Micro-organisms

function, form and environment

Second Edition

edited by
Lilian E. Hawker
Alan H. Linton

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Foreword

Micro-organisms are living things differing widely in form and life-cycle but resembling one another in their relatively small size, ranging from *ca.* 30 nm for particles of the smaller viruses and *ca.* 1.0 μm diameter for small bacteria to *ca.* $30 \times 10\,\mu$m for certain unicellular algae. Since both the problems caused by small size and the methods used to study such small organisms are similar and since unrelated micro-organisms frequently occupy the same habitat and thus influence each other, it is convenient to study them within the same discipline i.e. *Microbiology*. This book is concerned with how micro-organisms live and multiply, their form and the roles they play in their varied habitats. Its aim is to survey the whole field of microbiology in a manner which we hope will be useful to students and specialist workers. It is an up-to-date account replacing two earlier books and while it contains some passages from these much is new.

We thank all those authors, editors and publishers who have provided illustrations. These are acknowledged in the figure captions. Also we are indebted to Helen Parker for preparing the index by computer.

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Part I

Biochemistry and physiology of micro-organisms

Chapter 1

Macromolecules in micro-organisms

Introduction

It is customary to think of bacterial macromolecules solely in terms of single and readily identifiable high molecular weight polysaccharides, lipids, nucleic acids, and proteins, but many more complex situations exist in microbial cells. There are intricate molecular arrangements in which two or more macromolecules are held together in specific ways by complementary ionic and hydrogen bonds. Much of the cell seems to be made up of chemical structures that are more than just an intimate mixture of two types of macromolecule joined together by stable covalent linkages. A good example of this situation is the mucopeptide that forms the rigid structural matrix of the cell wall of many bacterial species. In this molecule there is close cross-linking between polysaccharide and polypeptide chains in such a way that it is no longer possible to define the limits of the molecule accurately. Thus, with molecules of this type, such concepts as molecular weight and size cease to have much meaning. As far as mucopeptide is concerned, the entire bacterial cell seems to be enclosed by a single sack-like molecule that might not even have a similar repeating structure over the whole of its area.

Although such complex macromolecules do pose problems as far as isolation and identification are concerned, it is possible to consider simple polysaccharides, lipids, proteins and nucleic acids as single molecular entities that can be defined with some precision. In the following sections, therefore, the structures of some examples of each of these four groups will be considered before attention is turned to bacterial mucopeptide as an example of one of the more complex and less well-defined types of microbial macromolecule.

Polysaccharides

All simple polysaccharides have a repeating structure made up of either a single type or alternating types of monosaccharide. One of the simplest is amylose, a polysaccharide which is found in many types of micro-organism and in which the molecule consists of glucose units joined together to form a long chain (Fig. 1.1). The bonds linking the structure join the C_1 atom of one glucose residue to the C_4 atom of the next by an oxygen bridge, often known as a *glycoside bond*. The use of these bonds with each sugar residue leads to a molecule in which all the monosaccharide units have an identical linkage save the first and the last. In the first, the hydroxyl group on C_4 is unsubstituted, while on the last the —OH group on C_1 is in a similar state (Fig. 1.1).

The amylose molecule (Fig. 1.1) is one of the simplest types of polysaccharide, since it is made up solely from a single repeating glucose unit and all the bonds linking the monosaccharides are identical. In many other polysaccharides, however, two

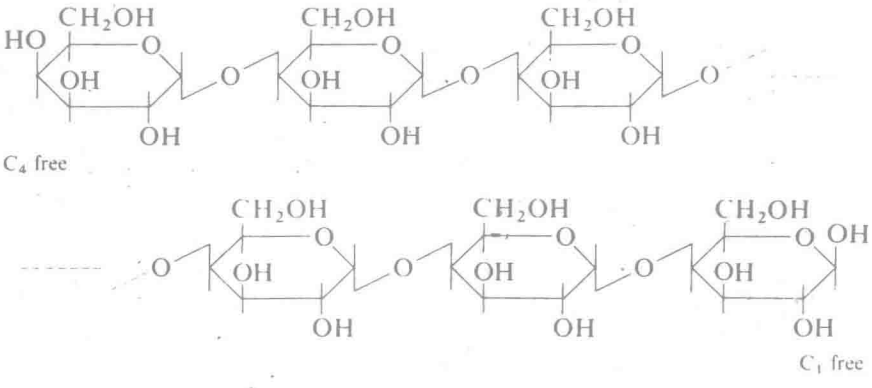


Fig. 1.1 Overall structure of amylose (poly-α-1 : 4-glucose). The free C_1 end of the molecule is responsible for the reducing properties.

different types of monosaccharide are involved in the chain. An example of such a molecule is the polysaccharide found in the Type III capsular material from certain strains of pneumococci. In this case the structure consists of chains of alternating glucose and glucuronic acid residues arranged as shown in Fig. 1.2

A further, and more complex, class of polysaccharides are those that are branched. Branching occurs where a monosaccharide residue in the chain is attached to three other monosaccharide units rather than to two, as in any straight-chain polysaccharide. An example of this type of molecule is the dextran molecule synthesized by *Leuconostoc mesenteroides*. This molecule, as in all dextrans (see Table 1.1), is made up entirely from glucose units which, in this case, are joined by a glycoside bond between C_1 of one glucose residue and C_6 of the next, rather than between C_1 and C_4 as with amylose. The branching points in the *Leuconostoc* dextran are introduced where occasional glycosidic bonds are formed between C_1 and C_4 or between C_1

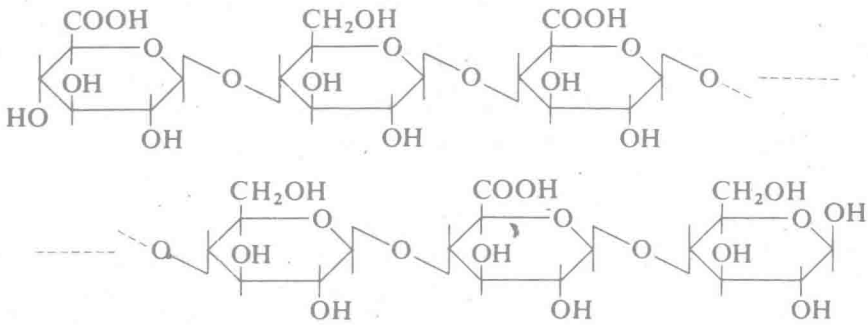


Fig. 1.2 The overall structure of the polysaccharide from the Type III capsular material found in some pneumococci.

Table 1.1 Trivial names and chemical constitution of various microbial polysaccharides

Trivial name	Constitution	Source
Glucan (general term)	Poly-glucose	Many yeasts and bacteria
Dextran	Poly-1 : 6-glucose	*Leuconostoc* and many other microbial species
Mannan (general term)	Poly-mannose	Yeasts
Amylose	Poly-α1 : 4-glucose	Many bacteria
Chitin	Poly-β1 : 4-*N*-acetyl-glucosamine	Fungi
Cellulose	Poly-β1 : 4-glucose	*Acetobacter xylinum*

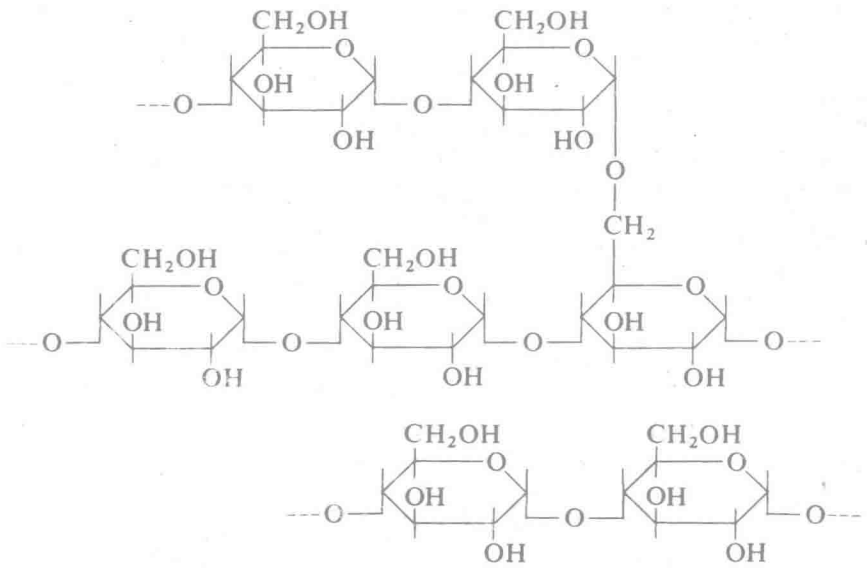


Fig. 1.3 A part of the structure of a branched polysaccharide to show the molecular nature of the branching points.

and C_3 of two glucose residues rather than between C_1 and C_6 (see Fig. 1.3).

Mucopolysaccharides

The term mucopolysaccharide is often used for those polysaccharides containing residues of *N*-acetyl-amino sugars such as *N*-acetyl-glucosamine or *N*-acetyl-galactosamine (Fig. 1.4).

One of the simplest mucopolysaccharides, and undoubtedly one of the most important in many moulds since it forms a great part of their cell walls, is *chitin*. This molecule consists of unbroken chains of *N*-acetyl-glucosamine linked from the C_1 of one residue to the C_4 of the next. In point of fact this polymer is usually present in an organism in association with protein, but whether there are a small number of covalent bonds between the two or whether the mixture is stabilized solely by ionic and hydrogen bonds, is unclear at the moment.

Not all mucopolysaccharides contain amino-sugars unmixed with non-nitrogenous monosaccharides. As an example, the mucopolysaccharide component of the Type XIV capsular material from pneumococci contains *N*-acetylglucosamine, glucose and galactose in the overall molecular arrangement shown in Fig. 1.5. The various general names used to describe simple polysaccharides usually give some idea of their composition and a list of the most common of these names is given in Table 1.1.

Lipids

All lipids share a common property of being soluble in fat solvents, such as chloroform or ether, and almost insoluble in water. A wide range of compounds with different structures fall within this classification and it is convenient to consider lipids under the following groups:

1 Fatty acids
2 Triglycerides
3 Phospholipids, phosphatidic acids and glycolipids
4 Steroids
5 Carotenoids

Fatty acids

Fatty acids are long-chain monocarboxylic acids of the general formula R.COOH. Usually the R-group has a long chain, commonly unbranched, consisting of an even number of between 8 and 24 carbon atoms. The fatty acid may be described as *saturated* or *unsaturated* depending on whether the R-group contains any double bonds; acids with one double bond are known as mono-enoic, those with two as di-enoic, and so on. The structure of a number of fatty acids and their trivial names is given in Table 1.2. Little more need be said about their structure at this stage since their greatest importance, apart from the role of the lower examples as metabolic

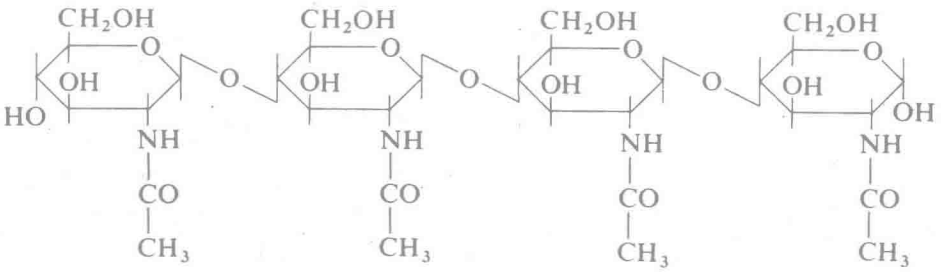


Fig. 1.4 The overall structure of chitin.

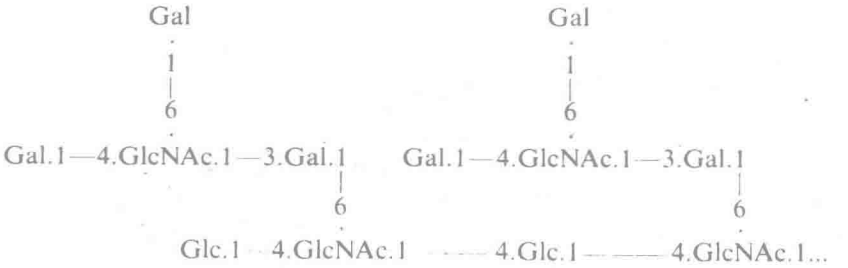


Fig. 1.5 The overall structure of the polysaccharide from the Type XIV capsular material found in some pneumococci.

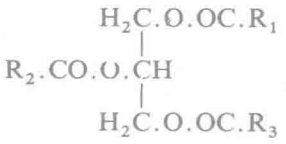
Table 1.2 Trivial names of some of the various fatty acids to be found in microbial cells

Molecular formula	Common name	Systematic name
Saturated acids:		
$C_4H_8O_2$	Butyric	*n*-Butanoic
$C_6H_{12}O_2$	Caproic	*n*-Hexanoic
$C_{10}H_{20}O_2$	Capric	Decanoic
$C_{12}H_{24}O_2$	Lauric	Dodecanoic
$C_{14}H_{28}O_2$	Myristic	Tetradecanoic
$C_{16}H_{32}O_2$	Palmitic	Hexadecanoic
$C_{18}H_{36}O_2$	Stearic	Octadecanoic
$C_{20}H_{40}O_2$	Arachidic	Eicosadecanoic
$C_{24}H_{48}O_2$	Lignoceric	Tetracosanoic
Unsaturated acids:		
$C_{16}H_{30}O_2$	Palmitoleic	Hexadec-9-enoic
$C_{18}H_{34}O_2$	Oleic	Octadec-9-enoic
Doubly unsaturated acids:		
$C_{18}H_{32}O_2$	Linoleic	Octadeca-9,12-dienoic
$C_{18}H_{30}O_2$	Linolenic	Octadeca-9,12,15-trienoic
$C_{20}H_{32}O_2$	Arachidonic	Eicosa-5,8,11,14-tetraenoic

intermediates, is to form part of the higher molecular weight lipids described in the next two sections.

Triglycerides

Triglycerides consist of molecular complexes of glycerol with fatty acids and the generalized structure of all such molecules is:

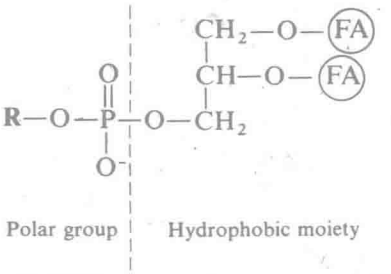


In view of the absence of charged groups in the molecule, these structures are sometimes known as neutral fats to distinguish them from the phosphatidic acids described below. In practice, some triglycerides have the same R-group in all positions, but in others two or three different R-groups may be represented in a single molecule.

It should be emphasized that fats as isolated from bacterial cells are unlikely to consist of single molecular entities, largely because of the wide variety of different fatty acid residues involved and the consequent difficulty of separating molecules of such close molecular similarity.

Phospholipids

These compounds, like triglycerides, are also



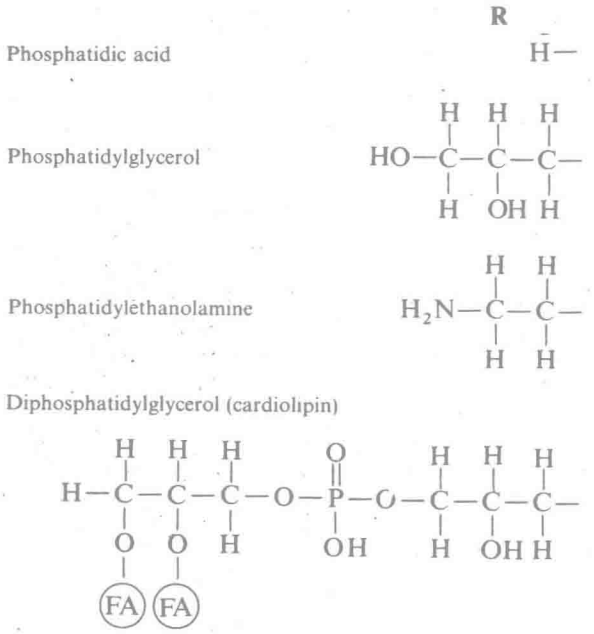
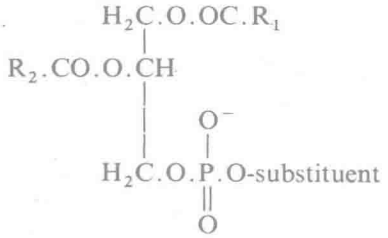


Fig. 1.6 Structures of some phospholipids from bacterial membranes. FA = fatty acid.

substituted glycerols, but all contain phosphorus; many also contain nitrogen. Most of the examples found in bacteria fall into the group known as phosphatidic acids and have the generalized structure:



where R_1 and R_2 are fatty acids and the 'substituent' may be choline, ethanolamine, serine, or inositol (Fig. 1.6 for examples). Where the substituent is choline, the phosphatidic acids are known as *lecithins*.

Steroids

Steroids are unknown in bacteria but certain derivatives are found in fungi where they may be essential for spore formation. One such compound is ergosterol (Fig. 1.7) and this is of particular industrial importance since chemical modification of this compound in the laboratory allows the synthesis of many medicinally important steroids on a commercial scale (p. 366).

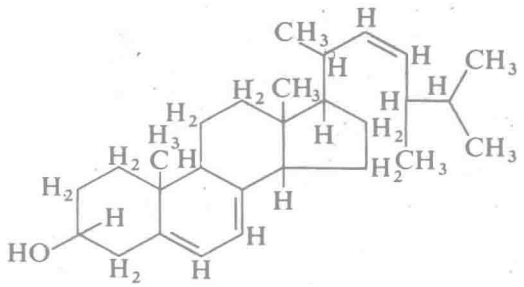
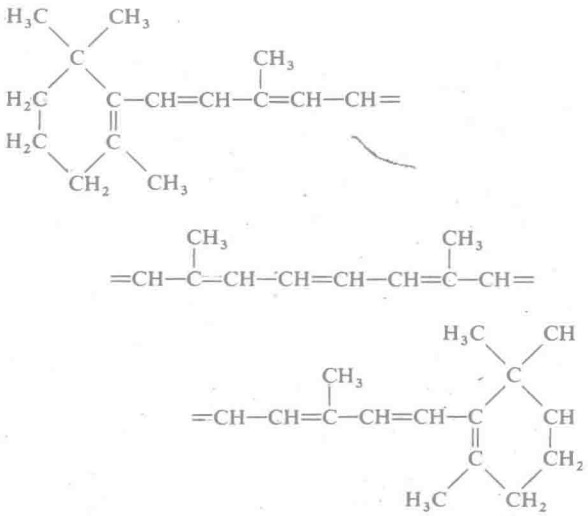


Fig. 1.7 Ergosterol—a steroid with important medicinal uses that is produced by some fungi.

Carotenoids

Carotenoids are a group of lipid substances which have a characteristic orange or red colour. They are compounds responsible for the pigmentation of carrots (hence their name), and also of many bacterial species, particularly the staphylococci and micrococci. All are molecular variants of β-carotene whose structure is as follows:



When present in bacteria cells these pigments are usually found in the cell membrane.

Proteins

Proteins may be classified into two types on the basis of their composition. *Simple* proteins consist solely of amino acids while *conjugated* proteins are structures of the same type but with one or more additional molecules attached. This additional molecule is usually known as the *prosthetic group* and is often involved in the physiological function of the protein, particularly if it is an enzyme, and in the immunological specificity of an antigen (p. 330). For example, electron transport is mediated by flavine prosthetic groups in the dehydrogenases and pyridoxal phosphate is present as a prosthetic group in many transaminases and amino acid racemases.

In both simple and conjugated proteins, the amino acid part of the structure consists of one or more unbranched polypeptide chains formed from amino acid residues joined together by peptide bonds (Fig. 1.8). Although twenty different types of amino acid may be found in such peptide chains, the common basic structure of all (namely $H_2N.CHR.COOH$, where R is one of 20 different chemical residues—see Table 1.3) ensures that the whole polypeptide chain can be formed by joining the amino acids together with a single type of bond. Examination of a number of proteins has shown that not all amino acids are present in the same molecular proportions in each; indeed their distribution may vary quite widely and some may even be missing completely. Although it is impossible to generalize, proteins often contain relatively small quantities of tryptophan, methionine and cysteine but large amounts of the non-polar amino acids valine, leucine and iso-leucine.

Many proteins consist of only one polypeptide chain (which may vary in length from 20 to about 300 residues in different proteins) but many others contain more than one chain, and some as many as six or eight. In such molecules the individual chains

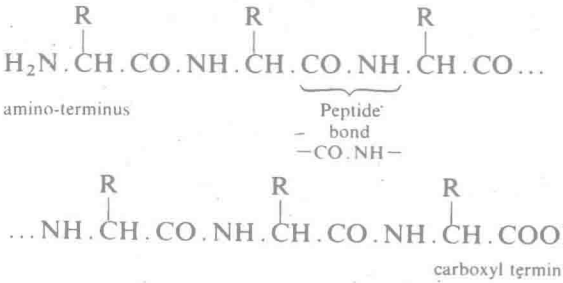


Fig. 1.8 The overall structure of a simple polypeptide chain as found in many proteins. The free $—NH_2$ residue at the left hand end is the *amino terminus*, and the free —COOH at the other end is the *carboxyl terminus*.

Table 1.3 The sidechain substituents (R-groups) of the amino acids commonly found in microbial proteins

General structure: $H_2N.CHR.COOH$		
Amino acid	(abbreviation)	R-group
Glycine	(gly)	H—
Alanine	(ala)	CH_3—
Valine	(val)	$CH(CH_3)_2$—
Leucine	(leu)	$CH_2.CH(CH_3)_2$—
Isoleucine	(ileu)	$CH(CH_3).CH_2.CH_3$
Phenylalanine	(phe)	CH_2—C_6H_5
Tyrosine	(tyr)	CH_2—C_6H_4—OH
Threonine	(thr)	$CH(OH).CH_3$—
Serine	(ser)	$CH_2.OH$—
Cysteine	(cys)	$CH_2.SH$—
Methionine	(met)	$CH_2.CH_2.S.CH_3$—
Tryptophan	(try)	CH_2—(indole ring)
Proline	(pro)	(pyrrolidine ring)—COOH
Aspartic acid	(asp)	$CH_2.COOH$—
Asparagine	(asn)	$CH_2.CO.NH_2$—
Glutamic acid	(glu)	$CH_2.CH_2.COOH$—
Glutamine	(gln)	$CH_2.CH_2.CO.NH_2$—
Arginine	(arg)	$CH_2.CH_2.NH.C(=NH).NH_2$—
Lysine	(lys)	$CH_2.CH_2.CH_2.CH_2.NH_2$—
Histidine	(his)	CH_2—(imidazole ring)

Note: The proline molecule, being an imino acid, does not fall into the general structural classification of amino acids; the structure shown here is the whole molecule and not just the R-group.

are held together by molecular bridges formed between the thiol groups of two cysteine residues, one in each chain (see Fig. 1.9). Such cross connexions are often referred to as —S.S— (disulphide) bridges and usually occur to the extent of about one to two bridges to every 100 residues, although considerable variation in this value is found.

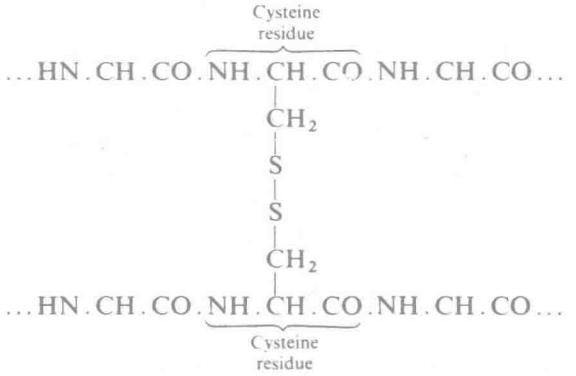


Fig. 1.9 The molecular nature of the —S.S— cross bridges that link different polypeptide chains (and sometimes two points on the same chain) in proteins.

Although all proteins are similar in that they consist of polypeptide chains that may be cross-linked with —S.S— bridges, this basic structure admits an enormous variety of detailed structure and, consequently, of detailed properties. This variety depends to a certain extent on the number and length of the polypeptide chains, but chiefly on the type and distribution of the individual amino acid residues along the chains themselves. The chemical nature of the R-groups found in the twenty different types of amino acid (see Table 1.3) show a wide variation in ionic properties, in polarity and in molecular shape (to mention only a few characteristics) and this ensures that each polypeptide chain has a correspondingly wide range of detailed chemical properties depending on the exact distribution of different types of amino acids along its length.

Although the order and nature of the amino acids along the polypeptide chains together with the position of the cross-bridges between the chains (the so-called *primary* and *secondary* structure of the protein) are important factors in the nature of the protein, the crucial element that determines the properties of the molecule is the way in which the structure folds up and this seems to be determined by the amino acid sequence of the polypeptide chains themselves. As an example, Fig. 1.10 shows

Amino terminus:

1
Lys . Val . Phe . Gly . Arg . Cys . Glu . Leu . Ala . Ala . Ala . . .
. . . Met . Lys . Arg . His . Gly . Leu . Asp . Asn . Tyr . Arg . Gly . Tyr . . .
2
. . . Ser . Leu . Gly . Asn . Try . Val . Cys . Ala . Lys . Phe . Glu . Ser . . .
. . . Asn . Phe . Asn . Thr . Gln . Ala . Thr . Asn . Arg . Asn . Thr . Asp . . .
. . . Gly . Ser . Thr . Asp . Try . Gly . Ileu . Leu . Gln . Ileu . Asn . Ser . . .
3
. . . Arg . Try . Try . Cys . Asp . Asn . Gly . Arg . Thr . Pro . Gly . Ser . . .
4 3
. . . Arg . Asn . Leu . Cys . Asn . Ileu . Pro . Cys . Ser . Ala . Leu . Leu . . .
4
. . . Ser . Ser . Asp . Ileu . Thr . Ala . Ser . Val . Asn . Cys . Ala . Lys . . .
. . . Lys . Ileu . Val . Ser . Asp . Gly . Met . Asn . Ala . Try . Val . Ala . . .
2
. . . Try . Arg . Asn . Arg . Cys . Lys . Gly . Thr . Asp . Val . Gln . Ala . . .
1
. . . Tyr . Ileu . Arg . Gly . Cys . Arg . Glu .

Carboxyl terminus.

Fig. 1.10 The primary and secondary sequence of egg-white lysozyme. Note that in this molecule there is only one polypeptide chain which is bridged at intervals by —S.S— bridges. There are four such bridges linking the molecule at intervals; they are formed between the pairs of cysteine residues labelled 1, 2, 3 and 4 respectively.

the primary and secondary structure of egg-white lysozyme, while Fig. 1.11 shows how this structure folds up to form the final, or *tertiary*, structure of the molecule. The nature of this folding of the chains is vitally important since the overall properties of the molecule are determined by the nature of the amino acid chains that are brought into structural juxtaposition with one another and with the external environment in the folded structure and not by the sequence of the amino acids in any one chain.

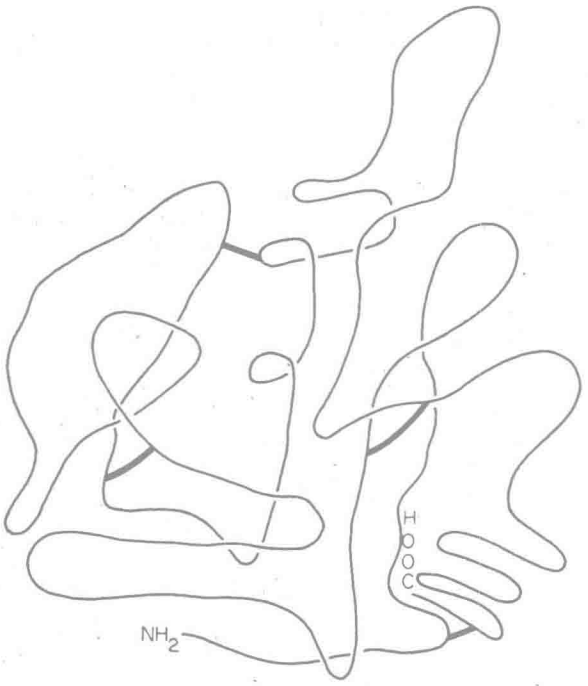


Fig. 1.11 The tertiary folding of the 129 residues of egg-white lysozyme shown in Fig. 1.10. The —S.S— cross bridges are shown as solid bars linking the chain.

Protein subunits

Although some proteins consist of one or more distinct polypeptide chains joined together by —S.S— bridges, others may be formed by the interaction of two or more subunits. In some cases the subunits have an identical structure but in others two, or even three, different subunits are grouped together to form a molecule. One type of protein that usually consists of subunits is any enzyme that is subject to feed-back inhibition (see p. 18). In this case one subunit is the enzyme *sensu stricto* and is responsible for recognizing and metabolizing the substrate. The other subunit recognizes the inhibitor, which is usually the product of the pathway. The inhibitory action is mediated by interaction between the subunits in such a way that reaction of one subunit with the inhibitor reduces the action of the other against the normal substrate. Such an effect transmitted between subunits is known as an *allosteric* effect.

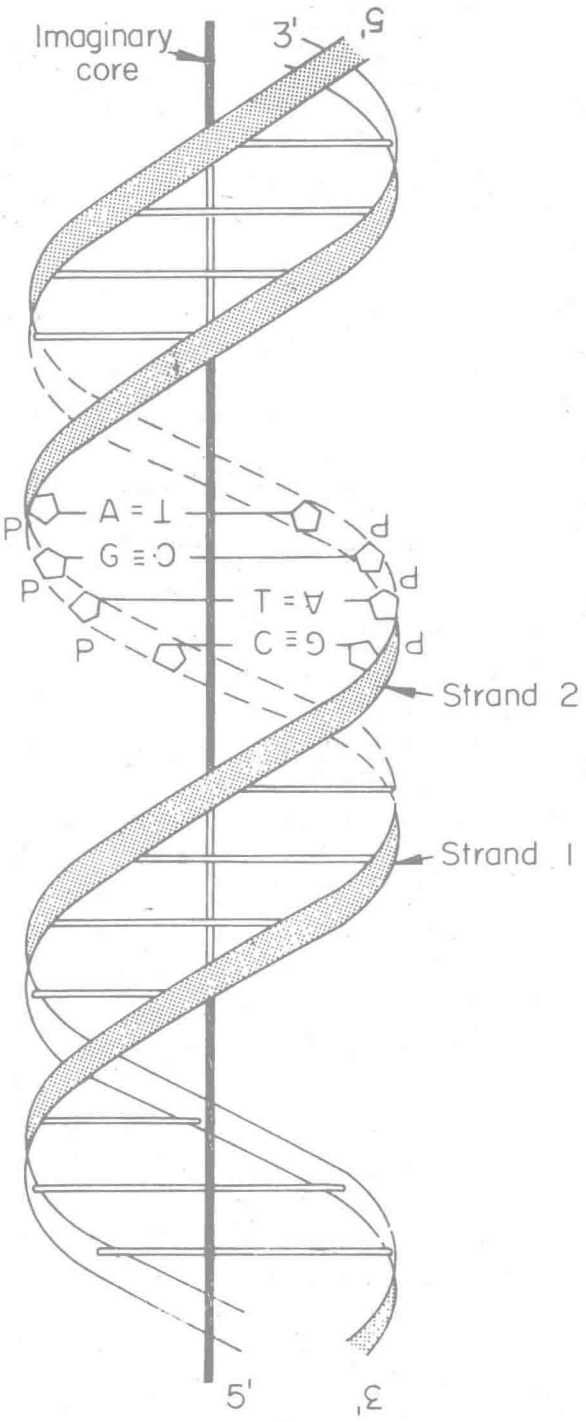


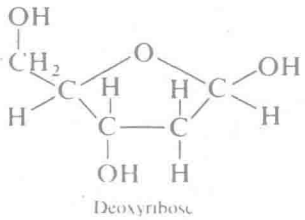
Fig. 1.12 The overall arrangement of residues in the anti parallel double strand of a DNA molecule. A = adenine, G = guanine, C = cytosine, T = thymine, and P = phosphate.

Nucleic acids

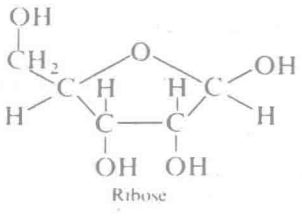
Deoxyribonucleic acid (DNA)

DNA is an extremely long chemical thread made up of two strands, but unlike most threads, the strands are not twisted round one another but wound together round an imaginary core to form a double spiral or, more accurately, 'double helix' (Fig. 1.12). Each thread of the molecule consists of a chain of deoxyribose (Fig. 1.13) and phosphate residues arranged alternately as shown in Fig. 1.14. This arrangement ensures that each individual sugar residue in the chain is joined to two phosphate groups, one substituted on the 3-hydroxyl of the sugar and the other on the 5'-OH group, and that all the phosphate groups in the strand are doubly substituted except the first and the last. Thus one end of a DNA strand carries a single substituted phosphate on C-3 of a deoxyribose residue and the other end has a similar phosphate on the C-5 of the sugar. Thus any chemical change, such as an enzyme reaction, that passes along one of the DNA strands can be thought of as moving in a direction that is either $3 \rightarrow 5$ or $5 \rightarrow 3$. This concept of direction in a DNA strand is important when one comes to examine the overall structure of the molecule, for the two strands are arranged to lie in the double helical thread so that one lies in the $5 \rightarrow 3$ direction and always faced by a strand running $3 \rightarrow 5$ (see Fig. 1.11). For this reason, therefore, DNA is said to exist in the form of an *antiparallel double helix*.

In addition to the substitution at the 3 and the 5 positions, each sugar residue in a DNA strand is also substituted at C-1 by one of a number of purine or pyrimidine bases. The bases commonly found in



Deoxyribose



Ribose

Fig. 1.13 The structure of deoxyribose and ribose sugars.

DNA are the purines, adenine (A) and guanine (G), and the pyrimidines, cytosine (C) and thymine (T) (Fig. 1.15). Examination of the overall structure of DNA shows that the double-stranded nature of the molecule is maintained by hydrogen bonding between the purine and pyrimidine bases in such a way that an adenine residue is always faced by a thymine while guanine is faced by cytosine (Fig. 1.16). Thus adenine and guanine are said to be a *complementary base pair*, and share two hydrogen bonds, while guanine and cytosine are a similar complementary pair and share three hydrogen bonds.

The fact that there is always an adenine opposite a thymine and a guanine opposite a cytosine in the molecule means that there is an equal amount of adenine and thymine in DNA and the same is true of guanine and cytosine. However, the ratio of each pair of bases (that is [A + T]/[G + C]) varies widely from one bacterial species to another. Analysis of the composition of DNA from a number of bacteria shows that the [A + T]/[G + C] ratio may vary from as much as 70/30 in *Clostridium perfringens (welchii)* at one extreme to 28/72 in *Micrococcus lysodeikticus* and 26/74 in *Actinomyces bovis* (Table 1.4). This wide variation in DNA base composition is confined to bacteria and similar relatively

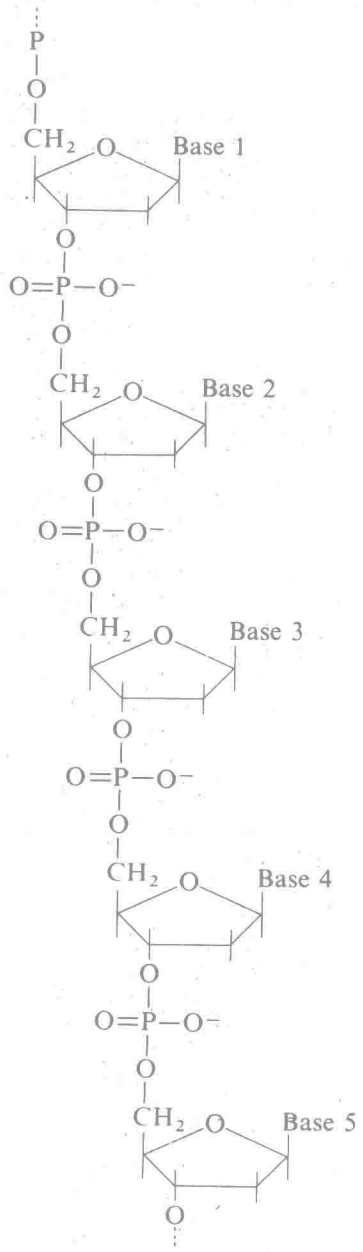
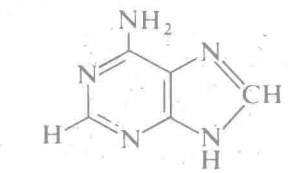
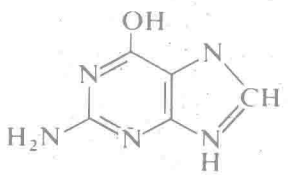


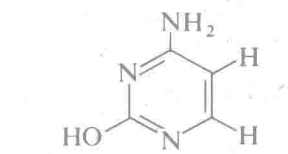
Fig. 1.14 A typical polynucleotide sequence as found in RNA and DNA. In RNA the sugar is *ribose*, while in DNA it is *deoxyribose*.



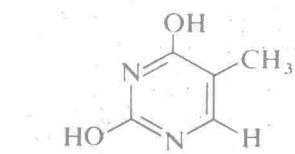
Adenine



Guanine



Cytosine



Thymine

Fig. 1.15 The structure of adenine, guanine, cytosine, and thymine.