MARTENSITE AND LIFE : DISPLACIVE TRANSFORMATIONS AS BIOLOGICAL PROCESSES

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Abstract.- Martensitic transformations in cylindrical protein crystals are found to perform life functions in primitive biological systems. Tail-sheath contraction in T-even bacteriophages can be described as an irreversible strain-induced martensitic transformation, while polymorphic transformations in bacterial flagella appear to be stress-assisted mechanically reversible martensitic transformations exhibiting a shape memory effect. Available information indicates that the geometric, thermodynamic, and kinetic aspects of these transformations are consistent with martensitic behavior. Similar transformations involving the motion of partial (coherency) dislocations under chemical forces may underly the mechanism of motion in higher organisms as well.

Introduction.- Recent advances in molecular biology have revealed that a remarkable number of biological structures involve periodic or crystalline arrays of protein molecules. Even more remarkable, from the viewpoint of a materials scientist, is the fact that displacive phase transformations between metastable states frequently occur and provide the mechanism of important life processes. While crystal structures of importance to materials science, and metallurgy in particular, have been known for quite some time and considerable attention has focused on the mechanism and kinetics of solid-state transformations, the question of transformation mechanisms in the recently determined molecular crystal structures is just now being addressed in the field of biology. These systems may provide important tests of the generality of fundamental concepts in materials science.

We here examine the relevance of martensitic transformation theory to biological systems adapting the theory to reduced dimensionality using two examples of displacive transformations in cylindrical protein crystals performing life functions in viruses and bacteria.

Bacterial-Virus Tail-Sheath Contraction.- A transformation for which the most precise structural information is available is the case of tail-sheath contraction in T-even bacteriophages, viruses that infect E.coli bacteria. The construction of a bacteriophage and the process of contraction are illustrated in Figure 1. The virus consists of a DNA-filled icosahedral head or capsid attached to a tail assembly composed of a cylindrical sheath surrounding a narrow tubular core. At the end of the tail is a hexagonal baseplate from which extend six long and six short tail fibres. The virus head is a two-dimensional protein crystal which closes on itself as a result of a periodic array of disclinations. The tail sheath is also a two-dimensional protein crystal which closes to form a cylinder. The latter crystal is apparently in a metastable state formed by "epitaxial" growth of the sheath on the baseplate and core during the initial assembly process of the virus (2). When the
virus tail contacts a bacterium, attachment of the tail fibres to the bacterial cell wall transforms the baseplate from the hexagonal to a "star-shaped" form. This in turn triggers a transformation in the tail sheath involving a contraction which drives the rigid core through the bacterial cell wall, injecting the virus DNA into the bacterium.

Figure 1. Tail-sheath contraction process in T4-bacteriophage (1).

The crystal lattice structure of the tail sheath has been precisely determined by electron microscopy and X-ray diffraction for the case of the T4 bacteriophage. The cylindrical crystal can be described as a stack of 24 annular rings of six globular gp18 protein subunits each. In the "extended" form the hexagonal rings are spaced 4nm and each is rotated about the cylinder axis relative to its neighbor by 17°. "Unwrapping" the cylinder to form a plane lattice gives the structure depicted in Figure 2a. As discussed by Harris and Scriven (4) the structure of a cylindrical crystal can be specified by combining a two dimensional lattice of primitive vectors \( \mathbf{a}_1 \) and \( \mathbf{a}_2 \) with a characteristic vector \( \mathbf{C} \) which follows the circumference of the cylinder. The vectors \( \mathbf{a}_1 \) and \( \mathbf{a}_2 \) in Figure 2a were chosen along directions of closest packing. On the closed cylinder, each of the directions defines six helices, left-handed and right-handed, respectively.

Upon tail-sheath contraction, the spacing of the annular decreases to 1.8nm, the annular rotation between them increases to 32°, and the cylinder outer dia-

Figure 2. Crystal lattice structure of T4-bacteriophage tail-sheath in (a) extended and (b) contracted forms, showing corresponding lattice vectors.
meter expands from 24 to 34 nm, giving the lattice structure depicted in Fig. 2b. Electron microscopy observation of tail-sheaths in an artificially-induced state of partial transformation not only indicates that the transformation is displacive (and diffusionless) in nature, but allows a direct determination of the operative lattice correspondence (5). This correspondence is depicted by the corresponding vectors $a_1'$, $a_2'$, and $c'$ in Figure 2b.

The distortions of corresponding vectors in Figure 2 define the lattice deformation accompanying this transformation. Inasmuch as the conversion of relative rotation or twist about the cylinder axis to shear strain in the two-dimensional lattice is dependent on the cylinder diameter, the lattices of Figure 2 were constructed using an effective initial diameter of 13 nm based on positions of the protein subunit "centers" estimated from electron density contours generated by electron microscopy (6). Adopting an orthogonal coordinate system with $x_1 \parallel C$ and $x_2$ along the cylinder axis, the total lattice deformation $\xi$ accompanying tail-sheath contraction is expressed by:

$$\xi = \begin{bmatrix} 1.4576 & 0.6050 \\ 0 & 0.4268 \end{bmatrix}$$

(1)

The deformation shear component of $\eta = 0.6050$ corresponds to a large twist about the cylinder axis by which the virus head (and tail core) makes one complete revolution. While tail-sheath contraction is often likened to the operation of a hypodermic needle, the analogy of a drill press, whereby the tail core "bores" through the bacterial cell wall, is more appropriate.

The total deformation can be factored into a rigid-body rotation $R$ and a pure deformation $\beta$ expressed as:

$$R = \begin{bmatrix} 0.9521 & 0.3057 \\ -0.3057 & 0.9521 \end{bmatrix} \quad \beta = \begin{bmatrix} 1.3879 & 0.4456 \\ 0.4456 & 0.5913 \end{bmatrix}$$

(2)

The rotation $R$ is a clockwise rotation of 17.8°. Expressed in principal coordinates $x_1', x_2'$ (defined by a counter clockwise rotation of 24.1°), the pure lattice deformation $\beta$ is:

$$\beta = \begin{bmatrix} 1.5872 & 0 \\ 0 & 0.3920 \end{bmatrix}$$

(3)

This is a relatively large lattice deformation, amounting to a ~60% expansion along one principal axis and a ~60% contraction along the other. It is, however, the smallest principal distortion relating the two structures of Figure 2. The lattice distortion is predominately deviatoric with the total shear strain exceeding 100%. Such a large shear-dominant lattice distortion would suggest that this diffusionless displacive transformation be classed as martensitic (7).

As will occur for any two-dimensional deformation in which the principal strains are of opposite sign, the lattice deformation $\xi$ leaves two vectors unchanged in length. The orientation of two undistorted lines $x_1$ and $x_2$ relative to the parent-crystal and deformation coordinate systems are depicted in Figure 3; $x_1$ is 29.2° from $x_1'$ with $x_2'$ 12.6° from $x_2$. The undistorted lines are fairly close to the [1 0] and [0 1] crystal close-packed directions, consistent with a relatively small change in near-neighbor separations during transformation. (It is interesting to note, however, that the [1 1] direction, nearly parallel to $x_2'$, undergoes such a large contraction that it becomes more close-packed than the original close-packed directions, see Figure 2). The strain energy associated with a martensitic interface in a planar two-dimensional crystal would be minimized if the interface lies
Figure 3. Orientation of undistorted lines \( \bar{x}_1 \) and \( \bar{x}_2 \) relative to parent-crystal and deformation coordinate systems. Deformation axes \( x_1 \), \( x_2 \); principal axes, \( \bar{x}_1 \), \( \bar{x}_2 \); crystal directions \([10]\) and \([01]\) parallel to \( a_1 \) and \( a_2 \).

Along an undistorted line, \( x_1 \) or \( x_2 \). Meeting of the structures along this line would leave the line unrotated such that the lattice deformation would then be an invariant-line strain, the two-dimensional equivalent of an invariant-plane strain. Thus, provided principal lattice strains are of opposite sign such that an undistorted line exists, no additional deformation (e.g. lattice-invariant shear) is required to achieve stress-free matching at a martensitic interface in a planar two-dimensional crystal. The situation is more complicated for the case of a cylindrical crystal. The periodic boundary conditions imposed by the characteristic vector \( C \), dictate that the only "straight" line which closes on itself, and therefore the only orientation of a "flat" interface, is parallel to \( C \). Imposed meeting of the two structures along \( C \) guarantees that this vector is unrotated across the interface and the parent-product orientation relation is thus specified by the condition:

\[
C' \parallel C,
\]

consistent with the observed behavior of partially transformed tail sheaths (5). The strain energy associated with an interface constrained to lie along \( C \) could be minimized if the interface is made semi-coherent by the introduction of a lattice-invariant deformation to make \( C \) a "macroscopically" invariant line. In view of the small finite dimension of \( C \), however, exact matching would be difficult to obtain through (anti-coherency) interfacial dislocations with lattice Burgers vectors. Whether the interface is fully or partially coherent, the orientation relation will always be specified by equation 4.

Observation of partially transformed tail sheaths indicates that the interface remains fully coherent (5). Elastic distortion in the coherent interface will make the interface less sharp than would be the case for an invariant line interface, and this is observed (5). Despite the more diffuse character of the interface, the nature of its long-range displacements and its underlying discrete-crystal step
structure allow its description via interfacial dislocation arrays. Resolving the total lattice deformation $\gamma$ into invariant line strains on the $[10]$ and $[01]$ close-packed directions, the fully coherent interface can be modelled by two sets of coherency (or transformation) dislocations (8,9) as depicted in Figure 4. The helical nature of the close-packed directions in the cylindrical crystal provides a built-in "pore mechanism" whereby only six dislocations of each type need spiral up the $[10]$ and $[01]$ directions (as indicated by the arrows in Figure 4) to completely transform the crystal. Diffuseness of the coherent interface is equivalent to a widening of the dislocation cores.

The possible relevance of dislocations moving along close-packed helices in tail-sheath contraction was first proposed by Harris and Scriven (4). However, their specific model amounts to deformation by slip, whereby dislocations with lattice Burgers vectors deform the crystal via a lattice-invariant deformation. In contrast to the coherency dislocation array of Figure 4, such a deformation involves severe bond-breaking distortions at the dislocation cores, does not transform the crystal to a new structure, and must be driven by externally-applied mechanical forces. By coherently transforming the crystal to a new structure of differing free energy the coherency dislocations propagate the lattice-deformation in response to "internal" chemical forces, thereby providing an effective means of converting chemical energy to mechanical work. The lack of disruption of near-neighbor bonds also provides the intrinsic potential for structural reversibility.

A recently proposed definition of martensitic transformations as a subset of diffusionless/displacive transformations requires that lattice-distortive shear displacements be sufficiently large that the transformation is dominated by strain energy (7); a corollary of this definition is that martensitic transformations are first-order in nature. While the transformation strains involved in tail-sheath contraction are quite large, the actual magnitude of elastic strain energy involved depends on the elastic moduli of the crystal. As will be discussed later, the shear modulus $\mu$ of cylindrical protein crystals is estimated to be two orders of magnitude smaller than that of metals. Since the effective transformation shear $\gamma$ is an order of magnitude higher than for typical martensitic transformations in metals, the strain energy product $\gamma\mu^2$ will be of comparable magnitude. The first order nature of the transformation is evident from calorimetric measurements which reveal a large latent heat of $\Delta H = 150 \text{kJ/mole}$ (10).

Another feature of tail-sheath contraction which is characteristic of a strain-energy-dominated martensitic transformation is the apparent difficulty of nucleation. Judging from the relatively high amount of work required to rupture the bacterial cell wall during contraction, the transformation must involve a substantial free-energy change. Maintaining the extended sheath in a highly metastable state requires a large barrier to martensitic nucleation. This is consistent with the need for strain-induced nucleation in which the tail base-plate becomes a heterogeneous nucleation site as a result of its distortion via displacement of the tail fibres. The interfacial dislocations of Figure 4 would then be generated from displacements in the baseplate.

Polymorphic Transformations in Bacterial Flagella.- Another important displacive transformation for which detailed structural and kinetic information is available involves the mechanism of motion of many bacteria including Salmonella, E. coli, and B. subtilis. These bacteria propel themselves by rigid rotation of "flagella", which are helical filaments consisting of distorted cylindrical crystals of the protein flagellin. A bacterium controls its travel by alternating between two modes of motion depicted in Figure 5. In normal swimming, the flagella are in a left handed helical form, termed the "normal" form, and are rotated counter-clockwise (viewed looking toward the bacterial cell) to act as screw-type propellers. Although the individual flagella are located randomly on the cell wall, motion causes them to group together to form a coordinated helical bundle as shown in Figure 5a. The direction of travel of the bacterium can be changed in a random manner by changing to a "tumbling" motion via reversal of the direction of
rotation of the flagella. Viscous drag of the surrounding fluid then initiates a transformation to a right-handed helical form with a different pitch angle, termed the "curly" form. A sharp change in direction of the helical axis across the transformation interface in partially transformed flagella causes the flagellar bundle to fly apart and renders the individual flagella ineffective as propellers, resulting in a random chaotic motion as depicted in Figure 5b. Reversal back to the original sense of rotation induces reversion of the flagella to the original left-handed state and net motion ensues in a new direction of travel. By adjusting the time spent in each mode, a bacterium can steer itself to a desired environment.

Studies of isolated flagella reveal that, in addition to the normal and curly forms important in bacterial motion, a wide variety of metastable helical forms exists, described as polymorphism, and reversible transformations between these forms can be induced by alteration of the thermodynamic environment. For the case of Salmonella and E. coli flagella, phase diagrams have been constructed mapping the stability of the various forms as a function of pH, ionic concentration, and temperature (12-14).

Among the observed flagellar forms is a perfectly straight form which permits direct determination of its crystal structure by electron microscopy; the structure for straight flagella of Salmonella is depicted in Figure 6. Although the corresponding precise structural information is not available for the helical flagellar forms, it is generally accepted that the various forms are associated with slight changes (diffusionless and displaceable) of the protein crystal structure, and specific structural models have been proposed consistent with observed correlations between twist and curvature of the helical forms (16). The straight cylindrical crystal of Figure 6 can be converted to a macroscopically helical form by inhomogeneous normal strains along the nearly longitudinal (axial) lattice rows. If these rows were exactly longitudinal, expansion on one side of the cylinder and contraction on the other would impart a simple curvature (bending) to the cylinder. By following nearly longitudinal rows which are helical in nature, these normal strains convert the cylinder into the form of a macroscopic helix. If the normal strains remain directed along these lattice rows, twist deformation about the cylinder axis can convert the pitch and handedness of the helical form. Referred to as initially rectangular unit cell, the lattice deformation accompanying displacive transformations between the helical forms is then of the type depicted in Figure 7. While the precise nature of the intra-cell shuffling accompanying the nearly-axial inhomogeneous displacements is not known, the shear deformation which
The occurrence of a macroscopic shape strain across the transformation interface, an important characteristic of martensitic transformations, plays an essential role in bacterial tumbling. Studies of the geometry of partially transformed flagella show that the angle relating the helix axis of the two helical forms across the interface is always equal to the difference between the two helical pitch angles (17). Equivalent to the usual geometric features of martensitic shape strains, this rule has been explained using the orientation relation of equation 4 (unrotated interface line) with the additional constraint that lattice rows of maximum and minimum axial distortion are continuous across the interface; the latter constraint is rationalized on the basis of minimum elastic energy of interfacial dislocation arrays (16). There is no evidence that the transformation interface is other than fully coherent. If the transformation displacements are only of the type depicted in Figure 7, the lattice deformation is an invariant line strain. Circumferential normal strains that would cause a deviation from an invariant line condition have not been detected so far.

The elastic moduli necessary for a quantitative determination of the strain energies involved in the flagellar polymorphic transformations can be estimated from a measured bending modulus for Salmonella flagella of 3x10^{-24} N/m² (18). Treating the crystal as a thick-walled cylinder of 19nm O.D. and 4nm I.D. (15) gives a Young's modulus of E = 4.7x10^{8} N/m². This modulus compares well with that estimated for F actin, a two-stranded helical fibre of a protein similar to flagellin, a measured bending modulus of 5.3x10^{8} N/m² (19) gives a Young's modulus of E = 4.5x10^{8} N/m². A Young's modulus of E = 5x10^{8} N/m² has also been reported for DNA (20). Assuming a Poisson's ratio of v = 1/3, these Young's moduli correspond to an isotropic shear modulus of μ = 2x10^{8} N/m², approximately two orders of magnitude lower than for metals and ceramics which undergo martensitic transformations.

In spite of the relatively soft elastic behavior, a significant transformation nucleation barrier exists as indicated by a hysteresis accompanying forward and reverse transformation. Stress-assisted transformation under forces induced by fluid flow has been studied in isolated flagella of Salmonella SJ25 with one end
attached to a glass slide, and the forces acting were quantitatively analyzed (21). The results support the martensitic character of the transformations in that axial loads exert little influence, but the transformation interacts strongly with torsional (shear) loads. The positive torque required for forward transformation and a smaller negative torque required for reversion were both measured, identifying the total transformation hysteresis. A sharp load drop following initiation of single-interface transformation indicated that a substantially higher driving force is required for nucleation than for growth. Transformations from the normal (N) to curly (C) forms and to a "semi-coiled" (SC) form were studied. The net torque necessary to drive the nucleation process can be estimated from one-half the total torque hysteresis, giving $7.5 \times 10^{-19}$ N-m for the N-SC transformation and $5 \times 10^{-19}$ N-m for N-C. Taking an average cylinder radius of 5.8 nm, the twist increments for these transformations (16) correspond to transformation shear strains of $\gamma_{N+SC} = 0.023$ and $\gamma_{N+SC} = 0.032$. Converting torques to maximum shear stress $\tau$ for a thick-walled cylinder, critical driving forces $\Delta G_c$ for nucleation can be determined from the work term $-\gamma W$ (22). With a protein molar volume of $7.8 \times 10^{-2}$ m$^3$, this gives critical values of $\Delta G_c$ N+SC = -1.01 kJ/mole and $\Delta G_c$ N+SC = -1.11 kJ/mole. As molar quantities, these values are similar to the critical driving forces for FCC-BCC transformation in steels; however, the comparison is misleading due to the much larger molar volume of the protein. Expressed as a free energy change per unit volume, $\Delta g$, and normalized to the estimated shear modulus, critical driving forces of $\Delta G_c$ N+SC = -7.4x10^-5 J/m$^3$ and $\Delta G_c$ N+SC = -8.2x10^-5 J/m$^3$ are comparable to those of metallic systems involving similar transformation shear of a few percent. Direct observation of these transformations revealed that they nucleated heterogeneously at the point of attachment to the glass slide, and whether the C or SC form nucleated depended on the detailed geometry of the distortion imposed by the attachment. It is interesting to note that, because of the low-pitch (nearly circumferential) helical lattice row in the structure of Figure 6 (a similar feature exists in the structure of E. coli (23) flagella), accomplishing the transformation shear requires the formation of only a single coherency dislocation which can spiral up this helix to completely transform the crystal.

Given the large number of polymorphic forms observed in isolated flagella, a problem of interest to biologists has been the question of why bacterial tumbling involves discrete transformation between the N and C states without involving structures such as the SC state which can be considered structurally intermediate between N and C. One explanation is that these intermediate states involve a large axial contraction which is opposed by the viscous drag of the surroundings (16). The characteristics of martensitic transformations suggest some additional factors. As has been well demonstrated for the case of the competing metastable $\beta'$ and $\gamma'$ martensitic phases in $\beta$ CuAlNi alloys (23), the thermodynamics of transformation under stress can favor the transformation with the larger transformation strain, even when the lower strain transformation gives the nearest metastable state (in free energy) under stress-free conditions. The "site specificity" aspect of heterogeneous martensitic nucleation observed in the experiments just discussed is another characteristic that warrants attention. Consistent with dislocation-dissociation theory of martensitic nucleation (24), details of the "hook" assembly where the flagellum is attached to the bacterium can control which coherency dislocations can be most easily derived from this nucleation site. Perhaps most important, the nature of crystalline bonding is such that relative free energies can not be simply inferred from structure. That the SC state can be regarded as structurally intermediate between N and C states does not imply that it is energetically intermediate. Calculating free energies from the midpoints of the experimental torque hysteresis measurements (21), the free-energy difference between the N and C states under stress-free conditions is $\Delta G_{N-C} = +3.71 \times 10^2$ J/mole, while the SC state has a higher free energy with $\Delta G_{N-SC} = +4.71 \times 10^2$ J/mole.

Following a procedure analogous to the Clausius-Clapeyron relation, the foregoing relative free-energy estimates can be combined with the available phase
diagram information to derive further thermodynamic information concerning the flagellar polymorphic transformations. Denoting chloride ion concentration as C, the phase diagram (12) for the Salmonella S25 flagella (at an ambient temperature of -30°C) indicates an N=SC equilibrium line of slope dC/dP = -0.05M passing through C=0 at pH=5. The shift of the equilibrium line with temperature is described by dP/dT = -0.037 K^-1. For the conditions of the stress-assisted transformation experiments (21) (C=0.15M, pH=7), the deviation from the N=SC equilibrium temperature T0 can then be estimated as T-T0 = -0.123K giving T0 = 180K. The AG N=SC value of 8.71x10^-2 J/mole estimated from the torque hysteresis midpoint then defines a transformation entropy change of \( \Delta S = -\Delta G/\Delta T = -\Delta G/(T-T_0) = -3.8 \text{J/mole}{ }^\circ \text{K.} \) The transformation enthalpy change then estimated as \( \Delta H = T_0\Delta S = 670 \text{J/mole.} \) This is two orders of magnitude smaller than the enthalpy change of the large-strain martensitic transformation in the case of virus tail-sheath contraction.

In contrast to the virus tail-sheath where the function is a one-time performance of a large amount of work requiring a large deviation from equilibrium, the N=SC flagellar transformation during bacterial tumbling need only produce a mechanically reversible change of flagellar shape, i.e., "shape memory effect," requiring a relatively small amount of work. Mechanical reversibility is insured by a small transformation strain promoting a relatively small critical driving force for nucleation such that conditions for forward and reverse transformation can be met by modest changes in thermodynamic conditions that do not destroy the crystal. The behavior is analogous to thermoelastic martensitic transformations. The incomplete nature of the N=SC transformation in tumbling is also suggestive of a thermoelastic growth force balance, but the origin of the growth restraining force is in this case yet unclear.

Discussion.- Thus far our treatment of biological processes as displacive phase transformations has not considered the nature of protein bonding as it differs from the bonding of metals and ceramics. Details of the short-range bonding interactions between protein subunits will be important to the structure and energy of interfacial dislocation cores, the intrinsic lattice resistance to dislocation motion, and to the physics underlying the observed thermodynamic quantities. However, the long-range constraints imposed by crystalline periodicity allow that many aspects of strain-energy dominated, first-order martensitic transformations can be predicted on the basis of crystal geometry, linear elasticity, basic dislocation theory, and macroscopic thermodynamics, without sensitivity to local bonding details; this forms the strength of the theory of martensitic transformations as it currently stands. The numerous parallels in the behavior of martensitic transformations in three-dimensional metallic crystals and the cylindrical protein crystals examined here, in spite of the bonding differences, attests to the usefulness of the approach.

In addition to the examples of contractile virus tail sheaths and bacterial flagella, other examples such as pili, tubules, and microtubules show that cylindrical crystals are ubiquitous in biological structures. Other forms of two dimensional crystals are also common, and may undergo martensitic transformations. A twinned structure representing the internal substructure of a martensitic transformation product is observed in phospholipid membranes (25) but it is not clear whether the structure arises from a martensitic mechanism. A two-dimensional dilatational displacive transformation apparently occurs in some icosahedral virus capsids. Arrays of cylindrical crystals with one dimensional periodicity along their lines of attachment are important to the mechanism of motion in higher organisms. Nabarro (26) has discussed the relative motion of muscle fibres in terms of dislocations moving along such one dimensional arrays. It appears that in many of these cases the displacements involved are partial lattice vectors and therefore produce a change in structure (lattice deformation) with an associated chemical free energy change. An important property of partial dislocations compared to lattice dislocations is their response to chemical rather than purely mechanical forces. Mechanical reversibility is also promoted by
the preservation of near neighbor bonds at partial dislocations in contrast to lattice dislocations. It is likely that a central feature of the mechanisms of motion and shape change in periodic biological structures of all dimensionalities is the movement of partial (coherency) dislocations in response to chemical forces.

As a final note, man is credited with making use of martensitic transformations in metallic systems for about three thousand years and the shape memory effect for a few decades. It now appears from the behavior of the viruses and bacteria examined here that the earliest application of these phenomena dates back 3.5 billion years. We may be unwittingly exploiting even more sophisticated applications as we live.

Conclusions.—Displacive phase transformations in virus tail-sheaths and bacterial flagella are identified as martensitic. Allowing for special constraints of cylindrical symmetry, the geometric, thermodynamic, and kinetic aspects of these transformations are consistent with strain-energy-dominated martensitic behavior, as dictated by the long-range constraints of crystalline periodicity. The transformations are describable by partial dislocation mechanisms which may be of broader relevance to the mechanisms of motion and shape change of periodic biological structures in general.

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References.—

1. KING, J., private communication.
23. Otsuka, K., Wayman, C.M., Nakai, K., Sakamoto, H., and Shimizu, K.,
26. Nabarro, F.R.N., Theory of Crystal Dislocations, Oxford Univ. Press,