

ZOOLOGY

ON THE CORRELATION BETWEEN THE CERVICAL MUSCLES
AND THE STRUCTURE OF THE SKULL IN *PHASIANUS*
COLCHICUS L. AND *PERDIX PERDIX* L. II

BY

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(Communicated by Prof. C. J. VAN DER KLAUW at the meeting of May 30, 1953)

4. *Musculus rectus capitis lateralis* (*m. r. cap. lat.*; fig. 4D, 5D, 17 and 18)

The *musculus rectus capitis lateralis* runs from the second, third and fourth cervical vertebrae to the caudal wall of the skull. In *Phasianus colchicus* this muscle consists of three flat bundles, attached respectively to the second, third and fourth cervical vertebra. From the cervical vertebrae these three bundles extend lateralwards between the *musculus rectus capitis superior* and the *musculus rectus capitis ventralis* and fuse quite laterally to one flat muscle bundle which turns markedly dorsalwards and proceeds dorsorostralwards laterally of the *musculus rectus capitis superior* to the place of attachment on the skull (fig. 18). The muscle fibres are directed about parallel to each other and constitute direct connections between the second, third and fourth cervical vertebra respectively and the caudal wall of the skull.

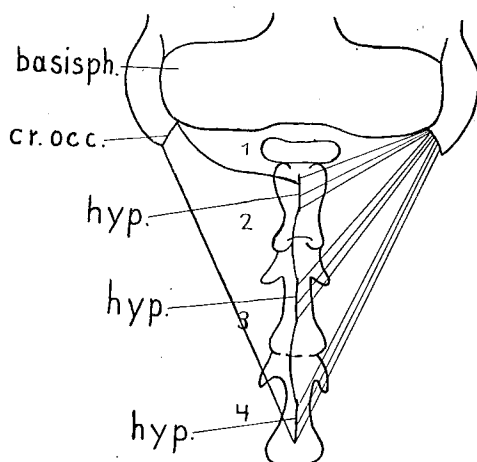


Fig. 17. Diagram of the *musculus rectus capitis lateralis* in *Phasianus colchicus* L. and in *Perdix perdix* L. in ventral view. *basisph.*, basisphenoid; *cr. occ.*, crista occipitalis; *hyp.*, hypapophyse.

The three flat bundles of which the musculus rectus capitis lateralis consists, are attached to the second, third and fourth cervical vertebra on the hypapophyses (fig. 17). At the places of attachment much connective tissue is found between the muscle fibres.

The place of attachment to the skull of the musculus rectus capitis lateralis, is situated on the most ventral part of the crista occipitalis. The attachment occurs by means of a weak aponeurosis to which the muscle fibres are attached on the median surface.

The most rostral part of the musculus rectus capitis lateralis is for the greater part covered by the musculus depressor mandibulae which is situated against its lateral surface. Connective tissue from the medial surface of the musculus depressor mandibulae is connected with the aponeurosis of the musculus rectus capitis lateralis (fig. 18).

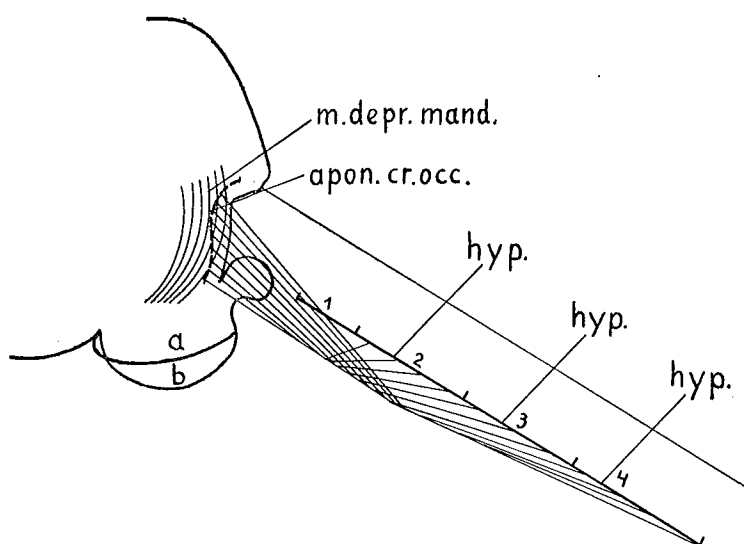


Fig. 18. Diagram of the musculus rectus capitis lateralis in *Phasianus colchicus* L. and in *Perdix perdix* L. in lateral view. *apon. cr. occ.*, aponeurose at the crista occipitalis; *hyp.*, hypapophyse; *m. depr. mand.*, musculus depressor mandibulae; *a*, surface of the basisphenoid in *Perdix perdix* L.; *b*, surface of the basisphenoid in *Phasianus colchicus* L.

In *Perdix perdix* no marked differences occur in the structure, neither in the attachment to the cervical vertebrae of the musculus rectus capitis lateralis, nor in the attachment to the skull.

5. Musculus rectus capitis superior (*m. r. cap. sup.*; fig. 4B, 5B, 19, 20, 21, 32 and 33)

The musculus rectus capitis superior runs from the first up to and including the fifth cervical vertebra to the caudal wall of the skull.

In *Phasianus colchicus* this muscle consists of two parts, a medial and a lateral part. The medial part is composed of 3 branches respectively

attached to the third, fourth and fifth cervical vertebra (fig. 19 and 21). The lateral part consists of five branches, attached respectively to the first up to and including the fifth cervical vertebra (fig. 19 and 20). The medial and the lateral parts of this muscle are situated against each other in such a way that the first branch of the medial part is situated against

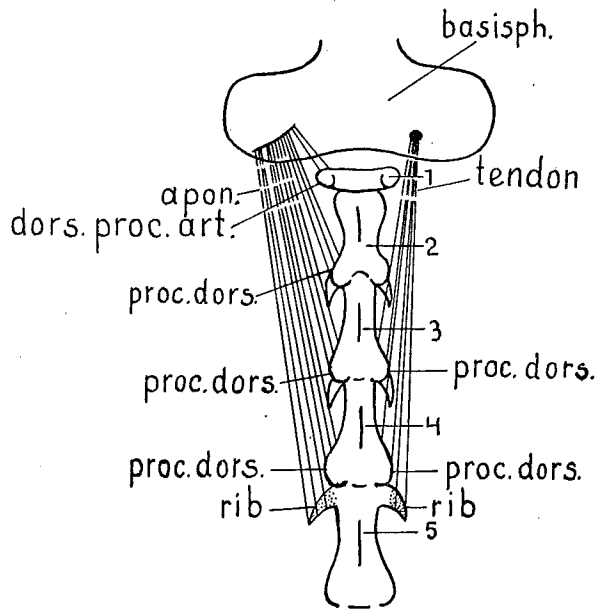


Fig. 19. Diagram of the musculus rectus capitis superior in *Phasianus colchicus* L. and in *Perdix perdix* L. in ventral view. *apon.*, aponeurose of the lateral part of the musculus rectus capitis superior; *basisph.*, basisphenoid; *dors. proc. art.*, dorsal process articularis of the atlas; *proc. dors.*, processus dorsalis.

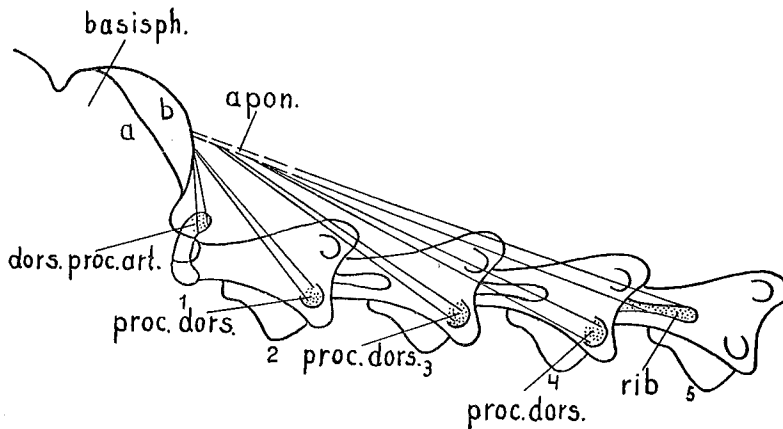


Fig. 20. Diagram of the lateral part of the musculus rectus capitis superior in *Phasianus colchicus* L. and in *Perdix perdix* L. in lateral view (dorsal side below). *apon.*, aponeurose of the lateral part of the musculus rectus capitis superior; *basisph.*, basisphenoid; *dors. proc. art.*, dorsal process articularis of the atlas; *proc. dors.*, processus dorsalis; *a*, surface of the basisphenoid in *Perdix perdix* L.; *b*, surface of the basisphenoid in *Phasianus colchicus* L.

the third branch of the lateral part, the second medial branch against the fourth lateral branch and the third medial branch against the fifth lateral branch.

The first medial branch and the third lateral branch are clearly distinct from each other; the second medial branch and the fourth lateral branch are more difficult to separate, while the third medial branch and the fifth lateral branch are so completely fused together that it remains doubtful whether the branch attached to the rib of the fifth cervical vertebra consists of two or of only one branch (probably belonging to the medial part of the muscle).

The third, fourth and fifth branch of the lateral part of the musculus rectus capitis superior are attached to the dorsal surface of a strong and broad aponeurosis (attached to the caudal wall of the skull); only the first and second branch are attached directly to the skull. The third branch is attached to the aponeurosis close to the skull, the fourth at some distance from the skull and so on (fig. 20). Especially the first branch of

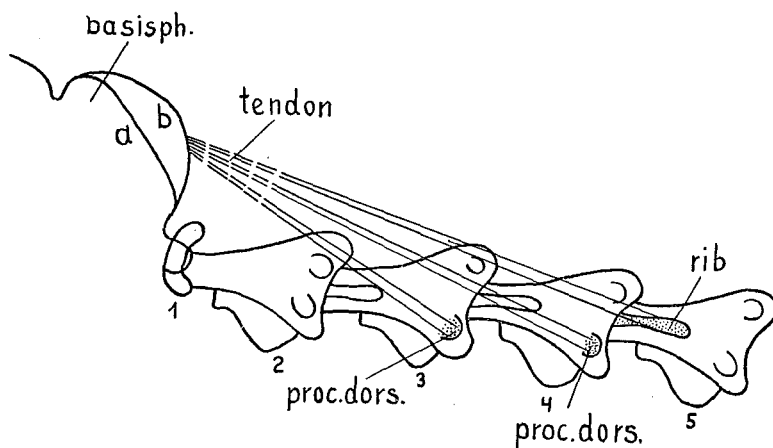


Fig. 21. Diagram of the medial part of the musculus rectus capitis superior in *Phasianus colchicus* L. and in *Perdix perdix* L. in lateral view (dorsal side below). *basisph.*, basisphenoid; *proc. dors.*, processus dorsalis; *a*, surface of the basisphenoid in *Perdix perdix* L.; *b*, surface of the basisphenoid in *Phasianus colchicus* L.

the lateral part is very weak; the second branch is much more developed; the third branch is very strong, the fourth is weaker again and the fifth somewhat weaker still.

The first and second branch of the medial part of the muscle are less developed than the corresponding third and fourth branch of the lateral part, while the third medial branch is stronger than the fifth lateral branch. These 3 medial branches are united in one tendon at some distance from the skull.

All branches consist of parallel muscle fibres which constitute direct connections between their places of attachment on the cervical vertebrae and on the skull, respectively aponeurosis, respectively tendon.

The lateral part of the musculus rectus capitis superior is attached with five branches to the five first cervical vertebrae, viz. the first branch to the dorsal processus articularis of the atlas; one branch (respectively the second, third and fourth) to the processus dorsalis and its surroundings of each of the three following cervical vertebrae and the fifth branch to the rib of the fifth cervical vertebra (fig. 19 and 20). The attachment to the cervical vertebrae is for the greater part muscular; in the fourth and fifth branch of the lateral part, respectively in the second and third branch of the medial part, much connective tissue is mixed with the muscle fibres. In the fifth branch of the lateral part resp. in the third branch of the medial part we are perhaps justified to speak of a weak aponeurosis.

The aponeurosis to which the third up to and including the fifth branch of the lateral part of the musculus rectus capitis superior are attached, is fastened to the skull on a weak crista just beside the median and directly dorsally of the place of attachment of the musculus rectus capitis ventralis, ventrally of the group of foramina for cerebral nerves.

The place of attachment of the first and second branch of the lateral part is situated in a faint excavation direct dorsally of the place of attachment of the aponeurosis, mentioned above. The attachment is muscular. The tendon which the three branches of the medial part have in common is attached to the skull directly medial of the attachment of the aponeurosis of the lateral part.

No marked differences in the structure of the musculus rectus capitis superior nor in its attachments to the cervical vertebrae and to the caudal wall of the skull, can be observed in *Perdix perdix* as compared with *Phasianus colchicus*.

6. Musculus rectus capitis ventralis (*m. r. cap. ventr.*; fig. 4D, 5D, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32 and 33)

This muscle runs from the first up to and including the sixth cervical vertebrae to the knob on the basisphenoid. In *Phasianus colchicus* the musculus rectus capitis ventralis seen from the ventral side is a large about triangular muscle, consisting of two parts: a large medial part and a smaller lateral part (fig. 22). The medial parts of the right and left muscle are firmly connected with each other in the median, so that in many specimens the right and left muscles are not clearly distinct from each other.

The median part of the muscle consists of four branches, which are attached to the first up to and including the fourth cervical vertebra respectively. These separate branches fuse close to their attachment to the cervical vertebrae to one powerful muscle running to the knob on the basisphenoid. The first branch of the medial part of the musculus rectus capitis ventralis is rather weakly developed, the second branch is somewhat more developed and the third and fourth branches are very strongly

developed. All muscle fibres constitute direct connections between their place of attachment on the cervical vertebrae and the knob on the basisphenoid.

Each lateral part of the musculus rectus capitis ventralis consists of two branches attached by means of membranes of connective tissue to the fifth and sixth cervical vertebra respectively. Both branches fuse relatively close to their attachment to the cervical vertebrae to one muscle attached to the knob on the basisphenoid by means of a tendon (fig. 24). Both branches of the lateral part are equally well developed. Here again

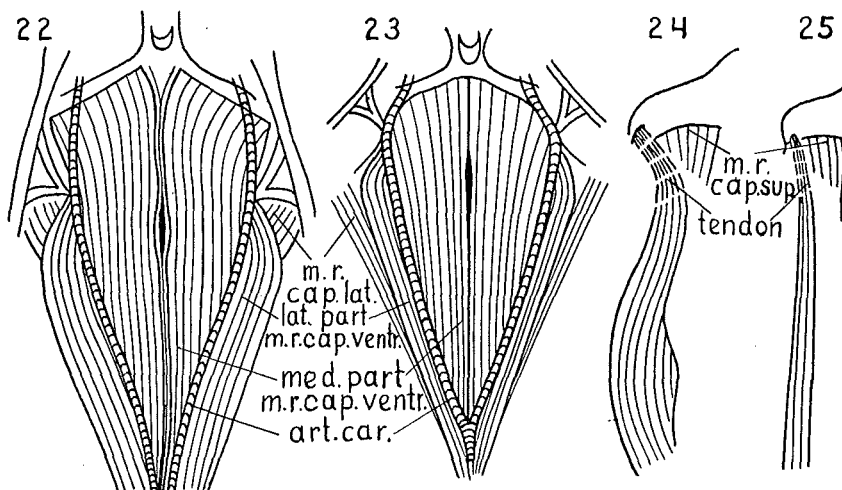


Fig. 22. *Phasianus colchicus* L. Ventral view of the musculus rectus capitis ventralis. *art. car.*, arteria carotis; *lat. part m. r. cap. ventr.*, lateral part of the musculus rectus capitis ventralis; *med. part m. r. cap. ventr.*, medial part of the musculus rectus capitis ventralis; *m. r. cap. lat.*, musculus rectus capitis lateralis.

Fig. 23. *Perdix perdix* L. Ventral view of the musculus rectus capitis ventralis. For abbreviations see fig. 22.

Fig. 24. *Phasianus colchicus* L. Ventral view of the lateral part only of the musculus rectus capitis ventralis. *m. r. cap. sup.*, musculus rectus capitis superior.

Fig. 25. *Perdix perdix* L. Ventral view of the lateral part only of the musculus rectus capitis ventralis. *m. r. cap. sup.*, musculus rectus capitis superior.

all muscle fibres constitute direct connections between their places of attachment on the cervical vertebrae and the tendon which fastens the muscle as a whole to the knob of the basisphenoid.

The demarcation between the medial and lateral parts of the muscle is defined by the arteria carotis. If we trace this arteria from its emergence from the skull, we observe that it is attached to connective tissue membranes which are connected with the cornua of the hyoid and with the roof of the mouth and then that it proceeds caudalwards between the medial and lateral parts of the musculus rectus capitis ventralis. So the right and left arteriae carotides converge caudally and finally are situated

side by side in the median, ventrally of the cervical vertebrae. As the arteriae carotides converge caudalwards their situation becomes more and more dorsal, that means nearer to the cervical vertebrae; when the median has been reached the arteriae lie entirely dorsally of the musculus rectus capitis ventralis and proceed farther caudalwards directly ventrally of the cervical vertebrae.

The location of the attachments of the four branches of the medial part of the muscle is as follows: the first branch is attached to the processus latus of the atlas, the three following to the hypapophyses of the epistropheus and the two following cervical vertebrae respectively (fig. 26 and 27). The attachment to the cervical vertebrae is for the greater part muscularous.

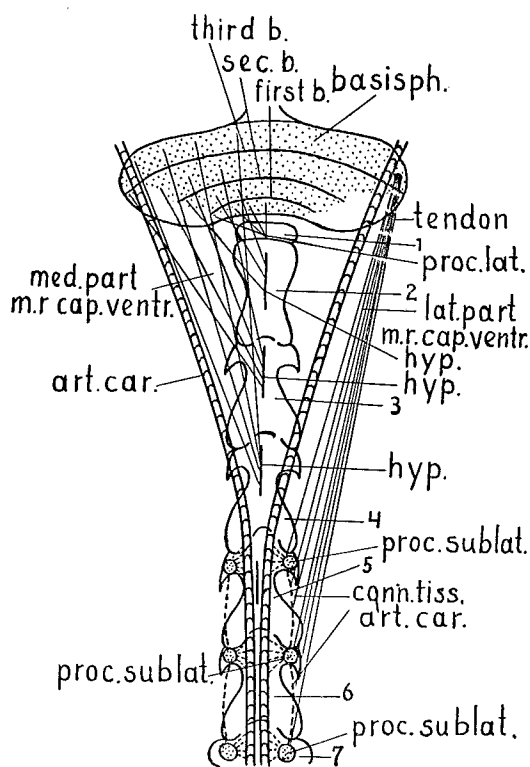


Fig. 26. Diagram of the musculus rectus capitis ventralis in *Phasianus colchicus* L. in ventral view. *art. car.*, arteria carotis; *basisph.*, basisphenoid; *first b.*, border between the places of attachment of the first and second branch of the musculus rectus capitis ventralis; *sec. b.*, idem of the second and third branch; *third b.*; idem of the third and fourth branch; *conn. tiss. art. car.*, connective tissue round the arteriae carotides; *hyp.*, hypapophyse; *lat. part m. r. cap. ventr.*, lateral part of the musculus rectus capitis ventralis; *med. part m. r. cap. ventr.*, medial part of the musculus rectus capitis ventralis; *proc. lat.*, processus latus of the atlas; *proc. sublat.*, processus sublateralis.

The attachment of the two branches of the lateral part of the musculus rectus capitis ventralis occurs by means of the connective tissue round the arteriae carotides. Where the arteriae carotides reach the median, *i.e.* a little rostrally of the demarcation between the fourth and fifth cervical vertebrae, the arteriae are connected by firm membranes of connective tissue to the processus sublateralis of the fifth, sixth and seventh cervical vertebrae. To these membranes between the fifth and

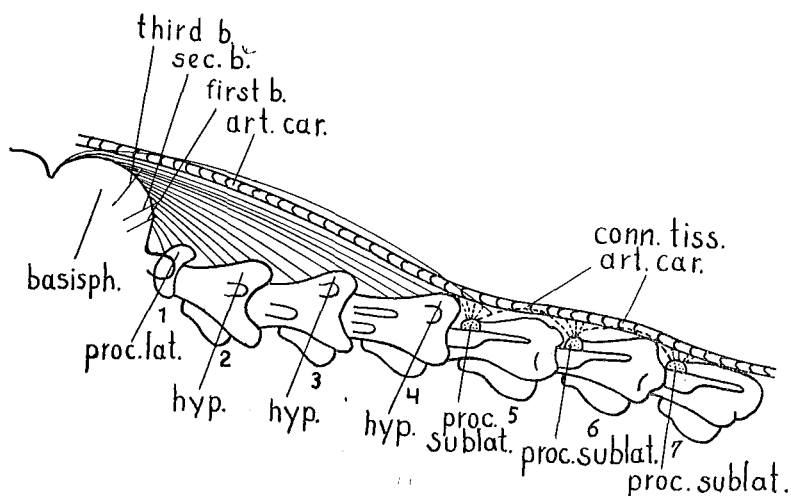


Fig. 27. Diagram of the medial part of the musculus rectus capitis ventralis in *Phasianus colchicus* L. in lateral view (dorsal side below). *art. car.*, arteria carotis; *basisph.*, basisphenoid; *first b.*, border between the places of attachment of the first and second branch of the musculus rectus capitis ventralis; *sec. b.*, idem of the second and third branch; *third b.*, idem of the third and fourth branch; *conn. tiss. art. car.*, connective tissue round the arteriae carotides; *hyp.*, hypapophyse; *proc. lat.*, processus latus of the atlas; *proc. sublat.*, processus sublateralis.

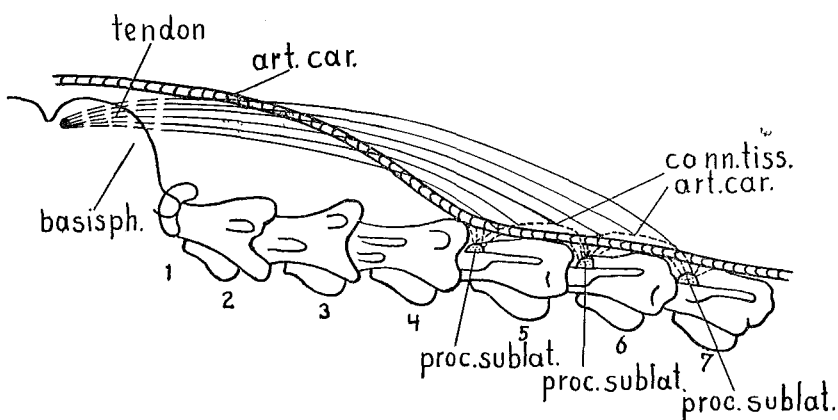


Fig. 28. Diagram of the lateral part of the musculus rectus capitis ventralis in *Phasianus colchicus* L. in lateral view (dorsal side below). *art. car.*, arteria carotis; *basisph.*, basisphenoid; *conn. tiss. art. car.*, connective tissue round the arteriae carotides; *proc. sublat.*, processus sublateralis.

sixth respectively between the sixth and seventh cervical vertebrae the two branches of the lateral part of the musculus rectus capitis ventralis are attached just ventrally of the arteriae carotides (fig. 28).

The attachment of the lateral part of the musculus rectus capitis ventralis to the connective tissue membranes is principally muscular, only the attachment to the processus sublateralis of the seventh cervical vertebra occurs by means of a tendon.

The median part of the musculus rectus capitis ventralis is attached to the skull on the knob of the basisphenoid. Rostroventrally the area of attachment is bordered by the place of attachment of the musculus adductor internus pterygoideus, laterally by the cornua of the hyoid and by the musculus depressor mandibulae and caudodorsally by the places of attachment of the muscoli recti capitis superiores (fig. 4D).

The attachment to the knob is entirely muscular.

The fibres of the first branch (coming from the processus latus of the atlas) are attached most caudally to the knob of the basisphenoid, those of the second branch (from the hypapophysis of the epistropheus) just

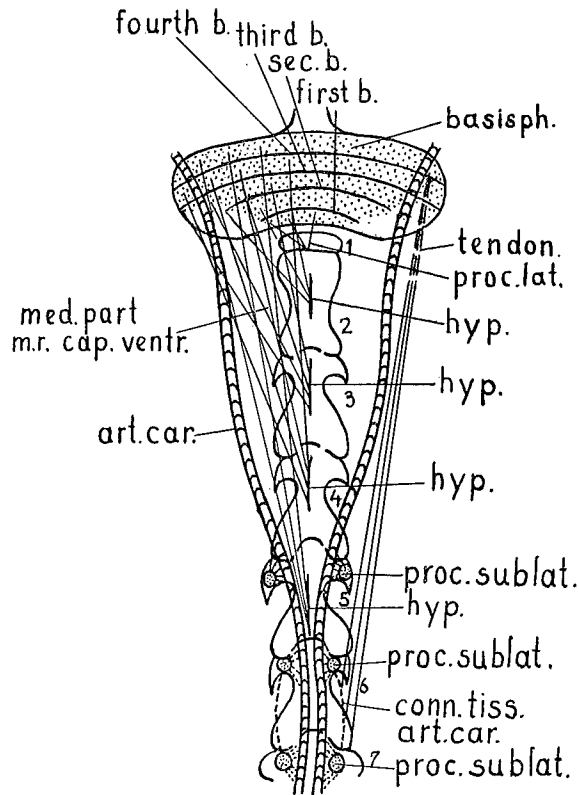


Fig. 29. Diagram of the musculus rectus capitis ventralis in *Perdia perdia* L. in ventral view. *fourth b.*, border between the places of attachment of the fourth and fifth branch of the musculus rectus capitis ventralis; For further abbreviations see fig. 26.

rostrally of the former, a.s.o.; so the fibres of the last branch are attached most rostrally on the knob (fig. 26 and 27). Consequently in the pheasant the fibres are attached to the knob of the basisphenoid at quite different angles, *viz.* in the fibres that are most caudally attached these angles are nearly 90° and in the fibres that are most rostrally attached these angles are practically 0° (so the attachment is about tangentially) (fig. 27).

The surface of the knob is somewhat rough, where the medial part of the muscle is attached to it.

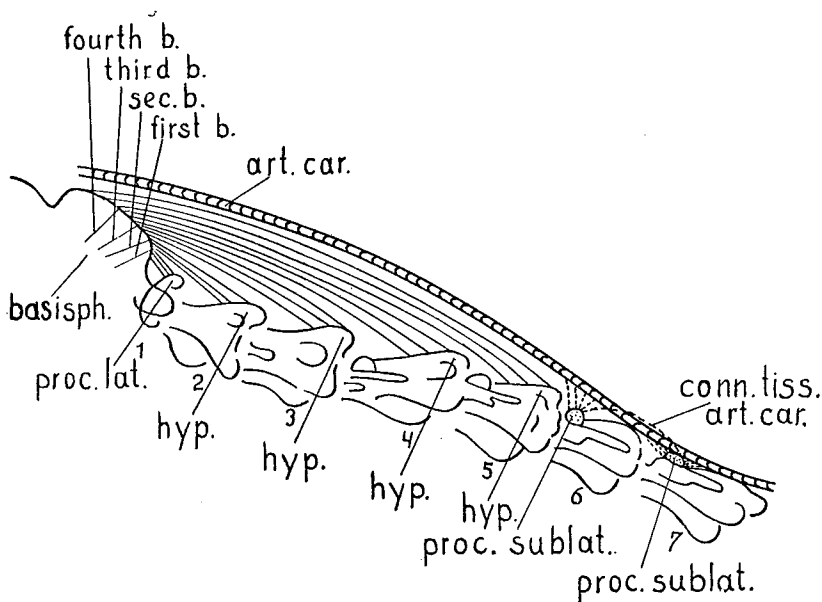


Fig. 30. Diagram of the medial part of the musculus rectus capitis ventralis in *Perdix perdix* L. in lateral view (dorsal side below). *fourth b.*, border between the places of attachment of the fourth and fifth branch of the musculus rectus capitis ventralis. For further abbreviations see fig. 27.

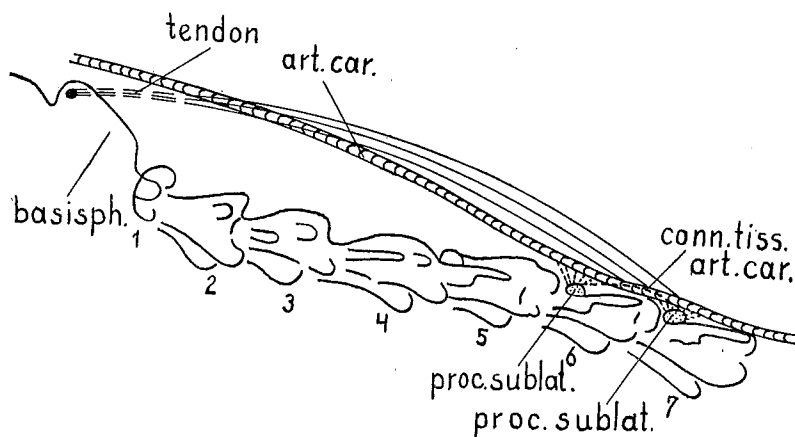


Fig. 31. Diagram of the lateral part of the musculus rectus capitis ventralis in *Perdix perdix* L. in lateral view (dorsal side below). For abbreviations see fig. 28.

The tendon of the lateral part of the musculus rectus capitis ventralis is attached to the knob of the basisphenoid quite laterally and rather far rostrally. This place of attachment of the tendon cannot be distinguished on the dry skull.

In *Perdix perdix* the structure of the musculus rectus capitis ventralis is in most respects the same as in *Phasianus colchicus*. An essential difference, however, is that the medial part of this muscle in the partridge consists of five branches respectively attached to the first up to and including the fifth cervical vertebra. The fifth branch of the medial part of the muscle is less developed than the third and the fourth (compared

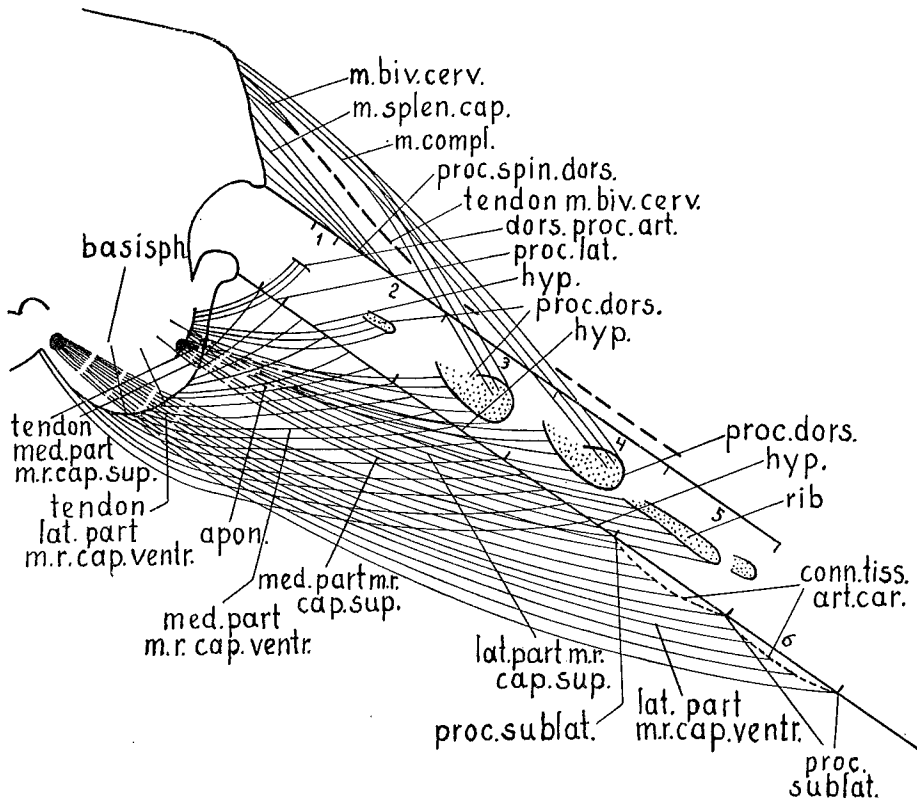


Fig. 32. Diagram of the musculus complexus, musculus biventer cervicis, musculus splenius capitis, musculus rectus capitis superior and musculus rectus capitis ventralis in *Phasianus colchicus* L. in lateral view. *apon.*, aponeurose of the lateral part of the musculus rectus capitis superior; *basisph.*, basisphenoid; *conn. tiss. art. car.*, connective tissue round the arteriae carotides; *dors. proc. art.*, dorsal processus articularis of the atlas; *hyp.*, hypopophyse; *lat. part m. r. cap. sup.*, lateral part of the musculus rectus capitis superior; *lat. part m. r. cap. ventr.*, lateral part of the musculus rectus capitis ventralis; *med. part m. r. cap. sup.*, medial part of the musculus rectus capitis superior; *med. part m. r. cap. ventr.*, medial part of the musculus rectus capitis ventralis; *m. biv. cerv.*, musculus biventer cervicis; *m. compl.*, musculus complexus; *m. splen. cap.*, musculus splenius capitis; *proc. dors.*, processus dorsalis; *proc. lat.*, processus latus of the atlas; *proc. spin. dors.*, processus spinosus dorsalis of the epistropheus; *proc. sublat.*, processus sublateralis.

to the pheasant). The lateral part of the musculus rectus capitis ventralis consists of only one branch attached to the sixth cervical vertebra.

From the description above it appears that the lateral part of the muscle must be far less developed in the partridge than in the pheasant (fig. 22 and 23; fig. 24 and 25). While this lateral part of the musculus rectus capitis ventralis consists of a rather considerable branch in the pheasant, it is represented in the partridge only by a remarkably thin branch of muscle fibres.

The attachment to the cervical vertebrae occurs in the same way as in the pheasant. The fifth branch is attached to the hypopophysis of the

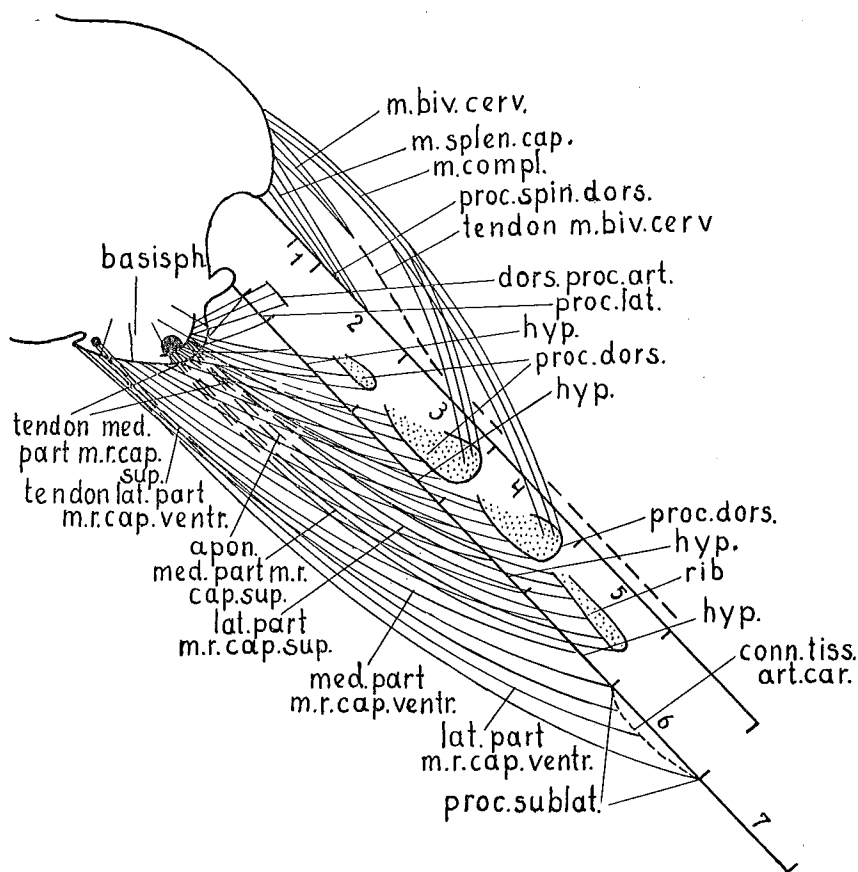


Fig. 33. Diagram of the musculus complexus, musculus biventer cervicis, musculus splenius capitis, musculus rectus capitis superior and musculus rectus capitis ventralis in *Perdix perdix* L. in lateral view. For abbreviations see fig. 32.

fifth cervical vertebra (fig. 30). The attachment of the only branch constituting the lateral part of the musculus rectus capitis ventralis to the sixth cervical vertebra occurs also in the partridge by means of connective tissue surrounding the arteriae carotides. In the partridge the arteriae carotides reach the median just rostrally of the articulation between the

fifth and sixth cervical vertebrae and are connected by membranes of connective tissue with the processus sublateralis of the sixth and seventh cervical vertebrae. So the lateral part of the musculus rectus capitis ventralis is attached to this connective tissue membrane (between the sixth and seventh cervical vertebrae), just ventrally of the arteriae carotides (fig. 29 and 31). The attachment to the skull occurs in the partridge in the same way as in the pheasant (fig. 4D and 5D). But the shape of the surface of the place of attachment (the knob of the basisphenoid) is essentially different in both species. As already mentioned the knob of the basisphenoid in the pheasant is strongly vaulted (nearly semicircular in section) while it is nearly entirely flat in the partridge (fig. 3A and 3E and fig. 1 and 2). So in the partridge the area of attachment of the medial part of the musculus rectus capitis ventralis will be relatively less extensive than in the pheasant.

To express this fact quantitatively, the surface of the knob of the basisphenoid was determined as exactly as possible in the partridge (one skull) and in the pheasant (two skulls) and compared with the total area available for the attachment of cervical muscles to the skull. It appeared that the surface of the knob amounted to 160.5 mm² respectively 173 mm² in the pheasants and 76 mm² in the partridge while the total area available for the attachment of cervical muscles on the skull proved to be 489.5 mm² resp. 510 mm² in the pheasants and 257.5 mm² in the partridge.

Thus the relation $\frac{\text{area of attachment of m. rect. cap. ventr.}}{\text{total area of attachment of cervical muscles}}$ is 0.328, resp. 0.339 in *Phasianus colchicus* and 0.296 in *Perdix perdix*. So the place of attachment of the medial part of the musculus rectus capitis ventralis indeed seems to be smaller in the partridge than in the pheasant (however, it is questionable whether this difference is real).

In the partridge the muscle fibres are nearly all attached to the knob at about the same angle (fig. 30).

(To be continued)

ZOOLOGY

ON THE CORRELATION BETWEEN THE CERVICAL MUSCLES AND THE STRUCTURE OF THE SKULL IN *PHASIANUS* *COLCHICUS* L. AND *PERDIX PERDIX* L. III

BY

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(Communicated by Prof. C. J. VAN DER KLAAUW at the meeting of May 30, 1953)

VII. *The significance of the difference in shape of the knob on the basisphenoid in the partridge and in the pheasant*

The most obvious consequence of the flat shape of the knob in the partridge is the fact that nearly all the fibres of the medial part of the musculus rectus capitis ventralis are attached to this knob at the same angle (fig. 30 and 33). In fig. 41 the area of attachment of the medial part of the musculus rectus capitis ventralis has been constructed on the skull by drawing a small piece of the area of attachment perpendicularly to each fibre. The total area obtained in this way has the same vaulting as the knob on the basisphenoid in the partridge.

It is probable that the effective functioning of a muscle fibre is only possible when it is attached to the surface at a special angle — or an angle little varying from this optimal angle — (principle of Mollier) and so it may be expected that the muscle in which nearly all the fibres are attached to the surface at the same angle, will function by contracting all the fibres at the same time. This applies to the medial part of the musculus rectus capitis ventralis in *Perdix perdix* L.

In the same way the strongly vaulted surface of the knob of the basisphenoid in the pheasant entails that the fibres of the medial part of the musculus rectus capitis ventralis are attached to this knob at strongly varying angles (fig. 27, 32 and 40).

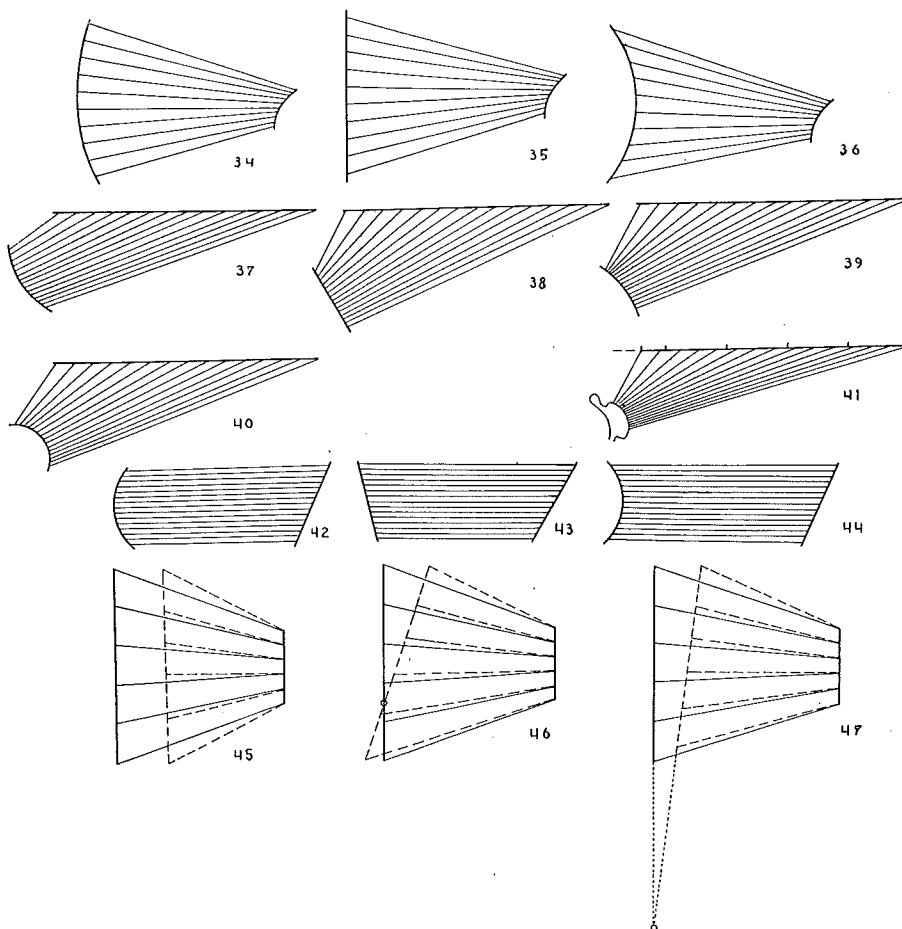
According to the principle of Mollier it is probable that the medial part of the musculus rectus capitis ventralis in the pheasant will function by contracting only part of the fibres at a time, *viz.* those that are at the most favourable angle to the surface. Which fibres will contract at a given moment will depend on the position of the head in relation to the neck at the moment of action.

So it seems that in the partridge the medial part of the musculus rectus capitis ventralis will function only when the head is kept in one (or a few) special position(s), while in the pheasant this muscle will be able to function with any given position of the head (assuming that the most favourable angle is the same for all the fibres of the muscle).

This difference in the way of functioning of the medial part of the

musculus rectus capitis ventralis in the partridge and in the pheasant probably will be correlated with differences in the functioning of the other cervical muscles and will be connected with special movements of the head which are different in the partridge and in the pheasant.

However, at present further analysis of these points is not yet possible; first the typical movements of the head in the living animals (in the partridge and the pheasant) must be studied with great exactness.



Figs. 34-36. Diagrams of muscles with diverging fibres, attached to different shaped areas. For further explanations see the text.

Figs. 37-39. Diagrams of muscles with converging fibres, attached to different shaped areas. For further explanations see the text.

Fig. 40. Diagram of the median part of the musculus rectus capitis ventralis in *Phasianus colchicus* L. For further explanations see the text.

Fig. 41. Diagram of the median part of the musculus rectus capitis ventralis in *Perdix perdix* L. For further explanations see the text.

Figs. 42-44. Diagrams of muscles with parallel fibres, attached to different shaped areas. For further explanations see the text.

Figs. 45-47. Diagrams of the movement of one place of attachment with respect to the other. For further explanations see the text.

VIII. *General considerations about structure and function of the cervical muscles in Phasianus colchicus L. and Perdix perdix L.*

According to the relative size of both places of attachment of a muscle, three cases can be distinguished in principle:

1. muscles in which the place of attachment at the origin is smaller than that at the insertion; the fibres are divergent.
2. muscles in which the place of attachment at the origin is larger than that at the insertion; the fibres are convergent.
3. muscles in which both places of attachment are about equal in size; the fibres run parallel to each other.

As the forces exercised by a muscle on both places of attachment are equal (at least when no important aponeuroses occur), the power per unit of surface will be greater at the smaller of the two places of attachment, when these areas are not equal in size.

Further microscopic-anatomical and histological investigation will be necessary to prove whether there is a correlation between the magnitude of the force exercised on the unit of surface and the number of muscle fibres or the quantity of connective tissue attached to this unit of surface on the one hand and the microscopical structure of the bone on which the force is acting on the other hand.

In the muscles mentioned under no. 1 the force exercised by the muscle is dispersed over a larger area of insertion.

In the muscles mentioned under no. 2 the force is concentrated on a smaller area of insertion.

In the muscles mentioned under no. 3 the force is transferred to an equally sized area of insertion.

1. To the first category belong the cervical muscles attached to an extensive area on the skull (area of insertion) and to a small area on the cervical vertebrae (area of origin) f.i. the musculus splenius capitis in the pheasant and the partridge. Assuming that the principle of Mollier (section VII) applies to these muscles the shape of both areas of attachment will also be important with respect to the functioning of the muscle. If the place of attachment at the origin is practically one point and the area of insertion is larger, three cases can be distinguished according to the shape of the area of insertion, *viz.*:

- a. the surface of insertion is concave (fig. 34);
- b. the surface of insertion is flat (fig. 35);
- c. the surface of insertion is convex (fig. 36).

If the area of insertion is concave and the place of origin is not too far from the centre of the sphere of which the area of insertion can be considered to be a sector, then all fibres will act upon the area of insertion at the same angle. This kind of construction might be advantageous, when a muscle acts by contracting all fibres at the same time (comp. section VII).

If the area of insertion is flat the angle at which different fibres act upon

it will not be the same; and this will be the more so when the area of insertion is convex. This divergency in the angles at which the fibres are attached to the surface may be important in cases where a muscle functions by contracting only part of its fibres at the same time (comp. section VII). The area of insertion of the musculus splenius capitis (which belongs to this category) in the pheasant and the partridge is flat in its dorsal part and strongly convex in its ventral part.

If the area of origin is not practically one point, but is more extensive, the shape of this area will also be important in relation with the functioning of the muscle. According to the shape of this area of origin the same three cases a, b and c can be distinguished and so in combination with the cases a, b and c, for the area of insertion, nine cases are theoretically conceivable.

2. The above argument of course also applies to muscles belonging to the second category (fig. 37, 38 and 39).

The area of insertion of the musculus rectus capitis superior (especially of the median part) and of the lateral part of the musculus rectus capitis ventralis may be considered as practically one point. In the median part of the musculus rectus capitis ventralis the area of attachment at the origin is also larger than the area of insertion, but the latter (the knob on the basisphenoid) cannot be considered as one point (fig. 40 and 41). The possible significance of the shape of the area of insertion (knob on the basisphenoid) for the functioning of the median part of the musculus rectus capitis ventralis in the pheasant and the partridge in relation with the principle of Mollier, has already been discussed in section VII.

Especially in cervical muscles the situation can be complicated when the area of attachment at the origin is extensive, which is the case when the muscle is attached to a number of cervical vertebrae. The area of attachment in this case is discontinuous. Moreover the cervical vertebrae each bearing a part of the area of attachment are movable in relation to each other and consequently the shape of the area of attachment is variable; it can change from concave to flat or to convex. This possibility to change the shape of the area of origin will be especially significant in the musculus rectus capitis superior, the lateral part of which is attached to five cervical vertebrae, while the median part is attached to three cervical vertebrae (section VI, 5). Likewise this point will be material for the median part of the musculus rectus capitis ventralis, which in the pheasant is attached to four and in the partridge to five cervical vertebrae.

3. With muscles belonging to the third category, in which both places of attachment are about equally sized, in the first place the case can be conceived in which both places of attachment can be considered as practically one point. The musculus biventer cervicis in the pheasant and in the partridge may be classed as a muscle of this kind. The tendon connecting the rostral with the caudal venter in my opinion must be seen only as a way of transition of the force in order to bridge over a greater distance than a bundle of parallel fibres could do.

If both places of attachment of parallel muscle fibres possess a certain extension it is theoretically possible to distinguish nine cases again according to the combinations of different shapes of the areas of attachment (concave, flat and convex).

It is obvious that the several muscle fibres of such parallel bundles will only be attached to the surfaces at about equal angles when both surfaces are practically flat.

The three cases conceivable with a flat surface of attachment on one side are reproduced in fig. 42, 43 and 44.

Among the cervical muscles in the pheasant and the partridge the musculus complexus and the musculus rectus capitis lateralis do not fit in any of the categories mentioned above. Probably they can best be brought under the last heading: parallel bundles with areas of attachment possessing a certain extension. The area of insertion is about linear in these muscles.

The relative change in position of the two areas of attachment of a muscle with the contraction of all or a number of the fibres may occur in two ways.

A. Considering one place of attachment as fixed, the other changes its position parallel to itself (fig. 45).

B. One place of attachment being fixed, the other changes its position not parallel to itself, in other words one place of attachment is rotated round a turning point (or -axis) in relation to the other. Here two cases may occur:

a. the centre of rotation is situated within one of the areas of attachment (fig. 46);

b. the centre of rotation is not situated in either of the areas of attachment (fig. 47).

Especially in many cases belonging to category B considerable changes may occur in the angles at which the muscle fibres apply their forces during the displacement of one area of attachment in relation to the other.

The situation mentioned under B will occur in all cervical muscles; the areas of insertion in the skull are rotated in relation to the areas of origin on the cervical vertebrae or *vice versa*, with the condylus occipitalis as centre of rotation.

The musculus splenius capitis in the pheasant and the partridge is an example of case B, a: centre of rotation within one of the areas of attachment (fig. 4C and 5C).

A consequence of this construction is that fibres ventrally of the condylus must relax when fibres dorsally of the condylus contract. And the same applies to contraction on the left and right sides.

All other cervical muscles in the partridge and the pheasant belong to case B, b: centre of rotation outside of either of the areas of attachment.

With the musculus rectus capitis superior the centre of rotation is

situated quite near to the area of insertion (of the median as well as of the lateral part of the muscle) (fig. 4B and 5B). Likewise the most caudally attached fibres of the median part of the musculus rectus capitis ventralis apply quite near to the condylus occipitalis, while the lateral part of this muscle inserts at a rather great distance ventro-rostrally of the centre of rotation.

The area of insertion of the musculus complexus, the musculus biventer cervicis and the musculus rectus capitis lateralis is situated as far as possible from the condylus occipitalis. The more distant from its centre of rotation a muscle applies the longer the arm and so the more extensive the movement achieved with the same force (greater moment) or the smaller the force needed to perform the same movement (equal moment).

The musculus complexus, musculus biventer cervicis, musculus rectus capitis lateralis and the lateral part of the musculus rectus capitis ventralis will be able to achieve considerable and quick movements of the head with relatively small forces (great arm). The musculus rectus capitis superior on the contrary will have to exert relatively large forces to effect small movements of the head (short arm).

Remark. With muscle fibres is always understood the smallest macroscopically discernible bundles of which a muscle consists. Whether these fibres are units of construction for all muscles dealt with, will have to be proved by further microscopic-anatomical research. Likewise further physiological investigation will have to prove whether these fibres represent functional units.

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REFERENCES

- BOAS, J. E. V., Biologisch-anatomische Studien über den Hals der Vögel. Kgl. Danske Vidensk. Selsk. Skr. 9, no. 1, 101-122 (1928-1929).
- DULLEMEIJER, P., The correlation between muscle system and skull structure in *Phalacrocorax carbo sinensis* (Shaw & Nodder). III. Proc. Kon. Ned. Akad. v. Wet., Amst., Series C, 55, no. 5, 533-536 (1951).
- , idem, IV. Proc. Kon. Ned. Akad. v. Wet. Amst., Series C, 55, no. 1, 95-102 (1952).