DEVELOPMENT—The early part of ontogeny from **zygote** to hatching or birth. The period during which the single-celled zygote divides into multiple cells, the cells differentiate and become fated to form specific structures, and organ development (**organogenesis**) occurs. Some organ development often continues even after birth or hatching (e.g., closure of the cranial fontanelle in human infants, development and growth of adult teeth in mammals), but usually the period of 'development' is considered to end at birth or hatching.

CLADE—A monophyletic group or lineage, i.e., a common ancestor and *all* of its descendants.

GRADE—A 'level' of organization that is not necessarily represented by a monophyletic group. For example, if we were able to look at a living, early **synapsid**, it would appear to us to be a 'reptile', even though it is in the synapsid (mammal) clade rather than the reptile clade. As such, some people would say that it represents a 'reptile grade' of structural organization.

GRADUALISM—A theory of **phenotypic evolution** suggesting that evolutionary change occurs more-or-less constantly, even if slowly. Gradual change is not associated with an particular point in the phylogeny, i.e., it occurs during both **anagenesis** and **cladogenesis** (but see **'punctuated equilibrium'**). Gradualistic changed has been demonstrated with evidence in the fossil record.

PUNCTUATED EQUILIBRIUM—An alternative theory for the main pattern of **phenotypic evolution** championed by **Stephen J. Gould**. It proposes that during most of evolutionary history, organisms remain more-or-less phenotypically **static** (i.e., they do not evolve, they are in **equilibrium**), but during **cladogenesis**, when one species gives rise to two, there is a relatively short period (in geological terms) when phenotypic evolution occurs rapidly. Hence, most phenotypic evolution occurs in **'punctuated'** steps during the process of **cladogenesis**, with little or no **anagenesis** (and gradualism) occurring in between. Some fossil groups seem to support the P-E model, but the evidence is controversial.

ANAGENESIS—Evolutionary change occurring through time in a population or species that does NOT speciate (there is no **cladogenesis**).

CLADOGENESIS—The formation of new species. When one ancestral species splits (usually because of physical separation or continental drift) into two descendant (or daughter) species. As such, the origin of a new clade (monophyletic lineage).

CHARACTER—A individual trait or characteristic of an organism that can be compared in other individuals or species to determine patterns of evolution, etc. When something is identified as a 'character' it is assumed that the identified trait or feature is (i) capable of evolving independent of other characters (**independent**); and (ii) is developmentally separated from other characters (**individuated**). These two assumptions must be violated on some level because all characters are connected to all other characters, if only by sharing the same body. However, usually identified characters are independent and individuated enough that they can be used in formal **'character analyses'** to create accurate **phylogenetic hypotheses**. Characters usually exist in variable forms in different species. These variable forms are called **character states**.

HOMOLOGY—A term coined by **Richard Owen in 1843**, referring to a **character** that is compared in two or more species. Owen's definition was "The same organ in different animals under every variety of form and function." In modern terms, we recognize that two characters are the "same" in two or more species if they evolved from the "same" character present in a common ancestor. In evolutionary terms, homology refers to, "The possession by two or more species of a trait derived, with or without modification, from their common ancestor." Importantly, characters that are homologous may or may not look the same and they may or may not have the same function—**homology refers to the continuity of evolutionary history; it says nothing about form or function**. Homology can be confusing. One must be specific. For example, while the wing of a bat and the wing of a bird are *not* homologous (because they evolved their wings independently (an example of **homoplasy**), the individual bones that make up the wings in both groups *are* homologous.

ANALOGY—Owen (1843) also coined this term: "A part or organ in one animal which has the same function as another part or organ in a different animal." Specifically, analogy refers to functional similarity in traits, e.g., gills and lungs are analogous, as are the tail fins of whales and icthyosaurs.

SYMPLESIOMORPHY—Similarity in form of two or more characters that results from their shared evolutionary history. As such, each of the species simply inherited the trait from their common ancestor and that trait failed to evolve. Consequently, the trait looks similar in each of the descendant species only because it hasn't changed (it retains its 'primitive' or ancestral state). In contrast to **homoplasy**.

HOMOPLASY—Refers to similarity in form or function of a character in two or more species that evolved independently (separately) within each species or clade, i.e., the similarity is *not* inherited directly from a common ancestor. When two or more species evolve similar characters from different ancestral conditions, the homoplastic characters are said to be **convergent**. Convergence is usually thought to be caused by similar environments with similar forms of selection.

ZYGOTE—An ovum fertilized by a sperm nucleus. A single, diploid cell. The cell may contain a lot of yolk (e.g., reptiles) or it may contain hardly any yolk (e.g., mammals).

MORULA—Once the zygote begins to divide into multiple cells, it eventually forms a solid ball of tinier cells called a morula. The morula is the same size as the **zygote**.

BLASTULA—Eventually a morula develops a cavity inside called the **blastocoel**, i.e., it becomes a hollow ball, still without growth.

GASTRULA—During **gastrulation** (formation of the gastrula) he cells of the **blastula** begin to migrate across the surface of the embryo to a single point (**the blastopore**), where they **involute** (move to the inside) forming layers of cells. These layers are called the **embryonic germ layers** (the **endoderm**, **mesoderm** [including **chordamesoderm**] and **ectoderm)**. In addition, a hollow tube is created through the middle of the embryo that becomes the **gut tube** (in the embryo it is called the **archenteron**). In **deuterostomes**, like vertebrates, the blastopore becomes the **anus** and the other end of the gut tube eventually opens to the outside to form the **mouth**. The endoderm forming the gut tube contains various amounts of acellular **yolk**, depending on the species. The yolk is eventually surrounded by the endodermal lining of the gut tube and is absorbed during further development and growth (sometimes one can find newly hatched turtles with a small bit of yolk sac still attached!).

NEURULA—During **neurulation**, the embryo begins to grow. A thickening forms in the **ectoderm** on the top of the embryo running anteroposteriorly (front to back). This thickened region is called the **neural plate**. Its sides roll up, sink down and join at the top to form a **neural tube** that runs the length of the embryo. Just beneath it, the **chordamesoderm** forms into the **notochord**, a stiff, turgid structure that supports the axis of the body and keeps it from collapsing during bending/locomotion. During neurulation, some ectodermal cells from the neural plate, on either side of the developing neural tube, bud off on either side of the neural tube, become **mesenchymal** and migrate into the head and throughout the body as **neural crest cells**. These eventually form various tissues, notably the skeletal elements of the visceral arches and the dermal bones of the skull. Another set of ectodermal cells lateral to the neural crest cells form the **neurogenic placodes**—thickenings of the ectoderm that interact with the underlying mesodermal **mesenchyme** to form various structures. In the head the neurogentic placodes sink down and enter the sensory capsules of the developing chondrocranium. They form the sensory cells of the nose and ear and the lens of the eye.

ENDODERM—The innermost of the **embryonic germ layers**, the endoderm includes the acellular **yolk** when present. The yolk is eventually metabolized to support development and all that is left of the endoderm in an adult animal is the single cell thick layer (**epithelium**) that lines the inside of the **gut tube** and some other organs.

MESODERM—The mesoderm is the embryonic germ layer more-or-less in the middle of the **gastrula.** The part of it that lies beneath the long axis of the embryonic body, corresponding to the place where the **neural plate** will form, differentiates into a special kind of mesoderm that will form the **notochord** (the **chordamesoderm**). The rest of the mesoderm will form segmented units along the body axis called **somites**, as well as a layer of unsegmented mesoderm along the body walls called the **lateral plate**. Mesoderm forms most of the **connective tissues**, including the **cartilages** and **bones** of the post-cranial skeleton, as well as the **musculature**.

ECTODERM—The third embryonic germ layer, it forms the outer covering of the **gastrula** and thickens on top to form the **neural plate** and **neural tube**. In the adult, ectodermal cells gives rise to **neurons** of the central and peripheral nervous system, the **neural crest**, the **neurogenic placodes** (and other placodes behind the head) and the **epidermis** (the outer layer of the skin).

NEURAL CREST—see **neurula**. Neural crest cells give rise to all the pigment cells of the body (**melanocytes** and others), but primarily contribute to the **head skeleton** and other head structures new to vertebrates, especially the **splanchnocranium** (**visceral arches**) and the **dermatocranium**.

NOTOCHORD—A tough, cylindrical structure that forms the main axial support for all vertebrate embryos. It was the only axial support structure for the chordate ancestors of vertebrates (before vertebrae evolved) and is also found in living non-vertebrate chordates. It is one of the shared, diagnostic characters of all chordates. It is covered by a strong, fibrous membrane and contains specialized cells that are filled with a fluid or 'gel' that stretches the tough outer tunic, making it **turgid** and fairly rigid. When vertebrae form in vertebrates, they develop either within or around the notochord. Many living fishes, including some bony fishes, still have a complete notochord, even as adults. The vertebrae simply form 'donuts' around it. However, in most vertebrates, development of the vertebrae actually replaces the notochord so it usually disappears. In adult humans, vestiges of the notochord remain within the intervertebral discs, forming a 'jelly center' that helps cushion compressive forces along the spine. It is called the **nucleus pulposus**. It is this notochordal gel that 'herniates' through the fibrous outer layer of the disc in a pathology called a 'herniated' or 'slipped disc'.

SOMITES—Segmented blocks of **mesodermal tissue** that form alongside the **neural tube** and **notochord** in the embryo dorsal to an unsegmented mesodermal layer called the **lateral plate**, which lies between the gut tube and the lateral body wall. Later, each somite grows down along the outside of the body wall, coming to lie lateral to the lateral plate mesoderm. The mesoderm of the somites gives rise to the dermis of the skin, the body musculature and most of the post-cranial skeleton.

LATERAL PLATE—Unsegmented mesoderm that forms a continuous sheet along the flanks of the embryo, between the gut tube and the body wall. It eventually splits in the middle to form the body cavity or **coelom**. The inner layer becomes associated with the gut tube to form the **splanchnic mesoderm** and the outer layer associates with the body wall to form the **somatic mesoderm**. The splanchnic mesoderm forms the smooth muscle and connective tissue of the gut tube (**viscera**) and a thin, smooth outer membrane covering them; the somatic mesoderm forms a similar thin, smooth, eptithelial layer lining the coelom. These slippery epithelia (**serosa**) keep the organs from adhering to themselves and the wall of the body cavity.

CONNECTIVE TISSUE—A type of tissue consisting to three components: (i) **living cells**; and a **matrix** consisting of (ii) **a ground substance** (usually a **proteoglycan gel**); and (iii) **fibers** (usually **collagen fibers**; sometimes **elastic fibers** or a mixture). Connective tissues include **bone**, **cartilage**, **tendon**, **ligament,** enamel, dentin (and other types of enamel-like tissues) and various types of **'loose' connective tissue**.

CARTILAGE—Cartilage forms the embryonic skeleton of all vertebrates and the internal skeleton of vertebrate ancestors. It remains the tissue forming the internal skeletons of agnathans and chondricthyans. Cartilage cells, or **chondrocytes**, secrete a **matrix** consisting of a **proteoglycan gel** and various types and amounts of **fiber**, depending on the location (and therefore, type) of cartilage. Chondrocytes lie within little holes (lacunae) often arrayed in rows that give cartilage its characteristic appearance.

HYALINE CARTILAGE—A smooth, almost glassy type of cartilage that is found in parts of the head skeleton and especially in most joints. In **synovial joints**, where the **articular cartilages** are covered with **synovial fluid**, there is very little friction between the bones moving at the joint. There is a lot of matrix with relatively few **collagen fibers**.

FIBROCARTILAGE—Found primarily in the **intervertebral discs** lying between the bodies of adjacent vertebrae. Contains very l**arge amounts of collagen fiber**, which makes fibrocartilage extremely tough and relatively incompressible. In most tetrapods, there is a small amount of soft gel in the center of each disc that represents the remnant of the **embryonic notochord**.

ELASTIC CARTILAGE—Found only in the **epiglottis** and parts of the **external ear** of mammals. The epiglottis forms a flexible cartilaginous flap in front of the **glottis** (opening of the trachea) that prevents aspiration of food into the trachea/lungs when food passes through the throat. Instead of collagen fibers, elastic cartilage has primarily **elastic fibers**, which are stretchy.

BONE—Forms either within an existing **cartilage model**, or by itself within the dermis of the skin or other connective tissue membranes. Bone is similar to cartilage except that **inorganic salts**, especially **calcium phosphate**, precipitate out on the collagen fibers within the **matrix** and **crystallize** in a form known as **hydroxyapatite**. The inorganic salts and crystallization make bone much stronger than cartilage, but less flexible. Bone cells are called **osteocytes** and the fibers within the matrix are mostly **collagen**. Bone can form dense layers or masses known as **compact bone**, or it can form delicate spicules creating a network or lattice of bone with many empty spaces in between, known as **spongy**, **trabecular**, or **cancellous bone**. Bone tissue is actively **remodeled** by continuous addition and removal of calcium and phosphate ions. It thickens and thins in areas in a way that reduces stress on the bone. Calcium and phosphate are also mobilized from bone for use in many physiological processes, including muscle contraction and the generation of nerve impulses.

CARTILAGE REPLACEMENT BONE—Bone that develops in association with pre-existing cartilage. It includes both **perichondral bone** and **endochondral bone**.

PERICHONDRAL BONE—A type of membrane bone that forms deep within the body, rather than superficially, like dermal bone. It forms compact bone around the outside of a pre-existing cartilage**.**

ENDOCHONDRAL BONE—Bone that forms within a pre-existing cartilage (the **model**). Bone cells invade the cartilage and start replacing the cartilage matrix with bone matrix.

MEMBRANE BONE—Forms de novo (i.e., with no cartilage precursor) within a **membrane**, often near the surface of the body within the **dermis** of the skin (= **dermal bone**), or sometimes within other mesodermal/connective tissue membranes deeper in the body associated with ossifying cartilages = **perichondral bone**). Such bones often attach directly to endochrondral bones with sutures. In adult vertebrates, it is difficult to distinguish dermal/membrane bone from endochondral bone.

TENDON—A type of connective tissue that is composed almost entirely of **collagen fibers** with practically no matrix. Living cells are called **fibroblasts**. Tendons connect **muscles to bones** and are continuous with the **epimysium** and **endomysium** of the muscle and the **periosteum** of the bone for a very strong connection. Muscle-tendon systems are used by some animals (e.g., kangaroos) to store **elastic energy** when the foot hits the ground. During the next push-off, the elastic energy is released (the streteched tendon-muscle rebounds), decreasing the amount of energy required for powerful hopping.

LIGAMENT—Similar to tendon, but connecting **bone to bone**. A few ligaments contain a high proportion of **elastic fibers**, rather than collagen fibers, permitting the ligament to stretch (e.g., the **nuchal ligament** of ungulates that supports the head so that no muscle contraction is needed to hold it up or to lift it from the ground).

PERIOCHONDRIUM—Collagen fibers forming a tough, fibrous layer over the outside of a cartilage; fibers are continuous with fibers within the matrix and continuous with fibers of any connecting ligaments, bones or muscles.

PERIOSTEUM—As for the **perichondrium**, except covering bones.