
By

F. H. Edgeworth, M.D.,
Professor of Medicine, University of Bristol.

With Plates 27—39.

This paper is a continuation of one published in this Journal (1914, vol. 59) on "The Development and Morphology of the Mandibular and Hyoid Muscles of Mammals." It deals with the structure of the pharyngeal, laryngeal, and hypobranchial muscles of Ornithorhynchus and Echidna, with the development of these muscles in Dasyurus viverrinus and some other Marsupials, in the pig and rabbit. The last few pages contain a summary of the similarities and differences between the cranial muscles of Monotremes, Marsupials, and Eutheria.

PLICE PALATO-PHARYNGE.

Göppert stated that palato-pharyngeal folds are absent in adult Monotremes, and did not describe them in developmental stages of Echidna. In a 25 mm. specimen of Echidna, however, they are present (Pl. 27, figs. 1–4)—continuous anteriorly with the soft palate and extending backwards on the lateral wall of the pharynx as far as the antero-posterior level of first branchial bars; they contain the pharyngo-palatinus muscles.

The palato-pharyngeal folds of Dasyurus are developed in...
stage iv; in the pharyngeal region they do not extend further back than the first branchial segment, where they form slightly marked projections into the lumen of the pharynx (Pl. 29, fig. 18). In stage A (just born) they are much more marked, have extended back in the pharynx, and end by meeting together in a dorsal median fold at the junction of the pharynx and oesophagus (Pls. 29, 30, figs. 15-23). It is not until stage H that the pharyngo-palatinus muscle begins to lie in the fold.

In the pig the palato-pharyngeal folds first appear in embryos of 17 mm. crown-rump length, and do not extend backwards beyond the first branchial segment (Pl. 37, figs. 64 and 65). At the same time a median dorsal pouch develops in the roof of the pharynx in the second branchial segment (Pl. 37, fig. 68) and projects backwards as a flat, hollow pocket of epithelium (Pl. 38, fig. 69). In 20 and 21 mm. embryos the palato-pharyngeal folds have extended a little backwards, but fall short of the median pharyngeal pouch. The soft palate becomes fully formed in 38 mm. embryos.

The palato-pharyngeal folds in the rabbit form continuous structures extending from the palate in front along the sides of the pharynx, and meeting in a median dorsal fold at the junction of the pharynx and oesophagus.

The primary condition of the palato-pharyngeal folds is probably that present in Echidna, where they do not extend further back than the first branchial segment. In the pig they extend backwards slightly further. In Dasyurus, Didelphys, Phascolarctus, and rabbit they reach to the hind end of the pharynx, where they meet each other in a median dorsal fold. They become more developed in Marsupials than in the other animals investigated, and form thin reduplications of the mucous membrane.

Rückert, who described the median pharyngeal pouch in the adult pig, was of opinion that it was formed by the hind ends of the palato-pharyngeal folds. As a matter of fact, however, the pouch is formed posterior to the hind ends of the folds and has no direct relationship to them.
EPIGLOTTIS.

The epiglottis of Monotremes has been described by Göppert. The epiglottis of Dasyurus is developed in stage IV as a fold of mucous membrane in the floor of the pharynx, in the first and second branchial segments, just in front of the aditus laryngis (Pl. 29, fig. 14). In stage A (just born) the soft palate is formed, and the epiglottis projects upwards into the nasopharynx, with its anterior surface close to the posterior edge of the soft palate; its lateral edges are embraced by the palato-pharyngeal folds, whilst below these folds there is, on each side, a wider space between the lateral edges of the epiglottis and the wall of the pharynx—the "fauces" of Gegenbaur (Pls. 29, 30, figs. 16 and 24). This condition remains up to the stage J—the latest investigated.

The formation of the epiglottis in the pig has been described by Kallius. It begins to develop in 8 mm. embryos.

PLACê ARY-EPIGLOTTICÆ.

In stages A to D of Dasyurus (stage A, Pls. 29, 30, figs. 16–20; stage D, Pl. 31, figs. 30 and 31) the lateral edges of the epiglottis are continuous, posteriorly, with the ary-epiglottic folds bounding the aditus laryngis. In stage E (Pl. 32, fig. 38) small prominences appear over the anterior ends of the arytenoid cartilages, projecting into the lumen of the larynx, on the inner sides of the ary-epiglottic folds, a little distance below their free edges. Slight grooves separate the prominences over the arytenoid cartilages from the dorsal edges of the original ary-epiglottic folds. In front of the prominences the original ary-epiglottic folds are continuous, as in former stages, with the lateral edges of the epiglottis (Pl. 32, figs. 35–37).

The prominences over the arytenoid cartilages become more marked, but they do not extend forward to the epiglottis. The original ary-epiglottic folds increase in height, and form thin, inward-arching folds whose free edges bound the aditus
The original ary-epiglottic folds thus become those called Plicae laterales by Symington and Partes laterales epiglotticae by Göppert. In the figures I have employed the former term. The folds subsequently developed over the arytenoid cartilages may be called secondary arytenoid folds.

In the pig the method of formation of the secondary arytenoid folds is different from that in Dasyurus. In a 11 mm. embryo (Pl. 36, figs. 60 and 61) the ary-epiglottic folds on either side of the aditus laryngis are continuous anteriorly with the lateral parts of the slightly developed epiglottis. In a 17 mm. embryo the lateral boundaries of the aditus are formed, posteriorly, by the ary-epiglottic folds (Pl.37, fig.67); a little further forwards (Pl. 37, fig. 66) grooves are visible on the dorso-lateral sides of the ary-epiglottic folds, separating median arytenoid folds from the lateral plicae laterales, at first partially, and still further forwards completely (Pl. 37, fig. 65). The plicae laterales are the original ary-epiglottic folds, as shown by the fact that they are continuous, anteriorly, with the epiglottis, as were the ary-epiglottic folds in the 11 mm. embryo. The secondary arytenoid folds have free forward projecting extremities on the floor of the pharynx a little behind the epiglottis (Pl. 37, fig. 64). The plicae laterales increase in height, and in a 32 mm. embryo (Pl. 39, figs. 76 and 77) form the lateral boundaries of the aditus laryngis, whilst the secondary arytenoid folds are prominences on the inner surface of the plicae laterales below the aditus. The secondary arytenoid folds have free anterior extremities just behind the posterior surface of the epiglottis in both this and the 38 mm. stage, but in the adult are continuous with the epiglottis forming secondary ary-epiglottic folds (Némai).

The developmental phenomena in the rabbit are similar to those occurring in the pig.

Gegenbaur (1892), Symington (1899), and Göppert (1902) have discussed the nature of the lateral boundaries of the larynx in Marsupials. Gegenbaur stated that the lateral edges of the epiglottis form plicae laterales, which pass
backwards and form a tube intro which project the arytenoids. Symington stated that in the majority of Marsupials there are no ary-epiglottic folds, and that the lateral boundaries of the epiglottis, turning back, form plicae laterales, separated from the arytenoids by sulci. In some of the smaller Marsupials, where the arytenoids are not so prominent, the plicae laterales may join the upper borders of the arytenoids to form ary-epiglottic folds. Goppert stated that in Marsupials, Rodents (Leporidae and Muridae), and Lemurs the partes laterales epiglotticæ become developed, so that the entrance to the larynx is raised into a tube projecting into the pharynx. In these cases the plicae ary-epiglotticæ lose in importance, but are visible inside the epiglottis tube.

The observations described above show that the primitive condition is one in which the aditus laryngis is bounded laterally by ary-epiglottic folds, which are continuous in front with the epiglottis. The arytenoid cartilages are developed in these ary-epiglottic folds. This is the condition in Monotremes, as described by Göppert.

In Dasyurus, pig, and rabbit this primitive condition is succeeded by one in which secondary arytenoid folds develop on the inner sides of the ary-epiglottic folds. The latter extend in height, and form plicae laterales bounding a new aditus laryngis. This condition becomes the permanent one in Marsupials.

The initial stages of formation of the secondary arytenoid folds are not identical in Dasyurus, pig, and rabbit. In Dasyurus, where they develop in extra-uterine life and subsequent to the formation of the arytenoid cartilages, they are formed on the inner side of the ary-epiglottic folds. In the pig and rabbit, where they develop in intra-uterine life and previous to the formation of the arytenoid cartilages, they are at first situated more dorsally than in Dasyurus and for a time bound the aditus laryngis, and only subsequently assume the position they have from the first in Dasyurus. This difference is apparently due to the relative
lateness in upgrowth of the original ary-epiglottic folds to form plicæ laterales in the pig and rabbit.

In the pig and rabbit the secondary arytenoid folds gain an attachment to the posterior surface of the epiglottis and form secondary ary-epiglottic folds, ventro-internal to the original ary-epiglottic folds, s. plicæ laterales.

It is probable that there is a similar development in the other classes of Mammals in which, according to Göppert, plicæ laterales occur, i.e. in Carnivora other than Canidae and Ursidae, Insectivora, Prosimiae, Platyrrhina, and Catarrhina other than Anthropomorphæ.

In stage A of Dasyurus (Pls. 29, 30, figs. 17 and 18) a solid outgrowth of the epithelium lining the cavity of the larynx is formed, which projects forwards between the two anterior cornua of the thyroid cartilage. There is no further development of this outgrowth until stage E, when it begins to enlarge and to become hollowed out, and forms a cavity opening posteriorly into the ventral part of the larynx (Pl. 32, figs. 36 and 37). A similar recess was described by Gegenbaur in Phalangista vulpina, by Albrecht in Cuscus, and by Symington in almost all the cases he examined.

Hyobranchial Cartilages.

In stage A of Dasyurus (Pl. 29, figs. 16 and 17) the cartilaginous ventral ends of the hyoid and first branchial bars are continuous with the median cartilaginous basi-branchial. The upper, precartilaginous, end of the first branchial bar passes backward and is continuous with the upper edge of the thyroid ala (Pl. 30, figs. 18 and 19). It becomes cartilaginous in stage C.

The development of the hyobranchial cartilages in the pig has been described by Kallius.

1 Plicæ ary-epiglotticæ (Göppert), Plicæ inferiores (Albrecht), Plicæ ary-epiglottidæ s. Plicæ inferiores (Némai).
THYROID CARTILAGE.

The morphology of the thyroid cartilage of Mammals has been the subject of many investigations. Dubois (1886) showed that the thyroid cartilage of Monotremes consists of a median copula and two bars on either side, which are homologous with the second and third branchial (fourth and fifth visceral) bars of lower Vertebrates. This opinion was confirmed by the embryological investigations of Göppert. Dubois also stated that the thyroid cartilage of Marsupials—consisting of a broad plate with marked anterior and posterior horns—is homologous with that of Monotremes, and probably due to fusion of two bars and a copula. He was also of opinion that the thyroid cartilage of Eutheria, though its posterior horns are less marked, has a similar derivation.

Investigations into the development of the thyroid cartilage in Eutheria have not yielded concordant results. His (1885), as stated by Göppert, found that the thyroid cartilage of man is developed in the second branchial arch.

Nicholas (1894), whose researches began with 22 mm. human embryos, showed that the thyroid cartilage develops from two independent lateral halves which fuse ventrally, at first in front and then behind. An unpaired median cartilaginous nodule subsequently develops in the cellular band connecting the alæ in the intermediate region and fuses with them. This nodule is to be distinguished from the intermediate piece of cartilage of the adult larynx, which is a secondary formation, and "resulte du remaisement dans une région limitée d'une lame cartilagineuse homogène." He doubted any homology of the primary median nodule with the basithyroid copula of Monotremes owing to its filling a part only of the interval between the alæ.

According to Kallius (1897), each half of the thyroid cartilage develops in human embryos of thirty-nine to forty

1 A difference of opinion between Dubois and Göppert in regard to the morphology of the Monotreme laryngeal cartilages is discussed later on (pp. 414, 415) in connection with the interthyroides muscle.
days, as a plate of dense connective tissue, chondrified at its cranial and caudal borders, and with a central foramen thyroideum. Chondrification spreads, and a cartilaginous plate is formed which extends ventrally in a dense connective tissue. A median thyroid copula, homologous with that of Monotremes, is developed in this tissue. The thyroid cartilage is thus formed by the fusion of elements homologous with the second and third branchial (fourth and fifth visceral) bars and an intermediate copula.

Soulié and Bardier (1907) investigated the development of the thyroid cartilage in man. They did not regard the presence of a foramen in the thyroid cartilage and of a notch in its border as certain indications of a formation from two pieces, but remarked that it was not possible to be absolutely sure of the morphology of the thyroid alae in man, inasmuch as the gill-clefts have disappeared in 14 mm. embryos, whilst cartilage is first developed in 19 mm. embryos. They concluded that "la partie médiane du quatrième arc est utilisée pour la formation de l'épiglotte, et le squelette de ses parties latérales donnera les lames latérales du thyroïde, dont les grandes cornes se constitueront aux dépens du squelette des portions latérales du troisième arc. Le cinquième arc, rudimentaire, ne fournit aucun dérivé." The vocal or intermediate nodule first appears in 37 mm. embryos, and they denied its equivalence to a thyroid copula, owing to this lateness in development.

Frazer (1910) stated that "the thyroid cartilage of man is primarily a fourth arch derivative, and if it has any fifth arch element this is a later addition, and its line of junction is not indicated by the occasional persistence of the foramen in the ala." The cartilage first appears at the end of the first month. In a 35 mm. embryo two small nodules of cartilaginous structure are interposed between the alae, probably representing the cartilages of Nicholas.

Grosser (1912), in the course of a description of the gill-clefts of man, stated that the skeletal portion of the fifth visceral (third branchial) segment "which is included in the
thyroid cartilage is, however, of considerable size," Soulié and Bardier, however (vide supra) had stated that the gill-clefts of man lose their connection with the pharynx before the thyroid cartilage begins to develop, so that determination of the segment or segments of origin of the thyroid cartilage is not possible in man. The same thing was shown by Soulé in the mole.

The development of the thyroid cartilage could not be followed in Dasyurus owing to the absence of the necessary stages. In stage iii β it is not yet developed; in stage iv it is present, and does not differ from that at birth (stage A), except in that chondrification has not yet taken place. In Trichosurus vulpecula, however, the process of development could be followed. In stage viii β (Pl. 34, figs. 50-52) the gill-clefts are still continuous with the pharynx. The thyroid cartilage consists of two primordia, the anterior between the third and fourth gill-clefts in the fourth visceral (second branchial) segment, and the posterior behind the fourth gill-cleft in the fifth visceral (third branchial) segment. In stage ix, a and b (Pl. 35, figs. 53-55), these primordia are more clearly defined. Their outer ends (Pl. 35, figs. 53-55) are united together, whilst a little nearer the middle line (Pl. 35, fig. 54) they are still separate. The upper end of the first branchial bar is continuous with the 1st thyroid primordium. The hind end of the second thyroid primordium abuts against the ill-defined primordium of the cricoid cartilage.

In stage A of Dasyurus (Pls. 29, 30, figs. 17-22 and 24-25) the thyroid alæ form slightly curved cartilaginous bars, the anterior ends of which are connected by precartilaginous tissue. Their ventral edges are connected by cells which form a membrane. The hind ends of the first branchial bars are continuous with the upper edges of the alæ. There is no thyroid copula.

In stage B the lower edges of the thyroid alæ have extended ventrally in the membrane connecting them. In stage C the precartilaginous tissue connecting the anterior ends chondrifies and a copula is developed in the ventral
membrane. Behind the copula the projecting wedge-shaped ventral part of the cricoid, hitherto separate, has become continuous with the thyroid alæ. In stage D the copula has chondrified (Pl. 31, fig. 31), and become continuous laterally with the alæ.

In 17 mm. pig embryos no definite primordium of the thyroid cartilage is present (Pl. 37, figs. 66-68). In 18 mm. embryos (Pl. 38, fig. 69) it is developed, on each side, lateral and ventro-lateral to the pharynx. The ductus pharyngobranchialis of the fourth gill-cleft passes outwards from the pharynx behind the primordium, which is consequently developed in the fourth visceral (second branchial) segment. In 21 mm. embryos (Pl. 38, figs. 71, 72) the primordium of the thyroid cartilage has extended ventrally, and the thyroid copula has appeared in the middle line. The fourth gill-cleft is no longer continuous with the pharynx. The epithelial body of the fourth gill-cleft lies just external to the hind end of the primordium of the thyroid cartilage. In 24 mm. embryos chondrification has occurred both in the thyroid alæ and copula. In 32 mm. embryos the alæ and copula form a continuous whole.

In the pig each thyroid ala is thus developed in one segment only—the fourth visceral (second branchial).

The morphology of the thyroid cartilage of Mammals would thus appear to be as follows: In Monotremes and Marsupials each lateral half is developed from two primordia developed in the fourth and fifth visceral (second and third branchial) segments, and homologous with the second and third branchial bars of Amphibia. In Monotremes the bars remain separate; in Marsupials they fuse and form the thyroid alæ. In Eutheria it appears probable that the thyroid ala is formed, as in the pig, from one primordium only, developed in the fourth visceral (second branchial) segment. In Eutheria the fifth visceral (third branchial) segment, marked in early stages by an aortic arch and segmental branch from the vagus, appears to have only an ephemeral existence.

This disappearance in the phylogeny of Eutheria of a
third branchial constituent of the thyroid cartilage offers an explanation of the observation of Dubois that the recurrent laryngeal nerve passes into the larynx ventral to the articulation of the thyroid and cricoid cartilages in Monotremes and Marsupials, dorsal to it in Eutheria. The articulations are not homologous.

A median thyroid copula was described by Dubois in Monotremes, and its existence was confirmed by Symington, Miss Walker, and Göppert.

A similar copula is developed in Dasyurus and in the pig. In man a median cartilage between the ventral edges of the thyroid alæ was described by Nicholas, and subsequently by Kallius, Soulié and Bardier, and Frazer. Its homology with the thyroid copula of Monotremes was affirmed by Kallius and Göppert, but denied by Nicholas, who called it the "cartilage vocal," and by Soulié and Bardier mainly on the ground of its very late appearance. Thus Soulié and Bardier state that the alæ develop in 19 mm. embryos, and the median cartilage only in 37 mm. embryos.

It appears doubtful if this relative lateness in development is a sufficient ground for denial of homology, as this is a constant feature of the copulae of the visceral bars.

Epiglottic Cartilage.

Dubois (1886) stated that the epiglottic cartilage represents a chondrification of the submucous tissue of the transverse glosso-laryngeal fold. Its intimate relations to the thyroid cartilage are to be regarded as secondary.

Gegenbaur (1892) put forward the theory that the epiglottic cartilage is derived from the fourth branchial (sixth visceral) bars. This view was based on the asserted hyaline condition of the cartilage in Monotremes and on the frequent paired condition of the base of the cartilage.

Symington (1900), however, showed that the epiglottic cartilage of Monotremes consists of elastic cartilage, and rejected Gegenbaur's theory.
Göppert (1894 and 1900) investigated a large number of Mammals, and showed that the condition of the base of the cartilage is variable—in some cases paired, in others not—and adhered to the view that the paired condition is the more primitive.

Schaffer (1907) advanced the following arguments against Gegenbaur's theory. The epiglottic cartilage has not been shown to have a hyaline primordium in any animal, as would be the case in a typical skeletal cartilage. It bears the character of a secondary chondrification, in agreement with its late formation and its frequent replacement by other connective tissues. Its first primordium has a close relation to the thyroid cartilage, varying from one of contiguity to cartilaginous continuity, and also to the mucous membrane of the epiglottis in its later development. He concluded that the epiglottic cartilage is not derived from a pair of branchial bars, but is a secondary formation. "Der Grund für diese Bildung wird ungezwungen darin zu suchen sein dass die glosso-laryngeale Schleimhautfalte durch eine neugewonnene Funktion einer festeren Stütze bedürfe."

Soulié (1909), in his paper on the development of the larynx of Talpa, expressed the opinion that the epiglottic cartilage was not derived from the branchial skeleton, and was a special formation, on the nature of which we cannot pronounce.

Dasyurus is born with a fully developed epiglottis (Pls. 29, 30, figs. 16 and 24), but the epiglottic cartilage is not developed until later. It is first visible in stage B (Pl. 32, fig. 35) as an aggregate of cells dorsal to the united anterior ends of the thyroid cartilage. It increases in size, and its lateral edges extend a little backward along the upper edge of the thyroid cartilage (Pl. 33, figs. 43 and 44). By stage H it consists of elastic cartilage. There is no intervening stage in which it consists of hyaline cartilage, nor any in which it shows indications of being formed by coalescence of two lateral halves.

The epiglottic cartilage of the pig is not yet developed in
24 mm. embryos, but is present in 32 mm. embryos (Pl. 39, fig. 76) as an aggregate of cells beneath the epithelium of the epiglottic fold.

The evidence suggests that the theory of Gegenbaur and Göppert may be rejected in favour of that of Dubois, Symington, and Schaffer. The epiglottis is developed in the floor of the pharynx just in front of the opening of the larynx, and its cartilage is subsequently formed in it as a supporting structure. Both are exclusively Mammalian structures and have been developed in association with the mammary function.

The segment of origin of the epiglottis appears to vary a little. In Echidna, Dasyurus, and pig it is the first and second branchial (third and fourth visceral) segments. In Talpa (Soulé) it is the second branchial (fourth visceral) segment. In man, according to Soulé and Bardier, it is the second branchial (fourth visceral) segment, whilst, according to Frazer, the epiglottis is derived from a central mass which has a first branchial (third visceral) element on its oral and upper aspect.

**Cricoid and Arytenoid Cartilages.**

In stage iii β of Dasyurus there are aggregated cells round the lower part of the larynx and upper part of the trachea, but no definite primordium of skeletal structures is visible. In stage iv these cells form a continuous precartilaginous primordium of the arytenoid-cricoid-tracheal cartilages—in the arytenoid region n-shaped with a connecting bridge dorsal to the lumen of the larynx, and behind that surrounding the posterior part of the larynx and anterior part of the trachea; the cricoid is slightly marked off from the tracheal skeleton.

In stages A to C (Pl. 30, figs. 19-22, 24-25) the arytenoid-cricoid forms a continuous structure. The cricoid is a cartilaginous ring, complete dorsally and ventrally. The two arytenoid cartilages project forward from the upper part of its anterior edge. These are distinct structures anteriorly, but continuous with each other and with the cricoid posteriorly.
The cartilaginous continuity of cricoid and arytenoid is not complete laterally, where the intercellular matrix is scarcely present. In stage D (Pl. 31, figs. 32, 33) the arytenoids are fully separated from the cricoid, but are united dorsally by a bridge which has lost its hyaline cartilage appearance and forms the primordium of the interarytenoid cartilage. The interarytenoid cartilage moves dorsally, and by stage J (Pl. 34, fig. 46) lies dorsal to the upper edges of the arytenoid cartilages. It is formed of elastic cartilage. The anterior parts of the arytenoid cartilages are rounded in stages A to C (Pl. 30, figs. 19, 20); the processus muscularis and ventral process begin to develop in stage D (Pl. 31, figs. 32, 33) and subsequently become still more marked (Pl. 34, fig. 46).

The position of the interarytenoid cartilage varies in Marsupials. Symington found it lying between the two arytenoids and articulating with their internal processes, and this position was also described by Henkel in Macropus rufus. Körner described and figured it in Halmaturus giganteus, lying dorsal to the arytenoid cartilages. This position was also described by Henkel in Phascolomys platiceps and Petrogale lateralis, and it exists in late pouch stages of Dasyurus and Didelphys aurea, and also in adult Monotremes (Göppert).

The interarytenoid cartilage primarily has an interarytenoid position in Echidna (Göppert) and in Dasyurus, and subsequently a dorsal one. The condition found by Symington in many Marsupials and by Henkel in Macropus rufus is thus probably due to persistence of a developmental stage. The cartilage was termed “interarytenoid” by v. Luschka and Symington, “cartilago sesamoidea sive paplionacea” by Körner and Henkel, “procricoid” by Göppert. The developmental phenomena suggest the use of the first name in preference to either of the other two.

In the pig there is no definite primordium of the cricoid and arytenoid cartilages until the stage of 18 mm. Previous to this—from the stage of 6 mm. to that of 17 mm.—there is a continuous layer of aggregated mesoblast cells round the tracheal
and laryngeal epithelium (Pls. 35, 36, 37, figs. 57–59, 61–63, 66–68). They extend from behind the sixth aortic arch into the second branchial segment. In the 18 mm. stage the primordium of the cricoid and arytenoids is visible, dorsal and lateral to the hinder portion of the larynx (Pl. 38, figs. 69, 70).

It is more marked and may be spoken of as precartilage in 21 mm. embryos (Pl. 38, figs. 71, 72). In 24 mm. embryos chondrification has taken place lateral to the laryngeal lumen, whilst dorsal and ventral to it the structures are still precartilaginous; and, anteriorly, what will become the arytenoids are precartilaginous. In 32 mm. embryos the arytenoids are separated from the cricoid; they are cartilaginous and are connected by a bridge, dorsal to the laryngeal lumen, of precartilaginous structure (Pl. 38, fig. 71); the cricoid is a cartilaginous ring, and patches of cartilage have appeared round the trachea. In 38 mm. embryos the interarytenoid cartilage has separated from the laterally lying arytenoid cartilages.

LARYNGEAL MUSCLES.

The development of the laryngeal muscles has been the subject of many investigations. Strazza (1888) found the first indication of the musculature of the larynx in human embryos of 12 and 13 mm. in intimate connection with that of the tongue.

Nicholas (1894) stated that in the first stages of development the laryngeal sphincter of man forms a complete ring, and subsequently becomes subdivided into three groups of muscles. He did not describe the derivation of this sphincter.

Kallius (1897) did not describe the development of the laryngeal muscles.

Göppert (1902) found the primordium of the laryngeal muscles of Echidna in stage 42 as a triangular mass of aggregated cells lying lateral to the mesodermal cells immediately surrounding the epithelium of the larynx. "Man kann sie an der Seite des Kehlkopfes caudalwarts verfolgen, bis in die Gegend des Beginnes der Trachea. Sie nimmt dabei an
Umfang noch etwas zu.” In stage 44 the cells had developed into embryonic muscle-cells, easily recognisable when cut longitudinally; the muscles of this primordium already had the same arrangement as in the adult larynx.

Soulié and Bardier (1907) were not able to confirm Strazza’s observation on man. They did not see any indication of intrinsic laryngeal muscles in 14 mm. embryos; in 19 mm. embryos, however, four muscle-groups were recognisable, corresponding to the interaryténoidien, crico-aryténoidien-postérieur, crico-thyroïdien, and thyro-crico-aryténoidien. No statement was made as to the origin of these primordia.

Soulié (1909) found the first indication of the laryngeal musculature of the mole (Talpa europæa) in 10 mm. embryos formed “par les muscles crico-aryténoidiens posté-rioure et par quelques rares faisceaux musculaires interposés aux divers précartilages.” He did not state the origin of these muscles.

Fraser (1910) stated that the intrinsic laryngeal musculature of man is developed from two planes, inner and outer, which are separated from one another by mesoblast of the fourth arch. The inner plane or constrictor, developing first, in 5 mm. embryos, is derived from the fifth visceral (third branchial) arch; the outer plane or constrictor, developing a little later, is derived from the fourth visceral (second branchial) arch, which becomes antero-external to the fifth arch. “The inner constrictor appears to be subsequently split up into the internal intrinsic muscles in its laryngeal part, and dorsally forms part of the pharyngeal musculature, whilst the outer constrictor becomes dorsally a part of this musculature, and in its laryngeal area gets a secondary attachment to the cricoid and thyroid, and seems to form the crico-thyroid muscles in consequence of the downgrowth of the inferior thyroid cornu into it.”

The early development of the laryngeal muscles could not be followed in Dasyurus, owing to want of the necessary stages. In stages i and iii of Trichosurus vulpecula the larynx and anterior part of the oesophagus and trachea are
surrounded by mesoblast cells in which no differentiation is visible. In stage v the primordia of the constrictor of the oesophagus and laryngeal muscles is found (Pl. 34, figs. 47-49). The latter lie lateral to the anterior part of the trachea, extending from behind the sixth aortic arch to the fourth gill-cleft. There is no connection between them and the oesophageal constrictor. The recurrent laryngeal nerve passes from the vagus directly inwards to the hind end of the laryngeal muscle primordium. In stage β viii (Pl. 34, figs. 50-52) the laryngeal muscle primordium has shifted forward—its hind end lies opposite the fourth aortic arch, and it extends into the second branchial segment.

In stage ix (Pl. 35, figs. 54, 55) it forms a continuous mass, in which the dilatator laryngis and laryngeus ventralis are distinguishable; the laryngeus dorsalis is not yet formed.

The intrinsic laryngeal muscles of Dasyurus in stage A consist of dilatator, laryngeus dorsalis, and laryngeus ventralis. The dilatator muscle (Pl. 30, figs. 20-22, 24) arises from the posterior cornu of the thyroid and dorsal surface of the cricoid, and is inserted into the dorsal and lateral surfaces of the arytenoid cartilage, the processus muscularis not being yet developed. The greater number of the fibres have a longitudinal direction, but a few fibres can be seen extending down from the dorsal portion of the muscle next to the cricoid cartilage and medial to the main mass of the muscle. By stage C (Pl. 31, figs. 26, 27) these descending fibres are much more marked. In stage H (Pl. 33, fig. 41) the original dilatator muscle is fully separated into a ventro-lateral portion—the kerato-crico-arytenoideus, and a dorso-median portion—the crico-arytenoideus posticus internus. The latter arises from the cricoid cartilage dorso-medial to the kerato-crico-arytenoideus, and also by fibres which pass upwards and inwards internal to the kerato-crico-arytenoideus. The developmental phenomena described are due to the occurrence of a lateral extension of the origin of the crico-arytenoideus posticus internus on the cricoid before separation of the dilatator into the two muscles it forms.
The laryngeus dorsalis forms the interarytenoides. In stages A (Pl. 27, fig. 6) to C (Pls. 30, 31, figs. 20, 28) it is represented by a very few muscle-cells only, and these lie dorsal to the upper surface of the arytenoid cartilage. It is not until stage D (Pl. 31, fig. 32), when the arytenoids have separated from the cricoid, that the muscle-cells increase in numbers and form a transverse muscle. On separation of the interarytenoid cartilage, in stage E, some of the fibres are inserted into it (Pl. 34, fig. 46 of stage J), whilst in front of the cartilage the fibres cross from side to side.

The laryngeus ventralis in stage A (Pl. 30, figs. 19, 20) of Dasyurus arises from the lateral surface of the wedge-shaped anterior projection of the ventral edge of the cricoid ring, and is inserted into the lateral surface of the arytenoid cartilage. In stage B its origin has spread uninterruptedly forwards so that it also arises from the membrane connecting the ventral edges of the thyroid alaæ. In stage D, when the thyroid alaæ have extended down, the anterior part of the muscle arises from the thyroid ala (Pl. 31, fig. 32). It thus forms the crico-thyro-arytenoideus (Pls. 33, 34, figs. 44–46).

Two theories have been advanced in regard to the morphology of the crico-arytenoideus posticus internus of Marsupials. Symington stated that this muscle and the kerato-crico-arytenoideus "represent the crico-arytenoideus posticus of the majority of Mammals, which has become split into two parts, and its attachments modified owing to the large size of the inferior cornu of the thyroid cartilage, the slight vertical extent of the posterior part of cricoid cartilage, the development of a large internal process to the arytenoid, and the existence of an interarytenoid cartilage."

Göppert, on the other hand, stated that the crico-arytenoideus posticus internus (which he called "crico-procricoides") of Marsupials, is a portion of the laryngeus dorsalis which has divided into the interarytenoideus (which he called "ary-procricoides") and this muscle. This opinion was founded on the homology of the laryngeal muscles with those of Monotremes and on the observation that in Echidna the
MUSCLES OF MAMMALS.

crico-procricoideus is formed by extension of the laryngeus dorsalis to the cricoid cartilage.

The above recorded observations on Dasyurus appear to prove the theory of Symington as regards the crico-arytenoideus posticus internus of Marsupials. In stage A of Dasyurus, when the muscle is beginning to be formed, there is a distinct gap between the anterior end of the dilatator muscle and the primordium of the laryngeus dorsalis (cp. Pl. 30, figs. 20 and 21). This suggests that the development of the muscle in the Monotreme larynx is worth reinvestigation.

The form of the crico-arytenoideus posticus internus in Dasyurus is not the most primitive present in Marsupials. It has been shown above that the origin of the medial portion of the original dilatator muscle of Dasyurus (which will form the crico-arytenoideus posticus internus) begins to spread laterally on the cricoid beneath the outer portion (which will form the kerato-crico-arytenoideus) even before the two muscles become fully separated from one another.

In Phascolarctus (Pl. 35, fig. 56), and also in Petrogale lateralis (Henkel), such a lateral extension of the crico-arytenoideus posticus internus does not take place, and it lies wholly medial to the kerato-crico-arytenoideus. But in many Marsupials the origin of the muscle spreads laterally, and the lateral portion may remain in continuity with the medial portion, e.g. in Dasyurus, Didelphys aurita, and also in Macropus rufus and Phascolomys platiceps (Henkel). Or the lateral portion may become a separate muscle, lying under the kerato-crico-arytenoideus; this is the case in Halmaturus giganteus and Billardieri (Körner), Macropus robustus and cervinus, and Onychogalea fennata (Henkel).

Körner, who described the condition in Halmaturus giganteus and Billardieri (where the lateral portion is a separate muscle), gave the name crico-sesamo-arytenoideus to the medial portion and that of crico-arytenoideus profundus to the lateral portion of the crico-arytenoideus posticus
Henkel described the crico-arytenoideus profundus as being absent in the cases where it did not form a separate muscle—both in those, e.g. Petrogale lateralis, where the crico-arytenoideus posticus internus remains medial to the kerato-crico-arytenoideus, and in those, e.g. Macropus rufus, where it spreads laterally on the cricoid. Comparison, however, of the various conditions shows that they are due to the non-occurrence or occurrence of a lateral spread, and in the latter case to the non-separation or separation of the lateral portion.

Möller stated that he had found the crico-arytenoideus profundus of Marsupials closely bound to the crico-thyro-arytenoideus, and was of the opinion that the former muscle was homologous with the crico-arytenoidens lateralis of higher Mammals. In Dasyurus, however, the lateral edge of the crico-arytenoideus posticus internus (which, as stated above, does not separate into two muscles) is at some little distance from the posterior edge of the crico-thyro-arytenoideus in stage A, and only in stage C do the two muscles come into contact. The same thing is true of Didelphys aurita—in 10 mm. specimens there is a gap between the two muscles, which is gone in 20 mm. specimens. The opinion of Möller, consequently, does not appear to be tenable.

Various names, as stated above, have been given to the laryngeal muscles of Marsupials. They are, in part, associated with those of the cartilage here called “interarytenoid.” The arrangement in the following tabular statement differs from that of Göppert in regard to the derivation of the crico-arytenoideus posticus internus. In it and the above discussion I have (1) employed the term “crico-thyro-arytenoideus” in preference to that of “thyro-crico-arytenoideus,” used by Symington and Göppert, as in the development of Dasyurus the first attachment of the muscle is to the cricoid cartilage, from which it spreads forward to the thyroid cartilage: (2) used the name “interarytenoideus”; and (3) have followed Symington in the nomenclature of the subdivisions of the M. dilatator.
In the pig the primordium of the laryngeal muscles is first visible in 8 mm. embryos, as a mass of cells continuous with, and apparently proliferated from, the primordium of the constrictor of the oesophagus, posterior to the sixth aortic arch. It extends forwards as far as, but not anteriorly to, the sixth aortic arch. The vagus nerve passes backwards and downwards lateral to the primordium of the laryngeal muscles (Pl. 35, figs. 57–59).

In 11 mm. embryos the laryngeal muscle-primordium has extended forwards and a little in front of the fourth gill-cleft, i.e. into the fourth visceral (second branchial) segment, though it is still continuous with the primordium of the constrictor of the oesophagus, posterior to the sixth aortic arch (Pl. 36, figs. 60–63). The recurrent laryngeal nerve which has now developed passes inwards and slightly forwards from the vagus to the hind end of the muscle-primordium, behind the sixth aortic arch.

In 14 mm. embryos the recurrent laryngeal nerve has been carried backwards by the “descent” of the sixth aortic arch, so that it passes into the laryngeal muscle-primordium from behind.
In 17 mm. embryos (Pl. 37, fig. 68) the anterior part of the laryngeal muscle-primordium has extended a little ventrally, and it lies lateral to the aggregated cells surrounding the posterior part of the larynx.

In 18 mm. embryos (Pl. 38, figs. 69, 70) the hind end of the laryngeal muscle-primordium is separated from the anterior end of the constrictor of the oesophagus, lying ventral to this and dorsal to the primordium of the cricoid cartilage.

The separation of the laryngeal muscle-primordium into M. dilatator (crico-arytenoideus posticus), laryngeus ventralis, and laryngeus dorsalis (lateral half of interarytenoideus) begins in 21 mm. embryos (Pl. 38, fig. 71), and is complete in 24 mm. embryos. In 32 mm. embryos the laryngeus ventralis has separated into thyro-arytenoideus and crico-arytenoideus lateralis.

The above-described phenomena show that in Trichosurus and pig the primordia of the laryngeal muscles are formed behind the sixth aortic arch, i.e. behind the branchial region. In the pig the primordia are at first continuous with, probably proliferated from, the primordium of the constrictor muscle of the oesophagus; in Trichosurus they are developed at the same stage as, though not in continuity with, the oesophageal constrictor.¹ The primordia grow forward into the branchial region, losing in the pig their continuity with the oesophageal constrictor, and develop into the dilatator laryngis, laryngeus ventralis, and laryngeus dorsalis on each side.

The primordia of the laryngeal muscles are thus post-branchial in origin, and are probably developed from the constrictor of the oesophagus.

These phenomena harmonise with the first development of the larynx as a post-branchial structure and its subsequent forward migration into the meso-branchial region. Thus Grosser showed that, in man, the primordium of the larynx

¹ Possibly the laryngeal muscle-primordium in stage iv of Trichosurus is continuous with the oesophageal constrictor, but this stage was not available.
appears caudal to the pharyngeal pouches as a ventral groove, developing simultaneously with the last pharyngeal pouches. The laryngeal portion of the groove encroaches on the mesobranchial region until it lies between the medial ends of the fourth and, later, between those of the third visceral arches. Similarly, I found that in a Dasyurus embryo of stage ii. α (of Hill) the opening of the larynx lies caudal to the fourth (the last) gill-cleft (Pl. 29, figs. 11, 12), and that in stage iii. β it has migrated forwards into the branchial region. In a 6 mm. pig embryo (the youngest investigated) the hind end of the aditus laryngis lies 230 μ caudal to the opening of the fourth gill-cleft; this distance gradually lessens until, in 14 mm. embryos, it lies on the same antero-posterior level.

The relationship of the aditus laryngis and intrinsic laryngeal musculature to the branchial region and thyroid cartilages is thus secondary and due to forward migration during development.

It has yet to be determined whether in the cases, e.g., man, mole, where the intrinsic laryngeal musculature has been described as originating in the branchial region, this is really so, or whether further investigation will show that the muscle-primordia can be traced back behind the sixth aortic arch to the oesophageal region. As quoted above, Goppert stated that the primordia of the laryngeal muscles in Echidna, at their first appearance in stage 42, could be followed backward to the beginning of the trachea, and he gave a figure which shows that they extended at least to the sixth aortic arch. But this is the only account, in previous investigations, of phenomena similar to those described above.

The primitive condition is probably that existing in Dipnoi (Protopterus), where the larynx opens behind the branchial region and its musculature other than the transversus ventralis v. is a direct derivative of the oesophageal constrictor. The phylogenetic history of the Mammalian larynx and its musculature from such a condition is clearly shown in its

1 The term used by Grosser is "branchial," but it is clear from the context that he uses it in the sense of "visceral" or "post-oral" and not in the restricted way employed in this paper.
ontogenetic development. The separation of this musculature into dilatator, laryngeus dorsalis, and laryngeus ventralis occurs also in Amphibia and Sauropsida.

**Pharyngeal and Palatal Muscles.**

Kostanecki described the pharyngo-palatinus muscle of Ornithorhynchus, but the stylopharyngeus and pharyngeal constrictor have not been described in either Monotreme nor the pharyngo-palatinus in Echidna.

In a 25 mm. specimen of Echidna (Pl. 27, figs. 1-4) the stylo-pharyngeus arises from the inner surface of the stylohyale and passes inwards, and then inward and upward in a dorsally convex curve over the pharynx and nasopharynx to meet its fellow in the mid-dorsal line. It thus forms an anterior pharyngeal constrictor. It has no fibres passing directly towards the lateral wall of the pharynx. The posterior pharyngeal constrictor forms a sheet of fibres arching over the pharynx (Pl. 27, figs. 3-8). It is attached, from before backwards, to the stylohyale (Pl. 27, figs. 3, 4), to both medial and lateral surfaces of the first branchial bar (Pl. 27, figs. 5, 6) and thyroid ala, to the first branchial and first thyroid cornua¹ of the thyroid ala (Pl. 27, fig. 7), and to the cricoid cartilage. It has no attachments to the second thyroid bar. No superior pharyngeal constrictor is present. The pharyngo-palatinus arises from the anterior part of the posterior pharyngeal constrictor (Pl. 27, figs. 5, 4), passes downwards and forwards into the palato-pharyngeal fold (Pl. 27, fig. 3), then forwards in it, ventral to the stylo-pharyngeus, to the soft palate (Pl. 27, fig. 2). In the soft palate many fibres spread forwards and inwards towards the median raphe; the most lateral fibres are attached to the hinder wall of the medial end of the Eustachian tube (Pl. 27, fig. 1). No levator veli palatini is developed from the pharyngo-palatinus.

In stage A (Pl. 29, fig. 17) of Dasyurus a stylo-pharyngeus

¹ I adopt the interpretation of Dubois in regard to the morphology of the cornua of the thyroid ala (vide p. 414, 415).
muscle is present; it is attached laterally to the stylohyale and spreads round the pharynx to the dorsal middle line, some of the fibres pass towards the epithelium of the lateral wall of the pharynx. Behind the stylopharyngeus is a sheet of mesoblast cells (Pl. 30, figs. 18-21), not yet muscle-cells, with long axes in the transverse plane, arching over the pharynx and attached laterally to the first branchial cornu and upper edge of the thyroid cartilage—this is the primordium of the posterior pharyngeal constrictor and palato-palatinus. It develops into muscle-cells in stage B. In stage C (Pl. 30, fig. 25) muscle fibres, with longitudinal long-axis, can be seen extending forwards from the primordium of the posterior pharyngeal constrictor and pharyngo-palatinus, past the stylopharyngeus, towards the soft palate, but not reaching it in either this stage or stage D (Pl. 32, figs. 28-31). These longitudinal fibres are the pharyngo-palatinus, and transverse sections show that, behind the stylo-pharyngeus, they lie internal to the transverse fibres of the posterior constrictor.

In stage D embryonic muscle-cells can be seen surrounding the oesophagus.

In stage E the front end of the pharyngo-palatinus muscle has reached the soft palate (Pl. 32, fig. 34); some of its fibres diverge laterally towards the floor of the Eustachian tube, forming a pars salpingia. The hind end of the muscle has extended a little further back.

In stage H (Pl. 33, fig. 41) there is a well-marked posterior pharyngeal constrictor round the hinder part of the pharynx; it is attached laterally to the posterior cornu of the thyroid cartilage, and is continuous posteriorly with the constrictor of the oesophagus. It forms a continuous sheet up to the stylopharyngeus muscle, with the constrictor fibres of which it mingles. The pharyngo-palatinus muscle lies between the wall of the pharynx and the posterior constrictor; some of its fibres penetrate the palato-pharyngeal fold; it ends posteriorly between the wall of the pharynx and the pharyngeal constrictor; it extends forwards to the soft palate and Eustachian tube (Pl. 33, fig. 40). No superior pharyngeal
constrictor is formed by forward extension of the posterior pharyngeal constrictor, nor is a levator veli palatini separated from the longitudinal pharyngo-palatal sheet. Longitudinal fibres are developed from the anterior part of the oesophageal constrictor and are attached anteriorly to the cricoid (Pl. 33, fig. 42).

In stage J some of the fibres of the posterior pharyngeal constrictor become separated from the others and form a middle constrictor, whilst the main mass forms the inferior constrictor. The hind end of the pharyngo-palatinus does not extend quite so far posteriorly as the median fold in which the palato-pharyngeal folds end.

The primordium of the pharyngeal constrictors, crico-thyroid, pharyngo-palatinus, and levator veli palatini of the pig is first visible in 12½ mm. embryos as a band of aggregated mesoblast cells latero-dorsal to the pharynx immediately outside the epithelium, in the second branchial segment. In 14 mm. embryos a similar primordium—that of the stylo-pharyngeus—appears in the first branchial segment. In 17 mm. embryos the primordium developed in the second branchial segment has spread forwards past the primordium of the stylo-pharyngeus into the hyoid segment, forming the longitudinal pharyngo-palatinus, whilst the part behind is the posterior pharyngeal constrictor (Pl. 37, figs. 64–68). The latter, in 18 mm. embryos, is attached laterally to the first branchial bar and thyroid cartilage, and has grown ventrally outside the posterior extremity of the thyroid cartilage (Pl. 38, fig. 69). This downgrowth has extended further down in 21 mm. embryos and forms the crico-thyroid muscle (Pl. 38, fig. 72). The stylo-pharyngeus gains an attachment to the stylohyale in 24 mm. embryos and passes towards the lateral wall of the pharynx, but does not develop any constrictor fibres over the pharynx (Pl. 39, fig. 76). The pharyngo-palatinus extends in 21 mm. embryos as far forwards as the soft palate and medial end.

1 I do not give any figures of the stages, as they are similar to those of the rabbit which I have previously described.
of the Eustachian tube, and it is penetrated by fibres of the stylo-pharyngeus passing towards the lateral wall of the pharynx (Pls. 38, 39, figs. 74–76). In 24 mm. embryos the hind end of the pharyngo-palatinus has extended backwards underneath the posterior pharyngeal constrictor, and ends over the median dorsal pouch (Pl. 39, fig. 77). In 32 mm. embryos the tensor veli palatini separates from the dorsal surface of the anterior end of the pharyngo-palatinus (Pl. 38, fig. 74). In 38 mm. embryos the anterior edge of the posterior pharyngeal constrictor, which hitherto had not extended further forwards than the stylo-pharyngeus, extends uninterruptedly forwards, covering in the longitudinal fibres of the pharyngo-palatinus, and forming the superior pharyngeal constrictor. The part of the posterior pharyngeal constrictor behind the stylo-pharyngeus separates into the constrictor medius arising from the first branchial bar and the constrictor inferior arising from the thyroid and cricoid cartilages.

The above-described phenomena show that the primitive condition of the stylo-pharyngeus is that of an anterior constrictor of the pharynx, developed in the first branchial segment and having a lateral attachment to the stylohyale. From this origin the fibres spread over the anterior part of the pharynx and naso-pharynx. This is present in Echidna.

In Marsupials additional fibres—dilatator fibres—passing towards the lateral wall of the pharynx are developed.

In the pig and rabbit, and in Eutheria generally (vide description by Rückert), the stylo-pharyngeus has no constrictor fibres, only those passing towards the lateral wall of the pharynx are developed.

The constrictor fibres of the stylo-pharyngeus—in Monotremes and Marsupials—are dorsal to the pharyngo-palatinus; those passing towards the lateral wall of the pharynx—in Marsupials and Eutheria—penetrate the pharyngo-palatinus.

The primordium of the posterior pharyngeal constrictor is developed in the mesoblast immediately surrounding the pharyngeal epithelium, behind the stylo-pharyngeus. Its
The primitive condition is that of a sheet of transverse fibres arching over the pharynx, with lateral attachments to the upper edge of the thyroid cartilage and first branchial bar, and in Eutheria also to the stylohyale.

The pharyngo-palatinus is developed from the posterior pharyngeal constrictor as a direct forward extension. This longitudinal sheet extends forwards, and also backwards internal to the pharyngeal constrictor. In Echidna its hind end extends only a little distance behind the anterior edge of the posterior constrictor; in Marsupials (Dasyurus, Didelphys, and Phascolarctus), pig, and rabbit to a greater extent. In the pig it ends on the dorsal surface of the dorsal pharyngeal pouch.

The front end of the pharyngo-palatinus grows forward past the stylo-pharyngens to the soft palate and medial end of the Eustachian tube.

A levator veli palatini is not formed in Echidna, Dasyurus viverrinus, Didelphys aurita, and Phascolarctus. Nor did Kostanecki describe this muscle in Didelphys cancrivora, D. azarae, D. virginiana, Dasyurus macrurus, D. ursinus, Perameles, Phalangista vulpina, Macropus spec. On the other hand, Symington stated that there is one in Macropus bennettii.

In the pig and rabbit the levator veli palatini is developed from the anterior end of the pharyngo-palatinus.

The relationship of the pharyngo-palatinus muscle to the palato-pharyngeal fold is not constant. In Echidna both muscle and fold are short, the muscle lies in the fold, and extends a little way behind its hind end (Pl. 27, figs. 3–5). In Dasyurus the fold is well marked at birth, but the muscle does not extend into it until stage H, and even in stage J does not penetrate to its free edge. This is generally true of Marsupials, as described by Symington. The folds extend the whole length of the pharynx and meet in a mid-dorsal fold, but the muscle does not extend so far back as does the fold. In the rabbit and pig the folds are not nearly so marked as in Dasyurus. In the rabbit the folds extend the
whole length of the pharynx and meet in a mid-dorsal fold; the muscle lies in the fold, but does not extend back to its hind end. In the pig, as in Echidna, the fold does not extend further back than the first branchial segment, the muscle lies in it and extends back beyond, ending over the median dorsal pouch.

Of these conditions, that of Echidna appears to be the primitive one; those found in other Mammals investigated are secondary developments.

In Echidna, Dasyurus, Didelphys, and Phascolarctus, the posterior pharyngeal constrictor retains its position relative to the constrictor fibres of the stylo-pharyngeus. In the pig and rabbit—where no constrictor fibres of the stylo-pharyngeus are formed—the anterior edge of the posterior pharyngeal constrictor extends forwards in front of the stylo-pharyngeus at a late stage of development, and forms the superior constrictor. The part behind the stylo-pharyngeus separates into the middle and inferior constrictors.

Konstanecki, who investigated adult forms only, came to the conclusion that the levator veli palatini and pars palato-salpingo-pharyngea are "Abkömmlinge des M. palato-pharyngeus und, dar dieser selbst ein Derivat des Constrictor superior ist, würden sie sich mittelbar von dem letzteren, also von der Ringsmuskulatur des Pharynx herleiten lassen."

The embryological phenomena as stated above suggest some modification of this opinion. The primitive condition appears to have been an anterior constrictor s. stylo-pharyngeus, and a posterior constrictor. From the posterior constrictor was developed a longitudinal stratum—the pharyngo-palatinus—which extended forwards to the soft palate. In Macropus bennettii (Symington) and in Eutheria the levator veli palatini was developed from the anterior end of the pharyngo-palatinus. In Marsupials dilatator fibres, passing towards the lateral wall of the pharynx, were additionally developed in the anterior constrictor s. stylo-pharyngeus. In Eutheria no constrictor fibres, but only dilatator fibres, were developed in the stylo-pharyngeus,
and in relation to this, the posterior constrictor extended forwards forming anteriorly a superior constrictor—which takes the place of, but is not homologous with, the constrictor fibres of the stylo-pharyngeus of Echidna and Marsupials.

These phenomena are at variance with the statements of Futamura that in man the M. levator veli palatini and M. uvulae are developed from a "Muskelblastemgewebe" which "deutlichen Zusammenhang mit dem tiefen Teil der Platysmaanlage erkennen lässt," and that in the pig they are derived from "Gewebe des Platysma colli das von der vorderen Seite des Oberkieferfortzès nach seiner medialen Seite zieht." On the other hand they offer an explanation of the experiments of Beevor and Horsley, who found that in Macacus sinicus movements of the palate occurred in intracranial stimulation of the vago-accessorius, and did not occur on intracranial stimulation of the N. facialis. Dr. Elizabeth Cords has traced a nerve from the pharyngeal plexus to the levator veli palatini, in man; and the motor impulses probably pass by this route.

Cricothyroid Muscle.

Miss Walker described a crico-thyroides muscle in both Monotremes, innervated in Echidna by a branch of the recurrent laryngeal nerve. This was confirmed by Göppert, who termed the muscle "thyreo-cricoidens," and denied its homology with the crico-thyroides muscle of Eutheria. He stated that it belongs to the group of the inner (intrinsic) laryngeal muscles. The evidence given in favour of this derivation does not appear very convincing.

No cricoid-thyroid muscle is developed in Dasyurus, nor is one present in 10 mm. specimens of Didelphys aurita, or 15 mm. specimens of Phascolarctus. Symington found a small crico-thyroides posticus in pouch specimens of Macropus, but not in any adult Marsupials. Henkel stated that the muscle is absent in Macropus rufus, robustus, and cervinus, Phascolomys platiceps, Petrogale
MUSCLES OF MAMMALS.

lateralis, and Onychogalea frenata. The non-development or atrophy of the muscle in Marsupials is related to the fusion of the cricoid with the thyroid cartilage.

In the pig the crico-thyroid is formed by a downgrowth of the posterior pharyngeal constrictor lateral to the hind end of the thyroid cartilage.

HYPOBRANCHIAL CRANIAL MUSCLES.

In Dasyurus only one hypobranchial cranial muscle—the branchio-hyoideus— is developed (Pl. 33, fig. 43). It is also present in Echidna (Fewkes) (Pl. 27, figs. 4, 5), Ornithorhynchus (Dubois), Didelphys, Trichosurus (Pl. 34, fig. 50), Phascolarctus, rabbit, pig, and many other Eutheria. It passes from the first branchial bar downwards and forwards to the ventral end of the stylohyal, is innervated by the ninth nerve, and in the pig is developed from the ventral portion of the first branchial muscle-plate.² Fewkes also described in Echidna, but did not figure, a second muscle passing from the first branchial bar forwards and outwards to the stylohyale, under the name stylothyroideus. It was not described by Coues, Dubois, Miss Walker, Fräulein Westling, or Göppert, but is present in both Monotremes (vide Pl. 27, figs. 3–5, and Pl. 28, figs. 9, 10 from a 25 mm. specimen of Echidna). In a 8·5 mm. specimen of Ornithorhynchus it lies just outside and is not fully separated from the branchio-hyoideus.³ I have called it the branchio-hyoideus dorsalis, as the name proposed by Fewkes is not very suitable.

Miss Walker described a muscle—the "thyro-hyoid"—in Echidna and Ornithorhynchus, passing between the first thyroid (second branchial) and the first branchial bar. In Echidna “its fibres are very short, and are to a great extent

1 S. cerato-hyoidens, hyothyroideus (Fewkes), interhyoideus (Dubois).
3 Ibid., vol. 59, part 4 (1914), fig. 33. The muscle is not named in the figure as I did not then know what it was.
replaced by ligament,” but in Ornithorhynchus is better developed. Göppert, who did not refer to Miss Walker’s statements, said that the interval between these bars is occupied by dense connective tissue. I found this to be the case in a 25 mm. specimen of Echidna (vide Pl. 28, figs. 9 and 10), and in an adult specimen of Ornithorhynchus, and in a 8.5 mm. embryo of the latter did not see any muscle-primordium between the first thyroid (second branchial) and first branchial bars. The muscle is therefore variable and its homology doubtful.

Dubois described an interthyroideus muscle in both Monotremes, passing from the cornu laterale to the cornu posticum of the thyroid ala, innervated by the superior laryngeal nerve, and serially homologous with the “interhyoideus” s. branchio-hyoideus between the hyoid and first branchial bars. The existence of this muscle was confirmed by Miss Walker and by Göppert (Pls. 27, 28, figs. 7, 9, 10).

The upper end of the first branchial bar in Echidna is continuous with the thyroid ala, which ends in two posterior cornua. The dorsal one enters the valve at the junction of the pharynx and oesophagus (Göppert), and the ventral one ends free (see figures by Dubois, Miss Walker, and Göppert, and drawings (Pl. 28, figs. 9, 10) of a model of a 25 mm. Echidna).

Dubois described the ventral cornu as the cornu laterale, and the second thyroid (third branchial) bar as the cornu posticum, and regarded the former as the posterior end of the first thyroid (second branchial) bar. Göppert, on the other hand, regarded the dorsal process of the thyroid ala as the upper end of the first thyroid (second branchial) bar, and its ventral process as a “processus muscularis,” but did not offer any embryological evidence for this view.

In a 8.5 mm. specimen of Ornithorhynchus—in which the upper ends of the first branchial and first thyroid (second branchial) bars were unconnected—I found the primordium of the “interthyroideus” muscle passing between the first thyroid (second branchial) and second thyroid (third
branchial) bars. This proves the correctness of the theory of Dubois. The dorsal cornu of the thyroid ala is thus a backward prolongation of the upper end of the first branchial bar, the middle portion of which has fused with that of the first thyroid (second branchial) to form a thyroid ala, and the ventral cornu is the posterior end of the first thyroid (second branchial) bar. The "interthyroideus" muscle thus passes between the first thyroid (second branchial) and the second thyroid (third branchial) bars.

The view of Dubois also harmonises with the place of entry of the superior laryngeal nerve into the larynx—between the first branchial and first thyroid bars, i.e. serially homologous with the ninth nerve between the hyoid and first branchial bars. (In Marsupials and Eutheria—vide Dubois and Henkel—the place of entry of the superior laryngeal nerve is variable.)

The branch of the superior laryngeal nerve to the interthyroideus muscle is given off just after the nerve passes between the first branchial and first thyroid cornua of the thyroid ala, and passes downwards and backwards internal to the first thyroid cornu (vide figure of Göppert). This muscle, theoretically, should be innervated by a second thyroid (third branchial) branch of the vagus, and Dubois took this view for the whole of the superior laryngeal nerve. But Göppert showed that in Echidna embryos the main stem of the superior laryngeal nerve lies just posterior to the third gill-cleft and fourth arterial arch, and must therefore be regarded as the nerve of the first thyroid (second branchial) arch, and that no branch corresponding to the second thyroid (third branchial) arch, homologous with the atrophying branch found by Froriep in calf embryos, was given off by the vagus.

It may be concluded that the superior laryngeal is the nerve to the first thyroid (second branchial) arch; that its motor branch to the "interthyroideus" is a second thyroid (third branchial) element which has been taken up into the superior laryngeal nerve in place of being a separate branch of the vagus.

MUSCLES OF MAMMALS. 415

VOL. 61, PART 4.—NEW SERIES. 28
These hypo-branchial cranial muscles are homologous with the Mm. interarcuales ventrales of Amphibia. The foremost, interarcualis ventralis i, passes from the first branchial bar to the hyoid bar, is represented in Monotremes by the branchio-hyoideus and branchio-hyoideus dorsalis, in Marsupials and many Eutheria by the branchio-hyoideus. Possibly the variable thyro-hyoideus of Miss Walker represents interarcualis ventralis ii. Interarcualis ventralis iii. passes from the second thyroid (third branchial) to the first thyroid (second branchial) bar, and is present only in Monotremes. Interarcualis ventralis i is innervated by the ninth and interarcualis ventralis iii by a branch of the superior laryngeal nerve.

In Sauropsida only interarcualis ventralis i is present—the branchio-hyoideus (Sphenodon) or branchio-mandibularis (other Sauropsida)—and has a secondary innervation from the hypoglossal nerve.

**Hypobranchial Spinal Muscles.**

Monotremes. The hypobranchial spinal muscles of Echidna were described by Fewkes, Führinger, Leche, Toldt, and myself. Dissection of an adult Ornithorhynchus showed the following: M. onio-hyoideus (employing the usual nomenclatures, see below) arises just within the thorax from the outer end of the clavicle and adjacent part of the scapula. It separates into a superficial and a deep layer. The former\(^1\) passes forwards and slightly inwards, ventral to the hypobranchial bars, to which it has no attachments, and is inserted into the longitudinal raphé a little in front of the hyoid bar. The median edges of the two muscles are in contact in the anterior third of their extent. The deep layer\(^2\) is very thin and not so broad as the superficial; it passes forwards and is inserted into the basithyroid and median ends of the first and second branchial bars. The

\(^1\)Coues did not give its origin, and stated that it is inserted to the os hyoidei. I found the same insertion as Schulman.

\(^2\)Not previously described.
M. sterno-thyroideus arises from the dorsal surface of the manubrium sterni; it passes forwards and is inserted into the ventral surfaces of the third and distal extremity of the second branchial bars. The median edges are fused in the cervical part of their extent.

There are no tendinous intersections in the sterno-thyroid and omo-hyoid muscles. These muscles are innervated by the descending branch of the twelfth nerve, with which—as shown by Fürbringer—the first and second cervical nerves anastomose.

The M. genio-hyoideus consists of a median and a lateral portion. The former arises from the distal extremity of the second branchial bar and passes forwards and slightly inwards, and is inserted into the median raphe anterior to the superficial portion of the omo-hyoid muscle. The lateral portion blends posteriorly with the superficial fibres of the M. laryngo-glossus, from which it diverges inwards and is inserted into the median raphe just in front of the superficial portion. The ascending branch of the twelfth nerve passes into the tongue between the median and lateral portions.

There is no muscle taking origin from the symphysis of the jaws and passing into the tongue which could strictly be called a M. genio-glossus. It is probably represented by a well-marked lingualis muscle which takes origin from the median raphe and passes vertically upwards into the tongue internal to the M. laryngo-glossus. It has no direct attachment to the hyoid bar. It is apparently the muscle described as the M. genio-hyo-glossus by Coues. It is homologous with the M. genio-glossus of Echidna.

1 Described by Coues as an unseparated sterno-hyoid and sterno-thyroid. I did not see any fibres passing to the hyoid bone, or continuous with the laryngo-glossus, as described by him.

2 According to Coues and Toldt the M. genio-glossus reaches the lower jaw. Schulman mentions the same insertion as I found.

3 Coues states that “The genio-hyo-glossus forms as usual a vertical plane in apposition with its fellow in the middle line; behind it has the ordinary attachment to the os hyoides and is considerably blended with the hyo-glossus; its anterior connections are rather with the genio-hyoid than with the jaw itself.”
In a 8.5 mm. embryo of Ornithorhynchus the anterior end of the M. genio-hyoideus reaches Meckel's cartilage, so that there is a secondary loss of the attachments of the Mm. genio-hyoideus and genio-glossus to the jaw.

The M. laryngo-glossus takes origin from the distal extremity of the second branchial bar and passes forward; its origin is small, it attains its maximum size at the level of the hyoid bar, to which it has no attachment, and then tapers as its fibres pass into the tongue. Its anterior end joins its fellow and passes to the tip of the tongue.

Thyro-hyoid, stylo-glossus, and palato-glossus muscles are not developed. The genio-hyoid, laryngo-glossus, and lingualis muscles are innervated by the ascending branch of the twelfth nerve.

The homologies between the hypobranchial spinal muscles of Echidna and Ornithorhynchus with those of other Mammals are doubtful owing to ignorance of their development. In Dasyurus, however (vide p. 420), the posthyoid longitudinal strip separates into three muscles—from within outwards, the sterno-thyroid, sterno-hyoid, and omo-hyoid, and subsequently the anterior part of the sterno-hyoid shifts inwards and lies ventral to the sterno-thyroid. The sterno-glossus of Echidna is formed of two constituents—a posterior part, homologous with the lateral portion of the sterno-thyroid of Ornithorhynchus, and an anterior part, homologous with a separated portion of the laryngo-glossus. The "omo-hyoid" muscles of the Ornithorhynchus and Echidna are homologous; in each case the muscle arises lateral to the sterno-thyroid, passes forwards and inwards so as to be ventral to it, and separates into two portions, of which the deep is inserted into the laryngeal cartilages and the superficial passes forwards to the median longitudinal septum.

Fürbringer was of opinion that the posterior part of the sterno-glossus of Echidna was homologous with the sterno-hyoid of other Mammals, and, like Coues, he designated the muscles just described as "omo-hyoid." In this he was
followed by Schulman, Bijvoet, and Toldt. Comparison, however, with Dasyurus suggests that their "omo-hyoid" is the sterno-hyoid, that a true omo-hyoid is not formed, and that the separation of the posterior part of the sterno-glossus of Echidna from the sterno-thyroid is a peculiarity of that animal.

The genio-hyoid of Echidna arises from the first branchial and second branchial (first thyroid) cartilages, that of Ornithorhynchus from the second branchial (first thyroid) only. The laryngo-glossus arises from the second branchial (first thyroid) bar in both animals. As in 8·5 mm. embryo of Ornithorhynchus the adjacent ends of the anterior and posterior portions of the primordium of the hypobranchial spinal muscles lie at the level of the first branchial bar, the more posterior attachments of the genio-hyoid and laryngo-glossus in the adult are due to a subsequent backward growth. Owing to this and the forward growth of the superficial part of the sterno-thyroid muscles, there is a partial overlapping of the anterior and posterior portions of the hypobranchial spinal muscles.

The condition of the hypobranchial spinal muscles of Dasyurus in stage iv (a little before birth) differs very slightly from that in stage A (just born). In stage A (Pls. 29, 30, figs. 15–24) they consist of intrinsic lingual muscle-fibres, genio-glossus, genio-hyoid, stylo-glossus, hyo-glossus, sterno-thyroid, sterno-hyoid, and omo-hyoid muscles. The intrinsic lingual muscle-fibres consist of well-marked transversalis and verticalis fibres. The genio-hyoid and hyo-glossus are attached posteriorly to the first branchial bar, and the stylo-glossus to the stylohyale. The sterno-hyoid and sterno-thyroid muscles form a common flat band, which arises from the dorsal surface of the sternum, as low down as the second rib, and passes forwards, with its inner edge close to that of its fellow; the median fibres are attached to the membrane uniting the two thyroid alae, whilst the more lateral fibres pass on and are attached to the first branchial bar. The omo-hyoid arises from the scapula and passes forward,
converging to the sterno-hyoid, and is inserted into the first branchial bar. There is no thyro-hyoid muscle.

In the immediately preceding stage iv the only difference is that the sternum is not yet formed, and (unseparated) sterno-thyroid and sterno-hyoid muscles are attached posteriorly to the sternal plate connecting the ventral ends of the first and second ribs.

In stage B the median united sterno-thyroid muscles have shifted a little upwards and lie dorsal to the medial edges of the sterno-hyoid muscles. In stage C (Pls. 30, 31, figs. 25, 28) the adjacent ends of the genio-hyoid, sterno-hyoid, and omo-hyoid muscles have lost their attachment to the first branchial bar and are united together by a short tendon. The sterno-thyroid muscles are inserted into the thyroid cartilage. In stage D (Pl. 31, figs. 32, 33) the thyro-hyoid is beginning to be proliferated from the medio-dorsal surface of the anterior part of the omo-hyoid. It becomes a separate muscle by stage F, though with smaller fibres than the omo-hyoid. It arises from the posterior cornu of the thyroid cartilage and is inserted into the common tendon of the genio-hyoid and sterno-hyoid. In stage E, and the process is still more marked by stage J (Pl. 33, figs. 43, 44), the outer fibres of the genio-hyoid extend a little more posteriorly than do the inner fibres, so that the inner fibres are connected with the sterno-hyoid and thyro-hyoid, and the outer fibres, which are connected with the omo-hyoid, overlap the anterior end of the sterno-hyoid.

The primordium of the hypobranchial spinal muscles posterior to the first branchial bar thus forms in Dasyurus a broad strip which separates into three muscles—from within outwards, the sterno-thyroid, sterno-hyoid, and omo-hyoid. The two sterno-thyroids subsequently lie dorsal to the sterno-hyoids. The thyro-hyoid is proliferated from the anterior portion of the omo-hyoid. The sterno-hyoid and omo-hyoid are at first attached to the first branchial bar, then lose this insertion, and become united to the posterior end of the genio-hyoid by a tendon to which also the thyro-hyoid becomes
attached. The union of the genio-hyoid with the sterno-hyoid, thyro-hyoid, and omo-hyoid is thus a secondary condition.

In Didelphys aurita (10 and 12 mm. pouch specimens) the sterno-hyoid and omo-hyoid muscles are inserted into a tendon from which arises the genio-hyoid. This tendon is situated dorsal to the transverse tendon connecting together the hyoid ventral constrictor s. posterior digastricus. The thyro-hyoid is inserted into the hinder edge of the lower end of the first branchial bar and the sterno-thyroid into the thyroid cartilage. The stylo-glossus arises from the stylohyale, and the hyo-glossus from the first branchial bar, by an extensive dorso-ventral origin. The posterior end of the anterior digastric is attached to the tendon of the hyoid ventral constrictor.

In Phascolarctus (15 and 25 mm. pouch specimens) the sterno-hyoid and omo-hyoid muscles are inserted into the transverse tendon of the hyoid-ventral constrictors. The thyro-hyoid is inserted into the basibranchial, and the sterno-thyroid into the thyroid cartilage. The stylo-glossus arises from the stylohyale; the hyo-glossus arises by two heads from the tendon of the hyoid ventral constrictor—an inner and an outer, the former of which, passing forwards and outwards to join the outer head, forms a band of muscle lying dorsal to the genio-hyoid, much as do the inner fibres of the hyo-glossus of Didelphys. The posterior end of the genio-hyoid is attached to the hyoid ventral constrictor. This account of Phascolarctus confirms that given by Young in most particulars.

The primary condition of the hypobranchial spinal muscles of Marsupials is thus one in which the adjacent ends of the genio-hyoid, sterno-hyoid, and omo-hyoid are attached to the first branchial bar. This may persist as e.g. in Cheironectes. Various conditions may ensue in which these attachments are lost and the muscles become connected together by tendon, but no uniform type of such secondary connection is present in these three Marsupials. In particular, no long retractor of the lower jaw, of constant elements, is formed.
The primordium of the hypobranchial spinal muscles in the pig forms in 11 and 12½ mm. stages an undivided strip of cells extending from the mandibular segment backwards in the hyoid and branchial segments into the neck. In 13 mm. embryos the primordia of the hyoid and first branchial bars are visible, but it is not until the stage of 17 mm. is reached that the muscle-primordium divides into anterior and posterior portions at the level of the first branchial bar. Previous to this, however, in the 14 mm. stage a longitudinal division begins at the hind end of the posterior portion; this extends forwards and in the 17 mm. stage separates the (lateral) omo-hyoid from the (median) primordium of the sterno-hyoid and sterno-thyroid; in the branchial region the muscle-strip is as yet undivided (Pl. 37, figs. 64–68). In 21 mm. embryos the thyro-hyoid is separated from the dorsal portion of the anterior part of the primordium of the sterno-hyoid and sterno-thyroid (Pl. 38, figs. 71, 72). In the 24 mm. stage the sterno-hyoid and sterno-thyroid have become separate.

The method of formation of the thyro-hyoid is thus not identical in Dasyurus and the pig—in the former it is developed from the anterior part of the omo-hyoid; in the latter from the anterior part of the primordium of the sterno-hyoid and sterno-thyroid, i.e. in the one case from the lateral, in the other from the medial of the two strips into which the primordium of the hypobranchial spinal muscles separates behind the first branchial bar.

The palato-glossus muscle of Dasyurus begins to develop in stage D by the upgrowth of fibres from the dorso-external edge of the stylo-glossus muscle into the soft palate (Pl. 31, fig. 29). It is better marked in stage F (Pl. 32, fig. 39) and stage H (Pl. 33, fig. 40), though still connected with the stylo-glossus. It has become separate in stage J.

The palato-glossus of the pig was mentioned by Kallius, but he did not describe its development. It is formed in 32 mm. embryos by an upgrowth into the soft palate from the dorso-external edge of the stylo-glossus (Pl. 38, fig. 73).
These phenomena show that in Dasyurus and the pig the palato-glossus is a derivative of the stylo-glossus, and not one of the pharyngeal group of muscles.

It is stated in "Quain" (Ed. Symington) and in "Cunningham" (Ed. Robinson) that the palato-glossus of man is innervated by the pharyngeal plexus. I found, however, in one subject that the muscle was innervated by a twig from the distal of the two branches of the hypoglossal nerve passing to the stylo-glossus. Further, my friend Dr. Fisher found in another subject that the stylo-glossus was supplied by four branches of the hypoglossal nerve, the two distal of which formed a loop from which twigs passed to the palato-glossus. The developmental phenomena and the innervation thus agree.

Comparison of the Cranial Muscles in Mammals.

The embryological history and adult condition of the muscles of the head in Monotremes, Marsupials, and Eutheria suggest the following conclusions:

Adult Monotremes are more primitive than Marsupials and Eutheria in the following particulars:

1. The presence of a pterygo-tympanicus (homologue of the tensor veli palatini) in Ornithorhynchus and in the embryo of Echidna—also in some Edentates. This condition is not fully developed during the pouch stage of Dasyurus.

2. The existence of a depressor mandibulæ anterior (homologue of the anterior digastric), with no attachment to the hyoid ventral constrictor, so that no digastricus mandibulæ is formed. This condition is present in the adult stage of Myrmecobius and in the pouch stage of Dasyurus.

3. The existence of a stapedius in a levator hyoidei form. This condition is present in the pouch stage of Dasyurus.

4. The existence of a hyoid ventral constrictor arising from the stylohyale. This condition is present in the pouch stage of Dasyurus and in the adult stage of Manis pentadactyla.
(5) The existence of relatively undifferentiated facial muscles.

(6) The existence of an Interthyroides s. Interarcualis ventralis iii. This is associated with the presence of a second thyroid (third branchial) bar, as a separate structure not fused with the first thyroid bar.

(7) The existence of a stylo-pharyngeus as an anterior constrictor of the pharynx.

(8) The absence of a stylo-glossus, palato-glossus, and thyro-hyoid.

On the other hand, some of the cranial muscles of Monotremes undergo modifications:

(1) The internal pterygoid atrophies.

(2) The pterygo-tympanicus atrophies in Echidna.

(3) The intermandibularis loses its attachments to the jaw in Echidna.

(4) The detrahens mandibulae and branchio-hyoideus dorsalis are probably secondary formations. Neither of these muscles has any representative in non-Mammals, Marsupials, or Eutheria.

(5) According to Göppert the crico-thyroides is absent and its place is taken by the thyreo-cricoides, which is innervated by the recurrent laryngeal nerve, and is developed from the intrinsic laryngeal musculature. The embryological evidence in favour of this last statement is not, however, convincing.

(6) In both Monotremes there is a secondary overlapping of the adjacent ends of the anterior and posterior elements of the hypobranchial spinal muscles—in Echidna a sternoglossus is developed and in Ornithorhynchus the genio-hyoid and genio-glossus lose their attachment to the jaw.

In Monotremes and Marsupials the dilatator laryngis separates into the kerato-crico-arytenoides and crico-arytenoides posticus internus. This does not occur in Eutheria, and is, perhaps, a secondary feature of both Monotremes and Marsupials.

No one of the cranial muscles of Marsupials is more
primitive than in Monotremes if, as above suggested, the
detrahens mandibulae and branchio-hyoideus dorsalis are
secondary formations.

Secondary changes occur in the attachments of the adjacent
ends of the anterior and posterior elements of the hypo-
branchial spinal muscles in Monotremes and some Marsupials,
but such changes are very different in character and have
been separately acquired.

Marsupials are more primitive than Eutheria in the follow-
ing particulars: (1) The presence of constrictor as well as
dilator fibres in the stylo-pharyngeus (in Monotremes only
constrictor fibres are present); (2) the absence of a superior
pharyngeal constrictor derived from the posterior constrictor
(also absent in Monotremes); (3) the absence of a levator
veli palatini, except in Macropus hennetti (Symington),
(also absent in Monotremes); (4) the presence of a second
thyroid (third branchial) bar (also present in Monotremes in
a more primitive condition).

In Myrmecobius the depressor mandibulae anterior and
hyoid ventral constrictor remain separate, as in Monotremes.
In all other Marsupials the hind end (morphologically, the
inner end) of the depressor mandibulae anterior fuses with the
hyoid ventral constrictor to form a digastricus.

In Eutheria, other than Edentates, the hyoid ventral con-
strictor divides into dorsal and ventral portions, which
partially lose their primary relative positions owing to up-
growth of the upper end of the ventral portion (stylohyoideus)
so that overlapping results. The digastricus is formed by
connection of the depressor mandibulae anterior with the
dorsal portion.

In Edentates, in general, the depressor mandibulae anterior
unites with (a portion or the whole of) the sternohyoideus to
form a sternomandibularis. The hyoid ventral constrictor
either remains single or divides into dorsal and ventral
portions which retain their relative positions. The lower end
of the undivided hyoid ventral constrictor, or of its lower
portion, has various relations to the sternomandibularis. A
digastricus of either the Marsupial or the Eutherian type is not developed.

Certain developmental changes which, on comparison with Monotremes, appear to be of importance in the phylogenetic history of the cranial muscles of Marsupials and Eutheria occur in the pouch stage of Dasyurus, but are omitted or slurred over in the development of the pig and rabbit. The majority of these are mentioned above in dealing with Monotremes. In addition there are (1) the existence at birth of two masticatory muscles only, a medial and a lateral; (2) after separation of the medial muscle into internal pterygoid, pterygo-tympanicus s. tensor veli palatini, and tensor tympani, there is a temporary origin of the tensor tympani from the (Mammalian) pterygoid bone. Neither of these conditions is preserved to the adult stage in any living Mammal. They and the others mentioned above are referable to the fact that Dasyurus is born at a very early stage of development, whereas the parallel stages in the pig and rabbit occur during intra-uterine life.

The pterygo-tympanicus retains more primitive conditions in some Edentates than in Marsupials.

I have in conclusion to express my thanks to Professor J. P. Hill for the loan of sections of Dasyurus and Trichosurus and for the opportunity of examining sections of an embryo of Ornithorhynchus; to Dr. Assheton for the loan of specimens of Echidna; and to J. M. Gillespie, Esq., for an adult specimen of Ornithorhynchus.

The expenses of this investigation and of the figures illustrating it have been defrayed by a grant from the Committee of the Bristol University Colston Society.

July 15th, 1914.

References.

MUSCLES OF MAMMALS.

Beevor, C., and Horley, V. (1888).—"Note on some of the Motor Functions of Certain Cranial Nerves (Fifth, Seventh, Ninth, Tenth, Eleventh, Twelfth) and on the First Three Cervical Nerves of the Monkey (Macacus sinicus)," 'Proc. Roy. Soc.'


Fürbringer, M. (1897).—"Uber die Spino-Occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie," 'Festschrift für Gegenbaur,' iii.


v. Luschk. (1871).—‘Der Kehlkopf des Menschen,’ Tübingen.


Möller (1902).—‘Beitrag zur Kenntniss der Kehlkopfmuskulatur,’” ‘Archiv f. Lary. u. Rhin.,’ Bd. xii.


Nicholas, A. (1894).—‘Recherches sur le développement de quelques éléments du larynx humain,’” ‘Bibliographie Anatomique,’ t. ii.

Rückert, J. (1882).—‘Der Pharynx als Sprach- und Schluckapparat,’” München.


Schulman, H. (1906).—‘Ueber die ventrale Facialismuskulatur einiger Säugethiere, besonders der Monotremen,’” ‘Festschr. f. Palmen.’


MUSCLES OF MAMMALS.

Walker, Mary L. (1889).—"On the Larynx and Hyoid of Monotremata," 'Studies from the Museum of Zoology in University College, Dundee,' No. iii.


EXPLANATION OF PLATES 27—39,
Illustrating Dr. F. H. Edgeworth's paper "On the Development and Morphology of the Pharyngeal, Laryngeal, and Hypobranchial Muscles of Mammals."

ABBREVIATIONS.

Omo-hyoideus muscle. pal. gloss. m. Palato-glossus muscle. pal. phary. plica. Palato-pharyngeal fold. phary. pal. m. Pharyngo-palatine muscle. post. branch. b. Post-branchial body. pri. of eric. cart. Primordium of cricoid cartilage. pri. of cons. asoph. m. Primordium of constrictor muscle of oesophagus. pri. of hypobr. sp. m. Primordium of hypobranchial spinal muscles. pri. of lary. m. Primordium of laryngeal muscles. pri. of post. phary. cons. m. Primordium of posterior pharyngeal constrictor muscle. pri. of thy. cart. Primordium of thyroid cartilage. recurrr. lary. n. Recurrent laryngeal nerve. sec. ary. plica. Secondary arytenoid fold. sternoh. m. Serno-hyoideus muscle. sternomast. m. Serno-mastoideus muscle. sternothy. m. Serno-thyroides muscle. stylogloss. m. Stylo-glossus muscle. stylohy. m. Stylo-hyoideus muscle. stylophary. m. Stylo-pharyngeus muscle. sup. cons. m. Superior constrictor muscle of pharynx. sup. lary. n. Superior laryngeal nerve. symp. n. Sympathetic nerve. tend. gen. hy. m. to omohy. m. Tendon passing from genio-hyoideus to omo-hyoideus. tend. gen. hy. m. to sternothy. m. Tendon passing from genio-hyoideus to sterno-hyoideus. tend. hyoid. vent. cons. m. Tendon connecting the two halves of the hyoid ventral constrictor muscle. thy. gl. Thyroid gland. thyro. eric. m. Thyreo-ericoid muscle (in Echidna). thyroid cart. Thyroid cartilage. thyrohy. m. Thyro-hyoideus muscle. 1st thyroid cornu. First thyroid cornu of thyroid ala (in Echidna). trach. ring. Tracheal ring. vent. aorta. Ventral aorta. Roman numerals. Cranial nerves.

Echidna, figs. 1-10.

Greatest length 25 mm. (stage 50 of Semon); figs. 1-8, transverse sections; No. 1 is the most anterior; figs. 9 and 10, sketches of a model of the hyoid, first branchial, thyroid, and cricoid cartilages; fig. 9 shows the ventral aspect, fig. 10 the lateral.

Dasyurus, figs. 11-46.

Stage A (embryo C '01; greatest length 4·3 mm.): fig. 11, slide 1, row 5, number 15; fig. 12, s. 2, t. 1, n. 3; fig. 11 is the more dorsal. The right side of the sections is a little more dorsal than the left.

Stage iv ('01; greatest length 4·7 mm.): fig. 13, s. 2, t. 3, n. 8; the right side of the section is a little anterior to the left side, and the upper part is posterior to the lower. Fig. 14, sagittal section, s. 5, r. 1, n. 11.

Stage A (just born; greatest length 5·5 mm., head length 2·5 mm.): fig. 15, s. 1, r. 7, n. 21; fig. 16, s. 1, r. 8, n. 9; fig. 17, s. 1, r. 8, n. 18; fig. 18, s. 1, r. 9, n. 2; fig. 19, s. 1, r. 9, n. 7; fig. 20, s. 1, r. 9, n. 11; fig. 21, s. 1, r. 9, n. 17; fig. 22, s. 2, t. 1, n. 6; fig. 23, s. 2, t. 1, n. 21; fig. 24, s. 2, r. 1, n. 2.
Stage C (few hours old; greatest length 5.75-6 mm., head length 3 mm.): fig. 25, s. 2, r. 2, n. 8; fig. 26, s. 2, r. 2, n. 12; fig. 27, s. 2, r. 3, n. 2; fig. 28, s. 2, r. 3, n. 7.

Stage D (26 hours old; greatest length 6 mm., head length 3.25 mm.): fig. 29, s. 1, r. 2, n. 14; fig. 30, s. 2, r. 2, n. 13; fig. 31, s. 2, r. 2, n. 14; fig. 32, s. 2, r. 3, n. 16; fig. 33, s. 2, r. 4, n. 2.

Stage E (5-6 days old; greatest length 8 mm., head length 4.5 mm.): fig. 34, s. 2, r. 8, n. 5; fig. 35, s. 2, r. 8, n. 20; fig. 36, s. 3, r. 1, n. 6; fig. 37, s. 3, r. 1, n. 10; fig. 38, s. 3, r. 2, n. 1. In fig. 38 the lower end of the section is broken away.

Stage F (about 7 days old; greatest length 8.5-9 mm., head length 5.5 mm.): fig. 39, s. 3, r. 1, n. 13.

Stage H (about 14 days old; greatest length 13.5 mm., head length 8.8-5 mm.): fig. 40, s. 6, r. 3, n. 5; fig. 41, s. 8, r. 2, n. 2; fig. 42, s. 8, r. 5, n. 3. In figs. 41 and 42 the left side of the sections is a little posterior to the right side.

Stage J (25 days old; greatest length 20 mm., head length 12.5 mm.): the plane of the sections is such that the upper part of the sections is anterior to the lower. Fig. 43, s. 14, r. 2, n. 7; fig. 44, s. 14, r. 3, n. 8; fig. 45, s. 15, r. 1, n. 5; fig. 46, s. 15, r. 3, n. 4. In fig. 46 the lower part of the section is broken away.

**Trichosurus vulpecula**, figs. 47-55.

Figs. 47-49.—Stage v (greatest length 6 mm. XI. '01): transverse sections; fig. 47 is the most anterior. Fig. 47, s. 4, r. 1, n. 3; fig. 48, s. 4, r. 2, n. 1; fig. 49, s. 4, r. 3, n. 2.

Figs. 50-52.—Stage viii b (greatest length 7.25 mm. XII. '02): Fig. 50 is the most anterior. The plane of the sections is from above downwards, nearly horizontal to the primordia of the thyroid cartilages. Fig. 50, s. 5, r. 1, n. 7; fig. 51, s. 5, r. 2, n. 1; fig. 52, s. 4, r. 3, n. 6.

Figs. 53 and 54.—Stage ix a (greatest length 8.5 mm.): sagittal sections; fig. 53 is the more lateral. Fig. 53, s. 4, r. 4, n. 2; fig. 54, s. 4, r. 4, n. 5.

Fig. 55.—Stage ix b (greatest length 8.5 mm.): the plane of the section is from above downwards and forwards, nearly horizontal to the primordia of the thyroid cartilages; s. 6, r. 4, n. 2.

**Phascolarctus** (greatest length 15 mm.) fig. 56.

Pig, figs. 57-78.

Figs. 57-59.—Transverse sections, embryo 8 mm. vertex-breech length; fig. 57 is the most anterior. The left side of the sections is a little anterior to the right side.

**VOL. 61, PART 4.—NEW SERIES.**
Figs. 60-63.—Transverse sections, embryo 11 mm. vertex-breech, length; fig. 60 is the most anterior.

Figs. 64-68.—Transverse sections, embryo 17 mm. vertex-breech length; fig. 64 is the most anterior.

Figs. 69-70.—Transverse sections, embryo 18 mm. vertex-breech length; fig. 69 is the more anterior.

Figs. 71-72.—Transverse sections, embryo 21 mm. vertex-breech length; fig. 71 is the more anterior. The right side of the sections is a little anterior to the left side.

Figs. 73-77.—Transverse sections, embryo 32 mm. vertex-breech length; fig. 73 is the most anterior.

Fig. 78.—Transverse section, embryo 38 mm. vertex-breech length.
Page 60

Pr. of lary. m.

Pr. of aorta arch.

Page 62

Pr. of cons. oesoph. m.

Pr. of lary. m.

Pr. of aorta arch.