THE STRUCTURAL ORGANIZATION OF THE SEPTATE AND GAP JUNCTIONS OF HYDRA

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ABSTRACT

The septate junctions and gap junctions of Hydra were studied utilizing the extracellular tracers lanthanum hydroxide and ruthenium red. Analysis of the septate junction from four perspectives has shown that each septum consists of a single row of hexagons sharing common sides of 50–60 Å. Each hexagon is folded into chair configuration. Two sets of projections emanate from the corners of the hexagons. One set (A projections) attaches the hexagons to the cell membranes at 80–100 Å intervals, while the other set (V projections) joins some adjacent septa to each other. The septate junctions generally contain a few large interseptal spaces and a few septa which do not extend the full length of the junction. Basal to the septate junctions the cells in each layer are joined by numerous gap junctions. Gap junctions also join the muscular processes in each layer as well as those which connect the layers across the mesoglea. The gap junctions of Hydra are composed of rounded plaques 0.15–0.5 µ in diameter which contain 85 Å hexagonally packed subunits. Each plaque is delimited from the surrounding intercellular space by a single 40 Å band. Large numbers of these plaques are tightly packed, often lying about 20 Å apart. This en plaque configuration of the gap junctions of Hydra contrasts with their sparser, more widely separated distribution in many vertebrate tissues. These studies conclude that the septate junction may possess some barrier properties and that both junctions are important in intercellular adhesion. On a morphological basis, the gap junction appears to be more suitable for intercellular coupling than the septate junction.

INTRODUCTION

Recent physiological studies have demonstrated low-resistance intercellular pathways in many tissues (Loewenstein and Kanno, 1964; Furshpan, 1964; Barr et al., 1965; Penn, 1966; Bennett et al., 1967; Payton et al., 1969) and have stimulated intensive investigation of the morphology of intercellular junctions. Gap junctions have been designated as the morphological site of these intercellular pathways in several vertebrate tissues (Furshpan, 1964; Barr et al., 1965; Penn, 1966; Bennett et al., 1967) as well as in invertebrate tissues (Payton et al., 1969; Pappas et al., 1971).

In Loewenstein’s initial studies in the Drosophila salivary gland, septate junctions were implicated in intercellular coupling (Wiener et al., 1964). However, later studies have shown that gap junctions are also found in this gland (Phillips and Rose, as cited by Hudspeth and Revel, 1971). Septate junctions are not confined to invertebrate epithelial tissues as originally thought. In a very few instances, they have also been described in vertebrate tissues (Barros and Franklin, 1968; Lasansky, 1969) including at least one site in the vertebrate central nervous system (Gobel, 1971). The function of the septate junction, some twelve
years after its discovery, is still poorly understood, and its possible role in intercellular communication is still being intensively investigated (Satir and Gilula, 1970; Gilula et al., 1970; Rose, 1971). In view of its distribution and the general lack of information about the functional properties of the septate junction, we have reexamined its structure utilizing extracellular tracers and uranyl acetate blockstaining techniques.

_Hydra_ was selected as a model for this study for several reasons. The septate junctions, which join the outer and lumenal margins of the cells of the two layers (epidermis and gastrodermis), are readily accessible to extracellular tracers. The hydroid septate junction is well suited for a two-dimensional analysis since it is made up of regularly spaced, parallel septa (Wood, 1959) in contrast to the corrugated or honeycombed septa found in the septate junctions of higher species (Locke, 1965; Danilova et al., 1969; Satir and Gilula, 1970). In addition, a micrograph in Wood’s study (1961) suggested to us that gap junctions also may occur in _Hydra_.

The present study describes a lattice-like organization of the septate junction in which individual septa consist of a chain of folded hexagons which are attached to the cell membranes and to each other by short projections. The cells of _Hydra_ are also connected by gap junctions organized in closely packed, rounded plaques. The septate and gap junctions of _Hydra_ are evaluated from a morphological standpoint with respect to their role in intercellular adhesion, as permeability barriers, and in intercellular coupling.

**MATERIALS AND METHODS**

Individual _Hydra_ (Pelmatohydra oligactis, General Biological Supply House, Inc., Chicago, Illinois) were sucked up into a medicine dropper from the water in which they were shipped, allowed to relax, and ejected into a large volume of fixative. The animals were fixed for 30–60 min in a mixture of 2.5% glutaraldehyde and 2% formaldehyde in 0.1 M sodium cacodylate buffer, pH 7.4 (Karnovsky, 1965). After an overnight wash in 0.1 M sodium cacodylate buffer with 7.5% sucrose, pH 7.4, they were postfixed for 30–60 min in a solution of 1% OsO₄ in either the cacodylate buffer or Veronal acetate buffer (Zetterqvist, 1956), and stained in block with 0.5% uranyl acetate (Karnovsky, 1967). _Hydra_ were also fixed in the above sodium cacodylate-buffered aldehyde solution which contained either 1–2% lanthanum hydroxide (Revel and Karnovsky, 1967) or 500 ppm ruthenium red (Luft, 1964). In these experiments, similar concentrations of these extracellular tracers were included in the buffer wash and in the OsO₄ solutions. In some experiments, _Hydra_ were initially fixed in aldehydes for 5–10 min before being placed in fixatives with lanthanum hydroxide. There were no observable differences between the two lanthanum procedures. After dehydration in ethanol and embedding in epoxy resin (Spurr, 1969), thin sections of the mouth and body column were cut transversely and longitudinally, and stained with lead citrate (Venable and Coggeshall, 1965).

**RESULTS**

**Septate Junctions**

The septate junctions of _Hydra_ are found between the outer regions of adjacent epidermal cells and between the lumenal regions of adjacent gastrodermal cells where they follow a tortuous course, frequently uniting interdigitating processes of adjacent cells. An analysis of these septate junctions as seen in different section planes has led us to propose the following three-dimensional model for the structure of the septa (Fig. 1). Each septum is composed of a backbone which consists of a single row of hexagons sharing common sides of 50–60 Å. Each hexagon is folded into a chair configuration, a term used to describe a

![Image of a model of a portion of a single septum. Each septum consists of a backbone made up of a row of hexagons sharing common sides and folded into chair configuration. V projections extend vertically from each corner of the hexagons. In addition, each hexagon emits two A projections. In succeeding figures this model has been photographed on end (Fig. 6), from above (Fig. 9), and from its side (Figs. 13 and 16).](image-url)

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_Venables_ and _Coggeshalls_ (1965).
FIGURE 2  Schematic drawing illustrating the interseptal relationships between three septa and the orientation of the section planes used in the analysis. The folds of the upper and middle septa are oriented parallel to each other (see text) and their $V$ projections are out of alignment. The folds of the middle and lower septa are inverted with respect to each other and show fusion of their aligned $V$ projections at the left. The membrane in the foreground has been cut away in order to reveal the $A$ projections which join the hexagons of the septa to the cell membranes.

The specific configuration of the hexagonal structure of the cyclohexane molecule, in which opposite corners of the hexagon lie on different sides of an equatorial plane through the hexagon. Projections extend vertically from each of the corners of the hexagons either above or below the backbone, depending on the position of the corner with respect to the equatorial plane (Figs. 1 and 2). Such projections will be referred to as $V$ projections. Another set of projections extend from each of the corners of the hexagons which face the cell membranes and attach the backbone to the membranes (Figs. 1 and 2). These projections will be referred to as $A$ projections. Consequently, each corner of the hexagons is formed by four intersecting lines which meet in tetrahedral fashion.

When the model (Fig. 1) is viewed either on end (Fig. 6), from above (Fig. 9), or from its side (Figs. 13 and 16), one obtains different images with respect to the form of the backbone and the periodicity of the $A$ and $V$ projections. These different images result from superimposition of parts of the model and from foreshortening of some of the angles. The following description correlates electron microscope observations of septate junctions viewed from different planes with the model which has been photographed from corresponding angles. The structure of septa from junctions between gastrodermal cells and epidermal cells is similar and the model is based upon observations of junctions in both locations.

When a septate junction is viewed at right angles to the long axis of the septa, each septum extends across the intercellular space between adjacent cell membranes, producing the typical ladder-like image of septate junctions (Fig. 3).
Such views are defined as plane 1 (Fig. 2). Each septum as seen in plane 1 appears as a moderately electron-opaque bar, which emits V projections that extend toward the adjacent septa (Fig. 3). The periodicity of the septa varies between 130 and 170 Å, although large interseptal spaces occasionally interrupt this pattern (Figs. 10 and 17). Lanthanum hydroxide and ruthenium red gain access to the septate junctions of both cell layers and fill the interseptal spaces. In the presence of these substances the septa span the intercellular space and are seen in negative contrast. They appear as folded electron-lucent bands 20–30-Å thick, with V projections extending from the peaks of the folds (Figs. 4 and 5). The V projections of adjacent septa occasionally appear connected across the interseptal space (Figs. 3, 4, and 5). Fig. 6 shows the model (Fig. 1) viewed on end and illustrates the folds and peaks which result from the superimposition of parts of the backbone as well as the alignment of the V projections seen in plane 1.

Septate junctions oriented so that the section plane passes between the septa provide opportunities to view the septa from above. Such views are defined as plane 2 (Fig. 2). The junction, as seen in plane 2, contains a rather amorphous band of...
FIGURE 10 In plane 3, the septa show gentle curvatures along their length and often enclose wide inter-
septal spaces (X). A few septa terminate without extending the full length of the junction (arrows). Epi-
dermis. Lanthanum hydroxide. X 117,000.

FIGURE 11 The septa appear as thin, flattened sheets in plane 3 views of routinely fixed junctions. The
curving nature of the septa is also evident. Gastrodermis. X 116,000.

FIGURE 12 Plane 3. A portion of Fig. 10 at higher magnification. In the presence of tracers the septa ap-
pear as a central band 20–30-A thick with V projections extending from each side at 40–50-A intervals.
X 246,000.

FIGURE 13 When the model is viewed from the side, the backbone partially superimposes to form a
central band, with V projections extending from both sides of the backbone.

moderately electron-opaque material between the
membranes (Fig. 7). When the interseptal spaces
are filled with lanthanum or ruthenium red, a
row of small hexagons is outlined. These hexagons
share common sides 50–60-A-long, and have a
center-to-center spacing of 80–100 A (Fig. 8). A
projections, about 30-A–long, leave the corners of
the hexagons which face the cell membranes and
appear to contact the latter perpendicularly, in
effect joining the hexagonal backbone to the cell
membranes (Fig. 8). The A projections are also
spaced 80–100-A apart. Fig. 9 shows the appear-
ance of the model when viewed from above and
illustrates the hexagons and the A projections.
The V projections are not evident in this plane
because of superimposition, and the folded nature
of the hexagons cannot be discerned because of
foreshortening.

Section planes which pass through septate
junctions parallel to the cell membranes are de-

defined as plane 3 (Fig. 2), and provide side views of
the long axis of the septa. In plane 3, the septa
appear as thin, flattened sheets which commonly
exhibit gentle curvatures (Fig. 11). Groups of
septa parallel each other for varying distances
but may occasionally diverge to encompass fairly
large interseptal spaces (Fig. 10). In most junc-
tions, a few septa can be found which do not
extend the full length of the junction (Fig. 10). In
the presence of lanthanum or ruthenium red
each septum consists of a linear backbone 20–30-A
–thick. The V projections on each side of the back-

ARTHUR R. HAND AND STEPHEN GOBEL  Septate and Gap Junctions of Hydra  401
bone are spaced about 40–50 Å apart (Fig. 12). The V projections from adjacent septa occasionally appear in register and probably fuse in the interseptal space. Fig. 13 is a photograph of the long axis of the model viewed from its side, illustrating the partial superimposition of the backbone and the alignment of the V projections.

If one end of the model, oriented as in Fig. 13, is raised to a point where the model forms an angle of 30° with the plane of the page, the backbone and the V projections assume a configuration which is shown in Fig. 16. The form of the backbone seen in septate junctions viewed in this plane (Figs. 14 and 15) is a result of the superimposition of the sides of the hexagons and the A projections. The periodicity of the V projections on either side of the backbone is ~100 Å, or about twice that of the V projections as they appear in plane 3 views.

**Gap Junctions**

The epidermal and gastrodermal cells are also joined extensively by gap junctions. These junctions span the intercellular space at numerous points basal to the septate junction (Fig. 17). They are also found between muscular processes which lie on the mesoglea (Fig. 18) and between processes of each layer which meet within or cross the mesoglea (Fig. 19). A gap junction may also lie quite close to a septate junction (Figs. 17 and 22). When sectioned transversely, the gap junctions are short (usually 0.5 µ or less), occur in series, and are separated by short irregular dilations of the intercellular space (Figs. 18 and 20). On rare occasions one finds what appears to be an exceptionally long gap junction (Figs. 21 and 22). The cell membranes lie 30–40 Å apart within the junction (Fig. 18).

When Hydra are fixed in the presence of lanthanum hydroxide, the lanthanum permeates the gap junctions and appears as a 75-Å-thick line within transversely sectioned gap junctions (Fig. 22). Lanthanum is always retained in the gap junctions, although it is usually lost from the irregular intercellular spaces between adjacent gap junctions during processing of the specimens. In a few instances, however, the lanthanum is also retained within these spaces as well as within the gap junctions. When such areas are sectioned approximately parallel to the cell membranes, i.e., en face, the topographical and structural organization of the gap junctions is clearly revealed (Fig. 22). Each junctional region consists of numerous, tightly packed, rounded plaques surrounded by irregular pools of intercellular space. The plaques range from 0.15 to 0.5 µ in diameter. 65 individual plaques have been counted in an 8 µ² area. In this en plaque configuration, some plaques lie within 20 Å of each other (Fig. 22). Each plaque is encircled by a thin electron-lucent band ~40 Å-thick. The interior of each plaque consists of hexagonally packed subunits. Each subunit is clearly outlined by the lanthanum, and is ~85 Å in diameter. A central electron-opaque particle, ~20 Å in diameter, is visible in most of the subunits. As in vertebrate gap junctions, the subunits have a center-to-center spacing of 95–110 Å. The subunits are separated from the electron-lucent band by a relatively amorphous, lanthanum-filled zone 50–150 Å-thick.

**DISCUSSION**

From our observations we have drawn the following conclusions about the distribution of the intercellular junctions of Hydra. Septate junctions join the outer and lumenal surfaces, respectively, of
the epidermal and gastrodermal cells. While they completely encircle the apical regions of adjacent cells, their extent with respect to the short axis of the animal varies considerably. In some instances they are quite long and tortuous, while in others they are short and consist of only a few septa. Some junctions may run parallel to the outer or lumenal cell membranes for short distances.

Basal to the septate junctions, adjacent cells of each layer are joined extensively by numerous gap junctions in en plaque configuration. Gap junctional plaques also join the muscular processes in each layer as well as those which connect the layers across the mesoglea. While desmosome-like structures occur between muscular processes (Haynes et al., 1968), they are conspicuously absent from other areas of the cells. Tight junctions (zonulae occludentes) have not been found in *Hydra*.

**Morphology of the Septate Junction**

Since the initial description of the septate junction (Wood, 1959), several models of the septa have been suggested. Generally these models were similar, and, like Wood's original one, each proposed that the septa consisted of separate barlike plates. These plates were, depending upon the species, either parallel to each other (Wood, 1959; Wiener et al., 1964; Danilova et al., 1969), somewhat corrugated (Gilula et al., 1970), or organized into a honeycomb (Locke, 1965; Bullivant and Loewenstein, 1968; Danilova et al., 1969). Recent advances in preparative techniques such as uranyl acetate block staining (Karnovsky, 1967) and the use of electron-opaque intercellular...
The gap junctions are separated by irregular dilations of the intercellular space. Epidermis. X 70,000.

**Figure 20** A series of five short gap junctions (1–5), each less than 0.5 µ long, join two epidermal cells.

**Figure 21** Rarely, one encounters a long gap junction; this one is about 4 µ. Gastrodermis. X 68,000.

Tracers such as lanthanum hydroxide (Revel and Karnovsky, 1967) and ruthenium red (Luft, 1964) have provided an opportunity to examine the structure of the septate junction in greater detail. It has been possible to depict the three-dimensional structure of a septum as well as some interseptal relationships by utilizing the side length of the hexagon and by comparing the periodicity of the projections and the form of the backbone in the four different views. The four views used in the analysis were selected because they provide critical alignments of the projections and the backbone of the septa. Small deviations from these alignments produce thickened, blurred images of the septa. Essentially, each septum consists of a chain of hexagons, each of which is folded in chair configuration. V projections emanate from each of the corners of the hexagons and extend alternatively above or below each hexagon toward the adjacent septa. Two A projections join each hexagon to the cell membranes.

Considerable variation in interseptal relationships exists within a septate junction. Plane 1 views show that adjacent septa are inserted within the junction either inverted or parallel to each other with respect to the folds of their backbones (Figs. 4 and 5). Of 104 pairs of septa counted, 57 were in the inverted configuration. In addition, groups of three or more septa may be either parallel or inverted.

V projections often appear to connect adjacent septa (Figs. 3 and 4). The opportunity for such interseptal connections involves two factors: inverted versus parallel pairing of adjacent septa; and superimposition of the hexagons of adjacent septa (Fig. 2). Maximum opportunity for interseptal connections exists in two situations: (a) adjacent septa are inverted and their hexagons are superimposed (middle and lower septa of Fig. 2); and (b) adjacent septa are parallel and their hexagons are out of phase. Of course, such considerations are based on a rigid model that cannot encompass possible elastic properties or small irregularities in a septum. They nevertheless suggest considerable variation in interseptal connections and in the rigidity of the junction itself.
Morphology of the Gap Junction

The gap junctions of Hydra consist of rounded plaques, generally 0.5 μ or less in diameter. The term en plaque configuration has been chosen to denote the tight packing of the individual plaques which make up a gap junctional area. The en plaque configuration contrasts with the distribution of gap junctions in vertebrate tissues where individual junctions are more widely separated from each other. The shape of individual vertebrate gap junctions has not been determined, although there are suggestions that some may also be rounded plaques (Robertson, 1963; Kreutziger, 1968; McNutt and Weinstein, 1970).

FUNCTIONAL IMPLICATIONS OF THE INTERCELLULAR JUNCTIONS OF HYDRA

Intercellular Adhesion

The septate junctions as well as the gap junctions are undoubtedly of prime importance in maintaining topographical relationships within the two epithelial sheets of Hydra as the individual cells undergo drastic changes in shape during contraction and relaxation. The structure of the septa, their interseptal connections, and the manner in which they are attached to the cell membranes suggest that the septate junction is a site of firm intercellular adhesion. Gap junctions are also known to be sites of firm intercellular contact which resist osmotic (Brightman and Reese, 1969) and mechanical disruption (Gooenough and Revel, 1970). The en plaque configuration of the gap junctions suggests a firm adhesion of the more basal parts of the cells of Hydra.

Permeability Barriers

In several different systems (Revel and Karnovsky, 1967; Brightman and Reese, 1969) electron-opaque tracers such as lanthanum hydroxide have been demonstrated within gap junctions. These observations have suggested the existence of extracellular channels within the junction (Pappas et al., 1971) which are presumably permeable to water and small ions. The present study demonstrates that lanthanum hydroxide and ruthenium red readily penetrate the spaces in the lattice-like structure of the septate junction and gain access to the more basal intercellular spaces. However, in spite of these observations and the “open” appearance of the septa, several factors suggest that the septate junction may possess some barrier properties. (a) In preliminary studies, we have tested septate junctions in vivo by soaking living Hydra in horseradish peroxidase (mol. wt. 40,000, equivalent radius 25–30 A [Karnovsky, 1967]) or cytochrome c (mol. wt. 12,000, equivalent radius 15 A [Karnovsky and Rice, 1969]). (b) The spaces in the septal lattice may actually be filled by substances which are not revealed by our preparative methods. Ruthenium red, which stains acid mucopolysaccharides (Luft, 1964), may be staining components of the intercellular space rather than inertly filling a potential space in the lattice. There is some evidence to suggest that lanthanum hydroxide also stains or binds to some extracellular substances (Doggenweiler and Frenk, 1965; Lesseps, 1967; Overton, 1968). (c) If the hexagonal backbone and projections of a septa bear even a weak electrical charge, a septate junction consisting of a stack of 30 or more septa would present a considerable barrier to the movement of many substances through the junction. (d) Independent electrophysiological studies of Hydra (Josephson and Macklin, 1967, 1969) have demonstrated a high resistance across the body wall and suggest that a barrier to the flow of ions exists at some point in the path from the digestive cavity to the exterior.

Intercellular Coupling

To date, intercellular coupling has not been demonstrated in Hydra. However, the paucity of neural elements, especially in the body wall, suggests that such mechanisms may be important in contraction and relaxation of the animal. There are at least two factors which, from a morphological standpoint, suggest that the gap junction is better suited for intercellular coupling than the septate junction. The minimum intercellular distance between cells at the gap junction is ~30 A compared to ~200 A through the septal backbone. A 10–20-A intercytoplasmic channel (McNutt and Weinstein, 1970; Pappas et al., 1971)
A wide separates the subunits from the surrounding band. X 185,000.

units with their 20-A central electron-opaque particle. In each plaque, a relatively amorphous zone -100-

lucent band '40-A-thick. The interior of the plaques contains the typical hexagonally packed 85-A sub-

higher magnification. Each plaque is sharply delimited from the intercellular space by a thin electron-

seen at the left. Gastrodermis. Lanthanum hydroxide. X 59,000. Inset: The gap junctional plaques at

septate junction (SJ) which has been sectioned in plane 3. A few transversely sectioned gap junctions are

20), or one long junction as in plane

through this junctional area would show either a series of short gap junctions as in plane

ameter. Each plaque is surrounded by irregular pools of intercellular space(IS). Transverse sections

FIGURE 22 In the presence of extracellular tracers, face views reveal the organization of the gap junc-

tions of Hydra. The gap junctions are organized in rounded plaques ranging from 0.15 to 0.5 µ in di-

diameter. Each plaque is surrounded by irregular pools of intercellular space (IS). Transverse sections

through this junctional area would show either a series of short gap junctions as in plane AA' (see Fig.

20), or one long junction as in plane BB' (see Fig. 21). At the upper right, several plaques lie against a

septate junction (SJ) which has been sectioned in plane S. A few transversely sectioned gap junctions are

seen at the left. Gastrodermis. Lanthanum hydroxide. X 59,000. Inset: The gap junctional plaques at

higher magnification. Each plaque is sharply delimited from the intercellular space by a thin electron-

lucent band ~40-A-thick. The interior of the plaques contains the typical hexagonally packed 85-A sub-

units with their 20-A central electron-opaque particle. In each plaque, a relatively amorphous zone ~100-

A-wide separates the subunits from the surrounding band. X 185,000.

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