



动物胚胎学

Embryology of animals

- 胚胎学 (embryology) 是研究动物个体发育过程中形态结构及其生理功能变化的科学。
- 个体发育包括生殖细胞的起源、发生、成熟、受精、卵裂、胚层分化、器官发生，直至发育为新个体，以及幼体的生长、发育、成熟、衰老和死亡。

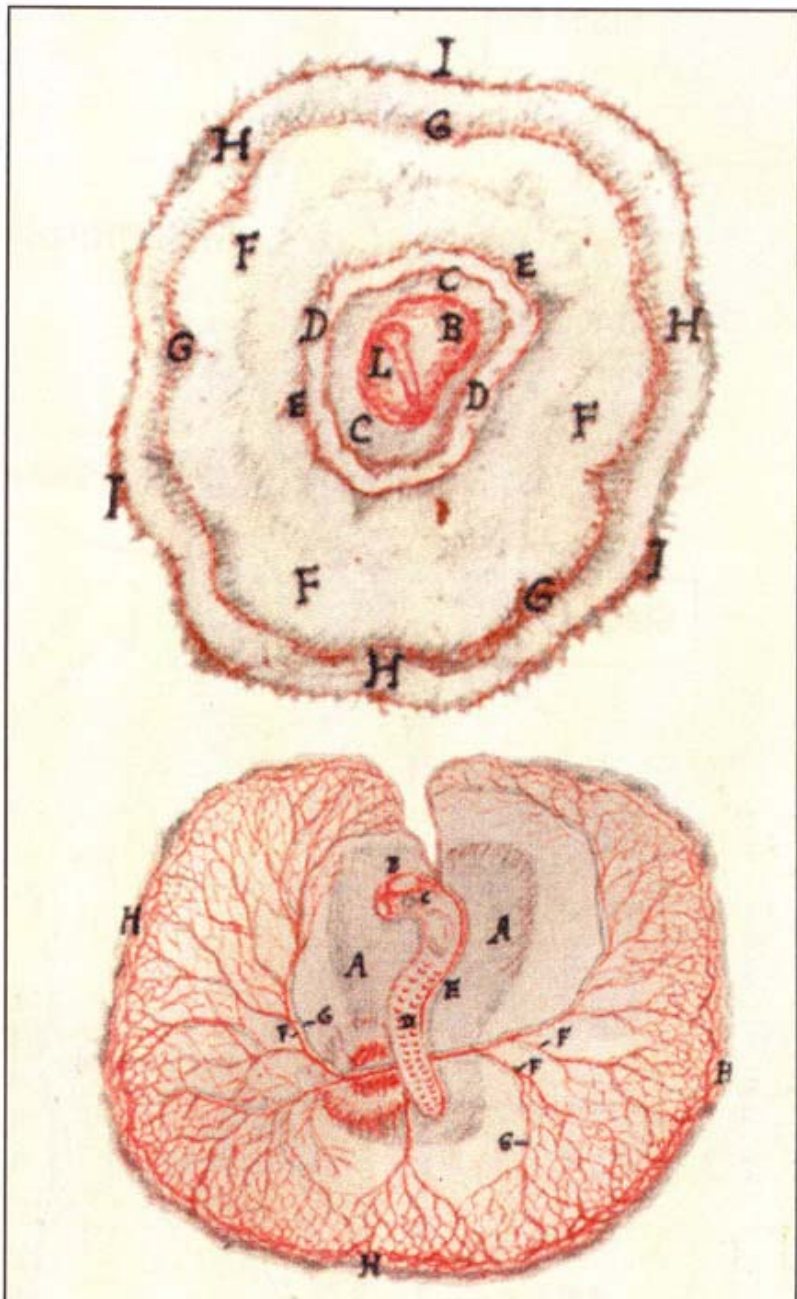


Fig. 1:4 Malpighi's description of the chick embryo. The figure shows Malpighi's drawings, made in 1673, depicting the early embryo (top), and at 2 days' incubation (bottom). His drawings accurately illustrate the shape and blood supply of the embryo. Reprinted by permission of the President and Council of the Royal Society.

**17世纪，意大利胚胎学家
Marcello Malpighi观察到的
鸡胚**



Fig. 1.5 Some preformationists believed that a homunculus was curled up in the head of each sperm. An imaginative drawing, after Nicholas Hartsoeker (1694).

17世纪，精原学说的代表人物Nicholas Hartsoeker所想像的精子中的微型人

法国科学家Bonnet(1745)提出胚胎发育套装论

3、Mosaic and Regulative Development

19世纪80年代，Weismann提出了mosaic development学说：合子中的大量特殊因子在细胞分裂中不均等分配，导致了不同细胞向不同命运的发育。

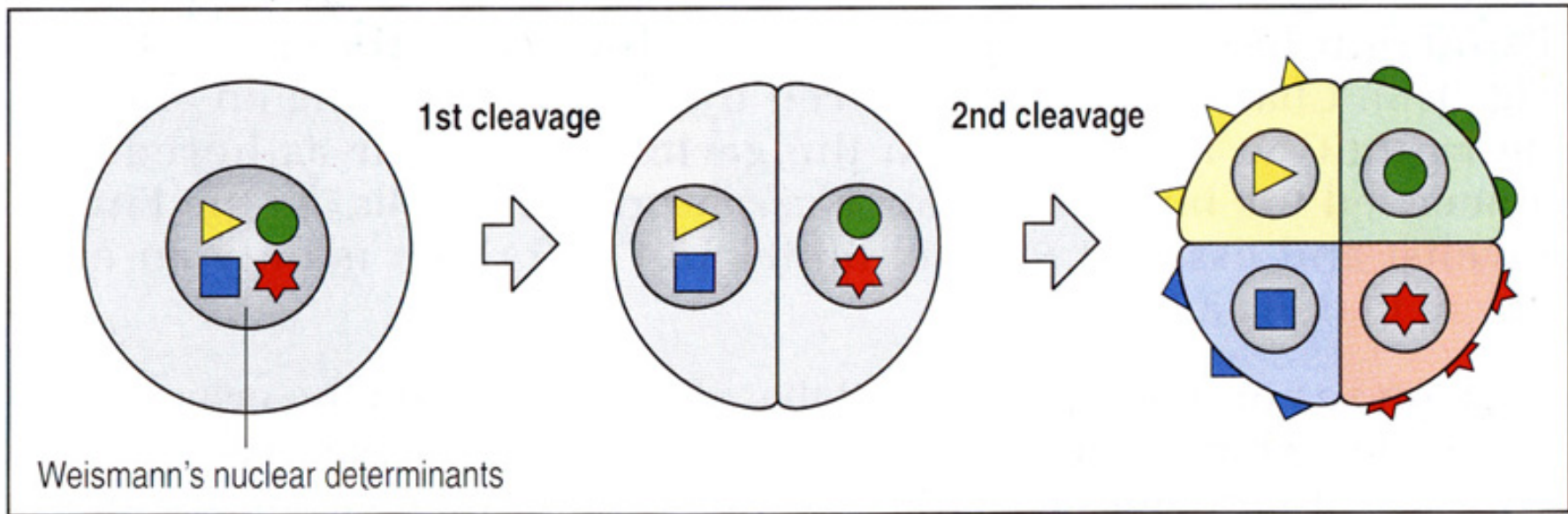


Fig. 1.7 Weismann's theory of nuclear determination. Weismann assumed that there were factors in the nucleus

that were distributed asymmetrically to daughter cells during cleavage and directed their future development.

3、Mosaic and Regulative Development(续)

支持嵌合体学说的实验证据：**Wilhelm Roux**的实验：

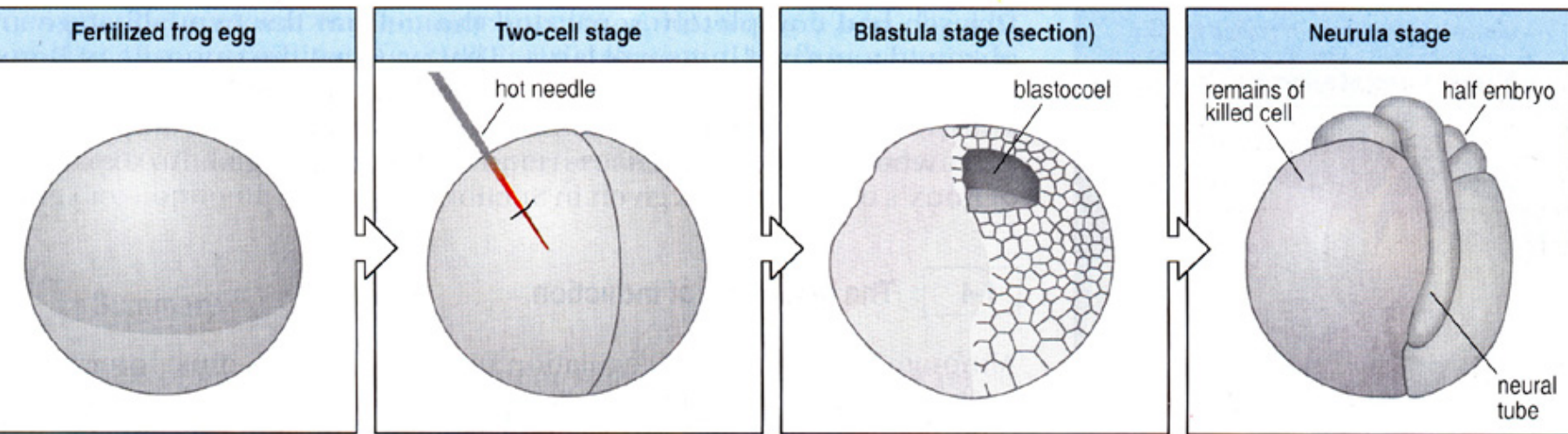


Fig. 1.8 Roux's experiment to investigate Weismann's theory of mosaic development. After the first cleavage of frog embryo, one of the two cells is killed by pricking it with a hot needle; the other remains undamaged. At the blastula stage the undamaged cell can be seen to have divided as normal into many cells that fill half of the embryo.

The development of the blastocoel is also restricted to the undamaged half. In the damaged half of the embryo, no cells appear to have formed. At the neurula stage, the undamaged cell has developed into something resembling half a normal embryo.

3、Mosaic and Regulative Development(续)

Wilhelm Roux的同事Hans Driesch的下述实验表明，胚胎具有在局部被排除或受损伤后仍正常发育的能力，即胚胎发育是可调节的。

Normal development of sea urchin larva from two-cell stage



Driesch's separation of cells at two-cell stage resulted in the death of one cell.
The surviving cell developed into a small but otherwise normal larva



Fig. 1.9 The outcome of Driesch's experiment on sea urchin embryos, which first demonstrated the phenomenon of regulation. After separation of cells at the two-cell stage, the remaining cell develops into a small, but whole, normal larva. This contradicts Roux's earlier finding that if one of the cells of a two-cell frog embryo is damaged, the remaining cell develops into a half-embryo only (see Fig. 1.8).

1924年，Hans Spemann和Hilde mangold的移植实验表明，胚胎的一种组织可以指导另一种相邻组织的发育。

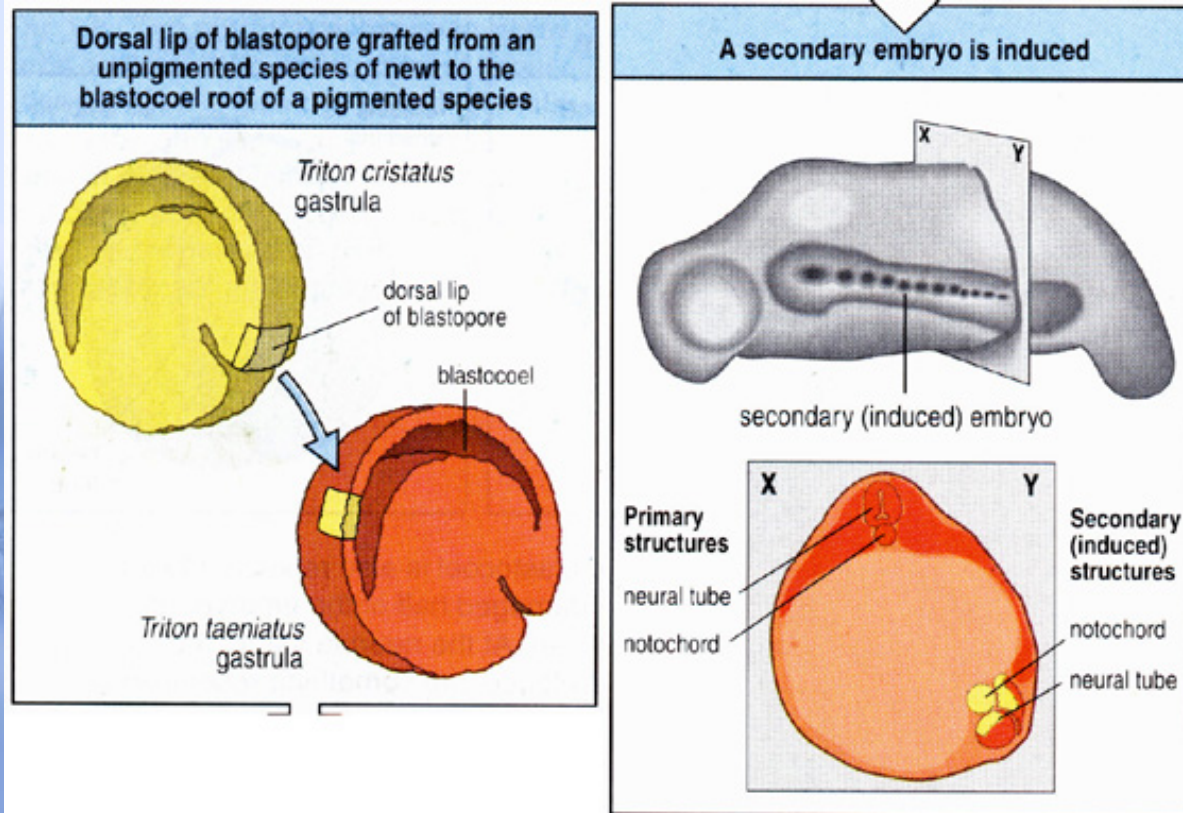


Fig. 1.10 The dramatic demonstration by Spemann and Mangold of induction of a new main body axis by the organizer region in the early amphibian gastrula. A piece of tissue (yellow) from the dorsal lip of the blastopore of a newt (*Triton cristatus*) gastrula is grafted to the opposite side of a gastrula from another, pigmented, newt species (*Triton taeniatus*, pink). The grafted tissue induces a new body axis containing neural tube and somites. The unpigmented graft tissue forms a notochord at its new site (see section in lower panel) but the neural tube and the other structures of the new axis have been induced from the pigmented host tissue.

- 分胚前发育、胚胎发育和胚后发育
- 胚前发育研究生殖细胞的起源、配子的发生、形成和成熟，到形成单倍体的精子和卵子
- 胚胎发育是指从受精到分娩
- 胚后发育包括出生的幼体的生长发育、性成熟、体成熟，以及以后的衰老和死亡
- 胚胎学主要研究胚前发育和胚胎发育

- 近来，人工授精、体外受精、胚胎移植、胚胎冷冻、性别鉴定、胚胎细胞和体细胞克隆、胚胎干细胞等成为胚胎学的热点。

学习提纲

- 两性生殖细胞的形成、结构及成熟
- 精子获能
- 受精
- 卵裂
- 附植
- 原肠胚与胚层形成
- 中胚层的形成
- 胚层分化与中轴器官的形成
- 胎膜
- 胎盘

一、生殖细胞与受精

- (一) 精子的形成与结构
- (二) 卵子的形成与结构

原生殖细胞

- Primordial germ cell, PGC
- 生殖细胞的前体细胞称原生殖细胞，原生殖细胞经迁移，进入发育中的生殖腺原基（genital anlage）分化为生殖细胞。

(一) 精子的形成与结构

■ 1、精子在睾丸曲精小管形成

- 雄性动物原生殖细胞到达生殖嵴后生殖腺分化睾丸，精原细胞首先分裂产生A型精原细胞，有丝分裂产生B型精原细胞。B型精原细胞再分裂，并生长变大形成初级精母细胞，后者进入减数分裂。每一初级精母细胞经历第一次减数分裂产生一对次级精母细胞，后者完成第二次分裂产生单倍体的精子细胞。

- 精子细胞是一圆形、无尾的细胞。精子细胞经过一系列变化后，由圆形逐渐分化转变为蝌蚪形的精子，这一过程称为精子形成。
- 首先，染色质极度浓缩，核变长并移向细胞的一侧，构成精子的头部。由高尔基复合体形成的顶体泡以后逐渐增大，并凹陷成为双层帽状覆盖在精子核的头端，形成顶体。中心粒形成精子尾巴，尾巴将伸入曲细精管腔中。在精子发生的后期，剩余的细胞质被丢弃，而线粒体则聚集于近段轴丝的周围，盘绕成螺旋形构成线粒体鞘。

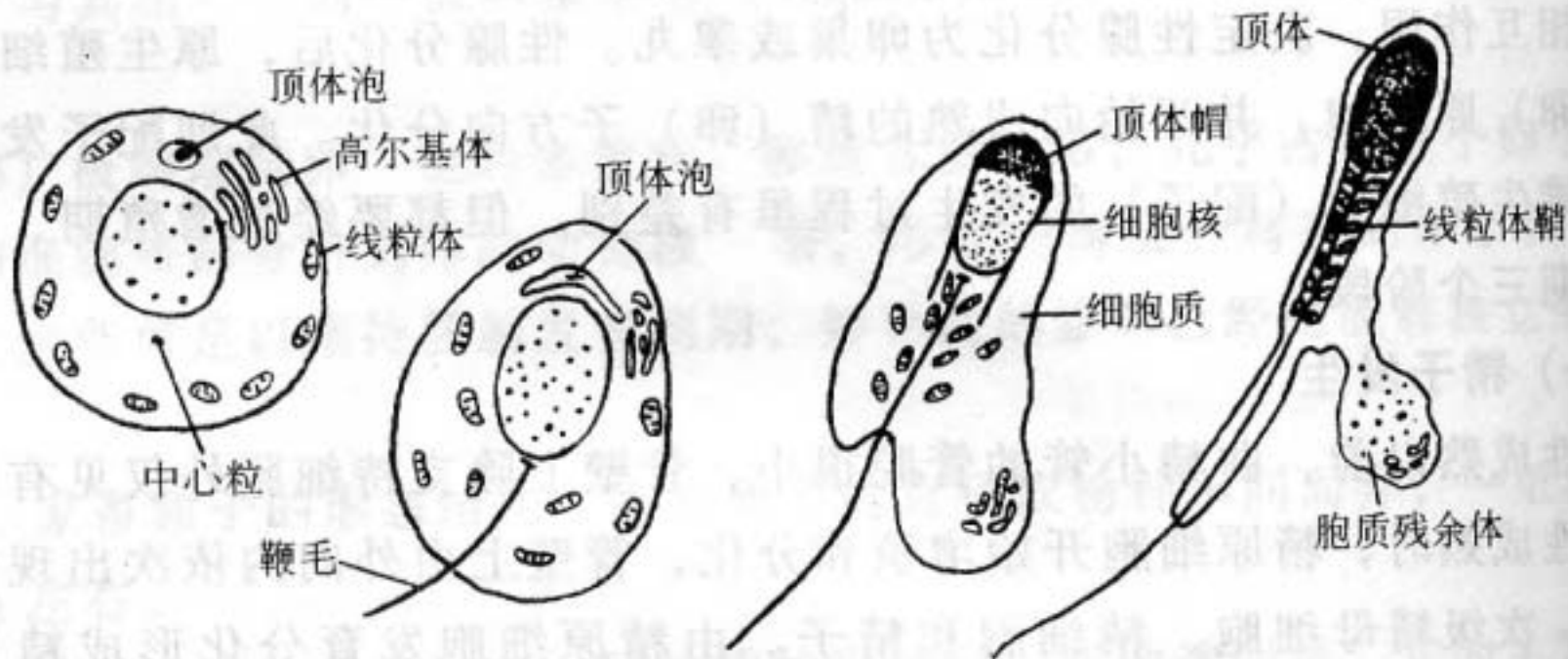


图 20-3 精子成形的过程

(绘自王铁恒等, 1989)

精子的发生

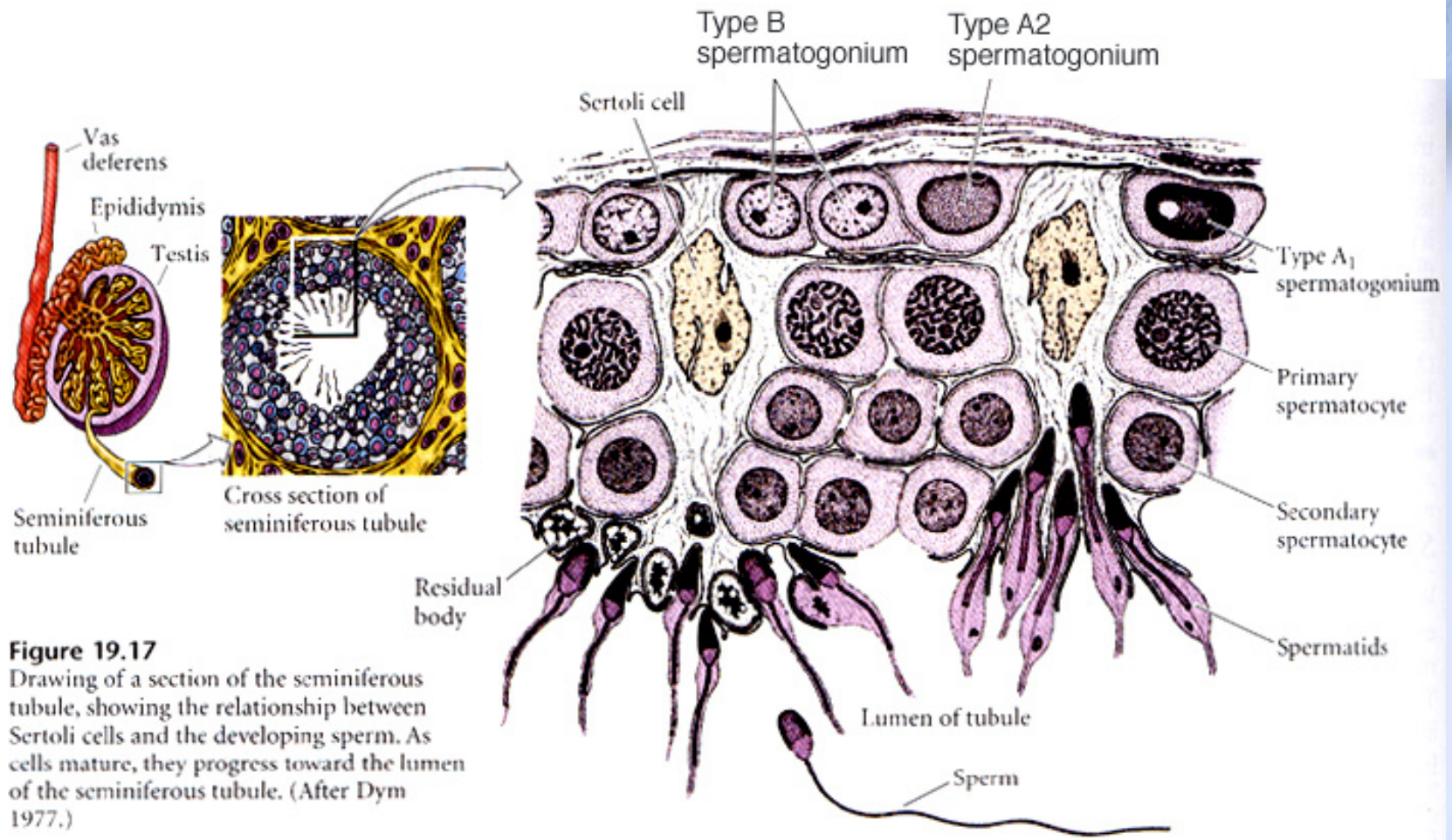
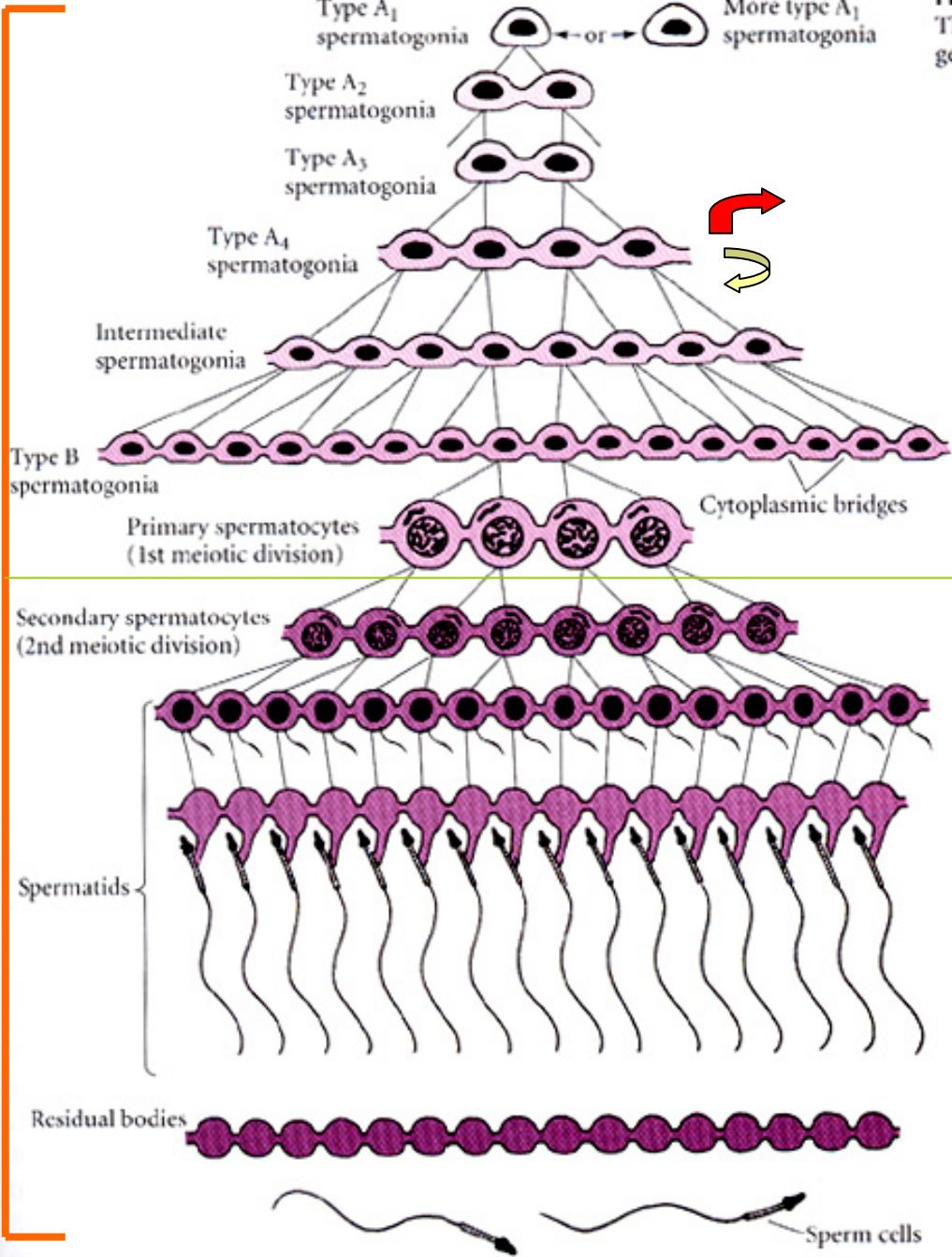


Figure 19.16
The formation of syncytial clones of human male germ cells. (After Bloom and Fawcett 1975.)



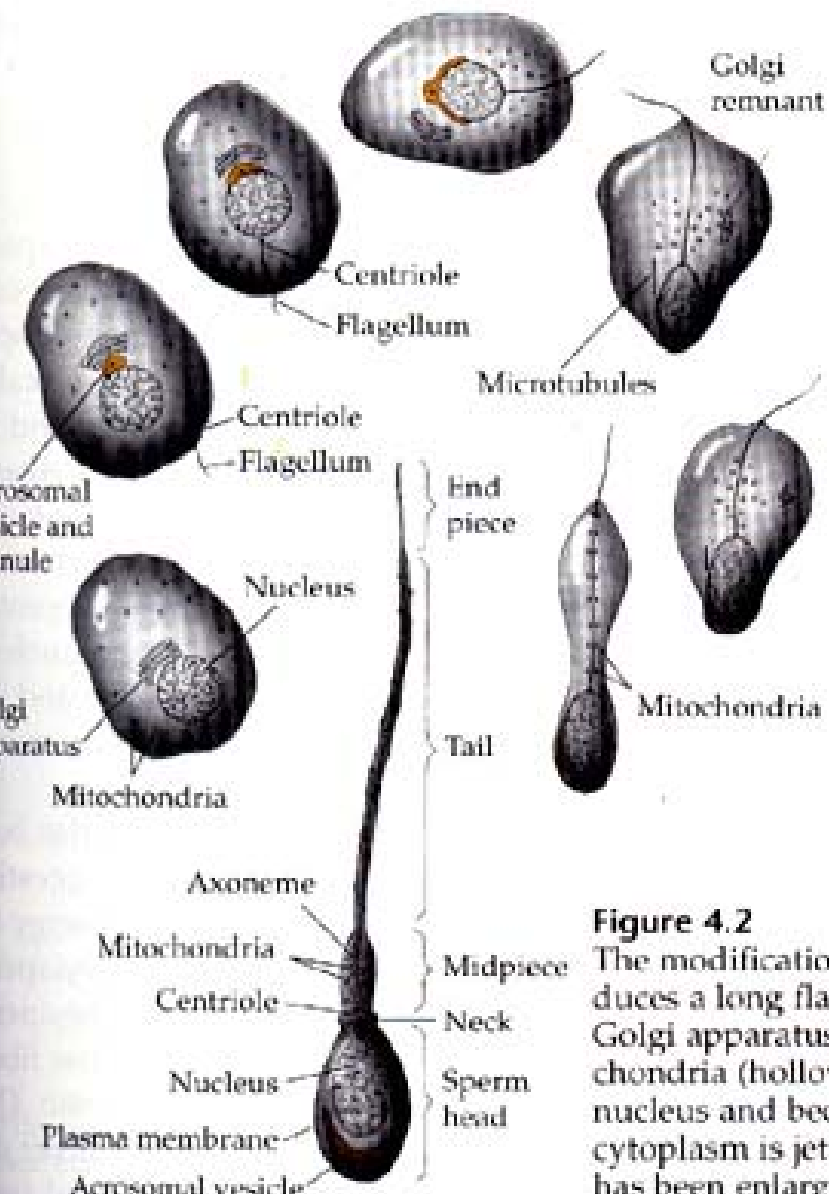


Figure 4.2

The modification of a germ cell to form a mammalian sperm. The centriole produces a long flagellum at what will be the posterior end of the sperm, and the Golgi apparatus forms the acrosomal vesicle at the future anterior end. The mitochondria (hollow dots) collect about the flagellum near the base of the haploid nucleus and become incorporated into the midpiece of the sperm. The remaining cytoplasm is jettisoned, and the nucleus condenses. The size of the mature sperm has been enlarged relative to the other figures. (After Clermont and Leblond, 1959)

2、精子的形态和结构

- 家畜的精子形态各异，长度在55—75um左右，主要由头部、颈部和尾部构成。尾部从前到后又可分为中段、主段和末段。

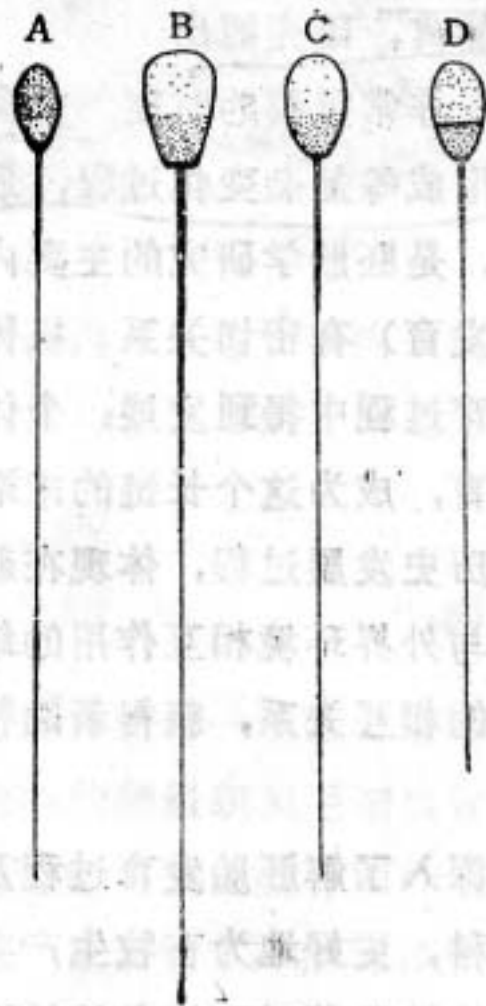


图 11—1 各种家畜的精子

A. 马 B. 牛 C. 绵羊 D. 猪

(1) 头部

- 精子头部由细胞核和顶体组成
- 细胞核主要由高度致密化的染色质构成
- 顶体为单单位膜包的囊状结构，富含透明质酸酶等。
- 当精子发生顶体反应时释放这些酶，有利于精子通过卵外的各层结构。

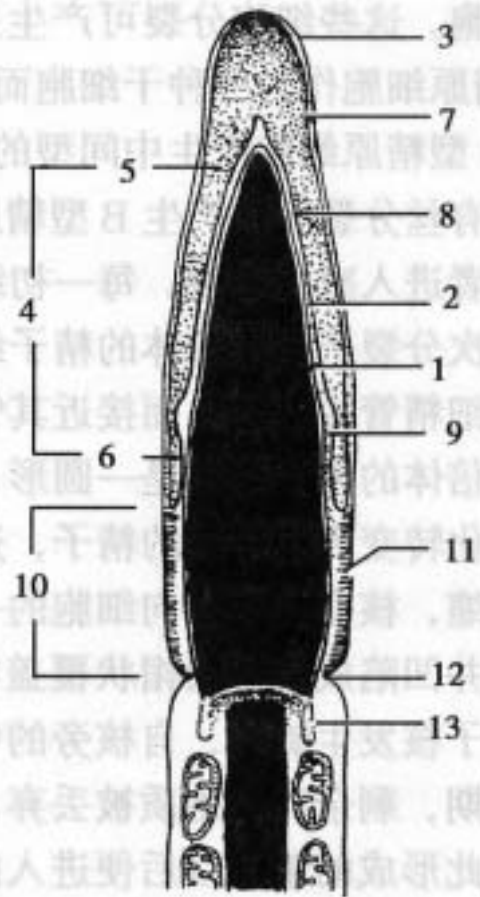


图 11-3 精子头部结构模式图

1. 核 2. 核膜 3. 质膜 4. 顶体
 5. 顶体帽 6. 赤道段 7. 顶体外膜
 8. 顶体内膜 9. 顶体下物质
 10. 后顶体区 11. 后顶体致密层
 12. 后环 13. 残余核膜

(2) 颈部

- 介于头部和尾部之间，从近端中心粒起到远端中心粒止。近端中心粒横位附着于核底部的浅窝中，远端中心粒则变为基粒，由它产生精子尾部的轴丝。
- 颈部最易受损破坏，使头尾分离。

(3) 尾部

- 尾部分为中段、主段和末段三部分
- 精子尾部的轴丝由中央的2条单根纤维和外围9对纤维构成。
- 尾部中段轴丝外还有自颈部延续而来的9条粗纤维纵行排列;再外由螺旋形排列的线粒体鞘包围。
- 中段是精子活动的能量供应中心，线粒体内含有精子氧化代谢的各种酶。
- 主段是尾部最长的部分，线粒体鞘消失
- 末段为精子最后的一段，仅由中央的轴丝和外围的质膜构成。

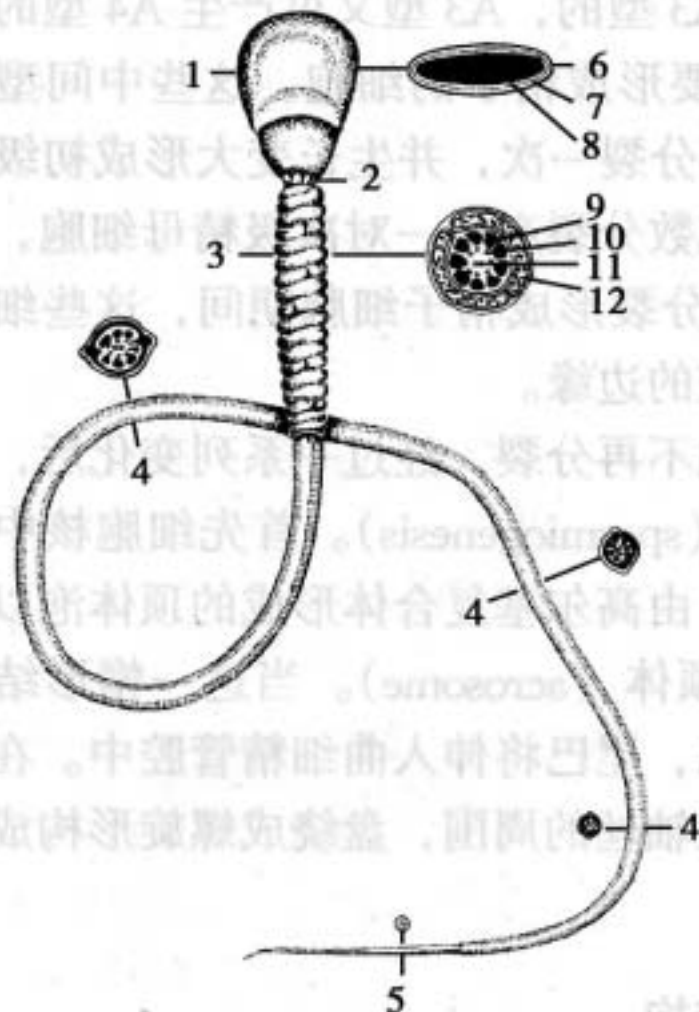


图 11-2 精子外形及其各部切面模式图

1. 头部 2. 颈部 3. 尾部中段 4. 尾部主段
 5. 尾部末段 6. 细胞膜 7. 顶体 8. 细胞核
 9. 周围 9 根粗丝 10. 9 对内部纤丝 11. 中

精子的运动能力

- 精子尾部的节律性收缩，使精子绕纵轴旋转前进，牛精子尾部每秒钟摆动10次，在生理盐水中前进10um左右，而在子宫颈黏液中前进较快
- 家畜的精子在母畜生殖道内，一般只能生存1—2天，马精子生存时间较长，可达5—6天，一直保持受精能力
- 精液冷冻技术，精子在-78~-196 下长期保存

(二) 卵子的形成与结构

■ 1、卵子的形成

■ (1) 增殖期

- 来源于原生殖细胞的卵原细胞经多次有丝分裂，数目显著增多而成为初级卵母细胞的过程。经过细线期、偶线期和粗线期而到达双线期。
- 大多数家卵原细胞的增殖期都于接近胎儿出生前结束，出生后不再形成新的初级卵母细胞。

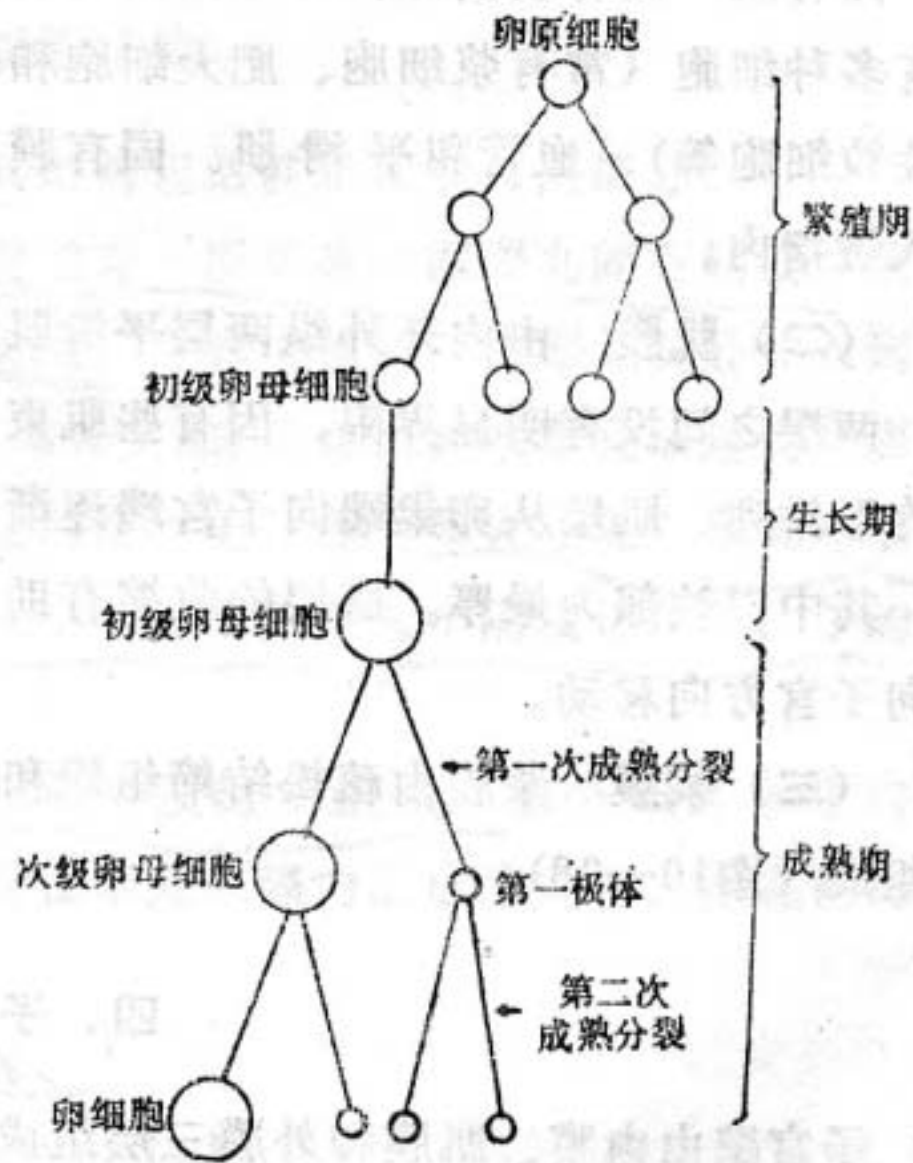


图 10—37 卵子发生过程示意图

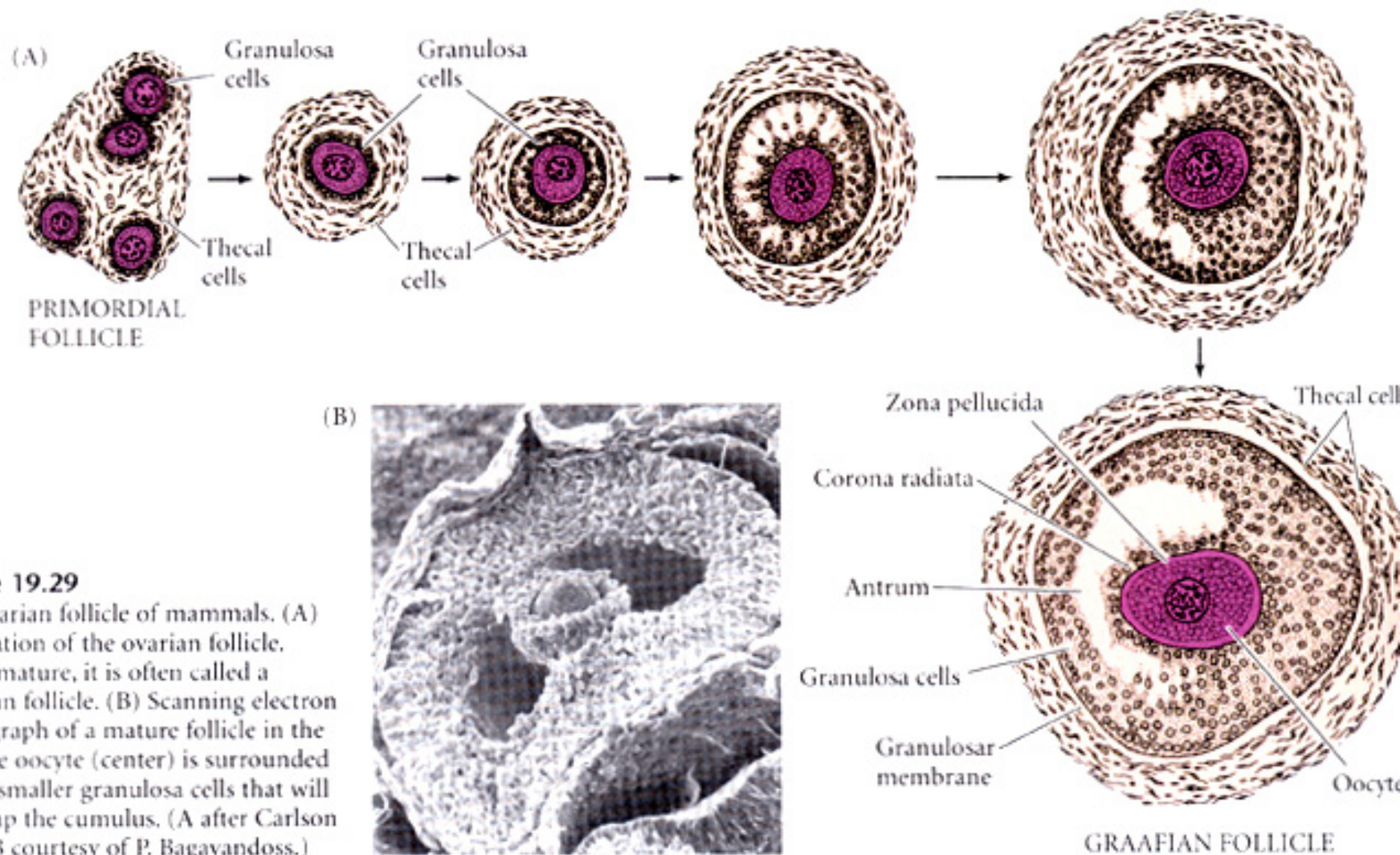
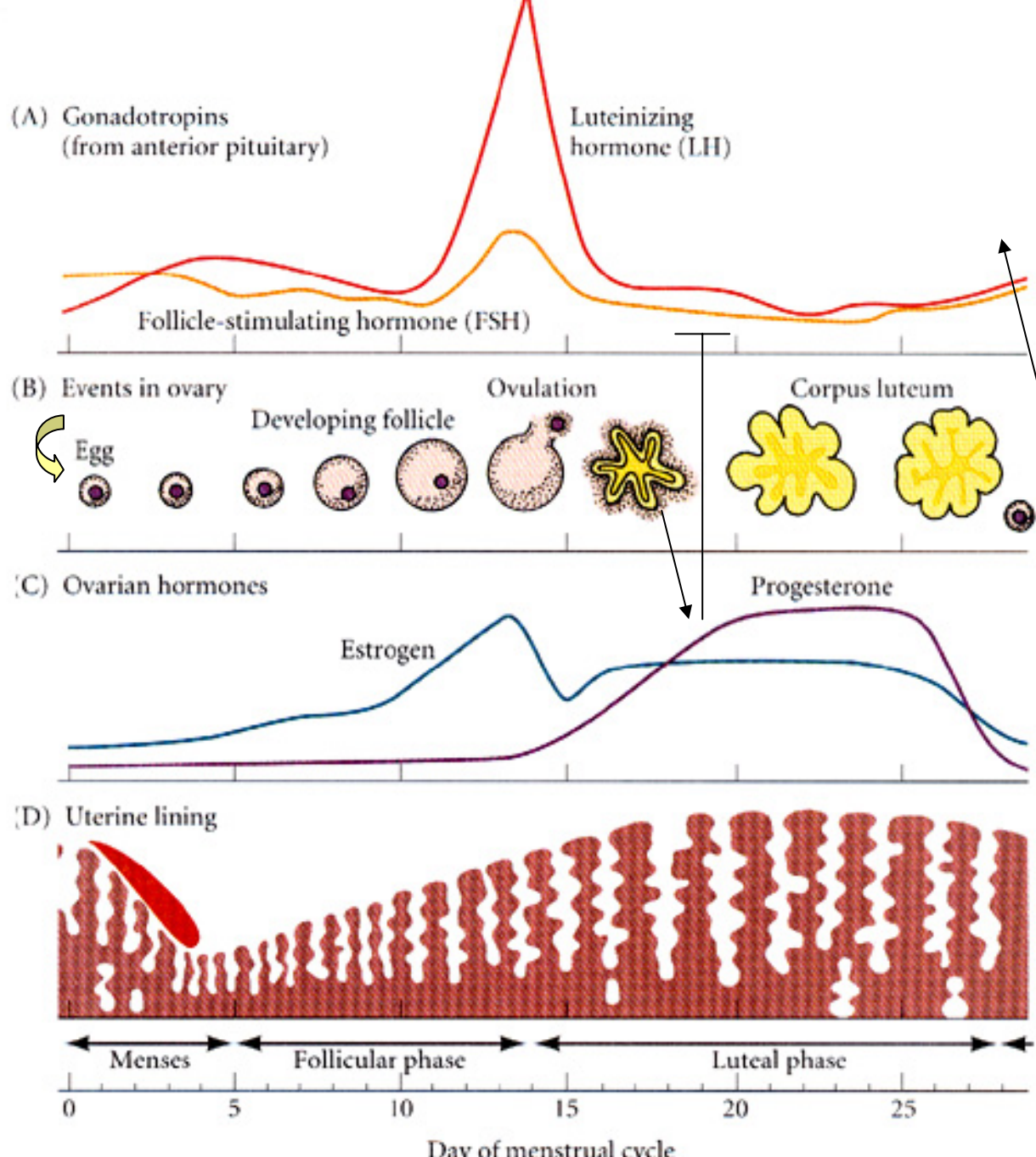


Figure 19.29
 The ovarian follicle of mammals. (A) Maturation of the ovarian follicle. When mature, it is often called a Graafian follicle. (B) Scanning electron micrograph of a mature follicle in the ovary. The oocyte (center) is surrounded by the smaller granulosa cells that will make up the cumulus. (A after Carlson 1981; B courtesy of P. Bagavandoss.)

Figure 19.50
 The human menstrual cycle. The coordination of (B) ovarian and (D) uterine cycles is controlled by (A) the pituitary and (C) the ovarian hormones. During the follicular phase, the egg matures within the follicle, and the uterine lining is prepared to receive the blastocyst. The mature egg is released around day 14. If a blastocyst does not implant into the uterus, the uterine wall begins to break down, leading to menstruation.

人的排卵周期



(2) 生长期

- 是指进入生长期的初级卵母细胞，由于胞质内不断蓄积大量供早期胚胎发育用的营养物质(如卵黄等)和蛋白合成装置(核糖体和mRNA)等而体积明显增大的过程。
- 如在生长期期间，小鼠卵母细胞的直径由12um增加到85um。
- 伴随体积的增大，卵母细胞外形成透明带。

(3) 成熟期

- 是指初级卵母细胞经过两次减数分裂，使染色体数目减少到体细胞的一半而变为成熟卵子的过程。初级卵母细胞经过第一次减数分裂形成一个次级卵母细胞和一个第一极体。
- 有些低等动物(如海胆)，次级卵母细胞很快完成第二次减数分裂，形成一个大的成熟卵子和一个很小的第二极体。
- 大多数家畜，次级卵母细胞则停止在第二极体。伴随细胞核的成熟分裂，卵母细胞微绒毛和卵丘细胞突起自透明带中撤出，细胞质内的细胞器发生重新分布，呈受精前状态。

2、卵子的形态结构与发育

- 家畜卵子的直径为 $100\ \mu\text{m}$ 左右，家畜卵子的卵黄含量少，卵子体积不大，胚胎在体内发育成熟，发育期间利用母体营养，无须很多营养贮备。
- 家畜在胎儿时期由生殖嵴形成的卵巢内有大量的由原生殖细胞形成的卵原细胞，这些细胞在胎儿出生前后进入第一次减数分裂前期。

- 成熟卵泡的卵泡腔最大，颗粒层很薄，颗粒细胞不再增殖。此时的卵母细胞又恢复成熟分裂，在排卵前36~48h完成第一次减数分裂，产生一个次级卵母细胞和一个很小的第一极体。第一极体位于次级卵母细胞和透明带之间的卵周隙中。次级卵母细胞随即进入第二次减数分裂中期，一直停留在此期，等待受精。

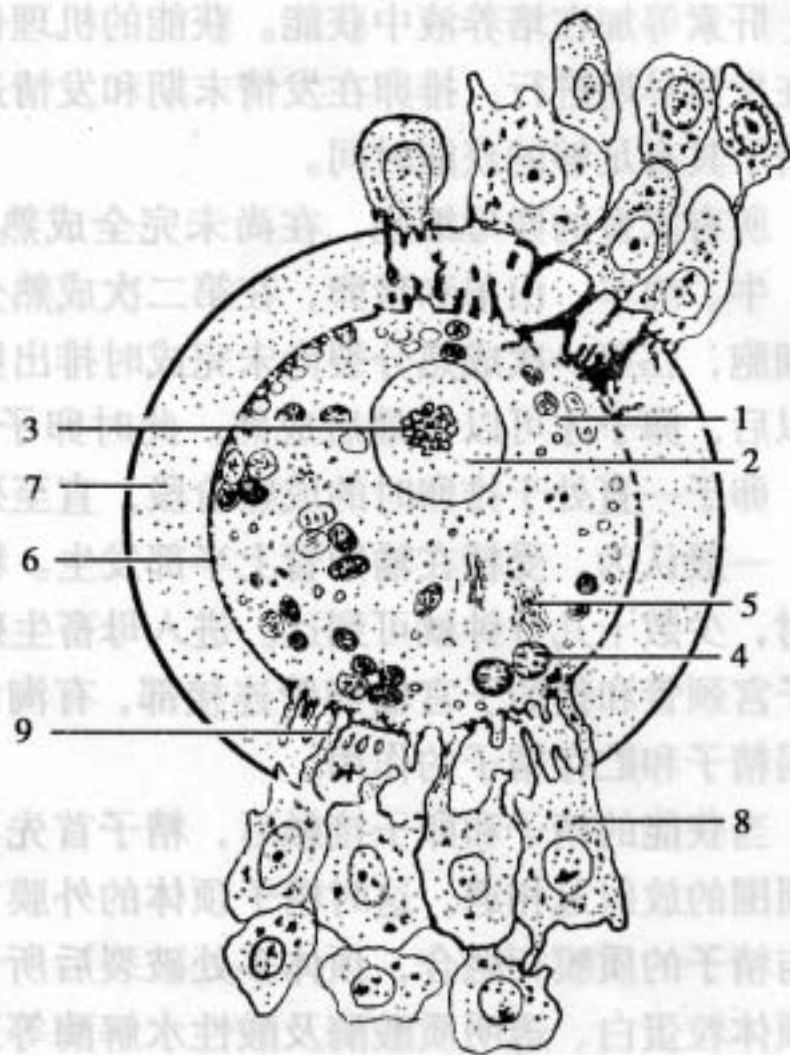


图 11-4 哺乳动物排卵时卵细胞结构示意图

1. 细胞质 2. 细胞核 3. 核仁 4. 线粒体 5. 内网器
 6. 卵黄膜 7. 透明带 8. 放射冠 9. 卵细胞的突起及放射冠的突起伸到透明带中

二、精子获能

- 精子在睾丸中产生，在附睾内发育成熟，直接从睾丸中取出的精子没有受精能力。进入母畜生殖道内的精子，要在子宫、输卵管内渡过一段时间（2~4h），才能获得受精能力，此过程称精子获能。

- 获能过程在于精子发生形态生理和生物化学变化，有利入卵。在体外可用输卵管、卵泡液、血清、咖啡因、肝素等加在培养液中获能。获能的机理仍不清楚。未获能的精子不能进入卵内。通常自然交配在发情早期进行，排卵在发情末期和发情过后，精子和卵子在母畜生殖道内出现的时间差异，使精子具有足够的获能时间。

■ 家畜的卵母细胞，在尚未完全成熟以前，由卵巢排出进入输卵管，但成熟程度并不一样。牛、绵羊、山羊和猪卵，在第二次成熟分裂中期排出，此时第一极体已经排出；狗和狐狸的卵细胞，在第一次成熟分裂尚未完成时排出卵巢受精。当精子入卵以后，卵子才可以说最后成熟。此时卵子完成第二次成熟分裂，排出第二极体。

三、受精

- (一) 定义 成熟的精子与成熟的卵子融合，形成受精卵的过程。
- (二) 位置 受精在输卵管壶腹部，距顶端1 / 3处，精子进入母畜生殖道，到达受精部位需几十分钟到数小时。

(三) 过程

■ 1、顶体反应

- 当获能的精子和卵子接触后，精子首先与卵周围的放射冠相遇，这时精子顶体的外膜首先与精子的质膜相融合，顶体多处破裂后所含的顶体粒蛋白、透明质酸酶及酸性水解酶等逐渐释放出来。精子顶体的这种变化称为顶体反应。

■ 2、透明带反应

- 精子经过顶体反应、释放出透明质酸酶，溶解放射冠，通过透明带接近卵黄膜。精子进入后，卵母细胞浅层细胞质内的皮质颗粒立即释放出溶酶体酶样物质，使透明带结构发生变化，称为透明带反应，从而阻止其他精子穿越透明带。

3、识别

- 穿过透明带的精子接触卵细胞膜，精子与卵细胞膜上都有同种抗原。识别后精卵细胞融合。精子进入卵细胞。

4、皮质反应

精子一旦与卵子质膜接触后，卵子发生一系列变化，使卵得以激活，首先精卵接触处的卵母细胞表层的皮质颗粒与质膜发生融合，然后整个卵子表层的皮质颗粒都发生胞吐作用，将整个过程称为皮质反应。

5、雌雄原核形成

- 精子入卵后，头尾分离，核内染色体解聚，头部迅速膨大，胞核出现核仁，形成明显的核膜。这种圆形核称雄原核。与此同时，卵排出第二极体；完全成熟并形成雌原核。

6、核膜融合

- 雌雄原核逐渐在细胞中部靠拢，核膜消失，染色体彼此混合，同源染色体配对，形成二倍体的受精卵，又称合子，受精过程到此结束。

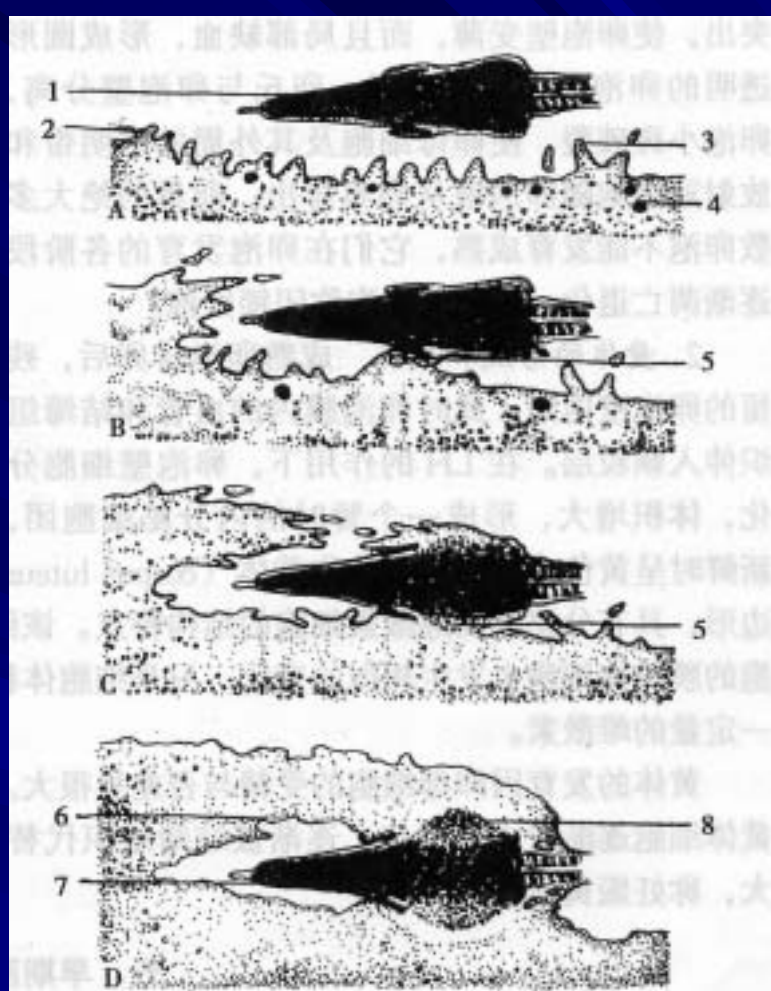


图 11-5 哺乳动物精子入卵和精卵融合过程

A. 顶体反应后精子穿过透明带进入卵周隙 B. 以赤道段质膜与卵质膜相融合 C. 融合后 CGs 胞吐，核开始去致密

D. 精子头部完全入卵，将一部分卵质膜带入

1. 进入卵周隙的精子 2. 卵质膜 3. 微绒毛 4. CGs

5. 精卵开始融合处 6. 带入的卵质膜 7. 顶体内膜

8. 精核去致密

(四) 意义

- 1、标志着新生命的开始
- 2、染色体得到恢复
- 3、染色体来自父、母双方，产生与双亲都不同的遗传特性
- 4、决定性别

四、卵裂

- 家畜卵的卵黄量少，分布均匀，进行不规则的异时全裂。
- 第一次卵裂沿动物极(极体所在的一端)向植物极方向，将单细胞合子一分为二成为两个细胞。分裂后的细胞称卵裂球。

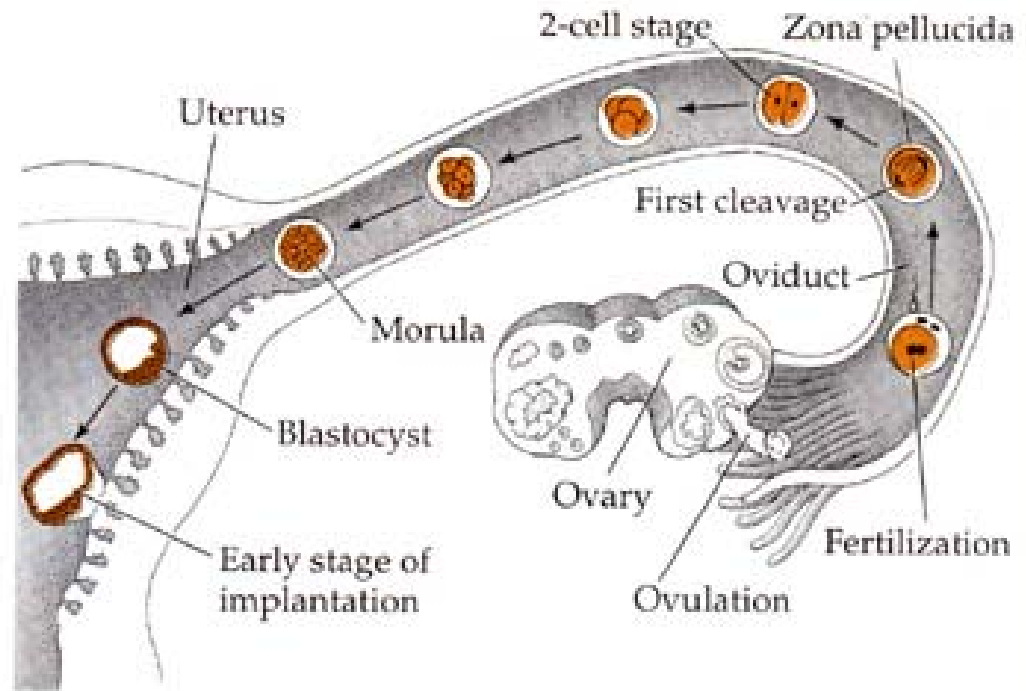
- 卵裂一直在透明带内进行，随着卵裂的进行，卵裂球数量增加，分裂后的细胞并不生长增大，卵裂球的体积随卵裂次数增多而逐渐变小。
- 进行几次卵裂后形成一实心的胚胎，形似桑葚，故称桑葚胚。
- 进入桑葚胚不久，卵裂球之间排列紧密，将此过程称为致密化。

- 卵裂开始在输卵管内进行，随后胚胎迅速通过输卵管峡部，进入子宫。

旋转型全卵裂

哺乳动物的早期卵裂发生在输卵管中

Figure 5.18
Development of a human embryo from fertilization to implantation. Compaction in human embryos takes place at day 4, when it is at the 10-cell stage. The egg "hatches" from the zona upon reaching the uterus, and the zona probably prevents the cleaving cells from sticking to the oviduct rather than traveling to the uterus. (After Tuchmann-Duplessis et al., 1972.)



哺乳动物旋转型全卵裂：第1次为经线裂，其后的2个卵裂球各采不同的卵裂方式。早期卵裂球的卵裂不同步，可产生奇数细胞的胚胎。

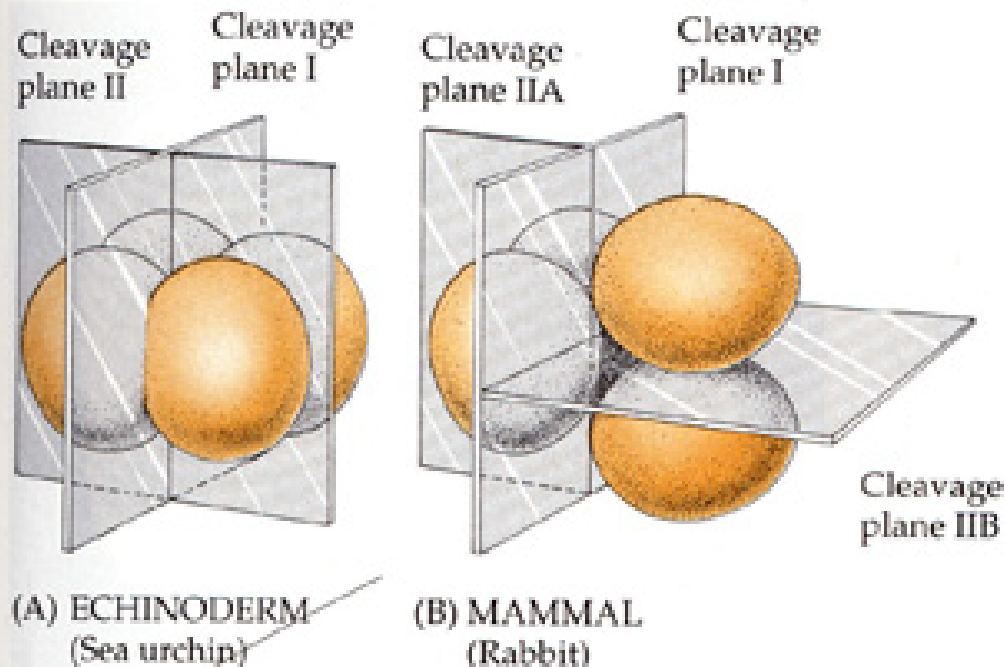


Figure 5.19

Comparison of early cleavage in (A) echinoderms (radial cleavage) and (B) mammals (rotational cleavage). Nematodes also have a rotational form of cleavage, but they do not form the blastocyst structure characteristic of mammals. Details of nematode cleavage will be given in Chapter 13. (After Gulyas, 1975.)

哺乳动物卵裂球的compaction:发生第三次卵裂后

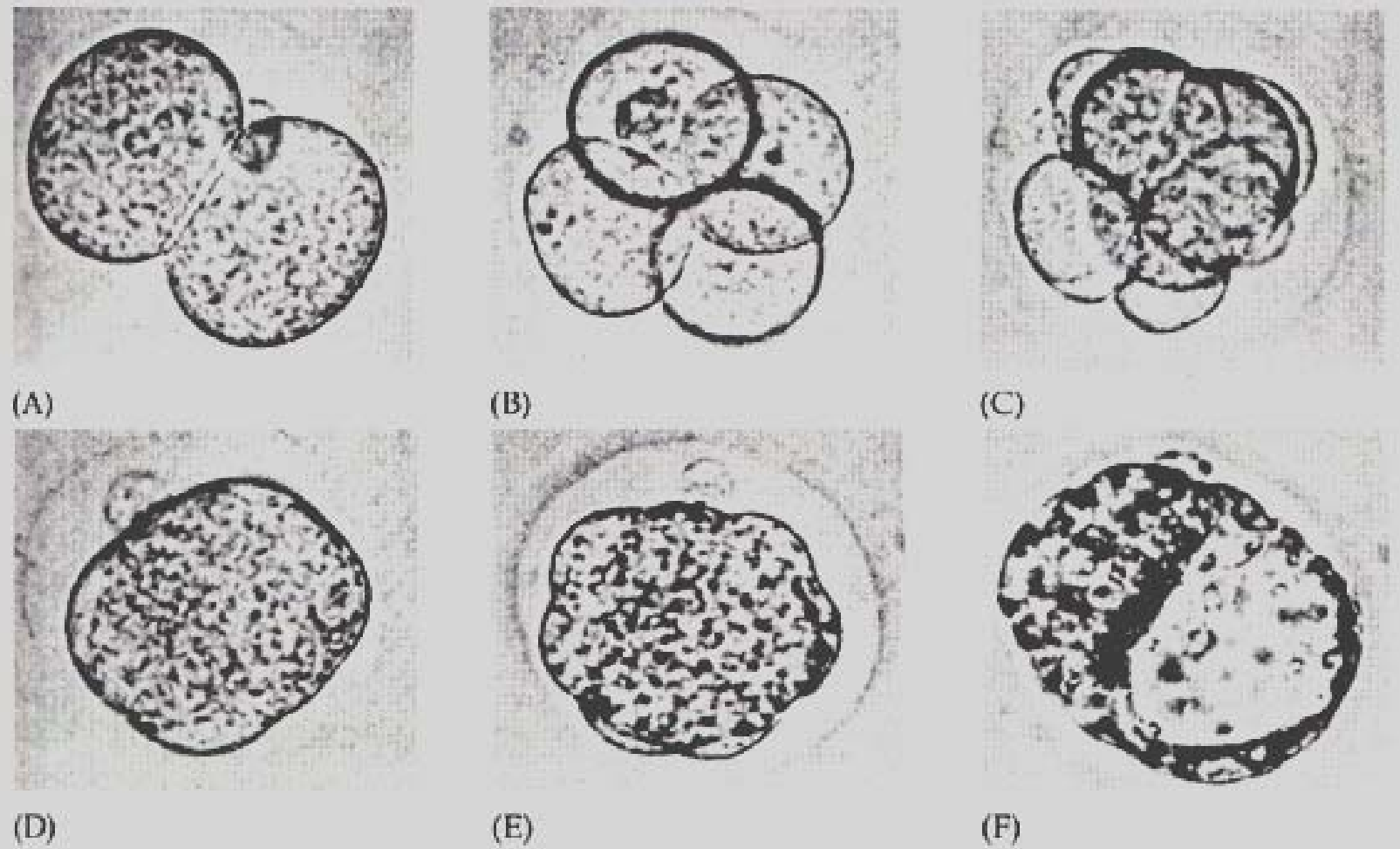
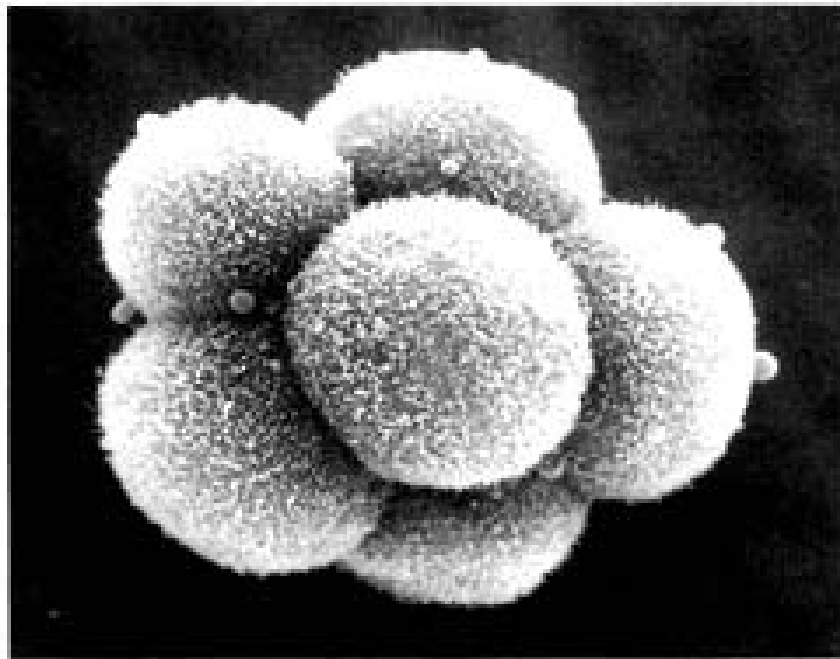


Figure 5.20

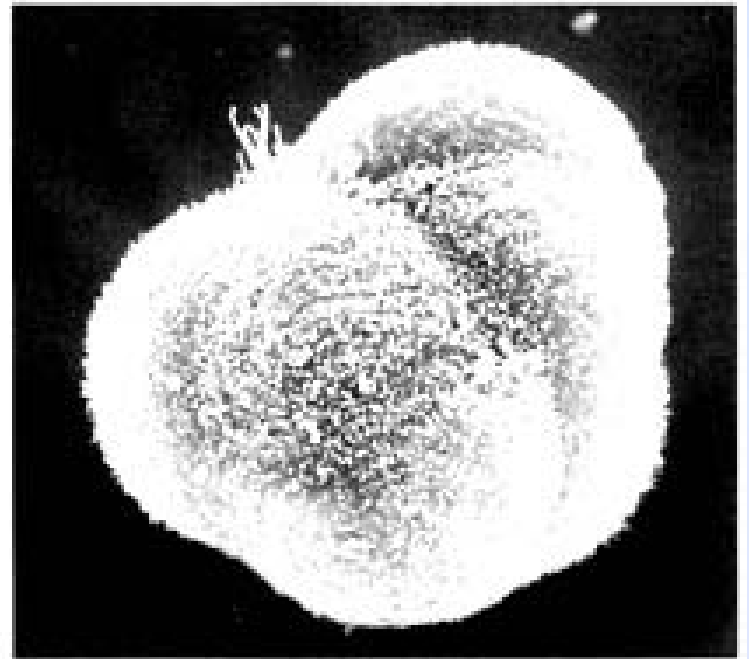
The cleavage of a single mouse embryo in vitro. (A) 2-cell stage. (B) 4-cell stage.

cell stage. (E) Morula. (F) Blastocyst. (From Mulnard, 1967, courtesy of J. G. Mulnard.)

小鼠8细胞胚胎 compaction前后



(A)

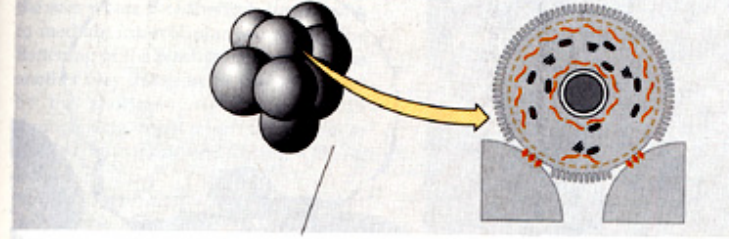


(B)

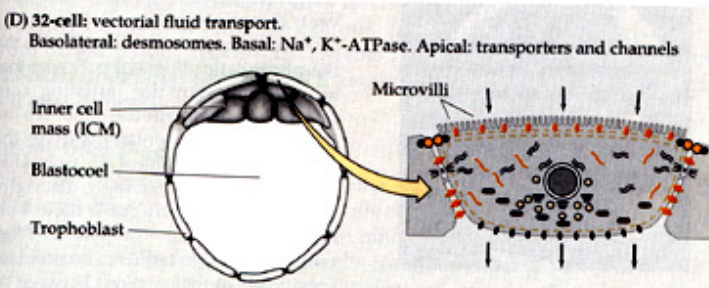
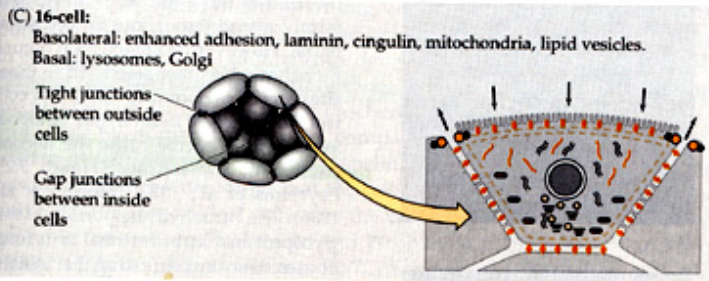
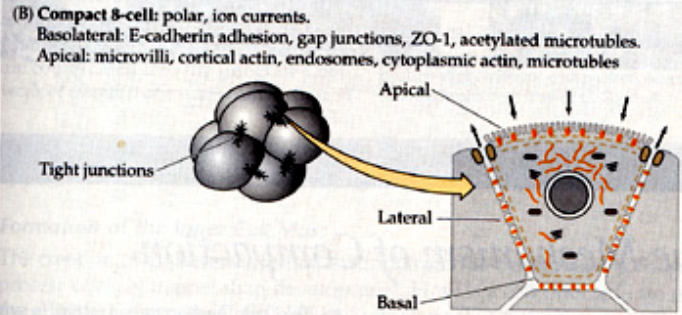
Figure 5.21

Scanning electron micrograph of (A) uncompact and (B) compacted 8-cell mouse embryos. (Courtesy of C. Ziomek.)

Compaction
 的机制:8细胞
 胚胎的外层胞
 间形成致密连
 接(tight
 junctions), 而
 内层胞间形成
 缝隙连接(gap
 junction)。



Compaction and the formation of mouse blastocyst. (A,B) 8-cell embryo. (C) 16-cell morula. (D) 32-cell blastocyst. The left side represents the entire embryo or its cross section. The right side details the changes associated with maturation of the trophoblast. (Revised hand figures after Fleming, 1992)



◆ E-cadherin	≡≡ Desmosomes	00 Tight junction (ZO-1)
Ion current direction	○ Secondary lysosomes	●● (ZO-1)+cingulin
● Na ⁺ , K ⁺ -ATPase	∇ Golgi	- - - Cortical actin
≡≡ Gap junctions	≈ Cytokeratin filaments	Microvilli

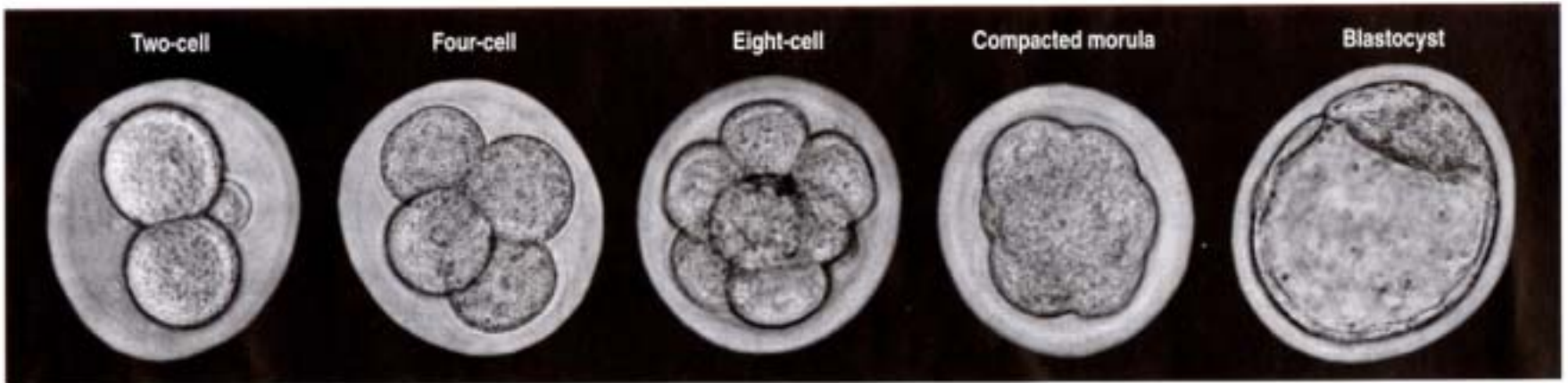


Fig. 2.21 Cleavage in the mouse embryo. The photographs show the cleavage of a fertilized mouse egg from the two-cell stage through to the formation of the blastocyst. After the eight-cell stage compaction occurs, forming a solid ball of cells, the morula, in which individual cell outlines can no longer be discerned. The internal cells of the morula give rise to the inner

cell mass, which can be seen as the compact clump of the top of the blastocyst. It is from this that the embryo proper forms. The outer layer of the hollow blastocyst—the trophoblast—gives rise to the extra-embryonic structures. Photographs courtesy of T. Fleming.

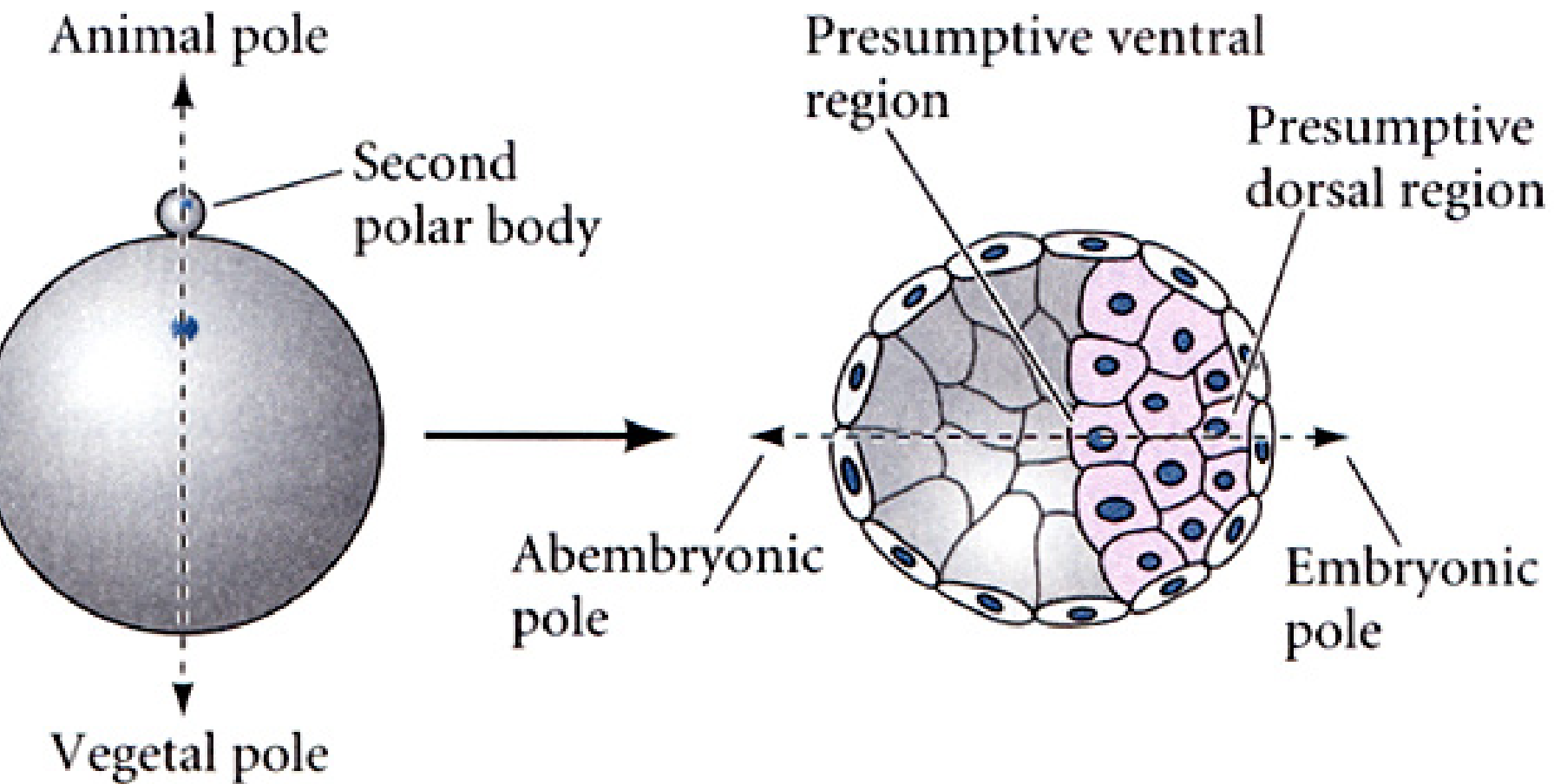


Figure 11.41

Relationship between the animal-vegetal axis of the egg and the embryonic-abembryonic axis of the blastocyst. The polar body marks the animal pole of the embryo. The dorsal-ventral axis of the embryo appears to form at right angles to the animal-vegetal axis of the egg.

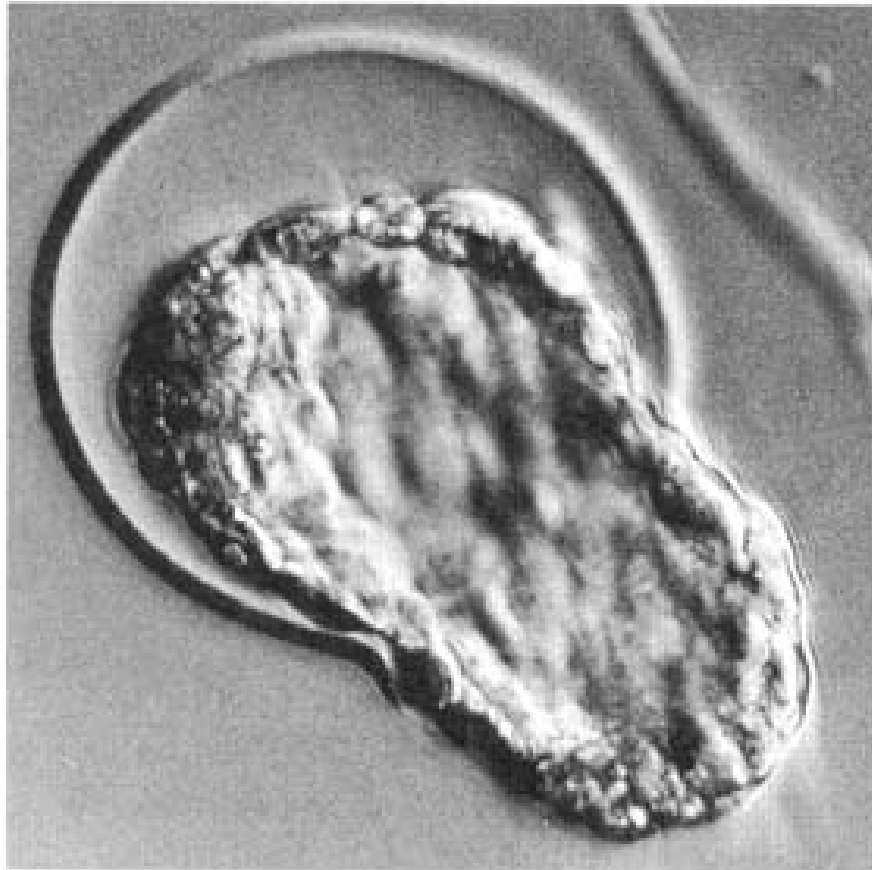


Figure 5.26

Mouse blastocyst hatching from the zona pellucida. (Photograph from Mark et al., 1985, courtesy of E. Lacy.)

人类的同卵双生的发生(占出

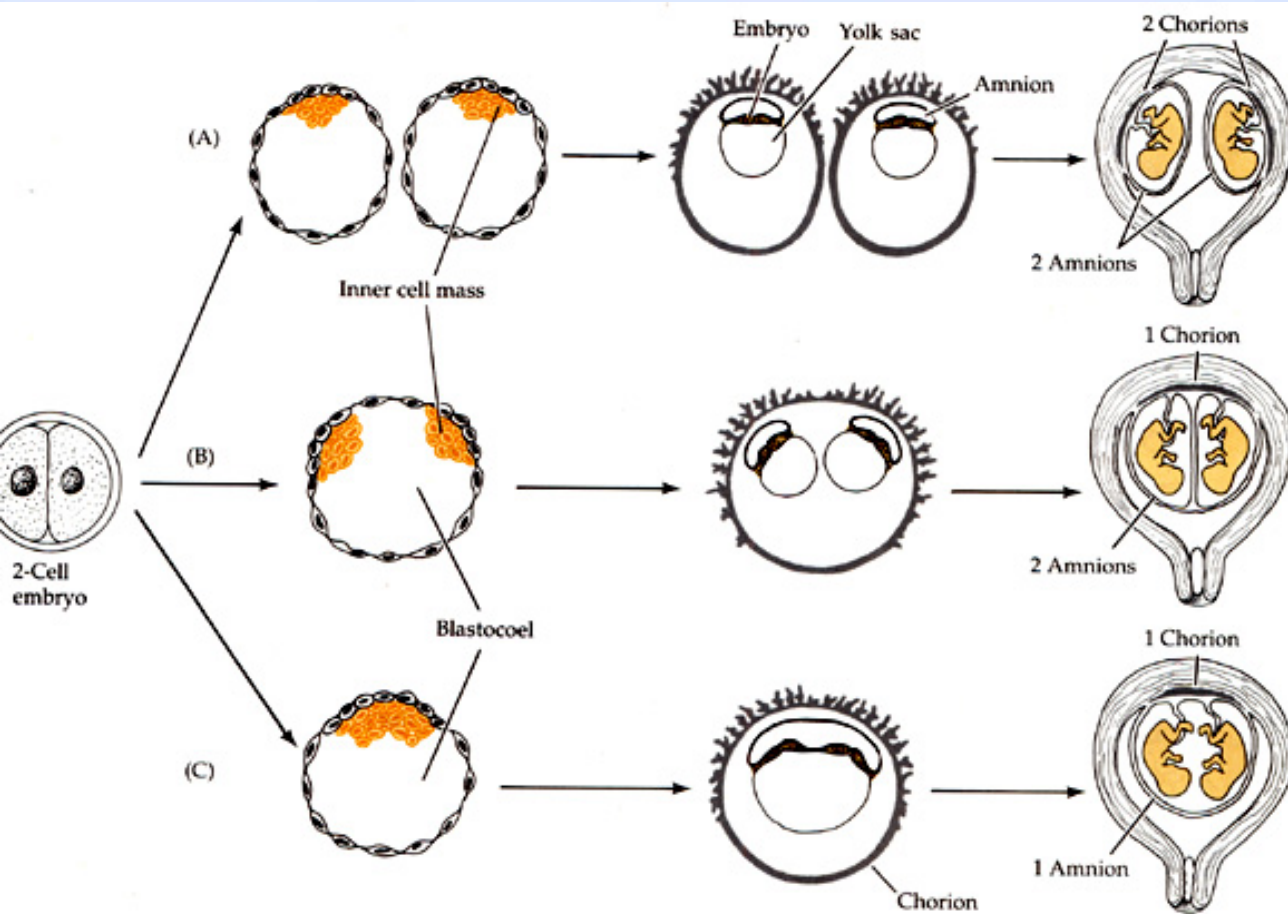


Figure 5.27 Diagram showing the timing of human monozygotic twinning with relation to extraembryonic membranes. (A) Splitting occurs before the formation of the trophoblast, so each twin has its own chorion and amnion. (B) Splitting occurs after trophoblast formation but before amnion formation, resulting in twins having individual amniotic sacs but sharing one chorion. (C) Splitting after amnion formation leads to twins in one amniotic sac and a single chorion. (After Langman, 1981).

人类的连体婴儿

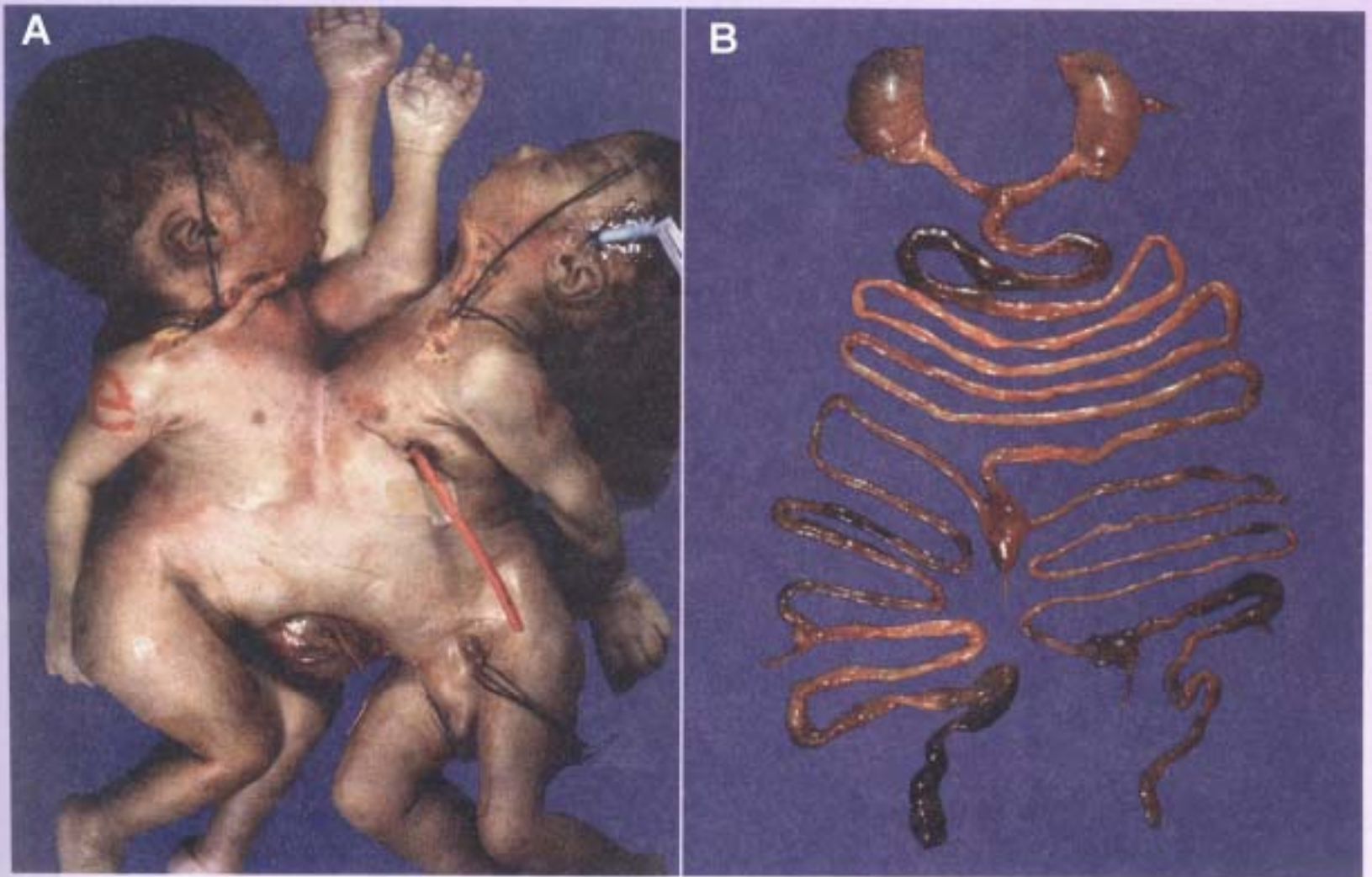


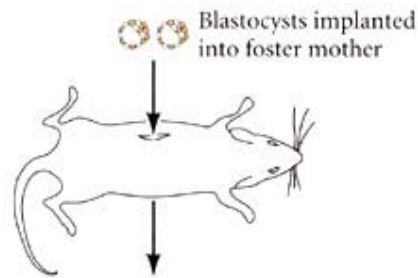
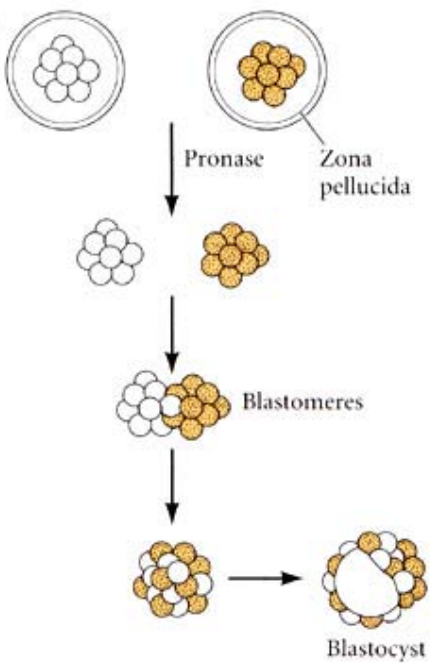
Figure 3-14 A, Conjoined twins with broad truncal attachment (thoracopagus). B, Dissected intestinal tracts from the same twins showing partial fusion of the small intestine and mirror image symmetry of the stomachs. (Courtesy M. Barr, Ann Arbor, Michigan.)

7月21日拍摄的手术前的连体女婴。9月9日，一对罕见的胸腹连体女婴在上海第二医科大学附属新华医院儿童医学中心成功分离。医生在分离连体女婴胸腔、腹腔共同心包和肝脏等组织的同时，一并纠正了其中一名女婴的血管畸形。





哺乳动物中的嵌合胚、胚胎



(B)

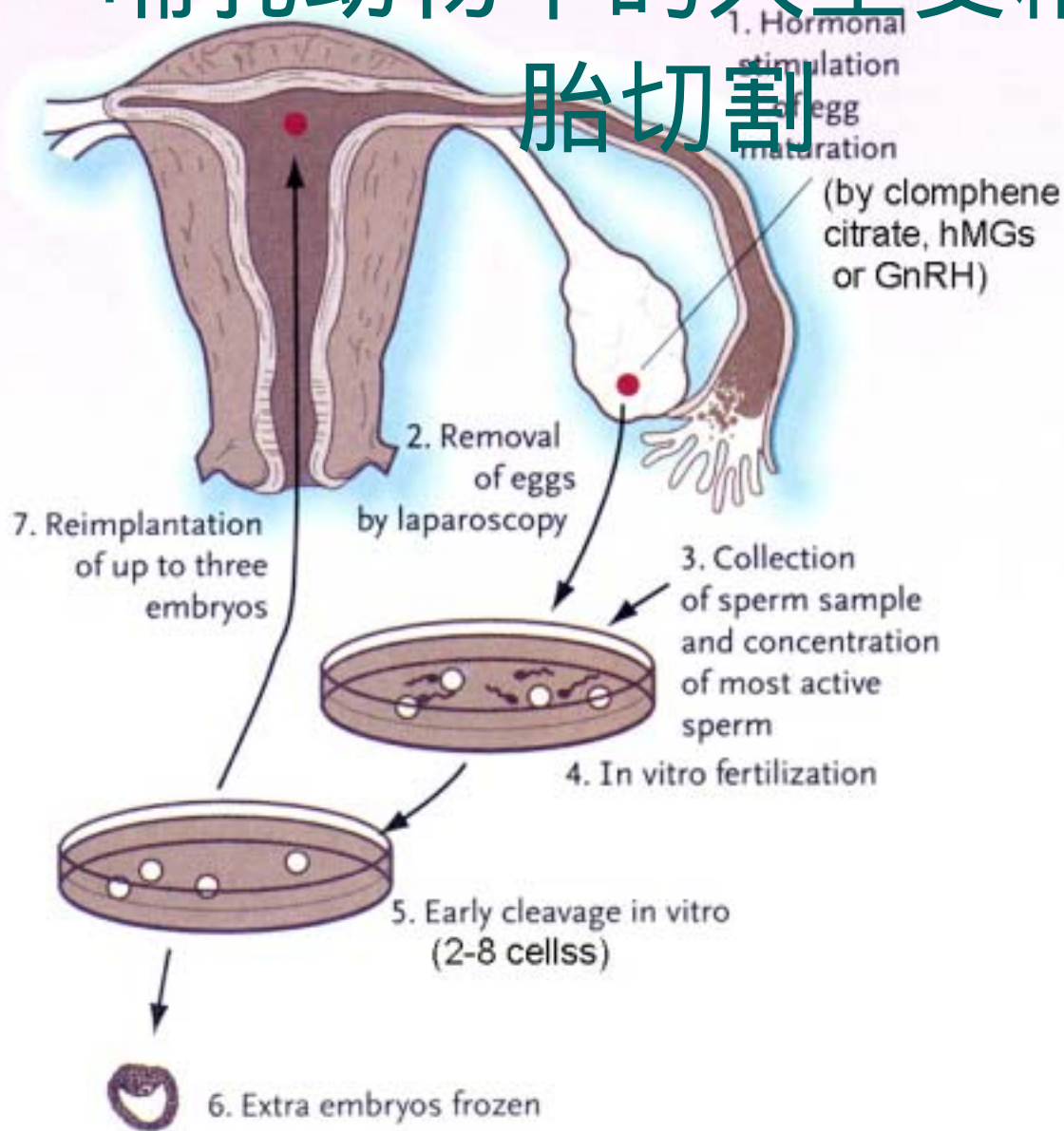


Figure 11.33

Production of chimeric mice. (A) The experimental procedures used to produce chimeric mice. Early 8-cell embryos of genetically distinct mice (here, with coat color differences) are isolated from mouse oviducts and brought together after their zones are removed by proteolytic enzymes. The cells form a composite blastocyst, which is implanted into the uterus of a foster mother. The photograph shows one of the actual chimeric mice produced in this manner. (B) An adult female chimeric mouse (bottom) produced from the fusion of three 4-cell embryos: one from two white-furred parents, one from two black-furred parents, and one from two brown-furred parents. The resulting mouse has coat colors from all three embryos. Moreover, each embryo contributed germ line cells, as is evidenced by the three colors of offspring (above) produced when this chimeric female was mated with recessive (white-furred) males. (A, photograph courtesy of B. Mintz; B from Markert and Petters 1978, photograph courtesy of C. Markert.)

嵌合胚：
如右图，说明早期卵裂球有同等的发育潜力。
自然人群中
也出现过同
时有XX型和
XY型细胞的

哺乳动物中的人工受精和胚胎切割



人工受精：如主要用于治疗不育症、保存和运输优良个体。

Figure 2-7 Schematic representation of a typical in vitro fertilization and embryo transfer procedure in

五、胚泡的形成及附植

- 桑葚胚形成之后，卵裂球之间出现小的腔隙，腔隙中的液体越来越多，腔也越来越大，将内部细胞挤向一侧，形成一个有腔的胚泡，也称囊胚。
- 在胚泡外围的一层细胞称滋养层，为将来形成胎膜的外胚层细胞。
- 中央的腔为胚泡腔，位于胚泡一侧的一群细胞称为内细胞团，将来发育成胚体和胚外部分

- 胚泡逐渐长大，透明带也随之逐渐变薄，胚泡从透明带中孵出，开始胚胎附植，即胚胎在子宫内膜相接触并附着或侵入子宫内膜的过程。

- 初期的胚泡仍然游动于子宫腔内。随后，胚胎在子宫角内调整间隔后均匀分布于子宫角中。由于胚泡变长变大，胚泡腔液体增多，胚泡在子宫内的运动受到限制，胚泡逐渐定位在子宫角内特定的位置，然后开始附植。附植过程在各种家畜略有不同。
- 附植开始的确切时间，观察尚少，其说不一，一般认为，猪配种后11—15天，绵羊16—17天，牛30—35天，马40—50天左右，胚泡开始附植。

- 胚胎附植是家畜妊娠过程中最关键的阶段，很多胚胎损失发生在此阶段。胚胎附植的成败，是早期胚胎存活的关键。因此，母畜妊娠初期，应该特别注意保胎，以免胚胎死亡流产。

六、原肠胚和胚层形成

■ 内外胚层形成

- 胚泡附植后，内细胞团继续增殖分化形成由两层细胞构成的圆盘状的胚盘，即靠近表面滋养层的外胚层和下面的位居胚泡腔顶侧的内胚层。
- 随后，在外胚层的近滋养层侧出现一个腔，为羊膜腔，腔壁为羊膜。这时外胚层构成羊膜腔的底部。而内胚层的周缘向下延伸形成卵黄囊。

5 哺乳动物的一层为下胚

层，将用于

形成yolk

sac；另一

层为上胚

层。上胚层

细胞间的缝

隙将合并、

扩大成头盖

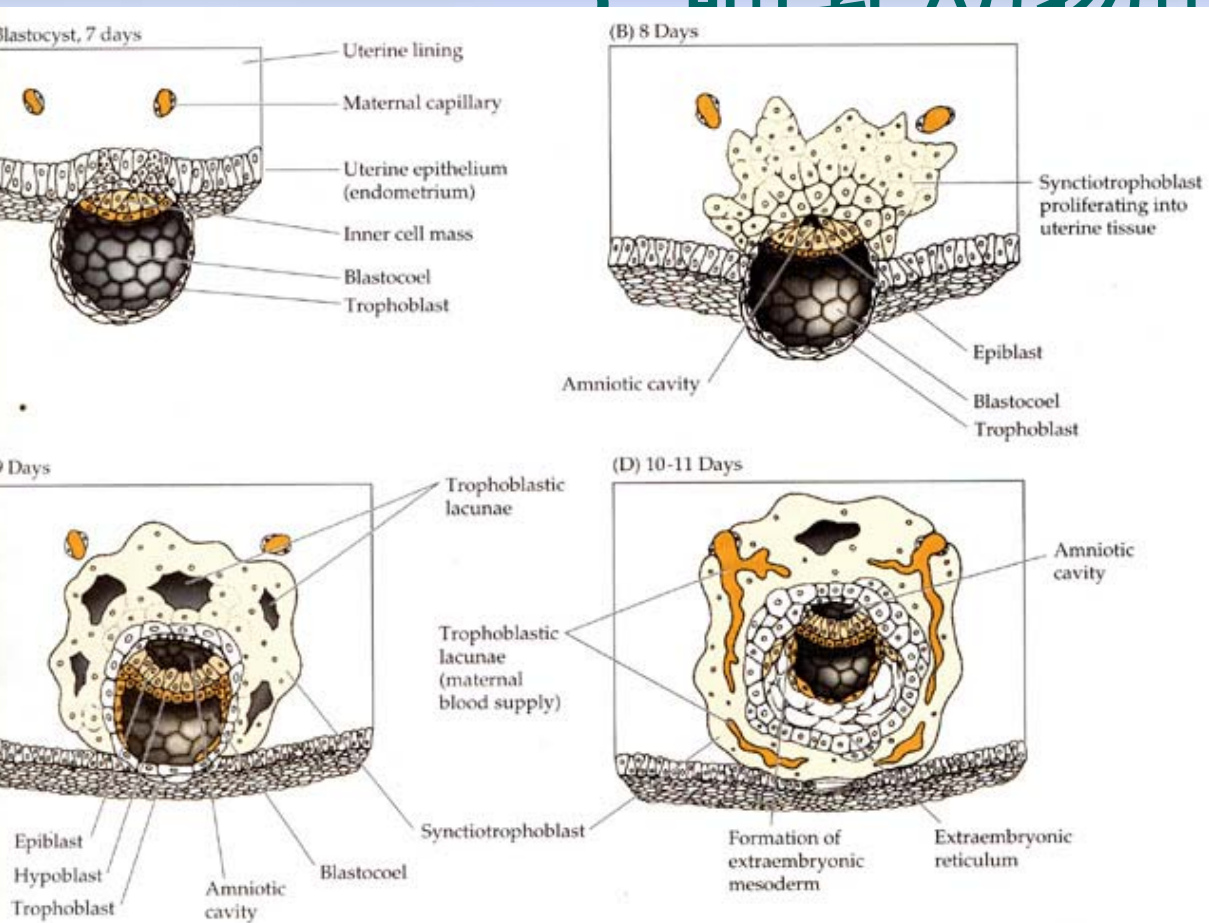
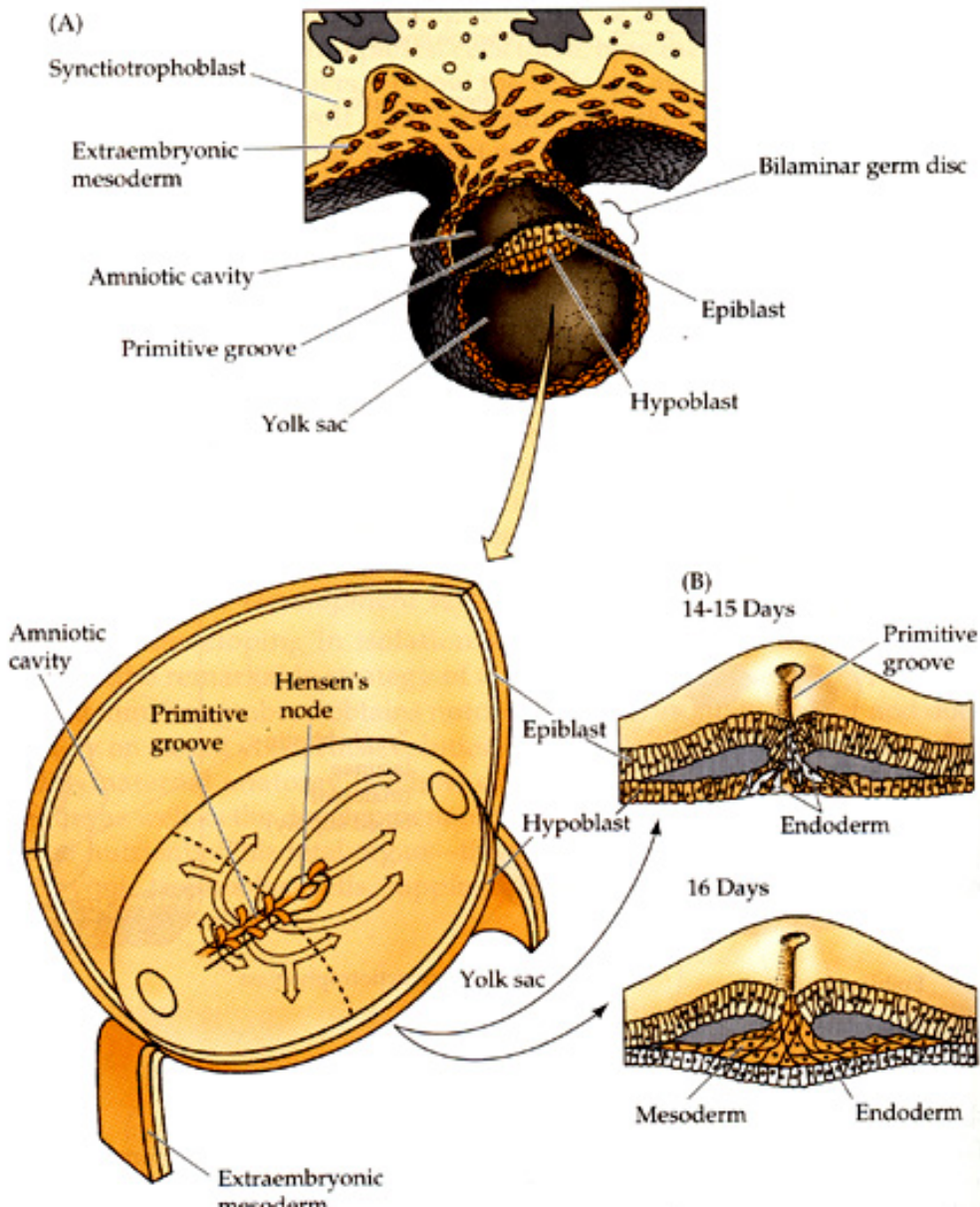


Figure 6.33
 Gastrulation and extraembryonic cavity formation in the human embryo between days 7 and 12. (A,B) Human blastocyst immediately prior to gastrulation. The inner cell mass delaminates into the epiblast and hypoblast that line the trophoblast, thereby forming the primitive yolk sac and a two-layered (epiblast and hypoblast) blastodisc similar to that seen in avian embryos. The trophoblast in some mammals can be divided into the polar trophoblast, which covers the inner cell mass, and the mural trophoblast, which does not. The trophoblast divides into the cytotrophoblast, which will form the villi, and the syncytiotrophoblast, which will ingress into the uterine tissue. (C) Meanwhile, the epiblast has split into the amniotic ectoderm (which encircles the amniotic cavity) and embryonic epiblast. The adult mammal forms from the cells of the embryonic epiblast. (D) The extraembryonic endoderm forms the yolk sac. (After Gilbert, 1989; Larsen, 1993.)

胚层的建立及其

Figure 6.34

Amnion structure and cell movements during human gastrulation. (A) Human embryo and uterine connections at 15 days' gestation. In the upper view, the embryo is cut sagittally through the midline; the lower view looks down upon the dorsal surface of the embryo. (B) The movements of the epiblast cells into the primitive streak and Hensen's node and underneath the epiblast are superimposed on the dorsal surface view. At days 14 and 15, the ingressing epiblast cells are thought to replace the hypoblast cells (which contribute to the yolk sac lining), while at day 16, the ingressing cells fan out to form the mesodermal layer. (After Larsen, 1993.)



人类新生胎儿的胚外结构

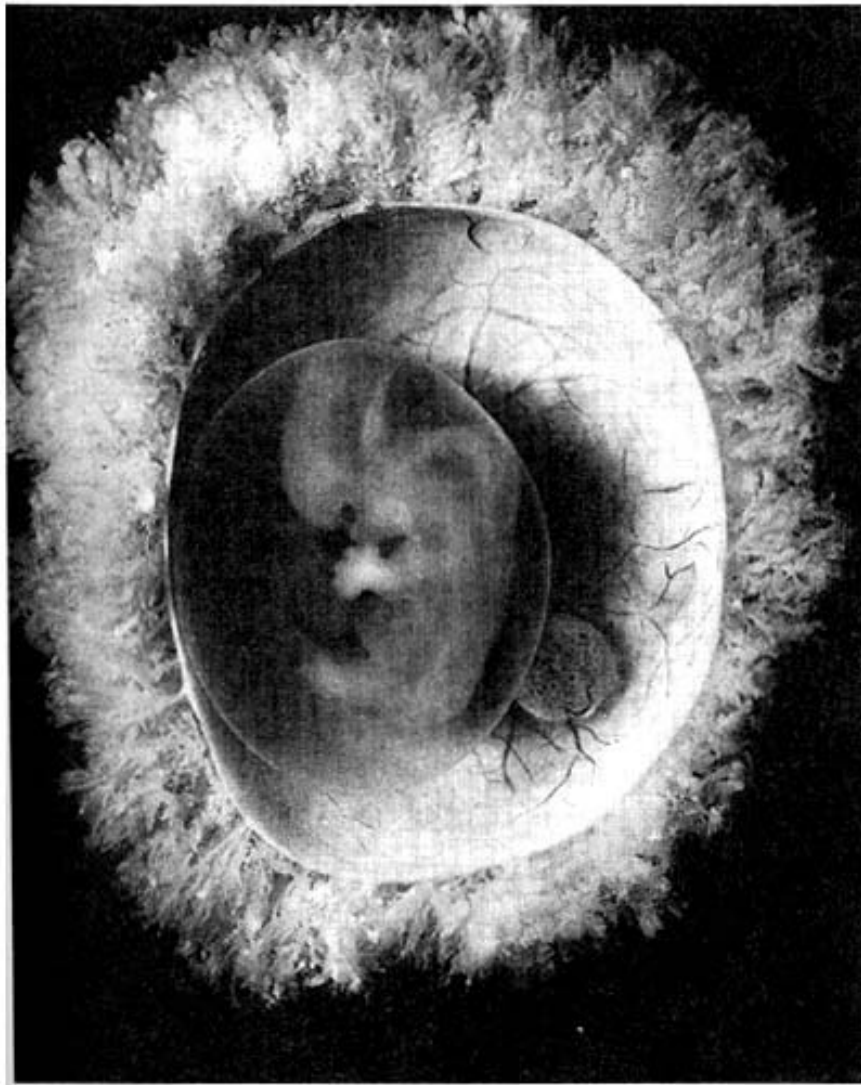


Figure 11.30

Human embryo and placenta after 40 days of gestation. The embryo lies within the amnion, and its blood vessels can be seen extending into the chorionic villi.

The small sphere to the right of the embryo is the yolk sac. (The Carnegie Institution of Washington, courtesy of G. F. Bunker.)

七、中胚层形成

- 随着胚泡变长，圆形的胚盘变成卵圆形。胚盘外胚层细胞迅速增殖并不断地自两侧向胚盘尾侧的中轴迁移，在尾侧中轴线上形成一条增厚的细胞索，称为原条。

- 原条出现后，在其前端膨大形成原结。在原结的后部有一凹陷，称原窝。以后原条的中央下陷形成原沟，两侧的细胞隆起形成原褶。此时，原条头端原结处的细胞继续向深部下陷，并在内外胚层之间的中轴线上向头侧生长，形成一条脊索。随着胚盘的继续发育，脊索继续增长，而原条则逐步缩短，最后消失。脊索在胚胎早期起支持作用，以后为脊柱所代替。

- 随着原条的形成，在胚盘后端的内外胚层之间逐渐分化出另一层细胞，即中胚层。中胚层细胞不断增殖，并向胚盘的后方、两侧及前方扩展，便在胚盘的外胚层与内胚层之间，以及胚盘区以外的滋养层和内胚层之间形成一个完整的中胚层。

- 在胚盘区的为胚内中胚层，而胚盘区外的称胚外中胚层。由于胚外中胚层细胞细胞聚集分为两层并贴附在滋养层的内面和羊膜腔与卵黄囊的外面，两层间的腔成为胚外体腔。

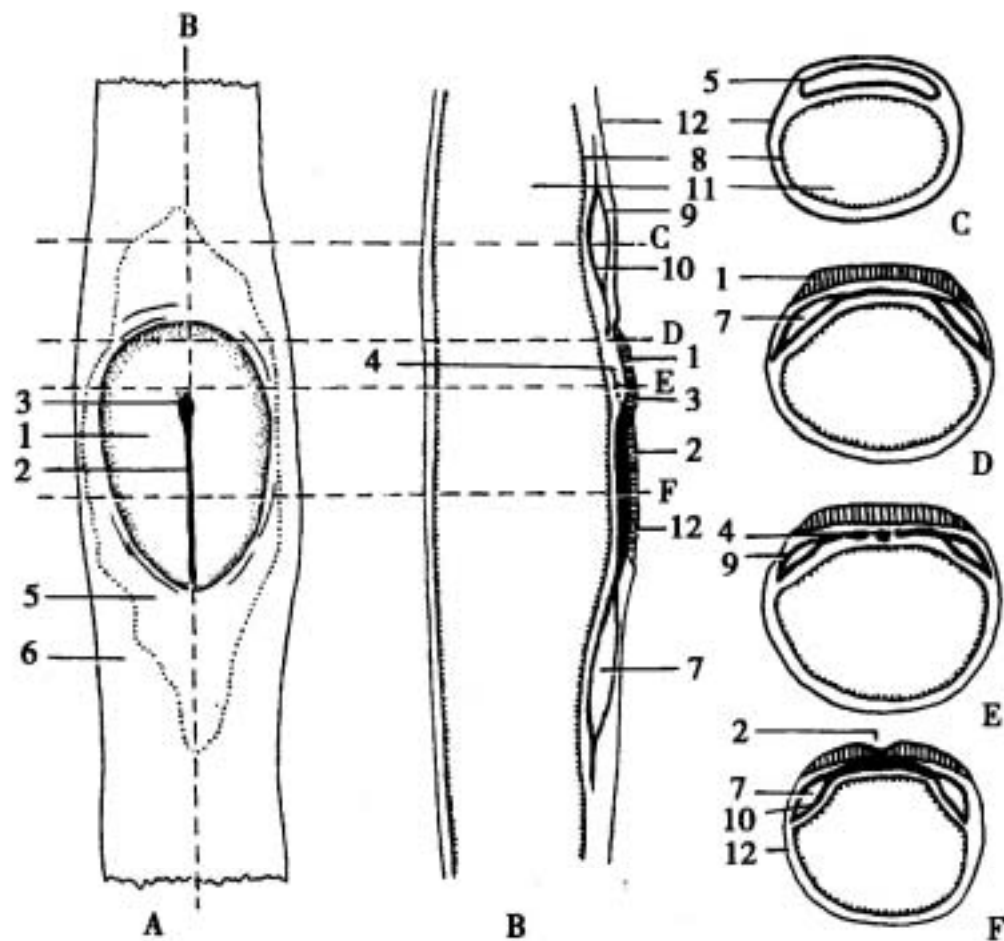


图 11-9 12 天猪胚泡背侧观及纵横断面

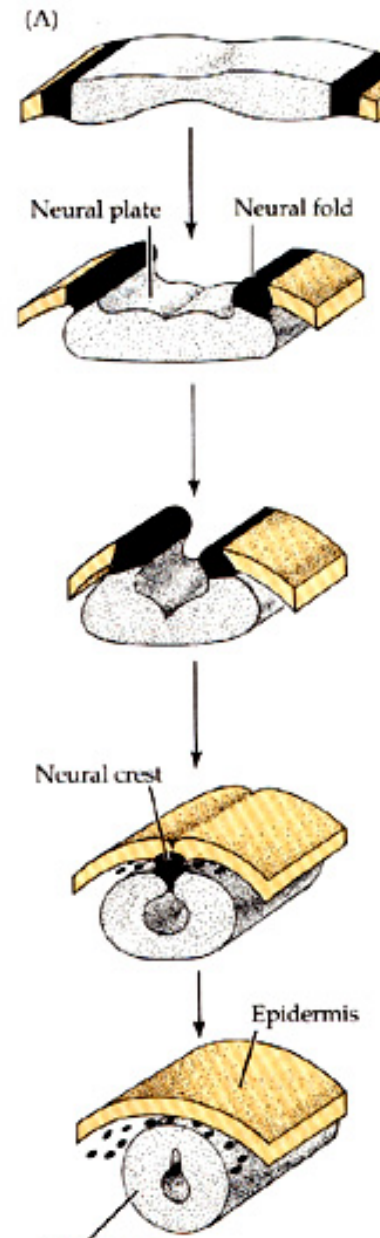
A. 背侧表面观 B. 纵切线和纵切面右半内侧观 C、D、E、F. 胚泡不同部位横断面

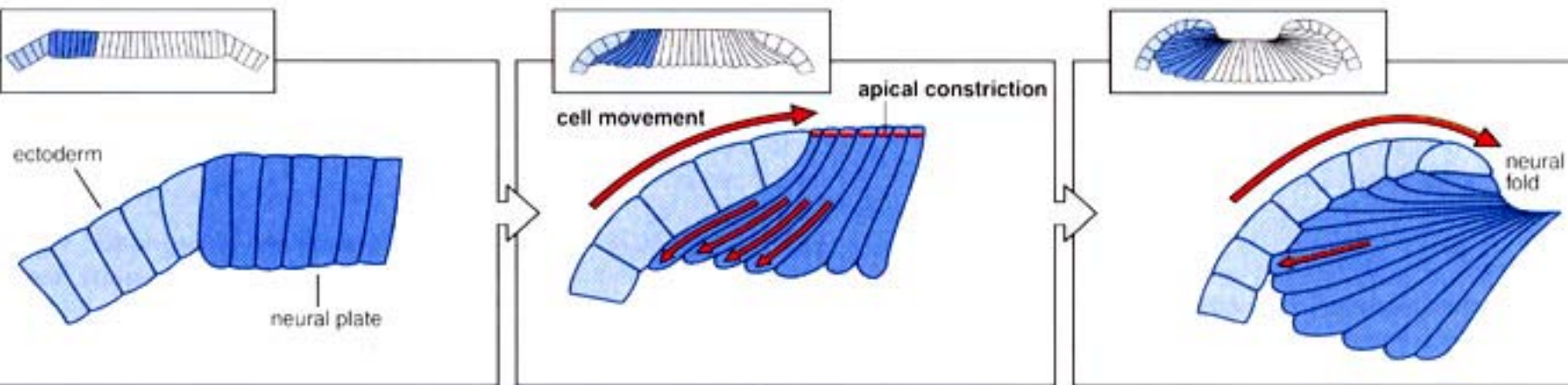
1. 胚盘 2. 原条 3. 原结 4. 脊索 5. 中胚层 (胚外部分) 6. 滋养层 7. 体腔 8. 内胚层 9. 体壁中胚层 10. 脏壁中胚层 11. 原肠 12. 外胚层 (滋养层)



Figure 7.2

Neurulation in amphibians and amniotes. (A) Diagrammatic representation of neural tube formation. The ectodermal cells are represented either as precursors of the neural crest (black) or as precursors of the epidermis (color). The ectoderm folds in at the most dorsal point, forming an outer epidermis and an inner neural tube connected by neural crest cells. (B) Photomicrographs of neurulation in a 2-day chick embryo. (C) Neural tube formation seen in transverse cross sections of the chick embryo at the region of the future midbrain (arrowheads in B). Each photograph in (C) corresponds to the one above it. (HF, head fold; HP, head process; HN, Hensen's node; M, midbrain; NP, neural plate.) (Photomicrographs courtesy of R. Nagele.)



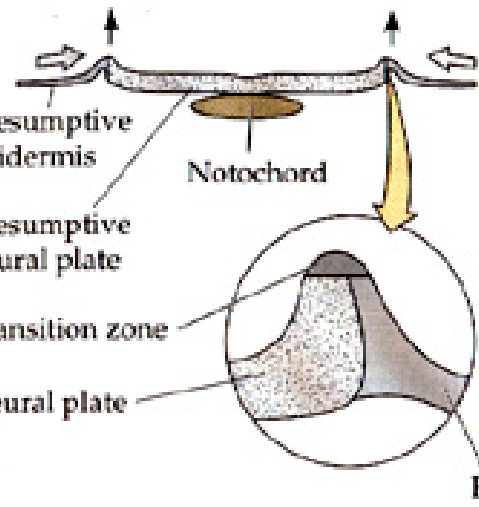


8.29 Change in cell shape and cell crawling may drive neural folding. Cells at the edge of the neural plate change their shape and appear to crawl along the undersurface of the adjacent

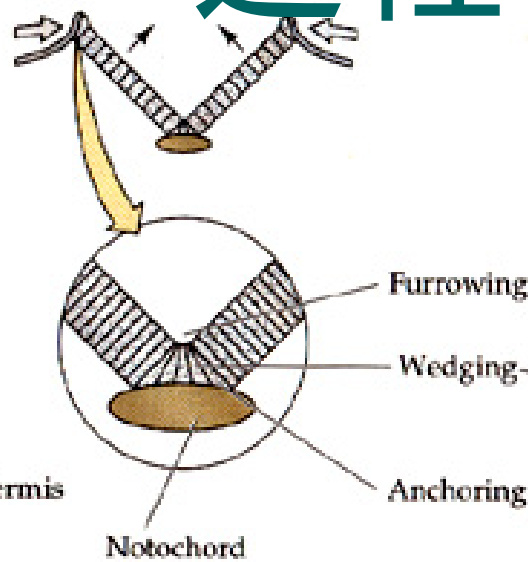
ectoderm. This may be partly responsible for causing the neural folds to develop.

Primary neurulation的过程

(A) Formation of neural folds



(B) Elevation of neural fold



(C)

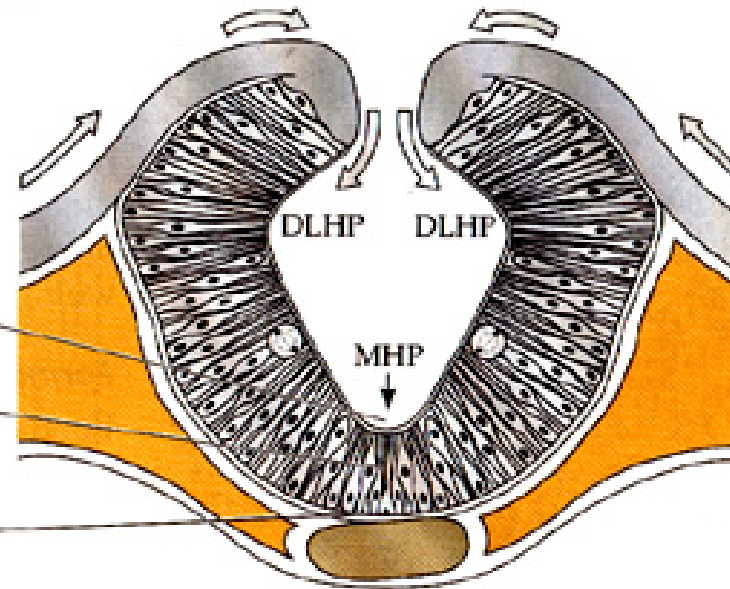
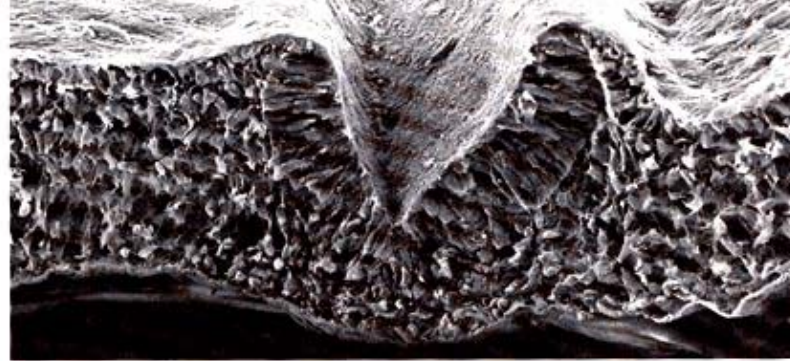


Figure 7.4

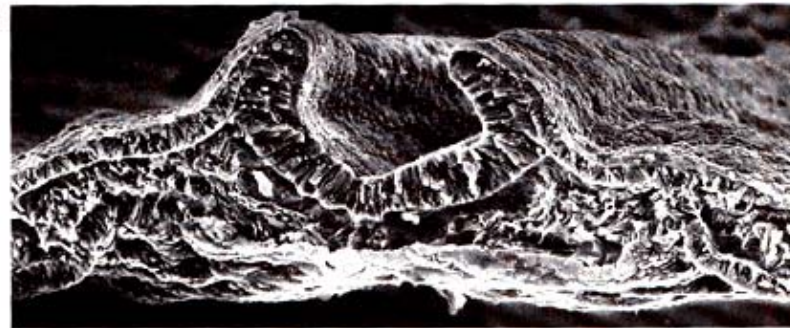
Schematic representation of the epithelial bending during chick neurulation. (A) Formation of neural folds occurs when presumptive epidermal cells move medially toward the center of the embryo. This presumptive epidermis pushes the neural plate under it as it moves. (B) As the midline cells of the neural plate (the floor plate cells) are

anchored to the notochord, the neural folds are elevated. These movements appear to be continued as the medially moving epidermis drags the neural plate with it, resulting in the apposition of the neural folds. (C) In the three hinge regions (the medial hinge point, MHP, and the two dorsolateral hinge positions, the DLHP), the neural plate cells change their length and constrict at their apices.

神经管形成的扫描电镜图



(B)



(C)

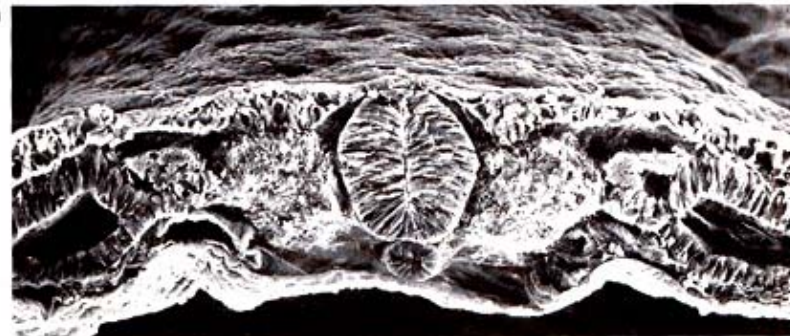
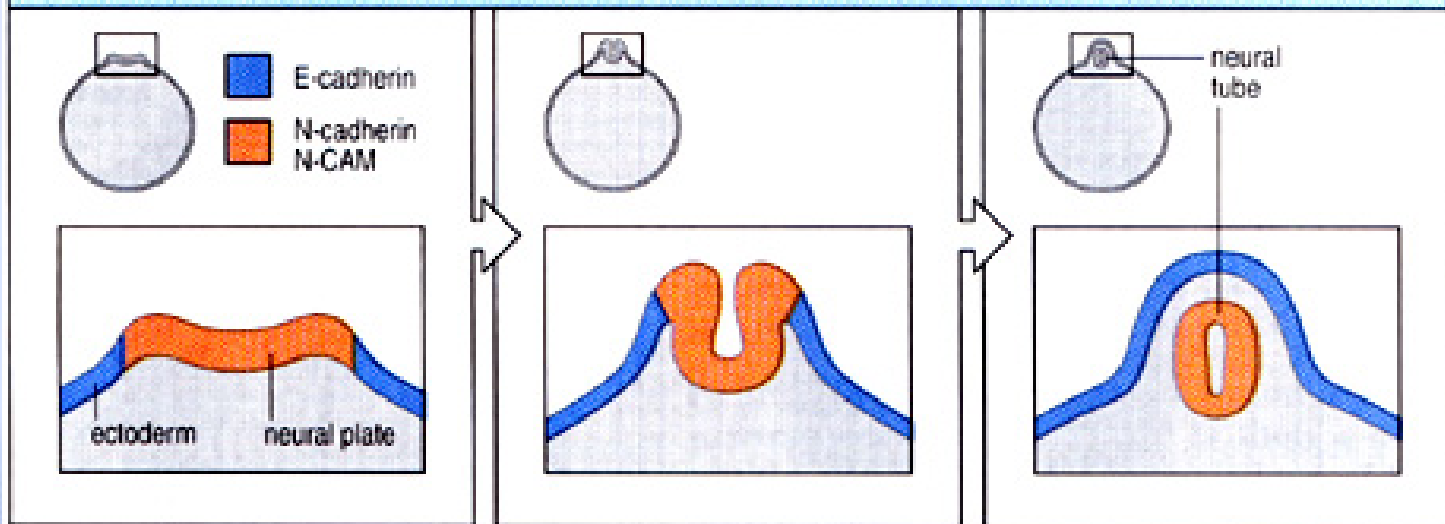


Figure 7.8

Scanning electron micrograph of neural tube formation in the chick embryo. (A) Neural groove surrounded by mesenchymal cells. (B) Elongated neural epithelium cells form a tube as the flattened epidermal cells are brought to the midline of the embryo. The MHP cells form a hinge at the bottom of the tube, while the neural plate cells attached to the basal area of the surface ectoderm form the dorsolateral hinge regions. These three hinges can be seen as furrows. (C) Neural tube formation is completed. The cells that had been the neural plate are now inside the tube. The presumptive epidermis lies atop the tube, and the neural tube is flanked on its sides by the mesodermal somites and on the bottom by the notochord.

Cadherin expression during neural tube formation in a *Xenopus* embryo



Misexpression of N-cadherin

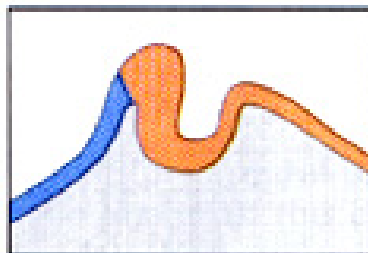
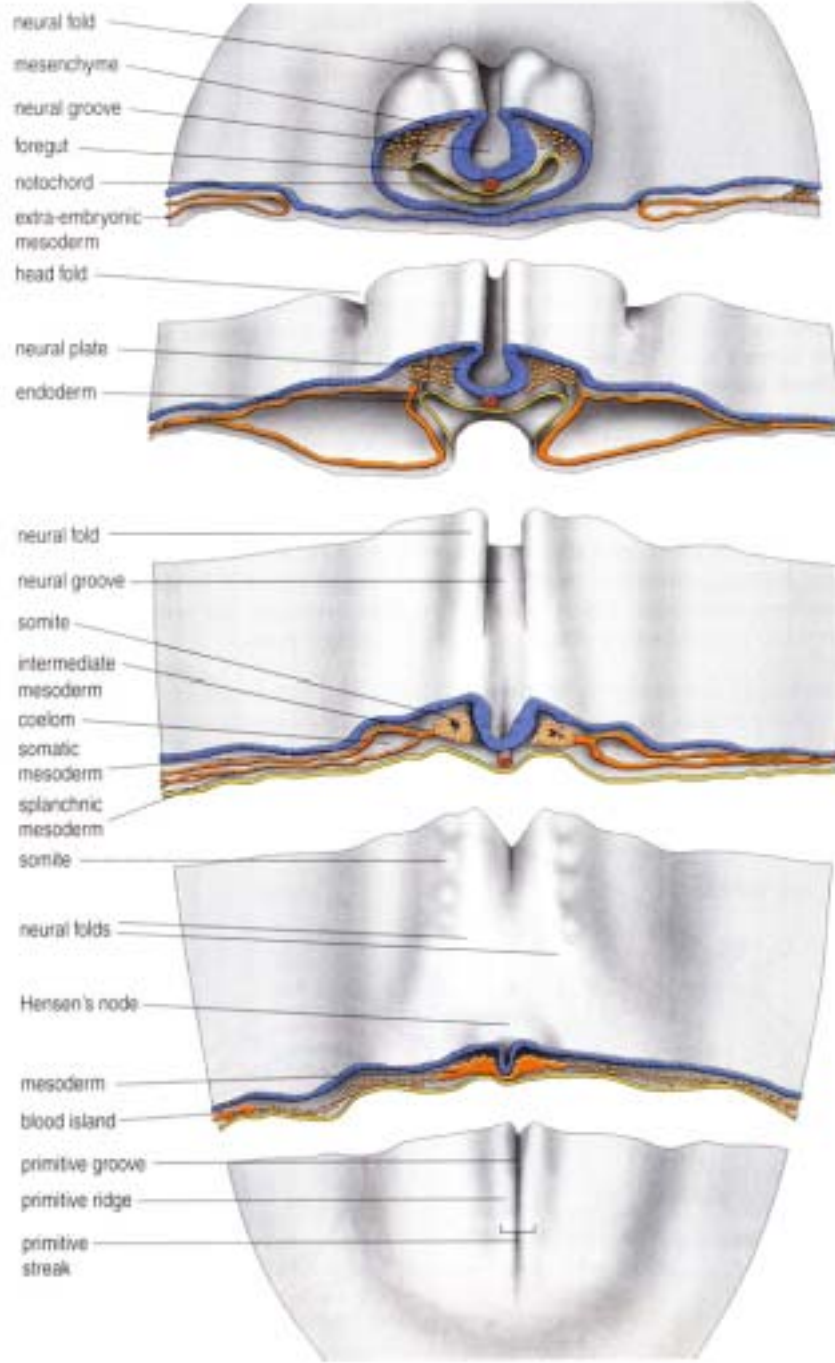


Fig. 8.31 Expression of cell adhesion molecules during neural tube formation in *Xenopus*. The cells of the neural plate express N-cadherin and the adjacent ectoderm expresses E-cadherin. If N-cadherin is misexpressed in the ectoderm on one side, there is a failure of the neural tube to separate at that site (right panel).



tube and mesoderm in the chick embryo. Once the notochord has formed, neurulation begins, following notochord formation in an anterior to posterior direction. The figure shows a series of sections along the antero-posterior axis of a chick embryo. Neurulation is well advanced at the anterior end (top two sections), where the head fold has already separated the future head from the rest of the blastoderm and the ventral body fold has brought endoderm from both sides of the body together to form the gut. During neurulation the neural plate changes shape: neural folds rise up on either side and form a tube when they meet in the midline. The mesenchymal mesoderm in this region will give rise to head structures. Further back (middle section), in the future trunk region of the embryo, notochord and somites have formed and neurulation is starting. At the posterior end, behind Hensen's node (bottom section), notochord formation, somite formation, and neurulation have not yet begun. The mesoderm internalized through the primitive streak starts to form structures appropriate to its position along the antero-posterior and dorso-ventral axes. For example, in the future trunk region, the intermediate mesoderm will form the mesodermal parts of the kidney, and the splanchnic mesoderm will give rise to the heart. The body fold will continue down the length of the embryo, forming the gut and also bringing paired organ rudiments that initially form on each side of the midline (e.g. those of the heart and dorsal aorta) together to form the final organs lying ventral to the gut. Blood islands, from which the first blood cells are produced, form from the ventral-most part of the lateral mesoderm.

After Patten, B.M.: 1971.

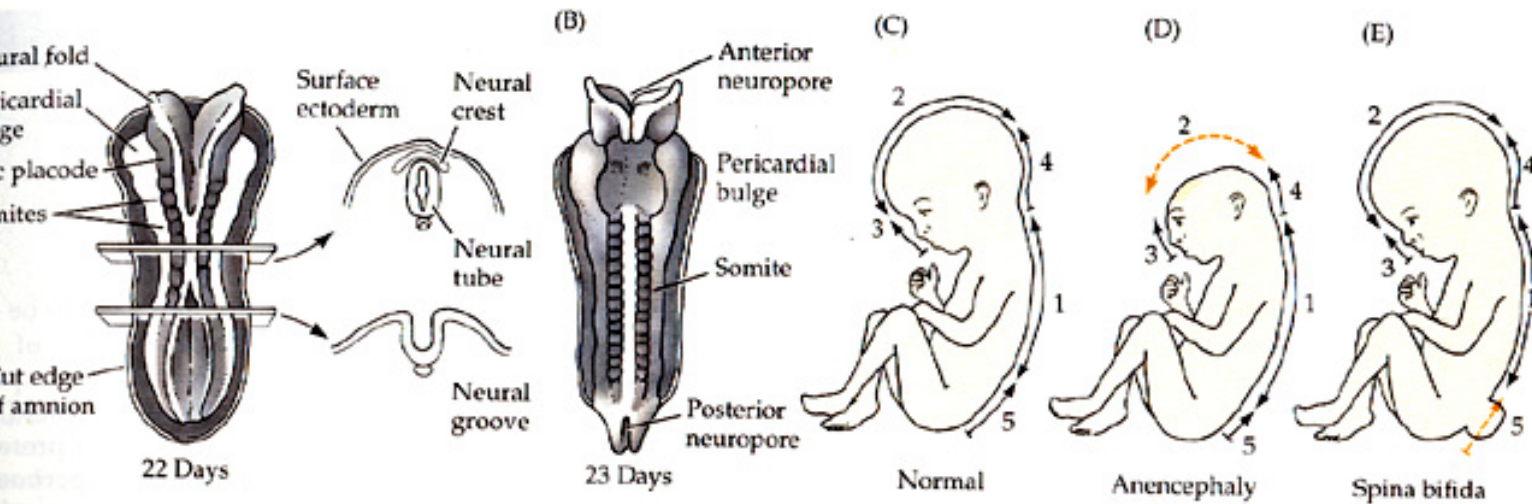
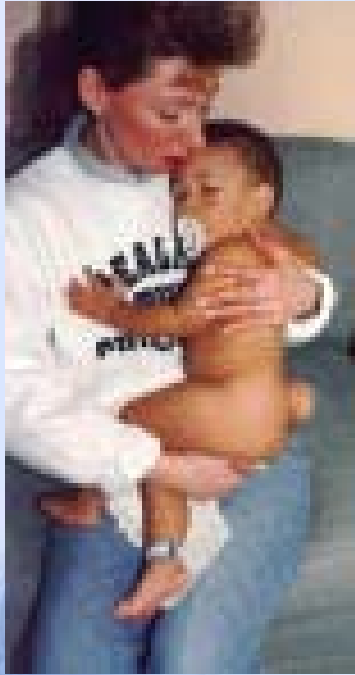


Figure 7.10
 Neurulation in human embryos. (A) Dorsal and transverse sections of a 22-day human embryo initiating neurulation. Both anterior and posterior neuropores are open to the amniotic fluid. (B) Dorsal view of a neurulating human embryo a day later. The anterior neuropore region is closing while the posterior neuropore remains open. (C) Regions of neural tube closure postulated by genetic evidence superimposed on newborn body. (D) Anencephaly due to failure of neural plate fusion in region 2. (E) Spina bifida due to failure of region 5 to fuse (or for the posteriormost neuropore to close). (C-E after Van Allen et al., 1993.)





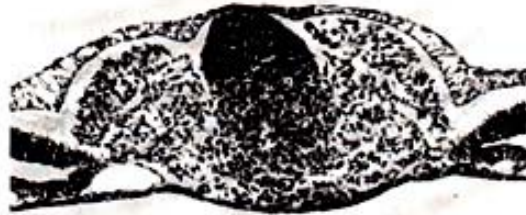
Secondary

Neurulation

(A)



(B)



(C)



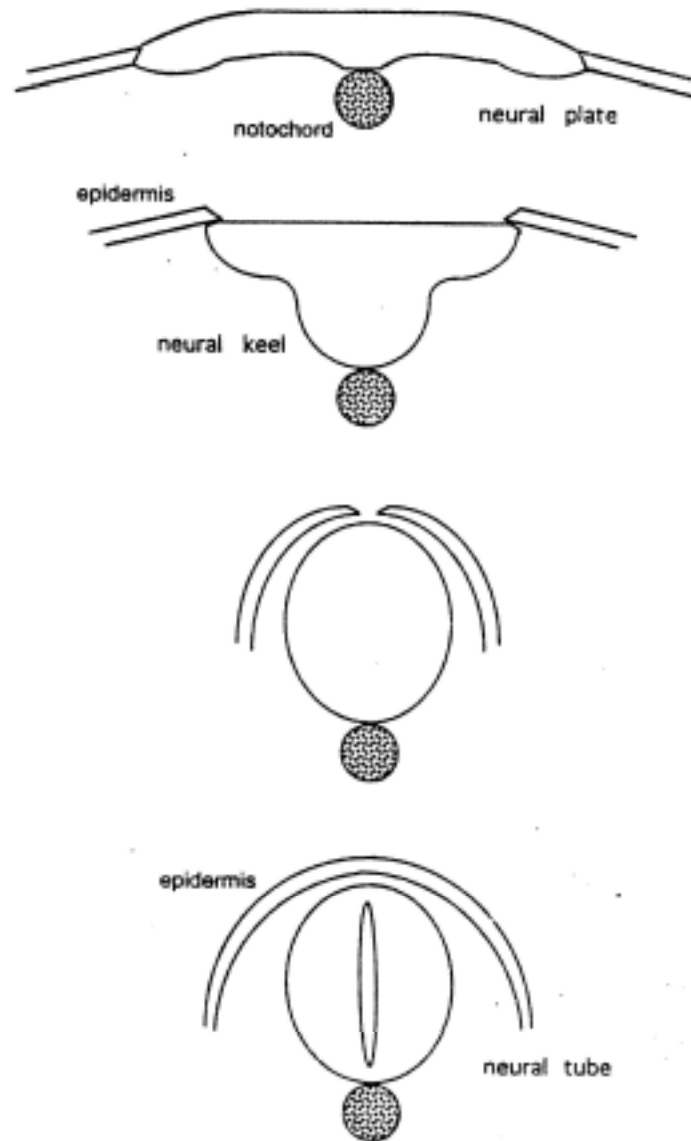
(D)



Figure 7-3

Formation of the secondary neural tube in the 25-somite chick embryo. (A) The medullary cord forming at the most caudal end of the chick tailbud. (B) Medullary cord slightly more anterior in the tailbud. (C) Cavitating neural tube and notochord forming. (D) Lumens coalesce to form the central canal of the neural tube.

斑马鱼神经管的形成



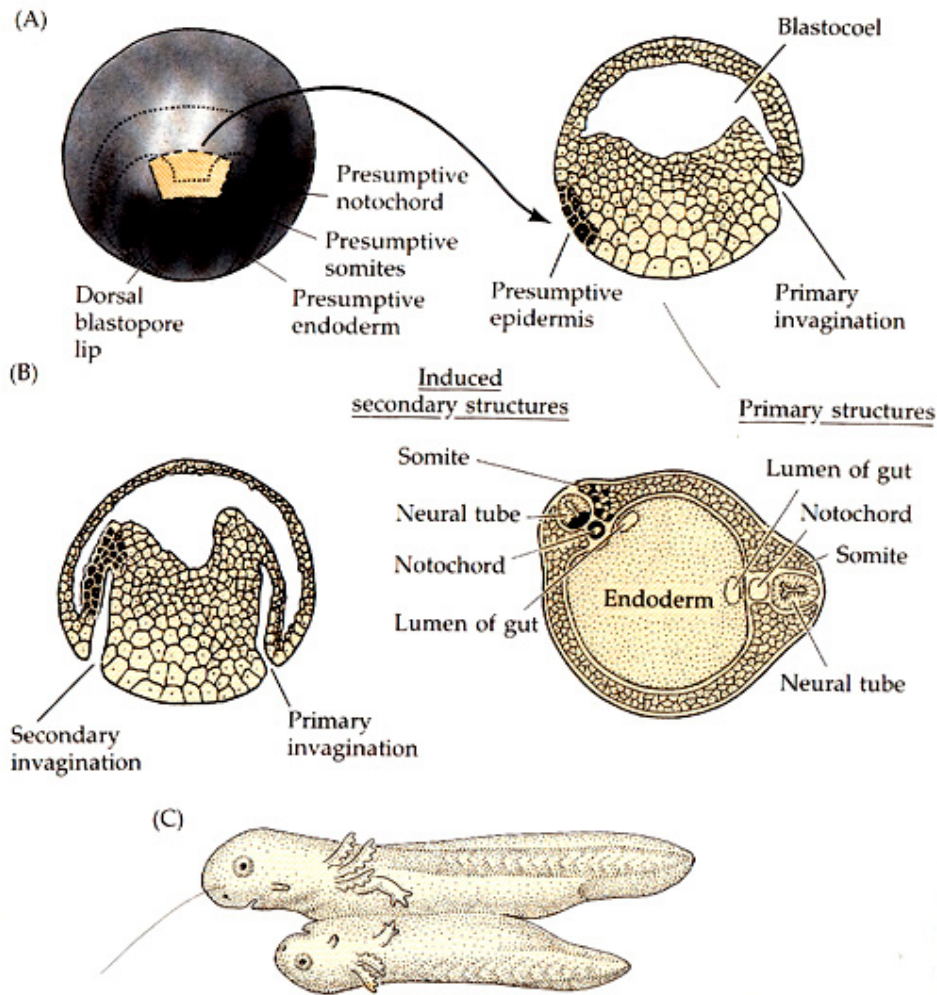


Figure 15.12

Self-differentiation of the dorsal blastopore lip tissue. (A) Dorsal blastopore lip from early gastrula is transplanted into another early gastrula in the region that normally becomes ventral epidermis. (B) Tissue invaginates and forms a second archenteron and then a second embryonic axis. Both donor and host tissues are seen in the new neural tube, notochord, and somites. (C) Eventually, a second embryo forms that is joined to the host.

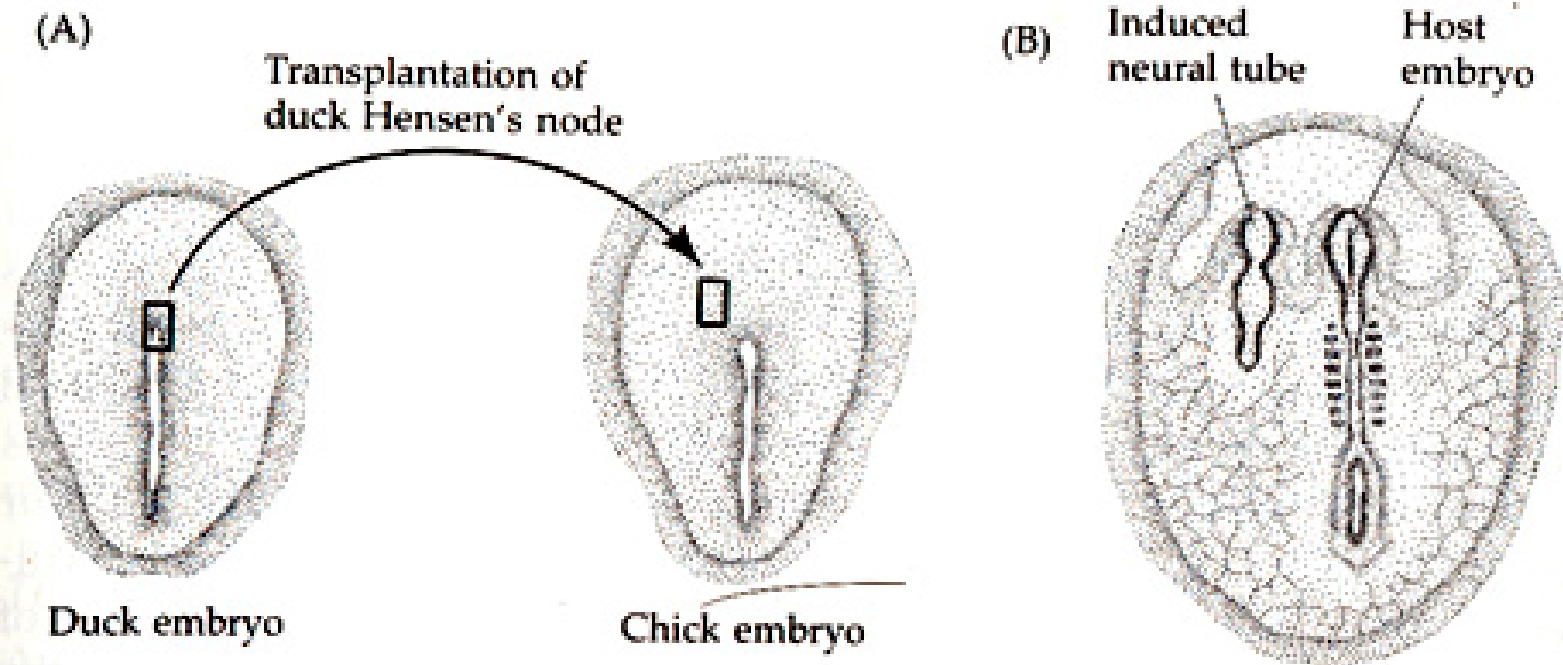


Figure 15.13

Induction of a new embryonic axis by Hensen's node. (A) Hensen's node tissue is removed from a duck embryo and implanted into a host chick embryo. (B) An accessory neural tube is induced at the graft site. (After Waddington, 1933.)

八、胚层分化和中轴器官形成

- 胚层分化成各种组织，称为组织发生；
- 由各种组织形成各种器官的过程，称为器官发生。

（一）胚体的形成

- 随着发育的进行，由于胚盘各部位的生长速度不同，扁平形的胚盘周区向腹侧陷入并向中央集中，逐渐使胚体变为圆柱形。这时胚盘中部的生长速度快于边缘部，外胚层的生长速度快于内胚层，使外胚层包在胚体的外部，而内胚层包在内部，形成头尾方向的原始消化管。

- 由于胚盘头部的生长速度快于尾部，前后方向的速度又快于左右方向，胚盘卷折形成头大尾小的筒状结构，且胚盘的边缘也向胚体的腹部汇合，最终在胚体腹侧形成条状的原始脐带。胚体通过边缘形成头褶、尾褶和左右褶，使胚体凸入羊膜腔的羊水中。

(二) 外胚层分化

- 由外胚层发育而来的主要有神经系统、感觉器官、皮肤的表皮层、毛和皮肤腺等。脊索出现后，诱导其背侧的外胚层增厚形成一条板状结构，称神经板。以后神经板随着脊索的生长而增长，且头部宽于尾部，神经板的两侧向上突起形成神经褶，中间凹陷成神经沟。

- 以后，神经褶在背侧合并围成神经管。神经管以后分化形成前脑、中脑、后脑及脊髓等中枢神经系统，以及松果体、神经垂体和视网膜等。在神经褶闭合形成神经管时，一部分细胞分离出来，在神经管的背外侧形成两条纵行的细胞索，称神经嵴。神经嵴以后形成周围神经系统及肾上腺髓质等。

- 家畜皮肤的表皮及衍生物由外胚层发育；真皮及皮下组织由中胚层发育而成。家畜毛和皮肤腺的发生，较其他器官晚，绵羊毛囊原基在胚胎发育50—110天左右发生。

家畜毛纤维长出以前，先在皮内形成毛囊。毛囊发生时，由表皮向真皮形成毛囊原基及其侧旁的汗腺、皮脂腺原基。毛囊原基初呈芽状，随后变长变大，外包结缔组织形成毛囊结构。毛纤维在毛囊内角化后长出体表。

- 根据毛囊发生的时间和形态结构，绵羊的毛囊可分为初级毛囊和次级毛囊。伴随初级毛囊发生的有汗腺、皮脂腺等附属结构；伴随次级毛囊的皮脂腺小，缺乏汗腺。初级毛囊发生早，约在羊胚50—90天时发生；次级毛囊发生晚，在90天以后出现。羔羊出生后，毛囊一般不再发生。
- 绵羊皮肤内由初级毛囊和次级毛囊组成毛囊群。每个毛囊群一般由三个初级毛囊和数量不等的次级毛囊（粗毛羊少，细毛羊多）组成。毛囊长出的毛纤维构成毛被。初级毛囊和部分次级毛囊的毛纤维，在胚胎中后期长出体表；有些次级毛囊要在羔羊出生以后，才能长出毛纤维，或者潜在皮内退化消失。

(三) 内胚层分化

- 由于体褶发生，胚体逐渐隆突于胚盘之上，胚内和胚外两部分的界限更加清楚。内胚层在胚体下部缩细，胚内为原肠，胚外为卵黄囊。原肠在脊索下方，纵贯前后，可分为前肠、中肠和后肠。中肠与卵黄囊连通。随着胚胎发育，前肠形成食管和胃，中肠形成小肠，后肠形成大肠。前肠前端头部下面与内陷的外胚层相贴近，形成口咽膜，口咽膜破裂形成口。后肠后端尾部腹侧与内陷的外胚层相贴近形成肛膜，后破裂形成肛门。

- 在发育过程中，初为直的肠管，后来形成肠袢。肠袢向脐部垂下形成降支和升支。两支相连处有卵黄囊柄与卵黄囊相连。在升支的初段，出现盲肠原基，形成盲肠；在胃后中肠的起始部的背腹侧，有肝胰的原基向外突出，形成肝脏和胰脏。其余肠段弯转盘曲形成小肠和大肠。在咽的后部，原肠腹侧形成一个盲管。盲管末端分叉形成气管和肺的原基。以后形成喉、气管、支气管和肺。

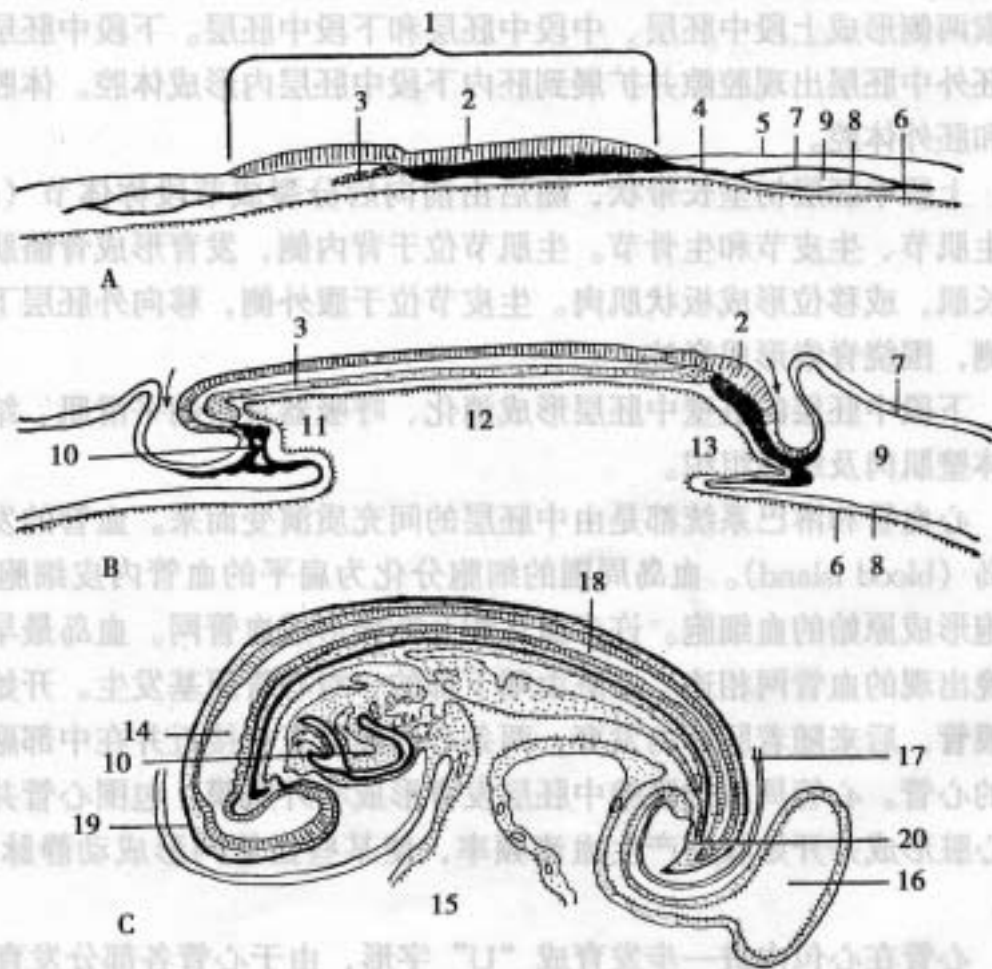


图 11-11 猪胚胚体分出与卵黄囊、尿囊形成

A. 原条期 B. 体节开始形成期 C. 25对体节期

1. 胚盘 2. 原条 3. 脊索 4. 中胚层 5. 滋养层 6. 内胚层 7. 体壁中胚层
 8. 脏壁中胚层 9. 胚外体腔 10. 心脏 11. 前肠 12. 中肠 13. 后肠 14. 脑
 15. 卵黄囊 16. 尿囊 17. 羊膜断端 18. 脊髓 19. 头部 20. 尾部

- 应该指出:内胚层细胞仅仅形成消化和呼吸系统的上皮和腺体 (口咽和肛门的上皮除外), 其余组织除神经成分外, 均由脏壁中胚层发生。

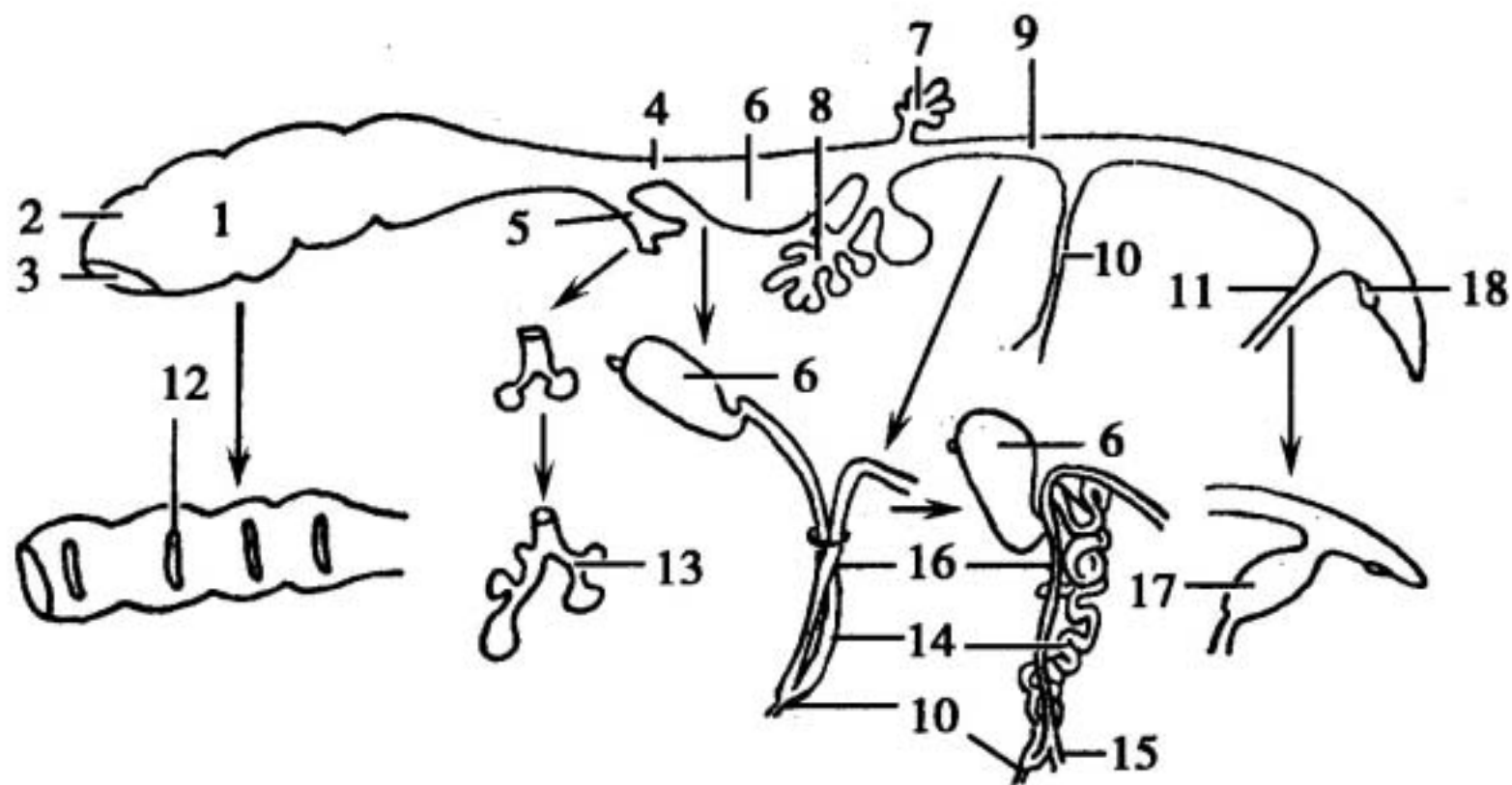


图 11-12 内胚层分化、消化呼吸器官形成模式图

1. 咽部 2. 咽囊 3. 口 4. 食管 5. 肺芽 6. 胃 7. 胰 8. 肝和胆囊 9. 小肠 10. 卵黄柄 11. 尿囊柄 12. 鳃裂 13. 支气管树 14. 肠环 15. 盲肠 16. 结肠 17. 膀胱 18. 肛门

(四) 中胚层分化

畜体全身的肌组织、结缔组织、心血管淋巴系统和泌尿生殖系统，都由中胚层分化形成。它们对畜体的物质代谢、运动、保卫和繁殖起重要作用。随着三胚层的形成，中胚层进一步分化。在脊索两侧形成上段中胚层、中段中胚层和下段中胚层。下段中胚层延续至胚外称胚外中胚层。随后胚外中胚层出现腔隙并扩展到胚内下段中胚层内形成体腔。体腔延续胚体内外，分别称胚内体腔和胚外体腔。

1、上段中胚层

上段中胚层初呈长带状，随后由前向后分裂成节段称体节。体节进一步发育分化为生肌节、生皮节和生骨节。生肌节位于背内侧，发育形成骨铬肌，分节的骨骼肌相互合并成大块长肌，或移位形成板状肌肉。生皮节位于腹外侧，移向外胚层下形成皮肤真皮。生骨节位于腹内侧，围绕脊索形成脊柱。

■2、下段中胚层

■ 下段中胚层的脏壁中胚层形成消化、呼吸器官壁的平滑肌、结缔组织和浆膜。体壁中胚层形成体壁肌肉及结缔组织。

■ 心血管和淋巴系统都是由中胚层的间充质演变而来。血管的发生，始于间充质细胞聚集形成血岛。血岛周围的细胞分化为扁平的血管内皮细胞形成原始血管。血岛中央的细胞形成原始的血细胞。许多血岛相互衔接形成血管网。血岛最早出现在卵黄囊上，以后与体内较晚出现的血管网相连。心脏由咽下部的一对心管原基发生。开始由脏壁中胚层分化形成1对心内膜管，后来随着胚体的发育，两条心内膜管互相接近并在中部融合，形成一条前后端都有2个权的心管。心管周围的脏壁中胚层发育形成心外肌膜，包围心管并分化形成心肌层与心外膜。由于心脏形成并开始收缩产生血流频率使某些血管网形成动静脉主干，从而形成原始的血管系统。

■ 心管在心包内进一步发育成 "U"字形，由于心管各部分发育不均衡，以致使外形扭曲，内部生出隔膜，将心脏分为心房和心室。

■3、中段中胚层

■ 中段中胚层又叫生肾节，形成泌尿生殖器官。肾脏的发生重演系统发生过程，先后形成前肾、中肾和后肾。其发生时间、位置和结构都不相同。前肾存在时间短，不起泌尿作用就消失；中肾及中肾管是胚胎早期的排泄器官；中肾消失，被终身存在的后肾代替。后肾发生时，中肾管离胚胎泄殖腔不远处的背侧形成突起，向前生长形成输尿管并伸入肾内形成肾盂、肾盏和肾乳头管等。

■ 家畜的生殖腺及主要生殖管道都由中胚层发生。当中肾还是胚胎主要排泄器官的时候，生殖腺在中肾腹内侧发育，该处脏中胚层细胞形成上皮团，突入中肾组织内形成生殖嵴。随后生殖嵴与中肾分开。生殖嵴表层为间皮和由卵黄囊内胚层迁移而来的原始生殖细胞构成的生殖上皮，内部为索状细胞团和间充质。索状细胞团是由表层细胞向内增殖而成。这个时期的生殖腺在形态结构上没有性别差异，属未分化时期或中性时期。这时，尚未分化的生殖管道也无性别差异，即在两条中肾管的外侧都有两条由脏中胚层内凹形成的缪勒氏管存在。在性别分化时，生殖腺、中肾管和缪勒氏管都发生相应的变化。当胚胎向雄性发展、生殖腺变为睾丸时，索状细胞团变成精小管索。精小管索间的间充质细胞构成间质组织。随后精小管变成曲细精管。这时，中肾小管与睾丸相连，形成睾丸输出小管；中肾管变成附睾管和输精管；缪勒氏管退化成为某些家畜残留的雄性子宫。

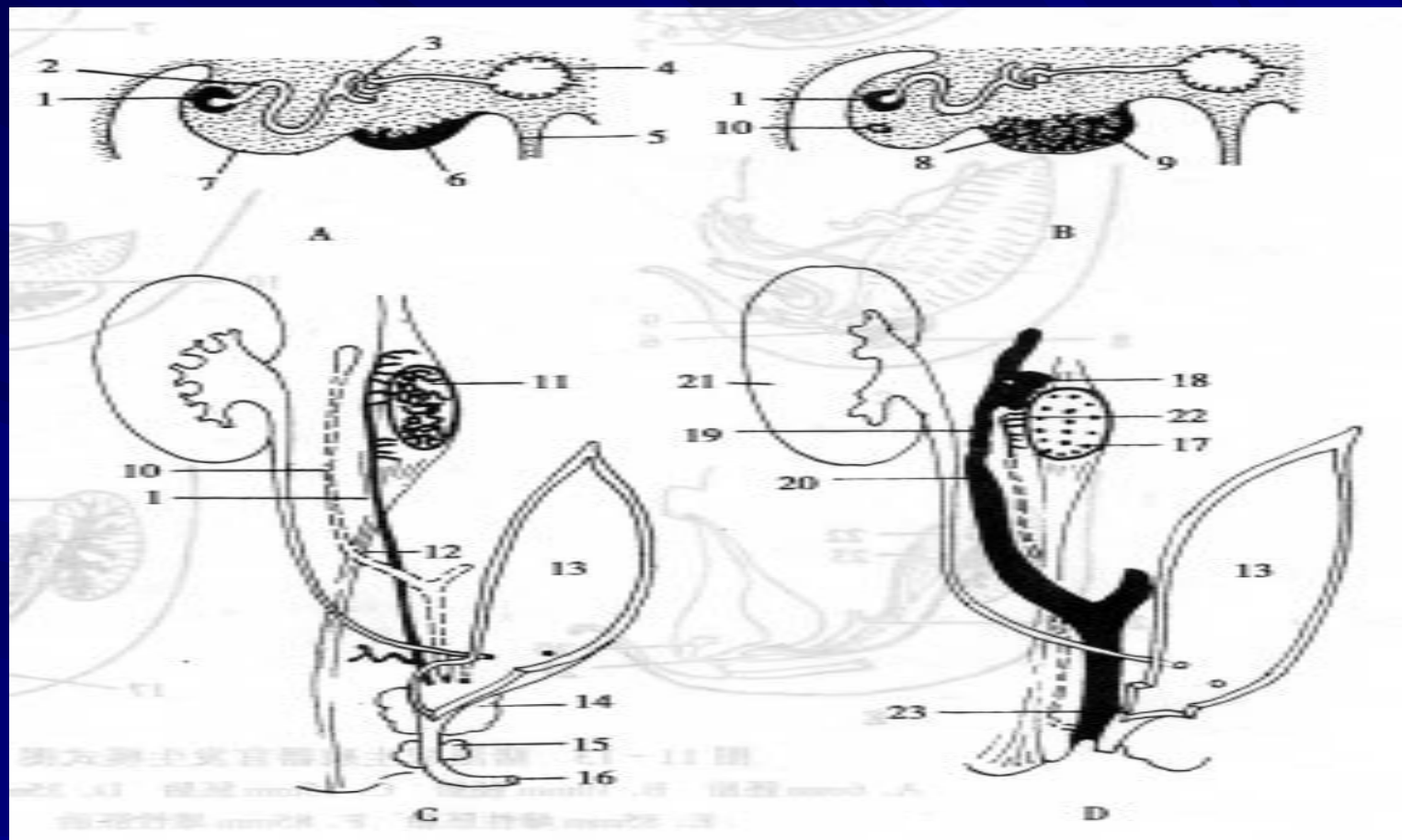


图 11-14 哺乳动物胚胎生殖器官的发育

A、B. 哺乳类生殖嵴的发育（无性别期的左半侧横断） C. 雄性生殖器官（右半侧腹侧） D. 雌性生殖器官（右半侧腹侧）

- 1. 中肾管 2. 中肾小管 3. 肾小球 4. 主动脉 5. 背肠系膜 6. 生殖嵴 7. 中肾嵴 8. 原始性索 9. 体腔上皮增生 10. 缪勒氏管 11. 睾丸 12. 雄性子宫
- 13. 膀胱 14. 前列腺 15. 尿道球腺 16. 尿道 17. 卵巢 18. 输卵管口 19. 输卵管
- 20. 子宫角 21. 后肾 22. 卵巢冠 23. 阴道

■ 当胚胎向雌性发展、生殖腺变为卵巢时，细胞索分散成许多细胞团，再分化形成原始卵泡。有些原始卵泡在胚胎期发育，出生后逐渐退化，有些原始的卵泡直至性成熟后才逐渐分别发育成熟。缪勒氏管前段发育成输卵管，中段形成子宫角，后段融合形成子宫体和阴道前部。雌雄间性在家畜中偶尔遇到，即在同一个体身上具有雌雄两性的生殖器官或是其中的一部分。这种现象是由胚胎发育时期性分化异常所引起。

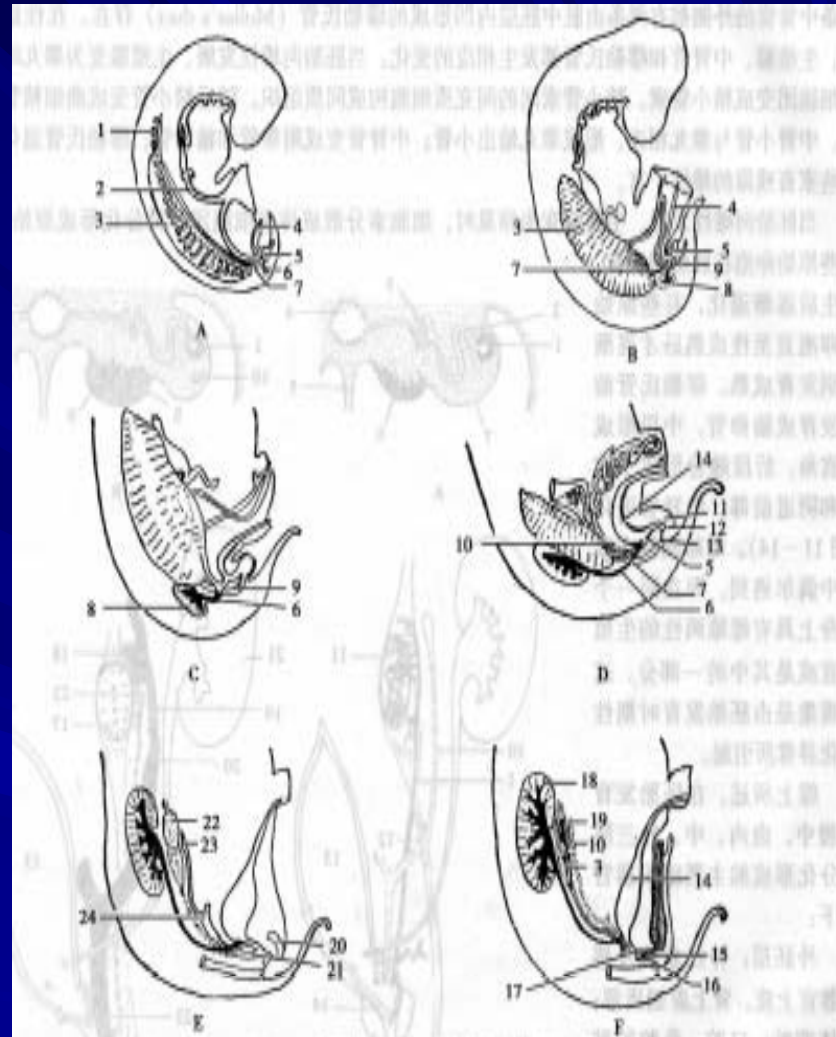


图 11-13 猪泌尿生殖器官发生模式图

A. 6mm 胚胎 B. 10mm 胚胎 C. 15mm 胚胎 D. 35mm 胚胎

E. 85mm 雌性胚胎 F. 85mm 雄性胚胎

1. 前肾 2. 消化道 3. 中肾 4. 尿囊 5. 泄殖腔 6. 后肾管 7. 中肾管 8. 后肾 9. 直肠
 10. 缪勒氏管 11. 生殖突 12. 尿生殖孔 13. 肛门 14. 膀胱 15. 尿道球腺 16. 前列腺
 17. 尿道 18. 集合小管 19. 睾丸 20. 阴蒂 21. 阴道 22. 卵巢 23. 输

■ 综上所述，在胚胎发育过程中，由内、中、外三胚层分化形成的主要组织器官如下：

■ 外胚层：神经系统及感觉器官上皮。肾上腺髓质部；垂体前叶；口腔、鼻腔的黏膜上皮；肛门、生殖道和尿道末端部分的上皮；皮肤的表皮及其衍生物、蹄、角、毛、汗腺、皮脂腺和乳腺上皮。

■ 中胚层：各种肌组织；各种结缔组织；心血管淋巴系统；肾上腺皮质部；生殖器官及泌尿器官的大部分；体腔上皮等。

■ 内胚层：消化系统从咽到直肠末端的上皮及壁内、壁外腺上皮；呼吸系统从喉到肺泡的上皮；甲状腺、甲状旁腺和胸腺上皮等。

■ 在器官形成过程中，由两种或两种以上胚层分化成的组织结合起来形成一个器官。

九、胎膜

家畜胚胎由于卵内所含的卵黄物质很少，在母体子宫内发育，借助胎膜和胎盘与母体进行物质交换，吸取营养，排泄废物，创造胚胎发育的条件，保证胎儿正常发育。

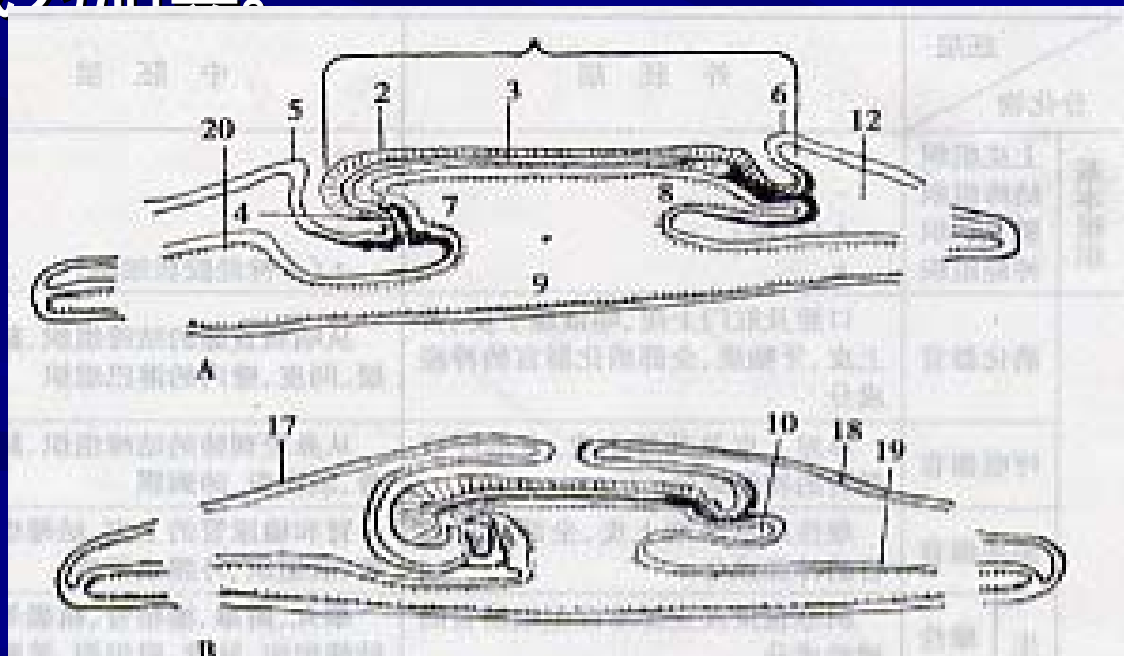
■ 家畜的胎膜也称胚外膜，依据结构部位和功能可分为卵黄囊、羊膜、绒毛膜和尿囊。

1、羊膜和绒毛膜

■ 早期胚胎体褶形成时，胚盘周围的胚外外胚层和胚外体壁中胚层，向胚体上方摺起形成羊膜摺。猪胚15天左右，羊膜摺在背侧会合形成羊膜和绒毛膜。羊膜在内，直接包围胎儿；绒毛膜在外，包围所有其他胎膜，并与子宫黏膜直接接触。羊膜和绒毛膜的胚层结构相同，但位置相反。羊膜壁的外胚层在内，体壁中胚层在外；绒毛膜壁的体壁中胚层在内，外胚层在外。

■

■ 羊膜腔内充满羊水。羊水由羊膜上皮细胞分泌。猪妊娠初期羊水较少，随后羊水分泌量增多，妊娠末期又重新减少。羊水呈弱碱性，所含成分不甚稳定，其中有蛋白质、脂肪、葡萄糖、果糖、无机盐、黏蛋白、尿素等，此外，还有脱落上皮和白细胞。随着胚胎胃肠发育和吞咽反射建立以后，胚胎吞食羊水，这种吞食现象，妊娠后期尤为显著。消化残渣积蓄在肠内成为胎粪。



■ 胎儿在羊水的液体环境中生长发育，既能调节温度，又能缓冲来自各方面的压力，保证胎儿正常的形态发生。分娩时，胎膜破裂，羊水连同尿囊液外流，能扩张子宫颈，润滑产道，有利于胎儿分娩。

■ 由于尿囊的接触与迅速扩大，绒毛膜与尿囊壁紧密相贴发育成尿囊绒毛膜。尿囊绒毛膜的表面着生绒毛与子宫黏膜紧密联系，通过渗透进行物质交换。这就构成了胎盘的基础。

2.卵黄囊

■ 家畜卵的卵黄含量少，但在胚胎发育过程中仍有卵黄囊形成。早在原肠胚形成时期，由于体褶发生，胚体上升，原肠缢缩成胚内的原肠和胚外的卵黄囊两个部分。卵黄囊早期较大，很快缩小退化。猪在胚胎13天左右形成，17天开始退化，1个月左右完全消失。牛、羊和猪的卵黄囊对胚胎营养作用不大。马的卵黄囊与绒毛膜接触，形成卵黄囊胎盘，并有丰富的血管吸收子宫乳，作为胚胎早期的营养。

3.尿囊 尿囊由后肠末端腹侧向外突出的盲囊发育形成。尿囊壁的结构同肠壁，由内层的胚外内胚层和外层的胚外脏壁中胚层构成。猪在13天时尿囊发生，突向胚外体腔。16天左右与绒毛膜接触，随后逐渐形成尿囊绒毛膜胎盘。通过分布于尿囊上的脐血管到达胎盘，与母体间进行物质交换。尿囊发展迅速，1个月左右扩展至整个胚外体腔并包围羊膜。但尿囊的形状和在胚外体腔内扩展的程度因家畜种类而异。马的尿囊呈盲囊状，充满整个胚外体腔，完全包围羊膜，形成尿囊绒毛膜和尿囊羊膜；牛、羊和猪的尿囊分成左右两支，且尿囊未完全包围羊膜。除有尿囊绒毛膜和尿囊羊膜外，还有羊膜绒毛膜存在。尿囊腔内贮存尿囊液。尿囊液初期清亮，以后变成黄色至淡褐色，内含胎儿排泄的废物。尿囊通过尿囊柄与胚体后肠部分相连通。胎儿出生后随着脐带的断离，残留在胚体内的尿囊柄闭合形成膀胱的韧带。多胎动物猪胚的胎膜，在子宫内常常相互靠接；多胎羊胎膜上的血管也很少相互吻合。然而，雌雄孪生犊牛胎膜上的脐血管常常吻合，雌雄胎儿的血液相互交流，而引起雌犊生殖器官发育不全的间性现象。

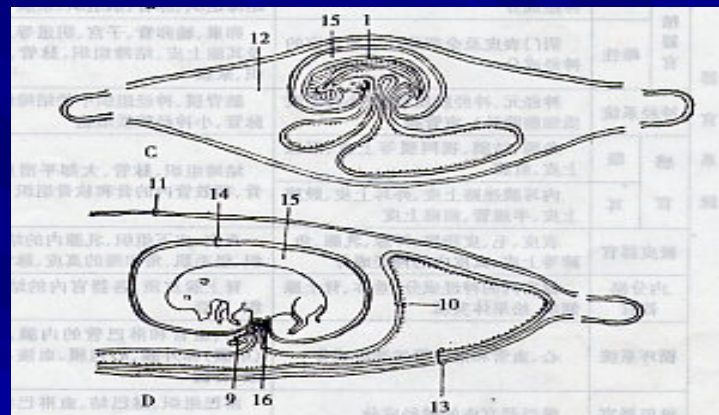


图 11-15 猪胚胎膜形成

- A. 体节开始形成期 B. 约 15 体节期 C. 约 25 体节期 D. 猪胚长 30mm
 1. 胚胎 2. 神经板 3. 脊索 4. 心脏 5. 羊膜头褶 6. 羊膜尾褶 7. 前肠
 8. 后肠 9. 卵黄囊 10. 尿囊 11. 绒毛膜 12. 胚外体腔 13. 尿囊绒毛膜
 14. 羊膜 15. 羊膜腔 16. 脐带 17. 胚外外胚层 18. 胚外体壁中胚层 19. 胚外脏壁 中胚层 20. 胚外内胚层

十、胎盘

胎盘由母体子宫内壁和胚胎的绒毛膜，即母体胎盘和胎儿胎盘组成。胚胎在母体子宫内发育，通过胎盘从母体获得营养并进行物质交换。随着胚胎的生长发育，胎儿和母体间通过胎盘的物质通透量不断增加。因而胎盘的形态结构也发生相应的变化，如胎盘体积增大，皱壁形成，绒毛和微绒毛的发生等，以此增加通透面积，适应功能变化的要求。胎盘通透面积的增大，在胚胎发育前半期特别明显。

家畜的胎盘属于尿囊绒毛膜胎盘，由尿囊部分的绒毛膜与母体子宫壁之间建立相互联系，营养通过尿囊血管传递给胚胎。依据胎盘的形态和尿囊绒毛膜上绒毛的分布不同，家畜的胎盘可以分为四种类型：

1、分散性胎盘 如猪、马。除尿囊绒毛膜的两端外，这种胎盘的绒毛或皱摺比较均匀地分布在绒毛膜表面。绒毛(马)或皱摺(猪)与子宫内壁相应的凹陷部分相嵌合。

2、绒毛叶胎盘 如牛、羊、山羊，胎盘的绒毛膜上的绒毛，在绒毛膜表面集合成叶状，构成绒毛叶或称子叶。子叶与子宫内壁上的子宫肉阜紧密嵌合。羊的子宫肉阜上有一大的凹窝，绒毛叶伸入凹窝内构成胎盘块；牛的子宫肉阜上无凹窝，由绒毛叶包裹子宫肉阜而构成胎盘块。

3、环状胎盘 此类胎盘见于猫、狗等肉食兽。胎儿绒毛膜上的绒毛仅分布在绒毛膜的中段(相当胚体腰部水平位)，呈一窄环带状。

4、盘状胎盘 胎儿绒毛膜上的绒毛集中在一盘状区域内。兔和人的胎盘属这种类型。

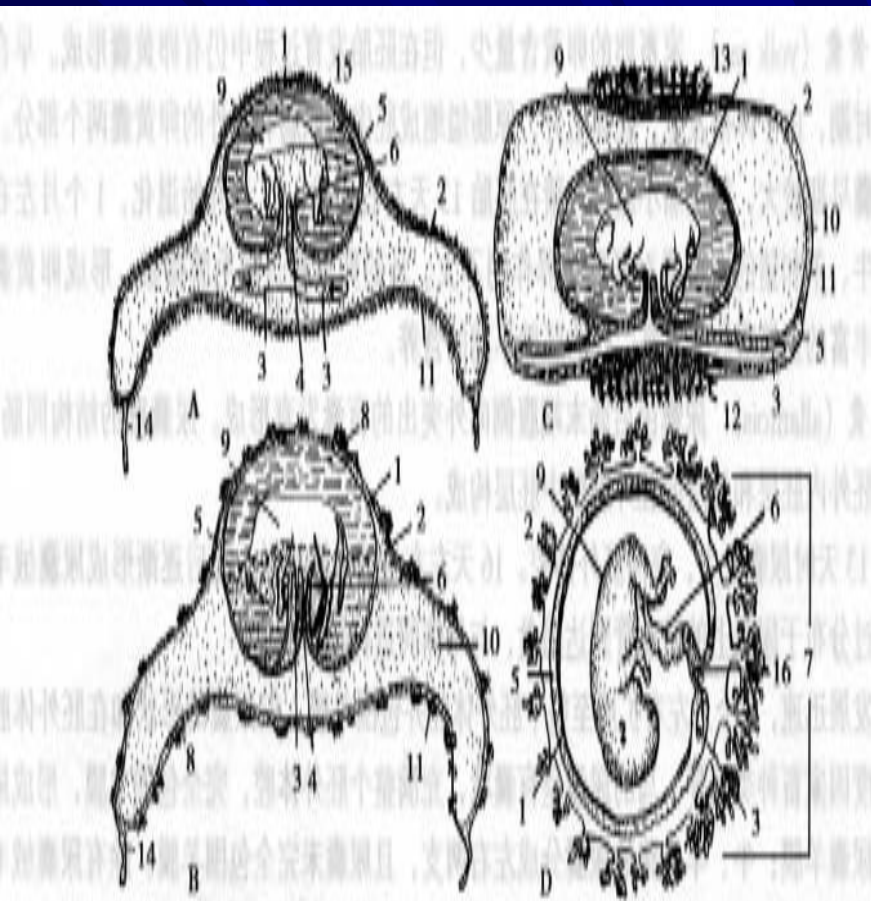


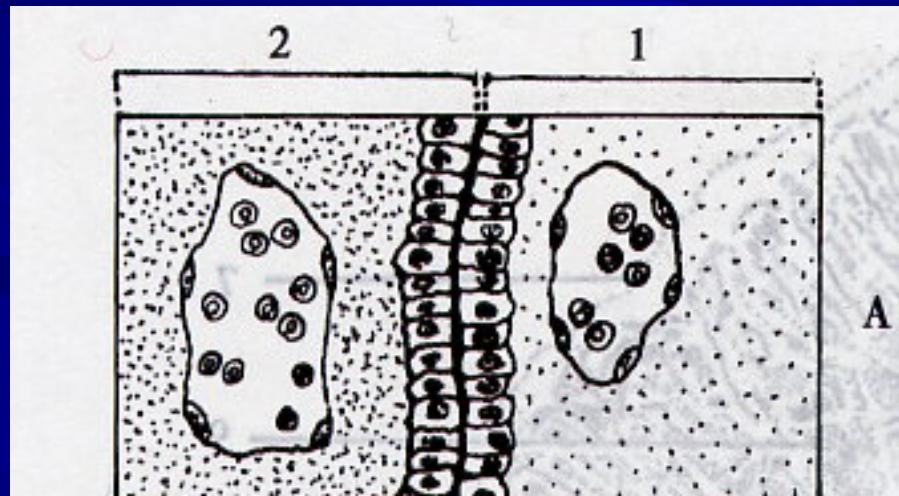
图 11-16 哺乳动物胎盘模式图

A. 猪分散型胎盘 (综合 Michel, 1983) B. 牛子叶型胎盘 (综合 Michel, 1983) C. 肉食兽环状胎盘 (综合 Michel, 1983) D. 人盘状胎盘 (综合 Patton, 1953)

- 1. 羊膜 2. 绒毛膜 3. 卵黄囊 4. 尿囊管 5. 胚外体腔 6. 脐带 7. 盘状胎盘 8. 子叶
- 9. 胎儿 10. 尿囊 11. 尿囊绒毛膜 12. 绒毛环 13. 环状胎盘 14. 退化的绒毛膜端
- 15. 卵 16. 尿囊血管

另外，根据胎盘的组织和结构以及对母体子宫内壁的破坏程度，又可将高等哺乳动物的胎盘分为以下四类。

(1) 上皮绒毛膜胎盘 这种胎盘屏障的组织层次结构比较完整，物质由母体血液渗透到胎儿血液中或反向渗透时，都要经过六道屏障：母体血管内皮；子宫内壁结缔组织；子宫内壁上皮；胎儿绒毛膜上皮；绒毛膜间充质；绒毛膜血管内皮。家畜中的猪、马、牛、羊属这种胎盘。



这种胎盘的绒毛膜上皮和子宫内壁上皮均比较完整，绒毛嵌合于子宫内壁上皮的凹陷内。电镜观察表明，绒毛膜上皮细胞和子宫内壁上皮细胞均可出现微绒毛，相互嵌合而增大物质交换的面积。据研究，牛在妊娠末期部分子宫内壁上皮细胞剥落而出现局部的结缔组织型屏障结构。绵羊的胎盘屏障结构，在妊娠期间虽有某些变化，但仍属上皮绒毛膜结构类型。

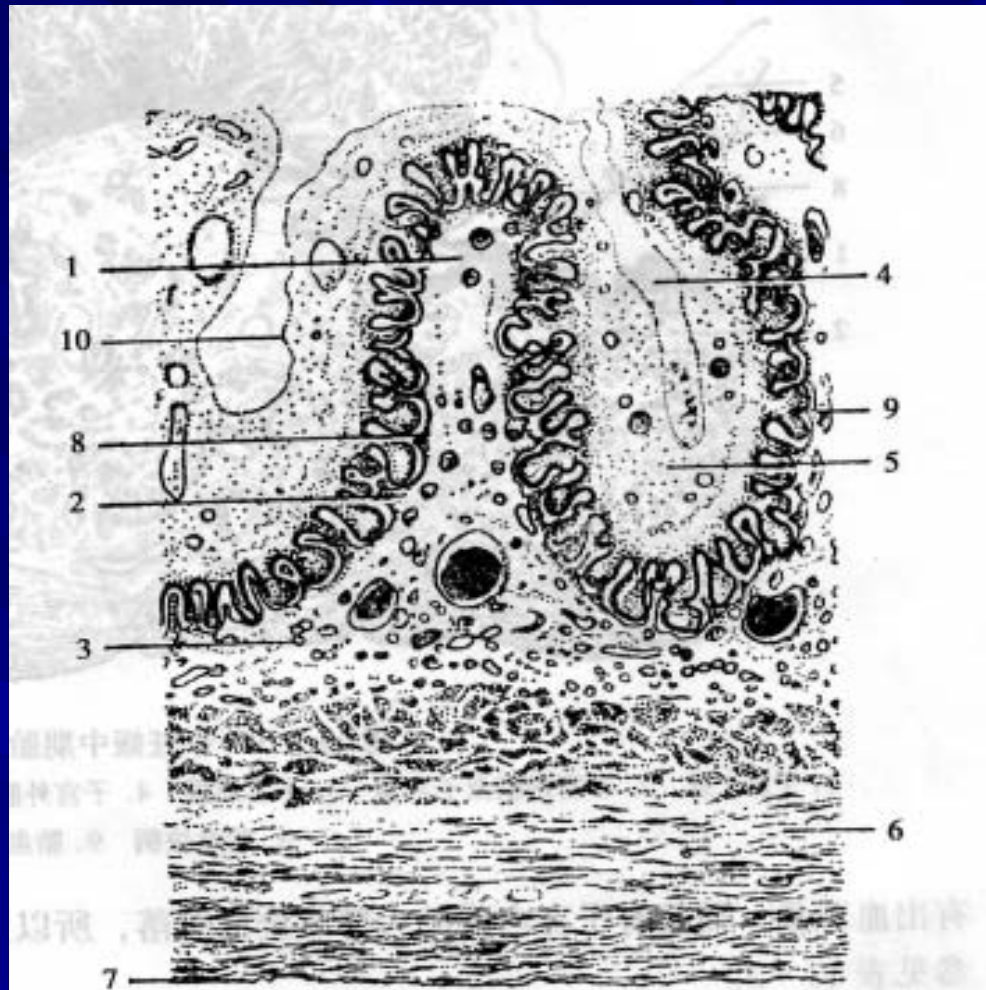


图 11-18 猪胎盘中后期横切

1. 初级皱襞 2. 次级皱襞 3. 子宫内膜及子宫腺 4. 尿囊腔
5. 尿囊绒毛膜 6. 子宫肌膜 7. 子宫外膜 8. 子宫上皮
9. 滋养层 10. 内胚层

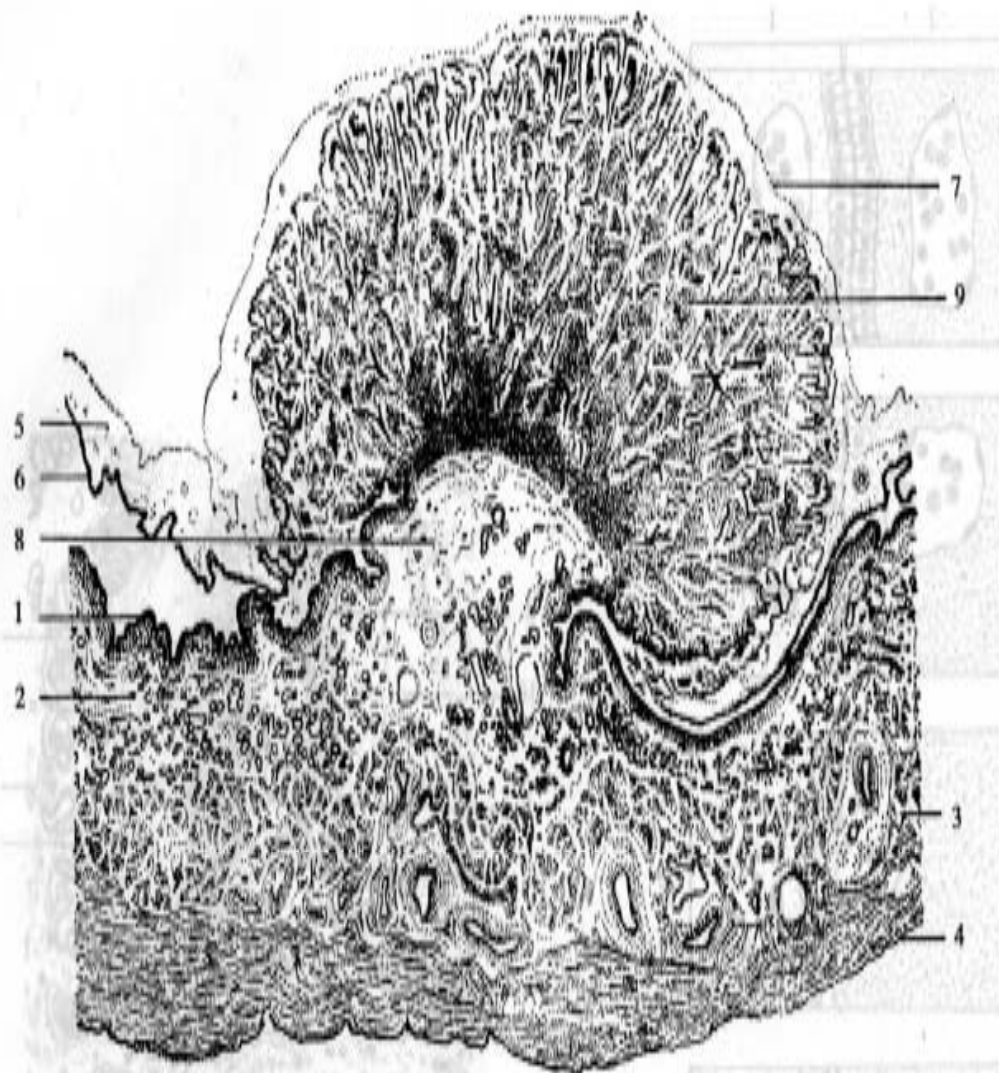
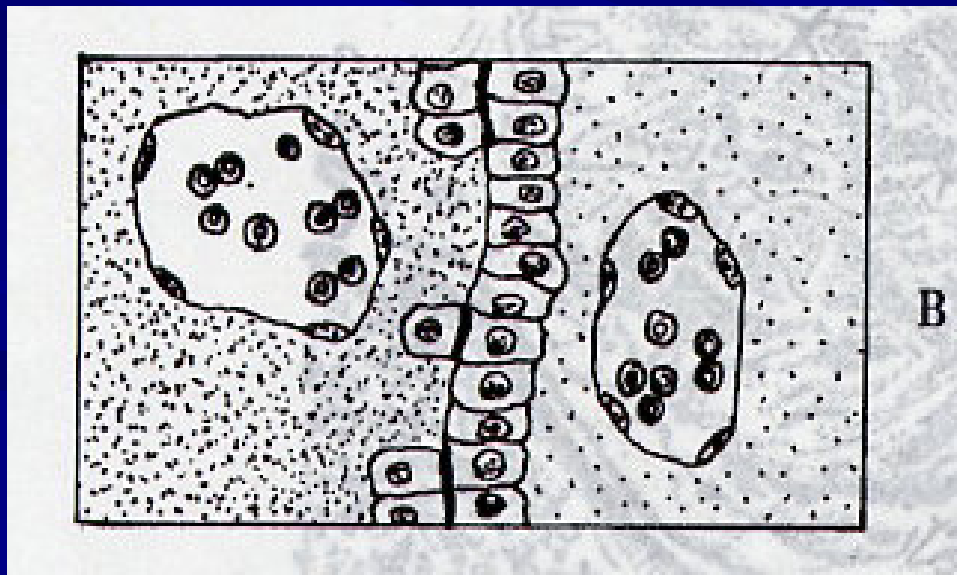


图 11-19 牛妊娠中期胎盘横切

1. 子宫上皮 2. 子宫内膜及子宫腺 3. 子宫肌膜 4. 子宫外膜 5. 尿囊绒毛膜 6. 滋养层 7. 内胚层
8. 胎盘块柄 9. 胎盘块

(2) 结缔绒毛膜胎盘

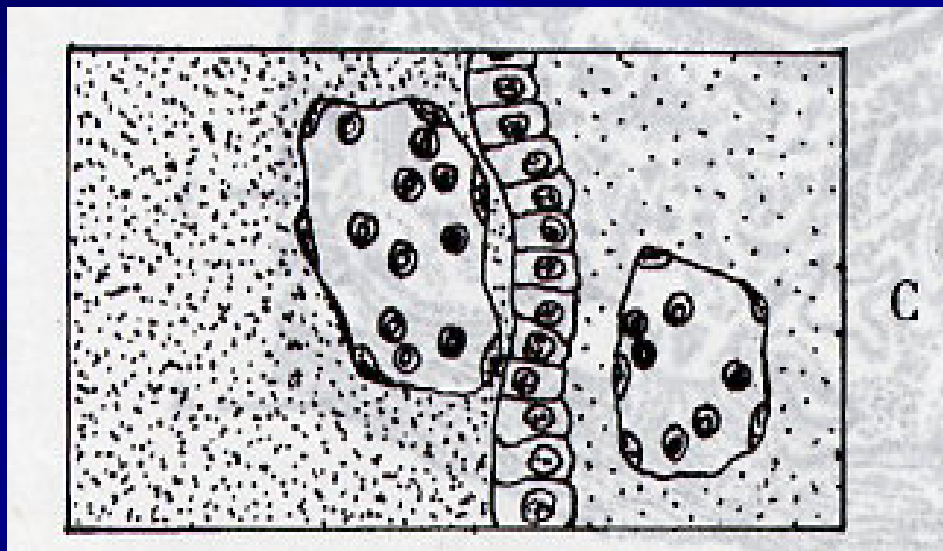
这种胎盘的子宫内膜上皮脱落，绒毛膜上皮直接接触子宫内膜的结缔组织。这种胎盘的联系较散布胎盘紧密，物质交换经过五道屏障：
子宫血管内皮； 子宫内膜结缔组织；
绒毛膜上皮； 绒毛膜间充质； 绒毛膜血管内皮。



上述两种胎盘，胎儿绒毛膜与子宫内膜接触时，子宫内膜没有破坏或破坏轻微。分娩时胎儿胎盘和母体胎盘各自分离，没有出血现象，也没有子宫内膜的脱落，又称非蜕膜胎盘。

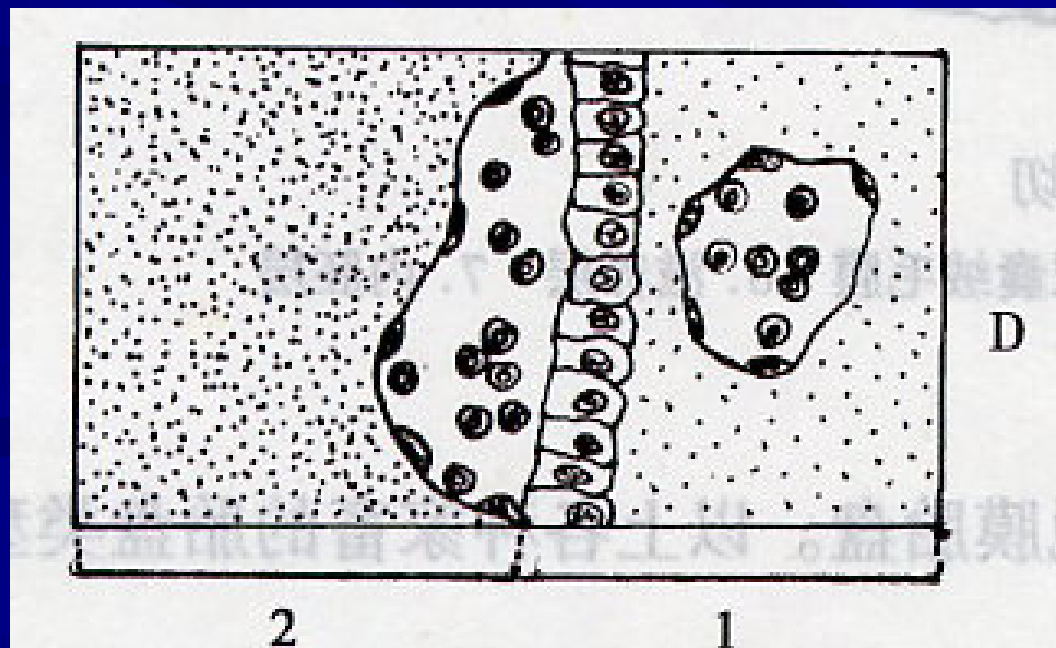
(3) 内皮绒毛膜胎盘

这种胎盘的绒毛深达子宫内壁的血管内皮，猫、狗等肉食兽属这种类型。物质交换经过四道屏障：子宫血管内皮；绒毛膜上皮；绒毛膜间充质；绒毛膜血管内皮。



(4) 血绒毛膜胎盘

兔和人的胎盘属这种类型。这种胎盘的绒毛浸在子宫内
膜绒毛间腔的血液中，物质经过三道屏障：绒毛膜上皮；
绒毛膜间充质；绒毛膜血管内皮。



- 上述两种胎盘，胎儿胎盘深入子宫内膜，子宫内膜被破坏的组织较多。分娩时不仅母体子宫有出血现象，而且有子宫内膜的大部或全部脱落，所以又称蜕膜胎盘。

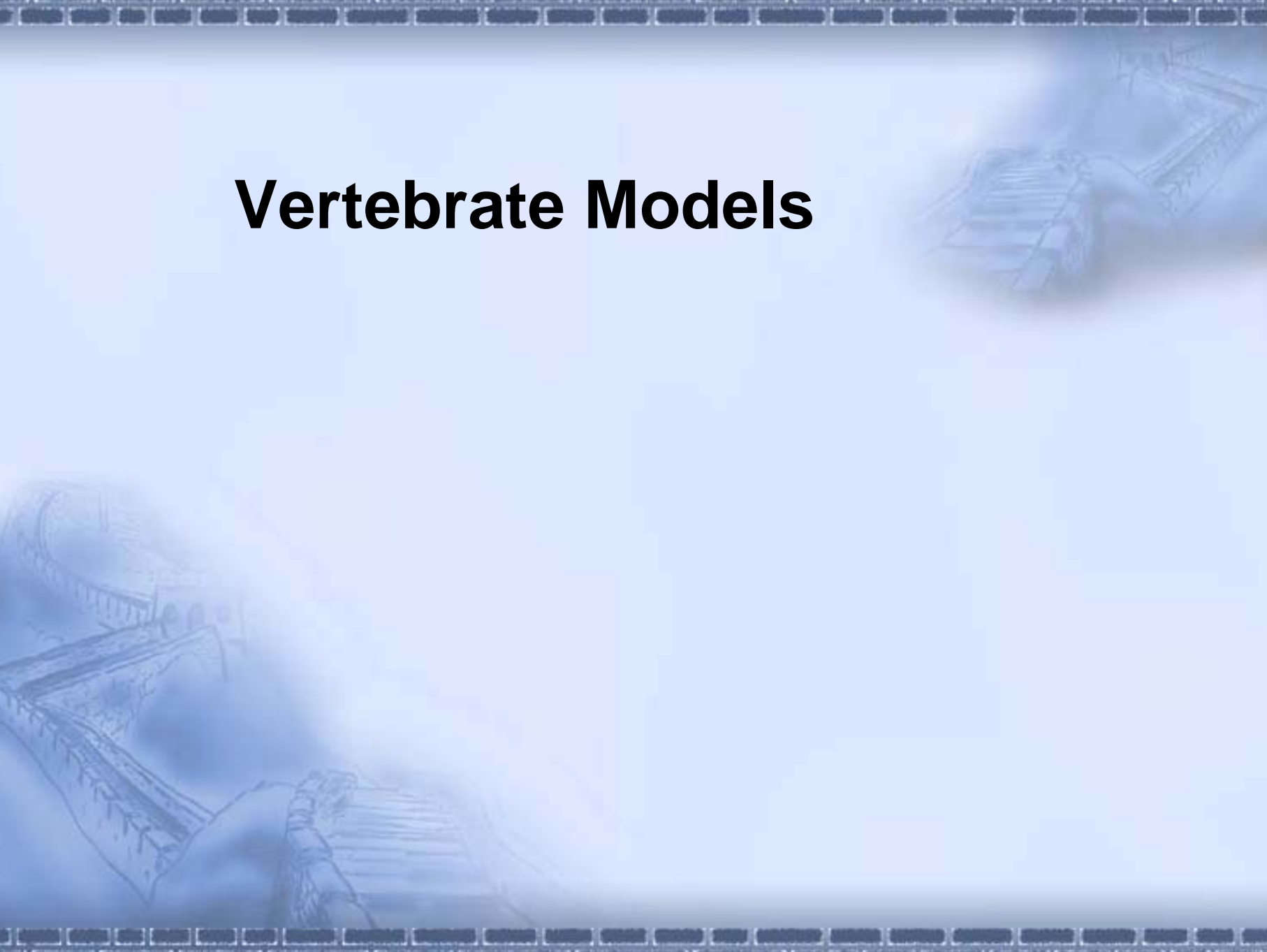
■ 胎盘是胎儿与母体进行物质交换的器官。胎儿所需营养物质和氧，从母体吸取；胎儿的代谢产物，如二氧化碳、尿素、肌酸、肌酸酐等，通过胎盘排入母体血液内。应该注意，胎儿循环血管和母体循环血管，并不直接连通，物质交换以渗透方式进行。但这种渗透具有选择性，物质通过主动运输而传递。有关试验表明，果糖在胎盘中形成并贮存于胎儿肝内作为能量贮备；绒毛膜上皮细胞含有大量核糖核酸，能合成蛋白质供胎儿生长。绒毛膜还能分泌促性腺激素和孕激素。因此，胎盘对于胎儿的作用，有如出生后动物的胃肠道、肺、肾、肝和内分泌腺一样，完成吸收、排泄、合成等重要机能，保证胎儿正常发育。

脐带

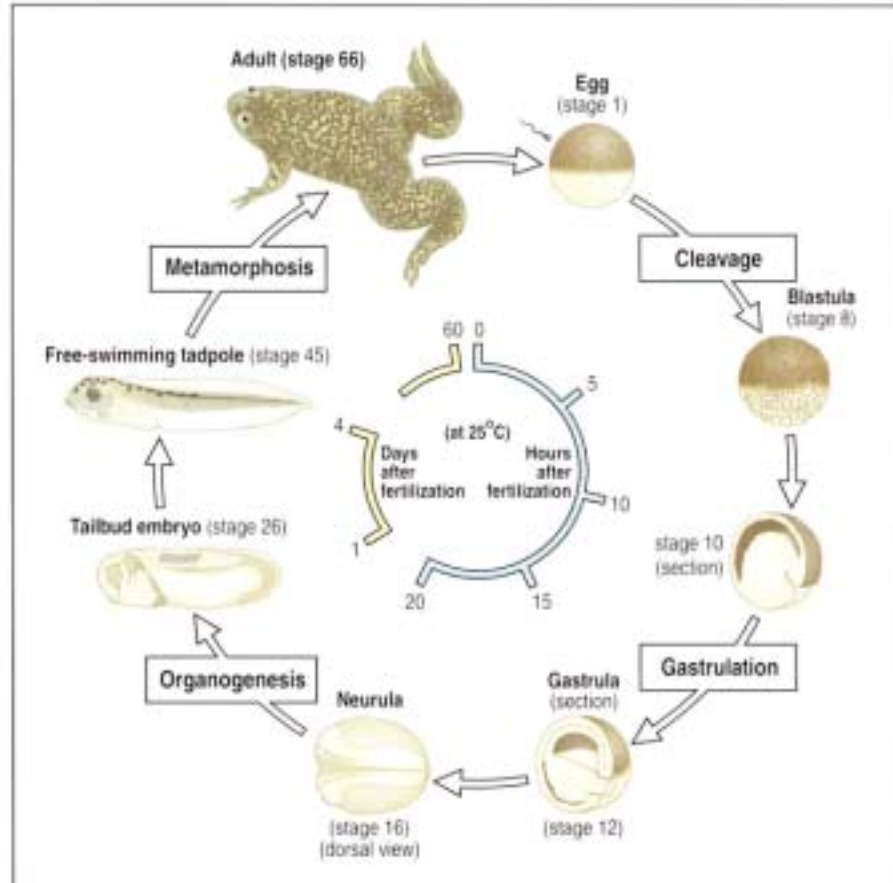
起源于胚胎早期的体褶，随着胚胎发育逐渐向胎儿腹部脐区集中缩细。由于羊膜腔的扩大，使尿囊柄和退化的卵黄囊柄靠拢缩细，并被羊膜包围形成长索状称脐带。

脐带外被覆着一层光滑的羊膜，内部主要为中胚层发生的黏性结缔组织。脐带的黏性结缔组织中有尿囊柄、脐动脉和脐静脉通过。胎儿体内的尿液可通过脐带中的尿囊柄贮于尿囊腔内。脐动脉将胎儿体内血液输至胎盘，而脐静脉将胎盘处的血液输送至胎儿体内。脐带中的脐动脉、脐静脉及其在胎膜上的分支，构成胎儿血液循环的体外部分。

Vertebrate Models



Xenopus laevis: Amphibian model



主要优点

1. 性成熟短；
2. 卵体大，易于操作；
3. 抗感染力强，易于组织移植；

2.3 Life cycle of the African claw-toed frog *Xenopus laevis*. The numbered stages refer to standardized stages of *Xenopus* development. More stages can be seen in the larger figure in Box 1A, page 4. The photographs show: an embryo at

the blastula stage (top, scale bar = 0.5 mm); a tadpole at stage 45 (middle, scale bar = 1 mm); and an adult frog (bottom, scale bar = 1 cm). Photographs courtesy of J. Slack (top, from Alberts, B., et al.: 1994) and J. Smith (middle and bottom).

Danio rerio (zebrafish)

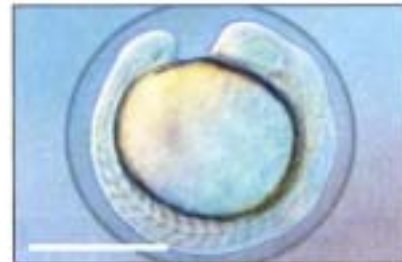
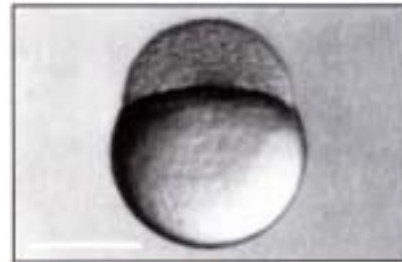
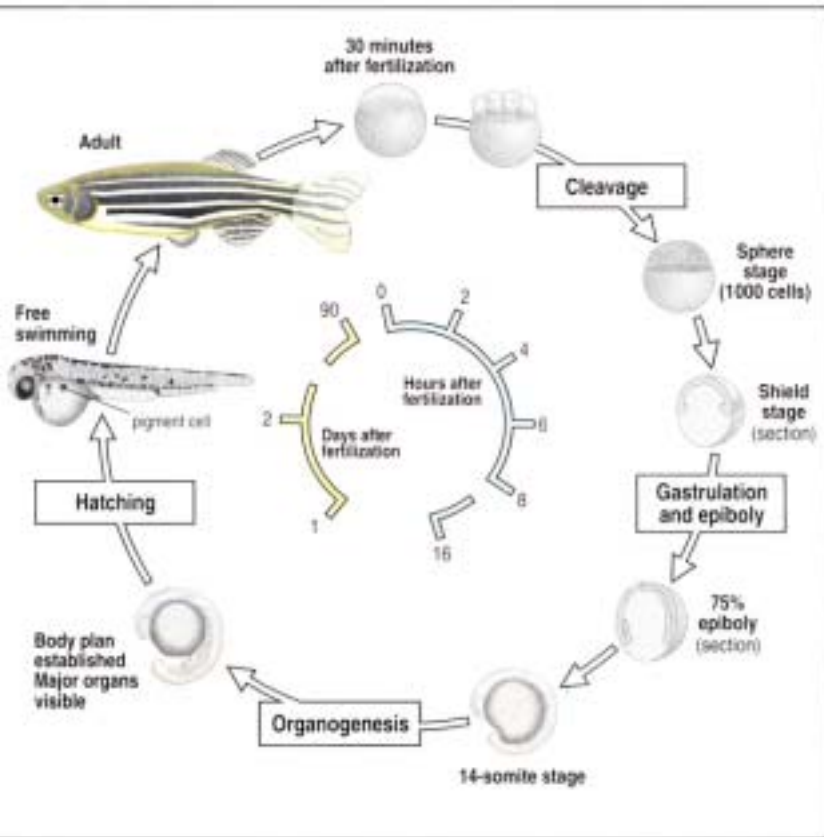


Fig. 2.26 Life cycle of the zebrafish. The zebrafish embryo develops as a cup-shaped blastoderm sitting on top of a large yolk cell. It develops rapidly and by 2 days after fertilization the tiny fish, still attached to the remains of its yolk, hatches out of the egg. The top photograph shows a zebrafish embryo at the sphere stage of development, with the embryo sitting on top of the large yolk cell (scale bar = 0.5 mm). The middle photograph

shows an embryo at the 14-somite stage, showing developing organ systems. Its transparency is useful for observing cell behavior (scale bar = 0.5 mm). The bottom photograph shows an adult zebrafish (scale bar = 1 cm). Photographs courtesy of C. Kimmel (top, from Kimmel, C.B., et al.: 1995), N. Holder (middle), and M. Westerfield (bottom).

主要优点

1. 体积小，易于饲养；
2. 产卵力强；
3. 性成熟短；
4. 易于遗传操作：如诱变；
5. 体外受精和发育，易于观察；
6. 基因组序列已全部测出。

Mus musculus (Mouse)

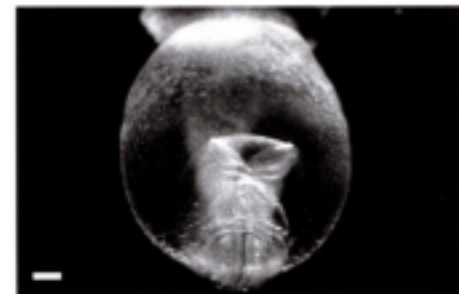
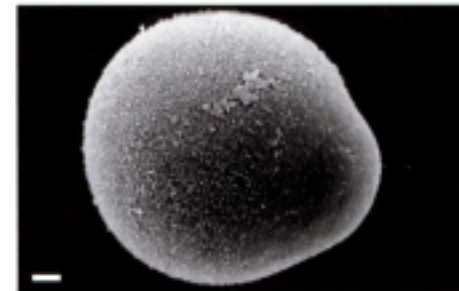
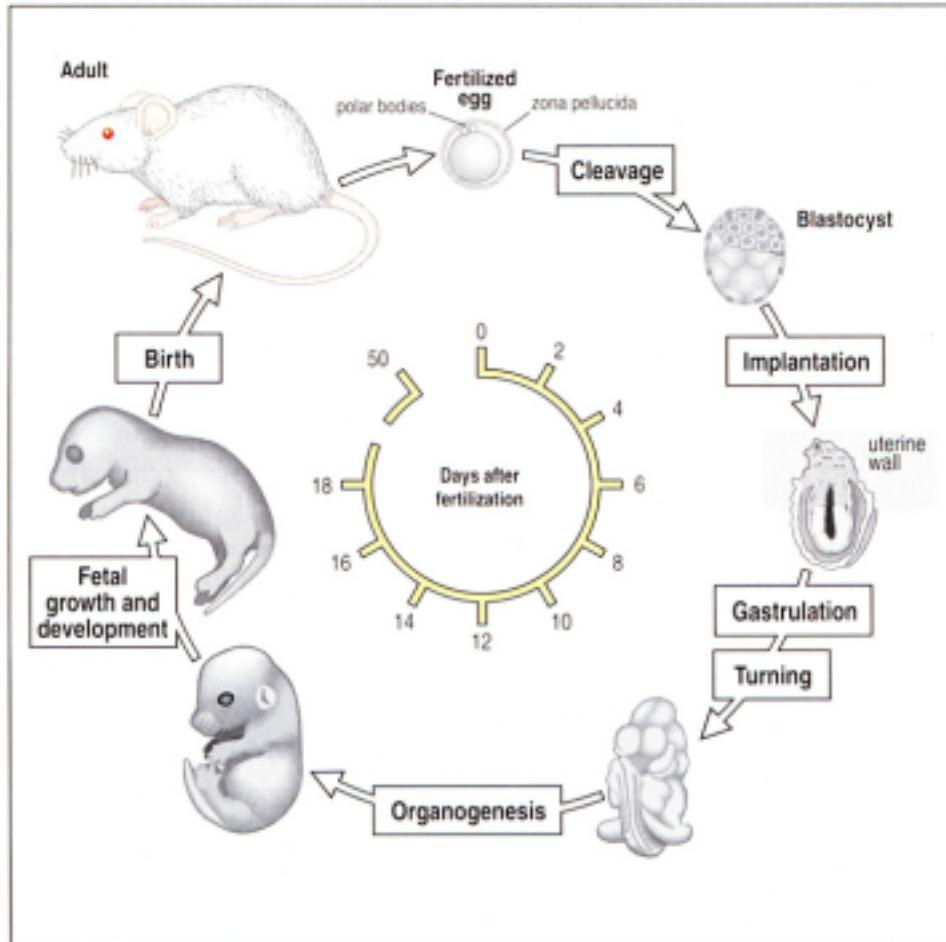


Fig. 2.20 The life cycle of the mouse. The egg is fertilized in the oviduct, where cleavage also takes place before implantation of the blastocyst in the uterine wall at 5 days after fertilization. Gastrulation and organogenesis then take place over a period of around 7 days and the remaining 6 days before birth are largely a time of overall growth. After gastrulation the mouse embryo undergoes a complicated movement known as 'turning' in which it becomes surrounded by its extra-embryonic membranes

(not shown here). The photographs show (from top): a fertilized mouse egg just before the first cleavage (scale bar = 10 μm); anterior view of a mouse embryo at 8 days after fertilization (scale bar = 0.1 mm); and a mouse embryo at 14 days after fertilization (scale bar = 1 mm). Photographs courtesy of: T. Bloom (top, from Bloom, T.L.: 1989); N. Brown (middle); and J. Wilting (bottom).

Gallus gallus (Chicken)

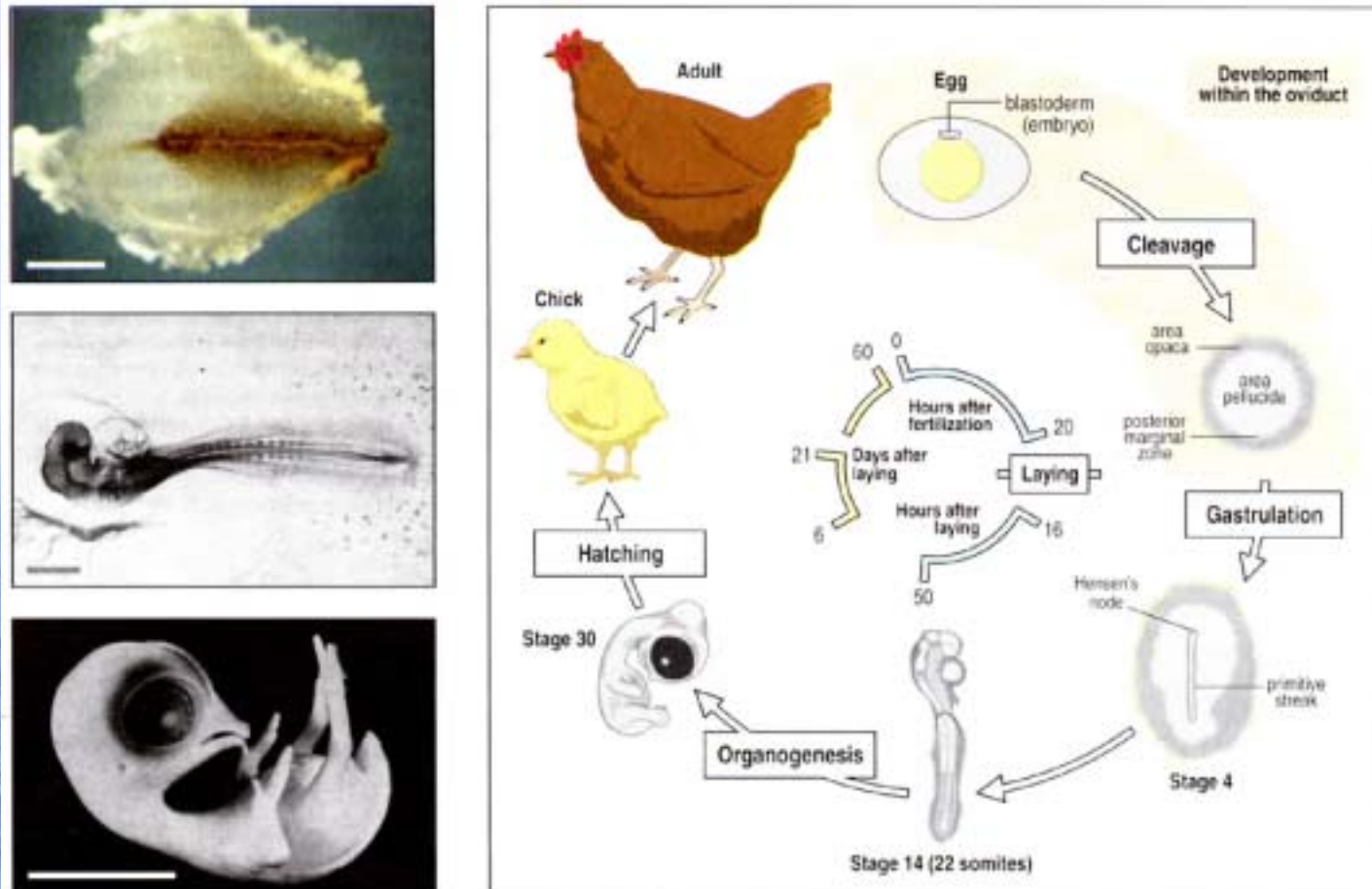


Fig. 2.11 Life cycle of the chicken. The egg is fertilized in the hen and by the time it is laid, cleavage is complete and a cellular blastoderm lies on the yolk. After gastrulation, the primitive streak forms. Regression of Hensen's node is associated with somite formation. The photographs show: the primitive streak surrounded by the area pellucida (top, scale bar = 1 mm);

a stage 14 embryo (50–53 hours after laying) with 22 somites (middle, scale bar = 1mm). The head region is well-defined. The transparent organ adjacent to it is the ventricular loop of the heart; a stage 35 embryo, about 8½–9 days after laying, with a well developed eye and beak (bottom, scale bar = 10mm). Top photograph courtesy of B. Herrmann, from Kispert, A., et al.: 1994.

三、发育生物学中的基本概念及规律

(一)、Five major developmental processes

1. Cell division:

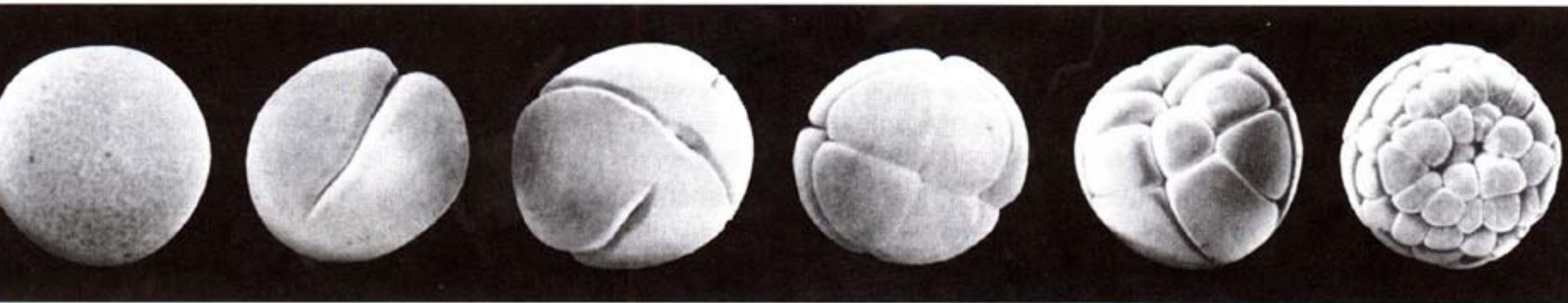
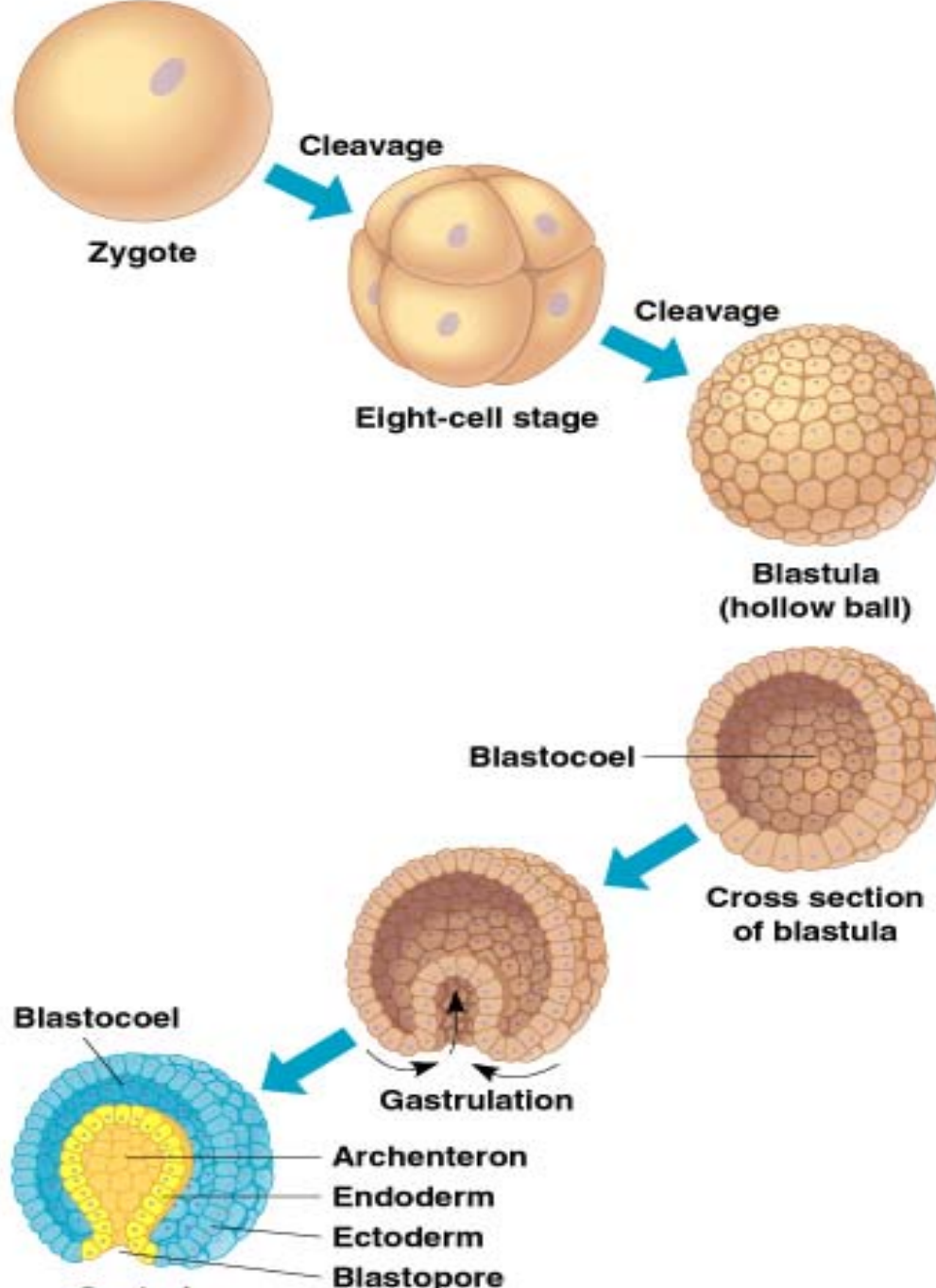
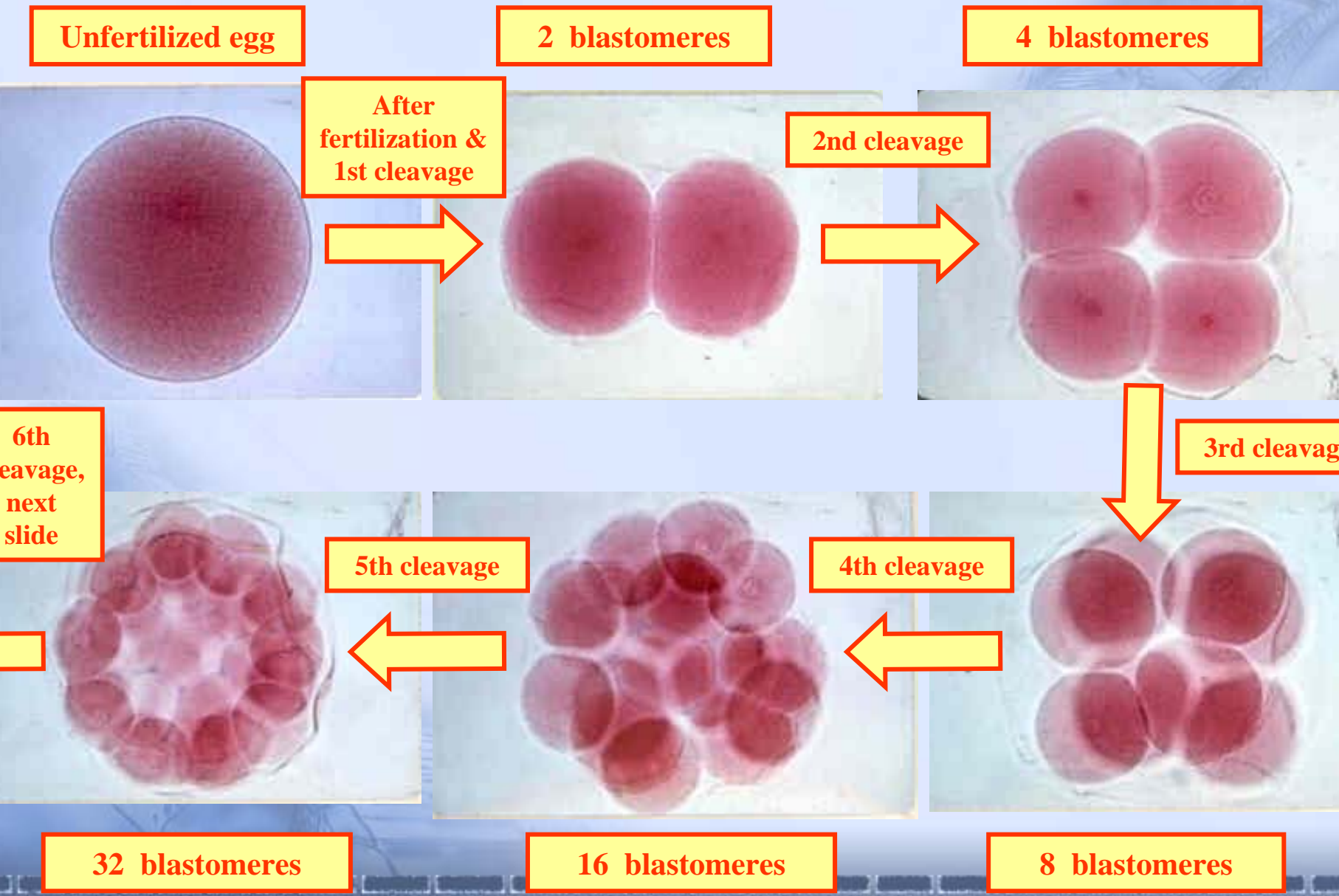


Fig. 2.5 Cleavage of the *Xenopus* embryo. The *Xenopus* embryo undergoes successive cleavages at intervals of about

20 minutes. Photographs courtesy of R. Kessel, from Kessel, R.G. *et al.*: 1974.



Starfish Development

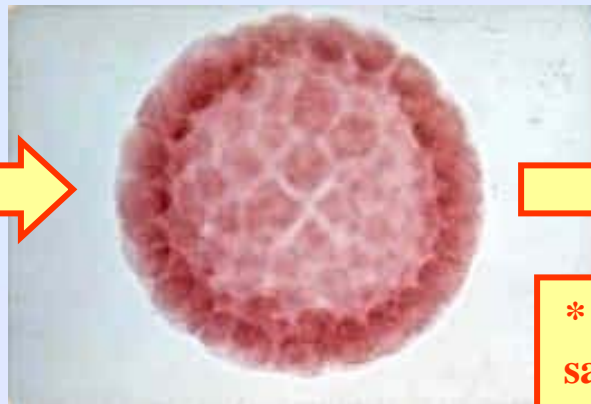


Starfish Development (continued)

64 blastomeres



Non-motile blastula



Ciliated blastula



* blastula is same size as unfertilized egg

Next slide



Gastrula: Archenteron, no mesenchyme



Gastrula: During invagination

blastopore



Gastrula: Beginning invagination

Starfish Development (continued)

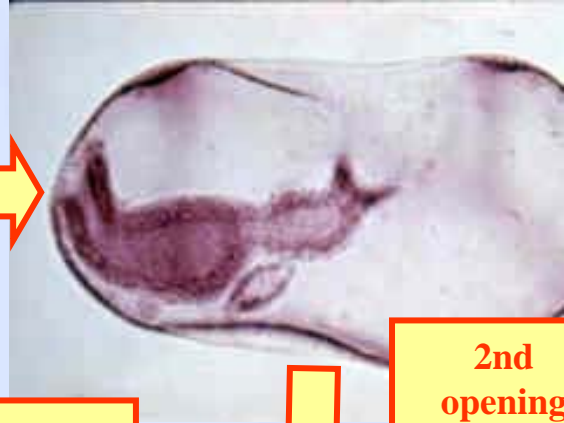
Gastrula: Archenteron with mesenchyme



Late gastrula: lateral view

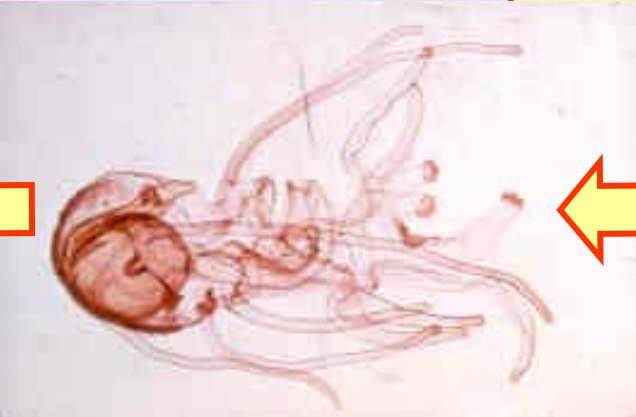


Early bipinnaria larva, lateral view



blastopore becomes anus

2nd opening becomes mouth



Young starfish

Brachiolaria larva

Late bipinnaria larva, lateral view



Pattern formation

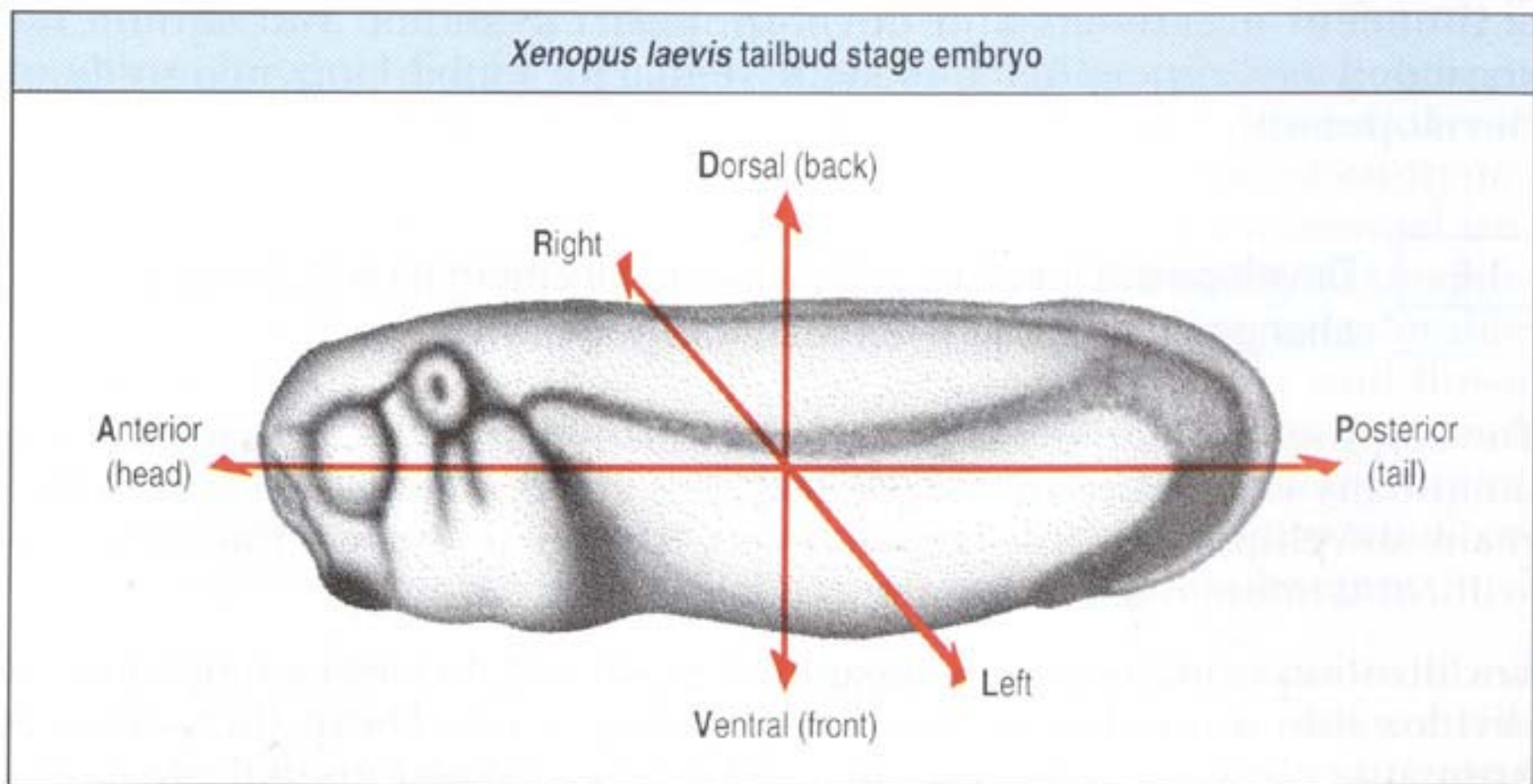
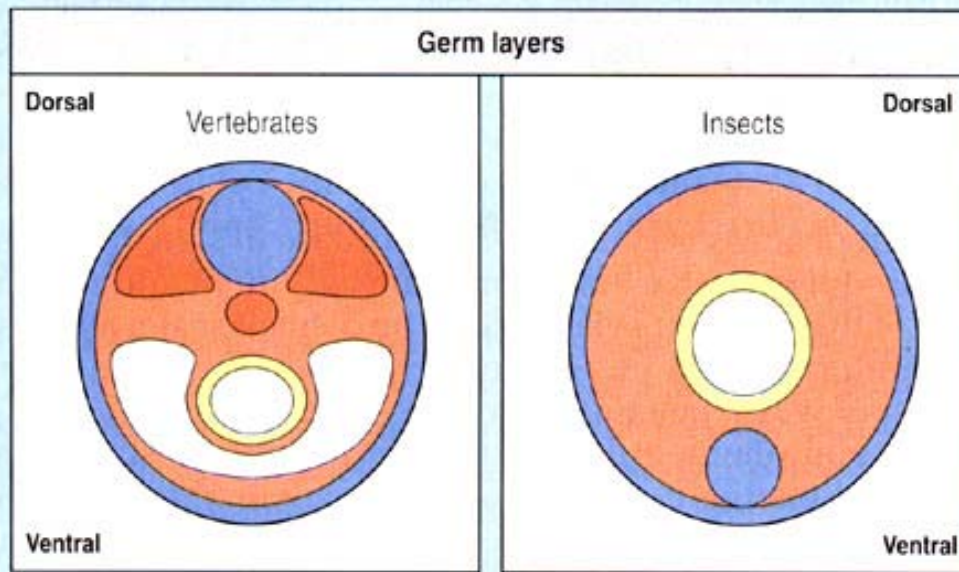


Fig. 1.13 The main axes of a developing embryo. The antero-posterior axis and the dorso-ventral axis are at right angles to one another as in a coordinate system.

Pattern formation:

胚层的形成

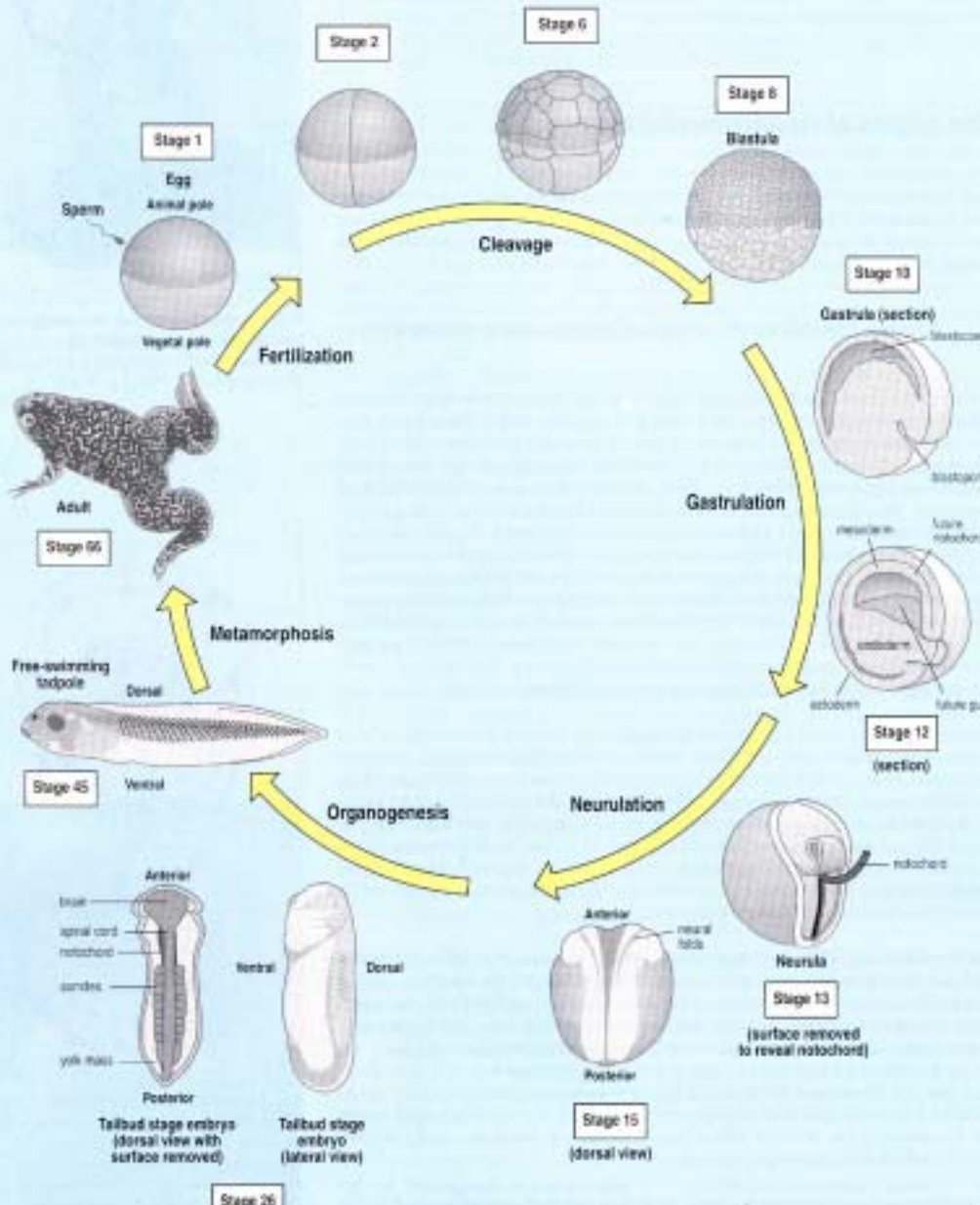
Box 1B Germ layers.



The concept of germ layers is useful to distinguish between regions of the early embryo that give rise to quite distinct types of tissues. It applies to both vertebrates and invertebrates. All the animals considered in this book have three germ layers: the endoderm, which gives rise to the gut and its derivatives, such as the liver and lungs in vertebrates; the mesoderm, which gives rise to the skeleto-muscular system, connective tissues, and other internal organs such as the kidney and heart; and the ectoderm, which gives rise to the epidermis and nervous system. These are specified early in development. The boundaries between the different layers can be fuzzy and there are notable exceptions. The neural crest in vertebrates, for example, is ectodermal in origin but gives rise both to neural tissue and to some skeletal elements, which would normally be considered mesodermal in origin.

Germ layers	Organs	
Endoderm	gut, liver, lungs	gut
Mesoderm	skeleton, muscle, kidney, heart, blood	muscle, heart, blood
Ectoderm	skin, nervous system	cuticle, nervous system

Box 1A Basic stages of *Xenopus laevis* development.



最突出的形态变化发生在原肠作用开始之后。

胚胎在基本的pattern形成之后，其体积会显著增长，原因在于细胞数量增加、细胞体积增加、胞外物质的积累。不同组织器官的生长速度也各异。

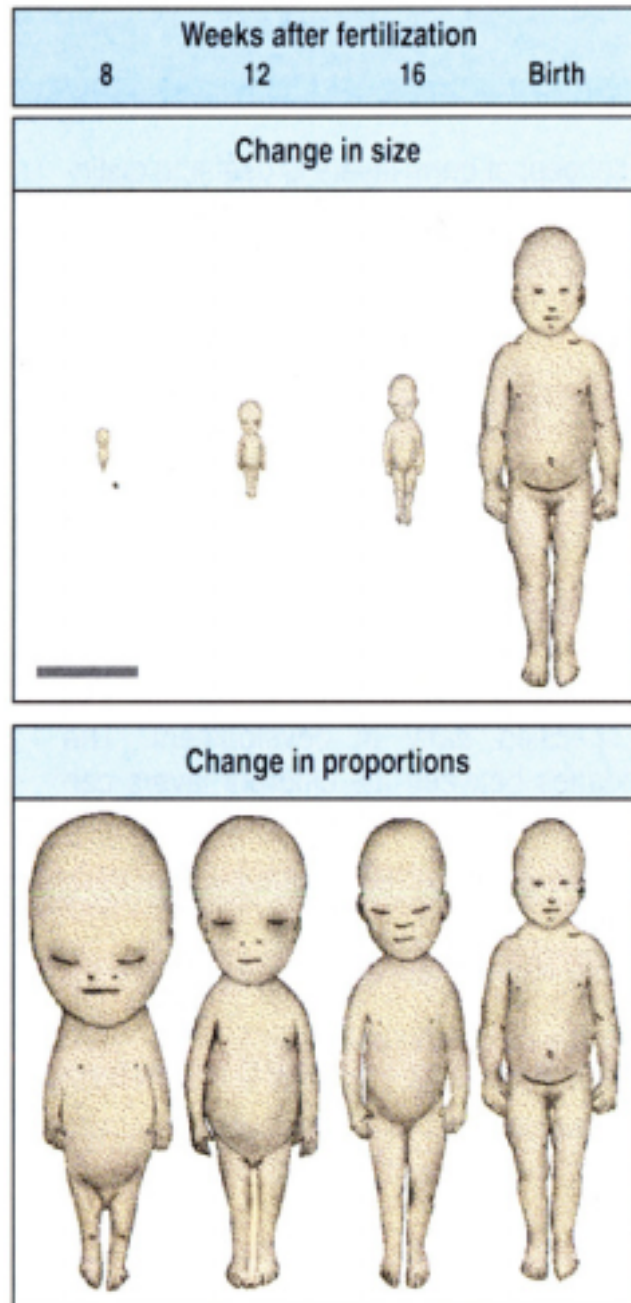


Fig. 1.15 The human embryo changes shape as it grows. From the time the body plan is well established at 8 weeks until birth the embryo increases in length some ten-fold (upper panel), while the relative proportion of the head to the rest of the body decreases (lower panel). As a result, the shape of the embryo changes. Scale bar = 10 cm. After Moore, K.L.: 1983.



Carnegie Stages of Human Development

Dr Mark Hirst, Cell Biology Lab, School of Medical Sciences (Anatomy), UMSW



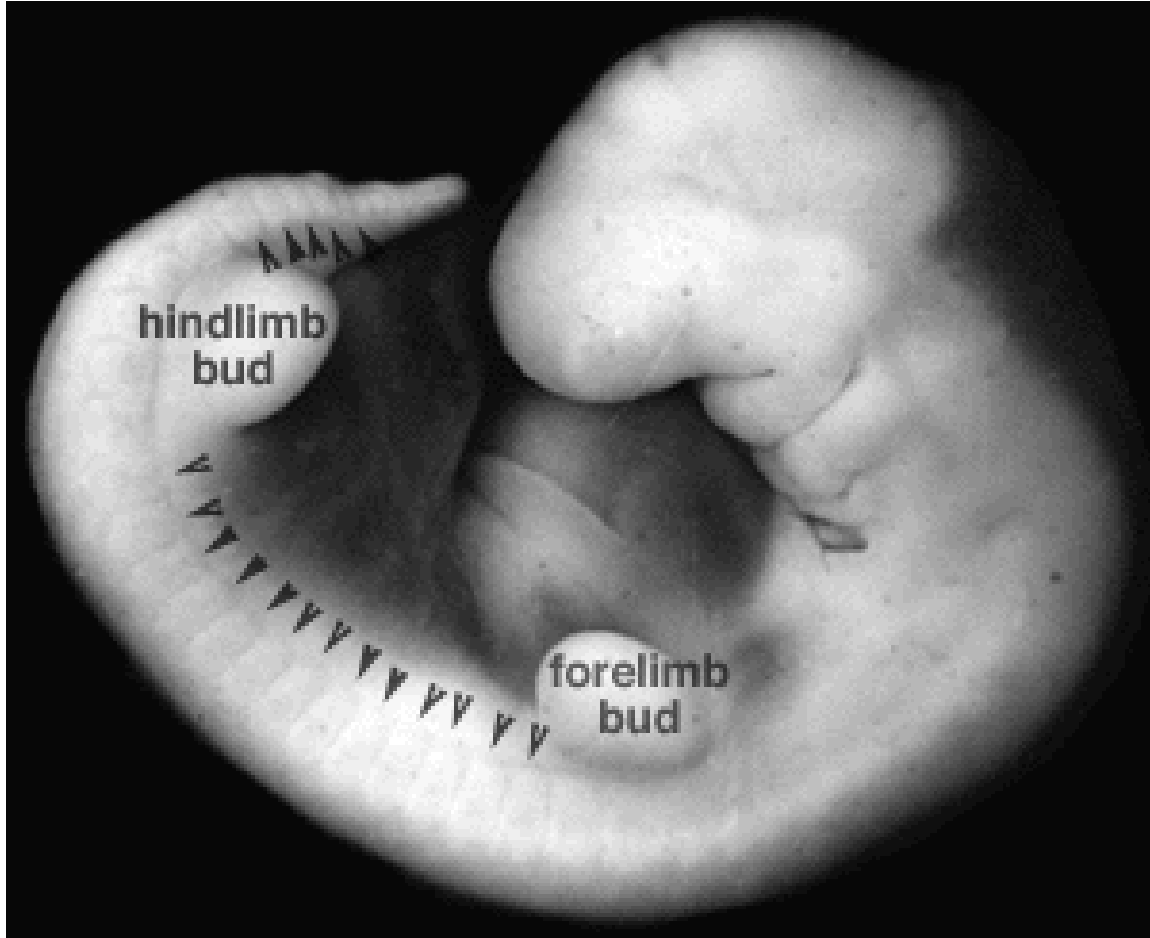
Anteriorly

Special thanks to Dr S. J. Willmore and Prof. Robert Slonick for allowing reproduction of their research images and material from the Human Embryonic Collection and Dr S. Hill for image preparation.

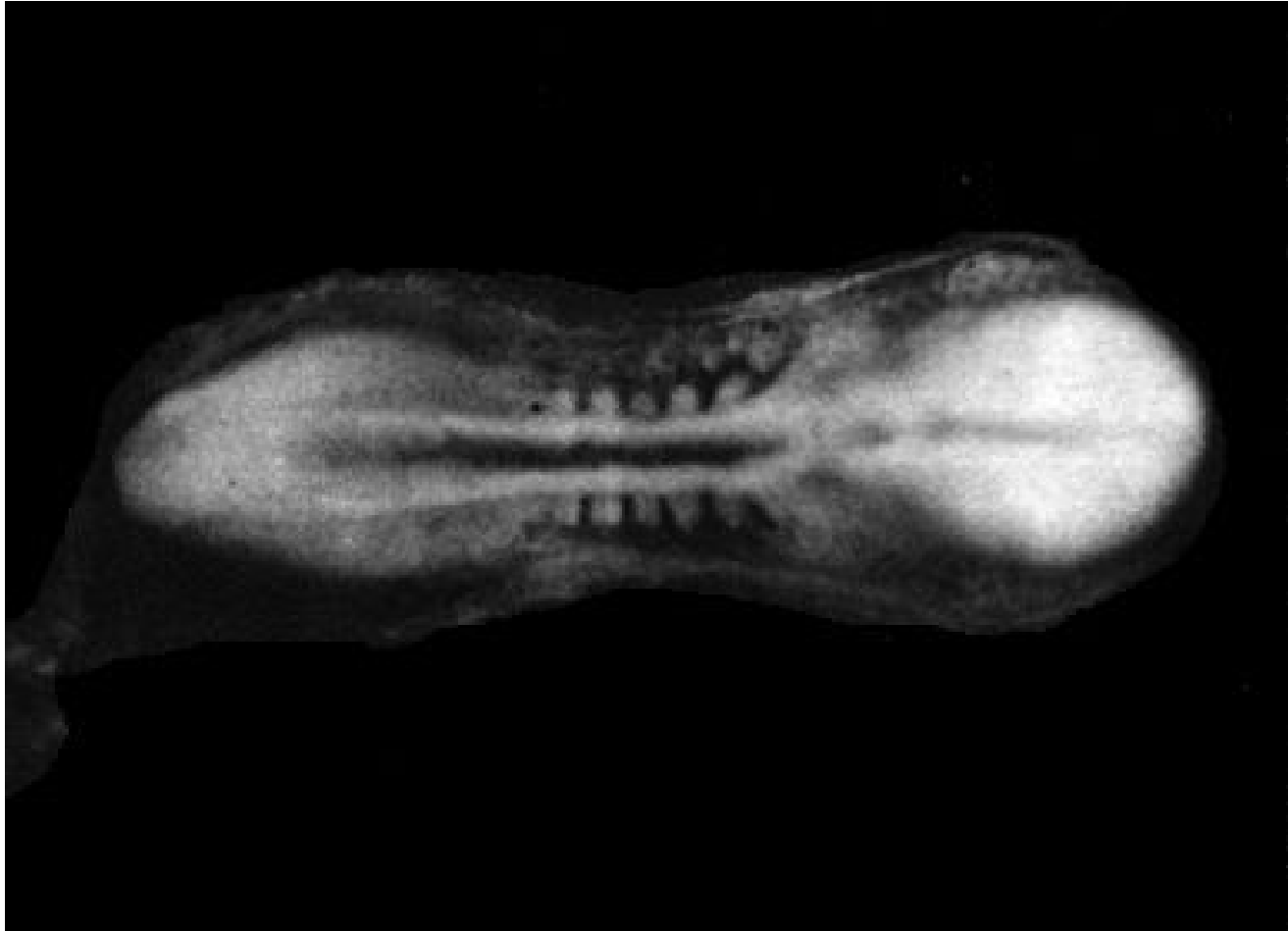
© Dr S. Hill, 2009

Carnegie Stages 1

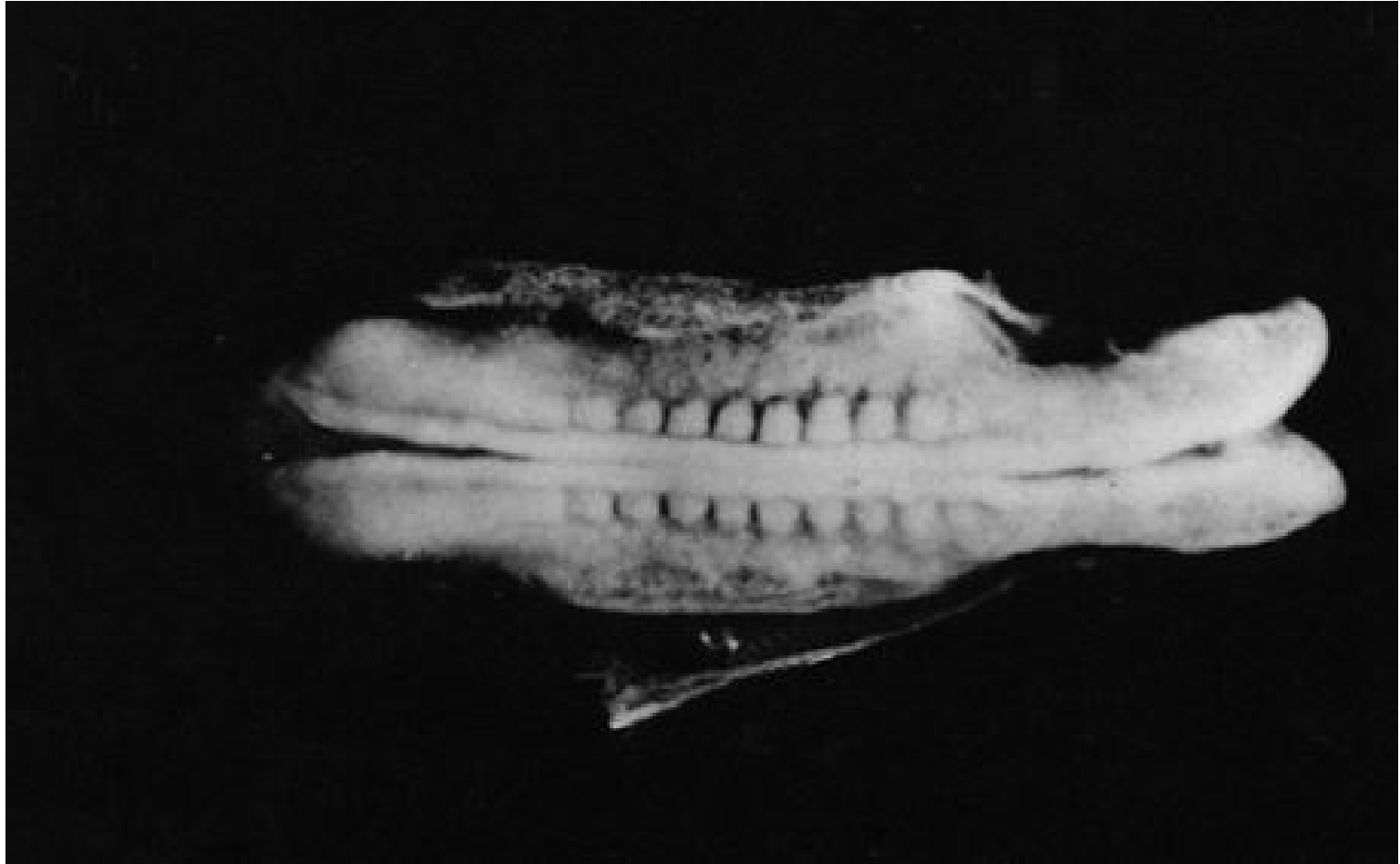




Carnegie Stage 10 (early)



Carnegie Stage 10 (late)



课后复习题:

- 1、 精子获能和受精的概念
- 2、 简述受精的过程及功能意义。
- 3、 简述家畜胚胎发育的基本过程。
- 4、 三胚层最终分化分别形成哪些器。
- 5、 何谓胎膜, 包括哪些结构?
- 6、 什么叫脐带以及胎盘, 胎盘有哪些类型?