THE MUSCLES AND NERVES OF THE POST-AXIAL REGION OF THE TETRAPOD THIGH

PART I

By A. B. APPLETON
Lecturer in Anatomy, University of Cambridge

CONTENTS

INTRODUCTION

WHILE the skeletal system has long occupied a prominent place in the comparative study of Tetrapoda, attention has been mainly directed to the study of features of direct classificatory value. The interpretation of bone form with consideration of the parts played by environment in ontogeny and phylogeny has been studied by comparatively few investigators.

Just as a study of bone form in ontogeny involves consideration of correlative differentiation (Roux) in relation to adjacent soft tissues such as musculature, so also in phylogeny the musculature requires consideration as an integral part of the immediate environment of bones.

The present investigation was undertaken for the purpose of tracing phylogenetic muscle changes among Tetrapoda, with a view to the subsequent examination of the relation in phylogeny between bone form and the muscular pattern.

It remains for subsequent work to extend the application of the criteria which have been developed for the determination of muscular changes in phylogeny. The main outlines alone of the structural evolution of the tetrapod thigh and pelvic region will be considered in this paper.

Attempts to reconstruct the soft parts and external form of the very numerous fossil Tetrapoda whose remains have come to light have given an impetus in recent years to the study of bones with reference to their relations with the soft tissues, especially with the muscles, in place of their study as isolated objects. In recent years, Watson, Gregory and Camp, von

Huene and Romer have essayed the detailed reconstruction of the musculature of various fossil groups. The principal difficulty, as Romer remarks, has consisted in the immature state of comparative myology.

Descriptions of the myology of many Tetrapoda, especially of mammals, are now available; but the diverse systems of nomenclature and the omission by many writers of all details regarding the course and distribution of nerves render the direct comparison of these forms by study of the literature both difficult and misleading. I have found that the attempt to infer the course of phylogenetic modifications of the muscular system through collation of existing accounts leads to many erroneous conclusions quite unjustified by the actual structural patterns of the animals concerned. The name "caudofemoralis" (and its variant "caudifemoralis"), for example, has been applied to at least three different mammalian muscles having distinct phylogenetic histories (*vide* Leche, Parsons, Forster and Carlsson, pp. 411 and 413), while the muscle to which Leche applied this name in menotyphlous Insectivora has in most descriptions of other mammals been either overlooked or described as pyriformis, quadratus femoris, or as some part of the semimembranosus or of the adductor musculature. Existing descriptions readily lend themselves to the support of views such as that of the former continuation of the biceps cruris as far as the caudal vertebrae, or that of the proximal migration of the insertions of the pyriformis and of the glutaeus maximus among mammals from more distal attachments to the middle of the femur and to the region of the knee respectively (*vide* pp. 424, 431). These views it has been found necessary to reject, as a result of re-examination of the animals on which they were based.

Of late there have been few substantial contributions to the myology of living Tetrapoda. The valuable study of the Salientia by Noble (1922) is important. Intensive studies of a restricted group like that of Noble on the frogs are indispensable alike for the tracing of adaptive changes within the group and for the morphological comparison of different groups. There can be no doubt that many of the mistaken homologies between reptilian and mammalian muscles, which have been suggested from time to time, are attributable largely to an inadequate knowledge of the mammals themselves (cf. p. 393, *infra*).

The conclusions I have reached are based on the dissection (aided in some instances by serial sections) of representatives of each class, and most of the recent orders of Tetrapoda, enumerated below. The data so obtained have been considered in conjunction with published figures and descriptions for the same or allied species.

At a meeting of the Anatomical Society (1923, p. 82) I drew attention to certain characteristic relations between the caudofemoralis (Leche) and the adjacent nerve trunks in Insectivora and other mammals. I further pointed out that the great retractor musculature of the hind-limb in reptiles and urodeles presents similar relations, and that these can be recognised also in birds and frogs, despite the vestigial character of this musculature in them. In this paper it will be shown that the resemblance of structural pattern extends throughout the whole post-axial region of the thigh, and that it is much closer than a perusal of published descriptions would lead one to believe. Considerable apparent differences have proved to be illusory and the structural pattern has proved to be so similar throughout Tetrapoda as to leave little doubt regarding the general trend of muscle modification in the specialisation of the Salientia, Reptilia, Aves and Mammalia.

THE HOMOLOGISATION OF MUSCLES AND NERVES.

The conception of homology rests upon the idea of a common descent of the organisms concerned ("homogeny," Lankester). The "identification" of a given nerve as a median nerve in various individuals (of the same or different species) is a method of structural classification, based upon the finding, after extensive comparative and variational studies, that the presence of a nerve with certain relations to adjacent muscles and bones is a conservative feature in limb structure.

Support is given to this mode of classifying nerves by the close relation which is found to hold between muscles and their nerve supply, provided only that the nerves are defined by means of their topographical relations in the limb.

The earlier attempts at the homologisation of muscles depended mainly on consideration of their relations to bones and to one another. Special value was attributed to a study of the site of "origin" (generally understood for this purpose to mean the more proximal attachment), as being more conservative in phylogeny than the distal attachment. The realisation of the close relation existing between muscles and their nerve supplies provided a valuable accession to the means of determining homologies, obscured as these sometimes are by the great changes of size and attachment which are involved in adaptive modifications of limbs and other parts. This really implied, however, the introduction of another parallel but independent conception—that of the homologisation of the nerves themselves.

This latter question has thus far remained in a generally unsatisfactory position. It is now desired to lay stress upon the importance of an adequate consideration of this factor.

Inasmuch as the "identification" of nerves is in common usage based, quite correctly, on topographical relations and not on central origin, the observed close relation of muscle and nerve supply implies a conservatism of the structural pattern of the thigh as a whole, involving not only muscles and their nerves, but also their topographical relations to the main nerve trunks of the limb. Neglect to consider this general structural pattern has led to the overlooking of close resemblances. The large buttock muscle, for example, of Monotremata has been generally but erroneously regarded as a "glutaeus maximus," evidently on the ground of its general position and extent, and in spite of peculiarities of nerve supply (cf. Frets, 1909, p. 94) and insertion. Its nerve was accordingly described as N. glutaeus inferior. It will, however, be shown that this muscle presents all essential features (apart from its great size) of the "caudal slips of the hamstrings" present in many mammals and is still more like a reptilian muscle mass which has commonly been misinterpreted (*vide* p. 420, *infra*). An extreme instance of the conservatism of appendicular structure, despite great differences in the central origin of peripheral nerves, is offered by von Ihering's well-known observations on the innervation of the pelvic fins of Teleostei. The segmental origin differs greatly according as these are in an abdominal or in a jugular position, but fin structure (including the course of nerves within it) appears to have undergone relatively little change.

I have on a previous occasion (1922) given a preliminary outline of a classification of the mammalian adductor muscles based on consideration of the course of the obturator nerve, and especially on the course of the nerve to the gracilis. Such topographical details constitute a part of the structural pattern of the thigh.

Certain well-known exceptions have been claimed in regard to the constancy of the innervation of muscles. There is little doubt that certain of these depend on unsatisfactory muscle comparisons. Others, on the other hand, suggest further examination of the "identification" of the nerve in question, while there are still others, such as the peculiar distribution of the femoral nerve among Monotremata (Ruge, Westling), and the innervation of the interosseous muscles of the mammalian foot (Cunningham), whose significance cannot yet be estimated. But such instances are rare.

Comparative studies[1] may be said then to point to the topographical course of the principal limb nerves as an integral part of the structural pattern of the thigh, suggesting that their course and distribution depend on peripheral reaction systems during ontogeny rather than on the central origin of the nerves. What we know of the processes of nerve and limb morphogenesis may be claimed in support of this view. The well-known experiments of Roux and Braus with transplanted limb buds in Amphibia point to the course of a nerve bundle being an expression of its behaviour in a given environment, such as that offered by the limb bud to an outgrowing nerve. The general course and distribution of limb nerves are found to be the outcome mainly of developmental processes within the limb bud itself and not in the central nervous system. Przibram, in his summary of recent work relating to trans plantation and regeneration, finds that "a nervous influence on developing organs does not seem to enter into morphogenesis proper at all, neither in early development nor in regeneration" (1926, p. 324). If we restrict our

---

[1] It is appropriate to recall an instance of similar constancy in the course of a nerve-bundle, in the mammalian foot. Ruge and Cunningham (*Voyage of H.M.S. "Challenger," Zool.* vol. v, pt. xvi, p. 121) have shown that the lateral plantar nerve almost invariably passes between the adductor and flexor brevis series of intrinsic muscles, a feature which assists in their mutual distinction.

attention to the provisional motor elements of peripheral nerves (which originate primitively as collaterals from intraspinal tracts—Coghill, 1926, p. 117) it indeed appears that their formation may be initiated in the first place through the effects produced upon the embryonic spinal cord by the contraction of neighbouring muscle tissue (*vide* Kappers, 1921, pp. 143, 144). Their connection, moreover, with muscle is attained before there is perceptible nervous function (Coghill, 1926, p. 125). At a later stage it has been shown that the size of the spinal ganglia is in Urodela modified by alteration in the extent of peripheral musculature and integumentary areas (Detwiler, 1926, p. 411; cf. also Detwiler, 1924, p. 64). Detwiler's transplantations of larval Amblystoma limbs indicate, moreover, that there exists between the limb and its normal nerves an intimate developmental relationship (1922, p. 158). To these conclusions comparative anatomy makes its contribution by claiming a very close relation throughout phylogeny between peripheral muscles and the courses of nerves supplying them.

The foregoing considerations regarding the homologisation of nerves have had reference primarily to muscular nerves. The point of view upon which emphasis has here been laid clearly requires, however, that the conservatism or otherwise of the course of cutaneous nerves among limb structures should be examined from the comparative point of view. Some attempt has been made in the following pages to study this aspect of the structural pattern of the tetrapod thigh, in addition to the mutual relations of muscles and muscular nerves. For data regarding the course of cutaneous nerves I have been obliged to depend almost entirely on original observations.

Romer (1922, p. 522), in discussing the means at our disposal for the determination of the homologies of nerves, has denied that the course of a nerve in relation to adjacent muscles will prove its "identity," though he admits some constancy for the relations of nerves to bones. He instances Sieglbauer's observation regarding the variability of the course of the tibial nerve in Urodela in relation to the femorofibularis[1]. It may be added that other variations in the relations of nerves to muscles have come to light in the present investigation. But these do not invalidate the general conclusion that these relationships are extremely conservative in phylogeny. Sieglbauer's description of the nerve in question as a "tibial" nerve implies that its relations and distribution were sufficiently characteristic in every urodele examined to distinguish this nerve from neighbouring nerve trunks. It will be subsequently shown (p. 400) that the muscular relations of N. tibialis suffice to distinguish it throughout Tetrapoda from Nn. ischiadicus ventralis, peronaeus, and ischiadicus dorsalis. And when these nerves are thus identified by their topographical relations in the various tetrapod groups, it is found that the muscle-masses respectively innervated by these nerves present close resemblances in the various groups (those supplied by N. ischiadicus dorsalis and N. ischiadicus ventralis are reviewed in Part II

---

[1] Romer evidently intends to refer to this muscle, though he writes "femoro-tibialis" (*vide* Sieglbauer, 1904, p. 390).

of this paper). This circumstance is confirmatory of the value of the distinction provided by muscle relations. The variation in the course of N. tibialis cited by Romer is but an illustration of the classificatory character of nerve homologies, and does not invalidate our recognition of topographical relations, principally those with muscles, as the basis of the homologisation of limb nerves.

It is worthy of note, on the other hand, that the skeletal relations on which Romer rightly places some reliance, also exhibit minor variations comparable with those between muscles and nerves. In fish, for example, the pectoral girdle shows great variation in its relations to the appendicular nerves (Braus, 1898, p. 267), and this seems to find its most probable explanation, notably in *Polypterus*, in a phylogenetic remodelling of the girdle (Braus, 1900). The supracoracoid nerve also appears to have acquired a course in mammals differing from its passage through the procoracoid of therapsid and many other reptiles, presumably as a result of skeletal modification. Minor variations must be recognised in the relation of the median and radial nerves to the humerus among Tetrapoda, and their passage through foramina in some of them seems to be related to skeletal change. It may be that the absence in the hind-limb of frogs of a diazonal nerve is similarly related to change in the pubic part of the girdle, permitting the union of the obturator with the femoral nerve as Hoffmann (1878, p. 245) suggested, though Noble has offered an alternative explanation (1922, p. 53).

Romer's statement that de Man's attempt at homologising the finer nerves of Salientia and Urodela has proved valueless cannot be accepted *in toto*. De Man's comparisons, for example, between the nerves 11, 12 and 13 in the two orders (1873, pp. 56, 58 and 75) are sustained by Noble's comparisons (1922, p. 54) and find further support in the additional data presented in this paper. The exact point at which a nerve bundle leaves the main stem is, on the other hand, admittedly variable, as is also the precise arrangement of nerve branches to a muscle (Noble, 1922, pp. 50, 51).

Many instances have come to light in the present investigation of nerve bundles varying in their mode of union into larger trunks (identification being based on their course and confirmed by their distribution). Such variation is far more common than variation in the relations of nerve bundles to muscles or bones. Noble has offered an instance (1921, p. 50), in the union of the nerves to dorsal thigh muscles in *Pipa* and *Xenopus* into a common trunk, unlike other Salientia; but it appears that the relation to adjacent muscles, notably to the iliofibularis, was unchanged. The occasional "accessory obturator" nerve of man (better described—adapting Paterson's suggestion of 1891[1] to the B.N.A. —as the "accessory femoral" nerve) provides a similar instance. The thigh nerves subsequently to be described as Nn. ischiadicus dorsalis and ischiadicus ventralis (p. 372) will be shown to vary in the extent to which various constituent bundles are bound to one another and to the tibial and caudofemoral nerves. But despite these variations there is some constancy in the mode of union of nerve bundles. Those classified as elements of N. ischiadicus dorsalis in

---

[1] *Journ. Anat.* vol. XXVI, p. 47.

Tetrapoda are more closely associated with N. peronaeus than with N. tibialis in all cases studied. Similarly those classified as elements of N. ischiadicus ventralis are associated in the early part of their course with N. tibialis. Muscles presumed on other evidence to have had a recent phylogenetic differentiation from a common mass do in various instances pursue a common path until they approach their destination, as Noble (1922, pp. 26 and 51) showed for the "pectineus" and "adductor longus" of the frogs.

On Muscle Homologies.

It is necessary to give further brief consideration to the meaning of homology in reference to musculature. The existence of intra-special *variations* in the muscular and nervous systems implies the classificatory character of our schemes of nomenclature. In the same way as the median nerves of various individuals can be grouped together, so the biceps muscles of the fore-limb can also be classified by the use of the name "biceps brachii." The term is applied even when one or two additional heads of origin are present, and from man is extended to the description of similar structures in apes and more remotely related animals. A limit is reached only when the necessary approximation of structure is wanting, and doubt exists as to which muscles should be considered "homologous" muscles. A hiatus in structural arrangement of this magnitude is not limited to groups supposed to have been delimited by the extinction of intermediate forms, but may occur as an intra-special variation, and anomalous muscles occur which cannot be closely compared with any normal ones.

No fundamental difference can be assumed to exist between "inter-specific" and "intra-specific" variation; such differences as there seem to be (e.g. Pearson, 1919, p. 373) may involve for the most part questions of interbreeding and its relation to geographical isolation or physiological isolation (e.g. through infertility). It is clear from experimental studies[1] that at certain developmental stages there are pluripotent tissues; a cell lineage in one individual might eventuate in the formation of muscle fibres, while in another it might result in the formation of areolar tissue. Thus we cannot yet say whether the musculature of an additional head to the biceps or of an anomalous abductor ossis metatarsi quinti in one man is represented in another by muscle tissue or by areolar or some other tissue. Slight genetic differences may lead to the formation of "anomalous" musculature by determining different histogenetic changes through altered metabolic or electrical gradients.

In the comparative study of muscles attention is focussed on their place in the developed organism as functional units in the mechanism of movement. Adaptive evolutionary changes are to be sought in modifications of attachments, internal structure or in changes of bone form which affect function. Muscles whose gross features show a definite evolutionary trend might well be found to show differences of cell lineage. But it is possible to trace the series of phyletic changes, even though the actual germinal differences

---

[1] *Vide* references provided by Przibram, 1926, p. 314.

and the epigenetic (or "apogenetic"—Przibram, 1926, p. 327) processes involved in muscle differentiation have not been analysed in detail.

It would seem essential for investigations of phylogenetic changes in a region such as the tetrapod thigh that comparisons should be made between the structures as a whole, *without* assuming too rigid an identity between the nerves of one animal and those of another, or a constancy of course and distribution of nerves throughout a phyletic series. Thus we may hope to trace phylogenetic changes, whether these consist in a change in course of a nerve bundle, in the relation between muscle cleavage and the zones of nerve distribution, in the attachments of muscles or in the courses of nerves supplying them. It is by means of such broad comparisons that the essential similarity of the thighs of Tetrapoda has come to light, obscured as it has been in published descriptions by the diverse terminologies employed; and it has proved possible to trace the main trends of phylogenetic modification in musculature.

MATERIAL AND ACKNOWLEDGMENTS

In the animals enumerated below, the detailed distribution of nerves and topographical relations of nerves and muscles have been studied in the post-axial region of the thigh and adjacent parts of the trunk and shank. The conclusions reached are based mainly on the data obtained from these dissections. In addition, certain points have been checked in microscopic sections of embryos of *Alligator miss.* and *Chrysemys* sp. and of larvae of *Cryptobranchus allegh.*

Many of the mammals dissected belong to Dr Duckworth's collection, and my thanks are due to him for his kindness in so freely placing them at my disposal. I am greatly indebted to Dr Beattie for the opportunities he has provided me for the dissection of valuable material derived from the Gardens of the Zoological Society in London. I have pleasure in thanking Prof. J. P. Hill for a specimen of *Dasyurus mac.*, Prof. Sir A. Keith for a *Hyrax* sp., Dr Gadow for a *Crocodilus nil.*, and Mr Forster Cooper for his kindness in facilitating the study of material in the Museum of Zoology, Cambridge.

I take this opportunity of recording my great appreciation of the invaluable assistance I have derived from discussions of neuromuscular problems with Prof. J. T. Wilson, and my thanks for his permission to make extensive use of material in the School of Anatomy, Cambridge.

The following animals have been employed in the present study of thigh nerves and muscles.

Mammalia. *Ornithorhynchus anat., Echidna acul.*
Manis sp., *Orycteropus cap., Tatusia peba, Myrmecophaga jub.*
Lepus cunic., Mus dec., Mus sylv., Erethizon dors., Dinomys branicki, Capromys melan., Capromys brach., Cynomys ludovic.
Macroscelides sp., *Elephantulus myurus jamesoni, Tupaia pict., Ptilocercus lowii borneanus, Erinaceus eur., Talpa eur.*

Mammalia (continued).	*Lemur lem.*, *Lemur var.*, *Lemur mac.*, *Tarsius spectr.*, *Loris grac.*, *Nycticebus tard.*, *Perodicticus potto*, *Galago crassic.* *Pteropus med.* *Hapale jacch.*, *Hepales pigm.*, *Chrysothrix sciur.*, *Ateles ater*, *Ateles* sp., *Callicebus* sp., *Cebus* sp. *Thepopithecus gel.*, *Cynocephalus maim.*, *Semnopithecus ent.*, *Macacus rhesus*, *Nasalis larv.* *Gorilla gor.*, *Anthropithecus trogl.*, *Simia sat.*, *Hylobates leuc.*, *Hylobates müll.* *Lutra vulg.*, *Meles tax.*, *Paradoxurus herm.*, *Mustela vison*, *Ursus himil.*, *Felis cat.*, *Canis vulg.*, *Genetta vulg.*, *Herpestes ichn.* *Bos taur.*, *Ovis ov.*, *Sus scrofa.* *Equus cab.* *Hyrax cap.* *Didelphys mur.*, *Belideus sciur.*, *Perameles obes.*, *Dasyurus mac.*, *Dendrolagus inustus*, *Sarcophilus harr.*
Aves.	*Gallus bank.* (*var. Wyandotte*), *Columba liv.*
Reptilia.	*Alligator miss.*, *Crocodilus nil.* *Varanus beng.*, *Ctenosaura multisp.*, *Uromastix spin.*, *Lacerta vir.*, *Gecko* sp., *Scincus* sp. *Testudo* sp.
Amphibia.	*Triton crist.*, *Salamandra mac.*, *Necturus mac.*, *Cryptobranchus allegh.* *Bufo vulg.*, *Rana temp.*, *Rana catesb.*

A. THE STRUCTURAL PATTERN OF THE TETRAPOD THIGH (POST-AXIAL REGION)

1. Urodela. (Figs. 1, 2, 12 and 13.)

The topographical relations of nerve bundles to muscles are shown in fig. 1. Metazonal nerves enter the thigh as a single trunk, N. ischiadicus. Two of these, however, are in certain Urodela distinct from the remainder as they enter the thigh (e.g. *Salamandra mac.*, fig. 2); they will be described below as *Nn. pudendus* and *cutaneus femoris posterior*. At the proximal border of M. caudalifemoralis (de Man, 1873), the great retractor muscle of the thigh in primitive Tetrapoda, two nerves leave the main stem (which is continued to the leg as *N. tibialis*). These will be described as *Nn. fibularis* (Hoffmann, 1878) and *ischiadicus ventralis*.

N. ischiadicus ventralis[1] (comprising de Man's nerves 5, 6, 7, 8 and 9—1873) passes *ventrally* to the caudalifemoralis, and supplies the ventral thigh

---

[1] Frets (1909, p. 90) applied this term to a similar nerve (*vide* p. 396, *infra*) in *Sphenodon* and certain mammals; but he failed to recognise the corresponding amphibian nerve. Ogushi (1913) has applied the name of "N. pudendus" to a similar nerve in *Trionyx*.

muscles, named by de Man as follows: puboischiofemoralis externus (partim) and ischiofemoralis forming the deeper musculature (fig. 12); and pubotibialis, puboischiotibialis and ischioflexorius (forming the more superficial musculature). It includes also a cutaneous element which accompanies the nerve to the pubotibialis and becomes superficial on the inner side of the knee between Mm. pub.-tib. and pub.-isch.-tib. This cutaneous bundle will be named *N. cutaneus femoris ventralis*, in the belief that it corresponds with the nerve which will be so described in Salientia and Reptilia. In these classes, however, the nerve in question has a distribution mainly in the thigh, while the urodele nerve is mainly distributed in the shank.

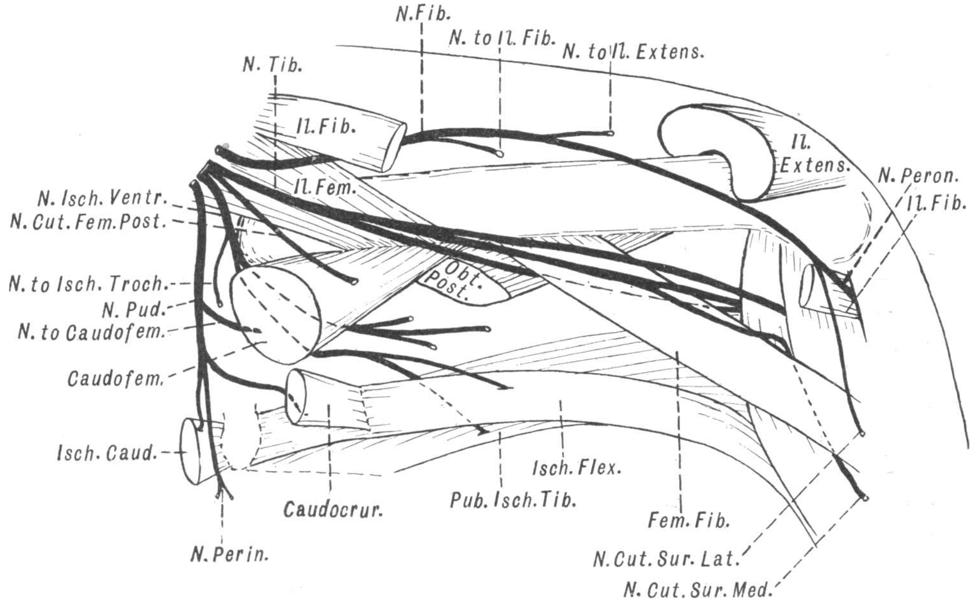

Fig. 1. Diagram of the post-axial region of the right thigh of *Cryptobranchus allegh.*, showing the topographical relations of nerve bundles to muscles. The structural pattern shown above is retained throughout Tetrapoda, apart from the presence here of two muscles, femorofibularis and the "caudocrural," which there is no reason to believe were present in the pro-amniota Amphibia. N. tibialis, distributed to the ventral part of the limb distal to the knee, passes between M. caudofemoralis[1] and M. iliofibularis. A small N. cut. fem. post. also emerges between these muscles. Nn. ischiadicus ventralis and pudendus, distributed to the ventral part of the thigh, and cloacal region, pass ventro-medially to M. caudofemoralis. The N. fibularis, distributed to the dorsal parts of the thigh, leg and foot, passes dorsally to M. iliofibularis from its pre-axial to its post-axial side, close to the knee. The relation of the tibial nerve (here shown as three trunks) to M. femorofibularis is variable among Urodela (cf. fig. 2).

---

[1] The names employed in the legends to illustrations are those which have been found appropriate for comparative tetrapod myology; their equivalents in the descriptions of various writers are provided on p. 434. M. caudofemoralis of the Urodela comprises M. caudalifemoralis (de Man) and perhaps also the caudo-crural of Humphry (*vide* p. 428).

N. pudendus, like N. ischiadicus ventralis, passes ventro-medially to M. caudalifemoralis, but is situated more caudally. It supplies this muscle, and also supplies three other caudo-appendicular muscles, viz. ileocaudalis[1], ischiocaudalis and caudalipuboischiotibialis (de Man)[1], the latter being the "caudo-crural" of Humphry (1872). Like N. ischiadicus ventralis, it includes a cutaneous element which will be named *N. perinaealis.* This nerve passes between the caudocrural and ischiocaudalis to reach the cloacal region.

The attachments and mutual relations of the above-mentioned muscles have been described by a number of writers[2]. It may be observed that the muscle described by de Man as a diploneural puboischiofemoralis externus is represented in some Urodela by two distinct muscles innervated respectively by Nn. obturatorius and ischiadicus ventralis (e.g. in *Salamandra mac.*, fig. 12). These will be distinguished as *M. obturator anterior* and *M. obturator posterior* respectively.

The remaining metazonal nerves pass *dorsally* to M. caudalifemoralis.

A cutaneous nerve (figs. 1 and 2) is distributed to the angle between the thigh and tail (a region it will be convenient to name the "*post-axial groin*"), emerging between M. ileofibularis[1] (de Man) and M. ischioflexorius (de Man). In view of comparisons to be made subsequently with mammalian anatomy (p. 399) it will be named N. cutaneus femoris posterior.

N. tibialis (figs. 1 and 2), like the N. cut. fem. post., passes dorsally to M. caudalifemoralis, but remains ventral to M. iliofibularis[1]. It divides into medial and lateral branches at the knee, if it has not already done so in the thigh (*vide* p. 375). Besides its branches to the muscles and skin of the calf and sole of the foot, it provides a small branch to the more distal part of the ventral thigh musculature (puboischiotibialis, cf. pp. 382, 399). Its cutaneous branch to the shank passes laterally to M. puboischiotibialis, a feature which distinguishes it from N. cut. fem. ventr. (*Necturus*—Appleton; *Siredon*—cf. Sieglbauer, 1904, p. 397). In view of its resemblance to the *N. cutaneus surae medialis* of mammals (p. 399), this cutaneous nerve will be given the same name.

N. fibularis differs from the above-mentioned nerves in regard to its relation to M. iliofibularis[1]. It is like N. tibialis and N. cut. fem. post. in its situation dorsal to M. caudalifemoralis, but (fig. 2) it passes between M. iliofibularis and the femur (clothed here by M. ileofemoralis[1]—de Man—and M. pectineus—Humphry), gains a superficial position by emerging between the iliofibularis and ilioextensorius of Sieglbauer (1904, p. 390) and Noble (1922, p. 47), and turns over the dorsal border of M. iliofibularis to reach the lateral (post-axial) surface of the fibula. It then disappears under cover of M. peroneus (Humphry)[3]. It innervates dorsal thigh muscles, Mm. iliofemoralis,

---

[1] The orthography employed by the various authors quoted has been respected. With this exception, the orthography employed in the text is that used in the table on pp. 434, 435, and in the legends to figures.

[2] Humphry (1872), de Man (1873), Hoffmann (1878), Sieglbauer (1904), and Noble (1922).

[3] M. femorofibularis—Hoffmann. 1878, p. 158. This name is, however, unsuitable since Humphry previously applied this name to another muscle (Mivart's "short head of biceps").

iliofibularis, and ilioextensorius, and enters the shank to provide muscular and cutaneous nerves for the dorsal parts of the leg and foot. It includes a cutaneous component which leaves the main stem as it winds over the dorsal surface of M. iliofibularis; it supplies the fibular side of the leg. In some urodeles a further cutaneous bundle leaves the main stem about the middle of the thigh and winds round the dorsal margin of M. iliofibularis (in *Salamandra mac.*). These bundles pursue so similar a course that they will be described together, as *N. cutaneus surae lateralis.*

It follows then that the large nerve bundles of the urodele thigh show differences in their relations to Mm. iliofibularis and caudalifemoralis. Nn. ischiadicus ventralis and pudendus pass ventro-medially to both (including the cutaneous components N. cut. fem. ventr. and N. perinaealis respectively). Nn. cutaneus femoris posterior, tibialis and cutaneus surae medialis pass dorsally to M. caudalifemoralis but remain ventral to M. iliofibularis, while N. fibularis (with its cutaneous component, N. cutaneus surae lateralis) passes dorsally to M. iliofibularis as well as M. caudalifemoralis. The cutaneous nerves subsequently pursue distinctive routes to the surface. N. perinaealis passes between two caudo-appendicular muscles, and N. cut. fem. ventr. between two of the long flexor muscles; N. cut. sur. lat. passes between two of the dorsal muscles (Mm. iliofibularis and ilioextensorius), while Nn. cut. fem. post. and cut. sur. med. pass between the flexor and the dorsal musculatures.

Differences occur among Urodela (even within a single species) in the distance over which nerve bundles are bound up together. The nerve to M. iliofemoralis may leave the main sciatic nerve independently of N. fibularis, or it may accompany the latter a short distance. Published descriptions illustrate these variations. Similar differences in the branches of N. fibularis have been observed by Noble in Salientia (p. 377 *infra*). The tibial nerve may divide into its medial and lateral terminal branches in the middle or even in the proximal part of the thigh, instead of at the knee. This difference appears to be related to a variation in the course of the nerve relative to M. femorofibularis (Humphry). Humphry has noted this variability (1872, p. 53), the two hind-limbs of an individual *Cryptobranchus jap.* differing in this respect; but whereas in one limb Humphry found the two nerves again joining after encircling the muscle, I have found in a *Cryptobranchus allegh.* that the medial branch divided into two bundles which re-united more distally (cf. figs. 1 and 2). In *Salamandra mac.* the whole of the tibial nerve passes laterally (post-axially) to M. femorofibularis, splitting to encircle the sciatic artery.

It is to be observed that the division of the tibial nerve into two branches, which occurs in some urodeles in the popliteal space, is not comparable with the division of the mammalian or salientian division of the sciatic nerve into tibial and (common) peronaeal nerves. It will be shown that the latter is a constituent part of the urodele N. fibularis (fig. 9). Thus Humphry's names for the two branches of the tibial nerve in Urodela ("internal" and "external popliteal" nerves) have been found unsuitable.

Variation in the course of a nerve relative to a muscle has been noted by Sieglbauer (1904) in regard to N. fibularis and M. peroneus (Humphry).

M. femorofibularis (Humphry) was described by Mivart as the "short head of biceps." But in its relation to N. tibialis (fig. 2) it differs from the mammalian muscle of that name; the latter, moreover, is justifiably claimed by Parsons and Klaatsch as a neomorph in mammals (fig. 10; further evidence of this is offered on p. 403). The phylogeny of this urodele muscle has not been determined. In view however of the absence of this muscle in Reptilia (and apparently also in birds and mammals), and of the undoubted specialisations which distinguish the hind-limb of modern Urodela from that of the early Tetrapoda (p. 427), it is presumed that this muscle is a caenotelic feature of the Urodela. Functionally, it offers a parallel to the short head of biceps found among Primates and Xenarthra.

The muscular branch of N. tibialis to the distal part of the long flexor musculature was described by de Man as entering M. pubotibialis in *Triton crist.* But in *Salamandra mac.* and *Cryptobranchus allegh.* I have found it supplying M. pubi-ischio-tibialis; Hoffmann confirms in respect of the former animal (1878, p. 243); in both of them the branch arose from the medial terminal branch of N. tibialis. Both it and N. cut. sur. med. leave N. tibialis *after* encountering M. femorofibularis (Humphry).

Some essential relations in Urodela may be summarised by enumerating structures in their topographical order on the post-axial side, in passing from the dorsal to ventral aspect: M. iliofemoralis, M. ilioextensorius and its nerve; N. fibularis[1]; M. iliofibularis and nerve; Nn. cut. fem. posterior, tibialis and cut. sur. medialis[2]; M. caudalifemoralis and nerve; Nn. ischiadicus ventralis and perinaealis; M. flexor cruris and Mm. ischiofemoralis (de Man) and obturator posterior.

Variation in the structural pattern of the urodele thigh involves the relative size and extent of attachment of muscles, and the distance along which nerves are bound up together. Two muscles exhibit variations in their relations to the larger nerve bundles, viz. Mm. femorofibularis Humphry and peroneus Humphry, femorofibularis Hoffmann (p. 375, *supra*). The general pattern of thigh structure, so far as the relations of muscles and nerves and the distribution of the latter are concerned, is found to be very similar throughout Urodela, with exceptions of the kind recorded.

2. SALIENTIA. (ANURA, fig. 9.)

For purposes of comparison with the Urodela, the salientian terms employed will be those mainly of Gaupp (whom Noble has followed in his recent contribution, 1922); the data provided by these authors have been supplemented and controlled by dissection of *Bufo vulg.*, *Rana temp.* and *Rana catesb.*, and by the descriptions of Perrin (1892) and Nussbaum (1898). Corresponding to the specialisation and increased number of separate muscles (p. 427, *infra*), there is some modification in the disposition of nerve bundles, but the essential topographical relations are the same as in Urodela.

A single nerve trunk, N. ischiadicus, enters the limb caudad to the pelvis.

---

[1] Including N. cutaneus surae lateralis.

[2] No muscle like M. biceps cruris in mammals (cf. p. 399) is inserted in the region of the knee between the last two and the first of these nerves.

It gives off two nerves which pass ventrally to M. "pyriformis" (fig. 9), while the main stem passes dorsally to that muscle, just as in Urodela two nerves (N. isch. ventralis and N. pudendus) pass ventrally to M. caudalifemoralis but the main stem (Nn. fibularis and tibialis) dorsally to this muscle. The distribution of these nerves also shows them to be comparable with the urodele nerves. The one is comparable with N. pudendus, for it innervates M. "pyriformis" (and a caudalipuboischiotibialis also in *Ascaphus*, the only frog in which this muscle is retained—Noble, 1922, p. 52), and continues ventrally to M. "pyriformis" to end as a cutaneous nerve like *N. perinaealis*. To the last-named nerve the term "N. cutaneus femoris posterior" is often applied; but it is inappropriate since commonly applied among reptiles and mammals to another nerve, represented (in some Salientia, only, according to Nussbaum, 1898, p. 455) by a small twig passing between Mm. iliofibularis and "pyriformis," and arising from N. ischiadici close to the N. pudendus. This twig will therefore be now described as N. cutaneus femoris posterior (as in other Tetrapoda). In *Rana catesb.* I found this nerve to be of fair size, little smaller, indeed, than the N. perinaealis which passes from N. pudendus to the skin on the other side of M. "pyriformis" (subsequently shown to be comparable with M. caudofemoralis of other Tetrapoda, pp. 379, 409). The other nerve passing ventrally to M. "pyriformis," named "ramus profundus posterior" by Gaupp, has an extensive distribution to the enormous flexor mass (Mm. flexor cruris and flexor profundus, *mihi*, p. 414), and comprises, as in Urodela, a cutaneous element reaching the surface by passing through that mass, viz. between Mm. gracilis and sartorio-semitendinosus (Nussbaum, 1898, p. 548). To this cutaneous element the name N. cutaneus femoris medialis was applied by Gaupp, but is unsuited for comparative work, owing to its employment in mammals for a branch of N. femoralis. A similar nerve has already been termed *N. cutaneus femoris ventralis* in Urodela (p. 373), and this name will be now given to it also in the frogs.

The urodele N. fibularis is represented by two nerve trunks, e.g. in *Pipa* and *Xenopus* (Noble), which both pass dorsally to M. "pyriformis," and round the pre-axial side of M. iliofibularis, supplying the muscles on the dorsal aspects of thigh and shank respectively; these will be distinguished as *N. ischiadicus dorsalis* and *N. peronaeus* respectively. The arrangement differs from that described in Urodela (fig. 9) in the early separation of nerve bundles destined for the dorsum of the thigh from those for the dorsum of the shank, and the close apposition of the latter, as a distinct peronaeal nerve, to N. tibialis in the thigh. In most Salientia the disintegration of the N. fibularis has proceeded further and N. ischiadicus dorsalis itself is represented by bundles leaving N. peronaeus at different points for M. iliofemoralis, M. iliofibularis, and M. glutaeus with cruralis. The cutaneous bundle N. cutaneus surae lateralis remains associated with N. peronaeus as far as the knee; it was described by Gaupp and Nussbaum as "ramus cruris lateralis" of N. peronaeus.

The N. ischiadicus dorsalis is figured by Nussbaum (1898, figs. 2 and 3) as passing between the "long" and "short" heads of "biceps"; these two muscles evidently are Gaupp's Mm. iliofibularis and iliofemoralis. The passage between them of the nerve to the dorsal post-axial thigh musculature is characteristically like the course of nerve bundles destined for that musculature in Urodela, between Mm. iliofibularis and iliofemoralis (de Man). It will be shown subsequently that the mammalian name of "biceps" is as misleading when applied to these muscles as is Gaupp's name of "pyriformis" for the salientian muscle now shown to exhibit all essential features of the urodele M. caudalifemoralis (de Man).

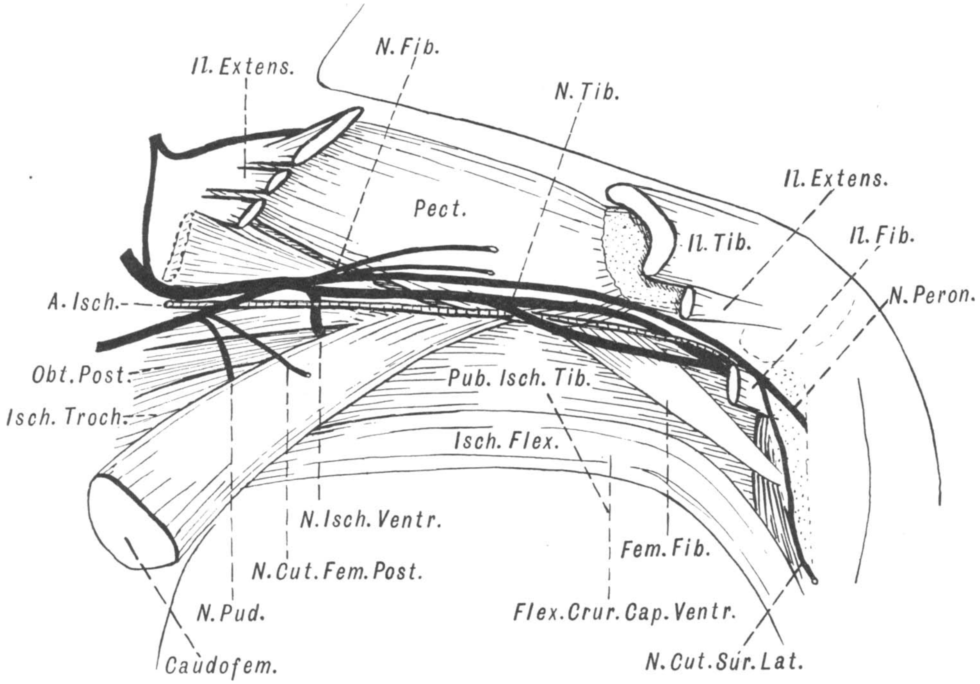

Fig. 2. Dorsal view of *Salamandra mac.*, with the right thigh in a position of medial (pre-axial) rotation, × 5. Parts of Mm. iliofibularis, ilioextensorius and iliotibialis have been removed. Two nerves, pudendus and ischiadicus ventralis, pass ventro-medially to M. caudofemoralis. The remaining trunks, Nn. tibialis and fibularis and the small N. cutaneus femoris posterior, all pass dorsally to that muscle. Of these N. fibularis passes round the pre-axial side of M. iliofibularis and over its dorsal margin to reach the leg. As it lies between M. iliofibularis and the Mm. iliofemoralis and pectineus it provides branches for dorsal thigh muscles; these branches are represented by N. ischiadicus dorsalis of other Tetrapoda (cf. figs. 3 and 9) and the continuation of the nerve, the N. fibularis, by their N. peronaeus. The figure shows the passage of N. tibialis laterally to the characteristic urodele M. femorofibularis, and its encircling of A. ischiadica; these relations are variable in Urodela (cf. fig. 1). It is to be observed that the whole of the musculature innervated through N. ischiadicus ventralis (long flexor muscles) passes to its pelvic attachment on the ventral aspect of M. caudofemoralis (cf. fig. 3).

N. tibialis is closely associated, as already mentioned, with N. peronaeus in the thigh, and thus passes between Mm. iliofibularis and "pyriformis" just as in Urodela it passes between Mm. iliofibularis and caudalifemoralis. I find no record of a branch leaving this nerve after passing dorsally to M. "pyriformis" for the supply of the distal part of any hamstring muscle (M. flexor cruris), comparable with the distal nerve supply recorded in Urodela (and in reptiles and mammals, p. 399).

The post-axial thigh nerves of Salientia are thus found to agree closely in course and distribution with those of Urodela, provided that Nussbaum's "long head of biceps" be admitted as the representative in frogs of M. iliofibularis and Gaupp's "pyriformis" as the vestige of the once large caudalifemoral musculature. These identifications have already been inferred by Noble (1922, pp. 52–54) on other grounds. According to Nussbaum (1898), the "pyriformis," now identified with the urodele caudalifemoralis, is absent in some of the Salientia.

3. REPTILIA. (Figs. 3, 12, 13 and 14.)

Gadow's descriptions have been supplemented and controlled by dissections of various Chelonia, Crocodilia and Lacertilia (p. 416), and by the accounts of *Sphenodon* published by Osawa and Frets, and of *Trionyx* by Ogushi. Subsequently to my dissection of *Alligator miss.* Romer published (1923) an account of its limb myology in which he reached the same conclusions as myself with regard to Gadow's M. pubi-ischio-femoralis internus Theil I + II, M. pubi-ischio-femoralis post. Haupttheil, and M. iliofibularis II. These are recognised as parts of M. obturator posterior and M. adductor (Gadow would call them M. pubo-ischio-femoralis externus and M. ischio-femoralis), and M. extensor iliotibialis, respectively.

As in Salientia, N. peronaeus is closely associated with N. tibialis till near the knee (fig. 9). A N. ischiadicus dorsalis is recognised, comprising two nerve bundles which leave the tibial-peronaeal stem independently (cf. figs. 1 and 2). The more proximal of these supplies M. iliofemoralis, the more distal one Mm. extensor iliotibialis (Gadow) and iliofibularis (Gadow); but in the Lacertilia, M. iliofemoralis receives no supply from this source, and (except in Monitors) M. extensor iliotibialis receives none (Gadow, 1882, p. 380).

Gadow's "Hautast d. N. peroneus profundus" (1882, pp. 352 and 354) is found in the alligator to be a cutaneous nerve, passing dorsally (fig. 3) to the insertion of M. iliofibularis near the knee; it is therefore now renamed *N. cutaneus surae lateralis*, like the similar nerve of Amphibia. This nerve has also been recognised in *Lacerta vir.* and *Varanus beng.* Nn. peronaeus and ischiadicus dorsalis pursue in reptiles the same course[1] relative to M. femoro-caudalis (Frets, 1909)[2], as that relative to M. pyriformis (Ecker, Gaupp and

---

[1] Gadow has shown certain of these relations in his figs. 34 and 37 (1882). His "iliofibularis I" of the alligator alone corresponds to the amphibian iliofibularis. His "iliofibularis II" presents all the features of a posterior differentiated portion of M. extensor iliotibialis or of a urodele M. ilio-extensorius; it presents a similar relation to N. peronaeus (cf. figs. 2 and 3).

[2] *Vide* Table on p. 434.

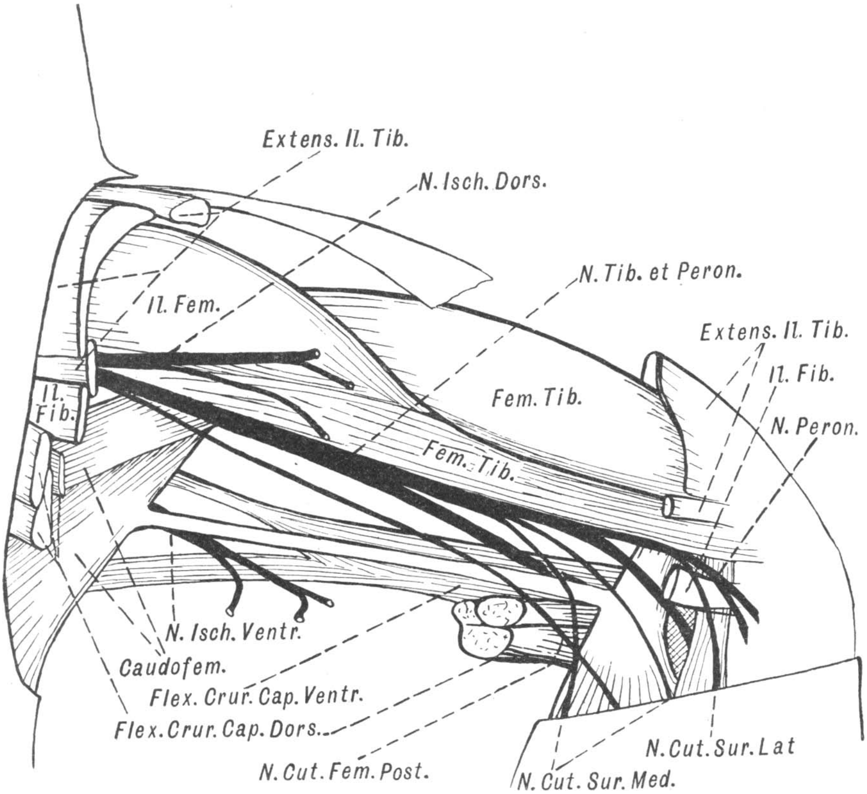

Fig. 3. Dorsal view of *Alligator miss.* × 1½, with the right thigh in a position of medial rotation, for comparison with fig. 2. As in that figure, the origins and insertions of Mm. extensor iliotibialis and iliofibularis are represented as cut short. In addition, the dorsal head of M. flexor cruris, which is wanting in Amphibia (figs. 1, 2 and 13), is represented as cut away in part, to show the course of N. ischiadicus ventralis ventrally to M. caudofemoralis. This nerve innervates the dorsal as well as the ventral head of M. flexor cruris, the nerves of supply being represented cut short as they pass dorsally on the distal side of M. caudofemoralis. The small ventral head of M. flexor cruris is provided with three heads of origin, the third of which is shown in fig. 12.

N. fibularis of Urodela is represented by two large nerve trunks, N. ischiadicus dorsalis and peronaeus, which, like the fibular nerve, pass round the pre-axial side of M. iliofibularis to their destinations; thus there has here been a segregation of muscular nerves destined for the dorsal part of the thigh from those destined for the leg and foot. A similar change has occurred in other Amniota and in Salientia (fig. 9). A N. cutaneus surae lateralis similar to that of Amphibia is again present.

N. cutaneus femoris posterior is unlike the corresponding nerves of Urodela and Salientia in its large size and distal extension beyond the knee; in this respect Reptilia resemble other Amniota. N. cutaneus surae medialis of Amphibia is represented in the alligator by two nerves.

Noble) in Salientia; the course is the same also as that relative to M. caudalifemoralis in Urodela (figs. 1, 2, 3, 9 and 14).

A N. ischiadicus ventralis leaves the main tibial-peronaeal stem and passes ventro-medially to M. femorocaudalis (Frets, 1909), a muscle to which the general tetrapod term of "caudofemoralis" will be found applicable (p. 409). This nerve forms a single trunk supplying superficial and deep ventral musculature in the post-axial region. It also supplies the dorsal head of M. flexor cruris (which comprises parts of the muscles described by Gadow as Mm. flexores tibialis internus and externus). The course of the nerve bundles to this dorsal head is like that of the bundles supplying the ventral head, as far as the distal margin of M. femorocaudalis; then they turn dorsally with a somewhat recurrent course (which is most pronounced in Lacertilia owing to the extension of the dorsal head into the tail, fig. 14). Gadow has recorded the innervation of the more dorsally attached flexor or "hamstring"[1] musculature from a nerve leaving the plexus independently, though pursuing a similar course to the nerve supply of the ventrally attached flexor musculature. I have not met with this condition. In the alligator and crocodile, in *Lacerta vir.*, *Uromastix spin.* and *Varanus beng.*, the nerve supply of the dorsal head of M. flexor cruris was closely associated with that of the ventral head on the ventral aspect of M. femorocaudalis, forming a single trunk, which I have named N. ischiadicus ventralis. It is inferred that the dorsal head of M. flexor cruris is a part of the same muscle as the ventral head, and that it has been formed by extension dorsally of a urodele-like M. flexor cruris, over the lateral surface of M. femorocaudalis (a conclusion which is considered further, on p. 416). The distribution of N. isch. ventr. to deep muscles is stated on p. 414. The cutaneous element of N. ischiadicus ventralis described in Amphibia (N. cut. femoris ventralis) is represented in Reptilia. It is identified as the nerve which pierces M. pubi-ischio-tibialis (in the alligator this muscle was described by Gadow as a part of "flexor tibialis internus"; that it is probably a part of M. pubi-ischio-tibialis was recognised by Gadow himself, 1882, p. 404, footnote).

N. pudendus of Amphibia is represented in reptiles by several distinct bundles arising directly from the plexus. There is a nerve supplying part of M. femorocaudalis (Frets)—Gadow's "caudi-ilio-femoralis," and several other nerves for the main mass of that muscle in Crocodilia and Lacertilia. A cutaneous element, mentioned by Gadow in the Crocodilia, and present also in Lacertilia as I have ascertained (*Lacerta vir.*), passes ventro-medially to M. femorocaudalis and emerges *between* the dorsal and ventral heads of

---

[1] The superficial ventral thigh musculature of reptiles is diploneural, as in mammals; the term "hamstring" or "M. flexor cruris" (p. 414) is reserved for that part which receives a metazonal innervation, though it is recognised that in various reptiles (mostly Lacertilians), in Monotremata, and rarely in Urodela, there is no plane of cleavage in the superficial ventral muscle mass corresponding to the boundary between the spheres of innervation of Nn. ischiadicus ventralis and obturatorius (*vide* p. 422, and the descriptions of Gadow, Westling and Noble).

M. flexor cruris. It is thus like that described in Amphibia as N. perinaealis; a similar nerve will be shown to exist in mammals.

Nerves to pelvi-caudal muscles also arise independently from the plexus (Gadow, 1882, pp. 362 *et seq.*); thus the pudendal nerve trunk described in Amphibia appears to be represented by a series of independent nerve bundles.

N. tibialis passes distally along the thigh dorsally to M. femorocaudalis just as in Amphibia it passes dorsally to M. caudalifemoralis (or the Salientian representative, p. 379), but it leaves the peronaeal nerve when the latter passes round to the dorsal aspect of M. iliofibularis, again resembling Amphibia. Its constituent bundles are subdivided near the knee by the long tendon of M. caudofemoralis (which is in most reptiles thus provided with a more distal insertion in addition to that on the femoral shaft). Cutaneous elements are distributed to the lateral aspects of thigh and shank after passing between Mm. femorocaudalis and iliofibularis. The most proximal of these, a long nerve, thus corresponds to the Amphibian N. cut. femoris posterior (figs. 3 and 9). Two other nerves pursue a similar course, but accompany the tibial nerve till nearing the knee; they are derived from Gadow's "Stamm III" and agree in their course and distribution with N. cut. surae medialis of the Urodela (the more distal of these appears to be that described by Gadow, 1882, p. 352).

The nerve which, in Urodela, supplies the distal part of M. flexor cruris after passing with N. tibialis dorsally to M. caudalifemoralis, is represented in the Crocodilia by the branch described by Gadow as leaving his "Stamm III" for the supply of M. flexor tibialis (1882, p. 353).

The post-axial thigh nerves of Reptilia thus present an arrangement closely resembling that of Amphibia; in the close association of N. peronaeus with N. tibialis in the thigh they are more like Salientia than Urodela. The additional nerve supplying M. flexor cruris caput dorsale (which is absent in Amphibia), accompanies N. ischiadicus ventralis as far as the distal margin of the great retractor of the thigh, M. femorocaudalis (Frets). M. femorocaudalis presents attachments and nerve relations like those of the urodele M. caudalifemoralis.

4. AVES.

A single N. ischiadicus enters the limb, and the nerves for dorsal thigh muscles separate early from those for the dorsum of the shank, as in frogs and reptiles; N. peronaeus proceeds with N. tibialis till close to the knee. A N. ischiadicus dorsalis is recognised, as in reptiles, arising in two stems from the main N. ischiadicus, the one for supply of Mm. glutaeus medius and glutaeus externus, the other for Mm. "tensor vaginae" and "biceps" (Selenka, 1869, and de Man, 1873, p. 98).

The cutaneous element already described for Amphibia and reptiles as N. cut. surae lateralis is represented again by a similar nerve leaving N. peronaeus near the knee, after passing with that nerve dorsally to the insertion of M. iliofibularis (cf. de Man's Plate II and p. 98, nerve No. XXIV).

In the fowl and pigeon I have verified the passage of Nn. peronaeus and ischiadicus dorsalis dorsally to M. caud-ilio-femoralis Gadow ("adductor longus"—de Man), and then round the pre-axial side of M. iliofibularis ("biceps"—de Man). These relations are like those relative to Mm. femorocaudalis and iliofibularis in reptiles, to Mm. "pyriformis" and iliofibularis in frogs, and to Mm. caudalifemoralis and iliofibularis in urodeles.

A nerve identified as N. ischiadicus ventralis supplies muscles named caud-ilio-flexorius and ischio-flexorius by Gadow (1891, pp. 162 and 166); it passes ventrally to Gadow's caud-ilio-femoralis, just as in other classes it has been seen to pass ventral to the caudofemoral musculature. These muscles correspond to the caput dorsale and caput ventrale respectively of M. flexor cruris in reptiles (pp. 381, 419). N. perinaealis (*vide infra*) passes between them.

The proximally situated M. ischiofemoralis Gadow ("quadratus femoris"—de Man) is innervated through an independent branch of the main sciatic stem, but its close resemblance to the reptilian M. ischiotrochantericus and to the urodele ischiofemoralis (de Man) points to this nerve being a segregated portion of the primitive N. ischiadicus ventralis. Gadow has described a cutaneous element (1891, p. 420) passing ventrally to M. caud-ilio-femoralis to reach the perinaeal region; its course and distribution identify it as N. perinaealis of other classes. Another cutaneous nerve mentioned by this author as reaching the shank after close association with the nerves to his muscles 36 and 37 (p. 420) appears to be the N. cut. femoris posterior; he clearly figures this nerve (e.g. Taf. XXIII *a*, fig. 1) passing dorsally to M. caud-ilio-flexorius and caud-ilio-femoralis, but ventrally to M. iliofibularis, and I have found it in the fowl and pigeon. It appears to be the nerve XVII of de Man (1873, p. 98).

The distal innervation for M. flexor cruris already mentioned for the alligator and various urodeles is closely reproduced by the nerve supplying the "accessory" insertion of caud-ilio-flexorius (Gadow, 1891, p. 421 and Taf. XXIII *c*); the nerve bundles have in each instance passed with N. tibialis dorsally to the caudofemoral musculature. Gadow (1891, p. 422) has mentioned a cutaneous branch of N. tibialis which appears to correspond to the N. cut. surae medialis of other classes.

The principal features of neuro-muscular topography are clearly shown in Gadow's Taf. XXIII *b*, figs. 2 and 4, and Taf. XXIII *a*, where the passage of Nn. peronaeus and ischiadicus dorsalis dorsally to Mm. iliofibularis and caud-ilio-femoralis, the passage between these muscles of Nn. tibialis and cut. femoris posterior, and the passage ventrally to both of them of N. ischiadicus ventralis, are seen to offer a close resemblance to reptilian conditions. M. caud-ilio-femoralis presents relations like those of the reptilian M. femorocaudalis (with which it is identified), and Mm. caud-ilio-flexorius and ischio-flexorius are respectively identified (p. 426 *infra*) as the dorsal and ventral heads of M. flexor cruris. The innervation of M. caud-il. fem. has, with reduction in size and a situation mainly in the thigh, become closely associated with N. ischiadicus ventralis (cf. mammals). N. pudendus has disintegrated with separation of perinaeal components from the motor nerve for M. caudilio-femoralis.

5. MAMMALIA. (Figs. 4–12, 14 and 15.)

The structural pattern of the thigh of the more primitive Mammalia has been misinterpreted in various respects, mainly owing to attempts to describe it in terms of the structures found in the more specialised mammals. The confusion may be attributed to our earlier and more exact acquaintance with a number of these mammals, among which may be cited man and various domestic animals.

An investigation of the thigh structure of some of the more primitive mammals has revealed a structure sufficiently like that in surviving reptiles (and birds) to justify the detailed comparisons which will be here attempted. The conclusion is reached that the structural pattern of the tetrapod thigh has become obscured in the more specialised mammals mainly by the loss of certain muscles[1], but also by the reduction in size or change of attachment of muscles; further, great extension and differentiation of certain muscles[2] has complicated the picture in other directions.

The most satisfactory account of thigh structure among the less specialised mammals is that provided by Leche for the Insectivora. He not only recognised Mm. caudofemoralis and femorococcygeus as distinct entities in mammalian myology, but he correctly recognised some of the resemblances between the thighs of Monotremata, Reptilia and Insectivora. His account will therefore be taken as a basis for the terminology and for a discussion of mammalian conditions. In regard to the Insectivora, it has been found that certain amendments of Leche's descriptions are necessary; and considerable additions have been required in regard to the course of cutaneous nerves.

(*a*) *Revision of the Insectivora.* (Figs. 4, 5 and 6.)

Menotyphla. Examples of *Tupaia pict.*[3] and *Macroscelides* sp.[3] have been dissected. It is worthy of note that Leche's descriptions[4] bring out several points of difference between these animals. Mm. femorococcygeus and glutaeus maximus are not at their origin distinct from one another in *Tupaia;* both arise from the vertebral column. In *Macroscelides*, M. femorococcygeus has a distinct origin from the tuber ischii, but, as in *Tupaia*, it overlies N. ischiadicus. To Leche's account we may add that *Tupaia* resembles *Macroscelides* in the presence of a separate insertion for M. femorococcygeus on capsular

---

[1] Caudofemoralis; tenuissimus; flexor cruris caput dorsale.

[2] Iliofemoralis; ischiotrochantericus; flexor cruris caput ventrale.

[3] By the kindness of Prof. Le Gros Clark I have recently had the opportunity of dissecting specimens of *Ptilocercus lowii born.* and *Elephantulus myurus jamesoni.* The features under discussion in this paper are similar in *Ptilocercus* and *Tupaia,* and in *Elephantulus* and *Macroscelides* respectively.

[4] Supplemented by Carlsson's descriptions (1909 and 1922) of various other Tupaiidae and Macroscelididae.

structures of the knee joint, while the glutaeus maximus is attached mainly to the third trochanter.

Leche observed that a M. caudofemoralis in *Tupaia*, with a caudal origin, is closely reproduced in *Macroscelides* by a muscle taking origin, not from the vertebral column, but from the tuber ischii. The characteristic relation to

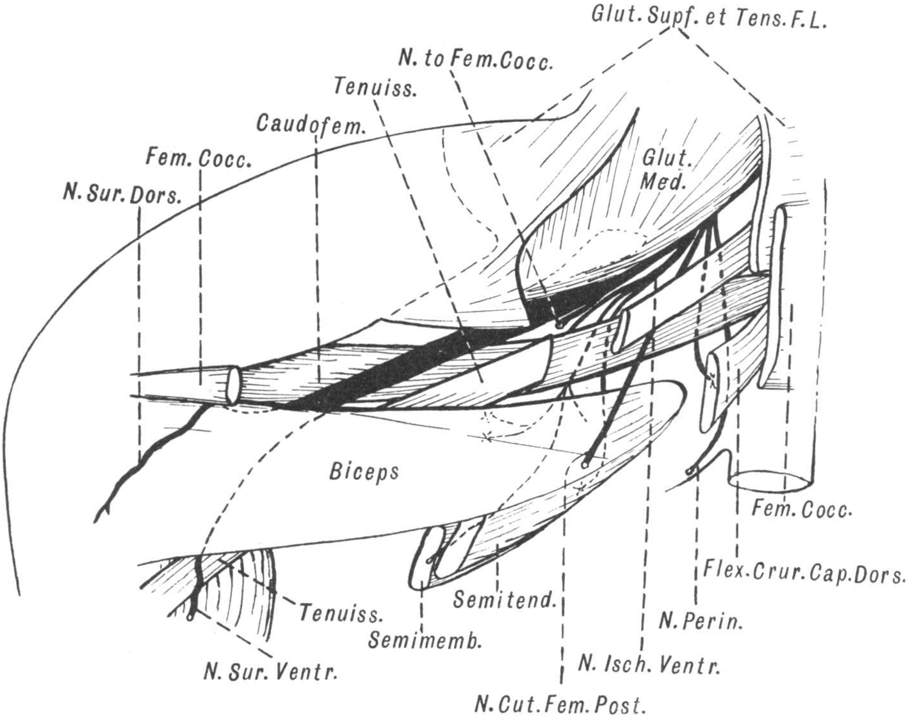

Fig. 4. *Tupaia pict.* × 2¼, illustrating most of the features of a primitive eutherian thigh (cf. figs. 5–14). Dorsal view, with the left thigh in a position of medial rotation; for comparison with fig. 3. Parts of Mm. glutaeus superficialis and femorococcygeus, of the dorsal head of M. flexor cruris, of Mm. semimembranosus and semitendinosus have been cut away, as also a short piece of M. iliofibularis (tenuissimus).

As in reptiles, M. flexor cruris comprises a dorsal as well as a ventral head, but the former is small and the latter large. Both are supplied by N. ischiadicus ventralis, which as in all Tetrapoda passes ventrally to M. caudofemoralis; the nerve to the dorsal head here pursues a somewhat independent course from N. ischiadicus. The ventral head of M. flexor cruris of mammals has acquired an attachment on the lateral side of the leg (M. biceps) besides its medial attachment (Mm. semimembranosus and semitendinosus); N. cutaneus surae lateralis is represented by two nerves, N. surae dorsalis and N. surae ventralis, passing respectively dorsal and ventral to M. biceps. As in reptiles, N. perinaealis passes ventrally to M. caudofemoralis (figs. 1 and 14) and between the two heads of M. flexor cruris; and M. cutaneus femoris posterior passes between Mm. iliofibularis and caudofemoralis. Nn. tibialis and peronaeus pass dorsally to M. caudofemoralis as in other Tetrapoda, the latter dorsally also to M. iliofibularis (fig. 9). A specialised feature of *Tupaia* consists in the differentiation of M. femorococcygeus from the glutaeal musculature. Its nerve, a component of N. ischiadicus dorsalis, passes dorsally to M. iliofibularis, like the latter nerve in other Tetrapoda.

N. ischiadicus (to which it is medial as it approaches the femur) and the relations to adjacent muscles are similar; the two muscles were homologised. He also observed that tenuissimus and the caudal head of semitendinosus, found in *Tupaia*, are unrepresented in *Macroscelides*. The latter animal is thus characterised by the suppression of four caudal muscle attachments. The origins of two muscles (femorococcygeus and caudofemoralis) have been transferred to the tuber ischii, and two other muscles have disappeared.

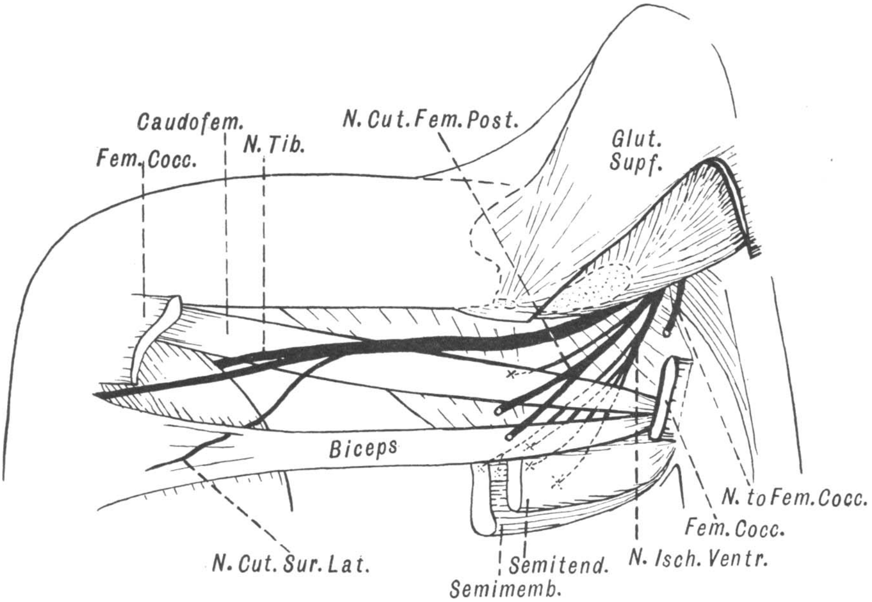

Fig. 5. *Macroscelides* sp. Left thigh, ×2¼, position and dissection similar to that of *Tupaia* in fig. 4. Modifications of the muscle arrangement seen in *Tupaia* consist in the loss of M. tenuissimus, and of the dorsal head of M. flexor cruris, and in the transference to the tuber ischii of the origins of Mm. femorococcygeus and caudofemoralis. Muscle-nerve relations are like those of *Tupaia*, excepting those involved in the above muscle changes; N. cutaneus femoris posterior, for example, is not separated from the nerve to femorococcygeus by a tenuissimus. The innervation of M. biceps from N. ischiadicus ventralis (and not as described by Leche) is illustrative of its derivation in phylogeny by differentiation of M. flexor cruris (cf. fig. 1). A single N. cutaneus surae lateralis is present (as in *Elephantulus*, p. 394).

Further examination of these animals serves to support and strengthen the inferences made from Leche's data. The resemblance of the two ischially attached muscles of *Macroscelides* with the Mm. caudofemoralis and femorococcygeus respectively of *Tupaia* is even closer than Leche realised.

M. femorococcygeus is in the Menotyphla superficially disposed between Mm. glutaeus maximus and biceps (figs. 4 and 5). Two cutaneous branches of the peronaeal nerve reach the surface on the lateral aspect of the knee[1]. Of these, one, the N. surae ventralis, passes in *Tupaia* (fig. 4) between tenuissimus and biceps, but in the Macroscelididae examined both tenuissimus

---

[1] This statement does not refer to the Macroscelididae.

and the N. surae ventralis are wanting. The other cutaneous branch, N. surae dorsalis, has a different course, for it passes between biceps and femorococcygeus (or pierces the margin of biceps), in all four members of the Menotyphla which have been examined (cf. footnote, p. 394).

The nerve to femorococcygeus passes dorsally (superficially) to the muscle identified as "caudofemoralis"; it thus differs from the course of the nerves to the hamstring muscles and of the nerve to the biceps in particular. The latter distinction fails in Leche's account owing to his erroneous account of the innervation of biceps (*vide infra*, p. 388). M. femorococcygeus is dorsal to both Nn. peronaeus and tibialis (like the glutaeal musculature).

Differences in the relations of this muscle in *Tupaia* and *Macroscelides*[1] depend mainly on its enormous size in *Macroscelides* and on special features in adjacent muscles, viz. (1) the loss of tenuissimus, (2) the loss of the caudal head of semitendinosus, and (3) the transference of the origins of both caudofemoralis and femorococcygeus from the vertebral column to the tuber ischii. Thus N. pudendus and the nerve to obturator internus pass deep to M. femorococcygeus in *Tupaia*, but do not do so in *Macroscelides.*

The present investigation has shown that in a large number of mammals there is present a muscle showing the characteristic features of M. femorococcygeus in *Tupaia* (pp. 394, 405). It is therefore inferred that *Macroscelides*[1] has been specialised in the acquisition of an ischial origin for M. femorococcygeus. This view finds support in the considerations that (1) its habits are specialised, (2) the origin is found on the tuber ischii in a few other mammals (including the gorilla, chimpanzee (fig. 10 C), gibbon, *Loris grac.* and *Erinaceus*), (3) the similar transference in a few mammals of the origin of M. caudofemoralis from the caudal vertebrae to the tuber ischii (*vide infra*, pp. 388, 397), (4) the evidence of specialisation in *Macroscelides*[1] presented in the loss of tenuissimus and of the caudal head of semitendinosus, as well as in certain other features which are beyond the scope of this paper.

M. caudofemoralis. The muscles so identified in *Tupaia* and *Macroscelides* agree in being placed between Mm. femorococcygeus superficially and Mm. quadratus femoris, adductores and semimembranosus on the deep aspect. They have similar insertions, in *Macroscelides* somewhat restricted in extent. In each animal the muscle is deep (ventro-medial) to the tibial and peronaeal nerves and the sural cutaneous elements in each of them, and deep also to the nerve to M. femorococcygeus. The nerve supplying the muscles identified as "caudofemoralis" agrees in *Tupaia* and *Macroscelides* in passing between Mm. femorococcygeus and quadratus femoris. The caudofemoral muscles are in each animal superficial to the nerves to biceps, semitendinosus and semimembranosus (the nerve to the first of these separating M. caudofemoralis from the two last)[2]. Differences in the relations of the muscles appear to be due to (1) loss in *Macroscelides* of certain muscles, mentioned above (figs. 4 and 5), and (2) the ischial origin of the muscle in question in *Macroscelides*[1],

---

[1] *Elephantulus* is similar.

[2] This account of the innervation of biceps differs from that of Leche (*vide infra*).

whereas in *Tupaia* this is caudal. Thus N. pudendus (with N. perinaealis) and the nerve to the obturator internus passing medially to the tuber ischii in *Macroscelides* come into no close relation to M. caudofemoralis. In *Tupaia*, as in *Macroscelides*, N. cut. femoris posterior passes superficially to this muscle, but the other two nerves lie deep to it.

It will be shown that among the more primitive mammals a muscle presenting features similar to those of the caudofemoralis of *Tupaia* is of widespread occurrence. The inference that the ischial origin in *Macroscelides* is the more specialised is supported by considerations similar to those already advanced for M. femorococcygeus. The ischial head of origin has been found in a few other mammals only, viz. in *Tarsius spectr.* (Appleton, 1921, Plate IV, and p. 468), in some Lipotyphlous Insectivora and in *Manis*. Parsons' descriptions of Rodentia point to its occurrence in various families of that order. Inasmuch as the thigh structure of *Hapale* (fig. 8) approximates closely to that of *Tupaia*, it will be seen that *Macroscelides* differs from *Tupaia* in regard to its M. caudofemoralis in a manner similar to that in which *Tarsius* differs from *Hapale*. In *Macroscelides*, however, as already mentioned, M. femorococcygeus has also acquired an ischial origin, but this is not so in *Tarsius* (Appleton, 1921, p. 467).

The innervation of M. biceps in Menotyphla (figs. 4 and 5). The nerve supplying this muscle intervenes between M. caudofemoralis and Mm. semimembranosus and semitendinosus (caput isch.). In *Tupaia* it comprised three bundles associated with the nerve to semitendinosus and less closely associated with that to semimembranosus, the series of nerves forming a trunk described by Leche as "4 i." This account of the innervation of biceps differs from that of Leche (1883, p. 44), who describes it as coming from the nerve "4 k," while he definitely states that "4 i" does not supply biceps. Le Gros Clark (1924) has described a nerve supply to biceps in *Tupaia* in its proximal part from N. tibialis and distally from N. peronaeus (where these nerves form a part of the sciatic nerve), apparently corresponding to Leche's nerves "4 k" and "4 i." The innervation from "4 i" was probably overlooked by Leche owing to its concealed position. I have been unable to detect any branch to the distal part of biceps from N. ischiadicus after this nerve has passed dorsally to M. caudofemoralis[1]. It is possible that both Leche and Le Gros Clark have regarded one of the above-mentioned sural branches of the peronaeal nerve (probably N. surae dorsalis, p. 387) as a motor twig ("4 k") to biceps, inasmuch as they have not described these cutaneous nerves.

Between the nerves named "4 k" and "4 i" by Leche there are two topographical differences which are significant for the study of comparative myology. Between them are situated both the caudofemoralis and tenuissimus muscles. This arrangement is general throughout Mammalia (except when one of these muscles is absent), and corresponds to the relations presented

---

[1] This statement refers to my dissections of *Ptilocercus* and *Elephantulus* as well as to those of *Tupaia* and *Macroscelides*.

by similar muscles in other classes of Tetrapoda (e.g. by Mm. femorocaudalis and iliofibularis respectively in *Sphenodon*, p. 379, cf. figs. 1 and 3, and the table of synonyms, p. 434).

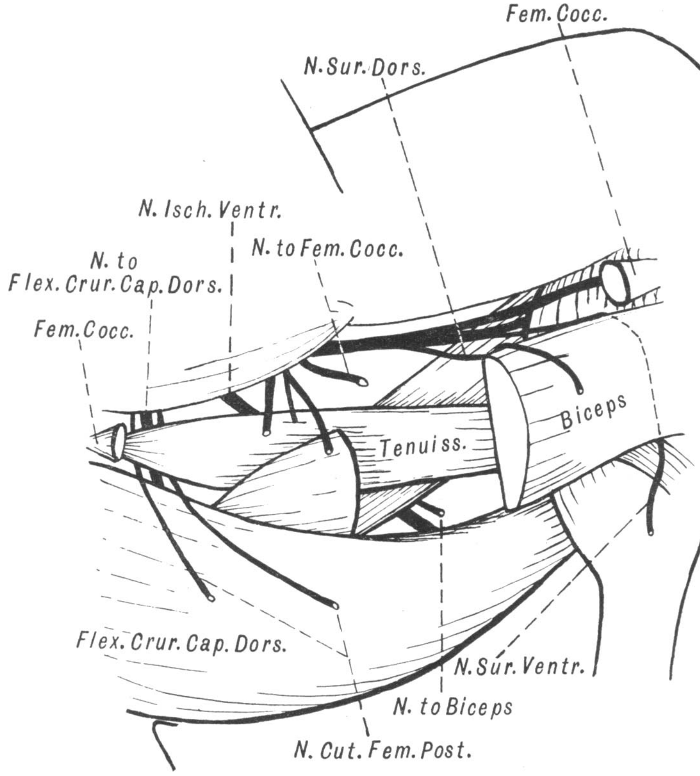

Fig. 6. *Talpa eur.* Right thigh, ×3½. Position and dissection similar to that of *Tupaia* in fig. 4, p. 385, except that M. biceps is divided and the dorsal head of M. flexor cruris has not been divided.

The structural pattern of the primitive eutherian thigh is preserved almost unaltered despite the enormous enlargement of certain muscles, especially biceps and the dorsal head of M. flexor cruris. One modification of the musculature, the transference of the origin of M. caudofemoralis from the tail to the tuber ischii, involves a failure of some nerves to come into direct relation with it, as in *Macroscelides* (fig. 5). The extensive skin area of the lateral thigh region is innervated by Nn. cut. femoris posterior and cut. surae lateralis, each of which is represented by more than one large bundle. As in Amniota generally, the nerves to M. flexor cruris (including the nerve supply of biceps and of the dorsal head) pass ventrally to M. caudofemoralis, N. cut. femoris posterior passes ventrally to M. iliofibularis, but N. cut. surae lateralis (comprising Nn. surae dorsalis and surae ventralis) and N. ischiadicus dorsalis (of which the nerve to femorococcygeus is a part) pass dorsally to it.

M. caudofemoralis is the unnamed muscle deep to tenuissimus.

Lipotyphla (fig. 6). Examples of *Talpa eur.* and *Erinaceus eur.* have been dissected. Leche stated that M. caudofemoralis is absent from all the Insectivora he examined except *Tupaia* and *Macroscelides*. I have, however, not found it possible to differentiate between the M. praesemimembranosus of *Talpa* and *Erinaceus* and the caudofemoralis of *Macroscelides* (which has already been homologised with that of *Tupaia*). It appears from Leche's account that in most Lipotyphla there has occurred a transference to the tuber ischii of the origin of M. caudofemoralis such as has undoubtedly occurred in *Talpa* and *Erinaceus* as well as in *Macroscelides*.

The relations claimed by Leche for "praesemimembranosus" (1883, p. 94) are equally true for the caudofemoralis of Menotyphla. Proximal attachments have been already discussed; distal attachments on the shaft of the femur present relations to neighbouring muscle attachments which are very much alike (cf. Leche's figs. 60, 63, with fig. 5 *supra*). It may be further pointed out that the relations already established for Menotyphla between M. caudofemoralis and nerves, viz. Nn. tibialis and peronaeus, surae dorsalis and surae ventralis (p. 387), and to the nerves to hamstring muscles (semitend., semimembr. and biceps), are identical with those presented by M. praesemimembranosus in *Erinaceus* and *Talpa*, and Leche's figures show that the same may be said for M. praesemimembranosus in certain other Lipotyphlous Insectivora (cf. *Chrysochloris*, fig. 93, with *Erinaceus*, fig. 75, Leche, 1883)[1]. The muscle thus identified in Lipotyphla as M. caudofemoralis (Leche's praesemimembranosus) differs from that of *Tupaia* in just those features which are incidental to the transference of its origin to the tuber ischii, as in *Macroscelides*. For example, the nerve to the dorsal head of M. flexor cruris caput dorsale does not pass ventrally to it (fig. 6).

It is significant, in connection with the identification here made between Leche's lipotyphlous praesemimembranosus and the menotyphlous caudofemoralis that Leche claimed a praesemimembranosus exclusively in those Insectivora in which he described caudofemoralis as absent.

Leche's account of the innervation of M. biceps in Lipotyphla requires amendment. Two nerves pass to it in *Talpa* from the hamstring nerve (Leche's "4 i"), which travels ventro-medially to M. caudofemoralis and supplies also the Mm. semimembranosus and semitendinosus caput ischiale. No twigs were found to supply it from N. surae dorsalis or N. surae ventralis. Now Leche described an additional innervation of M. biceps through a distal nerve "4 k," travelling dorsally to M. caudofemoralis as a part of N. ischiadicus. This is probably N. surae dorsalis whose cutaneous character he overlooked. In *Talpa* there are, besides the Nn. surae dorsalis and surae ventralis (resembling those of *Tupaia*, p. 386), four other cutaneous nerve bundles distributed to the extensive region over the greatly enlarged Mm. flexor cruris caput dorsale (semitendinosus caput caudale) and biceps (fig. 6). Two pursue a course like N. cut. femoris posterior ventrally to tenuissimus and then between femorococcygeus and biceps; they pass medially to the tuber ischii

---

[1] Leche's fig. 90 of *Erinaceus* appears to show the nerve "4 i" in incorrect relation with "M. praesemimembranosus," i.e. M. caudofemoralis. But in his fig. 75 and his statement on p. 44 there is agreement with my finding.

in company with the large nerve to M. semitendinosus caput caudale (Leche's "4 d"), like the single N. cut. femoris posterior found in *Macroscelides*. The other two present features suggesting separated portions of N. surae dorsalis.

Résumé. Concerning Mm. caudofemoralis, femorococcygeus and biceps, and the associated nerves in Insectivora.

The conclusions of Leche have been found to require modification. The "praesemimembranosus" of that author has been identified with his "caudofemoralis," and the latter name has been adopted for use throughout Insectivora (and mammals generally, p. 411). The lipotyphlous praesemimembranosus of Leche has been found to differ from the muscle so named in the cat (cf. fig. 12 I) and from the "ischiocondyloideus" of various Primates (with which muscles it was compared by Leche, 1883, p. 95), inasmuch as these are parts of the semimembranosus musculature, situated medially to the nerves to Mm. biceps and semitendinosus and medially also to M. caudofemoralis in such Carnivora and Primates as possess it (e.g. *Lutra*, fig. 7, and *Lemur*, Appleton, 1922, p. 301). M. biceps is found to be innervated solely through the main hamstring nerve trunk (Leche's "4 i"), which passes ventro-medially to M. caudofemoralis. It is thus found to be a part of the ventral or hamstring musculature, and not of the dorsal musculature, as Leche supposed (*vide* p. 424 *infra*). Leche's account of Insectivora would lead to the inference that Menotyphla and Lipotyphla differ (*a*) in the occurrence of a praesemimembranosus and a caudofemoralis, and (*b*) in the mode of innervation of biceps. But in none of these features is it found possible to maintain a distinction between these groups of Insectivora. The structure of the post-axial region of the thigh and buttock presents no difficulty to Carlsson's proposed separation of the Macroscelididae from the Tupaiidae, and her association of the former with the Lipotyphla.

The innervation of M. caudofemoralis in Insectivora is found to be through a nerve passing between Mm. tenuissimus and the ischially-attached hamstrings (M. flexor cruris cap. ventr.); it is closely associated at first with N. tibialis and with the nerves to M. flexor cruris cap. ventr. (biceps, semitendinosus and semimembranosus); it leaves N. tibialis in company with the nerve bundles to the last-named muscle mass in *Tupaia*, *Macroscelides* and *Chrysochloris*, but more proximally than those bundles in other Insectivora.

(*b*) *Comparison of Insectivora with other Mammalia.*

(Cf. figs. 4, 5 and 6 with figs. 7–15.)

The arrangement of structures already described in the thigh of *Tupaia pict.* and present also in a modified form in *Macroscelides* and other Insectivora, presents a close resemblance to that found in other mammals, and is especially like that in the more primitive ones. For example, in *Hapale jacch.* among

Primates (fig. 8), in *Genetta* and *Lutra* (fig. 7) among Carnivora, and in *Erethizon* (fig. 15) and *Mus* among Rodentia, the topographical relations of muscles to one another, to nerve bundles and the distributions of nerves agree very closely with those in *Tupaia*. Monotremata (fig. 14) and Marsupialia (fig. 11) present the same arrangement of structures, though in the former the enormous size of M. flexor cruris cap. dors. (cf. the caudal head of semitendinosus in Insectivora, *vide* p. 420) and the loss of tenuissimus, and in marsupials (fig. 11) the proximally displaced site of insertion of

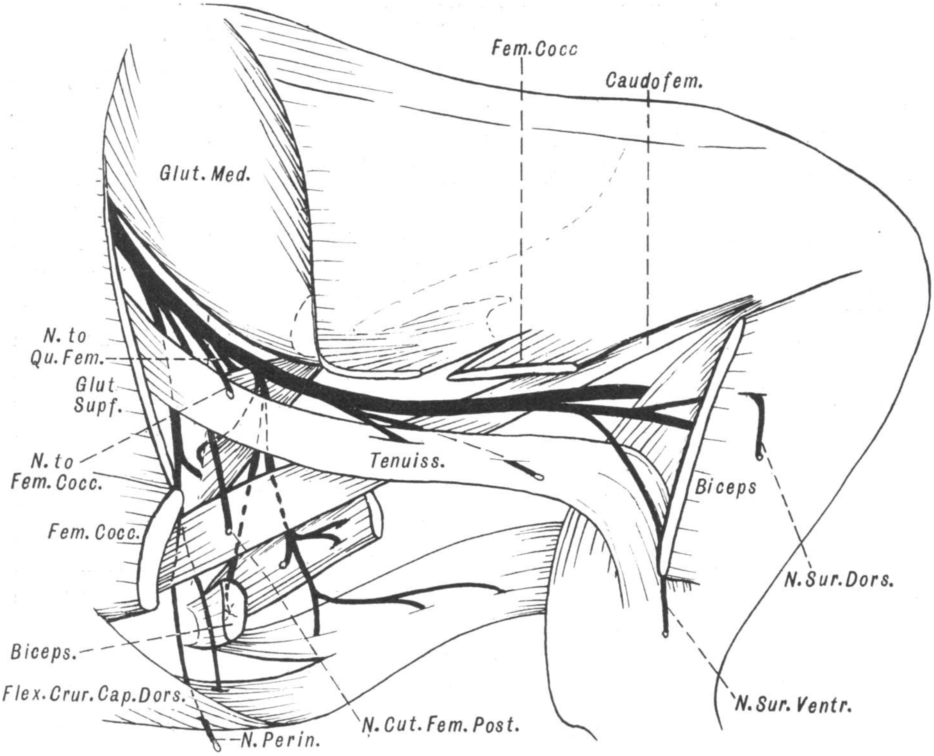

Fig. 7. *Lutra vulg.* Right thigh, × $\frac{3}{4}$. Position and dissection similar to that of *Tupaia* in fig. 4, p. 385, except that biceps has been removed in part, and the dorsal head of M. flexor cruris has not been divided. The relations of nerves to muscles (of which a primitive eutherian arrangement is retained) are similar to those found in Tetrapoda generally, excepting the passage of a nerve *through* M. iliofibularis and of N. perinaealis through M. flexor cruris cap. dors. N. ischiadicus ventralis is represented by (1) a large trunk supplying the ventral head of M. flexor cruris, (2) a nerve accompanying Nn. perinaealis and pudendus, and supplying the dorsal head of flexor cruris, (3) the nerve to quadratus femoris, (4) the nerve to obturator internus. All these pass ventrally to M. caudofemoralis. N. ischiadicus dorsalis is represented by (1) the nerve to tenuissimus, (2) N. glutaeus anterior (sup.), (3) N. glutaeus posterior (inf.), (4) the nerve to femorococcygeus. N. cutaneus surae lateralis is represented as in many other Eutheria by two nerves (Nn. surae dorsalis and ventralis); it passes dorsally to M. iliofibularis.

M. caudofemoralis, have in the past obscured the close resemblance of the three mammalian sub-classes.

Among Eutheria there has been a tendency, with specialisation of the limbs, to the loss of one or more of the muscles caudofemoralis (fig. **10 D**), tenuissimus (figs. 5 and 8), and flexor cruris cap. dors. (often described as the caudal head of semitendinosus) (fig. **10**). Failure to recognise them when present has been responsible for many misleading descriptions to be found in the literature of mammalian myology (pp. 395, 406, 411, 430). Errors may also be traced to the varied mode of union of the dorsal with the ventral head of M. flexor cruris (p. 424) and to the confusion by various writers of parts of the glutaeal (p. 406) and adductor (p. 431) musculature with "biceps" and "(pre-)semimembranosus" respectively.

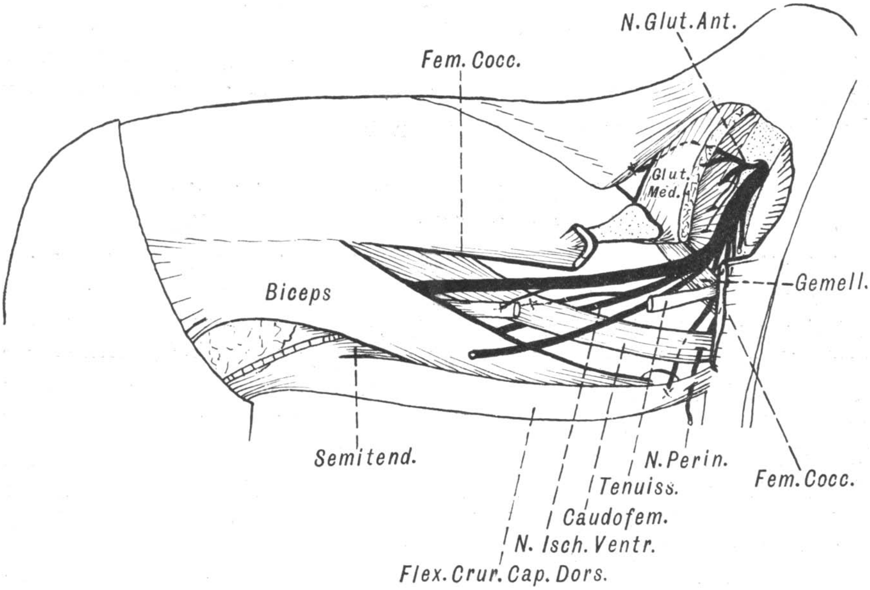

Fig. 8. *Hapale jacch.* Left thigh, × 2. Position and dissection similar to that of *Tupaia*, fig. 4, p. 385, except that the dorsal head of M. flexor cruris has not been divided. Mm. tensor fasciae latae and femorococcygeus are very incompletely differentiated from M. glutaeus superficialis, while other primitive eutherian features exhibited by *Tupaia* are also retained. Mm. caudofemoralis and tenuissimus present the relations to nerves which are characteristic of Tetrapoda generally (cf. fig. 1). N. ischiadicus dorsalis is represented by the anterior and posterior glutaeal nerves (whose distribution is indicated), and by the nerve to tenuissimus. The tetrapod, N. pudendus, is represented by the "N. pudendus," by the nerve to M. caudofemoralis (which has become bound up with N. ischiadicus ventralis), and by N. perinaealis. The dorsal head of M. flexor cruris is supplied by N. ischiadicus ventralis as in all Amniota (figs. 3 and 13). N. perinaealis, as an individual variation in *Hapale jacch.*, may pierce M. caudofemoralis and the dorsal head of M. flexor cruris (cf. fig. 7); the condition is shown in this figure. In other individuals examined it passed deep to both muscles, as in Amniota generally.

In mammals the sequence of structures in the proximal part of the thigh from the dorsal to the ventral aspect is the same as that found in the Insectivora (with modifications due to reduction of the part or whole of certain muscles), viz. Mm. glutaei and muscles derived therefrom (tensor fasciae latae, femorococcygeus, pyriformis, scansorius, glutaeus ventralis), Nn. surae dorsalis and ventralis[1], and N. peronaeus; M. tenuissimus with its nerve; N. cut. femoris posterior and Nn. tibialis and cut. surae medialis; M. caudofemoralis with its nerve; M. flexor cruris cap. dors.; N. perinaealis; M. biceps with its nerve, M. semitendinosus with nerve, M. semimembranosus with nerve; Mm. gemelli, obturator internus and quadratus femoris with nerves. In the distal part of the thigh M. biceps is interposed between Nn. surae dorsalis and ventralis[2] when both of these nerves are present (fig. 10).

Notes for guidance in the dissection of the glutaeal region and adjacent parts of the thigh, in Mammalia.

Attention should first be given to the distinction of superficial glutaeal from hamstring musculature. In the interval between them N. cut. femoris posterior comes to the surface, near the middle of the thigh. The interval should then be followed medially, and the hamstring muscles examined for a caudal head. N. perinaealis is found passing through or deep to the caudal head. If the latter is absent it emerges at the caudal margin of the superficial glutaeal musculature (frequently represented by a M. femorococcygeus). At this stage the nerve supply of the "caudal head of the hamstrings" (M. flexor cruris cap. dors.) is found. In the interval between Mm. biceps and glutaeus superficialis the sciatic nerve should be inspected, and the nerve to femorococcygeus secured; the origin of sural nerves from N. ischiadicus may be searched for at this stage. If a tenuissimus is present it is recognised by general relations, and more definitely by its relation to N. cut. femoris posterior (to which it is dorsal). If a M. caudofemoralis is present it will be found to intervene between the main sciatic nerve (Nn. tibialis and peronaeus) and the nerves to the hamstring muscles; N. perinaealis may be expected to be deep to it, but N. cut. femoris posterior superficial to it.

(*c*) *Absence of muscles in certain mammals.*

Reference has already been made (p. 393) to the frequency with which Mm. caudofemoralis, tenuissimus and flexor cruris cap. dors. are absent in mammals, mainly in the more specialised orders and members of orders. The distinctive features of the courses of certain nerves become obscured in these instances. Thus, when M. tenuissimus is absent, a valuable criterion for the distinction of N. cut. femoris posterior from Nn. surae dorsalis and ventralis is wanting (figs. 5 and 8). An approximate distinction is however

---

[1] In some mammals only one of these is present (cf. pp. 386, 398). These nerves are regarded as together constituting the mammalian representatives of the tetrapod N. cutaneus surae lateralis.

[2] See footnote on p. 376.

offered by the distribution of these nerves, mainly to the thigh and shank respectively. When, again, M. caudofemoralis is absent (fig. 10 D) the distinction between Nn. cut. femoris posterior and perinaealis is less clearly defined; they have indeed come to form, in Man and the giant anthropoids (except *Simia*), a single trunk, the perinaeal nerve being described as a branch of the former. When, further, as in many Primates and in Artiodactyla, both the muscles caudofemoralis and tenuissimus are wanting, the courses of a number of nerves have become similar, viz. Nn. ischiadicus dorsalis (represented by glutaeal nerves), peronaeus, tibialis and ischiadicus ventralis (represented by nerves to hamstrings, quadratus femoris, obturator internus and flexor cruris caput dorsale); and the cutaneous nerves surae superficialis and profundus, cutaneus femoris posterior and perinaealis. Comparison, however, of such Primates with their relatives (cf. figs. 10 D, 8, 5 and 4) which happen to be in possession of one or other of Mm. caudofemoralis and tenuissimus, suffices to establish the identity of the nerves, and assists in the correct homologisation of the musculature by which they are innervated. Thus the distinction[1] between the "ischio-femoralis" of the orang-outan and that of the gorilla and chimpanzee (p. 425) appears justified despite the absence of both Mm. tenuissimus and caudofemoralis.

(*d*) *Comparison of Mammalia with other Classes of Tetrapoda.*

(Cf. figs. 1 and 3 with figs. 7, 8, 14 and 15.)

The arrangement of structures in the thigh and buttock of Insectivora, summarised in the previous section, agrees closely with that which has been shown to exist in the Amphibia, Reptilia and Aves. The names, however, which are commonly employed in descriptive anatomy, obscure this similarity. As already indicated, the structural arrangement of Insectivora closely resembles that of the other mammals.

The name "tenuissimus" is employed in mammalian literature by Leche and others to describe a muscle presenting features like the iliofibularis of other tetrapod classes.

The name "caudofemoralis" was employed by Leche to describe an insectivore muscle which reproduces the relations of the reptilian femorocaudalis (Frets) and its equivalents in amphibians and birds. Given these identifications, the relations of the principal nerves to muscles are the same in mammals as in other groups, as illustrated by the summaries for dorsoventral sequence of post-axial structures provided for Insectivora (p. 394) and Urodela (p. 376).

Brief consideration will be given below (pp. 401–426) to the muscular changes involved in the representation in mammals by biceps, semimembranosus and semitendinosus of the reptilian caput ventrale of M. flexor cruris, those involved in the specialisation and subdivision of the reptilian

---

[1] By Fick and Kohlbrügge.

iliofemoralis and ischiotrochantericus (Osawa), and the not infrequent persistence in mammals of the reptilian femorocaudalis (Frets), iliofibularis and flexor cruris caput dorsale.

Ventrally to Mm. tenuissimus and caudofemoralis in mammals there are nerves which are identified as constituent bundles of Nn. ischiadicus ventralis and pudendus (pp. 372, 374); their course and distribution resemble those which in reptiles pass ventrally to Mm. iliofibularis and "femorocaudalis" (i.e. the tetrapod caudofemoralis) (figs. 1, 8 and 13).

The N. ischiadicus ventralis, which in reptiles comprises one large trunk destined for both ventral and dorsal heads of M. flexor cruris (p. 381) and one or more smaller ones for the short deep musculature (viz. ischiotrochantericus and in some reptiles parts of the pubo-ischio-femoralis externus and ischio-femoralis of Gadow), is represented in mammals by several nerve bundles. For the distinction of these bundles from those belonging to N. pudendus we are dependent on a study of their distribution, owing to the similarity of course pursued by Nn. ischiadicus ventralis and pudendus relative to muscles and bone (cf. figs. 1, 7 and 8).

N. ischiadicus ventralis (cf. fig. 7) in mammals comprises (*a*) the nerve to which Leche applied the term "4 i" in Insectivora (p. 391 *supra*), supplying M. flexor cruris cap. ventr. (i.e. Mm. biceps, semitendinosus and semimembranosus, but without their so-called "caudal heads"), (*b*) the nerve to M. flexor cruris cap. dors. (caudal head of hamstring musculature), which generally keeps close company with the cutaneous element of N. pudendus (fig. 7), and (*c*) the nerves to short deep muscles, represented in Monotremata by the nerve to M. ischiotrochantericus (Pearson's "obturator B"), but in most mammals by separate nerves to quadratus femoris and obturator internus (and associated gemelli). In Monotremata and Marsupialia (fig. 11), the first and last of these (*a* and *c*) leave N. tibialis as a single trunk to which Cunningham with some reluctance applied the name "nerve to the hamstrings," recognising the inclusion in this nerve of bundles destined for the deep muscles. Frets (1909, p. 90) named the same nerve N. ischiadicus ventralis, but this nerve differs from that to which he gave this name in *Sphenodon* in the absence of any component destined for M. flexor cruris cap. dors., and in the inclusion of bundles for short deep muscles. In this paper the term N. ischiadicus ventralis has been applied (p. 372) to a single comprehensive nerve stem destined for ventral thigh muscles and skin in Urodela (fig. 1); in other groups it has been found that certain of its constituent bundles, most commonly those destined for the short deep musculature, leave the main sciatic stem independently.

One point of difference in the N. ischiadicus ventralis of mammals deserves note: no cutaneous element comparable with the N. cut. femoris ventralis of other tetrapod classes is known to me in mammals.

N. pudendus is represented in mammals, as in birds, by two widely separated nerves. The cutaneous nerve already described in mammals as

N. perinaealis presents a course[1] and distribution in the Monotremata (fig. 14), Marsupialia (fig. 11), Rodentia (fig. 15), Carnivora (fig. 7), Insectivora (figs. 4 and 5), and Primates (figs. 8 and 10), so far examined, which identify it with the nerve which has been so termed in other tetrapod classes (pp. 374, 377, 382, 383). But with the reduction of the great caudofemoral retractor musculature of the more primitive Tetrapoda and its inclusion for the most part in the thigh (fig. 9), the nerve to M. caudofemoralis itself has become more distally situated and more closely associated with the branch of N. ischiadicus ventralis destined for M. flexor cruris cap. ventr. (figs. 5 and 8), or occasionally with that for the dorsal head (fig. 15). The transference in certain mammals of the origin of M. caudofemoralis from the tail to tuber ischii is responsible in these instances (e.g. Macroscelididae and *Tarsius*[2]) for its failure to present the customary relations to the more proximally placed nerves, viz. N. pudendus, and nerves to obturator internus, quadratus femoris, and flexor cruris cap. dors. (*vide* p. 388).

In mammals, then, both the nerve trunks, ischiadicus ventralis and pudendus, have undergone disintegration, and owing to the similarity of their courses the constituent bundles of these nerves require reference to their distribution for their distinction. Thus it has been concluded that a part of N. perinaealis has become closely associated in many mammals (fig. 7) with the nerve to M. flexor cruris cap. dors. (a component of N. ischiadicus ventralis), while the nerve to M. caudofemoralis has also become closely associated with the nerve bundles destined for M. flexor cruris (usually the ventral head).

The relations (to Mm. caudofemoralis and tenuissimus) and the distribution of N. peronaeus and Nn. surae dorsalis and ventralis, point to these nerves being the mammalian representatives of the N. peronaeus and N. cutaneus surae lateralis of other tetrapod classes. Similarly the glutaeal nerves present courses and distribution showing them to be components of the N. ischiadicus dorsalis; and a study of the musculature (p. 406 *infra*) points to their being differentiated from the nerve to M. iliofemoralis of pro-mammalian reptiles (cf. figs. 1, 9 and 12).

Inasmuch as M. tenuissimus presents every feature needed for its identification with the reptilian M. iliofibularis, the nerve to this muscle (fig. 9) and the glutaeal nerves together correspond to the N. ischiadicus dorsalis already described in other classes.

In mammals N. peronaeus and Nn. surae dorsalis and ventralis pass dorsally to M. caudofemoralis and round the pre-axial side of tenuissimus, just as in reptiles they[3] pass dorsally to M. femorocaudalis and pre-axially

---

[1] This nerve pierces the dorsal head of M. flexor cruris in some mammals, e.g. *Lutra vulg.* and in one of the examples of *Hapale jacch.*; in the latter instance it was found to pierce M. caudofemoralis also. These features are divergences from the usual tetrapod relations.

[2] Appleton, 1921, Plate IV, and p. 468.

[3] Represented by N. peronaeus and N. cutaneus surae lateralis.

to M. iliofibularis. The glutaeal nerves do not as a rule reach sufficiently far to show these relations clearly, though the relations are evident when N. glutaeus posterior becomes extended distally for the supply of M. femorococcygeus. The nerve to tenuissimus (figs. 6, 7, 8, 15) passes dorsally to M. caudofemoralis in those mammals which possess these muscles, just as in reptiles that to iliofibularis passes dorsally to the femorocaudalis (fig. 3).

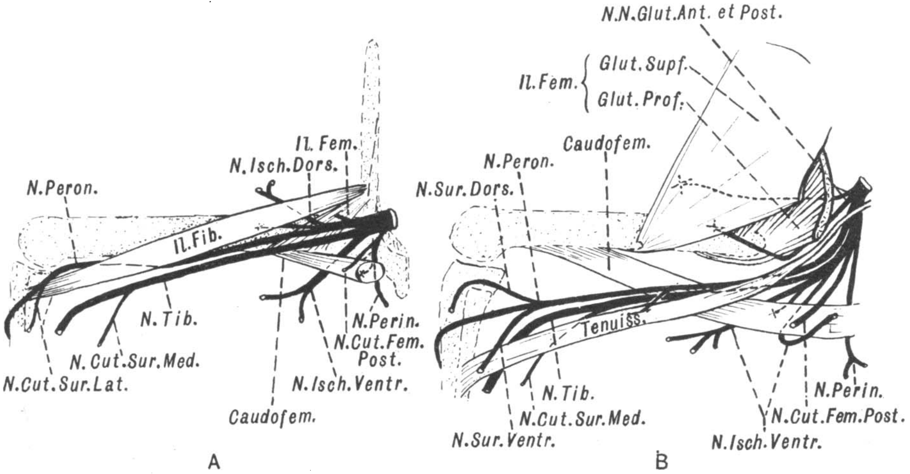

Fig. 9. Diagram showing the principal metazonal nerve-trunks of the thigh in the frogs (Salientia) and mammals. (A) Salientia, (B) Mammalia.

They alike show segregation of nerve bundles to dorsal thigh muscles (N. ischiadicus dorsalis) from the nerves to the dorsum of the leg and foot (N. peronaeus), cf. fig. 1. In both groups reduction of the primitive caudofemoral retractor musculature has occurred; but in mammals the vestige is situated mainly in the thigh and the nerve (a constituent of N. pudendus) travels into the thigh in company with N. ischiadicus ventralis. In mammals the nerve to iliofibularis (tenuissimus) is associated with N. peronaeus for some distance into the thigh, and is widely separated from the remainder of N. ischiadicus dorsalis (viz. Nn. glutaei anterior et posterior).

In both groups M. flexor cruris has become greatly elaborated; mammals have however retained a more or less vestigial representative of the Amniote dorsal head, which is innervated from a recurrent branch of N. ischiadicus ventralis (cf. figs. 3, 14 and 15). N. cutaneus femoris posterior is large in mammals as in other Amniota, small in frogs as in Urodela. N. cut. surae lateralis is often represented by two bundles in Mammalia (p. 394).

The relations of nerves to Mm. iliofibularis and caudofemoralis conform to the general structural pattern of Tetrapoda (cf. fig. 1).

In mammals N. peronaeus is closely associated with N. tibialis till near the knee; in this they resemble the frogs, birds and reptiles more closely than the urodeles in whom a N. fibularis is compounded from N. peronaeus and N. ischiadicus dorsalis (cf. figs. 1 and 9).

The two cutaneous nerves representative of the reptilian N. cut. surae lateralis have been found among Rodentia, Primates and Carnivora as well as in Insectivora, separated by the whole or part of M. biceps cruris (i.e. a part of M. flexor cruris caput ventrale, p. 425). In *Perameles* and *Canis*

I could only find one such nerve; in the former it pierced biceps, in the latter it was placed like a N. surae ventralis (described by Bradley by the name of "N. cutaneus surae lateralis"). In Macroscelididae the only one of these nerves present is situated like a N. surae dorsalis.

N. tibialis passes dorsally to M. caudofemoralis, but remains ventral to M. tenuissimus (iliofibularis), as in other tetrapod classes. It again provides a cutaneous element which is identified as a N. cut. surae medialis. The latter has a distribution similar to that in other tetrapod classes, but is peculiar in passing medially to the insertion of a part of M. flexor cruris (viz. M. biceps), a feature which appears attributable to the transference of this insertion to the lateral side of M. gastrocnemius (p. 424). The distal innervation of M. flexor cruris cap. ventr. through a nerve passing with N. tibialis dorsally to M. femorocaudalis, which has been found in certain Amphibia, reptiles and birds (pp. 374, 382, 383), is perhaps represented in mammals also, for in *Dasyurus mac.* I have found such nerve bundles reaching the distal parts of M. semitendinosus in addition to the innervation through N. ischiadicus ventralis. Cunningham evidently observed a similar distal innervation in certain Marsupialia (1881, p. 271).

A N. cut. femoris posterior has been found in all mammals examined. It is identified by its distribution and by its course between Mm. iliofibularis (tenuissimus) and caudofemoralis with the nerve to which this name has been applied in other tetrapod classes. The nerve is peculiar in *Meles tax.* and *Lutra vulg.* in its penetration of M. tenuissimus.

The relations of cutaneous nerves to muscles in mammals are therefore as follows: (1) *dorsal* to both caudofemoralis and tenuissimus[1], N. cutaneus surae lateralis, represented in some mammals by the Nn. surae superficialis and profundus (separated distally by the whole or part of biceps); (2) *between* caudofemoralis and tenuissimus, Nn. cut. femoris posterior (which emerges between femorococcygeus and biceps) and cut. surae medialis, the latter separated from the former by biceps; and (3) *ventral* to both caudofemoralis and tenuissimus, N. perinaealis, separated from N. cut. femoris posterior by caudofemoralis. The relations of muscular and cutaneous nerves to the thigh muscles of Mammalia are like those described in other tetrapod groups, save the relations of the distal part of biceps to adjacent nerves (cf. pp. 375, 379, 420 and 424).

6. REVIEW OF THE TETRAPOD METAZONAL NERVES.

(Fig. 1, p. 373, and fig. 9, p. 398.)

In Urodela, Salientia, Lacertilia, Chelonia, Crocodilia, Aves, Monotremata, Marsupialia and Eutheria, it has been found that the muscular and cutaneous nerves reaching the hind-limb on the caudad side of the os coxae fall into four categories differing in their course relative to the thigh muscles and possessing characteristic distributions.

---

[1] I.e. the tetrapod iliofibularis (cf. pp. 402, 425).

A: N. ischiadicus dorsalis is distributed to dorsal thigh muscles; it passes dorsally to M. caudofemoralis and round the pre-axial (medial) side of M. iliofibularis.

B: N. peronaeus (including a N. cutaneus surae lateralis) is distributed to muscles and skin on the dorsum of the shank and foot; it pursues a course similar to that stated for N. ischiadicus dorsalis (A).

Y: N. ischiadicus ventralis (including a N. cutaneus femoris ventralis) and N. pudendus (including a N. perinaealis) pursue similar courses ventrally to M. caudofemoralis (and iliofibularis); the former is distributed to ventral thigh musculature and skin, the latter to ventral musculature which is usually partly within the tail, and to skin near the anus.

Z: N. tibialis (including a N. cutaneus surae medialis) is distributed to muscles and skin on the ventral side of the shank and foot (and to the distal part of the ventral thigh muscles in some groups, p. 399); it passes dorsally to M. caudofemoralis but ventrally to M. iliofibularis. In the thigh a cutaneous nerve (N. cutaneus femoris posterior) pursues a similar course relatively to Mm. caudofemoralis and iliofibularis.

In Urodela, A and B form a single trunk which leaves the others in the proximal part of the thigh; in all other groups N. peronaeus (B) does not accompany A when the latter leaves N. tibialis (Z), but forms with Z a single trunk, commonly described as the sciatic, which is thus distributed to both dorsal and ventral parts of the shank and foot. The urodele nerve supplying the dorsal parts of both thigh and shank is known as N. fibularis. The nerves for the ventral thigh structures (Y) leave those for the ventral aspect of shank and foot (Z) in the proximal part of the thigh in all Tetrapoda. Amniota present a muscle (M. flexor cruris caput dorsale) which is not found in Amphibia; it is associated at its insertion with the superficial ventral musculature (M. flexor cruris cap. ventr.) and is innervated from N. ischiadicus ventralis (Y) which, in order to reach it, is prolonged round the latero-distal margin of M. caudofemoralis.

Either or both Mm. caudofemoralis and iliofibularis may be absent in mammals, the former occasionally also in birds and frogs. A specialised derivative of M. caudofemoralis in the Amphibia (p. 409), the caudocrural muscle, is only rarely retained in modern frogs.

In the second part of this paper the muscle homologies which are involved in the foregoing study of structural pattern in the tetrapod thigh will be critically reviewed. References to the literature concerned will be found at the end of the second part of this paper.