

fixation process depends on the properties of the individual soil—probably the quality of the calcium carbonate and its particle size.

The high concentration of calcium carbonate in soils of arid and semiarid regions could in some instances enlarge considerably the capacity of these soils for the strontium ion. The quantity of lime in these soils exceeds by far the amount of exchangeable ions in the double layer, and its importance in the fixation of strontium may be considerable.

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References and Notes

1. W. J. Kaufman, in *Radioactive Waste Disposal* (International Atomic Energy Agency, Vienna, 1960), pp. 533-546.
2. W. Beam, *Bull. U.S. Bur. Agr.* 3, 1721 (1916).
3. D. E. Williams, *Proc. Soil Sci. Soc. Am.* 13, 127 (1948).
4. G. Drouineau, *Ann. Agron.* 12, 441 (1942).
5. L. A. Richards, "Diagnosis and Improvement of Saline and Alkali Soils," *Agricultural Handbook Number 60* (U.S. Department of Agriculture, Washington, 1954).
6. I. Barshad, in *Clays and Clay Minerals*, E. Ingerson, Ed. (Pergamon Press, New York, 1960), pp. 350-364.
7. Supported by the Hazards Evaluation Committee of the Israel Atomic Energy Commission.

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Oysters: Composition of the Larval Shell

Abstract. *The shell of the free-swimming veliger larval stage of the common North American oyster Crassostrea virginica (Gmelin, 1791) is composed of aragonite. This composition contrasts with that of the adult shell, which is composed mainly of calcite, the rhombohedral allomorph of calcium carbonate, and minor amounts of aragonite.*

In view of the largely calcitic composition of the adult oyster shell, it is surprising to find that the prodissococonch, the shell of the free-swimming veliger larval stage, is composed of aragonite—for both the prodissococonch and the postlarval shell are secreted by the epithelium of the mantle of the same oyster, although not at the same time.

Adult oyster shells consist mainly of calcite, the rhombohedral allomorph of calcium carbonate, and minor amounts of aragonite, the orthorhombic allomorph of the same substance. Arago-

nite is restricted in the adult shell to five small, distinct areas: the resilium (1), which is the midportion of the ligament between the valves, the pads at which the ends of the large posterior adductor muscle are inserted, and the pads, one on each valve, at which Quenstedt's muscles are inserted (2).

Larvae of the common North American oyster *Crassostrea virginica* (Gmelin, 1791) were reared in breeding tanks at the Biological Laboratory of the U.S. Bureau of Commercial Fisheries, Milford, Connecticut. When any of them died, they were collected, washed with distilled water and dried at 35°C; no preservatives were used (3).

The dried larvae were picked carefully under a binocular microscope to avoid the inclusion in the sample of any accidental impurities or any larvae in the process of metamorphosis. Larvae in metamorphosis can be recognized by a narrow rim of white opaque postlarval shell encircling the hyaline prodissococonch. The sample thus selected included various larval stages, from the straight-hinge veliger larva with its shell, the protostracum, to the very latest stage of the umbo larva with its shell, the prodissococonch.

The shell of either larval stage is very thin, hyaline, and translucent. On the shell of a full-grown veliger larva, ready to settle on a substratum, the boundaries between the various stages are not sharply defined (Fig. 1); one has grown imperceptibly into the other, and there is no reason to suspect any differences in composition between them. The x-ray diffraction pattern (Fig. 2) shows that the sample is composed of aragonite; no calcite is indicated. The pattern proves that aragonite continues to be deposited through both stages.

In view of the largely calcitic composition of the adult shell, the question arises as to why the larval shell of the oyster is composed of aragonite. The specific gravity of aragonite is 2.95, and that of calcite is 2.72. As far as weight is concerned, no advantage would be gained by the planktonic or free-swimming animal if it built its shell of aragonite rather than calcite. The answer to the question is not to be found in a comparison with the adult oyster, but in a comparison with the larval shells of other Bivalvia. Although I have tested only larval shells of *Mercenaria mercenaria* (Linné, 1758) (Fig. 2), it is most likely that

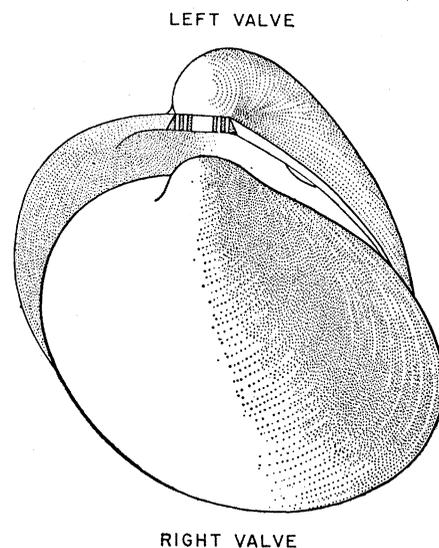


Fig. 1. Prodissococonch of veliger larva of *Crassostrea virginica*, modified from Ranson (4) ($\times 165$).

all, or nearly all, Bivalvia have aragonitic larval shells because the great majority of them have aragonitic adult shells (5). It may be assumed, therefore, that the larvae of the oysters merely conform to the general pattern in the Bivalvia. The larval oyster shells have aragonitic shells because their ancestors did, and there was and is no adaptive need for the free-swimming larvae to have shells of a composition other than aragonite.

The question should be put the other way around. Why do larval oysters suddenly begin depositing calcite after they have attached themselves to a substratum and begun metamorphosis? Adult oysters are permanently immobilized and live in an environment different from that of the larvae which requires different adaptations. Arago-

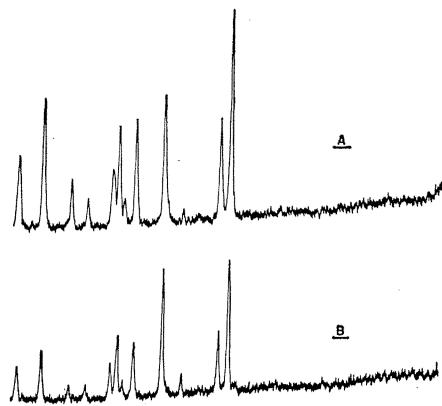


Fig. 2. X-ray diffraction pattern of veliger larvae of *Crassostrea virginica* (Gmelin, 1791) (A) and *Mercenaria mercenaria* (Linné, 1758) (B).

nitic shells may be more advantageous to free-moving bivalves, because aragonite is harder, has greater strength as a structural material, and is less prone to breakage by cleaving than calcite. On the other hand, calcitic shells may be more advantageous to bivalves permanently immobilized in certain environments, because calcite is more stable and much less subject to leaching in the sea water and because calcite can be secreted more economically than aragonite. Secreted calcite fills a larger volume per mole than aragonite. Adult oysters need a thick shell for defense against predators.

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References and Notes

1. H. B. Stenzel, *Science* **136**, 1121 (1962).
 2. ———, *ibid.* **142**, 232 (1963).
 3. I thank J. E. Hanks and W. S. Landers of the Bureau of Commercial Fisheries, Biological Laboratory, Milford, Conn., for the samples used.
 4. G. Ranson, *Inst. Oceanog. Bull. (Monaco)* **1183**, 13 (1960).
 5. O. B. Bøggild, *Kgl. Danske Videnskab. Selskabs Skrifte, Naturv. Mat. Afdel. ser. 9*, **2** (No. 2), 233 (1930).
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Femoral Expansion in Aging Women: Implications for Osteoporosis and Fractures

Abstract. *In femoral radiographs of 2030 aging women, the diameter of the midshaft periosteum increased as cortical thickness declined. Since the cortical area enlarged, periosteal accretion exceeded endosteal resorption. Since the section modulus increased more than did cortical area, the ratio of flexural failure resistance to crush resistance increased, in apparent contrast to the changes observed in the femoral neck.*

The great extent to which the human skeleton involutes with age is apparent in the high incidence of spontaneous vertebral and femoral fractures in elderly women. In studying the correlation between vertebral and femoral atrophy we obtained unexpected results in respect to femoral dimensions. These results are reported briefly here.

Standard anteroposterior radiographs of femurs were obtained in a study of 2030 women, aged 45 to 90 years. All were ambulatory outpatients or hospi-

Table 1. Dimensions and calculated derivatives for the femoral midshafts of subjects in different age groups.

Age group	Observed data			Calculated data*		
	No. of subjects (2030)	Periosteal diameter† (mm)	Cortical thickness† (mm)	Endosteal diameter (mm)	Cross-section cortical area (mm ²)	Section modulus (mm ³)
45-49	286	31.32 ± 0.15	18.67 ± 0.17	12.65	644	2935
50-54	303	31.60 ± 0.15	18.69 ± 0.14	12.91	653	3010
55-59	501	31.86 ± 0.13	18.17 ± 0.12	13.69	652	3065
60-64	424	32.12 ± 0.14	17.96 ± 0.14	14.16	653	3129
65-69	291	32.85 ± 0.16	18.08 ± 0.16	14.77	678	3336
70-74	162	33.03 ± 0.23	17.32 ± 0.22	15.71	661	3355
75-90	63	34.74 ± 0.32	17.68 ± 0.37	17.06	718	3875

* Based on group means of observed data. † Mean ± standard error.

tal personnel; none had skeletal disease and each entered the survey voluntarily. Cortical thickness and the periosteal diameter of the left femur were measured with a transparent plastic rule. Measurements to the nearest 0.5 mm were made at the point along the shaft where, in the anteroposterior projection, cortical thickness is maximal and femoral diameter is minimal. This position, roughly pear-shape in cross-section, approximates the mid-shaft (*I*) and corresponds closely to section 40 of Koch (2). Cortical thickness, as used here, represents the sum of the two projected cortices. To test the reliability of the measurements, 50 replicate readings of randomly selected radiographs were made 9 months apart, the sites for measurement being reselected. Reliability for cortical thickness was 0.93 and for diameter, 0.93.

The difference between the periosteal diameter and cortical thickness was recorded as the inner or endosteal diameter. Cross-sectional cortical areas were calculated from equation $\pi/4(2cd - c^2)$ where *c* is cortical thickness, *d* is periosteal diameter, and section shape is assumed to be circular. As a measure of bone volume, the cortical area is a determinant of resistance to longitudinal compression forces (stress equals force divided by area). To obtain a rough index of resistance to flexural failure, section moduli were calculated from the equation

$$Z = \frac{\pi}{2} \times \frac{\left[\frac{d}{2}\right]^4 - \left[\frac{d-c}{2}\right]^4}{d}$$

by appropriate substitution of *c* and *d* for *R*₁ and *R*₂, the outer and inner radii of a tubular structure, in the conventional equation

$$Z = \frac{I}{Y_{\max}} \text{ or } \frac{\pi}{4} \times \frac{R_1^4 - R_2^4}{R_1}$$

where *Z* is the section modulus or measure of applied bending moment required to gain a given level of stress in outermost fibers, *I* is the area moment of inertia, and *Y*_{max} is the distance of maximal stress from the neutral line. Chemical composition, porosity, and microstructure were assumed to be similar in all age groups. Cross-sectional areas and section moduli were calculated with mean measurement values for 5-year age groups; the percentages of change were computed, the data of the 45 to 49 age group being used as reference.

As shown in Table 1, the mean periosteal diameter increased successively by 0.2 to 0.3 mm per 5 years through age group 60 to 64, then by increments of 0.7, 0.2, and 1.7 mm to an overall 3.4 mm gain. Changes in cortical thickness were less, with reductions of 1.4 and 1.0 mm for the two oldest groups. By variance analyses of all data, the *p* value was <<.001 both for diameter and for cortex. Since periosteal diameter increased and cortical thickness decreased, endosteal diameter expanded faster with a gain of 4.4 mm (35 percent) between the youngest and oldest groups. These progressive increases in diameters result in similar gains in theoretical surface areas, 11 percent for periosteal and 35 for endosteal. In addition, an overall gain of 74 mm² in cortical area was found to be the net result of 177 mm having been added periosteally while 103 mm were resorbed endosteally. Expressed as rates, the outer accretion of femoral bone was 1.7 times faster than inner resorption. Finally, from gains in periosteal diameter and cortical area, the section modulus increased progressively, totaling 32 percent for the oldest femurs.

These observations are pertinent to the causality and effects of osteoporosis which is evidenced so commonly in