UNIT-I(SEM-II)

CHORDATE-:

A **chordate** (/ˈkɔːrdeɪt/ *KOR-dayt*) is a deuterostomic bilaterial animal belonging to the phylum **Chordata** (/kɔːrˈdeɪtə/ *kor-DAY-tə*). All chordates possess, at some point during their larval or adult stages, five distinctive physical characteristics (synapomorphies) that distinguish them from other taxa. These five synapomorphies are a notochord, a hollow dorsal nerve cord, an endostyle or thyroid, pharyngeal slits, and a post-anal tail.[8] The name "chordate" comes from the first of these synapomorphies, the notochord, which plays a significant role in chordate body plan structuring and movements. Chordates are also bilaterally symmetric, have a coelom, possess a closed circulatory system, and exhibit metameric segmentation.

In addition to the morphological characteristics used to define chordates, analysis of genome sequences has identified two conserved signature indels (CSIs) in their proteins: cyclophilin-like protein and inner mitochondrial membrane protease ATP23, which are exclusively shared by all vertebrates, tunicates and cephalochordates.[9] These CSIs provide molecular means to reliably distinguish chordates from all other animals.

Chordates are divided into three subphyla: Vertebrata (fish, amphibians, reptiles, birds and mammals), whose notochords are replaced by a cartilaginous/bony axial endoskeleton (spine) and are cladistically and phylogenetically a subgroup of the clade Craniata (i.e. chordates with a skull); Tunicata or Urochordata (sea squirts, salps, and larvaceans), which only retain the synapomorphies during their larval stage; and Cephalochordata (lancelets), which resemble fish but have no gills. The Vertebrates and Tunicates compose the clade Olfactores, which is sister to Cephalochordata (see diagram under Phylogeny). Extinct taxa such as the conodonts are chordates, but their internal placement is less certain. Hemichordata (which includes the acorn worms) was previously considered a fourth chordate subphylum, but now is treated as a separate phylum which are now thought to be closer to the echinoderms, and together they form the clade Ambulacraria, the sister phylum of the Chordates. Chordata, Ambulacraria, and possibly Xenacoelomorpha are believed to form the superphylum Deuterostomia, although this has recently been called into doubt.[10]

Chordata is the third-largest phylum of the animal kingdom (behind only the protostomic phyla Arthropoda and Mollusca) and is also one of the most ancient taxons. Chordate fossils have been found from as early as the Cambrian explosion over 539 million years ago.[11] Of the more than 81,000[12] living species of chordates, about half are ray-finned fishes (class Actinopterygii) and the vast majority of the rest are tetrapods, a terrestrial clade of lobe-finned fishes (Sarcopterygii) who evolved air-breathing using lungs.

History of name

[edit]

Although the name Chordata is attributed to William Bateson (1885), it was already in prevalent use by 1880. Ernst Haeckel described a taxon comprising tunicates, cephalochordates, and vertebrates in 1866. Though he used the German vernacular form, it is allowed under the ICZN code because of its subsequent latinization.[4]

Anatomy

[edit]

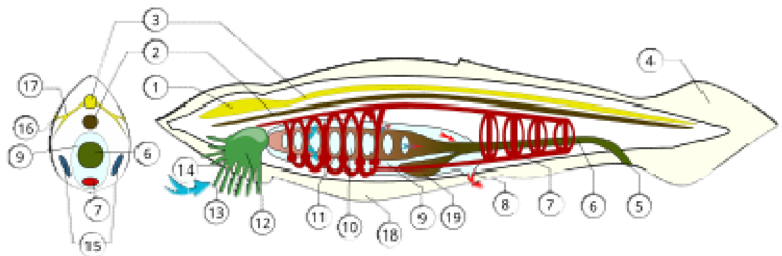

The glass catfish (*Kryptopterus vitreolus*) is one of the few chordates with a visible backbone. The spinal cord is housed within its backbone.

Chordates form a phylum of animals that are defined by having at some stage in their lives all of the following anatomical features:[13]

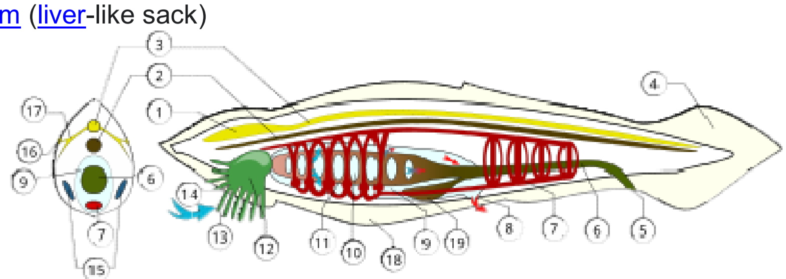
- A notochord, a stiff but elastic rod of glycoprotein wrapped in two collagen helices, which extends along the central axis of the body. Among members of the subphylum Vertebrata (vertebrates), the notochord gets replaced by hyaline cartilage or osseous tissue of the spine, and notochord remnants develop into the intervertebral discs, which allow adjacent spinal vertebrae to bend and twist relative to each other. In wholly aquatic species, this helps the animal swim efficiently by flexing its tail side-to-side.
- A hollow dorsal nerve cord, also known as the neural tube, which develops into the spinal cord, the main communications trunk of the nervous system. In vertebrates, the rostral end of the neural tube enlarges into several vesicles during embryonic development, which give rise to the brain.
- Pharyngeal slits. The pharynx is the part of the throat immediately behind the mouth. In fish, the slits are modified to form gills, but in some other chordates they are part of a filter-feeding system that extracts food particles from ingested water. In tetrapods, they are only present during embryonic stages of the development.
- A post-anal tail. A muscular tail that extends backwards behind the anus. In some chordates such as hominids, this is only present in the embryonic stage.
- An endostyle. This is a groove in the ventral wall of the pharynx. In filter-feeding species it produces mucus to gather food particles, which helps in transporting food to the esophagus.[14] It also stores iodine, and may be a precursor of the vertebrate thyroid gland.[13]

There are soft constraints that separate chordates from other biological lineages, but are not part of the formal definition:

- All chordates are deuterostomes. This means that, during embryonic development, the anus forms before the mouth does.
- All chordates are based on a bilateral body plan.[15]
- All chordates are coelomates, and have a fluid-filled body cavity (coelom) with a complete serosal lining derived from mesoderm called mesothelium (see Brusca and Brusca).[16]



1 = bulge in spinal cord ("brain")
2 = notochord
3 = dorsal nerve cord
4 = post-anal tail
5 = anus
6 = digestive canal
7 = circulatory system
8 = atriopore
9 = space above pharynx
10 = pharyngeal slit (gill)
11 = pharynx
12 = vestibule
13 = oral cirri
14 = mouth opening
15 = gonads (ovary / testicle)
16 = light sensor
17 = nerves
18 = metapleural fold
19 = hepatic caecum (liver-like sack)



Anatomy of the cephalochordate *Branchiostoma lanceolatum*. Bolded items are components of all chordates at some point in their lifetimes, and distinguish them from other phyla.

Classification

[edit]

The following schema is from the 2015 edition of *Vertebrate Palaeontology*.[17][18] The invertebrate chordate classes are from *Fishes of the World*.[19] While it is structured so as to reflect evolutionary relationships (similar to a cladogram), it also retains the traditional ranks used in Linnaean taxonomy.

- **Phylum Chordata**
  - Subphylum **Cephalochordata** (Acraniata) – (lancelets; 30 species)
    - Class **Leptocardii** (lancelets)
  - Clade **Olfactores**
    - Subphylum **Tunicata** (Urochordata) – (tunicates; 3,000 species)
      - Class **Ascidiacea** (sea squirts)

        - Class **Thaliacea** (salps, doliolids and pyrosomes)
        - Class **Appendicularia** (larvaceans)
        - Class **Sorberacea**
- Subphylum **Vertebrata** (Craniata) (vertebrates – animals with backbones; 66,100+ species)
    - Superclass '**Agnatha**' paraphyletic (jawless vertebrates; 100+ species)
        - Class **Cyclostomata**
            - Infraclass Myxinoidea or Myxini (hagfish; 65 species)
            - Infraclass Petromyzontida or Hyperoartia (lampreys)
        - Class †Conodonta
        - Class †Myllokunmingiida
        - Class †Pteraspidomorphi
        - Class †Thelodonti
        - Class †Anaspida
        - Class †Cephalaspidomorphi
    - Infraphylum **Gnathostomata** (jawed vertebrates)
        - Class †**Placodermi** (Paleozoic armoured forms; paraphyletic in relation to all other gnathostomes)
        - Class **Chondrichthyes** (cartilaginous fish; 900+ species)
        - Class †**Acanthodii** (Paleozoic "spiny sharks"; paraphyletic in relation to Chondrichthyes)
        - Class **Osteichthyes** (bony fish; 30,000+ species)
            - Subclass **Actinopterygii** (ray-finned fish; about 30,000 species)
            - Subclass **Sarcopterygii** (lobe-finned fish: 8 species)
        - Superclass **Tetrapoda** (four-limbed vertebrates; 35,100+ species) (The classification below follows Benton 2004, and uses a synthesis of rank-based Linnaean taxonomy and also reflects evolutionary relationships. Benton included the Superclass Tetrapoda in the Subclass Sarcopterygii in order to reflect the direct descent of tetrapods from lobe-finned fish, despite the former being assigned a higher taxonomic rank.)[20]
            - Class **Amphibia** (amphibians; 8,100+ species)[21]
            - Class **Sauropsida** (reptiles (including birds); 21,300+ species – 10,000+ species of birds and 11,300+ species of reptiles)[22][23][24]
            - Class **Synapsida** (mammals; 5,700+ species)

Subphyla

[edit]

See also: List of chordate orders


Cephalochordate: lancelet. Pictured species: *Branchiostoma lanceolatum*

Cephalochordata: Lancelets

[edit]

Main article: Lancelet

Cephalochordates, one of the three subdivisions of chordates, are small, "vaguely fish-shaped" animals that lack brains, clearly defined heads and specialized sense organs.[25] These burrowing filter-feeders compose the earliest-branching chordate subphylum.[26][27]

Tunicata (Urochordata)

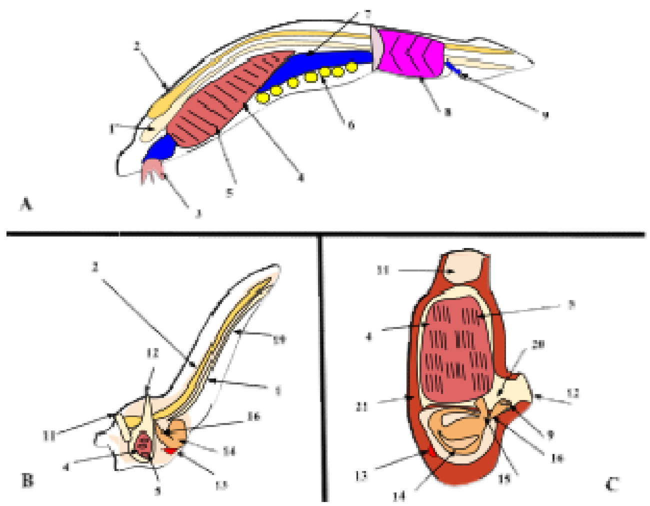
[edit]

Main article: Tunicate (Urochordata)


Tunicates: sea squirts

Most tunicates appear as adults in one of two major forms, known as "sea squirts" and salps. Both of these are soft-bodied filter-feeders that lack the standard features of chordates, which are only retained in their larvae. Sea squirts are sessile and consist mainly of water pumps and filter-feeding apparatus;[28] salps float in mid-water, feeding on plankton, and have a two-generation cycle in which one generation is solitary and the next forms chain-like colonies.[29] However, all tunicate larvae have the standard chordate features, including long, tadpole-like tails; they also have rudimentary brains, light sensors and tilt sensors.[28] The third main group of tunicates, Appendicularia (also known as Larvacea), retain tadpole-like shapes and active swimming all their lives, and were for a long time regarded as larvae of sea squirts or salps.[30] The etymology of the term Urochordata (Balfour 1881) is from the ancient Greek οὐρά (oura, "tail") + Latin chorda ("cord"), because the notochord is only found in the tail.[31] The term **Tunicata** (Lamarck 1816) is recognised as having precedence and is now more commonly used.[28]

Comparison of two invertebrate chordates



A. Lancelet, B. Larval tunicate, C. Adult tunicate

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1. Notochord, 2. Nerve chord, 3. Buccal cirri, 4. Pharynx, 5. Gill slit, 6. Gonad, 7. Gut, 8. V-shaped muscles, 9. Anus, 10. Inhalant syphon, 11. Exhalant syphon, 12. Heart, 13. Stomach, 14. Esophagus, 15. Intestines, 16. Tail, 17. Atrium, 18. Tunic

Craniata (Vertebrata)

[edit]

Main articles: Craniata and Vertebrata


Craniate: Hagfish

Craniates all have distinct skulls. They include the hagfish, which have no vertebrae. Michael J. Benton commented that "craniates are characterized by their heads, just as chordates, or possibly all deuterostomes, are by their tails".[32]

Most craniates are vertebrates, in which the notochord is replaced by the vertebral column.[33] It consists of a series of bony or cartilaginous cylindrical vertebrae, generally with neural arches that protect the spinal cord, and with projections that link the vertebrae. Hagfishes have incomplete braincases and no vertebrae, and are therefore not regarded as vertebrates,[34] but they are members of the craniates, the group within which vertebrates are thought to have evolved.[35] However the cladistic exclusion of hagfish from the vertebrates is controversial, as they may instead be degenerate vertebrates who have secondarily lost their vertebral columns.[36]

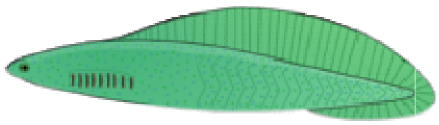
The position of lampreys is ambiguous. They have complete braincases and rudimentary vertebrae, and therefore may be regarded as vertebrates and true fish.[37] However, molecular phylogenetics, which uses biochemical features to classify organisms, has produced both results that group them with vertebrates and others that group them with hagfish.[38] If lampreys are more closely related to the hagfish than the other vertebrates, this would suggest that they form a clade, which has been named the Cyclostomata.[39]

Phylogeny

[edit]

Overview

[edit]



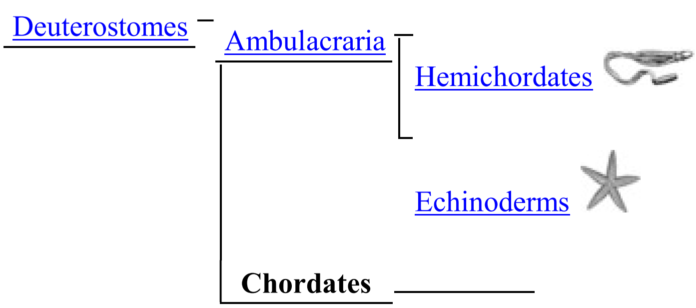
Haikouichthys, from about 518 million years ago in China, may be the earliest known fish.[40]

There is still much ongoing differential (DNA sequence based) comparison research that is trying to separate out the simplest forms of chordates. As some lineages of the 90% of species that lack a backbone or notochord might have lost these structures over time, this complicates the classification of chordates. Some chordate lineages may only be found by DNA analysis, when there is no physical trace of any chordate-like structures.[41]

Attempts to work out the evolutionary relationships of the chordates have produced several hypotheses. The current consensus is that chordates are monophyletic, meaning that the Chordata include all and only the descendants of a single common ancestor, which is itself a chordate, and that craniates' nearest relatives are tunicates. Recent identification of two conserved signature indels (CSIs) in the proteins cyclophilin-like protein and mitochondrial inner membrane protease ATP23, which are exclusively shared by all vertebrates, tunicates and cephalochordates also provide strong evidence of the monophyly of Chordata.[9]

All of the earliest chordate fossils have been found in the Early Cambrian Chengjiang fauna, and include two species that are regarded as fish, which implies that they are vertebrates. Because the fossil record of early chordates is poor, only molecular phylogenetics offers a reasonable prospect of dating their emergence. However, the use of molecular phylogenetics for dating evolutionary transitions is controversial.

It has also proved difficult to produce a detailed classification within the living chordates. Attempts to produce evolutionary "family trees" shows that many of the traditional classes are paraphyletic.



Olfactores

Tunicates 

Craniates (vertebrates) 

Diagram of the evolutionary relationships of chordates[14]

While this has been well known since the 19th century, an insistence on only monophyletic taxa has resulted in vertebrate classification being in a state of flux.[42]

The majority of animals more complex than jellyfish and other Cnidarians are split into two groups, the protostomes and deuterostomes, the latter of which contains chordates.[43] It seems very likely the 555 million-year-old *Kimberella* was a member of the protostomes.[44][45] If so, this means the protostome and deuterostome lineages must have split some time before *Kimberella* appeared—at least 558 million years ago, and hence well before the start of the Cambrian 538.8 million years ago.[43] Three enigmatic species that are possible very early tunicates, and therefor deuterostomes, were also found from the Ediacaran period – *Ausia fenestrata* from the Nama Group of Namibia, the sac-like *Yarnemia ascidiformis*, and one from a second new *Ausia*-like genus from the Onega Peninsula of northern Russia, *Burykhia hunti*. Results of a new study have shown possible affinity of these Ediacaran organisms to the ascidians.[46][47] *Ausia* and *Burykhia* lived in shallow coastal waters slightly more than 555 to 548 million years ago, and are believed to be the oldest evidence of the chordate lineage of metazoans.[47] The Russian Precambrian fossil *Yarnemia* is identified as a tunicate only tentatively, because its fossils are nowhere near as well-preserved as those of *Ausia* and *Burykhia*, so this identification has been questioned.

A skeleton of the blue whale, the largest animal, extant or extinct, ever discovered. Mounted outside the Long Marine Laboratory at the University of California, Santa Cruz. The largest blue whale ever reliably recorded measured 98ft (30m) long.

A peregrine falcon, the world's fastest animal. Peregrines use gravity and aerodynamics to achieve their top speed of around 242mph (390km/h), as opposed to locomotion.

Fossils of one major deuterostome group, the echinoderms (whose modern members include starfish, sea urchins and crinoids), are quite common from the start of the Cambrian, 542 million years ago.[48] The Mid Cambrian fossil *Rhabdotubus johanssoni* has been interpreted as a pterobranch hemichordate.[49] Opinions differ about whether the Chengjiang fauna fossil *Yunnanozoon*, from the earlier Cambrian, was a hemichordate or chordate.[50][51] Another fossil, *Haikouella lanceolata*, also from the Chengjiang fauna, is interpreted as a chordate and possibly a craniate, as it shows signs of a heart, arteries, gill filaments, a tail, a neural chord with a brain at the front end, and possibly eyes—although it also had short tentacles round its mouth.[51] *Haikouichthys* and *Myllokunmingia*, also from the Chengjiang fauna, are regarded as fish.[40][52] *Pikaia*, discovered much earlier (1911) but from the Mid Cambrian Burgess Shale (505 Ma), is also regarded as a primitive chordate.[53] On the other hand, fossils of early chordates are very rare, since invertebrate chordates have no bones or teeth, and only one has been reported for the rest of the Cambrian.[54] The best known and earliest unequivocally identified Tunicate is *Shankouclava shankouense* from the Lower Cambrian Maotianshan Shale at Shankou village, Anning, near Kunming (South China).[55]

The evolutionary relationships between the chordate groups and between chordates as a whole and their closest deuterostome relatives have been debated since 1890. Studies based on anatomical, embryological, and paleontological data have produced different "family trees". Some closely linked chordates and hemichordates, but that idea is now rejected.[14] Combining such analyses with data from a small set of ribosome RNA genes eliminated some older ideas, but opened up the possibility that tunicates (urochordates) are "basal deuterostomes", surviving members of the group from which echinoderms, hemichordates and chordates evolved.[56] Some researchers believe that, within the chordates, craniates are most closely related to cephalochordates, but there are also reasons for regarding tunicates (urochordates) as craniates' closest relatives.[14][57]

Since early chordates have left a poor fossil record, attempts have been made to calculate the key dates in their evolution by molecular phylogenetics techniques—by analyzing biochemical differences, mainly in RNA. One such study suggested that deuterostomes arose before 900 million years ago and the earliest chordates around 896 million years ago.[57] However, molecular estimates of dates often disagree with each other and with the fossil record,[57] and their assumption that the molecular clock runs at a known constant rate has been challenged.[58][59]

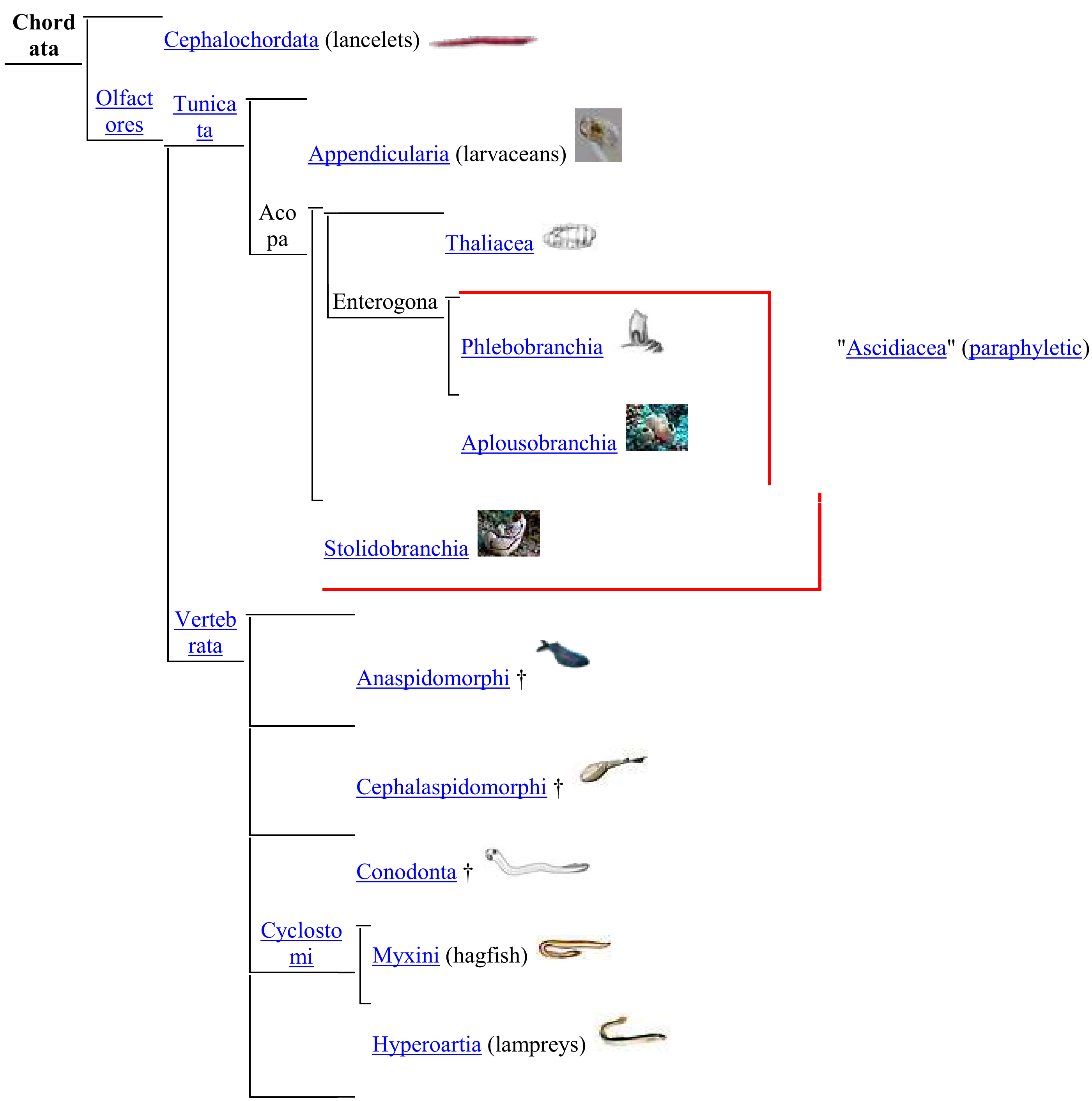
Traditionally, Cephalochordata and Craniata were grouped into the proposed clade "Euchordata", which would have been the sister group to Tunicata/Urochordata. More recently, Cephalochordata has been thought of as a sister group to the "Olfactores", which includes the craniates and tunicates. The matter is not yet settled.

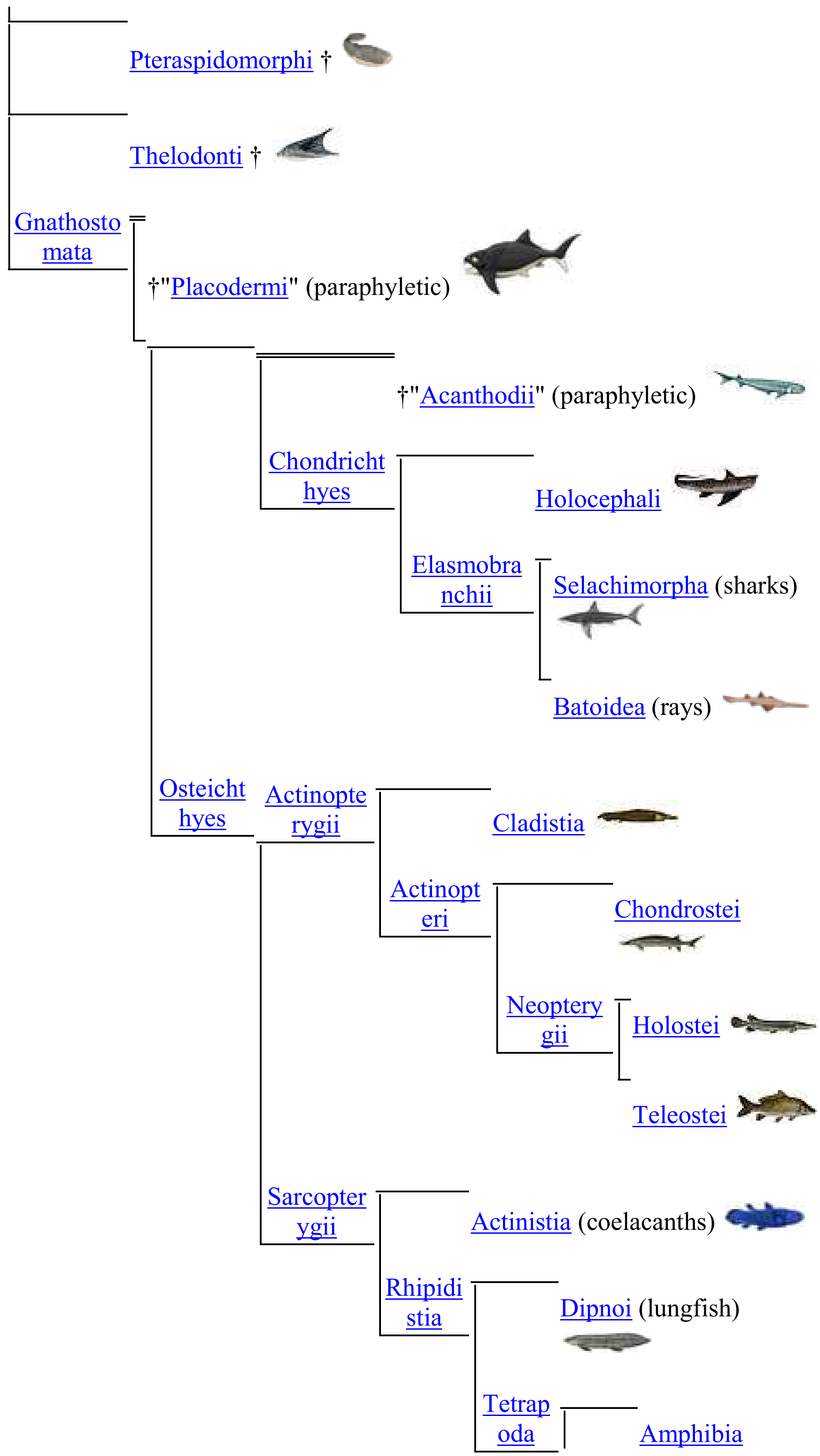
A specific relationship between Vertebrates and Tunicates is also strongly supported by two CSIs found in the proteins predicted exosome complex RRP44 and serine palmitoyltransferase, that are exclusively shared by species from these two subphyla but not Cephalochordates, indicating Vertebrates are more closely related to Tunicates than Cephalochordates.[9]

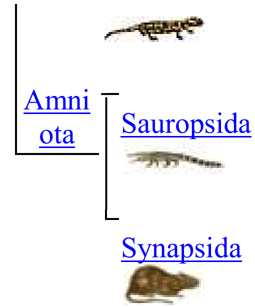
Cladogram

[edit]

Below is a phylogenetic tree of the phylum. Lines of the cladogram show probable evolutionary relationships between both extinct taxa, which are denoted with a dagger (†), and extant taxa. Relatives of vertebrates are invertebrates. The positions (relationships) of the lancelets, tunicates, and craniates/vertebrates are based on the following studies:[60][61][62][63]




Pteraspidomorphi †
Thelodonti †
Gnathostomata
†"Placodermi" (paraphyletic)
†"Acanthodii" (paraphyletic)
Chondrichthyes
Holocephali
Elasmobranchii
Selachimorpha (sharks)
Batoidea (rays)
Osteichthyes
Actinopterygii
Cladistia
Actinopteri
Chondrostei
Neopterygii
Holostei
Teleostei
Sarcopterygii
Actinistia (coelacanths)
Rhipidistia
Dipnoi (lungfish)
Tetrapoda
Amphibia



Closest nonchordate relatives

[edit]


Acorn worms or Enteropneusts are example of hemichordates.

The closest relatives of the Chordates are believed to be the Hemichordates and Echinodermata, which together form the Ambulacraria. The Chordata and Ambulacraria together form the superphylum Deuterostomia.

Hemichordates

[edit]

Main article: Hemichordate

Hemichordates ("half chordates") have some features similar to those of chordates: branchial openings that open into the pharynx and look rather like gill slits; stomochords, similar in composition to notochords, but running in a circle round the "collar", which is ahead of the mouth; and a dorsal nerve cord—but also a smaller ventral nerve cord.

There are two living groups of hemichordates. The solitary enteropneusts, commonly known as "acorn worms", have long proboscises and worm-like bodies with up to 200 branchial slits, are up to 2.5 metres (8.2 ft) long, and burrow though seafloor sediments. Pterobranchs are colonial animals, often less than 1 millimetre (0.039 in) long individually, whose dwellings are interconnected. Each filter feeds by means of a pair of branched tentacles, and has a short, shield-shaped proboscis. The extinct graptolites, colonial animals whose fossils look like tiny hacksaw blades, lived in tubes similar to those of pterobranchs.[64]

Echinoderms

[edit]


A red knob sea star, *Protoreaster linckii* is an example of Asterozoan Echinoderm.

Main article: Echinoderm

Echinoderms differ from chordates and their other relatives in three conspicuous ways: they possess bilateral symmetry only as larvae – in adulthood they have radial symmetry, meaning that their body pattern is shaped like a wheel; they have tube feet; and their bodies are supported by dermal skeletons made of calcite, a material not used by chordates. Their hard, calcified shells keep their bodies well protected from the environment, and these skeletons enclose their bodies, but are also covered by thin skins. The feet are powered by another unique feature of echinoderms, a water vascular system of canals that also functions as a "lung" and surrounded by muscles that act as pumps. Crinoids are typically sessile and look rather like flowers (hence the common name "sea lilies"), and use their feather-like arms to filter food particles out of the water; most live anchored to rocks, but a few species can move very slowly. Other echinoderms are mobile and take a variety of body shapes, for example starfish and brittle stars, sea urchins and sea cucumbers.[65]

See also

Neoteny (/niˈɒtəni/),[1][2][3][4] also called **juvenilization**,[5] is the delaying or slowing of the physiological, or somatic, development of an organism, typically an animal. Neoteny is found more in modern humans compared to other primates.[6] In **progenesis** or **paedogenesis**, sexual development is accelerated.[7]

Both neoteny and progenesis result in **paedomorphism**[8] (as having the form typical of children) or **paedomorphosis**[9] (changing towards forms typical of children), a type of heterochrony.[10] It is the retention in adults of traits previously seen only in the young. Such retention is important in evolutionary biology, domestication, and evolutionary developmental biology. Some authors define paedomorphism as the retention of larval traits, as seen in salamanders.[11][12][13]

History and etymology

[edit]

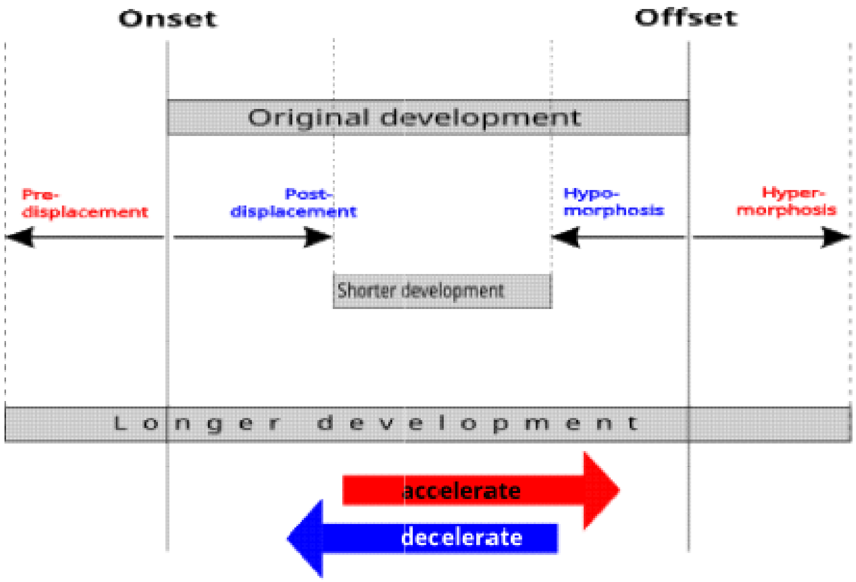


Diagram of the six types of shift in heterochrony, a change in the timing or rate of any process in embryonic development. Predisplacement, hypermorphosis, and acceleration (red) extend development (peramorphosis); postdisplacement, hypomorphosis, and deceleration (blue) all truncate it (paedomorphosis).

Julius Kollmann created the term "neoteny" in 1885 after he described the axolotl's maturation while remaining in a tadpole-like aquatic stage complete with gills, unlike other adult amphibians like frogs and toads.[14][15]

The word *neoteny* is borrowed from the German *Neotenie*, the latter constructed by Kollmann from the Greek νέος (*neos*, "young") and τείνειν (*teínein*, "to stretch, to extend"). The adjective is either "neotenic" or "neotenous".[16] For the opposite of "neotenic", different authorities use either "gerontomorphic"[17][18] or "peramorphic".[19] Bogin points out that Kollmann had intended the meaning to be "retaining youth", but had evidently confused the Greek *teínein* with the Latin *tenere*, which had the meaning he wanted, "to retain", so that the new word would mean "the retaining of youth (into adulthood)".[15]

In 1926, Louis Bolk described neoteny as the major process in humanization.[20][15] In his 1977 book *Ontogeny and Phylogeny*,[21] Stephen Jay Gould noted that Bolk's account constituted an attempted justification for "scientific" racism and sexism, but acknowledged that Bolk had been right in the core idea that humans differ from other primates in becoming sexually mature in an infantile stage of body development.[15]

In humans

[edit]

Main article: Neoteny in humans

Neoteny in humans is the slowing or delaying of body development, compared to non-human primates, resulting in features such as a large head, a flat face, and relatively short arms. These neotenic changes may have been brought about by sexual selection in human evolution. In turn, they may have permitted the development of human capacities such as emotional communication. Some evolutionary theorists have proposed that neoteny was a key feature in human evolution.[22] J. B. S. Haldane states a "major evolutionary trend in human beings" is "greater prolongation of childhood and retardation of maturity."[5] Delbert D. Thiessen said that "neoteny becomes more apparent as early primates evolved into later forms" and that primates have been "evolving toward flat face."[23] Doug Jones argued that human evolution's trend toward neoteny may have been caused by sexual selection in human evolution for neotenous facial traits in women by men with the resulting neoteny in male faces being a "by-product" of sexual selection for neotenous female faces.[24]

In domestic animals

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Further information: Domestication of animals

Neoteny is seen in domesticated animals such as dogs and mice.[25] This is because there are more resources available, less competition for those resources, and with the lowered competition the animals expend less energy obtaining those resources. This allows them to mature and reproduce more quickly than their wild counterparts.[25] The environment that domesticated animals are raised in determines whether or not neoteny is present in those animals. Evolutionary neoteny can arise in a species when those conditions occur, and a species becomes sexually mature ahead of its "normal development". Another explanation for the neoteny in domesticated animals can be the selection for certain behavioral characteristics. Behavior is linked to genetics which therefore means that when a behavioral trait is selected for, a physical trait may also be selected for due to mechanisms like linkage disequilibrium. Often, juvenile behaviors are selected for in order to more easily domesticate a species; aggressiveness in certain species comes with adulthood when there is a need to compete for resources. If there is no need for competition, then there is no need for aggression. Selecting for juvenile behavioral characteristics can lead to neoteny in physical characteristics because, for example, with the reduced need for behaviors like aggression, there is no need for developed traits that would help in that area. Traits that may become neotenized due to decreased aggression may be a shorter muzzle and smaller general size among the domesticated individuals. Some common neotenous physical traits in domesticated animals (mainly dogs, pigs, ferrets, cats, and even foxes) include floppy ears, changes in the reproductive cycle, curly tails, piebald coloration, fewer or shortened vertebra, large eyes, rounded forehead, large ears, and shortened muzzle.[26][27]

Neoteny and reduction in skull size – grey wolf and chihuahua skulls

When the role of dogs expanded from just being working dogs to also being companions, humans started selective breeding dogs for morphological neoteny, and this selective breeding for "neoteny or paedomorphism" "strengthened the human-canine bond."[28] Humans bred dogs to have more "juvenile physical traits" as adults, such as short snouts and wide-set eyes which are associated with puppies because people usually consider these traits to be more attractive. Some breeds of dogs with short snouts and broad heads such as the Komondor, Saint

Bernard and Maremma Sheepdog are more morphologically neotenous than other breeds of dogs.[29] Cavalier King Charles spaniels are an example of selection for neoteny because they exhibit large eyes, pendant-shaped ears and compact feet, giving them a morphology similar to puppies as adults.[28]

In 2004, a study that used 310 wolf skulls and over 700 dog skulls representing 100 breeds concluded that the evolution of dog skulls can generally not be described by heterochronic processes such as neoteny, although some pedomorphic dog breeds have skulls that resemble the skulls of juvenile wolves.[30] By 2011, the findings by the same researcher were simply "Dogs are not paedomorphic wolves."[31]

In other species

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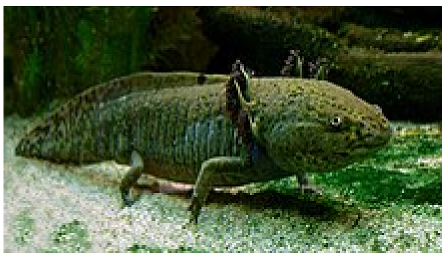
The axolotl is a neotenous salamander, often retaining gills throughout its life.

Neoteny has been observed in many other species. It is important to note the difference between partial and full neoteny when looking at other species, to distinguish between juvenile traits which are advantageous in the short term and traits which are beneficial throughout the organism's life; this might provide insight into the cause of neoteny in a species. Partial neoteny is the retention of the larval form beyond the usual age of maturation, with possible sexual development (progenesis) and eventual maturation into the adult form; this is seen in the frog *Lithobates clamitans*. Full neoteny is seen in *Ambystoma mexicanum* and some populations of *Ambystoma tigrinum*, which remain in larval form throughout their lives.[32][33] *Lithobates clamitans* is partially neotenous; it delays maturation during the winter as fewer resources are available; it can find resources more easily in its larval form. This encompasses both of the main causes of neoteny; the energy required to survive in the winter as a newly-formed adult is too great, so the organism exhibits neotenous characteristics until it can better survive as an adult. *Ambystoma tigrinum* retains its neoteny for a similar reason; however, the retention is permanent due to the lack of available resources throughout its lifetime. This is another example of an environmental cause of neoteny. Several avian species, such as the manakins *Chiroxiphia linearis* and *Chiroxiphia caudata*, exhibit partial neoteny. The males of both species retain juvenile plumage into adulthood, losing it when they are fully mature.[34] In some bird species, the retention of juvenile plumage is linked to the molting time in each species. To ensure no overlap between molting and mating times, the birds may exhibit partial neoteny in plumage; males do not attain their bright, adult plumage before the females are prepared to mate. Neoteny is present because there is no need for the males to molt early, and trying to mate with immature females would be energy-inefficient.

Neoteny is commonly seen in flightless insects, such as the females of the order Strepsiptera. Flightlessness in insects has evolved separately a number of times; factors which may have contributed to the separate evolution of flightlessness are high altitude, geographic isolation (islands), and low temperatures.[35] Under these environmental conditions, dispersal would be disadvantageous; heat is lost more rapidly through wings in colder climates. The females of certain insect groups become sexually mature without metamorphosis, and some do not develop wings. Flightlessness in some female insects has been linked to higher fecundity.[35] Aphids are an example of insects which may never develop wings, depending on their environment. If resources are abundant on a host plant, there is no need to grow wings and disperse. If resources become diminished, their offspring may develop wings to disperse to other host plants.[36]

Two environments which favor neoteny are high altitudes and cool temperatures, because neotenous individuals have more fitness than individuals which metamorphose into an adult form. The energy required for metamorphosis detracts from individual fitness, and neotenous individuals can utilize available resources more easily.[37] This trend is seen in a comparison of salamander species at lower and higher altitudes; in a cool, high-altitude environment, neotenous individuals survive more and are more fecund than those which metamorphose into adult form.[37] Insects in cooler environments tend to exhibit neoteny in flight because wings have a high surface area and lose heat quickly; it is disadvantageous for insects to metamorphose into adults.[35]

Many species of salamander, and amphibians in general, exhibit environmental neoteny. Axolotl and olm are perennibranchiate salamander species which retain their juvenile aquatic form throughout adulthood, examples of full neoteny. Gills are a common juvenile characteristic in amphibians which are kept after maturation; examples are the tiger salamander and rough-skinned newt, both of which retain gills into adulthood.[32]

Bonobos share many physical characteristics with humans, including neotenous skulls.[38] The shape of their skull does not change into adulthood (only increasing in size), due to sexual dimorphism and an evolutionary change in the timing of development.[38] Juveniles became sexually mature before their bodies had fully developed as adults and, due to a selective advantage, the skull's neotenic structure remained.[*citation needed*]

In some groups, such as the insect families Gerridae, Delphacidae and Carabidae, energy costs result in neoteny; many species in these families have small, neotenous wings or none at all.[36] Some cricket species shed their wings in adulthood;[39] in the genus *Ozopemon*, males (thought to be the first example of neoteny in beetles) are significantly smaller than females due to inbreeding.[40] In the termite *Kalotermes flavicollis*, neoteny is seen in molting females.[41]

In other species, such as the northwestern salamander (*Ambystoma gracile*), environmental conditions – high altitude, in this case – cause neoteny.[42] Neoteny is also found in a few species of the crustacean family Ischnomesidae, which live in deep ocean water.[43]

Subcellular neoteny

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Neoteny is usually used to describe animal development; however, neoteny is also seen in the cell organelles. It was suggested that subcellular neoteny could explain why sperm cells have atypical centrioles. One of the two sperm centrioles of fruit fly exhibit the retention of "juvenile" centriole structure, which can be described as centriolar "neoteny". This neotenic, atypical centriole is known as the Proximal Centriole-Like. Typical centrioles form via a step by step process in which a cartwheel forms, then develops to become a procentriole, and further matures into a centriole. The neotenic centriole of fruit fly resembles an early procentriole.[44]

See also

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- Ageing
- Cuteness
- Kawaii
- Larviform female
- Moe (slang)
- Neotenic complex syndrome
- Neotenin

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The development of phenotype

Key concepts	Genotype–phenotype distinction Reaction norm Gene–environment interaction Gene–environment correlation Operon Heritability Quantitative genetics Heterochrony Neoteny Heterotopy
Genetic architecture	Canalisation

	Genetic assimilation Dominance Epistasis Fitness landscape/evolutionary landscape Pleiotropy Plasticity Polygenic inheritance Transgressive segregation Sequence space
Non-genetic influences	Epigenetics Maternal effect Genomic imprinting Dual inheritance theory Polyphenism
Developmental architecture	Developmental biology Morphogenesis Eyespot Pattern formation Segmentation Metamerism Modularity
Evolution of genetic systems	Evolvability Robustness Neutral networks Evolution of sexual reproduction Tinkering
Control of development	**Systems**: Regulation of gene expression Gene regulatory network Evo-devo gene toolkit Evolutionary developmental biology Homeobox Hedgehog signaling pathway Notch signaling pathway

	Elements	Homeotic gene Hox gene Pax genes eyeless gene Distal-less Engrailed cis-regulatory element Ligand Morphogen Cell surface receptor Transcription factor
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