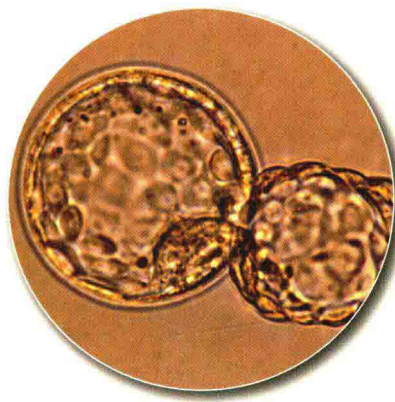
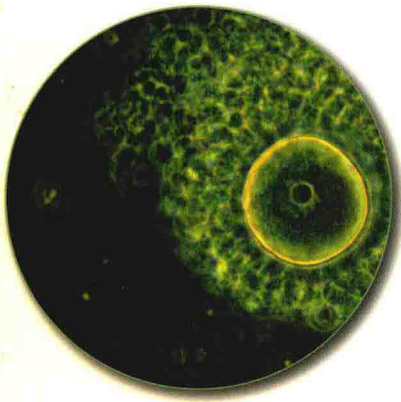


Second Edition

DICTIONARY OF

Developmental Biology and Embryology



FRANK J. DYE

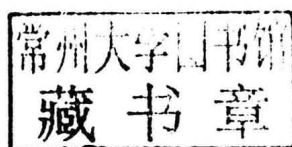
 WILEY-BLACKWELL

DICTIONARY OF DEVELOPMENTAL BIOLOGY AND EMBRYOLOGY

Second Edition

FRANK J. DYE

Western Connecticut State University



 **WILEY-BLACKWELL**

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**DICTIONARY OF
DEVELOPMENTAL
BIOLOGY AND
EMBRYOLOGY**

I dedicate this book to the memory of my high-school teachers, who unknowingly set the course of my life; my professors at Danbury State College (Western Connecticut State University), who raised my self-esteem; and especially to my professors at Fordham University, notably James Forbes and Alexander Wolsky, who fascinated me with embryology and developmental biology.

Preface

The motivation for the creation of the second edition of this work was a continued perceived need for such a book. Ten years have elapsed since the publication of the first edition, during which time developmental biology has rapidly progressed, in particular, developing the sub-discipline of evo-devo and giving birth to eco-devo. Unlike *The Dictionary of Cell Biology*, such a book does not exist for embryology and developmental biology; yet undergraduate students, graduate students, professors, and researchers would find such a book to be most convenient. Undoubtedly, most terms found in this book are accessible on the Internet; however, it is often not convenient to boot up the computer and initiate a search for the term in question. In addition to terminology, this book also presents historical vignettes of some major contributors, classical and modern, to embryology and developmental biology, as well as a number of concepts (as opposed to terminology per se).

This second edition will, perhaps, have omissions of some terms that you feel should be included. The author would greatly appreciate it if you would send suggested terms for possible inclusion in subsequent editions of this book to dyef@wcsu.edu.

I wish to acknowledge the contribution to the creation of this book of a sabbatical leave granted to me by Western Connecticut State University, during the Fall of 2006—it provided the momentum to get the ball rolling. Also, I wish to thank Dr. James Schmotter, president of Western Connecticut State University, for his support in obtaining the sabbatical leave. Additionally, I wish to thank Karen Chambers, Editor, Life Sciences, Wiley-Blackwell Publishing, for her belief in this project from the outset; Anna Ehler, Editorial Assistant, Life Sciences, Wiley-Blackwell Publishing, for her gentle nudging; Stephanie Sakson, Project Manager, Toppan Best-set Premedia Limited, for many helpful suggestions as we approached the completion of this project; and Sheree Van Vreede, who copyedited the manuscript. Finally, I thank the Connecticut State University System for providing an implantation site for the development of this developmental cell biologist.

Frank J. Dye
Western Connecticut State University

A

A23187 a calcium ionophore that increases the permeability of cell membranes to calcium ions; it has been used experimentally to trigger the cortical reaction of sea urchin eggs, which depends on an increase in the concentration of free calcium ions in the cytoplasm of the egg.

abaxial the side of the leaf facing away from the meristem, and can be thought of as the ventral side. *See:* **adaxial**.

abdominal cavity or peritoneal cavity, derived from the coelom and containing much of the viscera (internal organs).

ABO blood typing system a system of typing human blood, for the purpose of blood transfusion.

aboral surface the surface opposite the oral surface; in the sea urchin, this is the uppermost surface when the animal is in its normal, upright position. *See:* **oral surface**.

abortifacient that which induces abortion, e.g., RU486.

abortion the process of terminating a pregnancy with the demise of the conceptus.

abortus that which results from an abortion: an aborted embryo or fetus.

abruptio placentae premature separation of the placenta from the lining of the uterus.

abscisic acid (ABA) a plant hormone; it has been implicated in the developmental arrest of the plant embryo during seed dormancy. The increase in ABA levels during early seed development, in many plant species, stimulates the production of seed storage proteins and prevents premature seed germination. The breaking of dormancy in many seeds is correlated with declining ABA levels in the seed. *See:* **viviparous mutants**.

abscission the natural separation of flowers, fruit, or leaves from a plant.

accessory sex glands in humans: in the male, seminal vesicles (2), prostate gland (1), Cowper's glands (2), and the glands of Littre (multiple); in the female, Bartholin's glands (2) and Skene's glands (2). In female insects, accessory glands open into the vagina and they commonly secrete an adhesive substance for attaching the eggs to an external object or for cementing them in a mass; in male insects, in many cases, the accessory glands produce substances that go into the formation of a spermatophore.

accutane retinoic acid used to treat severe cystic acne. *See:* **retinoic acid**.

Acetabularia a large, marine, single-celled, green algae used in classical experiments to gather evidence that the nucleus provides the information determining phenotype.

acetylated histones histones enzymatically modified by the addition of acetyl groups; acetylated histones are relatively unstable and cause nucleosomes to disperse. *See:* **deacetylated histones**.

acetylation a type of chemical modification of histones, mediated by histone acetyltransferase enzymes, which destabilizes nucleosomes and allows for gene expression.

Achaete an example of a transcription factor encoded by proneural genes in *Drosophila*. *See:* **proneural genes**, **Scute**.

achondroplasia a typical, congenital dwarf, formed because of abnormal bone formation, specifically abnormal chondrification and ossification of the ends of the long bones; this birth defect is often inherited as a dominant trait.

acid blob *See:* **trans-activating domain**.

acoelomate animals lacking a coelom, e.g., Platyhelminthes (flatworms) and Nemertea (ribbon) worms.

acrania the partial or complete absence of the cranium.

acrocentric chromosome a chromosome in which the centromere is not equidistant from the two ends of the chromosome; therefore, the chromosome's two arms are of unequal length.

acrocephaly also called oxycephaly is a condition in which the head is roughly conical in shape caused by premature suture closure.

acrogen a nonflowering plant that grows only at the apex, as in a fern.

acron the preoral, nonsegmented portion of an arthropod embryo; a marker for the anterior terminus of the *Drosophila* embryonic axis.

acrosin a protease exposed on the sperm head after the acrosome reaction; may be involved in sperm digestion through the zona pellucida.

acrosomal filament an elongated filament, extruded by the heads of the spermatozoa of some species (e.g., *Saccoglossus*, a hemichordate), as part of their acrosome reaction. The extension of the acrosomal filament is a consequence of the underlying polymerization of G-actin to F-actin, resulting from increased intracellular pH (attributed to a release of hydrogen ions from the sperm head), which, in turn, is an early event of the acrosome reaction caused by altered spermatozoan plasma membrane permeability.

acrosomal vesicle *See: acrosome.*

acrosome an organelle, derived from the Golgi apparatus, found in the head of the spermatozoon, containing hydrolytic enzymes that play a role in the sperm reaching the plasma membrane of the egg; it is considered to be a modified lysosome. Also called the acrosomal vesicle.

acrosome reaction a change, during fertilization, undergone by the sperm of many types of animals that facilitates the breaching of the egg coats of the species by the spermatozoon; has been particularly studied in the fertilization of marine invertebrates, some of which produce dramatic acrosomal filaments as part of their acrosome reaction. In sea urchins, the acrosome reaction is initiated by a sulfated polysaccharide in the egg jelly coat; this allows calcium and sodium ions to enter the sperm head and to replace potassium and hydrogen ions; calcium ions mediate the fusion of the acrosomal membrane with the adjacent plasma membrane. In mice, the acrosome reaction occurs after the spermatozoon has bound to the zona pellucida; capacitation of mouse spermatozoa involves the unmasking of a specific enzyme on the sperm cell surface; the lock-and-key binding of zona *N*-acetylglucosamine by sperm glycosyltransferase links the spermatozoon and egg together; once this binding is complete, the acrosome reaction is initiated. During the acrosome reaction in the mouse, the sperm head loses the anterior part of the plasma membrane and the outer membrane of the acrosome, leaving the inner acrosomal membrane as the covering of the anterior part of the sperm head. From an evolutionary point of view, the primary role of the acrosome reaction seems to be the exposure or preparation of a specialized fusion surface on the sperm head.

acrotrophic ovariole an ovariole in which the trophocytes remain in the germarium but are connected with the developing oocytes by means of progressively lengthening protoplasmic strands that convey nourishment to them; found in Hemiptera and in some Coleoptera.

actin a ubiquitous protein in eukaryotic cells, occurring in especially abundant and organized form in skeletal muscle, where it is organized into thin filaments; in eukaryotic cells, in general, actin microfilaments make up one of the three major components of the cytoskeleton. Actin is enriched in the cortices of some eggs, e.g., amphibian eggs and sea urchin eggs.

actinomycin D an inhibitor of transcription; it prevents RNA synthesis by binding to DNA and blocking the movement of RNA polymerase.

activation of the egg *See: egg activation.*

activator a protein that positively regulates transcription of a gene.

active immunity immunity possessed by a host as the result of disease or unrecognized infection, or induced by immunization with microbes or their products or other antigens. *See: passive immunity.*

activin a member of the TGF- β family of growth factors, it plays a key role in the induction of dorsal mesoderm in *Xenopus* embryos; it is secreted by vegetal cells. *See: Brachyury, goosecoid.*

adaptive developmental plasticity when the organism alters its development in response to environmental cues such that the organism is more fit in that particular environment; e.g., plants grown in the shade often change their leaf structure and amount of branching. An inductive phenomenon. *See: niche construction.*

adaxial the side of the leaf that faces the meristem, and can be thought of as the dorsal side. *See: abaxial.*

adaxial cells cells that flank the chordamesoderm and are the precursors of the somites in the zebrafish embryo.

adenosine triphosphate (ATP) a, so-called, high-energy molecule, which is the almost ubiquitous source of immediate chemical energy for biochemical reactions.

adepithelial cells small numbers of cells that migrate into imaginal discs, which are composed primarily of epidermal cells, and which, during the pupal stage, give rise to the muscles and nerves that serve the structures formed from the imaginal discs.

adherens junctions a type of cell junction that binds one epithelial cell to another, and joins an actin bundle in one cell to a similar bundle in another.

adipocytes also called fat cells; growth hormone triggers fat cell differentiation; fat cell precursors that have been stimulated by growth hormone become sensitive to IGF-1, which stimulates the proliferation of differentiating fat cells. A fibroblast-like precursor cell is converted into a mature fat cell by the accumulation and coalescence of cytoplasmic lipid droplets.

adrenal glands a pair of endocrine glands found attached to the cephalic poles of the kidneys.

adrenal hyperplasia abnormally excessive growth of the adrenal glands attributed to an inherited enzyme deficiency; this leads to overproduction of male hormones that causes masculinization in females and may cause early sexual development in males.

adrenaline *See: epinephrine.*

adrenergic neurons the sympathetic neurons derived from neural crest cells of the trunk and that produce the neurotransmitter norepinephrine. *See: cholinergic neurons.*

adult hemoglobin the hemoglobin made up of two alpha polypeptide chains and two beta polypeptide chains; has a lower affinity for oxygen than fetal hemoglobin and releases oxygen in the placenta, which is taken up by fetal hemoglobin. *See: fetal hemoglobin, hemoglobin.*

adult stem cells stem cells found in mature organs, usually involved in replacing and repairing tissues of that particular organ, and can form only a subset of cell types, e.g., spermatogonia, muscle satellite cells, and hemopoietic stem cells.

adventitious structures or organs developing in an unusual position, as roots originating on the stem.

AER *See: apical ectodermal ridge.*

aequorin a luminescent protein, derived from luminescent jellyfish (*Aequorea*), which emits light in the presence of free calcium ions; it has been used experimentally to visualize the release of free calcium ions into the cytoplasm of the sea urchin egg upon fertilization.

afterbirth that which is born after the baby, namely the placenta, membranes, and part of the umbilical cord.

after-ripening a process required by some dormant seeds, during which low-level metabolic activities continue to prepare the embryo for germination.

agamospermy formation of seed without fertilization.

agenesis this type of birth defect is the absence of an organ or other structure from early development; the precise kind of agenesis refers to the missing organ, e.g., renal agenesis.

aggregation phase in the life cycle of *Dictyostelium discoideum*; the pseudoplasmodium of *D.d.* originates from the aggregation of many separate cells.

aging the time-related deterioration of the physiological functions necessary for survival and fertility. *See: life expectancy.*

AGM region aorta, gonads, and mesonephros region; the domain, near the aorta, where, in fishes, mammals, and frogs, the definitive hematopoietic cells are formed; mesodermal regions of the day 11 mouse embryo in which pluripotential hematopoietic stem cells and CFU-s cells can be found. These blood cell precursors will colonize the liver and constitute both the fetal and the adult circulatory system. Around the time of birth, stem cells from the liver populate the bone marrow, which then becomes the major site of blood formation throughout adult life.

Agnatha the class of vertebrates consisting of the jawless fish; it includes two subclasses, Ostracodermi (extinct) and Cyclostomata (with two extant orders, lampreys and hagfish).

agnatha without jaws. *See: gnathostomes.*

AIDS acquired immune deficiency syndrome, a viral disease that may be transmitted from mother to offspring.

air space *See: shell membrane.*

albinism a hereditary absence of pigment from the skin, hair, and eyes.

albino an organism lacking pigment.

albumen the white of an egg, composed principally of albumin.

albumin any of a group of plant and animal proteins that are soluble in water and dilute salt solutions.

albuminous seed a seed with albumen, the nutritive tissue in a seed.

alcohol a chemical teratogen.

alecithal eggs eggs without yolk. In placental mammals, the yolk is virtually absent.

aleurone protein granules stored in the outermost layer of the endosperm of the seeds of many grains.

aleurone layer a border of protein-rich cells that surrounds the endosperm of many seeds.

algae algae do not constitute a formal taxon (classification unit), but traditionally included the photosynthetic thallophytes, encompassing such plant divisions as chlorophyta, rhodophyta, chrysophyta, etc. The cyanobacteria (traditionally the "blue-green algae"), which are prokaryotes, were classified with the algae, which are eukaryotes; however, they are now classified with the bacteria, all of which are prokaryotes.

alkaline phosphatase an enzyme involved in the deposition of calcium phosphate crystals during ossification.

allantoic diverticulum an evagination or diverticulum of the hindgut, composed of endoderm and mesoderm. In human development, the endoderm of the allantoic diverticulum is rudimentary, but the mesoderm gives rise to important blood vessels of the umbilical cord.

allantoic stalk *See: allantois.*

allantoic vesicle *See: allantois.*

allantois one of the four extraembryonic membranes; originates from the hindgut and is not conspicuous in human development. In the chick, the allantois originates within the body of the embryo and its proximal portion remains intraembryonic throughout development; the distal portion is not incorporated into the body. Late in the third day of incubation, it originates as a diverticulum from the ventral wall of the hindgut; its walls are composed of splanchnopleure. During the fourth day, the allantois pushes out of the embryonic body into the extraembryonic coelom; the proximal portion is parallel to and just caudal to the yolk stalk while the distal portion enlarges. The narrow proximal portion is the allantoic stalk while the distal portion is the allantoic vesicle. The allantoic vesicle extends into the sero-amniotic cavity, flattens, and encompasses the embryo and yolk sac. The mesodermal layer of the allantois (splanchnic mesoderm) fuses with the mesodermal layer of the serosa (somatic mesoderm); in the double layer of mesoderm, a rich vascular network develops, connected with the embryonic circulation by allantoic arteries and veins; this highly vascular fusion membrane is the chorio-allantoic membrane. In mammals, the allantois originates as a diverticulum from the hindgut almost as soon as the hindgut is established, from splanchnopleure; the proximal portion gives rise to the allantoic stalk while the distal portion becomes enormously dilated. The allantois early acquires an abundant blood supply by way of large branches from the caudal end of the aorta; as yolk sac circulation undergoes retrogressive changes the plexus of allantoic vessels becomes more highly developed and takes over entirely the function of metabolic interchange between the fetus and the mother. In mammals with a saccular allantois (e.g., the pig), the chorion is essentially a layer of allantoic splanchnopleure fused with a layer of serosal somatopleure. In primate embryos, where the lumen of the allantois is rudimentary, endoderm is not involved in the formation of the chorion; allantoic mesoderm and blood vessels, however, extend distally beyond the rudimentary lumen and spread over the inner surface of the serosa, establishing the same essential relationships as in less highly specialized forms. The fusion of the allantois with the inner surface of the serosa brings to this hitherto poorly vascularized layer (serosa) an abundant circulation. In mammals, the embryo is dependent on the chorion (serosa) for carrying on metabolic interchange with the uterus.

allele most genes are present as two copies; each copy is called an allele; an allele is one of two (or more) forms of a particular gene.

allelic series a set of alleles having different degrees of loss of function arranged in order by the severity of the abnormal phenotype.

Allman, George (1812–1898) Anglo-Irish naturalist; coined the terms (in 1853) ectoderm and endoderm.

allogamy cross-pollination.

allometric growth *See: allometry.*

allometry the quantitative relationship between a part of an organism and the whole organism or another part of it as the organism increases in size. Also known as heterogony. Allometry occurs when different parts of the organism grow at different rates and can play a role in forming variant body plans within a *Bauplan*. In whale development, enormous growth of the upper jaw forces the nose (blowhole) to the top of the skull.

allosteric enzymes enzymes that have two functional sites: (1) the catalytic or active site that binds substrates as ligands and (2) the regulatory or allosteric site that binds allosteric effectors as ligands; the allosteric effectors may be positive or negative; i.e., they may activate or inhibit, respectively, the active site. *See: cooperativity.*

alopecia congenital loss of hair.

alternation of generations also called metagenesis; the phenomenon in which one generation of certain plants and animals reproduces asexually, followed by a sexually reproducing generation; a phenomenon generally exhibited by plants, wherein during their life cycle a haploid, multicellular, gamete-producing plant (gametophyte) alternates with a diploid, multicellular, spore-producing plant (sporophyte) (see Plate 17 in the color insert).

alternative RNA splicing pre-mRNAs may contain numerous introns; by the selective recognition of these one can have alternative RNA splicing; this results in alternative proteins from the same gene. This is one way in which development can be regulated by RNA processing.

alveolar period a period during lung development when the alveoli characteristic of the lung form.

alveoli terminal air sacs of the lungs.

amelia the congenital absence of limbs; a type of birth defect caused by the drug thalidomide.

ameloblasts the epithelial cells in the enamel organ of the tooth germ that will secrete enamel.

Ametabola those insects (Apterygota) in which the change of form from instar to instar is too slight and gradual to merit the term "metamorphosis."

ametabolous insects, e.g., springtails and mayflies, that have no larval stage and undergo direct development.

AMF formerly known as AMH. *See: anti-Müllerian factor.*

AMH *See: anti-Müllerian duct hormone.*

amino acids the building blocks of protein molecules.

ammocoete the larval stage in the life cycle of the lamprey.

ammonia in the life cycle of *Dictyostelium discoideum*, ammonia is produced by the migrating slug, which inhibits culmination; depletion of ammonia allows culmination to begin.

ammonotelic organisms organisms, such as freshwater fishes and frog tadpoles, that excrete ammonia. *See: ureotelic organisms.*

amnio-cardiac vesicles the pericardial regions of the coelom; in the chick embryo, these first appear as marked local enlargements of the coelomic chambers in the region of the anterior intestinal portal; later in development, they will form the pericardial cavity (see Fig. 19).

amniocentesis a prenatal diagnostic procedure initiated by obtaining a sample of amniotic fluid from the amniotic cavity; this procedure provides fetal cells as well as fluid for analysis (see Fig. 1).

amniocyte a cell found in the amniotic fluid.

amnion one of the four extraembryonic membranes formed during the development of higher vertebrates, including humans; it makes up the wall of the amniotic cavity. The functional significance of the amnion is emphasized by the observation that it appears only in embryos of non-water-living forms (amniotes). In chick development, the amnion and serosa (chorion) are closely associated in origin so they are here considered together; they are both derived from extraembryonic somatopleure. At approximately 30 hours, the head of the chick embryo sinks into the yolk and, at the same time, the extraembryonic somatopleure anterior to the head is thrown into a fold, the head fold of the amnion. Subsequently, two growth processes occur: (1) As the embryo increases in length, its head grows into the amniotic fold; and (2) growth of the somatopleure extends it over the head of the embryo; the head comes to lie in a double-walled pocket of extraembryonic somatopleure. The caudally directed limbs of the head fold of the amnion continue posteriorad as the lateral amniotic folds, which grow dorsomesiad and eventually meet in the midline, dorsal to the embryo. During the third day, the tail fold of the amnion appears. Continued growth of the

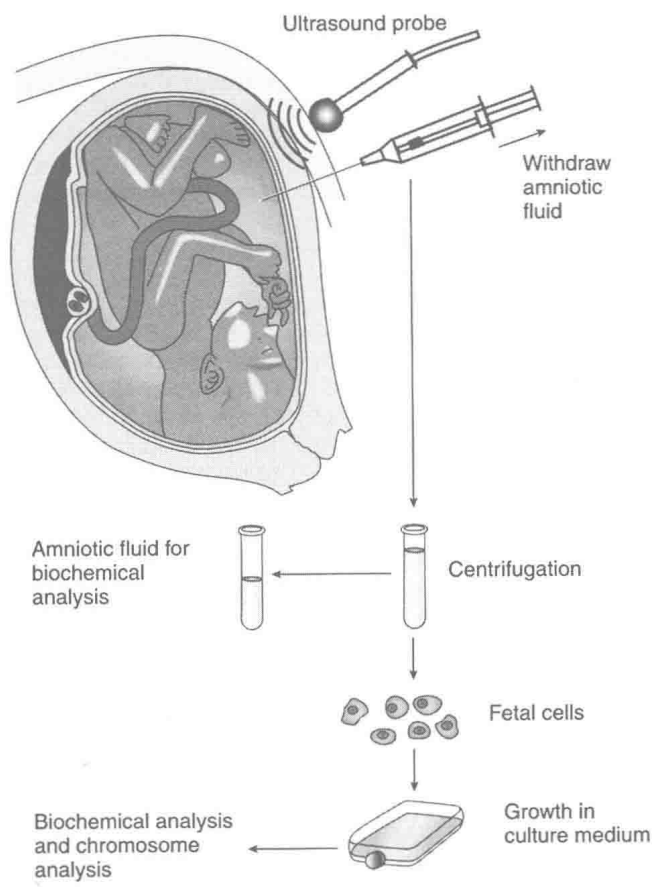


Figure 1. Diagram illustrating technique of amniocentesis. The amniotic fluid obtained by this technique contains both cells and liquid for prenatal diagnosis. Reprinted from Frank J. Dye, *Human Life Before Birth*, Harwood Academic Publishers, 2000, fig. 19-15, p. 173.

head, lateral, and tail folds results in their meeting and fusion above the embryo, providing the formation of a scar-like thickening, the sero-amniotic raphe, and the amniotic cavity, completely lined by ectoderm and continuous with the superficial ectoderm of the embryo. The outer layer of somatopleure becomes the serosa; the inner layer becomes the amnion. The cavity between the serosa and the amnion is the sero-amniotic cavity, a part of the extraembryonic coelom. The serosa eventually encompasses the embryo and all the other extraembryonic membranes. In all mammalian embryos, the amnion is formed at an exceedingly early stage of development; in some forms (humans), the amniotic cavity appears even before the body of the embryo has taken definite shape. In the pig, it is formed more leisurely (than in humans) and is easier to analyze; the first indication appearing shortly after the primitive streak stage; amniotic folds on all sides come together above the mid-dorsal region of the embryo; where the folds come together there persists for a time a cord-like mass of tissue between the amnion and the outer layer of the blastocyst; when this is obliterated, the embryo and its amnion lie free in the blastocyst. The amnion is attached to the body of the embryo where the body wall opens ventrally in the region of the yolk stalk; this ventral opening becomes progressively smaller giving rise to the umbilical ring; meanwhile the yolk stalk and the allantoic stalk are brought close together in the belly stalk (see Figs. 5, 6, 19, and 35).

-amnios- this word part refers to the amnion and, in the context of human development, is a part of terms describing abnormal amounts of amniotic fluid. See: **oligohydramnios**, **polyhydramnios**.

amniota with amnion. See: **amniotes**, **anamniota**.

amniote egg *See: cleidoic egg.*

amniotes vertebrates that develop with an amnion; reptiles, birds, and mammals. *See: anamniotes.*

amniotic cavity a fluid-filled cavity characteristic of amniote development; begins to form on the eighth day of human development; during their development, both the embryo and the fetus float in this, their private aquarium (see Figs. 6 and 44). *See: amnion.*

amniotic fluid the fluid that fills the amniotic cavity and in which the embryo and, later, the fetus float during their development; amniocentesis is a prenatal diagnostic procedure that begins with procuring a sample of this fluid (see Fig. 1).

amniotic folds in insect development, folds that originate from the edges of and then enclose the germ band; when these folds grow and fuse, the germ band is enclosed in a space known as the amniotic cavity. Coverings membranes also result from this fusion: the outer layer or serosa, continuous with the extra-embryonic blastoderm, and the inner membrane or amnion, continuous with the margins of the germ band. The amniotic cavity, serosa, and amnion protect the growing embryo from injury. *See: amnion.*

amniotic sac the sac that surrounds the embryo with amniotic fluid.

amoebocyte an amoeba-like cell found in the body fluid of coelomates; it is frequently phagocytic.

amorphous without any definite form; shapeless; lacking symmetry.

Amphibia the class of vertebrates composed of amphibians; includes three extant orders, Anura, Urodela, and Apoda.

amphibians members of the class of vertebrates (Amphibia) that includes frogs and salamanders.

amphiblastic cleavage the unequal but complete cleavage of telolecithal eggs.

amphimixis the union of paternal and maternal elements by syngamy. \rightarrow

Amphioxus a cephalochordate traditionally studied in embryology/developmental biology courses as a representative of an evolutionarily primitive chordate; encompasses two genera, *Branchiostoma* and *Asymmetron*. Amphioxus lacks neural crest cells (see Plate 1 in the color insert).

amplexus the physical interaction between male and female amphibians during mating, involving the embrace of the female by the male but not the intimacy of copulation.

ampulla literally, "a flask": (1) the portion of the fallopian tube, closest to the ovary, in which fertilization normally occurs, and (2) the enlarged segment of the vas deferens, just before it receives the seminal vesicle (see Fig. 16).

anagenesis *See: phyletic transformation.*

anal agenesis literally, "the lack of the anal opening" (anus) but also used to refer to an abnormal opening as into the vulva in females or the urethra in males; the latter variety results from incomplete partition of the cloaca by the urorectal septum.

anal evagination an outpocketing of the hindgut endoderm toward the proctodeal invagination of ectoderm.

anal membrane the membrane formed of proctodeal ectoderm and hindgut endoderm; its normal breakdown creates the opening called the anus.

anal plate *See: anal membrane.*

anal stenosis a narrowing of the anal canal, probably resulting from urorectal septum deviation in partitioning of the cloaca.

analgesic a drug that relieves pain.

analogous structures that are similar in function but do not have the same origin, e.g., the wing of a bird and the wing of an insect.

analogous organs body organs/parts of different species that have different evolutionary origins but have become adapted to serve the same purpose (e.g., wings of a bat and wings of an insect).

anamniota no amnion. *See: anamniotes, amniota.*

anamniotes vertebrates that develop without an amnion; fish and amphibians. *See: amniotes.*

anaphase the stage of mitosis or meiosis when the daughter chromosomes are moving toward opposite poles of the spindle (see Fig. 29).

anatomic position standing erect with the arms at the sides and the palms forward (see Fig. 2).

-andr- a man, e.g., as in polyandry.

androecium collectively, all of the stamens in a flower.

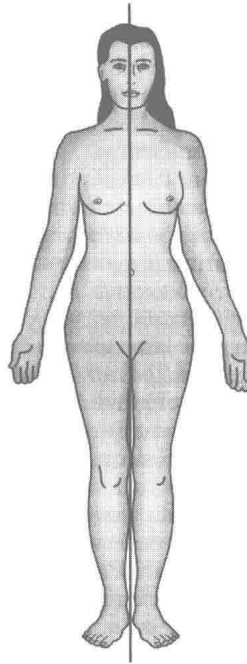


Figure 2. Anatomic position and bilateral symmetry. The body is erect, the arms are at the sides of the body, and the head, palms, and feet face forward. The line is in the median plane of the body, which is also the plane of bilateral symmetry. Reprinted from Frank J. Dye, *Human Life Before Birth*, Harwood Academic Publishers, 2000, fig. 1-1, p. 3.

androgen insensitivity syndrome the result of a mutation in which XY individuals (chromosomally male) do not make a functional testosterone *receptor*. *See: testicular feminization.*

androgenesis development of an embryo from a fertilized irradiated egg, involving only the male nucleus.

androgenic merogony the fertilization of egg fragments that lack a nucleus.

androgens male sex hormones, e.g., testosterone.

anencephaly a type of birth defect in which most of the brain is missing; a term literally meaning “without a brain”; more specifically, it refers to the absence of the cerebrum, cerebellum, and flat bones of the skull. *See: anterior neuropore.*

aneuploid the number of chromosomes in a cell that is not an exact multiple of the haploid number of chromosomes for the species. *See: euploid.*

angioblasts mesodermal cells that organize themselves into capillary blood vessels.

angiogenesis a type of blood vessel development that may occur in adults as well as in embryos, in which new capillaries sprout from existing vessels. In the adult, new vessels are produced only through angiogenesis; outside of female reproductive cycles, angiogenesis in the adult is largely controlled by pathological situations, such as wound healing and tumor growth. *See: Bacteroides thetaiotaomicron, vasculogenesis.*

angiogenetic clusters also called blood islands. *See: blood islands.*

angiopoietin-1 (Ang1) a protein involved in vasculogenesis; mediates the interaction between the endothelial cells and pericytes, smooth muscle-like cells recruited by the endothelial cells to cover them. *See: FGF2, vascular endothelial growth factor (VEGF).*

angiopoietins paracrine factors that mediate the interaction between endothelial cells and pericytes.

angiosperms the flowering plants.

animal has been defined (Slack et al.) as an organism that displays a particular spatial pattern of *Hox* gene expression.

animal cap the upper portion of the animal hemisphere of the frog blastula, above the equatorial region. Isolated by itself, animal cap tissue will give rise to only ectoderm, but

combined with vegetal cells of the blastula, it may be induced to form mesodermal tissue, such as muscle and notochord.

animal gradient one of two gradients of “principles” that are mutually antagonistic but that must interact with each other if normal sea urchin development is to occur. The animal gradient is centered at the animal pole. *See: animalized.*

animal hemisphere that half of the egg that has the animal pole at its center.

animal pole that point on the surface of an egg where the polar bodies are formed during the meiotic divisions of maturation (see Plate 3 in the color insert).

animalculist a preformationist who believed that the new individual is already preformed in the spermatozoon and that development involves essentially the growth of the preformed organism.

animalization the sea urchin embryo becoming animalized; may be caused by factors such as zinc, trypsin, and Evans blue dye.

animalized a term used in the context of experimental embryology of, primarily, sea urchins; when the sea urchin develops to excess those parts pertaining to the animal gradient, e.g., the tuft of cilia at the animal pole. If the vegetal gradient is weakened or suppressed, the animal gradient becomes preponderant and the embryo is animalized. *See: animal gradient, vegetalized.*

animal-vegetal axis of the embryo, an imaginary line joining the animal and vegetal poles.

animism the belief that inanimate objects possess a personal life or soul.

aniridia absence of the iris; caused by a mutation of the *PAX6* gene.

anisogamy sexual reproduction involving the fusion of unlike gametes.

ankyloglossia sometimes referred to as tongue-tie, refers to an abnormal attachment of the tongue to the floor of the oral cavity (mouth).

anlage the rudiment or primordium of a structure. *See: primordium.*

annual a plant that germinates from seed, flowers, sets seed, and dies in the same year.

anoikis rapid apoptosis that occurs when epithelial cells lose their attachment to the extracellular matrix.

anovulation the lack of ovulation.

Antennapedia complex of *Drosophila*, comprises five homeobox genes, which control the development of the parasegments anterior to parasegment 5 in a manner similar to the bithorax complex. The Antennapedia complex controls parasegment identity in the head and first thoracic segment. The order of genes in the complex is the same as the spatial and temporal order in which they are expressed along the anteroposterior axis during development. *See: bithorax complex.*

Antennapedia gene a gene responsible for the specification of fly body parts; mutations in it lead to bizarre phenotypes; specifies the identity of the second thoracic segment in *Drosophila*. In the dominant mutation of this gene, legs rather than antennae grow out of the head sockets; in the recessive mutation of this gene, antennae sprout out of the leg positions.

anteriad toward the anterior.

anterior group Hox genes Hox genes expressed in the anterior region of bilaterians and located toward the 3' end of Hox clusters; include the *Hox1* and *Hox2* genes in vertebrates.

anterior intestinal portal in the chick embryo, the opening from the midgut into the foregut (see Plate 2b in the color insert).

anterior neuropore the temporary opening at the cephalic end of the early neural tube. In the chick embryo, the anterior neuropore is almost closed at 33 hours. In human development, an improperly closed anterior neuropore gives rise to the birth defect known as anencephaly (see Fig. 30). *See: spina bifida.*

anterior organizing center classic embryological experiments demonstrated that there are at least two “organizing centers” in the insect egg, one is the anterior organizing center, and the other the posterior organizing center; in *Drosophila* embryos, the product of the wild-type *bicoid* gene is the morphogen that controls anterior development. *See: posterior organizing center, terminal gene group.*

anterior pole of the insect egg is that pole of the egg that lies in the ovariole directed toward the head of the parent insect.

anterior tip the anterior tip of the migrating pseudoplasmodium of *Dictyostelium discoideum* acts as an embryonic organizer in the sense that (1) a grafted tip will produce a new

individual and (2) the tip is a source of an inhibitory gradient regarding the formation of tips.

anterior visceral endoderm one of two signaling centers in the mammalian embryo; works together with the node ("the organizer") to form the forebrain; expresses several genes necessary for head formation, including genes for transcription factors, *Hesx-1*, *Lim-1*, and *Otx-2*, and for the paracrine factor *Cerberus*. *See: node*.

anteroposterior axis the axis joining the head and tail; also called head-to-tail, craniocaudal, or rostrocaudal axis. *See: axes*.

anther that portion of the stamen of a flower that produces pollen.

anther sac one of the pollen chambers of the anther.

antheridiophore a stalk that bears antheridia; found in some liverworts.

antheridium (1) a male gametangium, a container of sperm, formed by, for example, ferns; (2) a type of reproductive structure in algae that produces the male gametes or spermatozoa, e.g., as in the filamentous green alga, *Oedogonium*; and (3) a unicellular or multicellular structure which produces spermatozoa; the male reproductive structure in moss and fern gametophytes (see Plate 16 in the color insert).

antheridogen substance secreted by young fern gametophytes to stimulate the development of antheridia.

Anthropocene successor of the Holocene epoch, an epoch characterized by a human-dominated environment.

anticlinal divisions cell divisions that take place in planes perpendicular to the surface of the structure of which they are a part; these divisions increase the number of cells in a layer. *See: periclinal divisions*.

anticodon the triplet of nucleotides in a transfer RNA molecule that hydrogen bonds to a codon of messenger RNA.

antifertilizin a receptor molecule thought to exist on sperm heads of sea urchin sperm that would combine with fertilizin (sea urchin egg jelly coat) causing sperm agglutination experimentally; thought to function as the species-specific sperm receptor during fertilization.

antifungal symbiotic bacteria bacteria found associated with embryos that protect the embryos from fungal infection, e.g., in the outer coats of embryos, such as those of American lobster embryos. *See: embryo defenses*.

anti-Müllerian duct hormone one of two major hormones produced by the fetal testis (the other is testosterone); AMH destroys the Müllerian duct.

anti-Müllerian factor TGF- β family paracrine factor secreted by the embryonic testes that induces apoptosis of the epithelium and destruction of the basal lamina of the Müllerian duct, preventing formation of the uterus and oviducts. *See: anti-Müllerian duct hormone*.

antipodal cells those three cells found opposite the end of the embryo sac that contains the egg and synergid cells; they have no known function.

antisense oligonucleotides antisense oligonucleotides refer to short, synthetic oligonucleotides that are complementary in sequence to its cognate gene product and upon specific hybridization to its cognate gene product induces inhibition of gene expression. Oligonucleotides, as short as a 15 mer, have the required specificity to inhibit gene expression of a particular gene by annealing to the cellular mRNA. The mechanism of inhibition of gene expression is based on two properties; the first is the physical blocking of the translation process by the presence of the short double-stranded region, and the second is the presence of the RNA-DNA duplex that is susceptible to cellular RNase H activity. RNase H cleaves the RNA-DNA duplex region of the mRNA, thus preventing the faithful translation of the mRNA.

antisense RNA an RNA complementary to a mRNA; the reverse of the original message; i.e., a transcript that is complementary to the natural one. When introduced into a cell, the antisense RNA binds to the normal message resulting in a double-stranded RNA, which is digested by cellular enzymes; this causes a functional depletion of the message, allowing developmental biologists to determine the function of genes during development. *See: redundancy*.

antral vacuoles tiny fluid-filled spaces found among the follicle cells of a developing ovarian follicle.

antrum the fluid-filled cavity of the mature graafian follicle (see Fig. 33).

Anura tail-less amphibians; the frogs and toads.

anus the caudal opening of the gut to the outside of the body.

aorta the largest arterial blood vessel in the body, which carries blood away from the heart to various parts of the body. In mammals, the right fourth aortic arch degenerates and the left one gives rise to the arch of the adult aorta. In birds, the left fourth aortic arch degenerates and the right one gives rise to the arch of the adult aorta. Early in development the aorta gives rise to a segmentally arranged series of small vessels, the dorsal intersegmental arteries, which extend into the dorsal body wall. In the adult, three vessels originating from the dorsal aorta supply the abdominal viscera: the coeliac artery and the superior and inferior mesenteric arteries. The omphalomesenteric arteries develop as paired vessels; in the closure of the ventral body wall, they are brought together and fuse to form a single vessel. With the atrophy of the yolk sac, the proximal portion of the omphalomesenteric artery persists as the superior mesenteric; the coeliac and inferior mesenteric arteries originate from the aorta independently.

aorta-gonad-mesonephros region See: **AGM**.

aortic arches a series of six arterial blood vessels that originate in early development in conjunction with the pharyngeal arches. The aortic arches lie embedded in tissue of the branchial arches of corresponding numbers. Although all six aortic arches do not persist, several give rise to important prenatal and adult arterial blood vessels. In the chick embryo, the endothelial lining of the heart is continued cephalad as the ventral aorta (beneath the foregut), which bifurcates to form the paired ventral aortic roots, which curve around the cephalic end of the foregut as the first pair of aortic arches and extend caudad as the paired dorsal aortae. In the chick embryo, at 33–38 hours, there is a single pair of aortic arches; at 50 hours, there is a second pair and capillary sprouts of the third pair; and at 60 hours, there is a third pair and capillary sprouts of the fourth pair. By the fourth day, two more pairs of aortic arches appear posterior to the four formed in the 55–60-hour chick embryo; The first, second, and fifth pairs eventually disappear. The members of the fourth pair of aortic arches have different fates on opposite sides of the body. In mammals, the left generally becomes greatly enlarged to form the arch of the adult aorta, whereas the right forms the root of the subclavian artery; the short section of the right ventral aortic root proximal to the fourth arch persists as the brachiocephalic artery from which both the right subclavian and right common carotid arteries develop. Regarding the fate of the members of the sixth pair of aortic arches: branches extend from both toward the lungs; after these pulmonary vessels are established, the right side of the sixth aortic arch loses communication with the dorsal aortic root and disappears. On the left side, the sixth aortic arch retains communication with the dorsal aortic root; the portion of it between the dorsal aorta and the point where it is connected to the pulmonary artery gives rise to the ductus arteriosus. See: **aorta, carotid arteries**.

Apaf-1 apoptotic protease activating factor-1; the mammalian homologue of CED-4 of *Caenorhabditis elegans*, which plays a role in mammalian apoptosis; i.e., it participates in the cytochrome *c*-dependent activation of caspase-3 and caspase-9.

apical dominance regulation of the branching patterns of plant shoots by the shoot tip; the presence of a terminal (apical) bud inhibits the growth of lateral (axillary) buds beneath it; it is hypothesized that indole-3-acetic acid (IAA) coming from the shoot tip stimulates cells around lateral buds to make ethylene that, in turn, inhibits bud growth.

apical ectodermal cap when a salamander limb is amputated, epidermal cells from the remaining stump migrate to cover the wound surface, forming the wound epidermis, which proliferates to form the apical ectodermal cap.

apical ectodermal ridge (AER) a thickening of ectoderm found at the distal-most end of the developing vertebrate limb bud; interaction between the AER and the underlying mesenchymal mesoderm cells of the limb bud is necessary for limb development. The AER is induced by the underlying mesodermal cells.

apical meristem a meristematic part of a plant, the activity of which leads to growth in length of a plant part, such as a root or shoot. See: **meristem**.

apical notch the notch at the top of the cordate-shaped fern prothallus, at which there is meristematic activity (see Plate 15 in the color insert).

Apoda legless amphibians; the caecilians.

apomixis (apogamy) the formation of embryos from haploid eggs within embryo sacs and from cells that have not divided meiotically; seed production without fertilization.

apoplastic continuity continuity that occurs outside the cell's cytoplasm, in the spaces between cell walls. See: **symplastic continuity**.