Studies on the Development of the Foregut in the Chick Blastoderm

2. The Morphogenetic Movements

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INTRODUCTION

The first of this series of papers (Bellairs, 1953) outlined the morphological changes occurring in the endoderm of the chick up to the stage of about ten pairs of somites; it also showed that the presumptive foregut area in the primitive streak stage blastoderm lies around the anterior end of the primitive streak, and at a slightly later stage around the head process. The present paper is concerned with the pattern of morphogenetic movements which occur in the endoderm during the early stages of foregut development.

METHOD

The technique involved the use of carbon marks upon the exposed endoderm of blastoderms grown dorsal side downwards in tissue culture by the watchglass method (Waddington, 1932; Bellairs, 1953). During the period of development investigated an expansion of the blastoderm as a whole took place over the plasma clot; the use of external reference points was therefore essential, although even with such aids it was not always possible to tell whether certain displacements of marked cells were in fact merely the expression of a general expansion or were due to a specific morphogenetic migration. Long straight lines of carbon were consequently used in most experiments; they were applied with a fine knife and placed either at right angles to the primitive streak and head process or parallel to them, and extended across the area opaca and on to the clot surface. In some cases splinters of glass were placed on the clot as external reference points. Each blastoderm was drawn to scale and the position of the mark plotted, both before and after incubation. The individual dots and lumps of carbon which composed each line frequently became broken up with the expansion of the blastoderm. A total of fifty-seven blastoderms have been used.

The terms L and h.p. have been employed throughout to signify the long or

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definitive primitive streak stage (as defined by Waddington, 1952, and Abercrombie, 1950) and the head process stage respectively. The following abbreviations are also used in the paper: p.s. for primitive streak; a.p.l. for area pellucida length.

RESULTS

1. Marks placed at right angles to the primitive streak or head process

Specimen No. 1 (L stage; p.s. 2.0 mm.; a.p.l. 2.6 mm.). Two parallel lines were placed across the blastoderm at right angles to the primitive streak (Text-fig. 1A), the anterior one being immediately in front of and touching the primitive node,

![Area Pellucida and Area Opaca](image1)

and the posterior one crossing the primitive streak half-way along its length. After 24 hours part of the anterior mark had become enclosed in the developing foregut. The carbon which formerly lay just anterior to the node had moved forward slightly and was found in the roof. The parts of the mark which originally lay immediately to either side, however, had moved posteriorly and were adherent to the developing foregut floor. The change in position which the hinder carbon line had undergone showed that an extensive backward migration had occurred along the posterior part of the primitive streak and in the area pellucida endoderm at either side of the midline.

Specimen No. 2 (L stage; p.s. 2.2 mm.; a.p.l. 2.8 mm.). A line of carbon was placed across the blastoderm at right angles to the primitive streak; it passed just behind the primitive node (Text-fig. 2A). After 24 hours a backward movement had again occurred, and had been confined to the area opaca and the regions
lateral to the primitive streak. There appeared to have been no movement of the mark where it crossed the primitive streak.

**TEXT-FIG. 2.** Specimen No. 2. Structures shown as in Text-fig. 1. A. Position of a carbon mark placed on the endoderm of an L-stage blastoderm. B. The same mark after 24 hours.

**TEXT-FIG. 3.** Specimen No. 3. Structures shown as in Text-fig. 1. A. Position of carbon marks placed on the endoderm of an h.p. stage blastoderm. B. The same marks after 5 hours. C. The same marks after 24 hours.

*Specimen No. 3 (h.p. stage; p.s. 2·0 mm.; h.p. 0·6 mm.; a.p.l. 3·1 mm.).* Two lines of carbon were placed across the head process and at right angles to it, one half-way along its length, and the other just touching the tip of the primitive node (Text-fig. 3A). *After 5 hours* a slight forward movement had taken place in the
region of the anterior line, but there was no evidence of any displacement of the hinder mark (Text-fig. 3b). *After 24 hours* some of the material of the anterior mark had become enclosed in the foregut (Text-fig. 3c). The more anterior part of it lay in the roof and had undergone a slight forward movement. The more posterior part was adherent to the foregut floor and had moved backwards. In the extra-embryonic area pellucida on either side of the head process the lines had been displaced backwards. The posterior mark showed that an extensive migration had taken place along the primitive streak and, to a lesser degree, in the regions on either side.

![Text-fig. 4](image)

**Text-fig. 4.** Specimen No. 4. Structures shown as in Text-fig. 1. A. Position of carbon marks placed on the endoderm of an *h.p.* stage blastoderm. B. The same marks after 4 hours. C. The same marks after 18 hours.

*Specimen No. 4. (h.p. stage; *p.s.* 1.8 mm.; *h.p.* 0.9 mm.; *a.p.l.* 2.8 mm.).* Two transverse marks were placed at right angles to the primitive streak, the anterior one being immediately anterior to the head process, whilst the posterior one was just in front of the node (Text-fig. 4a). *After 4 hours* part of the anterior mark had become enclosed in the developing foregut and appeared to have migrated slightly forward (Text-fig. 4b). *After 18 hours* (Text-fig. 4c) more of this mark had become enclosed in the foregut. The part which lay farthest forward was mainly adherent to the roof and had moved anteriorly since the first inspection.
Behind this a small clump of carbon was discovered on the floor at one side. Farther posteriorly still, carbon was found centrally in the foregut floor. At the level of the anterior intestinal portal particles were again found on the lateral border of the developing floor. In this region the mark had moved posteriorly, for it lay behind the external reference marks. The displacement of the posterior carbon line showed again that a backward movement had again occurred along the primitive streak and the adjacent area pellucida. A few marked cells in the midline, however, had apparently moved only a short distance posteriorly, an unusual occurrence.

Text-fig. 5. Diagram showing: A, a line of carbon across the presumptive foregut area; B, an early stage of foregut formation with the enclosed carbon in a V-formation; and C, a later stage with the enclosed carbon arranged in a diamond shape.

These four specimens are characteristic of 20 marked with transverse lines, 9 at the L stage and 11 at the h.p. stage. In every case a backward movement took place in the posterior part of the area pellucida; usually the maximum displacement was along the hinder half of the primitive streak. In specimens which were marked at the L stage across the anterior end of the primitive streak, regression was greatest in the regions just lateral to the midline (2 specimens) or at the edge of the area pellucida (4 specimens).
Specimen No. 2 demonstrates the relative immobility of the endoderm lying just behind the primitive node at the L stage. A similar result was shown by six other specimens marked in the same region. The forward movement which occurred in the head process region was less well marked than the displacement which took place at the posterior end of the area pellucida; yet in eight out of twelve specimens where marks were placed just anterior to the primitive node in the L stage, or across the head process in the h.p. stage, a forward movement was found to occur. Three of these specimens were examined every 4 hours after marking, and it was found that the forward movement not only took place in the flat presumptive foregut but was continued in the developing foregut itself. If development had not proceeded far the enclosed carbon was usually arranged in a V-formation (Text-figs. 1B, 4B; schematized in Text-fig. 5 A and B), the anterior medial part being in the roof, the more posterior lateral parts in the floor. With further development the mark on the presumptive floor at each side of the anterior intestinal portal was brought into the midline to meet its fellow from the opposite side (Text-fig. 4C). The linear carbon mark inside the foregut had at this stage become disrupted. Had it stayed complete it would presumably have been transformed from a V-shape to a diamond-shape (schematized in Text-fig. 5C).

2. Marks parallel to the primitive streak and the head process

a. Marks placed on the primitive streak endoderm. These marks were placed on the endoderm in the medial part of the presumptive foregut area (Bellairs, 1953). They thus lay on the presumptive foregut roof.

Specimen No. 5 (h.p. stage; p.s. 1·8 mm.; h.p. 0·5 mm.; a.p.l. 2·9 mm.). The head process and the anterior half of the primitive streak were covered with a single, continuous carbon mark (Text-fig. 6A). After 5 hours (Text-fig. 6B) the primitive node had regressed farther. The arrangement of the marks indicated that a mediolateral movement had occurred in the endoderm. After 8 hours (Text-fig. 6C) the embryonic axis had begun to form and the carbon was
distributed along the roof and the presumptive roof of the developing foregut. Towards the posterior end of the primitive streak a few of the marked cells had migrated farther laterally, whilst others had undergone the usual regression.

Ten specimens in all were marked in this way; they were examined and redrawn to scale every 2–3 hours. In each case a small mediolateral movement was found to have taken place in the endoderm. This was most evident in the mid-primitive streak region of the head process stage. This slight mediolateral movement seldom exceeded 0.3 mm. at either side of the primitive streak.

![Text-fig. 7. Specimen No. 6. A. Position of two carbon marks placed on the endoderm of an h.p. stage blastoderm. B. The same marks after 12 hours. Three pairs of somites have developed. C. Schematic diagram to show the arrangement of the carbon on the left side in the foregut region. The structure outlined is the head in ventral view. Broken lines show the mark in the foregut floor.](image)

**b. Marks placed lateral to the primitive streak.** These marks passed through the lateral borders of the presumptive foregut area (Bellairs, 1953), i.e. presumably the presumptive foregut floor.

**Specimen No. 6 (h.p. stage; p.s. 1.6 mm.; h.p. 0.5 mm.; a.p.l. 3.0 mm.).** Two lines of carbon were placed parallel to the primitive streak and head process and about 0.2 mm. to 0.3 mm. from it, one on either side (Text-fig. 7A). After 12 hours the area opaca had expanded and covered the external reference marks. A latero-medial movement appeared to have taken place in the foregut region, however (Text-fig. 7B). The arrangement of the carbon is shown diagrammatically in Text-
fig. 7c. The anterior part of each mark lay along the yolk-sac endoderm ventral to the head. It passed through the medial part of the anterior intestinal portal into the foregut floor and traces of it were found some distance forward. The marks were traced out of the lateral border of the anterior intestinal portal and continued posteriorly, one on either side of the developing somites.

*Specimen No. 7 (h.p. stage; p.s. 2·2 mm.; h.p. 0·7 mm.; a.p.l. 3·5 mm.).* Two parallel lines of carbon were placed at about 0·4 mm. from the primitive streak on either side (Text-fig. 8A). After 24 hours (Text-fig. 8B) a latero-medial movement had occurred on either side of the anterior part of the developing axis, the anterior part of each mark extending along the extra-embryonic endoderm ventral to the head and almost meeting its fellow in the midline. A small portion of each mark was enclosed in the foregut, but stretched a little farther anteriorly than the posterior end of that which remained on the yolk sac. Most of the enclosed carbon lay in the foregut floor, but some particles were found in the roof as well. In this place, however, a large clump of carbon adherent to the floor lay in the lumen of the foregut. It seemed likely therefore that the roof had become marked secondarily after the foregut had formed.

It is possible that the loss of continuity which occurred between that part of the mark which remained on the yolk sac and that which became included in the floor of the foregut was an artefact brought about by the stretching of the marked region. It seems more probable, however, that the arrangement of the carbon demonstrates an advance in development on that shown by specimen No. 6. Thus it may be that as each side of the foregut floor had become fused, level for
level with the other side, the floor in the midline had lost contact with the extra-embryonic endoderm with which it was previously continuous, the splanchnic mesoderm becoming interposed between floor and yolk-sac endoderm (Text-fig. 8 b and c).

Eighteen specimens were marked in this way and all demonstrated the latero-medial movement in the endoderm. These movements appeared to be closely correlated with the actual ventral closure of the gut itself, since the longitudinal marks were displaced medially as they became enclosed in the floor of the developing organ. Inspection of specimen No. 6 suggests that the carbon which came to lie ventral to the anterior part of the head in the yolk-sac endoderm was derived from the area pellucida anterior to the presumptive foregut area as determined by Bellairs (1953). The more posterior, medially situated yolk-sac endoderm, however, appears to have arisen from a more posterior and lateral position (specimen No. 7). In fifteen of these specimens which were examined every 2 hours during the course of the experiment it was found that no mediolateral displacement took place at the edges of the presumptive foregut area prior to ventral closure of the foregut. On the other hand, in two specimens in which longitudinal marks were placed well outside the presumptive area a mediolateral movement was found to occur; each mark came to lie along the area pellucida border and remained there. In eight cases the posterior ends of the marks on the area opaca moved laterally, and in four of these a similar movement took place in the anterior end. In two specimens only was there a convergence toward the midline of the endoderm at the posterior end of the primitive streak. It is possible that these mediolateral movements in the area pellucida were merely an expression of the lateral expansion of the blastoderm as a whole.

The relationship of the transverse movements just described and the longitudinal migrations shown by the experiments using transverse marks will be discussed later. To investigate more fully the mechanism of closure of the foregut, however, a further series of marking experiments are described below. In the head-fold stage a V-shaped ridge of endoderm forms the ventral border of the anterior intestinal portal and projects backwards on either side of it. It was not clear whether the latero-medial movement simply directed the two arms of the ridge as such into the midline where they joined to form foregut floor and yolk-sac roof, or if in addition there was a rolling in of cells over the ridge; in other words, it was not known whether the ridge represents the limit of the presumptive foregut or not. This problem was tackled by additional marking.

3. Marks placed on the ridge

Specimen No. 8 (Head-fold stage; p.s. 1.9 mm.; h.p. 1.0 mm.; a.p.l. 3.6 mm.). Four small carbon marks were placed on the endodermal ridge bordering the anterior intestinal portal (Text-fig. 9A). They were inspected and drawn at intervals of 2 hours. After 24 hours a well-proportioned embryo had formed, and the
carbon lay on the yolk-sac endoderm. None of the marks had become enclosed (Text-fig. 9B). The two which were placed lateral to the anterior intestinal portal were subsequently found in a medial position and were somewhat elongated. The two marks which originally lay on the ventral (anterior) border of the ridge had, however, moved only slightly farther medially.

**Text-fig. 9.** A. Specimen No. 8. Position of four carbon marks placed on the endoderm around the anterior intestinal portal. B. The same marks after 24 hours. The marks all lie on the yolk-sac endoderm. C. Specimen No. 10. Position of five carbon marks placed on the endoderm around the anterior intestinal portal. D. The same marks after 24 hours. Only one mark has become enclosed in the foregut (diffuse shading).

*Specimen No. 9* (Early embryo with 2 pairs of somites; p.s. 2.2 mm.; h.p. 1.7 mm.; a.p.l. 4.0 mm.). Five marks were placed on the endodermal ridge around the anterior intestinal portal (Text-fig. 9C). They were inspected and drawn every 2 hours. *After 24 hours* only one mark had become included, and that had originally been placed on the extreme edge of the ridge (Text-fig. 9D).

Nine specimens were marked in this way, and in only two cases (specimen No. 9) did there appear to be a rolling in of a mark over the ridge. Marks placed on the ventral border of the ridge moved only slightly medially. Marks placed on the lateral parts of the ridge, however, were directed bodily into the midline, where they were subsequently found in the yolk-sac endoderm. Some elongation of such marks in an antero-posterior direction was frequent. It seems therefore that, on either side, the lateral limits of the presumptive foregut area coincide with the ridge.

**DISCUSSION**

Waddington (1952) has drawn attention to the fact that distortion of morphogenetic movements may occur when experiments are made like the present ones in tissue culture, even though an apparently normal embryo develops. For this reason it is unfortunate that direct marking of the endoderm *in ovo* is at present technically impossible. A second disadvantage of the method is that carbon particles, though excellent when used for marking a small group of cells (Bellairs, 1953), are not completely satisfactory when a large tract of the blastoderm
is to be covered. In addition to the discontinuities which develop between individual clumps of carbon, it is difficult with such extensive marks to prevent some of the many granules present from becoming dislodged from the endoderm (e.g. specimen No. 7). Whilst these are frequently washed away at fixation, their presence may lead to error in interpretation. Despite these difficulties, the present results have been obtained with considerable regularity and receive support from earlier observations (Pasteels, 1937; Spratt, 1937; Bellairs, 1953).

The movements which occur in the endoderm in the earliest stages in the formation of the foregut may be classified broadly as:

1. 'Two-dimensional movements', that is the shiftings of tissues which take place more or less in the original plane of the endoderm (Text-fig. 9, unbroken arrows). These movements consist of migrations of groups of cells in the presumptive foregut roof and in the hinder part of the area pellucida. In addition, the blastoderm as a whole expands radially.

2. 'Three-dimensional movements' (Text-fig. 9, broken arrows), that is the movements which ultimately lead to folding and ventral closure of the foregut.

In the experiments described above the following 'two-dimensional' movements have been identified. Firstly, there is a forward movement of the endoderm in the developing head process region; this is illustrated by specimens No. 1 and No. 3. A small region toward the anterior end of the primitive streak in the L stage, however, appears to move neither anteriorly nor posteriorly, as in specimen No. 2. Specimen No. 1 illustrates that the endoderm beneath the anterior border of the primitive node is not included in this area but migrates forward.

Secondly, there is an extensive regression in the endoderm of the posterior half of the area pellucida, some of the midline cells moving as much as 1 mm. from the middle of the primitive streak to its posterior end. The regions at either side of the midline undergo a similar movement, though usually not so extensively (20 specimens, e.g. Nos. 1, 3; and 4).

Thirdly, some evidence has been presented for a slight mediolateral movement in the endoderm on either side of the primitive streak (e.g. specimen No. 5). It is possible that one or more of these movements may be responsible for, or contributory to, the thinning of the presumptive foregut roof which takes place about this time (Bellairs, 1953).

Fourthly, there is a continual radial expansion of the blastoderm as a whole as it spreads over the yolk. This is incorporated in, and affects, all the other tissue movements occurring in the blastoderm. In the endodermal layer it is demonstrated especially by certain mediolateral movements described in section 2b of the results.

Lateral to the presumptive roof region there is an oblique and backwardly directed 'three-dimensional' movement at each side in the area pellucida endoderm (Text-fig. 10). This has been deduced from a study of the transverse and
longitudinal shifts of carbon marks which have been placed longitudinally and transversely respectively. Lying originally in the flattened endoderm, the tissues which are destined to form the floor of the foregut are gradually swung medioventrally by the oblique movements. Thus the latter, which at first are of a 'two-dimensional' character, gradually become 'three-dimensional.'

Text-fig. 10. Diagram showing the morphogenetic movements occurring in the area pellucida endoderm during foregut formation. Broken arrows show 'three-dimensional' movements. Unbroken arrows show 'two-dimensional' movements. The stippled region shows developing foregut. Thick black lines show the position of head process and primitive streak.

The first steps in the formation of the foregut in the early head-fold stage embryo are probably due to the forward migration in the midline combined with the backwardly directed oblique movement of the material on either side. It is probable that the forward movement results in the accumulation of more endoderm at the anterior end of the head process than can be accommodated in a single flattened sheet. Such a situation could lead to the development of a fold of the tissue layer; this would be crescentic, arching forward medially and taper-
ing out laterally (Text-fig. 10). Similarly, the material brought in from the sides by the oblique movements would probably result in the formation of folds at right angles to their direction. The two oblique folds and the transverse fold would thus enclose a small diverticulum, the anterior end of the foregut. Because of the close fusion between the medially situated endoderm and the overlying mesoderm (Adelmann, 1922) the forward moving tissue would tend to stay dorsal to the material brought in from the sides; the latter lies ventral to loose

Text-fig. 11. Diagram of two stages in the ventral closure of the foregut showing the importance of the 'three-dimensional' movements. The endoderm is seen from its ventral side. Broken arrows represent 'three-dimensional' movements. The anteriormost one on the left side and the two most anterior on the right show oblique movements which have already taken place. Unbroken arrows show 'two-dimensional' movements. The curved broken lines indicate the position of the foregut which is concealed by the yolk-sac endoderm.
mesenchyme. The posterior border of the endodermal pocket formed in this manner would be horseshoe-shaped with backwardly projecting arms, that is, it would have the characteristic outline of the ridge which flanks the anterior intestinal portal.

As development proceeds, the oblique movements take place at progressively posterior levels and in this way the ventral closure of the foregut gradually spreads backwards (Text-fig. 11). Marks placed on the ventral lip of the anterior intestinal portal (see section 3 of the results) show that there is no rolling in of cells medially over the ridges which extend back from the anterior intestinal portal; that is, the oblique movements direct the ridges bodily into the midline. Here they fuse together to form the keel of the foregut floor and this becomes separated from the subjacent extra-embryonic area pellucida endoderm, the two sides of the latter also becoming continuous. The three-dimensional oblique movement merges into the two-dimensional longitudinal movement in the posterior end of the area pellucida. This backward movement is part of the mass migrations of endodermal cells which take place in the hinder part of the blastoderm, marks placed in the middle of the area pellucida being subsequently discovered at its posterior borders (these are among the ‘two-dimensional’ movements described above). The absence of the oblique movements posteriorly explains why in an embryo with several pairs of somites the foregut closes ventrally only in the anterior half of the area pellucida.

The oblique movements believed to be responsible for the ventral closure of the foregut do not appear to have been described before. The displacements occurring in the endoderm at the hinder end of the area pellucida, however, have not escaped notice. Pasteels (1937) carried out vital marking experiments using vital dyes in ovo. Where the mark remained a discreet unit, a movement involving all the layers was deduced; that is, these displacements were occurring in the endoderm as well as in the superficial layers. Although Pasteels’s schemes deal primarily with blastoderms at the primitive streak and earlier stages, he includes one diagram representing the h.p. stage. The combined movements shown in this map consist essentially of a backward extension of the posterior end of the area pellucida. This receives full support from the present work. In Pasteels’s map there is a convergence towards the midline at the extreme posterior end of the area pellucida. This phenomenon occurred also in my specimens as in two cases referred to in section 2b of the results. Usually, however, the marks placed in this region were found to have moved laterally.

The extensive backward movement which I have suggested takes place along the endoderm beneath the primitive streak is represented by Pasteels as a phenomenon of the superficial layer only, although his fig. 17 (specimen 14) is strongly suggestive of a regression having occurred in the endoderm. Against this may be placed the evidence of Bellairs (1953), who reported that in certain specimens endoderm cells marked with carbon particles as they lay in the posterior half of the primitive streak region (actually in area F. 3 in the terminology used) were
sometimes subsequently found at the posterior end of the area pellucida, and
the similar findings of Spratt (1947) who marked blastoderms with Nile blue sul-
phate and neutral red.

It is possible that in the normal embryo some of the mass movements of the
mesoderm and endoderm are similar at these stages and take place simulta-
aneously. Unfortunately, however, despite the valuable investigations of Gräper
(1929), Wetzel (1929), Pasteels (1937), and Spratt & Condon (1947), there is still
some doubt as to the exact course taken by the migrating mesoderm during the
early stages of organ formation. Pasteels (1937) and Spratt (1947) have given
evidence of the backward migration of the primitive node and of the regions
lateral to the primitive streak, and Spratt believes that this is contemporaneous
with that of the endoderm. He carried out a number of experiments using vital
dyes in a manner similar to that of Pasteels (1937) and reported that at least along
the primitive streak itself there seemed to be 'no differential displacement of one
layer relative to another'.

During the backward movement the endoderm is so closely applied to the
mesoderm that a simultaneous movement of the two layers might be expected.
There is not, however, a complete correspondence of movement between the
mesoderm and endoderm during regression, for whereas the primitive node is
involved in the backwards migration of the mesoderm (Wetzel, 1929; Pasteels,
1937; Spratt, 1947), the present experiments suggest that the endoderm of that
level remains in relatively the same place.

Certain deductions as to the movement of the anterior part of the splanchnic
mesoderm may also be made as a result of the present work. It seems likely from
the study of serial sections that the close association which exists between the
endoderm and the splanchnic mesoderm is retained throughout this period.
Except in the region of the cardiac vesicles the contours of the thickened gut
wall are closely followed by those of the similarly thickened splanchnic meso-
derm at all stages in the formation of the closed gut. It is not improbable, there-
fore, that the two layers undergo simultaneous and identical movements; that is,
the oblique lateral movement is common to both.

The forces which actually initiate and control the tissue movements in the
chick blastoderm at this stage are but little understood. The close association of
the developing head fold and the anterior end of the foregut is well known and
has led many authors to imply that the presence of one is responsible for that of
the other, e.g. Lillie (1952) states: 'The head fold thus produces an internal bay
in the endoderm, the beginning of the Foregut.' The independence of the de-
velopment of the foregut and the formation of the head fold has, however, been
demonstrated (Waddington & Cohen, 1936; Abercrombie & Waddington, 1937)
and I have obtained specimens which confirm it. A further point is that, even
were the head fold responsible for mechanically initiating foregut formation,
some other influence must also be sought, since the ventral closure of the foregut
rapidly outstrips the backward extension of the head fold.
SUMMARY

1. The morphogenetic movements which take place in the endoderm of the chick during foregut formation have been traced by means of carbon marking on blastoderms explanted in vitro.

2. Two types of movement are distinguished, called ‘two-dimensional’ and ‘three-dimensional’, the former occurring in the original plane of the endoderm, the latter folding certain regions medio-ventrally to form the floor of the foregut.

3. The most anterior tip of the foregut is believed to be formed as a pocket between two sets of opposing movements in the endoderm: (a) a forward, two-dimensional movement beneath the head process, and (b) an obliquely backward, three-dimensional movement on either side.

4. During the formation of the foregut the oblique movements result in a U-shaped ridge in the endoderm bordering the anterior intestinal portal. These movements spread progressively backwards and result in the two limbs of the ridge being brought together in the midline, where they fuse and thus gradually close off the cavity of the foregut ventrally from that of the yolk sac.

5. Some forward movement takes place at the anterior end of the developing foregut.

6. In the posterior half of the area pellucida there are extensive displacements of endoderm cells in a posterior direction.

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REFERENCES


