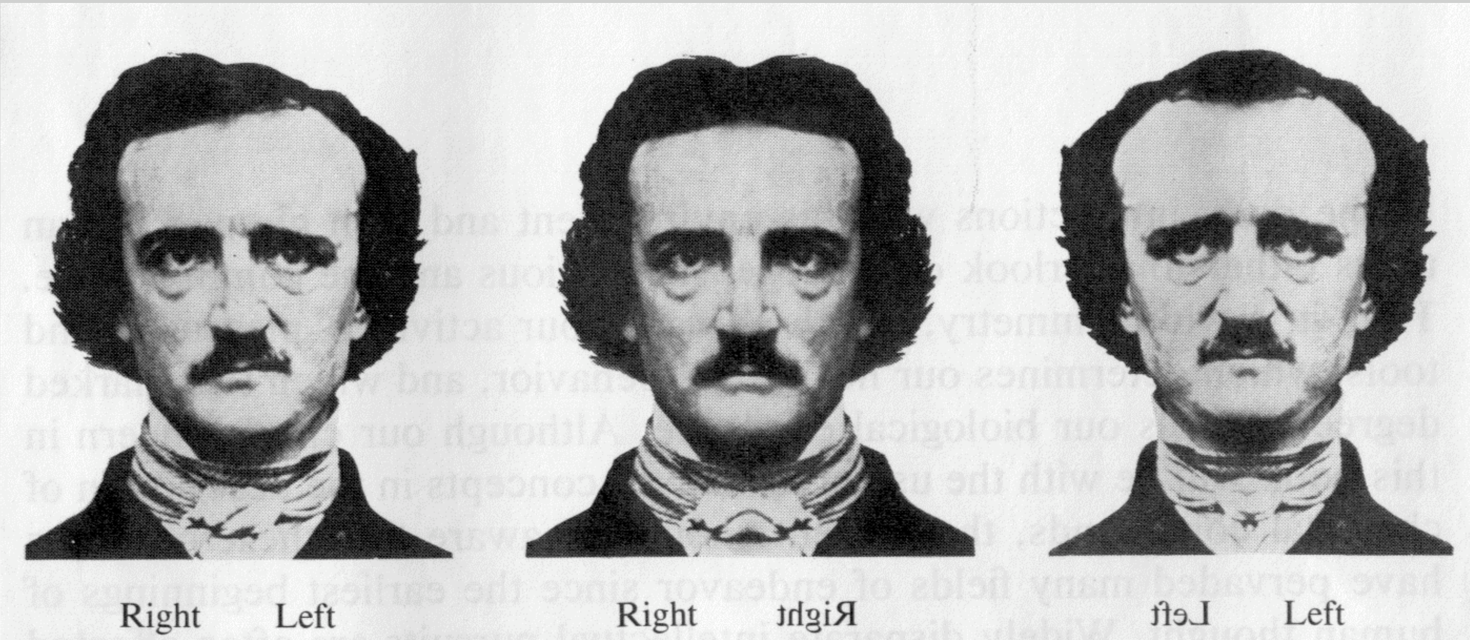
BioSci737: Fundamentals of Symmetry

Notion of symmetry depends on the existence of equivalent parts in a pattern or object

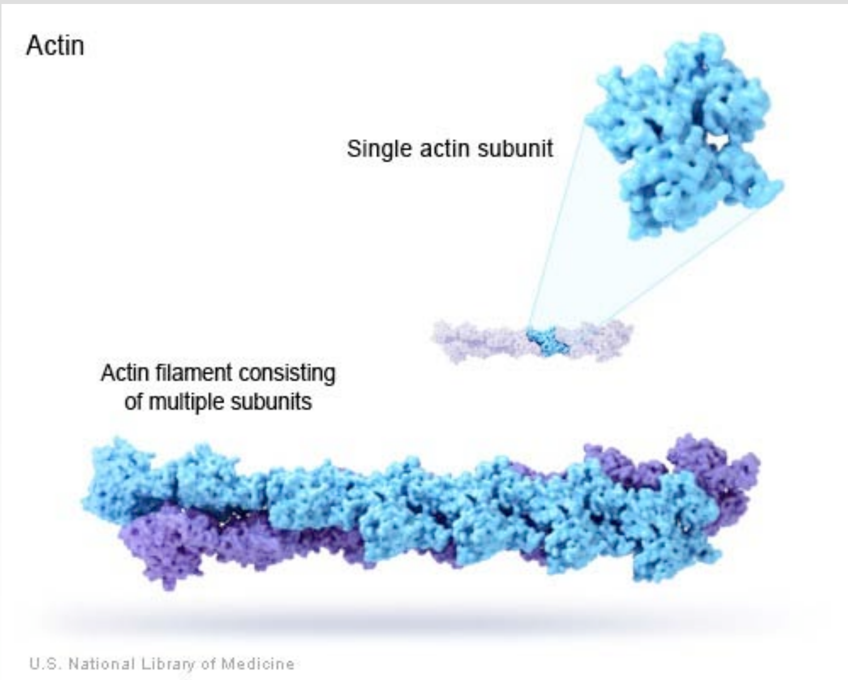


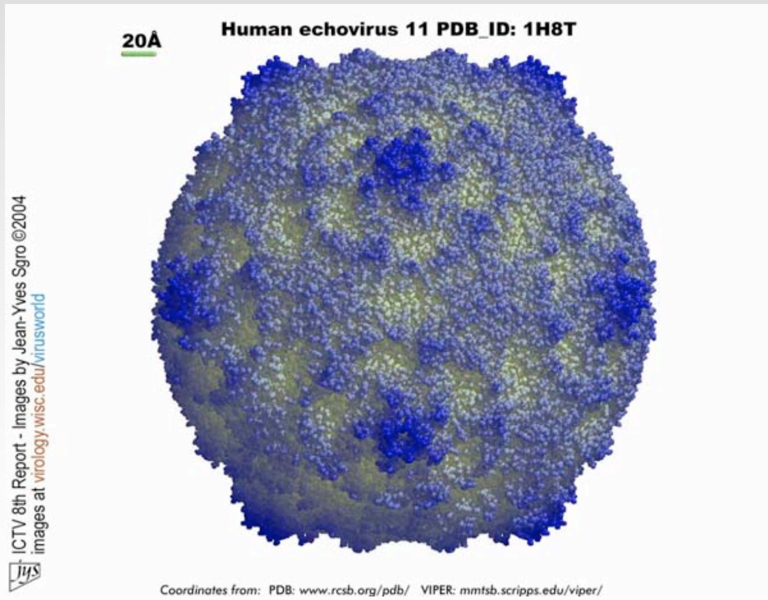
From Bernal, Hamilton & Ricci (1972)

If there are motions which carry or map any part of an object to the original position of any other, while leaving the appearance of the object unchanged, then the object is symmetrical. Such motions are called symmetry operations for the object.
Symmetry is a mathematical ideal and may be imperfectly realized in nature.

Why is symmetry important in structural biology?

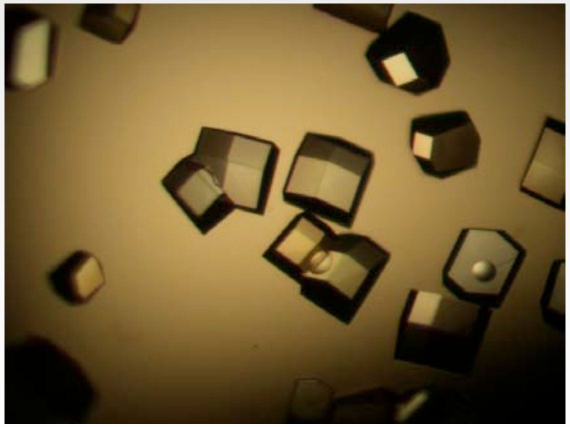
1. Many biological molecules assemble into symmetric or nearly symmetric structures … this is critical to their function.



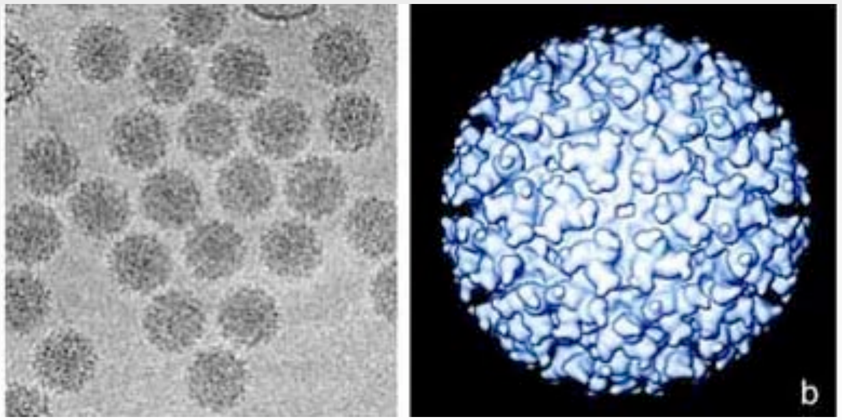


Why is symmetry important in structural biology?

1. We take advantage of symmetry in scattering-based techniques (e.g. electron microscopy and X-ray crystallography) … it massively increases the signal-to-noise ratio. Understanding symmetry is critical to proper data analysis in both methods.



3D Protein Crystals



Electron micrograph of icosahedral virus particles (L) and a derived 3D reconstruction (R).

Images courtesy Tuli Mukhopadhyay

The purpose of this lecture …

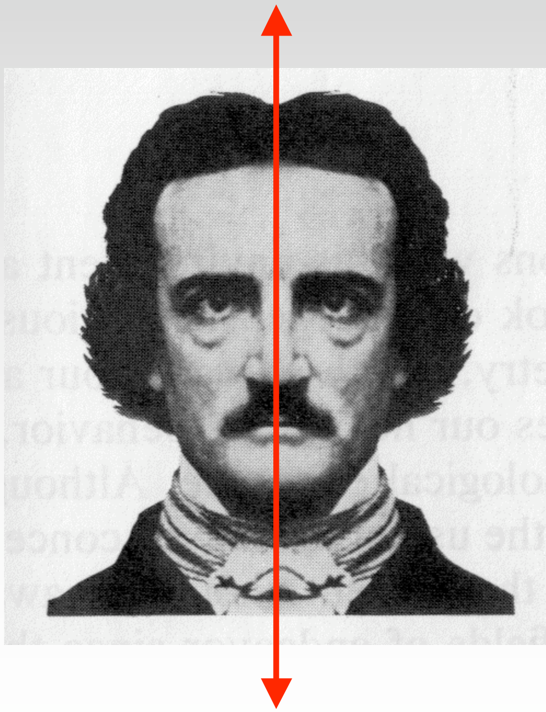
1. To introduce the basic concepts and language of symmetry.

2. To provide some tables and notation … reference material for the electron microscopy and X-ray crystallography lectures.

Symmetry operations and symmetry elements

A symmetry operation may keep some points fixed in place; the set of such points is called the symmetry element for the operation. In the case of reflection in the plane, the symmetry element is a line.

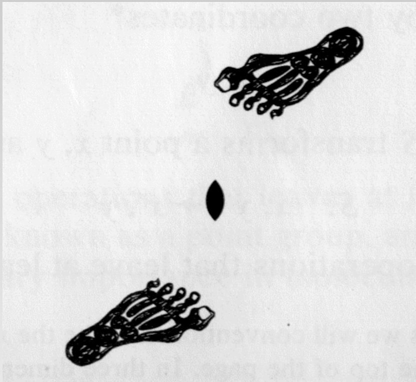
Symmetry operation: reflection in the plane

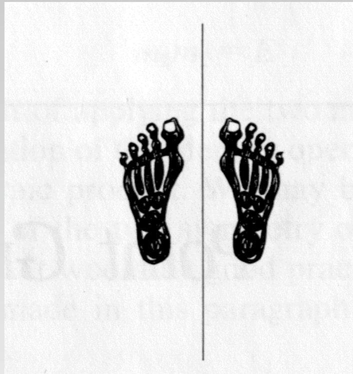


Symmetry element

Symmetry in 2D
Rotations, Reflections and Translations

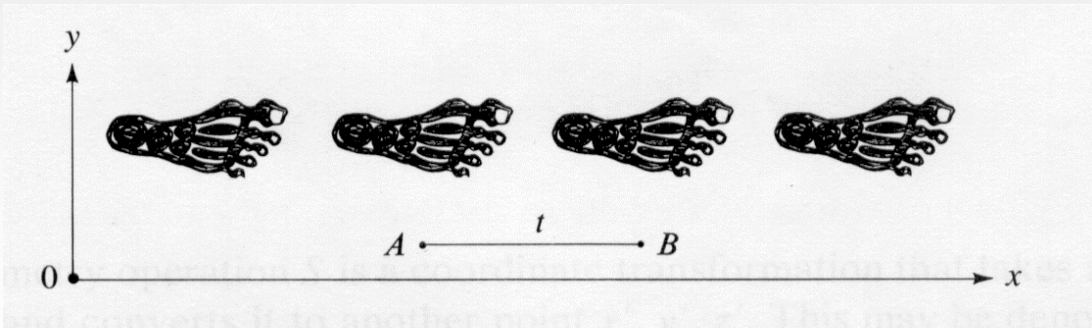
Rotation and Reflection are "Point symmetry Operations" … they leave at least one point of the object fixed





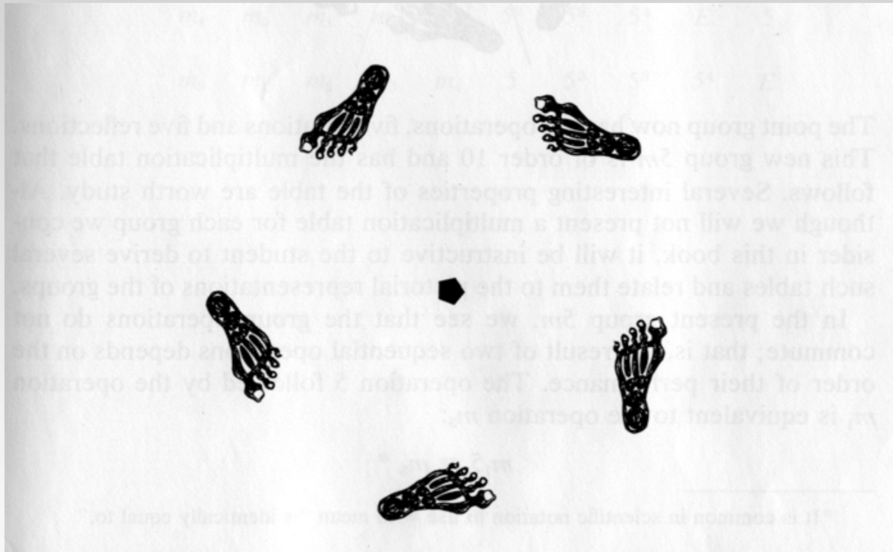
From Bernal, Hamilton & Ricci (1972)

Translation is a "space symmetry operations" … it leaves no point of the object fixed.



Symmetry operations are rigid motions, motions which do not alter the distances between points. Rigid motions are also called isometries

A 2D object with five fold rotational symmetry … an example of a symmetry group



From Bernal, Hamilton & Ricci (1972)

What is a “group”?

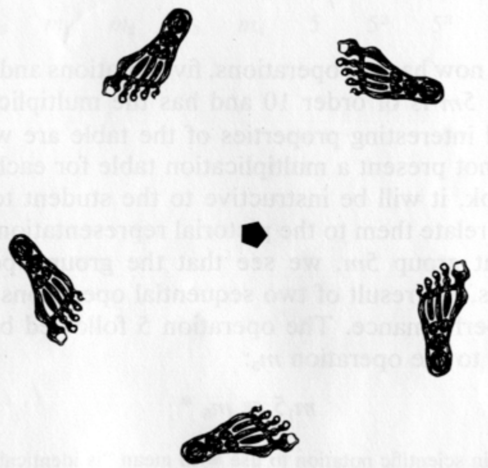
A group of movements is a set that satisfies the following conditions

1. The product of any two movements in the set, or of any movement with itself, is a member of the set.
2. The identity is included as a movement
3. For every movement there is an inverse, a member of the set such that the product of the movement and its inverse is the identity
4. For three successive movements the associative law applies.

Which is all best illustrated by example …

Our object is described by a symmetry group

The name of this group is simply '5', since all elements are generated by the single 5-fold rotation axis. The *order* of the group – the number of different symmetry operations – is also 5.



The operations of the group

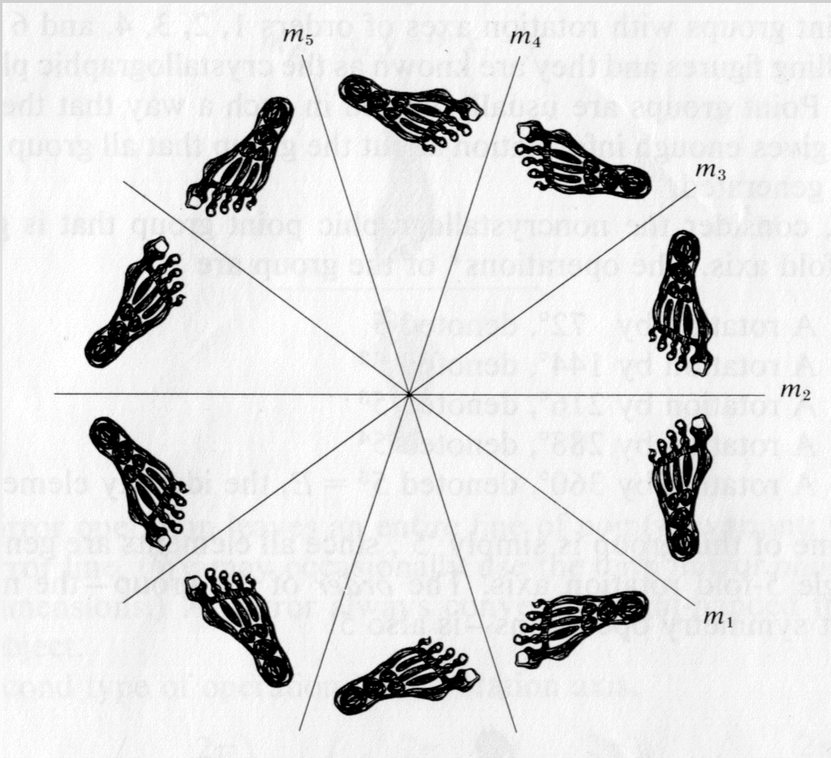
(1) A rotation by 72°, denoted 5
(2) A rotation by 144°, denoted 5^2
(3) A rotation by 216°, denoted 5^3
(4) A rotation by 288°, denoted 5^4
(5) A rotation by 360°, denoted $5^5 = E$, the identity element.

The multiplication table for the group is

E	5	5^2	5^3	5^4
5	5^2	5^3	5^4	E
5^2	5^3	5^4	E	5
5^3	5^4	E	5	5^2
5^4	E	5	5^2	5^3

From Bernal, Hamilton & Ricci (1972)

A more complicated point group in the plane.



From Bernal, Hamilton & Ricci (1972)

The asymmetric unit / fundamental region of a symmetric object.

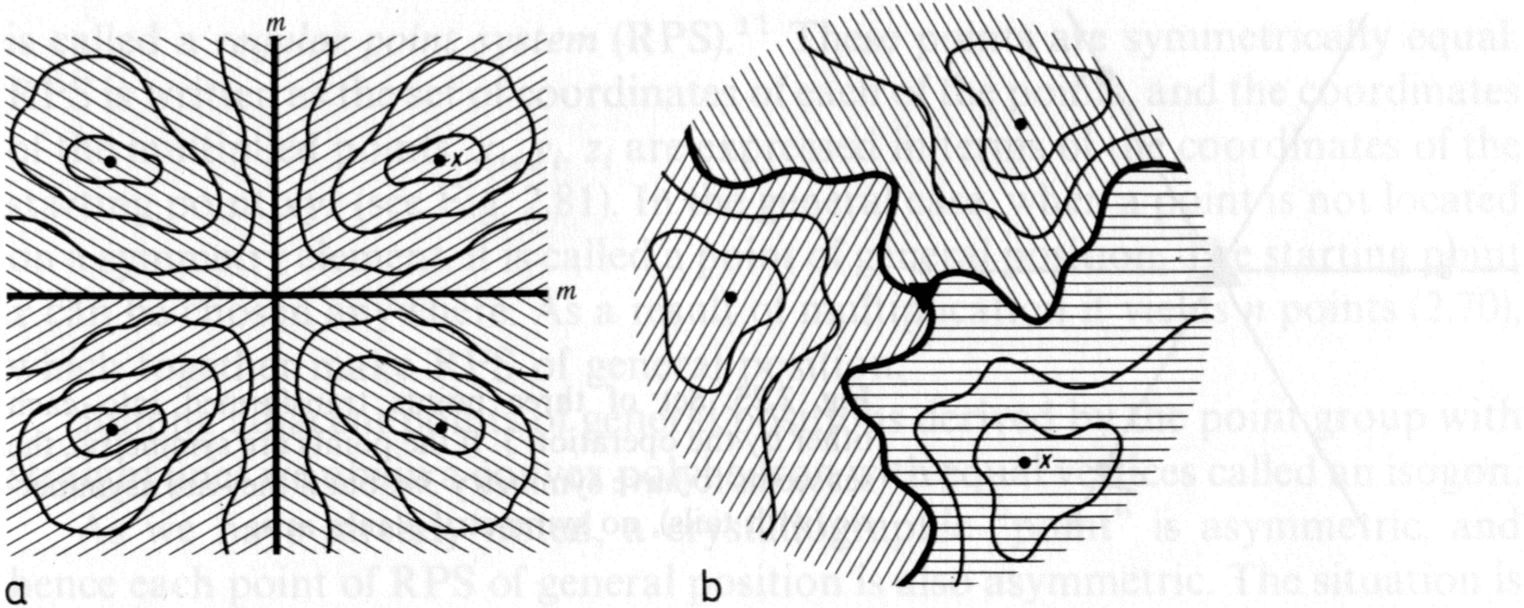


Fig. 2.26a,b. Formation of asymmetric independent regions as exemplified by two-dimensional groups *mm* (**a**) and 3 (**b**)

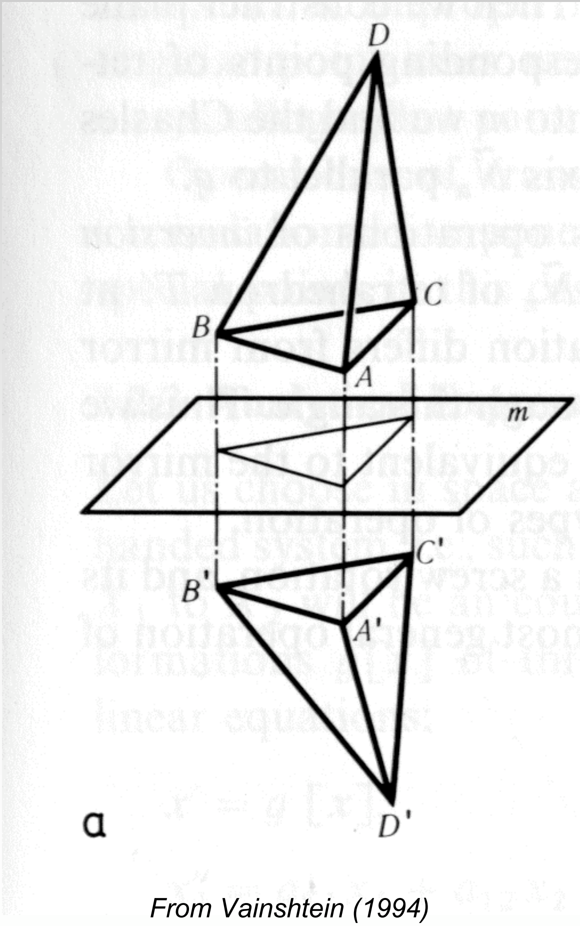
From Vainshtein (1994)

Symmetry operations in 3D

One useful way to classify symmetry operations is by the number of points they keep fixed

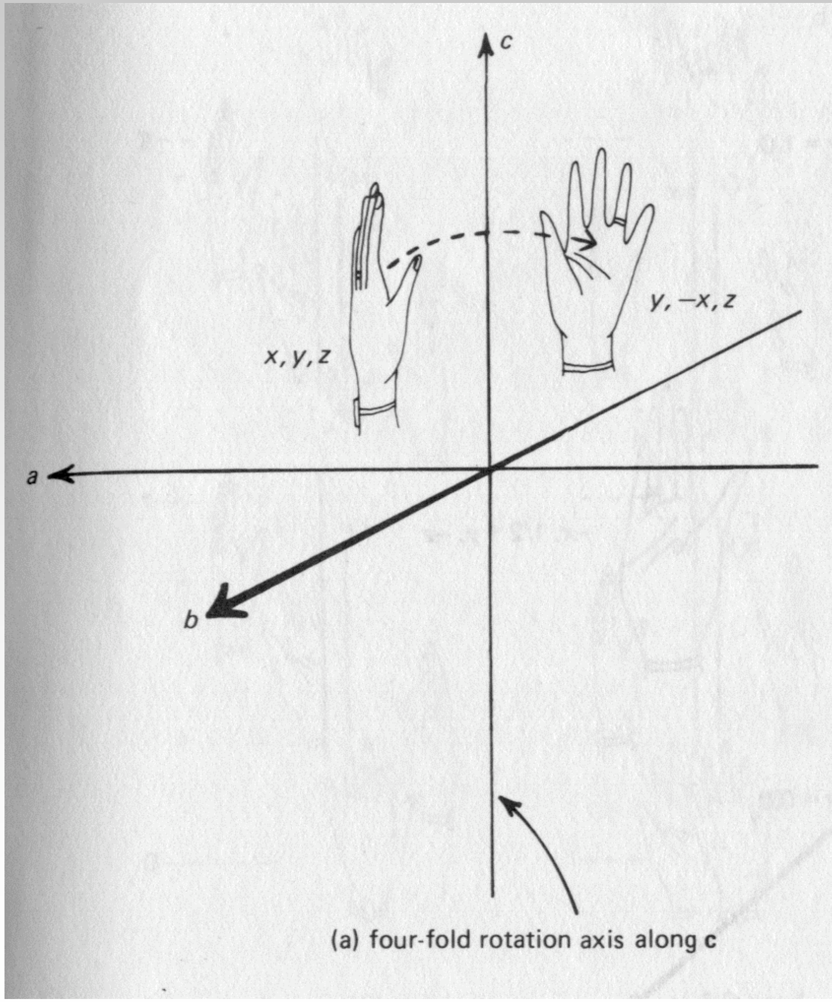
Point symmetry operations	The identity	Fixes 4 non-coplanar points
	Reflection	Fixes 3 non-colinear points
	Rotation	Fixes 2 points
	Rotary inversion/ Rotary reflection	Fixes 1 point
Space symmetry operations	Translation	Fixes no points
	Glide Reflection	Fixes no points
	Screw Rotation	Fixes no points

Symmetry operations in 3D: Reflection



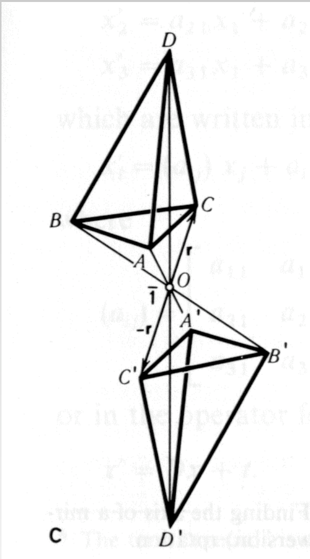
From Vainshtein (1994)

Symmetry operations in 3D: Rotation



From Glusker & TrueBlood (1985)

Symmetry operations in 3D: Inversion and Rotary Inversion (Rotary Reflection)



From Vainshtein (1994)

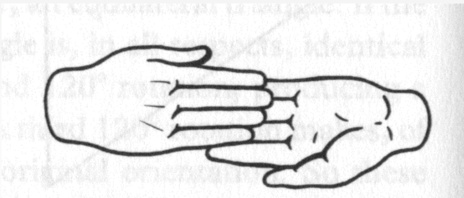
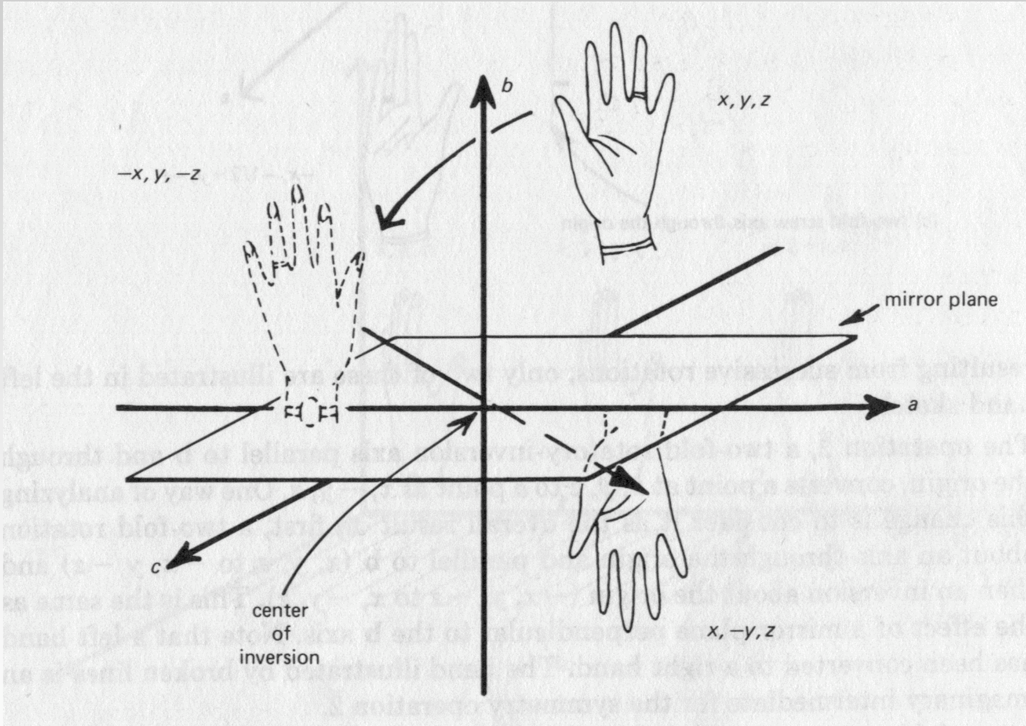


Fig. 2.8 Inversion symmetry of a pair of hands.

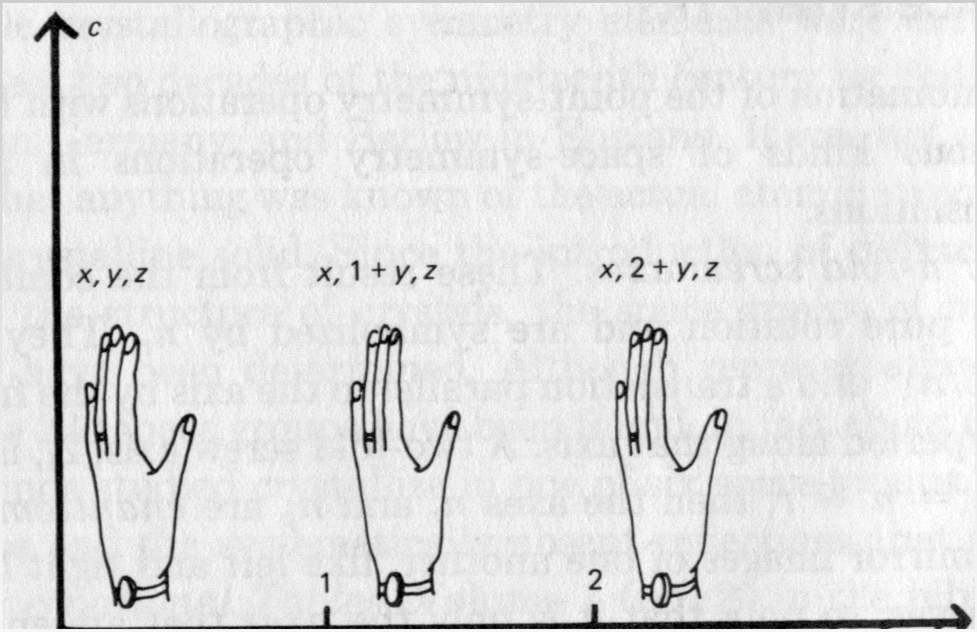
From Blow (2002)



(b) two-fold rotatory-inversion axis *or* mirror plane

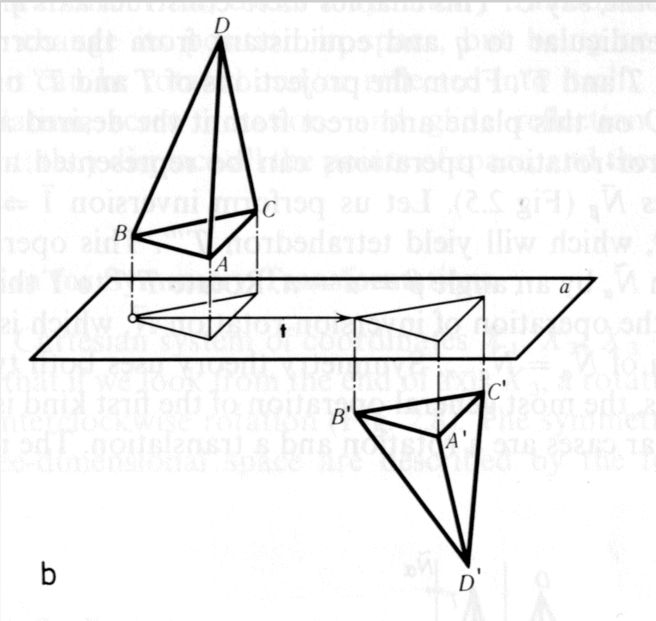
From Glusker & TrueBlood (1985)

Symmetry operations in 3D: Translation

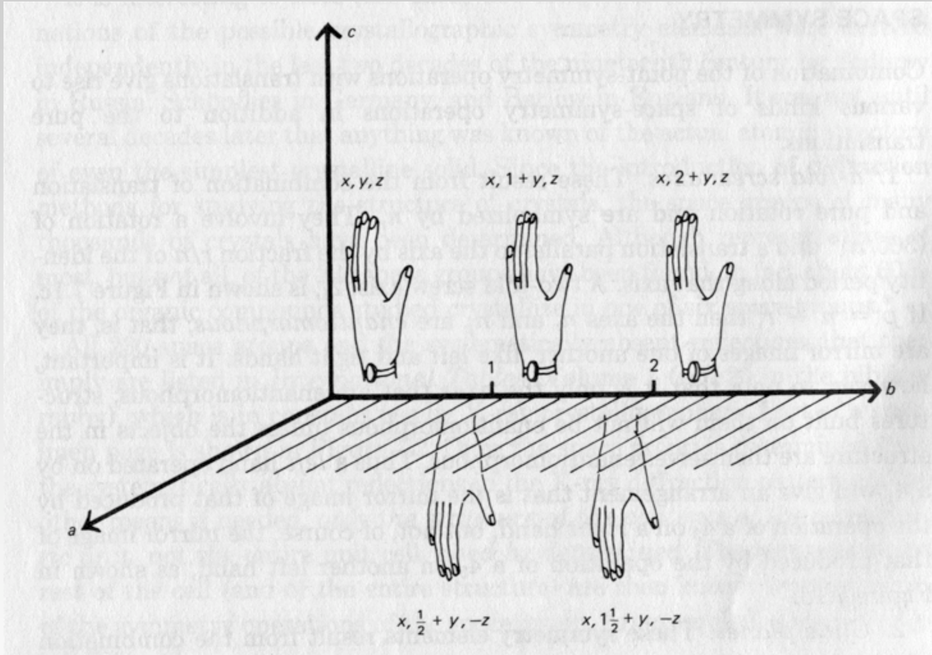


From Glusker & TrueBlood (1985)

Symmetry operations in 3D: Glide reflection



From Vainshtein (1994)

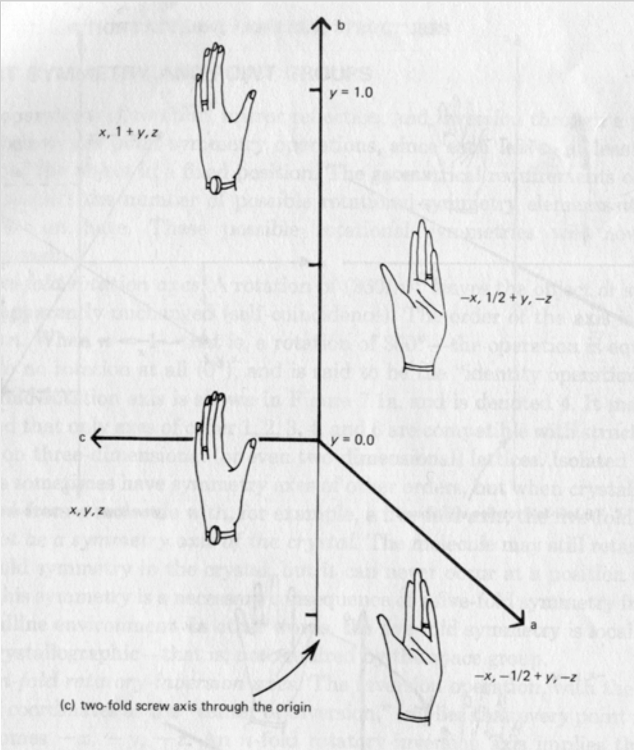


(e) *b*-glide plane through the origin and normal to c

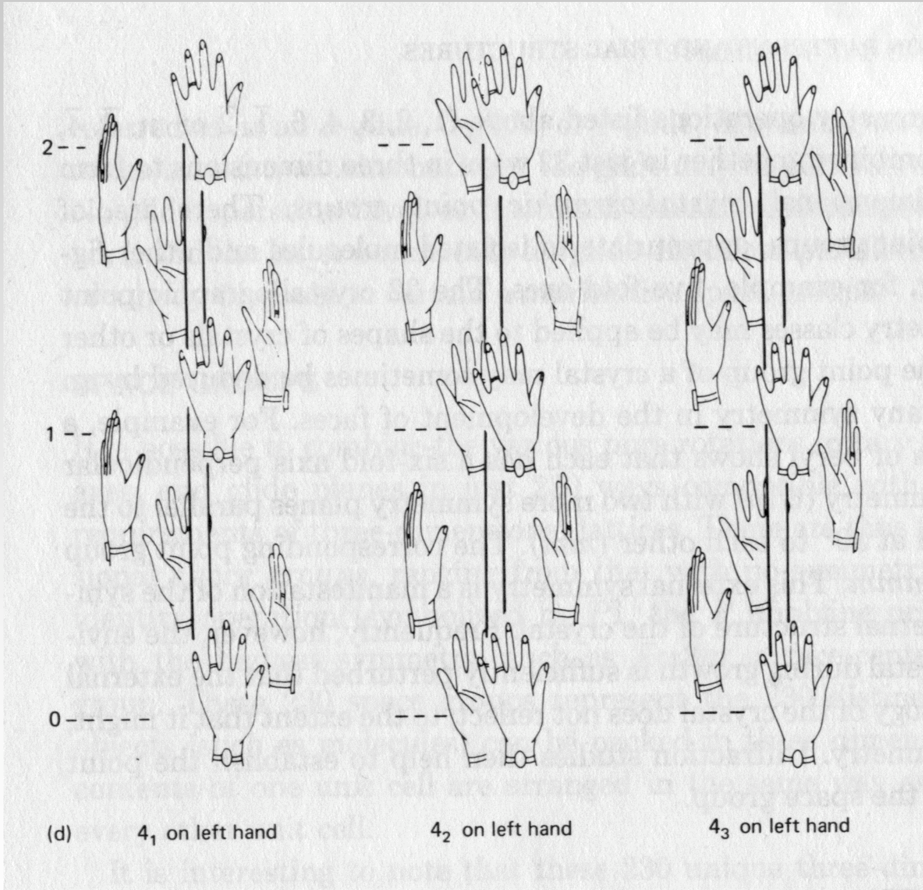
From Glusker & TrueBlood (1985)

Symmetry operations in 3D: Screw Rotation

From Glusker & TrueBlood (1985)



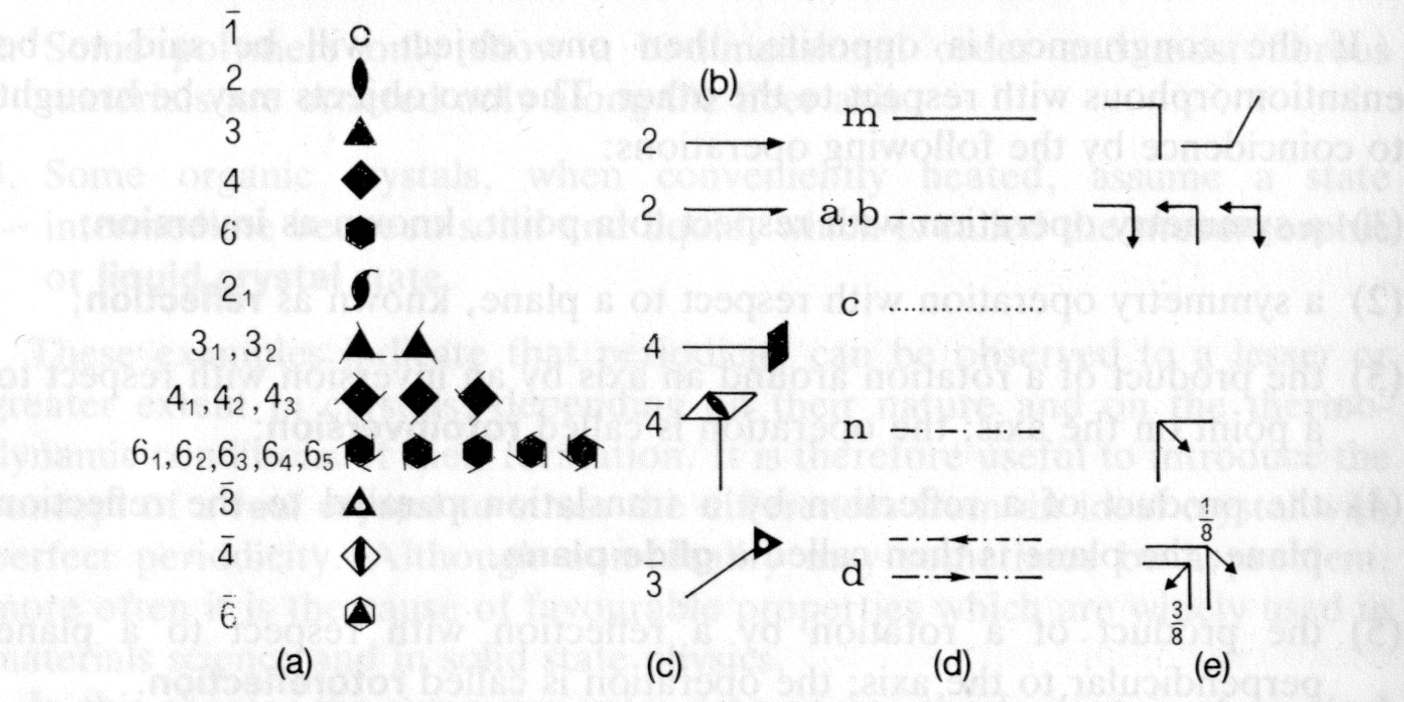
From Glusker & TrueBlood (1985)



An n_m screw axis involves a rotation of 360/n° accompanied by a translation of m/n of the fundamental repeat distance.

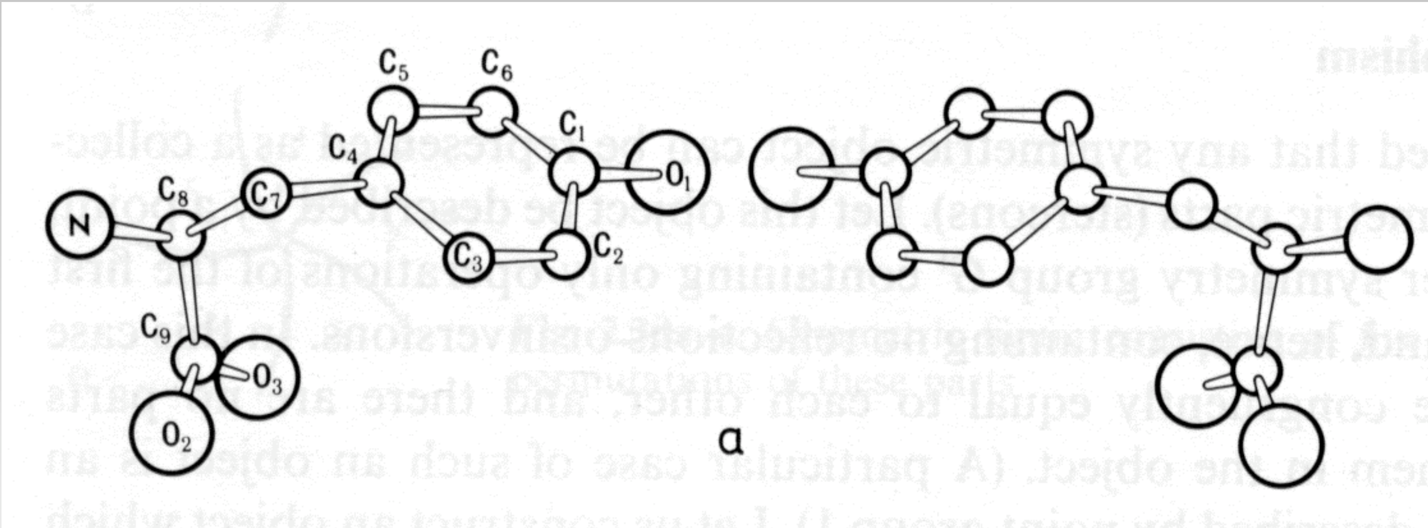
Graphical representations of symmetry operations

Table 1.1. Graphical symbols for symmetry elements: (a) axes normal to the plane of projection; (b) axes 2 and 2_1 parallel to the plane of projection; (c) axes parallel or inclined to the plane of projection; (d) symmetry planes normal to the plane of projection; (e) symmetry planes parallel to the plane of projection



From Giacovazzo (1992)

Enantiomorphism and the symmetries of biological specimens



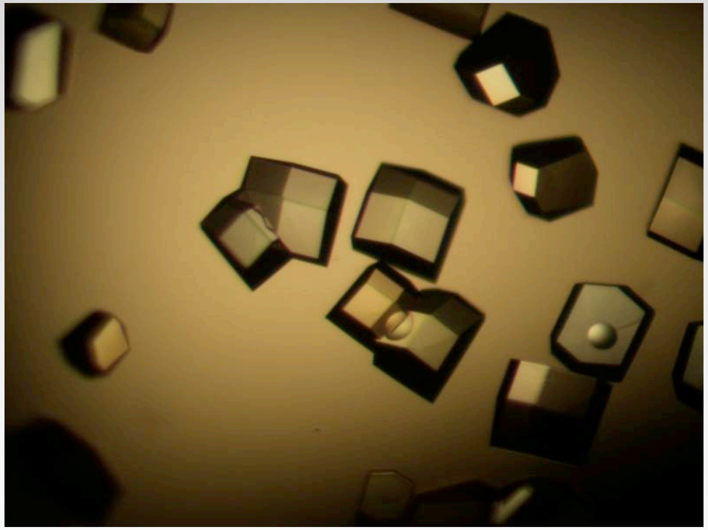
From Vainshtein (1994)

Many biological molecules are chiral. This includes the amino acid; the building blocks of proteins. Natural proteins are made of L-amino acids. The enantiomers … D-amino acids … are used very rarely in nature.

This means that for proteins and protein assemblies reflections and inversions are not “permitted” since they switch the handedness of an object. They would convert a protein made up of L-amino acids into a protein made up of D-amino acids.

Enantiomorphism therefore limits the symmetries we observe with biological specimens

While a biological assembly cannot accommodate mirror planes and centers of inversion, its diffraction pattern may …



Tetragonal crystals of lysozyme

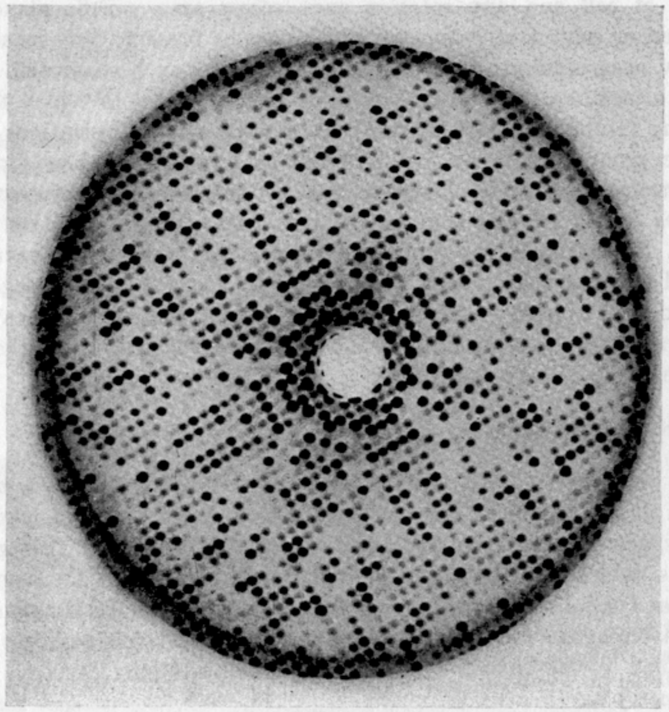


FIG. 7. X-Ray diffraction pattern taken down the 4-fold axis of a tetragonal crystal of hen egg lysozyme using a precession camera (courtesy of Dr. C. C. F. Blake). The array of reflections belong to a section through the reciprocal lattice. The effects of the 4-fold symmetry axis on the diffraction pattern are clearly visible.

From Fraser & Macrae (1969)

Symmetry groups in 3D

- We'll deal first with the symmetry groups that don't include translational symmetry (**Point groups**)

- Then we'll deal with the symmetry groups that include translational symmetry (**Line groups**, **Layer Groups**, **Space groups**)

Point groups

The symmetries of non-periodic objects

A group of symmetry operations that leaves at least one point invariant (in the same place) is known as a **point group**

There are three families of point groups that can accommodate chiral molecules of fixed hand … the **cyclic**, **dihedral** and **cubic** point groups. They involve only rotations (reflections and inversions being disallowed).

Unluckily for you, point groups containing reflections and inversions are important for describing the symmetry of diffraction patterns, so we can't ignore them entirely.

“Biological” Point Groups part 1. Cyclic point groups

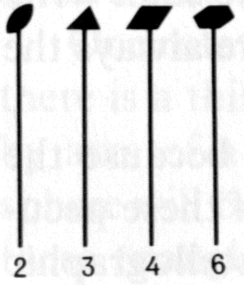


Fig. 2.38. A set of symmetry elements of crystallographic groups of rotations $N - C_n$

From Vainshtein (1994)

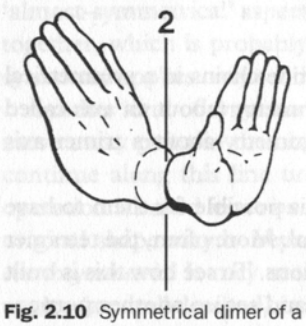


Fig. 2.10 Symmetrical dimer of a chiral object. The 2-fold rotational symmetry axis is indicated.

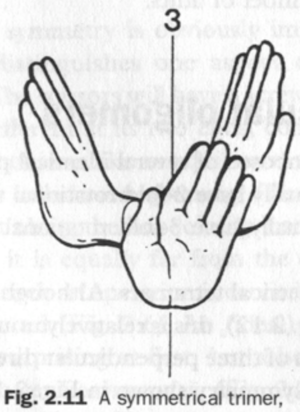


Fig. 2.11 A symmetrical trimer, showing its 3-fold axis.

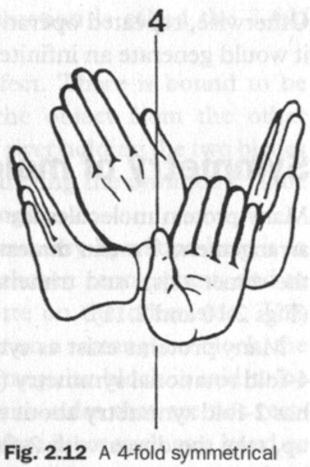
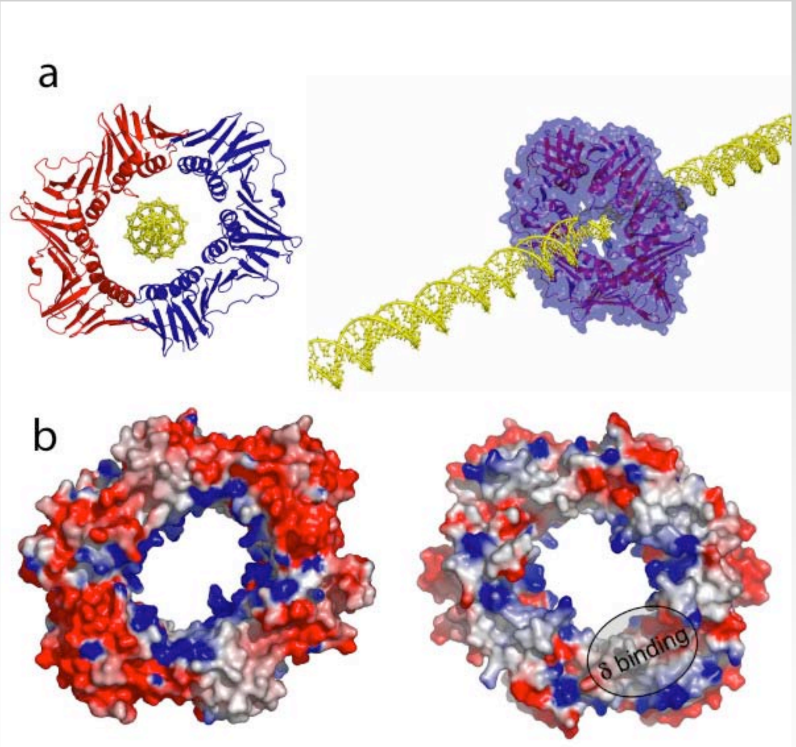


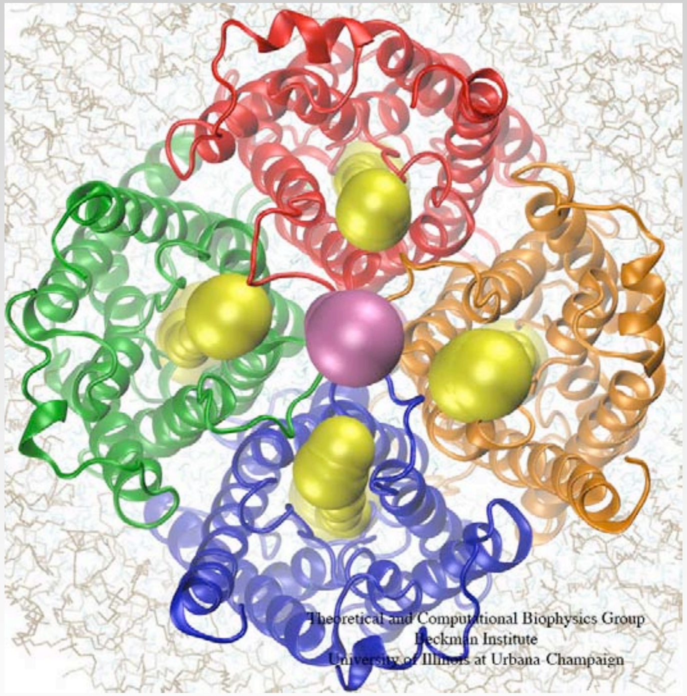
Fig. 2.12 A 4-fold symmetrical tetramer.

From Blow (2002)

Cyclic point groups: examples



Dimeric sliding DNA clamp
from S. pyogenes



Tetrameric Aquaporin-1

“Biological” Point Groups part 2. Dihedral point groups

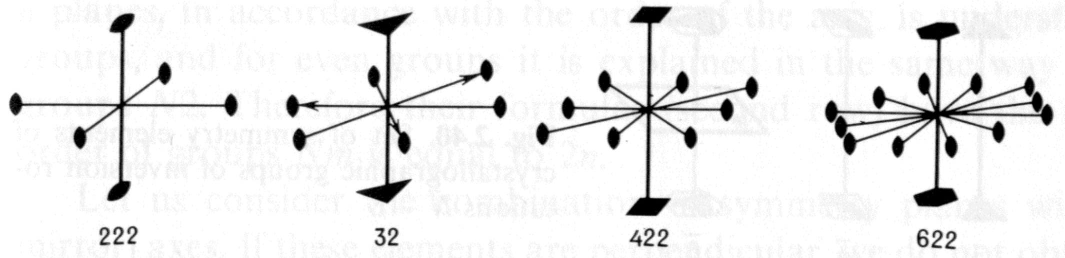


Fig. 2.39. Set of symmetry elements of crystallographic groups of family $N2 - D_n$

From Vainshtein (1994)

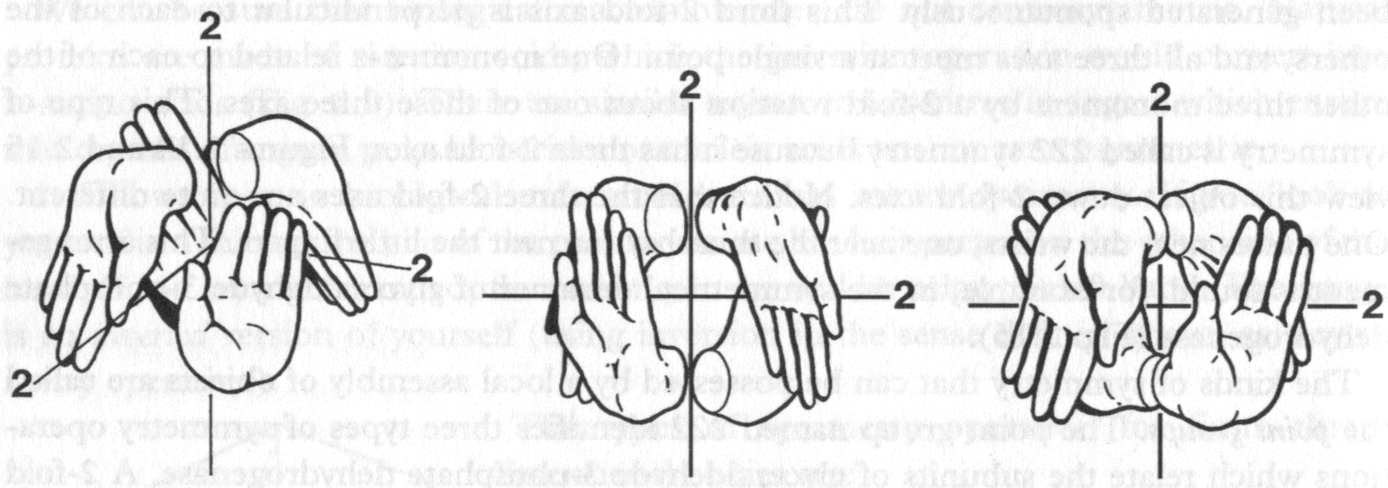


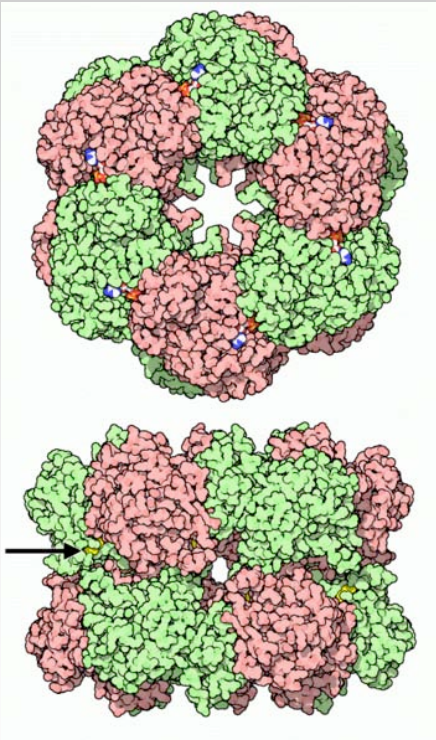
Fig. 2.13 A symmetrical tetramer with 222 symmetry.

Fig. 2.14 The 222 tetramer viewed along one of its 2-fold axes.

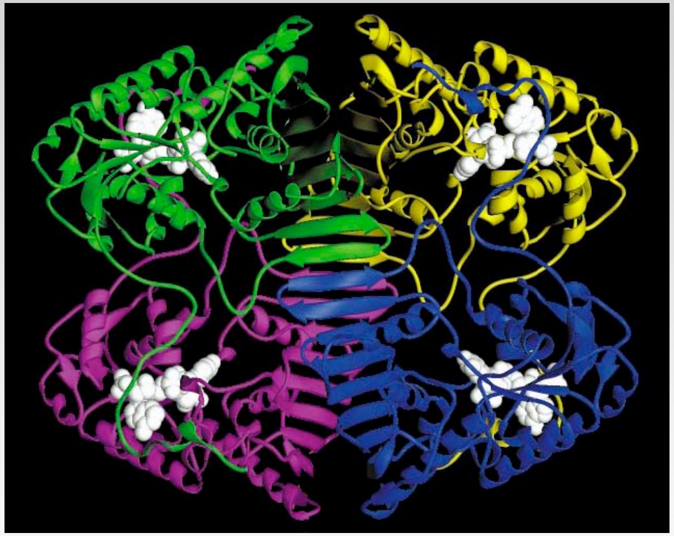
Fig. 2.15 The 222 tetramer viewed along a different 2-fold axis.

From Blow (2002)

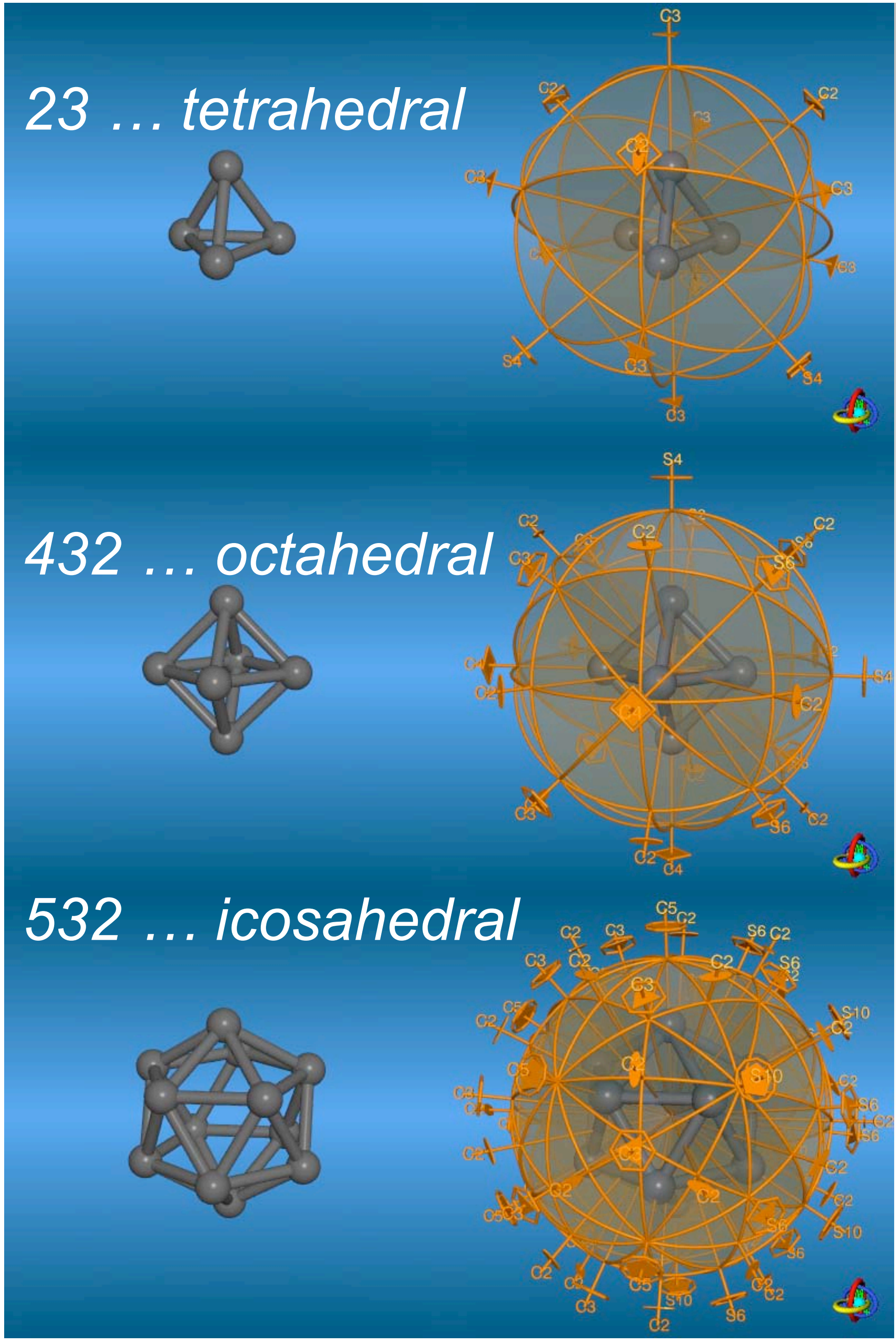
Dihedral point groups: examples



Glutamine synthetase: 622 pg symmetry



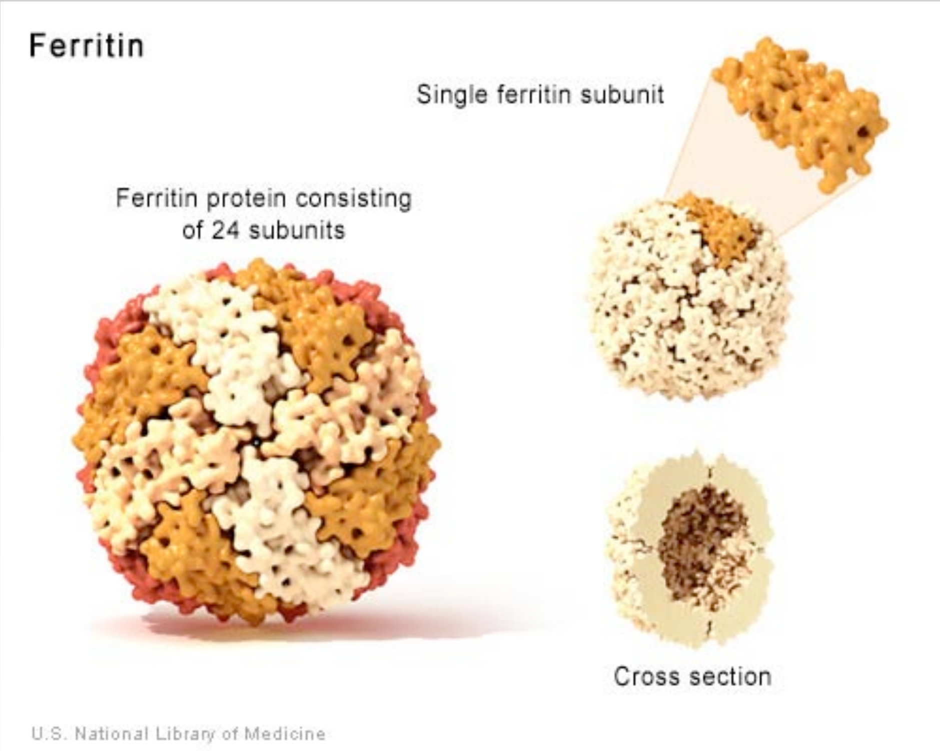
Glucose fructose oxidoreductase: 222 pg symmetry

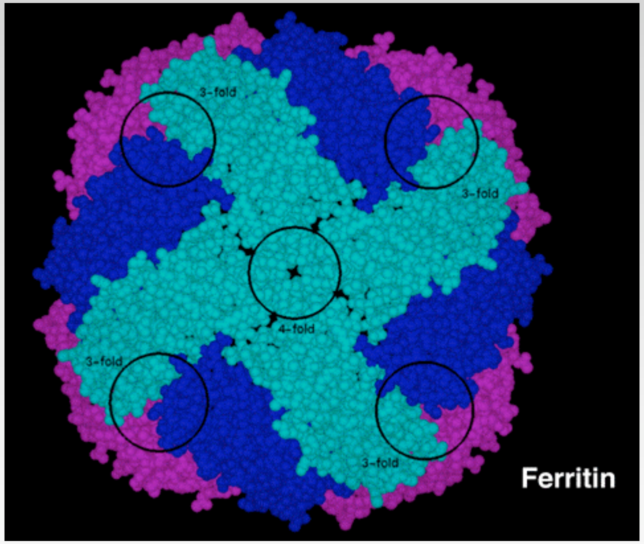


“Biological” Point Groups part 3. Cubic point groups

Images courtesy Dr Stefan Immel
http://csi.chemie.tu-darmstadt.de/ak/immell

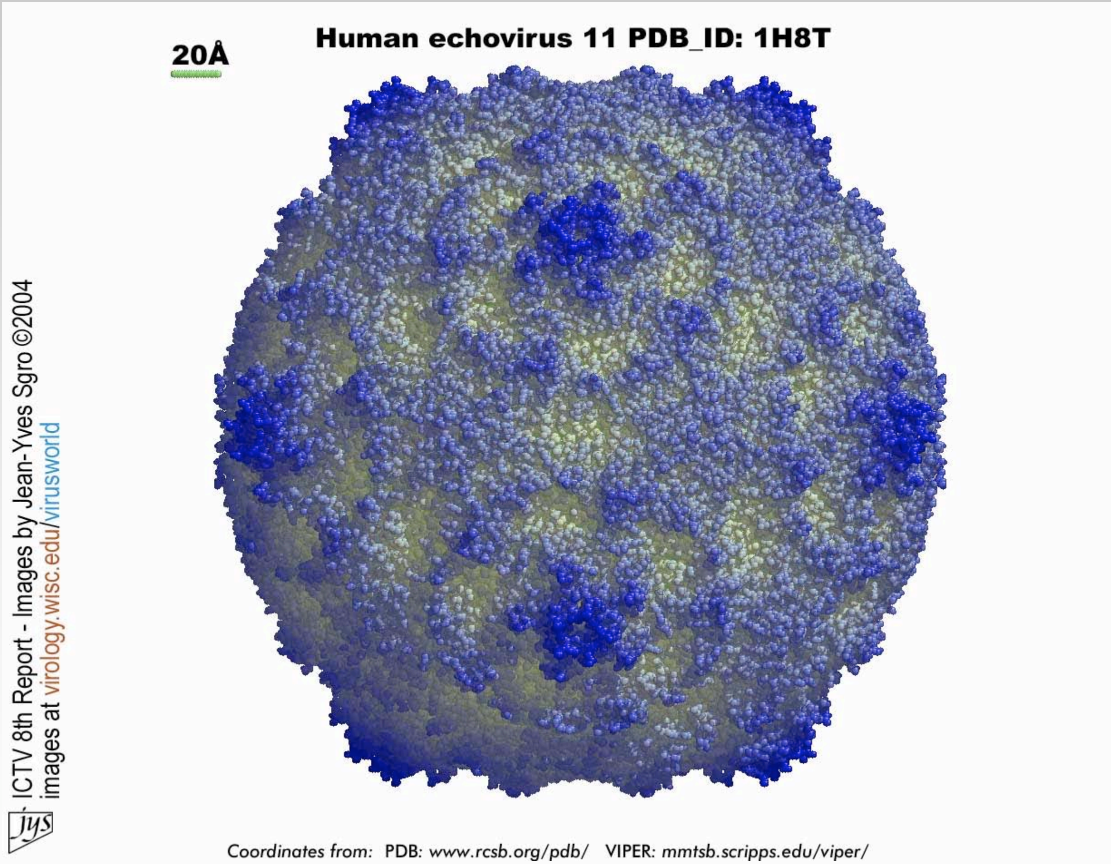
Cubic point groups: examples





Ferritin 432 octahedral symmetry

Cubic point groups: examples



Human echovirus … 532 icosahedral symmetry

Other Families of Point Groups.

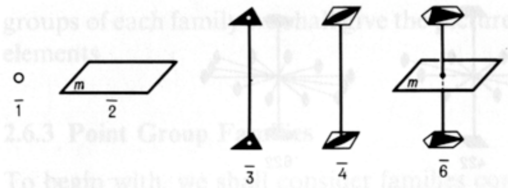


Fig. 2.40. Set of symmetry elements of crystallographic groups of inversion rotations $\bar{N} - S$

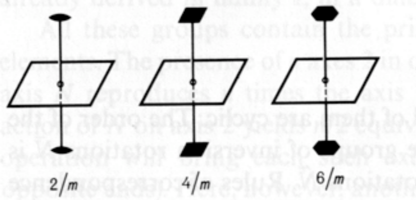


Fig. 2.41. Set of symmetry elements of crystallographic groups of rotations with reflections in planes perpendicular to the principal axis, $N/m - C_{nh}$

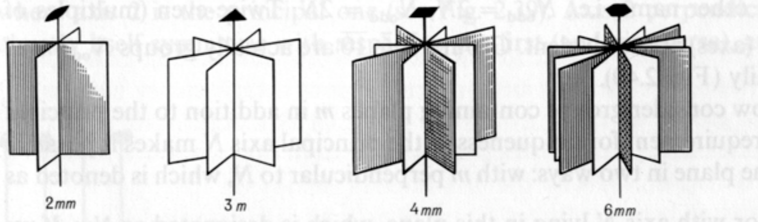


Fig. 2.42. Set of symmetry elements of crystallographic groups with reflections in planes coinciding with the principal axis, $Nm - C_{nv}$

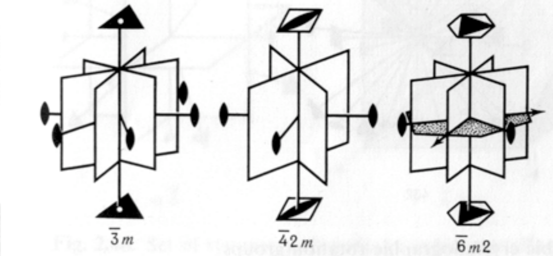


Fig. 2.43. Set of symmetry elements of crystallographic groups of inversion rotations with reflections in planes coinciding with the inversion-rotation axis, $\bar{N}m - D_{nd}$

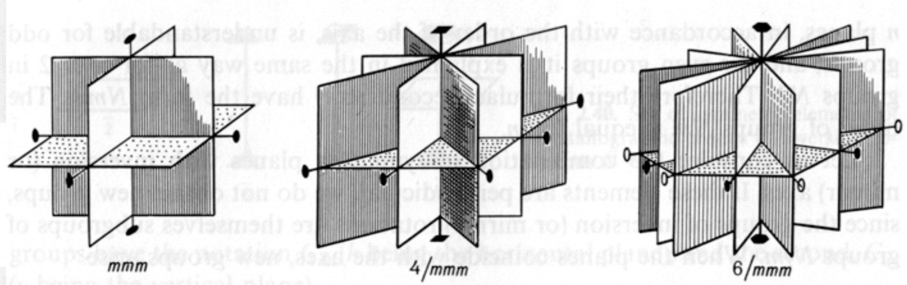


Fig. 2.44. Set of symmetry elements of crystallographic groups of rotations with reflections in symmetry planes coinciding with the principal symmetry axis and perpendicular to it, $\left(\frac{N}{m}m - D_{nh}\right)$

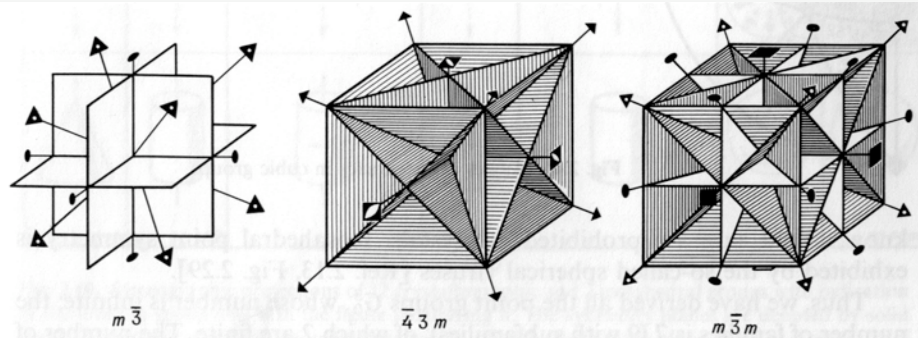


Fig. 2.46. Set of symmetry elements of cubic crystallographic groups with reflections

Images from Vainshtein (1994)

Important sets of point groups I. The protein crystallographic point groups.

Crystals (which we’ll come too shortly) can only accommodate rotation axes of a certain order. 1,2,3,4 and 6 fold symmetries are okay. 5 fold symmetry is out.So is 7-fold, 8-fold and all higher rotational symmetries. There are consequently only 11 “crystallographic” point groups involving pure rotations. Here they are …

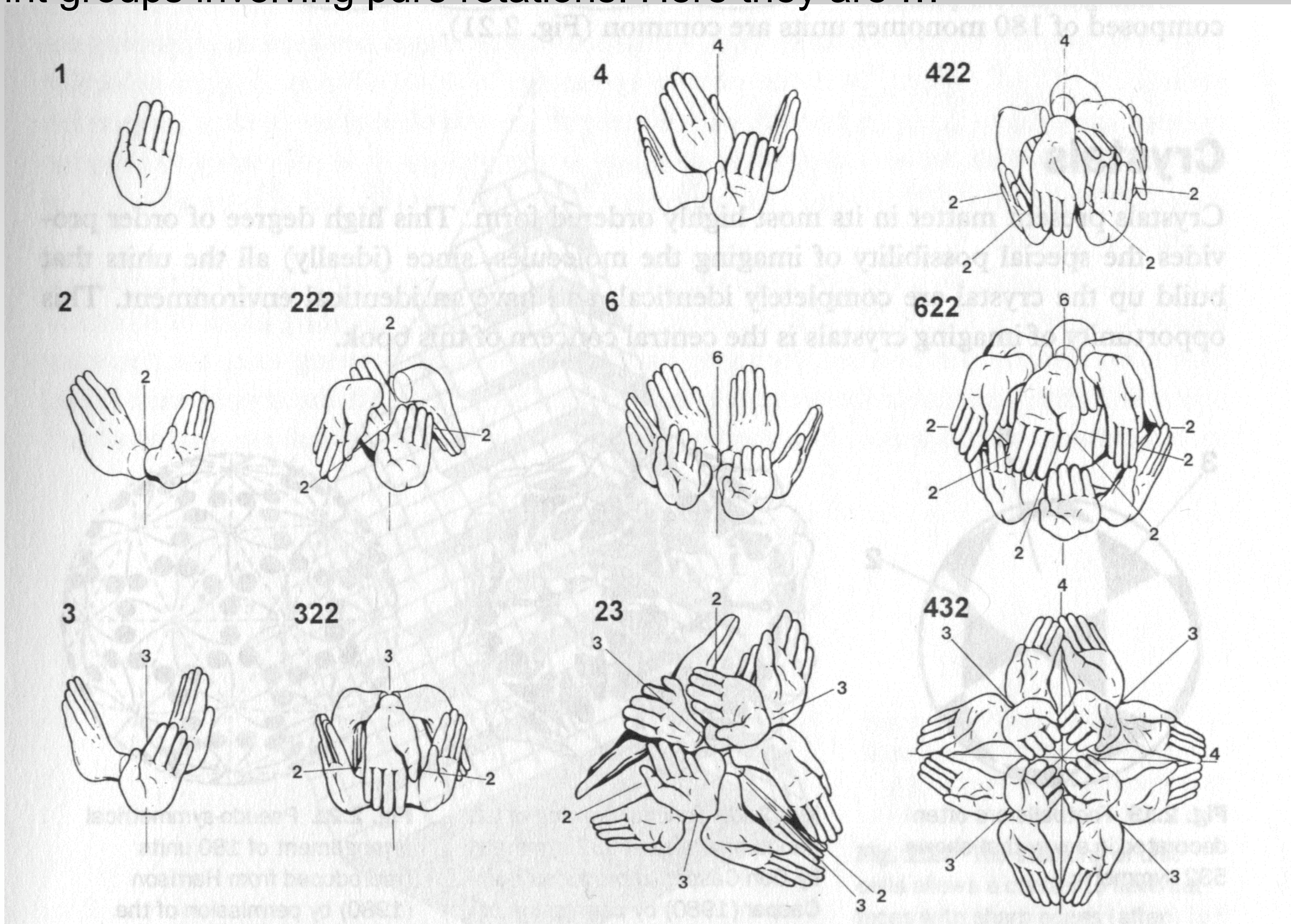
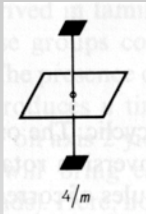
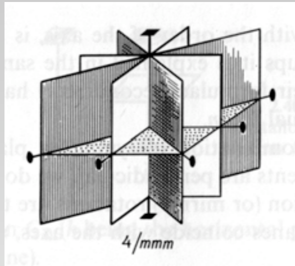


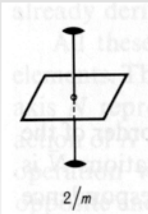
Fig. 2.18 The point groups that can exist in protein crystals.

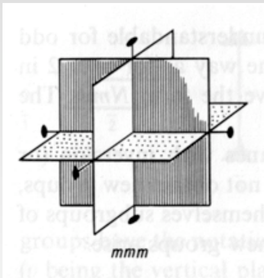
From Blow (2002)

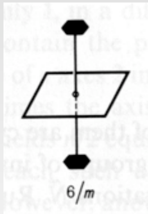
Important sets of point groups II. The Laue groups which describe the point symmetry of X-ray diffraction patterns

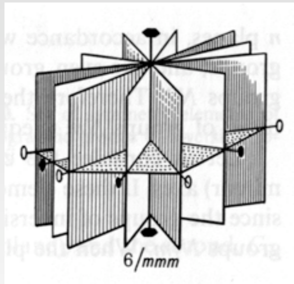


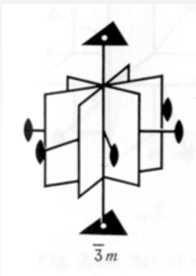


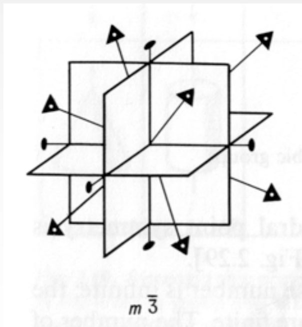


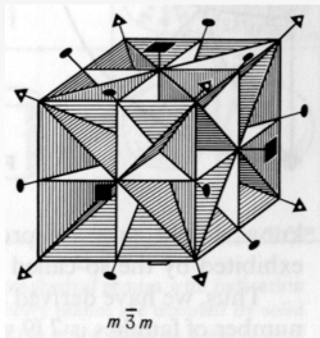












Images from Vainshtein (1994)

Lattices and Translational periodicity

- A lattice is a convenient representation of translational symmetry.
- Lattices are the framework on which much crystallographic theory is built.

It’s all best illustrated by example …

A crystal is the convolution of an object and a lattice

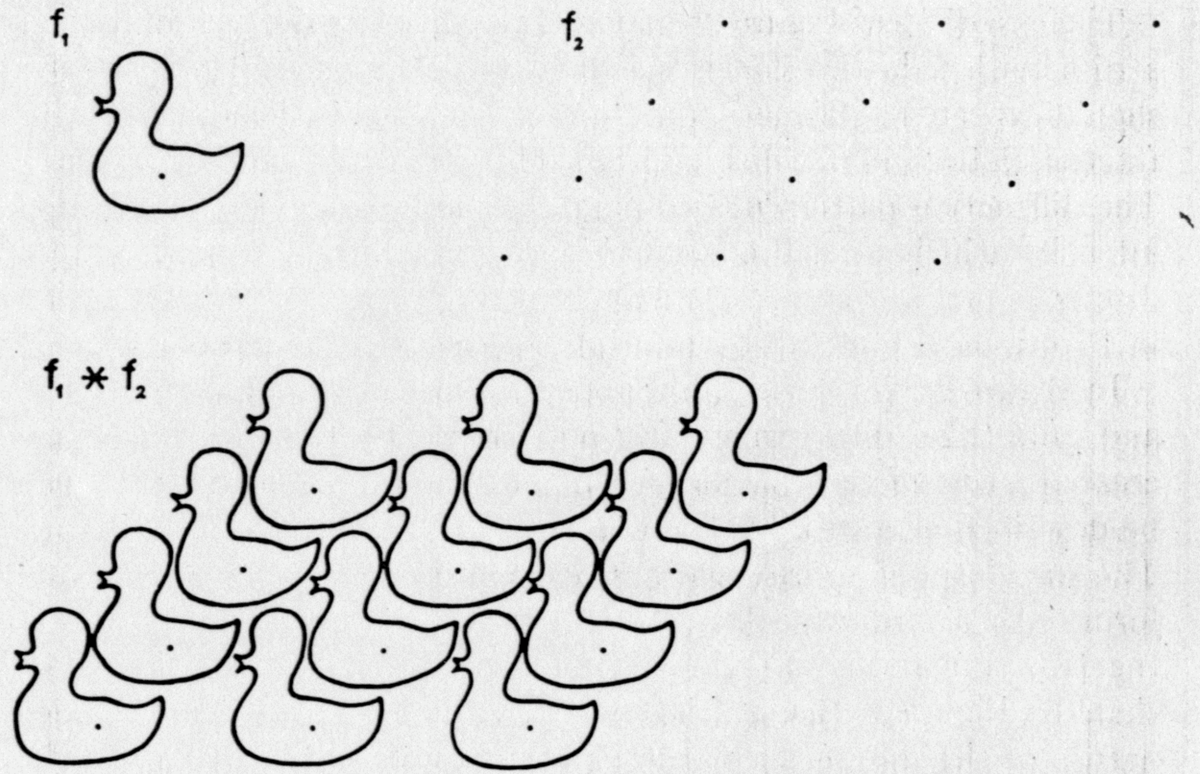
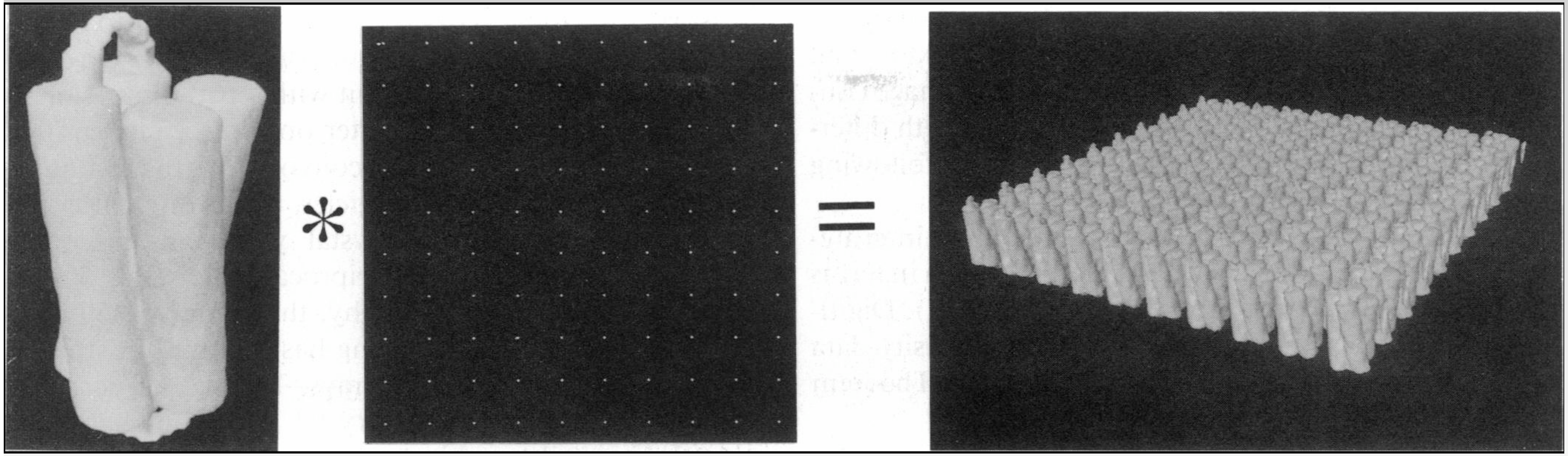


Fig. 4. A simple example of convolution. One function is a drawing of a duck, the other is a two dimensional lattice. The convolution of these functions (shown by the * sign) is accomplished by putting the duck on every lattice point.

From Holmes and Blow (1965)

A crystal is the convolution of an object and a lattice



From Chiu, Schmid and Prasad (1993)

Lattices in 1 and 2 dimensions

There is 1 unique 1-dimensional lattice …

A 1D lattice is generated by a single translation

There are 5 unique 2-dimensional lattices

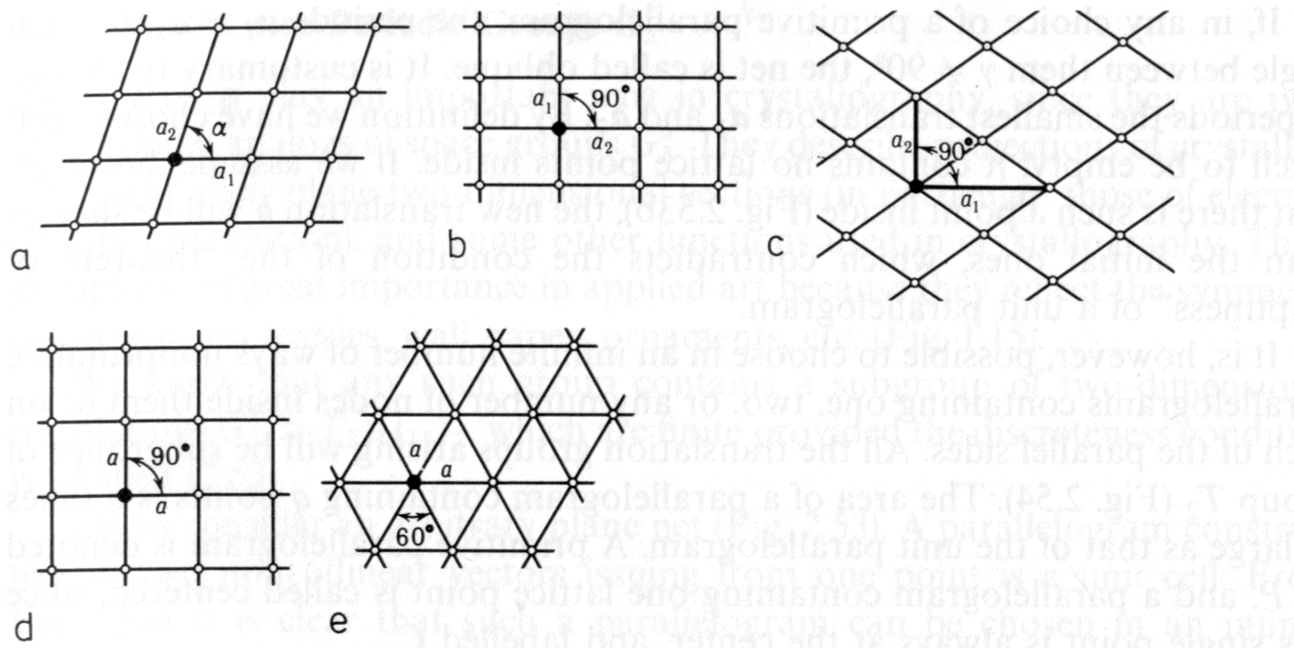


Fig. 2.55a–e. Five types of plane net illustrating two-dimensional Bravais groups. (**a**) oblique, (**b**) orthorhombic primitive, (**c**) orthorhombic centered, (**d**) square, (**e**) hexagonal

From Vainshtein (1994)

A 2D lattice is generated by 2 linearly independent translations

Lattices in 3 dimensions. The 14 Bravais Lattices

A 3D lattice is generated by 3 linearly independent translations

Figures from Woolfson (1970)

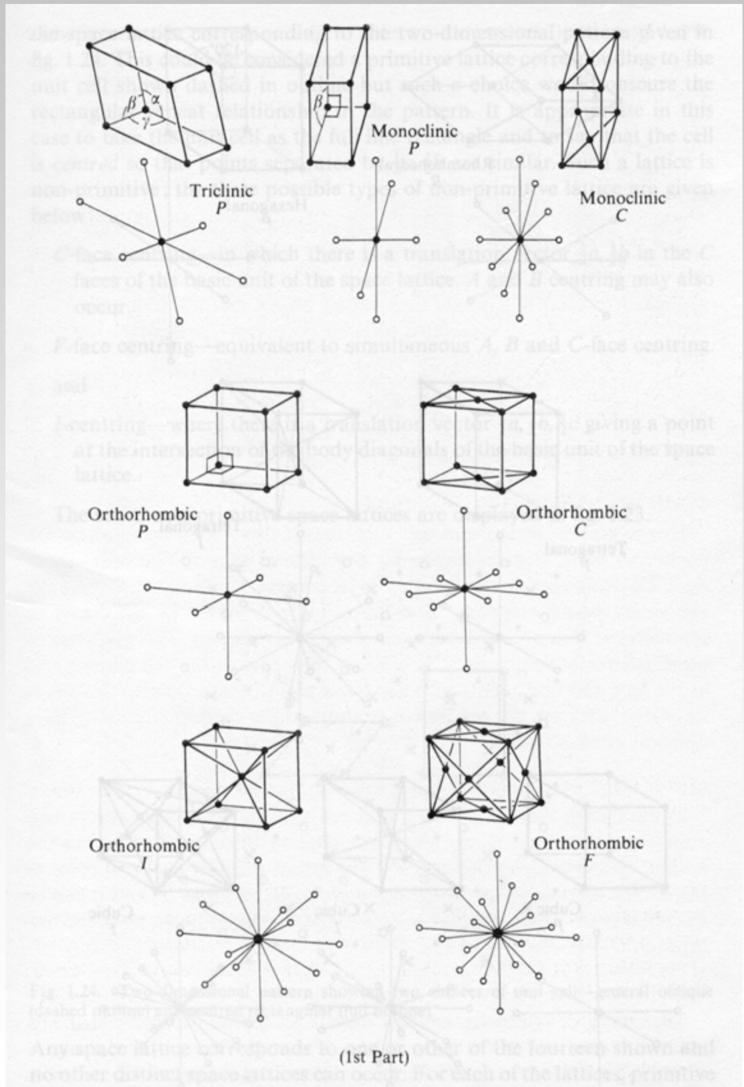


Fig. 1.23. The fourteen Bravais lattices. The accompanying diagrams show the environment of each of the lattice points.

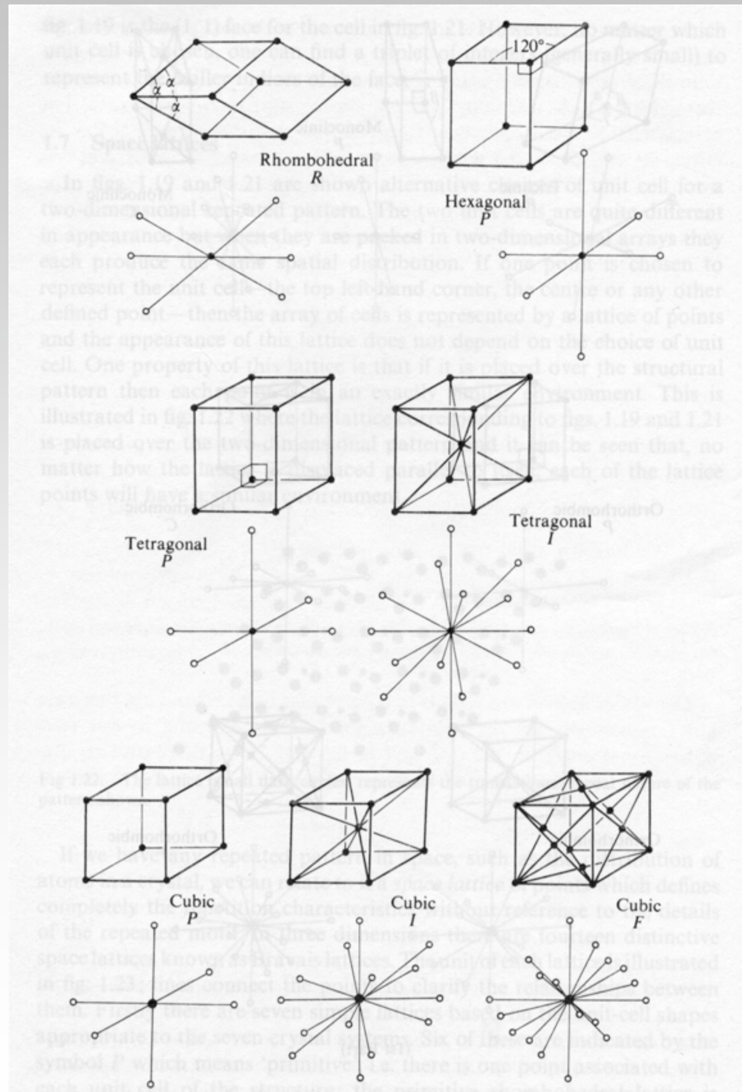


Fig. 1.23. (2nd Part)

Unit cells …

The generators of a 3D lattice form three edges of a box **. . .** if we complete the box we have a unit cell.

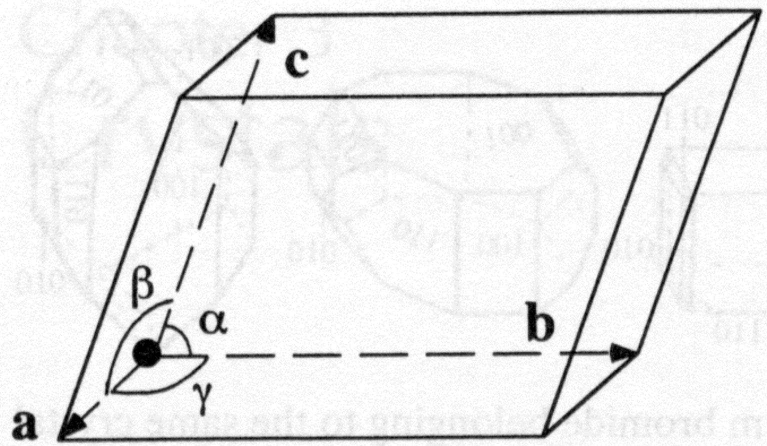


Figure 3.3. One unit cell in the crystal lattice.

From Drenth (2002)

The entire lattice can be constructed from a single unit cell by stacking these boxes together.

“Centered unit cells”

The choice of unit cell is not unique. Crystallographers have conventions for choosing the unit cell so that it reflects the symmetry of the lattice. Sometimes this puts lattice points at the center of a unit cell, or on its faces. This drives mathematicians crazy, but is actually quite sensible and convenient.

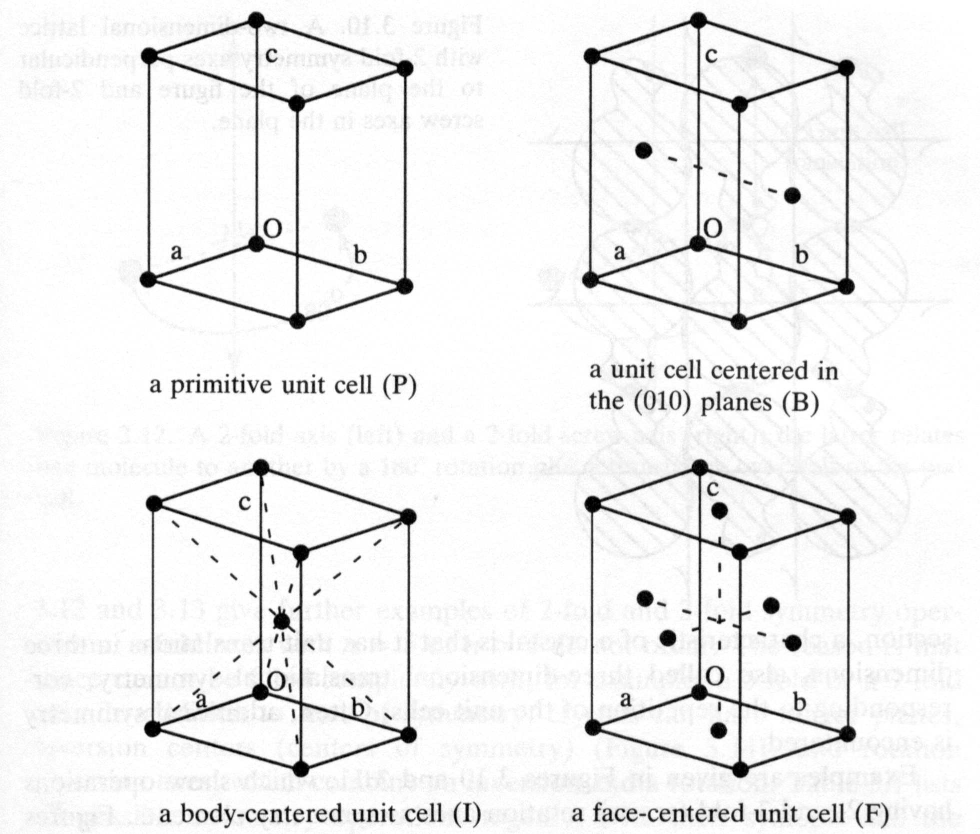


Figure 3.9. Noncentered and centered unit cells.

From Drenth (2002)

Symmetry of the lattice imposes constraints on the unit cell dimensions

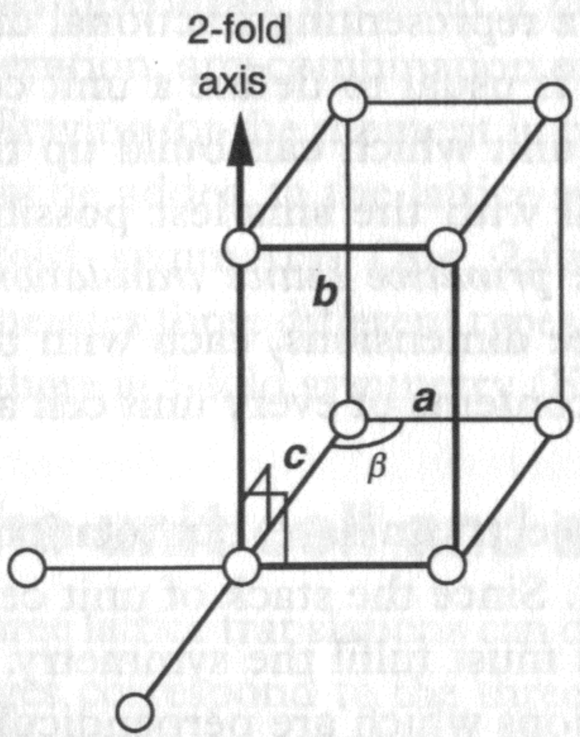


Fig. 2.31 A three-dimensional lattice can only have 2-fold symmetry if two of the lattice translations are perpendicular to the 2-fold axis.

From Blow (2002)

Lattices are assigned to crystal systems according to their symmetry though mathematicians and crystallographers do this slightly differently. This time we're going to side with the mathematicians (The argument centers over where to place the Rhombohedral Lattice).

The seven crystal systems

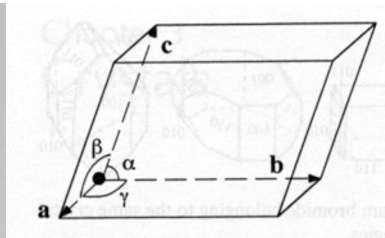


Figure 3.3. One unit cell in the crystal lattice.

System	Essential rotational symmetry	Conventional choice of axes	Unit Cell restrictions	Possible Lattices
Triclinic	None	No constraints	None	P
Monoclinic	Two-fold axis	**b** parallel to 2-fold	$\alpha = \gamma = 90°$	P,C
Orthorhombic	Three perpendicular 3-fold axes	**a, b, c** parallel to 2-fold axes	$\alpha = \beta = \gamma = 90°$	P,C,I,F
Trigonal/Hexagonal	3-fold or 6-fold axis	**c** parallel to 3-fold or 6-fold	a = b $\alpha = \beta = 90°$, $\gamma = 120°$	P
Rhombohedral	3-fold axis	**a, b, c** related by three fold axis	a = b = c $\alpha = \beta = \gamma$	R
Tetragonal	4-fold axis	**c** parallel to 4-fold	a = b $\alpha = \beta = \gamma = 90°$	P,I
Cubic	4 3-fold axes	**a, b, c** related by three fold axis	a = b = c $\alpha = \beta = \gamma = 90°$	P,I,F

Symmetry groups involving translational periodicity.

Skipping over the mathematical complexities, these groups are derived by combining point group symmetry with a lattice. The lattice might be 1, 2 or 3 dimensional leading to …

The **Line (or Rod) groups** …
the symmetries of helices

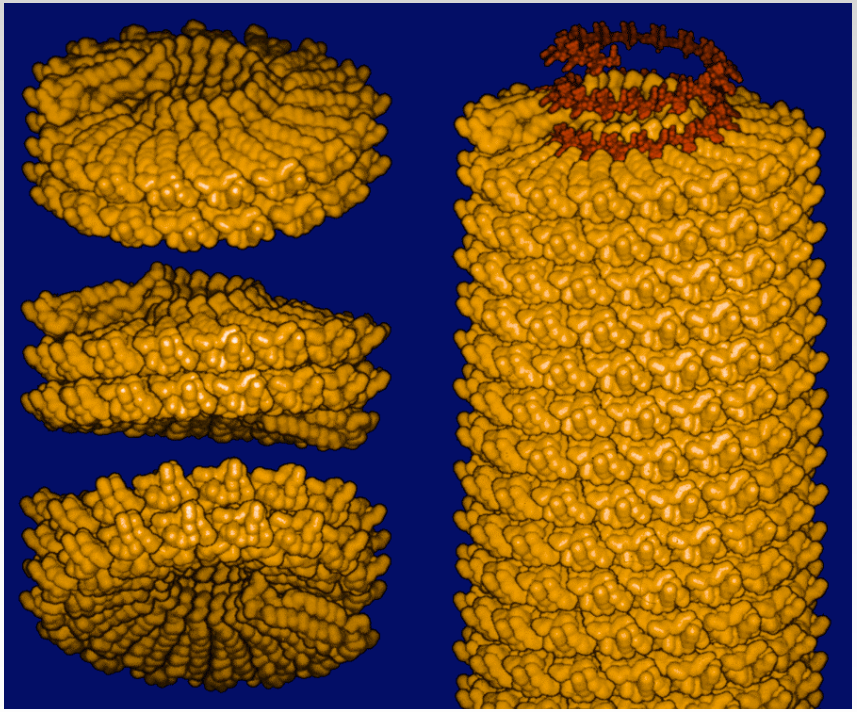
The **Layer (or Two-sided Plane) groups** …
the symmetries of 2D crystals

The **Space groups** …
the symmetries of 3D crystals.

Line Groups: The symmetries of 3D objects periodic in 1 Dimension

These groups describe the symmetries of helices and rods.

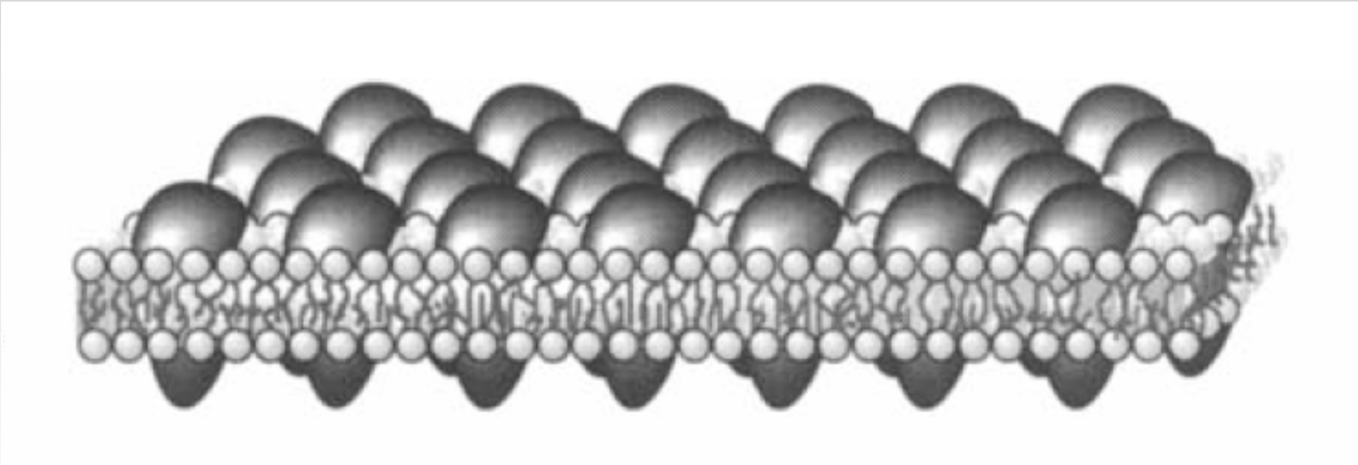
Very important in X-ray Fiber diffraction and Helical image reconstruction. They are constructed by combination of a point group and a 1D lattice. We do not consider them in detail in this course.



Tobacco Mosaic Virus … image from Don Caspar

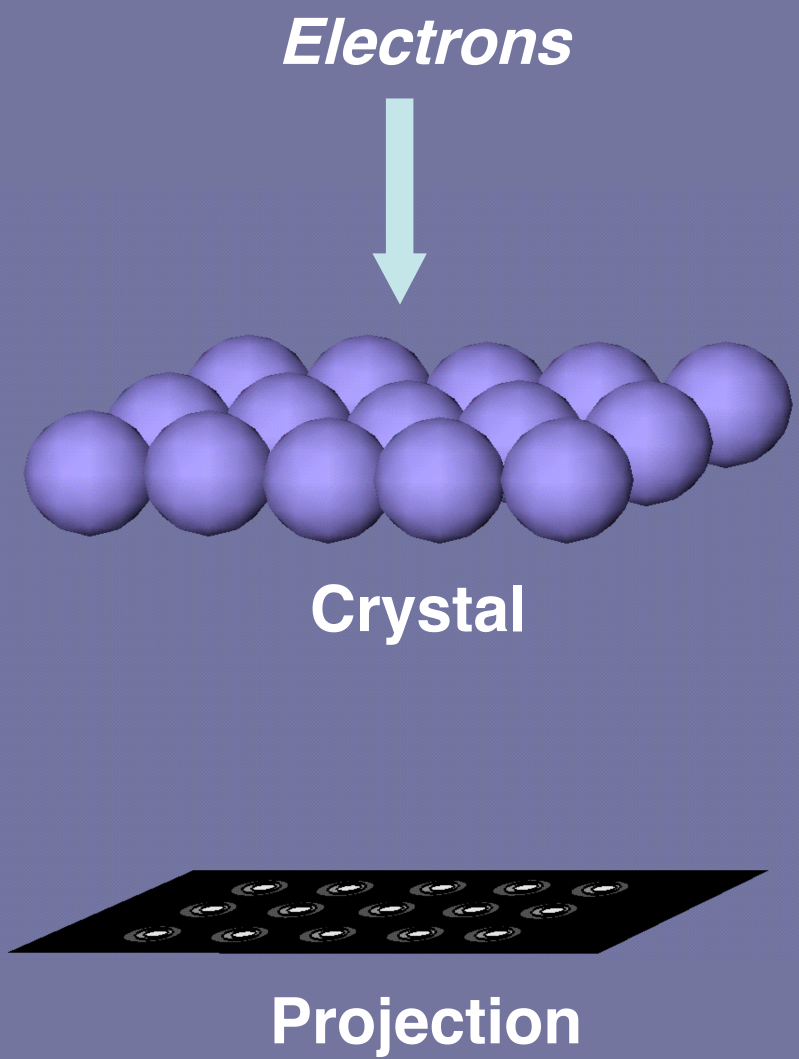
Layer Groups (Two-sided plane groups): The symmetries of 3D objects periodic in 2 Dimensions

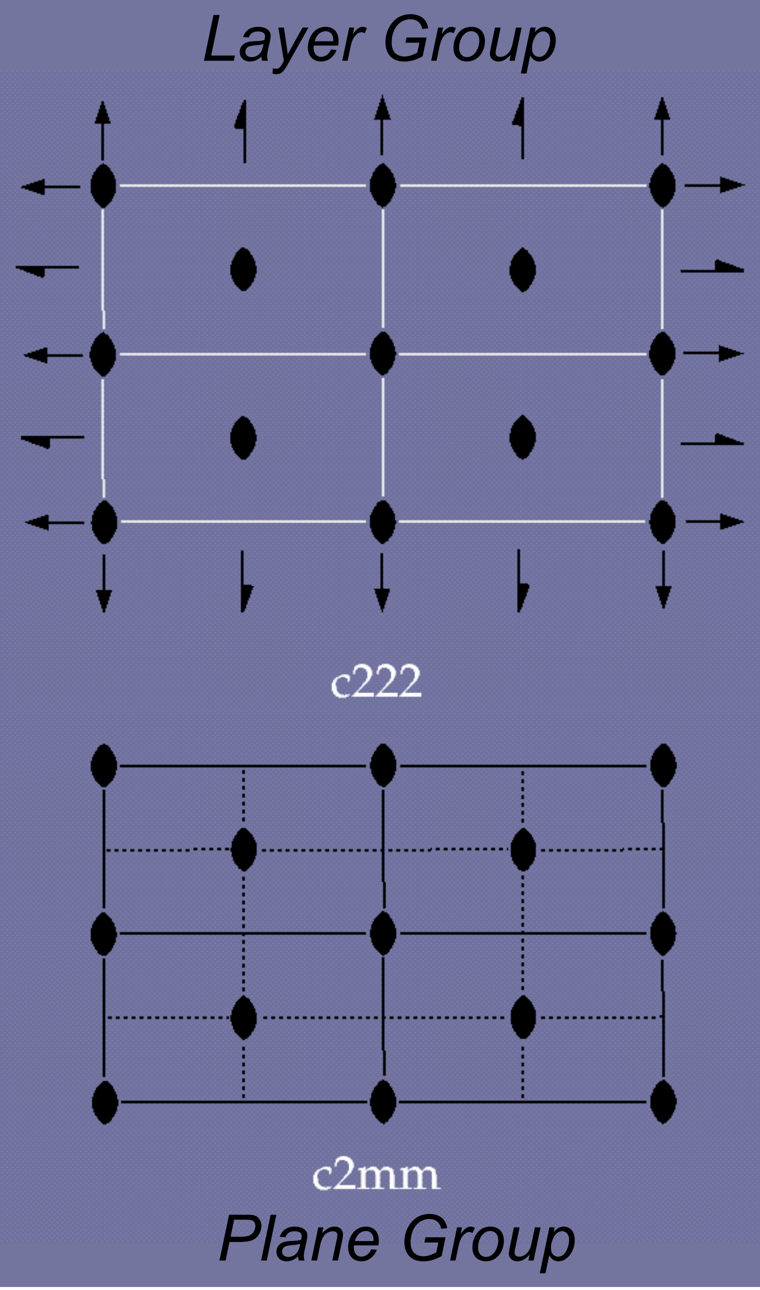
These groups describe the symmetries of “2D” crystals. They are constructed through combination of a point group and a 2D lattice.



From Mosser (2001)

Transmission electron microscopy … The relationship between the Layer groups and the Plane groups





Layer Groups (Two-sided plane groups): The symmetries of 3D objects periodic in 2 Dimensions

These groups describe the symmetries of “2D” protein crystals. There are 80 Layer groups in total, but only 17 can accommodate biological specimens.

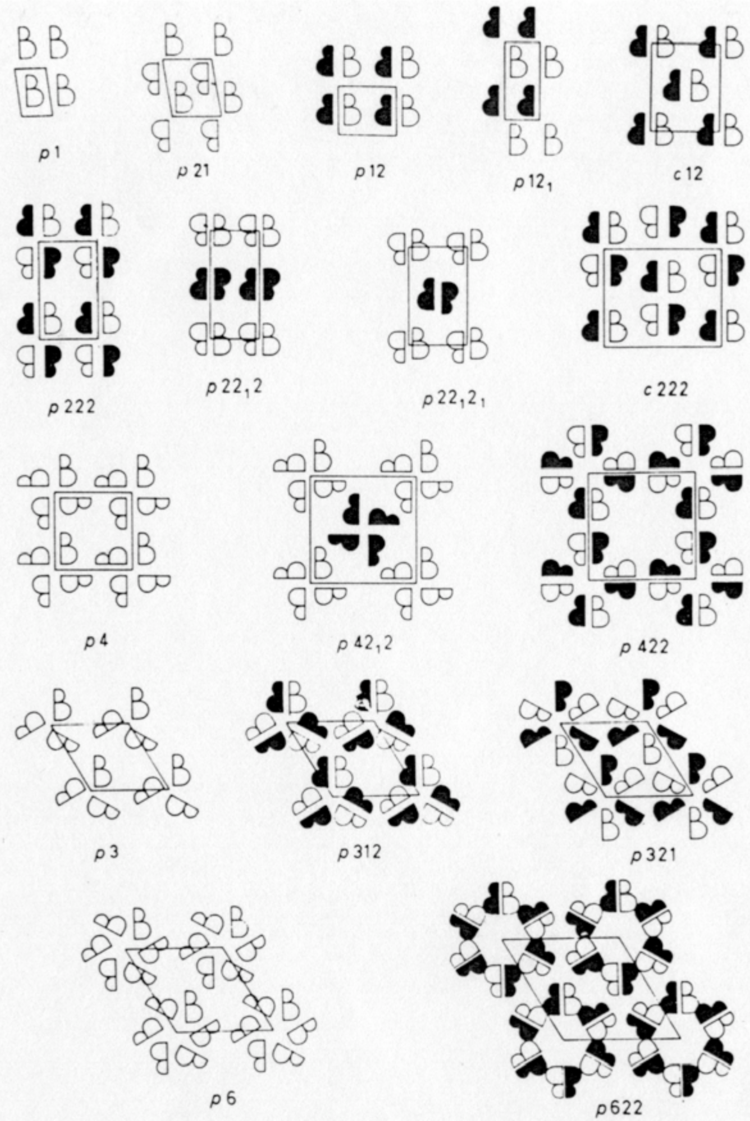


Fig. 4. Vertical projections of 2-D crystals from chiral molecules (symbolized by a B), representing the 17 two-sided plane groups. Black symbols represent molecules rotated by 180° around an axis in the crystal plane (“bottom view”). The unit cell boundaries are indicated, the positions of the axes of rotational and mirror symmetries are given in Fig. 5. The nomenclature of the plane groups follows the rules of Holser (1958). The cell type is indicated by a *p* (primitive) or *c* (centred), the rotational symmetry around the *z*-axis (perpendicular to the crystal plane) is described by the first number following the cell type (from Hovmöller, 1986, with permission).

From Engelhardt (1988)

Plane Groups: The symmetries of 2D objects periodic in 2 Dimensions

These groups describe the symmetries of crystals in projection. They are therefore of critical importance in electron crystallography. Happily the 17 “Biological” Layer groups each have a unique corresponding Plane group.

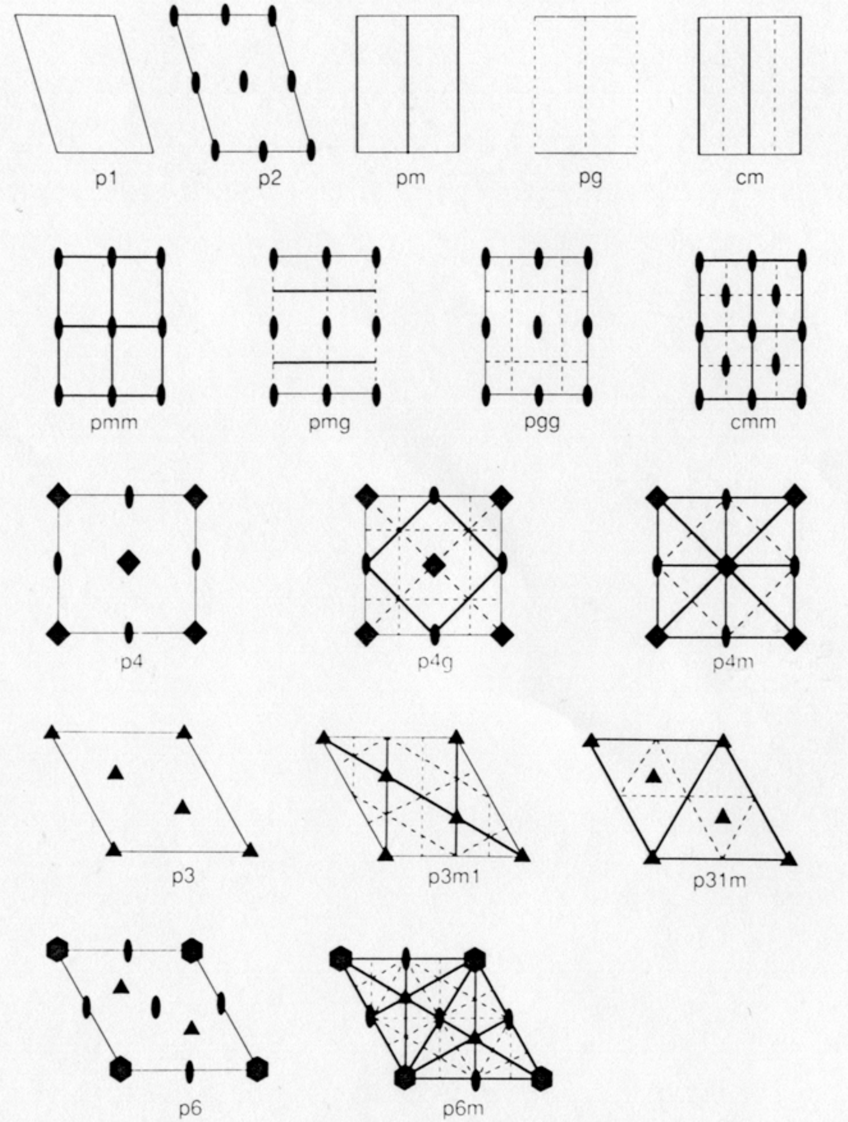
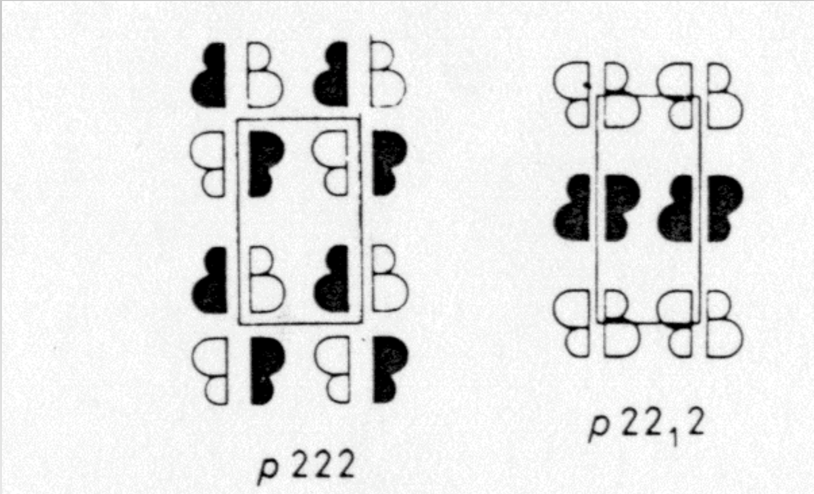


Fig. 5. Scheme of the centres of rotational symmetry and the axes of mirror symmetry in *vertical projections* of 2-D crystals belonging to the 17 two-sided plane groups. The arrangements of molecules in the unit cells are given in Fig. 4 (same order). The nomenclature describes the *projection symmetries* of the crystal types (Holser, 1958). Symbols: faint lines identify unit cell boundaries, ⬮ centre of 2-fold, ▲ 3-fold, ◆ 4-fold and ⬢ 6-fold symmetry, respectively. Solid lines represent mirror axes and dotted lines glide (mirror) axes. Scheme adapted from Vainshtein (1981).

From Engelhardt (1988)

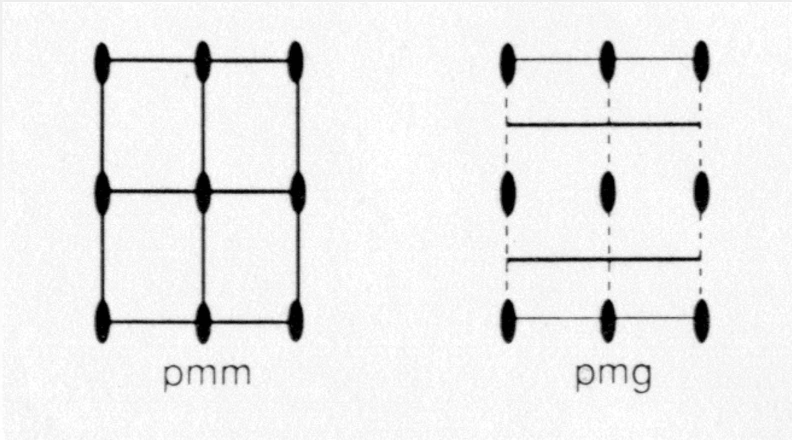
A closer look at some pairs of Layer and Plane Groups

Layer Groups



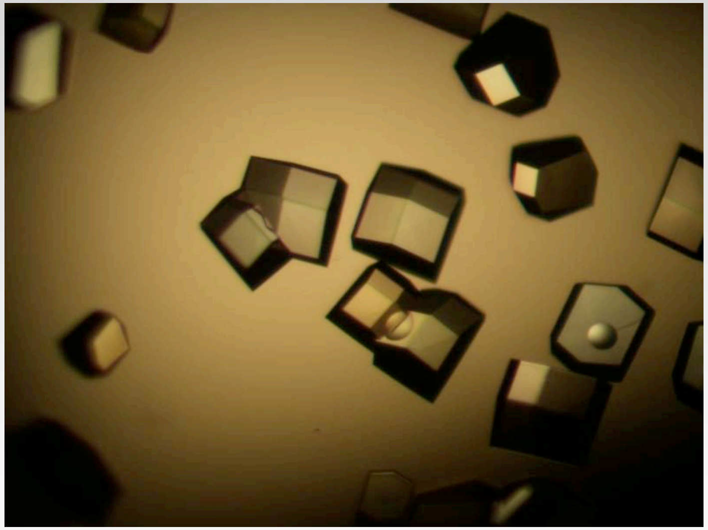
From Engelhardt (1988)

Corresponding Plane Groups



Space Groups: The symmetries of 3D objects periodic in 3 Dimensions

These groups describe the symmetries of 3D crystals. They underpin X-ray crystallography. They are constructed by combining a point group with a 3D lattice.



There are 230 Space groups in total. 65 of these do not involve reflection or inversion, and can accommodate biological molecules of a fixed hand.

A very simple space group … P2

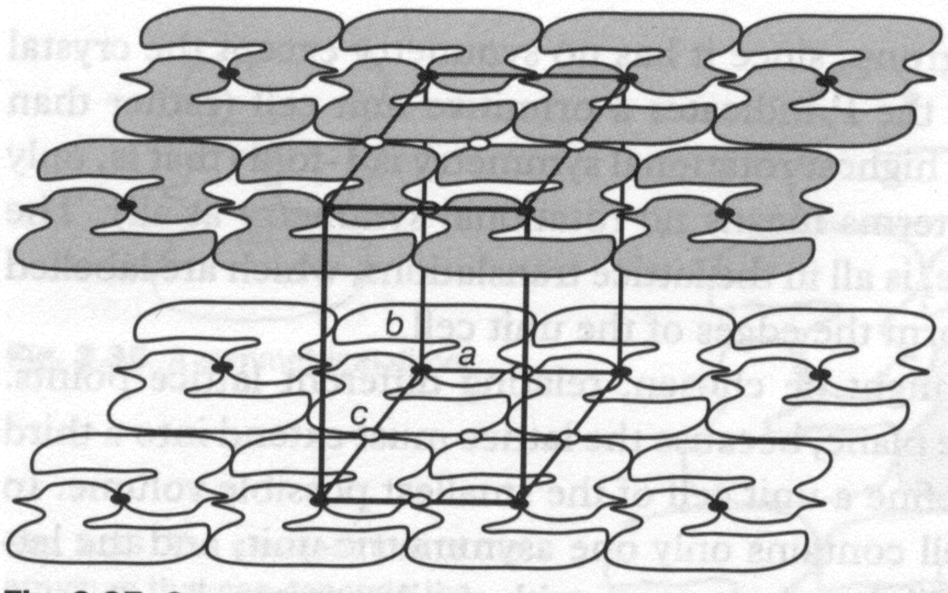


Fig. 2.37 Symmetry and equivalent positions in space group P2. A 2-fold axis along ***b*** creates two asymmetric units in the unit cell. Each unit has four 2-fold axes associated with it, at $x,z = (0, 0)$ (black circles), and at $(0, 1/2)$, $(1/2, 0)$, $(1/2, 1/2)$ (open circles).

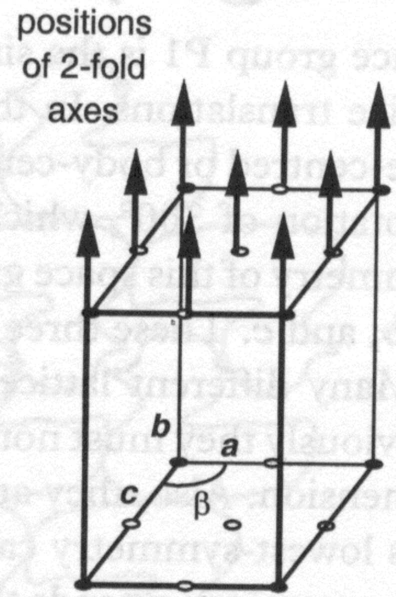


Fig. 2.38 A unit cell of space group P2.

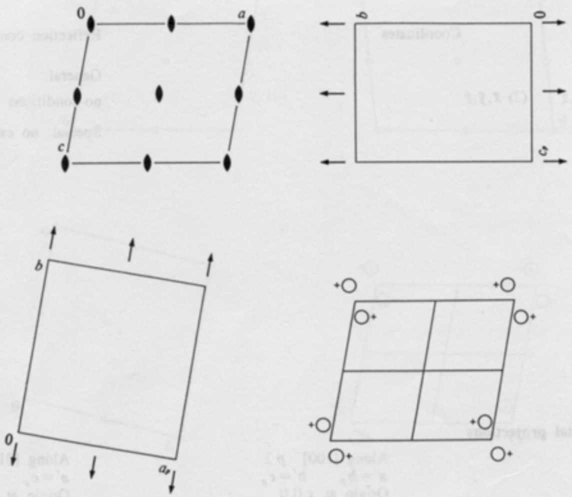
From Blow (2002)

International Tables:Space Group P2

$P2$ C_2^1 2 Monoclinic

No. 3 $P121$ Patterson symmetry $P12/m1$

UNIQUE AXIS b



Origin on 2

Asymmetric unit $0 \le x \le 1$; $0 \le y \le 1$; $0 \le z \le \frac{1}{2}$

Symmetry operations

(1) 1 (2) 2 $0,y,0$

106

CONTINUED No. 3 $P2$

Generators selected (1); $t(1,0,0)$; $t(0,1,0)$; $t(0,0,1)$; (2)

Positions

Multiplicity, Wyckoff letter, Site symmetry			Coordinates		Reflection conditions
2	e	1	(1) x,y,z	(2) $\bar{x},y,\bar{z}$	General: no conditions
					Special: no extra conditions
1	d	2	$\frac{1}{2},y,\frac{1}{2}$		
1	c	2	$\frac{1}{2},y,0$		
1	b	2	$0,y,\frac{1}{2}$		
1	a	2	$0,y,0$		

Symmetry of special projections

Along [001] $p1m1$
$\mathbf{a}'=\mathbf{a}_p$ $\mathbf{b}'=\mathbf{b}$
Origin at $0,0,z$

Along [100] $p11m$
$\mathbf{a}'=\mathbf{b}$ $\mathbf{b}'=\mathbf{c}_p$
Origin at $x,0,0$

Along [010] $p2$
$\mathbf{a}'=\mathbf{c}$ $\mathbf{b}'=\mathbf{a}$
Origin at $0,y,0$

Maximal non-isomorphic subgroups

I $[2]P1$ 1

IIa none

IIb $[2]P12_11\,(\mathbf{b}'=2\mathbf{b})(P2_1)$; $[2]C121\,(\mathbf{a}'=2\mathbf{a},\mathbf{b}'=2\mathbf{b})(C2)$; $[2]A121\,(\mathbf{b}'=2\mathbf{b},\mathbf{c}'=2\mathbf{c})(C2)$; $[2]F121\,(\mathbf{a}'=2\mathbf{a},\mathbf{b}'=2\mathbf{b},\mathbf{c}'=2\mathbf{c})(C2)$

Maximal isomorphic subgroups of lowest index

IIc $[2]P121\,(\mathbf{b}'=2\mathbf{b})(P2)$; $[2]P121\,(\mathbf{c}'=2\mathbf{c}$ or $\mathbf{a}'=2\mathbf{a}$ or $\mathbf{a}'=\mathbf{a}+\mathbf{c},\mathbf{c}'=-\mathbf{a}+\mathbf{c})(P2)$

Minimal non-isomorphic supergroups

I $[2]P2/m$; $[2]P2/c$; $[2]P222$; $[2]P222_1$; $[2]P2_12_12$; $[2]C222$; $[2]Pmm2$; $[2]Pcc2$; $[2]Pma2$; $[2]Pnc2$; $[2]Pba2$; $[2]Pnn2$; $[2]Cmm2$; $[2]Ccc2$; $[2]P4$; $[2]P4_2$; $[2]P\bar{4}$; $[3]P6$; $[3]P6_2$; $[3]P6_4$

II $[2]C121(C2)$; $[2]A121(C2)$; $[2]I121(C2)$

The 65 “Biological” Space Groups

Bravais Lattice	**Possible space groups**	**Associated point group symmetry**
Primitive Cubic	P23, P$2_1$3 P432, P$4_1$32, P$4_2$32, P$4_3$32	23 432
I centered Cubic	I23, I$2_1$3 I432, I$4_1$32	23 432
F centered Cubic	F23 F432,F$4_1$32	23 432
Rhombohedral	R3 R32	3 32
Primitive Hexagonal	P3, P3_1, P3_2 P312, P$3_1$12, P$3_2$12, P321, P$3_1$21, P$3_2$21 P6, P6_1, P6_2, P6_3, P6_4, P6_5 P622, P$6_1$22, P$6_2$22, P$6_3$22, P$6_4$22, P$6_5$22	3 32 6 622
Primitive Tetragonal	P4, P4_1, P4_2, P4_3 P422, P42$_1$2, P$4_1$22, P$4_1$2$_1$2, P$4_2$22, P$4_2$2$_1$2, P$4_3$22, P$4_3$2$_1$2	4 422
I centred Tetragonal	I4, I4_1 I422, I$4_1$22	4 422
Primitive Orthorhombic	P222, P222$_1$, P2$_1$2$_1$2, P2$_1$2$_1$2$_1$	222
C Centered Orthorhombic	C222, C222$_1$	222
I Centered Orthorhombic	I222, I2$_1$2$_1$2$_1$	222
F Centered Orthorhombic	F222	222
Primitive Monoclinic	P2, P2$_1$	2
C Centered Monoclinic	C2	2
Triclinic	P1	1

Sources for the material presented / Suggested Further reading (*)

Books

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