


Homology, An Unsolved Problem

Sir Gavin de Beer

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De Beer, Gavin *Evolution and Homology, an unsolved problem*. Nelson.

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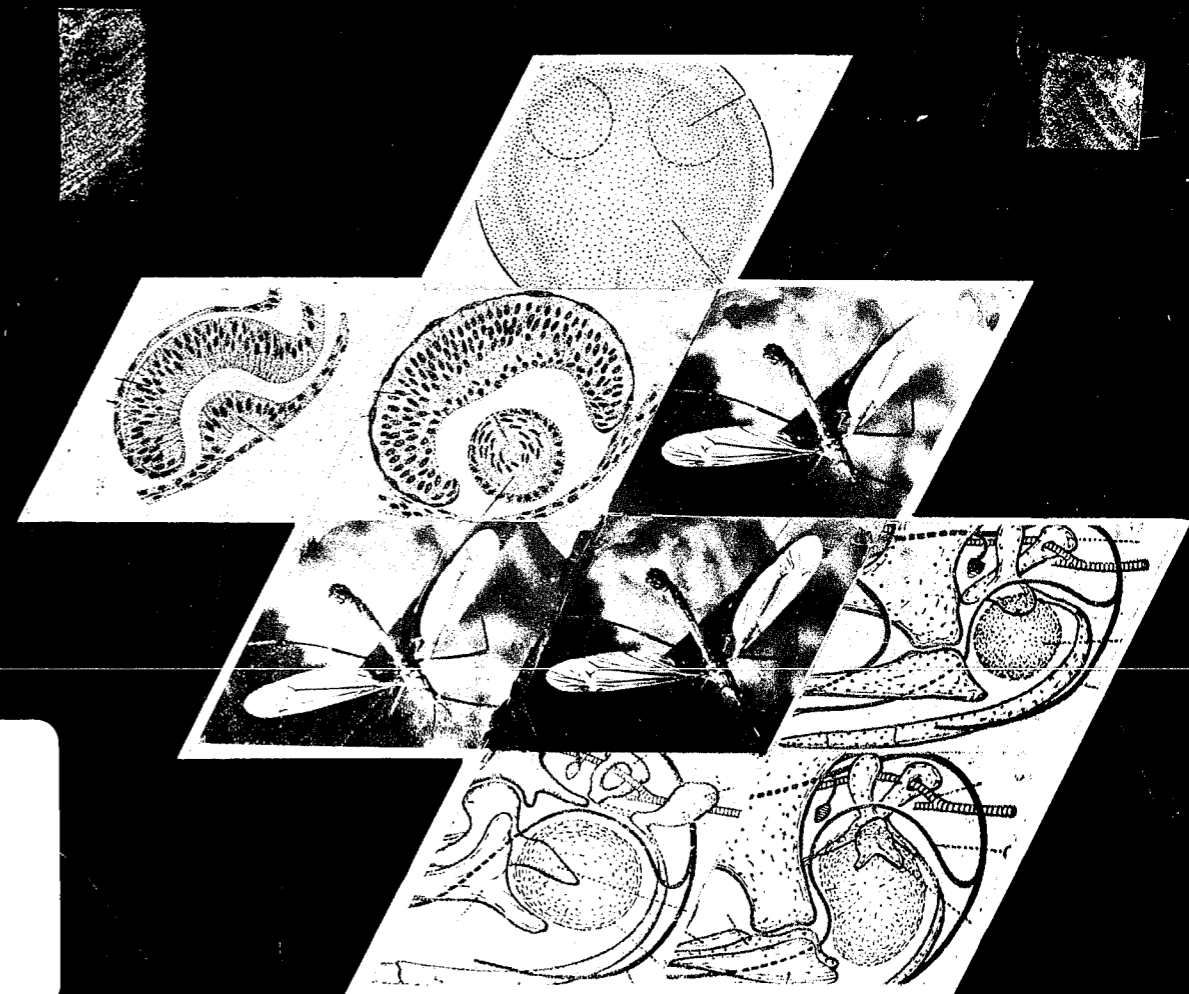
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now clear that the pride with which it was med that the inheritance of homologous tures from a common ancestor explained ology was misplaced; for such inheritance ot be ascribed to identity of genes. The npt to find 'homologous' genes, except in ely related species, has been given up as less. As S. C. Harland said: 'The genes, as a ifestation of which the character develops, t be continually changing . . . we are able to ow organs such as the eye, which are common ll vertebrate animals, preserve their essential arity in structure or function, though the s responsible for the organ must have become lly altered during the evolutionary process'. it if it is true that through the genetic code, s code for enzymes that synthesize proteins h are responsible (in a manner still unknown mbryology) for the differentiation of the us parts in their normal manner, what anism can it be that results in the production omologous organs, the same 'patterns', in of their *not* being controlled by the same s? I asked this question in 1938, and it has been answered.

is-useless to speculate on any explanation in bsence of facts. But attention may be drawn e work of T. M. Sonneborn (1970) on 'Gene n in development', in which he describes ts obtained by him on the unicellular proto- *Paramecium*, which show that although the ern' of the cortex of that organism must be result of genetic action, parts of that cortical rn are necessary for the development of cal structures at the next cell division. To question 'Is the whole of development encoded NA (that is to say, in the genes)?' the answer *amecium* is 'No'. Whether this is applicable to erns' in higher organisms, and whether ologous structures are controlled by non- A mechanisms awaits further research.

FURTHER READING

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Oxford University Press, Ely House, London W.1
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 DELHI BOMBAY CALCUTTA MADRAS KARACHI LAHORE DACCA
 KUALA LUMPUR SINGAPORE HONG KONG TOKYO

© Oxford University Press 1971
 ISBN 0 19 914111 8

First published 1971
 Reprinted 1974

Sir Gavin de Beer, F.R.S., who is now retired, was formerly Professor of Embryology in the University of London and Director of the British Museum (Natural History). He is author of a large number of books on biology, embryology, and evolution which include *Introduction to experimental embryology* (Clarendon Press 1926), *Development of the vertebrate skull* (Clarendon Press 1937), *Embryos and ancestors* (Clarendon Press, third edition 1962), *Charles Darwin* (Nelson 1963), and *Atlas of evolution* (Nelson 1964)

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1. The concept of homology

The term *homology* is derived from the Greek *homologia* which means 'agreement', and is applied to corresponding organs and structures of plants and of animals which show 'agreement' in their fundamental plan of structure, as for example the leaf of an oak tree with the leaf of an ash tree, or the right forelimb of a dog with the right forelimb of a horse. Richard Owen introduced the term into biological language in 1843 to express similarities in basic structure found between organs of animals which he considered to be more fundamentally similar than others.

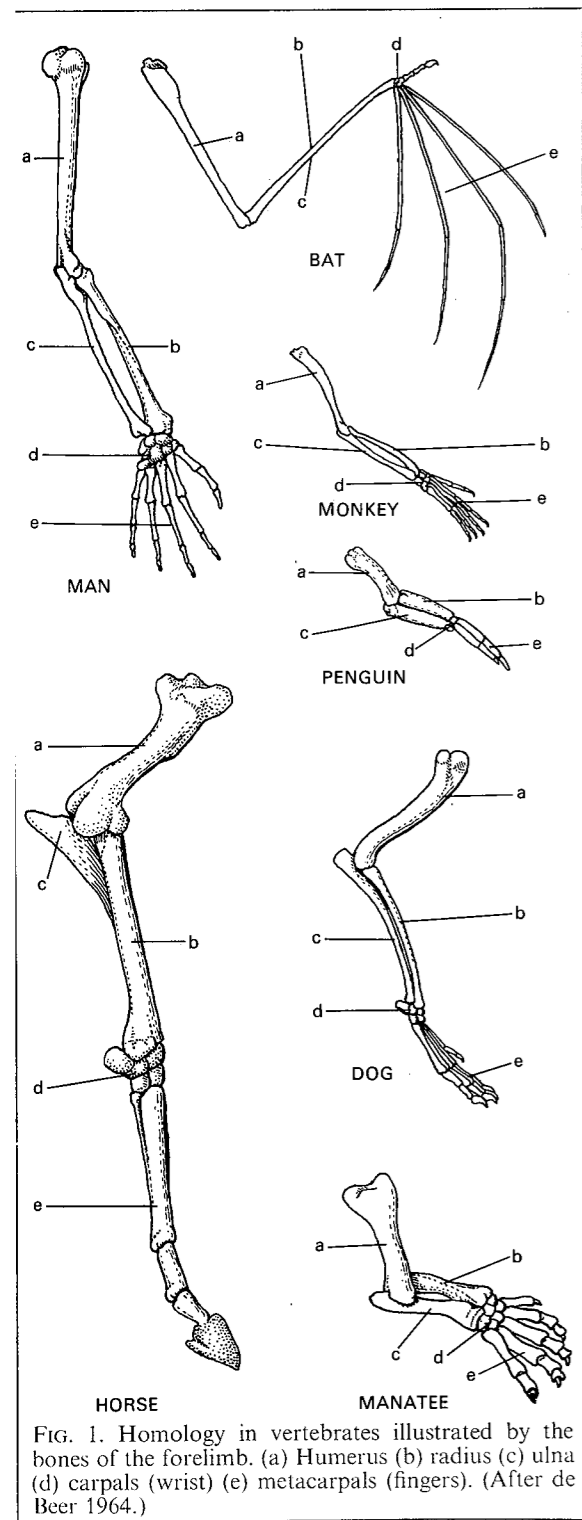
The basis of such similarity and its fundamental nature was for Owen, as for other anatomists of the Transcendental School who considered ideas that grouped facts to be more important than the facts themselves, that such organs corresponded to their representatives in a hypothetical 'archetype', a primeval pattern which was regarded as a sort of blueprint on which groups of similar animals had been created. This concept was pre-Darwinian and pre-evolutionary. The way to define an archetype was to make an abstraction of all the similarities that could be found in common in a group of animals, paying no attention to the variations which individuals and populations showed. The archetype was therefore nothing but a metaphysical concept, and views such as these were held widely by anatomists towards the end of the eighteenth century, and especially by those of the German school of *Naturphilosophie*.

As it turned out, Owen was right in basing homology and homologous organs, or homologues, on their structure regardless of their function. An organ is homologous with another because of what it *is*, not because of what it *does*. Homologous organs are the 'same' organs however modified in detailed form and in the function that they carry out. The forelimb of a horse is homologous with the wing of a bat, although the former serves for locomotion on land and the latter for flight in the air. Homology is therefore to be distinguished sharply from *analogy*, the term applied by Owen to structures that perform similar functions but do not correspond to the same representative in the archetype. The wings of an insect serve the same function as the wings of a bird and are analogous to them, not homologous with them. The entire science of comparative anatomy is concerned with the recognition of homologous organs in different groups of organ-

isms, plants and animals, and their distinction from analogous organs.

Like other people, Owen had predecessors in his way of thinking, and the earliest was Aristotle who may be said to have founded comparative anatomy in his *Historia animalium*, when he wrote: 'There are living beings such that all the parts of one recall the corresponding parts of others'; forelimb of quadruped, wing of bird, fin of fish. Aristotle, who based his views largely on external comparative anatomy, did not carry the analysis very deep, and it had to wait two thousand years before further progress was made. But Aristotle also did something else, which is reflected in the views of Owen and many of his contemporaries; like Plato, Aristotle believed that absolute reality resided not in a thing itself, but in the idea or essence of a thing, and this metaphysical notion is evident in the views of Owen. It was killed stone dead for biology by T. H. Huxley who, in his *Theory of the vertebrate skull*, published in 1858, showed that the Transcendental idea of the skull being only a variation on the theme of a vertebra, so that the skull 'was' modified vertebrae, was as absurd and untenable as the converse idea that vertebrae were modifications of the skull. From then on, transcendental anatomy was killed in England, and facts counted more than idealistic hypotheses and concepts.

To return to the development of comparative anatomy, Pierre Belon (1517-74) published a figure of the skeletons of a man and of a bird, showing that the bones corresponded, bone for bone. Felix Vicq d'Azyr (1748-93) made an important contribution when he analysed the correspondence of such structures and organs in great detail, by paying particular attention to their bones, joints, blood-vessels, ligaments, muscles, glands, etc., thereby establishing the 'correspondence' on a broad anatomical basis. Goethe (1749-1832) was so deeply interested in the correspondence of form that he coined the term morphology, the science of shape, to express the meaning of comparative anatomy; but he was so imbued with the idealistic conceptions of interpretation in anatomy that, on seeing a sheep skull broken into three rings, lying on the ground in the Jewish cemetery in Venice, he immediately concluded that the skull was only modified vertebrae, a blunder, as has been seen above. His recognition that parts of flowers are essentially modifications of leaves has more to be said for it.



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,

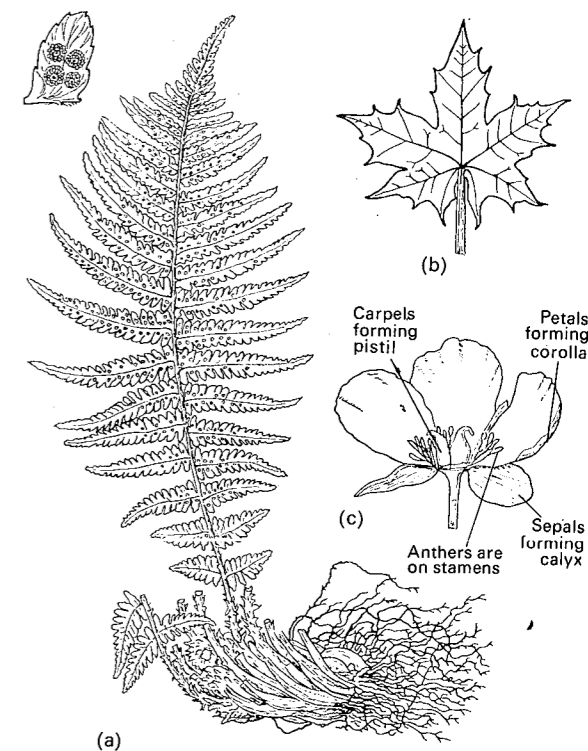


FIG. 2. Homology in plants illustrated by sporophylls, foliage, and floral leaves. (a) Fern sporophyte, showing frond or sporophyll bearing sporangia on its under surface. (b) Foliage leaf of maple. (c) Floral leaves (flower) of *Paeonia*. (After E. Strasburger (1921) *Textbook of botany*, Macmillan.)

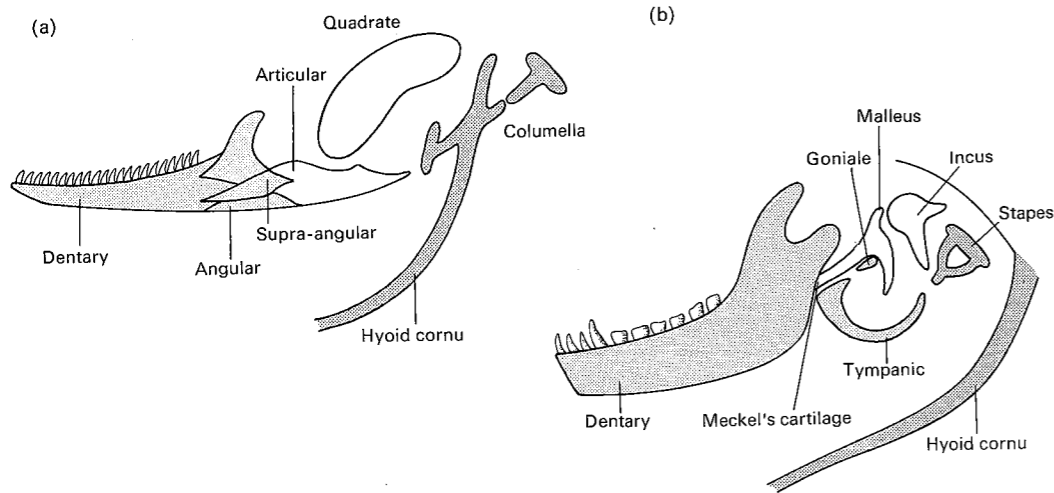


FIG. 3. Homology in vertebrates illustrated by the hinge of the lower jaw in reptiles (a); and the ear-ossicles (stapes) in mammals (b). (After E. S. Goodrich (1930) *Studies on structure of vertebrates*, Macmillan.)

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.

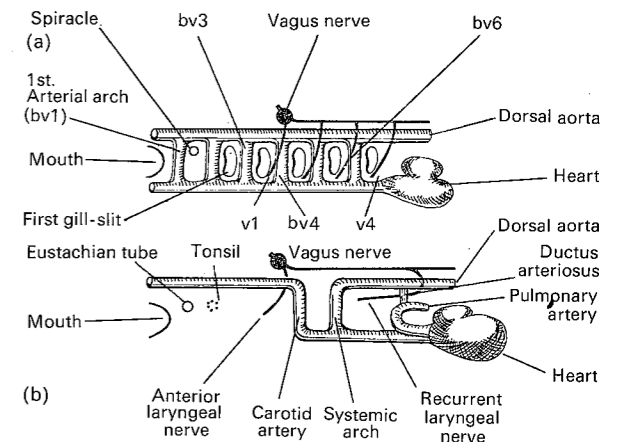


FIG. 4. Morphology of the arterial arches and the vagus nerve in (a) dogfish; (b) rabbit. bv 1, 3, 4, 6, blood-vessels running in the 1st, 3rd, 4th, and 6th visceral arches; v, vagus nerve; v1, 4, 1st, 4th branch of vagus. (After de Beer 1966.)

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

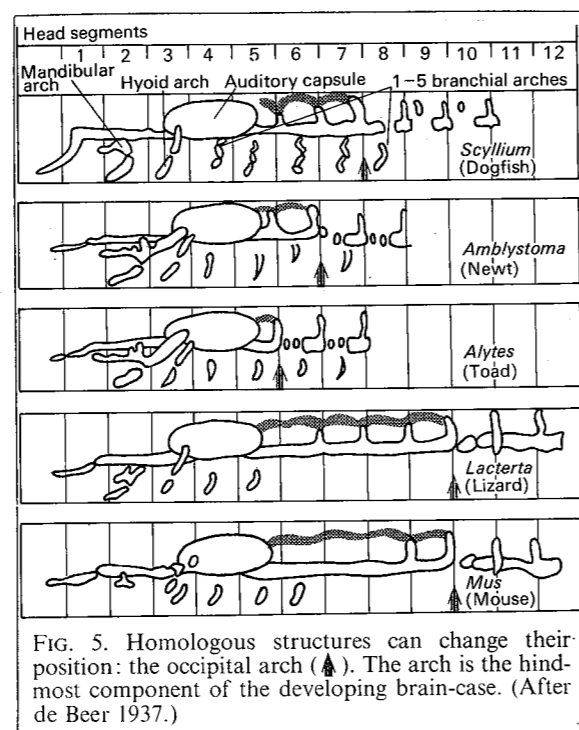


FIG. 5. Homologous structures can change their position: the occipital arch (▲). The arch is the hindmost component of the developing brain-case. (After de Beer 1937.)

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

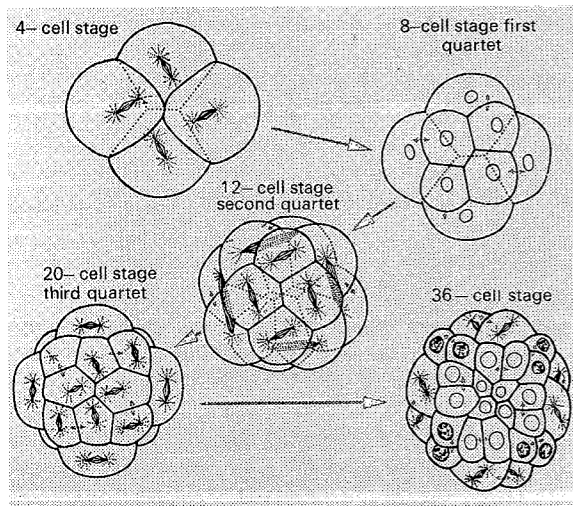


FIG. 6. Spiral cleavage of the egg, found in polyclad Turbellaria, Nemertinea, marine Annelida, Mollusca (other than Cephalopoda), showing the determinate succession and orientation of cell-divisions; probably a sign of latent homology. (After E. J. W. Barrington (1967) *Invertebrate structure and function*, Nelson.)

orientated first half-left, then half-right, then half-left again, with the precision of a drill, so that at the 64-cell stage it is possible to work out a cell lineage with indications of the prospective fates of the cells and their progeny in subsequent development. Spiral cleavage occurs in polyclad turbellarians, nemertines, marine annelids, and molluscs other than Cephalopoda. It surely indicates a general affinity between the different groups in which it is found, because it is difficult to see how such a complicated mechanism could have been evolved separately in each group, and this affinity is supported by other embryological and morphological considerations. But did the common ancestor of all these groups itself develop by spiral cleavage? It is impossible to say and difficult to assert, because in many species of these groups it does not occur. Development by means of 'polar lobes', as found in the annelid *Sabellaria* and in the mollusc *Dentalium*, present an analogous problem, because so many of their close relatives do not. These are perhaps other cases of latent homology, and another may be that of the evolution of social instincts in wasps, bees, and ants, because in each of these groups there are examples of solitary and social species, and although they are all Hymenoptera it is impossible to believe that

their common ancestor had social instincts.

Latent homology therefore conveys the impression that beneath the homology of phenotypes, there is a genetically based homology which provides some evidence of affinity between the groups that show it.

8. Homology and functional change

It is one of the definitions of homology that homologous organs can vary in the functions that they perform. There are several proofs of this, of which one of the simplest is the case of muscles and electric organs in fishes. Every time that a muscle contracts there is an output of electromotive force which in normal cases is so slight that it exerts no effect. In some fishes, however, the muscles of certain parts of the body are modified to produce electric organs which are batteries of muscles, insulated in series, which can make electric discharges powerful enough to deter predators and to kill prey. As it was difficult to imagine how these specializations arose by natural selection, and what advantages could have been conferred by initial stages of such specialization, Darwin warned that 'it would be extremely bold to maintain that no serviceable transitions are possible by which these organs might have been gradually developed'. This prophecy has been fully verified by H. W. Lissmann, who showed that weak electric discharges given off by the muscles of certain fishes function in a manner analogous to radar and provide the fish with information of the proximity of other objects, by reflection of the electric waves and their perception by the sense organs of the lateral line of the fish. This is not so much a change of function as the exaggeration of a function with the result that it serves a different purpose.

The original method of feeding of the primitive vertebrates was by the production of a ciliary current of water directed towards the mouth, wafting in particles of food. But the water must then pass out through the gill-slits, and to prevent the loss of food particles with it, an endostyle was present, as in amphioxus, consisting of bands of cilia along the floor of the throat and bands of mucus-secreting cells, the mucus of which catches up the food particles like a moving fly-paper. True vertebrates feed by means of predatory jaws, and lampreys by means of a specialized sucking mouth and rasping tongue; but the larval form of the lamprey, the ammocoete, preserves

the ciliary method of feeding, with an endostyle, and when it metamorphoses into the adult lamprey, the endostyle closes up, and from the opening that connected it with the floor of the throat there develops the thyroid gland. In all other vertebrates the thyroid develops in the same way from a downgrowth of the floor of the throat, partially homologous therefore with the endostyle.

Other ductless glands in vertebrates probably have a comparable origin: the pineal gland of mammals is homologous with the pineal eye of lower vertebrates which, even in the lizard embryo, still has the layer of melanin pigment. The thymus may be homologous with the excretory organs, the nephridia which, like those of amphioxus, develop from the epidermis of the dorsal end of the gill-slits.

Perhaps the most striking example yet found of function change is that of the hinder pair of wings in Diptera, common flies, which are modified into little rods, the halteres, which vibrate so fast that they serve as gyroscopic organs, as J. W. S. Pringle showed.

9. Non-homology

Just as morphology can provide proof that certain organs and structures are homologous, it can also show that others are not. In the hyoid arch of sharks, the cartilaginous skeletal elements, hyomandibular above and ceratohyal below, articulate with one another on the median side of the afferent hyoidean artery, laterally to which are the cartilaginous hyal rays some of which are joined together at their bases forming dorsal and ventral pseudohyoid bars. These stiffen the edge of the hyoid arch in the front wall of the 1st gill-slit.

In skates, the lower cartilaginous element of the hyoid arch is lateral to the afferent hyoidean artery, and therefore cannot be homologous with the ceratohyal cartilage of the sharks, but is the ventral pseudohyoid bar. In *Rhynchobatus*, a form somewhat intermediate between sharks and skates, an intermediate condition is found with a reduced ceratohyal cartilage in addition to the ventral pseudohyoid bar.

FIG. 8. (a) Dorsal view of a dipteran fly showing the hind wing converted into a gyroscopic organ (haltere). (b) Enlarged view of the haltere. (Courtesy of J. W. S. Pringle.)

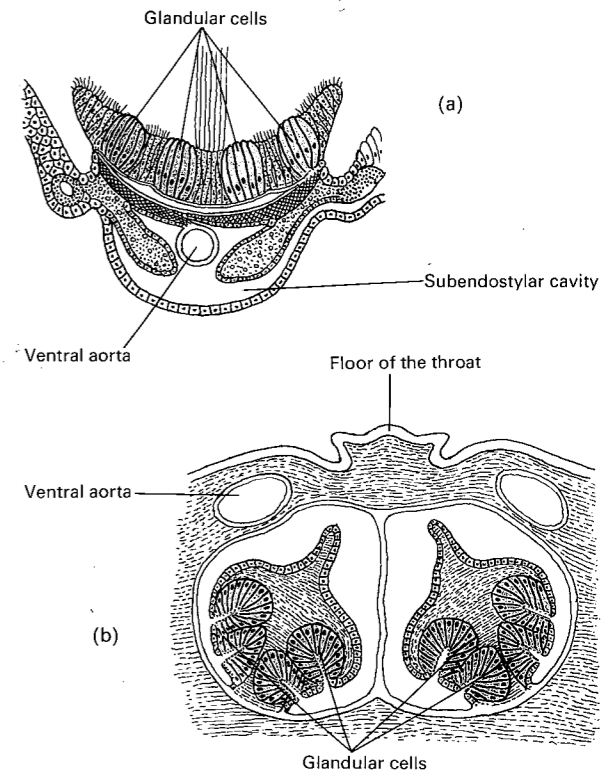
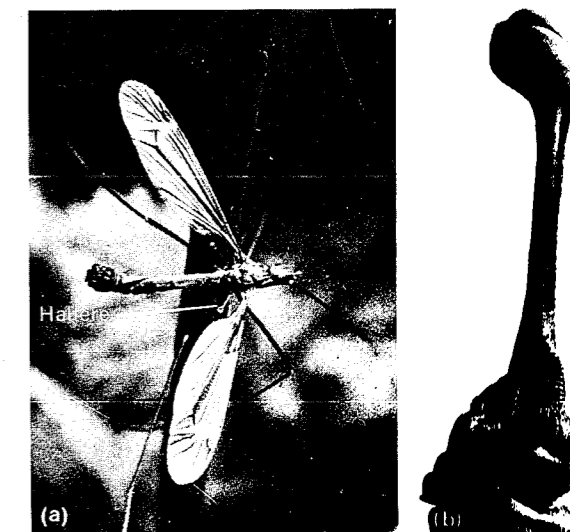
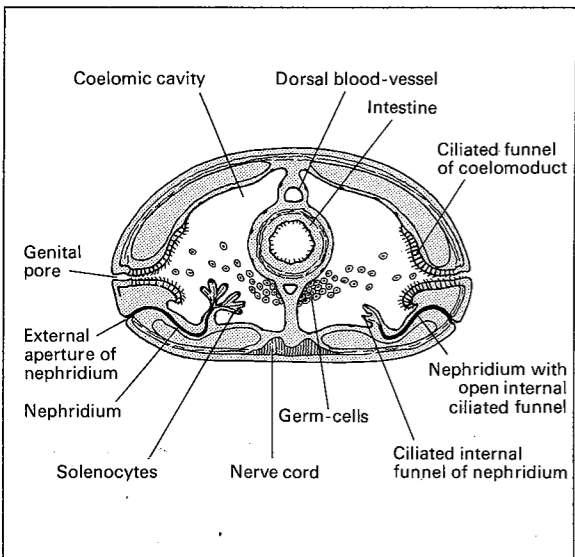
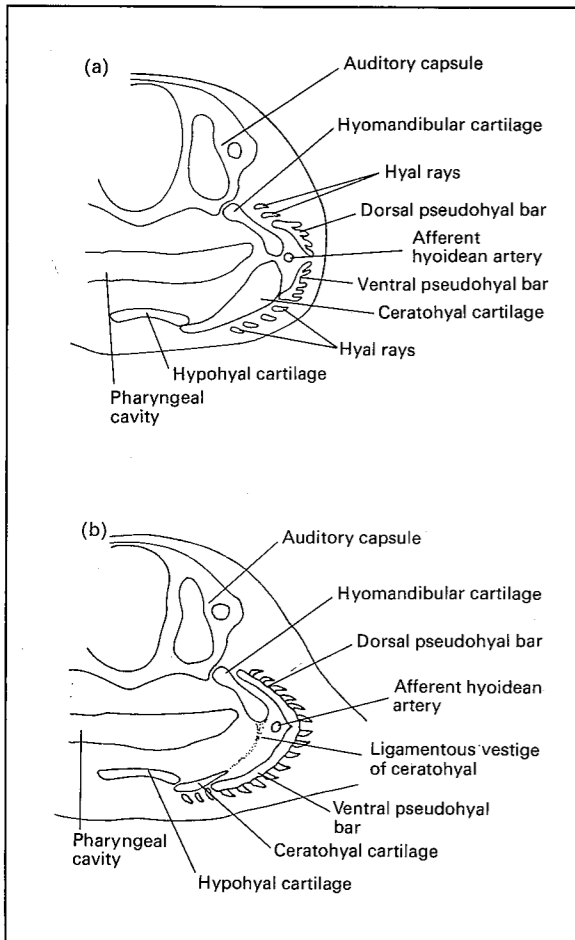


FIG. 7. Changes of function of homologous organs. (a) Transverse section through the endostyle of amphioxus showing the four tracts of ciliary and of glandular cells; (b) through the endostyle of the ammocoete larva of the lamprey shortly before metamorphosis when the thyroid gland will develop from the endostyle. (After de Beer 1966.)





One of the most fundamental facts in the morphology of animals is the body cavity or coelom, in all above the evolutionary level of the flatworms. This cavity serves primarily for the formation and temporary storage of the germ cells, which are eventually evacuated into the surrounding medium by means of tubes known as coelomoducts. A completely different set of tubes, nephridia, serve to void excretory products out of the body, and these are found even in the flatworms which have no coelom. Where a coelomic cavity exists the nephridia project into it.

The distinction between the two sets of tubes was made clear 75 years ago by E. S. Goodrich, who showed that nephridia are developed inwards from the ectoderm, whereas coelomoducts are developed outwards from the mesodermal wall of the coelomic cavity. Both kinds of tubes can be seen in annelid worms. The difficulty in interpreting these two kinds of structure in any given form is partly that both nephridia and coelomoducts may end internally in the coelomic cavity with open funnels surrounded by beating cilia which create a current of fluid serving to expel their content whether excretory products or germ cells. Another difficulty is that in some animals the function of the nephridia has been taken over completely by the coelomoducts and the nephridia disappear, as for example in molluscs and in vertebrates. This is why man has a urinogenital system, while annelids have separate excretory and genital systems. Nephridia and coelomoducts are not homologous at all. Even today, this fundamental fact of morphology is often ignored by continental European zoologists.

10. Homology and embryology

Since every organ and structure in any organism has come into existence only as a result of embryonic development, it is natural to look to embryology for evidence on homologous structures. At late stages of development, when

FIG. 9. Non-homology, demonstrated by morphological relations of the afferent hyoidean artery in the hyoid arch of sharks and skates, as seen in transverse sections of heads of (a) shark, and (b) skate. (After de Beer (1932), *Q. Jl microsc. Sci.*)

FIG. 10. Non-homology of nephridia and coelomoducts, shown by the separate presence of both pairs of structures in annelid worms. Solenocytes are blind internal endings of primitive nephridia. (After Goodrich 1946.)

morphological relations between structures are established, such studies may yield valuable results, as in the case of the ear ossicles mentioned above. But at very early stages, such research leads to disappointment.

Progress in early embryology has made such strides that there are two levels on which the relations of homology and embryology can be studied. The first concerns the correspondence of places of origin of homologous structures in the fertilized egg or young embryo of related species, because the prospective fates of portions of embryos are now well known, and they can be plotted back on to the egg. In many cases it can be observed and proved by experiment, e.g. on the mollusc *Dentalium* and in tunicates, that there are extensive translocations and movements of these 'organ-forming substances'. Structures as obviously homologous as the alimentary canal in all vertebrates can be formed from the roof of the embryonic gut cavity (sharks), floor (lampreys, newts), roof and floor (frogs), or from the lower layer of the embryonic disc, the blastoderm, that floats on the top of heavily yolked eggs (reptiles, birds). It does not seem to matter where in the egg or the embryo the living substance out of which homologous organs are formed comes from. Therefore, *correspondence between homologous structures cannot be pressed back to similarity of position of the cells of the embryo or the parts of the egg out of which these structures are ultimately differentiated.*

The same conclusion arises from cases of larval divergence. *Polygordius* is a primitive worm. In one species, *P. lacteus*, the trunk of the future worm develops all coiled up inside the body of the trochophore larva; in *P. neapolitanus* the trunk develops outside the larva as a worm-like extension of it. In spite of these developmental differences, the fully formed worms of the two species are practically indistinguishable. G. Fryer has drawn attention to the remarkable differences in larval structure and development between two bivalve molluscs, *Mutela* and *Unio*, the adults of which are so similar.

The other level of embryology at which the relations between it and homology can be studied is the induction of tissues to undergo differentiation, as a result of diffusion of substances from a master structure called an *organizer*. It was found by Hans Spemann that the dorsal lip of the blastopore of a newt embryo at the gastrula

stage, has the power, when grafted anywhere into the body of another embryo, of inducing the tissues by which it by accident finds itself surrounded to differentiate into all the structures characteristic of a vertebrate embryo: notochord, segmental muscle plates, kidney tubules, spinal cord, brain with eyes, etc. If they had been left undisturbed these tissues would have differentiated into very different structures. This is another proof that the quality of a structure is not dependent on the place of origin of the material out of which it is formed.

It was a problem to know why the lens of the vertebrate eye, which develops from the epidermis overlying the optic cup, should develop exactly in the 'right' place, and fit into the optic cup so perfectly, until it was discovered that the optic cup is itself an organizer which induces the epidermis to differentiate into a tailor-made lens. At least, this is what it does in the common frog, *Rana fusca*, in the embryo of which, if the optic cup is cut out, no lens develops at all. But in the closely related edible frog, *Rana esculenta*, the optic cup can be cut out from the embryo, and the lens develops all the same. It cannot be doubted that the lenses of these two species of frog are homologous, yet they differ completely in the mechanism by which determination and differentiation are brought about.

This is no isolated example. In true vertebrates, the spinal cord and brain develop as a result of induction by the underlying organizer; but in the 'tadpole larva' of the tunicates, which has a 'spinal cord' like the vertebrates, it differentiates without any underlying organizer at all. All this shows that *homologous structures can owe their origin and stimulus to differentiate to different organizer-induction processes without forfeiting their homology.*

Attention must now be paid to the germ layers. It was discovered a hundred and fifty years ago by C. Pander and K. E. von Baer that the fertilized eggs of all animals above the jelly-fish give rise to layers of tissue, three in number: ectoderm, endoderm, and mesoderm, which become folded up in different ways. It was then found that in general, ectoderm gives rise to epidermis, nervous system, sense organs, and nephridia; endoderm to the alimentary canal and its derivatives (in vertebrates: thyroid, lungs, liver, pancreas, appendix, urinary bladder); mesoderm to dermis, connective tissue, cartilage, bone, muscles, germ cells,

coelomoducts or genital ducts, and also to kidneys where nephridia have been lost.

Very soon, this generalization became a dogma, and it was held that homologous organs *must* always arise from the 'correct' germ layer. This position was first shaken when experiments involving extirpation of the neural crest (from which nerve cells arise) in newt embryos also resulted in absence of cartilages of the jaws and other visceral arches. It was morphological heresy to think that cartilage could arise from ectoderm. The orthodox view was that no valid conclusions could be drawn from experimentally mutilated embryos. It therefore became necessary to demonstrate the facts from the study of embryos on which no experiments had been performed, and this is what I did in 1947.

In newt eggs, ectodermal tissues arise from the upper superficial part of the egg which is black, because of the presence of innumerable small melanin granules, which persist for a long time in the cells derived from it, and indicate their ectodermal origin. On the other hand, endodermal and mesodermal cells contain small globules of yolk which betray their origin. By means of these natural indicators I was able to show that not only the cartilages of the jaws and visceral arches consist of cells containing the tell-tale melanin granules, but also the osteoblasts of the dermal bones of the skull (frontal, parietal), and the odontoblasts in the papillae which secrete the dentine that composes the body of the teeth. Enamel had always been regarded as an ectodermal product, formed from the stomodaeal epidermis which grows in and lines the front of the mouth cavity. But enamel can be formed from ectodermal stomodaeal cells (with melanin granules), or from endodermal cells (with yolk globules), according to where the tooth rudiments are, for they act as enamel organizers.

So the imagined embryological specific monopoly of the germ layers and what they invariably give rise to was shattered. This had an effect outside zoology, for the old dogma had cut so deep that even malignant cancers used to be classified according to the germ layer of origin of the tissues in which they arose.

It is therefore necessary to give the lie direct to the entry on 'Homology' in the glossary by W. S. Dallas which Darwin most unfortunately appended to the 6th edition of the *Origin of Species*. It defines homology as 'That relation

between parts which results from their development from corresponding embryonic parts.' This is just what homology is *not*. The real situation was well defined by E. B. Wilson in 1894, when he pointed out that 'Embryological development does not in itself afford at present any absolute criterion whatever for the determination of homology . . . comparative anatomy, not comparative embryology, is the primary standard for the study of homologies.'

As if this were not enough, there are also the processes in regeneration and asexual reproduction, whereby organs are replaced or new individuals differentiated. Such cases of morphogenesis differ completely from the sequence of events in embryonic development from the egg. In many cases, as can be seen most strikingly in nemertine regeneration, and polyzoan and ascidian asexual reproduction, no respect whatever is paid to the germ layers from which the structures of the new organism are made.

Before leaving embryology, there is a further aspect of the subject that is worth consideration. It is sometimes called sexual homology, and it refers to the correspondence between organs of the genital system that have undergone different

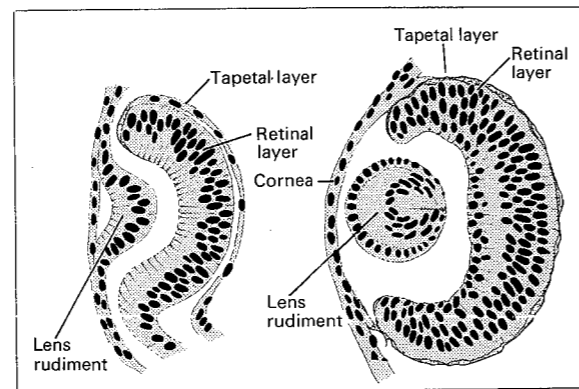


FIG. 11. Induction of the lens in Amphibia by organizer-action of the eye-cup. The eye-cup develops as an outgrowth from the brain, but the lens develops from the epidermis overlying the mouth of the eye-cup. In *Rana fusca*, the common frog, this is brought about by diffusion of an inducing substance from the eye-cup acting on the overlying epidermis, exactly in the right place. This is proved by the fact that if the eye-cup is removed, no lens is formed. But in *Rana esculenta*, the edible frog, removal of the eye-cup does not prevent the formation of a lens, which therefore owes its origin to a different mechanism. (After Huxley and de Beer 1934.)

development in the two sexes. For instance, the testis corresponds to the ovary; the scrotum containing the testes of the male corresponds to the labia majora of the vulva of the female, and the correspondence is made even more obvious in abnormal cases where the ovaries undergo 'descent' like testes, and pass by the canal of Nuck into the labia. The penis corresponds to the clitoris which, although diminutive, also contains erectile tissue. Part of the prostate corresponds to the uterus, and this fact can be made use of in certain pathological cases where enlargement of the prostate can be treated by sex hormones.

Are these corresponding organs homologous? Not in the strict sense, since it is not possible to refer them to a single representative in a common ancestor, which in vertebrates was certainly not hermaphrodite. They are the result of divergent embryonic development consequent on sexually dimorphic differentiation, due in part to genes and in part to sex hormones. The rudiments from which they have developed are homologous.

11. Homology and genetics

Because homology implies community of descent from a representative structure in a common ancestor it might be thought that genetics would provide the key to the problem of homology. This is where the worst shock of all is encountered.

It was seen in the section on latent homology that the theory of homology is concerned with homologous structures as phenotypes; but as their essence is hereditary descent from a common ancestor, it is natural to investigate the question how homology applies to genotypes. But what can be made of a gene such as that in certain fowls which not only controls the formation of a crest of feathers, but also brings about a cerebral hernia, with upswelling of the skull in the form of a knob, to accommodate it? There is no homology whatever between these two conditions. What is more, the feather crest character controlled by this gene is dominant in the wild-type gene complex, but the cerebral hernia is recessive. In the Japanese silky fowl, the gene complex suppresses the formation of the cerebral hernia altogether, while the production of the feather crest is unaffected.

Another example is that of the gene 'antenna' which, in *Drosophila*, controls the production of an extra antenna instead of an eye, structures that are not homologous. This phenomenon

recalls that known as heteromorphosis in regeneration where the organ regenerated is different from that which was lost or amputated: e.g. a leg instead of an antenna, or an antenna instead of a stalked eye, described by H. Przibram and by H. W. Lissmann and A. Wolsky.

Cases are known where identical, 'homologous' genes (as can be proved by breeding experiments) control characters which can be shown to have evolved independently. *Triphaena comes* is a moth which on the mainland of Britain is grey, but in the Orkneys and the Hebrides has dark races. But as E. B. Ford showed, the manner in which the genetic control of the dark races was built up was quite different in the Orcadian and Hebridean forms, which means that the dark colour in the two is not homologous.

What all this means is that *characters controlled by identical genes are not necessarily homologous*.

The converse is no less instructive. In *Drosophila* there is a gene, 'eyeless', which deprives its possessor of eyes. It is a recessive character, which is important because it means that when its effect is produced, the fly has inherited the 'eyeless' allele from both parents, and no normal eye-controlling allele is present. If a stock of individuals pure (homozygous) for the 'eyeless' gene is inbred for many generations, there is high mortality as would be expected from the adverse effects of natural selection acting on a gene with such lethal effects. But eventually, flies appear in the offspring possessing normal eyes. It can easily be shown that the 'eyeless' gene has not changed, because when one of these phenotypically eye-possessing but genotypically homozygous 'eyeless' flies is mated with the original wild stock, i.e., the 'eyeless' gene is put back into the original gene complex, the virulent effects of the 'eyeless' gene reappear. What has happened during the inbreeding is that all the other pairs of alleles making up the gene complex have been reshuffled until a gene complex has been produced that prevents the phenotypic manifestation of the 'eyeless' allele. Other genes must therefore deputize for the absent normal gene that controls the formation of eyes. But why should they, and by what mechanism? Nobody can deny that the restored eyes that develop in genetically 'eyeless' stocks are homologous with the original normal eyes. Therefore, *homologous structures need not be controlled by identical genes, and homology of phenotypes does not imply similarity of genotypes*.

12. Revision

It is now clear that the pride with which it was assumed 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 hopeless. As S. C. Harland said: 'The genes, as a manifestation of which the character develops, must be continually changing . . . we are able to see how 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 wholly altered during the evolutionary process'.

But if it is true that through the genetic code, genes 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 spite 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 results obtained by him on the unicellular protozoon *Paramecium*, which show that although the 'pattern' of the cortex of that organism must be the result of genetic action, parts of that cortical pattern are necessary for the development of cortical structures at the next cell division. To the question 'Is the whole of development encoded in DNA (that is to say, in the genes)?' the answer in *Paramecium* is 'No'. Whether this is applicable to 'patterns' in higher organisms, and whether homologous structures are controlled by non-DNA mechanisms awaits further research.

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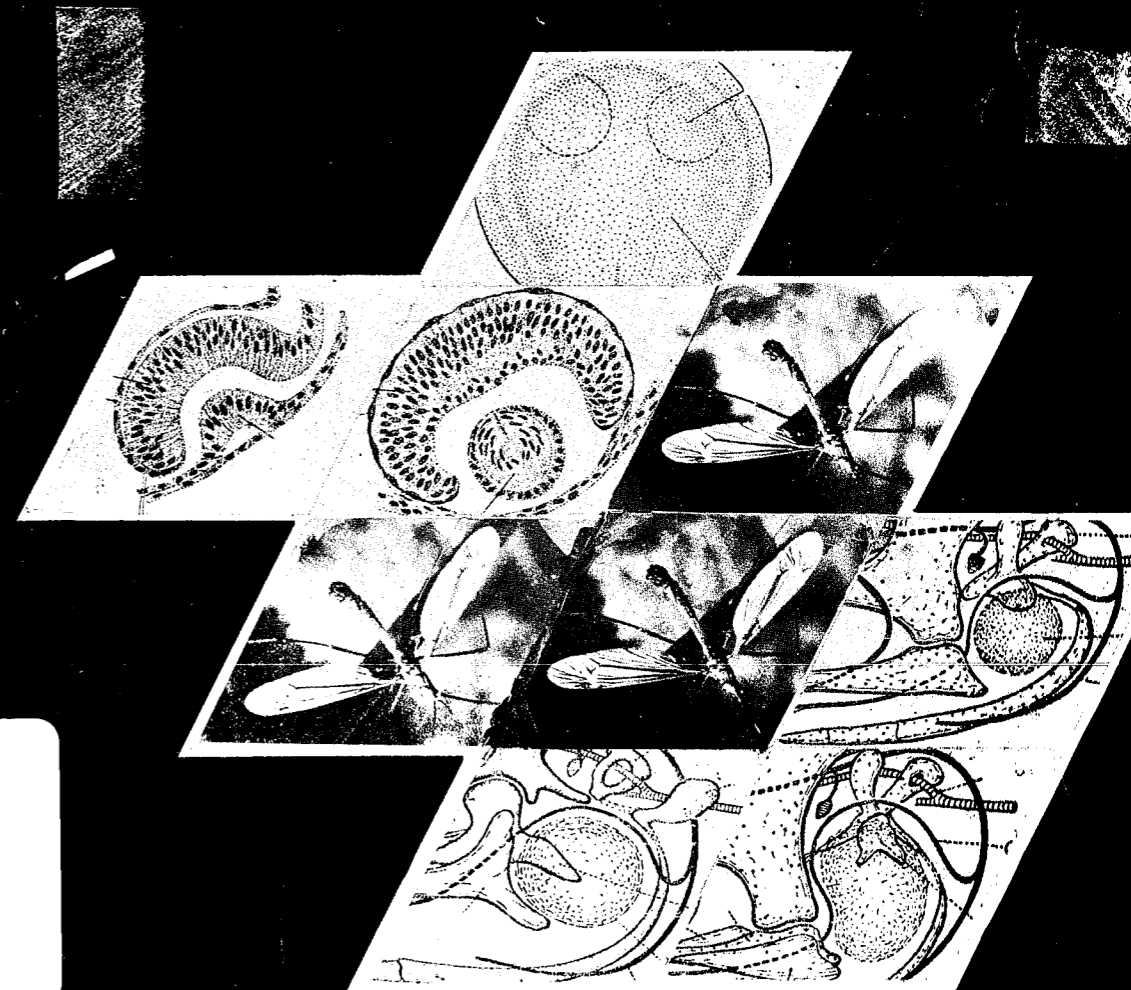
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Sir Gavin de Beer



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