

Homology, An Unsolved Problem

Sir Gavin de Beer

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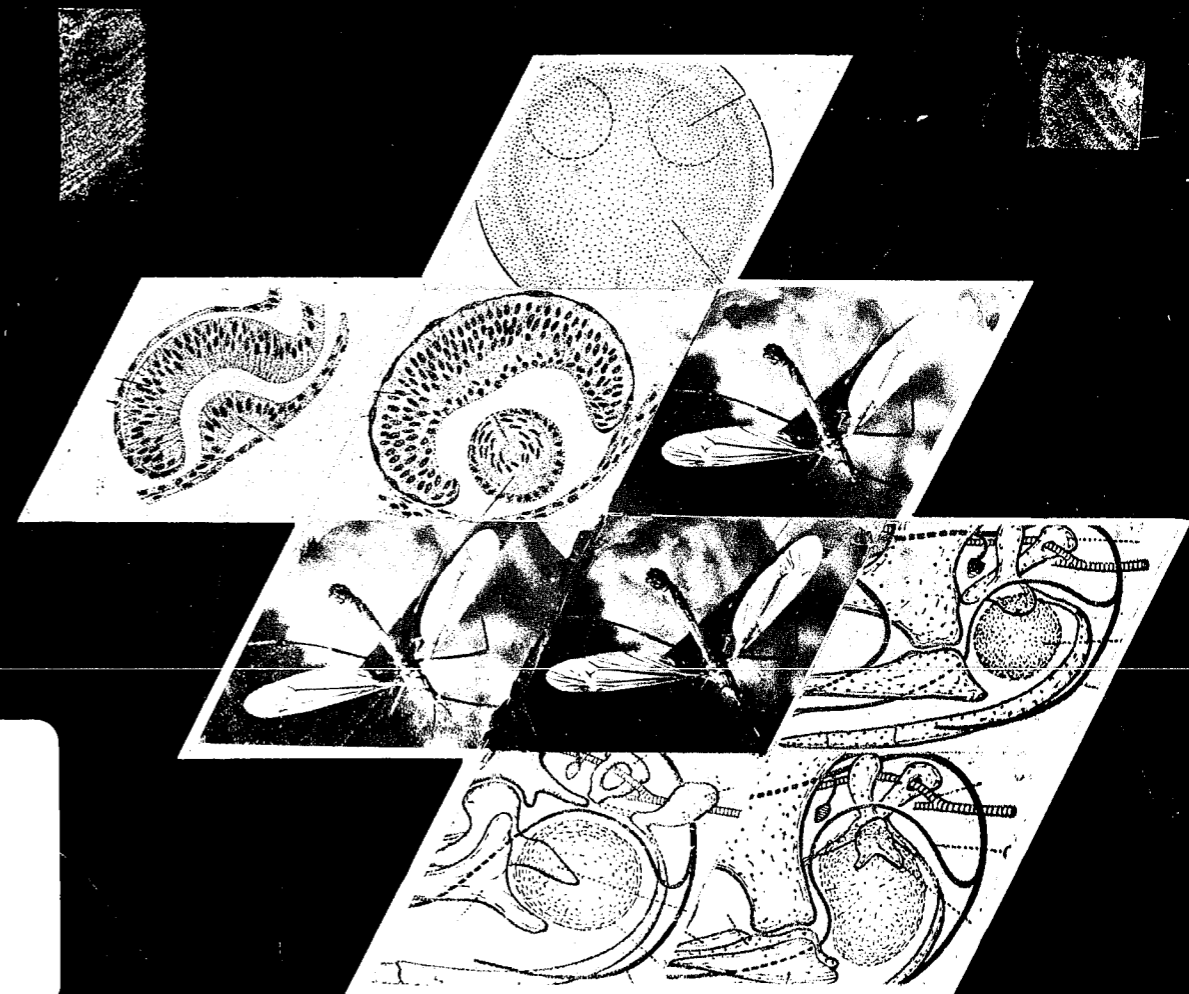
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now clear that the pride with which it was held that the inheritance of homologous structures from a common ancestor explained homology was misplaced; for such inheritance cannot be ascribed to identity of genes. The attempt to find 'homologous' genes, except in closely related species, has been given up as useless. As S. C. Harland said: 'The genes, as a manifestation of which the character develops, must be continually changing . . . we are able to show organs such as the eye, which are common to all vertebrate animals, preserve their essential similarity in structure or function, though the genes responsible for the organ must have become genetically altered during the evolutionary process'. It is not true that through the genetic code, the same code for enzymes that synthesize proteins which are responsible (in a manner still unknown in embryology) for the differentiation of the various parts in their normal manner, what mechanism can it be that results in the production of homologous organs, the same 'patterns', in the absence of their *not* being controlled by the same genes? I asked this question in 1938, and it has not been answered.

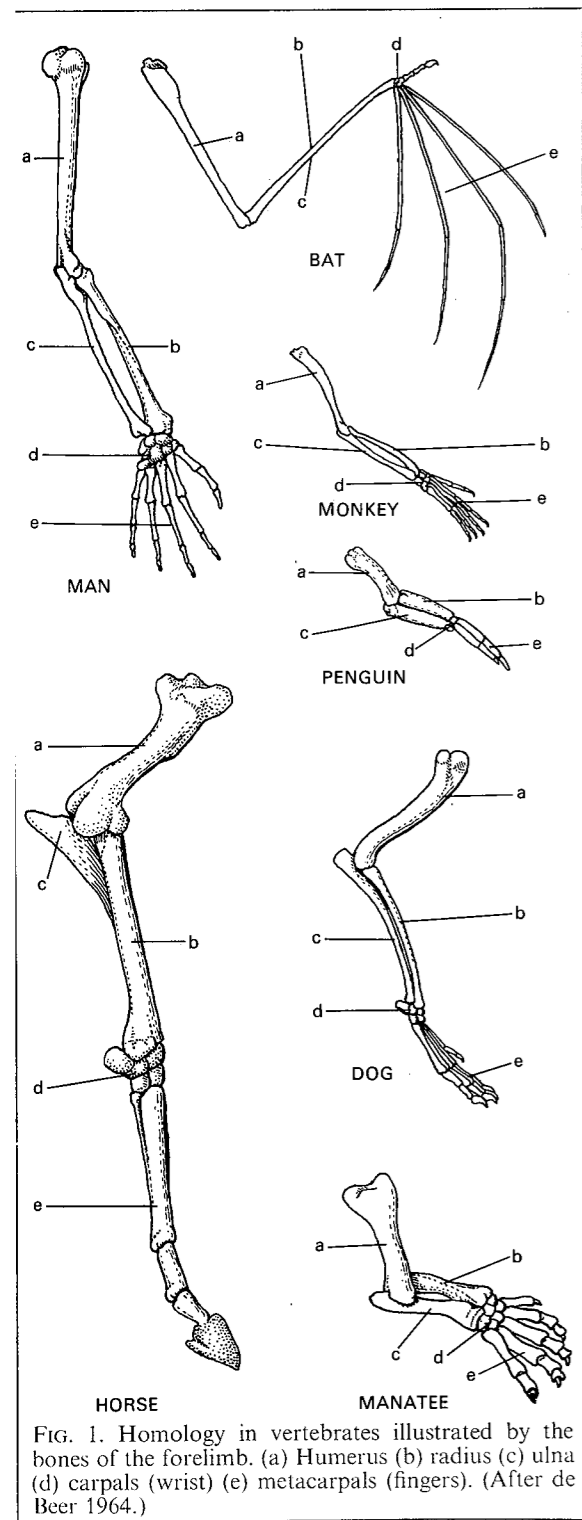
It is useless to speculate on any explanation in the absence of facts. But attention may be drawn to the work of T. M. Sonneborn (1970) on 'Gene action in development', in which he describes the results obtained by him on the unicellular protozoan *Paramecium*, which show that although the 'patterns' of the cortex of that organism must be the result of genetic action, parts of that cortical pattern are necessary for the development of local structures at the next cell division. To question 'Is the whole of development encoded in the DNA (that is to say, in the genes)?' the answer for *Paramecium* is 'No'. Whether this is applicable to 'patterns' in higher organisms, and whether homologous structures are controlled by non-genetic mechanisms awaits further research.

FURTHER READING

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Mention must also be made of Étienne Geoffroy-Saint-Hilaire (1772–1844) whose obsession with unity of type led him to believe that *all* animals were built on the same plan of structure, a view in the tradition from Aristotle to Owen, which was shattered by Cuvier (1769–1832) who contended that there were four plans of structure in animals. Geoffroy-Saint-Hilaire did, however, put forward a criterion in comparative anatomy: 'the only general principle that can be applied is given by the position, the relations, and the dependences of the parts, that is to say by what I name and include under the term *connections*.' This was an extension of Vicq d'Azyr's work, and is still the way in which a comparative anatomist studies the morphology of organs to satisfy himself that they are, or are not, what is called homologous.

Darwin's bombshell of evolution, which burst in 1859, had a profound effect on the concept of the explanation of homology, but without touching the criteria by which it is established. At one stroke, it was obvious that metaphysical 'archetypes' do not exist, and that homology between organs is based on their correspondence with representatives in a common ancestor of the organisms being compared, from which they were descended in evolution. 'What can be more curious,' asked Darwin, 'than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should be all constructed on the same pattern, and should include similar bones, in the same relative positions?' In the 6th edition of the *Origin of species* (1872) he went on to quote Sir William Flower: 'We may call this conformity to type, without getting much nearer to an explanation of the phenomenon, but is it not powerfully suggestive of true relationship, of inheritance from a common ancestor?'

In other words, it is homologous organs that provide evidence of affinity between organisms that have undergone descent with modification from a common ancestor, i.e. evolution. Furthermore, since evolution is the explanation of the 'agreement' between homologous organs, their study, if they are hard parts susceptible of fossilization, is not restricted to the morphology of living organisms, but the entire range of palaeontology is available for it. So, provided with a cast-iron explanation in terms of affinity, of

inheritance in evolution from a common ancestor, it looked as if the concept of homology was at last soundly based and presented no more problems of principle; however, as will be seen below, it unfortunately does.

2. Homology in plants: leaves and flowers

The leaf of a land plant is a lateral appendage of the stem, morphologically different from the stem, with, typically, a bud in the axil between the leaf-base and the stem. The leaf contains plastids with chlorophyll and is therefore green; a foliage leaf is exposed to sunlight with the energy of which the chloroplast performs the chemical reactions of photosynthesis. Foliage leaves can differ widely in detailed shape, from the needles of conifers to the stalked undivided blades of lilies, the indented leaf of the oak, the subdivided compound leaf made up of leaflets of the pea. The whole leaf, or a leaflet, can be modified into a tendril of a climbing plant as in the vine, ending in adhesive discs as in Virginia creeper. In the fly-catching sundew, the leaf bears tentacles that secrete a sticky substance that catches the fly, digests it, and then absorbs it. Leaves can also be modified into scales and bracts, but the most interesting modification is into floral leaves.

The flower of an angiosperm typically consists of four concentric whorls of elements. The frond or foliage leaf of a fern shows in its simplest form that it is a sporophyll: it forms and bears spores on its under surface. The innermost whorl of the elements of a flower is formed by the carpellary leaves, the carpels, which usually grow together to form an enclosed chamber, the ovary, surmounted by its style and stigma; but the carpels betray their sporophyll nature by the fact that they produce spores. These spores which develop into embryo-sacs, are contained within the ovules or future seed-coats. As sexual dimorphism, with its great genetical selective advantages, affects the flowering plant (the sporophyte), the spores produced by the carpels are sedentary macrospores, which is why the carpels are regarded as the female elements in the flower.

The second whorl of floral elements consists of the stamens, thin stalked structures ending in anthers which produce pollen-sacs containing the pollen grains which are microspores, adapted to travel and dispersal to find the macrospores, which is why the stamens are regarded as male sporophylls. The third whorl is made up of petals,

which show clear similarity to the structure of foliage leaves in spite of the fact that they may be of different colours. These colours attract insects, an adaptation to the pollination of flowers by insects which increases the chances of cross-pollination of the stigma of the flower of one plant by the pollen of a different plant. As Darwin noticed, no flower that is wind-pollinated, like those in catkins, has coloured petals. The evolution of the modification of floral leaves into petals that attract insects and of insects that pollinate flowers is a striking result of the fact that both flowering plants and insects evolved at the same time, in the late Mesozoic era, each thereby contributing to the rapid evolution of the other.

The evolutionary derivation of the parts of a flower from the unspecialized leaves of an ancestor is supported by the facts that in some Cycads,

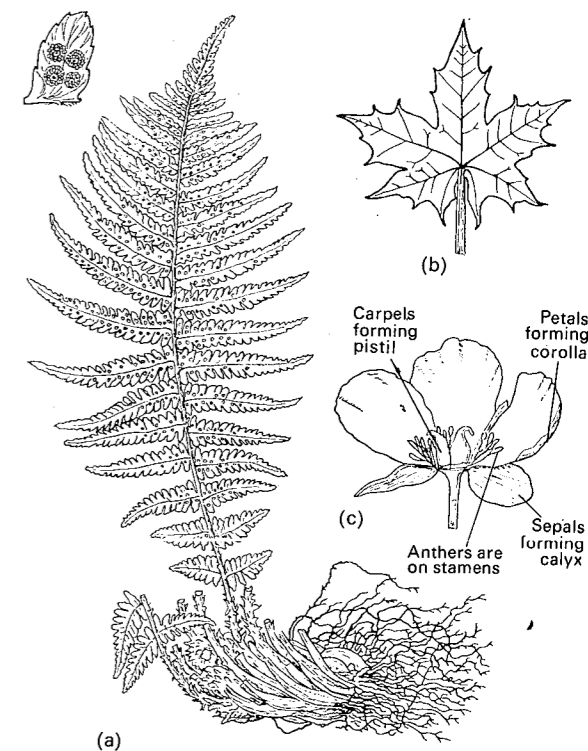


FIG. 2. Homology in plants illustrated by sporophylls, foliage, and floral leaves. (a) Fern sporophyte, showing frond or sporophyll bearing sporangia on its under surface. (b) Foliage leaf of maple. (c) Floral leaves (flower) of *Paeonia*. (After E. Strasburger (1921) *Textbook of botany*, Macmillan.)

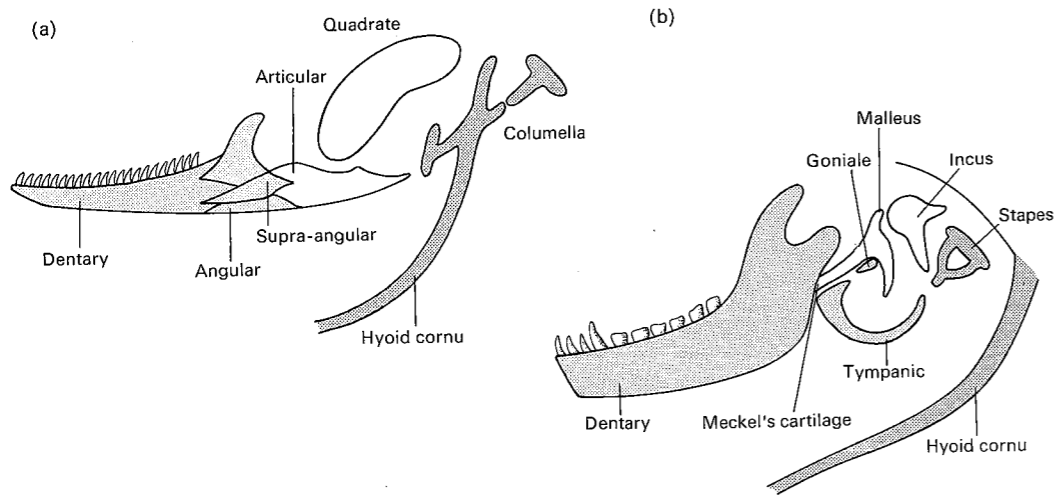


FIG. 3. Homology in vertebrates illustrated by the hinge of the lower jaw in reptiles (a); and the ear-ossicles (stapes) in mammals (b). (After E. S. Goodrich (1930) *Studies on structure of vertebrates*, Macmillan.)

the most primitive gymnosperms living, the carpels are simple sporophylls, like foliage leaves bearing ovules, and that in the Magnoliaceae, the most primitive living angiosperms, the stamens are often broad sporophylls, bearing their spores (pollen grains) on their under surface.

3. Homology in animals: the ear ossicles

In reptiles the hinge between the upper and lower jaws is the joint and articulation between two bones: the quadrate of the upper jaw and the articular of the lower jaw. The quadrate abuts against the side of the auditory capsule by its otic process. Both quadrate and articular are cartilage-bones, preformed in cartilage which then becomes ossified. The reptilian lower jaw also contains a number of membrane-bones, ossifications without cartilaginous precursors, such as the dentary in front, which bears the teeth, the angular and supra-angular behind situated laterally to the articular, the pre-articular and coronoid on the inner side of the jaw. Some fossil reptiles show even more bones.

The jaws are part of the 1st visceral or mandibular arch which is separated from the 2nd or hyoid arch by the tympanic cavity, derived from the 1st visceral pouch, and connected with the

throat by the eustachian tube. In the hyoid arch, the uppermost skeletal element is the columella auris, cartilage-bone, a rod conveying vibrations of sound from the tympanic membrane on which sound waves impinge, to the fenestra ovalis of the auditory capsule where the vibrations are imparted to the lymph fluid which stimulates the sense organs of hearing. As the tympanic cavity lies between the 1st (or mandibular) arch and the 2nd (or hyoid) arch, the quadrate and articular bones project into the tympanic cavity from in front, and the columella auris from behind, and the latter is able to vibrate in an open space instead of in thick tissue.

In mammals the conditions at first sight seem to be very different, because the lower jaw consists of a single bone, the dentary, from which an uprising extension articulates with the fossa of a membrane-bone of the brain case, the squamosal. The hinge of the lower jaw in mammals is therefore different from that in reptiles. When the question is asked what has happened in mammals to the old hinge bones of the reptiles, the answer is sensational. These bones have become inserted between the columella auris and the tympanic membrane and are known as the incus and malleus respectively, while the columella, now

called the stapes, continues to fit into the fenestra ovalis, receiving the vibrations from the incus which in turn receives them from the malleus impinging on the tympanic membrane. The leverage which these bones can exert on one another makes the transmission of vibrations more sensitive. So there is a chain of three ear ossicles in mammals, and between two of them, the incus and the malleus, is the old hinge joint of the lower jaw of reptiles.

The other bones of the reptilian lower jaw have also changed their functions and their names. The angular in mammals has become the tympanic bone which surrounds and protects the tympanic cavity; the pre-articular (also called goniale) becomes attached to the front of the malleus; the coronoid and supra-angular disappear.

The important point to notice in these changes is the perfect morphological correspondence between the conditions in reptiles and in mammals. All the elements that are cartilage-bones in the former are so also in the latter: the same is true of the membrane-bones and their relative positions correspond exactly. This correspondence also extends to minute details. The columella in reptiles is frequently pierced by a hole through which the stapedia artery passes; this is constant for the stapes of mammals, and is the reason why it is called the 'stirrup'. The lateral head vein runs back medially to the quadrate in reptiles and to the incus in mammals. The facial nerve passes out of the brain case and runs backwards on the median side of the quadrate in reptiles and of the incus in mammals. The nerve passes above the tympanic cavity on the outer side of the stapedia artery and gives off a branch, the chorda tympani, which runs forwards above the tympanic cavity and then down on the median side of the lower jaw elements, articular or malleus, in exactly the same way in reptiles and in mammals.

Minute morphological analysis of the conditions in reptiles and in mammals, carried out on embryonic and on adult material, proves beyond possibility of error that the reptilian quadrate, articular, and columella are respectively homologous with the mammalian incus, malleus, and stapes. This is a good example of the detailed 'correspondence' looked for by Vicq d'Azyr and of the 'connections' sought by Geoffroy-Saint-Hilaire. What makes this study even more significant is that the results of comparative anatomy are confirmed by those of palaeontology, for

there are fossil reptiles that show advances towards the mammalian condition, and the superseding of the quadrate-articular hinge of the lower jaw by the squamosal-dentary articulation. All this evolution took place without any functional discontinuity. It is a sobering thought that every man carries in his ear ossicles the homologue of the lower jaw hinge of his reptilian ancestors. This is one of the most demonstrative examples of how comparative anatomy can determine homology of structures inherited from common ancestors in evolution.

4. Conservative effects of homology

The courses taken by certain nerves and blood vessels in adult mammals are determined by the structure of their embryos which repeat the embryonic conditions of the ancestors' embryos. The recurrent laryngeal nerve is an example of how the topology of homologous structures determines some curious anomalies in adult anatomy. The recurrent laryngeal nerve is a branch of the vagus nerve which in fishes has four branchial branches, each of which passes down behind visceral pouches 3, 4, 5, and 6, and runs forwards ventrally but on the median side of the arterial arches that also run down behind those visceral pouches which, in fishes, are pierced as gill-slits.

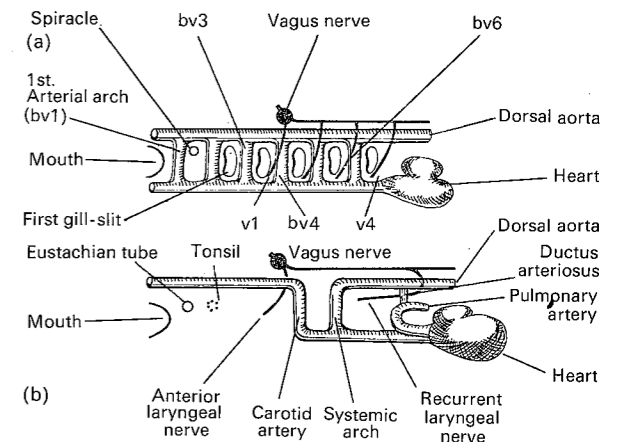


FIG. 4. Morphology of the arterial arches and the vagus nerve in (a) dogfish; (b) rabbit. bv 1, 3, 4, 6, blood-vessels running in the 1st, 3rd, 4th, and 6th visceral arches; v, vagus nerve; v1, 4, 1st, 4th branch of vagus. (After de Beer 1966.)

In mammals these arterial arches are reduced in number by the disappearance of arches 1, 2, and 5. The 3rd or carotid, the 4th or systemic aorta, and the 6th or pulmonary persist. The systemic aorta persists only on the left side where there is still the old connection between the aorta and the pulmonary artery by means of the ductus arteriosus, which is of great importance to the embryo when still in the uterus where respiration is carried out by the placenta. At birth respiration immediately becomes pulmonary, and the ductus arteriosus closes up and becomes nothing but a ligament. But the old 4th branchial branch of the vagus, now called the recurrent laryngeal nerve still loops round the remains of the ductus arteriosus, remnant of the old 6th arterial arch.

In early stages of development, the heart lies far forward, in the neck, and the laryngeal nerve does not have far to go to innervate the larynx. But as development proceeds, the heart and the arterial arches are drawn back into the thorax. This is why the recurrent laryngeal nerve on the left side, after running backwards and looping round the ductus arteriosus, then runs forwards again to innervate the muscles of the larynx. In man, this course of the nerve is several inches longer than it need have been in the adult if it went straight to the larynx from the point where the nerve emerges from the skull. In the giraffe its course must be several feet longer. The explanation is the homology between the mammalian ductus arteriosus and the 6th arterial arch of the fish, which is respected in descendant forms, resulting in apparently anomalous conditions.

5. The displacement of homologous structures

There is no doubt whatever that the forelimb in the newt and the lizard and the arm of man are strictly homologous, inherited with modification from the pectoral fin of fishes 500 million years ago. They have identical elbow and wrist joints and their hands end in five fingers. The bones and muscles that they contain also correspond. But a minute examination of their comparative anatomy reveals the astonishing fact that they do not occupy the same positions in the body. The limbs of vertebrates are always formed from material that is contributed from several adjacent segments of the trunk. So, in the newt the forelimb is formed from trunk segments 2, 3, 4, and 5; in the lizard from 6, 7, 8, and 9; in man from

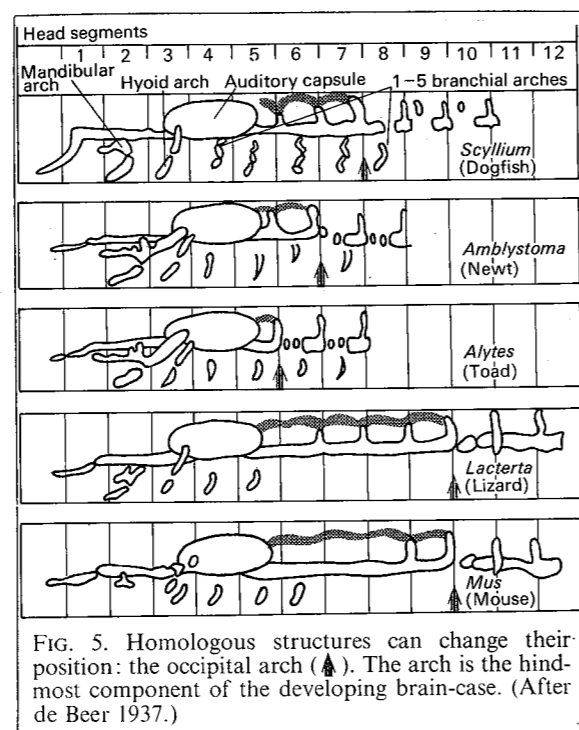


FIG. 5. Homologous structures can change their position: the occipital arch (▲). The arch is the hindmost component of the developing brain-case. (After de Beer 1937.)

trunk segments 13 to 18 inclusive. This can be determined embryologically by observing the contributions made by the segmental muscles to the muscles of the limbs, and anatomically in the adult by studying the ordinal numbers of the spinal nerves that make up the brachial plexus and innervate the muscles of the limbs, because ventral motor nerve roots are always 'faithful' to the muscle plates of their own segments. So the undoubted homology of the forelimb in newt, lizard, and man does not imply that they occupy identical positions in the body. They have shifted in position during evolution.

There is no shifting in position during embryonic development, but what has happened is that in the course of evolution, transposition has occurred; new adjacent segments further back in the trunk have been drawn into contribution to the formation of the limb, and segments further forward, which previously contributed, cease to do so. The limb is a pattern which has been transposed over the long axis of the vertebrate body, like a tune that can be transposed over the keys, as E. S. Goodrich showed.

Another example of the same phenomenon is the position of the occipital arch of the skull

which marks its hind end and the hinder limit of the head. In sharks the occipital arch is in the septum separating the 7th from the 8th segment, counting from the front of the head. In newts it is between the 6th and 7th segments, in frogs between the 5th and 6th; in reptiles and mammals between the 9th and 10th segments. Man therefore has 9 segments in his head. Without forfeiting its homology, the occipital arch has been transposed up or down the segments of the body.

These examples illustrate the important principle of the *pattern* which is where the problem of homology lies, not in identity of position in the body. A completely independent but comparable case is the shifting in position of the pattern of teeth in mammals. Extensions of the pattern of typical premolar teeth to teeth immediately in front of or behind them can be seen in related species, but do not always affect the 'same' teeth if 'sameness' means identical numerical position of the teeth in the jaws.

The realization that homologous organs conform to a pattern is valuable, and will appear again below.

6. Serial homology

Serial homology is really a misnomer, because it is not concerned with tracing organs in different organisms to their representatives in a common ancestor, that is to say with evolution, but with the similarity between organs repeated along the anteroposterior axis of one and the same organism. Such organisms are those that show metameric segmentation, orderly repetition of parts. Examples of serial homology include the parapodia of marine annelid worms, in which one pair corresponds to each segment of the body, and the segmental nerve roots, muscle plates, and ribs of vertebrates. Aristotle was interested in the correspondence between forelimbs and hindlimbs; in mammals for instance, each shows one bone in the upper arm and thigh, two bones in the forearm and shank, several bones in the wrist and ankle, and several more in hand and foot each of which ends in five digits, fingers or toes. This is not real homology, as forelimb and hindlimb cannot be traced back to any ancestor with a single pair of limbs. At most it might be said that there had been reduplication of a pattern. At the hands of Transcendental anatomists, serial homology has led to abject nonsense, such as attempts to claim serial homology for the soft palate of a mammal's

mouth cavity and the diaphragm.

One aspect of serial homology may have an indirect bearing on homology. In the paired limbs of arthropods, one pair of which corresponds to each segment, the limbs near the mouth serve, not for locomotion or respiration, but for feeding, and are modified into 'mouth-parts'. Higher crustacea have a pair of mandibles, 2 pairs of maxillae, and 3 pairs of maxillipeds, followed posteriorly by the series of swimming, walking, or respiratory limbs. Insofar as these mouth-parts really are serially homologous with ordinary paired limbs, it is possible to argue that in the ancestor the mouth-parts were ordinary limbs that have become modified. In a sense the homology of the elements of a flower with foliage leaves is a kind of serial homology, because a plant grows in height.

7. Latent homology

The concept of homology which refers organs to a representative in a common ancestor concerns itself with homologous organs as visible phenotypic structures, but it is more than possible that the criterion is over-exacting in insisting that the representative structure must be visible in the common ancestor. This suspicion arises from many sources. One example is the Titanotheres, extinct mammals, in many lineages of which knobs appeared on the head as soon as they reached a certain size. It is difficult to deny the homology between these knobs, but they cannot be referred to anything visible in a common ancestor. It must be inferred that these separate lineages inherited a trait, as a result of which each lineage would have exhibited the structure as soon as a limiting factor was removed, in this case presumably insufficient size.

On a simpler level, there is the problem of recurrent mutations. In the fruit fly *Drosophila* there have been repeated mutations from the normal red eye to white. It is difficult to rule out the possibility of a common inheritance, of a tendency for this mutation to occur, even if the common ancestor did not have white eyes.

More complex is the problem of spiral cleavage. This is a very precise set of manoeuvres by which the fertilized egg is cleaved. First, four sub-equal cells are formed by the first two cleavage divisions, but after that there is a sort of quadrille as successive quartets of smaller cells are formed above the four original cells, by division spindles

