the body can expand only dorsoventrally and hence forces the shell open. Harmful deformation of the body and lateral shifting of the valves are prevented by a complex muscular system. Such a system is indispensable in the few inarticulates (lingulids) that burrow with a valve-shifting mechanism (*1*). However, for all epibenthic brachiopods, any evolutionary change that permitted a reduction of the muscular-coelomic apparatus and a consequent enlargement of the mantle cavity with its lophophores

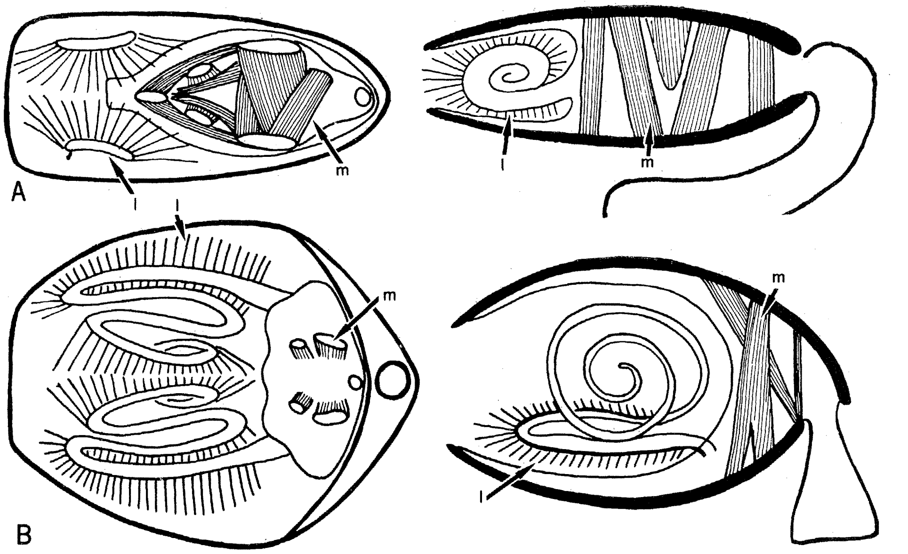

Fig. 1. Schematic representation of (A) an inarticulate brachiopod (*Lingula*) and (B) an articulate brachiopod (*Magellania*) in dorsal and lateral views to show the differential relationships between muscle (*m*) volume and mantle cavity volume with the contained lophophores (*l*). [Modified from figures of several authors (*15–17*)]

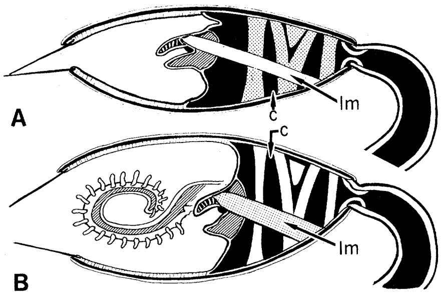

Fig. 2. An inarticulate brachiopod with (A) closed and (B) opened valves. The valves are closed by direct action of adductor muscles. They are opened by indirect action of longitudinal muscles (*lm*), which pulls the body into the posterior part of the shell. The resulting hydraulic pressure of the fluid-filled coelom (*c*) forces the valves open. Active muscles are stippled.

would have considerable adaptive advantage. Can the modification from the inarticulate to the articulate morphology be explained as a gradual series of sequential changes, with each evolutionary step being a biomechanical improvement with adaptive value?

Many Inarticulata have a small lamina near the posterior end of their valves (Fig. 3) that forms a line of contact or hinge between the opened valves. Anterior growth of the interarea space formed by this lamina results in a longer hinge line, which would be an adaptive improvement of the contact between the valves. The umbonal or posterior adductor muscles hinder continued enlargement of the interarea, which can occur only by enclosure of these muscles by the hinge line (Fig. 3C). This results in an anteriorly open triangle, the so-called delthyrium, as the hinge continues its forward growth past the umbonal muscles. At this stage (Fig. 3, D and E) the umbonal changes in function from an adductor to a diductor muscle—that is, from a closing to an opening muscle. The hinge line separates the umbonal muscle from the remaining adductor muscles and reverses its action because of the changed relationship between the force vector of the muscle and the fulcrum between the valves. Movement of the valves is stabilized by subsequent evolution of teeth and sockets along the hinge.

The morphology of the oldest Articulata from the Lower Cambrian supports our model. The genera *Nisusia*, *Eoconcha*, and *Matutella* have an enlarged interarea with a delthyrium and a long straight hinge with weakly developed teeth. Their delthyrium is primarily a muscle aperture, not a pedicle opening (*2*), which is formed by a special apical foramen.

The elongation of the hinge line by anterior growth of the interarea and resulting shift of the umbonal muscles from adductors to diductors resulted in an innovation of special significance for the evolution of the brachiopods. The articulate brachiopods were able to reduce their bulky hydraulic shell-opening system and substitute for it a much smaller directly operating muscular system in the posterior part of the shell. Reduction in size of the shell-opening mechanism freed space within the shell for the lophophore, which enlarged and thus enhanced feeding and respiration.

A subsequent step in the evolutionary improvement of the opening mechanism was mineralization of the shell, which was previously chitinous with a high organic content. Direct muscle action and short leverage of the diductor muscles required a more rigid shell to be effective.

The shells of most Inarticulata are fairly flat because the mechanics of hydraulic opening works better with flattened valves; this restriction disappeared with the appearance of the muscular opening system. Thereafter the space requirements of the lophophore exerted the primary influence on the evolution of shell shape. The food-collecting capacity of the lophophore is directly proportional to the area of its filaments (*3*). A three-dimensionally looped or coiled lophophore has the greatest filament area for shell surface. Hence the best-adapted shell form is a globular one, which offers the largest space for the mantle cavity with the least shell secretion. Although a sphere would be the ideal shape, the ellipsoidal shell form exists as a compromise because of the conflicting demands of ontogenetic growth, need of space for pedicle muscles, and so forth.

Our model suggests that globular ellipsoid brachiopods would prevail in food- and oxygen-deficient environments because of their larger lophophore relative to shell surface. We could prove such relations for the Middle Devonian rocks in the Eifel region of Germany and in Morocco (*4*).

Considering the adaptive advantage of the globular shell form, the success of very flat articulate brachiopods in the Paleozoic is surprising. The order Strophomenida achieved evolutionary diversity and longevity despite their planoconvex and concavoconvex shapes. The largest brachiopods belong to this order. In three groups (Plectambonitacea, Strophomenacea, and Chonetacea), the space within the shell is so restricted that only two-dimensional lophophores with small filter areas could be accommodated. Possibly these forms produced the necessary water current by periodic "flapping" of the valves, as suggested by several authors (*5–7*). Water "pumping" may be an archaic feeding method which brachiopods inherited from their forerunners (see below). Larvae of recent brachiopods filter-feed by pumping. Adults close the valves abruptly—probably at regular intervals (*3*)—for removal of wastes from their mantle cavity.

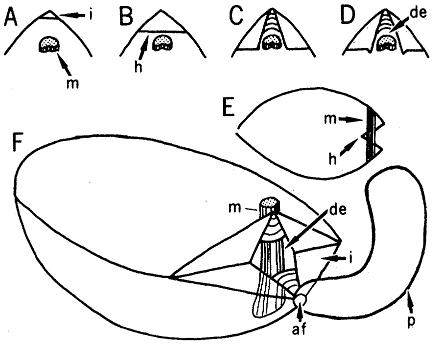

Fig. 3. Model of the evolution of articulate brachiopods from the inarticulates. (A) The series starts with a small interarea (*i*) as seen in many inarticulates. (B) The interarea enlarges with resulting elongation of the hinge (*h*) line as an adaptive improvement of the contact between valves. (C) Further elongation of the hinge is possible only if the anterior edge of the interarea bends around the umbonal muscle (*m*) to form a delthyrium (*de*). Consequently, the position of the umbonal muscle shifts relative to the hinge; the muscle now lies posterior to the hinge (D and E) and changes from an adductor to a diductor muscle. (F) The final stage is shown by the oldest Articulata in the Lower Cambrium. Originally the delthyrium is not a pedicle opening but a muscle aperture. The pedicle (*p*) enters the shell by a special apical foramen (*af*).

Our functional morphological analysis of the inarticulate hydraulic shell-opening mechanism provided several new insights into the evolutionary origin of the brachiopods. One of these features is the pair of transverse partitions possessed by the brachiopods (Fig. 4), consisting of connective tissue walls fixed at both sides of the body. They not only are lateral connections between the body wall and the digestive tract but also contain the metanephridia (two pairs in the Rhynchonellida) and support the gonads (two pairs in *Discinisca*). Thus we find these transverse bands to be homologous with the dissepiments of annelids. The mesenteries of brachiopods have been described. Further, in *Lingula* the pedicle is protected by a cuticle and its muscles surround a coelomic cavity. The larvae of most brachiopods and the adult *Lingula* possess setae that can be moved by muscles. All of these features are characteristic elements of metameric polychaete animals.

The ancestry of brachiopods must be suggested by phylogenetic reconstruction because direct paleontological evidence probably will never be found. Such reconstructions should be based on a sequential series of gradual changes formulated on the biomechanical requirements and interdependences of structure in recent soft-bodied animals (*8–10*). We present here a model of a series of changes linking an ancestral polychaete-like organism with a primitive brachiopod (Fig. 5). Our model begins with a metameric ancestor and hence differs from other derivations (*11, 12*) in which metamerism is considered to be a secondarily derived feature.

Our series begins with a tube-dwelling polychaete-like metameric worm having a hydraulic body construction (*13, 14*). Food is acquired by sucking in small organisms by respiratory movements rather than by active predation. Adaptations to less active movements and to a microphagous mode of feeding could develop gradually. Intensification of filter feeding led to the evolution of specialized organs, in this case a tentacular lophophore.

The first stage in our series (Fig. 5A) required peristaltic movements for respiration and for expulsion of feces into the open water column. Less energy would be required for these movements if the animal expelled excrement directly into the water. This was achieved by shifting the anus forward with the evolution of a U-shaped gut. Respiration was assumed by the tentacles. These morphological changes were accompanied by reduction of metamerism in the posterior part of the animal, which was possible because the tubular walls of the burrow take over the mechanical role served by the metameric body construction of free-living worms. Only the first segments were retained as support for the anterior part of the body with the lophophore. The form at this step (Fig. 5B) is nearly identical to the morphology of phoronid worms, which are reported to possess two transverse ("lateral") mesenteries in addition to the true (sagittal) mesentery; we believe that the so-called lateral mesenteries are dissepiments because they support the nephridia.

The next step in our model is the evolution of a collarlike fold into which the tentacles could be withdrawn (Fig. 5C)

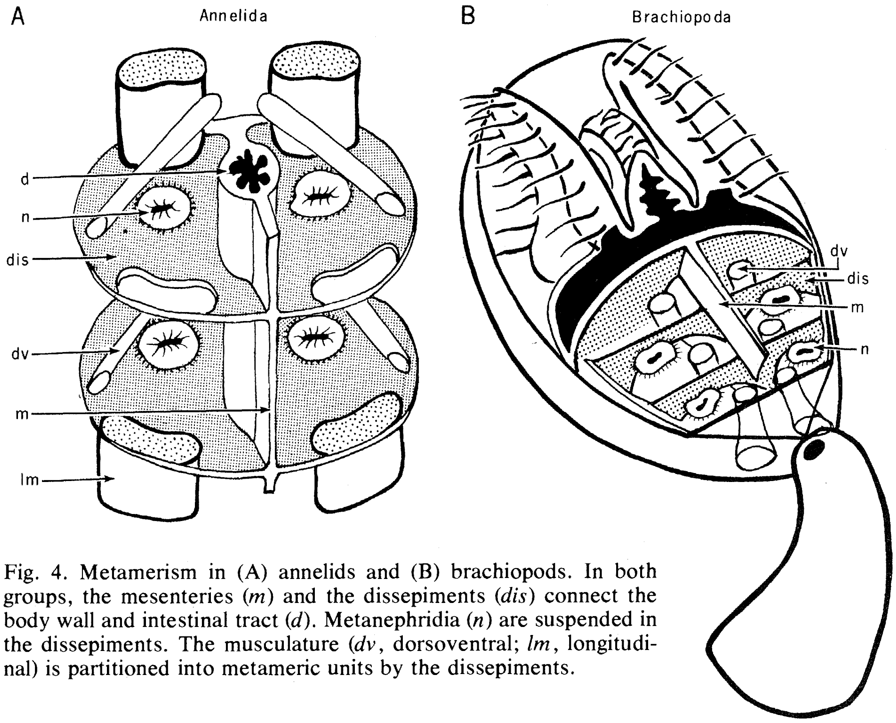

Fig. 4. Metamerism in (A) annelids and (B) brachiopods. In both groups, the mesenteries (*m*) and the dissepiments (*dis*) connect the body wall and intestinal tract (*d*). Metanephridia (*n*) are suspended in the dissepiments. The musculature (*dv*, dorsoventral; *lm*, longitudinal) is partitioned into metameric units by the dissepiments.

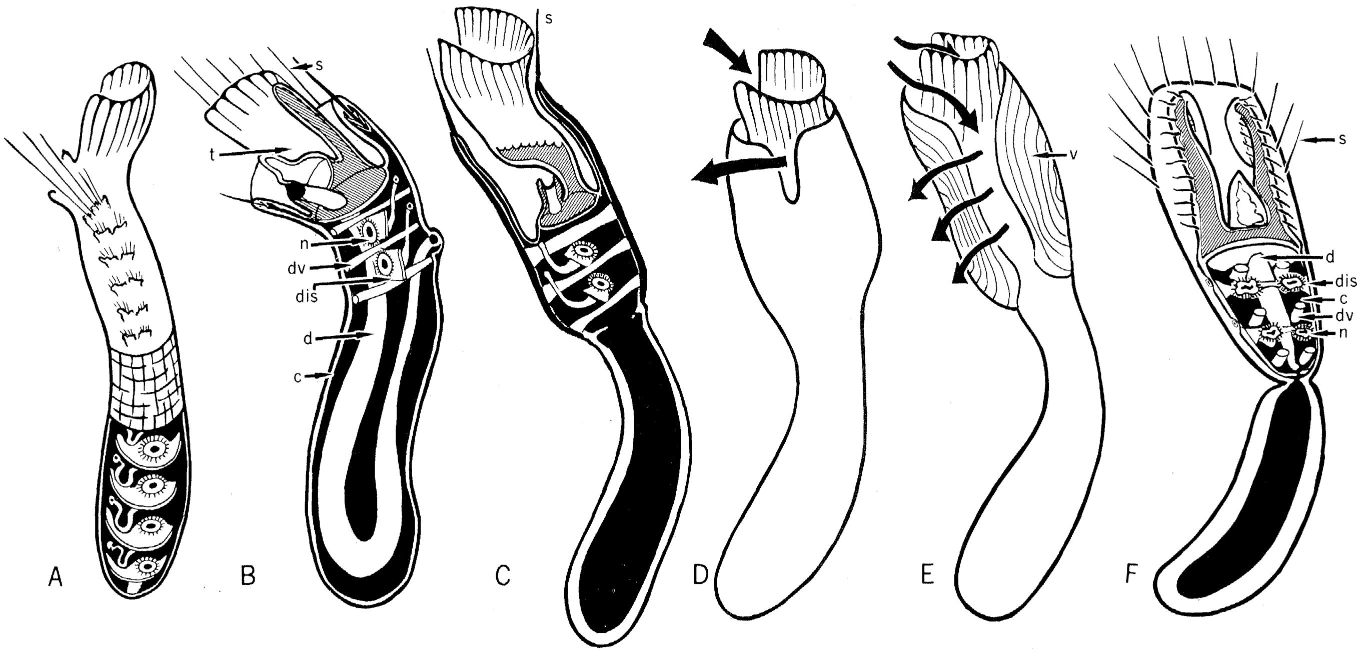

Fig. 5. Model of brachiopod origin by a sequence of gradual steps. (A) Annelid-like ancestor of tentaculates with a metameric hydraulic system. (B) Phoronid-like stage with two dissepiments and two pairs of metanephridia after shifting of anus anteriorly and loss of posterior metamerism. (C) Transitional stage showing development of a collarlike fold into which the tentacles can be withdrawn. (D) Transitional stage showing development of lateral slits in collar to improve water flow; current direction may be reversed. (E) Transitional stage showing development of valves to prevent collapse of mantle lobes. (F) Final stage showing a *Lingula*-like inarticulate brachiopod. Abbreviations: *c*, coelom; *d*, intestinal tract; *dis*, dissepiment; *dv*, dorsoventral muscles; *n*, metanephridia; *s*, setae; *t*, tentacular crown; and *v*, valves.

and its subsequent enlargement for further protection. This collar would be a key event in the evolution of the future mantle and shell of the brachiopods. Water current through the collar would be improved by the formation of two slits which divide the collar into two "mantle lobes" (Fig. 5D). Collapse of these soft lobes would be prevented by the formation of a skeletal support—that is, the evolution of two external valves of organic and later mineralized material (Fig. 5E). The final stage in our model (Fig. 5F) is an animal with a two-valved shell protecting a tentacular cavity, and with a soft body containing a coelomic cavity and two dissepiments supporting two pairs of metanephridia and gonads and suspending the intestinal canal. The dissepiments are an important part of the mechanism by which lateral body swelling is prevented during hydraulic shell opening. The posterior part of the wormlike ancestor is retained as the pedicle; its metamerism is lost but the muscular wall around the coelomic tube and the cuticular coat are retained. Existing transverse muscles could insert directly on the shell, and some could function as adductor muscles. The shell-opening mechanism is achieved by an indirectly operating system formed by a complex of laterally placed longitudinal muscles, fluid-filled coelomic cavities, and transverse bands, all parts of the existing hydraulic locomotor system of the metameric wormlike ancestors. The morphology as abstracted in the final stage of our series is that of the *Lingula*-like Inarticulata described at the onset (Figs. 1A and 2).

W. F. GUTMANN
Forschungsinstitut Senckenberg, D 6000
Frankfurt am Main, West Germany
K. VOGEL
H. ZORN
Geologisch-Paläontologisches Institut,
J. W. Goethe-Universität,
D 6000 Frankfurt am Main

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Cholestyramine: Use as a New Therapeutic Approach for Chlordecone (Kepone) Poisoning

Abstract. *In rats, as reported in humans, chlordecone (Kepone) is excreted predominantly in the feces. Cholestyramine, an anion exchange resin, binds chlordecone in rat intestine, increases its excretion into the feces, and decreases its content in the tissues. The resin appears to offer a practical method for treating chronic poisoning with this and possibly with other lipophilic toxins.*

Workers in a factory that manufactured chlordecone (Kepone) (*1*) were exposed to large quantities of this organochlorine pesticide for many months. The workers had high concentrations of chlordecone in their blood and fat associated with clinical evidence of toxicity to the nervous system, liver, and testes (*2*). No treatment is available for patients poisoned with organochlorine pesticides, such as chlordecone, except for measures aimed at relief of symptoms. One approach to therapy would be to accelerate the elimination of chlordecone from the body. This procedure is based on the assumption that the continued presence of the chemical in the tissues at high concentrations is necessary for overt toxicity and may also carry the potential for development of malignancy. The latter concern has been raised by the demonstration that chlordecone is carcinogenic in rats and mice (*3*).

In man chlordecone passes through the liver into bile, but only a small fraction of the biliary chlordecone entering the intestine appears in the stool (*2*). These observations suggest that elimination of chlordecone from the body is curtailed by reabsorption of the chemical from the contents of the intestine, creating an "enterohepatic recirculation" of chlordecone. If this hypothesis is correct, then the rate of elimination of chlordecone would be augmented by oral administration of a nonabsorbable agent that would bind chlordecone in the intestinal lumen. Cholestyramine, an anion exchange resin, binds chlordecone in vitro (Fig. 1). In short-term clinical tests of this resin, we have found that treatment of six patients with cholestyramine for 3 days produced an average sixfold increase in excretion of chlordecone in the stool (*2*). These results in patients are encouraging and suggest that a clinical trial of cholestyramine therapy is warranted. However, it seemed important to test first in animals the effect of the resin not only on fecal excretion but also on tissue content of chlordecone. Furthermore, the concentration of organochlorine pesticide may be underestimated in human samples since metabolites of chlordecone, if present, may escape detection by gas-liquid chromatography (GLC). Animals given ^{14}C-labeled chlordecone provide a ready means for studying the excretion of total organochlorine material and the stimulation of this process by cholestyramine.

Male Sprague-Dawley rats weighing 175 to 200 g were selected for study because the toxic manifestations of chlordecone in these animals (*4*) resembles those observed in man. The animals were housed individually in metabolic cages and allowed free access to food and water. After being fasted overnight, rats were given chlordecone (40 mg/kg) in solution by gastric tube. The solution of chlordecone was prepared by dissolving one part of [^{14}C]chlordecone (Pathfinder Labs, St. Louis, Mo.) with stated specific activity 19.68 mCi/mmole and 49 parts of unlabeled chlordecone (Allied Chemical) in warmed corn oil. The purity of both chlordecone products was greater than 97 percent, as judged by GLC and thin-layer chromatography. The total output of feces from the labeled rats was collected at 24-hour intervals. The stool was weighed and homogenized (20 percent, weight to volume) in distilled water. Portions (0.2 g) of the stool homogenates were vaporized (Packard 306 Tri-Carb Oxidizer) with the use of Carbosorb. Radioactivity was measured by liquid scintillation spectrometry with [^{14}C]toluene as an internal standard for counting efficiency. (Permaflow was used as counting fluid.) Urine, collected