Developmental Correlation

Correlated progression

The modular nature of development predicts that modules will aggregate to form larger modules. One evolutionary consequence of this phenomenon is **correlated progression**, in which changes in one part of the embryo induce changes in another. Skeletal cartilage informs the placement of muscles, and muscles induce the placement of nerve axons. In such cases, if one structure changes, it will induce other structures to change with it (Thomson 1988). The dramatic changes in bone arrangement from agnathans to jawed fishes, from jawed fishes to amphibians, and from reptiles to mammals were coordinated with changes in jaw structure, jaw musculature, tooth deposition and shape, and the structure of the cranial vault and ear (Kemp 1982; Thomson 1988; Fischman 1995).

The mechanism through which the jaw apparatus has maintained its integrity from agnathans to amniotes is a remarkable example of embryonic modularity. The neural crest-derived structures of the vertebrate head include the pharyngeal arches (the precursors of the jaw, middle ear, tongue skeleton, etc.) as well as the dermal bones of the face and the facial musculature (see Chapter 13). The braincase is produced from mesodermal tissues. Köntges and Lumsden (1996) were able to map the fates of the neural crest cells associated with particular rhombomeres by replacing individual chick rhombomeres with those of quail. Antibody staining of the quail neural crest cells showed that each rhombomere gives rise to particular skeletal elements *and to the muscles attached to them*. Moreover, the muscle-and-skeleton modules from each rhombomere were found to be innervated by a particular cranial nerve. For instance, the neural crest cells from rhombomere 4 generated four skeletal tissues: the retroarticular process of the lower jaw (found in birds, but not mammals), a portion of the tongue skeleton, the stapes bone of the middle ear, and, surprisingly, the small portion of the braincase where the jaw-opening muscle attaches to the otherwise mesodermally derived skull. The muscles connecting these four skeletal elements also came from the r4 neural crest cells. These muscles are all innervated by the seventh cranial nerve. Thus, this rhombomere forms a modular unit, comprising the pharyngeal arch skeletal elements, the muscles that move them, the attachment site of the muscles to the braincase, and the nerves that innervate the muscles. Because these muscles and bones are formed from the same cells, their relationships can be maintained despite the dramatic changes in position and function that these elements might undergo over time.

One can also see correlated progression over a shorter time in domesticated animals. Humans have a great talent for selecting hereditary variants in domestic animals that involve those neural crest cells forming the frontonasal and mandibular processes. In some cases, such as that of bulldogs, the breed is selected for a wide face with very little angle between head and jaw. Other breeds, such as the collie, are selected for a narrow snout with a long jaw protruding away from the head. All breeds of dogs can move their jaws, shake their heads, and bark, despite the differences in the way their bones are shaped or positioned. Each variation is genetically determined, and it is important to note that each represents a harmonious rearrangement of the different bones with each other and with their muscular attachments. As the skeletal elements were selected, so were the muscles that moved them, the nerves that controlled their movements, and the blood vessels that fed them.

Correlated progression has also been shown experimentally. Repeating the earlier experiments of Hampé (1959), Gerd Müller (1989) inserted barriers of gold foil into the prechondrogenic hindlimb buds of a 3.5-day chick embryo. This barrier separated the regions of tibia formation and fibula formation. The results of these experiments were twofold. First, the tibia is shortened, and the fibula bows and retains its connection to the fibulare (the distal portion of the tibia). Such relationships between the tibia and fibula are not usually seen in birds, but they are characteristic of reptiles (Figure 1). Second, the musculature of the hindlimb undergoes changes in parallel with the bones. Three of the muscles that attach to these bones now show characteristic reptilian patterns of insertion. It seems, therefore, that experimental manipulations that alter the development of one part of the mesodermal limb-forming field also alter the development of other mesodermal components. This was crucial in the evolution of the bird hindlimb from the reptile hindlimb. As with the correlated progression seen in facial development, these changes all appear to be due to interactions within a module, in this case, the chick hindlimb field. These changes are not global effects and can occur independently of the other portions of the body.

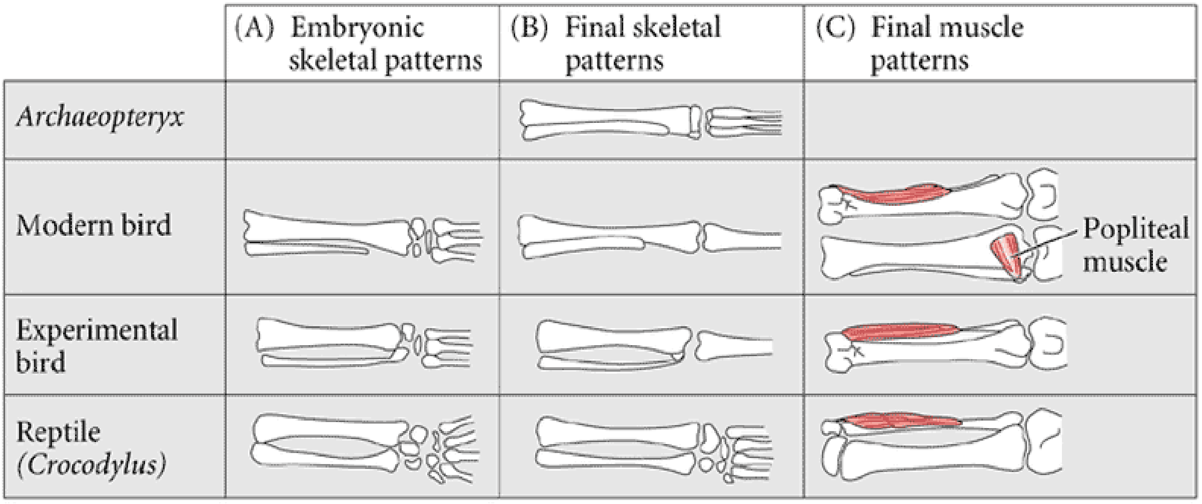

Figure 1 Experimental "atavisms" produced by altering embryonic fields in the limb. (A—C) Results of Müller's experiments using gold foil to split the chick hindlimb field. (A, B) The embryonic and final bone patterns, indicating that the fibulare structure was retained by the experimental chick limb, as it is in extant reptiles and as it is thought to have been in Archaeopteryx, the earliest known bird. (C) Some of the correlated muscle patterns. The popliteal muscle is present in the normal chick limb, but is absent from reptile limbs and from the experimental limb. The fibularis brevis muscle, which normally originates from both the tibia and fibula in chicks, takes on the reptilian pattern of originating solely from the fibula in the experimental limb. (A—C after Müller 1989.)

Correlated progression has also been seen in the domestication of animals. Here, domestication appears to be selection for neotenic conditions. In selecting for behavioral plasticity, changes in skull shape and pigment patterns are also produced. This phenomenon can also be seen in current attempts to domesticate wild wolves and foxes.

Coevolution of ligand and receptor

Another example of developmental correlation involves the ability of one tissue to interact with another. In development, things have to fit together if the organism is to survive. Ligands have to fit with receptors, and they have to be expressed at the right place and at the right time. Changes in the ligand must be accommodated by complementary changes in the receptor if the receptor is to function. If a mutation in a gene encoding ligand (or receptor) produces too great a change, it will not bind to its complementary receptor (or ligand), and development will stop. When duplications of ligand and receptor genes occur, they can diverge and acquire new functions. This is seen in the evolution of hormone families and their receptors (Moyle et al. 1994).

Such separation of functions can cause reproductive isolation and the separation of species when the receptor and ligand are proteins on the sperm and egg. While most proteins of closely related marine species are very similar, the proteins responsible for fertilization are often extremely different (Metz et al. 1994). In sea urchins, the bindin of the sperm and the complementary receptors of the egg have coevolved such that the bindin of one species often does not recognize the bindin receptors on the oocytes of other species. Hofmann and Glabe (1994) have proposed a model whereby there are several distinct recognition sites on bindin and its receptor. Mutations would cause some of these sites to be altered, and these alterations would select for complementary alterations on the opposite gamete. There would be a stage wherein some unaltered sperm could bind, albeit weakly, to altered eggs, but eventually, this process of alteration and accommodation would produce two reproductively isolated groups within the species. Moreover, these changes in bindin proteins appear to be rapid and correlate with speciation (Shaw et al. 1994; Metz and Palumbi 1996; Lyon and Vacquier 1999).

A similar situation has been seen in abalones. Clark and colleagues (2009) have looked at the genetic association of lysine (a small protein on the sperm heads) and VERL (the vitelline envelope receptor of lysine) to which it binds. The interaction between these proteins is very species-specific. If there were multiple forms of these proteins, then those that fit the best would have the most successful fertilizations. If this were the case, then you would expect to find in the zygote an association of the alleles encoding these compatible proteins. In other words, one would expect to find “linkage disequilibrium.” This, indeed, was found to be the case. There was an association between certain alleles for lysine and certain alleles for the lysine receptor. The abalone gamete recognition proteins indicate how male-female coevolution can lead to the reproductive barriers that can drive speciation.

The survival of those who fit

When one is talking about mating, shape is also important. In insects, the shape of genitalia is one of the most variable anatomical markers; in beetles it’s the shape, not the size, that matters. Macagno and colleagues (2011) have shown that male and female copulatory organs must mechanically fit together for efficient sperm transfer, so there is co-evolution between male and female beetles with respect to genital shape.

In water striders, the male holds the female’s head while mating, so that she doesn’t swim away. The antennae of the male have been modified so that there are four critical points of contact between the male antennae and the female’s eye, head capsule, and thorax. The traits are each regulated by the *distal-less* gene, and if the Distal-less protein is suppressed, the male’s grasping ability is lost (Khila et al. 2012).

It’s all about shape. Whether one is talking about ligands binding to receptors, substrates binding to enzymes, antigens binding to antibodies, or sperm binding to egg, it’s all a matter of shape. Stereocomplementary is a major rule of nature (Gilbert and Greenberg 1984).

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