ON THE PHYLOGENY AND THE ONTOGENY OF THE HUMAN LARYNX

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A MORPHOLOGICAL AND FUNCTIONAL STUDY

J. WIND

ON THE PHYLOGENY AND THE ONTOGENY OF THE HUMAN LARYNX

On the phylogeny and the ontogeny of the human larynx

A morphological and functional study

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Contents

PART I.

Chapter 1. *Phylogeny and ontogeny in general.*

Chapter 2. *Phylogeny of man with special reference to his larynx.*

PART II.

Chapter 3. *Comparative zoology.*

Chapter 4. *Discussion of the phylogeny of the human larynx.*

PART III.

Chapter 5. *Ontogeny of the human larynx.*

PART IV.

Introduction

The intention of this work is to describe the development of the human larynx in two ways: firstly, the evolution of the larynx as it must have taken place in our forebears; and secondly, the development of the larynx after its first appearance in the individual human, these two processes being called the *phylogeny* and *ontogeny* of the larynx respectively.

The very existence of the words phylogeny and ontogeny (*φυλοσ* = race, species, *ὀντοσ* = of the being, and *γευεσισ* = origin) indicates the eagerness with which man looks for relationships, rules and even laws in nature. From a study of the history of biology it is soon apparent how much satisfaction man has achieved from the discovery of the properties of nature. It may be that by his recognition of order amid complexity man finds identification with the forces of nature. Moreover from the history of biology it is possible to learn another typical human feature: the observer may anticipate the satisfaction he expects, and, not finding it, may attempt himself to establish these laws of nature.

The present work is not only an attempt to describe the phylogeny and ontogeny of the human larynx, but also, by studying their relationships, to obtain a clearer view in this field of the confusing yet beautiful picture of biology.

Since the introduction of terms like "organic evolution", "phylogeny" and "ontogeny", much has been and still is being published on these subjects and it is clear that there were and still are many complicated and unsolved problems.

I do not intend, nor am I able, to give a complete review of this complex matter or to add new theories, but a short introduction may be useful to remind the reader of the development of existing ideas and the meaning of the terms used. This will ensure a better understanding of the problems tackled in the succeeding chapters.

Part 1

CHAPTER I

Phylogeny and ontogeny in general

1. *PHYLOGENY*

It is now commonly accepted that since life started on earth there must have been a gradual change in its forms and that modern animal species evolved from others, most of which no longer exist, this process being called organic evolution.*

Aristotle (Singer, Simpson-1950, Hardy-1965) had already proposed a complete series of animals, the "scale of beings", which basically resembles the evolutionary sequence as we now know it and it is not impossible that he had some idea of one kind of animal changing into another. However, for centuries, mainly under the influence of the Christian Church, another concept existed (Simpson-1950), that of "special creation", according to which all living beings had been created as they now are. This idea persisted until the 19th century, when evolution and its mechanisms were first seriously considered and expounded. The two most influential theories of the time, which we will briefly describe, were *Lamarckism* and *Darwinism*; later evolutionary theories may be related to one or other of these.

Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck, commonly known as Lamarck, supposed in his *Philosophie Zoologique* of 1809 that the environment of the individual which brought about the need for new characters induced changes in the body. These changes would then be transferred as hereditary characters to the descendants.

In 1859 Darwin published his famous book *On the Origin of Species by Means of Natural Selection.* At about the same time the ideas of natural selection had occurred to Alfred Russel Wallace, who diverged from Darwin in so far as he applied the principle mainly to man's intelligence (Eiseley) and his mental and moral qualities (Dunn). According to Taylor, conceptions like these had already been put forward at the beginning of the 18th century by de Maupertuis. Zirkle, Zeller (cited by Uschmann), Hardy-1965 and Waddington emphasize that even the ancient Greeks, e.g. Empedocles (400 B.C.) and others, had expressed ideas of this sort long before the era of Darwin. However, by the 19th century the time was ripe for this concept to be discussed more thoroughly. From his observations Darwin concluded (1) that there is in nature a constant struggle for the continuation of each individual in spite of adverse environmental stresses imposed on it, (2) that the strongest and fittest individuals will survive, and (3) that their descendants will show the same characteristics by virtue of heredity. In this way new species could develop.

A third theory should be mentioned here, that of discontinuous variation by means of *mutations*. This theory, originated by de Vries at the beginning of the 20th century, was based on his botanical observations and postulated that seemingly spontaneous changes in the genetic pattern sometimes occur, that they can be constant in the offspring and that in this way new characteristics and possibly new species can originate. The science of genetics, in recent years, has provided a firm basis for this theory which has been supported by microscopy, biochemistry and biophysics. However, we know today that the value of mutations for evolution is smaller than was supposed by de Vries and his contemporaries (Mayr-1963, p. 176. For a discus-

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* As this study deals with zoological problems, we shall in this introduction consider only animal evolution, especially that of the vertebrates; it should be remembered, however, that most of these considerations can be applied to botany as well.

sion of the value of genetics in natural selection, see further Wright.)

A relatively young science is *palaeontology* (Romer -1958a, Patterson); "it supplies the annals of morphologic and ecologic events and their time and space relationships for five million centuries of the adaptive organizations of protoplasm; it historifies the geological records of time" (Jepsen). Reviews of the relationships of palaeontology to other sciences contributing to evolutionary theory are given by e.g. Olson and Krommenhoek.

In recent years attention has been drawn to the fact that it is not only morphology that helps us to understand evolution but also *physiology* (Wittenberger, Prosser-1960, Smit, Sollberger), *ethology* (Lorenz-1943, -1964, Portmann-1951, Tinbergen-1951, -1960, -1965, von Eickstedt, Baerends-1958, Simpson-1958*b*, Wynne-Edwards, Mayr-1963, Hardy-1965, -1968, Wickler, Hinde), *ecology* (Mayr-1963, Bates), and *biochemistry* (I. I. Geschwind, Tarlo, Broda, Grünewald, Sarich, Wang *et al.*, Goodman, and others cited by the last author).

When after this short historical review, we come to consider the question of organic evolution in the light of present knowledge, we have to conclude that up till now a completely satisfactory explanation of the mechanisms of evolution has not been found. As Murray (p. 453) states, however, evidence for the existence of organic evolution comes from all branches of the biological sciences: "palaeontology, comparative anatomy and embryology, geographical distribution, systematics, the study of domesticated animals and plants and immunology", and few biologists doubt its existence.

Today *Lamarckism* is regarded by most biologists as giving an unsatisfactory explanation of animal evolution (e.g. Simpson-1958*a*, Mayr-1963). "Although this hypothesis provides an explanation of the modifications of existing structures it also implies, in its wider application, that is, the *need* for a structure which induces its appearance, a not particularly tenable line of argument, for it seems to confer upon the organism an awareness of itself and its needs and power of modification which is not borne out by observation" (Grove & Newell, p. 692). Lamarckism often attracted philosophically minded scientists, adherents of the more-or-less mystical and metaphysical conceptions like "vis vitalis", "Vervollkommnungsprinzip", "entelechia", "teleology" and the "internal creative principle", all of which tend to be strongly opposed by the exact sciences (Lam).

It is true that there are some remarkable facts seemingly in favour of Lamarckism.

For instance the presence of skin callosities found in embryos at the site where they may be expected to develop after the birth of the animal because of its manner of living. This has been described by Duerden in ostriches (criticised by Lowe) and by Antony & Cuénot in pigs. In 1754 Albin* reported the same in human embryos (callosities on the soles of the feet). Kükenthal described teeth in the embryonal Indian sea-cow *Dugong dugon*, which at an early stage show unworn conical cusps and ridges, but at a later stage flat surfaces as if they were worn down by friction. These facts are remarkable, but are they more remarkable than the fact that from one cell, the zygote, grows a complete living individual, with legs so well fashioned for running and kneeling and teeth so well fashioned for grinding? Mayr-1963 thinks that natural selection gives sufficient explanation for the existence of these callosities.

More recently some French authors have favoured a Lamarckian view of evolution. Thus Retterer, a well-known anatomist, explains certain morphological differences in a Lamarckian way, which most modern biologists would not hesitate to explain by natural selection. Similarly in the ethological field we find Bouvier (1918, p. 124) firmly convinced that there is inheritance of "acquired instinctive characteristics", a most confusing idea for modern biologists who would consider such a statement as a *contradictio in terminis*. Another anatomist, Rouvière, concludes in his *Anatomie philosophique* (1941), that morphology gives sufficient evidence for the acceptance of a *finalité* in organic

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* Quoted by Semon, who also gives a circumstantial account of the publications in favour of and opposed to this finding. Other authors, like Johnson, described these pads on the palms and soles of human foetuses as being mesodermal rather than epidermal as normal callosities are.

evolution. Wintrebert attempts to revalidate Lamarckism and draws attention to the fact that characters might possibly become hereditable through the function of the protoplasm. Teilhard de Chardin's philosophy, with its teleological tendencies and its assumption that non-human materials possess an awareness of themselves, tends towards Lamarckism.

Defendants of Lamarckism claim furhtermore that the reason why experiments have hitherto failed consistently to prove this theory might be due to their necessarily short duration compared with the duration of organic evolution (Nopcsa).

Recent bacteriological findings seem to provide another argument in favour of Lamarckian evolution: acquired resistance against antibiotics can be transferred from one strain to another, the descendants of which maintain this characteristic (Smith & Armour). In general, however, such resistance can be explained in terms of the selection of the mutations concerned (Kaplan). It must be said therefore that it is possible that there exists some direct environmental influence on the genetic pattern. Equally such a mechanism exists where mutations are provoked by external stimuli like irradiation. Whether this kind of mutation has actually worked in evolution, e.g. as the result of cosmic radiation, remains questionable. Binge's hypothesis that there might be a relationship between periods of rapid vertebrate evolution, like that of the mammal-like reptiles, on the one hand, and synchronous periods of greater radiation activity from the sun with accompanying changes in the climate on the other, is concerned with such a mechanism. Nevertheless Mayr-1963 (p. 596, p. 617) concludes from his elaborate and elucidating studies on animal evolution, that in these cases too natural selection offers a sufficient explanation.

Therefore, although some arguments favouring his evolutionary theory may be found, it remains questionable whether or not Lamarck himself would have accepted the mechanisms adduced by them. In the absence of definite proof we shall not in this study base our premises on the least probable of the evolutionary theories, that of Lamarck and his followers.

Darwin's theory of selection, complemented by modern concepts based on genetic, palaeontological, ecological, ethological and other studies, is regarded by most biologists as giving a reasonable explanation of evolutionary processes and this is illustrated by a variety of well-known publications (e.g. Simpson-1950, Cuénot-1952, Rensch-1959, J. S. Huxley-1960, -1963, Mayr-1963). Weisz (p. 628) states: ". . . while fine details of the theory might well have to be adjusted to possible new evidence, the bedrocks of the theory—genetic variation and natural selection—are likely to be permanently valid descriptions of real evolutionary mechanisms", and Mayr-1963 (p. 185): "Natural selection is not only the keystone of evolution, but one of the most stimulating phenomena to have challenged the human mind". Mayr emphasizes, and probably most modern evolutionists agree with him, that next to natural selection it is the effect of mutations and of new gene combinations, as a result of *gene flow* between populations, which causes animal evolution. (For a recent review of the mechanism of these recombinations, see Simchen & Stamberg).

It is remarkable to note that Darwin himself was probably less Darwinian than most modern biologists. This may be illustrated by some examples. The first is a quotation from "The Expression of the Emotions in Man and Animals" (p. 354) ". . . there are no grounds for believing that any muscle has been *developed* or even *modified* exclusively *for* the sake of expression. The vocal and other soundproducing organs seem to form a partial exception; but I have elsewhere attemped to show that these organs were first *developed for* sexual purposes, in order that one sex might call or charm the other." (italics by the present author). The second can be found in the above mentioned article of Semon, according to whom Darwin expressed himself in favour of a Lamarckian explanation of the callosities. The same is reported by Vallois-1967 (p. 2177) with regard to Darwin's ideas about the reduction of the human jaws and teeth in relation to the change of diets in ancestral man, and by Mayr-1960 (p. 350) and -1963 (p. 165) with regard to ecological influences. Elsewhere too, Darwin discusses organs . . ."constructed for the purpose of . . ." (Mayr-1960, p. 362, and "The Descent of Man", p. 87 and 89). He accepted even inheritance of acquired characters (Greenberg).

In recent years too we find some writers unable to accept organic evolution of this kind.

Romer-1948 (p. 4) for instance, clearly expresses doubts: "Much seeming orthogenesis* may thus be explained through mutation and selection. There are still however many puzzling facts; and we are far from a complete and satisfactory solution to all of our problems of vertebrate evolution". And Dobzhansky-1963: "more than a century after Darwin, the concept of natural selection is still in need of clarification".

Doubts may further arise by the presence of many gaps in the fossil record. Indeed a real phylogenetic series can only be proved by a complete palaeontological series, and this is seldom available (de Beer, Bettenstaedt). Lever records the sudden appearance of the major groups of invertebrate animals in the Cambrian, Romer-1950 (p. 519) that of the Osteoichthyes (bony fishes) and that of the first Amphibia (p. 521). That this evolution should have been saltatory, is however denied by Mayr-1963 and Rensch-1959.

Although from a statistical point of view it might seem that the evolution of man (and other species) is only inadequately explained on the basis of selection, mutation and gene flow (this in view of the relatively short time during which a relatively great number of evolutionary changes in our ancestors must have taken place), in recent years the old, orthogenetic and anthropocentric conception of human evolution has begun gradually to disappear. Most of the recent discussions on human evolution are indeed based on the mechanisms mentioned (Strandskov, Haldane, Tappen-1953, Heberer-1956*b*, Rensch-1959, Dobzhansky-1960, Mayr-1963, Glass, Campbell and many others cited in Chapter 4, § 9). Spuhler-1959 and Dobzhansky-1968 emphasize that the mutation rate of human genes is not higher than that of other species, though in modern man it might rise as a result of the increased number of mutagenic agents, such as ionizing radiation and various chemicals (Dobzhansky-1960).

Whether we need to resort to more materialistic or more metaphysical explanations, we shall not attempt to discuss in detail here. For this study it is sufficient to follow the generally accepted line from fish through amphibians, reptiles and mammals up to man (Figure 3, p. 18). For more information the reader is referred to the works of Simpson-1950, Rensch-1954, -1959, Mayr-1963, J. S. Huxley-1963, Heberer-1949, -1956*b*, Romer-1950, -1966, or to any other of the great number of publications on this subject.

2. *ONTOGENY*

The mechanism of the development of each living individual has always been and remains a great mystery. If we limit ourselves to the vertebrates, we start once again with Aristotle who was the first to make accurate descriptions of his observations on chicken embryos. He saw that different organs appeared at different times and that the embryo gradually developed the shape of a chicken. He considered the heart "the first to live and the last to die" (Singer, p. 35). This could be the first mention of the idea of the low vulnerability of ontogenetically and phylogenetically early structures. According to T. S. Hall, the first after Aristotle to make similar observations was the Dutchman Coiter in 1572, but nevertheless the theory of "preformation", according to which the individual is present in its final shape in the egg or spermatozoon as suggested by Swammerdam (T. S. Hall), was accepted for a long time, even after van Leeuwenhoek in 1674 initiated the techniques of microscopy. (The date is usually given erroneously as 1675 or 1676—see Schierbeek, p. 58). After the detailed, descriptive, morphological embryology of the 19th century of which C. F. Wolff was the important founder (Dankmeijer), there came experimental embryology, introduced by Pflüger, His, Roux and Spemann (T. S. Hall).

After Aristotle, who may have foreseen the first of the laws listed below (Hardy-1965), it was probably von Baer in 1828 who first described the ontogeny of several different animals and found relationships between them. From his accurate observations came the following "laws" (rendered by T. S. Hall):

1. The more general characters of a large group of animals appear earlier in their embryos than the more special characters.

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* The term orthogenesis according to Overhage-1959 was first used by Eimer meaning *Zielgerichte Entwicklung*, evolution seemingly heading towards a certain form, "straight-line-evolution". A classical example seems to be the evolution of man; however its validity has never been proved. For a recent and critical discussion of orthogenesis, see Heberer-1956*b*.

2. From the most general forms the less general are developed, and so on until finally the most special arise.
3. Every embryo of a given animal form, instead of passing through the other forms, rather becomes separated from them.
4. Fundamentally, therefore, the embryo of a higher form never resembles any other form, but only its embryo.

Though nowadays a few exceptions are known (Rensch-1959), von Baer's "laws" are generally accepted as reliable rules applying to most vertebrate embryogenesis. In the 20th century modern genetics, microscopy and biochemistry have provided new evidence of the mechanism of embryogenesis, which is nowadays thought to be regulated both by inherited internal factors, present in the egg protoplasm and the chromosomes, and by a number of external factors of a physical and chemical nature.

3. *RELATIONSHIP BETWEEN PHYLOGENY AND ONTOGENY.*

The idea of parallelism between these two processes seems first to have been described by Harvey in 1645, by Meckel in 1811 and by Serres in 1824, although they did not assign the same meaning to the word phylogeny as we do today; in 1850 Agassiz added to Meckel-Serres law, changing it into the "law of parallelism" between systematic classification, embryonic development and palaeontological succession (de Beer). Nobody could give any exact picture of this parallelism however, or suggest how it worked except von Baer. His laws threw some light on the problem and in 1828 he stated (p. 224): "Die individuelle Entwicklung der höheren Thierformen durchlauft nicht die ausgebildeten Formen niederer Thiere": the individual development of higher animals does not pass through the adult forms of lower animals. It is apparent that von Baer had become interested in this problem even earlier, because on p. 202 he mentions he had already doubts about it in 1825.

Nevertheless Haeckel in 1866 (p. 500), apparently ignoring von Baer's observations, launched his famous "biogenetic law", according to which *ontogeny is a short recapitulation of phylogeny and phylogeny is the mechanical cause of ontogeny*. It cannot be denied that Haeckel greatly stimulated the study of biology, but the "biogenetic law" has caused much confusion. During his lifetime and since his death this "law" has been so severely criticized that it seems hardly necessary to add to the criticism here.

It is usually felt nowadays that the "biogenetic law" is a

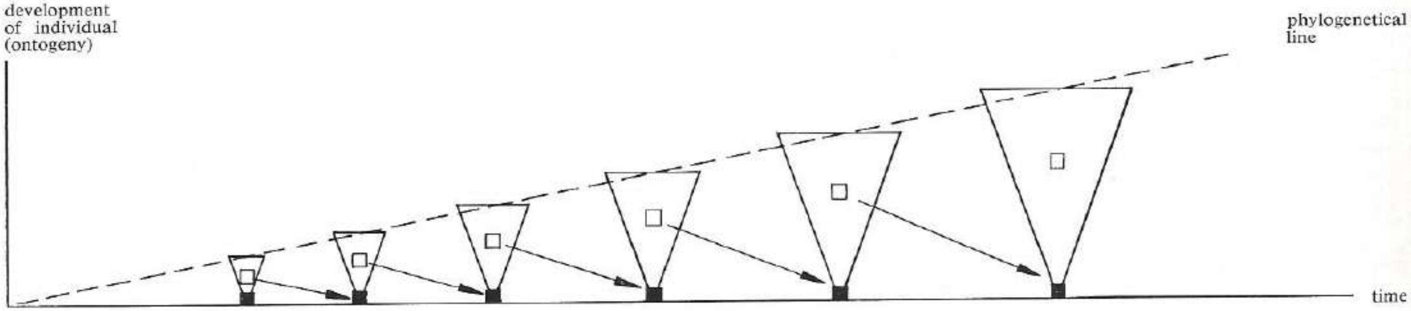

FIG. 1.
Diagram illustrating the relation between ontogeny and phylogeny of successive species. Each triangle represents the development (ontogeny) of an individual genotypically different from its ancestors and its descendants; each white square represents a sex cell; each black square represents a fertilized egg (zygote).

mistaken generalization, even though Zimmermann stated that applied to botany it holds good in 80% of cases examined by him. For a detailed discussion the reader is referred to Kingsbury, Garstang, Sewertzoff-1928, -1931, Jezhikov, Lebedkin, Kryzanowsky, Rouvière, Remane-1956*b*, de Beer and Smit and, so far as the evolution of behaviour is concerned, to Tinbergen-1951.

Objections to the "biogenetic law" may be summarized as follows. In sexually reproducing organisms the only influence exerted by phylogeny over ontogeny consists of the production of a fertilized egg cell by a male and a female of the preceding generation. To Haeckel phylogeny meant "the chain of manifold animal forms which represent the ancestry of an organism, *i.e.* the phyletic line of succession of adults" (Garstang). But do these adult forms really constitute a chain, a continuity, a line? According to de Beer (p. 170) "phylogeny is provisionally to be regarded as a series of adult forms, which are disconnected and causally unrelated to one another, each adult form being the result of an ontogeny which differs from the previous one". This concept is illustrated in Figure 1, partly based on Garstang, who summarized the matter as follows: "ontogeny does not recapitulate phylogeny: it creates it" (p. 82).

Similarly, the evolution of an organ, as it must have happened during human phylogeny and which for reasons of simplicity we shall call in this study the "phylogeny of the organ", may be illustrated in a comparable diagram (Figure 2).

From the fact that the "phylogenetic line" in Figures 1 and 2 is drawn as ascending, it could be inferred that descendants should necessarily be considered more highly developed than their ancestors. This, however, is not true, because words like *higher* and *lower* used in relation to the development of animals only have a relative value (Franz-1920, J. S. Huxley-1958, p. 452 and -1963, p. 556, Greenberg), and such usages are often the result of a subjective and anthropocentric way of thinking.

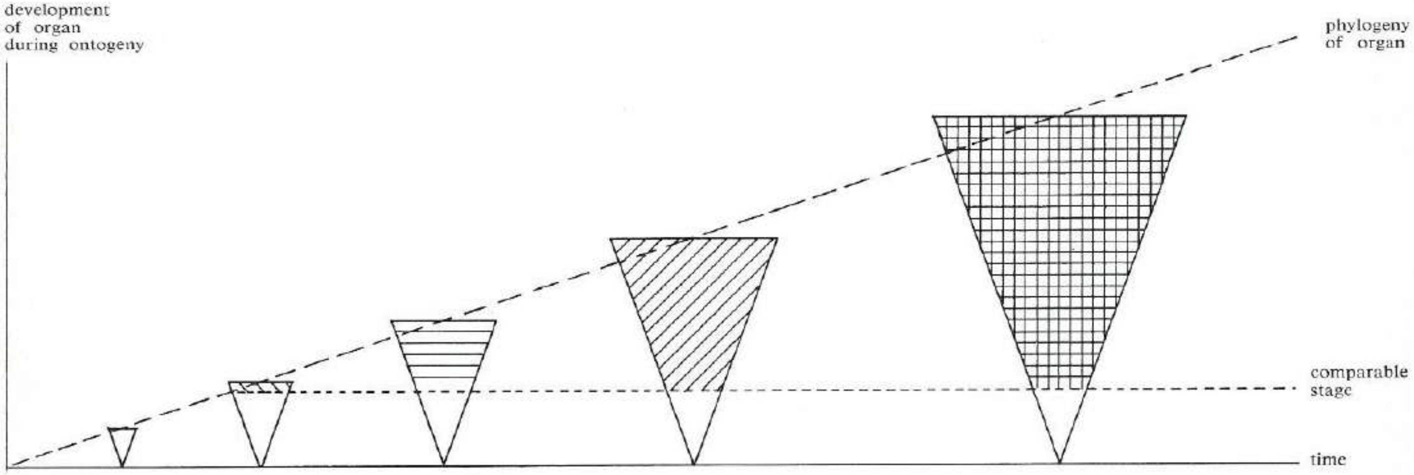

FIG. 2.
Diagram illustrating the relation between comparable organs during their development in individuals (ontogeny) of a seccessive series of phylogenetically related species. Each triangle represents such an ontogeny in these species. The different shading of the areas above the line labelled "comparable stage" indicates that after a more-or-less common stage the organ in each individual develops in the way typical of its species.

Attempts to define these meanings have been made, for instance by Wurmbach-1962, p. 62: an organism may be considered higher when it is able to make use of its environment better than its predecessor by means of changes in its anatomy and extension of its senses and influences, or when it is able to conquer new ecological niches (*Lebensräume*). Overhage-1957 and Rensch-1959 (p. 281-299) also use this criterion, the latter author providing an extensive discussion on the whole problem in the course of which he mentions still other factors. Nevertheless, defining lower and higher in this context remains difficult; for instance the question remains open as to what exactly is meant by "making better use of environment". Therefore when in these two diagrams phylogeny is illustrated by a series of triangles of increasing size, it is not because we are convinced that the final product, in this case man, has reached a higher level (*Vervollkommnung*) than his ancestors. It is only to indicate that there must have been a change in most morphological and functional characters during the evolution from "lower" forms towards man, and to adopt common usage, according to which, for example, protozoans are called lower than mammals.

The diagram in Figure 2 was composed from a theoretical point of view, but is only applicable to organs that are *homologous* in different species, which means that they must have been proved (1) to originate from comparable embryological structures, (2) to show a similarity in topography, and (3) to possess reliable phyletically intermediate forms (Remane-1955). It has only been realized in recent years that in a number of cases anatomists have been misled by observing only the adult forms of different animals, since it has transpired that seemingly similar organs with similar functions could have an entirely different ontogeny in different species, probably because of the interaction of form and function. From the point of view of the present study too, we must remain aware of homology, since it is entirely possible that seemingly similar parts of the adult functioning larynx may have a different ontogeny in different species.

Consequently for a valid comparison the complete ontogeny of each animal in the series should be available. For the present study this has not been possible, although it would have been of great importance and interest. For a detailed discussion of the value of comparative anatomy and embryology, see de Beer's chapter on embryology and homology.

Thus because the commonly known phylogenetic line does not show real continuity, it is to some extent an artificial construction. Why, then, is it frequently taken to show the development of certain species or their organs, as it is here with the larynx?

In our case there are three reasons. (1) Because the larynx could be called a mirror in which many properties of the owner are reflected. (2) Because it is interesting from a functional—ethological and physiological—point of view to see how the adult, functioning larynx has altered in the course of evolution. (3) Because Haeckel's "law" still has so much influence on people's thinking, even that of biologists, that it seemed useful to check which parallels are really there, so far as the larynx is concerned.

Some examples from the literature issued more than 60 years after Haeckel's publication may illustrate this third statement. When investigating the phylogeny of bill morphology in certain birds, von Boetticher (1928, p. 550) bases his study on the ontogeny of these species. Böker & Pfaff (1931, p. 539-540) attempt to prove the presence of tree-climbing in the early mammals, basing their views on ontogenetic observations of embryonic tree-shrews. Groth (1937) in a discussion of the mastoid process, derives evidence from the late appearance of this structure in man's ontogeny for its late appearance in his phylogeny. Basing his arguments on the biogenetic law, Stein (1942, p. 46) expects to find traces of the development of speech in evolutionary time in that of the growing child. E. Frey (1955) derives evidence from the ontogeny of the optic nerve and optic chiasma for their morphology in the primitive ancestral vertebrates, mentioning the biogenetic law. Balinsky (1961) explains ontogeny with Haeckel's concepts, although it must be admitted that he writes that "ontogeny is a shortened and modified recapitulation of phylogeny". An Haeckelian method of embryogenesis is suggested by Spatz (1958) in regard to the development of the human brain and by Duke-Elder (1958, p. 239) who seeks evidence for the evolution of the vertebrate eye in its ontogeny. The concepts of Negus-1929, -1949, -1962 about the phylogeny and ontogeny of the human larynx, which also give the impression of favouring recapitulation in an Haeckelian sense, are discussed in Chapter 4. N. Geschwind (1964, p. 165) supposes that "much of the human brain is evolutionarily late since it matures so late in the life of an individual". Mägdefrau (1966) in his botanical studies attempts to prove the validity of the biogenetic law.

Many of the differences between the ontogeny of different species may be classified according to the stage during which comparable characters appear. When, as is often the case, they do not appear at the same stage the term *heterochrony* is applied. We shall follow de Beer in his classification of eight different kinds of heterochrony, illustrating them with some examples. For a more recent but shorter discussion of the problem of the relationship between ontogeny and phylogeny, the reader is referred to Remane-1956*b*, to Rensch-1959 or to Starck-1965*a*, all of whom give a somewhat different classification of heterochrony.

1. CAENOGENESIS

Characters, which are present or make their appearance in the young stage of an ancestral animal, may appear in the ontogeny of a descendant in the young stage without affecting the phylogenetic adult series. For instance the mammalian lungs develop first as solid masses of mesenchyme into which later the typical epithelium and blood vessels grow. However, according to Haeckel's views, the lung could be expected to develop as a simple saccular organ lined with epithelium and bloodvessels.

2. DEVIATION

Characters, which are present or make their appearance in the young stage of an ancestral animal, may appear in the ontogeny of a descendant in the young stage but become changed in the adult stage, thereby producing a substitution of a new adult condition for the old. This results in progressive deviation in the ontogeny of the descendant from that of the ancestor. These cases are covered by von Baer's third law. An example is the gill-slits, better called visceral pouches, which are present in the same form in embryonal fish, amphibians, reptiles, birds and mammals, but which develop into gills in fish and in some amphibians only, and into other structures like the Eustachian tube, thymus, etc. in other classes.

3. NEOTENY

Characters, which are present or make their appearance in the young stage of an ancestral animal, may appear in the ontogeny of a descendant in the adult only as the result of a relative retardation of the development of the bodily structures as compared with the reproductive organs, resulting in so called neoteny. This process was called paedogenesis by von Baer-1866, proterogenesis by Schindewolf-1936, -1937 and foetalization by Bolk-1926*a*, -*b*, -1929*. A classical example is the Mexican amphibian *Ambystoma mexicanum*, the larval form of which (the axolotl) is nevertheless able to reproduce. According to Cuénot-1945, -1952 neoteny plays an important role in vertebrate evolution and, according to Bolk-1926*a*, -1929, de Beer, Montagu-1962*b*, Coon and Campbell, it must have played a part in human evolution as well. In several respects human beings, both children and adults, bear resemblance to the foetal forms of many other mammals. This applies to the relative size of the head, the relatively large amount of brain, the localization of the foramen magnum, the cranial flexure, the late closure of the skull-sutures, the dentition, the flatness of the face, the position of the vagina, the position of the big toe, the scanty distribution of hair, the light colour of the skin and other characters (see Montagu-1962*b*).

4. REDUCTION

Characters present in the young and adult stages of an ancestor, may appear in the young stage only in the ontogeny of a descendant, resulting in the reduction of the character to a vestige. Classical example: the disappearance of the tail of the frog tadpole. (One might add the hind limbs of foetal cetaceans, Slijper-1962, an example of both deviation and reduction). The phenomenon of reduction is in accordance with von Baer's observations.

5. ADULT VARIATION

Characters, which are present or make their appearance in the adult stage of an ancestor, may appear in the adult stage in the

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* According to Swingle the choice of the word *neoteny* is unfortunate, because it has come to be associated exclusively with sexual maturity in the larval stage, in which sense Kollmann was the first to use the word. Literally it means prolongation of the period of youth, and this is how it is used by many authors. Rensch-1968 also points out the problem of the definition of the word neoteny. In the literature several authors criticize the importance which Bolk and de Beer credit to neoteny (Ewer, Slijper-1936, Overhage-1959, Mayr-1963, Smit, Starck-1962, -1965*a*). It is beyond the aim of this study to discuss this problem. We shall use the word neoteny in de Beer's sense, as defined above, without considering it as a mysterious driving force or a general principle active in the evolution of all human characters, as suggested by Bolk. See pp. 76 and 77.

ontogeny of a descendant, resulting in those usually small differences which distinguish individuals, varieties, and races. Adult variation is in fact a special case of deviation.

6. RETARDATION

Characters which are present or make their appearance in the adult stage of an ancestor, may appear too late in the adult stage in the ontogeny of a descendant and so result in the reduction of such characters to a vestige by retardation. The human third molar erupting too late or not at all may be called an example of retardation.

7. HYPERMORPHOSIS

Characters, which are present or make their appearance in the adult stage of an ancestor may appear at the same stage in the ontogeny of a descendant. But if this is no longer the adult, the end of the adult stage being relatively delayed, the condition results in "overstepping" the previous ontogeny, which can be called hypermorphosis. For instance the lengthening of the young gibbon's arms reflects the lenghtening that must have occurred in the phylogeny of gibbons from ancestors with arms of normal length.

8. ACCELERATION

Characters, which are present or make their appearance in an older stage of an ancestor, may appear at a younger stage in the ontogeny of a descendant, producing precocious appearance of the ancestral character, or acceleration. This phenomenon thus *resembles* Haeckel's recapitulation, although Haeckel meant recapitulation of the *complete* adult ancestor. Acceleration can be illustrated by precocious formation of the heart in the chicken embryo (as described by Aristotle, see p. 6) and by the appearance of the human amnion, extra-embryonic coelom and allantoic mesoderm before that of the embryo itself, whereas in lower mammals this sequence is reversed.

4. *CONCLUSIONS*

The relations between phylogeny and ontogeny are not so simple as Haeckel supposed: there is repetition but seldom of adult shapes. In the following chapters we shall try to find out what relations exist between the phylogeny and ontogeny of the human larynx and how they can be classified.

A few words should however be said about the material and methods of investigation.

As explained on p. 6 a real picture of the phylogeny of man would be given by a complete palaeontological series. This, however, is very difficult to obtain: there are many gaps in that part of the phylogeny which interests us here, *i.e.* the period after the appearance of the fish. Especially in regard to the evolutionary history of the primates, to which man and his direct ancestors belong, are we poorly informed. These species being mostly arboreal, they rarely provide fossil specimens, presumably because of the forest's soil acidity (Le Gros Clark-1962, Mayr-1963, Romer-1966).

A second difficulty arises from the properties of the organ under consideration: the larynx is mainly composed of tissues not likely to produce the fossil evidence necessary for a reliable description of its development during the course of millions of years. The hyoid alone is bony in a number of species, whereas in the laryngeal skeleton proper of animals which may represent human ancestors, only partial ossification has been described in the thyroid cartilage of the gorilla (Raven) and of the chimpanzee (Starck & Schneider, p. 460), comparable with that in man. So, if our ancestors really did have bone in their laryngeal skeletons, they must have produced loose pieces unsuited to comparative morphology. The only direct palaeontological information in regard to the larynx may possibly be given by the stylohyoid process, which can give some indication as to the site of the hyoid and hence of the larynx.

Another pitfall in consideration of the phylogeny of respiratory organs is the substantial changes which have occurred in the atmosphere since the first appearance of air-breathing creatures: the oxygen content has probably doubled over the last 300 million years (Vangerow). This circumstance necessarily implies differences in morphology and/or function between modern animals and ancestral ones.

So it is clear that an exact picture of the phylogeny of the human larynx cannot be given; one can only suggest probabilities. Firstly, evidence comes from palaeontology which, on many grounds which cannot be discussed here in detail, points to evolution from fish through amphibians, reptiles and lower mammals up to man. Secondly, several representatives of groups through which evolution probably ran still exist, some of them only slightly changed. So by extrapolating the facts obtained from studying these representatives (by means of comparative anatomy and physiology) and fossils (by means of palaeontology) one can form a concept of a species' phylogeny, though Tinbergen-1962 (p. 2) rightly states: "The speculative element here lies in the fact that we 'translate' *differences between present-day species* into *changes of time*". Inquiries into animal behaviour during evolution may be based on the same methods, though with a somewhat greater risk of failure (Tinbergen-1951).

As to ontogeny, we encounter fewer difficulties, because a series of human embryos from about 3 mm in length, and anatomical specimens from older human beings, give a good picture of the development of the larynx of a human, the only source of uncertainty being possible individual variation. (In this study we use the word ontogeny in Kryzanowsky's sense: development from the fertilized egg cell to death. For a detailed discussion of the definition of the word ontogeny, see Smit).

CHAPTER 2

Phylogeny of man, with special reference to the larynx

1. *INTRODUCTION*

In this chapter we shall attempt to describe the main features of evolution from the lower vertebrates up to man. In so doing, as mentioned in the first chapter, one frequently meets enigmas and probabilities rather than facts. However, modern sciences have given sufficient evidence to assume that the picture rendered below is a fairly reliable one. Problems are mainly caused by gaps in the known phylogenetic series and doubts about the sequence of the species composing it.

The next difficulty concerns the starting point of our own series, lost in the misty dawn of vertebrate evolution, 300 million years ago, in the search for which it will be understood that the organ commonly called the larynx is not easily defined. So a short review of the palaeontological data is given in this chapter.

The evolutionary development of the larynx has been the subject of previous publications which either covered only some steps of the ladder of evolution, or else only parts of the matter, or did not follow the phylogenetic line, dealing only with comparative anatomy and physiology. Gegenbaur-1892, -1901 and Negus-1924, -1929, -1949, -1962 seem to be the only ones to discuss the matter more-or-less systematically. It therefore seemed useful to reconsider the whole problem independently of previous observations; indeed in several respects our own observations and discussions lead to conclusions different from those of the authors mentioned above. A short review of the available literature will be given in Chapter 4.

2. *DEFINITION OF LARYNX. LUNGS AND SWIM-BLADDERS*

In higher vertebrates the definition of the larynx offers no difficulty: it is the organ located in the ventral part of the pharynx around the oral opening of the tube, the trachea leading towards the lungs.* But in fish we meet difficulties caused by questions of *homology*: in the majority of bony fish we find hollow organs, often communicating with the pharynx, filled with air or gas, which in most species are called *swim-bladders*, but in some *lungs*, because they are supposed to be homologous to the lungs of higher vertebrates. Now it is clear that structures surrounding the opening in the latter group are commonly called laryngeal, whereas those of the first group are not. In point of fact no distinct borderline can be drawn between these groups. About the differences between lungs and swim-bladders and their evolution there has been much discussion, which we shall not follow in detail here. The reader is referred to the thorough work of Marcus-1937, and to the more recent one of Ballard; and, as far as the air-breathing organs and swim-bladders in fish are concerned, to Carter or Bertin, and to Denton, respectively.

As to the origin (phylogeny) of both these organs, there are 4 possibilities.

(1) Both evolved independently from non-homologous structures, showing convergence towards similar anatomy and physiology (Thomson cited by Barell, Brien & Bouillon, Bertin).

(2) Lungs evolved from swim-bladders, as one could easily assume after comparing the developmental level of

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* Though other structures in this region are also morphologically and functionally interesting, like the hyoid or tongue, we limit ourselves in this study to those structures that are commonly considered to constitute the proper larynx. The word "glottis" we will attempt to avoid in this publication because it is apt to cause some confusion, though according to authorative dictionaries (Dorland) it means "the vocal cords and the opening between them" but the word is sometimes used to indicate other parts of the larynx (Elze).

living species (Bert, Darwin-1875, p. 161, Boas, Wiedersheim-1886, Merkel cited by Marcus-1937, Krogh, Prosser-1950, Negus-1949, -1962, Bryan); palaeontology, however, fails to prove this hypothesis.

(3) Both evolved from homologous structures, as concluded by various authors, e.g. Parker, Gegenbaur (cited by Marcus-1937), Marcus-1937, and Ballard after elaborate studies in comparative anatomy and embryology.

(4) Swim-bladders evolved from lungs, probably first suggested by Sagemehl in 1885 and later by Kerr-1909-b, Barell and Jaekel; this possibility is mentioned more recently by Torrey, Eaton, Kuhn-Schnyder, Carter, Romer-1950, -1966, Mayr-1960, -1963 and Schmalhausen, and is favoured by the palaeontological data, as explained below.

Because palaeontology, supported by comparative anatomy and embryology, seems to give the most reliable evidence for tracing a phylogenetic line, we shall assume the last hypothesis. The characteristics of both organs may be summarized in a table (next column).

3. *SHORT REVIEW OF VERTEBRATE EVOLUTION*

The evolutionary history of the vertebrates probably begins in the early Ordovician, some 500 million years ago, when from simple sea-dwelling creatures (Amphioxus-like?) animals evolved, possibly by means of neoteny (Young, Teilhard de Chardin-1955, Romer-1958b, Mayr-1963), which may have been the ancestors of the vertebrates. The latter seem first to have appeared more than 100 million years later, in the Silurian, (*cf.* Figure 3, p. 18).

The first known vertebrates were jawless fish, called *ostracoderms* (covered with bony plates), and thanks to Stensiö we are well informed about these fossil Agnatha. They appear to be closely related to the modern jawless fish, the hagfish and lampreys, forming the Class Cyclostomata. These first vertebrates probably lived in fresh water, only later migrating to seawater (Barell, Kuhn-Schnyder, Romer-1958a, -1966). Denison, on the other hand, introduces arguments favouring a marine origin for the early vertebrates.

character	*lungs*	*swim-bladder*
number	mostly paired	mostly single
habitat of animal	aquatic and/or terrestrial	aquatic
function	mainly respiratory	mainly hydrostatic
contents	air	air or gas
blood supply	6th branchial artery	dorsal aorta
position in body	dorsal in aquatic species, partly dorsal in terrestrial species	dorsal
communication with pharynx	ventral, with specialized structures	absent or dorsal, with no specialized structures
phylogenetic relationship	probably older than swim-bladder	probably evolved from lungs
ontogeny	derivative of foregut	derivative of foregut
nerve supply	vagus	vagus
histomorphology	in most species seemingly suited to gas exchange.	in most species seemingly unsuitable for gas exchange.

(It may be noted that the difference between fresh and salt water in those days was probably somewhat smaller than it is nowadays, owing to the steadily increasing amount of ions in the sea since the cycle of the water in the atmosphere began).

Oxygenation took place, and in almost all vertebrates still does take place, mainly by means of the *branchial system* (or its derivatives), whose basic structure consist of a number of paired "segments" in the anterior, lateral and partly ventral regions of the body, each containing a rod of supporting tissue (cartilage or bone), an afferent and an efferent blood-vessel, and two nerves. In this system close contact is possible between the oxygen-containing environment and the body fluids of the animal. We shall see that the branchial system played an important* role in vertebrate evolution.

From the ostracoderms originated the *placoderms* in the Silurian, fish in which the anterior segments of the branchial system had evolved into primitive *jaws*. Although these animals are now extinct, their class is interesting in that it gave rise to all other vertebrates except the Agnatha. Moreover they are important to the present study, because amongst others, Romer-1966 and Schmalhausen suggest the probable existence of *lungs* in these early bony fish which enabled them to survive the dry periods of the Devonian. Whether the placoderms, when in water, used their lungs as respiratory organs or as hydrostatic organs is obscure. They certainly had an extensive branchial system (Stensiö), but even if we assume that their metabolism would be comparable to that of modern vertebrates, their oxygenation may have been hampered by lower oxygen levels in their environment, such as is likely to have existed in the Devonian (see p. 11).

From the placoderms originated the Actinopterygii, to which most modern bony fish belong, and the *crossopterygians* (sometimes called Choanichthyes) fish which are of greater importance to this study because they probably provide a link in the evolutionary chain towards the land-dwelling vertebrates. It should be remarked, however, that their choanae (internal nostrils) are probably not homologous with those in higher vertebrates (Arambourg & Guibé, Atz, K.S. Thompson, Schmalhausen).

To the Crossopterygii belong the Dipnoi (lungfish) and the Coelacanthini**, both of which have succeeded in surviving 300 million years in approximately the same form. Until some years ago the Coelacanthini were known only as fossils, but recently a few living specimens have been captured in the Indian Ocean called *Latimeria chalumnae*. Because their skeleton bears a striking resemblance to that of the tetrapods, the Crossopterygii are believed to form a link between fish and amphibians (Dollo, Romer-1966, Schmalhausen). A relationship is also suggested between modern lungfish and amphibians because of similarities in the pituitary and the endocrine pattern (I. I. Geschwind, Janssens-1964*a*, Kerr & van Oordt, van Oordt & Kerr).

The first *amphibians* appeared at the end of the Devonian, being able to stay longer and move more freely on land than their ancestors, although they still need aquatic surroundings for reproduction and to prevent the loss of too much water through their skin. According to Kuhn-Schnyder only the modern salamanders approximate in morphology to the early amphibians which were, however, much larger. For the rest, all existing species have changed considerably compared with their Devonian ancestors. Exact classification of these fossil amphibians is not yet possible, but the evolutionary line towards the reptiles probably runs through the *Labyrinthodontia*, whose descendants are also believed to have given rise to the modern Anura, such as frogs and toads. More information about the evolution of the amphi-

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* A problem I would like to draw attention to is that caused by using terms like "important" etc. in discussions of organic evolution which introduces a *prospective* element in our considerations, where necessarily they should bear a *retrospective* character. As Davis (p. 213) says: "Phylogeny looks orderly and purposive, like the unfolding that the word "evolution" implies, but actually it looks purposive only in retrospect". Moreover it introduces a suggestion of a human influence on a course of events which is clearly out of the grasp of man. One would be happy if the point had been reached, where one were able to deduce, from the rather static picture of modern man and some scanty indications from palaeontology, the course of events which led to the highly complex picture of numerous interacting facets, which together constitute the mosaic of the final stage of the phylogenetic series which concerns us here: that of man. Students of evolution are, however, only able to discover some of the elements which may have been involved in its course, and to base on these an attempt to describe the events on which man could only exert an influence, after his mental capacities had reached a level never before seen in the course of organic evolution. Properly speaking all the factors are of equal importance, since each factor, merely by its discovery, must necessarily be considered indispensable to human evolution. From our point of view we can only guess, what would have happened if one of the "important" factors had not been able to exert its influence. But since we are only able to observe these events from our point of view, we attempt to reproduce suprahuman meanings in human ones. Only when we are aware of this situation are we perhaps allowed a modest use of these terms.

** The taxonomic position of actinopterygians, crossopterygians and lungfish is still a matter of debate, and four different classifications are rendered here as given by four different workers in this field: *(ctd. p. 16)* bians is given by D. M. S. Watson-1926, -1940, and Romer-1950, -1966.

One step further in evolution appears a *reptile*-like animal developing from the above amphibians 250 million years ago, in Carboniferous times, called Seymouria which, together with the other members of its order, the Cotylosauria, constitute the starting point of the Class Reptilia (D.M.S. Watson-1918). They were less dependent on water than their ancestors, but on the other hand appeared well able to adapt to aquatic surroundings (Darwin, cited by Peterson, found that one of the great lizards of the Galapagos Isles was able to survive submersion for over an hour). The reptiles developed further in several respects of their anatomy and physiology (skeleton, circulation, water-metabolism) occupying such different habitats as land, water and air during 150 million years, after which they had to yield to the mammals. From the earliest reptiles (only known as fossils) lines probably branched off in the Carboniferous or Permian towards numerous reptiles, both living and extinct (and also the birds), and a line leading to the mammal-like reptiles, all extinct (Colbert).

But no direct descendants of the Cotylosauria remain amongst modern reptiles. The Rhynchocephalia, to which *Sphenodon* (the Tuatara) of New Zealand belongs, and maybe the Crocodilia more or less resemble the earliest reptiles, amongst other things because their roots can be traced back as far as the Triassic.

Mammals are considered to be higher animals because of their homoithermy, cerebral functions, their way of protecting and feeding their young, etc. Their origin is still obscure,

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Continued from p. 15

Grassé 1958 (*ed.*):

- Subphylum Gnathostomata — Superclass Pisces — Class Osteichthyes
  - Subclass Actinopterygii
  - Subclass Crossopterygii
  - Subclass Dipnoi

Norman:

- Class Pisces
  - Subclass Actinopterygii
  - Subclass Crossopterygii
    - Order Actinistia
    - Order Dipnoi
    - Order Rhipidistia

Romer-1966:

- Class Osteichthyes
  - Subclass Actinopterygii
  - Subclass Sarcopterygii (= Choanichthyes)
    - Order Dipnoi
    - Order Crossopterygii — Suborder Coelacanthini (fossils and *Latimeria*).

Young:

- Superclass Gnathostomata
  - Class Actinopterygii
  - Class Crossopterygii
    - Order Rhipidistia — Suborder Coelacanthini (fossils and *Latimeria*)
    - Order Dipnoi

For more details of lungfish phylogeny, *cf.* Dollo, Westoll-1943, -1949 or Schaeffer.

though the general conviction is that it has to be sought in early reptilian forms such as the Triassic Therapsida (Starck-1965*a*, Colbert, Thenius). Most probably the mammal-like reptiles and the mammals hardly succeeded in maintaining themselves in the shadow of the successful reptiles and only got their chance after the extinction of giants like the dinosaurs at the end of the Cretaceous, 70 million years ago.

The monotremes and the marsupials resemble in many features the primitive Jurassic and Cretaceous mammals, but on the other hand have in many respects evolved in their own way. All the other living mammals, Placentalia or Eutheria, probably originated from small shrew-like Jurassic or Cretaceous insectivores (Thenius & Hofer, Hofer); for a discussion of the evolution of the insectivores, see Saban or McKenna. The line towards man is then supposed to take its course through the Order *Primates*, most of whom are characterized by an arboreal habitat and a relative large brain size.

The Tupaiiformes may be considered the simplest primates (Le Gros Clark-1924*a*, -1924*b*, -1926, -1962); the tree-shrews are the living representatives. They probably originated in the Palaeocene (Remane-1956*a*, Fiedler, Patterson, Teilhard de Chardin-1955), or later in the Eocene or Oligocene (Young). In the last few years they have been classified by most authors in the primates and it has even been proposed that they should be put in a special suborder, the "Stirpisimiae" (Broers), although this kind of classification is rejected by Osman Hill-1953 (p. 25). For a detailed and more recent discussion on primate systematics, see Remane-1961 or Washburn-1963. The next stage in primate evolution came with the origin of the Prosimii, modern representatives of which are, for instance, the lemurs and tarsiers (Woollard-1928).

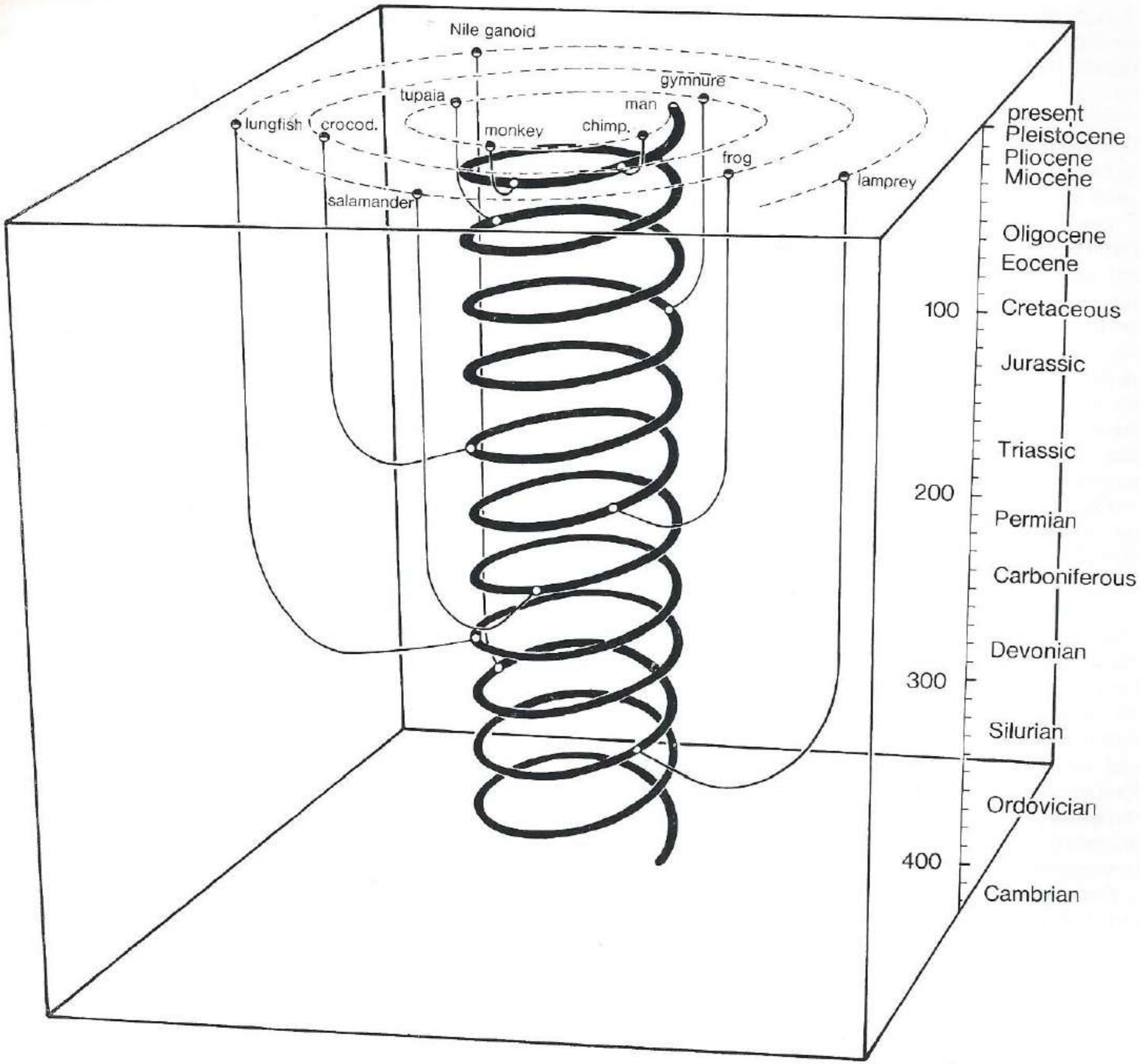
The origin of *man* and his relationship to the other living primates is not yet fully clarified. The old idea of man descending from a modern type ape is now generally rejected. However, there is little doubt that both have common ancestors (Le Gross Clark-1958, -1964, Simpson-1966), one of which was a tree-shrew-like animal. Evidence for this comes not merely from morphology, but also from serology (Goodman-1963, Sarich). Between these primitive Cretaceous ancestors and the earliest man several links in the fossil record are missing, which anthropologists and palaeontologists suppose to be formed by the Palaeocene and Eocene Prosimii and Anthropoidea. In the latter suborder monkeys, apes and man are classified.

According to Kurtén, the probable sequence and chronology of the evolution of the Hominoidea, the superfamily to which apes and man belong, is as follows: *Propliopithecus* in the early Oligocene, 30-35 million years ago; *Dryopithecus* (to which *Proconsul* belongs, Simons-1963) in the Miocene, 12-25 million years ago; *Ramapithecus* (the earliest member of the Hominidae, the family to which man and his direct ancestors belong, especially studied by Simons-1961, -1963, -1967 and Pilbeam & Simons) in the late Miocene and early Pliocene, 5-12 million years ago; *Australopithecus* (supposed by Leakey-1960, Broom & Robinson, Tobias-1967, -1969, and many others to represent the oldest form most closely related to modern man) in the early Pleistocene, 1-2 million years ago; *Homo erectus* in the middle Pleistocene, a million to $\frac{1}{2}$ million years ago; and *H.sapiens* since $\frac{1}{2}$ million years ago (or maybe even longer, Day).

This short and incomplete review of the essentials of vertebrate evolution and palaeontology is only meant to illustrate the problems met with in this special study. For further details and arguments the reader is referred to some of the sources used in this section: Thenius & Hofer, Kuhn, Kuhn-Schnyder, Romer-1948, -1950, -1966, Mayr-1963 and Young for the evolution of the vertebrates in general, and the Cold Spring Harbor Symposium No. 15 (1950), Fiedler, Remane-1956a, -1961, Le Gros Clark-1962, Washburn-1963, Campbell and Simons-1963, -1967 for the evolution of the primates.

4. *CONCLUSIONS*

From the foregoing we may conclude that the study by comparative anatomy and physiology of existing animals is only of relative value for building up a phylogenetic series, but handled with care it certainly can be used (Figure 3).


Nile ganoid
gymnure
tupaia
man
lungfish
crocod.
monkey
chimp.
frog
salamander
lamprey
present
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
100
Cretaceous
Jurassic
Triassic
200
Permian
Carboniferous
Devonian
300
Silurian
Ordovician
400
Cambrian

For a more detailed discussion of the value of comparative anatomy for tracing a phylogenetic line, see Davis. It is, however, wrong to represent organic evolution as a simple tree, as the old notion had it, whose stem and main branches represent modern "lower" animals and whose upper and smaller branches modern "higher" animals. If one wants to compare evolution with a tree, it must be a particular one: a tree in a flooded country, only the top of which is visible. The greater part remains unseen beneath the surface, indications of its architecture only being found in old, destroyed material occasionally coming up from lower branches in hidden depths. In recent years one has realized that the invisible branches may often lie much lower than had previously been thought.

So each case, where a modern animal is taken to demonstrate events from the past, should be judged on its palaeontological and comparative anatomical merits. Only where there are gaps in the known phylogenetic series, or where the sequence is obscure, may one possibly be allowed to take one organ alone as a guide, since the development of such an organ may only just be representative for the animal as a whole. For instance, it is very probable that during vertebrate evolution there has been a fairly constant increase in relative brain size, and if one therefore composes a random series of modern vertebrates of increasing brain size there would be a chance of these indeed being representative of vertebrate evolution. However, one must be cautious in following this path without regard to palaeontological evidence, as Negus-1949, -1962 seems to have done in regard to the larynx, which does not show such easily assessible parametres like increase in size. Another difficulty can be encountered when observations on a certain organ in a series of modern animals, selected for illustrating a phylogenetic line, do not yield a picture of continuous evolution; in these cases one can try to find such continuity by observing other, related, species of the same class or order.

← FIG. 3.

An attempt to illustrate the relations between man's phylogeny and comparative zoology. The upper surface of the cube represents the present in which direct comparative zoological observations are possible. The contents of the cube represent the past in which no direct observations are possible. At right some of the geological periods are pictured in a time scale indicating millions of years. The real phylogeny of man is indicated by the thick vertically placed spiral; the seeming phylogeny by the dotted horizontally placed spiral in the upper surface as deduced from comparative zoology. (The names here refer to the species described in Chapter 3).

Part 2

CHAPTER 3

Comparative zoology

1. *COMPOSITION OF THE SERIES OF SPECIMENS STUDIED*

As stated in Chapter 2, we have to begin the series of modern animals illustrating the phylogeny of the larynx, with a jawless fish representing the Silurian ostracoderm, a vertebrate without a larynx. Because the modern Agnatha, the Cyclostomata, resemble the ostracoderms, one of them, the river lamprey, *Lampetra fluviatilis*, is taken for this purpose. It may give some idea of the branchial system in these fossil vertebrate ancestors, although the Cyclostomata have changed in several ways, during evolution e.g. their bone has been replaced by cartilage and the adult forms live as parasites on higher fish.

The first larynx is likely to have been present in the placoderms, as they were probably the first animals with lungs. Though no direct descendants of these fish are to be found amongst modern species, the Polypteridae, which are considered to be direct descendants of the earliest Actinopterygii, may possibly give some indication of the situation in the placoderms. For this purpose, one of the two members of the Polypterid family, the Nile ganoid *Polypterus senegalus*, will be considered; it bears so much resemblance to its Palaeozoic ancestors that it is often called a living fossil (Daget, Franz-1924, Schmalhausen).

Next comes a representative of the Choanichthyes, which have probably not changed much during evolution (Brien & Bouillon). Observations on specimens of the African lungfish *Protopterus annectens*, therefore, may provide a picture of the animals which came between the fish and the amphibians. *Latimeria* is more like these animals in most respects, but does not serve very well for our purpose because it has no functioning air-breathing system: its (single) lung has degenerated into a fat-organ (Anthony & Millot, Nevenzel *et al.*). Specimens of *Latimeria* are also very rare and hard to obtain for dissection. Romer-1966 supposes the *Polypterus* lung to be of similar type to that of the typical crossopterygian.

Since the urodeles probably come closest to the earliest amphibians (Kuhn-Schnyder finds resemblance in morphology and D. M. S. Watson-1926 in physiology), the larynx of *Amphiuma* spec. will be described.

Since a reliable modern representative of the labyrinthodonts—the extinct amphibian ancestors of the reptiles — does not exist, *Rana*, the modern frog, is chosen, although little is known about the possible anatomy and physiology of these fossils and their possible resemblance to the modern Anura. In fact the latter show a high degree of specialization in many features, and, as will be seen later in this study, this also applies to their larynx, both from a morphological and a functional point of view. Thus the frog is only chosen for lack of a better representative. The same can be said of the early (fossil) and modern reptiles. Because the crocodiles can be traced back to the Triassic we take one of them, *Osteolaemus tetraspis*. Perhaps *Sphenodon* would have been a better representative, but it is very rare and was impossible to obtain.

The primitive mammals, the monotremes and marsupials, are too specialized, so we prefer to observe the insectivores, which are supposed to be similar to the stem forms of all eutherian mammals (Starck-1965*a*). Of the Order Insectivora the gymnures, such as the moonrat *Echinosorex gymnurus*, small shrewlike animals living in South-East Asia, bear so much resemblance to the earliest, Cretaceous, proto-insectivores (Viret, Grassé-1967*b*, Thenius & Hofer), that they are often called living fossils. To the Lesser gymnure *Hylomys suillus* this statement would apply even more, as it appears to be the most primitive of the 4 gymnure genera

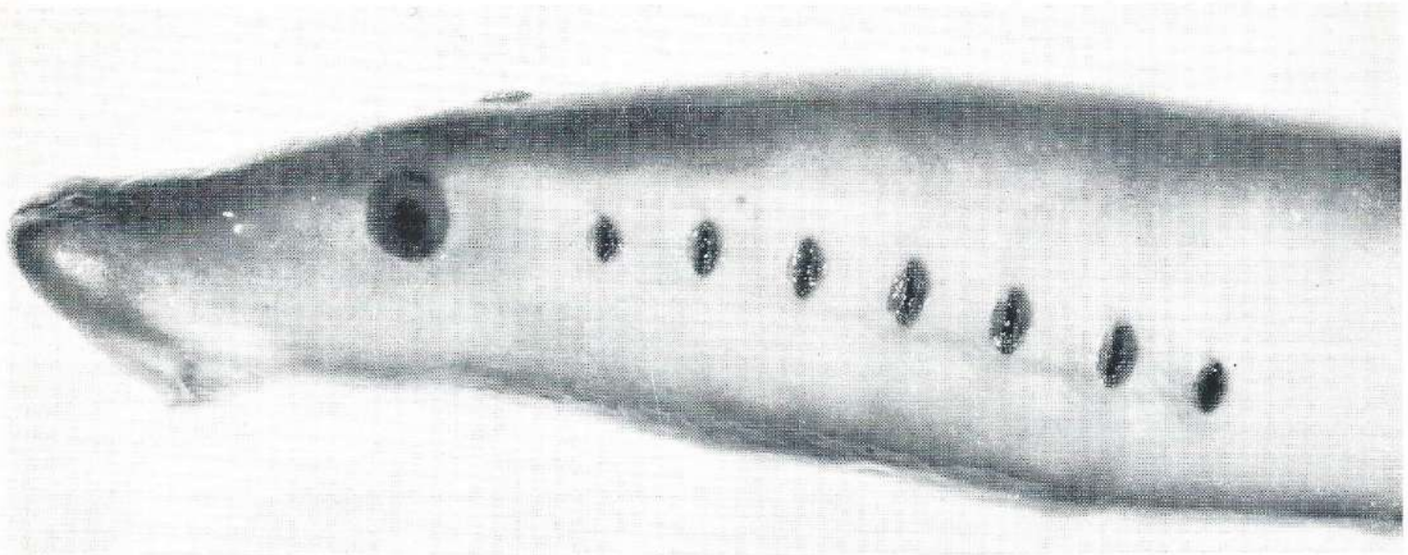
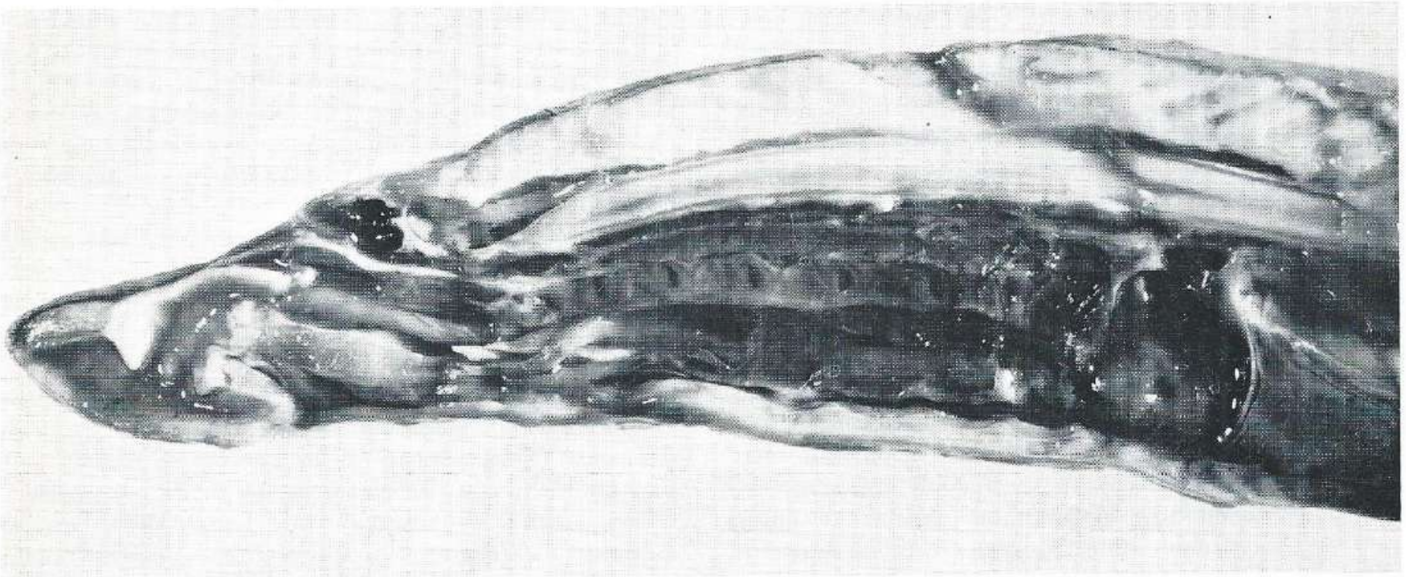


FIG. 4. ↑
River lamprey (*Lampetra fluviatilis*), a primitive jawless fish in many ways similar to the first vertebrates living 400 million years ago. Lateral view of head region, showing the 7 external gill slits. 1,8×.

FIG. 5. ↓
River lamprey (*Lampetra fluviatilis*). Sagittal section of head region, showing the 7 internal gill openings and the absence of an airway. 1,8×.



(Brehm). Other modern insectivores like the hedgehog would also serve the purpose reasonably well because they retain many ancient features (Young, Grassé-1967). Indeed Dobson found the hedgehog larynx to be very similar to that of the gymnure.

The tree-shrew *Tupaia glis* in most characters (and therefore probably also in its larynx) resembles the early primates; indeed Davis suggests behaviour studies of the tree-shrew for further elucidation of human evolution.

As a representative of the early Anthropoidea the Rhesus monkey *Macaca mulatta* is taken, because it belongs to the Cercopithecidae (Old World monkeys or Catarrhina) which probably branched off from the common stem in the late Eocene. Though the taxonomic position of the Old World monkeys in the primate order is not yet established, there are so many fundamental similarities that these monkeys must be considered in any analysis of primate and human evolution (Tappen-1960).

Perhaps the apes are more like the common ancestor of apes and man than man himself, although they doubtless evolved in their own way. According to Keith (cited by Kuhn-Schnyder), von Krogh and von Koenigswald-1955, the chimpanzee *Pan troglodytes* has most features in common with man; this applies equally to its larynx (Giacomini, Kleinschmidt-1938, -1950). Schultz however (cited by von Koenigswald-1955) thinks the gorilla has more features in common with man, and Simpson-1966 supposes both apes to be closely related to man. It seems improbable that the larynx of the direct human ancestors could have shown characters essentially different from that of apes or recent man.

Concerning the larynx of each species we will describe the main features of its anatomy, topography, physiology and (as far as possible) ontogeny. Because of poor quality, histological examination of most specimens was fruitless. As far as physiology and ontogeny are concerned, I had to rely primarily on the literature since mainly adult cadavers were observed. A third limitation is that only a few specimens of each species could be observed, which means that there were few controls on possible individual variation.

2. *RIVER LAPMREY (LAMPETRA FLUVIATILIS)*

A specimen of the river lamprey illustrates the situation in the jawless vertebrate ancestors without a larynx. The anterior part of their body clearly shows metameric division: the branchial system consists of 7 paired gills (Figures 4 and 5) in other Cyclostomata numbering up to 14 pairs, as in *Bdellostoma*. It is supported by a rather complex cartilaginous skeleton. There are no lungs (nor swim-bladder), and hence no larynx. As in other fish, blood is supplied by afferent branchial arteries branching off from the ventral aorta from the heart. Lampreys are purely aquatic animals and so is their respiration.

For more detailed information about the Cyclostomata the reader is referred to Fontaine; and about their embryology to W. B. Scott, Pasteels or Damas. Older publications mentioning the development of the branchial system can be found in the studies of Göppert-1906 and Goette.

3. *NILE GANOID (POLYPTERUS SENEGALUS)*

This species is one of the few which may still resemble the first animals to evolve a larynx, the placoderms. It is called Bichir and, since it inhabits the Nile and its contributaries, the Nile ganoid (Figure 6). After removing the bony-hard ganoid scales and the mesodermal tissues from the dorsum, it is easy to see the 4 paired gill-clefts (Figure 7) and the elongated air-filled organs in the dorsal part of the coelom, sometimes called swim-bladders (Müller-1844, Wiedersheim-1886, Budgett-1902, Franz-1924, Gérard, Prosser-1950, Daget, Young, de Smet), and by others lungs (Bert, Boas, Rauther, Marcus-1937, Mayr-1960, Ballard, Negus-1965). It seems more reasonable to consider these organs as lungs since (1) they are paired, (2) they open into the ventral part of the pharynx, (3) they are supplied with blood from the last efferent branchial artery (probably homologous with the 6th embryonal visceral artery), and (4) since the palaeontological data point in this direction.

The modern Polypteridae are purely aquatic and some authors (Bertin, Brien & Bouillon, Daget, Prosser-1950,

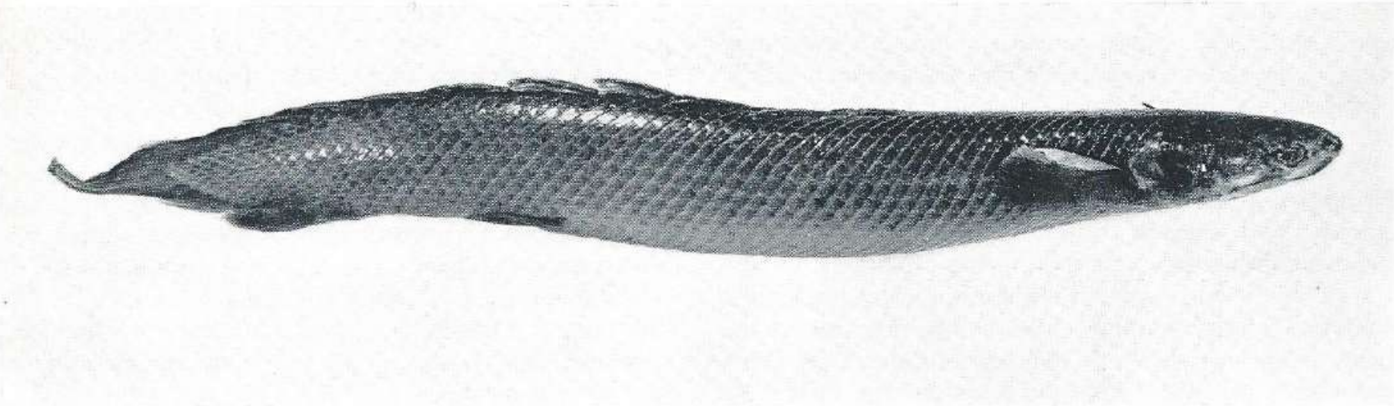


FIG. 6.
Nile ganoid, Bichir (***Polypterus senegalus***), often called a living fossil, in several features resembling the earliest actinopterygians from which most later bony fishes originated. 0,6 ×.

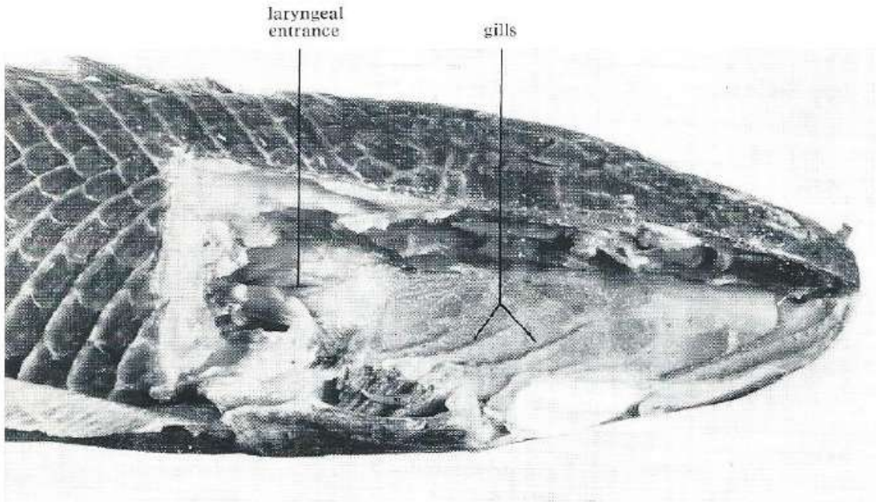


FIG. 7.
Nile ganoid, Bichir (***Polypterus senegalus***), specimen of 28 cm length, sex unknown. Right half of cranium removed to show the gills and the small slit-like laryngeal opening. 2,5 ×.

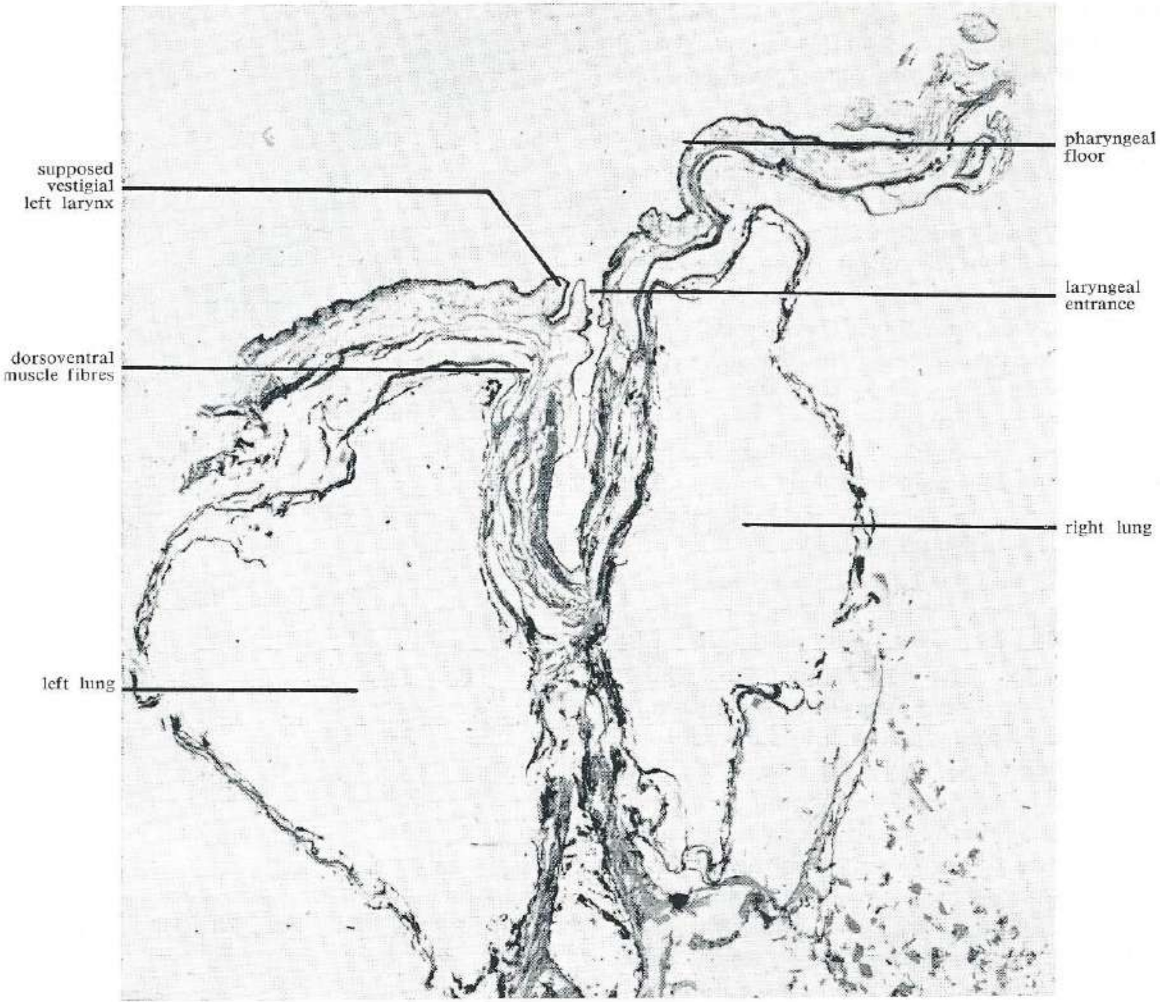


FIG. 8*a*.
Nile ganoid (*Polypterus senegalus*), specimen of 35 cm length, sex unknown. *a*. Cross-section through laryngeal region just cranial to the connection between the "trachea" and the right lung. It shows the laryngeal entrance, its surrounding muscle fibres, both lungs, and the small blind slit supposed to represent a vestigial left larynx. H.E.-stain. 12×.

de Smet) believe that they only very rarely use their lungs for oxygenation. Others (Budgett-1900, Harrington, Young) believe that even in well-oxygenated water they need aerial respiration. These doubts about the physiology of the Polypteridae do not matter to the nomenclature problem above, because there are examples of adaptation in which lungs are no longer used for oxygenation like *Latimeria* (Anthony & Millot, Nevenzel *et al.*), and others in which the swim-bladder is used for oxygenation, like the gar-pike *Lepisosteus* spec. and the bowfin *Amia calva* (Carter).

It is remarkable that the right lung is about twice as large as the left one, which communicates with the pharynx via the right lung. The inner surface of the lung is macroscopically smooth and does not seem to serve very well for easy gas exchange (Gérard, de Smet), but Rauther concludes from his histological observations, that there is quite close contact between the blood in the lung capillaries and the air. The same is suggested by Harrington.

The *larynx* consists of a small slit-like opening medially in the bottom of the pharynx, 5 mm in length in a 28 cm specimen and 6 mm in a 35 cm specimen, and a connection between this slit and the right lung, comparable with the trachea of the higher vertebrates. The slit is surrounded by slightly elevated rounded edges (Figure 7), and, according to de Smet, by a well-developed sphincter muscle. In dead specimens it is always closed. Presumably during life it is normally also closed, preventing water from entering the lungs, and only opening during relaxation of the sphincter and simultanous raising of the air-pressure in the mouth and pharynx by swallowing movements, whilst the oesophagus will probably be closed by sphincteric action. There is no clear dilator muscle, though Wiedersheim-1903 in a drawing of the laryngeal region reproduces some non-circular fibres in the sphincter, parallel to the floor of the pharynx, which he calls "dilators". On the other hand Müller-1844, in a similar drawing, shows only more-or-less circular fibres. My observations also indicate the latter condition, but must remain inconclusive on this point by lack of sufficient material. Hitherto probably undescribed are the muscle fibres present in dorsoventral direction around the aditus and "trachea" (Figure 8*a*). These might be able to produce some dilating effect on the laryngeal entrance.

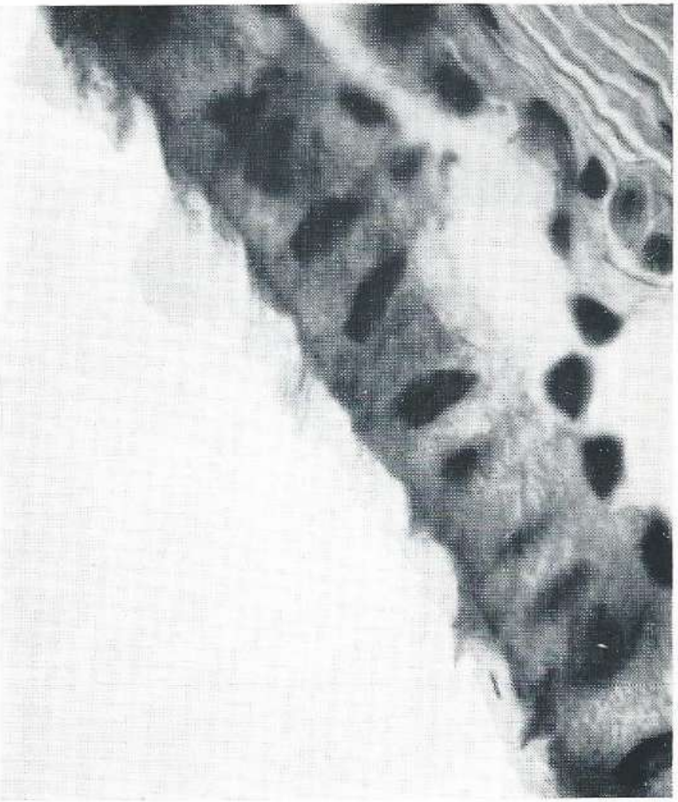


FIG. 8*b*
Nile ganoid *(Polypterus senegalus)*. Same section as shown in Fig. 8*a*. Ciliated epithelium of the supposed vestigial left larynx. The same type of epithelium is found in the larynx and the "trachea". H.E. stain. 545×.

In the above two specimens I could confirm the remarkable presence of a blind slit-like sac, 1 to 2 mm left and parallel to the above entrance, by Bumiller and Marcus-1937 supposed to represent a *vestigial left laryngeal entrance* (Figure 8*a*). De Smet, on the other hand, feels that this slit is similar to the folds present over the full width of the pharyngeal floor. However, I found it lined by the same type of ciliated epithelium present in the larynx and the "trachea", different from that of the pharyngeal floor (Figure 8*b*).

Little is known about possible expiration; the air-bubbles reported by Budgett-1900 to escape from the spiracles during or immediately after inspiration, may well be caused by leakage during air-swallowing as a result of the raised intrapharyngeal pressure. It is, however, reasonable to assume that real expiration does occur in *Polypterus*; though it will not result in reduction in the carbon dioxide level of the blood (which has already passed through the gills), and though probably most of the inhaled oxygen will be absorbed because of the long stay in the lungs, the inhaled nitrogen has to removed. Sound production by the respiratory tract of *Polypterus* is not mentioned in the literature, though it is known to be produced in other fishes via the swim-bladder (Ballard, Fish).

About the *Polypterus*' ontogeny, we encounter the same lack of knowledge as concerning its physiology (only Kerr, Budgett-1901, -1902 and de Smet have published observations on it), but until more up-to-date research indicates otherwise, one can accept the generally held view of the homology of the lungs and larynx with those of higher vertebrates.

4. *AFRICAN LUNGFISH (PROTOPTERUS ANNECTENS)*

This lungfish, living in tropical West Africa and first described in 1839 by Owen and (as far as the larynx is concerned) by Henle, serves to illustrate the branchial system and the larynx in the probable ancestors of the tetrapods. It is certainly a fish, but its anatomy and physiology let it adapt to a temporary terrestrial habitat. In this respect the lungfish and its Devonian ancestor may be considered more highly developed than their fellow-fish, which cannot survive drought. The lungfish can do this, however, being able to move out of their dried up pools to look for water.

Reports of *Protopterus* moving around on land come from Nichols & Griscom, and Smith. Moreover the African lungfish, if it does not find new water, can encapsulate itself in a mud case and thus survive dry periods (Johnels & Svensson, Parker, Poll, Smith, Negus-1932, -1949, -1962). It is evident that in the oxygenation of these animals aerial

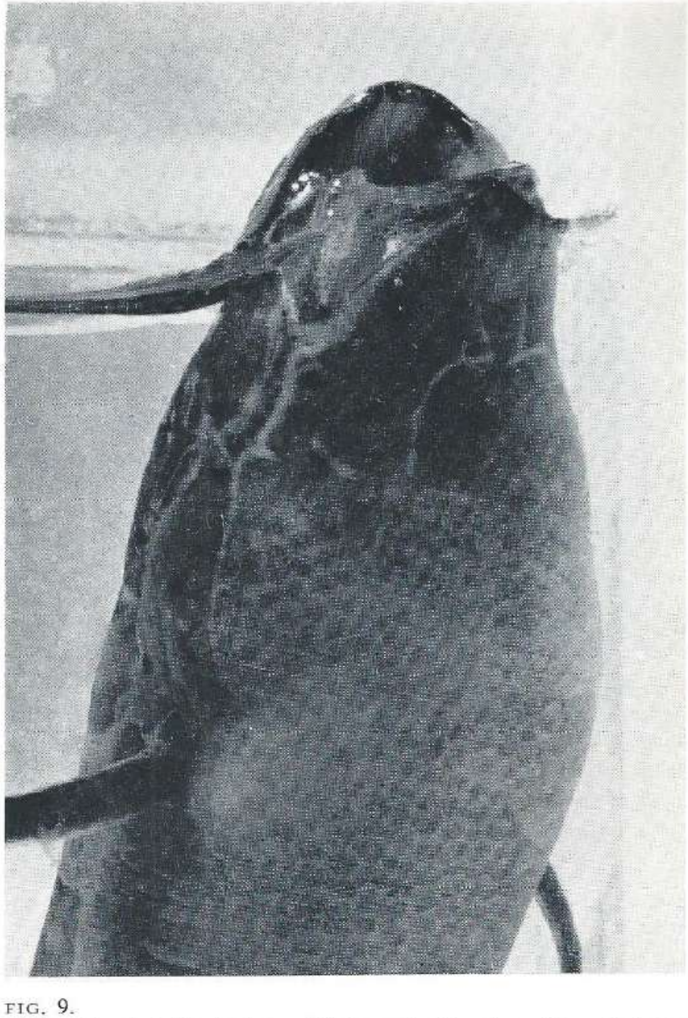


FIG. 9.
African lungfish (*Protopterus dolloi*), a primitive bony fish which can be traced back into the Devonian and possesses some similarities with the ancestors of the amphibians. It has both lungs and gills, and the animal is shown here while surfacing and inspiring air. Note the widely opened mouth and the distended region of the mouth bottom. Right ventral view. 1,5×.

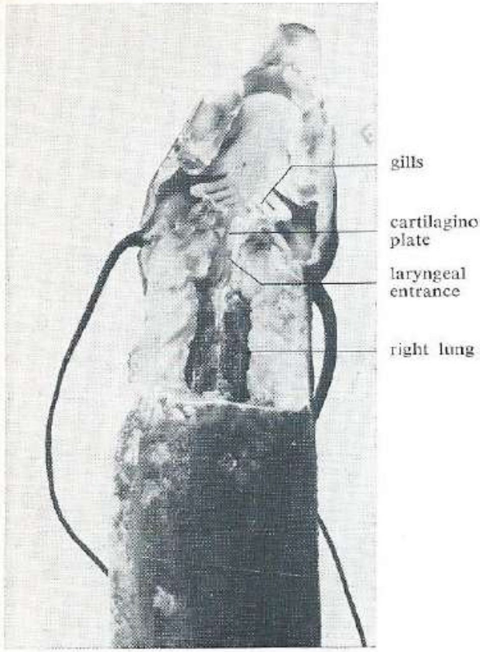


FIG. 10.
African lungfish (*Protopterus annectens*). Cranium and dorsal part of anterior body region removed to show gills and lungs. Dorsal view. 0,6 ×.

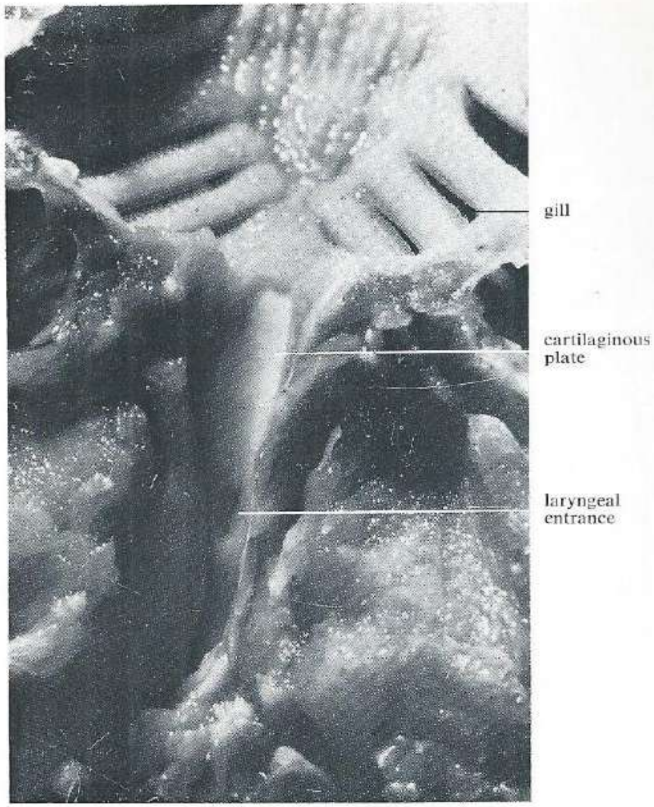


FIG. 11.
Same as FIGURE 10, laryngeal region enlarged to show cartilaginous plate and slit-like laryngeal entrance. 3,5 ×.

respiration plays an important part (Figure 9). Its part in the total oxygenation is even reported to be as high as 98% (Young), the rest being provided by gill respiration.

This great dependency on aerial respiration is reflected in the anatomy and physiology of the larynx and lungs. Although the topography and the volume of the latter are much like those of *Polypterus*, more oxygen can be absorbed, because the inner surface is increased by the presence of alveoli (Spencer). The larynx, macroscopically scarcely visible (Figures 10 and 11), seems to consist once more of a small median slit in the floor of the pharynx (about 2,5 mm long in a specimen 45 cm long*), but its more complicated and finer anatomy indicates its adaptation to the greater need for air: besides the simple sphincter (as in *Polypterus*), in microscope sections there are clearly visible muscle fibres originating from the lateral wall of the pharynx running transversely through the sphincter fibres and inserted in the margins of the laryngeal slit (Figure 12). These fibres, which are present along the whole length of the laryngeal entrance, no doubt pull the margins apart by their contrac-

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* According to Chardon the different subspecies of *Protopterus* may show some morphological differences in their branchial and circulatory systems, possibly including their larynx. These minor differences are neglected in this study, because they do not seem to bear any relation to phylogenetic considerations.

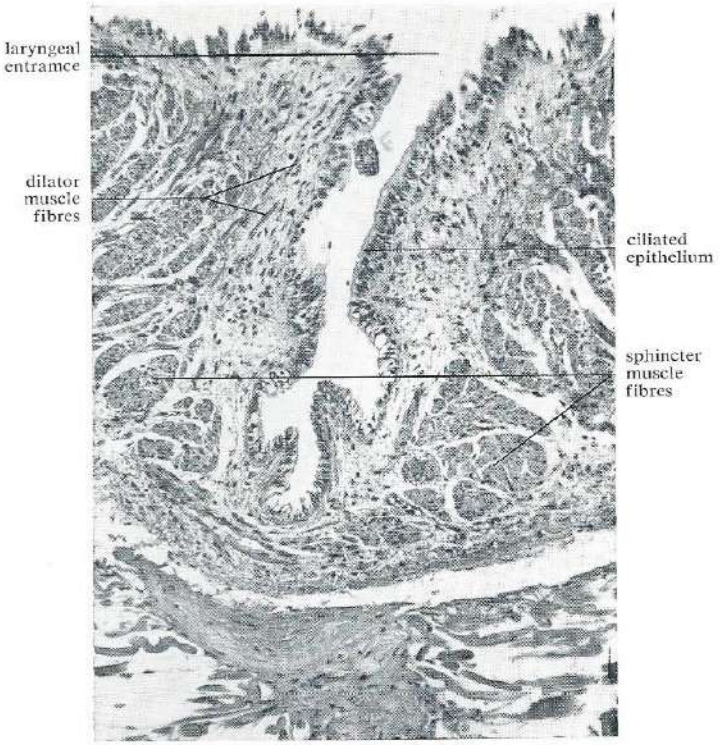


FIG. 12.
African lungfish (*Protopterus annectens*). Cross-section through laryngeal entrance, showing transversely cut bundles of sphincter muscle through which the weaker dilator muscle fibres penetrate, inserting into the margins of the laryngeal opening. Haematoxylin-eosin stain. 20×.

tion and may thus be called M. dilatator laryngis; because of its course it is called M.pharyngo-laryngeus by Göppert-1904.

A second differentiation from *Polypterus* is the presence of a fibro-cartilaginous plate (considered by Göppert-1904 to be purely fibrous), situated just below the mucosa of the pharyngeal floor in front of the laryngeal entrance (Figures 10 and 11), described already by Henle in 1839 and Owen-1841 and later by Peters and others. It has three small processes at its caudal end, two projecting alongside the anterior part of the aditus, and one projecting medially and ventrally just under the larynx and the beginning of the "trachea". Wiedersheim-1930 reports a number of fibro-cartilaginous elements supporting the borders of the laryngeal entrance, which I was not able to confirm. By some authors the plate is called the epiglottis (Bisschoff, R. Dubois, Howes-1887, Young), which for reasons to be explained on p. 54 seems confusing. A better name would be "anterior laryngeal cartilage".

There are five gills on each side, only the caudal three of which are capable of diffusion of gases, since the others do not bear sufficient lamellae. Histological examination of the laryngeal entrance and the pharyngeal floor reveals the presence of ciliated epithelium and small mucous glands which might indicate adaptation for air-breathing: according to Sagemehl-1885*b* all *aquatic* vertebrates lack mucous glands in their mouth. The posterior nostrils are located in front of the upper jaw a few millimetres behind the border of the mouth.

Most authors agree that even in normal conditions *Protopterus* needs aerial respiration. Inspiration thus occurs at a higher rate than in *Polypterus*: R. Dubois reported in *Protopterus* spec. a rate of 28 p.h. during stress and 128 p.h. during oxygen-deprivation and Smith in *P. aethiopicus* 2 p.h. during rest. Brien & Bouillon found a rate of 3-4 p.h. for larvae of *P. dolloi* in average conditions whereas Budgett-1901 did not see any air respiration in larvae of *P. annectens*. My own observations concerning a 30 cm specimen of *P. dolloi* in water containing about 4 ml oxygen per litre showed a rate of $1\frac{1}{4}$ p.h. at rest and about 6 p.h. during excitation. During its short stay at the surface the animal inspires air by lowering the hyoid region and it probably presses the air into the lungs by swallowing movements (Figure 9). According to Negus-1949, -1962, the cartilaginous plate has an inspirational function propelling the bolus of air, whilst Göppert-1904 found dilating fibres originating from it. Active expiration is described by Brien & Bouillon in larvae of *P. dolloi* and by R. Dubois in adult *Protopterus* spec.

Whether the "*choanae*" are used for respiration is very doubtful: Parker confirms it, Broman-1939, R. Dubois and Bertin deny it. From my few observations the conclusion may be drawn that they are not used for respiratory purposes, because the animal is seen to push its head well above the surface so that both the external and the internal nostrils are above water. Inspiration then takes place after opening the mouth wide, heard as a weak but clearly audible hiss. So during inspiration the pressure in the anterior and the posterior nostrils will presumably be about the same, and passage of air through the nose is therefore very unlikely. Also, in expiration the nose does not seem to take any part: the air bubbles, occasionally seen escaping from the animal between inspirations originate, from under the operculum, and the air frequently seen to escape immediately after inspiration has the same origin.

Sound production is reported by several authors, e.g. Johnels & Svensson "when specimens are handled in such a way that the air is violently forced out of the lungs". R. Dubois, Bisschoff and others cited by Parker also mention active sound production during expiration, described as a squeaking or catlike mewing. Tait even called this sound production a "voice". However, nothing is known about communication by such sounds (see p. 67).

The ontogeny of *Protopterus* is discussed by Brien & Bouillon, Budgett-1901, Gérard, Kerr and others. It should be noted that the lungs are found to be developed and functioning as respiratory organs before the gut is formed, again proving the inaccuracy of Haeckel's "law". Since they appear to originate from the ventral part of the foregut and there is evidence from vascularisation, the lungs can be considered to be homologous with those of the higher vertebrates.

For more data on the anatomy and physiology of *Protopterus* the reader is referred to Parker, Johnels & Svensson, Brien & Bouillon or Chardon. An analysis of metabolism during aestivation is given by Janssens-1964*b*.

5. *SALAMANDER (AMPHIUMA SPEC.)*

This salamander, representing here the primitive amphibians, belongs to the Subclass Urodela or tailed Amphibia. These are mainly aquatic and their outer forms resemble the fish, though sufficient palaeontological evidence for the shape of *Amphiuma* really representing that of the ancestral proto-amphibian is lacking. During the larval stage all urodeles show functioning gills, which some retain in the adult form. In *Amphiuma*, however, they disappear.

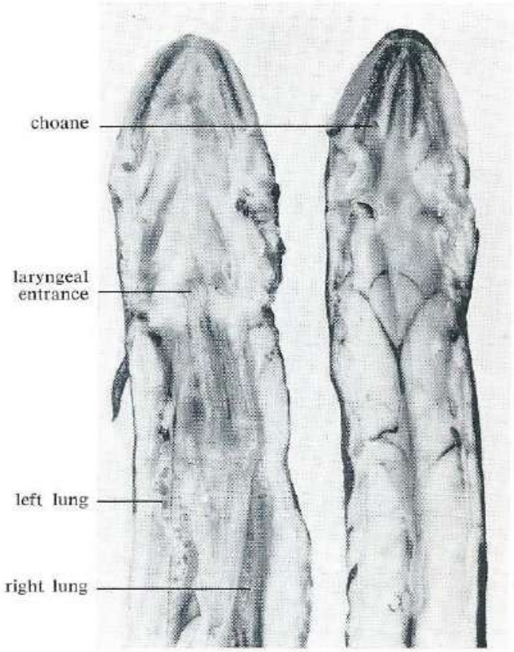


FIG. 13.
Salamander (*Amphiuma* spec.), a urodele or tailed amphibian. It displays some features in common with the earliest Carboniferous amphibians. The animal is photographed cut in a frontal plane; on the left the ventral part is seen from the dorsal side, showing the lungs and the scarcely visible slit of the laryngeal entrance; on the right, the dorsal part, in which the position of the choanae is shown, is seen from the ventral side. 0,8 ×.

The pharynx and larynx are topographically very similar to those of the lungfish, as are their elongated paired saccular lungs. As in *Protopterus*, there is a considerable distance between the larynx and the choanae (Figure 13), but the latter are placed more caudally than in the lungfish.

There are other differentiations indicating further developed respiratory functions. The laryngeal entrance is

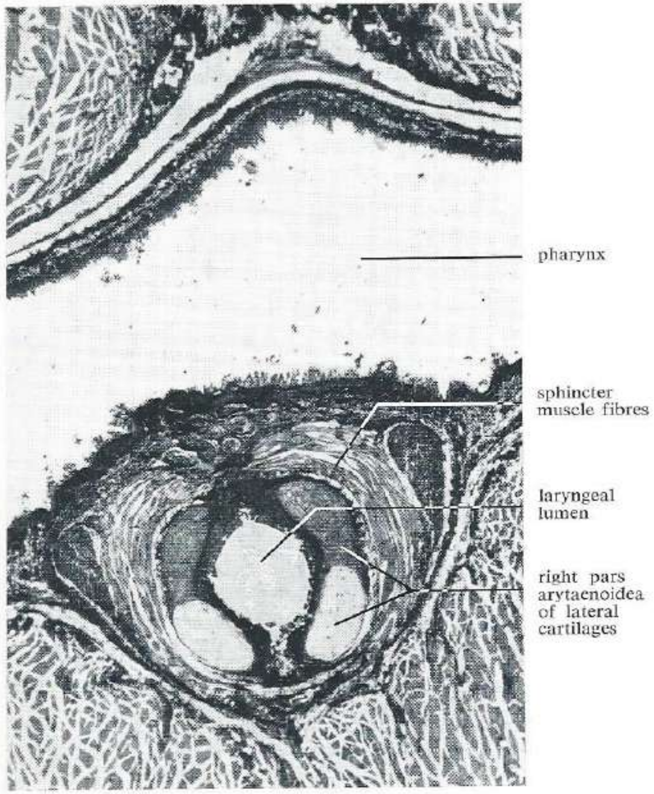


FIG. 14.
Salamander (*Amphiuma* spec.). Transverse section through laryngeal region just caudal to the laryngeal entrance, showing the arytenoid cartilages and, encircling these, the sphincter muscle fibres. Haematoxylin-eosin. 15 ×.

situated on top of a small eminence and shows sharp edges, which can thus act as a valve system (see p. 64).

Alongside this slit-like entrance, which is about the same size as in *Protopterus*, there are two pieces of cartilage, the paired *pars arytaenoidea*, which, together with the more caudal equally non-circular crico-tracheal cartilages alongside the trachea, are called the lateral cartilages (Figure 14). There is a specialized paired dilator muscle, the dorso-laryngeal (R. Dubois), inserted in the lateral cartilages. As in most amphibians, the sphincteric fibres surrounding the cartilages form a paired muscle which in *Amphiuma*, unlike the condition in other amphibians, do not show a clear division into a ventral and a dorsal portion. The muscular system as a whole gives the impression of being stronger than in lungfish.

I cannot find any exact information in the literature about *Amphiuma's* respiratory physiology, e.g. the amount of air used by the animal or the frequency of breathing movements. However, most authors dealing with respiration in the Urodela agree on some points: the lungs only constitute part of the oxygenation system, which also comprises the skin and probably the pharyngeal mucosa. Aeration of the urodele lungs is effected by swallowing movements after the air is inhaled through the nose, produced by lowering the floor of the mouth to give a negative pressure (Noble, Spurway & Haldane). Expiration is by mouth (D. M. S. Watson-1926, Negus-1965). The frequency of the breathing movements is subject to great variation, depending on the state of activity of the individual and the environmental temperature, as in all poikilotherms. Sound production by the salamanders has been reported, through rarely; Noble credits the production of whistling sounds to *Amphiuma*, but doubts whether this really results in communication. (See the discussion on p. 67 on the evolution of the larynx as an organ of communication).

About the ontogeny of the *Amphiuma* larynx the available literature yields no information. On the pharyngeal and laryngeal morphology of larval stages in some urodeles, Göppert-1889 published observations, to which the reader is referred for further data on the adult stages; observations on the branchial arches in early stages of other urodeles have been published by e.g. Stone and Starck-1937.

6. *FROG (RANA CATESBIANA AND R. ESCULENTA)*

The frogs belong to the subclass of anurous (tail-less) amphibians and the adults have a more terrestrial habit than the Urodela. They are even reported to drown when prevented from surfacing (Hempelmann). Consequently the adult forms rely for their oxygenation more on respiration of air than do salamanders. Nevertheless pulmonary respiration in frogs is only partly responsible for oxygenation, since this is also secured by respiration through the skin and the mucous membranes of the mouth, which for instance in *R.esculenta* provide about the same amount of oxygen as pulmonary respiration (Krogh-1904). Adult anurans have lost their functioning gills, which were present in the tadpoles. Since for many years the frog has been used as a laboratory animal, we are well informed about its anatomy, physiology and ontogeny. As there appear no obvious differences in laryngeal morphology between the various species of the genus *Rana*, we will consider the American bull-frog *R. catesbiana* and the European frog *R. esculenta*.

The laryngeal entrance is visible just behind the tongue as a small fissure on top of a hemispherical eminence, the length being about 6 mm in *R. esculenta* and a few mm greater in *R. catesbiana*. The long axis of this fissure does not run parallel to the ventral side of the pharynx but is tilted about 45⁰ (Figure 15). The eminence is mainly formed by the two arytenoid cartilages, which on their medial sides, normally not visible from the pharynx, bear a fold of mucous membrane generally called the vocal folds. (This name is criticized by Negus-1949, -1962 because not all frogs use them for vocal purposes). Just behind these we find a pair of very short bronchi, leading towards the saccular lungs, whose walls are well supplied with blood vessels and show alveolar enlargement of the inner surface.

The laryngeal skeleton is rather complicated compared with that of the Urodela. It consists of 7 cartilages: the two *arytenoids* (oral and lateral), below these the feeble, single, circular *cricoid* with an outgrowth supporting the "trachea" (together forming the crico-tracheal cartilage), and 4 very small accessory cartilages, the paired apicals and basals. The well-developed hyoid bears a narrow relationship to the larynx, because it supports it and gives origin to several laryngeal muscles.

Naturally the muscle system has a more complex anatomy than that of lower vertebrates; there is a strong paired dilator, originating from the cricoid and the hyoid, and inserted into the arytenoid, and three U-shaped sphincter muscles (Figure 16). About the exact size of the surface of the laryngeal entrance when opened nothing is known. Howes-1887 found in several frogs a small paired membranous fold in front of the laryngeal entrance and considered it to be homologous with the epiglottis of higher vertebrates, which seems very questionable (see Chapter 4, § 2). The

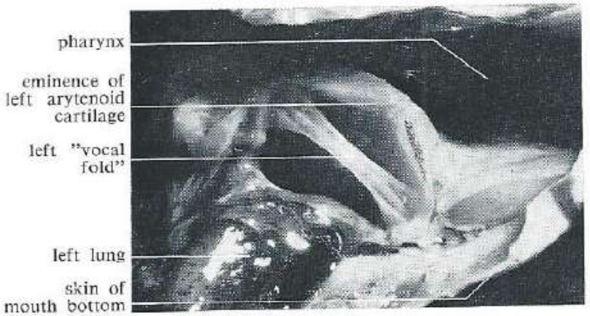


FIG. 15.
Frog (*Rana esculenta*). ♂, adult. Sagittomedial section through head region showing position of larynx and valvular character of "vocal folds". 5,5 ×.

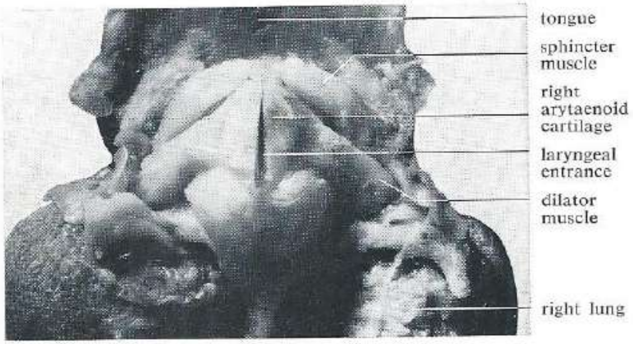


FIG. 16.
American bull-frog (*Rana catesbiana*) adult, sex unknown. Dorsal view of the pharyngeal floor of which the mucous membranes have been removed, showing the nearly closed slit-like laryngeal entrance, the well-developed constrictor and dilator muscles, and the lungs. 1,6 ×.

choanae lie in the front part of the upper jaw, just in front of the eyes.

The mechanism of *pulmonary respiration* in frogs is more complex, but probably more efficient, than that of lower vertebrates: the laryngeal anatomy together with other characters enables the animal to adapt itself to both aquatic and terrestrial habitats. In the former the lungs are protected against invasion by water and other foreign material by the action of the sphincter muscles, aided by the valve-like action of the dome-shaped laryngeal entrance and of the oral border of the vocal folds (which resemble human aortic cusps in form and function). At the same time the air in the lungs is prevented from escaping by means of the same sphincter action, aided by the non-return valves formed by the down-turned folds of the caudal margins of the vocal folds (Negus-1949, -1962). Movements for pulmonary respiration take place in three phases. (1) Aspiration: air is sucked through the nose and choanae into the mouth by lowering the floor of the mouth whilst the larynx remains closed. (2) Expiration: by raising the intra-abdominal pressure by contraction of the abdominal muscles air is forced out of the lungs, while the larynx is opened (according to Krogh-1941 there is only passive expiration). (3) Inspiration immediately follows expiration: the fresh air is pressed into the opened aditus whilst the outer nasal openings remain closed, followed by closure of the larynx and opening of the nostrils.

The rate of these movements depends on the animal's activity and temperature; during hibernation it may even be absent.

There is no doubt about many male frogs using their respiratory tract, including the larynx, for vocal purposes.

During larval stages (in the tadpoles) lungs and larynx are seen to develop from the medio-ventral part of the fore-gut (von Baer-1837, Märtens-1895, -1898, Rugh). This fact, together with the vascular and nervous supply of lungs and larynx, provides sufficient evidence for considering them homologous with those of other vertebrates.

For a more detailed description of the frog's general anatomy the reader is referred to the excellent, classic work of Gaupp-1896, -1904, and for the laryngeal anatomy to Henle or Göppert-1898. Its ontogeny is discussed by e.g. Märtens and Rugh, the biology of the amphibians in general by Noble.

7. *CROCODILE (OSTEOLAEMUS TETRASPIS)*

The crocodile is a typical reptile showing a better adaptation to a terrestrial habitat than the amphibians, while at the same time, probably by secondary adaptation, being able to pass a great part of its life in water. Since its skin is cornified, it is able to preserve a maximum of water within the body (aided by re-absorption in the metanephros). There is no skin respiration, and for oxygenation the crocodile probably relies entirely on pulmonary respiration.

The laryngeal entrance in dead specimens of the small species *Osteolaemus tetraspis* is a triangular opening with upturned edges caudal to the tongue, with its apex pointing cranially and its plane parallel to that of the floor of the mouth (Figure 17). In front of it there is an epiglottis-like structure formed by the anterior edge of the very large hyoid cartilage, which reaches the palatum. This enables air to pass through the nostrils and choanae directly into the larynx, and thence into an elongated and capacious trachea, reinforced by rings of cartilage, and into the lungs. The hyoid bears a narrow relationship to the larynx, because the latter is ventrally completely enclosed by it. Because of its semi-cylindrical form it gives the impression of being a thyroid cartilage and from a phylogenetic point of view there are reasons for calling it so (see p. 54).

The laryngeal skeleton proper consists of two well-developed, U-shaped *arytenoids* (the base of the U being at the caudal end of the aditus) and a circular *cricoid* (Figure 18). The muscular system again consists of sphincteric and delating fibres, both of which are well developed. Göppert-1899, -1937 described the sphincter as being divided into a ventral and a dorsal part. The paired dilating muscle orginates from the cricoid, and is attached to the arytenoids, which by its contraction are drawn laterally, and thus give the aditus a larger surface by elongating the basis of the triangular opening.

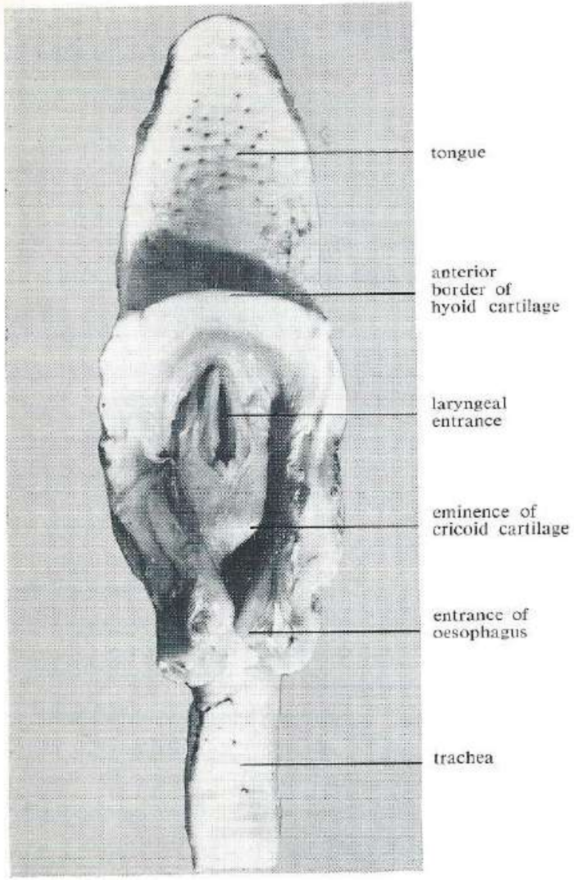


FIG. 17.
Crocodile (*Osteolaemus tetraspis*). Tongue, larynx and part of trachea seen dorsally. The triangular laryngeal entrance, with slightly upturned edges, and the epiglottis-like anterior ridge of the hyoid are clearly visible. ½×.

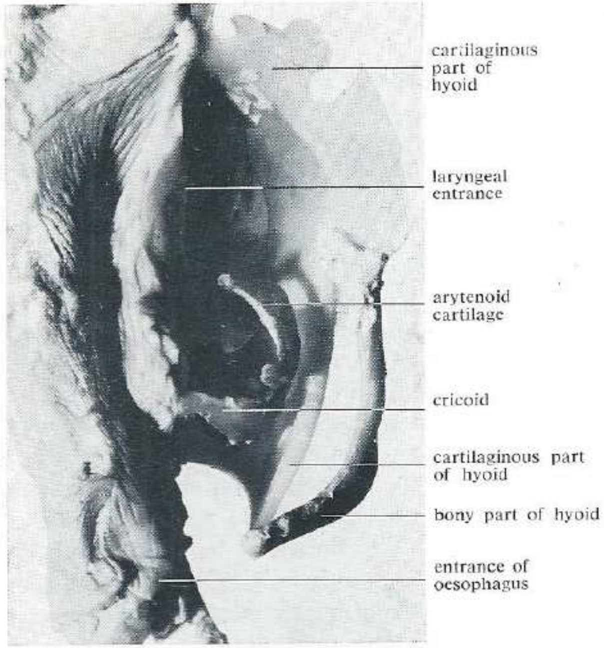


FIG. 18.
Same as FIGURE 17, enlarged view of laryngeal region, soft parts of right half of larynx removed, showing its cartilages and the hyoid. Natural size.

Respiratory movements of crocodiles are essentially different from those of amphibians: inspiration takes place by suction rather than by swallowing, since rib movements cause lowering of the intra-thoracic pressure. Inspiration in crocodiles is further effected by the action of the diaphragm similar to that in mammals. Such a structure is, however, absent in most other reptiles. Expiration is probably partly passive and partly active, by contraction of the abdominal muscles. Usually a few breathing movements can be observed, ending with an inspiratory one followed by a relatively long pause (Bert, Serfaty & Peyraud).

The action of the crocodilian larynx during respiration was studied by Bert and Boelaert in alligators. On looking into the open mouth the laryngeal entrance was seen to open during respiratory movements only, and during the long pauses it remained closed. Bert (p. 308) showed that this closure serves to keep the inspired air in the lungs. About the average respiration rate little is known; it probably shows great differences according to the state of activity and the surrounding temperature, since reptiles are poikilothermic. Nielsen found the respiratory frequency of lizards to vary linearly with metabolic rate. During diving, which in other crocodilians like the alligator may last 2 hours (Andersen-1961), or as many as 5 (G. H. Parker, cited by Dill & Edwards), respiratory movements are completely absent.

Although the crocodile's oxygenation is exlusively secured by pulmonary ventilation, the anatomy and topography of its larynx permit the animal to live an amphibian way of life. With only the tip of its nose above the water's surface the crocodile can inspire air through the nostrils, nose, choanae, and larynx, because the upper border of the hyoid acts as an epiglottis does in many mammals (Negus-1949, -1962, Ballard), by shutting off the respiratory tract from the alimentary tract. This is probably effected by elevating the floor of the mouth and the hyoid region, aided by a transverse ridge of the mucous membrane of the palate. During diving the upturned edges of the laryngeal entrance, and the well developed sphincter, presumably keep the laryngeal entrance tight shut, allowing the animal to swallow prey under water.

Sound production by the crocodilian larynx consists of hissing, which is used, as in other reptiles, as a means of intimidation, and of roaring during the mating season (Henle, Negus-1949, -1962, Landois, Villiers, Carr). Von Humboldt, cited by Grützner, recorded yelling cries in newborn alligators. I know of no investigations into the ontogeny of the larynx, and some doubt exists about the homology of its elements with those of the higher vertebrates.

For more information on the biology of *Osteolaemus* the reader is referred to Villiers or Pope; on respiratory mechanisms of reptiles in general to Bert, Serfaty & Peyraud, and on the early ontogeny of crocodilians to Keibel. Unfortunately little is known about the respiratory physiology and the precise laryngeal anatomy of crocodiles. Original work on the anatomy of the crocodile larynx was done by Henle, Göppert-1937, Söller and Negus-1929, -1949, -1962; on the physiology recent work has been done on the alligator by Boelaert and Andersen, and in the older literature we find only the work of von Humboldt, cited by Landois and Bert.

8. *LESSER GYMNURE (HYLOMYS SUILLUS)*

Little is known about the biology of the primitive insectivores belonging to the Subfamily Echinosoricinae, which are supposed, more than any other living species, to approach the common Cretaceous ancestor of all Placentalia (Thenius & Hofer). According to Brehm (p. 346), of the Echinosoricinae it is the Lesser gymnure, *Hylomys suillus* (Figure 19), which shows the most primitive features. Some data on the biology of the Lesser gymnure are given by Medway; the animal seems to be strictly terrestrial.

Topographically the larynx shows typical mammalian features, being in close contact with the nasopharynx (Figure 20). Equally mammalian is the laryngeal scaffolding, which next to the arytenoids, with their well developed corniculate cartilages, and cricoid consists of the thyroid cartilage and the epiglottis (Figure 21). The latter clearly shows an antevelar position projecting high into the pharynx with well

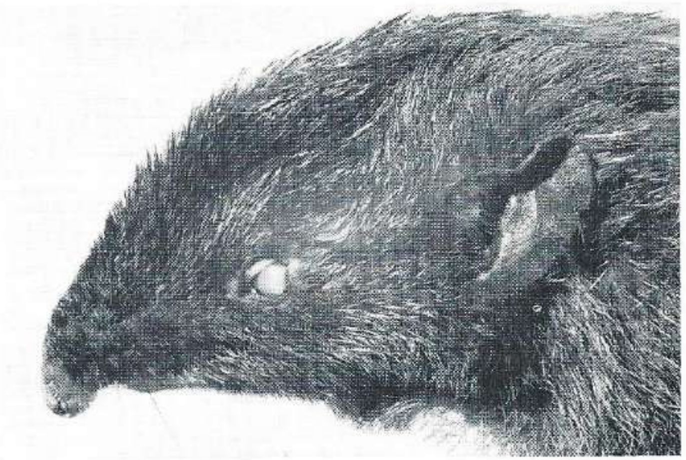


FIG. 19.
Lesser gymnure (*Hylomys suillus*). This small Malayan insectivore of which a male specimen is shown, is probably the most primitive living Placental, and is supposed in many respects to be similar to forms from which all the mammals (except the marsupials and the monotremes) originated. The slight downward pointing of the nose tip is an artifact: in the normal state it is in an even line with the rest of the nose. 1,5 ×.

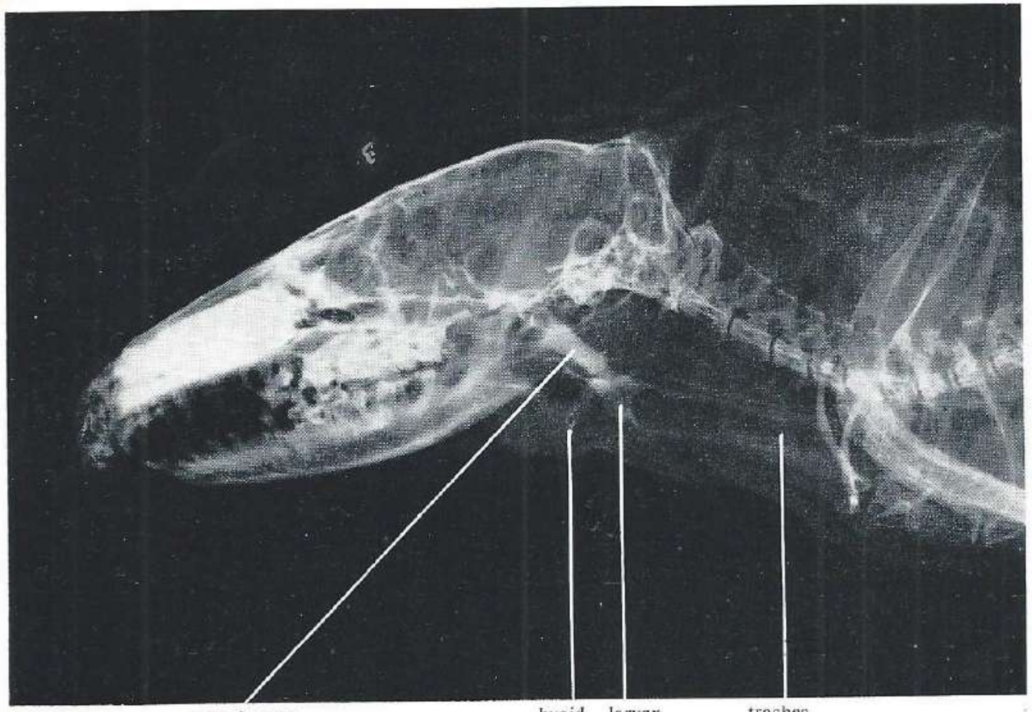


FIG. 20.
Same specimen as FIGURE 19. Lateral X-ray of head and neck; the nose and mouth are filled with an iodine-containing fluid to show the contours of the lumina. The epiglottis is antevelar. 2 ×.

developed aryepiglottic folds, thus establishing lateral channels for the foodpassage, and enabling the air to pass direct from nose to larynx. The dimensions of the larynx in the dorsoventral direction appears to be somewhat larger than the diameter of the trachea. Laterally in the larynx there is one smoothly edged thyroarytenoid fold on each side, whose length is about half that of the dorsoventral diameter of the larynx, the other half being occupied by the arytenoid cartilages. For the rest the laryngeal walls are smooth (Figure 22). In accordance with the presence of more cartilaginous parts in the gymnure larynx as compared with the reptiles, the muscular system shows a further differentiation into muscles connecting the newly-developed cartilages.

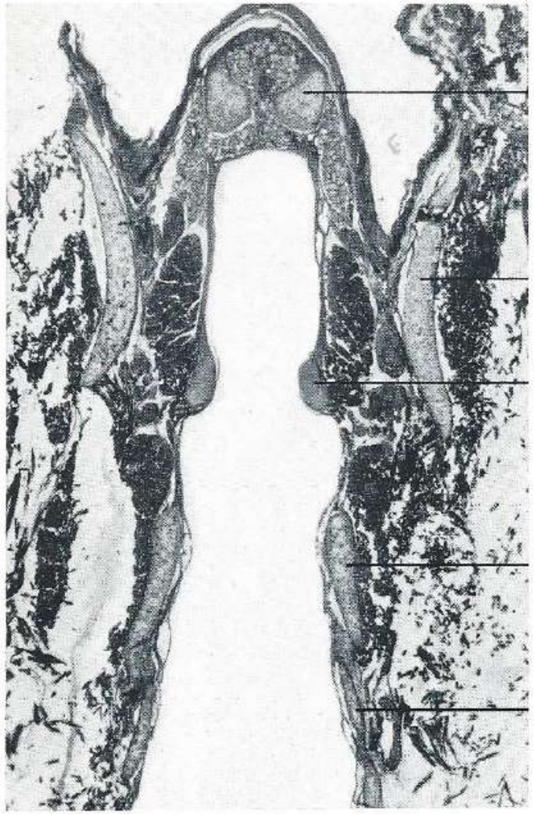


FIG. 21.
Same specimen as FIGURE 19. Section in a frontal plane through the larynx, showing the thyroid, cricoid, epiglottic and arytenoid cartilages, At right is an opening in the thyroid cartilage (*foramen thyreoideum*), through which a nerve passes. Mason-aniline-blue. 15,5 ×.

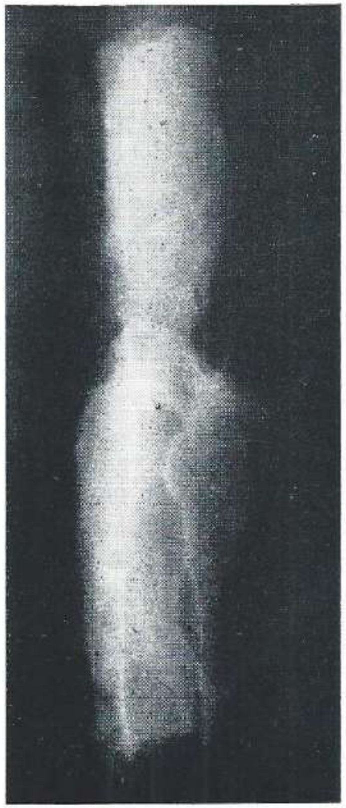


FIG. 22.
Lesser gymnure (*Hylomys suillus*). A dorsoventral X-ray of the tongue (left half removed) with the larynx and the cranial part of the trachea. The lumen is filled with an iodine-containing fluid to show its contours A simple fold is seen protruding on either side of the laryngeal lumen. 5 ×.

Presumably this more complex morphology is reflected in the laryngeal functions, but unfortunately very little is known about these. We may assume that in view of the higher respiratory rate associated with homoiothermy, the laryngeal respiratory movements occur with a much higher frequency than in the reptiles and that regulation of the airstream by the more differentiated muscular and skeletal system is likely to be of greater importance than in the reptiles.

Probably the sole description of the voice of *Hymolys* is given by Medway: "A shrill squeak or series of squeaks, penetrating although not very loud".

I know of no investigations into the ontogeny of gymnures.

9. *TREE-SHREW (TUPAIA GLIS)*

The tree-shrew (*Tupaia*, Figure 23) is supposed to represent the common Cretaceous ancestor of the primates, and may therefore be considered as occupying an important taxonomic position in the phylogenetic line of the primates. The habitat of these active and sometimes aggressive animals is only partly arboreal and is limited to South-East Asia (Napier & Napier). Though according to Le Gros Clark-1962 the digits are effective for grasping purposes, the tree-shrews do not use their limbs like the monkeys as suspension organs.

In a median section of a tree-shrew's head (Figure 24) the typical mammalian topography of the larynx can readily be observed: the entrance reaches the nasopharynx. In the specimen dissected here the epiglottis has an antevelar position, but it does not seem impossible that in living specimens it occupies a retrovelar position, displacement in the prepared specimen possibly being an artifact, due to fixation, retraction and manipulation. DuBrul indeed describes the epiglottis as being intranarial. The arytenoid eminences appear well developed, and in the dorsoventral direction are as long as the thyroarytenoid folds. The latter appear to show a shallow division into a lower and a upper part. Ventrally they partially pass over into the entrance of a subepiglottic, retrothyroid air-sac (Figure 25), but there is no ventricle, as in higher primates. The diameter of the larynx definitely appears to be larger than that of the trachea. As in the gymnure the skeleton is composed of epiglottis, arytenoids with corniculate cartilages, thyroid and cricoid. (A spatial reconstruction of a *Tupaia*'s laryngeal skeleton has been made by Schneider, see Starck & Schneider, p. 426).

The musculature connects the different skeletal parts, the thyrocricoid muscle being well developed and the thyroarytenoid being divided into a medial and lateral part (Starck & Schneider).

Little is known about the respiratory physiology in general, but sound production appears to be well differentiated, according to Hofer, Andrew-1964, Kaufman and Sprankel; the latter describes 8 different sounds, such as high pitched cries used in different situations. For more details on the biology of the tree-shrew in general, the reader is referred to Sprankel and to Napier & Napier.

No published observations are known concerning the ontogeny of the tree-shrew's respiratory system.

FIG. 23.
Tree-shrew (*Tupaia glis*). This species, of which an adult male is shown, is supposed to resemble the Cretaceous ancestors of all later primates. The position of the limbs is somewhat abnormal, the picture having been taken after death. ½ ×.

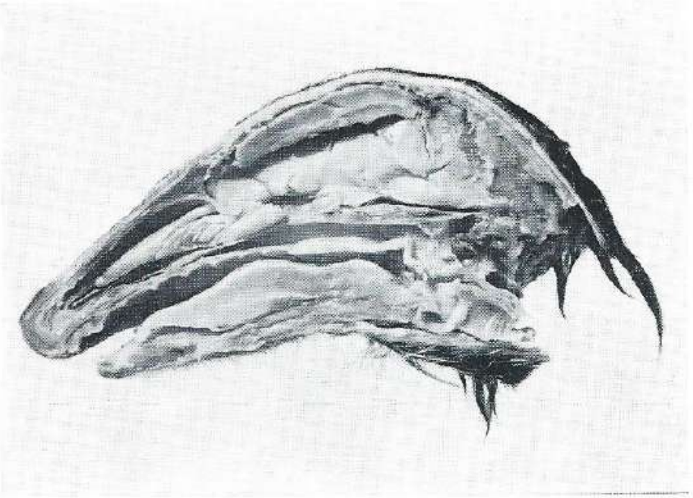


FIG. 24.
Same specimen as FIGURE 23. Sagittomedial section through head. Natural size.

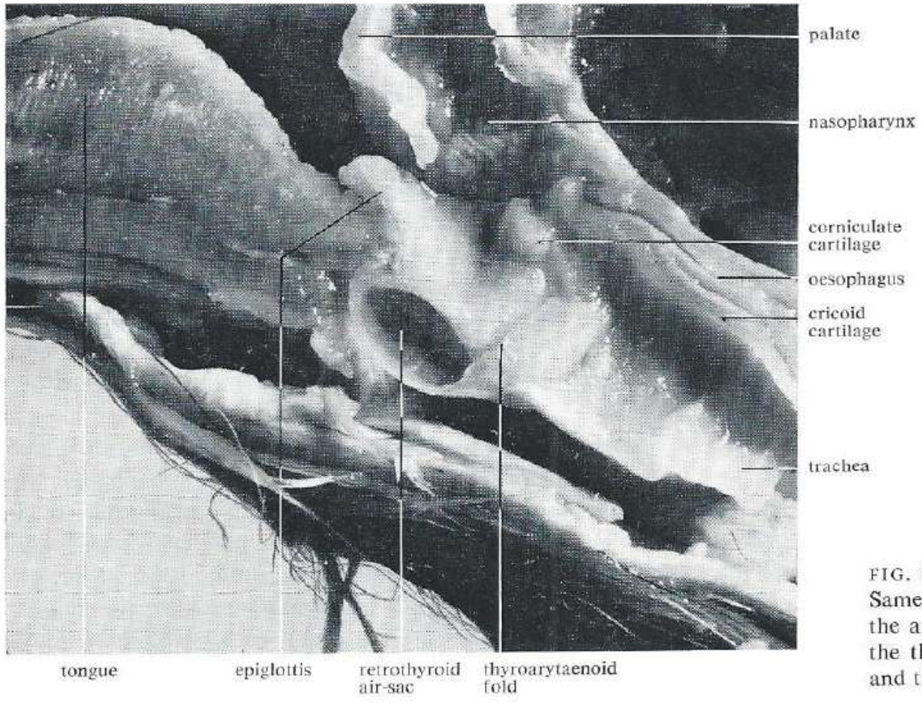


FIG. 25.
Same as FIGURE 24, laryngeal region enlarged, showing the antevelar position of the epiglottis, the division of the thyroarytenoid fold into an upper and a lower part, and the retrothyroid air-sac. 4×.

10. *RHESUS MONKEY (MACACA MULATTA)*

This species belongs to the Cercopithecidae, supposed to bear some resemblance to the ancestral primates preceding the Hominoidea. Though Rode, cited by Tappen-1960, states that it is less arboreal than other African monkeys, it is better adapted to this habitat than the tree-shrew, since it is able to move through the trees with greater dexterity. This is mainly effected by (1) "brachiation": the forelimbs are more easily movable at the shoulder joints (Napier suggests one should not ascribe real brachiation to the Rhesus monkey, such as seen in the gibbon. For more details on this subject the reader is referred to him or to Erikson), (2) a process which analogously can be called "chiriation": the development of hands and feet into effective grasping organs, for which the opposable first fingers are important, (3) stereoscopic vision, and (4) corresponding cerebral development together with an increase in intelligence, which may be as well developed as in the apes (Hill-1957).

The larynx is of typical mammalian appearance. Its entrance reaches high into the pharynx with a retrovelar position of the epiglottis (Figure 26); compared with other mammals the lateral food channels are rather poorly developed (Negus-1965). According to F.D. Geist and Bernstein the inferior border of the cricoid lies at about the level of the superior border of the 4th cervical vertebra. This is confirmed by our own observations. The larynx is essentially built up of the same components as in the tree-shrew, the only extra parts of the skeleton being the paired small cartilages of Wrisberg and Santorini, the cuneiform and the corniculate.

However, aside from some other less obvious differences, one should be mentioned here because of its interest from a phylogenetic point of view: the inner surface of the larynx, which in the tree-shrew only shows a slight, paired prominence caused by the presence of the thyroarytenoid muscles, is in monkeys provided with two pairs of clearly inbending folds, parallel to (but not in all Cercopithecidae shaped by) the thyroarytenoid muscles (Figure 27). These folds on each side enclose a small space, the ventricle.

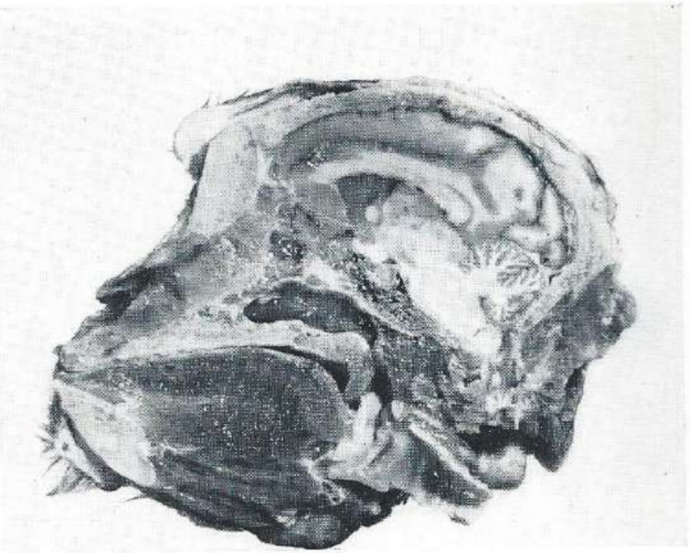


FIG. 26.
Rhesus monkey (*Macaca mulatta*). Adult ♀. Sagittomedial section through head to show position of larynx. 0,7×.

The cranial folds are directed somewhat caudally and have smooth edges; the caudal ones have sharp, cranially turned edges, thus forming an inlet-valve. According to Negus-1924, -1925, -1929, -1949, -1957, -1962 all primates with active brachiation possess such valves, which he supposes to be functional: effective brachiation is only possible when the origin of the pectoral muscles can be fixed, obtained by a constant negative intrathroacic pressure. This can be effected by the inlet-valve action (see p. 65 for the valve action of the larynx).

Together with the establishment of the thyroarytenoid folds there is a reduction in the relative dorsoventral size of the arytenoids as compared with lower primates. The Rhesus monkey shows another difference from *Tupaia*: the presence of a subhyoid air-sac (or Saccus laryngeus medianus superior), whose entrance is at the base of the epiglottis. In other monkeys and in apes there are often more and larger air-sacs connected with the larynx.

No direct observations are known as to the part the monkey's larynx takes in breathing, but since on most

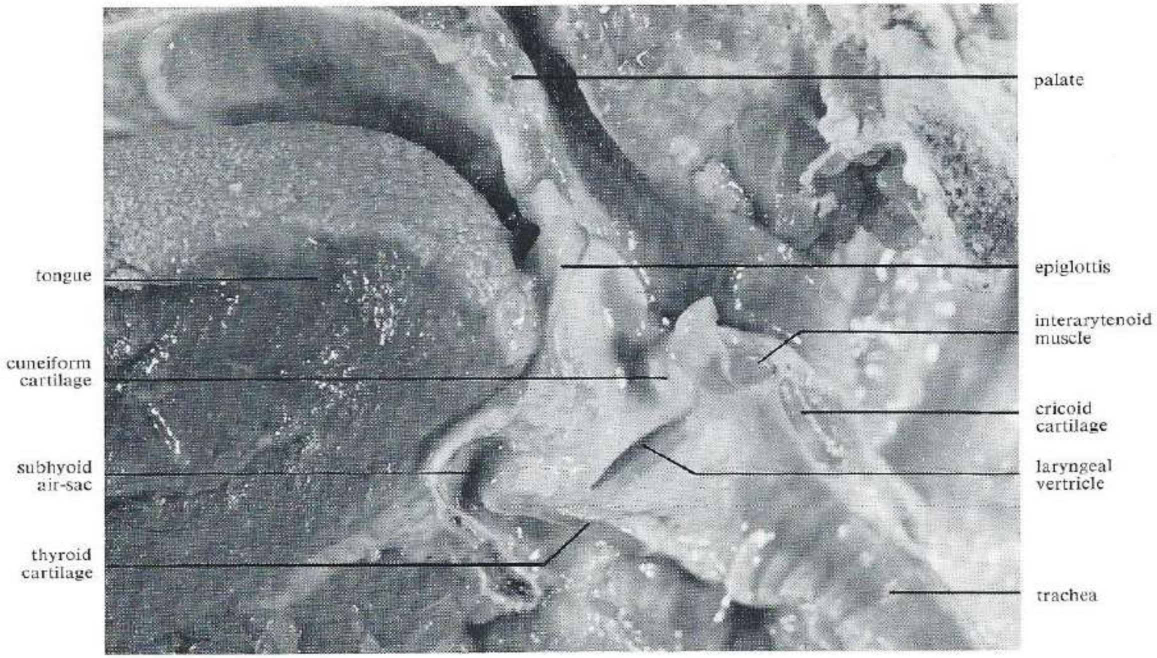


FIG. 27.
Rhesus monkey (*Macaca mulatta*). Adult ♀ . Sagittomedial section through laryngeal region. 2,5 ×.

points its physiology can be considered very similar to man's, one may assume the same in regard to the larynx. Sound production by the *Macaca* larynx is well known and consists of differently pitched sounds. It has been described by Garner-1900, Hill-1957, Rowell, Itani, Andrew-1963*a*, -b, -1964, Struhsaker (cited by Marler), and Altmann.

We also lack extensive information on the monkey's ontogeny; some data are given by e.g. Hill-1957, but because of its resemblance to other primates we will assume the laryngeal elements to be homologous in all.

For further anatomical details the reader is referred to Starck & Schneider, or F. D. Geist; Wilson, too, gives some anatomical and functional data on the Rhesus monkey. Behaviour studies of the Rhesus monkey are made e.g. by Carpenter, Koford and Altmann and of the related Japanese macaques by Imanishi. Napier & Napier recently gave an excellent short review of all the important data on the genus *Macaca* in general.

11. *CHIMPANZEE (PAN TROGLODYTES)*

The chimpanzee belongs to the Hominoidea, and of all modern species most nearly approaches man, morphologically and ethologically; the other apes are more specialized and less similar to man (see p. 25).

Though they are very dexterous in their arboreal habitat, chimpanzees are known to move around just as well on the ground and even seem to prefer it. It is only in recent years that we have begun to become informed on their ecology and their ethology in their orginal habitat, by the observations of e.g. Nissen, Kortlandt-1962, Kortlandt & Kooy,

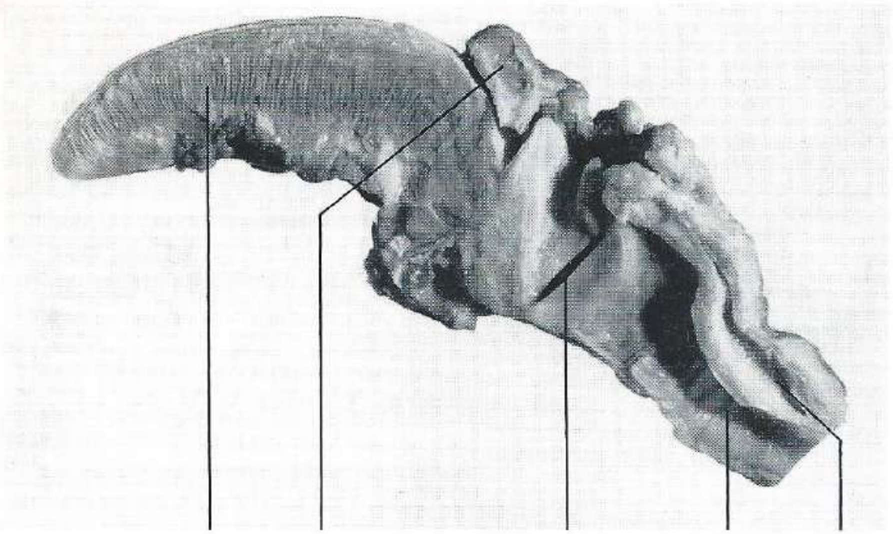


FIG. 28.
Chimpanzee (*Pan troglodytes*, subspecies unknown), 3 year old ♂.
Medial section of tongue, larynx and cranial part of trachea. Because of fixation there is in this specimen an abnormal approximation of the soft palate to the tongue and the epiglottis. 0,8 ×.

and Goodall-1963, -1965. Behaviour in captivity is described by Yerkes and Köhler. In point of fact these observations are very interesting from a phylogenetic point of view.

The larynx, like many other organs, is very similar to man's, at least from a morphological viewpoint (Figures 28, 29 and 30). Topographically the chimpanzee shows one difference from the monkey: its laryngeal aperture projects less far in the pharynx, so its epiglottis does not reach the palate and has an antevelar position. Consequently there is a small gap between the two structures, resembling the human condition.

The plane of the aperture is almost frontal and faces the dorsal pharyngeal wall (Figure 28).

The *skeleton* closely resembles that of man; two less obvious characteristics are the fusion of Santorini's cartilage with the arytenoids and the presence of two of Wrisberg's cartilages (Avril). The relative size of the arytenoids in the dorsoventral direction is somewhat smaller than in the monkey (Bernstein) (Figure 29). The cricoid shows in the sagittal direction a more pronounced funnel shape than in man (Figure 29).

Concerning the *soft tissues*, the conspicuous system of *air-sacs* in the apes should be mentioned. These are relatively large spaces communicating with the large ventricle and with each other, situated along the ventral side of the neck and cranial part of the thorax, and lined with mucosa. It is smaller in the chimpanzee than in the orang and the gorilla. About its function there is no general agreement: Negus-1949, -1962 supposes it to be mainly respiratory (its air could be used in an emergency by means of rebreathing), whereas its involvement in voice-production is described by Kelemen-1948 in the orang-outang, and by Itani in the goril-

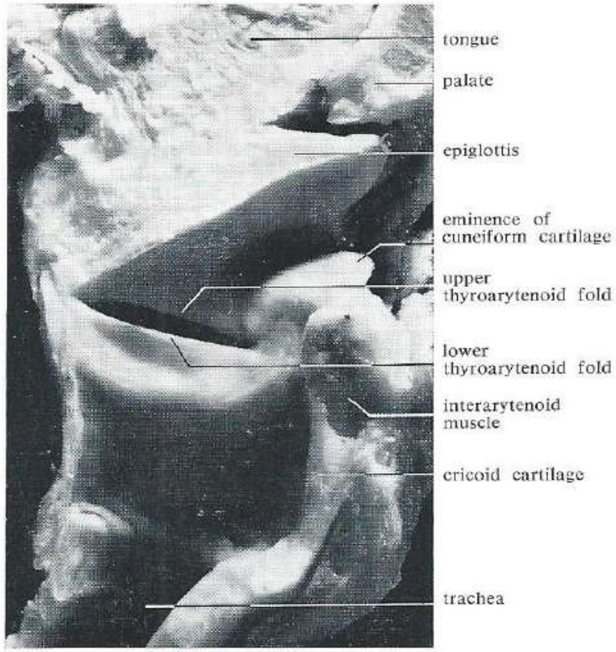


FIG. 29.
Same as FIGURE 28. Detail of larynx 1,5×.

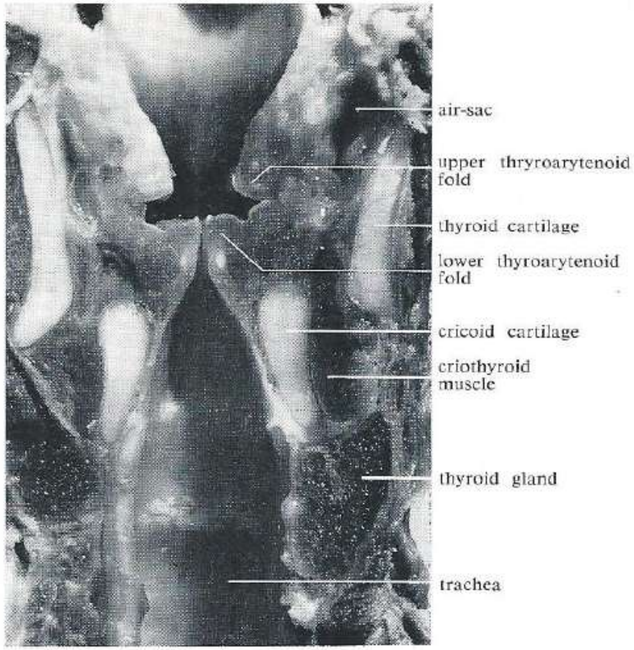


FIG. 30.
Chimpanzee (*Pan troglodytes*, subspecies unknown), 3 year old, ♂ Frontal section of larynx showing the upturned inferior thyroarytenoid folds. 1,5×

la. The chimpanzee also possesses two smaller air-sacs, the entrance of which is to be found in the pharynx, somewhat lateral and caudal to the aryepiglottic folds (Figure 30).

About the muscular system, which appears to be of generalized mammalian type, one possible difference from the human should be noted: the fibres of the thyroarytenoid muscles do not insert into the vocal folds, as Goerttler-1951 described in man (Avril). Of the thyroarytenoid folds, the inferior show a sharp upturned edge (Figures 29 and 30) which seems to accord with the brachiation and arboreal habitat of the chimpanzee (see p. 65).

The chimpanzee larynx is actively involved in *sound production*. Observations on voice and "speech" have been made by Garner-1896, Yerkes & Learned, Kohts, Nissen, Hayes and Andrew-1963*a*, -*b*.

In regard to the physiology and ontogeny the same remarks apply as to the Rhesus monkey. More about the laryngeal anatomy and differences from other Hominoidea can be found in Avril, Kleinschmidt-1950, Negus-1949, -1962 or Starck & Schneider. The latter also give an illustration of a foetal chimpanzee larynx. A detailed account of the biology of the chimpanzee is given by Yerkes & Yerkes (1929) and by Yerkes (1943), and a review of behaviour studies by Reynolds & Farrer.

12. *MAN (HOMO SAPIENS)*

As the reader is presumably already sufficiently informed about the anatomy and physiology of the human larynx, this topic will be dealt with briefly.

In most respects the human larynx is like that of other primates, but its *topography* is somewhat different from that in apes. The larynx as a whole lies farther down the neck (Figure 31): in the average adult the inferior border of the cricoid lies approximately opposite the VIth or VIIth cervical vertebra (von Lanz & Wachsmut), the most caudal point of the laryngeal entrance being about opposite the C IV (Negus-1949, -1962). There is thus a considerable distance between epiglottis and palate, which is greater because the palate is short, in accordance with the reduction in size of the jaws compared with the apes. The axis of the airway in the laryngeal entrance runs from caudally and somewhat ventrally to cranially and somewhat dorsally. The larynx projects into the pharynx by means of the epiglottis and the aryepiglottic folds, which are rather poorly developed compared with other mammals. Adult man thus has rather

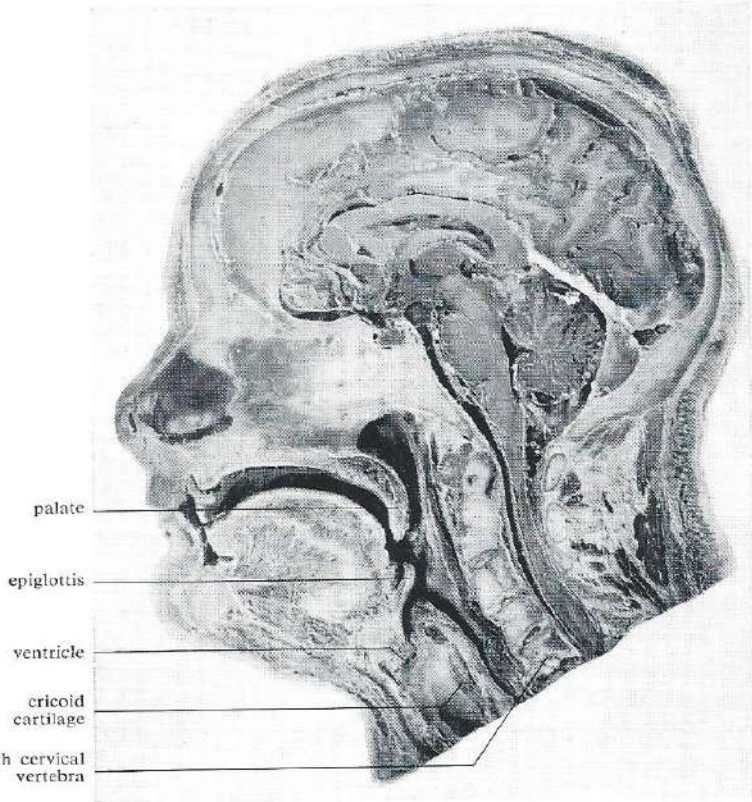


FIG. 31.
Man (*Homo sapiens*), ♀, 71 year old. Sagittomedial section through head and neck. $\frac{1}{3}$×.

poorly functioning lateral food-channels and food passes over the epiglottis rather than alongside it (Hafferl).

The *skeleton* essentially consists of the same elements as in other mammals: arytenoids, cricoid, thyroid, epiglottis and the small cartilages of Wrisberg and Santorini.

The morphology of the skeleton is about the same as that of the chimpanzee; the capacity of the airway impresses one as being relatively smaller, whereas the comparative size of the arytenoids in the dorsoventral direction seems to be somewhat larger.

The soft tissues including the muscular system are much like the chimpanzee's. Again we find downturned upper thyroarytenoid folds and upturned lower thyroarytenoid folds, also called false and true vocal cords; the latter, however, showing a more triangular shape on cross-section. Between the two folds a quite small ventricle is present. The space between the true vocal cords forms the narrowest point in the airway. It has roughly the shape of a triangle whose apex in a maximally opened larynx subtends about 30°.

Though apart from the air-sacs the human larynx shows few morphological differences from that of the chimpanzee and the other apes, it is evident that in regard to its *function* it reaches a higher level: its muscular control and the resulting vocalization seem to be better developed than in any other animal. This characteristic of the human larynx may play a part in speech, and may be reflected morphologically in the great number and the special arrangement of mitochondria in the internal part of the thyroarytenoid (or vocal) muscle reported by Berendes & Vogell. Zenker & Anzenbacher, and Anzenbacher & Zenker found by histological examination of the vocal muscle fewer cholinesterase-positive receptors in monkeys than in man. There seems to be some indication for a typical human arrangement of the muscle fibres in the vocal folds as described by Goerttler-1951, but such an arrangement is denied by Mayet-1955 and Sonneson.

There are some morphological differences between the different human races as far as the larynx and other speech organs are concerned (Gibb, cited by Darwin-1875 on p. 566, Duckworth, Brosnahan, Wilson), which do not, however, seem relevant here.

The ontogeny of the human larynx is described in detail in Chapter 5.

CHAPTER 4

Discussion of the phylogeny of the human larynx

Having reviewed the larynx in a series of animals which were supposed to represent man's ancestors, we may try to discover some continuity in these descriptions and thus establish its possible phylogeny. For this purpose a number of topics will be discussed in the various species: their topography, skeleton, relations with branchial system, musculature, larynx as a protective, respiratory, valvular and communicatory organ, the emergence of speech, and other functions.

1. *TOPOGRAPHY*

As far the position of the larynx in the body is concerned, it is invariably found in the ventral part of the pharynx, caudal to the tongue. However, its relations to other organs clearly show variation in different species. From a functional point of view the relationship to the choanae is the most interesting (Figure 32).

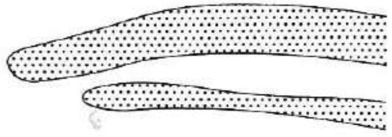
In *Polypterus* there are no internal nostrils. In *Protopterus* the choanae, if they may be called that (see p. 15), are located in the upper jaw just behind its anterior border. There is thus a relatively great distance between the choanae and the laryngeal entrance. This suggests that there is no functional relationship between these organs; indeed *Protopterus* is seen to inspire with its mouth wide open (Figure 9), and the nose probably has no respiratory function. Observations on the respiratory mechanism of other lungfish are unknown to me.

In salamanders there is some distance between the choanae and the larynx (Figure 13), but a functional relationship between them does exist, since in Urodela the nose is in fact used for respiration. The same applies to the frog and other Anura, which also breathe through their noses. But in all amphibians the interrelationship is not a close one, due to the distance between these structures.

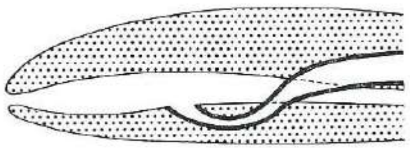
When we come to the *crocodile* however, we find the larynx, hyoid and the choanae constituting an anatomical and functional unit which enables the animal to breathe with only the tip of its nose above the water, meanwhile shutting off the respiratory system from the digestive tract. In this respect the crocodile bears some resemblance to mammals. In gymnures (Figure 20), tree-shrews (Figure 25), Rhesus monkeys (Figure 27) and most other mammals, we find the same sort of functional separation between the respiratory and the digestive tract: the epiglottis shows close contact with the palate, whereby the air-current passes directly from the nose into the larynx and back. But that the topography in crocodiles really represents that of the ancestral mammal-like reptiles is improbable, since many other reptiles show a gap between the choanae and the larynx (Göppert-1937), and these could equally be taken to illustrate the ancestral reptile anatomy. Moreover, in the crocodile the close contact between the laryngeal entrance and choanae, and the separation between the respiratory and the digestive tract is formed by other structures than in mammals (*viz.* by the hyoid, against the epiglottis and the aryepiglottic folds in mammals).

The topography in *Sphenodon* would be of interest, but from the literature one cannot get a reliable idea about it. Even the detailed studies of Günther, Osawa, O'Donoghue and Fürbringer-1922, do not mention it, though from their illustrations one gets the impression of a small gap between the larynx and the choanae. On the other hand the turtles, belonging to the very ancient Order Chelonia, show a close relationship between the choanae and the larynx (Göppert-1901).

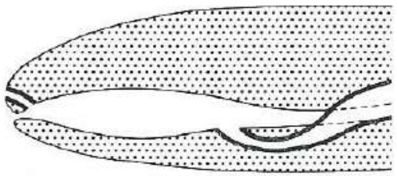
So the resemblance between the laryngeal topography in



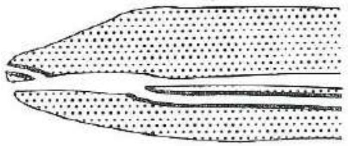
1. Agnatha



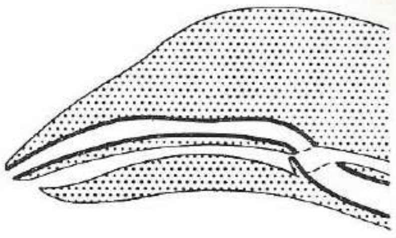
2. Primitive fish *(Polypterus, Protopterus)*



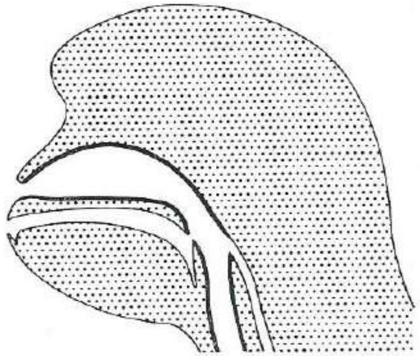
3. Amphibians



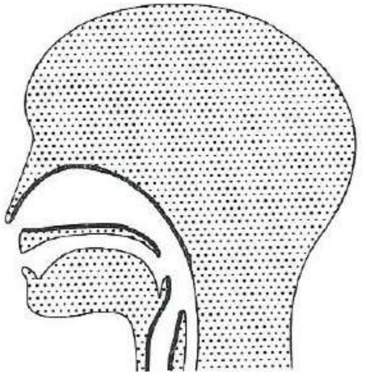
4. Reptiles



5. Primitive placental mammals



6. Catarrhine monkeys



7. Man

FIG. 32.
Schematic illustration of the possible evolution of the upper airway (thick lines) during human phylogeny as indicated by some modern species. (In *Protopterus* the nostrils are not pictured because they have no function in breathing and because they are not homologous with those of higher vertebrates).

mammals and in crocodiles may very well be the result of convergent evolution by adaptation to a secondary aquatic habitat by the crocodile rather, than representing a stage between amphibians and mammals.

From a functional point of view, the crocodilian anatomy may be considered as being at a lower developmental level than the mammalian: though separation between the two tracts is made possible, presumably only one can be used at a time because the epiglottis-like projection of the hyoid extends along the full width of the pharynx. In mammals both tracts can function at once, because the larynx only projects upwards into the pharynx *medially*, thus allowing food to be swallowed lateral to it through the "lateral food channels".

What, then, was the situation in man's *mammalian ancestors*? In the Lesser gymnure we find a high antevelar position of the epiglottis (Figure 20), with well developed aryepiglottic folds, as in other insectivores (Starck & Schneider) and many other mammals, by which good lateral food channels are established. When we come to the Tupaioidea and Lemuriformes, there is still close contact between the palate and epiglottis, but the aryepiglottic folds are somewhat degenerate (Starck & Schneider), whereas in the Rhesus monkey we see the epiglottis just reaching the palate (Figure 27), the aryepiglottic folds being relatively less well developed.

Finally in the Hominoidea one finds in the chimpanzee (Avril, Bernstein, Negus-1949,- 1962), the gorilla and the orang-outang (Negus- 1949, -1962) a small gap between the palate and the laryngeal entrance. (It is true that R. Brandes found the epiglottis in a retrovelar position in the orang-outang, but this might be an artifact, according to Starck & Schneider and Avril; DuBrul reports the epiglottis in the chimpanzee just touching the velar tip). In man this gap is much larger (Figure 31), but here, too, the laryngeal entrance protrudes somewhat into the pharynx by means of the epiglottis and the aryepiglottic folds.

In several respects this anatomy is important for mammals. Firstly, in regard to a function related to the very name of this class, sucking, which can be performed without interference with breathing. This circumstance, already described by Bowles in 1889, is of vital importance to mammals, with their necessarily high frequency of respiration due to their intense metabolism, requiring more oxygen than do poikilothermic animals. Human infants with choanal atresia may actually die of it (Stupka), and other mammals with the same malformation may die of starvation soon after birth. Secondly, this topography is important for adult mammals with a herbivorous and liquid diet, such as the ancestral arboreal primates were possibly accustomed to. These animals need more food than the carnivores and thus spend a great part of their life eating and swallowing, during which they continue to breathe. Moreover this food, being most often liquid or semi-liquid, would tend to enter the lower airways. Thirdly, during eating the sense of smell, which acts as a warning system in many mammals, can be used all the time and is not interfered with by the smell of the food (von Bonin, Vallancien). Also Negus-1927, -1949, -1962 considers the epiglottis to be mainly an olfactory organ.

So the gap between the laryngeal entrance and the palate in man is not homologous with that in amphibians or reptiles, but constitutes a secondary development during primate evolution, partly by a shortening of the palate and partly by descent of the larynx. This development played a part in human evolution by giving greater opportunities for speech, since the expiratory airstream could now voluntary be distributed through the nose and mouth (Negus-1949, -1962, von Bonin, Bernstein, DuBrul & Reed, Kipp), whereas most other mammals are obligatory nose breathers.

When the relations between the food passages and airways in vertebrate evolution are compared, another interesting phenomenon can be observed: the reduction of the former in proportion to the latter. Not only do we see a gradual enlargement of the airways but also a diminution in resistance to the passage of air as a result of a straightening out of the tortuosities, one cause of which is the gradual tilting of the laryngeal entrance (Negus-1949, -1962).

The relationship of the larynx to other organs, namely the *heart* and *cervical vertebrae*, should be mentioned here. In *Polypterus*, *Protopterus* and the amphibians the heart, branchial blood vessels and laryngeal nerves are to be found in the head just ventral to the larynx. Along with the evolution of the neck which, according to Reiter and Rensch-1959, must already have been present in the primitive reptiles, offering greater mobility of the head and thus more chance of observing the surroundings and catching prey, the heart, together with the caudal branchial blood vessels and nerves, moved caudally into the thorax. This displacement caused the loss of the clear metameric anatomy of the branchial muscles, blood vessels and nerves, resulting in the typical course of the recurrent laryngeal nerves. Compared with the *base of skull*, the laryngeal aperture shows a quite constant position just ventral to it during the evolution of the vertebrates up to the higher primates. In the primates there is a tendency for displacement in a caudal direction. The deepest descent of the larynx is seen in adult man, in whom the most caudal point of the aperture lies opposite the C IV whereas in most animals it is opposite the base of the skull or C I.

According to Bernstein and Starck & Schneider, the inferior border of the cricoid lies opposite CII-C IV in Rhesus monkeys, in the chimpanzee opposite C IV-C VI and in adult man C VI or C VII.

The human topography has some *pathophysiological* consequences. (1) The elongated course of the recurrent laryngeal nerves make them much more vulnerable than the laryngeal nerves in the lower vertebrates: intrathoracic diseases frequently cause damage to them. (2) The downward position of the larynx in the neck can cause asphyxia in unconscious people, because the tongue can fall backwards and obstruct the pharynx and the laryngeal entrance. This is less likely to occur in apes and is highly improbable in other animals (except perhaps in the Sirenia like the Manatee *Trichechus manatus* which has a very small degenerate epiglottis that does not reach the palate).

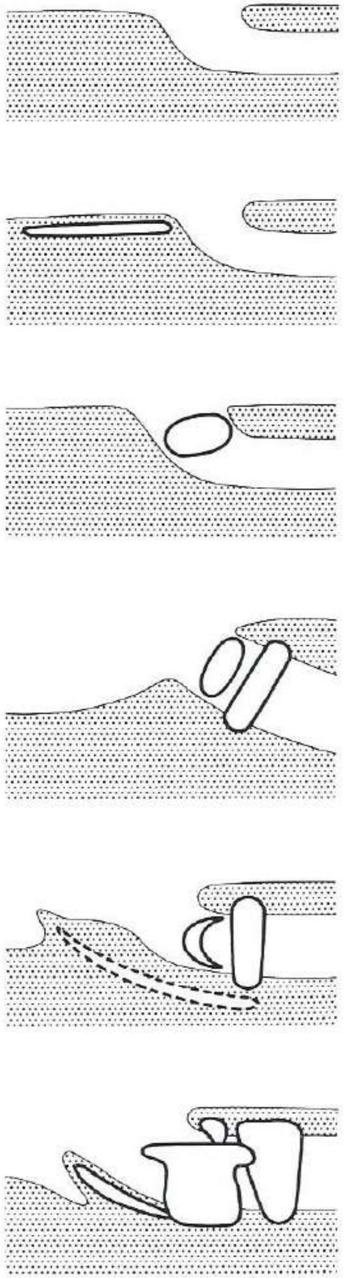
The size relationship between the airways and the food passages is discussed in §6 of this chapter.

2. *SKELETON*

The first larynx in our series, that of *Polypterus*, is without any supporting skeleton (Figures 33 and 34). However in *Protopterus* we find a fibrocartilaginous plate in front of the laryngeal entrance (Figure 11). Whether the amphibian ancestors possessed this structure seems uncertain; in other lungfish genera a similar cartilage may appear, present in the Australian form *Neoceratodus* since Negus-1949, -1962 reported it, though Wiedersheim, cited by Göppert-1937, denies its existence. Negus-1949, -1962 found no such cartilage in the South-American lungfish *Lepidosiren*. If this cartilage is considered representative, it could be the precursor of the arytenoids and not of the epiglottis as is suggested by Bisschoff, Howes-1887, R. Dubois and Young.

Its two small caudal processes are interesting, because they are present alongside the laryngeal fissure (in its anterior part) and thus remind one of the arytenoids of higher animals. So it could be that the anterior laryngeal cartilage of the *Protopterus*-like ancestor evolved into the *arytenoids* of the amphibian ancestor by division in two parts. It is however also possible that the arytenoids developed spontaneously in the proto-amphibian. Anyway, there is sufficient evidence for assuming that the first amphibians possessed a pair of cartilaginous bars alongside their laryngeal entrance, and most probably these arytenoids may be considered phylogenetically to be the oldest part of the laryngeal skeleton. They represent a level of development higher than that which must have been present in previous forms by making more efficient use of the larynx possible: a cartilaginous reinforcement alongside the whole length of the laryngeal aperture on which muscle fibres were inserted, presumably resulted in a larger opening of the larynx during respiratory movements.

The arytenoids remained the only laryngeal cartilages until (preceded maybe by non-circular cartilages as in the modern Urodela) the *cricoid* developed, because we see it in the modern Anura, which could be an indication for their presence in the Labyrinthodontia. The evolutionary history of the additional small cartilages of the frog's larynx remains obscure; they may be the homologues of the "tracheal" cartilages of the Urodela. It is not clear from a functional point of view if the presence of the cricoid in the frog's larynx may be considered to be a higher level of



1. Nile ganoid *Polypterus*

2. African Lungfish *Protopterus*

3. Salamander *Amphiuma*

4. Frog *Rana*

5. Crocodile *Osteolaemus tetraspis*

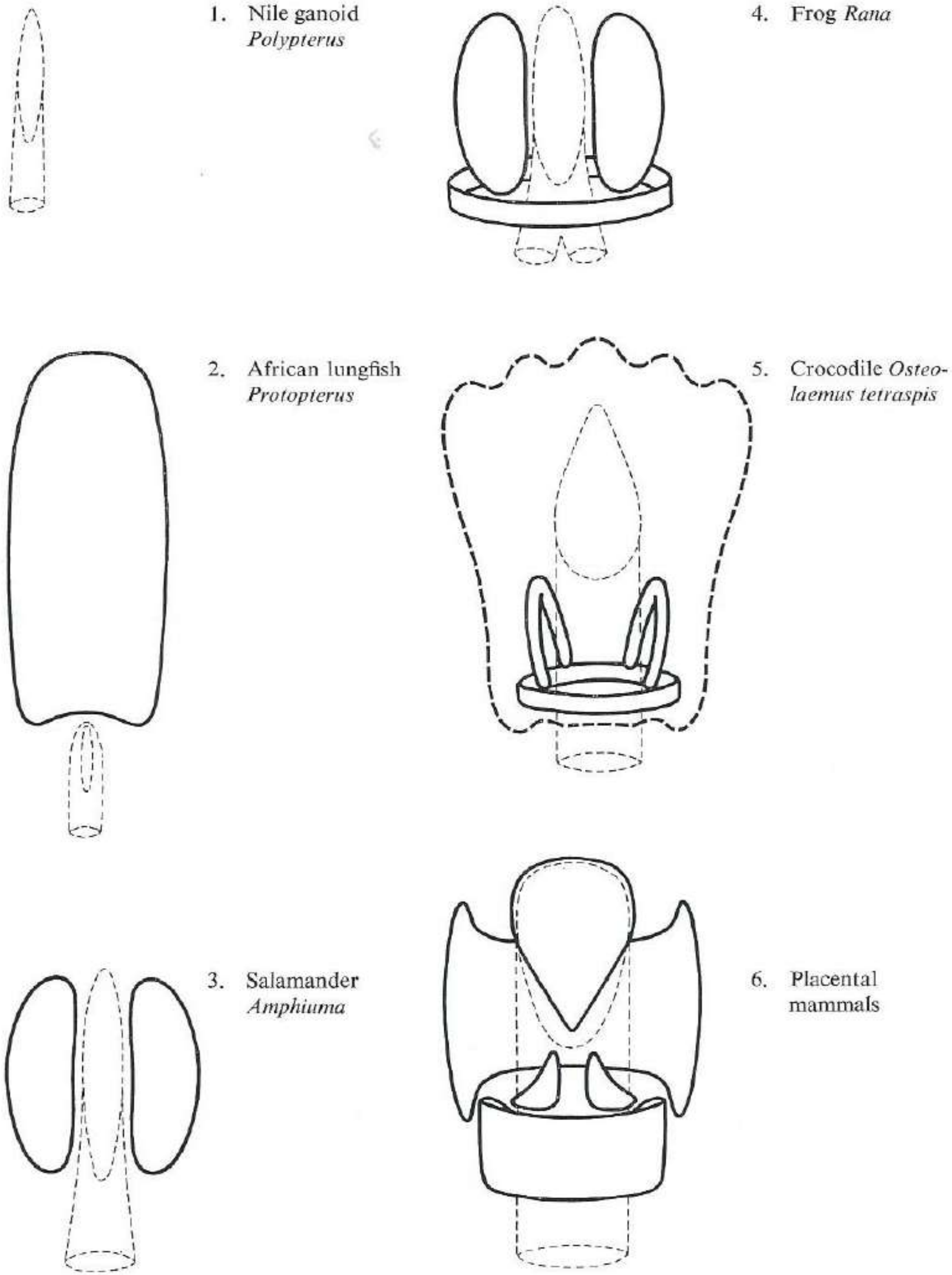
6. Placental mammals

FIG. 33.
Possible evolution of the laryngeal skeleton (thick lines) during human phylogeny, illustrated schematically by some modern species. The hyoid though not belonging to the laryngeal skeleton has been indicated in the crocodile by a dotted line because of its close anatomical, functional, and possibly embryological relationships to the larynx. Lateral view.

development: it provides an origin for the dilating muscles and may have some protective function, but the greater capacities of the anuran larynx in regard to the amount of air passing through it, are more likely to be explained by its relatively greater size as compared to the larynges of lower animals. Nor in regard to sound production does the cricoid seem to have any important function.

In reptiles and mammals, on the other hand, support of the airways by the cricoid and the tracheal cartilages is useful, because during inspiration in most reptiles and in all mammals there is a negative pressure in the larynx and trachea: inspiration here is the result of lowering the intra-abdominal and intrathoracic pressure rather than raising the intrapharyngeal pressure as in amphibians and fish. A second function of the cricoid lies in its giving origin to the dilating muscles. During vertebrate evolution the shape of the cricoid cartilage has remained constant: in all vertebrates it is circular. In most mammals it is dorsally elongated in a cranio-caudal direction, forming the *lamina*.

The laryngeal skeleton in all reptiles including *Sphenodon* (Göppert-1900, -1901, -1937) appears to be composed of the same elements as in the Anura, the arytenoids and the cricoid, and in both groups there is a close morphological and functional relationship between the larynx and the *hyoid*, different from other vertebrates (Figure 18). In reptiles, however, a further development of the hyoid, as compared with the Anura, is not only indicated by its function, but also by its embryological morphology: the structure called the hyoid in reptiles is probably formed ontogenetically from material of the 2nd, 3rd and 4th visceral arches (see Figure 35), the last of which is supposed to give rise to the thyroid cartilage in mammals. Thus part of the reptilian hyoid can be considered to be homologous with the mammalian to which, at least in crocodilians and in *Sphenodon*



1. Nile ganoid *Polypterus*
2. African lungfish *Protopterus*
3. Salamander *Amphiuma*
4. Frog *Rana*
5. Crocodile *Osteolaemus tetraspis*
6. Placental mammals

FIG. 34.
Possible evolution of the laryngeal skeleton during human phylogeny, illustrated schematically by some modern species. The dotted lines indicate the laryngeal entrance and the airway. The hyoid though not belonging to the laryngeal skeleton has been indicated in the crocodile by a dotted line because of its close anatomical, functional, and possibly embryological relationship to the larynx. Dorsal view.

(Fürbringer-1922), it bears some resemblance in shape. When therefore the reptilian cricoid is called a "crico-thyroid" by Henle (p. 44) and Negus-1949, -1962 (p. 11), -1965 (p. 94), this does not seem to be supported by accurate embryological observations but appears to be based on a vague similarity in adult reptiles and mammals.

With the origin of mammals two new cartilages were added, the *thyroid* and the *epiglottis*, both of which can be considered from a functional point of view to give the larynx a higher level of development. The former gave rise to the vocal cords (or rather the thyroarytenoid folds); the latter has a function in deglutition, breathing and smelling, as mentioned previously.

There have been several authors who have used the name "epiglottis" in relation to structures in non-mammals, but this is rather confusing because the homology between these structures and the mammalian epiglottis is very questionable. Bisschoff, Howes-1887, R. Dubois, and Young named the laryngeal cartilage of *Protopterus* the "epiglottis". The objections to this name are as follows: (1) The homology is not proved by embryological observations. (2) South-American lungfish, amphibians and most reptiles do not possess a similar cartilage. (3) In *Protopterus* this cartilage has a function different from that in mammals.

In amphibians the name "epiglottis" was propagated by Howes-1887. He found in some Anura a paired fold in the mucous membrane just oral to the laryngeal entrance and associated it with the epiglottis of higher animals. In my opinion the same objections apply to this nomenclature. According to Henle, Göppert-1937 and Negus-1949, -1962 a structure is found in some reptiles, such as the boa and some lizards, which resembles the mammalian epiglottis and which it is therefore called. Though homology with the mammalian epiglottis is not impossible, evidence from comparative embryology is lacking. For a more detailed account on the phylogeny of the epiglottis the reader is referred to Gegenbaur-1892 or Schaffer.

The phylogenetic history of the small cartilages of Santorini and Wrisberg is not yet fully elucidated, though Göppert-1894 finds evidence for the latter being a derivate of the original larger epiglottis present in the Insectivora.

3. *THE LARYNX AND THE BRANCHIAL SYSTEM.*

Along with the development of the larynx during vertebrate evolution, a gradual disappearance can be observed of the clear metameric (or polyisomeric) structure of the branchial system, which makes it probable that material from the branchial system, originally transforming into gills, progressively took part in the formation of the larynx. The development of the branchial system in the ontogeny and phylogeny of a number of vertebrates has been the subject of several studies since the end of the 19th century, and one now has a general though incomplete idea of these developments. The problem is that for good comparison one needs a complete series of ancestral animals, as well as a complete picture of the ontogeny of the vertebrate species concerned, in this case man. The first requirement is evidently very difficult, if not impossible, to fulfill; the second imposes fewer difficulties. For that reason the evidence we have today for the evolution of the branchial system is mainly derived from comparative anatomy and embryology. These reveal that in all vertebrate embryos the presence of the branchial system can be recognized, but the higher the species the less clear it is. So when comparing lower and higher vertebrates one should be aware of homologies: in the past, findings in other mammals have been erronously extrapolated into human embryology and anatomy, whereas it later turned out from further study on the human embryogenesis that seemingly homologous structures in fact have a different origin. This is clearly illustrated in the thymus by de Beer.

Another difficulty arises from the numbering of the branchial elements: when comparing the number of these elements in those Chordata (the phylum to which the Subphylum Vertebrata belongs) which may represent the successive ancestors, one sees in course of their evolution a decrease in their number (Figure 35) together with a gradual specialization of these elements, which is in full accordance with "Williston's law".

In 1914 Williston showed from numerous palaeontological findings that during the evolution of reptiles there is a steady decrease in the number of skull bones. He concluded that there is "a law in evolution that the parts in an organism tend toward reduction in number, with the fewer parts greatly specialized in function. . ." (p. 3). Similar statements had been made earlier e.g. by T. H. Huxley in 1880 concerning the evolution of the foot in horses. In 1933 Gregory worked out these statements and called it "Williston's law" and in 1935 gave it a wider appliance, namely to the skull bones from the earliest vertebrates up to man.

Independently a more general application of this principle (change from polyisomerism into oligoanisomerism) had been visualized by Bronn in 1853 and 1858, and Barge in 1937, and according to Remane-1956*b* at the beginning of the 19th century by Treviranus. Goethe seems to have had ideas in this direction (Franz-1920, -1924, Uschmann). However, it should be emphasized that all these 19th century authors considered this "polyisomerism *v.* oligoanisomerism" as applying exclusively to "lower" and "higher" *i.e.* modern species, and they apparently did not see it in an evolutionary setting.

Though it should perhaps have been called a rule rather than a law, because there are in the science of evolution few laws in the strict sense of the word (Olson), this principle is in my opinion neglected too much in most considerations of vertebrate evolution, because it is not limited to the skull bones or branchial elements, but can equally be applied to a number of other structures during vertebrate evolution and possibly even to functional characters. For a discussion on this subject the reader is referred to Remane-1956*b*, Franz-1920 or Uschmann.

It is hard to say how many of these branchial elements must have been present in the Ordovician or Silurian stem chordate, because palaeontological evidence is lacking. If we consider modern Amphioxus, however, as being indicative for these early chordates (Young), we may assume that the ancestors of the vertebrates possessed a larger number of branchial elements than the vertebrates themselves.* It is equally difficult to find out which of the supposed original multitude did remain during evolution to form the average of 9-15 in the ostracoderms (Stensiö) meanwhile changing their function from a digestive to a respiratory one. This applies equally to the evolution from ostracoderms into placoderms. Since the appearance of the placoderms things seem to be less obscure, because in most higher vertebrates only 7 elements can be found and it is generally accepted that these are homologous. In comparative anatomy their mesodermal reinforcements are commonly called *visceral arches* (*Kiemenbogen* or *primäre Bogen*, Gegenbaur-1892) and they are numbered from head to tail. A rather confusing habit is calling the 3rd-7th visceral arches the 1st-5th *branchial* arches, but the terms are in common use in mammalian and human embryology and can probably be explained on historical grounds.

The data in the diagram in Figure 35 are obtained from different sources (amongst others Gegenbaur-1892, Gasc, Romer-1950, Starck-1965*a*, -1967, Starck & Schneider, and Wustrow) and correspond to each other in the main. A somewhat aberrant view is given by Noble (p. 169), who supposes the laryngeal cartilages of the amphibians to originate from 8th and 9th visceral arches.

The reader should be reminded of Figure 2 which can be applied to this matter: in the process of evolution all the larynges showed a common stage during their individual development, one in which the branchial elements are present, but with evolution came a progressive divergence, and in human embryos metameric division of the branchial system is only vaguely discernible. In adult mammals a metameric arrangement of the laryngeal skeleton can be recognized in the monotremes, such as the spiny ant-eater *Echidna* (E. Dubois, Gegenbauer-1901, Symington-1900 Göppert-1901, Negus-1949, -1962), whose thyroid cartilage consists of two fused U-shaped parts. Already in 1839 Henle supposed the thyroid foramen of modern mammals to represent a phylogenetically older division of the thyroid into an cranial and caudal part.

In several species the hyoid apparatus of adults bears a resemblance to the two visceral arches of which it was originally composed.

For a discussion on the metameric characters of the branchial system in primitive and higher chordates the reader is referred to Dalcq & Pasteels or to Starck-1965*a*.

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* About the maximal number of branchial elements in modern Amphioxus, *Branchiostoma lanceolatum*, there is no unanimity in the literature: Sewertzoff-1931 reports 90, Starck-1965*a* 100, Gasc 180 and Young 200. It may depend on the individual's age (Young).

stem chordata	Agnatha	Teleostei	Amphibia	Reptilia	Mammalia	*Visceral arches*
about 100 branchial elements?	9-15 branchial elements	jaw, Meckel's cartilage	columella, Meckel's cartilage	Meckel's cartilage	Meckel's cartilage, malleus, incus.	*1*
		hyoid	hyoid	hyoid (basihyal)	cornu minus hyoidei (*Homo*), proc.styloid., lig.stylo-hyoid., stapes.	*2*
		gill bar	gill bar	hyoid (thyrohyal	cornu majus hyoidei (*Homo*)	*3 (=1st branchial arch)*
		gill bar	gill bar	hyoid	cartilago thyreoidea	*4 (=2nd branchial arch)*
		gill bar	gill bar *(rudimentary)*	*(absent)*	cartilago thyreoidea	*5 (=3rd branchial arch)*
		gill bar	gill bar *(rudimentary)*	*(absent)*	cartilago epiglott.?	*6 (=4th branchial arch)*
		gill bar (rudimentary)	cart. lat.? (cart. aryt). cart. cric.?	cart. aryt.? cart. cric.?	cart. aryt.? cart. cric.?	*7 (=5th branchial arch)*

FIG. 35.
Diagram illustrating the probable homogies of the branchial arches in the Chordata (from different sources, see text).

For a complete review on the hyoid apparatus in vertebrates see the detailed study of Fürbringer-1922 or the more recent one of Gasc (1967) and for a general discussion on metamerism Remane-1950.

4. *MUSCULAR SYSTEM*

In securing the primary functions of the larynx, protecting the lungs and offering passage to air, the muscular system plays the central part, the sphincter muscles in regard to the former function and the dilating muscles to the latter. These two systems can be recognized in all species representing the human ancestors, but with the increasing complexity of the larynx during vertebrate evolution, the muscular system differentiated into a number of mostly paired elements connecting the newly evolved parts of the laryngeal skeleton. Because the latter is closely related ontogenetically and phylogenetically to the branchial system, the same can be said of the laryngeal muscles, which may be supposed to originate from the branchial musculature. However, their precise relationship to the branchial system is even less clear than that of the laryngeal skeleton. Göppert has occupied himself in finding homologies between the laryngeal muscles in the different species. I have not been able to check these homologies personally, and the data in Figure 36 are based on Göppert and others (Wustrow, Starck & Schneider, von Lanz & Wachsmut). Before considering the possible homologies, it may be useful briefly to review the conditions in the various species.

In *Polypterus* we find a simple sphincter round the glottal fissure. Active dilatation in this species is questionable (Figure 8). The precursor of the amphibians, illustrated by the lungfish, probably possessed a more highly developed muscular system, equipped, next to a surrounding sphincter, with specialized dilating fibres, in *Protopterus* running transversely through the sphincter fibres (Figure 12). In primitive amphibians a clear division is visible between these two systems, and the sphincter muscles appear to be divided into a ventral and a dorsal portion. According to Göppert-1937 this division can be recognized in all higher vertebrates as well. Because the muscles in the Urodela give the impression of being stronger than those of the lungfish, it is probable that in the early amphibians too the larynx worked more effectively, as it could open wider. The same applies to the anuran larynx, though this seems to be based on its relatively larger size rather than on the characters of the muscular system proper. The latter differs from that in the Urodela in the origin of the dilating muscles, which is to be found on the pharynx in the Urodela (Göppert-1895, -1937). Their attachment from the Urodela onwards is invariably the arytenoid cartilage, in the amphibians often distributed along its lateral surface.

In association with the increased air passage the reptilian larynx possesses stronger muscles. The dilating muscle fibres originate exclusively from the cricoid, and are inserted into a relatively smaller area of the arytenoids which in Crocodilia are situated at the caudal end of the triangular laryngeal aperture (Figure 18). In mammals, next to the ventral and dorsal sphincter, an external sphincter is added consisting of the paired cricothyroid muscles, which are supposed to be a derivative of the 4th visceral arch, and the laryngopharyngeal muscles, which possibly evolved from the sphincter muscle fibres round the pharynx of lower vertebrates (von Lanz & Wachsmut, Jordan). The insertion of the dilating fibres is again to be found in a specialized area of the arytenoids, the muscular process.

The continuity we are thus able to recognize when reviewing the muscular system in the consecutive vertebrates consists of (1) increasing strength, (2) division of the single sphincter in the lungfish into a ventral and a dorsal portion in the higher species, (3) displacement of the origin of the dilating fibres from dorsally to ventrally, and (4) increasing concentration of the insertion of the dilating fibers on the arytenoid and parts of it.

5. *THE LARYNX AS A PROTECTIVE ORGAN*

Reviewing the development of the larynx during the phylogeny of man since its first appearance in the placoderms, it has shown a steady rise in qualities. Apart from its function

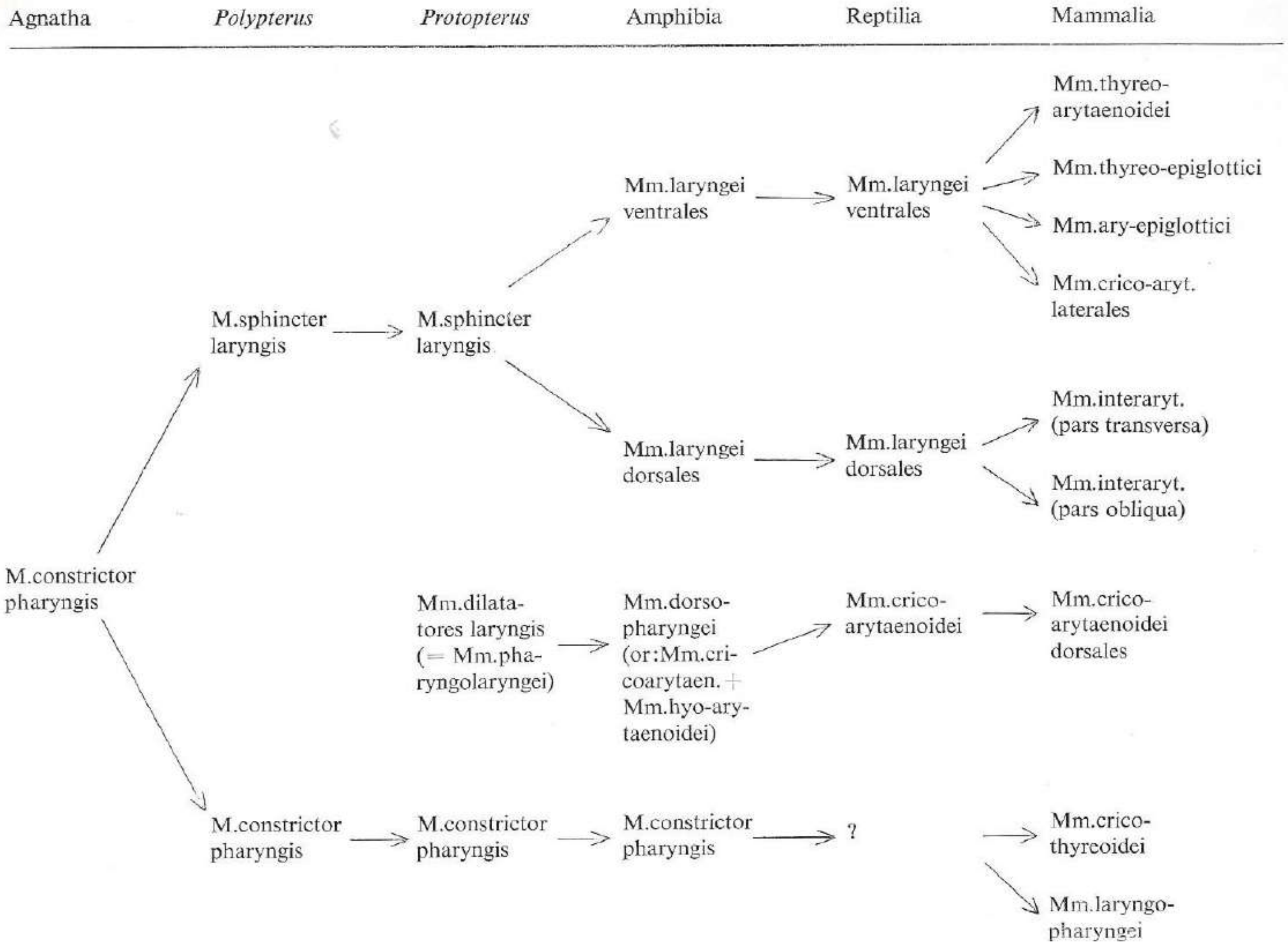


FIG. 36.
Diagram indicating the possible homology (and evolution) of the laryngeal muscles in the vertebrates. *Polypterus* and *Protopterus* are supposed to represent the primitive early fish and the amphibian's ancestor respectively.

as a communication organ, this mainly applies to its capacities for air passage. However, when we consider what was possibly its oldest function from the phylogenetic point of view, which is, as may be concluded from the present study and others the protection of the lungs (Negus-1924, -1929, -1957b, -1962, Lullies, Berendes, Pressman, C. Jackson, Wilson, Némai-1926*b*, Terracol *et al.*), we see no clear upward evolution. On the contrary, in this respect the mammalian and not least the human larynx could even be considered to possess *fewer* qualities than those of lower species. It should be emphasized, however, that in all man's ancestors with lungs such a protective mechanism *must* have existed because of its survival value.

Let us first consider *Polypterus*. Inspiration takes place here only in abnormal conditions, the passage of air through the larynx being an exception. When it actually does occur a small amount of air is taken in by the mouth, after which the mouth is shut and the bolus of air swallowed, during which manoeuvre the larynx is opened for a very short time. Thus the rarity of inspiration, the small size of the laryngeal aperture and the protective ciliated epithelium make aspiration of foreign material (water etc.) unlikely. The same applies to lungfish, in which on the other hand the higher respiration rate may possibly increase the risk of aspiration.

Inspiration in *amphibians* takes place through the nose and the inspired air stays a short time in the mouth, which possibly acts as a warning system, after which the larynx is opened for a moment to allow the passage of air. Moreover in Anura there is an effective valvular protection. Hence in amphibians penetration to the lungs by foreign material via the larynx is unlikely.

When we comes to the ancestral *reptiles*, however, these conditions seem to have changed. Along with the greater activity of the reptiles and the increase of dead space due to the development of the trachea associated with a greater oxygen demand, the respiration rate rose and the laryngeal aperture widened. It is not impossible that it remained open during the period of rest between the respiratory movements; at least this is to be observed *post mortem* in crocodiles (Figure 17), though other modern reptiles like lizards do not show this so clearly and though Boelaert reports closure between respiratory movements in alligators and lizards. Protective nose breathing is likely to have existed in ancestral reptiles because it is used by all modern ones.

In accordance with their increased oxygen requirements, the larynx in *mammals* is necessarily open throughout most of their lifetime, and this is one of the reasons that aspiration of foreign material in abnormal conditions is more likely to occur than in the lower animals. As we have seen in the section Topography of this chapter, many mammals are obligatory nose breathers and in these species, including the gymnure, tree-shrew and Rhesus monkey, the lungs are protected by (1) the ciliated epithelium, presumably also present in the respiratory tract of lower animals, (2) the mechanical barrier of the nose (external nostrils with hairs, and mucous membranes), (3) the sense endings of the glossopharyngeus and vagus nerves in the pharynx, larynx and lower respiratory tract which when stimulated cause *reflex closure* of the larynx or *coughing*.

Protective closure of the larynx in man, and therefore presumably in other mammals, is most often the result of stimulation by the food bolus in the posterior pharynx. Probably less well known is a reflex originating from the mucous membranes of the nose as described by Sercer, which is understandable from a phylogenetic point of view.

It is not improbable that the inspiratory cry many people produce seemingly instinctively when startled, has its roots in a generalized vertebrate pattern for the protection of the lower air passages by closure of their entrance. The squealing of a frightened dog, which according to Scheminzky is inspiratory, may be regarded in this light. The same applies to the sound produced by a frightened frog which, according to C. Jackson, results partly from sudden closure of its larynx. Stein (p. 49), in his discussion on the ontogeny of speech, concludes: "... the glottal stop, which was originally designed to protect the body from material danger, has in the course of time become a symbolic attitude towards any danger and consequently a symptom of fearful anticipation". Andrew-1963*a*, -1964 too in his discussion of protective responses in mammals, considers glottis closure to be one of them (and even suggests it having given origin to mammalian vocalization).

For the rest, *voice production during inspiration* in man is too common to be interpreted solely as a reflex sign based on fright. It is a normal way of voice production in infants (Nadolecny); in children and stammerers it is frequently encountered (Sokolowsky, Kelemen-1932) and ventriloquists also use it (Tschiassny). True inspiratory words are reported by Panconcelli-Calzia to exist in a Camerounian language. Sapir-1921, Gray, Stein and Moses describe inspiratory words in the Hottentot and Bushman languages, but here, as in some cases in Western culture which Moses considers to have a neurotic significance, these sounds are due to a negative *intraoral* pressure rather than to a negative *infralaryngeal* one, and are therefore better not called inspiratory. Kelemen-1932 feels that the ape's inspiratory voice might be an expression of pleasure.

Coughing in potential mouth breathers like apes, man, and some Carnivora is sometimes the only protection; indeed only in mammals is it both useful, as mentioned above, and possible, requiring the powerful mammalian expiratory muscles and a closing system of the larynx of such effectiveness that it withstands considerable infralaryngeal pressure. Though coughing in reptiles with the most highly developed respiratory system like the crocodilians does not seem absolutely impossible, it was never observed by Anderson-1967 during his drowning experiments on alligators, nor did information from several zoos reveal such a phenomenon.

These characteristics of human anatomy and physiology to which should possibly be added the exaggerated influence of gravity due to his upright posture, are probably why man coughs more frequently than any other species. The other reasons are (1) the high incidence of respiratory disease, which exceeds that in other species, (2) pollution of the inhaled air, for instance by smoking, (3) the presence of what in terms of comparative psychology may be called *displacement* phenomena in human respirational behaviour patterns. Ethologists speak of displacement when the actual utterance does not belong to the motor pattern of the instinct that is activated at the moment of observation (Tinbergen-1951, -1965), e.g. coughing is often used to attract attention and can often be considered as a display of confusion or shyness.

In association with mouth breathing the above animals appear to have the most effective way of coughing with their exit valves formed by the down-turned upper thyroarytenoid folds. In man not only do the two pairs of thyroarytenoid folds protect the lower airways, but also the sphincter formed by the aryepiglottic folds and muscles which, according to Pressman, is more effective in preventing entrance by foreign bodies than the thyroarytenoid folds.

What, then, is the *pathophysiological consequence* of these human conditions? Aspiration of foreign material is no exception in human pathology, and may be due to dysfunction of the nervous warning system such as lowering of the state of consciousness, intoxication, neurological disease etc., and it even seems to be the rule in elderly people, according to the observations of Pontoppidan & Beecher. Man deprived of his exit valves, e.g. after laryngectomy, may have considerable difficulty with coughing and thus the clearing of the lungs.

6. *THE LARYNX AS AN ORGAN OF RESPIRATION*

When comparing the relationships between the cranial food passages and airways during vertebrate evolution, an interesting phenomenon can be observed, the reduction of the former in proportion to the latter. The respiratory tract, once an insignificant appendix of the foregut, became from a morphological point of view its equivalent or even its dominating partner. Negus-1925 pointed out that in mammals the oesophagus is suspended from the larynx, whereas in lower vertebrates the larynx is suspended from the pharynx. Not only do we see a gradual enlargement of the airways, but also a diminution in the resistance encountered by the air, due to straightening out of the tortuosities. These changes are in accordance with the increasing use of air in the successive species. In this development the larynx also played its part; however, it would be too bold to state that the *pharyngolarynx rate* or the *size of the laryngeal opening* can be considered as the only deciding factor for oxygen intake, for this is also dependent on a number of other factors such as the calibre of the other respiratory passages, the frequency and duration of respiratory movements, the structure of the lungs, the chemical characteristics of the transporting and storing tissues, e.g. the blood and muscles, and the physical characteristics of the circulatory system. So, only after taking these factors into account, may one in comparative physiological studies consider the ratio of the cross-section of the maximally opened laryngeal aperture to the body weight as a measure of the larynx in regard to the passage of air.

Such observations may never have been published, and they are beyond the limits of this study, but it seems probable that they would reveal an increasing efficiency of the larynx in the series of animals representing man's ancestors, at least up to the monkeys. This hypothesis is based on the *shape of the laryngeal opening*, which is mainly dependent on the size and position of the arytenoid cartilages. On the maximal laryngeal opening in the lower vertebrates we are rather poorly informed. On the mammals we are better informed and Negus-1929, -1949, -1962 demonstrated clearly that the mammals with the best capacities for prolonged running are those with arytenoid cartilages which, measured along the thyroarytenoid folds, are about 0·7 of the diameter of the larynx in length; for in these animals abduction of the vocal processes results in a square and thus maximum opening of this, the narrowest, portion of the larynx (Figure 37). Examples may be given from many ungulates and also the Lesser gymnure and the tree-shrew. Species whose arytenoids are shorter (man and several other mammals) or longer (birds) have a relatively smaller opening in consequence. When comparing the possible conditions in the human mammalian ancestors, a decrease in length of the arytenoid cartilages is observed, necessarily accompanied by a lengthening of the thyroarytenoid folds, giving the human folds greater ease for vocal use, but at the same time making the passage of air more difficult.

As a matter of fact not only the shape of the area of cross-section, but also the relative size of the larynx as a whole has to be considered in such comparative studies. It was again Negus-1929, -1949, -1962 who made observations on the ratio of the cross-sectional area of the maximally opened larynx to the cross-sectional area of the trachea in various species. He found that for a horse it was about 1·1, for some other ungulates and some carnivores about 0·7, and for man (adult woman) about 0·5. Our estimate of this ratio in the Lesser gymnure and the tree-shrew range from 0·8 to 1. The greater ratio in some animals is caused by the shape of the laryngeal opening, and also by its relatively greater size, as shown by the funnel shape seen in sagittal sections (Negus-1949, -1962). Némai and Kelemen-1948 described this shape in the orang-outang, and Kleinschmidt-1938, -1950 performed exact measurements of the angles between the dorsal part of the cricoid cartilage and its caudal plane, from which the same funnel shape appears to be present in other apes. (Though Kleinschmidt-1950 also found in regard to the shape of the thyroid that man has more of a funnel shape than the apes). Man's disadvantageously small laryngeal opening and poor running are compensated for by his intellectual capacities, ability to use tools, his keener sight, etc.

From its site in the respiratory tract and the subtle con-

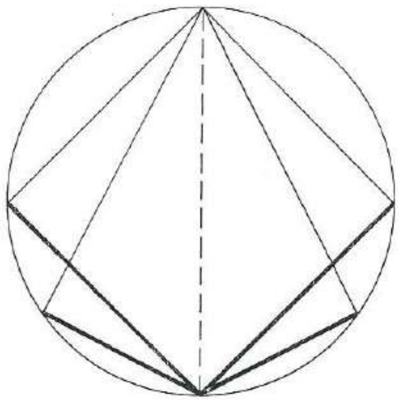


FIG. 37.

Schematic cross-section of the mammalian larynx at the level of the thyroarytenoid folds. Arytenoids (indicated by thick lines) measuring about 7/10 of the laryngeal diameter enable the species concerned to obtain maximal opening of this area, the narrowest in the airway. This condition is found in many ungulates and also, in the Lesser gymnure and tree-shrew (upper thick lines). Man with his shorter arytenoid cartilages has a relatively narrower larynx (lower thick lines). (Slightly modified from Negus-1929, -1949, -1962).

trol of its opening it will be obvious that the larynx is used in several species for *regulation of the volume of air* passing through the airways.

Unfortunately there are but few observations on this matter, and our considerations are therefore speculative. In *Polypterus*, *Protopterus* and the amphibians this mechanism does not seem very important because (1) their morphology does not give the impression of being able to do it, (2) there does not seem much use for it, because the lungs in these species should be looked on as auxiliary respiratory organs, and (3) their oxygen requirements probably do not fluctuate greatly because of their lower bodily activity.

Therefore their laryngeal opening will probably always be about the same size during breathing movements, and though McCutcheon states that such a mechanism exists in amphibians, this does not seem to be supported by actual observations.

From a theoretical point of view, however, its existence in *reptiles* seems more probable where a larger opening during periods of greater activity and higher temperature and a smaller during period of rest would be of physiological significance. This is also reported by McCutcheon, though descriptions of actual observations are lacking. Boelaert, probably one of the few actually to have observed laryngeal movements in reptiles, does not report such movements of the laryngeal entrance in lizards and alligators.

In *mammals*, which show greater fluctuations in their oxygen requirements, and whose larynges show much finer control thanks to their more highly developed anatomy and physiology, regulation of the amounts of air passing into the lungs seems highly probable and is indeed proved by observations.

We know more about such mechanisms in man than in other mammals whose larynges are difficult to observer during life without risk of disturbing the normal movements. Three mechanisms will be discussed here.

(1) During quiet breathing the human inferior thyroarytenoid folds can be seen to *abduct slightly during inspiration* and to *adduct slightly during expiration*. These movements were first described well before the era of laryngoscopy by H. Mayo in 1833 in his *Outlines of Human Physiology*, after his observations of a man who had attemped suicide by cutting his throat (Müller-1840).

This mechanism, probably controlled by a reflex of the vagus nerve, can be considered of great use if one takes account of Bernoulli's law that the pressure in the narrower sites in a tube is lowered when a current of gas or fluid is passed through it. Though Daniel Bernoulli formulated this law already in 1734 (Burckhardt), Bergmann (1845) was probably the first to foresee its importance to laryngeal physiology.

According to Negus-1929, -1949, -1962 and C. Jackson this reflex is under the control of the respiratory centre in the hind brain, stimulated by the CO_2-level of the blood. However, these movements can still be observed in man when he voluntarily raises his respiratory frequency, during which regulation by the CO_2-level would be far too inert a mechanism. A purely neural reflex is therefore also likely to have influence on this regulation. The same conclusion is drawn by Lullies (p. 186) and suggested by Evans (p. 728), Semon (cited by Weiss-1931), Weiss-1914 and von Skramlik.

Thus in modern man *abduction during inspiration* is of vital importance because the area between the vocal cords, even when abducted, forms a narrowing in the airway. Moreover the cords form an inlet valve which has a tendency to close as a result of a reduction in pressure within. The same mechinism is found in the anaesthetized rabbit (Negus-1949, -1962) and cat (Negus-1949, -1962, Floersheim), and in the unanaesthetized dog which is also provided with inlet valves.

I observed the thyroarytenoid folds of 4 tracheostomised dogs (two adult, a ♀ and a ♂, weighing about 16 kg, and two half-grown specimens, a ♀ and a ♂, weighing about 4 kg at the start of the experiment) whose stoma was kept open with canulae, for about 2 months by means of a 90° bronchoscope optic introduced without anaesthesia through the stoma. Neither function nor morphology seemed to be changed by these circumstances. During normal breathing and during panting on exertion the folds made the movements seen in man, slight abduction during inspiration and slight adduction during expiration. During panting related with cooling off the inferior thyroarytenoid folds remained nearly closed, only forming a small ovoid opening in the middle of the relaxed folds. At rest a shallow longitudinal ridge on the dorsal wall of the trachea could sometimes be observed, as can also be seen in the dog's trachea after death. Vallancien seems to have obser vedabduction during inspiration and adduction during expiration, but only in anaesthetized dogs.

Though their larynges may have formed a somewhat less narrow point in their airways the arboreal ape-like and monkey-like ancestors most probably possessed more efficient inlet valves than modern man with thyroarytenoid folds showing sharply upturned edges. Therefore the existence of such a mechanism in these ancestral primates seems very likely.

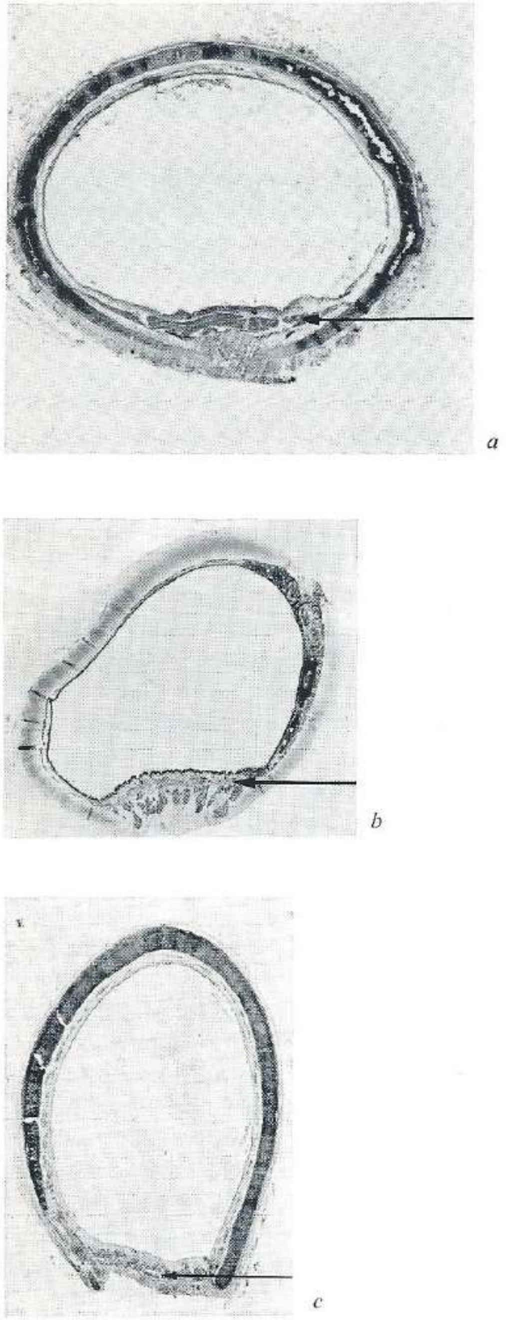
Speculations on its possible existence in earlier ancestors would require intricate aerodynamic calculations because the size of their larynx and the speed of the air currents concerned, probably differed considerably from those in the species mentioned. We can only say that in most species with a larynx, its dilating muscles are of vital importance, the larynx either being closed at rest or being provided with a valve system. Even the horse with its roomy larynx seems to get dyspnoea and die, when its dilating muscles are put out of action by severing the recurrent nerves (Weiss-1914). The degree of closure during expiration in man appears to be due to a subtle regulation dependent on the degree of resistance encountered (Rattenborg).

(2) In man, whose larynx clearly forms a choke in the airway, the vocal folds can be seen drawn apart maximally during periods of raised oxygen need, whereas during normal breathing they form a much smaller triangle with a sharp apex. Hence in man, regulation is limited to enlarging the opening when needed. However, in species with relatively larger air passages the contrary is likely to exist. Here the lungs have to be *protected against too much air* entering when there is no need for much oxygen. The above observations seem to prove that the latter mechanism is present in dogs, who use an increased respiration rate for cooling off by evaporation from the surfaces of their mouth and tongue, during which the thyroarytenoid folds remain nearly closed. (For an analysis of the biochemical and biophysical changes during the dog's panting, see Thiele & Albers). We can only guess about the existence of such a mechanism in man's ancestors. It could have existed in the tree-shrew-like primates.

(3) Another mechanism with the same effect, though not produced in the larynx itself, consists of the *muscle movements within the bronchiotracheal tree*. Negus-1928, -1949, -1962 found that in horse the cross-sectional area of the trachea can be considerably diminished by means of contraction of relatively strong muscle fibres in its dorsal wall, and he supposes it capable of diminishing the dead space in the airpassages and contributing to the expulsion of air. It is probably less well known that dogs are also likely to possess such a control over their trachea, as may be inferred from my above observations.

In man, similar mechanisms are present in the more peripheral airpassages of the lungs (Negus-1928, -1949, -1962, Evans), the trachea being provided only with rudimentary muscle fibres. In man's primate ancestors, which probably had relatively more capacious airpassages, such regulation by the trachea is likely to have played a more important role than in modern man, as seems to be confirmed by the presence of relatively well developed muscle fibres in the dorsal wall of the chimpanzee and monkey trachea (Figure 38). The same cannot be said of the reptiles, whose trachea is reinforced by closed bony or cartilaginous rings and which lack a bronchial tree (Engel).

These mechanisms in mammals are probably part of a feedback system controlling the inflow of blood to the chest and heart which is increased by negative pressure. In lower vertebrates its existence is less likely, because of the absence or limited value of the negative pressure round the heart. It does not seem impossible that the ancestral primates, with their relatively larger larynx, used the latter mechanism. In modern man, active narrowing of the laryngeal opening for building up a negative intrathoracic pressure probably hardly exists except in association with the function of the pectoral muscles (p. 65), because even in periods of great oxygen need and maximal opening, man's larynx offers considerable resistance.



Negus-1929, -1949, -1962 ascribes other functions to the laryngeal movements seen during respiration, namely preventing the peripheral parts of the lungs from collapse by raising the intrapulmonary pressure (effected by an increase in the expiratory resistance), and secondly retardation of the Hering-Breuer reflex.

7. *THE LARYNX AS A VALVULAR ORGAN*

The valve action of the larynx has already been briefly referred to in this study, but a somewhat more extensive discussion considering the larynges of the different animals may be illustrative of the implications of the laryngeal valve actions to the ecology and ethology of the species concerned.

In *Polypterus* we find the laryngeal entrance as a slit in the floor of the mouth, the slightly rounded and elevated edges of which pass smoothly from the mouth into the "trachea". For this reason the *Polypterus* larynx may be considered as hardly possessing any valvular action. In *Protopterus* the edges may be somewhat sharper, and are therefore likely to be pressed against each other when pressure is exerted, as may happen when water enters the mouth while submerged. But in lungfish the sphincter fibres round the laryngeal entrance are probably of greater importance than this valve mechanism in preventing penetration by foreign material.

In amphibians we see in the Urodela a condition very similar to that in lungfish, apart from the presence of quite sharp edges sited on top of a shallow eminence. There is thus a more efficient inlet valve than in *Protopterus*: the lungs can be protected with less muscular effort. In anuran amphibians the laryngeal entrance is found on an hemispherical eminence and has sharp edges. The membranous folds on the

FIG. 38.

Cross-section through the upper part of the trachea of *a*. Rhesus monkey *Macaca mulatta* (age and sex unknown), *b*. chimpanzee *Pan troglodytes*, 3 years old ♂, *c*. man *H. sapiens*, 60 years old ♀. The arrows indicate the muscle fibres in the dorsal wall, which in the monkey and the chimpanzee are relatively better developped than in man in whom regulation of respiration by narrowing of the trachea therefore is of little, if any, significance. *a*. 6,8×, *b*. 4×, *c*. 2,3×.

medial surfaces of the arytenoids act as inlet valves and may work somewhat less effectively as exit valves. These species may therefore be considered as possessing a very effective laryngeal valve system, in accordance with their amphibian way of life. But one should be cautious in considering this condition representative of that in the amphibian ancestors of the reptiles, for the modern Anura have moved away in various respects from these ancestors and are too specialized.

In regard to valvular action, the crocodilian larynx and the reptilian larynx in general do not possess the qualities described in the Anura. We have seen on p. 36 that the crocodilian laryngeal entrance shows only slightly upturned edges which do not protrude into the pharynx, nor are any valvular structures to be found caudal to the aditus, the protection of the lower airways being secured by other structures—flaps of tongue and palate. In other reptiles there is often a prominent entrance with more-or-less sharp edges. I have not been able to discover the situation in *Sphenodon*, though one gets the impression from the figures in Göppert-1900, -1937 that there are rather sharp edges. The detailed studies of Osawa and Günther on *Sphenodon* unfortunately do not deal with this subject at all.

The primitive mammals do not seem to have been provided with clearly developed valvular mechanisms, since neither the Lesser gymnure nor the tree-shrew appears to have them. The more highly evolved primates possibly had such qualities, as seen in monkeys; here and in the higher primates, it is most often not the laryngeal entrance which constitutes a valvular mechanism, but the typically mammalian thyroarytenoid folds. In most primates there are two on each side of the laryngeal lumen and the caudal ones show sharp and upturned edges in lemurs (Otto, Starck & Schneider) as well as in most monkeys (Starck & Schneider). Their function is not, as seen in the lower vertebrates, primarily a protective one, but seems to serve for maintainance in the habitat. Negus-1924, -1925, -1949, -1957, -1962, probably first* drew attention to the combination of these *inlet valves and the arboreal habitat*, which he explains as follows: the pectoral muscles involved in brachiation, namely moving the forelimbs from laterally and dorsally to medially and ventrally, as all muscles need a fixed point of origin, here formed by the ribs. Such fixation is obtained by a constant negative pressure within the thorax, which in its turn is made possible by closure of the larynx. As a matter of fact this can be performed most effectively by an inlet valve system such as described above. All brachiating animals possess such a mechanism, and these include the apes and, to a lesser degree, man, in which the arboreal habitat of his ancestors might be reflected, though Erikson states that our present knowledge does not permit much to be said about brachiation in Miocene apes. Experimental evidence for this hypothesis, at least as applied to modern man, seems to be given by Pressman, Griesman and C. Jackson.

A pathophysiological consequence of the human inlet valve action is the occurrence of the inspiratory laryngeal dyspnoea often seen in children, in which subglottic oedema, by the Bernoulli effect, causes closure of the inlet valve during inspiration.

After these inlet valves a system of *outlet valves* came into being during primate evolution. In the lemur, which for several reasons can be placed between our *Tupaia*-like and our monkey-like ancestors, the larynx seems only to be capable of acting as an inlet valve whereas in most Cercopithecidae and in all higher primates there is a division into paired upper en lower thyroarytenoid folds, the first down-turned and the latter upturned. That the inlet valves of man work more effectively than the outlet valves was shown by Müller in 1840, though not to that end: he could more easily produce sounds in isolated human larynges by an "inspiratory" air-stream than by an "expiratory" one.

A functional consequence of the existence of outlet valves is the possibility of raising the *intrathoracic* and *intra-abdominal* pressure. I do not know if the valvular action of the upper thyroarytenoid folds produced during straining in monkeys and apes is used frequently. Negus-1949, -1962 (p. 111) thinks it exists only in gibbons, chimpanzees, gorillas and man. Human physiology provides evidence of its importance to man. Firstly there is the ability to *cough*

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* Though Brunton & Cash (1883) wrote: "Closure of the [human] glottis plays a most important part in . . . those muscular actions where it is necessary to have the thorax fixed. . .", they probably meant the upper thyroarytenoid folds and a high intrathoracic pressure.

effectively for which high intrathoracic and intra-abdominal pressures are needed (p. 60); regular clearing of the lower airpassages in man is of vital importance. But the role of the larynx in coughing is possibly less important than often assumed, as seems to be suggested by the experements of Floersheim with cats, and coughing in laryngectomized patients.

From a phylogenetic point of view the second use is probably equally important: raising the intra-abdominal pressure during straining occurs mainly in two circumstances:

(1) *Parturition* which in man (and to a lesser degree also in apes and monkeys) requires forceful and prolonged rise of intra-abdominal pressure, more than in most lower vertebrates (Naaktgeboren gives some examples of mammals), firstly, because the human full-grown foetus reaches quite a large relative size; and, secondly, because the evolution of man's upright posture has been accompanied by changes in the pelvis that have resulted in a more tortuous birth canal (see p. 76, section on speech emergence).

(2) *Defaecation*, which perhaps requires more straining in man than in his ancestors, as comparative physiological observations give the impression that the lower in the primate series the less obvious is straining during defaecation. This is most probably associated with the absence of effective exit-valves, and possibly also with differences in peristalsis, expiratory muscles or diet. It seems possible that analogous to the condition in the higher primates, whose birth canal lacks peristalsis (de Snoo-1939, -1942), these species also show this lack in their bowel evacuation, in contrast to the condition in many mammals, and this might have something to do with straining in the higher primates.

Next to the valve systems mentioned man, and possibly apes, have a third one formed by the *laryngeal entrance* which may act as an inlet valve in two ways.

(1) The T-shaped entrance in the human foetus and young children forms a narrow point in the airways, and is surrounded by rather lax folds, which may be sucked together in certain aerodynamic changes such as may occur in infants during crying or excitement. This mechanism may be responsible for a number of cases of so-called "benign" congenital laryngeal stridor*, possibly combined with the same effect from the inferior thyroarytenoid folds.

In cases where no obvious abnormalities are found in the larynx, most authors suppose the laxity of the tissues surrounding the laryngeal entrance to be the cause (e.g. Crooks, Pinson, Leading Article Brit. Med. J.), and a tendency for spasm or tetany (Perelman), a disturbance of the coordination of the respiratory movements (Thomson & Turner) or micrognathia (Schwartz). However, it seems more reasonable not to blame these causes alone, since it is very possible that this laxity, whether combined with the other abnormal conditions or not, can be found in other individuals too. Maybe it is rather the smaller size of the air passage combined with the higher velocity of the air, *i.e.* the *Bernoulli effect*, which constitutes the main cause of this stridor (for a discussion of the Bernoulli effect in the human larynx, see van den Berg & Zantema).

(2) The epiglottis in old age many act as an inlet valve by moving against the posterior pharyngeal wall, which may happen during relaxation of the surrounding tissues when the state of consciousness is lowered, resulting in snoring.

8. *THE LARYNX AS AN ORGAN OF COMMUNICATION*

Many people think of the larynx primarily as a voice producing organ. As stated in §5 of this chapter such a concept is not confirmed by the phylogenetic evidence, the original functions of the larynx being protection of the lungs and the admission of air. Because voice and speech played such an important part in human evolution, a discussion of their development in our ancestors is justified here.

Before the situation in the different species is discussed, it is necessary to consider the meaning of the words "sound", "voice" and "speech" frequently used in this context. In this

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* That this stridor is often *not* benign is shown by Benians *et al.* demonstrating intellectual impairment in a high percentage of these cases due to cerebral anoxia.

study we understand by *sound* vibrations perceived by the human ear; by *voice* those vibrations produced in the respiratory tract of certain species (in animals mainly by reflex and/or instinct) seemingly with the purpose and often with the result of communication with the surroundings, in most instances used for relation with other members of the same species, but also for predation, threat, echolocation, etc. (It should be noted that the voice vibrations are not necessarily identical with sound vibrations in the above sense, since the first may be of a frequency imperceptible to the human ear). Finally, the means of communication resulting from the acquired, non-instinctive use of the human voice are called *speech* (or *language*, see p. 74) in agreement with Simpson-1966 and Tavolga. For further discussion of communication in biology, see Sebeok-1968 (*ed.*).

Let us first consider *Polypterus*, as a representative of the primitive fish. As far as I know, sound production in its respiratory tract has never been reported, and its anatomy gives no clear indications for its existence. However, in general fish are not silent, since many produce sounds, which in some could be considered as voices, as they seem to be used for purposes of communication (Fish, Tavolga); and it should be remarked that any sound emitted by an individual and perceived by another of the same species certainly has an great selective value.

But these fish voices are most often produced by the swim-bladder and specialized muscles which have never been reported in *Polypterus*; and as long as observations on sound production by this fish are lacking, nothing on this subject can be certain. When therefore *Polypterus* is considered as a representative of the earliest Actinopterygii, one might conclude that sound production, or at least voice production in these species, and thus in their direct ancestors the placoderms, is unlikely to have existed.

Coming to the *lungfish*, one gets the impression that the evolution of sound production is a small step on its way to voice and speech. In *Protopterus* sound production in the respiratory tract has been reported in some publications and our scanty observations give some indications in this direction. Johnels & Svensson found crying sounds when specimens were handled in such a way as to force air violently out of the lungs, and R. Dubois reported them sometimes crying like a newborn babe when they were excited. According to Bell (cited by Negus-1929, p. 297) the Australian lungfish could make sounds, and according to Tait all lungfish could use their respiratory tract as vocal organs, but this does not seem to be supported by reliable observations. The only sound I have been able to observe in one specimen of *P. dolloi* was limited to a weak hissing sound during inspiration, when air was sucked into the mouth. Occasional expirations under water also produce sound. But it seems doubtful whether all these sound productions may be called "voice", since there is no evidence of their resulting in communication with the surroundings. They should be interpreted as accidental circumstances of the respiratory movements, and until new evidence is produced from ethological studies on lungfish, these species, and therefore maybe the ancestral amphibians too, should be considered as voiceless. Darwin-1875 (p. 567) too supposed the vertebrate voice to originate in accidental sound production in the airways, later evolving by adaptation and the forces of selection. Wynne-Edwards (p. 42) concludes: "Sound signals. . . generally appear to have evolved through the development of what were in the first place accidental noises".

The *Urodela*, representing the primitive amphibians, are generally considered to be silent (Ballard), but in the older literature we find authors reporting the occurrence, though rare, of weak croaking sounds. Landois found these in salamanders during the mating season when they emerged from the water; v. Leydig (cited by Landois) and Scheminzky when the animals were handled somewhat roughly during catching. Brehm (cited by Scharrer) and Kainz report the production of whistling sounds by salamanders when threatened; more recently Nobel describes these sounds in *Amphiuma*. Spurway & Haldane found squeaking in newts. So it is not impossible that the Urodela should be considered as having voice qualities (because of the sounds produced during the pairing season), but evidence equally exists that the sound production may consist of the involuntary sequels of respiratory movements or artificial and forceful removing of the air from the lungs.

The *Anura* certainly produce sounds in their larynx often resulting in communication with their surroundings, and for that reason may be considered as having a voice. (For a recent review of anuran communication systems, see Blair). Because of the possession of a tympanum, Noble supposes that the first tetrapods may have possessed a voice, like the modern frogs. One must, however, be careful of considering the frog's voice a stage in the evolution of the vertebrate voice, standing between the silent primitive amphibians and the voice-producing higher animals, as done by Tait. There are 4 reasons for such caution. (1) The frog is a poor representative of those ancestral amphibians which gave rise to the reptiles, evidence for which comes from palaeontology. (2) The frog shows a number of specializations and adaptations. These can be encountered in the morphology of its laryngeal skeleton (p. 34), and also in its laryngeal functions. The so-called "vocal folds" of the frog are certainly not homologous to the mammalian ones: the first are membranous folds on the medial surface of the arytenoid cartilages, the latter folds are stretched between the arytenoids and the typically mammalian thyroid cartilage, consisting of mucous membrane and the thyroarytenoid muscle, and are subjected to variable tension. (3) We find no evolutionary stage between the frog's characters and mammalian ones, neither from the morphological point of view, nor the functional. (4) The frog's voice is mostly used by the males, though according to Grützner the females may sometimes produce weak sounds.

Reptiles in general do not possess very elaborate vocal abilities. In most species these are limited to a weak hissing sound (Ballard, Scheminzky, Weiss-1914) whilst others seem to be completely silent. On the *crocodile's* sound production there are a few orginal observations in the literature. Villiers recorded roaring or bellowing in African crocodiles, and Landois quotes other authors besides himself observing hissing sounds when the animals were disturbed slightly and making grunting sounds when in pain. Darwin-1875 (p. 567) and Bartram (cited by Landois) recorded roaring by alligators during the mating season, during which the animals appeared swollen. Weiss-1914 cites some observations on the crocodile's voice. During reproductive activities *turtles* are reported to produce whistling or roaring sounds (Pope and de Sola, quoted by Blair). The most differentiated reptile voice is probably to be found in the *geckos*, small lizards which exchange various clicking and cheeping sounds.

Observations on *Sphenodon*'s voice are certainly more interesting than those on the crocodile's. Unfortunately little is known about it: Oliver, cited by Pope, reported croaking like a frog when a specimen was picked up, and Bogert considers *Sphenodon*'s croaking to be a call. It is therefore uncertain if the sound production in its air passages should be regarded as accidental or communicatory.

Nothing is known for certain, however, about the *mechanism of reptile voice production*, for instance whether it is produced during inspiration or expiration. Presumably the *hissing* sound is caused by forceful passage through the nearly closed larynx. This is more likely to be produced by expiration than inspiration, since (1) forceful inspiration through a nearly closed larynx in most species is likely to result in immediate and complete closure because of the inlet valve system, the upturned edges (though Weiss-1914 records swelling of some snake species during the hissing and concludes that their voice production must be inspiratory), and (2) most reptiles have no diaphragm (and if they have it is a weak one) which implies presumably that their inspiratory muscle system is weaker than their expiratory.

On the other hand the so-called *roaring* of the crocodilians might very well be produced by forceful inspiration through the semi-closed laryngeal aperture, by which the edges may vibrate at a relatively low frequency. An indication in this direction is the swollen appearance of the animals during roaring. The grunts produced by the animal in pain could be evidence, since closure of the larynx might be a general reaction of vertebrates to sudden anxiety (p. 59). Another argument in favour of the above hypothesis is the observation by Müller (cited by Weiss-1914): he produced a falsetto sound when he blew air from the trachea of dead alligators upwards through the larynx.

Because we may only conclude from comparative zoology that some reptiles have a primitive voice, used e.g. for catching prey or in mating, it is probable that the ancestral reptiles, including the Carboniferous or Permian mammal-like reptiles, also used their respiratory systems for purposes of communication. But what the voice of the mammalian ancestor was like remains obscure. It is likely to have been limited to simple hisses, since reptilian laryngeal anatomy in general does not seem to allow production of variable tones, consisting of a limited range of frequencies such as we see in many mammals, due to the lack of folds whose tension can be controlled. Moreover, many primitive modern mammals only produce hissing sounds (see below).

The transition to the *mammalian* voice is a great step, and we know nothing about possible transitional phases. Along with the development of the thyroid cartilage, the thyroarytenoid folds probably also developed, because they are present in most modern mammals including the Lesser gymnure, the tree-shrew and other primates. This development gave new opportunities to the voice, since the tensions and movements of these folds could now be controlled by means of the thyroarytenoid and cricoarytenoid muscles, and a great variety of more-or-less pure tones could now be produced. The increased mobility of the tongue (Rensch-1959, p. 296), the better developed system of respiratory muscles and the higher respiration rate may also have contributed to the development of the mammalian voice.

In the *primitive primates* and their direct ancestors vocalization probably consisted of hissing, as produced by the moonrat (Medway), the pen-tailed tree-shrew *Ptilocercus lowii* and some insectivores (Walker) including the hedgehog *Erinaceus* (Schmid), or high pitches and squeaks such as are found in the Lesser gymnure *Hylomys suillus* (Medway), the hedgehog (Negus-1929), the pen-tailed tree-shrew (Le Gros Clark-1926) and another tree-shrew, *Tupaia glis*. Andrew-1964 feels that the voices of our insectivore ancestors are illustrated by that of the modern *Sorex*: twitters and clicks.

Primitive mammalian species belonging to the Order Marsupialia are generally voiceless, though when threatened some may produce hissing or barking sounds. Vocal communication between members of the same species is only poorly developed (Bergamini, Tembrock).

Presumably the voices of primates are generally produced during expiration, because their larynges give the impression of being only suitable for this, and because most mammals are reported to have expiratory voices; exceptions are man, horse, donkey, panther, cat and occasionally the dog (Grützner, Scheminzky). Andrew-1963b supposes voice production in primates to be often expiratory. A factor which may be associated with the development of the voice in the primates is their arboreal habitat: Negus-1949, -1962 pointed out that most arboreal species use their voices as a means of communication in contradistinction to those living on the open plains, which are mostly silent. The upturned edges of the thyroarytenoid folds, which are probably associated with an arboreal habitat because of their function in brachiation (Negus-1924), may also have contributed to the evolution of the primate voice by shaping the vocal folds of man.

The range of frequency in the *monkey* and *ape* voice is greater than in the lower primates and consequently contributes to communication which is also effected by sounds produced by the tongue, mouth, lips and teeth, and by numerous facial expressions described and analyzed in detail by van Hooff and Andrew-1963*a*, -1964. Rowell stated that, at least in Rhesus monkeys, "these visual signals appear to be the primary method of communication, and the noises have not evolved independence from them". And Thorpe feels that "apart from circumstantial evidence for rhesus monkey (*Macaca mulatta*) and the night monkey (*Aotus trivirgatus*) there seems to be nothing in the literature which is at all convincing" for the existence in primates of individual recognition by means of vocal signals. For a recent and detailed review on primate communication systems, see Altmann.

There are several observations on the voice and "words" produced by the *chimpanzee*, as cited by Scheminzky, Mathis and Portmann-1962. Yerkes & Learned observed two young captive chimpanzees which appeared to use 32 different "speech elements", each with a different meaning and built into a great number of different melodies, though only two of these elements were used in common by the two individuals. Kohts reported in a year-old chimpanzee 23 such sounds; Nissen described 5 kinds of sound, each with a special meaning, used by chimpanzees in their natural habitat. Hayes reported her chimpanzee being able to produce some seeming words: vocalizations acquired by learning and used spontaneously and repeatedly in the same situation. True words, however, are parts of an "open system": they are used in various combinations, and this has not been found in animals.

Yerkes & Yerkes conclude (p. 301) from their elaborate studies on chimpanzees that the motor mechanism of voice in this ape is adequate not only to the production of a considerable variety of sounds, but also to definite articulations similar to those of man. The orang-outang, formerly supposed to be silent, seems to use its voice for emotional expression (G. Brandes); the same is reported by Schaller-1963, -1964 concerning the gorilla in the wild.

9. *THE EMERGENCE AND EVOLUTION OF SPEECH*

The human voice and its resulting means of communication, *speech**, deserve our special attention because of their high importance in human evolution and in present human life. Language is the most diagnostic single trait of man (Simpson-1966), and the most salient subsystem of human communicative behaviour (Diebold). (For the differences between "language" and "speech", see p. 74). Similarly Tolman and G. Frey, considering human speech from psychological and philosophical points of view, consider it the most distinctive character of man compared with animals.

To assume that it evolved from a voice such as the ape's is not allowed from the present state of our knowledge: although from a morphological point of view a gradual transition from an ape-like ancestor into man is likely, as far as the larynx is concerned we lack sufficient evidence for this from a functional point of view, since there is a wide gap between the communication resulting from ape's voice and that from the human voice. Kainz (p. 96) concludes from his elaborate considerations of the essential differences between animals' and man's vocal communication systems that the ape's voice does *not* constitute a bridge between these two. Révész, considering the question from a psychological point of view, concludes that the roots of human language cannot be found in the vocal communication of animals.

On the other hand psychologists like Groos, Tolman (p. 238), Benedek (p. 48), Höpp and Bastian, and linguists like Buyssens-1949, Gardiner (p. 123), Whatmough (p. 172) Hockett-1959, -1960, -1964 and Sebeok-1965 introduce several arguments in favour of animal roots for human speech. De Laguna (p. 76, p. 259), Stein (p. 47), Koehler-1950, -1955, Spurway & Haldane (p. 23), Zuckerman-1932 (p. 18), Yerkes (p. 193), Itani and Andrew-1963*a*, -b come to the same conclusion, the last four after elaborate observations of ape and monkey behaviour. Indeed, if one assumes a gradual evolution from ape-like ancestors to primitive man, as is generally done in regard to morphological characters, one might assume the same in regard to the evolution of speech capabilities, though the intervening stages are still obscure.

In which aspects, then, *do the vocal communication systems of man and apes differ*? As far as *physiology* is concerned, we see that man is indeed able to produce a large range and a rapid change of frequencies, different from most animals, but I doubt whether the vocal organs of apes (and monkeys) are really incapable of making such sounds (*cf.* the numerous reports of monkey and ape vocalization in §8 of this chapter).

As far as *anatomy* is concerned: there have been several authors, who laid stress upon the importance for speech of the morphology of the human vocal organs. Already in 1779 the Dutch scientist Camper wrote in his letter to the Royal Society that the orang-outang would be unable to speak even had he the intellectual capacities for it. More recently Kelemen-1948 and Zenker & Anzenbacher expressed the same kind of doubt in regard to the chimpanzee and monkey larynx, had they been directed by human brains. These

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* Other means of communication via man's respiratory tract, like whispering and whistling are phenomena in which the larynx is only indirectly involved; from a phylogenetic point of view they are not particularly interesting, because it is likely that they came into being only after man had acquired speech, both mechanisms essentially being the result of man's ability for symbolic expression. Whistling by birds has very little to do with that by man, both being common only in some physical characters of the sound. Crying and other comparable non-acquired, instinctive, uses of the human voice are discussed in Chapter 5.

doubts are based on the anatomical differences between the human and the simian larynx. Camper's are founded on the presence of the large air-sacs in the orang-outang*, Kelemen's on this and several other macroscopic differences, and those of the other authors on the histological findings mentioned on p. 47. Spuhler-1959 (p. 8) feels that the high position of the larynx "is one of the reasons why attempts to teach chimpanzees English have failed". Van den Broek, Goerttler-1954, Whatmough, Kelemen-1948, -1963, Bryan and Kipp attribute great value to the morphology of the vocal organs for the origin of speech in human evolution.

However, in my opinion morphology is not that important. We have seen that apart from the air-sacs there are only minor differences between the human and the simian anatomy. Furthermore, speech, at least in modern man, is still possible with an ill-functioning larynx and even without a larynx at all, as one sees in laryngectomized patients. (Similarly, deaf-mutes may acquire speech and language). Comparable to speech in laryngectomized patients, as an illustration of man's desire and ability to find means of symbolic expression, is the writing on a blackboard which everybody is able to perform with his arm who is able to do so with his hand, and the foot or mouth writing of people who have lost the function of their arms. It therefore seems probable that should surgery ever reach the level where the successful grafting of an ape's larynx (preferably that of a chimpanzee) into an otherwise normal human being is possible, such a person would be able to acquire a speech hardly discernible from the normal.

A characteristic of the human voice much more important than the more differentiated sound production lies in the superimposed cerebral control, clearly emphasized, probably for the first time, by Traill in 1821, who stated: "On reviewing the structure of the organs of respiration, of the tongue and larynx, there does not appear any reason why the Orang Outang** should not speak... we must therefore, refer its deficiency in this respect, not to corporeal, but to mental peculiarities" (p. 42-43). Later, in comparing primate vocal functions other authors like Darwin-1875 (p. 89), Lampert, Washburn-1959, Etkin, Schaller-1964, Roe and Lenneberg-1967 have stressed this point.

Man's will and ability to command the material substrate (consisting of various speech organs like larynx, pharynx, mouth, tongue, lips, facial musculature, etc.) and express himself and communicate by *symbols*, *i.e.* words, are unique in biology, and result in and are only made possible by abstract thinking. "In language we have the free, accomplished use of symbolism, the record of articulate conceptual thinking; without language there seems to be nothing like explicit thought whatever" (Langer, p. 94). It should be emphasized, however, that there is some evidence from the behaviour of apes that they may show traces of conceptual thinking (W. R. Thompson, Nissen-1958, Hayes, p. 83, Freedman & Roe, Gardner & Gardner). Whether the great difference in this respect between animals and man should be considered quantitative rather than qualitative remains inconclusive.

As a matter of fact the origin and evolution of speech has been the subject of numerous studies, because "he who considers the evolution of speech considers the evolution of man" (Portmann-1962). No satisfactory explanation of speech emergence has yet been given, and any author who seriously considers this problem, like Overhage-1959, comes to the conclusion that the matter appears much too complicated to be clarified by the too easy explanations and conclusions given by authors like de Snoo-1939, -1942, Weinert, Gottschick and Goerttler-1954. The problem is that science has to rely on the poor morphological evidence of scanty palaeontological remains, like skeletons and tools left by fossil man and his ancestors, insufficient to tell us much about a largely non-material phenomenon like speech.

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* It has since turned out that Camper's conclusions were incorrect, because G. Brandes and Kelemen-1948 observed voice production by the orang; the last author even supposes that the air-sacs take an active part in it.

** He meant the chimpanzee (Yerkes & Yerkes, p. 301). It may be remarked here that Camper (p. 147) gave a description of an "Orang Outang" from Angola, presumably a gorilla, though the "speech organs" described in this publication were apparently those of an orang-outang.

From observing the *casts of fossil skulls* and the morphology of fossil mandibles, conclusions have indeed been drawn indicating the ability for speech in ancestral man e.g. by Elliot Smith (p. 126), Black, Tilney (cited by Pannekoek), van den Broek, Shellshear & Elliot Smith, Childe (p. 28, 29, 49), Gieseler-1943, Keith-1948, Schepers, and von Koenigswald-1955, -1960, while such a relationship is suggested by Dart-1959 (p. 134) and Lilly (app. 2).

The same has been done in regard to intellectual capacities of different modern human races by Hauger and Shellshear (and Coon, plate XXXII, suggests it) on the basis of anatomical observations of brains. However, neither the shape, nor the absolute nor relative amounts of brain tissue in the vertebrates, are the sole deciding factors in determining intelligence or speech. The brain of a rat may be responsible for a greater intelligence than the much larger brain of a crocodile, or even of several of its fellow-mammals, and there have been several famous and learned scientists who appeared to have possessed an average or even subnormal amount of brains.

Apparently the explanation of a greater intelligence has also to be sought in the finer architecture of the brain, and in the sphere of biochemistry and biophysics, which might give indications for functions like association and memory. Indeed N. Geschwind supposes that man develops language because he can form associations between two non-limbic stimuli.

Though it does not seem impossible that in the future it will be shown that mammals with absolutely and relatively large brains, like the toothed whales, have opportunities for association and memory basically the same as the human ones (or even for language, as suggested by Lilly and Poulter), it should be remarked that the evolution of speech in the primate stem must have been possible by the interaction of a number of extra-cerebral factors, as will be shown later in this chapter. For the rest it should be realized that the possible similarity in functions between the brains of man and of Odontoceti should be considered as a result of convergent evolution, as shown by palaeontology and illustrated by their different morphology.

For a recent and lucid discussion on the problems of comparison between brain form and function in different individuals and species, the reader is referred to Mettler; for a discussion on brain size and language, to Lenneberg-1967.

However, authors like Hirschler, Duckworth, Weidenreich, Hayes & Hayes, Teilhard de Chardin-1956, Heberer-1956-a, -1965, Anthony, DuBrul & Reed, Vallois-1962, Le Gros Clark-1962, -1964, Coon*, J. Scott, Hockett & Ascher, Starck-1965-b, Simpson-1966 and Lenneberg-1967, -1968 have convincingly exposed the speculative nature of these conclusions.

Any explanation of speech emergence and evolution is necessarily of a speculative character, and if a new attempt is made here to illustrate this problem, I certainly do not pretend to have its solution, my aim being only to demonstrate the *multicausal origin*, which often seems to be neglected in publications on this subject, as Portmann-1948 points out. Only a few authors, like Critchley and Gray pay any attention to it, though possibly insufficient**.

When considering the factors that may have contributed to the origin of speech one discovers a close relationship between them, and as science progresses the whole problem seems to resemble a jigsaw puzzle, the pieces of which are gradually seen to fit into each other to form the complex pattern of human characteristics. However, such a comparison would present too static a picture, and therefore the gradual character of speech emergence could also be compared to a crystallizing substance, in which there may be one or more centres from which crystallization started and in which the origin of one crystal induced the other. An attempt to illustrate the emergence and evolution of speech in this way is shown in Figure 39 (p. 81) in which the relations between a number of factors involved are represented by connecting lines and arrows.

When considering the matter from such a point of view, one is often confronted with the question of the *direction of the causal relationship* between these factors, *i.e.* the direction of the arrows in the diagram. For instance, there is little doubt that in our primate ancestors the enlargement

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[*] Coon (p. 259) rightly criticizes Schepers who infers from *Australopithecus* casts the ability to speak, but falls into the same trap himself by concluding from the supposed brain size that it "is extremely unlikely that they could speak".

[**] It was only after completion of the manuscript that I obtained the paper of Hockett & Ascher, who approach the problem in a way more or less similar to mine, apparently "convergent evolution of thought".

of the brain, a prerequisite for speech emergence, must have been accompanied by an enlargement of the skull. The question is: what was the causal relationship between these two processes? Arguments in favour of bigger brains having caused bigger skulls (Mayr-1968) are as valid as those in favour of skulls having provided the opportunity for enlargement of brain (e.g. Childe, p. 27, p. 29, Prahl-Andersen). So the direction of the arrows in the diagram may sometimes be arbitrary. Objections against these directions might also be raised by considering the problem from a Lamarckian or teleological viewpoint, which is this study we do not support. Together with authors like Washburn & Howell, Brosnahan, Mayr-1963 and many others cited in this section I feel that the principles of mutations, gene flow and natural selection are responsible for the emergence of speech.

Some remarks are necessary before discussing the interconnections in Figure 39. Only a limited number of possible factors is given, but such a figure can be greatly extended: in this study we have deliberately limited ourselves to those factors more-or-less directly involved in the emergence of speech. In considerating the phylogeny of speech, evidence is sometimes derived from the ontogeny of speech (for instance by Negus-1929, p. 335, Pannekoek, p. 42, Buyssens-1957, Diamond, Bounak, Stein), a procedure we shall also follow in this study, with the proviso, that these two processes though closely related, are not identical (Jespersen, p. 417, Gray, p. 39, Simpson-1966, Lenneberg-1967. See pp. 113 and 114).

The numbers between square brackets in the following discussion refer to those of the lines in the diagram, but it should be noted that the sequence in which the various relationships are discussed, does not apply to the possible sequence of their establishment during this range of vertebrate evolution, which roughly covers the whole lifetime of the primate stem. Because the factors contributing to speech emergence appear to be very closely interwoven with a number of other factors contributing to hominisation, in the following discussion the latter have frequently to be taken in account. Since further explanation and discussion of these factors fall outside the scope of this study, the reader is referred to publications dealing with human evolution.

The present problem will be considered from the somatic and anthropological points of view, as might be expected from the education of the author. I am, however, fully aware of the existence of a large number of publications considering the same problem from a linguistic and psychological point of view.

Finally, it should be emphasized that a number of lines are hypothetical and are only mentioned to indicate the complexity of this matter and a possible way of its elucidation which, according to Portmann-1948, belongs to the most mysterious of evolutionary problems.

Commencing with laryngeal morphology: it can be stated that the *anatomy of the human larynx* and more especially the anatomy of the inferior thyroarytenoid folds is partly responsible for the human voice, *i.e.* for the typical timbre and the broad range of tone frequencies [1].

Diamond, who otherwise approaches the problem from a linguistic point of view, sees (in Ch. 17) another, indirect relationship between laryngeal anatomy and speech. He supposes speech to have originated from the spontaneous sounds produced by expiration after the use of forelimbs by our ancestors, in view of the inlet valve action of the vocal folds as supposed by Negus (see p. 65). Objections to this hypothesis may be summarized as follows. (1) According to Negus the negative intrathoracic pressure is more likely to be followed by a short inspiration than by an expiration. (2) This mechanism is supposed to be present only during forceful contraction of the pectoral muscles, which was probably present in our ancestors only during a small part of their lifetime. (3) As far as I know, such vocalization has never been reported in modern actively brachiating primates.

However, without effective muscular control the rapid changes of sound and pitch typical of the human voice, would be impossible, some morphological evidence for which may be derived from the observations of Berendes & Vogell and of Anzenbacker & Zenker [2]. But a fine effector system without a fine steering system such as is provided by the motor-areas of the human brain would be of no value [3]. Superimposed on these, and possibly of more importance for the evolution of speech, are the powers of the human intelligence that make possible the existence of processes necessary for speech, e.g. learning, the desire to express oneself, if necessary by organs other than the larynx, and the tendency towards symbolization [4]. Sapir-1938 states: "It is probable that the origin of language. . . is essentially a particular case of a much wider problem of the genesis of symbolic behavior, and of the specialization of such behavior in the laryngeal region. . .".

On the other hand, the development of speech, or perhaps in this context we should say language, in human ontogeny with certainty stimulates and in phylogeny probably stimulated the development of cerebral functions [5], as pointed out in 1868 by Geiger (cited by Pannekoek) and in 1875 by Darwin (p. 88). In fact many authors, for instance cited by Sapir-1921, de Laguna and Sayce, feel that conceptual thought is impossible without language: "thinking is largely subvocal talking" (J. B. Watson). Monod even states that rather than man creating language, language created man. Amongst others Gray and Janet feel that thought must have preceded language.

The difference between the meaning of the words "language" and "speech" may be illustrated by a quotation from Buyssens-1957: ". . . It is most probable that language began long before words and phonemes had been invented". In other words, language indicates the presence of abstract thinking in a community and the urge to express it (*c.f.* "geistige Kontakte" of Révész). Lewis', Gardiner's and Diamond's definitions go in the same direction. Sapir-1921 (p. 16) states: ". . . we must not imagine that a higly developed system of speech symbols worked itself out before the genesis of distinct concepts and thinking, the handling of concepts". For a number of definitions of "language" by various authors, see de Laguna and Gray; and for an extensive discussion on the differences between "speech" and "language", see Gardiner.

As we have seen, the descent of the larynx and consequently the *loss of contact between the palate and the epiglottis* gave wider opportunities to the primate voice, because, firstly, air could now be distributed more easily through the nose *and* the mouth, providing capabilities for the production of many more sounds; and secondly, as Némai-1933 and Negus-1949, -1957, -1962 pointed out, the roomy pharynx could act as a resonator [6]. But in the newborn and infant human a condition more similar to the general mammalian one is retained, enabling breathing during sucking. The latter may have played a part in the evolution of speech, because breast-feeding must have contributed to the relationship between mother and child [7], which in its turn is important in speech ontogeny.

The loss of contact between larynx and palate may have been caused partly by the *reduction of the jaws*, which in the evolution of primates shows a drastic decrease in relative size (DuBrul), and which in all living mammals is probably larger than in man. This reduction may have had two effects: (1). Reduction of the upper jaw and the palate—the human uvula may be a rudiment of the larger palate of our ancestors—, and (2). Reduction of the mandible with the maintenance of the large tongue, by which the larynx was pushed down into the neck (Negus-1949, -1962) [8].

This jaw and tooth reduction may have effected the development of the *face* (Washburn-1959) with its musculature [9], which according to Macbeth may be related to the presence and shape of the paranasal sinuses. This musculature, under the guidance of the cerebrum [10] and allied with the mobility of the tongue, is indispensable for speech (the laryngeal musculature is probably not). It has even been said that "buccal speech. . . must be seen as the most primitive form of speech known in the development of man" (Drost)[11]. The acquisition of differentiated facial expressions made possible by this musculature, must have contributed to the establishment of human social life [12].

Loss of prognathism may have had another and more direct influence on speech evolution, by means of easing the production of labial consonants; while Palmer (cited by Critchley), Gaudry and Piveteau feel that the shape of the human mandible, with its diverging ascending rami, must have contributed by giving the tongue greater mobility. On the other hand Kipp feels that the latter is mainly effected by man's high palate[13].

With the reduction of the jaws and, possibly causally related to it is the *reduction of the nose* in size and smelling capacities[14]. This reduction was compensated for by developments in *sight* and *hearing*, resulting in greater acuity of perception and better spatial orientation [15] [16]. These two mechanisms are again necessary for development of communication both in phylogeny and ontogeny, the first in regard to gestures and movements of face and lips, which need to be observed (Höpp) [17], and the second, more important, for perception of the sounds of speech. Many authors agree that speech is essentially an acoustic system (e.g. Grützner, Sapir-1921, Portmann-1948, Overhage-1959), both in regard to exteroceptive and to proprioceptive stimuli. Indeed the human acoustic system, and probably that of the chimpanzee (Elder-1934, -1935), shows its optimal performance at the frequencies predominating in the human voice[18]. Corresponding changes within the cerebrum accompanied the development of sight and hearing [19] [20]. Campbell (p. 78) points out that "primates. . . see the environment as a collection of objects rather than merely as a pattern, and the recognition of objects is . . . the beginning of conceptual thought". [19]

Not only did the reduction in jaws and nose make development of sight necessary for survival, it also contributed to it: primate *stereoscopic vision* was made possible by (1) flattening of the face, making the optical axes parallel, and (2) reduction in the decussation of the optic nerve fibres (Rohen)[15].

Duke-Elder (p. 697) points out, however, that total decussation of the optic nerve fibres, with laterally placed eyes, does not necessarily imply a lack of binocular and stereoscopic vision (which seems to be confirmed by the recent experiments of Knapp & Kang, and Ingle), but in primates these functions are no doubt on a higher level. And Andrew-1964 emphasizes that the reduction of the muzzle is not necessarily correlated with stereoscopy, because the lemur may look over its muzzle rather than along it. For an interesting discussion on the comparative anatomy of the optic chiasma, see Stanley-Jones.

Stereoscopy probably reached the simian level in the monkey-like ancestors, since the modern tree-shrews are supposed by Woollard-1926 to possess monocular vision only, though they may look frontally in curiosity (Andrew-1964). Von Bonin states that "the shift to optic impressions as the most important clue to the outside world. . . achieved its definitive status in the true monkeys". Stereoscopic vision may have contributed indirectly to speech because of the "realization of space and time, and a tremendous increase of range and precision in recognizing objects by their shape, colour, size and texture" (Elliot Smith, p. 172).

The acquisition of *colour vision* probably occurred between our lemur-like and the monkey-like ancestors, whereas Grether's experiments suggest that in the discrimination of hues the chimpanzee ranks between the Old World monkeys and man. Man's *visual acuity* appears to be possessed by modern monkeys (Yarczower *et al.*), making its existence in our monkey-like ancestors probable.

A consequence of stereoscopy, more important than the direct contribution to speech, was the resulting greater facility in catching prey, which accords with the change, as supposed by Oakley, Robinson-1954 and others, to have occurred from a mainly herbivorous diet during the arboreal habitat of our ancestors into an *omnivorous diet* after they left the trees, or we should rather say, after the trees left them, because of the change of climate in the Pliocene (Zuckerman-1932, -1958)[21]. In accordance with the loss of a mainly herbivorous semiliquid diet, such as can be observed in all modern monkeys and apes (Zuckerman-1932, -1958) including the chimpanzee (Nissen, Goodall-1963) and the gorilla (Schaller-1963), the descent of the larynx resulted in a reduction in the lateral food channels [22]. It is evident that the increase in intellectual capacities played its part in catching prey and also in eating (use of fire). On the other hand, the intellectual development, and possibly the origin of other human activities, may have been favoured by the shift from herbivorousness to omnivorousness: herbivores generally spend much of their lives on feeding activities, carnivores spend less and are thus able to use their time for other activities[23].

The reduction in the jaws was accompanied, by a reduction in number and specialization of the *teeth*, which in their turn made an omnivorous diet possible (Robinson-1954)[24]. It is not impossible that man's well-developed *cheeks* are related to the herbivorous habit of his ancestors, since most herbivorous mammals possess them, unlike the carnivores (Negus-1949, -1962)[25]. The absence of well-developed cheeks in modern tree-shrews and their presence in the other primates (Andrew-1964) possibly indicates their presence in the monkey-like ancestors.

The anatomy of the thyroarytenoid folds not only directly influenced the evolution of speech by means of the typical qualities of the human voice, but probably indirectly too. By their valve-like action they made, according to Negus-1924, -1925, -1957, -1949, -1962 effective brachiation possible (see p. 65)[26], and hence an *arboreal habitat*[27], which can be associated with speech because, as Negus-1957, -1949, -1962 pointed out, most arboreal species communicate by voice[28]. Eisely suggests that "the arboreal environment and its demands may well have played a part in the creation of that ideational insight which is known to exist in our living relatives and which may lie close to the root of language as one of the preadaptions of our fathers of the forest world". On the other hand, Kortlandt-1965 suggests that leaving the arboreal habitat may have contributed to human social life, because as far as the evolution of the large mammals is concerned, a savanna habitat tends to increase socialization, which a forest habitat inhibits[29]*. Possibly the arboreal life of the early primates can be related to the development of the optic system, since effective movement in the trees is only possible with good stereoscopic vision[30].

A circumstance accompanying the arboreal habitat must have been *brachiation* and "chiriation": use of the forelimbs and hands for grasping and climbing, for which the specialized first finger was essential[26]. (The concepts of Heberer-1956*b*, however, make it likely that brachiation such as the modern apes show is only a recent phenomenon, and may not have existed in man's ancestors). Again, guided by the motor areas and intellectual capacities of the brain[31], arms, hands and fingers must have been essential for the use and manufacture of tools, and these are even supposed by Washburn-1959 to have contributed by selection pressures to shaping man's hand[32].

Another indirect relationship between larynx and speech may have been the fact that the upper thyroarytenoid folds mainly act as an outlet valve, and without such an effective valve system labour during *childbirth* might have been difficult, or even impossible. Parturition in man is likely to be more difficult than in his ancestors, firstly because new-born man is relatively larger than the new-born apes, especially the head (e.g. Portmann-1951, Napier & Napier); and secondly, the birth-canal in woman is more tortuous than in other primates (see below)[33]. These circumstances are why at least in modern man birth often requires the help of others, a consequence of his social life[34]. This help is mainly based on the intelligent use of arms and hands[35], and is closely related to the power of speech. That parturition in man's ancestors must necessarily have been easier follows from the negative selection pressure which such a phenomenon would have exerted, because of its small survival value.

The difficult childbirth in man can be related to *neoteny* in two ways; firstly to the "foetalized" position of the human vagina (Bolk-1926*a*, -*b*), which leaves the birth-canal with a built-in tortuosity, and secondly to the large size of the new-born babe. The human child is characterized by relatively slow growth when compared with other primates (Portmann-1945, -1948, Schultz, Freedman & Roe, Washburn & Avis, Bartholomew & Birdsell, Montagu-1962*b*, Mayr-1963, Campbell) which can be considered as a prolonged youth[36].

According to Starck-1965*a* the prolonged youth of man cannot be considered to be neotenous in Bolk's sense because, as Portmann-1951 made clear, man is secondary nidicolous (*Nesthocker*) and therefore his youth should not be comparable to that of his ancestors. However, there seem to be sufficient reasons for calling this phenomenon neoteny. This is not the place for circumstantial arguments on this point, and objections may be summarized as follows.

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* Because of the increase in danger which our ancestors must have faced after leaving the trees, de Laguna (p. 53-55) supposes selective forces to have favoured groups with speech-like communication. In this discussion she probably overestimates, however, the value of the selective forces exerted by the large carnivorous mammals: dangers acting in selection and survival in these human ancestors are more likely to be sought in parasitic diseases (present both in the arboreal and ground-level habitat), and in feeding conditions. Moreover, as Leakey-1967 points out, the (modern) big cats seem to eschew human flesh. Livingstone too warns against this "Tarzan mentality".

(1). "Neoteny" literally means nothing more than prolongation of youth, as indeed Kollmann first used this word. (2). There are several reasons for ascribing a longer youth to man than to other primates. (3). Not just the state of nidicolousness should be considered, but also other criteria in comparing man's youth with that of other species. (4). Though newborn man does indeed differ from his newborn direct ancestors in being nidicolous, he is comparable with unborn higher primates and newborn lower primates and insectivores. (5). When we extend the meaning of "neoteny" beyond bare morphology and assume that man's behaviour during most of his lifetime is more similar to youthful ancestral forms than to adult ones, there is another reason for calling modern man neotenous.

Lorenz-1943 (p. 123, p. 125), Keith-1948, Montagu-1962-b, LaBarre and Morris (p. 30, p. 114) use the same term in relation to man. Apparently in recent years there has been a shift in the meaning of the word "neoteny" from applying it to lower vertebrate evolution towards applying it to human evolution as well. This shift was probably introduced by de Beer. Rensch-1959 stresses the importance to human evolution of "phylogenetic rejuvenation", "plasticity of juvenile behaviour" and "neomorphosis" (p. 304), Hocket & Ascher and Coon of "pedomorphism". See further the note on p. 10.

A result, or maybe the cause (Montagu-1962-b), of these circumstances is the reduction in the number of offspring in the higher primates as compared to lower ones[37]. A prolonged youth is indispensable for the acquisition of the multitude of knowledge typical of man, including speech[38], tool-using and tool-making[39].

In this context Hayes' observations are interesting: she reports her chimpanzee having passed through a period comparable to the infantile "babbling" stage which, however, started somewhat earlier and ended far earlier than in the human infant. This might be an indication for the neotenous character of human vocalization. Other, equally speculative, relationships between speech and neoteny can be inferred from Etkin's hypothesis (p. 141) that human vocal communication replaced grooming as a socializing factor, which could have been inhibited by the loss of body hair (another neotenous trait, Campbell, p. 31), and from Hocket & Ascher's that verbal *play* stimulated the evolution of language (see point 5 of the above discussion on neoteny).

The reduction in the number of offspring made for closer contact between members of one family such as exists in human *social life*[40], which has probably been another important factor in man's evolution*. For instance it must have contributed to the evolution of speech[41]. This hypothesis seems to be favoured by Ullrich's statement that the voice of animals living in groups is better developed than in others. Marler, Roe and de Laguna attribute great value to division of labour for the evolution of speech in early human society, as does Etkin in regard to the higher primates' sexual behaviour. Effective hunting must also have been stimulated by group life (Gieseler-1956), and accompanied by an increase in information exchange between the members (Spuhler-1959, Coon)[42]. Kortlandt-1965 even goes so far as to state that it was "apparently the socialization of the hunting techniques rather than the enlargement of the cortex, which has created the preadaptation from which human spoken language could evolve", in contrast to Dart-1959, who emphasizes that collaborative hunting demands silence rather than speech and that the mute aspects of imitation are often underestimated. Differentiation of social life must have been influenced by cerebral development, while Gottschick emphasizes the higher mental level which mankind could achieve by combining mental achievements within a community[43].

Neoteny may have acted in human evolution in other respects. The reduction in teeth and jaws already mentioned may be interpreted as such a phenomenon[44]. This view is supported by the observations of Spuhler in regard to Australopithecine dentition (Montagu-1962-b). Bolk-1926 further regarded it responsible for the large size of head and

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* Dobzhansky & Montagu are even ready to postulate that "the most important setting of human evolution is the human social environment". Also Keith-1948 stresses this point. Statements like this, however, by-pass the probability of the multicausal origin of human characters: a number of factors must have worked together. In fact social life as such is not typical of man, and it was probably the interrelationship of other factors, such as the mental capacities, that gave human social life its typical qualities. See also footnote, p. 15.

cerebrum*, the delayed closure of the cranial sutures[45], and the small cranial base angle. According to J. Scott and others the latter is associated with the acquisition of upright posture by man[46].

The human child's *long period of dependency* must have contributed to social relationships (also in view of the delayed appearance of adult proteins and hence of antibodies, Goodman-1963). Romer-1958-b (p. 72) states when comparing mammals with lower vertebrates: "Of major importance is the fact that continuous association of parent and young due to nursing habits marks the beginning of education... very probably and important factor here is that the brain is permitted to develop to a maximum degree before it is put to serious use". Dobzhansky-1950 considers educability to be the most important evolutionary trend in human species. Etkin feels that the postponement of sexual maturity must have caused a positive selection pressure, since the adult male primate is often seen to display competitive, non-socializing behaviour to other males[47].

Another neotenous character of man may possibly be shown in his larynx, since compared with other mammalian larynges it has, from a morphological point of view, a rather generalized or non-specialized appearance. Compared with other anthropoids, Kelemen-1948 and Kleinschmidt-1938 consider the human larynx to be primitive, the chimpanzee approaching man most closely[48]. Whether this condition should be considered neotenous or primitive can of course only be determined after the appropriate comparative anatomical and embryological investigations have been performed.

The evolution of man's *respiratory passages* including the larynx may be indirectly associated with speech evolution in another way. These passages must be considered to have gradually got smaller capacities in respect to the amount of air passing through them due to (1) the smaller relative size of the larynx[49], (2) the relative decrease in laryngeal cross-section[49], (3) the greater resistance to the passage of air by the cranial flexure, associated with upright posture, which furthermore according to Dart-1959, implies a more subtle breath control, useful for speech[50], and (4) maybe the reduction of the nose[51]. The diminution of the laryngeal opening, due to shortening of the arytenoid cartilages resulting in lengthening of the vocal folds, thus contributed to speech evolution (Negus-1949, -1962)[52].

It is probable that the human lungs also show signs of reduction. From the comparative anatomical studies of Marcus-1937 it follows that of all mammalian lungs, the human's have nearly the smallest respiratory surface to body weight ratio.

In respect to his running capacities, the reduction in the size of air passages put early man at a disadvantage compared with many of the animals he hunted or was threatened by. This was compensated for directly by his intellectual preponderance[53], and indirectly by his use of tools[54].

The making and use of *tools* has certainly been of great importance to the evolution of mankind (Washburn-1950, -1962), though animals, including a number of primates, also use tools. In this respect monkeys may be as highly developed as apes (Klüver, cited by Hill-1957) K. R. L. Hall therefore finds some evidence that human tool-using is rooted in primate tool-using. Because of the reduced canines and incisors Pilbeam & Simons suppose the late Miocene primate *Ramapithecus punjabicus* to have already been dependent on tool-using for feeding.

Circumstances that accompanied the *origin of tools* and the evolution of tool-making during human evolution have already been briefly referred to: brachiation and "chiriation"[32], neoteny[39] and poor running capacities[54]. To these should be added: (1) *Intelligence*, which made new inventions possible[55], but which according to Dobzhansky-1955 was stimulated in turn by handling objects[56]. A reverse relationship is propagated by soviet authors like Seppe and even Stalin, cited by Critchley: "speech functions are created from work". Clark supposes the improved intel-

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* Slijper-1936 (p. 525) emphasized that the great amount of human cerebral tissue cannot be considered as a foetalized character, being the result of a greater number of neurones compared with the larger size of individual neurones in lower primate ontogeny. On the other hand, von Bertalanffy & Pirozynski explain the high relative brain size at birth in other vertebrate species by the presence of the adult number of nerve cells.

lectual capacity of *Pithecanthropus* compared with *Australopithecus* and represented by increased cranial capacity to be the result of tool-making, which probably began in the Australopithecine stage (Washburn & Howell, Oakley-1968). Therefore Washburn-1960, Pilbeam & Simons, Mayr-1963, Robinson-1968 and Dart-1968 feel that tool-use and tool-making must have preceded the increase in brain size in the human ancestors. (2). *Group-life*, which gave new findings the chance of spreading and of being of continuous value[57]. (3). *Speech*, through which techniques could be communicated (Oakley-1952, -1962)[58]. Indeed the presence of tools or evidence for fire in fossil layers has been supposed to indicate the ability of speech by the makers (de Laguna, Pannekoek, Révész, Kraft, Weidenreich, Gieseler, Gottschick, Bounak, Dart-1959, Overhage-1959, Critchley, Montagu-1962-a, Bryan). On the other hand Bastian and Lenneberg-1968 consider such inferences as unreliable, and Pumphrey and Hallowell suppose the use, not manufacture, of tools to have preceded the development of speech. (4) The *arboreal habitat*, which may have introduced the use of tools, because of the grasping and the handling of branches and fruits[59], though naturally palaeontological evidence for this hypothesis does not exists.

The change from a mainly herbivorous diet during the arboreal stage into an *omnivorous diet* may also have had a relationship to toolmaking: hunting was advanced, and, according to Washburn & Avis, probably preceded by tools[60]. The reverse relationship equally holds true: regular tool-use started with the emergence of weapons rather than with gadgets (Kortlandt & Kooy), while handling bones and other parts of the prey probably induced their application as tools, as illustrated by Dart-1949, -1961, -1968 in regard to *Australopithecus*[61]. Also dental characteristics suggest tool use by Australopithecines, because of its necessity for predation and intrasexual combat (Bartholomew & Birdsell) and its protective function (Brace)[62]. Recently Tobias-1969 summarized a number of other arguments indicating the use and the making of tools by these early ape-men. It is evident that effective toolmaking was stimulated by good vision, as pointed out by Dobzhansky-1955[63]. This agrees with Linschoten's statement that man's stereoscopic vision is optimum within the range of the working hands.

After leaving the trees for a prairie-type landscape, man's ancestors probably acquired their *upright posture*, which may have already happened in the early Pliocene primate *Ramapithecus* (Simons-1967). One may postulate that by moving on the ground on foot man freed his hands for the use and manufacture of tools[64]* and his inferior thyroarytenoid folds for mainly vocal purposes, since they were now scarcely used any longer for the combination of valve action and voice production. From then on these folds are better called *vocal folds*, and man's voice attained its typical timbre instead of the somewhat stronger and harsher voice of his ancestors (Negus-1949, -1962)[65]. It is not impossible that the upright posture may have been causally related to the descent of the larynx (Vallois-1967, Hockett-1963). Mehnert supposes the forces of gravity to be responsible for the gradual descent during human ontogeny[66].

Bipedal gait may have given ancestral man's vision better opportunities by providing wider horizons, as suggested by Negus-1928, Etkin, Roe and R. C. Snyder.[67]. Negus-1925, Kipp, DuBrul, DuBrul & Reed, Andrew-1963-c and Campbell postulate a mechanical influence on the jaws from the upright posture, causing reduction in their size[68]. The same can be said of the human pelvis, whose shape brings a more tortuous birth-canal than in apes (de Snoo-1939, -1942) resulting in more difficult parturition[69].

Bipedal gait and the attendant change in function of the upper extremities must have contributed indirectly to human social life. In early hominids the exchange of information and expression of feelings and emotions by gestures is likely to have accompanied vocal communication or even to have preceded it (Sayce, Diamond)[70]. In fact Crawford (p. 278) concludes from his ethological studies of chimpanzees: "It may be that an important transitional step in the development of language behavior lies between the direct orientation of one animal by another through bodily manipulations

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* Washburn feels, and also quotes Darwin who was of the same opinion, that a reverse relationship exists: the use of tools may have caused bipedal gait. Hayes & Hayes suppose tool-using to have preceded upright posture.

and indirect orientation through pointing towards a distant object".

Another factor which may have contributed indirectly to the evolution of speech is the *increase in body weight*, which must have occurred during the evolution from lower primates to man. Rensch-1956, -1959 showed that in a number of vertebrate species an increase in body weight is positively correlated with an increase in intellectual capacity. Such a process may very well have contributed to the rise towards a higher level of cerebral function during human evolution [71]. Increased body weight may be associated with the arboreal habitat: it must either have led to the abandonment of such a niche, or a selection pressure in favour of larger individuals must have arisen after its abandonment [72].

The increased body weight may have had survival value not only because of the possibly greater intelligence, but also because of the increase in visual range the wider horizons made possible especially after upright posture had been obtained[73]; while the greater strength favoured the use and production of tools[74] and the predation of larger animals[75].

Rensch-1939, -1959 pointed out that increased body weight acts in *climatic selection*, larger individuals being able to sustain lower environmental temperatures better than smaller ones in view of the relative decrease in body surface. (Röhrs pointed out, however, that other factors are probably more important for this kind of selection). In spite of the progressive loss of hair during human evolution, possibly a neotenous character (Campbell, p. 31)[76], man has therefore been able to occupy new niches, a situation facilitated equally by a number of other factors. There may be another relationship between the increase in body weight during primate evolution and the scantily haired human skin. Albers supposes that animals able to *sweat* have generally evolved into larger forms than those depending on panting alone for temperature control. Panting loses efficiency with increase in size, and Montagu-1964 supposes the loss of body hair during human evolution to have increased sweating capacity. Whether such a relationship has actually been working in human evolution must remain hypothetical until the appropriate comparative anatomical and physiological observations have been made. (From the work of Perkins & Machida, and Machida, Perkins & Hu, and others it may be inferred that most primates are able to sweat on most parts of the body).

In *conclusion* we may state that the roots of human speech are probably to be found in a long era of *sound* production, gradually passing into communication: an even longer era of *voice* production. The emergence of *speech* based on this must have resulted from the interaction of a large number of characteristics and circumstances, some of them typically human, making up the greatest part of the human morphological and functional characteristics, in which process the larynx does *not* occupy a central place.

10. *OTHER FUNCTIONS*

In conclusion we must consider the part the larynx plays in the evolution of some less obvious respiratory phenomena.

The phenomenon of *hiccoughing* is characterized by a sudden forceful contraction of the diaphragm, and for that reason is probably only present in mammals, its existence in reptiles being uncertain because these, including *Sphenodon*, as far as can be understood from the publications of Osawa and Günther, usually possess no diaphragm, and when like the crocodilians they do, it is feeble (Negus-1925). Hiccoughing is accompanied by a sudden decrease in intrathoracic pressure and this results in various signs depending on the anatomy of the species concerned. Hiccoughing in man is usually accompanied by the typical hiccing sound, sometimes followed by a slight soreness in the throat or epigastrium.

In the comparatively rare publications on the hiccough, the phenomenon is always considered from a clinical point of view (e.g. Baily, Benke, Voorhoeve, Salem *et al.*, Gigot & Flynn, Munchenheim), and no explanation of the mechanisms mentioned is given. It must probably be sought in the valve action of the lower thyroarytenoid folds: by the sudden decline in subglottic pressure the usually relaxed folds are forcefully drawn together. The resulting closure may be

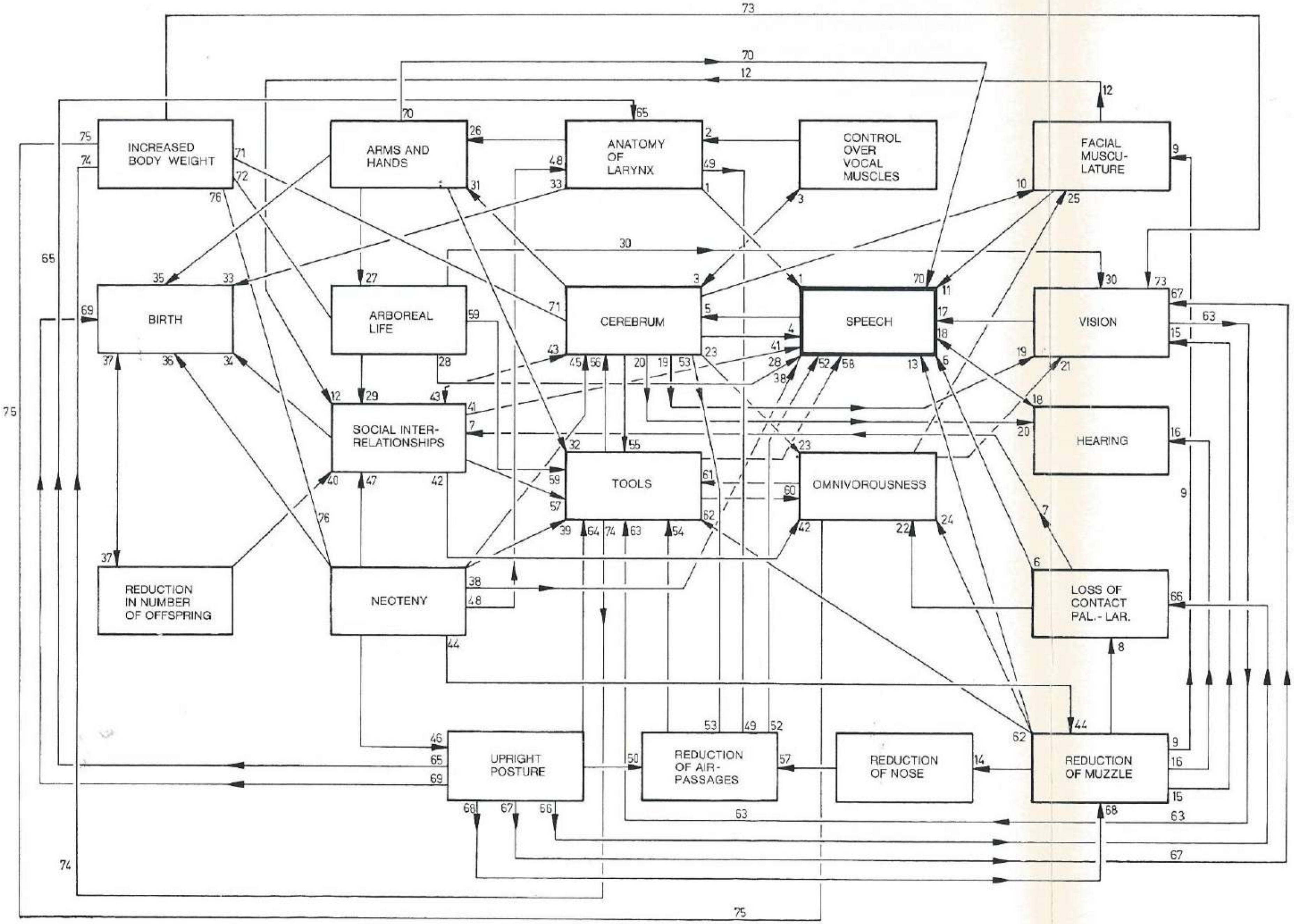

FIG. 39.
Diagram illustrating the emergence and evolution of speech (see text)

followed by another and steeper decline in subglottic pressure before diaphragmatic movement is complete. Painful sensations presumably occur in these cases.

Another explanation can be found in the simultaneous stimulation of the phrenicus and vagus nerves, resulting in contraction of the diaphragmatic and the laryngeal muscles. If the sphincter muscle fibres are stronger than the dilators, as suggested by the *Semon-Rosenbach law* and affirmed by the findings of Pfau in dog experiments, such stimulation would result in closure of the larynx, on whose tissues a considerable tension would then be exerted. A third explanation would be a combination of the two.

Unfortunately there are only few observations on *hiccoughing in animals*. Even in the extensive article by Kelemen-1932 on the inspiratory voice it is not mentioned. Schaller reports it in gorillas in the wild. Speculations about its existence in man's ancestors are therefore purely hypothetical. Our own observations indicate that in dogs it appears as a forceful sudden inspiration, not accompanied by sounds from the larynx but from the other bottleneck in the airways, the nose. For this reason the laryngeal phenomena of hiccoughs are more likely to be explained by the valve action of the vocal cords than by the simultaneous contraction of the laryngeal muscles. C. Jackson feels that the hiccoughing sound is produced by the valvular closure of the larynx. In the ape-like ancestors hiccoughing may have had human characteristics because of their valve systems which were probably even more effective than those of modern man. Indeed hiccoughing in modern apes shows many human characteristics. As far as our earlier ancestors are concerned, we encounter the same problems of aerodynamics as mentioned on p. 63. In the gymnure-like and *Tupaia*-like ancestors it seems unlikely to have existed because of the absence of inlet valves.

Another, largely physiological, phenomenon in which the respiratory tract and hence the larynx is involved is *yawning*. (In order to avoid confusion which is likely to result from reading different publications on animal yawning, I will in this discussion consider opening the mouth and taking one or a few deep breaths as yawning, only if it is accompanied by contraction of the respiratory and most of the other skeletal muscles). The inspiratory phase may be compared with the hiccough, but the larynx is opened maximally by reflex, and due to this and the slower passage of air through the inlet valves, is not closed.

Yawning seems mainly to be found in the carnivorous mammals and the primates. Heusner, in one of the few publications on yawning, comes to the same conclusion. In the above form it probably does not exist in non-mammals. The sole herbivorous mammals which, as far as I know, have been reported to yawn are the kangaroo *Macropus* (Breeden & Breeden), the North American moose *Alces alces andersoni* (V. Geist), and members of the horse family (Trumler, cited by Tembrock), but it seems uncertain if these herbivores show the mentioned muscle stretching; this is equally absent probably in tree-shrews, reported by Kaufman and Sprankel to yawn, and some non-mammalian vertebrates, which may sometimes show yawn-like mouth movements (Baerends-1969, Peiper).

The *phylogeny of yawning* is difficult to trace, if only because of the lack of sufficient reports on it in animals. The only speculation I have been able to find in the literature is that of Spurway & Haldane, who suppose it to have originated as a "displacement" of normal breathing movements, evidence for which, however, provisionally is unconvincing (Baerends-1969).

Ethology can perhaps give some indications. (1) It may mainly be found in species whose activities show considerable variation (carnivorous mammals, primates), and here it can be useful for the abolition or prevention of atelectasis in the lungs: presumably these contain during periods of rest extensive collapsed areas which only come into use during periods of increased activity like hunting. Contraction of the muscles supposedly removes metabolic products impeding their normal function. Yawning *before* periods of activity, normally seen in man and animals, may therefore have a physiological significance and hence a selective value. (2) Man, on the other hand, yawns also during fatigue, which may often be considered as *displacement* behaviour. (On the other hand, it is very likely that, at least in man, biochemical changes of the blood, other proprioceptive stimuli and neurological diseases, too, may cause yawning via the central nervous system. C. Jackson and Peiper suppose the yawning centre to be able to take over the function of the respiratory centre, and Selbach & Selbach that an interaction between the respiratory centre and the extrapyramidal motor system causes yawning. Similarly in animals it is sometimes present as displacement behaviour, e.g. in nervous dogs. (3) It is remarkable that yawning, and to a lesser extent coughing and clearing one's throat, at least in man, is "infectious": it is evoked by observing it in a member of the same species.

As a working hypothesis, I therefore propose that in many cases it can be considered as a *ritualized behaviour* and as a *social releaser* (in the sense of Tinbergen-1951, *i.e.* an innate response dependent on stimuli given by other individuals of the same species) acting as a socializing factor, and having selective value because of its use for preparing for the common bodily activities of the above carnivores, the primates, and our primate ancestors.

Other, equally hypothetical, explanations of yawning are rendered by Heusner, Selbach & Selbach and Peiper.

The first phase of *coughing* shows roughly the same phenomenon as that of hiccoughing: slight narrowing of the laryngeal lumen, as Yanagihara *et al.* found in human subjects, which they explain as a Bernoulli effect. Floersheim reports the same in cats. However, this narrowing does not pass over into complete closure. Apparently the velocity of the air is too low (indeed the inspiration preceding coughing does not even have the violent character of that during hiccoughing), or there is a different reflex mechanism. For a further discussion of coughing, see pp. 60, 65 and 66.

Whispering is of no particular interest here, since it probably originated after speech, as a modification thereof. Moreover the larynx has almost no function in whispering. The part the larynx takes in *sobbing* is very similar to that in hiccoughing, in view of the sudden involuntary contraction of the diaphragm and the valve action of the human vocal folds. However, since it has never been observed in animals, its existence in non-human ancestors is unlikely. The same applies to *laughing*. An involuntary and quite sudden inspiration also occurs in the initial phase of *sneezing*, during which the larynx however remains open, presumably because of the air current moving slower than during hiccoughing. Since sneezing can be observed in many other mammalian species, in which it shows quite human characteristics, it is likely to have existed in its present form in our mammalian ancestors.

11. *CRITICAL REVIEW OF THE AVAILABLE LITERATURE*

The development of the larynx during vertebrate evolution has been the subject of many publications in the past, especially in that great era of morphology and comparative anatomy, the second half on the 19th century. It can safely be stated that as far as morphology is concerned, these publications are still of great value and can be considered as giving a firm basis to most modern studies dealing with such topics. At that time, however, there was some confusion about the meaning of comparative anatomy and phylogeny, the two often being considered indentical (*cf.* Figure 3). In this section the majority of publications dealing with the phylogeny of the human larynx will be briefly discussed.

Henle-1839 was probably the first to give a comparative anatomical description of the larynx in a number of vertebrates, mainly amphibians and reptiles plus some data on *Protopterus*, birds and mammals. His study was based on the above concepts of comparative anatomy and evolution. Nevertheless it gives clear morphological descriptions, good pictures, and references to the older literature. Müller-1840 published accurate observations on the physiology of human and several animal larynges. Though these did not directly deal with phylogeny, they doubtless greatly contributed indirectly to this subject. Müller's book is of particular historical interest, because he gave many references to the older literature. Fürbringer-1875 was probably the first to write an extensive monograph on the morphology of the laryngeal musculature which, as usual in that era, comprised both the human and the mammalian anatomy in general. Although in his publication of 1922 some phylogenetic considerations are given concerning the hyoid apparatus, he hardly did so in regard to the larynx in either publication.

On the other hand, Gegenbaur-1892 in his detailed monograph on the epiglottis, and in his 1901 book on comparative vertebrate anatomy, did attempt to find evolutionary relationships in the various branchial elements and laryngeal cartilages. The essential features of the diagram in Figure 35 are derived from this study, though the modern view of his subject has somewhat changed, mainly in regard to newer evidence from palaeontology. Moreover, Gegenbaur's discussions applied almost solely to the laryngeal skeleton and, virtually disregarded e.g. musculature, topography and functions.

This lack of physiological considerations is also encountered in the otherwise excellent publications of Göppert, who with Negus, contributed most to the studies on the comparative anatomy, and therefore the phylogeny, of the larynx. In a series of clearly illustrated articles published around 1900 and summarized in 1937, Göppert systematically gave very detailed and reliable anatomical descriptions of the laryngeal anatomy, mostly avoiding the more speculative phylogenetic conclusions to be drawn from these observations.

Before and after Göppert, but mainly in the era of relatively great interest in comparative anatomy ending roughly with the First World War, a number of other studies were published on the comparative anatomy of the larynx without, however, dealing with its phylogeny, the majority of which is briefly mentioned here.

Brunton & Cash 1883	a review of the morphology (plus some physiology) of the thyroarytenoid folds in various mammals.
Simanowsky 1883	a morphological description of the ventricular bands and nerve endings in the laryngeal mucous membranes of man, dog, cat, pig, some rodents and some ungulates.
Koerner 1884	mainly the laryngeal musculature; fairly extensive description of the condition in the chimpanzee, orang-outang and monkeys; good pictures.
Waldeyer 1886	several mammals; some general remarks on the pharynx and deglutition; comments on the orang-outang.
Wiedersheim 1886	a number of mostly original observations concerning the larynx of different vertebrates.
Howes 1887	mainly topography of epiglottis in most mammalian orders including insectivores, lemur and orang-outang.
Bowles 1889	mainly anatomical data on pig and sheep; short discussion on the topography of the infant with probably the first recognition of the function of its lateral food channels.
Sutton 1889	some general remarks on the thyroarytenoid folds and hyoepiglottic muscle in seemingly random chosen mammals.
Albrecht 1895	short but accurate descriptions of the condition in the different mammalian orders, including the insectivores and primates.
Némai 1912, 1933	mainly ungulates; an early author to mention the lateral food channels.
Piérard 1963, 1965	mainly anatomy of dog and some other carnivores.

The phylogenetic line we attempt to follow has, of course, been dealt with before. But few of the early studies can be considered complete, since they only tell us about limited ranges of the line (from the Cyclostomata to man), or discuss incompletely the subjects reviewed in this chapter. These publications may be summarized as follows:*

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* After completion of the manuscript I obtained a recent publication dealing with this matter, a monograph by Paulsen, mainly an analysis of voice production in different vertebrates, and mentioning a number of morphological items of the phylogeny of the larynx. Seemingly based mainly on the work of earlier authors, it includes an original, though possibly somewhat bold, hypothesis concerning the topography and orientation of the arytenoids in the vertebrate phylogenetic series.

Wilder 1892	discussion of the origin of the arytenoids and laryngeal musculature from the viewpoint of the anatomy of the lower vertebrates, mainly amphibians, with some original observations.
Gaupp 1904	short discussion and review of the literature concerning the phylogeny of the laryngeal skeleton and musculature in Anura.
Némai 1921	a detailed, mainly morphological, study of the larynx of several Old World monkeys, with some phylogenetic considerations concerning the mammalian ancestors of man.
Marcus 1925, 1937	in the first publication the author discusses some problems concerning the larynx in *Polypterus*, *Lepidosiren* and amphibians; in the second he gives a very detailed study of the lung/swim-bladder problem, with many references to the older literature.
Elze 1925	a short morphological review of phylogeny with no original observations.
Némai 1926*a*, -*b*	a detailed, mainly morphological, study of the larynx of several New World monkeys and the gibbon.
Jaekel 1927	discussion of the evolutionary relations between lungs and swim-bladders. The author gives a most unusual view according to which fish evolved from land vertebrates.
Tait 1934	short, somewhat peculiar discussion of the evolution of the vertebrate voice, teleologically coloured; seemingly few original observations.
C. Jackson 1946	a short review of the common knowledge on the morphological and functional points of interest concerning the evolution of the human larynx.
Goerttler 1954	some observations on the embryological development of the human vocal cords, from which the author draws some bold conclusions about the evolution of man's voice.
McCutcheon 1954	general considerations on vertebrate respiratory physiology; hardly any information on the larynx; the author favours the probably incorrect view of modern crossopterygians using lung respiration.
DuBrul 1958	a relatively detailed study of the vocal organs in a series of primates representing man's ancestors, somewhat indirectly focussed on the larynx; original observations, anatomical (mainly topographical) and functional considerations.
Overhage 1959	a discussion on the problem of speech emerg- from a palaeontological and anthropological point of view. Few anatomical details.
Starck & Schneider 1960	a very detailed study of all the morphological problems of the primate larynx supported by many original observations and good illustrations, including a review of the phylogeny of the skeleton and musculature. Many references.
Wustrow 1963	short review of the evolutionary history of the human larynx, with no original observations; almost purely morphological.
Ballard 1964	a short discussion of the lung/swim-bladder problem.

Special note may be taken of the work of Negus who, in a series of publications, has contributed to elucidation of many of the questions regarding the phylogeny of the larynx, compiled and summarized in his well-known books *The Mechanism of the Larynx* (1929) and *The Comparative*

Anatomy and Physiology of the Larynx (1949, 1962). The great merit of his work lies in the combination of numerous original morphological *and* physiological observations. The latter, though dealing with most vertebrate classes, mainly apply to the condition in mammals. Without intending to minimize the most valuable work this author has contributed to the comparative biology of the larynx and nose, some criticism may be given of his view of the evolution of the human larynx. This is not the place to discuss it in detail, but the objections may be summarized as follows:

(1) His work shows teleological tendencies, which are generally rejected by biologists when applied to the evolution of animals or their organs. Teleology may sometimes be accepted in working hypotheses concerning the functions of organs in modern species, but even in these cases it is better to explain with Lorenz-1964 (p. 21), what exactly is meant when one states that "this animal has character *x* for reason *y*". Most biologists in this context do not mean a metaphysical teleology but a consequence of natural selection. As Slobodkin points out, in the majority of such statements the phenomena concerned may be explained by non-teleological reasoning.

(2) In his description of laryngeal evolution one gets the impression that Negus is guided not by the sequence of species indicated by palaeontology but by evidence derived solely from comparing modern species. In this way he places a modern Teleost (with a swim-bladder) at the beginning of his series (-1949, -1962, p. 1), and, in a diagram illustrating the evolution of the larynx, a bird between a reptile and a mammal (-1924, p. 988, -1949, -1962, p. 10, -1965, p. 97). Moreover in this diagram the mammalian epiglottis is lacking.

(3) Negus supposes the reptilian cricoid and hyoid cartilages to be homologous with the mammalian cricoid and thyroid (1949, 1962 p. 11, 1965 p. 94), which, as made clear on p. 54, is improbable.

(4) The author seems to favour Haeckel's "biogenetic law", as may be concluded from several of his publications (-1924 p. 987, 988; -1949, -1962 p. 6, 13, 180, 183, 186, 197) though it is generally rejected by biologists (see Chapter 1).

Part 3

CHAPTER 5

The ontogeny of the human larynx

1. MATERIAL AND METHODS. REVIEW OF THE LITERATURE

As mentioned on p. 12, the ontogeny of an individual is taken as its development from fertilization to death (Kryzanowsky). If we want to describe the development of the larynx in human ontogeny, which for the sake of brevity we shall refer to as the ontogeny of the human larynx, we shall have to observe human individuals from a stage at which the first signs of the larynx appear. These snapshot-like observations are necessarily taken from different individuals and so the view of the ontogeny we are attempting to establish may well be influenced by individual variations.

In regard to the *shape* of the larynx and its constituent parts, the main changes take place in the early embryonic stages of man, those in regard to their *size* in the prenatal and postnatal stages. To acquire information about shapes and sizes in the early embryonic stages, besides simple observation of microscope sections, it often appears necessary to use special methods such as spatial reconstructions. For this purpose enlarged copies of the sections are put one above another, making macroscopic observation of microscopic material possible.

From about 20 weeks on the human larynx can be observed macroscopically, though with some difficulty and inexactitude, and after birth macroscopic dissection and observation are possible.

Considering the complex character of the reconstructive method, it will be realized why only a few such observations on the early stages of the human larynx have been published. After the classic work of His on the development of the branchial system, dealing with the laryngeal entrance but not with the other parts, Kallius concentrated on the embryology of the human larynx and in 1897 published a detailed study illustrated with figures of his reconstructions, adding some more data in 1898. The text and the illustrations are of high quality, and have frequently been used since in many books on embryology and laryngology (Berendes *et al.*, Denker & Kahler, Broman-1911, -1927, Bonnet & Peter, Baily & Miller, Fischel, Hertwig, Keibel & Mall, Prentiss). Before Kallius some other work had been published by Roth in 1880 on the epiglottis and laryngeal entrance, by Strazza in 1889 on the early stages and Nicolas on several stages, while in 1898 Zuckerkandl gave quite a detailed description of the complete ontogeny. It seems, however, that none of these authors made reconstructions.

After Kallius we find but few original publications on the subject: the detailed ones of Soulié & Bardier-1906, -1907 and of Frazer-1910, -1940, using spatial reconstructions.

Unfortunately the latter hardly dealt with the laryngeal skeleton; moreover the quality of their illustrations does not reach the level of Kallius. This can also be said of two other publications, Broman-1911 and H. Frey, who do not discuss the subject in detail but give some reconstructions. One study, neglected later, was that of Lisser who in 1912 gave an excellent review of the development of all laryngeal structures in human embryos ranging from about 10 mm to 20 mm, illustrated with a number of clear pictures of his reconstructions.

Mention should also be made of an elaborate study of the pharyngeal floor and its derivatives by Kingsbury who, however, hardly considers the larynx, and one by Patzelt on the epiglottis at different ages. More recently Tucker & Smith gave an original review of the laryngeal connective tissue compartments in the human foetus. In most textbooks, even more recent ones, the embryological stages of laryngeal development are only superficially discussed, if at all (Arey, Patten, Hamilton *et al.*, Kollman, Gurwitsch, de Haan & Ursprung, Starck-1965-a, Tourneux, Prentiss, Corning), even when they give original observations, like those of Lederer or Hamilton & Harrison. When a more detailed account is given on this subject, it is based on Kallius' observations or on Frazer's (e.g. Negus-1949, -1962, Keith-1933, Grosser *et al.*) rather than on original work. Therefore it seemed useful to enquire into the embryological stages of laryngeal ontogeny based on newly-made spatial reconstructions.

Macroscopic observations on the human larynx have frequently been published in textbooks of anatomy and otorhinolaryngology, and in numerous incidental publications.

In this study we pay special attention to the main lines of early embryonic development for two reasons. Firstly, because at this stage the greatest changes in form take place; and, secondly, because there is not much information to be obtained from the literature on this subject. On the other hand, the final stage of laryngeal development, the postnatal, will only be discussed briefly, the reader being referred to the textbooks.

Since the disposable human material from the earliest stages of laryngeal development appeared to be too damaged for sufficient information, description of these stages is mainly based on the existing literature, which has in the past sometimes been based on observations of animal material rather than human. On the larynges of human embryos measuring from crown to rump (= C.R.length = sitting height) 8 mm, 23 mm and 47 mm (Laboratory of Anatomy, University of Leyden, series No. 78-WK 3461, 47-WK 1256 and 229-WK 592) a description mainly based on three dimensional reconstructions will be given. For later stages serial sections or macroscopic observations will be discussed. In all cases only the main features of laryngeal development are described, the aim being to examine the relations with phylogeny, not to give a detailed account on the embryology of the larynx.

The technique used for our reconstructions is somewhat different from that commonly applied for this purpose, namely the use of *transparent plastic* material (Figures 47 and 53).

The traditional method, probably first described by Born in 1883 and used since the great era of morphological embryology in the second half of the 19th century, consists of copying the microscope sections after magnification on wax plates dimensioned in proportion to the magnification used. The wax is then removed, except from the portion representing the organ to be reconstructed. Recently this method has again been applied to an adult larynx by Konig & von Leden. In another method cardboard sheets are used, and the organs are drawn and cut out. When these sheets or plates are placed one on top of another, one gets a three-dimensional picture of the organs concerned.

My technique was as follows. Using 10 μ haematoxylin-eosin stained sections and a projecting microscope, the structures to be reconstructed were drawn at an appropriate magnification, say x times, on paper sheets. Because of the shape and position of the laryngeal rudiments within the foetus, only cross-sections were used, about 50 in each of the three reconstructions. These drawings were divided into left and right halves by a sagittal line drawn according to the symmetry of the structures projected. Then the drawings were cut into halves which were put on transparent polymethylmethacrylate plates of the same size as the divided paper sheets. The thickness of these plastic plates was x times the distance within the embryo between the microscope sections drawn.

The paper sheets were then glued to the plastic or copied onto it with carbon paper, and the areas of the plastic corresponding to the structures to be reconstructed, namely the lumina lined by the epithelial surfaces and the cartilages of the larynx, were removed by means of a small fret-saw and discarded. To get the spatial model the plastic sheets, cleaned from the paper, were put on top of one another and their correct sagittal interrelations established with the help of a sagittal series from another embryo of about the same size, also guided by existing pictures showing neighbouring structures and the contours of the head region. For a correct reconstruction the angle between the long axis of the embryo and the plane of the cross-sections of the concerned series had to be taken into account. This was found by measuring the distance between two cross-sections in which a comparable left and right structure appeared. The eyes were used for this. Finally, the two piles were reinforced by vertical pins, their uneven vertical walls were smoothed by sawing and polishing to give transparency in the horizontal direction, and the cut plastic surfaces were coloured, epithelium red and cartilage blue.

The advantages of this method are two: the model lasts longer when handled, and the three-dimensional relationships of organs like the larynx can better be observed. A disadvantage is the greater amount of work necessary and the price of the materials, which are somewhat more expensive than in the traditional methods.

2. *THE EARLIEST STAGE OF THE HUMAN LARYNX*

The first sign of the lower respiratory tract in a human embryo consists of a median slit-like groove on the ventral side of the foregut, which is the beginning of the division of the respiratory from the digestive tract. This tracheal or *laryngo-tracheal groove* can be observed in embryos aged about three weeks. In the literature one finds different indications of size and age in regard to this sign: before the end of the third week* (Göppert-1906,) 2,5 mm (Arey), 7 somites* (His), 14 somites** (Patten), 2,7 mm (Fischel), 3 mm (Soulié & Bardier, Terracol), 3,2 mm (Negus-1965), 4-5 mm (Wustrow), 5 mm (Hamilton *et al.*), all C.R.lengths.

Shortly after this stage the branchial elements can be recognized, of which man has 5 pouches or entodermal evaginations on each side. The most caudal pair, the 5th,

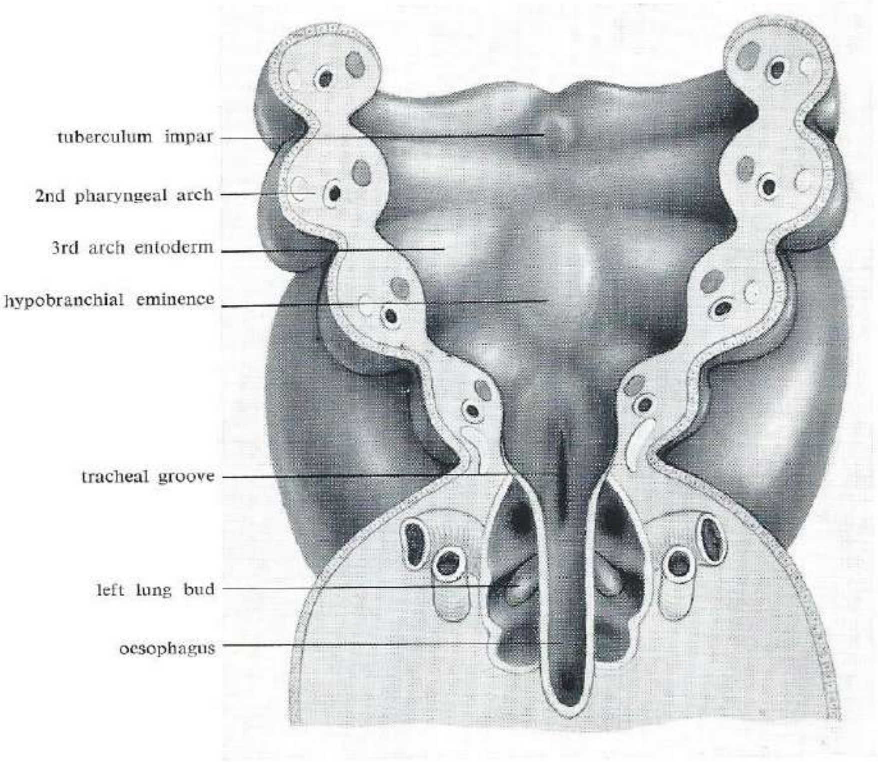

FIG. 40.
Floor of the pharynx in a 5 mm C.R.length human embryo showing the visceral arches (based on Hamilton, Boyd & Mossman). 40 ×.

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* which corresponds to a C.R.length of somewhat under 2,5 mm according to the measurings of Hamilton *et al.*

** which corresponds to a C.R.length of somewhat over 2,5 mm.

are only rudimentary. Between them the paired mesodermal branchial or visceral arches are situated (Figure 40). The branchial system and the entoderm which has been separated from the ventral part of the foregut, together form the major parts of the larynx. The relationship of the arches to the laryngeal skeleton was described in Chapter 4, §3. Unfortunately we have not been able to check these data and therefore rely on previous observations.

The laryngo-tracheal groove, situated just caudal to the 4th pouches, shows slightly upturned and rounded edges (Soulié & Bardier, Frazer-1910, -1940). The relief of the pharyngeal floor is further determined, next to the branchial arches, by an ovoid swelling between the 3rd and 4th arches in front of the groove, the *hypobranchial eminence* (Frazer's central mass), which represents the rudiment of the epiglottis. It becomes clearly visible at a somewhat lager stage (Kallius: 28 days, *i.e.* about 4 mm; Hamilton *et al.* 4,2 mm; Frazer-1910, -1940: 5 mm; Soulié & Bardier: 6 mm). Cranial to the hypobranchial eminence and the second arches another swelling can then be recognized, the *tuberculum impar* (His), from which the tongue develops.

The lateral walls of the groove are formed by dense mesenchyme which gives rise to the arytenoid cartilages; they are named the *lateral masses* (Frazer-1910, -1940) or *arytenoid swellings (Arytaenoidwülste, bourrelets aryténoidiens)*, which by their bulk seem to be pressed against each other and obstruct the lumen. This was probably first described by Roth in 1880. At this stage no cartilage can be found in the laryngeal region.

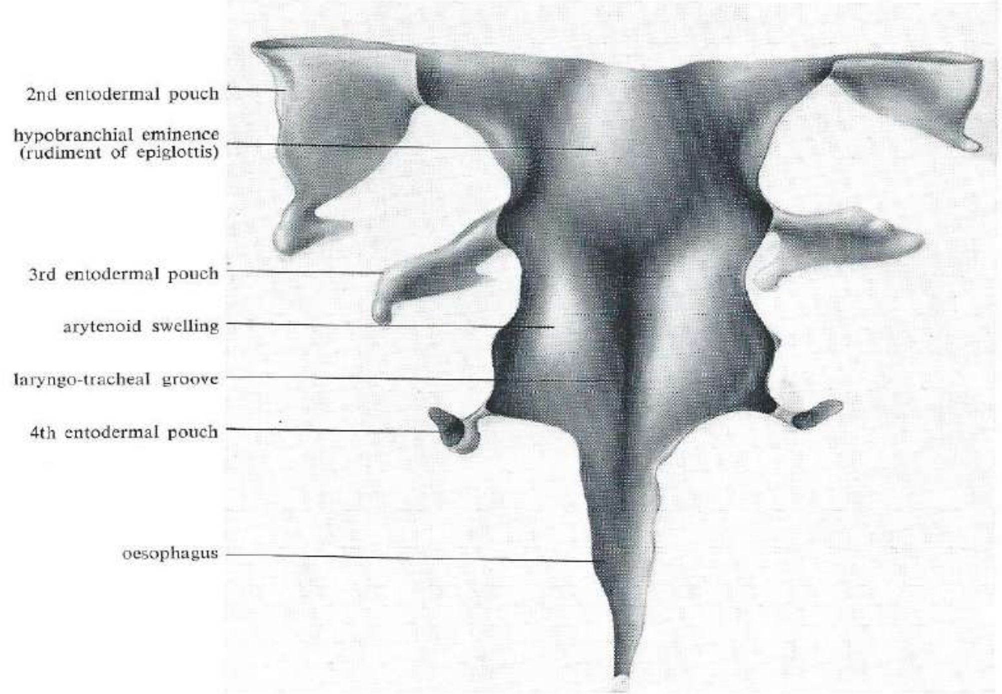


FIG. 41.
Human embryo, 8 mm C.R.length. Pharyngeal floor with laryngeal entrance between the arytenoid swellings, and 2nd, 3rd and 4th entodermal pouches. Artist's view based on spatial reconstruction. 85 ×.

3. *THE 8 MM EMBRYO*

Compared with the previous stage the ventral aspect of the pharynx in a human embryo of 8 mm C.R.length (age approx. 35 days), shows no essential differences except in size: the median laryngo-tracheal groove is flanked by the relatively large arytenoid swellings, and cranial to it is the hypobranchial eminence (Figure 41). The side walls show the 2nd entodermal pouches lateral to the hypobranchial eminence, the 3rd pouches lateral and cranial to the arytenoid swellings, and the 4th pouches lateral and caudal to these swellings. Within the relatively large masses of undifferentiated mesenchyme in this region there is as yet no trace of cartilage indicative of the future laryngeal skeleton; the same applies to muscular tissue.

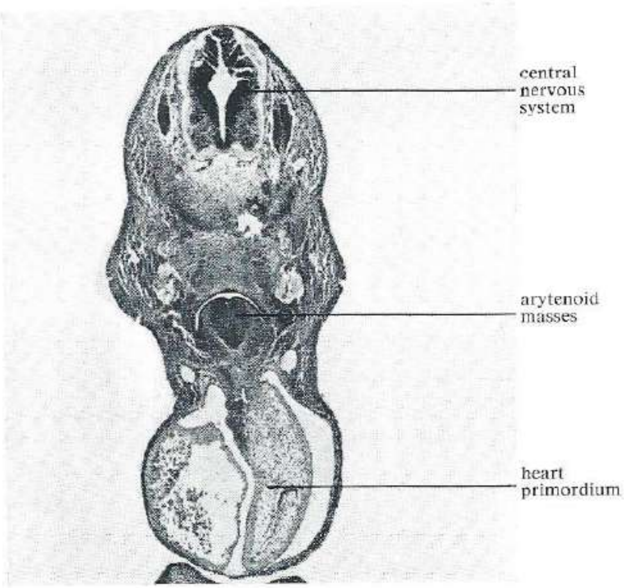


FIG. 42.
Horizontal section through an 8 mm C.R.length human embryo, showing the relatively large arytenoid masses just dorsal to the heart primordium. H.E.stain. 22 ×.

In contradistinction to earlier stages, the trachea has separated from the gut although in its cranial part there is still complete blockage of the lumen by the arytenoid masses (Figures 42, 43, 44). Concerning topography it should be noted that the laryngeal primordium is bordered ventrally by the heart (Figures 42 and 44).

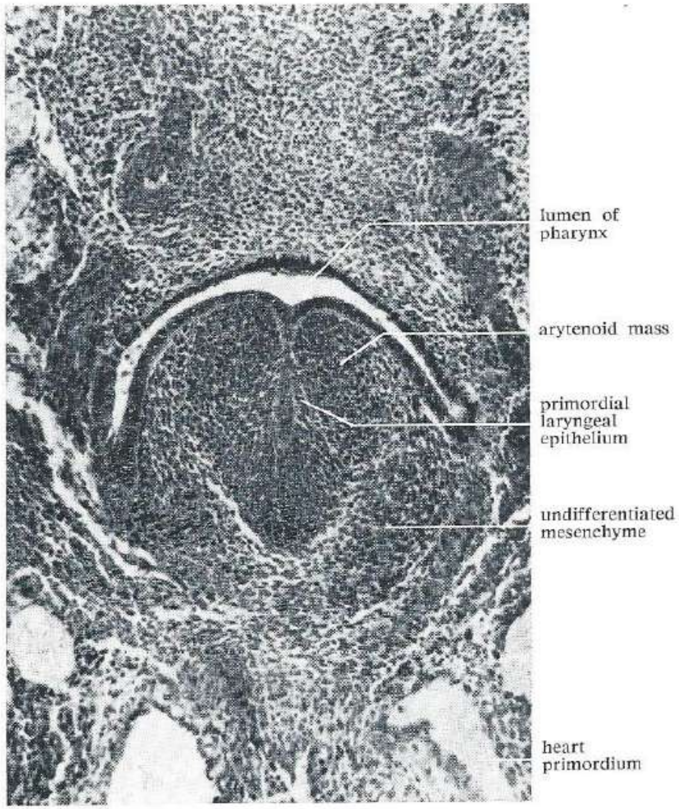


FIG. 43.
Same specimen as FIGURE 42, area of rudimentary larynx enlarged. The U-shaped pharyngeal lumen is clearly visible, the two arytenoid masses are pressed against each other obstructing the laryngeal lumen, which is only indicated by its epithelial lining. The tissue later differentiating into the laryngeal muscles and cartilages is at this stage present as simple mesenchyme. 118 ×.

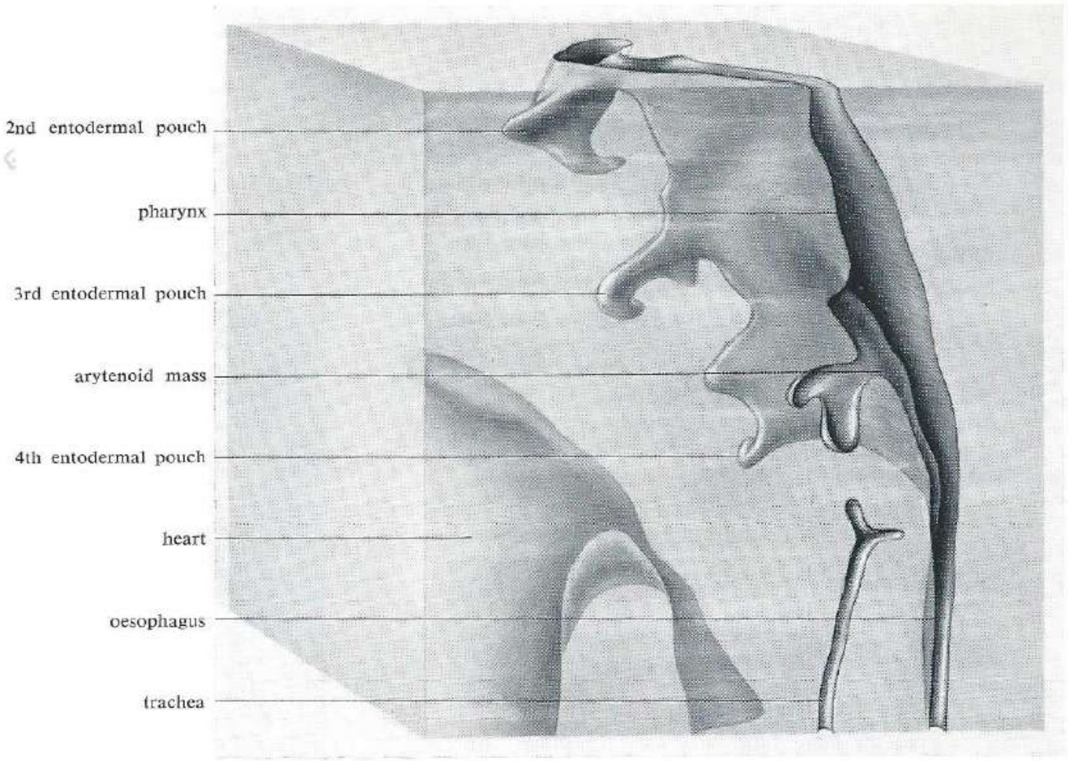


FIG. 44.
Medial and slightly ventral view of the right half of the pharyngeal, laryngeal and tracheal lumen of an 8 mm C.R.length human embryo. Artist's view based on an original spatial reconstruction, and showing the 2nd, 3rd and 4th visceral pouches. The laryngeal lumen is at this stage still obstructed and there is as yet no cartilage. For simplicity the other structures in this region have been omitted. The heart primordium has been vaguely reproduced to show the close relationship between larynx and heart at this stage. 85 ×.

4. *THE 23 MM EMBRYO*

In an embryo of 23 mm C.R.length (age approx. 50 days) some indications of the definitive shape of the laryngeal skeleton can already be recognized, the rudiments of the thyroid, arytenoids, cricoid and hyoid being present as pre-cartilaginous tissue. The contours of the lumen of the pharynx and larynx already resemble the postnatal condition. The relative size of the larynx-primordium has decreased (Figures 42 and 45).

Topographically the larynx still clearly shows a more cranial position than later, the top of the arytenoid swellings being well above the level of the hyoid body and reaching the level of the base of the skull, as illustrated in Figure 46 showing a somewhat earlier stage. The oesophagus and trachea are well established, but the laryngeal entrance is still blocked by the large arytenoid masses (Figures 46, 47 and 48). According to Kallius-1897, Broman-1911, -1927, Frazer-1910, -1940, Göppert-1906 and Soulié & Bardier-1906 at all stages of laryngeal development a connection remains between the pharynx and the trachea dorsal to the arytenoid masses. However in the 23 mm specimen observed in this study, a complete closure was suggested by the reconstruction, as the ventral channel, starting in the pharynx, had a dead end caudally, and the dorsal channel, starting in

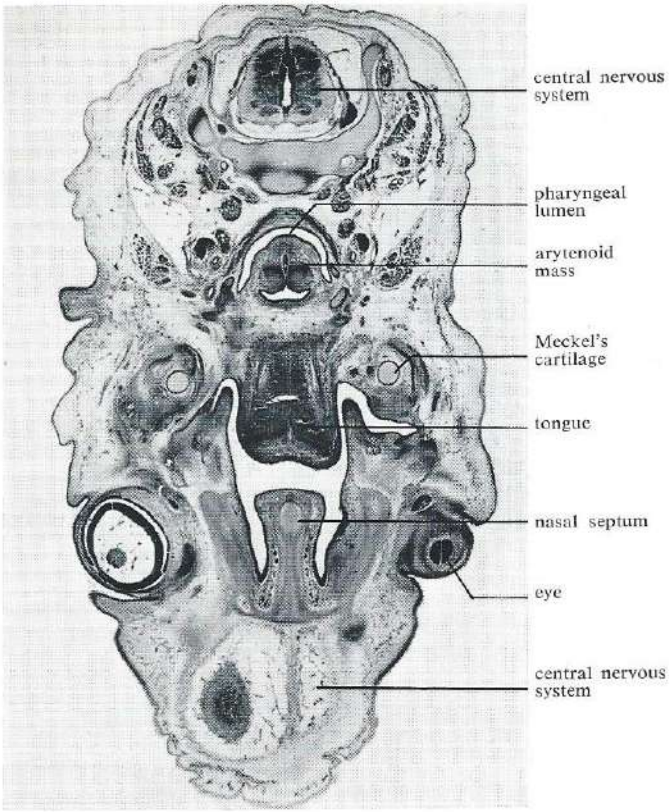


FIG. 45.
Cross-section through head region of a human embryo of 23 mm C.R. length showing the relative decrease in size of the arytenoid masses, as compared with the 8 mm stage (FIGURE 42). H.E. stain. 13 ×.

the trachea, seemed to have a dead end cranially, quite near the pharynx. Complete blockage of this sort is reported by Tourneux, Prentiss and Patten, whereas Fischel and Grosser *et al.* feel that in some cases a small channel remains and in others there is complete occlusion. It does not seem impossible that the blockage we found in this reconstruction may have been artificial because of aberrations in the model caused by the techniques used. As to the relationship between the parts of the skeleton, one clearly sees a condensation of these elements in a cranio-caudal direction, the upper border of the cricoid reaching well above the inferior

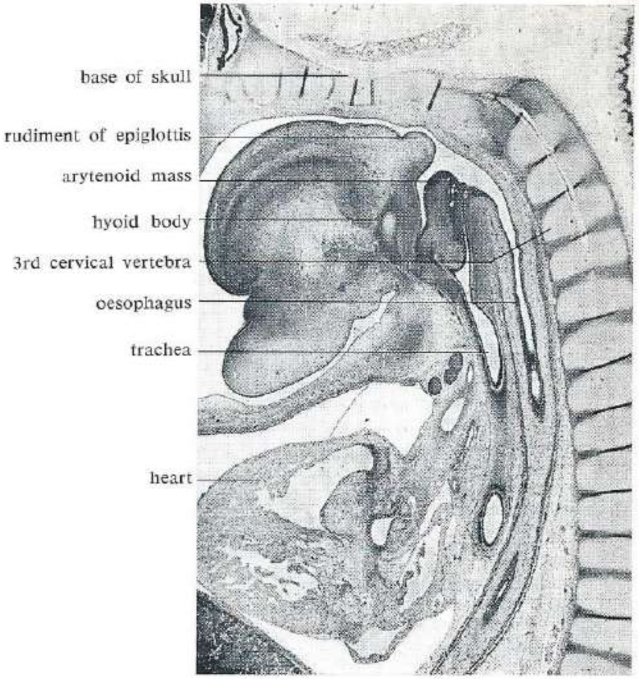


FIG. 46.
Sagittomedial section through the upper thoracic and pharyngeal region of a 19 mm C.R.length human embryo. Compared with FIGURE 44 there has been a caudal displacement of the heart. The laryngeal lumen shows a caudally blind ventral channel and a small dorsal channel which at its upper end is obstructed by an epithelial plug. The arytenoid masses are still relatively large. H.E. stain. 18 ×.

border of the hyoid, and the thyroid-primordium being at the level of the hyoid body for the most part.

When seen from cranially and caudally the *laryngeal entrance* shows the typical T-shape, formed by the dorsoventral groove as a result of the compressed arytenoid masses and the much deeper transversly placed groove between the epiglottis primordium and arytenoid masses.

The *hyoid* consists of a median body from which four horns diverge laterally, dorsally and cranially (Figures 49 and 50). These represent the original 2nd and 3rd visceral arches, the first of which becomes the lesser cornu, stylo-

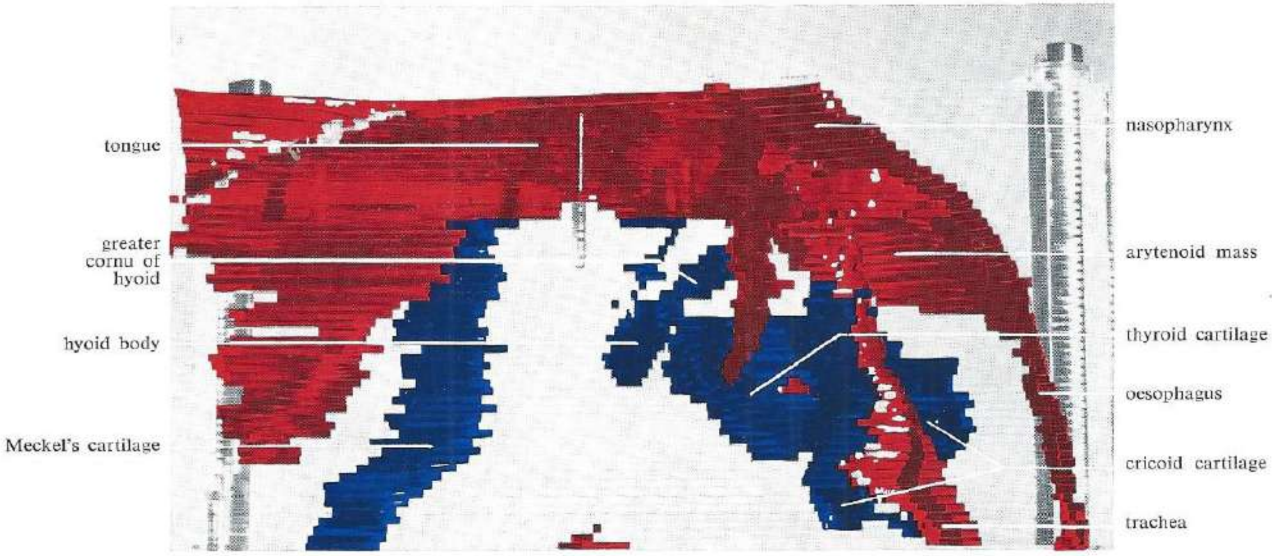


FIG. 47.
Spatial reconstruction of the laryngeal region in 23 mm C.R.length human embryo. Right half, medial view. The reconstruction is made by piling up transparent plastic plates in which the sites corresponding to the laryngeal cartilages and the epithelial lining of the region concerned have been cut out and coloured. The magnification of the original embryonic structures is in this figure. 22 ×.

hyoid ligament and process and stapes, the latter the greater cornu (see Chapter 4, §3). I found the future greater horn still united with the upper horn of the thyroid primordium in accordance with the findings of Kallius-1897 in his 13-14 mm embryo, Frazer-1910, -1940 in his 22 mm embryo, H. Frey in her 30 mm embryo and Nicolas in his 22 mm embryo. Broman-1911 in his 33 mm embryo suggests this connection.

The *thyroid cartilage* does not yet have the definitive shield form with its U-shape in cross section, but consists of two separate paramedian sections of pre-cartilage (also reported by Frazer-1910, Kallius-1897 and Nicolas). Their ventral border shows a slight prominence which probably constitutes the future incisura thyreoidea cranialis or Adam's Apple. It is here that the epithelium of the ventral side of the larynx shows the curve from a ventral to a dorsal direction seen in later stages at the base of the epiglottis, which Kallius-1897 considered to be typically human. However, this curve can also be recognized in adults of many other mammal species. The continuity of the upper horn with the hyoid has already been established, but there is no trace yet of the inferior one. In the upper part of the thyroid primordium a perforation is descernible, the foramen thyreoideum, by Kallius-1897 and later by e.g. von Lanz & Wachsmut supposed to represent the space between the 4th and 5th arches; this was however denied by Frazer-1910, -1940.

The *cricoid* completely encircles the trachea at this stage, but its shape is different from its definitive form, its ventral and lateral borders being somewhat higher, and its dorsal

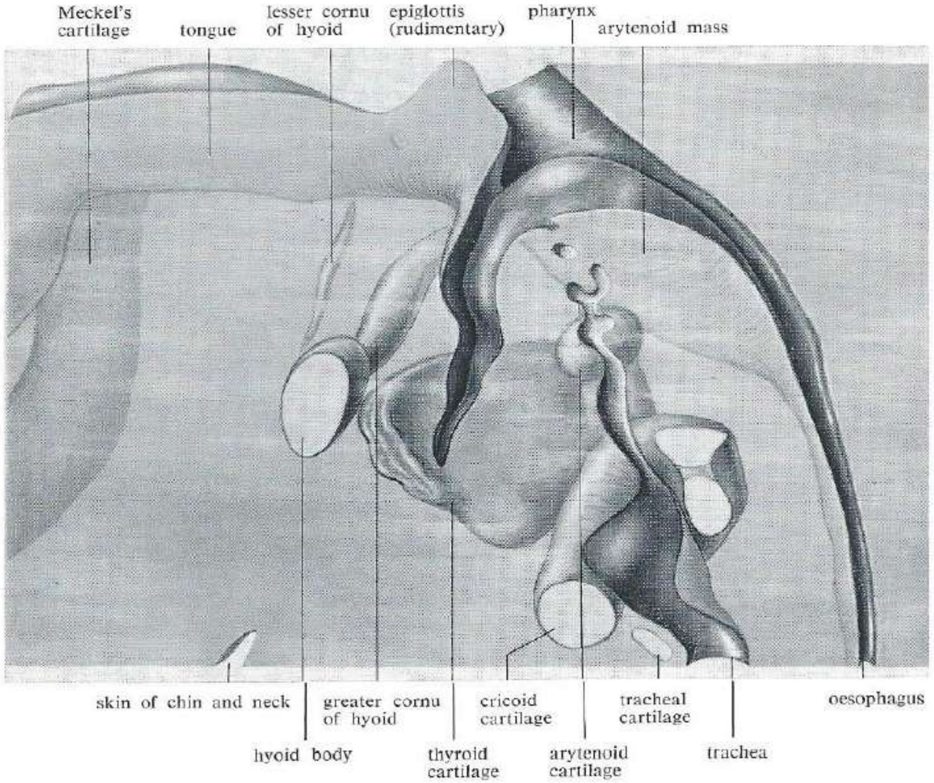


FIG. 48.
Medial view of the laryngeal region in a 23 mm C.R.length human embryo, right half. Artist's impression based on the reconstruction in Figure 47, showing the laryngeal and hyoid cartilages and the lumen of pharynx, oesophagus and trachea. At its cranial end the laryngeal passage is obstructed by the large arytenoid masses. 46×.

wall shows a medial perforation in the pre-cartilaginous tissue. Compared to the postnatal stages it is much more bulky, having relatively thick walls.

Contrary to the other skeletal parts of the larynx, the *arytenoids* are at this stage barely discernible in their definitive forms, being present as relatively small oval pre-cartilaginous bodies medial to the upper and dorsal parts of the thyroid primordium, enclosed in the comparatively large mesenchyme arytenoid masses. According to several authors these arytenoid rudiments represent the future muscular process, the vocal process being developed much later (Bardeen, Frazer-1910, -1940, Kallius-1897). Kallius describes the arytenoid primordium as originating from and being connected with the upper part of the cricoid, but this could not be seen from our reconstructions, though it may occur in intermediate stages. Possibly he meant the mesen-

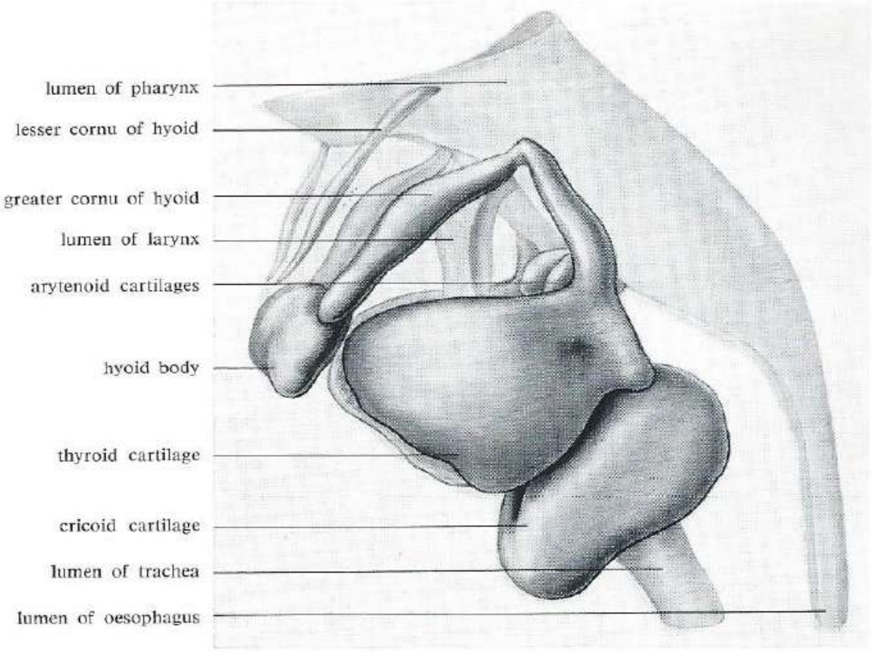


FIG. 49.
Laryngeal skeleton of a 23 mm C.R.length human embryo, seen from the left side and slightly ventral. All the laryngeal cartilages and the hyoid cartilage have been laid down at this stage. The epithelial lining of pharynx, larynx, oesophagus and trachea is indicated in more vague contours. Artist's view based on the reconstruction in FIGURE 47. 46×.

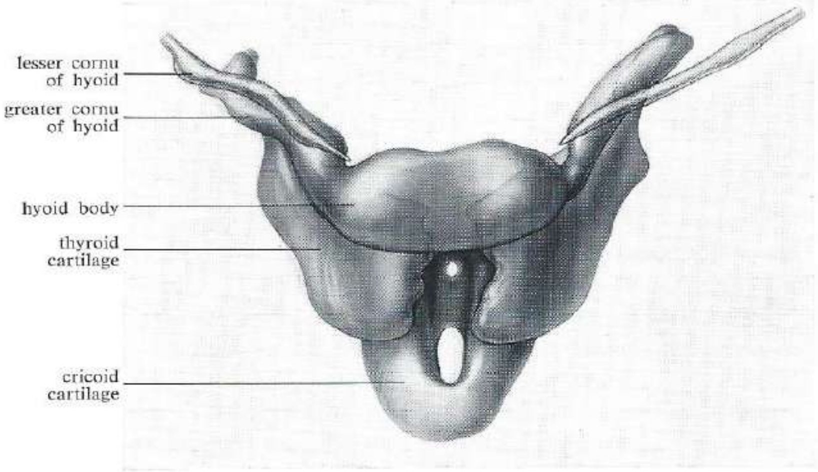


FIG. 50.
Laryngeal skeleton and hyoid of a 23 mm C.R.length human embryo, seen from ventrally and cranially. The two lateral parts of the thyroid cartilage have not yet fused. Artist's view based on the reconstruction in FIGURE 47. 45×.

chyme condensations in the arytenoid masses rather than the cartilaginous tissue.

Although the outer form and position of the *epiglottis* is easily recognized from the postnatal anatomy, any cartilaginous tissue related to it is still lacking at this stage. Its long axis already makes the typical sharp angle with the dorsal pharyngeal wall. The cranial position, its top as high as the most cranial part of the tongue, and the shallow groove between epiglottis and tongue which later becomes the relatively much deeper *vallecula glossoepigglottica*, are again different from later stages. Laterally, between the arytenoid masses and the epiglottis, there is a paired connection (mesodermal lined with epithelium) which later constitute the aryepiglottic folds.

The presence of the small *corniculate* and *cuneiform cartilages* (of Santorini and Wrisberg) seems to be indicated in this reconstruction by two paired shallow eminences at the ventral and cranial part of the arytenoid masses, but not as clearly as Kallius-1897 describes in his 4 mm and 14 mm embryos. His, in a figure of the laryngeal entrance of a 20 mm human embryo (p. 72), shows them still larger than Kallius does. The swellings show no cartilage and in fact are continuous with the mesenchyme of the arytenoid mass.

The *muscles* are hardly recognizable yet, their rudiments mainly consisting of undifferentiated mesenchyme; only dorsally and laterally to the arytenoids are any myoblasts to be found. The laryngeal lining mainly consists of non-ciliated cuboidal epithelium in 2 or 3 layers.

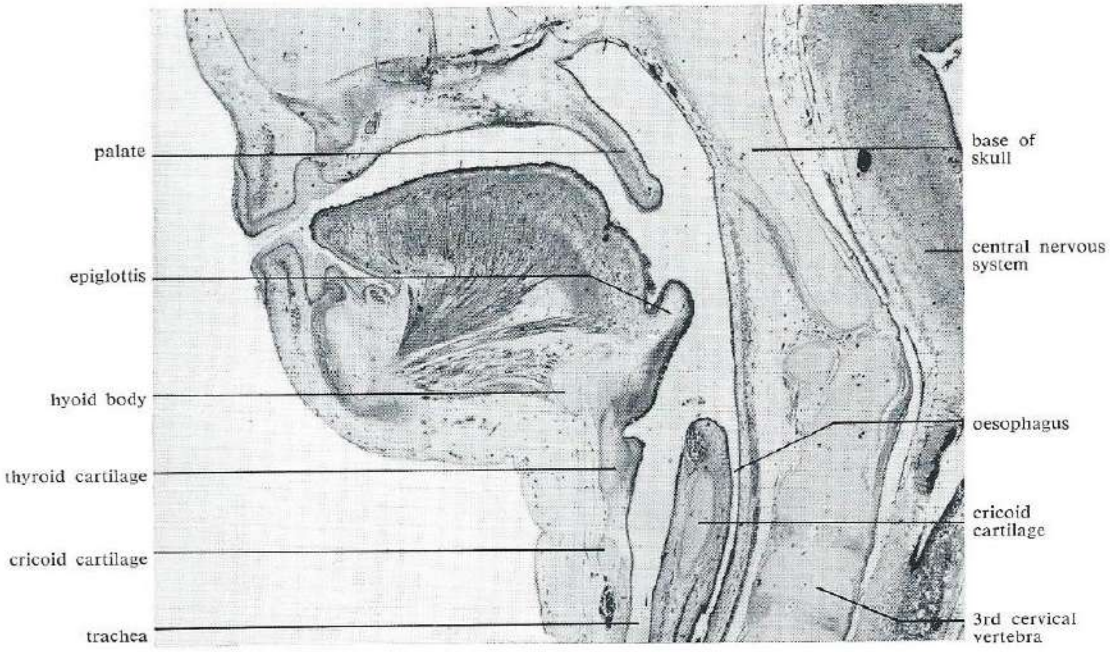


FIG. 51.
Sagittomedial section through pharyngeal region of human embryo, 55 mm C.R.length, showing position of larynx: low as compared with earlier stages, (figure 46), high as compared with later stages FIGURE 31). H.E. stain 4.×.

5. *THE 47 MM EMBRYO*

Topographically the larynx of a 47 mm C.R.length embryo (age almost 3 lunar months) still has typical foetal features, situated more cranially than after birth (Figure 51, showing a somewhat later stage). Its general morphology, however, approaches that of postnatal stages. The pharynx, especially the upper part, is spacious and the laryngeal lumen is now continuous with that of the trachea (Figure 52), though at the level of the arytenoids it is still limited to a slit-like opening whose dorsoventral dimension is about twice that of the trachea. The arytenoid masses are still relatively large and the epiglottis still feebly shows the T-shape typical of the early stages.

The laryngeal *skeleton* when compared with the 23 mm stage appears to be somewhat more elongated in the cranio-

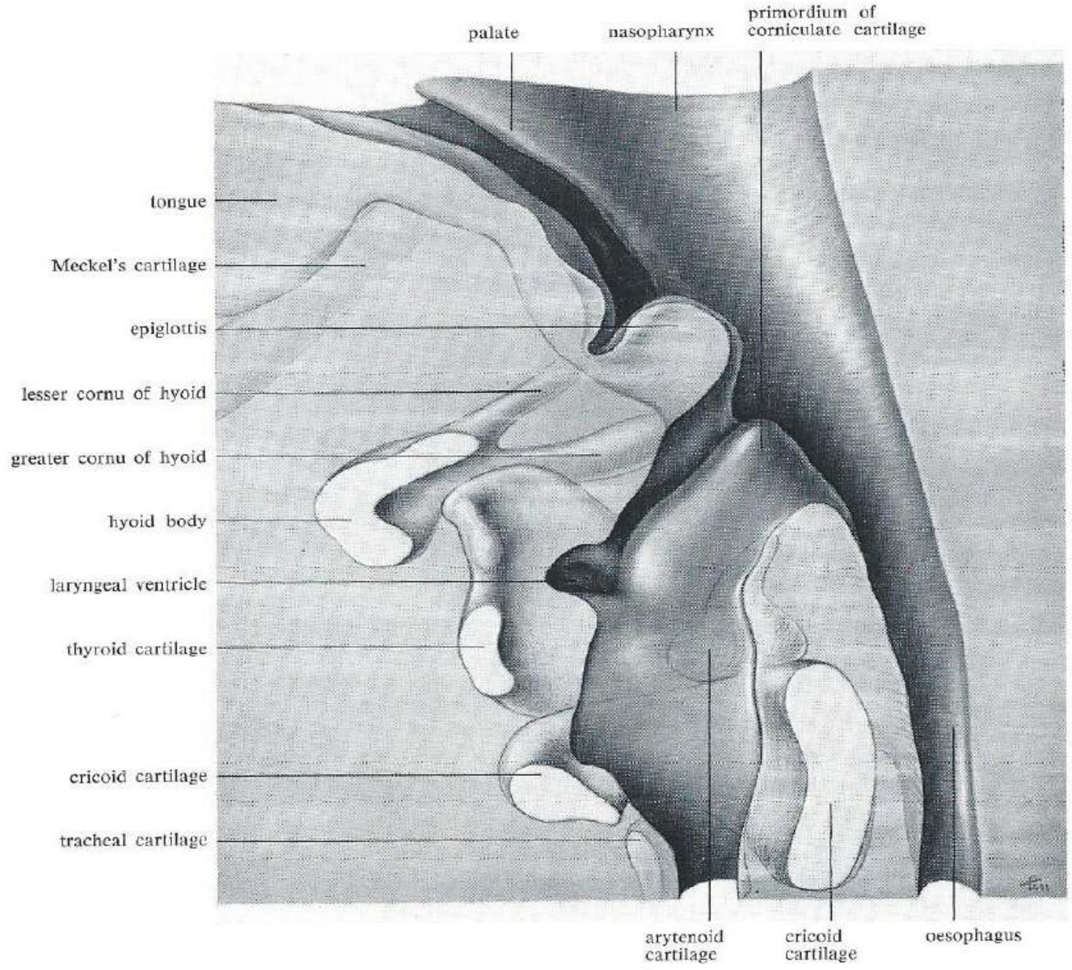
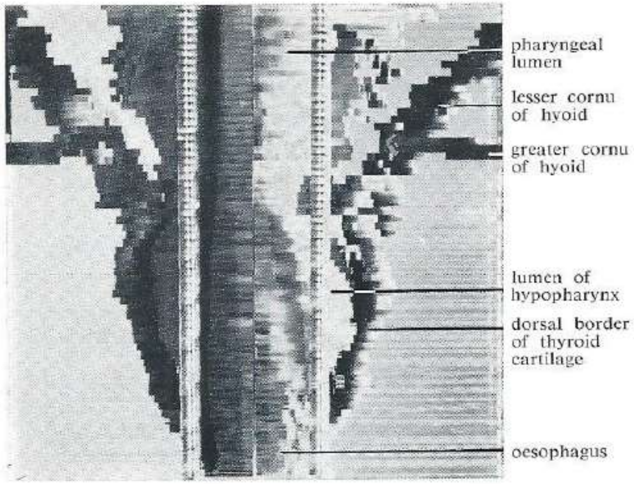


FIG. 52.
Sagittomedial section through pharyngeal region of 47 mm C.R.length human embryo, right half. All the laryngeal cartilages have been laid down at this stage, except the corniculate and cuneiform. Artist's view based on the reconstruction in FIGURE 53. 28×.



caudal direction (Figures 53 and 54), but not yet to the extent it has after birth. The *hyoid*, like the other parts of the skeleton still consisting of pre-cartilaginous tissue, shows a relatively large body from which the four horns radiate, the future greater ones still having the cartilaginous connection with the upper horns of the thyroid as we have seen in the 23 mm stage. The *thyroid cartilage* now shows a fusion of its two halves in its caudal end, thus establishing a deep cranial incisure. Its inferior horns articulate with the *cricoid* cartilage. This has its typical signet-ring appearance, but

FIG. 53.
Spatial reconstruction of the laryngeal region in a 47 mm C.R.length human embryo, seen from dorsally. The magnification of the original embryonal structures is in this figure 15×.

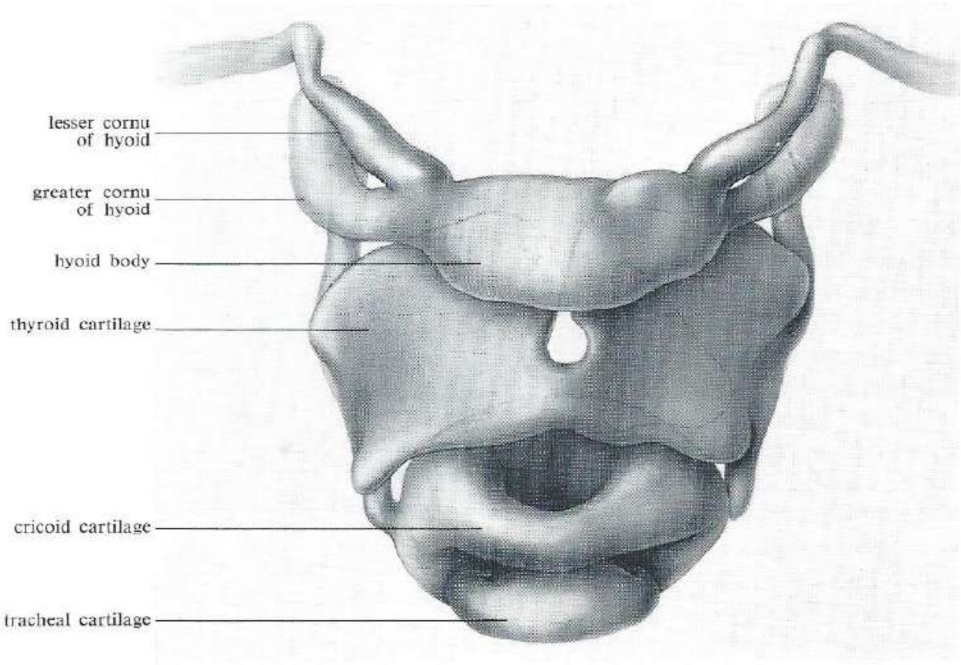


FIG. 54.
Laryngeal skeleton and hyoid of a 47 mm C.R.length human embryo, seen from ventrally and slightly cranially. Artist's view based on the reconstruction in FIGURE 53. 28×.

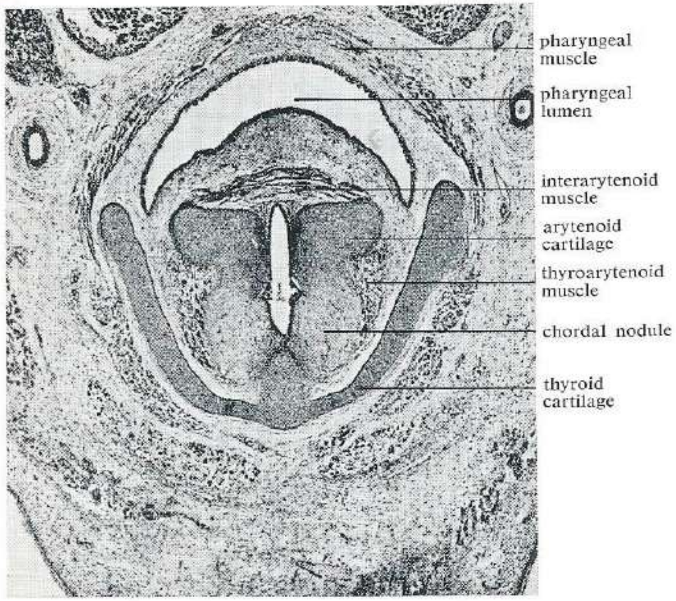


FIG. 55.
Cross-section through laryngeal region of human embryo, 47 mm C.R.length, showing the interarytenoid and thyroarytenoid muscles and the chordal nodules which indicate the future inferior thyroarytenoid or vocal folds. H.E. stain. 24×.

like the thyroid cartilage, with relatively thick walls and a deep superior incisure ventrally.

The arytenoid cartilages, articulating with the cranial dorsal border of the cricoid, at this stage only feebly show a muscular and a vocal process. An indication for the presence of the *corniculate* and *cuneiform cartilages* is given by a small groove dorsally and caudally in the future aryepiglottic folds, but still without cartilage. The *epiglottis*, though in its general form nearing its postnatal state, appears to consist entirely of mesodermal and not cartilaginous tissue.

Most of the laryngeal *muscles* can be recognized at the 47 mm stage (Figure 55). They contain elongated muscle cells in which striation is already present. The future laryngeal *ventricles* are represented by a small paired distension of the lumen ventral, lateral and slight caudal to the arytenoid masses. Just caudal to these distensions there is on each side an egg-shaped mesenchyme condensation with very fine collagen fibres, the chordal nodule (Frazer-1910), which indicates the future inferior thyroarytenoid (or vocal) folds (Figure 55). The *epithelium* shows no further differentiation compared with the 23 mm stage.

6. *THE FOETAL LARYNX AFTER THE 3RD MONTH*

During this period the larynx is present in a form which in its main features is similar to the neonatal one and, for that matter, to the adult larynx. There are, however, diffe-

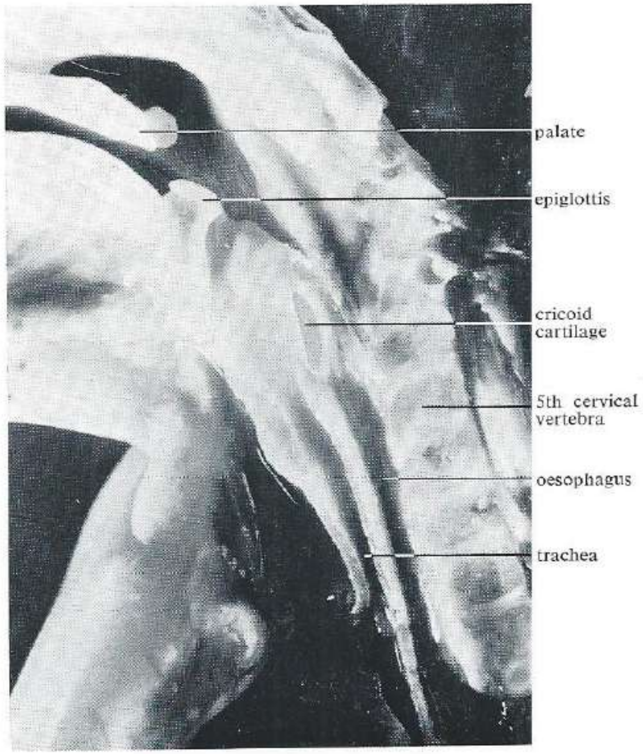


FIG. 56.
Sagittomedial section through laryngeal region of a human foetus of 240 mm standing height, showing the high position of the larynx compared with later stages, and the funnel shape of the lumen in sagittal direction. 4×.

rences, most apparent in topography. There is a gradual descent of the larynx as compared with the cervical vertebrae (*cf.* Figures 31 and 51).

In a sagittal direction the laryngeal lumen has a funnel shape (Figures 56 and 57), and the T-form characteristic of the foetal laryngeal entrance (Figure 58) is still visible at birth, though it has changed by a thickening of the crossbar of the T, as a result of the relative retardation in growth of the arytenoid masses. The skeletal parts are seen to draw gradually apart in a cranio-caudal direction, though at birth the upper border of the thyroid is still almost level with the inferior border of the hyoid body (Figure 57). This process continues after birth.

The foetal *epiglottis*, though already visible at very early stages as an eminence, only shows chondrification at about 5 months, which appears to result in elastic fibrocartilage and not in hyaline cartilage, as in the other parts of the laryngeal skeleton. This peculiarity has been used as an argument against a possible branchial origin of the epiglottis (Schaffer). The *thyroid* loses its cartilaginous connection with the hyoid by the cornu superior (Figure 54) during about the 4th month and its wings, beginning to join in the 47 mm embryo in their caudal region, appear in a 150 mm (standing height, S.H.), which corresponds to a stage somewhat further on than 3 months, to have reached a state very similar to its definitive form, though the cranial incisure

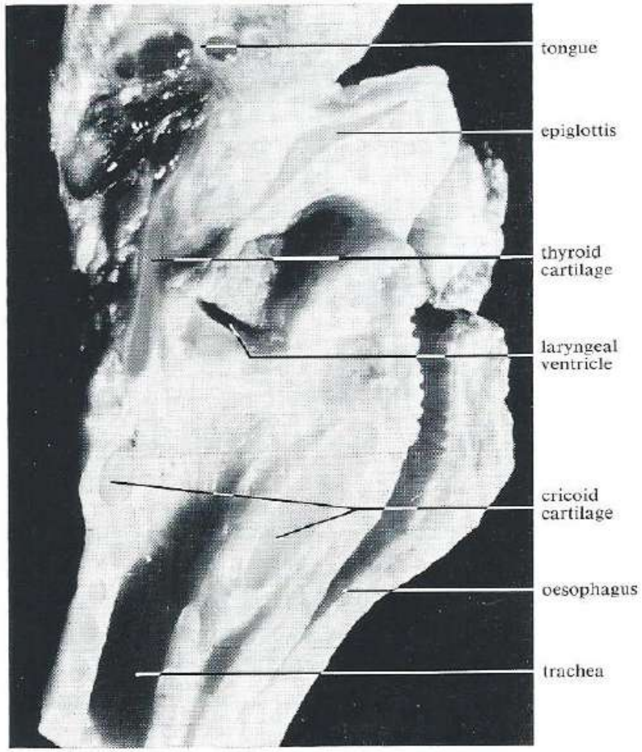


FIG. 57.
Sagittomedial section through the larynx of a newborn human showing the funnel shape of the laryngeal lumen. 5 ×.

FIG. 58.
Tongue and pharynx in a human foetus of 280 mm standing height, to show the T-shaped laryngeal entrance. The dorsal wall of the pharynx and oesophagus has been cut medially and the flaps turned laterally. Dorsal and slightly cranial view. 2·5 ×.

may still be somewhat deeper than in the postnatal thyroid cartilage. The union of its lateral parts has apparently progressed from caudal to cranial. The *cricoid*, already circular in the 23 mm stage, appears to have lost the deep cranial incisure in the 150 mm specimen (S.H.). However, at this stage there is still a small incisure, which can hardly be recognized in a 280 mm (S.H.) specimen. Another difference from the definitive cricoid is the rather bulky appearance, leaving a relatively small lumen (Figure 57), against the more slender signet-ring form in the adult.

The relative reduction in size of the *arytenoid* masses already discernible in the 47 mm specimen progresses in the later stages, giving rise to the arytenoid cartilages, which grow relatively and absolutely and in a 280 mm S.H. human embryo reach their maximum relative size. The presence of the vocal process, which in the 47 mm embryo is only vaguely recognizable, is in a 150 mm S.H. specimen clearly visible and the arytenoid cartilages may possibly be considered to have reached their definitive form at the 4th or 5th month.

The transformation of the undifferentiated mesenchyme into the laryngeal *muscles*, which was recognized at the 47 mm stage, appears to be well on its way in the embryo of 155 mm C.R.length. From this stage on the interarytenoid and thyroarytenoid muscles are present in a more-or-less sphincter-like form, being arranged somewhat circularly (Figure 59). The cricothyroid and lateral cricoarytenoid muscles are also discernible at this stage.

As far as the *laryngeal lumen* is concerned, it increases gradually during this period, also relatively, as a result of a reduction in the arytenoid masses, a widening of the cricoid cartilage and the establishment of a space in the lateral walls at the level of the arytenoid cartilages. This space is in the process of becoming the paired *ventricle*, at the same time giving rise to the upper and lower thyroarytenoid folds, in which it is enclosed. It extends rapidly after about 3 months, especially ventrally and cranially. The outgrowth formed in this way is called the *saccule* and at these foetal stages and later in infancy clearly has a relatively larger extension than in the adult (Figure 59). The inferior thyroarytenoid or vocal folds do not yet show the rather sharp edges seen in the postnatal stages, and are relatively shorter, together with the relatively larger arytenoids.

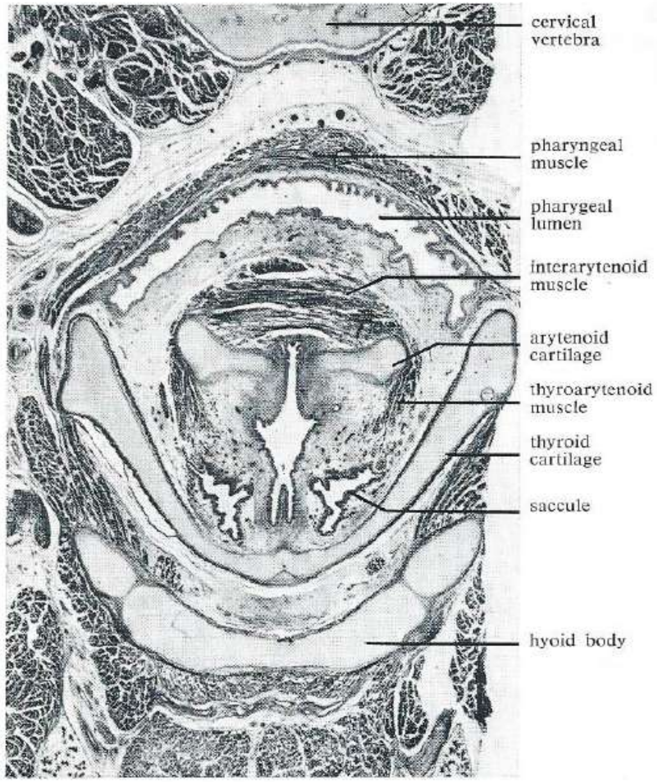


FIG. 59.
Cross-section through the larynx of a 155 mm C.R.length human foetus, cranial to the inferior border of the upper thyroarytenoid folds, showing the relatively large laryngeal saccules and the more-or-less sphincter-like arrangement of the muscle fibres. H.E. stain. 8 ×.

As far as the histology of the *epithelial lining* is concerned it should be remarked that in none of the prenatal specimens examined was clearly developed stratified epithelium observed. In most instances the laryngeal lumen was covered by 2-4 layered, cubical or cylindrical ciliated epithelium. Only in some specimens after the 150 mm C.R.length stage in the area of the future vocal folds were these epithelium cells much lower, seemingly a transition to stratified epithelium.

Differences between the two sexes are not seen in the prenatal stages.

7. *MORPHOLOGY OF THE LARYNX IN THE POSTNATAL PERIOD*

After birth the larynx grows, parallel with the increase in body weight of the child. A remarkable relative and absolute increase is presented by the male larynx during puberty.

The changes in *topography* are essentially the same as those in the previous stages: further descent of the larynx relative to the vertebrae (Figure 60). As mentioned on p. 79 this downward movement is explained by Mehnert, Vallois-1967 and Hockett-1963 as the result of man's erect posture. Symington-1885 supposed the growth of the skull's facial portion be the cause.

As far as the laryngeal skeleton is concerned, continuation of the process of the drawing apart of its elements in a cranio-caudal direction is to be observed. Apart from the increase in size of the individual laryngeal cartilages there are some less obvious changes in their form during development in childhood and puberty. The infant *epiglottis* may be somewhat more bulky than later and may also show, when seen from dorsally and cranially together with the aryepiglottic folds an Ω-appearance which may play a part in some cases of congenital laryngeal stridor. The two wings of the *thyroid* cartilage, which in the foetus and infant fuse to form a rounded shield ventral to the larynx, change their relationship so as to meet at an angle of about 90° in the adult. During childhood the *cricoid* looses its bulky appearance and takes on the more slender form of the adult, but otherwise its form shows no obvious changes postnatally. The same applies to the *arytenoid* cartilages but their size compared with the rest of the larynx tends to decrease, resulting in a relative increase in length of the vocal folds.

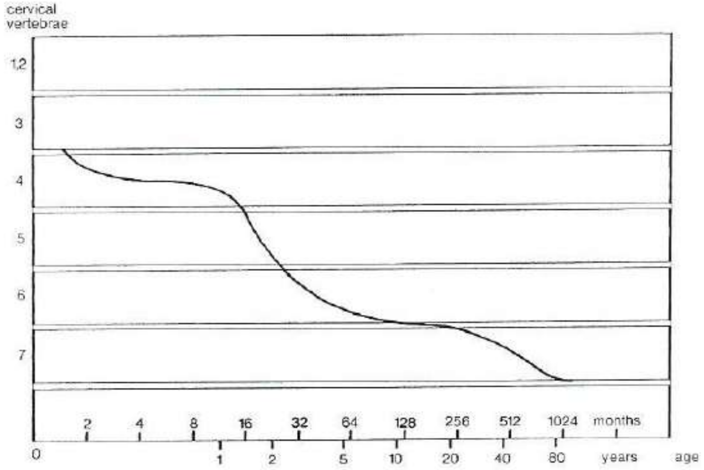


FIG. 60.
Diagram indicating the relationship of the lower border of the human cricoid cartilage to the cervical vertebrae at various ages, showing the gradual descent during ontogeny. Based on H. Frey, Symington, Mehnert and own observations.

During the first years of life the *entrance* of the larynx widens changing its T-shape gradually into a more rounded or oval opening. The cranial extension of the ventricle, the saccule, becomes relatively smaller, the ventricle itself meanwhile becoming elongated in a dorsoventral direction.

As to the *histology* of the laryngeal skeleton there are some changes to be observed. In contrast with the hyoid, which at birth appears to be partly ossified, the other parts of the laryngeal skeleton are entirely cartilaginous, but during postnatal life *ossifications* in varying degree may occur. Unlike the other problems encountered in laryngeal ontogeny, this one has been dealt with in numerous publications because of its interest from a clinical point of view, e.g. in regard to possible confusion with foreign bodies (Minnigerode). References to the older literature on this subject can be found in the articles of Hately *et al.* and Chievitz. In general, ossification starts after the 2nd decade (though Russo & Coin report a case of calcification in an infant), however, immediate correlation between age and degree of ossification is poor (Keen & Wainright). All cartilages may show these osseous changes except those of Wrisberg and Santorini (Hately *et al.*) and there appear to be only slight sex differences, the females showing somewhat denser ossification of the thyroid. In frequence of occurrence and density of ossification of the arytenoids, females show equal prevalence. According to Vastine & Vastine, calcification of the laryngeal cartilages depends on hereditary factors.

Miscroscopic examination of the inferior thyroarytenoid folds reveals changes in their mesodermal structures. With advancing age there is a progressive loss of the number of the submucous crossing elastic fibres (Mayet). This would imply a loss of elasticity in the vocal folds, which in turn might effect the vocal capabilities. On the other hand the laryngeal mucous membranes show no visible histological changes during postnatal life (Noell).

8. *EVIDENCE DERIVED FROM TERATOLOGY ILLUSTRATING EMBRYOLOGICAL DEVELOPMENT*

Indications for the embryological development of an organ may sometimes be provided by abnormal morphology of the organ after birth. Though this may apply e.g. to the heart, in which congential malformations are frequently found, the larynx yields but little evidence in this way, because malformations of this organ are rare, or at any rate those causing serious functional disturbances. There are even books on teratology like that of Guinard which do not mention laryngeal malformations at all. Some common abnormalities are discussed here.

The most detailed account of the subject is probably given by Schwalbe and Beck & Schneider, to which the reader is referred for malformations not mentioned here.

The most common congenital malformation is an abnormally shaped *epiglottis*, namely the Ω-shape, which in more extreme cases may show contact between the lateral parts, thus forming a narrow fissure. These conditions do not in general cause serious functional disturbances, nor can a clear relationship be found with the prenatal stages.

Though I know of no reports concerning the frequency of congenital malformations of the larynx, I suspect that next most common is probably partial or total *obstruction* of the laryngeal lumen, of which there are a number of reports in the literature (e.g. Beck & Schneider, Fox & Cocker, France & Stirling, Potter, Smith & Bain, Bigler *et al.*, McMillan & Duvall). The non-cartilaginous plugs, most often present at the level of the thyroarytenoid folds, may without much uncertainty be considered as a persistence of the blockage which normally disappears during the first months of foetal life. This view is supported by the fact that the total obstructions often leave a small channel dorsally and that partial ones exist only ventrally, often forming a web between the vocal cords.

A rarer obstruction is reported by France & Stirling, McMillan & Duvall and Potter who found a few cases with a cartilaginous obstruction formed by a circular thickening of the cricoid. This probably represents a persistence of the earlier stages in which this cartilage shows a bulky appearance (see p. 96).

Another rare malformation is a *cleft larynx*, in which a more-or-less deep dorsal cleft extends caudally as a continuation of the normal interarytenoid fissure. It may even continue into the trachea. Such an abnormality can possibly be traced back as a persistence of the laryngotracheal groove. Cases have been reported by Cameron & Williams, Beck & Schneider, and Lesbre.

A *ventral cleft* of the thyroid cartilage has been described by Hutter, which indicates its originally paired primordium. The original union between the upper horn of the thyroid and hyoid is illustrated in adults by the not infrequent presence of a bony or cartilaginous bridge between the two (Keen & Wainright).

An extension of the laryngeal ventricle, *laryngocele*, is probably not so rare as the previous malformations, nor are reports about it: authors cited by Beck & Schneider, Wustrow and Wilson. Next to a persistence of the foetal conditions, a causative factor may be pressure exerted on its walls by air, for instance by coughing (C. L. Jackson).

9. *ONTOGENY OF LARYNGEAL FUNCTION*

Information about human and animal laryngeal functions during prenatal stages is unfortunately not available. This is understandable when the difficulties which the observer meets in examing these functions even in postnatal stages are taken into account. However, some suppositions can be given here, partly based on observations in foetuses and partly on extrapolations back from observations after birth.

One of the main functions of the larynx is *respiratory*. Oxygenation in the human foetus is secured by the placental circulation, and the airways, including the larynx, have nothing to do with it. Nevertheless there are reasons for assuming that laryngeal respiratory movements exist in the human foetus. (1) Though there seems no use for laryngeal muscle movements before birth, it must be borne in mind that immediately after birth practically all muscles including the laryngeal ones, show contractions, which makes it probable that this must have happened before birth. This view is supported by the knowledge that no muscle is able to function unless it contracts frequently, and by the observations of Sullivan, who showed the necessity for skeletal muscle movements for the normal development of chicken embryos. (2) F. Snyder-1941, -1958 showed the presence of amniotic fluid in the airway of unborn rabbits which suggests respiratory movements. Indeed in human foetuses movements of thorax and abdomen, seemingly respiratory, have frequently been observed. (For a review of the literature on this subject the reader is referred to Potter, p. 239-241). Their rate appears to increase during anoxia of the foetus (Windle, Barcroft, Winton & Bayliss).

If considering the opening and closing of the glottis during respiration in the light of Bernoulli's law, one should notice that the law applies to gas and fluid alike, and because of its morphology it is probable that in the second half of foetal life the larynx already shows the valvular actions described in Chapter 4, § 7.

The function of *protection* will probably not be very important *in utero*. Though the penetration of fluid to the lower airways after birth causes violent reactions (closure of larynx, coughing), its presence before birth is apparently accepted by the foetus. This seeming paradox may be elucidated by the following: from postnatal pathology we know that constant mechanical stimulation of the laryngeal and tracheal lining rapidly dulls the above effects, and that it is a change in stimulus which causes the protective mechanism to come into action; and maybe the state of low vagotony which Reynolds reports in human and animal foetuses, and which he supposes to be the result of sensory deprivation, has something to do with it. Thus it seems probable that the entrance of air bubbles into the airway fluid by decompression of the thorax after birth, allied with other, vegetative stimuli, causes contractions of the respiratory muscles including the laryngeal ones.

During the rest of life there are no obvious changes in regard to the respiratory and protective functions of the larynx, except for a progressive loss of the cough reflexes in elderly people (Pontoppidan & Beecher), and an increase in average respiration rate during rest until about the 5th year, rising from about 14 to about 26 per minute, after which there is a decrease to about 17 per minute (Evans).

For the same reasons as mentioned above, the development of the *voice* in each individual is likely to begin *in utero*. A system able to produce cries immediately after birth must have been able to do so before, but the appropriate respiratory and laryngeal movements, though probably present *in utero*, do not result in easily audible sounds because of the presence of fluid. Most sounds produced in the airway of the newborn infant result in communication with its surroundings, and may therefore be considered as constituting the voice, according to our definitions (Chapter 4, § 8). But they clearly bear an involuntary and instinctive, or possibly even an reflex character for about the first 3 months.

This kind of sound production, the stimuli for which originate probably mainly in the brain-stem, in later life is often used for primitive emotional expressions (hunger, fear, pain), though altered by growth changes and the presence of the power of speech. In this context it may be noted that crying and smiling or laughing, in both of which the larynx plays a part, are among the first non-somatic contacts the baby establishes with its environment. From pathological conditions it may be concluded that these phenomena are strongly influenced by the brain stem. This suggests their instinctive or reflex character in the baby.

In human *speech*, on the other hand, the regulation responsible probably arises, for the greater part, in the cerebral cortex rather than in the stem, though both are of course necessary. The fundamentals of speech are represented by *babbling*. This is probably typically human, though our nearest relatives the chimpanzees may show traces of it (Hayes). In the babbling stage, which is added to the "instinctive" phase and in general ranges from about 3 months to a year or 18 months, the child seemingly uses all its vocal abilities at random. It is commonly considered as exercising the vocal organs. Babbling gradually passes over into true speech, the child imitating more and more the words perceived by it, abandoning most of the babbling sounds.

Presumably these contain the basic sound elements of all languages. An exact analysis of the phenomena exhibited in the babbling stage is given by Irwin.

It seems probable that in many children "language" should be considered as preceding "speech", *i.e.* children after 1-2 years of age may often be seen clearly to display the urge to express certain desires, emotions or even the beginning of conceptual thought, although still being unable to do so in the appropriate words, and so they use vocalizations invented by themselves or other means of communication. (For the differences between "language" and "speech", see Chapter 4, § 9).

It may further be remarked that closer observations of individual speech development might show that the child during and after the babbling stage, passes through a period in which there is a strong desire (and ability?) to find means of *symbolic expression*, different from later periods when speech has been achieved. I feel therefore that both during ontogeny and during phylogeny (*cf.* pp. 71, 74) symbolism plays a, presumably important, role in speech development.

Needless to say for adequate speech development a first requisite is a subtle coordination between normally functioning speech organs, such as the acoustic system, the perception, motor, association and coordination centres of the brain, and the peripheral motor organs (respiratory system, larynx, pharynx, palate, mouth, cheeks, lips). For reviews on the individual development of speech the reader is referred to Stein, Stern & Stern, Lewis and Lenneberg-1967.

Hiccoughing in the human foetus appears to occur from about the 5th month on; it has never been observed in animal foetuses (de Lee, cited by Windle). Since *yawning* can be observed very soon after birth its presence during human intra-uterine life is likely.

Part 4

CHAPTER 6

Relations between the phylogeny and the ontogeny of the human larynx

1. *INTRODUCTION*

Having reviewed the main features of the phylogeny and ontogeny of the human larynx, we shall now attempt to discover the relationship between the two processes. In some earlier publications on the comparative anatomy and embryology of the larynx, a parallelism in the sense of Haeckelian recapitulation was assumed to be self-evident (Howes-1887, Kallius-1897, Negus-1924, -1949, -1962). Such an assumption, however, often results in filling gaps in the knowledge of phylogeny with evidence derived from embryology which from a theoretical point of view is an unreliable method, as shown in Chapter 1.

Problems in comparing phylogeny with ontogeny may arise from lack of reliable means of comparison: because of their very nature the two processes are entirely different. Furthermore one should be aware of our incomplete and uncertain picture of human ancestry, and of the ontogeny of the larynx in the various vertebrate species, which must give indications for possible comparable stages: reasonable comparison in a Haeckelian sense between phylogeny and ontogeny is only possible when there is a comparable stage discernible between the two processes. Where this is so, we shall attempt to classify the heterochronia encountered in accordance with de Beer's classification (see Chapter 1).

Though it is uncertain if, in his recapitulation theory, Haeckel meant morphological characters alone, or functional ones as well, in order to be consistent and to consider the problem from all sides, we shall discuss both.

2. *COMPARISON OF MORPHOLOGICAL CHARACTERS*

The *first appearance* of the air tract, including the larynx, both in phylogeny and ontogeny, is to be found after that of the digestive tract, and here we may speak of comparable stages.

When, however, we come to *topography*, things are more complicated. If we first consider the relationship to the choanae, we see that the larynx in vertebrates up to the reptiles is some way from them (Figure 32). On the other hand in the early stages of human ontogeny there is a relatively more cranial position, the aditus reaching to about the area of the future choanae and during ontogeny there is a gradual displacement caudally instead of cranially, as the biogenetic law would suggest. Only when comparing conditions in the early stages of human ontogeny with those in the *later* human ancestors, a similarity is to be found in the topography: both in the mammals representing our ancestors and in the human foetus and infant, the larynx shows a close relationship to the choanae. If we therefore apply the biogenetic law to the mammalian ancestors only, and if we assume a homologous embryological development in the primates and their ancestors, these topographical conditions in phylogeny and ontogeny may be assumed to possess a comparable stage. From this comparable stage the human appears gradually to diverge, by descent of the larynx. This case of heterochrony should therefore be classified as *acceleration*, or possibly *deviation*.

Considering its relation to the base of skull, we invariably find in the early vertebrate ontogeny, the larynx present at about the junction of the first cervical vertebra and the base of skull; but as mentioned above, only in man's ontogeny and possibly in a lesser degree in the apes', is there a displacement in a caudal direction (*acceleration*).

As to the *size* of the larynx during phylogeny and ontogeny, one can see from Figures 42 and 45 that during the earliest stages of laryngeal development in the human embryo, it is considerably larger than in the earliest forms in phylogeny, so in this respect there is no comparable stage and no recapitulation.

Both the phylogeny and ontogeny depart from conditions with no cartilaginous scaffolding, but in later stages things are more complex. Though the sequence of origin of the different parts of the *laryngeal skeleton* during phylogeny is not certain, especially as far as the earliest stages are concerned, the probable sequence is: (1) arytenoids, (2) arytenoids + cricoid, and (3) arytenoids + cricoid + thyroid + epiglottis (Figures 33 and 34). The sequence of the first appearance of the cartilages in the human embryo is: cricoid, thyroid, arytenoids and epiglottis; and when the first non-cartilaginous primordia are considered: arytenoids together with epiglottis, cricoid and thyroid. As far as the individual cartilages are concerned, there appear to be certain similarities in regard to the size of the arytenoids only: we have seen in Chapter 4 that the lower primates possess rather large arytenoids compared with the adult human, and in Chapter 5 that the human foetus, and to some extent the infant too, have relatively well developed arytenoids (Figure 55). Perhaps we may consider this resemblance to be the result of a comparable stage, the lower primates retaining their large arytenoids during later life (*acceleration*). However, hardly any parallelism can be discovered between the cartilages of lower vertebrates and those in the earlier stages of human ontogeny, neither in size nor in shape.

The *musculature* probably originated during phylogeny from a simple sphincter, to which a dilator was added later, both differentiating into several other muscles. During ontogeny the differentiation of the mesenchyme into primitive muscle fibres starts after the differentiation into the primitive cartilage, in contrast to the sequence during the phylogeny. The primordia of the thyroarytenoid and interarytenoid muscles in the early stages of human ontogeny, form a somewhat sphincter-like configuration round the laryngeal lumen (Figure 59), thus showing some resemblance to the lower vertebrate situation. But the fibres of the dilator muscles appear at the same time as those of the constrictor, thus not showing a comparable stage. Moreover during ontogeny the dilating fibres are seen to originate from the cricoid region and not from the lateral wall of the pharynx, as seen in the early phylogenetic stages, nor does their insertion remind one of ancestral conditions.

The form of the *laryngeal entrance* in the lower vertebrates and the human foetus in the first month shows a remarkable resemblance, being present as a fissure (Figures 40 and 41). But whether this is based on a comparable stage, on homology, as suggested by Negus-1949, -1962, does not seem quite certain, the fissure in the lower vertebrates (Figures 7 and 11) being formed by the sphincter or the arytenoid cartilages, just caudal to which the trachea begins. In the human embryo on the other hand, it is formed by the large mesenchyme masses blocking the lumen over a comparatively long distance. Early in both processes the plane of the aditus lies parallel to the long axis of the primitive foregut and vertebral column. The dome-shaped arytenoid masses of the later human stages also resemble conditions in many amphibians and reptiles. More evidence can only be provided by comparative embryology, indications from which are provisionally lacking.

What is the place of the *branchial system* in this matter? This question cannot yet be answered with certainty while one is still so poorly informed about the origin of the laryngeal skeletal parts in the lower vertebrates. However, all the evidence incicates that the most clearly discernible comparable stages in the phylogeny and ontogeny of the human larynx are to be found in both processes in the early stages of the branchial system (*cf.* Figures 2 and 35). In all vertebrates the first stages in the development of the branchial system are much the same morphologically, in the lower species developing into the gill apparatus, in higher species into other structures, amongst which are parts of the larynx (heterochrony: *deviation*).

As far as the *soft tissues* of the larynx are concerned, human ontogeny shows some resemblance to the adult ancestors: the medial walls of the arytenoid masses are smooth at first, as in the Urodela, which might be considered a comparable stage. In later stages they give rise to the *thyroarytenoid folds*, of which the caudal (lower) and cranial (upper) appear almost simultaneously in the human embryo, in contrast to the sequence during phylogeny in which there probably were first undivided folds (*cf.* the gymnures), and later the division into upper and lower. The short inferior folds of the human foetus remind one of the conditions in the lower primates, and the relatively large *ventricles* bring to mind the conditions in the monkeys and the apes. Despite the lack of comparative primate embryology, we may perhaps assume, in view of the close relationship between the primates evidenced in so many other ways, that ventricles and saccules such as the human foetus shows also appear in the early ontogeny of many other Anthropoidea. The adult lower primates and insectivores, on the other hand, have small ventricles comparable with man's or else no such structures at all. These considerations make it likely that the common ancestor of man and the apes did not possess the large ventricles which C. L. Jackson, Negus-1949, -1962, Bounak and Andrew-1963-a have attributed to them, and that the condition in modern man is the same as in the common primate ancestor. Another explanation of man's small ventricles can be given by assuming *neotenous* evolution. Therefore when the occurrence of a pathological distension of the human ventricle, the *laryngocele*, is considered by C. L. Jackson to indicate the presence of large ventricles in our ancestors, this seems to me too bold a conclusion. In my opinion, it must be considered the result of an individual development starting from the same condition as in our ancestors and in modern apes, but in its course changed by abnormal inductive influences, which need not necessarily be the same as those in the apes: in many cases the non-congenital factor of high air pressures must be added to the aetiology.

3. *COMPARISON OF FUNCTIONAL CHARACTERS*

Respiration in the lower vertebrates and in the early ontogenetic stages of a human being are both non-aerial, but that is all that can be said concerning a resemblance between respiration during early phylogeny and ontogeny. Indeed, the larynx, which in almost all species is actively involved in respiration, has no such function in the human foetus. Here it reaches its final form, quite different from that of the lower vertebrates, capable of functioning months before it is suddenly called to its ultimate use at the moment of birth. Some laryngeal movements may be present before birth (p. 107), but the regulation of passage, the protection of the lower airways, the valvular actions and sound production probably only go into action after birth, whereas from a Haeckelian viewpoint one might expect this to happen much earlier.

It may be interesting here to compare *speech emergence* during phylogeny and ontogeny. As made clear in Chapter 4, sound production by the larynx appears very early in phylogenetic history, gradually passing over into its use for communication, which we call voice production, while the final, and phylogenetically very recent use, we consider to be human speech. The first sound production by the larynx in the human individual, which is not difficult to observe immediately after birth, may be considered as voice production, since it results in communication with the surroundings. The period of speech begins at the age of about 3 months, with the babbling stage. Because there is no period in which sound production by the human larynx can reasonably be considered identical with that in the lower vertebrates, *i.e.* sound production which must be considered to be accidental and not resulting in communication with the surroundings; and because from a Haeckelian point of view, one might expect the first signs of speech to be found in very old age, there is, as far as sound production is concerned, no recapitulation in the true sense of the biogenetic law. Nevertheless there is a very close relationship between the phylogeny and ontogeny of human vocal function. We may assume that during the evolution of man his culture, and therefore speech, evolved with him, each generation, each ontogeny, adding something to it and, while transferring it to the next, changing it somewhat. This transfer of experience and knowledge, though not completely unknown in other species, e.g. rats and birds (Darwin-1875, Haldane, Lorenz-1964, Tinbergen-1965) reaches an unique level in human evolution, both in quantity and in quality, and, it should be noticed, it is mainly effected by speech itself.

Each speech ontogeny is therefore essentially based on and results from speech phylogeny, if only that part after the appearance of *Homo sapiens*. So here is a case of *direct influence of phylogeny on ontogeny*. But this is most probably not what Haeckel meant when he stated that phylogeny is the mechanical cause of ontogeny, and this case probably forms one of the very few showing this influence. In the same sense in man's culture and language, a *transmission of acquired characters* is to be recognized, though it seems doubtful if this is the sense Lamarck meant, since he seems to have applied his theory only to morphological characters.

CHAPTER 7

Conclusions and summary

Many descriptions of organic evolution necessarily miss the exact logical character which mark most publications in the field of applied biology. The latter is largely based on more-or-less readily evaluated observations, while phylogenetic considerations are mainly based on speculative conclusions drawn from incomplete palaeontological evidence, supported by the more exact evidence of comparative biology. Nevertheless an endeavour to trace the phylogenetic history of the human larynx, based on probabilities rather than on exact measurable observations, seems to be justified by curiosity about man's past and by the new light that may be thrown on morphology and function of the larynx in modern man. However it is useful to be aware of these limitations which characterize several of the conclusions drawn from this study. As far as the ontogeny of the human larynx is concerned the value of the conclusions is much greater, though it is not claimed that this study offers a complete picture.

In *Chapter 1*, after a short historical review and discusison of the meaning of phylogeny and ontogeny in general, the relationship between these two processes is discussed, often illustrated by Haeckel's *biogenetic law* which postulates that the development of each individual is a short recapitulation of the evolution of its species, the latter process being the mechanical cause of the former. It is shown in this chapter that, despite the attractive and at the same time somewhat mystic character of this law, from a purely scientific point of view its truth seems very doubtful. Very often, when comparing cases of phylogeny and ontogeny, there appear to exist heterochronia or aberrations from this recapitulation.

In *Chapter 2* a short review is given of the main features of the special phylogenetic series with which this study is concerned: that of the possible human ancestors which possessed a larynx. After a discussion of the definition of the larynx in earlier vertebrates, it was made clear that the evolutionary history of man's larynx goes back 300 million years, to the appearance of the ostracoderms, primitive fish from which, through later fish, amphibians, reptiles and insectivorous mammals, a line can be discerned leading to man. Indications for the form and function of the larynx in these ancestors, however, are completely absent from or very scantily supplied by palaeontology, so one has to make use of comparative zoology. This science may offer reflections of past circumstances when, mainly guided by palaeontology, those modern species are selected which in a number of characters appear to resemble ancestral forms. Extrapolation from this knowledge may give some evidence for soft organs like the larynx such as must have existed in ancestral forms.

Data from comparative zoology are given in *Chapter 3* where, after a discussion of the species selected for this study, the main features of their laryngeal anatomy and physiology are described. These species include: *Lampetra fluviatilis* (river lamprey), *Polypterus senegalus* (Nile Ganoid), *Protopterus annectens* (African lungfish), *Amphiuma* spec. (a salamander), *Rana catesbiana* and *R.esculenta* (frogs), *Osteolaemus tetraspis* (a small crocodile), *Hylomys suillus* (the Lesser gymnure), *Tupaia glis* (tree-shrew), *Macaca mulatta* (Rhesus monkey), *Pan troglodytes* (chimpanzee) and *Homo sapiens* (man).

In *Chapter 4* a number of the topics discussed in these descriptions are compared. These comprise topography, skeleton, relations to branchial system, musculature, larynx as a protective, respiratory, valvular and communication organ, the emergence and evolution of speech and some less obvious functions. From this comparison it may be concluded that as fas as morphology is concerned, there has been a gradual increase in complexity and differentiation during vertebrate evolution, the branchial elements and their derivatives progressively being involved in formation of the parts constituting the larynx. It should be emphasized, however, that the morphology of man's larynx, as compared with other mammals, shows a quite general and unspecialized appearance: there may even be some arguments in favour of neotenous elements in its evolution. Indeed the larynx of man, as Albrecht remarked in 1895, shows much anatomical similarity with that of a primitive mammal like the hedgehog *Erinaceus*.

In regard to the relationship to the choanae there is firstly to be observed an approximation of the two structures, followed by a secondary division, such as seen in man. The relationship to the base of skull remains quite constant, the laryngeal entrance invariably being present just ventral to it, in the apes and man however showing a displacement in caudal direction. In regard to the protective function of the larynx there may have been some retrogression during the evolution of man's mammalian ancestors; this in contrast to the respiratory function which up to the monkey-like ancestors shows a clear progression, only in higher primates being less efficient. The valvular action of the larynx should be considered as showing a rise in its developmental level during the phylogeny of man.

The same can be said of the communicative function, which we considered to have evolved from a stage of accidental *sound* production through one in which this was used for communication—the era of *voice* production—into the relatively recent stage of *speech* production, in which communication reaches human level.

The emergence and evolution of speech are discussed somewhat more extensively in this chapter, because of their importance to human evolution and present human life. When reviewing the factors that may have played a role in speech emergence and evolution, one comes to the conclusion that they cannot be considered apart from a great number of other factors that have contributed to human evolution in general: in other words, that speech is essentially multi-causal in origin. This is illustrated in a diagram which shows 76 lines of connection between 21 different factors.

In *Chapter 5* the ontogeny of the human larynx, the development of this organ in each individual from its first appearance through to death, is described. This description is based on former observations, the main features of which are reviewed, and some original ones. The most obvious changes in form take place during the first months of embryonic life. These are illustrated with spatially reconstructed serial sections of human embryos of 8 mm, 23 mm, and 47 mm crown-rump length, for which transparent plastic was used, probably for the first time in such reconstructions. The development of the laryngeal functions, discussed in the preceding chapter, is briefly reviewed, a development which during the intra-uterine period is still obscure.

A comparison between the phylogeny and ontogeny of the human larynx is given in *Chapter 6*, in which the morphological and functional topics mentioned in Chapter 4 are considered, though any comparison of these two essentially different processes is a precarious task. It appears that the biogenetic law could not reasonably be applied to most of the characters considered. It could be concluded with some certainty that only in the earliest stages of phylogeny and ontogeny is there a common development in the branchial elements. In general, however, no Haeckelian recapitulation could be recognized. The only certain influence of phylogeny on ontogeny appeared to be present in the development of speech. Most probably, however, such a relationship, the transmission of knowledge, increasing from one generation to the next, was not what Haeckel meant by his biogenetic law.

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Index

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* *see also species concerned*

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* *see also species concerned*

Stellingen

1. De overgang van polyisomerie in oligoanisomerie gedurende de evolutie van de vertebraten krijgt in de literatuur niet die aandacht, die het, gezien zijn frequente voorkomen, verdient.

2. Convergentie in de evolutie van diersoorten wijst meestal op het bestaan van *survival value* van de betreffende overeenkomstige eigenschappen.

3. De in publikaties over de organische evolutie zo vaak gebruikte term *preadaptatie* is, hoewel zeer illustratief, vanuit neo-darwinistisch oogpunt een contradictio in terminis, en anderszins een uiting van een teleologische denkwijze.

4. De mening van sommige tandartsen, als zou de mens in de toekomst minder kiezen bezitten dan momenteel het geval is, berust op een onjuiste extrapolatie vanuit de palaeontologie.

5. Acute urineretentie e causa ignota bij een tevoren schijnbaar gezonde patiënt kan berusten op leukaemie.

6. Het bestaan van diabetische retinopathie kan niet worden uitgesloten d.m.v. oogspiegelonderzoek.

7. De wijze van behandeling van het carcinoma colli uteri wordt niet beïnvloed door de lymfografische bevindingen.

8. Indien men bij de behandeling van tijdelijke vernauwingen in het larynxgebied van jonge kinderen een tracheotomie geïndiceerd acht, dient eerst de behandeling d.m.v. nasotracheale intubatie overwogen te worden.

9. Ook indien er geen aantoonbare organische obstructies bestaan, is het discutabel de dyspnoe, die soms optreedt na verwijdering van een tracheacanule bij jonge kinderen, alleen te beschouwen als psychogeen.

10. De middenoordrainage heeft de bestraling van ingang van de tuba auditiva d.m.v. radium obsoleet gemaakt.

11. De meeste psychische afwijkingen optredend in aansluiting aan keel-neus-oorheelkundige ziekten of ingrepen worden veroorzaakt door verstoorde tussenmenselijke verhoudingen.

12. De localisatie in het lichaam van de ik-beleving is waarschijnlijk afhankelijk van het cultuurpatroon van de gemeenschap waarin dit begrip een rol speelt.

13. De doelstellingen van de „Anti Honger Actie" werden door haar naam onvoldoende aangeduid.

14. Het succes van physische therapie is in veel gevallen mede te danken aan de gunstige werking van die vorm van lichamelijk contact, welke in de dierlijke gedragsleer wordt aangeduid met *grooming*, en welke dus vergelijkbaar is met het z.g. vlooien bij apen.

15. De wetten van von Baer, volgens welke verschillende diersoorten in een jonger stadium meer op elkaar gelijken dan in een ouder, kunnen ook worden toegepast op verschillende individuen van éénzelfde soort maar van verschillend geslacht; indien deze wetmatigheid wordt toegepast op die individuen van de soort *Homo sapiens*, die streven naar uniformiteit tussen de twee geslachten in kleding en haardracht, dan zou deze gewoonte kunnen worden opgevat als een uiting van onvolwassenheid.

Stellingen behorende bij proefschrift J. Wind.