The Institute of Biology's
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Cellular Recognition Systems in Plants

J. Heslop-Harrison

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General Preface to the Series

It is no longer possible for one textbook to cover the whole field of Biology and to remain sufficiently up to date. At the same time teachers and students at school, college or university need to keep abreast of recent trends and know where the most significant developments are taking place.

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Readers' comments will be welcomed by the author or the Education Officer of the Institute.

1978

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Preface

The idea that cells and tissues in different parts of the plant or animal body can communicate through the agency of chemical messengers or hormones has been familiar in biology since the early years of the century. In the last two decades ideas about how cells interact at closer range, and indeed when in physical contact, have been taking shape. This text deals with such close-range communication between plant cells.

By selecting examples from various plant groups I have sought to trace some of the common threads, and wherever possible I have attempted to show the connections with parallel work on animal cells. In a rapidly advancing research field like this one speculation tends to outrun fact; but I have not hesitated to refer to some of the theories purporting to account for certain kinds of specific cell interactions. The need for much more work on these interactions in plants to fill some of the many gaps in our knowledge will be obvious enough from the text.

Plas Gogerddan, 1978

J. H. H.

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1 Introduction

1.1 The nature of intercellular recognition systems

In populations of unicellular organisms, cells associate during sexual reproduction and sometimes in such social activities as colony formation. In multicellular plants and animals, contiguous cells of the same individual necessarily interact in the normal course of growth and development; and here once again sexual reproduction requires that cells of different individuals of the same species should come together. Furthermore, cells of *different* species may be brought into close association in such relationships as commensalism, symbiosis and parasitism. In the various situations the interactions may be of the most general kind, or they may be quite specific, occurring only between particular types of cell and leading to responses of a highly characteristic kind in one or both partners. A cell that reacts in a special way in consequence of association with another must do so because it acquires 'information' from that other, information that must be conveyed through chemical or physical signals. In the shorthand of biological parlance, it is customary to refer to phenomena of this kind as 'recognition', in analogy with the way human individuals 'know' each other in the population at large. The terminology is not altogether satisfactory because human beings have to 'get to know' each other before there can be mutual recognition. Interacting cells behave in their characteristic ways because they are already programmed to transmit and receive their special signals. There is no learning stage, so that 'cognition' might be a better term for the form of awareness that one exhibits of the other.

Much the greater part of our present knowledge of the intimate details of cellular interactions has come from work on animal cells, which often reveal what appear to be cognitive properties in very dramatic ways. During embryo formation, cells make coordinated movements in the formation of organs, and in doing so they associate preferentially with other cells and become distributed in precise patterns within the population as a whole. An informative experiment illustrating the powers of sorting out and reassembly can be done with cells taken from embryos into culture. Artificial mixtures of cells from two different kinds of tissue do not form stable mixed aggregates; instead the cell types redistribute themselves in the course of time so that the classes separate. It is indeed as though the cells recognize like and unlike and undertake movements to maximize the degree of association within each class. Just *how* this works is

still unclear, but the experiment does highlight one important fact, namely that the properties of the cell surface are very significant in the social behaviour of animal cells. The cells sort themselves out and then adhere in more or less homogeneous aggregates, cell membrane to cell membrane. Adhesiveness evidently plays an important part in the whole complex process, and one can see that the specificity of the associations could itself be governed through modulations of the adhesive property. The mutual 'stickiness' might differ because at a molecular level there are precisely defined complementary binding sites, varying between cell classes. Or, possibly, the differential aggregation could result from different distributions or densities of binding sites without necessarily any great chemical differentiation.

The fact that animal cells do bear identifying markers is now well established from research on the surface antigens. One class of these is controlled by a group of major genes, the histocompatibility complex. The products of this complex participate in the control of certain types of interaction, being concerned, for example, in the discriminations between 'self' and 'non-self' that lead to the rejection of foreign tissue in grafting. A current theory of the evolution of the histocompatibility system holds that it is basically concerned with the control of development, being part of the mechanism responsible for the cell recognitions thought to play a part in embryogeny. Other functions are believed to have been derived from this fundamental one.

There is now a persuasive body of evidence indicating that surface properties also control many of the interactions of plant cells. Yet animal cells and plant cells differ a great deal in the nature of the surface they present to each other and their external environments.

1.2 The cell surface: animals

Earlier interpretations of the structure of the outer membrane of the cell (the plasmalemma), and indeed of the membranes within the cell, were based upon a model proposed in 1935 by J. F. Danielli and H. Davson. According to this model, the lipids (mainly phospholipids) of the membrane are distributed in two layers so that the hydrophobic 'tails' of the molecules are directed inwards towards each other and the hydrophilic 'heads' outwards to the aqueous phase of the cytoplasm on the one side and the intercellular space on the other. The proteins of the membrane are envisaged as being mainly distributed in two layers on the hydrophilic surfaces. This structure meets thermodynamic criteria for stability, and is consistent with various biophysical properties established both for membranes *in situ* and those separated from the cell. Moreover, electron microscopic images of animal and plant cell membranes generally show a three-layered structure readily reconciled with the Danielli–Davson model, a fact that led to the 'unit membrane' concept of J. D. Robertson, advanced in 1959.

The knowledge that biological membranes change their physical and chemical characteristics during the normal life of the cell, seen for example in variation in their permeability properties, has all along made it necessary to assume that the structure is to some extent dynamic. During the 1960s new evidence accumulated from many sources bearing on the nature of animal cell membranes, and this led to a reappraisal of their organization, culminating in the *fluid mosaic* model of SINGER and NICOLSON suggested in 1972. This preserves a basic feature of the Danielli–Davson model, the lipid bilayer, but proposes that the membrane-associated proteins are of two kinds, those embedded in the lipid bilayer or stretching through it (integral membrane proteins) and those distributed on the surface (peripheral membrane proteins). The special feature of this model and the one that required the most far-reaching re-consideration of membrane properties was the postulate that the integral membrane proteins are free to move *laterally* in the lipid layer. Their stability within the thickness of the membrane is presumed to be determined by an asymmetric distribution of hydrophilic and hydrophobic groups in each protein molecule, a distribution which establishes that part is firmly embedded in, or oriented across, the lipid bilayer, with part protruding from it. No forces constrain the protein molecules laterally, however, other than those they develop between themselves, or which may act from either side of the membrane on the protruding parts. A diagram of the fluid mosaic model of the membrane is given in Fig. 1–1.

The fluid mosaic model comfortably accommodates several features of the outer membrane of the animal cell established through recent research. The membrane lipids include glycolipids with short chains of sugar residues in the molecule; these would be disposed with the oligosaccharide portion extending into the aqueous phase and the acyl chains directed into the membrane. Among the most important classes of

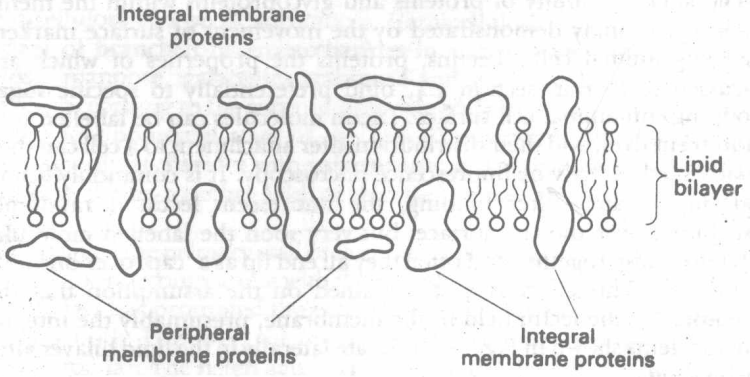

Fig. 1–1 Fluid mosaic model of the cell membrane (plasmalemma). (Based on SINGER and NICOLSON, 1972.)

membrane proteins are the glycoproteins, proteins with simple or branched carbohydrate chains covalently attached. The distribution of these is indicated in Fig. 1–2. The carbohydrate portions of glycolipids

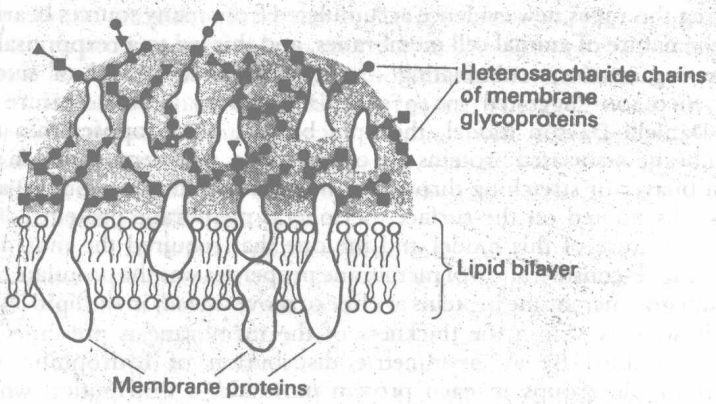

Fig. 1–2 Profile and surface of the cell membrane to show the possible disposition of the glycoproteins. The integral membrane glycoproteins emerge from the lipid layer, with the heterosaccharide chains forming the sugar-rich coating.

and glycoproteins form a sugar-rich coating on animal cells, to which the name glycocalyx has been given. With some cell types, the coating can be made visible in both light and electron microscopes by suitable staining procedures. The dye alcian blue stains acid polysaccharides, and cells stained with this often show the coating as a fuzzy layer on the outer face of the cell membrane, extending outwards with diminishing density for as much as 100 nm.

The lateral mobility of proteins and glycoproteins within the membrane is strikingly demonstrated by the movement of surface markers on living animal cells. Lectins, proteins the properties of which are discussed further in section 1.4, bind preferentially to specific sugar groupings on animal cell surface. Lectin molecules can be labelled with fluorescent dyes, and their distribution after attachment to a cell can then be observed directly by fluorescence microscopy. It is commonly found that, immediately after binding, the fluorescent lectin is randomly distributed over the cell surface, but very soon the labelled molecules begin to clump together and often they all end up as a 'cap' over one pole of the cell. This effect is best explained on the assumption that the receptors for the lectin held in the membrane, presumably the integral glycoproteins shown in Fig. 1–2, migrate laterally in the lipid bilayer after the binding.

Animal cell membranes are thus 'dynamic' in the sense that movements of molecules take place freely within them. They are dynamic also in

another sense, in that the characteristics of the coating change during development in such a way as to suggest that the exposed surface carbohydrates of the membrane glycoproteins undergo variation during the life of the cell. In fact, there may be a continuous and quite closely controlled flux of these components of the cell surface. The glycoproteins are probably synthesized in the endoplasmic reticulum and then passed through the Golgi apparatus of the cell, the sugars being attached to the protein later in the processing sequence by specific glycosyltransferases. They reach the cell surface with the discharge there of the dictyosome vesicles. These vesicles contribute new membrane to the plasmalemma, which itself is thus in a continuous state of change. This process provides one means through which the surface carbohydrates can be varied according to the metabolic state of the cell. Some observations suggest that changes may also be brought about by other processes after the incorporation of the glycoproteins into the cell membrane through the addition or excision of sugar groups.

1.3 The cell surface: plants

There is no reason to believe that the membranes of plant cells differ in any basic way from those of animal cells: they have broadly similar chemical compositions, and show much the same range of physical properties. However, the plasmalemma of the plant cell abuts a cell wall, and it is this fact that accounts for many of the differences between plant and animal cells. The primary wall, in general, consists of a microfibrillar component within a less well-ordered matrix material. In all higher plants and many algae the microfibrils are composed of cellulose, a β-1,4-linked glucan, the cellulose molecules in the interior of the microfibril being disposed in a crystalline manner with those towards the outside arranged more randomly. The microfibrils, which are 10 nm or more in diameter and of indeterminate length, are held in the matrix, itself composed of hemicellulose and pectic substances. Hemicellulose is the name given to a class of branched heterosaccharides in which the sugars are mainly xylose, mannose, galactose, arabinose and glucose, the combinations varying according to the taxonomic group and also sometimes according to the developmental state of the cell. The pectic substances are gel-forming polysaccharides with galacturonic and glucuronic acids in main and side chains together with arabinose, xylose, rhamnose and other sugars.

In so far as the primary wall of the plant cell is carbohydrate in nature it is in some sense comparable with the carbohydrate coat of the animal cell, and the fact has prompted the extension of the concept of the glycocalyx to cover both. However, for the older plant cell the analogy cannot be pressed too far. The heterosaccharides of the animal cell coat are parts of the membrane glycoproteins and are thus anchored into the membrane. Even though they may be lost slowly into the intercellular spaces by

ablation from the membrane due to the continuous turnover going on at the cell surface, they can scarcely be said to form a wall in the sense of the plant cell wall. This is much thicker, and has considerable mechanical strength so that it forms a box enclosing the protoplast. One aspect of the different relationship is seen in the fact that the plasmalemma can be withdrawn from the wall of the mature plant cell by plasmolysis. Nevertheless, in the young cell the relationship of the cell surface with the wall may be very close indeed. The precursors of the cell wall polysaccharides are passed into the young wall by the activity of the Golgi apparatus of the cytoplasm, the dictyosome vesicles once again contributing portions of membrane to the plasmalemma as this happens. Moreover, the enzymes responsible for the synthesis of the cellulose microfibrils appear to be clustered in particles or aggregates held on, or more probably partly in, the cell membrane. Interestingly, the assembly of the long microfibrils may require the slow, controlled migration of the enzyme aggregates in the membrane, a concept entirely compatible with the fluid mosaic model. Also, at least in the younger wall, glycoproteins are often present, and sometimes abundantly so. These must be transferred through the plasmalemma, and presumably they are synthesized in much the same manner as the glycoproteins of the animal cell surface. A generalized diagram of the plant cell wall is given in Fig. 1–3.

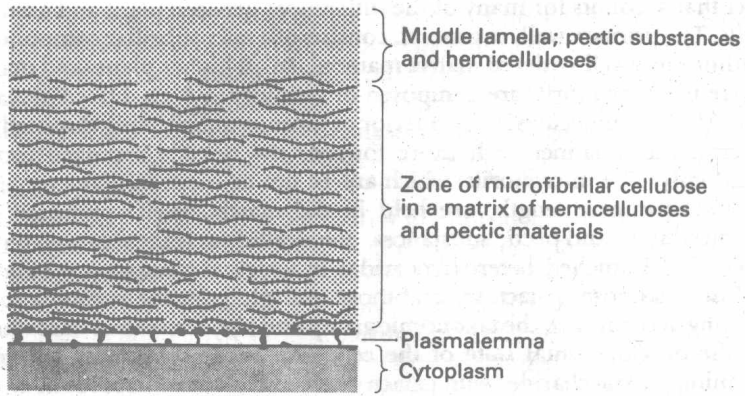

Fig. 1–3 Diagram of the primary wall of the plant cell.

The presence of walls necessarily precludes a direct membrane-to-membrane contact for most classes of plant cell. The exceptions are found among some lower groups, and universally in at least one phase of sexual reproduction in all plants – that stage when the gametes, or the cells carrying the gametes, come together as a prelude to fertilization. Even in reproduction, however, the initial overtures – comprising the courtship, so to speak – generally occur between walled cells. So in reproductive as

in somatic interactions plant cells mostly have to negotiate through polysaccharide walls. This may be achieved through the protoplasmic connections formed by the plasmodesmata; these give not simply membrane contact, but membrane continuity between contiguous cells. Or there may be one-way or reciprocal signalling through the agency of soluble, diffusible messengers, originating in one cell, passing across the wall and being received by receptors on or in the other. Or yet again the function of the cell membrane in communication may be transferred spatially so that some of the interactions are on the outer surface of the wall, secondary systems alerting the cell within as to what is going forward. Some of the possibilities in the tissues of a multicellular plant are summarized in a simple form in Fig. 1–4. It can be seen from a model of

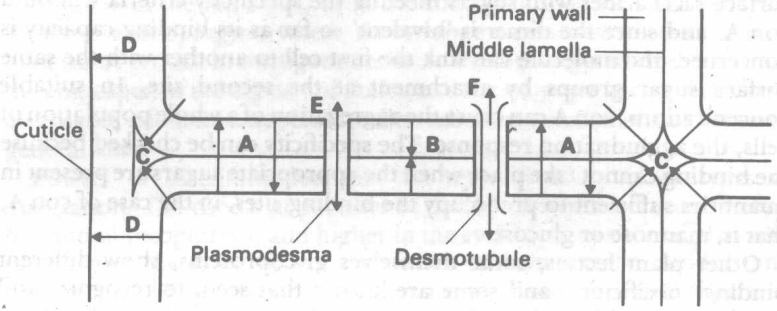

Fig. 1–4 Pathways of communication between plant cells. Signals can be passed by: A – diffusion from plasmalemma to plasmalemma across both intervening walls; B – diffusion from neighbouring cells, with interactions in the wall; C – diffusion into and through intercellular spaces; D – diffusion through the cuticle onto the outer surface; E – movement through plasmodesmata; F – movement through desmotubules.

this kind that close-range cell communication can be viewed as but one element in the wider system where diffusing molecules derived from remote tissues, the mobile hormones, also fulfil their functions.

1.4 A word about lectins

It so happens that one class of molecules produced by plants has played a very significant part in the investigation of cellular interactions in animals, namely the lectins. Lectins, sometimes also known as phytohaemagglutinins, were first detected almost a century ago as compounds, produced by plants, capable of causing the coagulation or agglutination of red blood cells. Today many hundreds of such compounds are known, from a thousand or so species of flowering plants, with the capacity of agglutinating various types of animal cells, and several have been typified chemically and structurally. Among those most

commonly used in experiments on animal cells is concanavalin A (con A), from the jack bean, *Canavalia ensiformis*. The structural unit of con A is a protein with a molecular weight of about 25 000 daltons. These units may be associated to form dimers or tetramers or larger aggregates, depending on the pH of the environment. The structural units are asymmetrical in shape, and each has a pocket in the molecule that can accommodate a sugar residue, the dimer thus having two and the tetramer four such binding sites. The binding property of con A is specific towards α-D-mannose and α-D-glucose residues, and the molecule attaches specifically to saccharides containing these residues, including those forming parts of glycoprotein molecules. It is to this property that con A owes its capacity for agglutinating animal cells. Cells with accessible surface saccharides with sugars meeting the specificity criteria will bind con A, and since the dimer is 'bivalent' so far as its binding capacity is concerned, the molecule can link the first cell to another with the same surface sugar groups by attachment at the second site. In suitable concentrations, con A can cause the aggregation of a whole population of cells, the agglutination response. The specificity can be checked because the binding cannot take place when the appropriate sugars are present in quantities sufficient to preoccupy the binding sites, in the case of con A, that is, mannose or glucose.

Other plant lectins, some themselves glycoproteins, show different binding specificities, and some are known that seem to recognize and attach to combinations of sugars terminating, or intercalated in, heterosaccharide chains. The binding affinity is reminiscent of that of enzyme for substrate, although the attachment is more persistent. The union is not due to the formation of covalent bonds, however, and it can be broken by appropriate treatments.

Because of their special properties, lectins provide a valuable method of 'probing' the cell surface, since their attachment can be taken to indicate the presence of the sugars for which they have specificity. In some instances the association with a lectin provokes far-reaching changes in the behaviour of the cell. Con A, for example, induces lymphocytes to undergo mitosis, and when applied to certain types of egg cell, can inhibit fertilization.

Like other proteins, lectins are probably synthesized in the endoplasmic reticulum of the plant cells. It is known that some at least are transferred into the cell wall, where they accumulate sometimes in surprisingly large amounts. Later some of the implications of lectin effects will be examined and the possible functions of these molecules in plants considered.

1.5 Types of recognition response in plants

The classical literature of botany is replete with examples of interactions which, with the wisdom acquired from recent research, one

can readily see must depend on recognition responses of greater or lesser specificity. Events associated with reproduction have already been mentioned. In every plant group with a sexual process there must be some selectivity at certain stages in the association of the conjugating partners. The gametic fusion of unicells clearly has to be selective, and the same must be true for the fusion of free-swimming gametes produced by multicellular algae and fungi like *Ulothrix* and *Allomyces*. The fertilization of static eggs by motile spermatozoa as in plants as widely diverse as *Vaucheria*, *Fucus*, *Monoblepharis*, *Funaria*, *Pteridium* and *Cycas* clearly requires a combination of chemotactic guidance together with more specific controls determining the kinds of cellular unions to be permitted. The same must apply when gamete nuclei are brought together through the association of non-motile cells, as in the contact of spermatium and trichogyne in the red algae, or in the conjugation of different filaments in *Mucor* and *Spirogyra*, where short-range interactions induce special patterns of growth in contiguous cells. In the higher gymnosperms and in the angiosperms the capture of pollen and the subsequent choice between acceptable and non-acceptable pollen tubes are phenomena of the same general kind.

Powers of discrimination may be seen in many other types of association. The choice of partners in the lichen symbiosis must depend on mutual recognition; and higher in the evolutionary scale of plants we can suspect the same in the association of host-specific dodders and their victims. The relationships of vascular plants and viral, bacterial and fungal pathogens embrace another whole field of recognition phenomena, where host specificity, resistance and susceptibility all imply specific interactions. In less natural situations, the results of artificial grafting where the genetic constitution of stock and scion determines whether the union will take or not suggest the operation of some form of cellular recognition system.

Grouping all of these different classes of phenomena under the general heading of recognition events acknowledges the feature they share in common, namely the expression of specificity or selectivity. This certainly cannot be taken to imply that the underlying controlling systems are identical or necessarily even broadly similar – even, say, in the interactions between gametes in the different groups. Nevertheless, a body of evidence is now accumulating which suggests that many responses do have much the same kind of molecular basis, and it is an intriguing fact that this may not be greatly different from that believed to underlie many recognition events in animal cells and tissues.

2 Recognition Systems in Algae and Fungi

2.1 Introduction

Algae and fungi have many advantages for the investigation of short-range cellular interactions. Their body-forms are simpler than those of the higher plant groups so that processes like fertilization can be more easily observed; many can be taken through complete developmental cycles under controlled laboratory conditions; and, where mass cultures can be raised, adequately large samples can be acquired for chemical analysis. It is therefore not surprising that a good deal of our present knowledge of cellular recognition systems in plants has come from these lower groups. There remains the question of how much use the gained knowledge is likely to be in seeking to understand the more complicated types of cell interaction found in the more advanced groups, particularly in the angiosperms. It is probable that the evolution of more elaborate body forms and more complex tissue systems has been accompanied by – indeed, has even been dependent upon – the development of a more sophisticated mechanism for cell communication. But one might at least expect the systems found among lower plants to be among those available to plants higher in the evolutionary scale, and it is therefore attractive to look for parallels.

2.2 Algae

2.2.1 *Gamete fusion in* Chlamydomonas

Chlamydomonas, a genus of unicellular freshwater alga belonging to the Chlorophyceae, has a sexual process in which morphologically similar, biflagellate gametes fuse to give the zygote. The gametes are transformed vegetative cells, formed when a population experiences nutrient deficiency. The gametes are not differentiated structurally, but many species show heterothallism, the gametes belonging to different mating types, designated as (+) and (–). No conjugation takes place within a gamete population of a single mating type but when (+) and (–) populations of gametes from the same species are mixed, agglutination begins. Clusters of gametes are formed containing mixtures of the two mating types, the clumping being due to adhesion between the tips of the flagella. Some time after this event, the clusters break up into pairs of gametes, each with a (+) and a (–) partner. The cells then link by the body region; the cell walls fuse, a conjugation tube is formed, and fusion of the cytoplasms and nuclei follows. Several features of this process make it a

favourable one for the study of contact and recognition events. Vegetative cells do not agglutinate, and because the transformation into gametes can be controlled, the development of the recognition system can be followed. The surfaces that come into contact during agglutination are precisely known: they are the membranes of the flagella tips. Finally, the responses are very specific: the fusion is between gametes of different sex, and beyond this there is species specificity, gametes of different species, with certain exceptions, being unable to fuse with each other whatever the mating type. These relationships are shown for three species in Table 1.

Table 1 Sex and species specificity in the mating of *Chlamydomonas*. A=agglutination when the cultures are mixed; O=no agglutination when mixed. (Data from WIESE, 1974.)

Species	*C. eugametos*		*C. moewusii*		*C. reinhardi*	
	(+)	(−)	(+)	(−)	(+)	(−)
C. eugametos						
(+)	O	A	O	O	O	O
(−)	A	O	O	O	O	O
C. moewusii						
(+)	O	O	O	A	O	O
(−)	O	O	A	O	O	O
C. reinhardi						
(+)	O	O	O	O	O	A
(−)	O	O	O	O	A	O

Most of our knowledge of the details of the conjugation process in *Chlamydomonas* has come from the work of Wiese and his collaborators (e.g. WEISE, 1974). One informative finding was that cells in the gametic state shed into the medium material which itself is capable of causing agglutination of gametes of opposite mating type; the material from (+) cells agglutinates (−) cells and the material from (−) cells agglutinates (+) cells. Agglutination of (+) gametes of *C. eugametos* by the material from the culture medium of (−) gametes is illustrated in Fig. 2–1. After this homosexual agglutination there is, of course, no cell fusion. These materials, referred to as isoagglutinins, have been shown to contain glycoproteins. They carry with them not only the *sex* specificity, but also the *species* specificity (Table 1). Their involvement in the adhesion and recognition responses is not therefore in doubt.

The analogy with animal-cell agglutination immediately suggests the possibility that the adhesion of the gametes might be something to do with membrane-held glycoproteins. Evidence favouring this idea comes from the fact that the lectin, con A, affects the agglutinability of the gametes. In high concentrations it brings about isoagglutination of

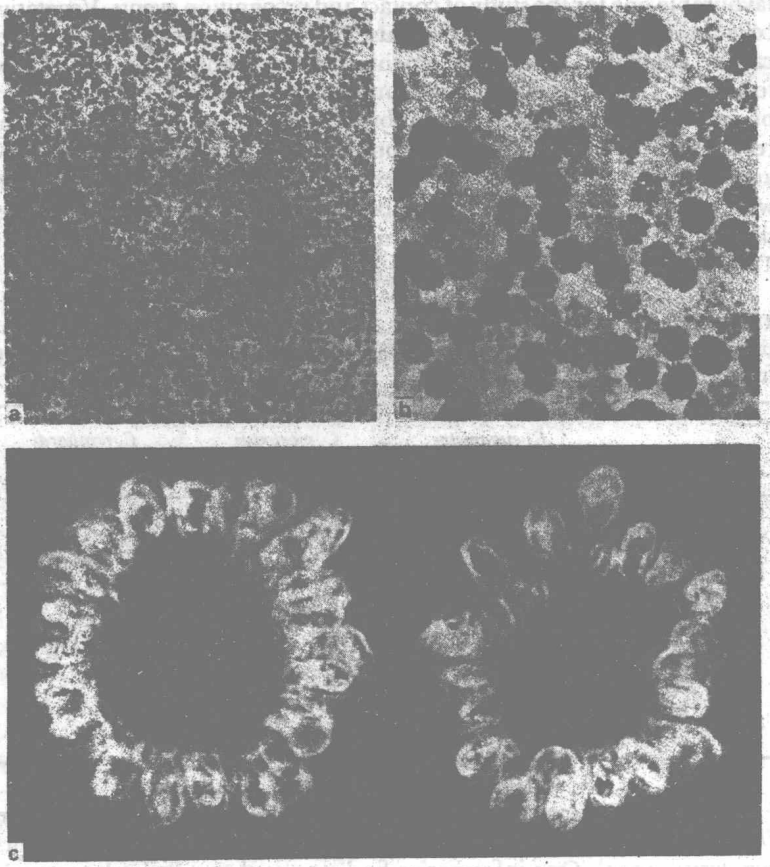

Fig. 2–1 Agglutination of (+) gametes of *Chlamydomonas eugametos* by isoagglutinin from the culture medium of (−) gametes. (a) Free-swarming cells in the absence of the isoagglutinin; (b) agglutination a few minutes after the addition of the isoagglutinin to the medium; (c) detail, showing two clusters of the agglutinated gametes as seen with dark-field illumination. The cells are held together in the rosette by the adhesion of the tips of the flagella. The body of each cell is about 12 μm long. (Micrographs reproduced by the courtesy of Professor L. Wiese.)

gametes of both sexes of certain species, and in the same species at lower concentrations it destroys the capacity of one sex to bring about agglutination when mixed with the other (Table 2). Con A does not induce isoagglutination when mannose is present, indicating that the effect depends on the specific sugar-binding capacity of the lectin. Furthermore, pre-treatment with α-mannosidase, an enzyme that might be expected to remove α-D-mannose residues from the flagellar surface,