



THE MUSCULATURE AND LIMB PLEXUSES
OF TRICHOSURUS VULPECULA.

by

Robert Angus Barbour, M.B., B.S. (Adel., 1955),

Department of Anatomy and Histology,

University of Adelaide.

Thesis submitted for the Degree of

Doctor of Medicine

in the University of Adelaide,

March, 1961.

I hereby certify that the text of this thesis is entirely my own composition, that the findings reported herein (except where due reference is made) are the result of my own personal investigations, and that no part of this work has been previously submitted for a Degree in this or any other University.

Department of Anatomy and Histology,

University of Adelaide,

January 16th., 1961.

SUMMARY.

A full account is presented of the anatomy of the skeletal musculature of the marsupial Trichosurus vulpecula, its innervation is noted, and an outline of the brachial and lumbo-sacral plexuses is given, the findings reported being the results of a study involving five separate animals.

All discrepancies between the findings of this investigation and those previously reported for the species are noted, a comparison is made with the muscles described for other marsupials and the relatively few unusual features shown by this species are pointed out. From this comparison it is concluded that the musculature shows a fairly generalized pattern, and bears a closer resemblance, both in its overall structure and in the few uncommon features that it presents, to the cuscus than to any other marsupial that has been adequately described. The cuscus, now generally known by the generic name Spilocuscus, has been described in the literature as Phalangista, Phalanger and Cuscus, and is the only other member of the Phalangerinae for which an adequate account of the muscular system is available.

This work, apart from providing the most comprehensive description yet given of the musculature of any single marsupial species, furnishes additional evidence for the view that the vulpine phalanger is a typical Phalangerine of a basic generalized marsupial structure such as probably characterized the original Diprotodont stock.

CONTENTS.

	page.
ACKNOWLEDGEMENTS	1.
INTRODUCTION AND HISTORICAL SURVEY	2.
MATERIAL AND METHODS	10.
DESCRIPTION AND DISCUSSION OF FINDINGS	12.
I. Limb plexuses	12.
(a). Brachial plexus	12.
(b). Lumbo-sacral plexus	21.
II. Musculature	28.
Subcutaneous musculature - panniculus carnosus	28.
(a). Panniculus in the head and neck	28.
(b). Panniculus of the trunk	34.
Deep musculature	38.
(a). Muscles of the head and ventro-lateral region of the neck	38.
1). Muscles of mastication	38.
2). Supra-hyoid and extrinsic lingual muscles	41.
3). Infra-hyoid muscles	48.
4). Lateral cervical muscles	51.
5). Prevertebral muscles	54.
6). Muscles of the palate	56.
7). Muscles of the pharynx	57.
8). Intrinsic laryngeal muscles	57.
9). Extra-ocular muscles	59.

	page.
(b). Muscles of the fore-limb and its girdle . . .	61.
1). Muscles connecting trunk to fore-limb and girdle	61.
2). Muscles of the shoulder	75.
3). Muscles of the upper arm	81.
4). Flexor muscle group of the fore-arm	86.
5). Extensor muscle group of the fore-arm	94.
6). Intrinsic muscles of the hand	101.
(c). Muscles of the abdominal and thoracic walls . . .	111.
1). Ventral longitudinal muscles	111.
2). Flat muscles of the body wall	115.
3). Muscles of the dorsal wall and roof of the abdomen	123.
4). Dorsal thoracic muscles	126.
(d). Deep dorsal muscles of the neck and trunk . . .	129.
(e). Muscles of the tail	137.
(f). Muscles of the perineum	144.
(g). Muscles of the hind-limb and girdle	146.
1). Ventral pelvic muscles	146.
2). Muscles of the gluteal region	149.
3). Muscles of the thigh	158.
4). Muscles of antero-lateral region of leg and dorsum of foot	170.
5). Muscles of the flexor aspect of the leg . . .	176.
6). Intrinsic muscles of the sole of the foot . . .	186.
CONCLUSIONS	196.
SUMMARY	200.

The regulations for the Degree of Doctor of Medicine in the University of Adelaide require:-

- (a). A declaration of originality of the thesis. This may be found immediately after the title page.
- (b). An indication as to where the thesis advances knowledge. This is included as the last paragraph of the summary on p. 200.
- (c). A historical survey of the subject on which the thesis is written. This is incorporated in the introduction beginning on p. 2.



ACKNOWLEDGEMENTS.

In connection with this work I would like to express my thanks to Professor A. A. Abbie for his assistance with the choice of subject, the provision of material in his Department and for his help in general discussion of the work and in the search for relevant literature, also to Dr. A. D. Packer for his helpful advice during Professor Abbie's absence overseas, and to Mrs. P. D. Kempster for her invaluable assistance with the preparation of the photographs and the labelling and reproduction of the diagrams. For the diagrams themselves and for the original exposure of most of the photographs the author must take full responsibility.

INTRODUCTION AND HISTORICAL SURVEY.

A considerable amount of work has been done, much of it many years ago, on the myology of marsupials. In some of the papers on this subject the vulpine phalanger, Trichosurus vulpecula, has received mention, the earlier authors referring to it by its previous name, Phalangista vulpina. None of these authors has, however, given anything like a complete account of the myology of Trichosurus, their references being either to one or a few muscles only, or brief statements by way of comparison with some other animal being treated more fully. The aim of this thesis is to provide a comprehensive account of the myology of this very common marsupial, usually regarded as a fairly generalized though typical member of the Phalangerinae, and to note the peripheral innervation of the various muscles - a feature of the muscular system that has received little attention in most of the accounts given for other marsupials. As an adjunct to this latter part of the work a study has also been made of the limb plexuses, and the report of this part of the investigation is included at the commencement of the main discussion. In the discussion of the muscles of Trichosurus vulpecula an attempt has been made to draw comparisons and contrasts between the features found and those reported for other marsupials. In reporting the works of other authors I have kept the generic and specific names that they use, making no attempt to bring these into line with modern nomenclature. The only alterations I have made are to eliminate upper case initial letters

from specific names in a few instances and to standardize the spelling of Didelphys.

One of the earliest workers of importance in the field of marsupial myology was Richard Owen who, in Todd's Cyclopaedia of Anatomy and Physiology (1839-1847), put together some points from the myology of several marsupials and made some general remarks on the subject; he dealt particularly with the abdominal muscles of Phalangista vulpina, the fore-limb muscles of Perameles lagotis, the psoas parvus of the kangaroo, and the muscles of the hind-limb of Dasyurus macrurus and Phalangista vulpina. He used substantially the same text and figures for the section on marsupial myology in his book on the anatomy of vertebrates (1868).

In 1866 came Haughton's fairly brief account of the myology of two species of Macropus and the opossum, and soon after that followed the work of Macalister. In 1868 this author made some remarks on the flexor muscles of the elbow in several marsupials in a broader consideration of this region of the vertebrate fore-limb; then followed (1870) his account of the myology of Phascologmys wombata and Sarcophilus ursinus which included passing references to some other marsupials including Phalangista vulpina. Two years later he published some further information on Sarcophilus ursinus (1872a) and a brief but comprehensive account of the muscles of Phascolarctos cinereus (1872b). At about the same time came Coues' (1872) important and comprehensive report on Didelphys virginiana.

A few more years brings us to the era of Young and Cunningham

in this field. In 1879, in his study of the male genital organs of Phascolarctos cinereus, Young dealt with the perineal muscles and cremaster of the male of that species; in 1880 he accounted for the intrinsic muscles of the hand in several marsupials, and in 1882 gave a fairly full account of the muscles of Phascolarctos cinereus with an occasional comparative reference to Phalangista vulpina. Also in 1882 came Cunningham's very important work, published in the Challenger Reports, on the muscles, plexuses and nerves of the limbs of Phalangista maculata and Thylacinus cynocephalus, the fore-limb muscles of Phascogale calura and the hand and foot musculature of several other marsupials including Phalangista vulpina. Some parts of this report were published earlier in the form of shorter papers (1878a, 1878b, 1878c, 1881a). This same year also saw the publication of Katz's work on the abdominal wall of a number of marsupials including Phalangista vulpina.

As the nineteenth century neared its end several more reports appeared. In 1885 Sidebotham gave a comprehensive account of the musculature of another American marsupial, Chironectes variegatus. MacCormick's study of the limb muscles of Dasyurus viverrinus, with some comparative references to Phalangista vulpina in the case of the fore-limb, followed in 1887, and in the same year Paterson published a few points about the brachial plexus of Phascolarctos cinereus. In 1890 Windle dealt with the long flexors of the fingers in Didelphys virginiana and Phalangista vulpina amongst other mammals, and in 1894 came Bardeleben's sketchy account of

some of the long and short muscles of the hand and foot in Didelphys marsupialis, Trichosurus vulpecula and Macropus bennetti (the hand only in the last). 1894 also saw the publication of Wilson's paper on the muscles - mainly of the fore-limb - of Notoryctes typhlops, with copious comparative notes, and in 1896 Parsons gave his account of the anatomy of Petrogale xanthopus which included a fairly complete cover of the muscles, their innervation and the limb plexuses. In 1897 Parsons, together with Windle, described the anatomy of another Macropod, Macropus rufus, giving some account of the muscles of the head, neck and limbs; and in the following year Kohlbrugge, dealing with two species of Cuscus and one of Macropus, presented information on the muscles and nerves of the face, neck and shoulder girdle regions. Another comparative account of this period was that of Leche in Bromm's Klassen und Ordnungen des Thier-Reichs, where he also recorded some of his own myological observations, principally on Myrmecobius.

In 1901 Alezais made some rather general remarks about the hind-limb muscles of Macropus bennetti, and Gössnitz dealt with the brachial plexus in three marsupial species with special reference to the phrenic nerve origin. The next year saw Tobler's account of the anatomy and innervation of the panniculus carnosus in Macropus bennetti and other mammals; and in 1905 the more important works of Carlsson on the sphincter marsupii and some abdominal and inguinal muscles in several marsupials, and of Parsons on the anatomy (including a brief account of the muscles) of Choeropus castanctis

made their appearance. A further addition to the knowledge of Notoryctes tyhlops came in 1905 with Thompson and Hillier's account of the hind-limb myology which included some allusions to the conditions in Trichosurus, and in the same year Taylor and Bonney dealt with the deep calf muscles of a range of vertebrates including Trichosurus among the few marsupials discussed.

Several reports appeared in 1908: Bijvoet, in his comparative studies on the digastric muscle, described some of the submental musculature of Trichosurus vulpecula and some other marsupials; Labosch gave an account of the muscles of mastication in several marsupials; Boas and Paulli dealt with the facial muscles - especially the ear muscles of Didelphys, and Frets included one marsupial - Didelphys cancrivora - in his work on the peronei and foot extensors. In this year also appeared Glaesmer's work on the flexors of the leg and foot in Didelphys cancrivora, Dasyurus hallucatus and Trichosurus vulpecula, where she noted the innervation of the muscles and made comparisons with the monotremes: in 1910 she followed this with a similar study of several other marsupials and compared them with other mammals. Also in 1910 Kajava gave his account of the long flexors and intrinsic muscles of the hand in several marsupials, and van den Broek described the perineal muscles and some muscles of the inguinal region in a wide range of marsupials including Trichosurus vulpecula (and also Phalangista vulpina, as if he thought it was a different species).

In 1914 Carlsson's account of Dendrolagus dorianus was published.

In this she also dealt briefly with four Macropods and Trichosurus vulpecula (representing the Phalangerinae) for purposes of comparison. Then in 1921 followed Osgood's important and comprehensive study of Caenolestes, and in the same year Sonntag (1921a, 1921b) described some of the neck muscles of several marsupials, of which Trichosurus vulpecula was one. A further work by Sonntag on many of the muscles of Phascologys wombata, Phascolarctos cinereus, Phalanger orientalis and Pseudochirus peregrinus followed in 1922.

The late 1920's saw the revival of work (and dispute) on the innervation of the facial muscles and platysma (Huber, 1924a, 1924b, 1925; Huber and Hughson, 1926; Adams, Wheeler and Edgeworth, 1929; Smith, 1931), and in 1930 Huber included some discussion of marsupials in his evolutionary considerations of the facial musculature.

The brachial flexors of Didelphys virginiana were considered by Howell and Straus in 1931 in dealing with the corresponding muscles in Primates, and in 1932 the opossum was subject to further study by Langworthy who described the pectorals and panniculus together with their innervation.

In 1934 Miller made a study of the brachial plexus in several vertebrates, including Trichosurus vulpecula as the marsupial example. In the following year, in his book on the cranial muscles of vertebrates, Edgeworth dealt with the branchial muscles of marsupials, and in 1937 he gave a short account of the digastric

and related muscles in two species of cuscus.

1939 saw the publication of Harris's extensive work on the vertebrate brachial plexus in which he dealt with five marsupials, and in this year Heighway submitted her comprehensive thesis (unpublished) on the anatomy of Hypsiprymnodon moschatus which included a large section on the muscles. Also in 1939 Haines, in a comparative study, described the fore-arm extensors of Didelphys virginiana, Campbell dealt with the interossei of Didelphys from a morphological and embryological approach, Lightoller gave some space to Trichosurus vulpecula and other marsupials in his comparative account of the mandibular and hyoid arch muscles, and Abbie (1939a) gave the results of a study of the region of attachment to the mandible of the masseter and medial pterygoid muscles in many marsupials.

One of the most recent anatomical studies in this field is that of Boardman (1941) on the chest wall and shoulder region of Macropus robustus, and in 1942 Straus described the fore-arm flexors of Didelphys in a comparative study of tetrapods in general.

Some further references to work on very restricted aspects of the field are given in the main text of this thesis but would be, I feel, rather out of place here.

The above review is not completely exhaustive. Some works not available locally (especially some of the older ones) have not been obtained elsewhere as it was felt that, since in most cases the genera concerned have been dealt with in other accounts, the result

would not have been worth the time and trouble involved. A fairly recent example is Carlsson's article on Hypsiptymmodon moschatus (1915. Kungl. Svensk. Vetenskapsakad. Hand. 52, 3.) quoted by Heighway (1939). Vrolik, Cuvier and Ruge are perhaps the most important early workers whose names do not appear in the foregoing review.

MATERIAL AND METHODS.

All the findings reported in the following text are the result of gross dissection of formalin preserved specimens; five animals in all were used in the work the details being as follows:-

No. 1 and No. 2 were male animals that had been decerebrated and stored in formalin for a number of years, both appeared to be full-grown, the former was not measured, the latter measured 71 cm. from tip of nose to tip of tail. No. 1 was used only for a preliminary examination of the limb plexuses, No. 2 for the first detailed study of the muscles.

No. 3 was a female that had been killed by perfusion of saline followed by formol saline into the aorta under barbiturate anaesthesia, and had had the brain, spinal cord and all the thoraco-abdominal viscera removed. It measured 72 cm. in overall length, was used only towards the end of the study for the verification of certain doubtful points.

No. 4 was also a female, killed in the same way as the last, measuring 72.5 cm. in length: this animal was used for further detailed study of the muscles and the main investigation of the motor nerves and the limb plexuses.

No. 5 was a male killed in the same way as the two females above under anaesthesia with ether and barbiturate: it was not quite full-grown, measuring 65 cm. This animal was used for further examination of the brachial and lumbo-sacral plexuses, and also many points in the anatomy of the muscles and their nerve supply.

The photographs are all of specimen No. 4 except that of the lumbo-sacral plexus (pl. II), which is of No. 5, and those of the intrinsic laryngeal muscles (pl. X), which came from No. 3.

DESCRIPTION AND DISCUSSION OF FINDINGS.I. LIMB PLEXUSES.(a). Brachial plexus (fig. 1; pl. I).

The brachial plexus is made up of fibres derived from the ventral rami of six spinal nerves, it receives part of the fifth cervical, all of the sixth, seventh and eighth, the major part of the first thoracic and a small branch from the second thoracic. It lies on the ventral surface of the scalene muscles and the proximal parts of the roots are covered by the longus capito-cervicis.

The roots from the fifth and sixth cervical nerves unite soon after leaving the intervertebral foramina to form the upper trunk, this almost immediately gives two branches, one being the large suprascapular nerve, the other a root of the phrenic. The latter is derived only from the fifth cervical nerve; it is joined by a branch from the fourth to form the phrenic nerve which runs ventral to the plexus into the thorax.

The middle trunk is formed by the seventh cervical nerve alone. On the lateral border of the scalenus it joins the upper trunk and at the same time both trunks divide into ventral and dorsal divisions. Actually the union of the trunks involves principally the dorsal divisions as the ventral can be fairly easily distinguished for a considerable distance further (they have been so separated in the figure and plate). The dorsal division of the upper trunk provides the upper subscapular nerve, while much further laterally the ventral division of the same trunk gives off the nerve

Figure 1 (cf. pl.I). Brachial plexus. Some of the nerves are displaced from their normal positions for the sake of clarity. xi.

Cl.f.	- Clavicular facet on sternum.
Cx.N.	- Circumflex nerve.
L.C-c.	- Longus capito-cervicis.
L.Pec.N.	- Lateral pectoral nerve.
L.S-s.N.	- Lower subscapular nerve.
L.Tr.	- Lower trunk.
M-c.N.	- Musculo-cutaneous nerve.
M.Cu.N.	- Medial cutaneous nerve.
Med.N.	- Median nerve.
M.Pec.N.	- Medial pectoral nerve.
M.Tr.	- Middle trunk.
N.L.D.	- Nerve to latissimus dorsi.
N.S-cl.	- Nerve to subclavius.
N.St.	- Nerve to sternalis.
Ph.N.	- Phrenic nerve.
R.A.	- Rectus abdominis.
Ra.N.	- Radial nerve.
S-cl.	- Subclavius (cut near origin).
Sc.M.	- Scalenus medius.
Sc.P.	- Scalenus posterior.
St.	- Sternalis.
St-hy.	- Sterno-hyoid.
Sup-s.N.	- Suprascapular nerve.
UL.N.	- Ulnar nerve.
U.S-s.N.	- Upper subscapular nerve.
U.Tr.	- Upper trunk.

Figure 2. Lumbo-sacral plexus. $\times \frac{7}{8}$.

Figure 3 (cf. pl. II). Post-fixed type of lumbo-sacral plexus.

$\times \frac{7}{8}$.

- A.F. - Accessory femoral nerve.
- D3-4, D4-5, etc. - Intervertebral discs.
- D.P. - Nerve to deep head of pectineus.
- F. - Femoral nerve.
- G-f. - Genito-femoral nerve.
- H. - Hamstring group of nerves.
- L3, L4, etc. - Lumbar vertebral bodies.
- L2N, L3N, etc. - Ventral rami of lumbar nerves.
- L.Cu. - Roots of lateral cutaneous nerve of thigh.
- Lo.L2. - "Long nerve of the abdominal wall".
- Lo.L2, 5. - "Long nerve of the abdominal wall".
- m. - Motor branch of accessory femoral nerve.
- N.Ta. - Nerves to tail.
- N.Ta.&Pu. - Nerves to tail and pudendal nerve.
- Ob. - Obturator nerve.
- Pa.L2, L3. - Parietal branches of lumbar nerves.
- Ps. - Nerves to psoas major.
- S1, S2. - Sacral vertebral bodies.
- S1N, S2N. - Ventral rami of sacral nerves.
- s. - Sensory branch of accessory femoral nerve.
- Saph. - Saphenous nerve.
- Sc. - Sciatic group of nerves.
- S.Gl. - Superior gluteal nerve.

Fig. 1.

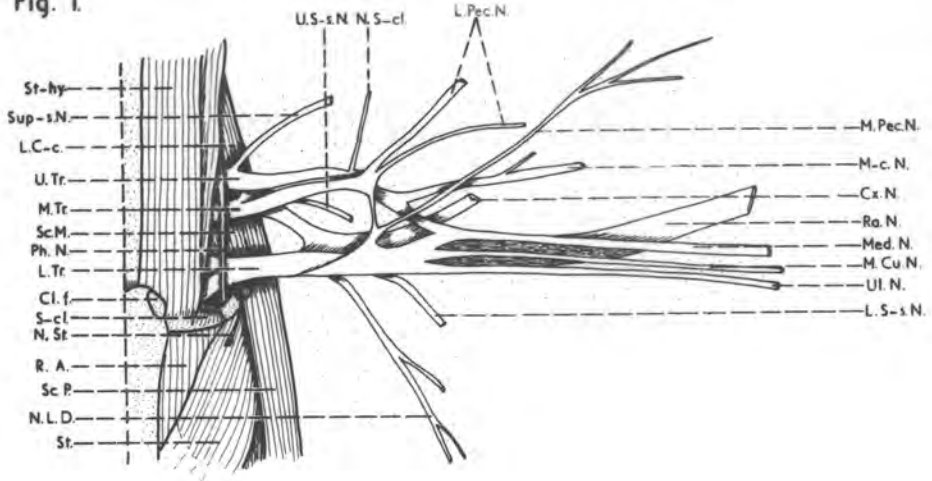


Fig. 2.

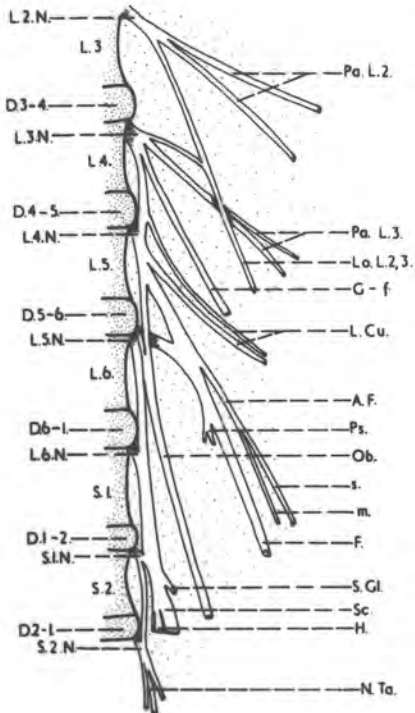


Fig. 3.

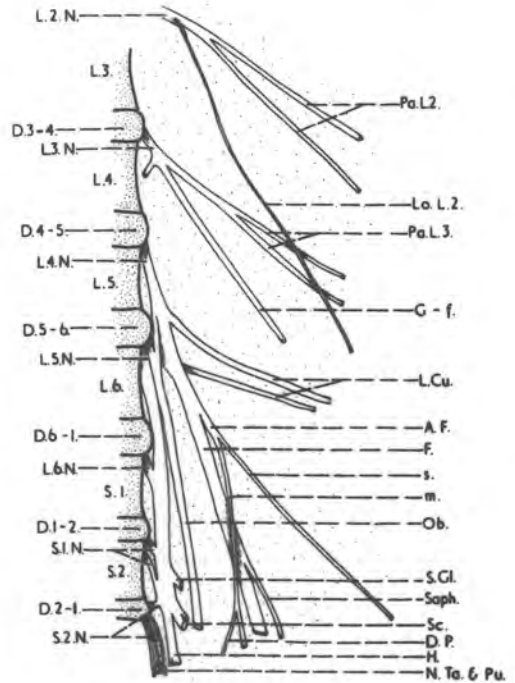
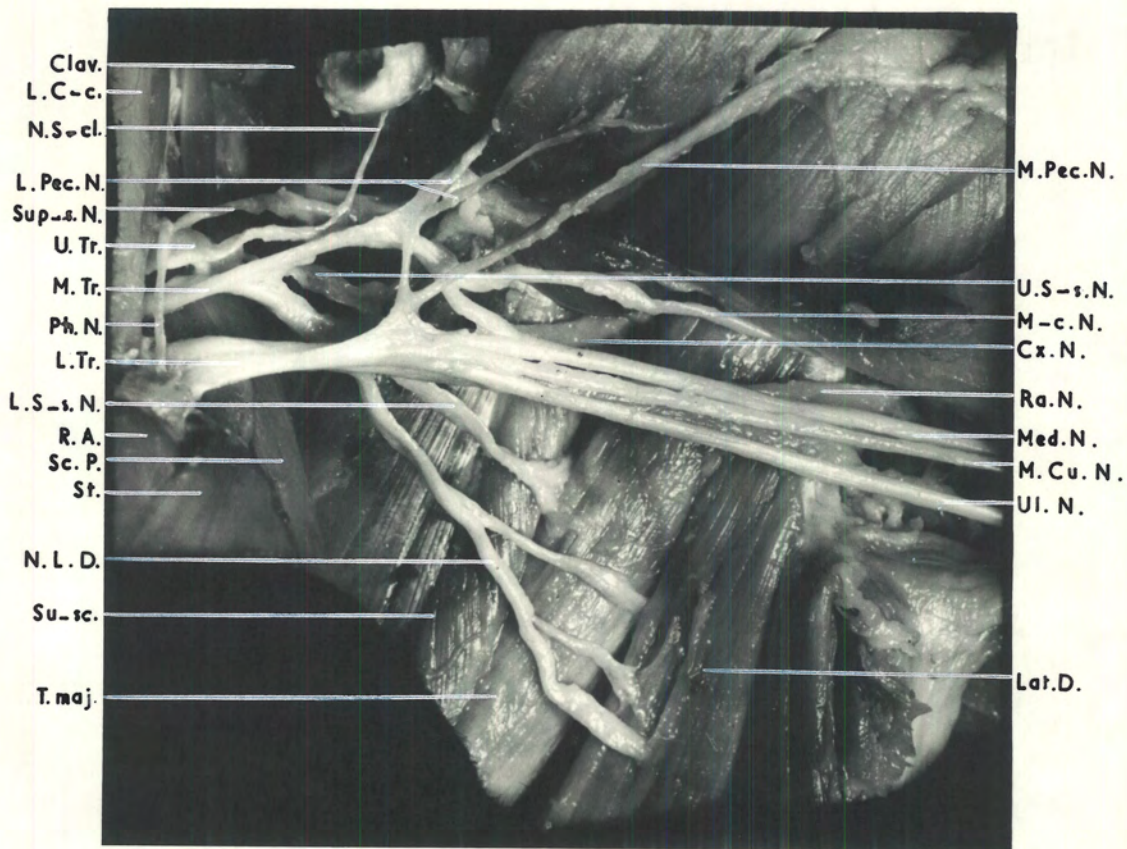


Plate I (cf. fig. 1). Brachial plexus. The pectoral muscles and the sterno-clavicular joint are divided and the fore-limb drawn dorso-laterally. The pectoral muscles are also turned cranially so the pectoral nerves are displaced from their normal position. $\times 1\frac{1}{2}$.

- Clav. - Sternal end of clavicle.
- Cx.N. - Circumflex nerve.
- Lat.D. - Latissimus dorsi.
- L.C-c. - Longus capito-cervicis.
- L.Pec.N. - Lateral pectoral nerve.
- L.S-s.N. - Lower subscapular nerve.
- L.Tr. - Lower trunk.
- M-c.N. - Musculo-cutaneous nerve.
- M.Cu.N. - Medial cutaneous nerve.
- Med.N. - Median nerve.
- M.Pec.N. - Medial pectoral nerve.
- M.Tr. - Middle trunk.
- N.L.D. - Nerve to latissimus dorsi.
- N.S-cl. - Nerve to subclavius.
- Ph.N. - Phrenic nerve.
- R.A. - Rectus abdominis.
- Ra.N. - Radial nerve.
- Sc.P. - Scalenus posterior.
- St. - Sternalis.
- Sup-s.N. - Suprascapular nerve.
- Su-sc. - Subscapularis.
- T.maj. - Teres major.
- Ul.N. - Ulnar nerve.
- U.S-s.N. - Upper subscapular nerve.
- U.Tr. - Upper trunk.



to subclavius. The conjoined dorsal divisions of these two trunks form a cord that gives a substantial branch to the dorsal part of the lower trunk - which is still undivided at this stage - and then divides into the lower subscapular nerve and the much larger circumflex nerve. The ventral divisions also unite, somewhat more laterally, and the resultant cord gives off the lateral pectoral nerve, finally dividing into the musculo-cutaneous nerve and the lateral root of the median. The lateral pectoral nerve gives a branch that joins the medial pectoral nerve near its origin.

The eighth cervical and first thoracic nerves (the latter including the small contribution from the second thoracic) unite early to form the lower trunk of the plexus. This trunk runs laterally and, while still undivided into ventral and dorsal divisions, receives the cord consisting of the dorsal divisions of the other two trunks and gives off the nerve to latissimus dorsi. When the lower trunk does finally divide the dorsal division simply continues as the radial nerve without giving off any more branches. The remaining ventral division, right at its origin, provides the medial pectoral nerve and then divides into the ulnar and medial cutaneous nerves and the medial root of the median.

The nerve to serratus anterior is not seen in the straight dissection of the brachial plexus, it arises deep to the scalenus posterior by two roots from the sixth and seventh cervical nerves (Miller, 1934, gives fifth as well) and finally appears at the dorsal border of this muscle on the medial wall of the axilla.

Miller (1954) includes the fourth cervical nerve in the plexus in Trichosurus, and she recognizes no separation of upper and middle trunks. Her figure shows a definite dorsal division of the lower trunk which joins that of the upper-middle trunk to form a posterior cord.

Of the other marsupials where this plexus has been described the fifth cervical nerve is only partly involved in Thylacinus cynocephalus (Cunningham, 1878a, 1882), Petrogale xanthopus (Parsons, 1896), Macropus robustus and, perhaps, Didelphys marsupialis azarae (Harris, 1959), and, according to the diagrams of Gössnitz (1901), in Macropus giganteus, Perameles gunii and Didelphys virginiana. The fifth ventral ramus enters the plexus completely in Phascolarctos cinereus (Paterson, 1837) and Phalangista maculata (Cunningham, 1878a, 1882), while in Bettongia penicillata, Dendrolagus bennettianus and Dasyurus viverrinus (Harris, 1959) there is also a contribution from the fourth cervical nerve - as Miller (1954) gives for Trichosurus (v.s.).

A small branch from the second thoracic nerve is present in all the species described by Harris and Gössnitz (v.s.), but is not mentioned by Cunningham for either of the two studied by him; Kohlbrugge (1898) gives it as a component of some of the branches of the plexus in Cuscus maculatus, Cuscus orientalis and Macropus brunii. Todd (1912) found this connection present in two out of three specimens of Phascolomys ursinus that he examined, in one of two examples of Potorous sp., and in one example each of Macropus

bennetti and Macropus rufus.

The arrangement of the plexus itself shows considerable variation amongst the different marsupials that have been studied. The variations are best discussed, I feel, not in general terms but with the discussion of the individual nerves that are affected by the features of the plexus.

By splitting the cords and trunks of the plexus it is found that the various nerves do not necessarily contain fibres from all the roots that could theoretically contribute to them by virtue of the gross arrangement of the plexus described above. Those that do contribute may do so in a disproportionate fashion. Such peculiarities are noted in the following discussion.

The suprascapular nerve contains predominantly fibres from C5 and relatively few from C6, in fact most of the ventral ramus of C5 passes into this nerve. The constitution of the suprascapular nerve is given as C5,6 for Trichosurus by Miller (1954) and in all other marsupials described except B. penicillata and Das. viverrinus in both of which Harris (1959) gives its roots as C4 and C5, Dend. bennettianus where the same author gives the source of fibres as C4,5,6, and Did. virginiana where Gössnitz (1901) shows a small branch from C7.

The nerve to subclavius (in agreement with the finding of Miller, 1954) has fibres from C5 and C6 as in Ph. maculata and Thyl. cynocephalus (Cunningham, 1878a, 1882); in the figure given for M. robustus by Harris (1959) the nerve looks as if it could contain

fibres from C4 as well. Gössnitz (1901) gives C6,7 for M. giganteus and Per. gunii, C6 only for Did. virginiana.

The phrenic nerve derives its fibres from C4 and C5, the same origin as given for C. maculatus by Kohlbrugge (1898), for Per. gunii by Gössnitz (1901), and for M. robustus and, judging from his figure, for Dend. bennettianus by Harris (1959); in the last author's figure of the plexus in Das. viverrinus the nerve could conceivably come all from C4. In Ph. maculata and Thyl. cynocephalus Cunningham (1878a, 1882) gives the roots of the phrenic nerve as C5,6, as does Parsons (1896) for Pet. xanthopus. Kohlbrugge (1898) gives C4 for C. orientalis and C3,4,5 for M. brunii, the latter being the roots given by Gössnitz (1901) for M. giganteus and Did. virginiana.

The lateral pectoral nerve contains fibres of C5,6,7 and by tracing these back C7 is found to provide the great majority with hardly any from C5. This appears to be the usual fibre content of the nerve in marsupials, though the proportions may differ. Cunningham (1878a, 1882) gives only C7 as the source of the fibres in Thyl. cynocephalus. Harris's (1959) figure for M. robustus shows a branch from the lateral to the medial pectoral nerve as was found here. Miller (1954) mentions three anterior thoracic nerves in Trichosurus, all arising by anastomosing branches from the lateral and medial cords.

The musculo-cutaneous nerve also has fibres of C5,6 and 7 (as given by Miller, 1954), but appears to be mainly C6 with very little C7. From the figures of Harris (1959) these three roots also

contribute to the nerve in Dend. bennettianus, C6 and 7 only in Did. marsupialis azarae, while in B. penicillata, Das. viverrinus and M. robustus there is no contribution from C7; in Dasyurus, however, the nerve to the brachialis arises from the median and could contain C7 fibres. The diagrams of G6ssnitz (1901) seem to show C6,7 only for Per. gunii and Did. virginiana, while in Thyl. cynocephalus Cunningham (1878a, 1882) gives the root as C7 only. According to Parsons (1896) there is no musculo-cutaneous nerve in Pet. xanthopus, the relevant muscles being supplied from the lateral root of the median nerve.

The upper subscapular nerve contains, as appears from its origin in the plexus, fibres from C5 and 6. The lower subscapular, arising from the fused dorsal divisions of the upper and middle trunks, could receive fibres from C7 as well, but these appear to be very much in the minority. Miller (1934) gives these same three roots for the subscapular nerves in Trichosurus but says there is some origin from the trunk of the circumflex nerve. Separate subscapular nerves are not given in all accounts and figures for other marsupials, but considering the two together they receive fibres from these three roots in C. maculatus and C. orientalis (Kohlbrugge, 1898) and also in Pet. xanthopus (Parsons, 1896) and Did. marsupialis azarae (Harris, 1939). In M. brunii (Kohlbrugge, 1898), M. robustus, Dend. bennettianus, B. penicillata and Das. viverrinus (Harris, 1939) there are no fibres from C7, in M. robustus, indeed, there is no communication of any sort between the

dorsal division of the upper trunk and those of the other trunks. C5,6 also appear to be the roots in Gössnitz's figure for M. giganteus. Cunningham (1878a, 1882) gives the roots as C6,7 in Thyl. cynocephalus, while in Ph. maculata one receives fibres from as far caudally as C8.

The circumflex nerve, since it arises from the same source as the lower subscapular, contains the same fibres, C5,6,7; the main contributor is C6 with, again, very few fibres from C7: Miller (1934) gives C6 and 7 only. My findings agree with the roots given for Pet. xanthopus by Parsons (1896), C. maculatus and C. orientalis by Kohlbrugge (1898) and Dend. bennettianus and Did. marsupialis azarae, judging by the diagrams of Harris (1939). In M. robustus (Harris, 1939) the isolation of the dorsal ramus of the upper trunk precludes C7 fibres from this nerve, and from the other figures in his work C7 is also absent from the circumflex nerve in B. penicillata and Das. viverrinus. Cunningham (1878a, 1882) gives the fibre content as C6,7,8 in Ph. maculata and C7 only in Thyl. cynocephalus.

The nerve to latissimus dorsi in theory could contain fibres of all the five main nerves of the plexus; by tracing back, however, it seems to contain predominantly C7 and C8 with some C6 and little if any T1 or C5: Miller (1934) gives C5,6,7. The nerve likewise could carry fibres from all the main roots of the plexus in Harris's (1939) figures for B. penicillata and Dend. bennettianus; in the same author's diagram for M. robustus it looks to have only C8 and

T1, in Did. marsupialis azarae C7,8, T1, and in Das. viverrinus C5,6,7. Parsons' (1896) figure for Pet. xanthopus also shows C5,6,7 as the roots in that species.

The radial nerve, like the last mentioned, also has the possibility of containing fibres from all the roots of the plexus, C5,6,7,8, T1, if we judge from its gross origin, and Miller (1934) gives its roots as such: it appears, however, to be made up mainly of contributions from C7,8 and T1 with little if any C5 or C6. The first three roots mentioned here, C7,8 and T1, are the only contributors to the nerve in Ph. maculata and Thyl. cynocephalus according to Cunningham (1878a, 1882), and also, going on the figures of Harris (1939), in Did. marsupialis azarae and M. robustus; in the last mentioned, as previously noted, the dorsal division of the upper trunk is separate from the others, while in Didelphys the dorsal division of the middle trunk divides to join both the upper and lower but there are still no fibres from the upper trunk to the cord which gives rise to the radial nerve. From the diagrams of Gössnitz (1901) the nerve appears to receive fibres from C7,8, T1 in Per. gunii, and mainly C8, T1 in Did. virginiana. In the other three marsupial plexuses figured by Harris (1939) and in that of Pet. xanthopus (Parsons, 1896) the nerve may have contributions from all the roots of the plexus.

The medial pectoral nerve, as is apparent from its origin, contains fibres from C8 and T1, and also receives the previously noted branch from the lateral pectoral nerve carrying mainly C7

fibres. Although some accounts do not distinguish between the two pectoral nerves there is usually some contribution to the pectoral nerve group from C8 and T1; in Thyl. cynocephalus Cunningham (1878a, 1882), however, gives only C7 as the origin of the pectoral nerves, while in the figure given by Harris (1939) for Dend. bennettianus there is no contribution caudal to C7.

The ulnar nerve receives its component fibres from the roots of the lower trunk, i.e. C8 and T1. This is in agreement with Harris's statement (1939) that in none of the Marsupialia does the ulnar nerve receive fibres from C7, and none of the other accounts I have seen contradicts this, though Miller (1954) gives C5,6,7 in brackets with C8 and T1 as the roots of origin in Trichosurus, and Cunningham (1878a, 1882) mentions that the nerve springs from a trunk containing fibres from all the roots of the plexus in Ph. maculata but he does not specify which fibres actually enter the ulnar nerve.

The medial cutaneous nerve has the same roots as the ulnar - C8, T1. This agrees with all other marsupials I have noted in the literature for which the roots are given. Miller (1954) does not mention this nerve in her account of the plexus in Trichosurus.

The median nerve arises by the usual two roots, one from the cord formed by the ventral divisions of the upper and middle trunks, the other from the ventral part of the lower trunk. The former has fibres of C5,6,7 (like the radial nerve having very little C5 or C6), the latter has fibres of C8 and T1, so that the nerve as a whole is mainly C7,8, T1. Miller (1954) gives C5,6,7,8, T1 for this

species. Cunningham (1878a, 1882) gives C7,8 and T1 as the fibre content of the nerve in Thyl. cynocephalus, while in the plexus of Did. marsupialis azarae figured by Harris (1939) the nerve receives no C5 and relatively little C6. Similarly in the diagrams of Gössnitz (1901) for Per. gunii and Did. virginiana there appears to be no C5 contribution. In the other plexuses figured by Harris (1939), and in Pet. xanthopus (Parsons, 1896), the nerve apparently arises from all the roots of the plexus.

The nerve to serratus anterior is derived from C6 and C7, as in Thyl. cynocephalus (Cunningham, 1878a, 1882), M. robustus and Dend. bennettianus (Harris, 1939). Harris's figure for Das. viverrinus shows it arising from C5,6,7 while in Pet. xanthopus Parsons (1896) gives the origin as C4,5. Gössnitz (1901) shows C6,7,8 in his figure for Did. virginiana.

(b). Lumbo-sacral plexus (figs. 2, 3; pl. II).

Some variation was noted in this plexus in the animals examined, two specimens (Nos. 1 and 5) showing a considerably more post-fixed plexus than the other three. The account given here is a composite one based on the three more pre-fixed examples which I take to represent the commoner form of the plexus in this species; the differences shown by the post-fixed variety are noted afterwards.

The plexus is buried to a large extent in the psoas muscles, the quadratus lumborum and the muscles on the ventral aspect of the sacrum, and is formed from the ventral rami of the spinal nerves from the second lumbar to the first caudal. Beyond this the caudal

plexus begins.

The second lumbar nerve is mainly distributed as a parietal nerve to the body wall but should be considered as part of the plexus by virtue of the root it gives to the "long nerve of the abdominal wall".

The third lumbar nerve also gives a parietal branch to the body wall, provides the second root of the "long nerve of the abdominal wall", gives rise to the genito-femoral nerve, and sends a large branch to join the fourth lumbar nerve. This last branch gives off the first root of the lateral cutaneous nerve of the thigh.

The combined trunk formed by the third and fourth lumbar nerves gives off the rest of the lateral cutaneous nerve of the thigh and then divides into two branches which enter respectively the femoral nerve and the obturator nerve, the latter one containing only fibres from L4.

The fifth lumbar nerve gives a large branch to the femoral nerve and at about the point where this joins the contribution from L5,4 the accessory femoral nerve arises from the L5,4 trunk. The fifth lumbar nerve also provides the second, smaller root of the obturator nerve, and then runs caudally to join the whole of the ventral ramus of the sixth lumbar nerve together with which it forms the lumbo-sacral trunk.

The lumbo-sacral trunk gives off from its lateral side the superior gluteal nerve and almost immediately is joined by a branch of the first sacral nerve. The continuation of the lumbo-sacral

trunk containing S1 fibres then splits into two groups of branches; the lateral group consists of nerves that leave the pelvis cranial to the piriformis muscle and includes the sciatic and inferior gluteal nerves and the posterior cutaneous nerve of the thigh. The medial group of nerves runs on the ventral surface of the piriformis and leaves the pelvis caudal to it; this group contains the hamstring nerve and, medial to that, the smaller nerves to quadratus femoris and obturator internus and the pudendal nerve. Another branch of S1 forms a second separate pudendal nerve and the rest runs to join the second sacral nerve, the combined trunk formed by these two giving several branches to the muscles and skin at the base of the tail and also initiating the superficial and deep longitudinal nerve cords of the tail: most, if not all, of the branch from S1 enters the nerve to the ischio-coccygeus, the other nerves from here containing mainly fibres from S2.

In the case of most of the branches of this plexus, unlike the brachial, the roots composing the nerves are obvious without splitting the plexus to elucidate them: some discussion of the nerves arising in the plexus is, however, necessary.

The "long nerve of the abdominal wall" deriving its fibres from L2 and L3 runs a more oblique course than the ordinary parietal nerves of the abdominal wall (some of which it crosses on their internal aspects as it goes) and appears to be distributed to the caudal part of the transversus abdominis. Of the significance of this nerve I am not sure; I would have liked to be able to trace it

through to the skin of the thigh and then consider it as a separated cutaneous part of the genito-femoral nerve, but this I was unable to do. It perhaps corresponds to a long nerve from L5 to the abdominal wall mentioned by Cunningham (1881a, 1882) in Ph. maculata, and may still represent a sort of "accessory genito-femoral nerve" to a portion of the transversus that has not separated off as a cremaster.

The genito-femoral nerve arises from L5 only and is entirely spent in supplying the cremaster. Cunningham (1881a, 1882) gives its roots as L5,4 in Ph. maculata and L2,3 in Thyl. cynocephalus, the latter also being the roots given for Pet. xanthopus by Parsons (1896) whose figure shows it coming from L2 only. In a female thylacine Cunningham found a sensory branch of this nerve to the nipples; in the others mentioned, however, the nerve, as found here, goes entirely to the cremaster.

The lateral cutaneous nerve of the thigh has two roots, one from L4, the other from the L5,4 trunk, which remain separate until somewhere about the point where the nerve leaves the abdomen near the anterior superior iliac spine. These same two lumbar nerves provide the fibres for the lateral cutaneous nerve also in Ph. maculata and Thyl. cynocephalus according to Cunningham (1881a, 1882). In Pet. xanthopus Parsons (1896) says the nerve arises from the femoral but his figure shows it coming from L2.

The femoral nerve contains fibres from L5,4 and 5, as in Pet. xanthopus (Parsons, 1896) and Ph. maculata (Cunningham, 1881a, 1882). In Thyl. cynocephalus, according to Cunningham (1881a, 1882), only

the third and fourth lumbar nerves contribute.

The accessory femoral nerve, containing fibres from L3 and L4, provides the motor supply to the pectineus and gives a large cutaneous branch to the front of the thigh: I have not found it described in any other marsupial.

The obturator nerve has fibres of L4 and L5, the same as in Ph. maculata (Cunningham, 1881a, 1882) and Pet. xanthopus (Parsons, 1896). In Thyl. cynocephalus Cunningham (1881a, 1882) gives the derivation as L3,4.

The superior gluteal nerve contains only fibres from L5 and L6 as it arises from the lumbo-sacral trunk proximal to the point where the trunk is joined by the branch of S1. It contains the same fibres in all three marsupials mentioned in the last paragraph.

The inferior gluteal nerve and the posterior cutaneous nerve of the thigh can be fairly easily traced back beyond the point where the branch of S1 joins the lumbo-sacral trunk, and therefore probably contain, like the superior gluteal, only L5 and L6. The assumption from Parsons' (1896) account of Pet. xanthopus is that these nerves there contain S1 as well as L5,6. Taking Cunningham's (1881a, 1882) special nerve to ecto-gluteus as the inferior gluteal, these two nerves appear to be L5,6, S1,2 in Ph. maculata, while in Thyl. cynocephalus the inferior gluteal is L5,6 and the posterior cutaneous S1.

The sciatic nerve has fibres of L5,6 and S1 as in Pet. xanthopus (Parsons, 1896). From Cunningham's (1881a, 1882) account Thyl.

cynocephalus lacks the S1 contribution, while in Ph. maculata S2 apparently donates fibres as well.

The hamstring nerve derives its fibres from the same roots as the sciatic. This is also the case in the two marsupials reported by Cunningham (v.s.), and can probably be assumed from Parsons' (1896) assertion that the nerve arises from the sciatic in Pet. xanthopus. The nerves to quadratus femoris and obturator internus in T. vulpecula also have the same roots, though these appear to have very little S1.

The pudendal nerve appears to be mainly S1 though it does have some fibres from the lumbo-sacral trunk as well. Cunningham (1881a, 1882) gives this nerve as S1 in Thyl. cynocephalus and S2 in Ph. maculata, Parsons (1896) as S1 and quite separate from the sciatic in Pet. xanthopus (his figure appears to show S1,2).

The basic roots involved in the plexus in T. vulpecula are the same as those given for Pet. xanthopus by Parsons (1896), similar to those which Cunningham (1881a, 1882) gives for Ph. maculata where S2 comes into it as well - as it may do in Trichosurus when the plexus is post-fixed (q.v.), but rather different from those that the latter author gives for Thyl. cynocephalus; there the plexus is formed from the nerves from L1 to L6, and L5 contributes only to the lumbo-sacral trunk, taking no part in the formation of the lumbar portion of the plexus. Although the first sacral nerve does not join the lumbo-sacral trunk in Thylacinus it gives rise to two nerves that are usually considered as arising from the plexus so probably

should strictly be considered as entering into its formation. In Phase. cinereus (Paterson, 1837) the plexus involves the nerves from L4 to L8; when we consider, however, that this species has only eleven thoracic nerves and eight lumbar this might be compared to L2 to L6 on the basis of the nerves in Trichosurus, which is not far removed from the findings of this investigation.

Finally the differences between this and the condition of the plexus in those animals where it is post-fixed are to be noted. Animal No. 5 will be taken as an example of this condition and the noteworthy points of difference shown by it were as follows:-

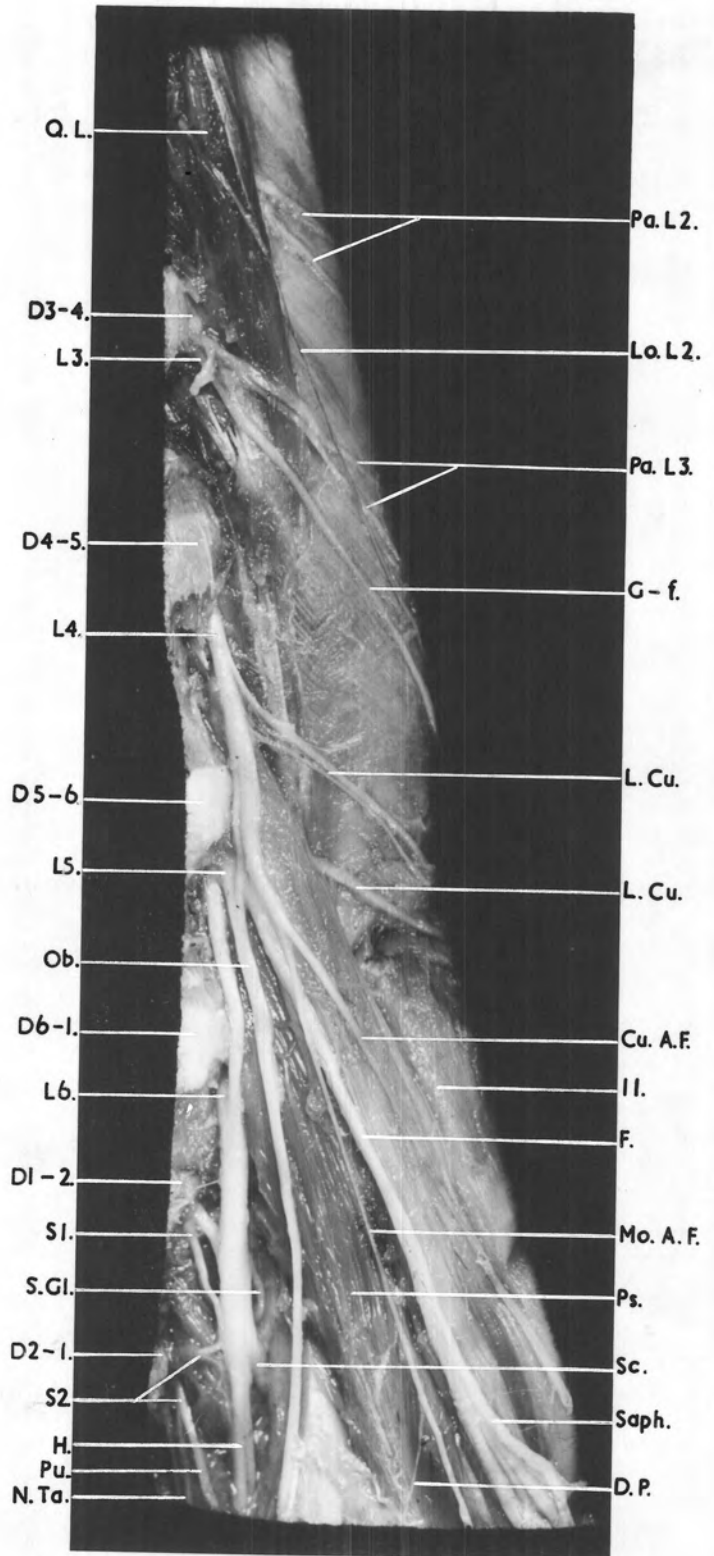
- (i). There was no branch from L3 to L4 so the femoral nerve derived its fibres from L4 and L5 only, the accessory femoral nerve from L4 only.
- (ii). For the same reason the lateral cutaneous nerve of the thigh had no fibres of L3, but in addition to its contribution from L4 it had an extra root, not present in the others, from L5.
- (iii). The obturator nerve had the same roots but got its larger contribution from L5 instead of L4.
- (iv). S1 did not give any fibres to S2, but instead there was a branch from S2 to the lumbo-sacral trunk, so that S2 entered the plexus and was distributed in much the same way as was S1 in the plexus as previously considered. The pudendal nerve was mainly S2.

Other differences, probably of less significance than these,

Plate II (cf. fig. 3). Post-fixed example of lumbo-sacral plexus.

Psoas minor and much of quadratus lumborum and psoas major are removed. x2.

- Cu.A.F. - Cutaneous branch of accessory femoral nerve.
- D3-4, D4-5, etc. - Intervertebral discs.
- D.P. - Nerve to deep part of pectineus.
- F. - Femoral nerve.
- G-f. - Genito-femoral nerve.
- H. - Hamstring group of nerves.
- Il. - Iliacus.
- L3, L4, etc. - Ventral rami of lumbar nerves.
- L.Cu. - Roots of lateral cutaneous nerve of thigh.
- Lo.L2. - "Long nerve of the abdominal wall".
- Mo.A.F. - Motor branch of accessory femoral nerve.
- N.Ta. - Nerves to tail.
- Ob. - Obturator nerve.
- Pa, L2, L3. - Parietal branches of lumbar nerves.
- Ps. - Psoas major.
- Pu. - Pudendal nerve.
- Q.L. - Quadratus lumborum.
- S1, S2. - Ventral rami of sacral nerves.
- Saph. - Saphenous nerve.
- Sc. - Sciatic group of nerves.
- S.Gl. - Superior gluteal nerve.



that should be noted are that the "long nerve of the abdominal wall" had no root from L5, and the accessory femoral nerve arose from the femoral rather more distally than usual.

Further points concerning the motor distribution of the nerves arising in the plexuses are considered with the discussion of the musculature.

II. MUSCULATURE.

SUBCUTANEOUS MUSCULATURE - PANNICULUS CARNOSUS.

(a). Panniculus in the head and neck (figs. 4, 5, 6).

Platysma (fig. 4). This muscle forms a thin sheet of pale muscle fibres and is quite distinct from the panniculus of the trunk. It arises along a line that begins on the ventral aspect of the upper arm then, turning around to the dorsum of the shoulder, crosses the dorsal scapular region towards the midline and runs cranially almost in the midline to the occiput. From this origin the fibres sweep ventrally and rostrally, the most caudal decussating over the cranial end of the sternum, others reaching the midline in the neck and over the chin. The fibres arising most frontally sweep around below the ear into the face and pass towards the angle of the mouth and into the lower lip. The form of the muscle seems to conform closely with the excised specimen photographed by Lightoller (1939).

Sonntag (1921a) indicates that the muscle is much better developed in Phasc. cinereus, and arises from the rest of the panniculus in that species, a fact also mentioned by Young (1882), while Macalister (1872b) is another who notes that the muscle is

Figure 4. Ventro-lateral aspect of face and neck to show extent of platysma and sphincter colli profundus. $\times \frac{2}{3}$.

Figure 5. Musculature of face and scalp from dorsal aspect. $\times \frac{3}{4}$.

Figure 6. Facial musculature from lateral aspect. $\times 1$.

- Au.P. - Post-auricular part of occipito-auricularis.
- Au.S. - Auricularis superior.
- Bu. - Buccinator.
- Ep.Ap. - Epicranial aponeurosis.
- Fr-au. - Fronto-auricularis.
- Man. - Mandible.
- Mass. - Masseter.
- Ment. - Mentalis.
- M-n-l. - Maxillo-naso-labialis.
- N-l. - Naso-labialis.
- Oc-au. - Occipito-auricularis.
- O.Oc. - Orbicularis oculi.
- O.Or. - Orbicularis oris.
- Plat. - Platysma.
- S.C.P. - Sphincter colli profundus (shown in broken lines deep to platysma).
- T. - Tongue.

Fig. 4.

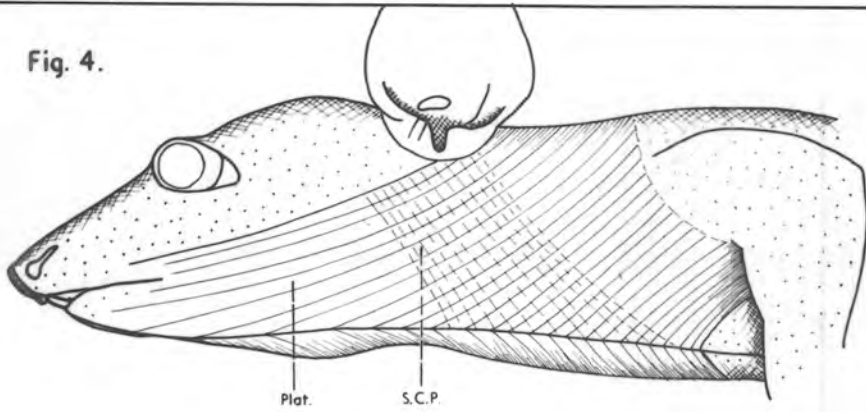


Fig. 5.

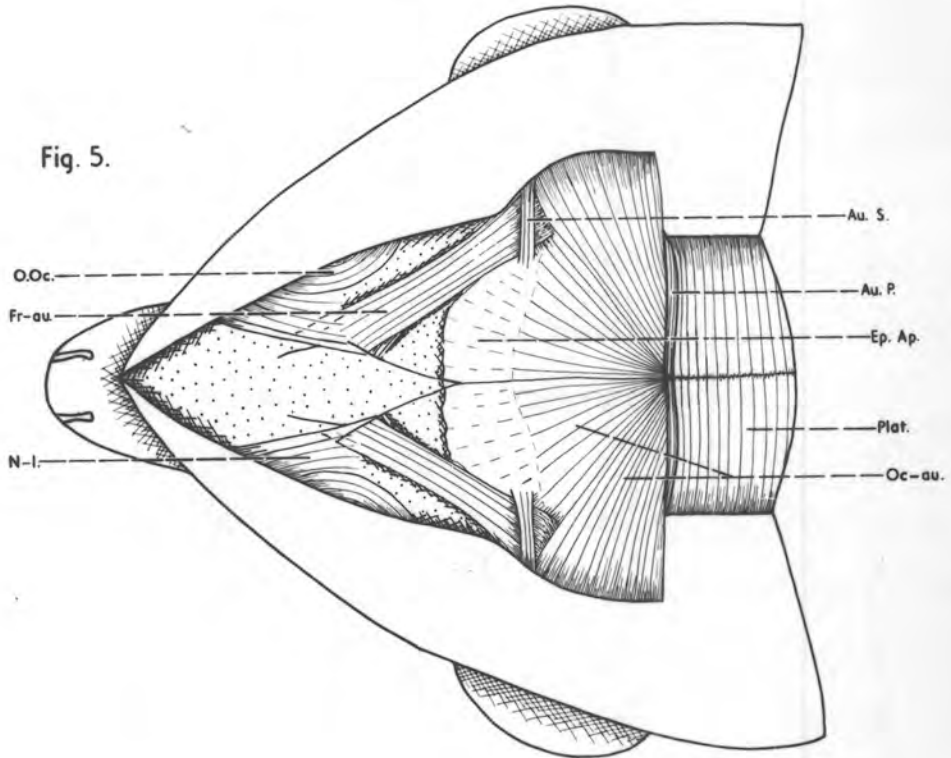
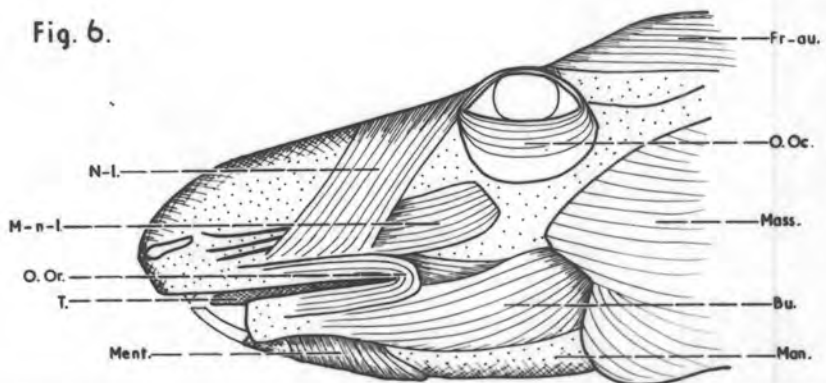


Fig. 6.



thick in Phascolarctos. The schematic figure given by Kohlbrugge (1898) for the marsupials he examined (C. maculatus, C. orientalis, M. brunii) shows a similar arrangement to that found here for Trichosurus though his platysma does not appear to extend so far caudally. Edgeworth (1955) states that the platysma is well developed in marsupials, though in Phascolomys wombata, Sarcophilus ursinus (Macalister, 1870) and Notoryctes typhlops (Wilson, 1894) this would not seem to be the case; in a later paper, however, Macalister (1872a) reports the muscle as being strong in Sarcophilus. In M. rufus (Windle and Parsons, 1897b; Sonntag, 1921b) and Dendrolagus ursinus (Sonntag, 1921b) the platysma is fleshy only in the face, being aponeurotic in the neck, while in Perameles obesula (Sonntag, 1921b) the reverse is the case.

Sphincter Colli Profundus (fig. 4) is a band nearly two centimetres wide whose fibres, running ventrally and caudally deep, and roughly at right angles, to those of the platysma, extend from the fascia ventral and rostral to the ear to the ventral midline of the neck where they meet their fellows of the opposite side along a line extending cranially from the manubrial end of the sternum for two or three centimetres. The muscle seems rather narrower than that figured by Lightoller (1939) but otherwise similar. Most accounts of marsupial myology omit this muscle; Parsons (1905) describes it in Choeropus castanotis as not reaching the sternum, while the figures of Huber (1930) for Did. marsupialis and M. rufus show it extending rather further into the face.

Both the above muscles receive a substantial branch from the facial nerve and I believe this is their only supply. Adams, Wheeler and Edgeworth (1929), agreeing with Kohlbrugge (1898), and going on the evidence of dissection alone, give some of the supply of the platysma in Did. marsupialis, Dasyurus, M. giganteus, Petrogale and Phascolarctos to the anterior cervical nerves; in Macropus dorsalis, Macropus ruficollis and Bettongia they found no innervation at all from the facial nerve. The experimental work of Huber (1924b) with Did. marsupialis, and of Huber and Hughson (1926) and Smith (1931) with Did. virginiana, which indicates that the sole supply to these muscles comes from the facial nerve, is far more convincing.

Muscles of the face and scalp (figs. 5, 6).

Occipito-auricularis (Auriculo-occipitalis) has the form of a flat sheet with its origin mainly from the occipital end of the ligamentum nuchae. From here the muscle fibres fan out over a ninety degree angle, the medial ones passing frontally, the lateral ones, which lie parallel with and adjacent to the frontal fibres of the platysma, running laterally. The medial fibres end about half way across the temporalis fascia in a thin aponeurotic sheet (the epicranial aponeurosis) that soon fades away into the skin of the snout; the majority of the more lateral fibres spread out over and attach to the free part of the cartilage of the pinna. Between these two parts a few of the middle fibres, joining some from the fronto-auricularis, turn down along the frontal margin of the auricle to be

inserted into the buried part of the cartilage of the external auditory meatus. Finally, a bundle of fibres separates off from the caudal border of the muscle and attaches to the caudal margin of the auricle; by comparison with the figure given by Boas and Paulli (1908) for Didelphys, where the muscle appears to be very similar, this portion seems to correspond to the part that they homologize with the postauricularis of placental mammals.

Fronto-auricularis. Edgeworth (1935) calls this muscle the orbito-auricularis and says that it represents the frontalis with some of its fibres attaching to the ear; by analogy with the occipito-auricularis which he describes as the occipitalis with fibres attaching to the ear I feel that fronto-auricularis is the better name. In Trichosurus the muscle passes from the ridge on the frontal bone above the orbit (the fibres arising furthest from the snout running to the deep aspect of the muscle) to the frontal and proximal part of the pinna where it is covered by a part of the occipito-auricularis.

Auricularis Superior is a small slip from the epicranial aponeurosis to the base of the auricle; it crosses superficially over the caudal end of the fronto-auricularis. It appears to correspond to the "pars transiens scutularis" which Boas and Paulli (1908) describe for Didelphys - referred to by Edgeworth (1935) as the medial part of the orbito-auricularis. Leche (1874-1900) also includes the auricularis superior with the frontalis under the general heading "orbito-auricularis".

Mandibulo-auricularis is a well defined bundle extending from the caudal border of the ramus of the mandible to the cartilage of the auricle just proximal to the point where it enters the free pinna - thus agreeing with Bijvoet (1908). A mandibular origin for this muscle is also found in Cuscus maculosus and Didelphys opossum (Bijvoet, 1908), N. typhlops (Wilson, 1894), Did. marsupialis (Huber, 1925; Adams, Wheeler and Edgeworth, 1929), Bettongia and Dasyurus maculatus (Adams, Wheeler and Edgeworth, 1929). These last authors give only an origin from the zygomatic arch in Phascolarctos, an origin from both the mandible and the zygomatic arch in M. dorsalis, M. giganteus, M. ruficollis and Petrogale, as does Huber (1925) for Macropus billardieri. The only reference to the absence of this muscle is in an unidentified species of Didelphys by Cords (1922) who gives a list of synonyms for mandibulo-auricularis.

Orbicularis Oculi is a rather feeble band around the palpebral fissure with some attachment medially to the medial palpebral ligament and the adjacent bone.

Naso-labialis (Levator labii superioris) commences in the same region as the fronto-auricularis and passes rostrally and towards the mouth reaching the upper lip near the angle of the mouth and lying superficial to the maxillo-naso-labialis.

Maxillo-naso-labialis takes origin from the maxilla and to a lesser extent from the zygomatic bone below the medial angle of the eye; the belly runs rostrally, covering the infra-orbital foramen, and gives way to several fine tendons that are inserted into the skin of

the side of the snout as far as the nostril, their main attachment being in the region of the large vibrissae on the side of the snout. Orbicularis Oris. Apart from the fibres of the naso-labialis and the buccinator that enter the lips there are also some fibrae propriae that curve around the angle of the mouth but do not reach the midline in either lip.

Mentalis arises from the mandible oral to the mental foramen and mainly rostral to it; its fibres, diverging somewhat, pass ventrally and caudally to the skin over the chin. The mental nerve emerges caudal to the muscle and the latter is overlapped by a few of the most rostrally extending fibres of the buccinator.

Buccinator (figs. 6, 9, 10; pls. V, VI) has a fleshy origin from the maxilla and the palatine bone adjacent to and caudal to the upper molar teeth. It passes rostrally and a little ventrally at first, then, coursing below the zygomatic process of the maxilla, it turns rostrally into the face where most of its fibres go into the lower lip and are inserted into the mucous membrane of the lower part of the cheek as far as a point beyond the mental foramen. A few of its deeper fibres go into the upper lip.

The facial muscles appear to agree in general with the common marsupio-placentalian ground plan and the figures for Did. marsupialis and M. rufus given by Huber (1950), the main difference being that in Trichosurus there is rather less undifferentiated sphincter colli profundus in the face than his figures show.

As would be expected all the muscles of the face and scalp are

supplied by the facial nerve. A considerable amount has been written about the innervation of the mandibulo-auricularis, Cords (1922) gives the supply from the auriculo-temporal nerve in some non-marsupial mammals at the same time noting that there are connections between the mandibular and facial nerves. Huber (1925) gives a posterior auricular supply in Did. marsupialis and M. billardierii, and has proved this supply in the former case by electrical stimulation (1924b); he has also shown in the same marsupial, as well as some placental mammals, that branches given to this muscle from the auriculo-temporal nerve are sensory (1924a). Adams, Wheeler and Edgeworth (1929) point out that a post-auricular supply is not invariable but cite no marsupials amongst the exceptions; they give the supply from the posterior auricular branch of the facial nerve itself in M. ruficollis, Phascolarctos, Das. maculatus and Did. marsupialis, and from a separate branch that leaves the Fallopian canal independently in M. dorsalis, M. giganteus, Petrogale and Bettongia; this latter is also the case in T. vulpecula. Parsons (1905), in his account of Choer. castanotis, describes as a third part of the masseter a muscle that is almost certainly the mandibulo-auricularis, though he uncertainly ascribes the innervation to the third division of the fifth nerve.

(b). Panniculus of the trunk (figs. 7, 8; pls. III, IV).

The panniculus carnosus of the trunk is a well developed sheet of muscle confined to the region caudal to the axillae and extending into the proximal parts of the hind-limbs. The cranial part of the

Figure 7. Dorse-lateral aspect of trunk showing arrangement of fibres of panniculus carnosus. $x\frac{1}{2}$.

Figure 8 (cf. pls. III, IV). Ventral aspect of trunk showing arrangement of fibres of panniculus carnosus. $x\frac{1}{2}$.

- Ax.Pann. - Axillary slip of panniculus carnosus.
- Dec. - Decussation of fibres caudal to marsupium.
- Mars. - Opening of marsupium.
- P.maj. - Pectoralis major.
- P.qu. - Pectoralis quartus.

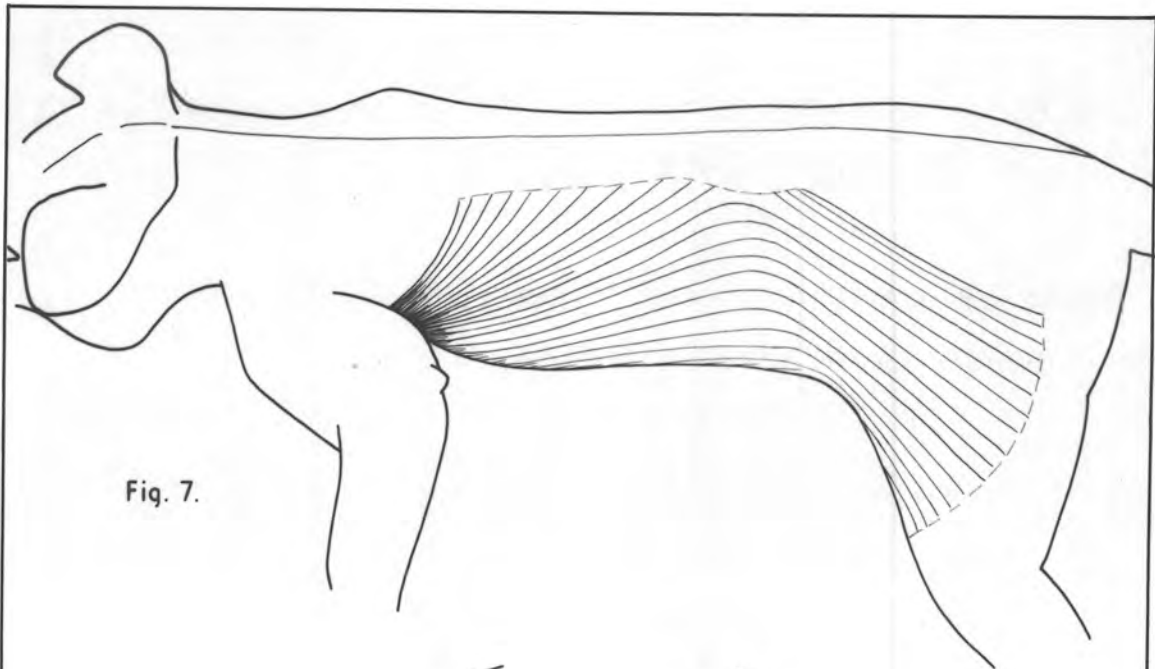


Fig. 7.

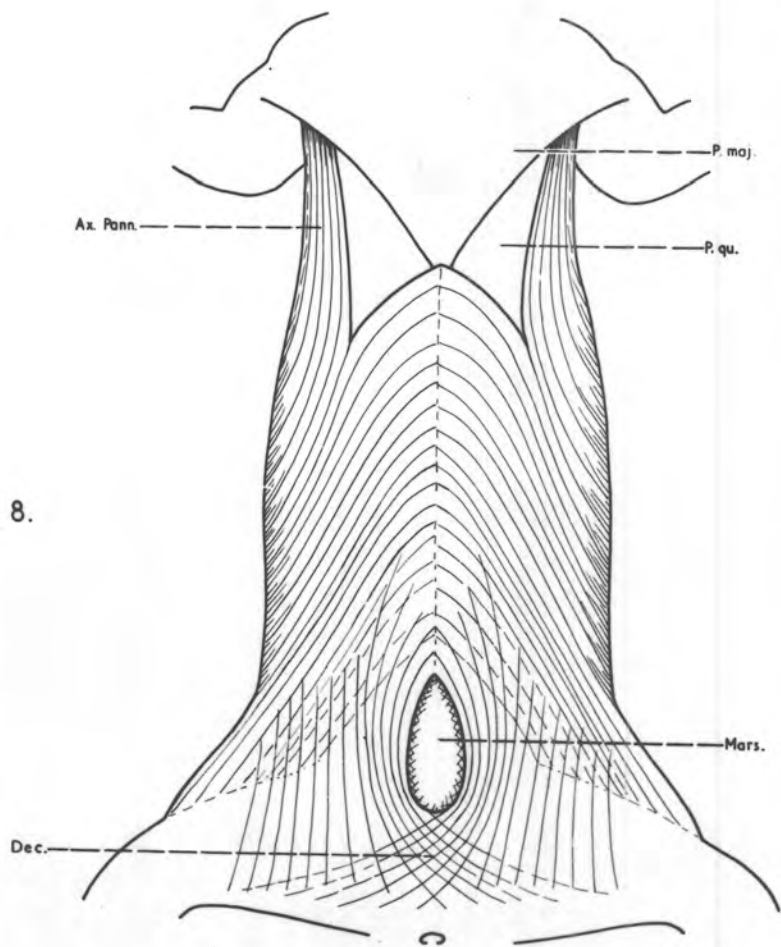
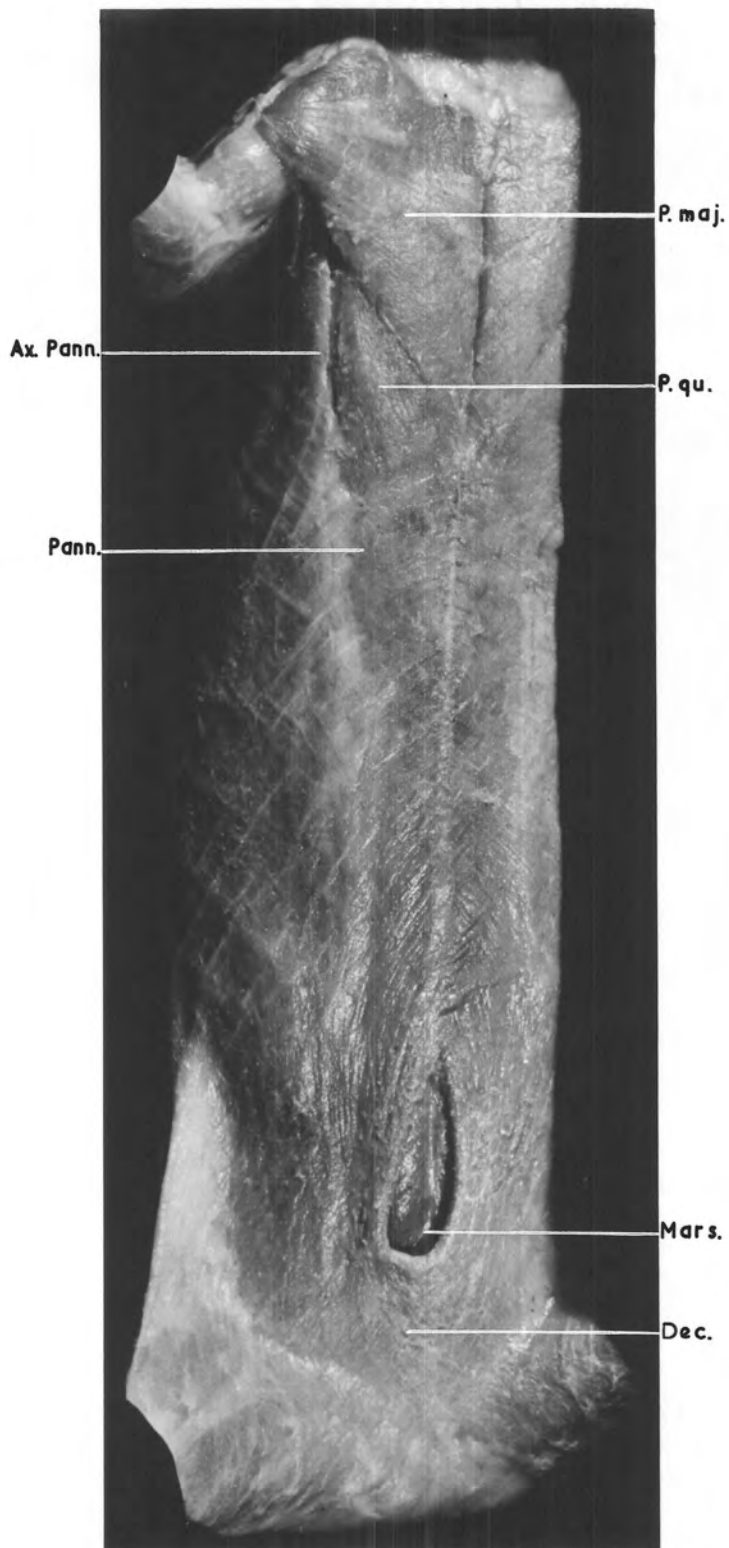


Fig. 8.

Plate III (cf. fig. 8). Ventral view of trunk with panniculus
carnosus in position. $\times 3/5$.

- Ax.Pann. - Axillary slip of panniculus carnosus.
- Dec. - Decussation of fibres caudal to marsupium.
- Mars. - Opening of marsupium.
- Pann. - Part of panniculus passing to midline.
- P.maj. - Pectoralis major.
- P.qu. - Pectoralis quartus.



sheet takes origin from the skin of the back along a line about two centimetres from the median plane and extending caudally for some ten centimetres from a point just caudal to the scapula; these fibres run cranially and ventrally around the body wall. The next part of the origin is from the distal two thirds of the lateral aspect of the thigh; from here fibres run cranially and somewhat dorsally, the most dorsal ones ending in the fascia of the back near the origin of the most caudal fibres of the first part of the sheet described above; most of these fibres, however, turn cranially and ventrally here and join the caudal border of this aforementioned section of the sheet. Most of the fibres so far described turn cranially on the ventro-lateral aspect of the chest wall to enter the axilla and attach to a tendinous arch that stretches across the axilla from the latissimus dorsi to the pectoralis quartus and so gain indirect attachment to the humerus; this is the thickest part of the whole panniculus - the "cutaneous maximus" of some authors. Some of the most caudal fibres of the dorsal portion of the sheet, however, turn more medially towards the ventral midline of the body instead of into the axilla and so form the cranial part of the main sheet as seen from this aspect, the caudal portion being formed of fibres running a similar cranio-medial course from their origin on the medial side of the thigh. This ventral section of the main sheet is inserted into a median raphe extending from the caudal part of the sternum to a point some distance cranial to the opening of the marsupium and adherent throughout much of its extent to the linea

alba. The fibres arising nearest the knee on both the medial and lateral sides of the thigh form a "web" between the thigh and the trunk, the fibres in the free edge of which run to about the middle of the raphe.

Other fibres arising more caudally from the medial aspect of the thigh pass cranially superficial to the main sheet and fade away just cranial to the level of the anterior end of the pouch opening. Arising in the same region as these and lying deep to them is a further band of fibres whose origin also extends more medially towards the anus; these fibres run cranially and medially, decussate in the interval between the marsupium and the cloacal orifice, and then curve cranially around the side of the opening of the marsupium, the ones nearest to the edge of the opening being inserted into the raphe mentioned above which is therefore extended back to reach the cranial limit of the pouch, those further out stopping slightly away from the median plane superficial to the main sheet. This last part of the panniculus constitutes the sphincter marsupii of this animal.

The arrangement is essentially the same in both sexes, in the male the opening for the "marsupium" is just as large and transmits the spermatic cords to the scrotum which lies over the caudal border of the opening.

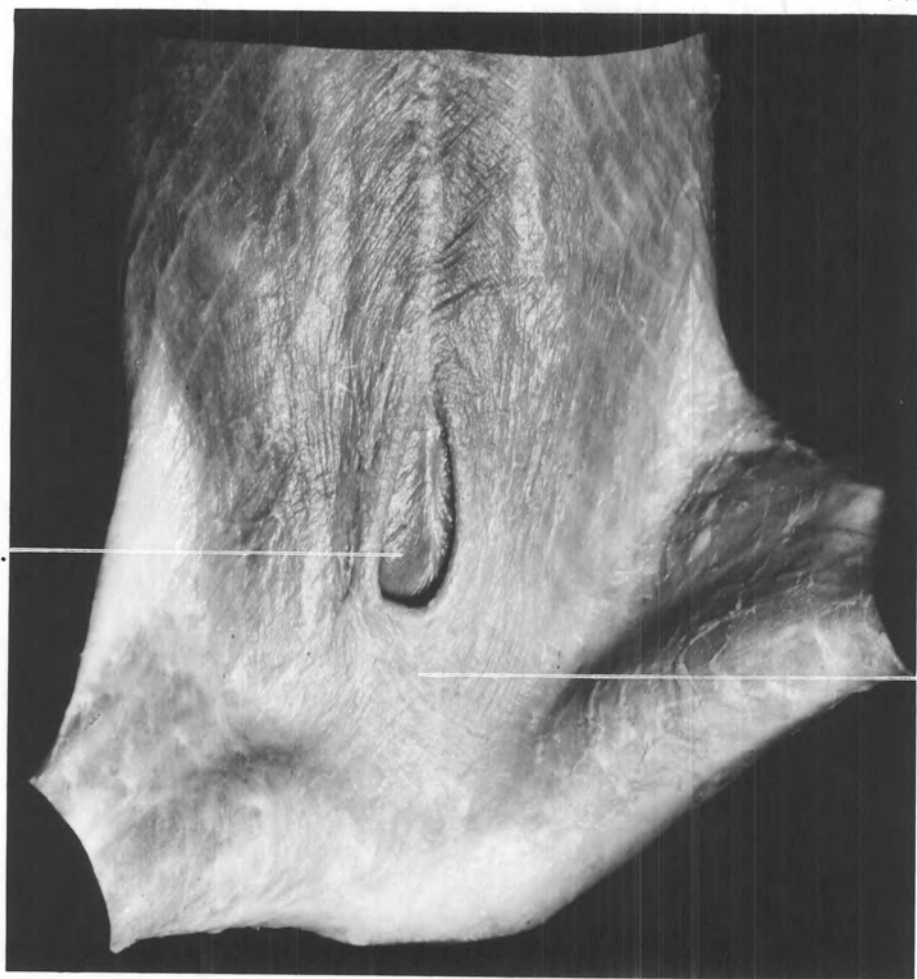
The arrangement of the panniculus of the trunk appears from the accounts given in the literature to vary considerably in different marsupials, the most constant part being the axillary slip. The

Plate IV (cf. fig. 8). Ventral view of abdominal wall to show the arrangement of the fibres of the panniculus carnosus in the region of the marsupium. $\times \frac{3}{4}$.

Dec. - Decussation of fibres caudal to marsupium.

Mars. - Opening of marsupium.

Mars.



Dec.

sphincter marsupii has no common pattern; in N. typhlops (Wilson, 1894) the fibres that constitute it pass caudally, some of them surrounding the opening and others attaching to the skin of its margins; in Phasc. cinereus Young (1882) describes the fibres as almost surrounding the opening. In Thyl. cynocephalus (Cunningham, 1882; Carlsson, 1905) the fibres of the two sides of the pouch decussate cranial to the opening while caudal to it they meet and are inserted into fibrous tissue over the symphysis, thus showing a very similar arrangement to that described for Per. obesula by Katz (1882); in Hypsiprymnodon moschatus (Heighway, 1959) the fibres that form the sphincter arise on the medial sides of the thighs and, sweeping caudally and medially, become continuous with their fellows across the midline caudal to the pouch opening. In the opossum (Langworthy, 1952) the fibres run caudally on both sides of the opening from the ventral midline of the abdomen cranial to the pouch but do not meet caudal to it. Leche (1874-1900), Katz (1882) and Carlsson (1905) go further into the comparative aspects of this muscle.

In Trichosurus a large branch passes from the medial pectoral nerve to the axillary part of the panniculus and is probably the only source of supply to the whole layer. Boardman (1941) gives the supply from the anterior thoracic nerve only in M. robustus, as does Tobler (1902) for M. bennetti and Langworthy (1952) for the opossum.

DEEP MUSCULATURE.

(a). Muscles of the head and ventro-lateral region of the neck.1). Muscles of mastication.

Masseter (figs. 9, 17; pls. V, VIII) is a large muscle incompletely divided into superficial and deep parts, the superficial being further separable into two portions that are quite distinct except at their origin. The superficial part arises from the lower area on the lateral surface of the zygomatic arch, and from most of this origin the fibres pass caudally and a little ventrally forming a mass that has many aponeurotic fibres on the surface and another aponeurotic layer deeper within and which is inserted into the ventral and caudal edges of the ventral half of the ramus of the mandible and into the lateral part of the inflected portion of the bone; this insertion extends up to overlap the origin of the mandibulo-auricularis. The most rostral fibres of origin of the superficial part of the muscle coming from the rostral end of the zygomatic bone and the zygomatic process of the maxilla are much more aponeurotic and fan out, the ventral ones passing ventrally and caudally, the dorsal ones passing directly caudally and overlapping the portion of the muscle described above; this section of the muscle is inserted into the medial part of the inflected portion of the mandible as far as the edge of the pterygoid fossa and the inflected angle. The insertions of both these superficial sections of the muscle are partly fleshy and partly tendinous. The deep part of the masseter arises from the ventral border and deep surface of the

Figure 9 (cf. pl. V). Masseteric region and side of neck. $x1\frac{1}{4}$.

Figure 10 (cf. pl. VI). Infra-temporal region from lateral aspect. Masseter and temporalis and the zygomatic arch are removed and most of the ramus of the mandible chipped away. $x1\frac{1}{4}$.

Figure 11. Deep infra-temporal and sub-lingual regions. The masseter, temporalis, pterygoid muscles, sterno-hyoid and the zygomatic arch are removed and the right half of the mandible turned downwards and laterally. $x1\frac{1}{8}$.

Figure 12 (cf. pl. VII). Deep infra-temporal and sub-lingual regions. The right half of the mandible with the masseter, temporalis, pterygoids, digastric and mylo-hyoid, the zygomatic arch, the tensor palati and the sterno-hyoid are removed. $x1\frac{1}{8}$.

Key to figs. 9, 10, 11 and 12.

- A.B.D. - Anterior belly of digastric.
- Bu. - Buccinator.
- Cl-occ. - Cleido-occipitalis.
- C.Ph. - Constrictor pharyngis.
- C.Sh. - Carotid sheath.
- C.T.D. - Central tendon of digastric.
- G-gl. - Genio-glossus.
- G-hy. - Genio-hyoid.
- H-g.N. - Hypoglossal nerve.
- Hy-gl. - Hyo-glossus.
- I.AL.N. - Inferior alveolar nerve.
- Int. - Tendinous intersection in genio-hyoid.
- I-o.N. - Infra-orbital nerve.
- Lac.N. - Lacrimal nerve.
- L.Ca. - Longus capitis.
- L.N. - Lingual nerve.
- L.P. - Levator palati.
- L.Pt. - Lateral pterygoid.
- Man. - Mandible.
- Mass. - Masseter.
- M-au. - Mandibulo-auricularis.
- M.N. - Mandibular nerve.
- M.Pt. - Medial pterygoid.
- Myl. - Mylo-hyoid.
- O.C.S. - Obliquus capitis superior.
- Omo. - Omo-hyoid.
- O-t.v. - Omo-trachelien ventralis.
- Pa-m. - Paramastoid process.
- P.B.D. - Posterior belly of digastric.
- Pt.H. - Pterygoid hamulus.
- S.M. - Symphyseal surface of mandible.
- St-gl. - Stylo-glossus.
- St-hy. - Sterno-hyoid.
- St-m. - Sterno-mastoid.
- St-th. - Sterno-thyroid.
- T. - Tongue.
- T.B. - Thyroid bulla.
- Th-hy.d. - Dorsal part of thyro-hyoid.
- Th-hy.v. - Ventral part of thyro-hyoid.
- T-m.J. - Temporo-mandibular joint.
- T.P. - Tensor palati.
- Tr. - Trapezius.
- Z. - Zygomatic arch (cut).

Fig. 9.

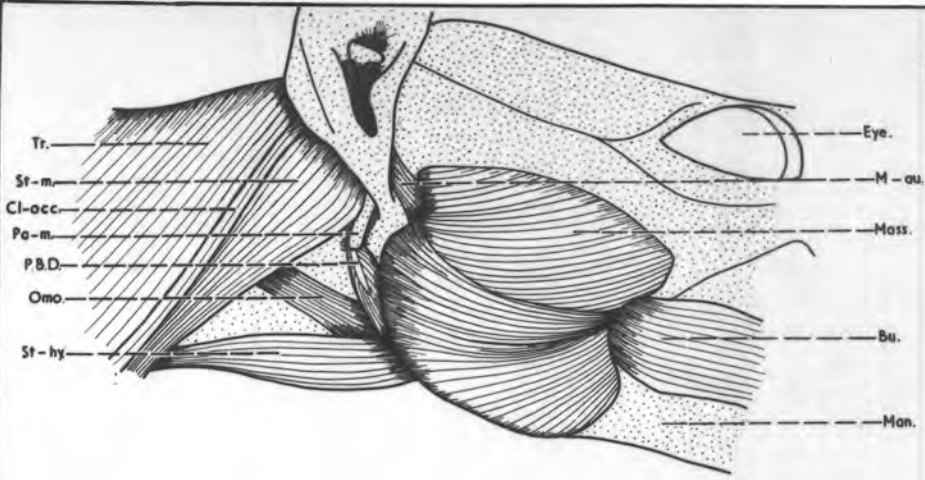


Fig. 10.

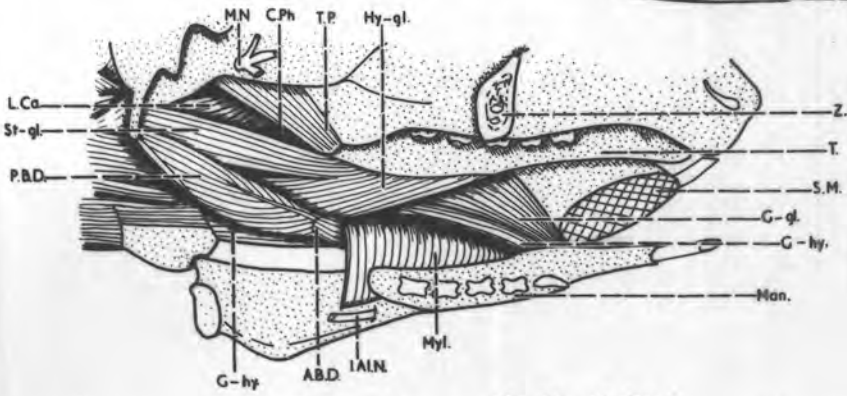
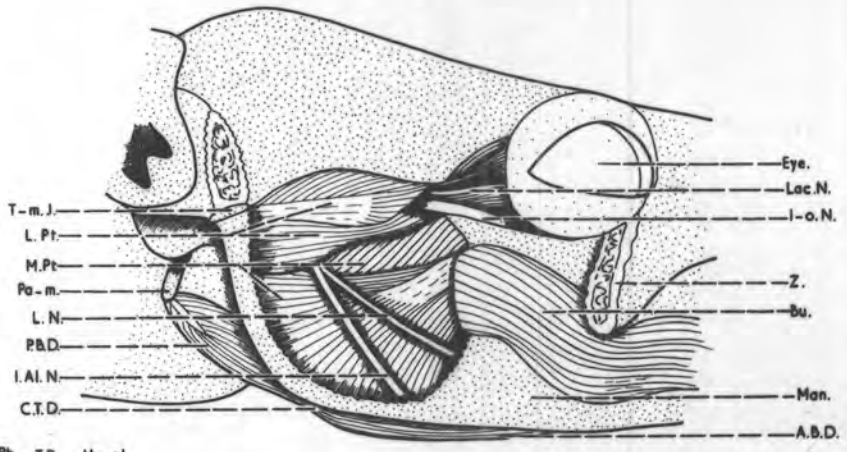


Fig. 11.

Fig. 12.

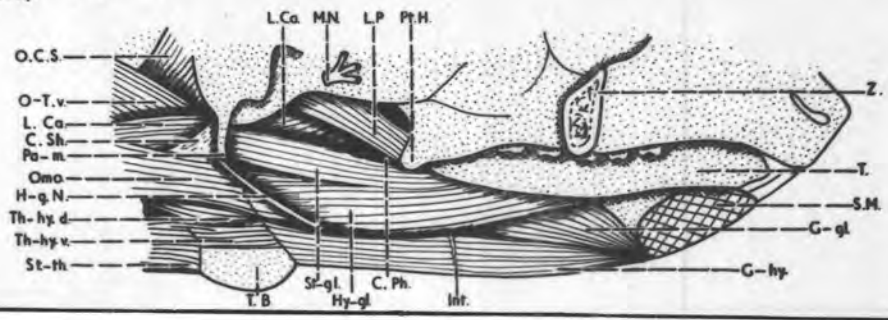
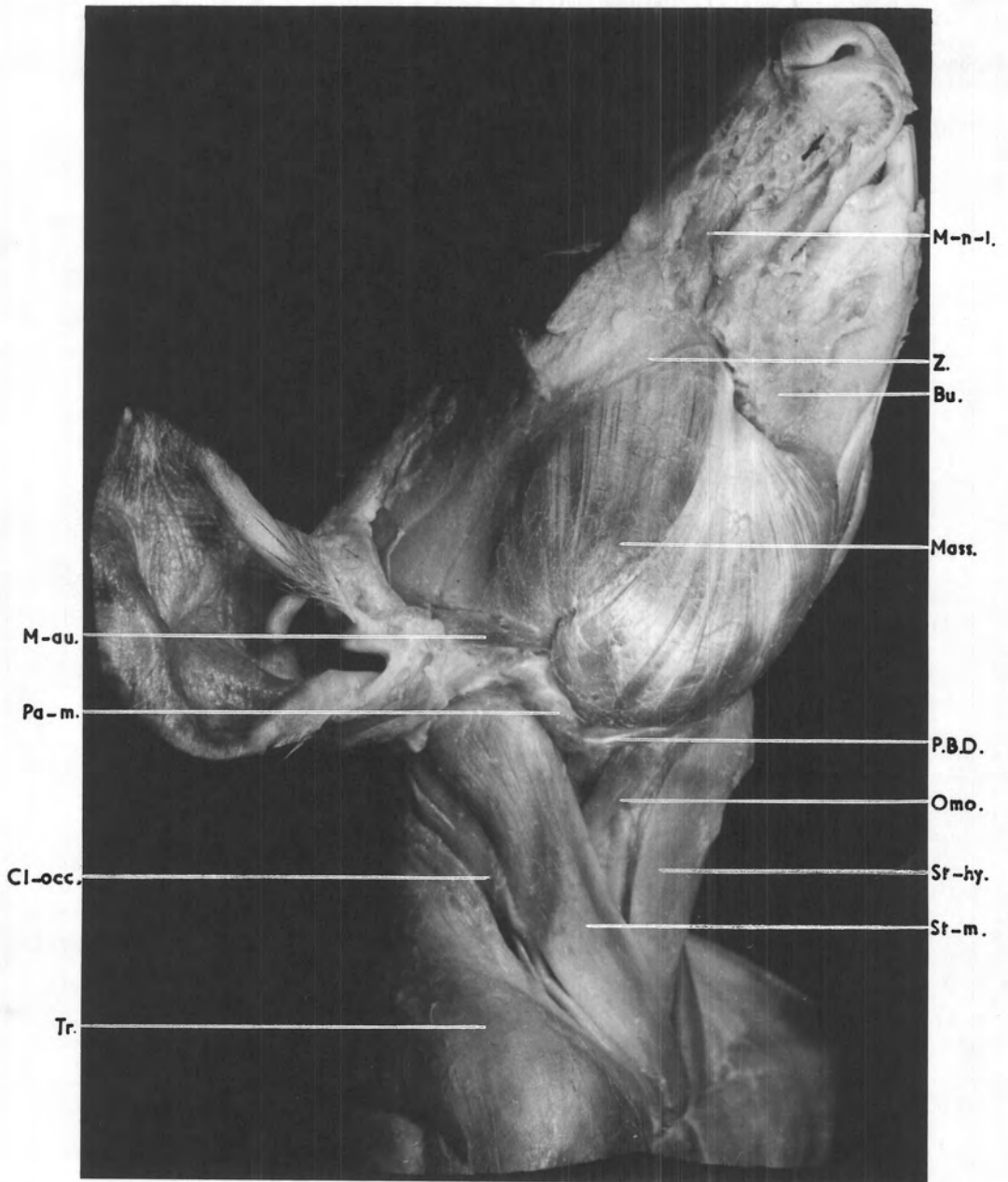


Plate V (cf. fig. 9). Ventro-lateral view of masseteric region and neck. $\times 1\frac{1}{3}$.

- Bu. - Buccinator.
- Cl-occ. - Cleido-occipitalis.
- Mass. - Masseter.
- M-au. - Mandibulo-auricularis.
- M-n-l. - Maxillo-naso-labialis.
- Omo. - Omo-hyoid.
- Pa-m. - Paramastoid process.
- P.B.D. - Posterior belly of digastric.
- St-hy. - Sterno-hyoid.
- St-m. - Sterno-mastoid.
- Tr. - Trapezius.
- Z. - Zygomatic arch.



zygomatic arch, its fibres run more ventrally than those of the superficial part and find insertion to the whole of the lateral aspect of the ramus except the coronoid: as noted by Abbie (1939a) there is no masseteric canal in this animal. The deep aspect of the muscle is directly continuous with the temporalis and the two cannot be separated.

A well developed masseter is characteristic of marsupials, and it is usually partly or completely divisible into two or three strata, the superficial or frontal extending its insertion to the inflected angle as in Did. virginiana (Coues, 1872), Chironectes variegatus (Sidebotham, 1885), Choer. castanotis (Parsons, 1903), Hyps. moschatus (Heighway, 1959), Dendrolagus dorianus (Carlsson, 1914), Pet. xanthopus (Parsons, 1896) and Thylogale stigmatica and others (Abbie, 1939a).

Deep union with the temporalis has also been mentioned for Caenolestes (Osgood, 1921), Chir. variegatus (Sidebotham, 1885), Hyps. moschatus (Heighway, 1959), Perameles, Didelphys, Dasyurus, Petaurus, the wombat and the Macropodidae (Lubosch, 1908) and Phasc. cinereus (Young, 1882) though in the last the same author found the muscles quite separate in two other specimens.

Temporalis has its origin from the temporal fossa of the skull to within a few millimetres of the infra-temporal ridge and from the whole of the temporal fascia except its caudo-medial corner, the origin extending to the nuchal crest and adjoining the midline for about three centimetres along the median sagittal crest. The muscle

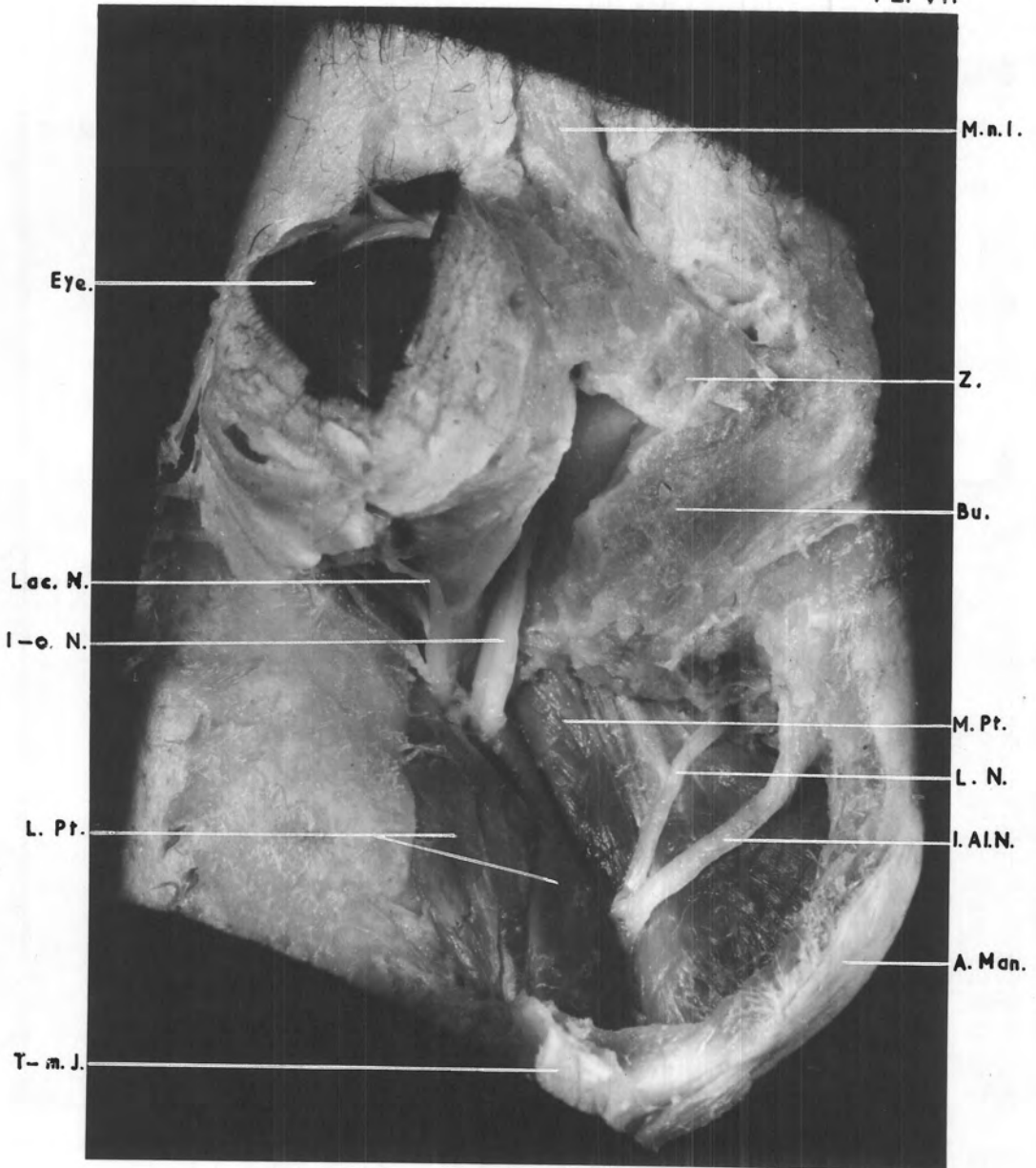
is inserted into the lateral surface of the coronoid and the frontal border and medial surface of the ramus, this latter part of the insertion extending down to within one or two millimetres of the floor of the pterygoid fossa. The area of origin from the temporal fascia and that from the part of the temporal fossa just frontal to the ear are directly continuous with the origin of the masseter from the deep surface of the zygomatic arch and the two must be considered as forming one muscle in this animal. In the presence of this continuity I have arbitrarily included all the fibres arising from the zygomatic arch with the masseter and those from the temporal fascia and fossa in the temporalis.

Lateral Pterygoid (fig. 10; pl. VI) is by far the smaller of the two pterygoid muscles and is clearly separable into upper (dorsal) and lower (ventral) heads the relative sizes of which varied in different specimens but which, on the average, appear to be roughly equal. The upper head arises from the sphenoid bone below the infra-temporal crest and extending frontally to a point just above the optic foramen; the lower has its origin from the crest representing the lateral pterygoid plate, from the lower part of the infra-temporal surface of the sphenoid and, further frontally, from the palatine bone just below the foramen rotundum. The two heads unite and are inserted into the head and neck of the mandible, the capsule of the temporo-mandibular joint and indirectly, through this, into the articular disc. Abbie (1939b) points out that the presence of an articular disc is characteristic of only the

Plate VI (cf. fig. 10). Lateral view of infra-temporal region.

Masseter and temporalis and the zygomatic arch are removed and most of the ramus of the mandible chipped away. $\times 2\frac{1}{2}$.

- A.Man. - Angle of mandible.
- Bu. - Buccinator.
- I.Al.N. - Inferior alveolar nerve.
- I-o.N. - Infra-orbital nerve.
- Lac.N. - Lacrimal nerve.
- L.N. - Lingual nerve.
- L.Pt. - Lateral pterygoid.
- M-n-l. - Maxillo-naso-labialis.
- M.Pt. - Medial pterygoid.
- T-m.J. - Temporo-mandibular joint.
- Z. - Zygomatic arch (cut).



Diprotodont members of the Marsupialia.

The only great divergence from the insertion given here appears to be in Chcer. castanotis where Parsons (1905) gives the insertion to the mandible just above the inferior dental foramen.

Medial Pterygoid (fig. 10; pl. VI). The larger of the two pterygoid muscles springs by fleshy fibres from the (medial) pterygoid plate, from the tubercle of the palatine bone as far rostrally as the foramen rotundum, and from the pterygoid fossa of the sphenoid as far caudally as the foramen ovale. The insertion fills the pterygoid fossa of the mandible, the muscle fibres attaching to the whole of the inflected part of the bone except for small areas in the rostral and caudo-lateral corners. A small portion arising from the basal part of the pterygoid plate and the palatine bone is somewhat separate at first but there is no clear division into two heads.

I have found one mention of fusion of the two pterygoid muscles in a marsupial, that in Phasc. cinereus (Macalister, 1872b); Young (1882) and Sonntag (1922), however, do not agree with Macalister on this point.

The muscles of mastication are all innervated by the mandibular nerve.

2). Supra-hyoid and extrinsic lingual muscles.

Digastric (figs. 9, 10, 11, 17, 20; pls. V, VIII, IX). The posterior belly of this muscle, which Lightoller (1939) says is representative of the stylo-hyoid in marsupials, arises in Trichosurus by tendon

and some fleshy fibres from the frontal aspect of the tip of the paramastoid (paroccipital) process and ends in an oblique tendinous intersection a little more than one centimetre beyond the angle of the mandible. The anterior belly runs from this intersection to attach to the base of the mandible by a short flat tendon about one centimetre wide that does not quite reach to the symphysis menti. From the intersection a small triangular aponeurosis extends medially to the middle of the hyoid bone and also to meet its fellow in the midline rostral to the hyoid where the union of the two virtually produces a continuation of the mylo-hyoid raphe back to the hyoid bone. This aponeurosis binds the central intersection of the digastric to the hyoid bone and has the appearance of being an aponeurosis of insertion for the caudal fibres of the mylo-hyoid which find their insertion into the deep surface of the intersection and then indirectly, through this aponeurosis, to the hyoid bone and to the caudal end of the raphe that extends from here to the symphysis menti. This aponeurosis is mentioned by Bijvoet (1908) who says that it gives part origin to the mylo-hyoid, and by Lightoller (1959) who describes it as an extension of the posterior belly of the digastric. The attachments noted here are in general agreement with those given by Bijvoet (1908) and Carlsson (1914) though the latter puts the attachment of the anterior belly in the middle of the lower jaw. The posterior belly receives a small branch from the facial nerve, the anterior belly being supplied in typical fashion by the mylo-hyoid branch of the inferior alveolar

nerve.

As indicated by Lightoller (1959), an origin from the paramastoid is the usual thing in marsupials, though Carlsson (1914) gives it from the mastoid in Dend. dorianus as does Leche (1874-1900) in Myrmecobius, and Heighway (1959) describes that of Hyps. moschatus on the base of the skull near the paramastoid. The attachment to the mandible varies somewhat in position in different marsupials, in Caenolestes (Osgood, 1921) it occupies the whole length of the base.

No central tendon is present in the digastric muscle in Dend. ursinus, Per. obesula or Metachirus opossum (Somntag, 1921b), nor does Osgood (1921) mention one for Caenolestes. Carlsson (1914) notes its absence also in Dend. dorianus and Petrogale penicillata, while an incomplete one is described for Did. virginiana by Coues (1872), for Pet. xanthopus by Parsons (1896) and for M. robustus by Bijvoet (1908). In Notoryctes (Lightoller, 1959) and Myrmecobius (Leche, 1874-1900; Lightoller, 1959) the two bellies are entirely separate from one another. The long intersection that gives rise to the anterior belly in Phascolarctos has the sterno-hyoid and the omohyoid, as well as the posterior belly of the muscle, attaching to its caudal edge (Macalister, 1872b; Lightoller, 1959); a somewhat similar description is given for this animal by Young (1882), and Bijvoet (1908) gives a comparable account for a marsupial that he names Phascologmys wombat but calls the koala in his text. Somntag (1922) describes the muscle as monogastric in Phasc. cinereus and

also in Pseudochirus peregrinus.

In a number of marsupial genera - Caenolestes (Osgood, 1921), Didelphys and Halmaturus (Bijvoet, 1908), Cuscus (Bijvoet, 1908; Edegworth, 1937), Macropus (Bijvoet, 1908; Lightoller, 1939), Petrogale, Phascolarctos and Dasyurus (Lightoller, 1939) - tendinous medial extensions to the midline have been noted, in some cases arising from a separate part of the muscle, and nearly always coming from the posterior belly, thus indicating that this aponeurosis belongs to this belly and not to the mylo-hyoid as appeared from my dissections of Trichosurus. This conclusion is in agreement with the account of the digastric given by Lightoller (1939).

The usual double innervation of the digastric has been verified by Bijvoet (1908) for C. maculosus, Did. opossum, M. robustus and Halmaturus ualabatus, and by Parsons (1905) for Choer. castanotis and (1896) for Pet. xanthopus.

Mylo-hyoid (figs, 11, 17) has its origin from the inner surface of the mandible adjacent to the last two molar teeth and further caudally as far as the mandibular foramen. The fibres pass medially and caudally, most of them being inserted into a median raphe extending from the symphysis, the caudal ones, however, having their attachment to the deep aspect of the central intersection of the digastric; through the medial aponeurotic expansion from this (as described above with the digastric muscle) they gain indirect attachment to the hyoid bone and to the caudal end of the mylo-hyoid raphe which is extended to reach the hyoid by the union in the mid-

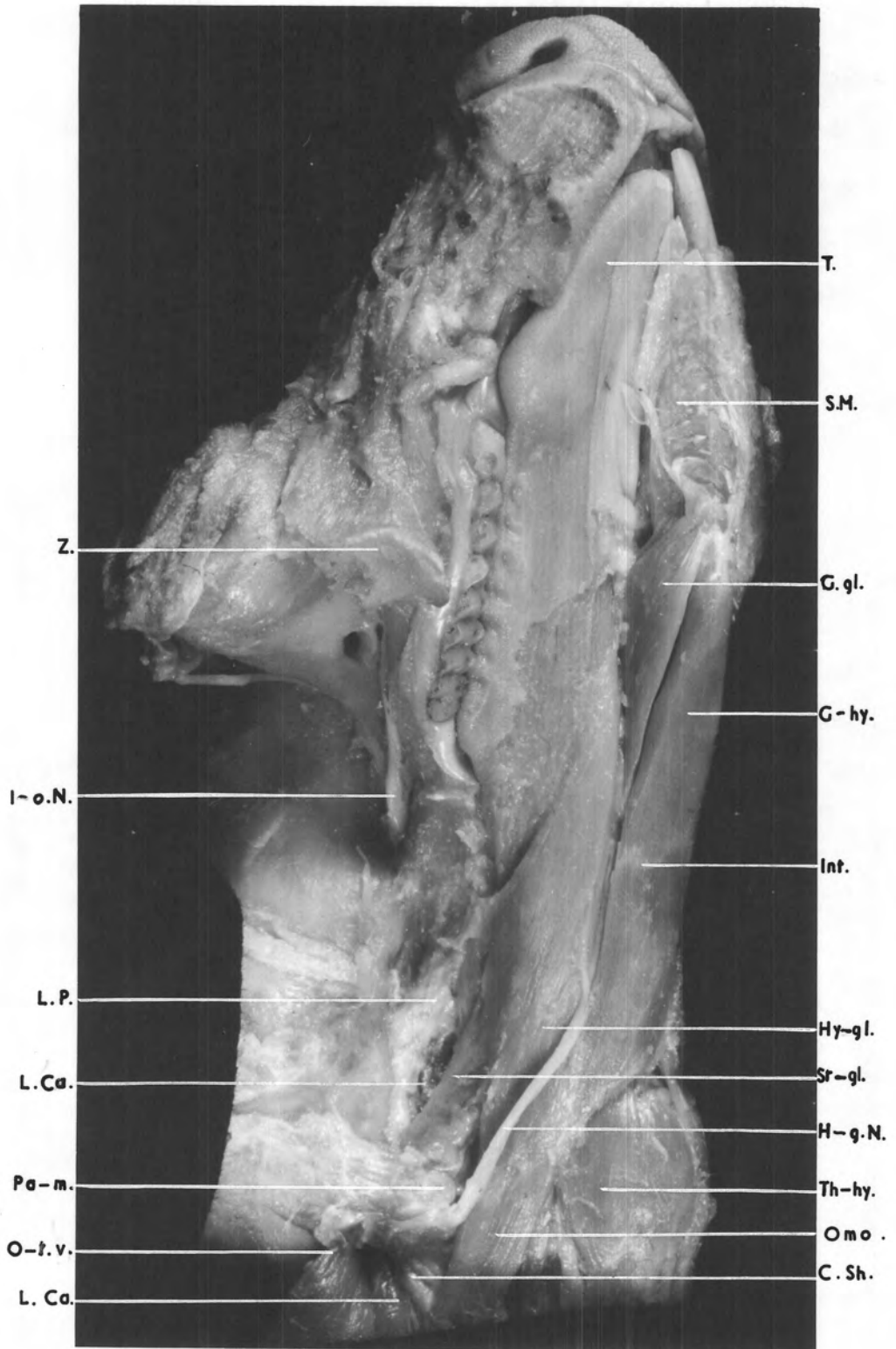
line of these two expansions. The account given for this muscle by Bijvoet (1908) agrees in most respects with this description though he gives the attachment of the caudal fibres to the aponeurotic expansion from the digastric and not to the intersection itself; he also gives the same outline for both C. maculosus and Did. opossum. As noted by Bijvoet (1908), the muscle is supplied by the mylo-hyoid nerve.

In most marsupials the insertion of the mylo-hyoid reaches the hyoid bone, other exceptions noted being Phasc. cinereus (Young, 1882), Did. virginiana (Coues, 1872), Caenolestes (Osgood, 1921) and Chir. variegatus in which Sidebotham (1885) describes the attachment of the caudal fibres to the extension from the posterior belly of the digastric apparently closely resembling the condition found by Bijvoet (1908) in the marsupials mentioned above. The raphe stops short of the symphysis in Pet. xanthopus (Parsons, 1896), Myrmecobius and Phascogale (Leche, 1874-1900); and in C. maculatus and C. orientalis Edgeworth (1937) describes the "intermandibulares" as radiating from the transverse aponeurosis between the digastrics, there being no raphe at all. Sonntag (1922) notes the continuity of the muscle with the sterno-hyoid and connection with the digastric in Phasc. cinereus.

Genio-hyoid (figs. 11, 12; pl. VII) arises by a short tendon from an impression on the inner aspect of the mandible near the base and adjacent to the symphysis. It is a relatively large muscle adherent to its fellow and to the overlying mylo-hyoid raphe; it is inserted

Plate VII (cf. fig. 12). Ventro-lateral view of deep infra-temporal and sub-lingual regions. The right half of the mandible with the masseter, temporalis, pterygoids, digastric and mylo-hyoid, the zygomatic arch, the tensor palati and the sterno-hyoid are removed. $\times 2\frac{1}{4}$.

- C.Sh. - Carotid sheath.
- G-gl. - Genio-glossus.
- G-hy. - Genio-hyoid.
- H-g.N. - Hypoglossal nerve.
- Hy-gl. - Hyo-glossus.
- Int. - Tendinous intersection in genio-hyoid.
- I-o.N. - Infra-orbital nerve.
- L.Ca. - Longus capitis.
- L.P. - Levator palati.
- Omo. - Omo-hyoid.
- O-t.v. - Omo-trachelien ventralis.
- Pa-m. - Paramastoid process.
- S.M. - Symphyseal surface of mandible.
- St-gl. - Stylo-glossus.
- T. - Tongue.
- Th-hy. - Thyro-hyoid.
- Z. - Zygomatic arch (cut).



into the body of the hyoid bone from the midline out to the medial border of the omo-hyoid. At its middle is a well marked tendinous intersection. A branch from the hypoglossal provides its nerve supply; the hypoglossal nerve has a communicating branch from the first cervical nerve and the fibres to the genio-hyoid might well come from this source.

In Phasc. cinereus Sonntag (1921a, 1922) describes an extension onwards to the larynx that appears to represent the thyro-hyoid; Young (1882), in his account of the same species, gives the insertion to the greater cornu of the hyoid and he, together with Macalister (1872b) and Bijvoet (1908), note the great length of the muscle that results from the marked caudal displacement of the hyoid bone in Phascolarctos (the last author calling it Phascolomys wombat but referring to it in the text as the koala as mentioned before). In Chir. variegatus Sidebotham (1885) notes a slip given off to the genio-hyo-glossus. Otherwise there appear to be no remarkable features about the genio-hyoid in this group of mammals. I have found no other reference to a tendinous intersection in this muscle in a marsupial.

Genio-glossus (figs. 11, 12; pl. VII) takes origin from the inner surface of the mandible near the base and close to the symphysis, just above the attachment of genio-hyoid: the fibres spread out into the tongue adjacent to the midline. The most ventral fibres of the muscle run deep to the hyoid bone and end in the pharyngeal end of the tongue very close to this bone; there is, however, no direct

attachment to the hyoid as there is in Hyps. moschatus (Heighway, 1939), Phasc. cinereus (Young, 1882), Chir. variegatus (Sidebotham, 1885) and Did. virginiana (Coues, 1872).

Hyo-glossus (figs. 11, 12; pl. VII) has its origin from the whole length of the body and greater cornu of the hyoid, the attachment extending medially to the midline. Some of the dorsal fibres of the muscle pass deep to the stylo-glossus and blend with its deep surface, the others form a band running alongside and fused with the ventral border of this muscle with which they pass into the tongue; some of the deepest fibres run amongst and even deep to those of the genio-glossus. In Pet. xanthopus Parsons (1896) gives some of the origin from a raphe frontal to the hyoid bone; in Phasc. cinereus there is no true hyo-glossus according to Sonntag (1921a, 1921b, 1922), though Young (1882) describes a transverse slip of muscle that runs from one side of the tongue to the other between the genio-glossi and the genio-hyoids and which he thinks represents it.

Stylo-glossus (figs. 11, 12; pl. VII) arises blended with the stylo-pharyngeus from the frontal aspect of the paramastoid process, the stylo-glossus forming the superficial part of this origin. The fibres are inserted into the tongue overlapping and fusing with the dorsal portion of the hyo-glossus. The long slender cartilaginous extension of the lesser cornu of the hyoid reaches this muscle and receives the insertion of some of its fibres; these fibres presumably do not represent the stylo-hyoid as Bijvoet (1908) and Huber (1930) indicate that the stylo-hyoid is not present in marsupials, while

Lightoller (1939) considers that it forms the posterior belly of the digastric in this group of mammals. Windle and Parsons (1897b), however, mention a stylo-hyoid for M. rufus.

The genio-glossus and the hyo-glossus receive their nerve supply from the hypoglossal nerve; no branch to the stylo-glossus was found.

5). Infra-hyoid muscles.

Sterno-hyoid (figs. 9, 17, 20, 24; pls. V, VIII, IX, XVI) has a fleshy origin from the caudal third of the deep surface of the manubrium, to a small extent from the second costal cartilage and from rather more of the first costal cartilage, this last part of the origin forming the lateral two thirds of the muscle. Passing cranially in the neck, not quite bordering on the midline, it is inserted into the ventral aspect of the hyoid bone: in one specimen (No. 5) both the muscles had incomplete tendinous intersections just caudal to the middle. Kohlbrugge (1898) also mentions an inscription in this muscle in C. orientalis.

The origin of the sterno-hyoid shows considerable variation, attachments as far caudally as the third piece of the sternum and from one or more of the first three costal cartilages have been described for different marsupials. Macalister (1872b) also gives some clavicular origin in Phascolarctos; in this species there is no attachment to the hyoid (Sonntag, 1922; Young, 1882). Sonntag (1921b) mentions a fusion with the underlying sterno-thyroid in Per. obesula.

Plate VIII (cf. fig. 17). Ventral view of submandibular region and neck. x⁵/₆.

- A.B.D. - Anterior belly of digastric.
- Cl-m. - Cleido-mastoid.
- Del.cl. - Clavicular part of deltoid.
- Mass. - Masseter.
- Myl.ap. - Aponeurotic expansion from central intersection of digastric (mylo-hyoid aponeurosis).
- Omo. - Omo-hyoid.
- P.B.D. - Posterior belly of digastric.
- P.maj. - Pectoralis major.
- St-hy. - Sterno-hyoid.
- St-m. - Sterno-mastoid.
- St-th. - Sterno-thyroid.

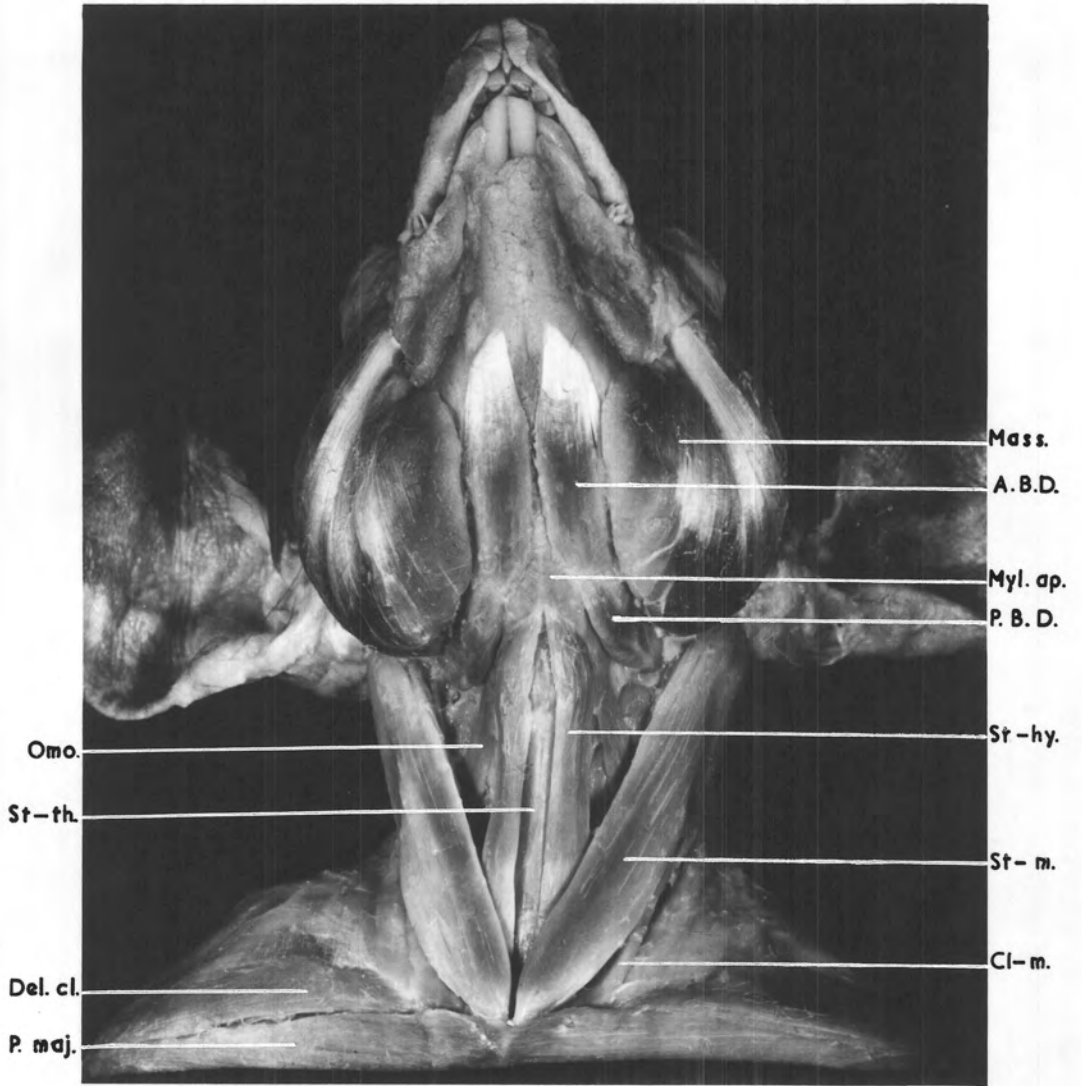
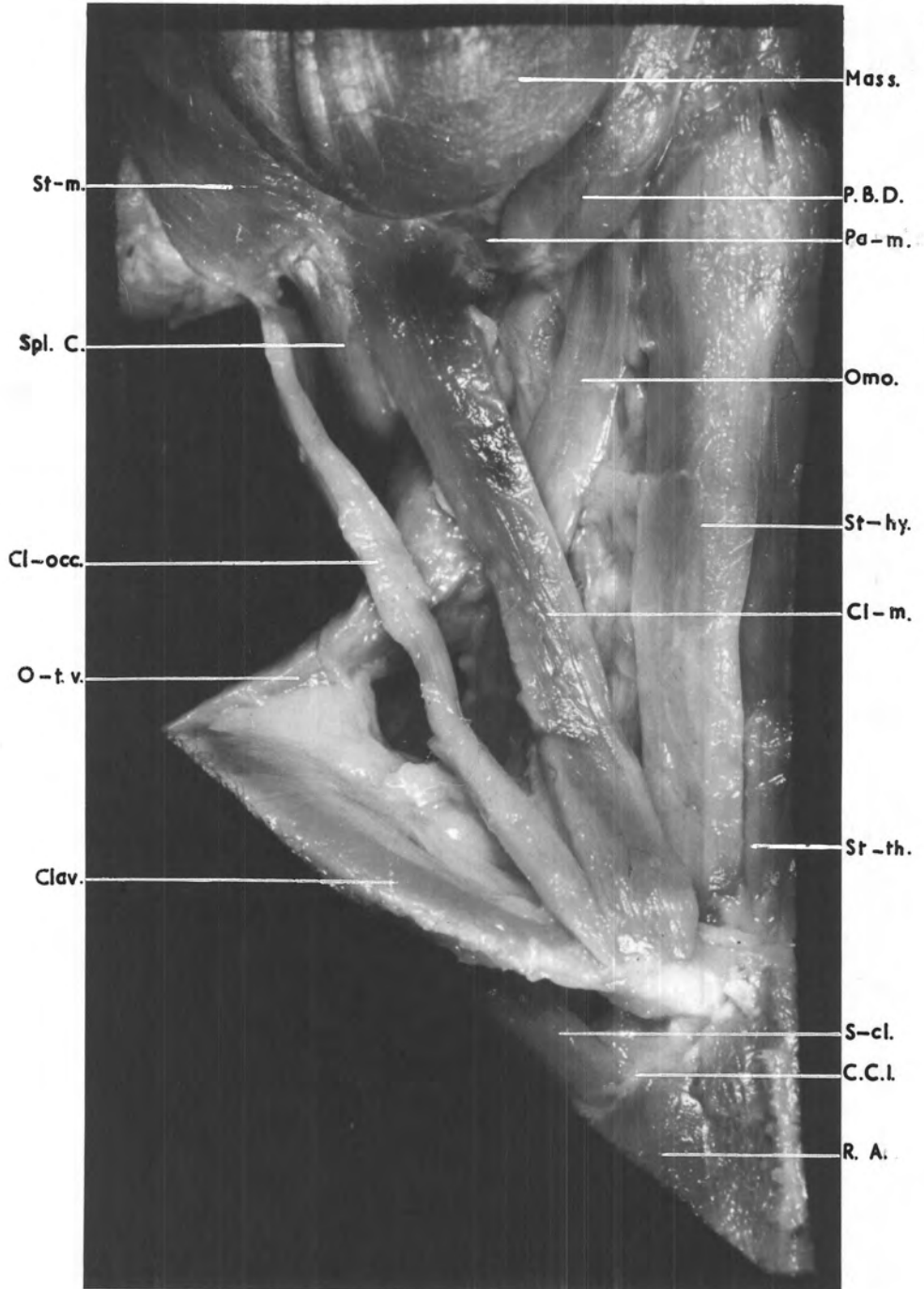


Plate IX (cf. fig. 20). Ventral aspect of neck after removal of trapezius and pectoral muscles and reflection of sternomastoid. x2.

- C.C.1. - First costal cartilage.
- Clav. - Clavicle.
- Cl-m. - Cleido-mastoid.
- Cl-occ. - Cleido-occipitalis.
- Mass. - Masseter.
- Omo. - Omo-hyoid.
- O-t.v. - Omo-trachelien ventralis.
- P.B.D. - Posterior belly of digastric.
- Pa-m. - Paramastoid process.
- R.A. - Rectus abdominis.
- S-cl. - Subclavius.
- Spl.C. - Splenius capitis.
- St-hy. - Sterno-hyoid.
- St-m. - Sterno-mastoid (reflected cranially).
- St-th. - Sterno-thyroid.



Sterno-thyroid (figs. 12, 17, 18, 19; pls. VIII, IX) also has a fleshy origin from the manubrium and the manubrio-sternal cartilage; it is slightly narrower than the sterno-hyoid, especially in its caudal part, and is united to its fellow in the midline. The insertion is into the crico-thyroid cartilage at the caudal edge of the thyroid bulla, some of the lateral fibres, however, pass straight on into the thyro-hyoid. Just caudal to the middle of the muscle is a tendinous intersection which in one case had the form of an aponeurosis four or five millimetres long.

As in the case of the sterno-hyoid the origin of this muscle shows some variation amongst the marsupials, in some instances involving costal cartilages and not being confined to the sternum as described here for Trichosurus. An intersection has been noted also in Did. virginiana (Coues, 1872), Pet. xanthopus (Parsons, 1896) and by Kohlbrugge (1898) in Cuscus and Macropus. Some degree of union between the muscles of the two sides appears to be the rule in this mammalian group.

Thyro-hyoid (fig. 12; pl. VII) consists of two fairly distinct parts, the more ventral or medial of which continues the line of the sterno-thyroid and is partly continuous with it; this part arises from the side of the crico-thyroid cartilage caudal to the bulla and runs cranially on the side of the bulla to be inserted into the hyoid bone, mainly deep to the sterno-hyoid. The more dorsal or lateral portion of the muscle springs from the cranial part of the bony wing of the crico-thyroid cartilage and is at first separated by a narrow

triangular interval from the first part; it runs cranially and a little ventrally, overlapping the first part slightly near its insertion which is into the hyoid bone - mainly the greater cornu deep to the omo-hyoid.

Omo-hyoid (figs. 9, 12, 17, 20, 24; pls. V, VII, VIII, IX, XVI) passes from a prominent point on the cranial border of the scapula (which I do not think represents the cranial or anterior angle) to the greater cornu of the hyoid bone opposite the lateral part of the origin of the hypo-glossus. The origin is by a short thin aponeurosis and the muscle has a faint tendinous inscription just toward the hyoid side of the centre. There is no hyoid attachment in Phasc. cinereus according to Sonntag (1922) and Young (1882), though Macalister (1872b) gives partial attachment to this bone; in Phascolarctos most or all of the muscle continues over the hyoid to unite with the supra-hyoid musculature. Most marsupials studied lack a tendinous inscription in this muscle; one has been noted in Das. viverrinus (MacCormick, 1887) and in a pouch-young specimen of M. rufus though not in the adult (Windle and Parsons, 1897b). Leche (1874-1900) says there is never a long central tendon in marsupials.

The nerve that supplies the sterno-hyoid, sterno-thyroid and omo-hyoid derives its fibres directly from the first and second cervical nerves and, although it gives a branch to the hypoglossal nerve that appears to contain fibres from C1 only, the supply to these muscles runs no part of its course in the trunk of the hypoglossal nerve. A twig to the thyro-hyoid could not be found. A

direct supply from the first two cervical nerves occurs also in Pet. xanthopus (Parsons, 1896), and Kohlbrugge (1898) seems to indicate the same condition in Cuscus and Macropus in the latter of which some fibres come from the third spinal nerve as well.

4). Lateral cervical muscles.

Sterno-mastoid (figs. 9, 17; pls. V, VIII) is separate from the cleido-mastoid. It arises by a short tendon from the ventral surface of the cranial end of the sternum and passes to a mainly fleshy insertion into the tip and frontal and lateral aspects of the mastoid process. Carlsson (1914) mentions that this muscle is separate from the next in this species but gives the insertion to the base of the paramastoid. An insertion to the paramastoid has also been reported for Petrogale (Parsons, 1896; Carlsson, 1914), Dend. dorianus (Carlsson, 1914), M. brunii, C. orientalis and C. maculatus (Kohlbrugge, 1898) and Phasc. cinereus (Macalister, 1872b) though Young (1882) gives the attachment in the last to the outer part of the occipital ridge; some attachment to this ridge is also present in Caenolestes (Osgood, 1921) and C. maculatus (Kohlbrugge, 1898).

Cleido-mastoid (figs. 17, 18, 19, 20, 22; pls. VIII, IX, XIII) arises from the clavicle near its medial end, the origin occupying five or six millimetres and leaving a similar distance clear adjacent to the sterno-clavicular joint. The muscle is fleshy throughout and is inserted along a line extending medially from the mastoid process to the base of the paramastoid. It is deep to the

sterno-mastoid except for a small area near the origin. MacCormick (1887) gives the origin in this species simply from the medial end of the clavicle, while Carlsson (1914) puts the insertion at the tip of the paramastoid. The muscle is said to be absent in Choer. castanotis (Parsons, 1903) and N. typhlops (Wilson, 1894). Some degree of fusion between this muscle and the sterno-mastoid towards their insertions occurs in a number of marsupials; in Dend. ursinus (Sonntag, 1921b) they are apparently fused throughout.

The nerve supply of the above two muscles is derived from the accessory nerve and branches of the second and third cervical nerves, some of the fibres of which join the accessory and are distributed with it. The accessory nerve runs deep to the sterno-mastoid and either deep to or through the cleido-mastoid. In Cuscus and Macropus Kohlbrugge (1898) gives the spinal contribution to the innervation of these muscles from the third and fourth cervical nerves.

Scalenus Anterior is absent - there is no part of the scalene muscle mass ventral to the brachial plexus and vessels. This is a general finding throughout the Marsupialia; the scalenus anticus described for Caenolestes by Osgood (1921), for Did. virginiana by Coues (1872) and for Chir. variegatus by Sidebotham (1885), although these authors do not mention the relationship to the brachial plexus, is almost certainly the scalenus medius.

Scalenus Medius (fig. 24; pl. XVI) takes origin from the caudal six cervical transverse processes and is inserted into the first rib; some of the deeper fibres from the more cranial transverse processes

are inserted into those further caudally - perhaps some of these fibres represent the cervical intertransverse muscles. The muscle is largely covered by the scalenus posterior, only a small portion being visible at the ventral border.

Scalenus Posterior (figs, 24, 25; pl. XVI) arises from the surface of the medius at about the middle of its length and passes caudally to be inserted into the third and fourth costal cartilages and sometimes by a few fibres into the fascia of the fourth intercostal space. The insertion is by three slips that interdigitate with some of the slips of origin of the serratus anterior, the dorsal one goes to the third cartilage, the other two to the fourth, the fibres to the fourth space coming from the ventral slip. MacCormick (1887), who says the condition here is the same as in Das. viverrinus, apparently found this last slip extending to the fifth rib.

The scalene muscles of marsupials are easily comparable in all the cases studied though they show some variation in their attachments. The number of cervical transverse processes involved in the origin varies considerably. The scalenus posterior, or longus (the name recommended by Windle and Parsons, 1897a), is inserted into two or more of the first five costal arches, usually not beyond the fourth. The insertion of the medius, or brevis (Windle and Parsons, 1897a), accepting that Osgood (1921) has misnamed his muscles, into the first rib appears to be the most constant feature, the only exception I have found being in Hyps. nosechatus where Heighway (1939) gives the insertion to the first two ribs.

Kohlbrugge (1898) also describes some deep fibres connecting the transverse processes in Cuscus and Macropus which he suggests are the representatives of the levatores costarum; I would prefer to relate them to the intertransversarii.

The scalene muscles in Trichosurus are innervated by branches of the last three or four cervical nerves; Kohlbrugge (1898) gives the last four for Macropus.

5). Prevertebral muscles.

Longus Cervicis has two parts, lateral and medial, separated by the longus capitis. The lateral part consists of fibres arising from the cervical transverse processes from the sixth to the third and inserted into those from the fifth to the second and also to a tubercle on the lateral mass of the atlas. The medial part has an arrangement reminiscent of the muscle in man; its caudal oblique section passes from the first five thoracic bodies to the prominent flange on the sixth cervical vertebra; the fibres that make up the cranial oblique portion come from this flange and also from the transverse processes from here to the third cervical and have their insertion to the lateral parts of the bodies from the fifth to the second cervical and to the ventral arch of the atlas. The third or longitudinal group of fibres passes from the last cervical and first thoracic bodies to the third, fourth and fifth cervical bodies. The caudal extent of this muscle varies a little in the few cases reported for marsupials, the extremes being the third and the fifth thoracic bodies; the same extremes have been given by different

authors for one species, viz. Phasc. cinereus, where Sonntag (1922) and Young (1882) take it to the third, while Macalister (1872b) extends it to the fifth.

Longus Capitis (Rectus capitis anterior major, or, as Windle and Parsons, 1897a, suggest, rectus capitis ventralis major) (figs. 24, 25; pl. XVI) is to some extent fused with the foregoing muscle, it arises from the ventral surface of the longus cervicis in the caudal half of the cervical region, having some attachment to the transverse processes in the cranial part of this origin where the medial and lateral parts of the cervicis are more separate. It is inserted into the occipital bone of the skull caudo-lateral to the pharyngeal tubercle. Some degree of fusion between this muscle and the longus cervicis seems to be common amongst marsupials.

Rectus Capitis Anterior (Minor) (Windle and Parsons, 1897a, would substitute "ventralis" for "anterior") is a small slip of muscle lying deep to the cranial end of the longus capitis from which it is not easily separated; it passes from the ventral aspect of the lateral mass of the atlas to the occipital bone just frontal to the condyle. This muscle is not definable in Myrmecobius (Leche, 1874-1900), Phasc. cinereus (Somntag, 1922; Young, 1882; Leche, 1874-1900), Phalanger orientalis or Phascolomys mitchelli (Somntag, 1922), apparently being fused with the longus capitis in these cases.

Rectus Capitis Lateralis is very small and runs somewhat medially as well as cranially from its origin on the medial part of the cranio-ventral edge of the transverse process of the atlas to its insertion

just lateral to the insertion of rectus capitis anterior and just caudo-medial to the base of the paramastoid.

These last two muscles are supplied by the ventral ramus of the first cervical nerve which emerges between them; the longi are innervated by the other cervical ventral rami. Kohlbrugge (1898) mentions the supply of the rectus capitis lateralis from C1 in Cuscus and Macropus, and of the long muscles from C2-3 in the former, C2-7 in the latter.

6). Muscles of the palate.

Tensor Palati (fig. 11) takes origin from the sphenoid bone just lateral to the auditory tube and slightly from the cartilage of the tube itself, runs ventrally and rostrally parallel with and slightly overlapping the caudal margin of the pterygoid plate and finally, on the lateral side of the large pterygoid hamulus, becomes a flat ribbon-like tendon that turns at right angles around the lower border of the hamulus into the soft palate. A small branch of the mandibular nerve which emerges through a foramen caudo-medial to the foramen ovale appears to supply the muscle.

Levator Palati (fig. 12; pl. VII). The deep fibres of origin of the tensor palati separate off and give rise to a musculo-aponeurotic band that lies deep to the caudal edge of the tensor; this I take to represent the levator palati, it is inserted into the upper border of the pterygoid hamulus and appears to be undergoing regression and fibrous replacement.

7). Muscles of the pharynx.

Constrictor Pharyngis, as reported for Chir. variegatus by Sidebotham (1885), forms a single sheet not divisible into separate constrictor muscles. Its fibres arise from the dorsal border of the crico-thyroid cartilage and both cornua of the hyoid bone and are inserted into a dorsal median raphe in the pharyngeal wall and to the base of the skull (pharyngeal tubercle). Sonntag (1922) says that there is no hyoid origin in Phasc. cinereus.

Branches from the glossopharyngeal and vagus nerves run to the wall of the pharynx, it is presumed that only the latter supplies its muscle.

Stylo-pharyngeus arises with the stylo-glossus from the paramastoid process, its fibres springing from the fronto-medial aspect and running medially to the dorsal wall of the pharynx. It is supplied by a minute twig from a branch of the glossopharyngeal nerve to the pharyngeal wall.

8). Intrinsic laryngeal muscles (figs, 15, 16; pl. X).

There are four fairly distinct intrinsic muscles on each side of the larynx, all of them connecting the arytenoid cartilage to the compound crico-thyroid. In this animal the cricoid has the usual ring shape but its ventral part is continuous with the thyroid cartilage, the cranial section of which is ballooned out into a large bulla with a thin cartilaginous wall. The dorsal parts of the laminae and cornua of the thyroid are composed of bone, the "inferior" (caudal) cornua also being continuous with the cricoid.

Figure 13 (cf. pl. XI.A). Extra-ocular muscles from the lateral side with the eyeball lifted dorsally. $x2\frac{3}{4}$.

Figure 14 (cf. pl. XI.B). Extra-ocular muscles from the dorso-lateral aspect with the eyeball turned laterally. $x2\frac{3}{4}$.

- Ab.N. - Abducent nerve.
- Fr.N. - Frontal nerve.
- I-o.N. - Infra-orbital nerve.
- Lac.N. - Lacrimal nerve.
- L.P.S. - Levator palpebrae superioris.
- O.I. - Obliquus inferior.
- O.S. - Obliquus superior.
- R.I. - Rectus inferior.
- R.L. - Rectus lateralis.
- R.M. - Rectus medialis.
- R.O. - Retractor oculi.
- R.S. - Rectus superior.
- S.A.N. - Superior alveolar nerve.
- Z. - Zygomatic arch (cut).

Figure 15 (cf. pl. X.A). Intrinsic muscles of larynx from lateral aspect. $x3$.

Figure 16 (cf. pl. X.B). Intrinsic muscles of larynx from dorsal aspect. $x3$.

- Ar. - Arytenoid cartilage.
- Bo. - Bony part of thyroid lamina.
- Cri. - Cricoid cartilage.
- D.C-a. - Dorsal crico-arytenoid.
- D-l.T-a. - Dorso-lateral thyro-arytenoid.
- Ep. - Epiglottis.
- L.C-a. - Lateral crico-arytenoid.
- S.C.T. - Superior cornu of thyroid lamina.
- T.B. - Thyroid bulla.
- T.R.1. - First cartilaginous ring of trachea.

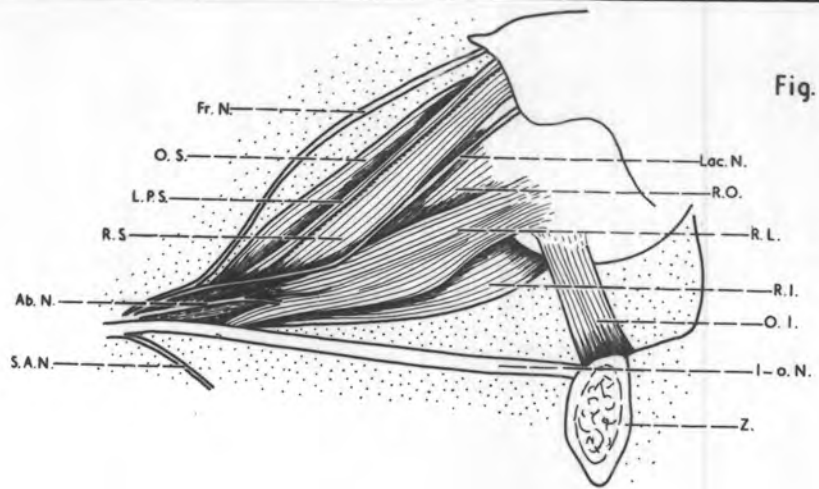


Fig. 13.

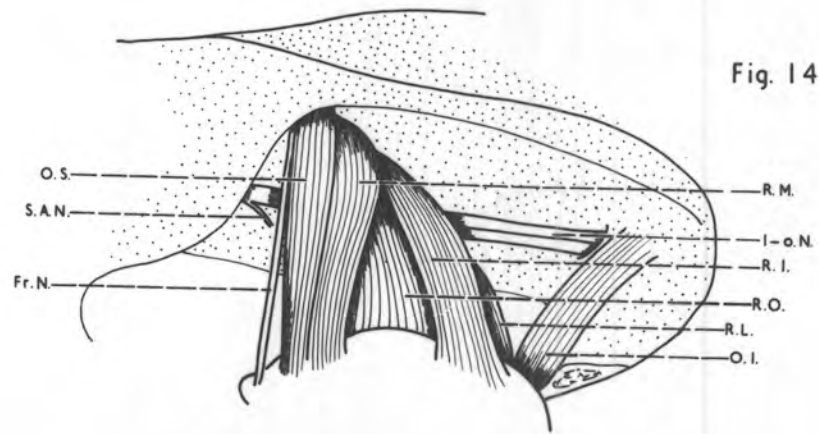


Fig. 14.

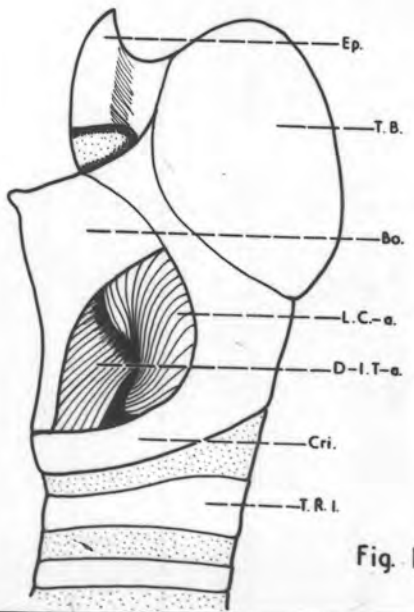


Fig. 15.

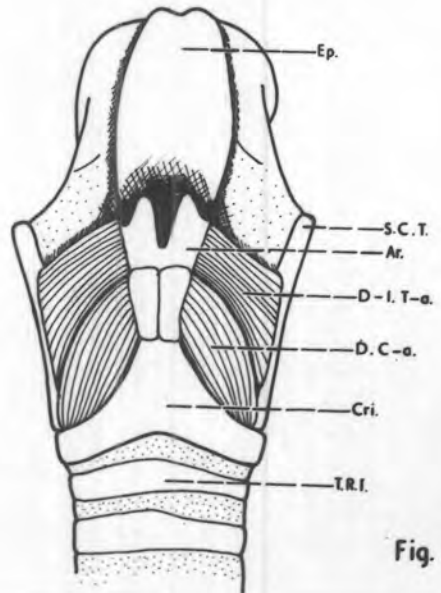


Fig. 16.

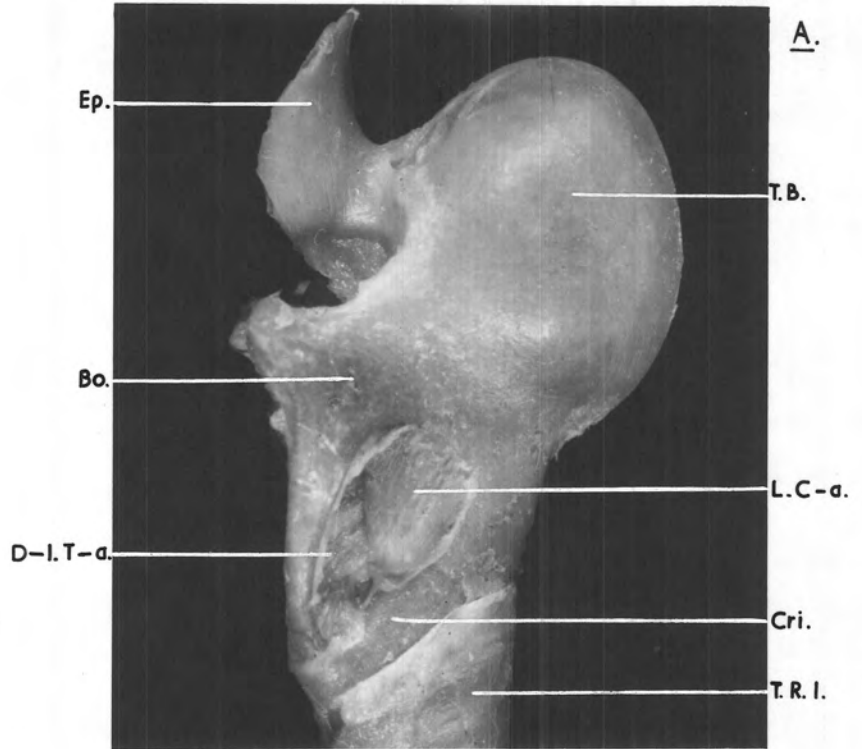
Plate X (cf. figs. 15, 16). Larynx with all extrinsic structures removed.

A. Lateral view. $x4\frac{3}{4}$.

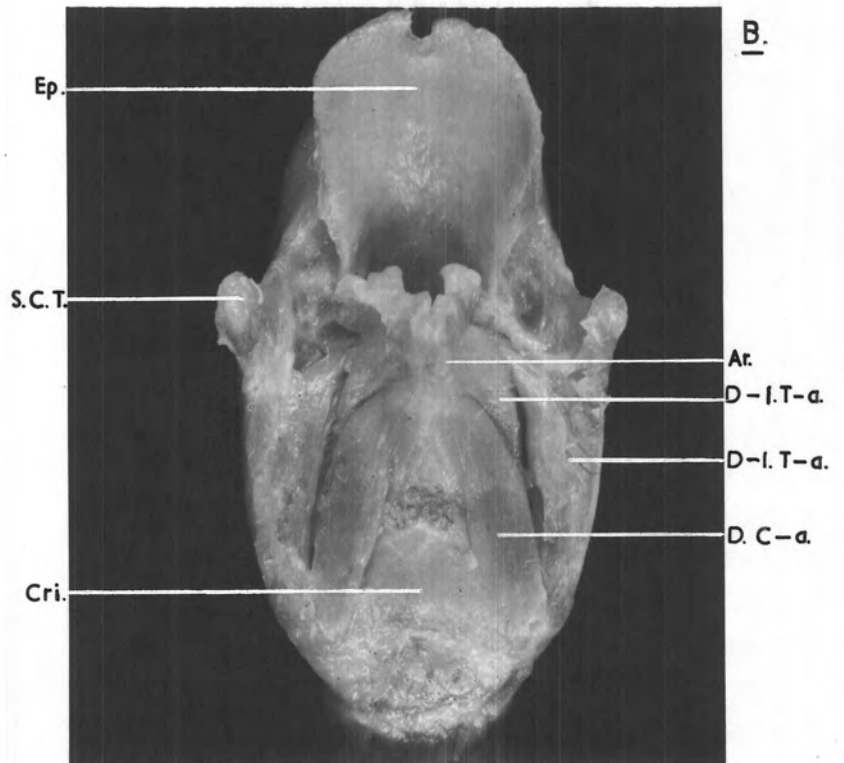
B. Dorsal view. $x4\frac{1}{2}$.

- Ar. - Arytenoid cartilage.
Bo. - Bony part of thyroid lamina.
Cri. - Cricoid cartilage.
D.C-a. - Dorsal crico-arytenoid.
D-l.T-a. - Dorso-lateral thyro-arytenoid.
Ep. - Epiglottis.
L.C-a. - Lateral crico-arytenoid.
S.C.T. - Superior cornu of thyroid lamina.
T.B. - Thyroid bulla.

A.



B.



Dorsal Crico-arytenoid is seen only on the dorsal surface of the larynx; it arises from the lateral part of the cricoid lamina and runs cranially and somewhat medially to the arytenoid.

Lateral Crico-arytenoid, seen on the lateral surface, radiates from the lateral process of the arytenoid to the dorsal margin of the conjoined ventral parts of the cricoid and thyroid and to the caudal edge of the osseous thyroid lamina.

Dorso-lateral Thyro-arytenoid, seen on both the lateral and dorsal aspects of the larynx, arises from the long "inferior" (caudal) cornu of the bony part of the thyroid and its fibres converge on the lateral end of the arytenoid; when viewed from the dorsal side some of its more ventral fibres may come to the surface between the rest of the muscle and the dorsal crico-arytenoid giving the appearance of an extra small muscle here.

Ventral Thyro-arytenoid is situated deeply and is not seen from the surface of the larynx. It arises from the inner aspect of the crico-thyroid cartilage near the midline and passes dorsally to the arytenoid.

All these muscles are supplied by the recurrent laryngeal nerve.

Edgeworth (1935) mentions as typical of marsupials in general posterior and lateral crico-arytenoids (? my dorsal and lateral), a thyro-arytenoid (? corresponding to both my ventral and dorso-lateral) and also an inter-arytenoid, no representative of which was found in my specimens. This author notes that the crico-thyroid muscle is absent owing to the fusion of the cricoid and thyroid

cartilages.

9). Extra-ocular muscles (figs. 13, 14; pl. XI).

Recti Oculi arise around the entrance of the optic nerve into the orbit, partly from the bone and partly, especially in the case of the medial and inferior, from the sheath of the optic nerve. The superior rectus has its origin on the lateral side of the nerve and runs upwards to gain its superior aspect, at first lying between the optic nerve and the retractor oculi muscle. The medial and inferior recti begin on the inner side of, and below the nerve respectively. The lateral rectus has two heads of origin, one arising in common with the upper edge of the medial rectus and passing below the superior rectus on its way to the lateral side of the nerve, the other beginning in connection with the lateral side of the inferior rectus and joining the first well back on the lateral side of the nerve: in one animal (No. 3) the first head gave a few fibres to the superior rectus as it passed beneath it. Each of the rectus muscles is inserted by a thin aponeurosis into the sclera two or three millimetres from the corneo-sclerotic junction.

Obliqui Oculi. The superior oblique arises from the bone above the medial rectus and has a muscle belly only about half the size of the superior rectus: it runs forwards in the orbit and, giving way to a small tendon, turns laterally through a loop of fascia that is anchored to the medial palpebral ligament and is inserted immediately into the tissues of the upper eyelid, any connection with the eyeball appearing to be only secondary through the fascia

Plate XI (cf. figs. 13, 14). Extra-ocular muscles.

A. Lateral view with eyeball lifted dorsally. $\times 5\frac{1}{2}$.

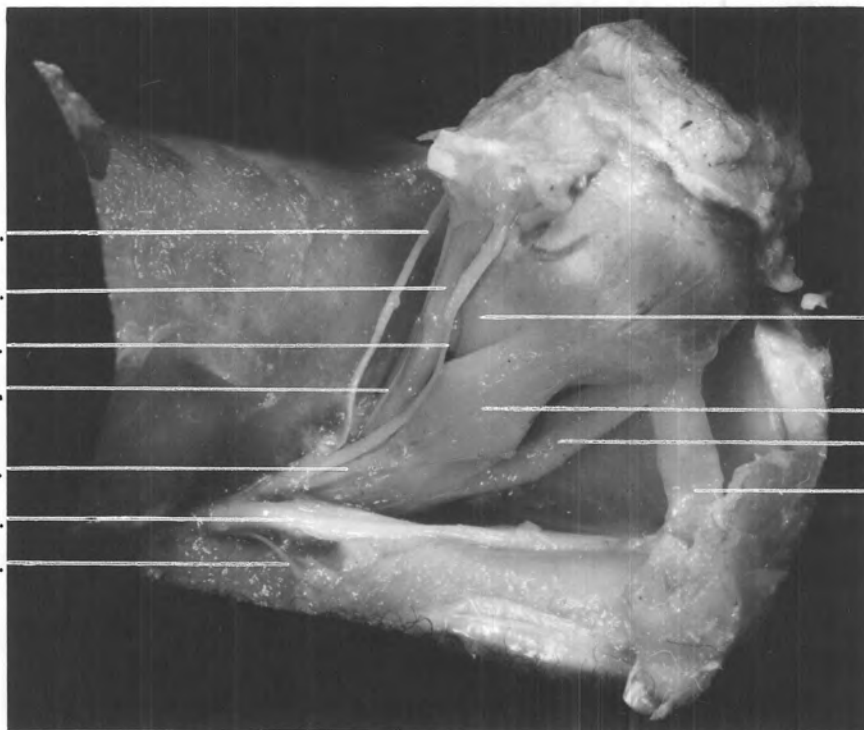
B. Dorso-lateral view with eyeball turned laterally. $\times 5\frac{1}{2}$.

- Ab.N. - Abducent nerve.
- Fr.N. - Frontal nerve.
- I-o.N. - Infra-orbital nerve.
- Lac.N. - Lacrimal nerve.
- L.P.S. - Levator palpebrae superioris.
- O.I. - Obliquus inferior.
- O.S. - Obliquus superior.
- R.I. - Rectus inferior.
- R.L. - Rectus lateralis.
- R.M. - Rectus medialis.
- R.O. - Retractor oculi.
- R.S. - Rectus superior.
- S.A.N. - Superior alveolar nerve.

A.

Fr. N.
R. S.
Lac. N.
L. P. S.
Ab. N.
I-o. N.
S. A. N.

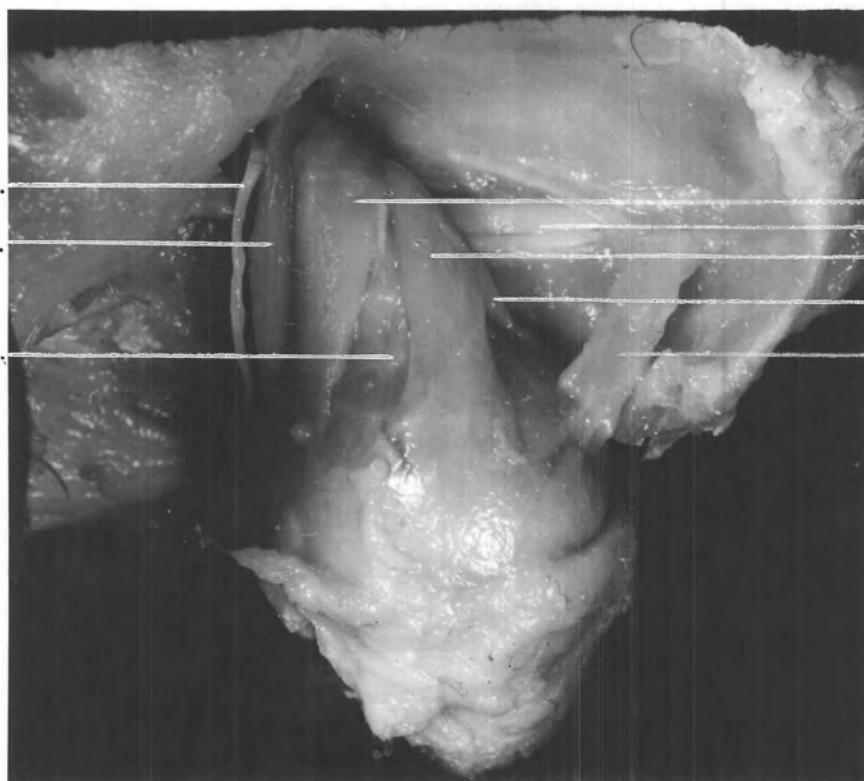
R. O.
R. L.
R. I.
O. I.



B.

Fr. N.
O. S.
R. O.

R. M.
I-o. N.
R. I.
R. L.
O. I.



of the orbit.

The inferior oblique begins in a small depression on the floor of the orbit just in front of the entrance to the infra-orbital canal, passes laterally and caudally below the inferior rectus and is inserted into the sclera as a thin aponeurosis at the level of the lower border of the lateral rectus muscle, a few of its tendinous fibres extending deep to those of the lateral rectus in the hinder part of the insertion.

Retractor Oculi has its origin from the bone lateral to the optic nerve entrance, gradually approaches the nerve as it passes forwards and spreads out to enclose it, mainly below at first. It is inserted into the sclera around the whole circumference of the eyeball a millimetre or two behind the equator.

Levator Palpebrae Superioris is a muscle smaller even than the superior oblique: it arises with the superior rectus lateral to the nerve and runs forwards on the upper surface of that muscle, finally spreading out to form a thin aponeurosis that attaches to the tissues of the upper eyelid and the superior conjunctival fornix.

The innervation of the extra-ocular muscles conforms to the general plan that Edgeworth (1955) says is common to all vertebrates. The superior oblique is supplied by the small trochlear nerve which enters its supero-lateral border in the posterior part of the orbital space. The abducent nerve supplies the retractor oculi and terminates in the lateral rectus, entering its lateral surface just after the two heads have joined. The other muscles are all supplied

by the oculomotor nerve, the branch to the inferior rectus and inferior oblique passing down between the optic nerve and the retractor oculi muscle.

(b). Muscles of the fore-limb and its girdle.

1). Muscles connecting trunk to fore-limb and girdle.

Pectoralis Major (figs. 17, 18; pl. XII) consists of superficial and deep strata that are fairly easily separable from one another. The superficial stratum arises from the whole length of the sternum excluding the xiphoid and is inserted into the lateral tubercular crest of the humerus, cranially it is fused with the deltoid and some of its most cranial fibres are overlapped by the deltoid near their insertion. The caudal fibres of this stratum fold under the others so that it is bilaminar at insertion, the deeper layer being more aponeurotic and attaching neither as high nor as low as the superficial. The deep stratum springs from the manubrium only and runs more cranially than the rest of the muscle, its insertion to the lateral tubercular crest being a proximal extension of that of the superficial stratum and reaching up to the base of the greater tuberosity so that the lateral part of this stratum is deep to the deltoid. The description given by MacCormick (1887) has no points of disagreement with this account. The superficial part in Did. virginiana (Coues, 1872) arises from the same extent of the sternum, though Langworthy (1932) indicates a little less in his opossum.

The origin of this muscle occupies less than the length of the sternum in Das. viverrinus (MacCormick, 1887), Thyl. cynocephalus

Figure 17 (cf. pls. VIII, XII). Pectoral region and neck from the ventral aspect. $\times \frac{2}{3}$.

Figure 18. Pectoral region from the ventral aspect after the reflection of the superficial part of pectoralis major. $\times \frac{2}{3}$.

Figure 19 (cf. pl. XIII). Pectoral region from the ventral aspect after the reflection of the whole of pectoralis major and the removal of trapezius and deltoid. $\times \frac{2}{3}$.

Figure 20 (cf. pl. IX). Ventral aspect of neck after the removal of the trapezius and the pectoral muscles and the reflection of sterno-mastoid. $\times \frac{2}{3}$.

A.B.D.	- Anterior belly of digastric.
Ax.Pann.	- Axillary slip of panniculus carnosus.
B.P.V.	- Brachial plexus and vessels.
Bu.	- Buccinator.
C.C.1.	- First costal cartilage.
Clav.	- Clavicle.
Cl-m.	- Cleido-mastoid.
Cl-occ.	- Cleido-occipitalis.
Del.cl.	- Clavicular part of deltoid covered by the supra-clavicular continuation of trapezius.
In-sp.	- Infraspinatus.
Lat.D.	- Latissimus dorsi.
Man.	- Mandible.
Mass.	- Masseter.
Myl.	- Mylo-hyoid.
Myl.ap.	- Aponeurotic expansion from central intersection of digastric (mylo-hyoid aponeurosis).
O.E.A.	- Obliquus externus abdominis.
O.E.A.ap.	- Aponeurosis of obliquus abdominis.
Omo.	- Omo-hyoid.
O-t.v.	- Omo-trachelien ventralis.
Pa-m.	- Paramastoid process.
P.B.D.	- Posterior belly of digastric.
P.maj.	- Pectoralis major.
P.maj.d.	- Deep part of pectoralis major.
P.maj.s.	- Superficial part of pectoralis major.
P.min.	- Pectoralis minor.
P.qu.	- Pectoralis quartus.
R.A.	- Rectus abdominis.
S-cl.	- Subclavius.
Spl.C.	- Splenius capitis.
S-sc.	- Subscapularis.
St-hy.	- Sterno-hyoid.
St-m.	- Sterno-mastoid.
St-m.r.	- Sterno-mastoid reflected cranially.
St-th.	- Sterno-thyroid.
Su-sp.	- Supraspinatus.
Tr.	- Trapezius.

Fig. 17.

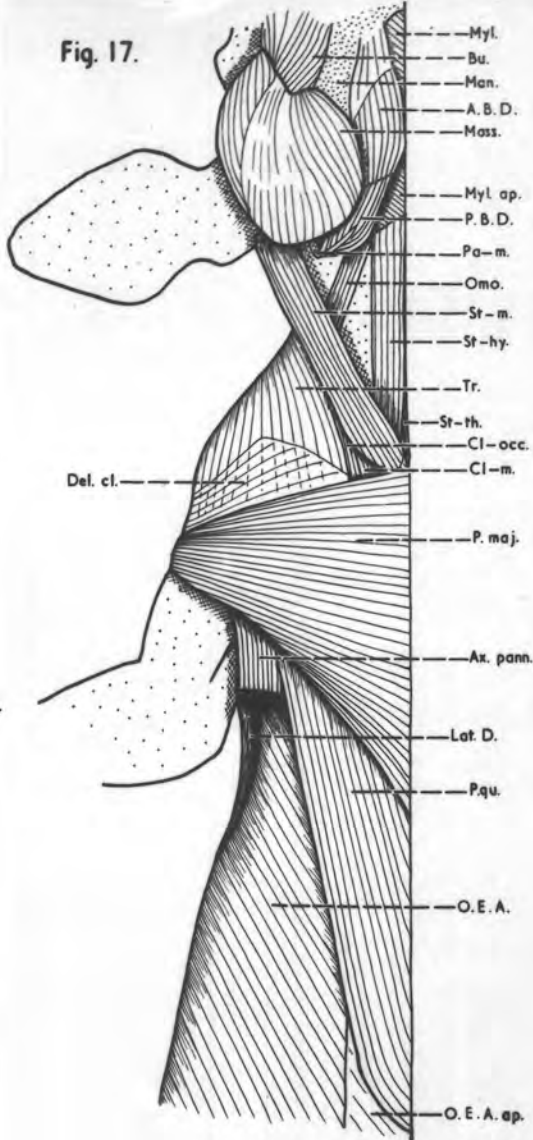


Fig. 18.

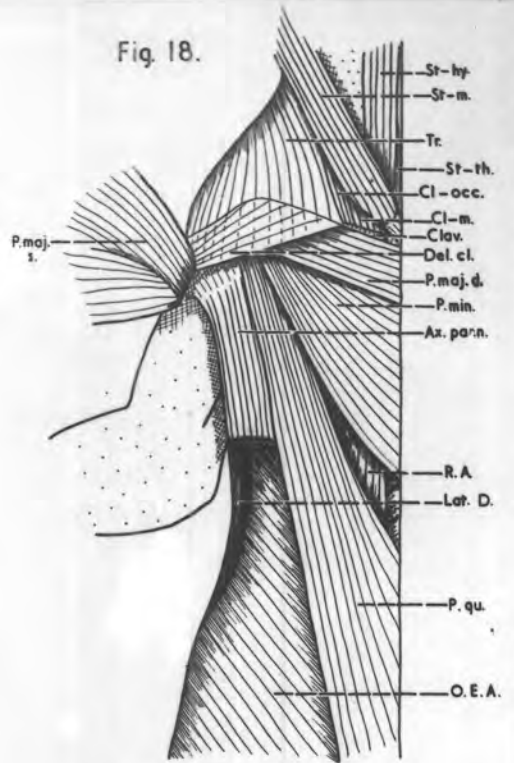


Fig. 19.

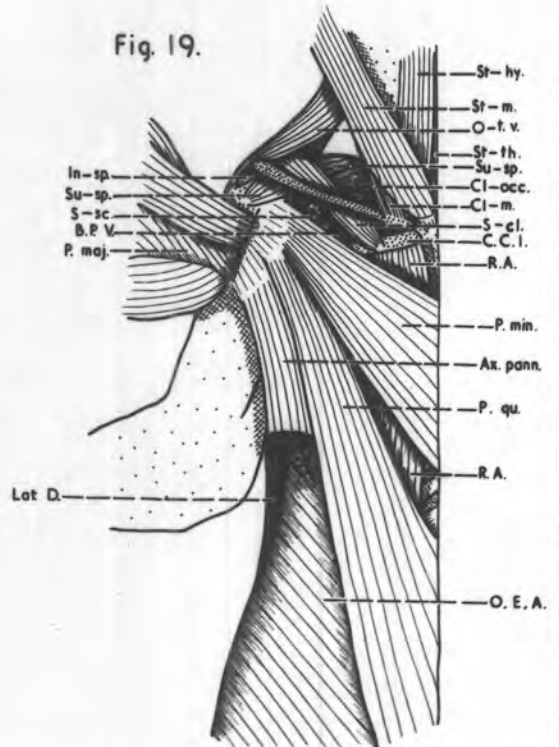


Fig. 20.

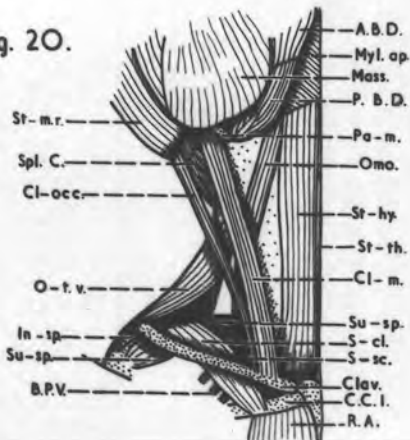


Plate XII (cf. fig. 17). Ventral view of superficial pectoral
muscles. Slightly reduced.

Ax.Pann. - Axillary slip of panniculus carnosus.

Cl-m. - Cleido-mastoid (origin).

Del.cl. - Clavicular part of deltoid.

O.E.A. - Obliquus externus abdominis.

P.maj. - Pectoralis major.

P.qu. - Pectoralis quartus.

St-m. - Sterno-mastoid.

Tr. - Trapezius.

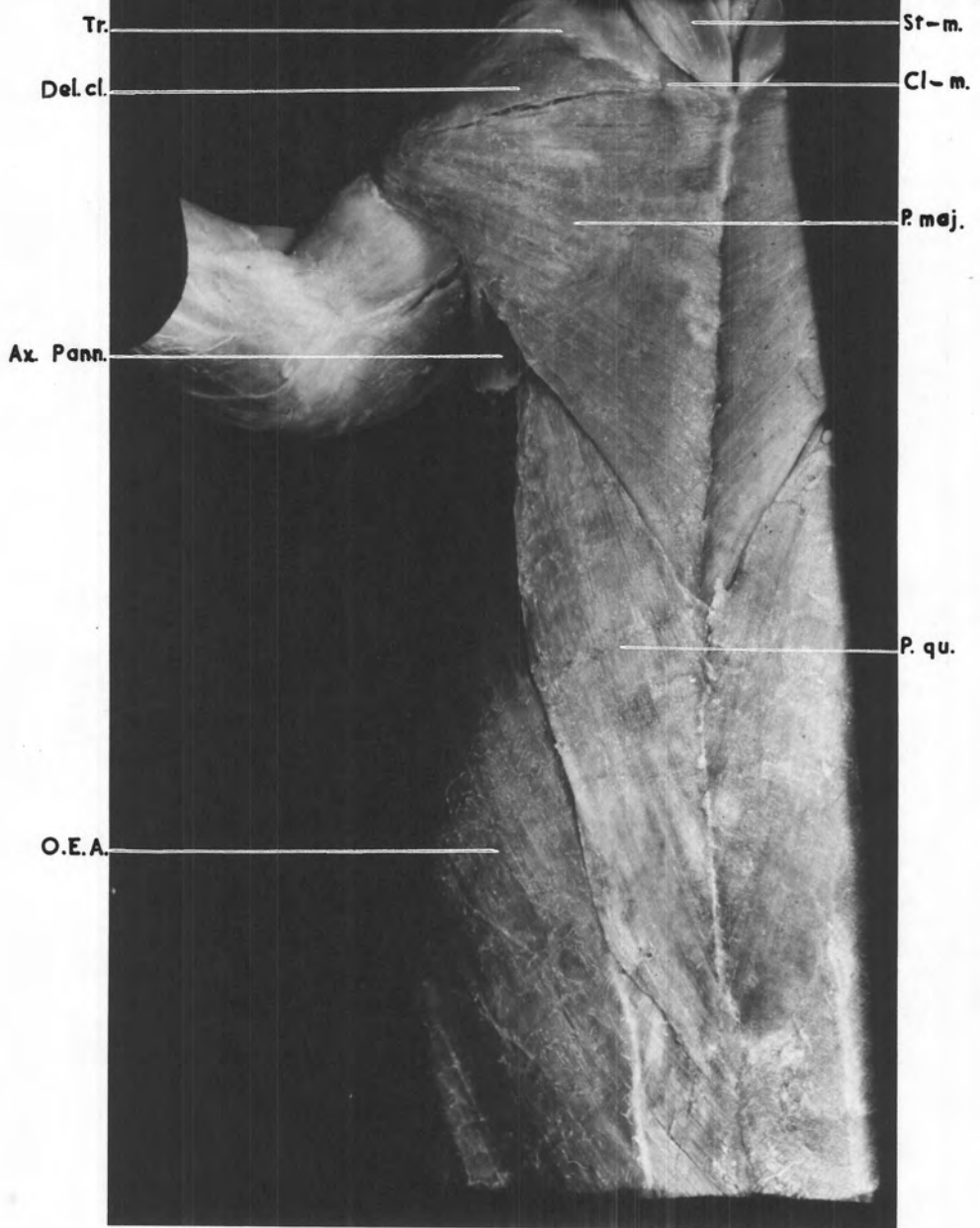
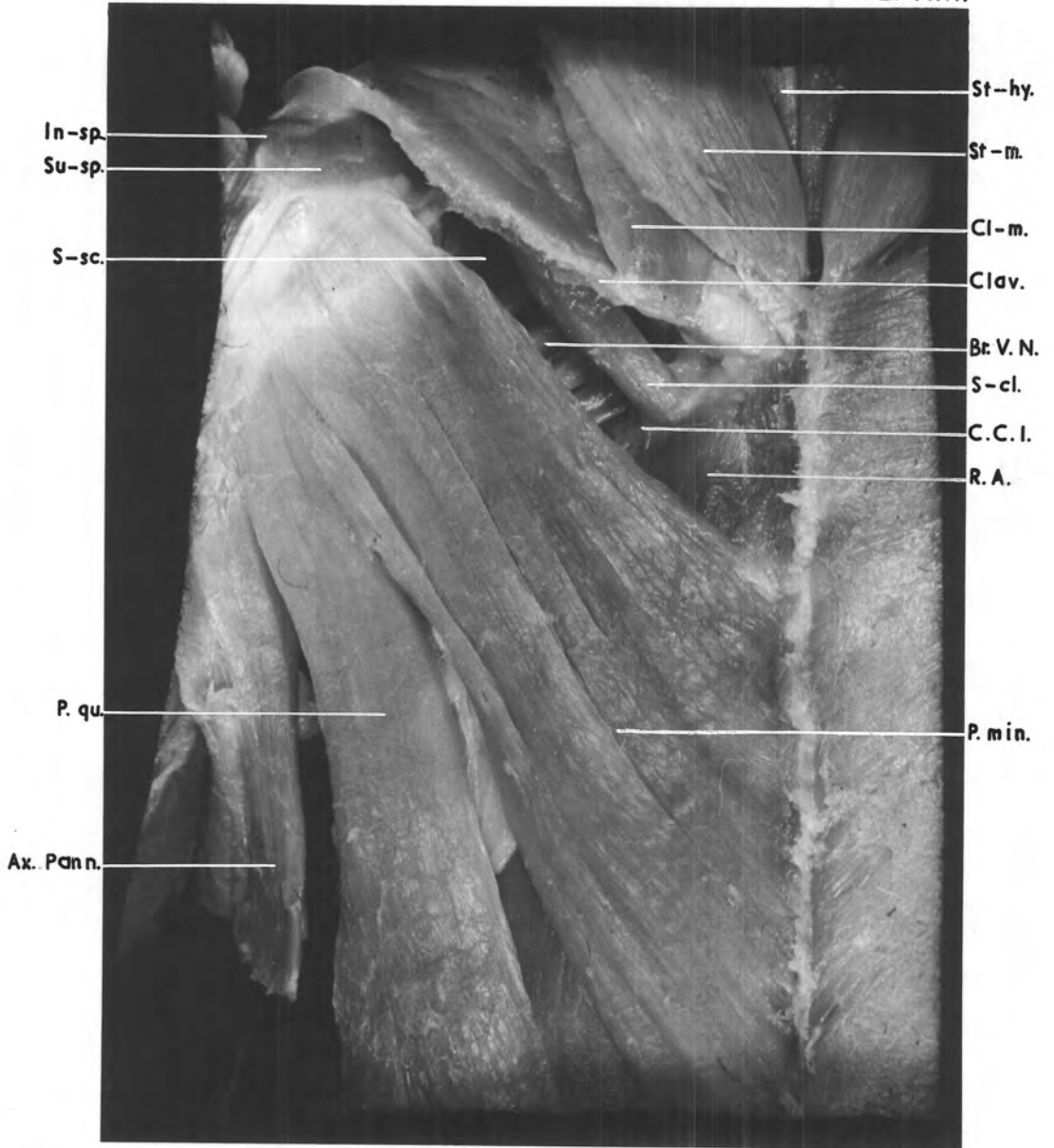


Plate XIII (cf. fig. 19). Ventral view of deep pectoral region.

Trapezius and deltoid are removed and pectoralis major is reflected. $\times 2\frac{1}{4}$.

- Ax.Pann. - Axillary slip of panniculus carnosus.
- Br.V.N. - Brachial vessels and nerves.
- C.C.1. - First costal cartilage.
- Clav. - Clavicle.
- Cl-m. - Cleido-mastoid.
- In-sp. - Infra-spinatus (insertion).
- P.min. - Pectoralis minor.
- P.qu. - Pectoralis quartus.
- R.A. - Rectus abdominis.
- S-cl. - Subclavius.
- S-sc. - Subscapularis.
- St-hy. - Sterno-hyoid.
- St-m. - Sterno-mastoid.
- Su-sp. - Supra-spinatus (insertion).



(Cunningham, 1882) and Ph. orientalis (Somntag, 1922), also in Choer. castanotis if we take the superficial part of the pectoralis described by Parsons (1903) to correspond here. There is attachment to the clavicle in Dendrolagus and Aepyprymnus (Carlsson, 1914), Petrogale (Carlsson, 1914; Parsons, 1896), Phasc. cinereus (Somntag, 1922) and in Hyps. moschatus (Heighway, 1959) where it is the deep part that has this connection. In Phasc. wombata, S. ursinus (Macalister, 1870) and N. typhlops (Wilson, 1894) there is attachment to both clavicle and ribs (or more probably costal cartilages). The origin extends beyond the sternum to the abdominal fascia in Phasc. mitchelli (Somntag, 1922) and, according to Young (1882), in Phasc. cinereus. The deep part is said to be absent in Phascogale calura and Thyl. cynocephalus (Cunningham, 1882) and is not specifically described in a number of other reports; the deep part described by Sidebotham (1885) for Chir. variegatus sounds more like the pectoralis minor which he does not otherwise mention. In M. giganteus and Macropus vallabiensis Haughton (1866) notes only one pectoral muscle which arises from the whole length of the sternum.

In T. vulpecula I found this muscle supplied by the lateral pectoral nerve only: Boardman (1941) gives slight supply from the medial pectoral to the superficial part (his part alpha) in M. robustus.

Pectoralis Minor (fig. 19; pl. XIII) arises from the sternum between the second and sixth costal cartilages and passes laterally and

cranially to its insertion into the greater tuberosity of the humerus and the deep surface of the supraspinatus tendon, there being no attachment to the coracoid. Towards its insertion it is overlain by the deep part of the pectoralis major. MacCormick (1887) gives, as well as these attachments, some origin from the sixth costal cartilage and part of the insertion into the shoulder capsule; these were not present in my specimens. The muscle is innervated from the lateral pectoral nerve: Boardman (1941) gives some supply from the medial pectoral in M. robustus.

Marsupials vary in the number of sternal segments contributing to the origin of this muscle: in M. robustus (Boardman, 1941), Ph. maculata, Phasc. calura and Thyl. cynocephalus (Cunningham, 1882) there is also some origin from costal cartilages, while in Phasc. cinereus (Macalister, 1872b; Young, 1882) and in N. typhlops, if we take Wilson's (1894) pectoralis C to represent this, the muscle arises only from costal cartilages with no attachment to the sternum. In S. ursinus Macalister (1870) gives the origin from the linea alba and the lower ribs as well as the sternum. Some insertion to the coracoid is given for Perameles lagotis by Owen (1839-1847, 1868), for Ph. maculata and Phasc. calura by Cunningham (1882) and for Phasc. wombata and S. ursinus by Macalister (1870); while the attachment to the supraspinatus tendon noted in Trichosurus has also been reported in Das. viverrinus by MacCormick (1887) and in Ph. maculata, Phasc. calura and Thyl. cynocephalus by Cunningham (1882). Part insertion to the capsule of the shoulder joint is also present

in a number of marsupials.

Pectoralis Quartus (figs. 17, 18, 19; pls. XII, XIII) lies in the same plane as the pectoralis minor which abuts its cranial or medial border, and the axillary slip of the panniculus carnosus which lies along its caudo-lateral edge: it is partly covered by the pectoralis major towards its cranial end. It arises from the cranial third of the linea alba and runs cranio-laterally to be inserted into the lateral tubercular crest of the humerus by a thin aponeurotic tendon that is continuous proximally (cranially) with that of the pectoralis minor and which is joined distally by the arch that extends across the axilla from the latissimus dorsi and receives the fibres of the cutaneous maximus part of the panniculus carnosus. Its motor nerves are branches of the medial pectoral; an innervation in agreement with that given for M. robustus by Boardman (1941).

Origin from the linea alba and an intimate association with the panniculus carnosus appear to be typical features of this muscle in marsupials, Wilson (1894) could not separate it from the panniculus in N. typhlops. In Das. viverrinus MacCormick (1887) has the origin extending cranially to the caudal third of the sternum. Coues' (1872) third part of the pectoralis major in Did. virginiana seems to be the pectoralis quartus as does the muscle that Sidebotham (1835) describes under the name "chondro-humeral" for Chir. variegatus, while the muscle that the latter author calls pectoralis quartus sounds more like the axillary panniculus. Owen (1839-1847, 1868) describes what is probably the pectoralis quartus as part of

the pectoralis major in Per. lagotis.

Subclavius (figs. 19, 20, 26; pl. XIII) extends from a small origin in the middle of the ventral surface of the first costal cartilage to a much broader insertion that is partly into the dorsal border of the outer half of the clavicle and partly, owing to the more cranial fibres of the muscle that pass deep to the clavicle, into the lateral part of the supraspinatus fascia. MacCormick (1887) says the muscle is similar to that of Das. viverrinus thus suggesting some attachment to the acromion, but in my specimens this was only an indirect connection through the supraspinatus fascia.

A similar insertion shared between the clavicle and the scapula and/or supraspinatus fascia occurs also in Hypsiprymnodon (Heighway, 1959), Phascolomys (Macalister, 1870; Sonntag, 1922), Sarcophilus (Macalister, 1872a) and in the opossum (Haughton, 1866; Macalister, 1870). In Macropus (Haughton, 1866; Macalister, 1870; Boardman, 1941), Petrogale (Parsons, 1896), Caenolestes (Osgood, 1921), Phascogale, Phalangista (Gunningham, 1882), Phalanger, Pseudochirus (Sonntag, 1922) and Phascolarctos (Sonntag, 1922; Macalister, 1872b) the insertion is wholly into the clavicle; while there is no attachment to this bone in Thylacinus (Cunningham, 1882), Notoryctes (Wilson, 1894) or Choeropus (Parsons, 1903) in the last of which there is no clavicle and where the muscle has an unusual origin from the manubrium. In Chironectes (Sidebotham, 1885) most of the muscle is inserted to the clavicle but takes further origin here also. Trapezius (figs. 17, 18, 21; pls. XII, XIV) arises from the whole of

the nuchal crest of the occipital bone, the nuchal ligament and the thoracic spines to the eighth or ninth, the part coming from the caudal portion of the nuchal ligament and the first thoracic spine beginning as a thin aponeurosis. The fibres from the lateral end of the nuchal crest separate from the rest of the sheet and the great auricular nerve passes between the two; this portion of the muscle is inserted into the clavicle on its ventral surface just lateral to the origin of the cleido-mastoid and apparently represents the cleido-occipitalis (fig. 20; pl. IX): it lies adjacent to the sterno-mastoid at the cranial end and to the cleido-mastoid at the clavicular end, though in one animal it was along the sterno-mastoid throughout thus covering the origin of the cleido-mastoid. The next fibres, i.e. the most cranial fibres of the true trapezius, also attach to the clavicle just lateral to the cleido-occipitalis, the next ones sweeping over the clavicle (lateral two thirds or more) and the acromion to be inserted into the fascia over the clavicular part of the deltoid, some of them gaining direct attachment to the humerus at the dorsal edge of this section of the deltoid. The next part of the muscle finds its insertion into the cranial border of the spine of the scapula, while the last fibres attach to the caudal border of the spine and to the infraspizatus fascia. The fibres that run transversely to the medial end of the spine are inserted through a small aponeurosis. In Carlsson's (1914) description she makes no mention of the part going over the clavicle, and takes the origin only to the seventh thoracic spine. MacCormick (1887) gives

some attachment to the clavicle about its middle and describes the cleido-occipitalis in agreement with my account. The arrangement of the muscles here obliterates the posterior triangle of the neck, as described for Dend. ursinus and Pet. xanthopus by Sonntag (1921b).

The caudal limit of origin of this muscle in marsupials reported varies from the fourth thoracic spine in S. ursinus (Macalister, 1872a) - though the same author gives the ninth or tenth for this species in another paper (1870) - and the fifth spine in Cuscus (Kohlbrugge, 1898), to the last thoracic spine in Das. viverrinus (MacCormick, 1887), the opossum (Macalister, 1870; Coues, 1872) and the phalanger (Macalister, 1870); the most popular point being at the seventh. The cranial limit seems much more constantly on the occiput, though Haughton (1866) does not take the muscle as far as this in Macropus and Leche (1874-1900) gives no origin from the occipital crest in Myrmecobius. The muscle is divided into two separate parts in Caenolestes (Osgood, 1921), and into three in N. typhlops (Wilson, 1894). The continuation of some fibres over the clavicle or acromion to the deltoid is common in marsupials, Macalister (1870) even describes such fibres as replacing the clavicular deltoid in Phasc. wombata; the genera Macropus (Kohlbrugge, 1898; Macalister, 1870; Boardman, 1941) and Petrogale (Parsons, 1896) provide some of the exceptions. The cleido-occipitalis is said to be absent in Phasc. mitchelli and Phasc. cinereus (Sonntag, 1922), Thyl. cynocephalus (Cunningham, 1882) and N. typhlops (Wilson, 1894), in the last, however, the author

Figure 21 (cf. pl. XIV). Superficial muscles of back and scapular region from the dorsal aspect. $x\frac{1}{2}$.

Figure 22. Dorsal aspect of neck and scapular region after the removal of trapezius and cleido-occipitalis. $x1$.

Figure 23 (cf. pl. XV). Dorsal aspect of neck and scapular region after the removal of trapezius, cleido-occipitalis, latissimus dorsi, rhomboid, deltoid, sterno-mastoid and cleido-mastoid. $x1$.

Acr.	- Acromion.
ap.	- Aponeurotic parts of trapezius.
Au.P.	- Post-auricular part of occipito-auricularis.
Bi.Ce.	- Biventer cervicis.
Bi.	- Biceps brachii.
Br.	- Brachialis.
Cl.	- Lateral end of clavicle.
Cl-m.	- Cleido-mastoid.
Del.ac.	- Acromial part of deltoid.
Del.cl.	- Clavicular part of deltoid.
Del.sp.	- Scapulo-spinal part of deltoid.
In-sp.	- Infraspinatus.
Lat.D.	- Latissimus dorsi.
L.Sc.	- Levator scapulae.
Mass.	- Masseter.
O.E.A.	- Obliquus externus abdominis.
Omo.	- Omo-hyoid.
O-t.d.	- Omo-trachelien dorsalis.
O-t.v.	- Omo-trachelien ventralis.
P.maj.	- Pectoralis major.
P.qu.	- Pectoralis quartus.
Rh.	- Rhomboid.
Sc.sp.	- Crest of spine of scapula.
Se.A.	- Serratus anterior.
Se.P.S.	- Serratus posterior superior.
Spl.C.	- Splenius capitis.
S-sc.	- Subscapularis.
St-m.	- Sterno-mastoid.
Su-sp.	- Supraspinatus.
T-l.f.	- Thoraco-lumbar fascia.
T.maj.	- Teres major.
T.min.	- Teres minor.
Tr.	- Trapezius.
Tri.lat.	- Lateral head of triceps.
Tri.Lo.	- Long head of triceps.

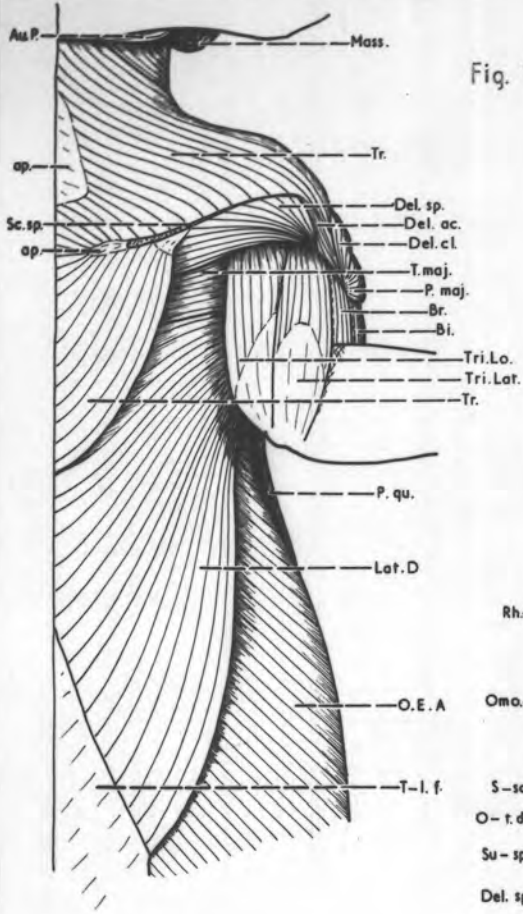


Fig. 21.

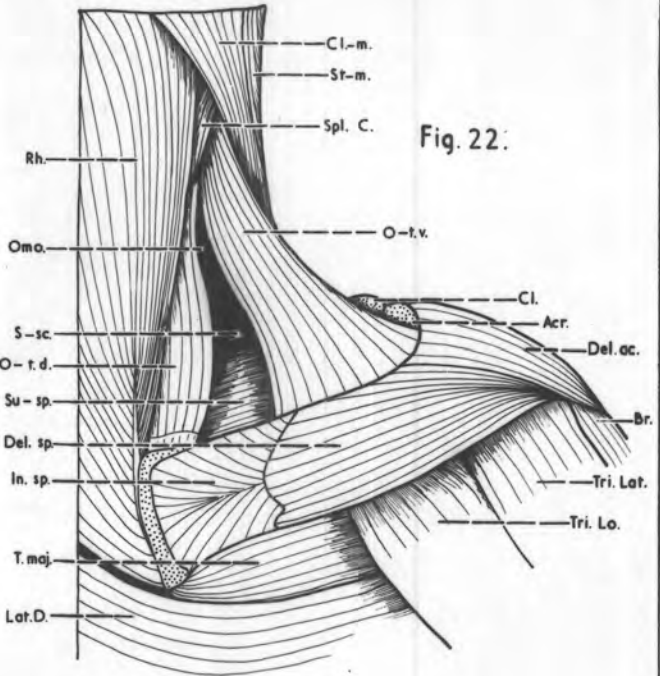


Fig. 22.

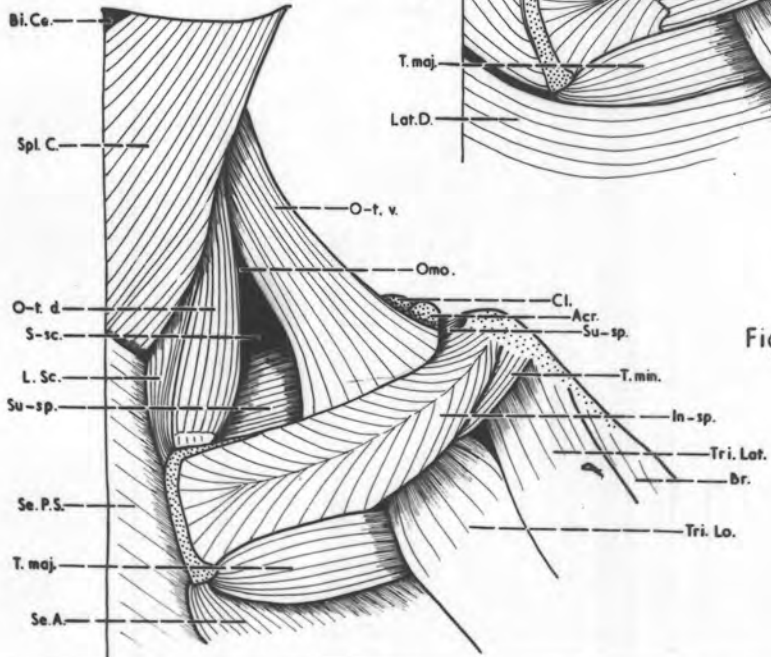
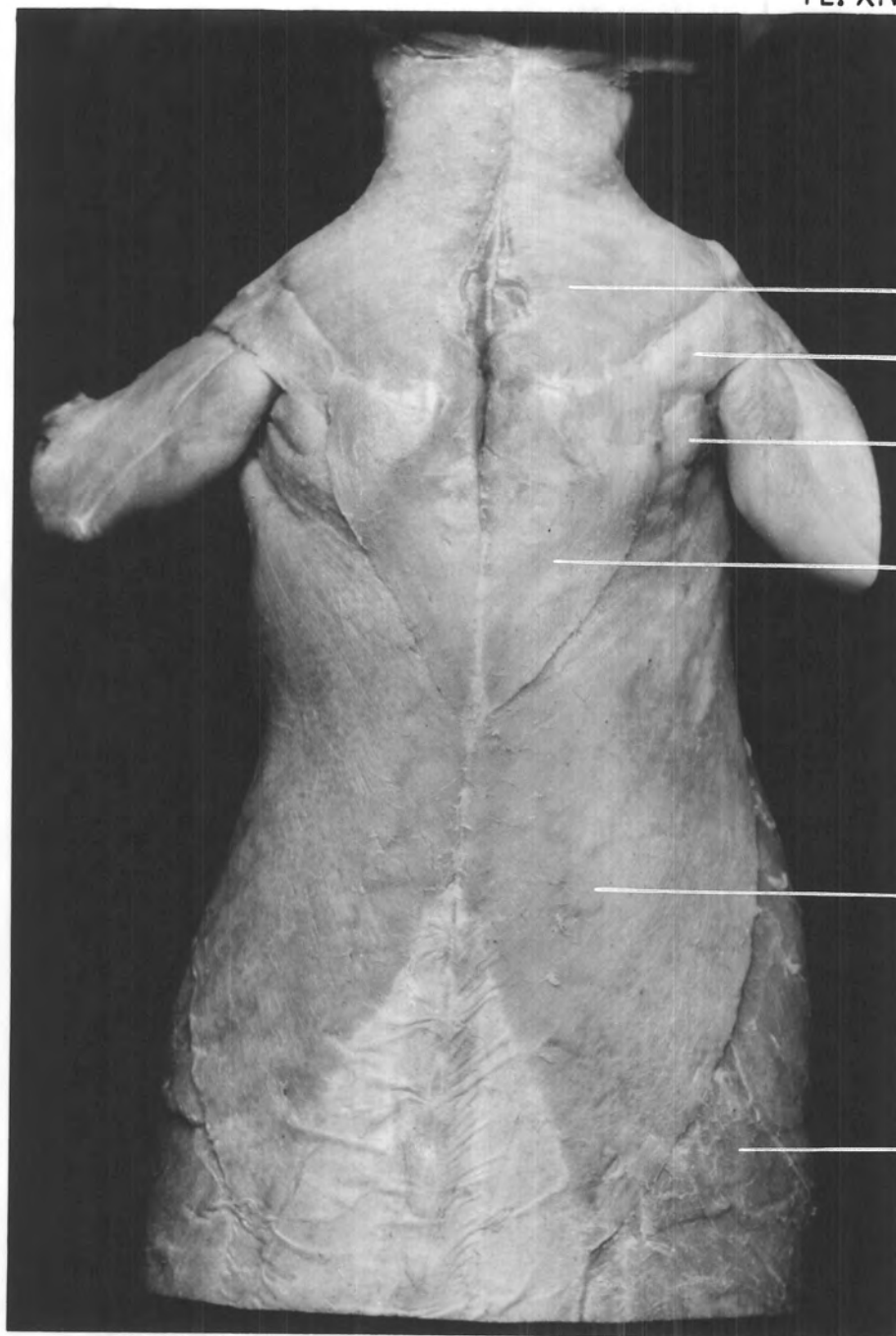


Fig. 23.

Plate XIV (cf. fig. 21). Dorsal view of superficial muscles of
back and scapular region. x⁵/₆.

- Del.sp. - Scapulo-spinal part of deltoid.
- Lat.D. - Latissimus dorsi.
- O.E.A. - Obliquus externus abdominis.
- T.maj. - Teres major.
- Tr. - Trapezius.



Tr.

Del. sp.

T. maj.

Tr.

Lat. D.

O.E. A.

mentions that it may be included in the trapezius, and in Phascolarctos Young (1882) describes a slip of muscle that sounds very like it.

The nerve supply in T. vulpecula comes from the accessory and the third and fourth cervical nerves; the second cervical nerve may also contribute through the branch that joins the accessory before the latter passes the sterno- and cleido-mastoids. Kohlbrugge (1898) gives accessory and C5 and 4 for C. maculatus, C. orientalis and M. brunii, while Boardman (1941) gives accessory and C4 for M. robustus. In N. typhlops Wilson (1894) gives the supply to the part inserted into the spine of the scapula from the nerve to latissimus dorsi.

Latissimus Dorsi (figs. 21, 22, 27, 29; pls. XIV, XVIII, XIX) arises from the thoracic spines from the third to the tenth and caudal to this from the lumbar fascia along a line that diverges from the median plane and extends to the transverse level of the second lumbar spine. The fibres run laterally and cranially converging on the dorsal fold of the axilla where most of them end in the main tendon of insertion which attaches to the floor of the inter-tubercular groove ventral to the insertion of the teres major. The cranial fibres of this main insertion pass dorsal to the rest and, fusing with the caudal border of the teres major, are inserted most distally. From the caudal edge of the tendon springs the axillary arch which crosses to join the pectoralis quartus and forms the insertion of the caudal fibres of the muscle; in one animal, however,

it arose by fleshy fibres from the latissimus tendon so appearing to be a separate muscle. The arch receives the insertion of the axillary part of the panniculus; it must vary considerably in this species because MacCormick (1887) describes it as stretching between the pectoralis quartus tendon and the medial tubercular crest and receiving many of the fibres of the latissimus dorsi itself, while the panniculus joins the fleshy part of the latissimus at the dorsal border of the axilla. As appears to be the rule in marsupials, there is no origin from the scapula, nor is there any from the ribs. Carlsson (1914) gives the origin in Trichosurus from all thirteen thoracic vertebrae and the last two ribs. Some origin from one or more ribs occurs in Dendrolagus and Aepyprymnus (Carlsson, 1914), Petrogale (Carlsson, 1914; Parsons, 1896), Hypsiprymnodon (Heighway, 1959), Phascologmys (Somntag, 1922; Macalister, 1870), Phalanger (Somntag, 1922), Phalangista, Phascogale and Thylacinus (Cunningham, 1882), Sarcophilus (Macalister, 1870, 1872a) and Choeropus (Parsons, 1905).

In N. typhlops Wilson (1894) describes the peculiar condition where the latissimus has no humeral insertion but passes to the fore-arm fascia over the flexor carpi ulnaris, this attachment apparently representing the dorso-epitrochlearis which is otherwise absent.

The latissimus dorsi receives, as usual, a special nerve from the brachial plexus.

Dorso-epitrochlearis (fig. 27; pl. XVIII), for which Windle and

Parsons (1897a) suggest the name "latissimo-olecranalis" and which Owen (1859-1847, 1868) calls "omo-anconeus", is a broad sheet of muscle arising from the caudal edge of the latissimus dorsi tendon. It passes distally on the medial side of the triceps, with which it has a loose fascial connection along its dorsal border, and is inserted through a thin aponeurosis that is blended with the fascia of the upper arm into the proximal two centimetres or so of the posterior border of the ulna including the olecranon.

This appears to be the usual arrangement of this muscle in the marsupials. It is noted as being small or narrow in Das. viverrinus (MacCormick, 1887), Pet. xanthopus (Parsons, 1896) and Aepyprymus rufescens (Carlsson, 1914); in the last and in Thyl. cynocephalus (Cunningham, 1882) it joins the triceps. Haughton (1866) describes it in the opossum as a fourth head of the triceps. Leche (1874-1900) quotes Gruber (1871. Mémoires de l'Acad. des sc. de St. Pétersbourg. 7. sér. 16.) as giving some origin from the scapula in Perameles.

The dorso-epitrochlearis is supplied by the radial nerve. Rhomboid (fig. 22), as is usual in marsupials (Osgood, 1921), is a single undivided sheet arising from a variable amount of the nuchal crest (all of it in one specimen), the nuchal ligament, the first two thoracic spines and some of the following supraspinous ligament. The fibres from the cranial part of the origin form a thin portion of the muscle that is inserted through a small intra-muscular tendon, visible near the lateral border of the muscle, into the

medial end of the spine of the scapula; the caudal part of the muscle is considerably thicker and its fibres run more and more transversely to their attachment to the medial border of the scapula caudal to the spine. The caudal edge of the muscle abuts the cranial border of the latissimus dorsi.

The rhomboid is supplied by branches from the third, fourth and fifth cervical nerves; Miller (1954) does not mention the third in the supply of this muscle.

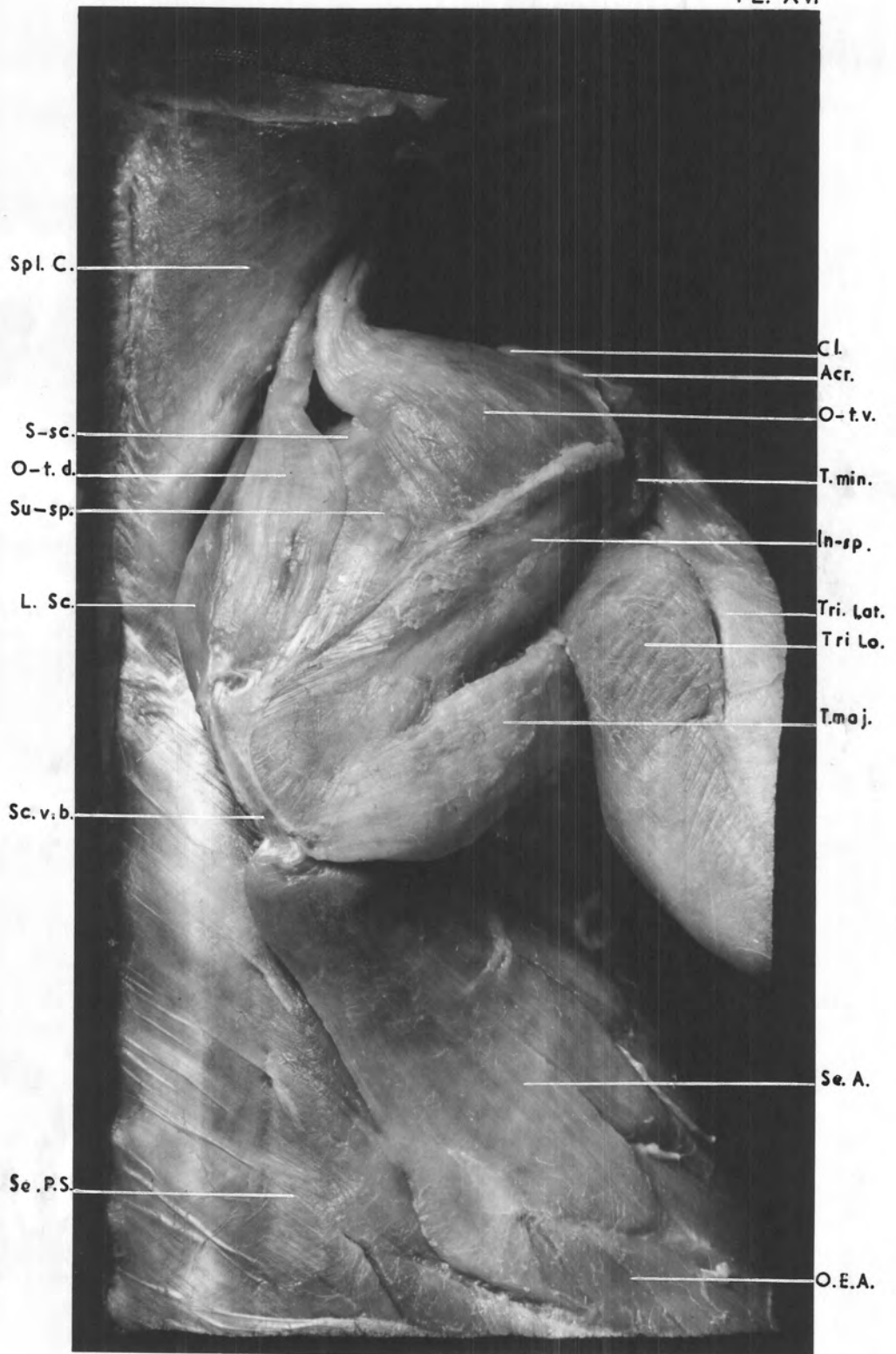
Some origin from the occiput occurs in nearly all marsupials; Windle and Parsons (1897b) found none in a pouch-young specimen of M. rufus though it was present in their adult, and Parsons (1896) gives none for Pet. xanthopus. The caudal limit of origin is more variable, usually being at about the second or third thoracic spine but sometimes extending as far as the fifth or sixth as in Choer. castanotis (Parsons, 1903), Caenolestes (Osgood, 1921), Chir. variegatus (Sidebotham, 1885), Phascolomys (Macalister, 1870; Sonntag, 1922), the opossum (Haughton, 1866; Macalister, 1870) and the phalanger (Macalister, 1870). In S. ursinus (Macalister, 1870) and Caenolestes (Osgood, 1921) the muscle is divided into separate occipital and vertebral parts.

Serratus Anterior (Serratus Magnus) and Levator Scapulae (figs. 25, 24, 25; pls. XV, XVI). These two muscles arise by a continuous series of slips from the transverse processes of the last five cervical vertebrae and the first eight ribs: the costal origins are covered as far as the fourth rib by the scalenus posterior and from

Plate XV (cf. fig. 23). Dorsal view of scapular region and neck.

Trapezius, cleido-occipitalis, latissimus dorsi, rhomboid, deltoid, sterno-mastoid and cleido-mastoid are removed. x 1½.

- Acr. - Acromion.
- Cl. - Lateral end of clavicle.
- In-sp. - Infra-spinatus.
- L.Sc. - Levator scapulae.
- O.E.A. - Obliquus externus abdominis.
- O-t.d. - Omo-trachelien dorsalis.
- O-t.v. - Omo-trachelien ventralis.
- Sc.v.b. - Vertebral border of scapula.
- Sc.A. - Serratus anterior.
- Se.P.S. - Serratus posterior superior.
- Spl.C. - Splenius capitis.
- S-sc. - Subscapularis.
- Su-sp. - Supra-spinatus.
- T.maj. - Teres major.
- T.min. - Teres minor.
- Tri.Lat. - Lateral head of triceps.
- Tri.Lo. - Long head of triceps.



Spl. C.

S-sc.

O-t. d.

Su-sp.

L. Sc.

Sc. v. b.

Se. P.S.

Cl.

Acr.

O-t. v.

T. min.

In-sp.

Tri. lat.

Tri. Lo.

T. maj.

Se. A.

O.E.A.

Figure 24 (cf. pl. XVI). Thoracic wall and neck from ventro-lateral aspect. Trapezius, cleido-occipitalis, sterno-mastoid, cleido-mastoid and latissimus dorsi are removed, the sterno-clavicular joint, brachial plexus and vessels, pectoral muscles and subclavius divided and the whole fore-limb pulled dorso-laterally. $x\frac{2}{3}$.

Figure 25. View of thoracic wall similar to that shown in fig. 24. In addition the omo-hyoid is removed, the omo-trachelien ventralis reflected cranially and the limb pulled further laterally to display the serratus anterior and levator scapulae more fully. $x\frac{2}{3}$.

Figure 26. Acromio-clavicular region from cranial aspect to show the insertion of subclavius. $x2$.

Acr.	- Acromion.
B.P.V.	- Brachial plexus and vessels (cut).
C.C.1.	- First costal cartilage.
Clav.	- Clavicle.
Cor.	- Coracoid process of scapula.
E.I.	- External intercostal.
In-sp.	- Infraspinatus.
L.C-c.	- Longus capito-cervicis.
L.Sc.	- Levator scapulae.
O.E.A.	- Obliquus externus abdominis.
O.E.A.ap.	- Aponeurosis of obliquus externus abdominis.
Omo.	- Omo-hyoid.
O-t.d.	- Omo-trachelien dorsalis.
O-t.v.	- Omo-trachelien ventralis.
Pa-m.	- Paramastoid process.
P.B.D.	- Posterior belly of digastric.
R.A.	- Rectus abdominis.
S-cl.	- Subclavius.
Sc.M.	- Scalenus medius.
Sc.P.	- Scalenus posterior.
Se.A.	- Serratus anterior.
Se.A.c.	- Costal slips of serratus anterior.
Se.A.tr.	- Slip of serratus anterior from seventh cervical transverse process.
Spl.C.	- Splenius capitis.
S-sc.	- Subscapularis.
St.	- Sternalis.
St-hy.	- Sterno-hyoid.
Su-sp.	- Supraspinatus.
T.maj.	- Teres major.

Fig. 24.

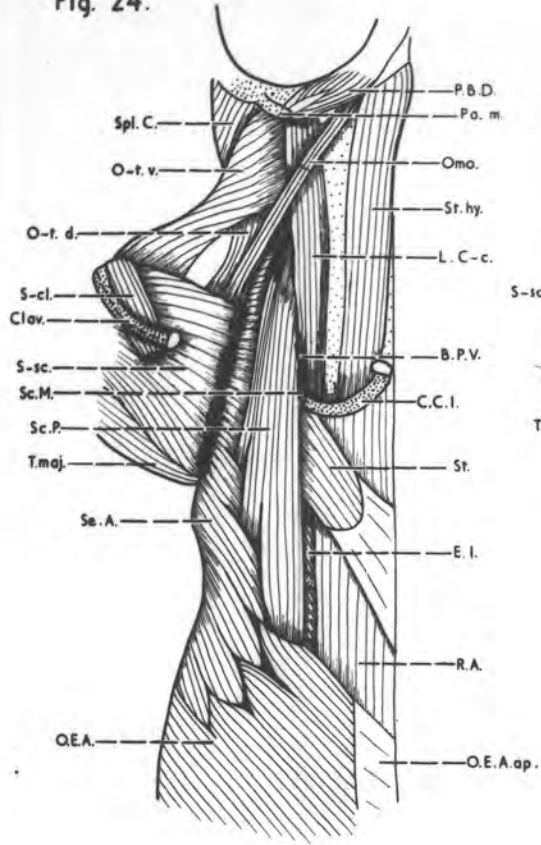


Fig. 25.

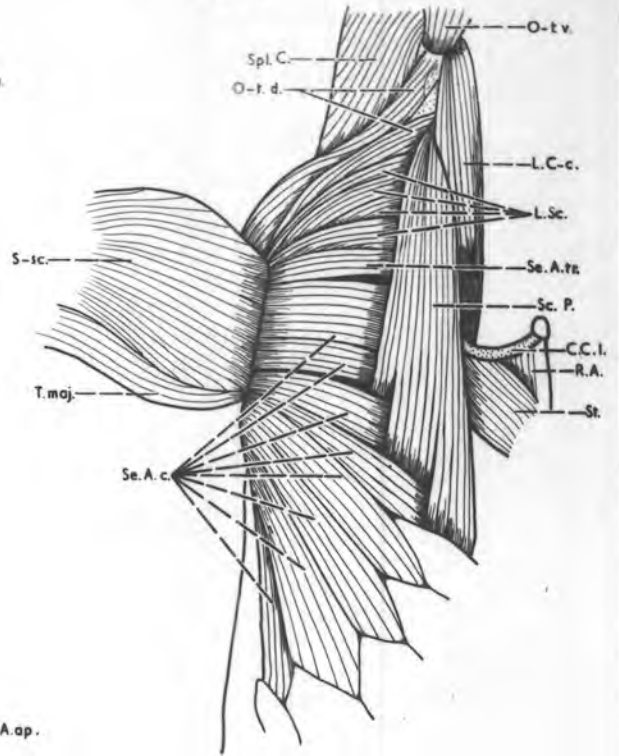


Fig. 26.

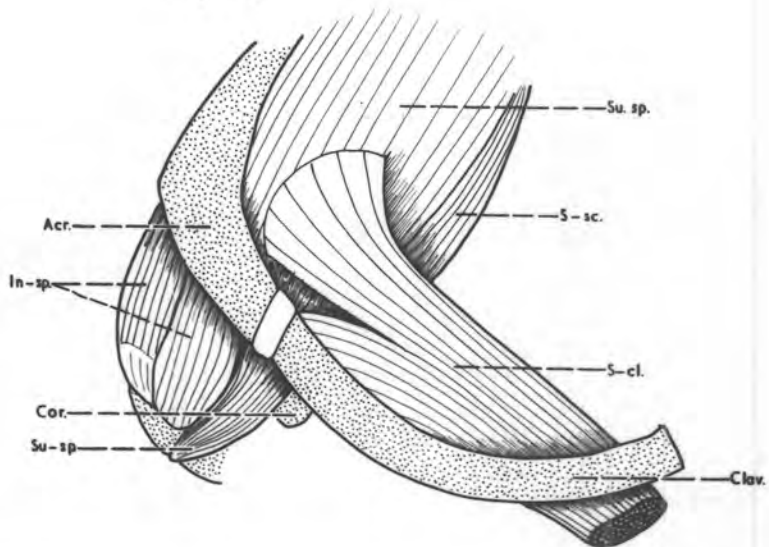
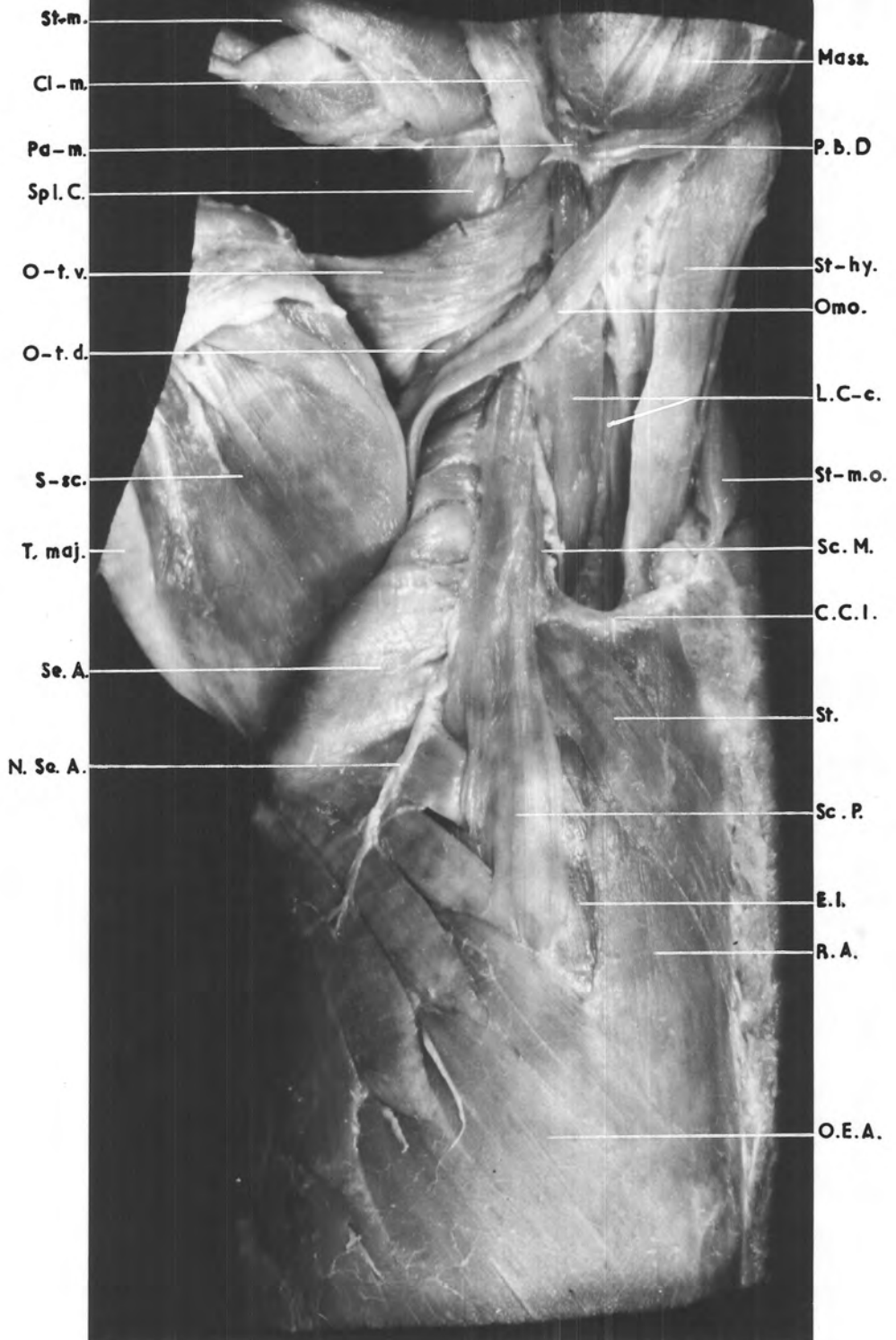


Plate XVI (cf. fig. 24). Ventro-lateral view of thoracic wall and neck. Trapezius and cleido-occipitalis are removed, sternomastoid and cleido-mastoid reflected cranially, the sternoclavicular joint, brachial plexus and vessels, pectoral muscles, subclavius and latissimus dorsi divided and the whole fore-limb pulled dorso-laterally. $\times 1\frac{1}{4}$.

- C.C.1. - First costal cartilage and rib.
- Cl-m. - Cleido-mastoid (reflected).
- E.I. - External intercostal.
- L.C-c. - Longus capito-cervicis.
- Mass. - Masseter.
- N.Sc.A. - Nerve to serratus anterior.
- O.E.A. - Obliquus externus abdominis.
- Omo. - Omo-hyoid.
- O-t.d. - Omo-trachelien dorsalis.
- O-t.v. - Omo-trachelien ventralis.
- Pa-m. - Paramastoid process.
- P.B.D. - Posterior belly of digastric.
- R.A. - Rectus abdominis.
- Sc.M. - Scalenus medius.
- Sc.P. - Scalenus posterior.
- Se.A. - Serratus anterior (continues into neck as levator scapulae).
- Spl.C. - Splenius capitis.
- S-sc. - Subscapularis.
- St. - Sternalis.
- St-hy. - Sterno-hyoid.
- St-m. - Sterno-mastoid (reflected).
- St-m.o. - Sterno-mastoid (of opposite side).
- T.maj. - Teres major.



there on interdigitate with slips of origin of the external oblique of the abdomen. There may also be a few fibres from the second cervical transverse process. The slips from the ribs together with that from the seventh cervical vertebra (and in one animal the sixth also) converge to be inserted into the ventral aspect of the medial border of the scapula and so constitute the serratus anterior. The slips arising from the sixth transverse process (or in one case the fifth) frontally form a mass separated from the rest by a definite cleft and which is inserted dorsal to it into the cranial part of the medial border of the scapula to a point just caudal to the spine; it seems reasonable then to call this part the levator scapulae, or, as Windle and Parsons (1897a) would have it, the "serratus colli". MacCormick (1887) and Carlsson (1914), neither of whom distinguishes between the serratus anterior and the levator scapulae, both give the origin in this animal as extending from the third cervical vertebra to the seventh rib only.

The slips from the cervical vertebrae receive their innervation from the fourth and fifth cervical nerves, this finding apparently being in agreement with that of Miller (1934). The slips from the ribs are supplied by the special nerve to the serratus anterior from the brachial plexus containing fibres from the sixth and seventh cervical nerves. Kohlbrugge (1898) gives the innervation of the levator scapulae as third and fourth cervical nerves in M. brunii, fourth only in C. maculatus and fourth and fifth in C. orientalis, with supply to the serratus from the fifth, sixth and seventh in

all; he puts the division between the two muscles, however, at the interval between the fourth and fifth cervical vertebrae in Cuscus, and between the third and fourth in Macropus, so that comparison becomes difficult.

Although it seems more usual for these two muscles to form a continuous sheet in marsupials other examples of their separation have been described, as in Caenolestes (Osgood, 1921), Ph. maculata (Cunningham, 1882) and in the animals treated by Kohlbrugge (v.s.). The muscle that Haughton (1866) calls levator scapulae in the opossum appears to correspond to my omo-trachelien dorsalis; the same probably applies in Sonntag's (1922) account of Phasc. mitchelli and Ph. orientalis, and to the slip from the atlas mentioned for Pet. xanthopus by Parsons (1896). The levator scapulae described by Young (1882) for Phasc. cinereus and by Sidebotham (1885) for Chir. variegatus is fairly obviously the omo-trachelien ventralis. In Phasc. wombata (Macalister, 1870) and N. typhlops (Wilson, 1894) there is a different subdivision of the muscle into two parts occurring more caudally in the costal region.

The origin of the serratus anterior usually extends to the seventh or eighth rib, though it reached only to the fifth in one example of M. rufus examined by Windle and Parsons (1897b), and to the sixth in M. robustus (Boardman, 1941) and Thyl. cynocephalus (Cunningham, 1882). In N. typhlops (Wilson, 1894) it extends to the tenth rib and in Phasc. wombata (Macalister, 1870) to the eleventh. Omo-trachelien (Acromio-trachelien, Trachelo-acromialis, Omo-cleido-

transversarius, Omo-atlanticus, Omo-cervicalis) consists of two quite separate muscles - the dorsal (or superior) and the ventral (or inferior).

The omo-trachelien dorsalis (figs. 22, 23; pl. XV) arises by two slips that are separate almost to their insertion by a thin aponeurosis to the medial centimetre of the crest of the spine of the scapula. One slip springs from the ventral aspect of the transverse process of the atlas near the tip, the other from the tip of the transverse process of the axis, and they appear to be in series with the slips of origin of the levator scapulae. The attachments given by Carlsson (1914) agree with this, MacCormick (1887) does not mention any origin from the axis.

The omo-trachelien ventralis (figs. 22, 23; pl. XV) also has two slips of origin, one from the ventral aspect of the base of the transverse process of the atlas, the other from the base of the skull just medial to the paramastoid process. These two slips soon unite and the muscle so formed spreads out to be inserted into the lateral half of the crest of the spine of the scapula extending as far out as the acromial angle. Neither Carlsson (1914) nor MacCormick (1887) mentions the attachment of this muscle to the skull, the former author gives an additional origin from the axis and the insertion to the outer third of the scapular spine.

Both the above muscles are supplied by the third and fourth cervical nerves, as in C. maculatus, C. orientalis and M. brunii (Kohlbrugge, 1898). In the case of the dorsalis the third supplies

the atlantic slip, the fourth the axial; the ventralis may also receive some fibres from the fifth cervical nerve through the branch that it gives to the fourth.

An omo-trachelien dorsalis is not described for some marsupials: this need not, however, indicate its absence, since some investigators include it as all or part of the levator scapulae. In other instances it may be represented as the cranial part of an undivided levator scapulae-serratus anterior complex when the origin of that complex extends as far as the atlas and axis. Leche (1874-1900) considers that the "omo-cleido-transversarius" and the levator scapulae are most probably derived from the same muscle group.

The omo-trachelien ventralis is more constantly described; Wilson (1894) notes its absence in N. typhlops. The origin of this muscle extends as far caudally as the fourth cervical vertebra in M. robustus (Boardman, 1941) and Pet. xanthopus (Parsons, 1896). The only other mention I have found of any attachment of the ventralis to the skull is in Kohlbrugge's (1898) account of Cuscus; in Chir. variegatus there is some origin of the dorsalis from the basi-occiput (Sidebotham, 1885).

2). Muscles of the shoulder.

Deltoid (figs. 17, 18, 21, 22; pls. XIII, XIV) has three parts that may be described separately. The clavicular part arises from the lateral three fourths of the ventral border of the clavicle and passes to an insertion into the deltoid tuberosity of the humerus and a line that runs proximally from this towards the base of the

greater tuberosity diverging, as it ascends, from the lateral tubercular crest. It is partly covered by the fibres of the trapezius that cross the clavicle and by the fascia into which these are inserted; it is adherent along its caudal edge to the superficial stratum of the pectoralis major and it covers some of the deep part of this muscle. The acromial part is separated from the clavicular by a wide V-shaped interval, it is the smallest of the three parts and takes origin from the lateral border of the acromion; its fibres, many of which diverge in bipenniform fashion from an intra-muscular tendon, are inserted into the deltoid tuberosity and the line described above. The third portion is the scapulo-spinal, the largest part, which has its origin from the lateral half of the caudal lip of the crest of the spine of the scapula, from the infraspinatus fascia along a line dividing the infraspinatus muscle into a medial one third and lateral two thirds, and from the lateral border of the scapula at the end of this line. It is inserted in the same way as the other two parts, blending first with the acromial part. Carlsson (1914) and MacCormick (1887) do not recognize the separation between the acromial and scapulo-spinal parts of this muscle; certainly they are not as obviously defined from one another as are the acromial and clavicular parts but they can be separated without any trouble except near their insertion. All three parts of the deltoid are supplied by the circumflex nerve which runs around the neck of the humerus just proximal to their insertion.

A division between the clavicular and acromial parts separating

the deltoid into two occurs in many marsupials; a double muscle with the separation between the acromial and scapulo-spinal parts is described for Caenolestes by Osgood (1921) and for Myrmecobius by Leche (1874-1900). There is no separation of parts in Phascologmys (Sonntag, 1922), M. giganteus and M. bennetti (Macalister, 1870) and Phasc. cinereus (Sonntag, 1922; Macalister, 1872b), though Young (1882) gives the usual division into two parts in the last. In Das. viverrinus (MacCormick, 1887) and Phasc. calura (Cunningham, 1882) three parts are described. Part origin from the infraspinatus fascia is reported for Dend. dorianus (Carlsson, 1914), M. robustus (Boardman, 1941), Hyps. moschatus (Heighway, 1939), Ph. maculata (Cunningham, 1882) and Per. lagotis (Owen, 1839-1847, 1868).

Supraspinatus (figs. 28, 29; pls. XVII, XIX) is about twice the size of the infraspinatus. It arises from almost the whole of the supraspinous fossa and also from the fascia that it shares with the subscapularis beyond the cranial border of the scapula. Its tendon passes across the shoulder joint to which it is partly adherent and is inserted on the summit of the greater tuberosity.

Infraspinatus (figs. 25, 28; pls. XV, XVII) has its origin from most of the infraspinous fossa; the muscle is hard to separate from the supraspinatus where the two are in contact in the spino-glenoid notch and further laterally their tendons are fused. The tendon of the infraspinatus is, like that of the supraspinatus, adherent to the capsule of the shoulder joint and finally attaches to the dorsal aspect of the greater tuberosity near the summit.

Both the spinati are supplied by the suprascapular nerve.

The infraspinatus is the larger of these two muscles in Dend. dorianus (Carlsson, 1914), M. robustus (Boardman, 1941), M. rufus (Windle and Parsons, 1897b), M. bennetti (Macalister, 1870), Pet. xanthopus (Parsons, 1896) and Phasc. cinereus (Young, 1832; Sonntag, 1922). They are about equal in M. giganteus (Macalister, 1870), while in the others reported the supraspinatus is the larger, the approximate two to one proportion noted here also being found in Hyps. moschatus (Heighway, 1959), Thyl. cynocephalus (Cunningham, 1832), S. ursinus (Macalister, 1872a) and Caenolestes (Osgood, 1921). The greatest disparity in size mentioned is in Das. viverrinus (MacCormack, 1887) and Phasc. calura (Cunningham, 1832) where the supraspinatus is three times as large as the infraspinatus.

Increased development of the supraspinous musculature is associated with improved climbing ability (Gregory, 1910), though it is retained in some marsupials that are now terrestrial. Fusion of the two spinati towards their insertion similar to that found here has been described for M. robustus by Boardman (1941).

Teres Major (figs. 22, 25, 27, 28, 29; pls. XV, XVII, XVIII, XIX) is a well developed muscle arising from the caudal two thirds of the lateral border of the scapula and beyond this border from the fascia that it shares with the subscapularis. It is inserted into the distal half of the medial tubercular crest of the humerus, this insertion lying dorsal to and blended with that of the latissimus dorsi and also extending further proximally than that of the

latissimus. It is supplied by the lower subscapular nerve.

Teres Minor (figs. 25, 26; pls. XV, XVII) is very small and is covered completely by the scapulo-spinal deltoid: it extends from the juxta-glenoid third of the lateral border of the scapula to the dorsal aspect of the greater tuberosity of the humerus immediately distal to the insertion of the infraspinatus, its tendon being somewhat adherent to the capsule of the shoulder joint where it lies in relation with this structure. It is supplied by the circumflex nerve, as in M. robustus (Boardman, 1941), Pet. xanthopus (Parsons, 1896), Ph. maculata and Thyl. cynocephalus (Cunningham, 1878a, 1882). MacCormick (1887) seems to indicate some origin of this muscle in Trichosurus from the metacromion and a fibrous arch connecting this to the axillary border of the scapula, while Macalister (1870) could not separate a teres minor from the infraspinatus; neither of these reports agrees with the findings of my present investigations.

The teres minor is not present as a separate muscle in M. giganteus (Macalister, 1870; Windle and Parsons, 1897b), Per. lagotis (Macalister, 1870), Did. virginiana (Macalister, 1870; Coues, 1872), Caenolestes (Osgood, 1921), Phasc. calura (Cunningham, 1882), N. typhlops (Wilson, 1894) and in some of Young's (1882) specimens of Phasc. cinereus. It is represented by fascia in Phascotomya (Sonntag, 1922; Macalister, 1870). It has been reported as present though small in quite as many other marsupials - Choer. castanotis (Parsons, 1905), M. robustus (Boardman, 1941), M. rufus (Windle and Parsons, 1897b), Pet. xanthopus (Parsons, 1896), Hyps.

moschatus (Heighway, 1939), Ph. maculata and Thyl. cynocephalus (Cunningham, 1832), Das. viverrinus (MacCormick, 1837), S. ursinus (Macalister, 1872a) and Chir. variegatus (Sidebotham, 1835).

Subscapularis (fig. 27; pl. XVIII) has an extensive origin from the ventral surface of the scapula (excepting an area laterally near the glenoid and the medial strip for the insertion of serratus anterior) and also from the fasciae separating it from the supraspinatus and the teres major. As its tendon crosses the shoulder joint on its way to the lesser tuberosity of the humerus it is adherent to the capsule. The muscle is supplied by the subscapular nerves, receiving no additional branch from the suprascapular such as Parsons (1896) describes for Pet. xanthopus.

Coraco-brachialis (figs. 27, 29; pls. XVIII, XIX). In T. vulpecula this muscle consists typically of two elements, the brevis (profundus, rotator humeri) and the medius, though the latter was absent from one arm of one animal I examined (No. 4). Both arise from the coracoid process of the scapula by a tendon that is joined to the medial side of that of the biceps brachii; the coraco-brachialis brevis forms a wide mass that is inserted into the medial surface of the humerus above the attachment of the teres major and in front of the lateral head of the triceps. The medius is a much narrower muscle whose fibres spring from a very thin continuation of the tendon of origin that extends over the superficial surface of the brevis: it is inserted, also by a thin short tendon, into the humerus just proximal to the entrance to the supracondylar foramen.

Figure 27 (cf. pl. XVIII). Ventro-medial aspect of scapular region and upper arm after removal from the trunk. All extrinsic muscles except latissimus dorsi, serratus anterior and levator scapulae are removed and the clavicle and acromion are excised. $\times 1\frac{1}{4}$.

Figure 28 (cf. pl. XVII). Dorso-lateral aspect of scapular region and upper arm after removal from the trunk. All extrinsic muscles, the deltoid, acromion and clavicle are removed. $\times 1\frac{1}{4}$.

Figure 29 (cf. pl. XIX). Ventro-medial aspect of scapular region and upper arm after removal from the trunk. All extrinsic muscles, teres major, subscapularis, dorso-epitrochlearis, biceps brachii, the clavicle and acromion are removed. $\times 1\frac{1}{4}$.

Acr.	- Acromion (cut off).
An.M.	- Anconeus medialis (epitrochleo-anconeus).
Bi.	- Biceps brachii (superficial part).
Bi.ap.	- Bicipital aponeurosis.
Bi.d.	- Biceps brachii (deep part).
Br.	- Brachialis.
C-b.br.	- Coraco-brachialis brevis.
C-b.m.	- Coraco-brachialis medius.
Cor.	- Coracoid process of scapula.
Del.Tu.	- Deltoid tuberosity of humerus.
D-ep.	- Dorso-epitrochlearis.
In-sp.	- Infraspinatus.
Lat.D.	- Latissimus dorsi.
L.Sc.	- Levator scapulae (retracted to the right).
Med.Ep.	- Medial epicondyle of humerus.
Ol.	- Olecranon.
P.q.sl.	- Slip from latissimus dorsi tendon to pectoralis quartus.
S.Cap.	- Capsule of shoulder joint.
Scap.	- Scapula.
Se.A.	- Serratus anterior (retracted to the right).
S-sc.	- Subscapularis.
Su-sp.	- Supraspinatus.
T.maj.	- Teres major.
T.min.	- Teres minor.
Tri.Lat.	- Lateral head of triceps.
Tri.Lo.	- Long head of triceps.
Tri.Lo.d.	- Dorsal part of origin of long head of triceps.
Tri.Lo.v.	- Ventral part of origin of long head of triceps.
Tri.Med.	- Medial head of triceps.

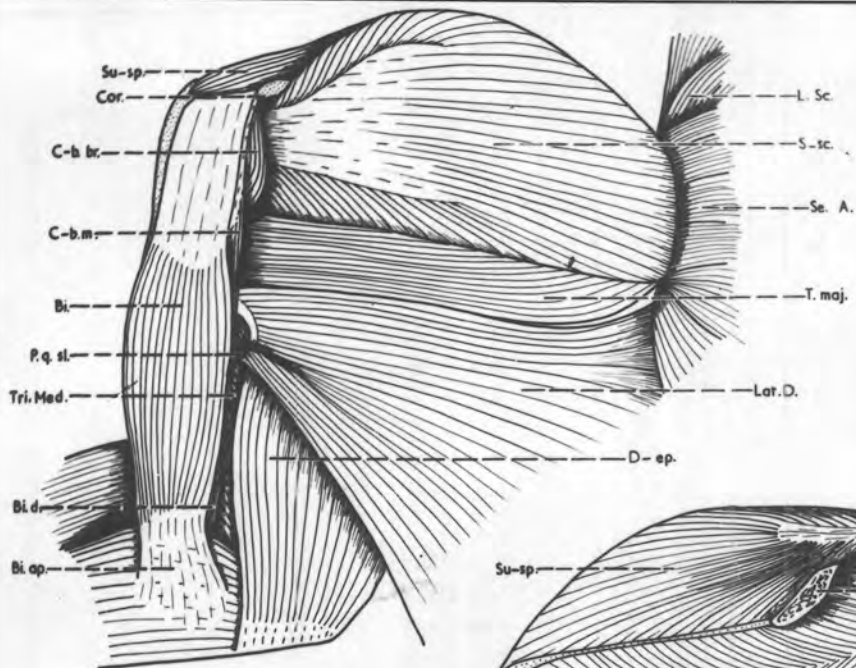


Fig. 27.

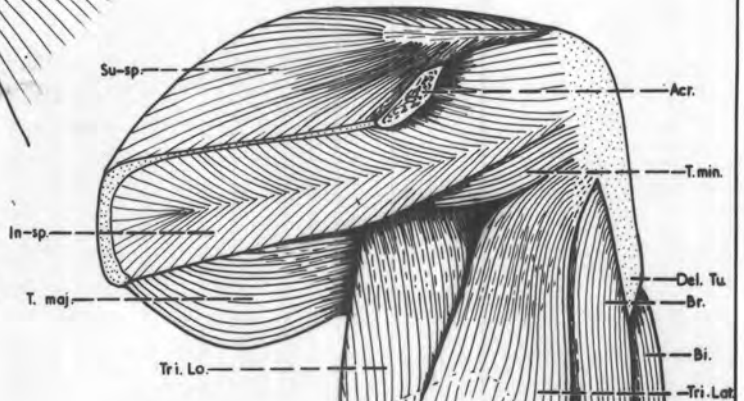


Fig. 28.

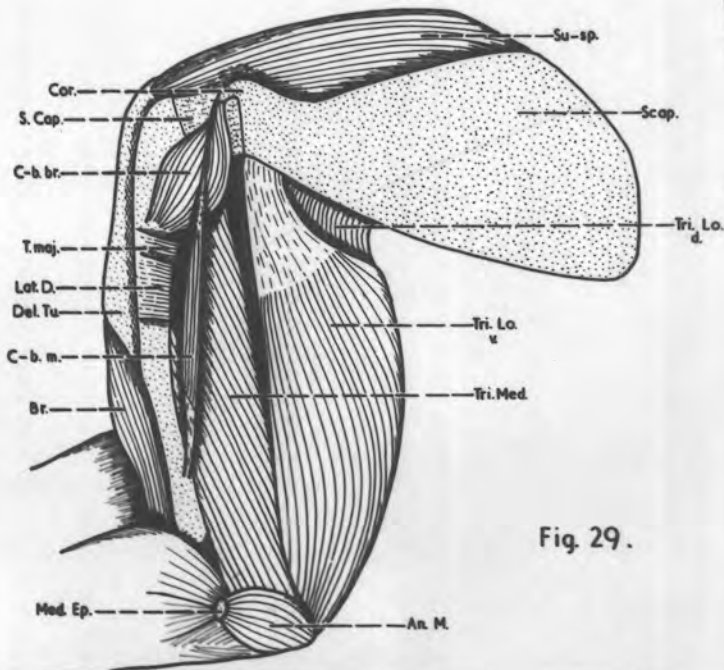


Fig. 29.

Plate XVII (cf. fig. 28). Dorso-lateral view of scapular region and upper arm. The limb is removed from the trunk leaving behind all muscles attaching it to the trunk: the deltoid and acromion are excised. $\times 1\frac{1}{2}$.

- | | |
|----------|----------------------------------|
| Acr. | - Acromion (cut). |
| Bi. | - Biceps brachii. |
| Br. | - Brachialis. |
| Del.Tu. | - Deltoid tuberosity of humerus. |
| In-sp. | - Infra-spinatus. |
| Lat.Ep. | - Lateral epicondyle of humerus. |
| Ol. | - Olecranon. |
| Su-sp. | - Supra-spinatus. |
| T.maj. | - Teres major. |
| T.min. | - Teres minor. |
| Tri.Lat. | - Lateral head of triceps. |
| Tri.Lo. | - Long head of triceps. |

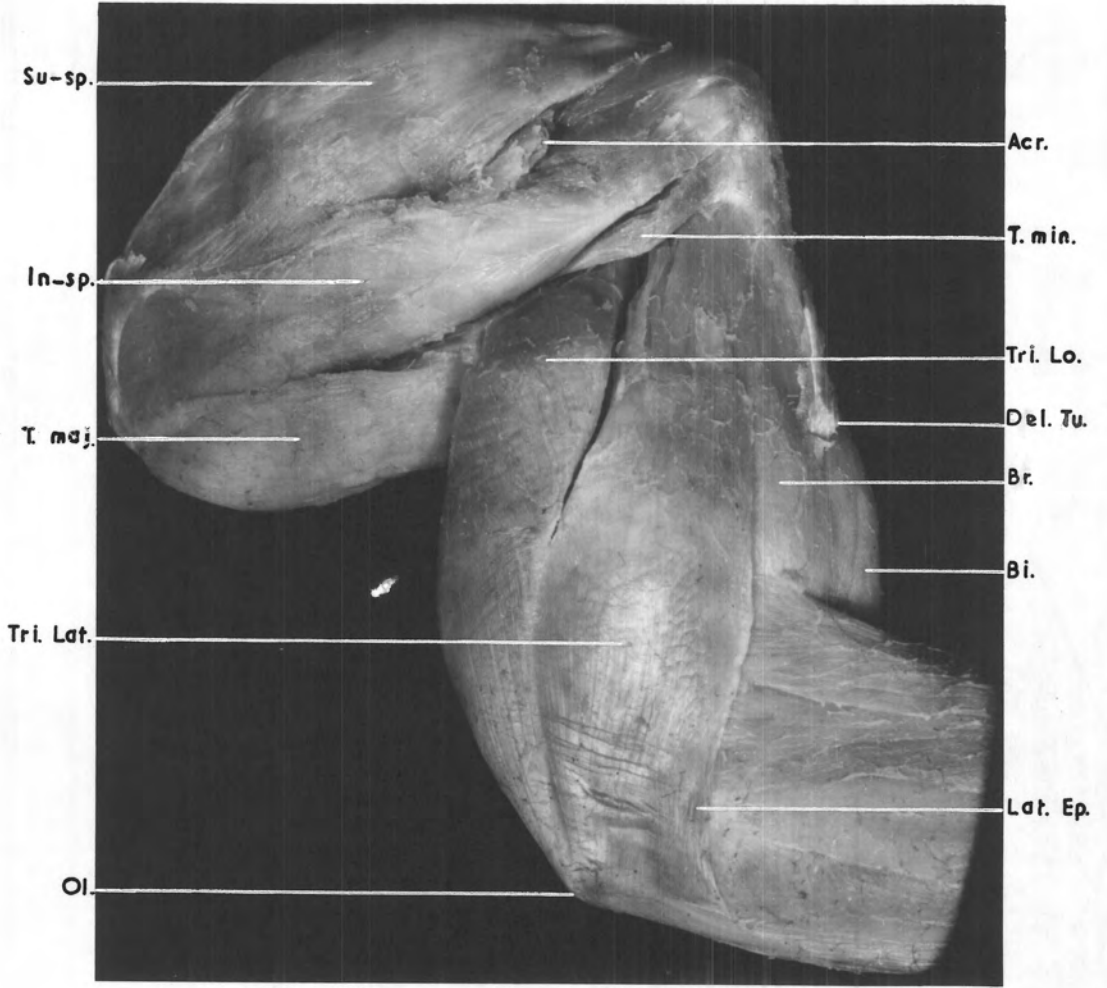
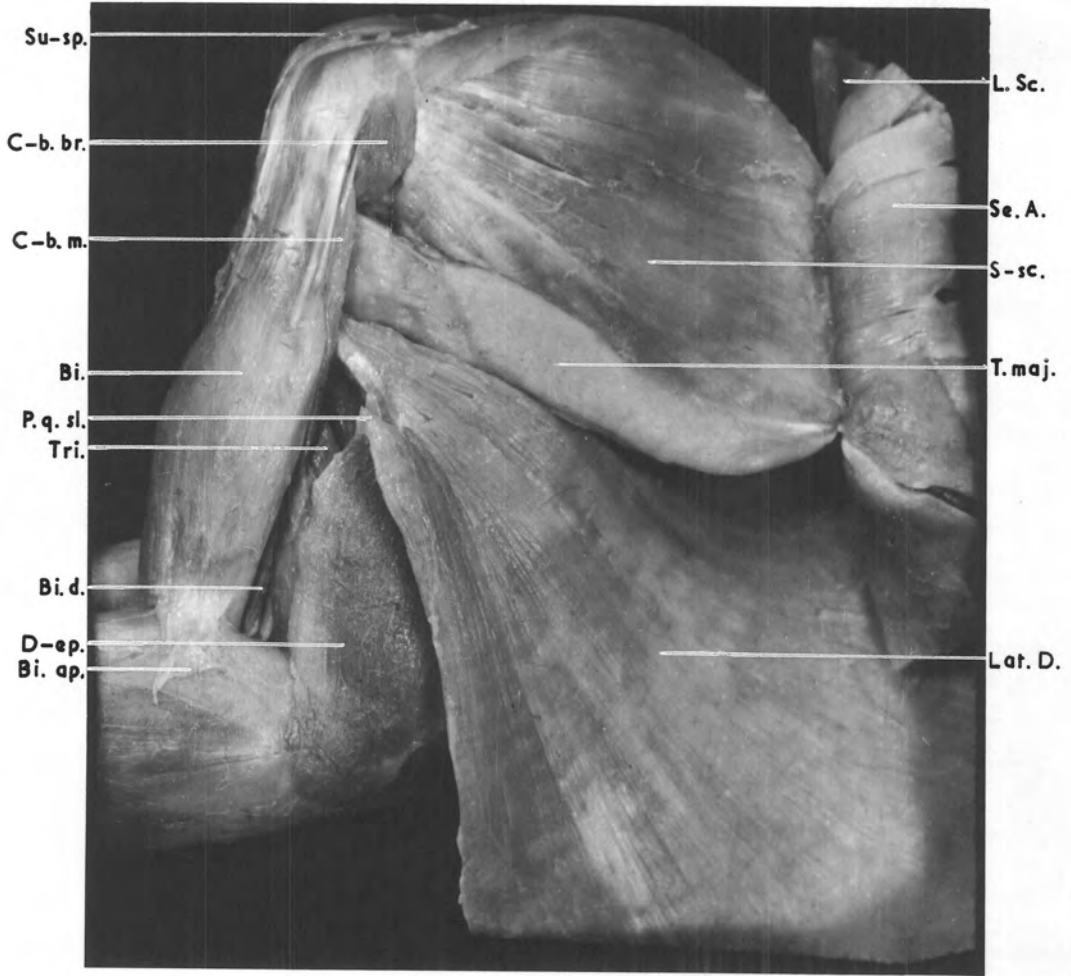


Plate XVIII (cf. fig. 27). Ventro-medial view of scapular region and upper arm. The limb is removed from the trunk and the clavicle and acromion are excised. Of the muscles that connect the fore-limb to the trunk only latissimus dorsi, serratus anterior and levator scapulae remain attached. $x1\frac{1}{2}$.

- Bi. - Biceps brachii (superficial layer).
- Bi.ap. - Bicipital aponeurosis.
- Bi.d. - Biceps brachii (deep layer).
- C-b.br. - Coraco-brachialis brevis.
- C-b.m. - Coraco-brachialis medius.
- D-ep. - Dorso-epitrochlearis.
- Lat.D. - Latissimus dorsi.
- L.Sc. - Levator scapulae (retracted to the right).
- P.q.sl. - Slip from latissimus dorsi tendon to pectoralis quartus.
- Se.A. - Serratus anterior (retracted to the right).
- S-sc. - Subscapularis.
- Su-sp. - Supra-spinatus.
- T.maj. - Teres major.
- Tri. - Triceps.



MacCormick (1887) gives the insertion of the medius rather more proximally, Carlsson (1914) - calling it the longus - found it to be absent in one of her specimens though present in the other: both noted the brevis.

Both parts of the coraco-brachialis are supplied by the musculocutaneous nerve which has no cutaneous distribution in this animal; the nerve is purely motor also in Thyl. cynocephalus and Ph. maculata (Cunningham, 1878a, 1882) where this muscle has the same supply. In Pet. xanthopus Parsons (1896) gives the supply from the lateral root of the median nerve, which probably amounts to the same thing.

The majority of marsupials described have only one part to the coraco-brachialis - the brevis. In Choer. castanotis (Parsons, 1903) and N. typhlops (Wilson, 1894) the muscle is entirely absent. Cunningham (1882) describes two muscles in Phasc. calura, where the second is the medius going to the middle of the shaft of the humerus, and also in Ph. maculata where the second (which he calls the longus) is inserted into the bridge over the supracondylar foramen. Young (1882) considers the longer of the two present in Phasc. cinereus to represent both the medius and the longus since it is inserted into the medial border of the humerus all the way from the latissimus dorsi to the internal condyle.

3). Muscles of the upper arm.

Biceps Brachii (figs. 27, 32; pl. XVIII) has a double origin from the scapula, a thick supraglenoid tendon and a thinner coracoid

tendon, the two being fused along their adjacent margins so that there is really only one tendon of origin. Most of the fibres from the supraglenoid part of the tendon form a separate deep part of the muscle that is inserted into the ulna with the brachialis, the muscle fibres from the coracoid portion of the tendon and some of those from the supraglenoid form the superficial stratum inserted into the tuberosity of the radius. The supraglenoid tendon provides about the lateral one third of the superficial layer and on the medial side this layer gives a distinct fasciculus to the deeper stratum. From the surface of the superficial layer arises a bicipital aponeurosis that blends with the fascia over the mass of flexor muscles arising from the medial epicondyle of the humerus. As noted by Carlsson (1914) none of the tendon of origin is within the shoulder capsule. The muscle is supplied by the musculocutaneous nerve.

Most marsupials show a partial or complete subdivision of the biceps into coraco-radial and gleno-ulnar parts, any connection between the two being usually at the tendon of origin. In Choer. castanotis (Parsons, 1905) and N. typhlops (Wilson, 1894) only the radial insertion is present and in both these animals the tendon of origin passes through the shoulder joint. The bicipital aponeurosis is rarely mentioned, Howell and Straus (1951) specifically note that there is no lacertus fibrosus in Did. virginiana. Parsons (1896) gives the nerve supply in Pet. xanthopus from the outer root of the median nerve, as does Boardman (1941) for M. robustus. Leche (1874-

1900) seems to indicate that supply from the median nerve is the general rule in mammals.

Brachialis (figs. 28, 29, 32; pls. XVII, XIX) is a relatively small muscle arising from the lateral aspect of the humerus; there is no origin in front of the line of the deltoid tuberosity. It is inserted into an impression on the ulna just distal to the coronoid process after fusing with the deep part of the biceps the attachment of which extends somewhat more distally on the bone. Its innervation comes from the musculo-cutaneous nerve; there is no branch from the radial nerve, a point also noted in Choer. castanotis (Parsons, 1905) and Pet. xanthopus (Parsons, 1896), in the latter of which the supply again comes from the lateral root of the median nerve.

The arrangement of the muscle as found here seems to be typical of most marsupials. In the accounts of Das. viverrinus (MacCormick, 1887), Did. virginiana (Howell and Straus, 1931) and Hyps. moschatus (Heighway, 1959) some origin is given from the anterior surface of the humerus.

Triceps Brachii (figs. 21, 28, 29; pls. XVII, XIX). The long head of this muscle arises by two quite separate origins from the axillary border of the scapula adjacent to the glenoid; the dorsal one is a broad sheet, partly fleshy and partly fibrous, the other is a narrow ribbon-like tendon lying on the ventral surface of the first. The two form one single belly which develops its aponeurosis of insertion on its superficial and lateral surfaces, this

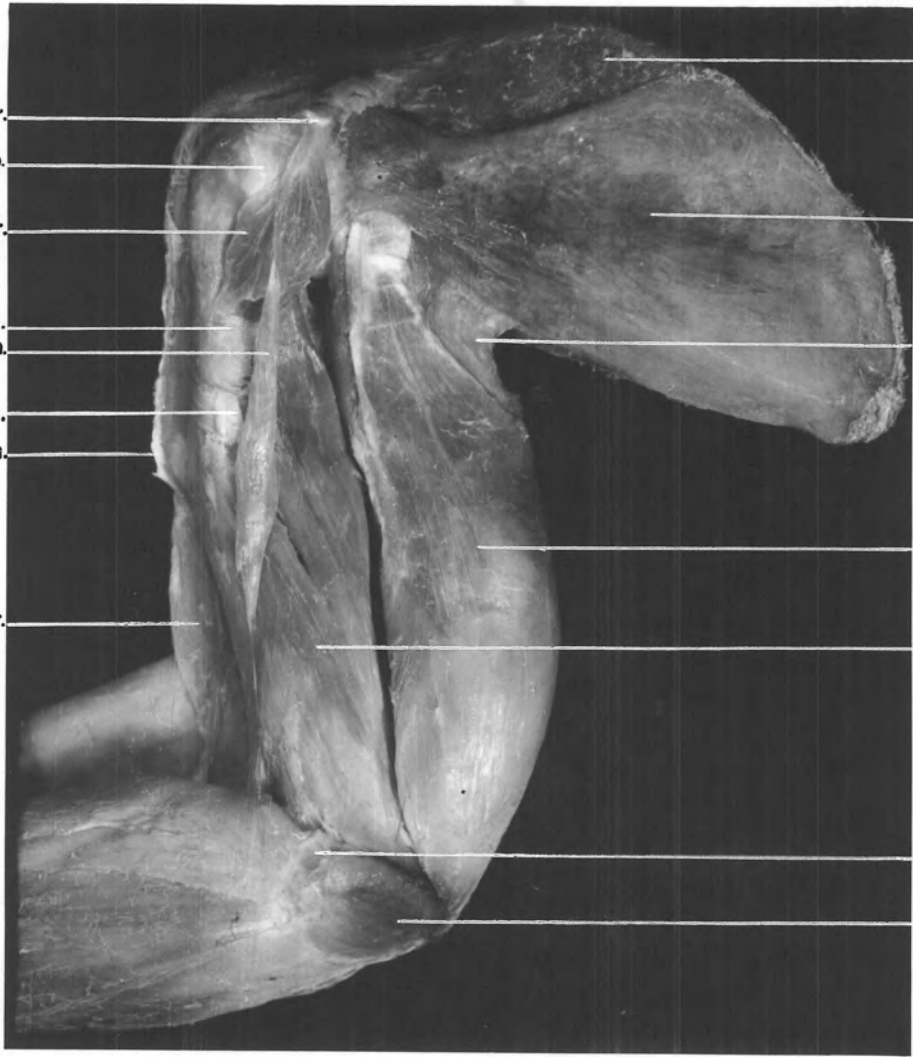
Plate XIX (cf. fig. 29). Ventro-medial view of scapular region and upper arm. The limb is separated from the trunk, and all extrinsic muscles, teres major, subscapularis, dorso-epitrochlearis, biceps brachii, the clavicle and the acromion are removed. $x1\frac{2}{3}$.

- An.M. - Anconeus medialis (epitrochleo-anconeus).
- Br. - Brachialis.
- C-b.br. - Coraco-brachialis brevis.
- C-b.m. - Coraco-brachialis medius.
- Cor. - Coracoid process of scapula.
- Del.Tu. - Deltoid tuberosity of humerus.
- Lat.D. - Latissimus dorsi (insertion).
- Med.Ep. - Medial epicondyle of humerus.
- S.Cap. - Capsule of shoulder joint.
- Scap. - Scapula.
- Su-sp. - Supra-spinatus.
- T.maj. - Teres major (insertion).
- Tri.med. - Medial head of triceps.
- Tri.Lo.d. - Dorsal part of origin of long head of triceps.
- Tri.Lo.v. - Ventral part of origin of long head of triceps.

Cor.
S. Cap.
C-b.br.
T. maj.
C-b. m.
Lat. D.
Del. Tu.

Br.

Su-sp
Scap.
Tri. Lo. d.
Tri. Lo. v.
Tri. med.
Med. Ep.
An. M.



aponeurosis is formed mainly from the dorsal part of the origin and the fibres arising from the ventral tendon are inserted into it - mainly into the lateral part that faces the lateral head of the muscle. The long head is easily separable throughout from the others and is inserted into the angle of the olecranon. The lateral and medial heads are to some extent fused with one another especially at their origin; the lateral has its origin from the back of the neck of the humerus and is inserted by a thin aponeurosis into the lateral border of the olecranon; the medial, which is joined to the deep surface of the lateral head, arises from the proximal three fourths of the back of the humerus and along the lateral supracondylar line to the lateral epicondyle where it becomes continuous with the anconeus lateralis. The medial head is inserted into the back of the capsule of the elbow and the tip and anterior and lateral surfaces of the olecranon deep to the lateral head. The three heads are all supplied by the radial nerve which runs through the medial head as Cunningham (1832) describes for Thyl. cynocephalus, not between the medial and lateral heads as in N. typhlops (Wilson, 1894), Chir. variegatus (Sidebotham, 1835), Ph. maculata (Cunningham, 1832) and Hyps. moschatus (Heighway, 1939). In Choer. castanotis (Parsons, 1903) and Caenolestes (Osgood, 1921) the medial head unusually remains separate throughout.

Carlsson (1914) briefly notes the double nature of the long head of this muscle in T. vulpecula; the nearest approach to the condition in any other marsupial appears to be in Thyl. cynocephalus

where Cunningham (1882) describes separate tendinous and fleshy parts which, however, apparently do not overlap as in Trichosurus; a similar arrangement also occurs in Chir. variegatus (Sidebotham, 1885).

Anconeus Medialis (Epitrochleo-anconeus) (figs. 29, 30, 31, 32; pls. XIX, XX) has a broad oval outline as it passes from its origin on the back of the medial epicondyle of the humerus to its insertion on the medial side of the half of the olecranon nearest the free end. Adjacent to its distal border is the fibrous arch that gives part origin to the flexor carpi ulnaris. The muscle is innervated by the ulnar nerve which runs deep to it, this supply agreeing with that given for Pet. xanthopus by Parsons (1896) and for Thyl. cynocephalus and Ph. maculata by Cunningham (1878a, 1882), and being the supply that Howell and Straus (1951) say is typical of a true epitrochleo-anconeus; the last mentioned authors describe a different anconeus internus in Did. virginiana representing a triceps element and supplied by the radial nerve. Heighway (1959) says that the medial anconeus appears to be constant throughout the Marsupialia; Parsons (1903), however, mentions the absence of the epitrochleo-anconeus in Choer. castanotis.

Anconeus Lateralis (fig. 35), as in most marsupials, is continuous with the medial head of the triceps through which it receives its nerve of supply. Its origin is from the back of the lateral epicondyle of the humerus and from the capsule of the elbow and is a direct continuation of the origin of the medial head of the triceps.

The insertion occupies some of the lateral aspect of the olecranon (deep to the triceps) and the posterior surface of the ulna, adjacent to the posterior border, extending nearly half way along the shaft: this extent of insertion agrees with that given by MacCormick (1887). The muscle is largely covered by the extensor carpi ulnaris and the extensor digitorum profundus.

4). Flexor muscle group of the fore-arm.

Pronator Teres (fig. 30; pl. XX) takes origin from the front of the medial epicondyle of the humerus and from the septum that separates it from the flexor carpi radialis; there is no deep head from the ulna. Passing distally and radially it is inserted into rather more than the middle two fourths of the outer border of the radius. It is supplied by the median nerve as in a number of other marsupials reported (Cunningham, 1878a, 1882; Kajava, 1910).

So far as I can ascertain a deep ulnar head for this muscle has never been found in a marsupial, the muscle varies chiefly in the position and extent of its radial attachment. The insertion given here for T. vulpecula, or, very similarly, the middle third of the bone, occurs in a wide range of marsupials - e.g. Das. viverrinus (MacCormick, 1887; Kajava, 1910), Thyl. cynocephalus (Cunningham, 1882), S. ursinus (Macalister, 1870), Phasc. cinereus (Young, 1882; Kajava, 1910; Sonntag, 1922), Chir. variegatus (Sidebotham, 1885), Caenolestes (Osgood, 1921), Didelphys (Coues, 1872; Kajava, 1910), Myrmecobius fasciatus, Ph. orientalis, M. robustus and Macropus affinis agilis (Kajava, 1910). In M. vallabiensis (Haughton, 1866),

Figure 30 (cf. pl. XX). Flexor muscle group of fore-arm with fore-arm in semi-pronation and dorso-epitrochlearis removed. $x1\frac{1}{8}$.

Figure 31. Flexor muscle group of fore-arm after the removal of pronator teres, palmaris longus, flexor carpi radialis, flexor carpi ulnaris and biceps brachii. Fore-arm in semi-pronation and showing especially flexor digitorum profundus. $x1\frac{1}{8}$.

Figure 32. Flexor aspect of fore-arm in semi-pronation showing pronator quadratus. All other muscles of the flexor group are removed and biceps brachii is cut near its insertion. $x1\frac{1}{8}$.

An.M.	- Anconeus medialis (epitrochleo-anconeus).
Bi.d.	- Deep layer of biceps brachii.
Bi.s.	- Superficial layer of biceps brachii.
Br.	- Brachialis.
Br-r.	- Brachioradialis.
E.C.R.B.	- Extensor carpi radialis brevis.
E.C.R.L.	- Extensor carpi radialis longus.
E.O.M.P.	- Tendon of extensor ossis metacarpi pollicis.
F.C.R.	- Flexor carpi radialis.
F.C.R.t.	- Cut tendon of flexor carpi radialis.
F.C.U.	- Flexor carpi ulnaris.
F.C.U.t.	- Cut tendon of flexor carpi ulnaris.
F.Dig.P.	- Flexor digitorum profundus.
F.Dig.P.co.	- Condylar parts of flexor digitorum profundus.
F.Dig.P.r.	- Radialis proprius part of flexor digitorum profundus.
F.Dig.P.u.	- Ulnaris proprius part of flexor digitorum profundus.
F.Dig.S.	- Flexor digitorum superficialis.
I-c.M.	- Interosseous membrane.
Med.Ep.	- Medial epicondyle of humerus.
Pa.L.	- Palmaris longus.
Pi.	- Pisiform bone.
Pr.Q.	- Pronator quadratus.
Pr.T.	- Pronator teres.
R.	- Radius.
Su.	- Supinator.
Tri.Lo.	- Long head of triceps.
Tri.Med.	- Medial head of triceps.
U.	- Ulna.
UL.N.	- Ulnar nerve.

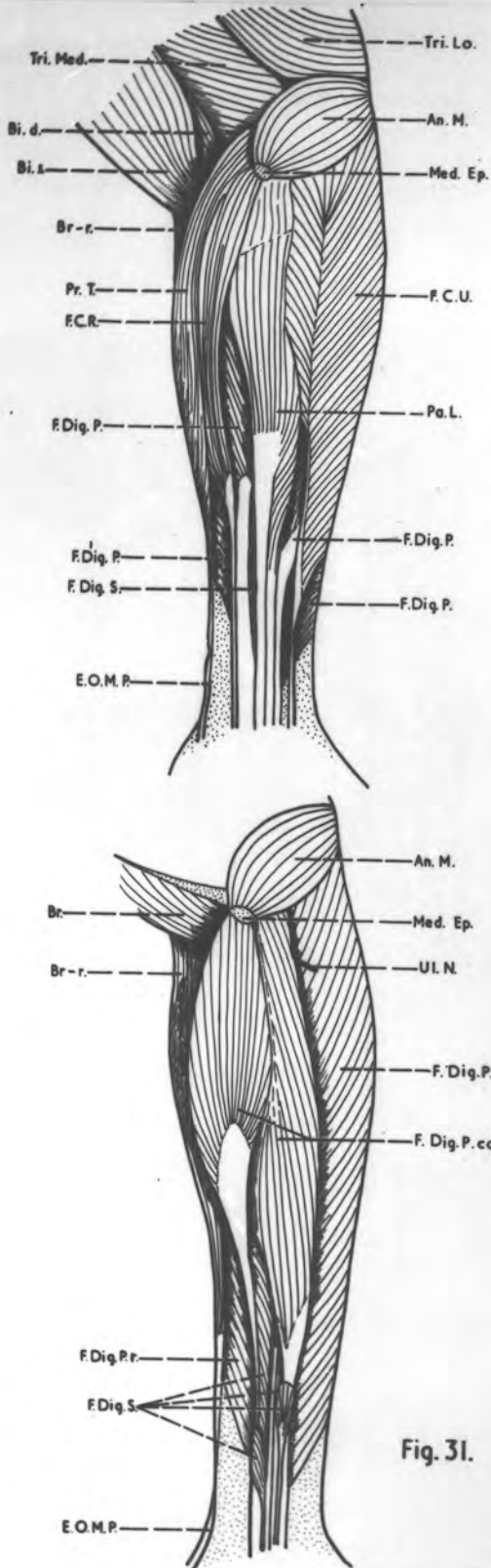


Fig. 30.

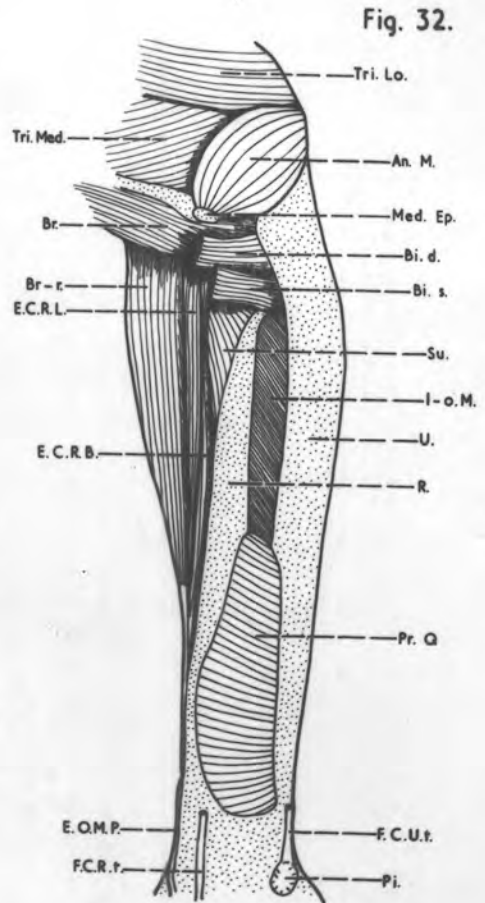
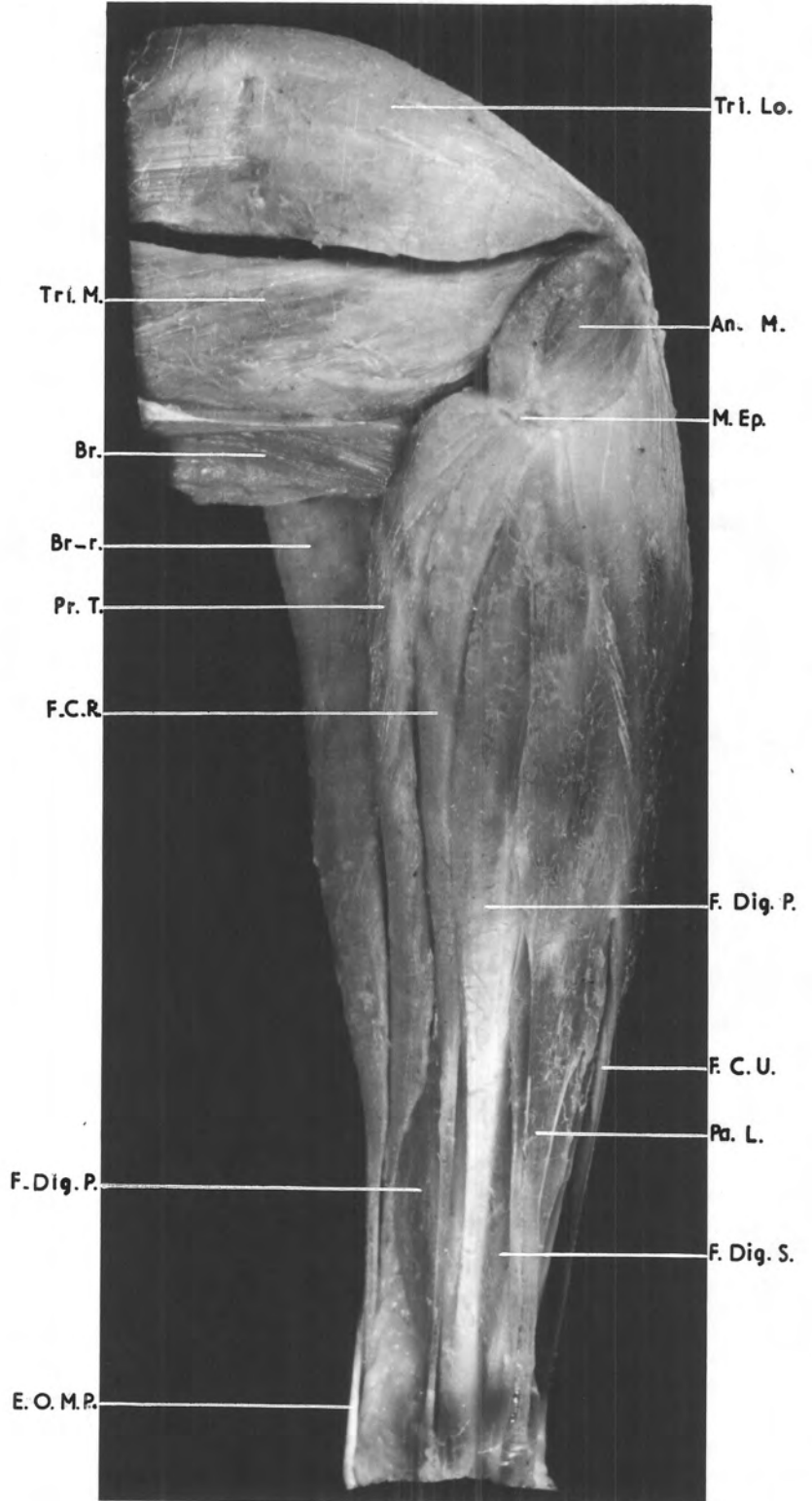


Fig. 32.

Fig. 31.

Plate XX (cf. fig. 30). Superficial view of flexor muscle group of fore-arm. Fore-arm in semi-pronation; biceps brachii and dorso-epitrochlearis are removed. $\times 1\frac{5}{6}$.

- An.M. - Anconeus medialis (epitrochleo-anconeus).
- Br. - Brachialis.
- Br-r. - Brachio-radialis.
- E.O.M.P. - Extensor ossis metacarpi pollicis tendon.
- F.C.R. - Flexor carpi radialis.
- F.C.U. - Flexor carpi ulnaris.
- F.Dig.P. - Flexor digitorum profundus.
- F.Dig.S. - Flexor digitorum superficialis.
- M.Ep. - Medial epicondyle of humerus.
- Pa.L. - Palmaris longus.
- Pr.T. - Pronator teres.
- Tri.Lo. - Long head of triceps.
- Tri.M. - Medial head of triceps.



M. giganteus and M. bennetti (Macalister, 1870) and Hyps. moschatus (Heighway, 1939) the insertion occupies the proximal half or third of the radius, in Phascolomys (Macalister, 1870; Sonntag, 1922) the distal half, in N. typhlops (Wilson, 1894) the distal fourth.

Cunningham (1882) gives the insertion to the whole length of the radius in Ph. maculata, while in Choer. castanotis (Parsons, 1903) and Perameles anurus (Kajava, 1910) the insertion is much more restricted and occupies only a small fraction of the length of the bone proximal to the middle.

Flexor Carpi Radialis (fig. 30; pl. XX) arises from the front of the medial epicondyle of the humerus and the septa on both sides separating it from pronator teres and flexor digitorum profundus respectively. The muscle belly gives rise to a thin tendon that is inserted into the tubercle of the scaphoid and the bases of the second and third metacarpals. Carlsson (1914) gives the insertion to the trapezium (greater multangular) and the second metacarpal. As reported for a number of marsupials by Cunningham (1878a, 1882) Kajava (1910) and Straus (1942) the nerve supply here too comes from the median nerve.

The insertion of this muscle in marsupials usually involves one or two of the first three metacarpal bones, the second being the most commonly included. Often there is also some attachment to the trapezium, or this may be the only bony insertion as in Phase. calura (Cunningham, 1882) and Hyps. moschatus (Heighway, 1939). The only other references to the scaphoid providing part of the insertion

come from Leche (1874-1900) in regard to Myrmecobius and Kajava (1910) who found some attachment to this bone in Thyl. cynocephalus, M. robustus and M. affinis agilis.

Flexor Digitorum Profundus (figs. 30, 31, 36; pls. XX, XXII) is a large and complex muscle and includes the flexor pollicis longus within its structure. It has an extensive origin from the front of the medial epicondyle, the proximal three fourths of the radius and ulna (reaching onto the medial side of the olecranon on the latter) and from the proximal part of the interosseous membrane. From the mass so formed springs a very thick and strong tendon that passes into the palm of the hand and divides into five parts, one for each digit. Each tendon runs through the fibrous flexor sheath of the corresponding finger and is inserted into the terminal phalanx, each having at its insertion a small vinculum breve.

The superficial surface of the muscle has a double bipenniform appearance with fibres converging on both margins of the tendon of insertion which if traced proximally presents a well marked groove on its surface which further up still is converted into an almost completely enclosed tunnel with an aponeurotic lining; this tunnel and groove give origin to the flexor digitorum superficialis. The fibres that run from the central part of the origin towards the sides of the tendon spring from the epicondyle and from a septum or intramuscular tendon shared with the flexor carpi ulnaris and the palmaris longus and presumably represent the condylo-ulnar and condylo-radial parts of Windle (1890). Those fibres that run

inwards towards the edges of the tendon come from the radius and ulna and form some of Windle's (1890) *radialis proprius* and *ulnaris proprius*; the rest of these parts are seen on the deep surface of the muscle where they are continuous with one another and join the central part of the main tendon. The deep surface of the muscle thus shows none of the apparent division into two sections seen on the superficial aspect since here the *radialis proprius* and *ulnaris proprius* are fused where they have origin from the interosseous membrane. Windle's (1890) fifth part, the *centralis*, is also present arising deeply from the condyle and joining the other condylar parts high up. The five parts of the muscle are considerably fused in this species and are not easily defined from one another.

The finding of the *flexor digitorum profundus* and the *flexor pollicis longus* as a single muscle that produces a tendon dividing into five is practically general throughout the Marsupialia. In N. typhlops Wilson (1894) describes the muscle as inserted into the palmar sesamoid from which only three tendons continue on to the index, medius and annularis; Kajava (1910) gives three tendons to these same digits in Per. anurus - as does Owen (1859-1847, 1868) for Per. lagotis - and four tendons only in Thyl. cynocephalus where the tendon to the first digit is the absent one. Young (1882) describes the tendon to the fifth digit in Phase. cinereus arising independently of the main tendon.

The *flexor digitorum profundus* is supplied by both the median

and ulnar nerves, as is the case in the various marsupials noted by Cunningham (1873a, 1882), Kajava (1910) and Straus (1942), the only variation apparently being in the relative amount of the muscle supplied by each nerve. In Pet. xanthopus Parsons (1896) states that there is no supply from the ulnar nerve.

Flexor Digitorum Superficialis (figs. 30, 31, 36; pls. XX, XXII) is a small muscle that gives rise to four very fine tendons for the ulnar four digits. It arises from the tunnel and groove formed by the proximal part of the tendon of insertion of the flexor digitorum profundus and is fairly easily separable into four small fleshy bellies, those giving the middle two tendons coming from further up in the tunnel than the other two which have part of their origin from the sides of the main profundus tendon more distally. The fine tendons of the superficialis run on the surface of the profundus tendon and diverge in the palm towards their respective fingers. Here they lie in the flexor sheaths, splitting to transmit the profundus tendons and being inserted into the middle phalanges in typical fashion: they possess vincula longa (which connect each to the base of the proximal phalanx of its finger from its point of splitting and consist of two parts straddling the profundus tendon) and vincula brevia, and are also adherent to the proximal end of the corresponding flexor sheath. Windle (1890) gives the origin of this muscle only from the condylo-ulnaris portion of the profundus, Bardeleben (1894) says the tendons end mostly in the flexor sheaths, while Carlsson (1914) gives the attachment of the four tendons to

the radial four digits.

The flexor digitorum superficialis shows more variation amongst marsupials than the profundus: it arises from the profundus tendon, from its fleshy part, or with the profundus from the epicondyle itself, as for example in Choer. castanotis (Parsons, 1903) and Phasc. wombata (Macalister, 1870). It usually gives rise to three or four tendons or, in a few species, only two. Wilson (1894) says the muscle is absent in N. typhlops, while from the description of Kajava (1910) it is represented either within the profundus itself or by small tendons coming from the deep surface of the palmaris longus in Per. anurus.

In T. vulpecula I found a branch of the median nerve providing its innervation, thus agreeing with the supply given for a number of other marsupials by Kajava (1910).

Palmaris Longus (fig. 50; pl. XX) is a small muscle arising partly from the fascia over the flexor digitorum profundus which provides an indirect aponeurotic attachment to the medial epicondyle of the humerus, and partly from the intramuscular tendon it shares with the condylo-ulnar part of the flexor profundus and with the flexor carpi ulnaris. The muscle belly divides into two parts, a deep and a superficial, the former remaining fleshy to a somewhat lower level than the latter, and these in turn provide two tendons of insertion for the muscle, the deeper one lying slightly ulnar to the superficial. The superficial tendon is adherent to the flexor retinaculum, sends expansions to the palmar sesamoid ("praepollex"

of Bardeleben, 1894) on the radial side and to the pisiform on the ulnar side, and then passes into the palmar fascia where it soon becomes inseparable from the skin. The deeper one runs through the ulnar part of the retinaculum and is inserted into the fascia on the ulnar side of the palm. In one specimen (No. 5) the muscle also gave rise to two more tendons, both extremely minute, one on either side of the muscle, that were lost in the fascia at the wrist; they suggested a partial regression to a state of affairs where this muscle constituted a third and most superficial digital flexor.

The basic account given here differs little from that of Bardeleben (1894) who, however, describes the palmaris longus as two separate muscles. Carlsson (1914) mentions no second tendon and managed to trace fibres through the palmar fascia to the middle three fingers.

In some marsupials there is only one tendon to this muscle; the presence of two tendons or a bifurcating tendon seems to be the commoner condition, however, having been reported in Caenolestes (Osgood, 1921), Didelphys (Bardeleben, 1894; Kajava, 1910), Thylacinus, Dasyurus, Myrmecobius, Perameles and in one example of Phascolarctos (Kajava, 1910). In Ph. maculata (Cunningham, 1882) and Ph. orientalis (Kajava, 1910) the muscle has three parts. Parsons (1905) says the muscle is absent in Choer. castanotis, as does Wilson (1894) for N. typhlops. Haughton (1866) mentions a peculiar insertion into the flexor digitorum profundus tendon in the palm in the opossum.

In T. vulpecula the palmaris longus appears to be supplied only by the ulnar nerve, I could trace branches of the median through the flexor digitorum profundus very close to it but not actually into it. Innervation from the ulnar nerve alone has also been given for Macropus (Bardleben, 1894; Kajava, 1910), Didelphys (Kajava, 1910; Straus, 1942) and Perameles (Kajava, 1910); the last author gives supply from both median and ulnar nerves in Dasyurus, Phascolarctos and Phalanger.

Flexor Carpi Ulnaris (fig. 30; pl. XX) is a bipenniform muscle at its origin, this feature being most easily seen on the deep surface. The fibres of one side come from the medial epicondyle of the humerus and the intramuscular tendon that it shares with the flexor digitorum profundus and the palmaris longus, the others from the proximal three fourths of the posterior border of the ulna, the olecranon and the fibrous arch that connects the latter to the medial epicondyle and lies adjacent to the distal edge of the epitrochleo-anconeus. The tendon that emerges from the muscle, appearing first along its radial border, is inserted into the pisiform bone. The muscle is supplied as usual by the ulnar nerve.

The insertion of this muscle to the pisiform is constant in marsupials; in some cases it extends to nearby ligaments as well. The origin varies principally in the amount of the length of the ulna that it occupies; the fibrous bridge from the epicondyle to the olecranon is not always mentioned in accounts of marsupial myology and Wilson (1894) specifically records its absence in N. typhlops.

Macalister (1870) notes that there is no condylar origin in the great kangaroo or the wallaby. Parsons (1905) found the muscle wanting in Choer. castanotis.

Pronator Quadratus (fig. 52) is found in approximately the distal half of the fore-arm (Carlsson, 1914, gives two thirds), its fibres passing more or less transversely from the ulna to the radius but radiating slightly so that the muscle extends a little more proximally on the latter bone. It is supplied from the median nerve by a branch that runs on its superficial surface and which sometimes passes through the radialis proprius part of the flexor digitorum profundus.

The pronator quadratus varies a good deal in the fraction of the fore-arm that it occupies, a portion similar to that given here for Trichosurus being found also in Chironectes (Sidebotham, 1885), Phascolumys (Sonntag, 1922) and Sarcophilus (Macalister, 1870). In other marsupials it may occupy as little as the lower fifth or less, as in Phascolarctos (Macalister, 1872b; Young, 1882; Sonntag, 1922), Phalanger and Pseudochirus (Sonntag, 1922), or as much as the distal three fourths or even more, as in Perameles (Owen, 1859-1847, 1868), Hypsiprymnodon (Heighway, 1939) and Macropus (Haughton, 1866; Macalister, 1870), always, however, having its distal limit approaching the wrist. It is said to be absent in Caenolestes (Osgood, 1921) and Notoryctes (Wilson, 1894).

5). Extensor muscle group of the fore-arm.

Brachio-radialis (Supinator Longus)(figs. 52, 53, 55; pls. XX, XXI),

Figure 33 (cf. pl. XXI). Extensor muscle group of fore-arm. x1.

Figure 34 (cf. pl. XXI). Extensor tendons on dorsum of hand. $x1\frac{3}{4}$.

Figure 35. Extensor muscle group of fore-arm after the removal of extensor digitorum communis, extensor digiti minimi and extensor carpi ulnaris. A small part of the lateral head of triceps near its insertion is also cut away. x1.

- | | |
|------------|---|
| Ab.D.M. | - Abductor digiti minimi. |
| An.L. | - Anconeus lateralis. |
| Br-r. | - Brachioradialis. |
| E.C.R.B. | - Extensor carpi radialis brevis. |
| E.C.R.B.d. | - Deep origin of extensor carpi radialis brevis
from surface of supinator. |
| E.C.R.L. | - Extensor carpi radialis longus. |
| E.C.U. | - Extensor carpi ulnaris. |
| E.D.C. | - Extensor digitorum communis. |
| E.D.M. | - Extensor digiti minimi. |
| E.D.Pr. | - Extensor digitorum profundus. |
| E.O.M.P. | - Extensor ossis metacarpi pollicis. |
| H.R. | - Head of radius. |
| L.Ep. | - Lateral epicondyle of humerus. |
| Ol. | - Olecranon. |
| Su. | - Supinator. |

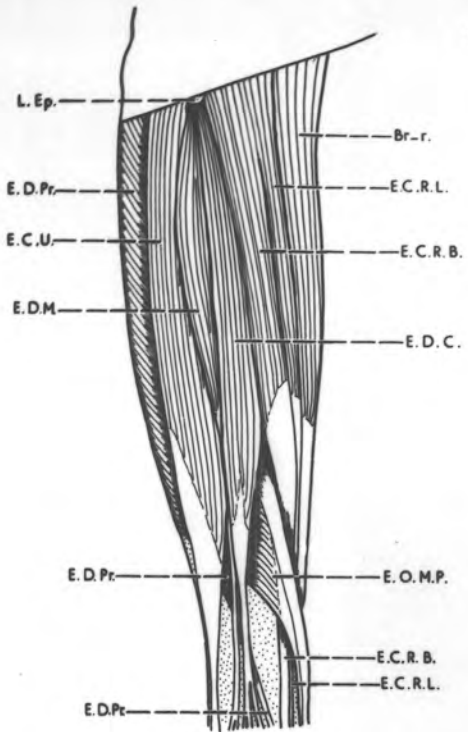


Fig. 33.

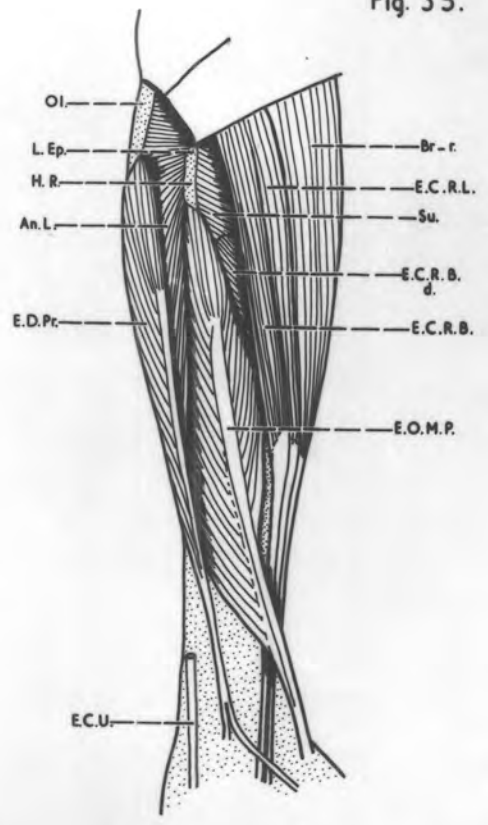


Fig. 35.

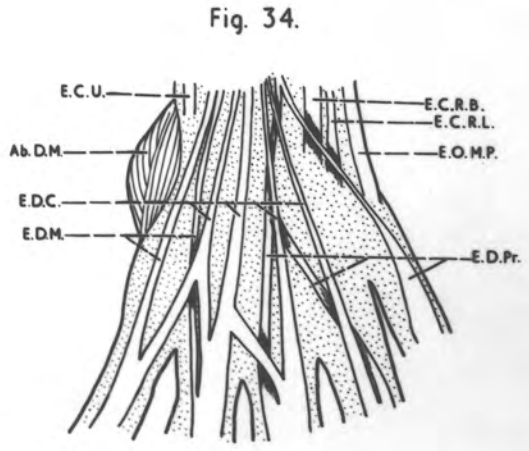
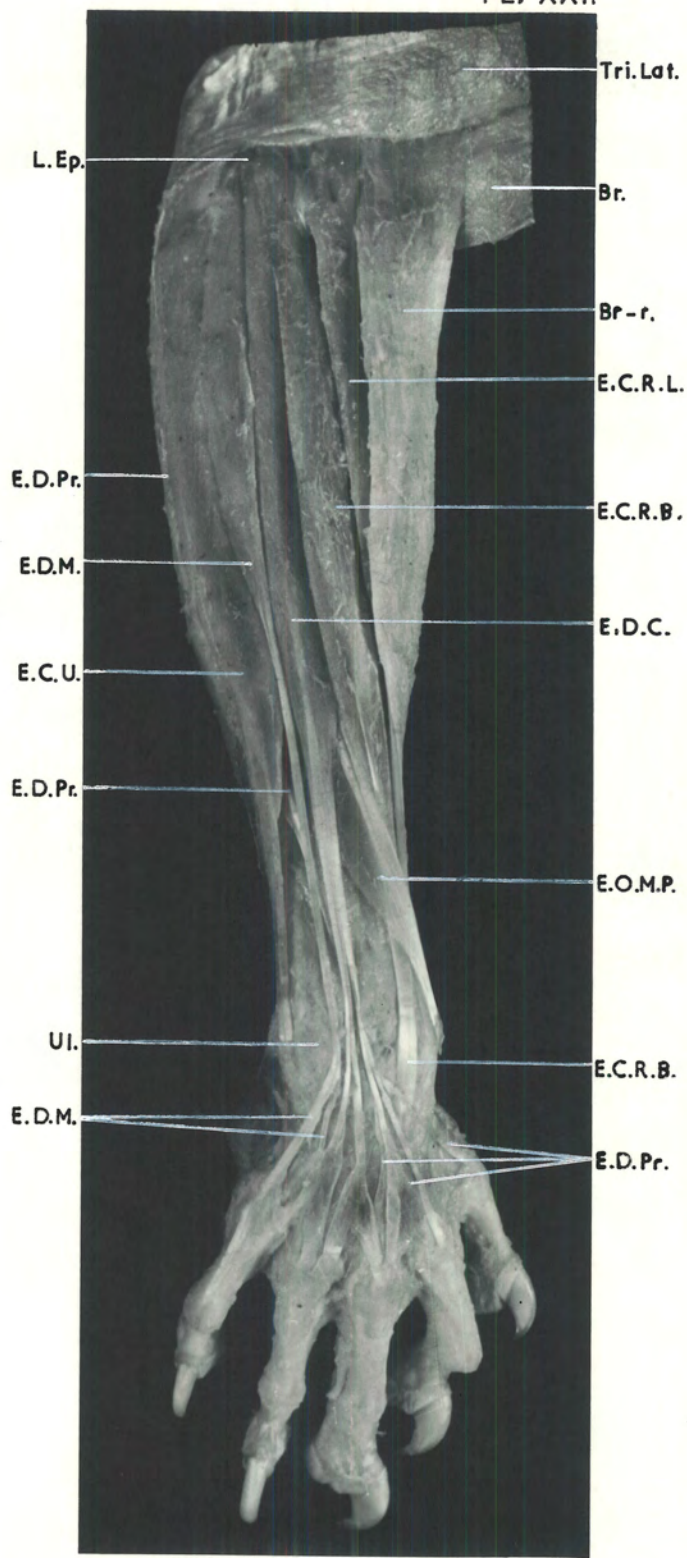


Fig. 34.

Plate XXI (cf. figs. 33, 34). Superficial view of extensor muscle group of fore-arm and hand. Fore-arm in semi-pronation; biceps brachii is removed. $\times 1\frac{1}{2}$.

- Br. - Brachialis.
- Br-r. - Brachio-radialis.
- E.C.R.B. - Extensor carpi radialis brevis.
- E.C.R.L. - Extensor carpi radialis longus.
- E.C.U. - Extensor carpi ulnaris.
- E.D.C. - Extensor digitorum communis.
- E.D.M. - Extensor digiti minimi.
- E.D.Pr. - Extensor digitorum profundus.
- E.O.M.P. - Extensor ossis metacarpi pollicis.
- L.Ep. - Lateral epicondyle of humerus.
- Tri.Lat. - Lateral head of triceps.
- Ul. - Dorsum of distal end of ulna.



L. Ep.

E. D. Pr.

E. D. M.

E. C. U.

E. D. Pr.

U. I.

E. D. M.

Tri. Lat.

Br.

Br-r.

E. C. R. L.

E. C. R. B.

E. D. C.

E. O. M. P.

E. C. R. B.

E. D. Pr.

a reasonably well developed muscle, arises from the proximal half of the lateral supracondylar ridge of the humerus where it is fused with the extensor carpi radialis longus. The tendon that passes from the muscle more than two thirds of the way down the fore-arm is inserted into the dorsal aspect of the scaphoid bone. These attachments agree with those given by Bardeleben (1894), though he also mentions some doubtful insertion into the "praepollex". The muscle is supplied by the radial nerve.

The insertion of this muscle shows great variation amongst marsupials, though part or the whole of the distal attachment to the scaphoid or scapho-lunar seems to be the commonest finding, occurring in Das. viverrinus (MacCormick, 1887), Dend. dorianus (Carlsson, 1914), Pet. xanthopus (Parsons, 1896), one example of M. rufus examined by Windle and Parsons (1897b), Phasc. calura, Ph. maculata (Cunningham, 1882), Phasc. cinereus (Macalister, 1872b; Young, 1882; Sonntag, 1922) and Did. virginiana (Haines, 1939). Other attachments noted include the distal end of the radius, the trapezium, the first or second metacarpal or both, and the ligaments of the wrist. In Phasc. cinereus the origin reaches as far proximally as the neck of the humerus (Young, 1882; Sonntag, 1922). Macalister (1872a) and Wilson (1894) say the muscle is absent in S. ursinus and N. typhlops respectively.

Extensor Carpi Radialis Longus (figs. 52, 53, 54, 55; pl. XXI) is connected with the brevis at its origin but very soon becomes separate. It arises from the distal part of the lateral supra-

condylar ridge of the humerus, from the bone in front of this and from the septum separating it from the extensor carpi radialis brevis, and is inserted by tendon into the dorso-radial aspect of the proximal end of the shaft of the second metacarpal bone.

Extensor Carpi Radialis Brevis (figs. 32, 33, 34, 35; pl. XXI)

extends from its origin in common with the longus to be inserted by tendon into the dorso-radial aspect of the third metacarpal at the junction of the base with the shaft. The muscle also receives a considerable fleshy or partly tendinous slip from the supinator which lies deep to it in the proximal part of the fore-arm.

Both the extensor carpi radialis longus and brevis are supplied by the same branch of the radial nerve.

These two muscles seem to have this typical arrangement in most marsupials, in some cases the muscles are fused but the insertion to both metacarpals shows that both are represented. In Das. viverrinus (MacCormick, 1887), Choer. castanotis (Parsons, 1905) and N. typhlops (Wilson, 1894) only one muscle is present inserted into the third metacarpal and hence apparently representing only the brevis, while in Caenolestes (Osgood, 1921) the two muscles are inserted into one of the phalanges of the corresponding fingers instead of the metacarpal bones.

The only other account of anything similar to the slip that I noted from the supinator to the brevis is in that given of this muscle in Ph. maculata by Cunningham (1882) where he describes some of the origin from the posterior border of the radius and a

tendinous expansion on the supinator.

Extensor Digitorum Communis (figs. 33, 34; pl. XXI) arises from the lateral epicondyle of the humerus and from the intermuscular septa separating it from the extensor carpi radialis brevis and the extensor digiti minimi; the muscle gives rise to four tendons that pass through a deep tunnel on the dorsum of the wrist and then spread out on the back of the hand. The first of these tendons goes to the index and in one limb examined gave a small slip to the medius; the second tendon goes to the medius; the third goes to the annularis with a large slip to the medius, and the fourth almost equally to the annularis and the minimus. On the dorsal aspects of the fingers the tendons are joined by others (e.g. extensor digiti minimi, extensor digitorum profundus, lumbricals, flexores breves, interossei, abductor digiti minimi) and broaden out into the extensor expansions that are inserted into the middle and distal phalanges of the fingers but do not divide into the central and collateral slips seen in the human hand, the deeper fibres attach to the middle phalanx and the more superficial ones simply pass over to the distal bone. The muscle is supplied by the radial nerve.

This muscle is typically distributed to the ulnar four digits in marsupials, usually after forming four tendons originally, but in Thyl. cynocephalus (Cunningham, 1832) and Chir. variegatus (Sidebotham, 1885) after initially forming only three. In Phase. cinereus it sends tendons to all five digits (Young, 1882; Sonntag, 1922), in Choer. castanotis (Parsons, 1905) and N. typhlops (Wilson,

1894) to the medius and annularis only, these animals having a very modified manus.

Extensor Digiti Minimi (Extensor Digitorum Secundus, Lateralis, Ulnaris) (figs. 53, 54; pl. XXI) is a comparatively small muscle arising from the lateral epicondyle and from the septa between it and the adjacent muscles, viz. extensor digitorum communis and extensor carpi ulnaris. It gives rise to two small tendons, one going to the fifth digit (this one was duplicated in one animal examined), the other passing deep to the tendon of the extensor digitorum communis to the minimus and then dividing into two slips for the fourth and fifth digits; in either case the slips join the extensor expansions. This muscle too is supplied by the radial nerve.

Here again Trichosurus shows what appears to be the commonest distribution of this muscle in marsupials, to the fourth and fifth digits. It has been found going to the third digit as well in some examples, but not all, of Phasc. cinereus (Macalister, 1872b; Young, 1882; Sonntag, 1922) and S. ursinus (Macalister, 1870, 1872a), and also in M. vallaensis (Haughton, 1866) and Did. virginiana (Haines, 1939), though Coues (1873) gives fourth and fifth or fourth only for the last species. Leche (1874-1900) gives insertion to the fifth finger only in Myrmecobius and Hypsiprymnus. The muscle is absent in N. typhlops (Wilson, 1894).

Extensor Digitorum Profundus (figs. 53, 54, 55; pl. XXI) apparently includes the extensor indicis and the extensor pollicis longus of

human anatomy. It arises from the proximal half of the posterior border of the ulna and the lower half of the olecranon, and, although it is one of the deep muscles of this region of the forearm, at its origin it lies superficially medial to all the other muscles of the group. The muscle passes distally and radially deep to the extensor carpi ulnaris and extensor digiti minimi and, in the hand, to the extensor digitorum communis, and gives rise to two tendons - one of these, which first appears high up on the radial border of the muscle, passes to the pollex and is inserted into the bases of both its phalanges (mainly the distal one), the other forms lower down and divides into two parts that go to the extensor expansions of the second and third digits and, in one animal, the fourth also.

The extensor pollicis longus is fused with the extensor indicis in most marsupials but is described as a separate muscle (extensor secundi internodii pollicis) by MacCormick (1887) in Das. viverrinus, by Macalister (1870) in S. ursinus and Phasc. wombata (where the extensor indicis is absent) and by Cunningham (1882) for Ph. maculata (where the "extensor indicis" goes only to the medius). In other cases the muscle usually sends tendons to the first two or three digits. The muscle is not represented in Phasc. cinereus (Young, 1882; Sonntag, 1922).

Like all the other muscles of the extensor group the extensor digitorum profundus is supplied by the radial nerve.

Extensor Ossis Metacarpi Pollicis (figs. 33, 34, 35; pl. XXI)

represents the abductor pollicis longus with the extensor pollicis brevis incorporated within it. Its origin is from the dorsal surfaces of the proximal half of the radius and two thirds of the ulna and the intervening interosseous membrane which is very thin. It is inserted by tendon into the base of the first metacarpal on its radial side. This insertion is also found in Das. viverrinus (MacCormick, 1887), N. typhlops (Wilson, 1894), Caenolestes (Osgood, 1921) and Chir. variegatus (Sidebotham, 1885). In many marsupials it also gives a slip to the trapezium; Leche (1874-1900) gives the whole insertion to the trapezium in Myrmecobius.

Extensor Carpi Ulnaris (figs. 53, 54; pl. XXI) takes origin from the lateral epicondyle of the humerus, from the septum joining it to the extensor digiti minimi and from the fascia over the anconeus lateralis. Its tendon begins, as Carlsson (1914) mentions, about two thirds of the way down the fore-arm and runs to the ulnar side of the hand where it gives off from its ventral border a thin expansion to the pisiform, the hook of the hamate and the pisohamate ligament, and then passes to its main attachment to the palmar surface of the base of the fifth metacarpal bone. As well as this insertion, however, there is also a part of the tendon passing radially, projecting into the palmar part of the joint between the fifth metacarpal and the hamate, and finding attachment to the palmar aspects of the bases of the second, third and fourth metacarpal bones. The standard insertion of this muscle in marsupials is into the fifth metacarpal only, I have found no other accounts of



attachment to other metacarpal bases such as I noted here; Bardeleben (1894) does mention some insertion into the volar ligaments in Did. marsupialis, while Cunningham (1882) gives some insertion into the unciform in Thyl. cynocephalus and Phasc. calura. Supinator (Brevis)(figs. 32, 55) passes from the lateral epicondyle of the humerus and the lateral part of the capsule of the elbow to the proximal third of the lateral surface of the radius. The continuation of the radial nerve into the back of the fore-arm runs deep to the muscle and supplies it.

The insertion of this muscle occupies about a quarter or a third of the radius in most marsupials reported, the variation recorded being from less than one fifth in Ph. orientalis (Sonntag, 1922), Ph. maculata, Thyl. cynocephalus and Phasc. calura (Cunningham, 1882) up to three fifths in N. typhlops (Wilson, 1894) and two thirds in Phascolumys (Macalister, 1870; Sonntag, 1922).

6). Intrinsic muscles of the hand.

Although the morphological significance of the arrangement of the muscles given by Cunningham (1882) has been disputed (Campbell, 1959) and other patterns for the palmar musculature have been given (McMurrich, 1905; Howell, 1956; Straus, 1946) Cunningham's plan still provides a useful grouping of the muscles for purposes of description, and I propose to use it with two modifications in the light of the more recent articles - viz. the description of the *abductores pollicis et digiti minimi* separately from the *interossei*, and the inclusion of the *lumbricals* in the field of the intrinsic

palmar musculature.

Lumbricals (fig. 36; pl. XXII). There were four of these muscles in all the hands I examined; they take origin from the adjacent sides of the flexor profundus tendons and from the palmar surface of the main tendon before it divides, the origin of the first lumbrical (i.e. the radial one), which is the smallest, extending furthest proximally along the tendon, in two animals reaching above the wrist. They pass to the radial sides of the ulnar four digits where they are partly inserted into the extensor expansion on the head of the first phalanx and also attach to the base of the middle phalanx. In one specimen (No. 2) the fourth muscle gave a slip to the ulnar side of the fourth digit as well as to the radial side of the fifth. Both Bardeleben (1894) and Carlsson (1914) also found four lumbricals in this species.

Four seems to be the commonest number of lumbricals to be found in marsupials although the number is reduced to three in several. In Phasc. cinereus there are only two (Young, 1882; Kajava, 1910); Parsons (1903) found only one in Choer. castanotis, and in N. typhlops Wilson (1894) did not find any. On the other hand Kajava (1910) found up to eight in M. robustus, the extra ones formed by splitting of the basic muscles so that they are inserted into both sides of the inter-digital space in a similar way to the fourth lumbrical I found in one animal (v.s.). Bardeleben (1894) also found eight in Did. marsupialis: here too, as in some cases where there are only four, some were inserted on the ulnar side of their

Figure 36 (cf. pl. XXII). Superficial muscles of palm. $\times 2\frac{1}{4}$.

Figure 37 (cf. pl. XXIII). Palmar musculature as seen after the removal of the long flexor tendons and lumbricals. $\times 2\frac{1}{4}$.

Figure 38 (cf. pl. XXIV). Flexores breves of middle three digits after the removal of all other intrinsic muscles except the interossei. $\times 2\frac{1}{4}$.

Figure 39 (cf. pl. XXV). Interossei of hand after the removal of all other intrinsic muscles. $\times 2\frac{1}{4}$.

Ab.D.M.	- Abductor digiti minimi.
Ab.P.	- Abductor pollicis.
Ac.4.	- Extra head of flexor annularis brevis from hook of hamate.
Ad.P.	- Adductor pollicis.
Ad.2,4,5.	- Adductors of second, fourth and fifth digits.
Arch.	- Arch of insertion of interosseous muscle.
E.O.M.P.	- Tendon of extensor ossis metacarpi pollicis.
F.B.1.	- Flexor pollicis brevis.
F.B.2,3,4.	- Flexores breves of middle three digits.
F.B.5.	- Flexor digiti minimi brevis.
F.C.R.	- Tendon of flexor carpi radialis.
F.C.U.	- Tendon of flexor carpi ulnaris.
F.Dig.P.	- Tendons of flexor digitorum profundus.
F.Dig.S.	- Tendons of flexor digitorum superficialis.
F.Ret.	- Flexor retinaculum.
H.H.	- Hook of hamate.
Int.1,2,3,4.	- Interosseous muscles.
L.F.T.	- Long flexor tendons.
L.1,2,3,4.	- Lumbrical muscles.
M-c.1,2,3,4,5.	- Metacarpal bones.
Pi.	- Pisiform bone.
r.	- Adductor raphe.
1 Trans.	- Transverse slip between 2nd and 4th digits.
2 Trans.	- Transverse slip between 2nd and 5th digits.

Fig. 36.

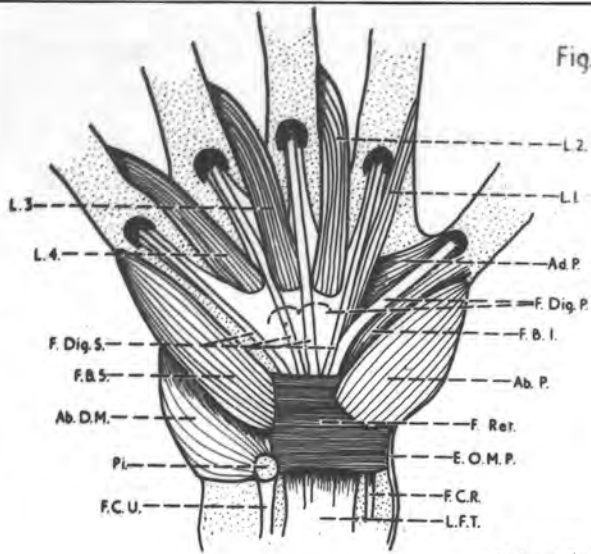


Fig. 37.

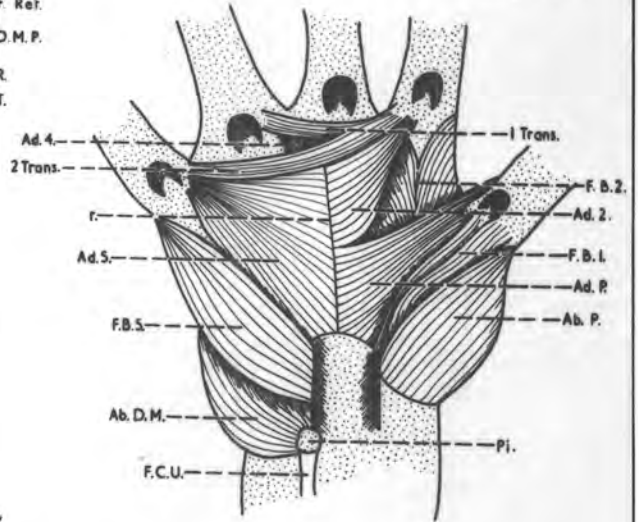


Fig. 38.

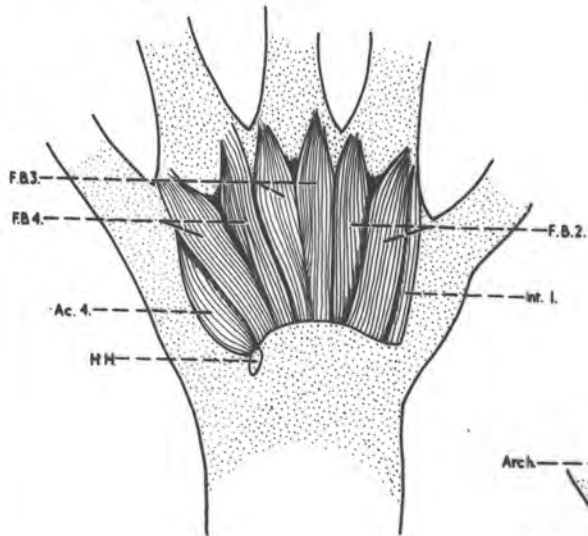


Fig. 39.

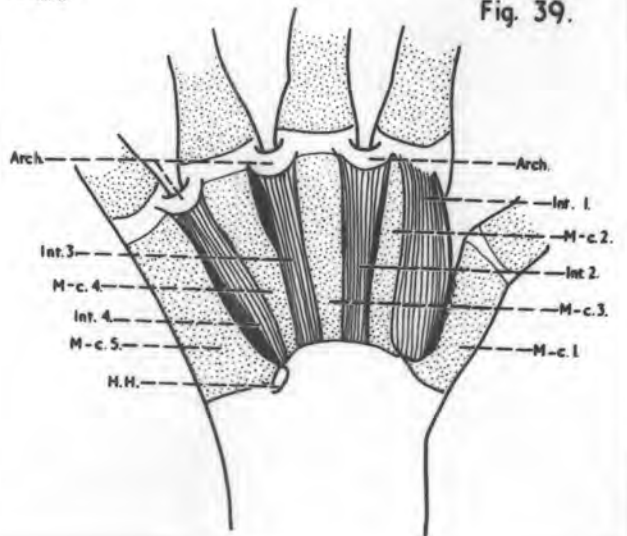
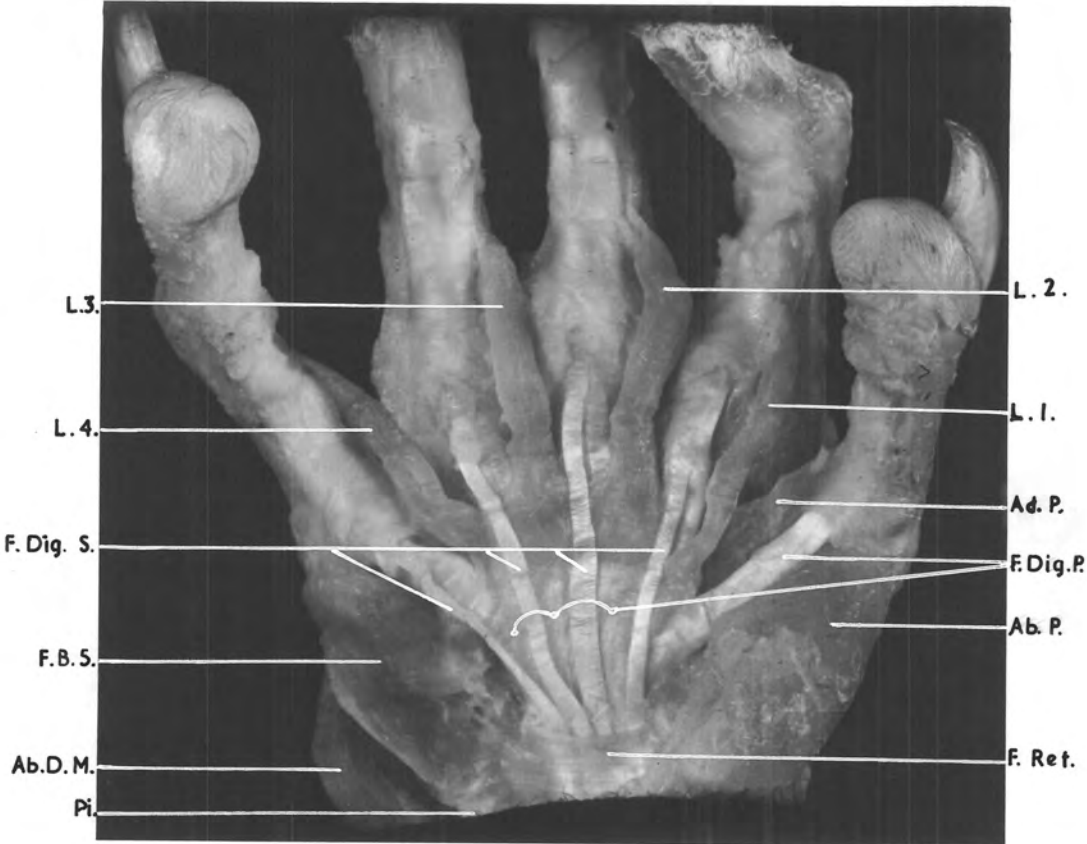


Plate XXII (cf. fig. 36). Superficial muscles of palm. $x3\frac{1}{2}$.

- Ab.D.M. - Abductor digiti minimi.
Ab.P. - Abductor pollicis.
Ad.P. - Adductor pollicis.
F.B.5. - Flexor digiti minimi brevis.
F.Dig.P. - Tendons of flexor digitorum profundus.
F.Dig.S. - Tendons of flexor digitorum superficialis.
F.Ret. - Flexor retinaculum.
L.1,2,3,4. - Lumbricals.
Pi. - Pisiform bone.



digits instead of on the radial side as usual. Partial origin of one or more lumbricals from far up along the flexor digitorum profundus tendon has also been reported by Kajava (1910) in Phalanger, Didelphys and Perameles.

Some of the nerves to these muscles are so small that they are difficult to distinguish from fascial strands but it appears that the first three are supplied by the median nerve, the fourth or ulnar one by the deep branch of the ulnar nerve. This corresponds to the supply given for Didelphys and Thylacinus and the partial supply given for Myrmecobius and Phalanger, in all of which there are four muscles arranged similarly, by Kajava (1910). In the other examples given by this investigator the muscles between the fourth and fifth digit tendons are always supplied by the ulnar nerve, the others by the median - a more general rule by which the instances given above also abide; in Macropus he gives some supply from the ulnar nerve to those muscles between the third and fourth digit tendons as well. In Thylacinus and Phalangista, however, Cunningham (1878a, 1882) gives the supply to all four muscles from the median nerve.

Abductor Pollicis (figs. 56, 57; pls. XXII, XXIII) takes origin from the trapezium, the flexor retinaculum and the palmar sesamoid plate and is inserted into the radial side of the base of the proximal phalanx of the pollex; it is hard to separate along its lateral border from the underlying radial head of the flexor pollicis brevis.

Abductor Digiti Minimi (figs. 54, 56, 57; pls. XXII, XXIII) arises from the flexor retinaculum and the pisiform bone and is inserted into the ulnar side of the base of the proximal phalanx of the fifth digit and slightly into the extensor expansion. At its insertion it fuses with the flexor digiti minimi brevis.

As in a number of marsupials reported by Kajava (1910), the abductor pollicis is supplied from the median nerve, the abductor digiti minimi from the ulnar.

These two abductor muscles are represented in most marsupials though Wilson (1894) indicates that the abductor digiti minimi is absent in N. typhlops, and Parsons (1905) gives both absent in Choer. castanotis.

Adductores (fig. 57; pl. XXIII). There appear to be typically four of these although that to the annularis is very small and in one animal was absent. As a group they arise from the fascia on the palmar surface of the carpal bones and from a raphe extending distally from the carpus along the line of the third metacarpal bone as far as the metacarpo-phalangeal joint.

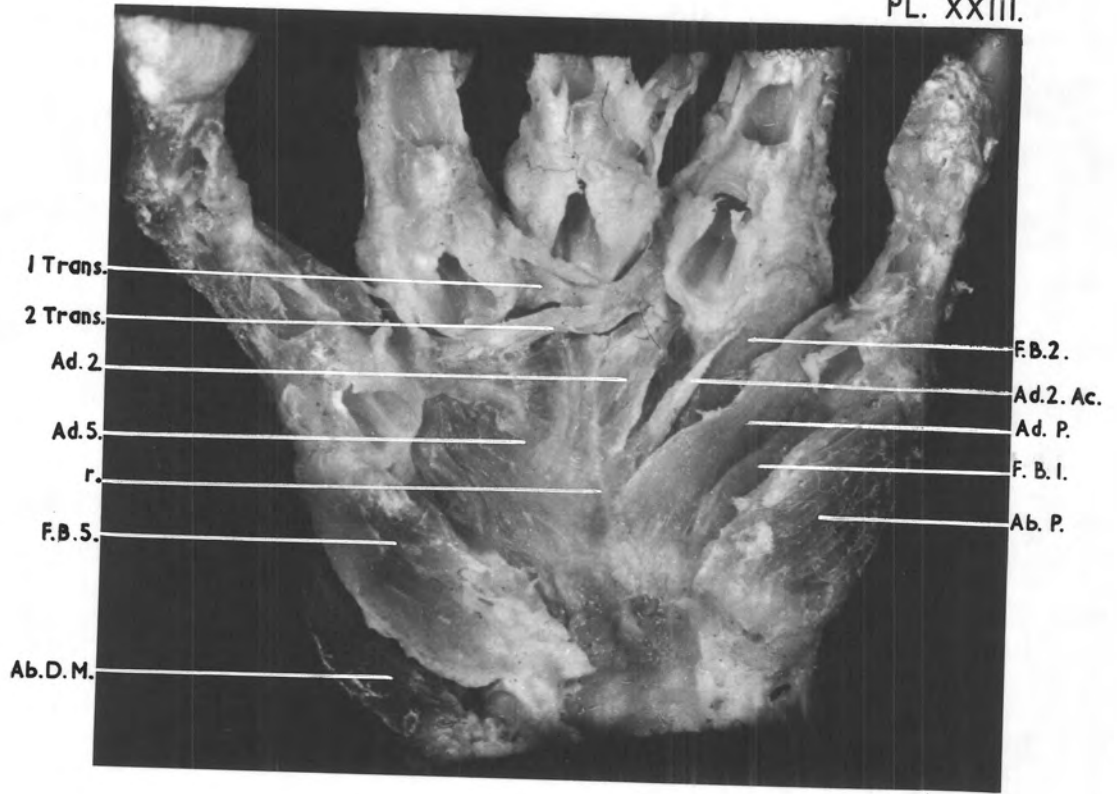
The adductor pollicis springs from the palmar fascia and from considerably less than the proximal half of the radial side of the raphe. It is inserted into the ulnar side of the base of the proximal phalanx of the pollex.

The adductor indicis has its origin from the distal part of the radial side of the raphe, being overlapped to a slight extent by the last muscle. It passes to the ulnar side of the base of the

Plate XXIII (cf. fig. 37). Adductor layer of palmar musculature.

Long flexor tendons and lumbricals are removed. $\times 3\frac{3}{4}$.

- Ab.D.M. - Abductor digiti minimi.
- Ab.P. - Abductor pollicis.
- Ad.P. - Adductor pollicis.
- Ad.2. - Adductor indicis.
- Ad.2.Ac. - Accessory slip of adductor indicis going to
radial side of digit.
- Ad.5. - Adductor digiti minimi.
- F.B.1. - Flexor pollicis brevis.
- F.B.2. - Flexor indicis brevis.
- F.B.5. - Flexor digiti minimi brevis.
- r. - Adductor raphe.
- 1 Trans. - Transverse slip between 2nd and 4th digits.
- 2 Trans. - Transverse slip between 2nd and 5th digits.



proximal phalanx of the index, in one animal (No. 4) also sending a small slip to the radial side of the same phalanx.

The adductor digiti minimi is the largest of the group, arising from the whole of the ulnar side of the raphe and from the carpal fascia as far as the hook of the hamate, and having its insertion on the radial side of the base of the proximal phalanx of the fifth digit.

The adductor annularis is a very small slip arising from the distal end of the ulnar side of the raphe deep to the last muscle and inserted on the radial side of the base of the first phalanx of the annularis.

The adductor sheet also includes a slip of muscle that passes transversely from the ulnar side of the base of the first phalanx of the index towards the ulnar side of the palm where it divides into two slips attaching to the radial sides of the bases of the proximal phalanges of the fourth and fifth digits; in one animal only the slip to the fourth finger was present. The only other account I have found of a slip of muscle similar to this is in the description of the muscles of Ph. maculata by Cunningham (1873b, 1882) where it is given as connecting the index and the annularis only. Kajava (1910) also describes a transverse slip from the index to the fifth finger in Ph. orientalis, but this is divided by a tendinous intersection looking like a separated part of the raphe and so differs slightly from the one I have described here.

Four adductors are usually present in the hands of marsupials,

the number sometimes being reduced to three by the absence of that of the pollex or annularis, more commonly the latter. They are said to be totally absent in Choer. castanotis (Parsons, 1905) and N. typhlops (Wilson, 1894), while Kajava (1910) and Leche (1874-1900) found only one distinctly in Myrmecobius (that of the fifth digit) the rest being intimately fused with the short flexors. Sidebotham (1885) describes five in Chir. variegatus, the extra one going to the radial side of the medius. Young (1880) gives the axis of action in Phascolarctos as the midline of the fourth digit instead of the third as is usual; the same author describes a slip of the adductor digiti minimi to the ulnar side of the annularis in a specimen of Phascolarctos that sounds reminiscent of the extra slip of the adductor indicis I found going to the radial side of its digit in Trichosurus.

Although the raphe noted here is absent in many marsupials it has been frequently described, e.g. in Aepyprymus and Petrogale (Carlsson, 1914), Phalangista (Cunningham, 1878b, 1882), Didelphys (Young, 1880; Kajava, 1910; Coues, 1872), Halmaturus (Young, 1880) and Phascolarctos (Young, 1882; Kajava, 1910) as well as Macropus, Phalanger and Thylacinus (Kajava, 1910). In all these cases it is in the line of the third metacarpal; Young (1880) describes a raphe over the second metacarpal in Phascolomys.

Campbell (1939) points out that these adductors are not the homologues of the palmar interossei of higher mammals, the latter being derivatives of the deep short flexors.

I found all the adductors to be supplied by the ulnar nerve, a finding in agreement with the supply given for several marsupials by Kajava (1910) who in one example of Phascolarctos found a branch from the median partly supplying the adductor pollicis. Parsons (1896) gives the whole supply in Pet. xanthopus, also, from the ulnar nerve.

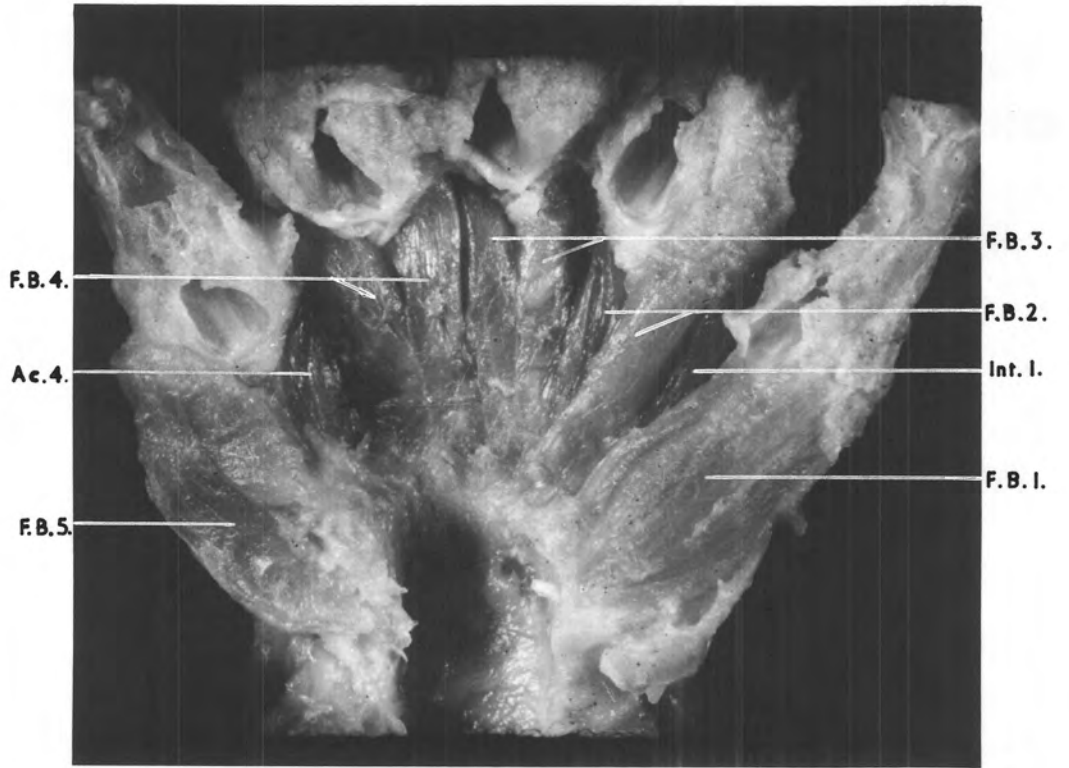
Flexores Breves (figs. 56, 57, 58; pls. XXII, XXIII, XXIV). Five muscles will be described under this head: the only short flexor of the fifth digit lies superficial to the deep branch of the ulnar nerve and appears to be more closely related morphologically to the abductor of this finger than to the deep flexors of the adjacent digits; functionally, however, it is a flexor so is here included in this group.

The flexor pollicis brevis is largely deep to the abductor and has two heads that remain separate throughout. It arises from the strong fascia over the palmar surface of the trapezium and trapezoid just deep to the distal edge of the flexor retinaculum, the two heads being inserted into the two sides of the base of the first phalanx of the pollex. The ulnar head is slightly the smaller and has its origin mainly from the region of the trapezoid bone.

The flexor digiti minimi brevis lies radial to the abductor of this digit; it has its origin from the hook of the hamate and from the medial end of the superficial surface of the flexor retinaculum and passes to an insertion on the ulnar side of the base of the proximal phalanx of the fifth digit where it also has some attach-

Plate XXIV (cf. figs. 37, 38). Flexores breves of hand. Long flexor tendons, lumbricals, abductors and adductors are removed. $x4\frac{1}{2}$.

- Ac.4. - Extra head of flexor annularis brevis
from hook of hamate.
- F.B.1,2,3,4,5. - Flexores breves.
- Int.1. - First interosseous muscle.



ment to the extensor expansion on the dorsum. A small bundle of fibres more or less separate from its deep surface extends from the hook of the hamate to the neck of the fifth metacarpal bone and apparently represents the opponens digiti minimi.

The flexores breves of the middle three digits arise from the palmar ligaments of the corresponding carpo-metacarpal joints, that of the annularis having an extra head of origin on its ulnar side from the hook of the hamate. Each muscle soon divides into two parts that are inserted into the sides of the base of the first phalanx of the respective finger, this insertion being mainly indirect through the palmar ligament of the metacarpo-phalangeal joint, and also sending an extension dorsally to join the extensor expansion.

The account given by Cunningham (1873b, 1882) of these muscles agrees on the presence of an opponens digiti minimi and the absence of a radial head of the flexor digiti minimi brevis, on the other hand he reports only a radial head for the flexor pollicis brevis and found some fibres of this attaching to the metacarpal possibly representing an opponens pollicis. The flexor pollicis brevis and the flexor digiti minimi brevis are occasionally wanting their ulnar and radial heads respectively in other marsupials reported in the literature.

The nerve supply of the flexor pollicis brevis showed some variation in different specimens, the others are all supplied by the ulnar nerve. The flexor pollicis brevis derives the innervation for

its radial head from the median nerve, that for the ulnar head from either the median or the ulnar. In the case where the muscle is completely supplied by the median nerve Kajava (1910) would, I think, take this as indicating that no part of it represented true flexor profundus: this conclusion is not necessarily correct, however, considering the views of Cunningham (1881b, 1882, 1890) and Haines (1955) who, in disagreement with the Fürbringer hypothesis, consider that nerve supply is not an infallible guide to muscle homology.

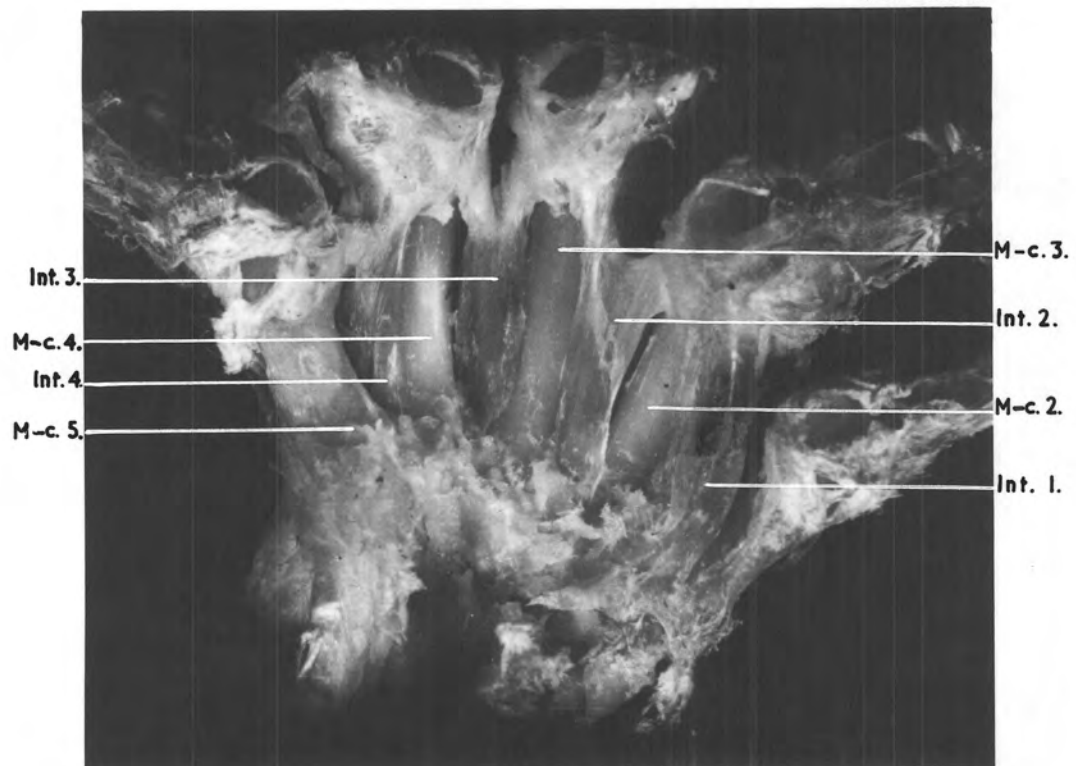
Interossei (fig. 59; pl. XXV). These muscles are not named "dorsal" here since Campbell (1939) considers that they are, in the marsupial hand, not wholly homologous with the dorsal interossei of placental mammals, but are at least partly formed by muscle structures peculiar to marsupials which he calls "flexores digitorum minimi" (after Ribbing).

In T. vulpecula there are four of these muscles, one to each interosseous space, all arising from the metacarpal bases: the first takes origin only from the base of the first metacarpal, the others from both those between which they lie - the second and third mainly from the bone on the radial side, the fourth mainly from that on the ulnar. Their insertions are to the bases of the proximal phalanges of the fingers and to the extensor expansions: the first attaches in typical fashion to the radial side of the index digit, the other three are each inserted into a fibrous arch that crosses the interosseous space at the level of the metacarpo-phalangeal joints and

Plate XXV (cf. fig. 39). Interosseous muscles of the hand. All
other palmar muscles are removed. $\times 4\frac{1}{4}$.

M-c.2,3,4,5. - Metacarpal bones.

Int.1,2,3,4. - Interosseous muscles.



connects the muscle to the fingers on both sides of its particular interosseous space. Accessory palmar slips such as Cunningham (1873b, 1882) describes for Thyl. cynocephalus and Ph. maculata, and Young (1880) notes in H. ualabatus, were not found.

The complete set of four of these muscles is nearly always present in the marsupial hand; they are completely absent, however, in Choer. castanotis (Parsons, 1905) and N. typhlops (Wilson, 1894). An arrangement similar to that noted here whereby the ulnar three muscles attach on both sides of their spaces has been described in M. affinis agilis (Kajava, 1910), Didelphys (Young, 1880; Kajava, 1910; Campbell, 1939) and Chir. variegatus (Sidebotham, 1885); these are the three muscles that Campbell (1939) says are not true dorsal interossei in Didelphys, the first one is. One or more such arches are also found in Thyl. cynocephalus (Cunningham, 1873b, 1882; Kajava, 1910), Ph. maculata (Cunningham, 1873b, 1882), Phasc. cinereus (Young, 1882; Kajava, 1910), H. ualabatus (Young, 1880) and in Didelphys cancrivora, Did. marsupialis, Das. viverrinus, Ph. orientalis and M. robustus (Kajava, 1910). The only reports of a muscle inserted on both sides of the first interosseous space are those of Kajava (1910) for Thyl. cynocephalus and M. robustus.

I was not able to trace the very fine nerves that pass from the deep branch of the ulnar through and between the short flexors as far as the interossei, but I have little doubt that these muscles are all supplied by the ulnar nerve as in the case of Pet. xanthopus (Parsons, 1896) and several marsupials examined by Kajava (1910).

(c). Muscles of the abdominal and thoracic walls.1). Ventral longitudinal muscles.

Pyramidalis (fig. 41; pl. XXVII) has an extensive origin from the medial edge of the longitudinal ramus of the marsupial bone and from a longitudinal raphe on the surface of the rectus abdominis in approximately the middle third of the length of the abdominal wall, which raphe marks part of the musculo-aponeurotic junction of the external oblique muscle of the abdomen (q.v.). It is inserted into the linea alba from a point nearly two centimetres from the pubic symphysis all the way to the xiphoid, and towards the cranial end it is hard to separate from the rectus; the caudal fibres pass transversely medially, the more cranial ones very obliquely cranially and medially. Carlsson (1914) describes the muscle as stopping half way to the xiphoid, probably she includes only the fibres from the marsupial bone. Owen (1859-1847, 1868) gives the origin from the marsupial bone only, and his figure shows the muscle reaching the symphysis. The insertion of the muscle extends at least as far as the xiphoid in Dend. dorianus (Carlsson, 1914), Phasc. cinereus (Young, 1882; Sonntag, 1922), Ph. orientalis (Sonntag, 1922), Hyps. moschatus (Heighway, 1959) and Did. marsupialis, S. ursinus, Phascogale flavipes and Sminthopsis (Carlsson, 1903) of those marsupials where the muscle has been described. Katz (1882) describes the origin of the cranial part of the muscle from the fascia of the external oblique beyond the tip of the marsupial bone in several marsupials - probably including

Phalangista vulpina - and figures this for Das. viverrinus, but he puts this line of origin at the lateral edge of the rectus: Parsons (1896) gives some origin from the fascia on the rectus in Pet. xanthopus; in most accounts, however, no such origin is mentioned. Heighway (1959) gives some origin from the pubis in Hyps. moschatus, as do Carlsson (1914) in Dend. dorianus and Coues (1872) in Did. virginiana; I found none in T. vulpecula.

The nerves to pyramidalis are derived from the spinal nerves from the seventh thoracic to the second, or possibly the third, lumbar.

Rectus Abdominis (figs. 41, 42; pls. XXVII, XXVIII). As this muscle always extends as far as the first costal arch in marsupials the name "rectus ventralis" suggested by Windle and Parsons (1897a) seems preferable; I have, however, kept here to the standard name.

The rectus abdominis has its origin from the deep surface, the cranial border and the cranial edge of the ventral surface of the transverse ramus of the marsupial bone, and as it runs cranially it gains some additional fibres from the middle third of the linea alba. Its principal insertion is into the first costal cartilage, there being small slips from the medial edge of the muscle to the second, third and fourth cartilages also; these slips get progressively smaller in the order given, in one animal (No. 4) the slip to the fourth costal cartilage was not present. The muscle has seven or eight tendinous intersections, the seventh one being at the level of the costal margin and the eighth, when present, cranial to

this: Owen (1839-1847, 1868) found these visible only on the deep surface.

The insertion found here is the same as that reported for Dend. dorianus by Carlsson (1914), and for Pet. xanthopus by Parsons (1896). Eight intersections have been described in Ph. orientalis and Ps. peregrinus by Sonntag (1922) and in Phasc. cinereus by Macalister (1872b) and Young (1882): this seems to be the usual number when there are any at all, the nearest approach I have found being the single one given for Chir. variegatus by Sidebotham (1885). There are none in Choer. castanotis (Parsons, 1903), Dend. dorianus (Carlsson, 1914), M. robustus (Boardman, 1941), Hyps. moschatus (Heighway, 1939), Did. virginiana (Coues, 1872) and Did. marsupialis (Carlsson, 1905).

Origin from the marsupial bone only, as I found in Trichosurus, has been reported by Sidebotham (1885) for Chir. variegatus and by Haughton (1866) for M. giganteus and the opossum; in most marsupials, however, the muscle has part or all of its origin from the pubis. Owen (1839-1847, 1868) gives some origin from the pubis in Ph. vulpina. In Trichosurus there is no insertion into the sternum as has been found in Caenolestes (Osgood, 1921), Chir. variegatus (Sidebotham, 1885), S. ursinus (Macalister, 1870), M. giganteus (Haughton, 1866), M. robustus (Boardman, 1941) and Hyps. moschatus (Heighway, 1939).

Origin of fibres of this muscle from the linea alba seems to be unique in Trichosurus; Haughton (1866) describes what appears to be

the insertion of some fibres in this region in M. giganteus and the opossum.

Branches were traced into the muscle from the spinal nerves from the fourth thoracic to the second lumbar; the third lumbar may also contribute.

Sternalis (Supracostalis) (figs. 24, 41; pls. XVI, XVII). This muscle has also been described under the names "rectus thoracicus" (Macalister, 1870), "rectus thoracis" (mentioned by Boardman, 1941), "rectus sternalis" (Sidebotham, 1885), "sterno-costalis" - obviously a very undesirable name for it - (Coues, 1872) and "transversus costarum" (mentioned, but not used, by Osgood, 1921, and Boardman, 1941): Haughton (1866) describes a structure that he calls simply "intercostal muscle" in the opossum which is apparently the same thing also, and in the same animal Langworthy (1952) refers to it as the fourth pectoral layer.

In T. vulpecula the muscle arises by a thin aponeurosis from the sides of the third and fourth and, sometimes, the fifth segments of the sternum. It passes cranio-laterally, becoming muscular where it lies on the rectus abdominis, and is inserted into the first rib just lateral to the insertion of the rectus and partly covered by the scalenus posterior.

The sternal attachment of the muscle shows considerable variation in different marsupials, Parsons (1896) says it is attached to the costal cartilages in Pet. xanthopus. The insertion into the first rib appears to be more constant, but Haughton (1866)

gives it to the second in the opossum, Macalister (1870) to the second and third in Phasc. wombata and to the first four ribs in S. ursinus. The fibres of the muscle lie parallel to those of the external oblique of the abdomen.

The nerve to the sternalis arises from the trunk of the first thoracic nerve to the brachial plexus where this lies on the first rib. This innervation agrees with that of the opossum given by Langworthy (1952), and Cuscus and Macropus given by Kohlbrugge (1898) - the "C1" given in his text fairly obviously being a misprint.

2). Flat muscles of the body wall.

Obliquus Externus Abdominis (figs. 24, 40, 46; pls. XVI, XXVI, XXX) takes origin by fleshy slips from the last ten ribs (i.e. ribs 4 to 13 inclusive) - the cranial slips interdigitating with the serratus anterior - and from the thoraco-lumbar fascia just lateral to the edge of the erector spinae to within nearly a centimetre of the anterior superior iliac spine. This fascial part of the origin has the appearance of being separated into three more large digitations which are, considering all thirteen of them, more distinct from one another cranially than caudally. The muscle has the form of a flat sheet with its fibres passing caudo-medially. The main cranial part of the sheet remains fleshy to a line nearly half way across the rectus abdominis where it gives way to a thin aponeurosis; this line extends caudally to the tip of the marsupial bone and along it the aponeurosis is very adherent to the underlying rectus, the raphe so

Figure 40 (cf. pl. XXVI). Ventral abdominal wall after the removal of all pectoral muscles. The hind-limb is disarticulated at the hip. $x\frac{1}{2}$.

Figure 41 (cf. pl. XXVII). Ventral aspect of trunk after the removal of all pectoral muscles and the obliquus externus abdominis. The hind-limb is disarticulated at the hip. $x\frac{1}{2}$.

Figure 42 (cf. pl. XXVIII). Caudal part of ventral abdominal wall after the removal of obliquus externus abdominis, obliquus internus abdominis and pyramidalis. The hind-limb is disarticulated at the hip. $x\frac{1}{2}$.

Ac.	- Acetabulum.
C.C.1.	- First costal cartilage.
Crem.	- Cremaster (cut).
E.I.	- External intercostal.
F.Sh.	- Femoral sheath.
Il-ps.	- Ilio-psoas.
Ing. lig.	- Inguinal ligament.
In.I.	- Internal intercostal.
Int.	- Tendinous intersection.
M.B.	- Marsupial bone.
Ob.Ex.	- Obturator externus.
O.E.A.	- Obliquus externus abdominis.
O.I.A.	- Obliquus internus abdominis.
O.I.A.ap.	- Aponeurosis of obliquus internus abdominis covering transversus abdominis.
Pec.	- Deep head of pectineus.
Pub.	- Pubis.
Pyr.	- Pyramidalis.
Pyr.c.	- Pyramidalis covered by aponeurosis of obliquus externus abdominis.
R.A.	- Rectus abdominis.
R.3,5,10.	- Third, fifth and tenth ribs.
Sc.P.	- Scalenus posterior.
Se.A.	- Serratus anterior.
St.	- Sternalis.
St-c.	- Sterno-costalis.
Tr.A.	- Transversus abdominis.
Tr.A.ap.	- Aponeurosis of transversus abdominis.

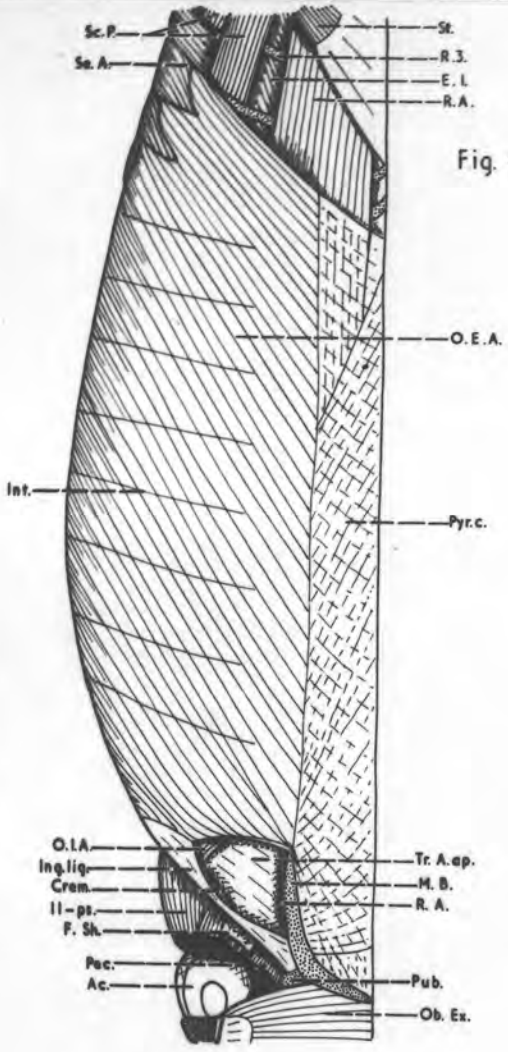


Fig. 40.

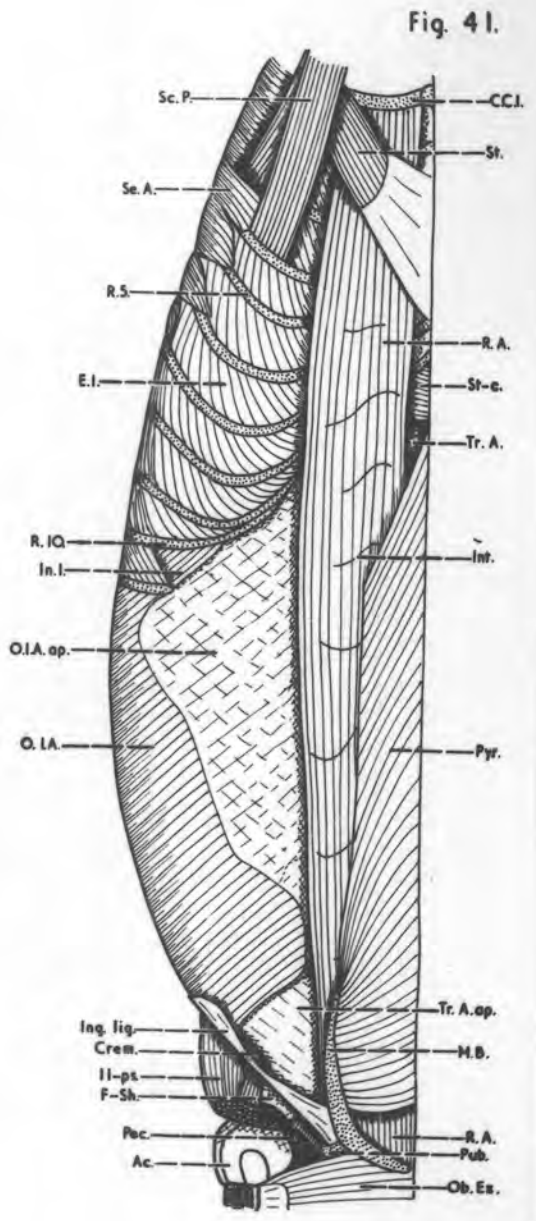


Fig. 41.

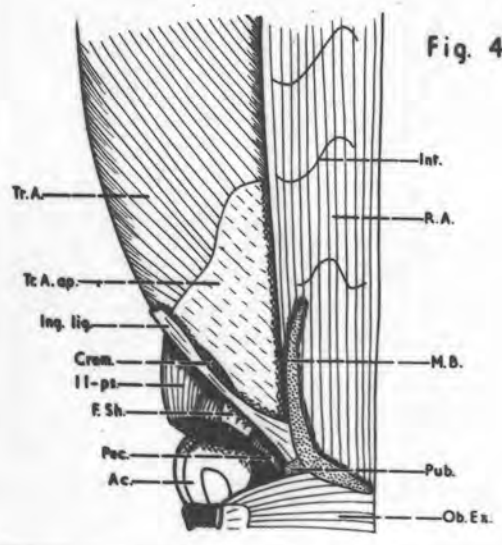


Fig. 42.

Plate XXVI (cf. fig. 40). Caudal part of ventral abdominal wall and superficial inguinal ring. Hind-limb disarticulated at hip. $\times 1\frac{2}{3}$.

- Ac. - Acetabulum.
- Crem. - Cremaster (cut off).
- F.Sh. - Femoral sheath.
- Il-ps. - Ilio-psoas.
- Ing.lig. - Inguinal ligament.
- L.A. - Linea alba.
- M.B. - Marsupial bone.
- Ob.Ex. - Obturator externus.
- O.E.A. - Obliquus externus abdominis.
- O.I.A. - Obliquus internus abdominis.
- Pec. - Deep head of pectineus.
- Pyr. - Pyramidalis (covered by external oblique aponeurosis).
- R.A. - Rectus abdominis.
- Tr.A.ap. - Aponeurosis of transversus abdominis.

O. E. A.

Pyr.

L. A.

O. I. A.

Tr. A. ap.

Ing. lig.

Crem.

Il-ps.

F. Sh.

Pec.

Ac.

R. A.

M. B.

Ob. Ex.



formed giving origin to the cranial fibres of the pyramidalis along part of its length and therefore corresponding to the lateral border of this part of the pyramidalis muscle. The insertion of the main aponeurosis of this part of the external oblique is into the linea alba, the fibres that reach the midline within a centimetre or two of the pubic symphysis (i.e. beyond the caudal border of the pyramidalis) decussating with those from the opposite side and gaining attachment to the transverse ramus of the contra-lateral marsupial bone: in this region of one animal examined (No. 5) there was no decussation, but the fibres of the left aponeurosis crossed superficially over those of the right so that the caudal end of the linea alba was incomplete. The fibres next caudal to those that form the external oblique aponeurosis find insertion into the lateral edge of the marsupial bone for a centimetre or so next to the tip, some of them by direct fleshy insertion, but more through a fibrous cord that forms the cranial crus of the superficial inguinal ring. The most caudal part of the muscle, in fact most of that from the lumbar fascia, remains fleshy for somewhat less than half of its extent, giving way to a thin aponeurotic ribbon that is separated from the rest of the muscle by the superficial inguinal ring: this ribbon is the inguinal ligament. It is not attached directly to the anterior superior iliac spine, but is adherent to the edge of the "ilio-gluteal fascia" (the name I choose to give to the fascia that separates the iliacus from the gluteal muscles beyond the ventral border of the ilium) near the origin of sartorius. The inguinal

ligament is inserted into the angle of the marsupial bone and also for a few millimetres cranial to this into its lateral border, and for a few millimetres caudo-laterally into the pubis: Owen (1839-1847, 1868) does not mention any pubic attachment.

The superficial inguinal ring is a large triangular opening bounded medially by the longitudinal ramus of the marsupial bone, caudo-laterally by the inguinal ligament, and cranially by the fibrous strand through which some of the fibres of the main body of the muscle are inserted into the marsupial bone.

I found usually eight tendinous inscriptions present in this muscle, one specimen (No. 5) having a very small ninth one. This is more than I have found described for any other marsupial, Parsons (1905) reporting five in Choer. castanotis and (1896) three in Pet. xanthopus, while Carlsson (1914) gives two in Pet. penicillata.

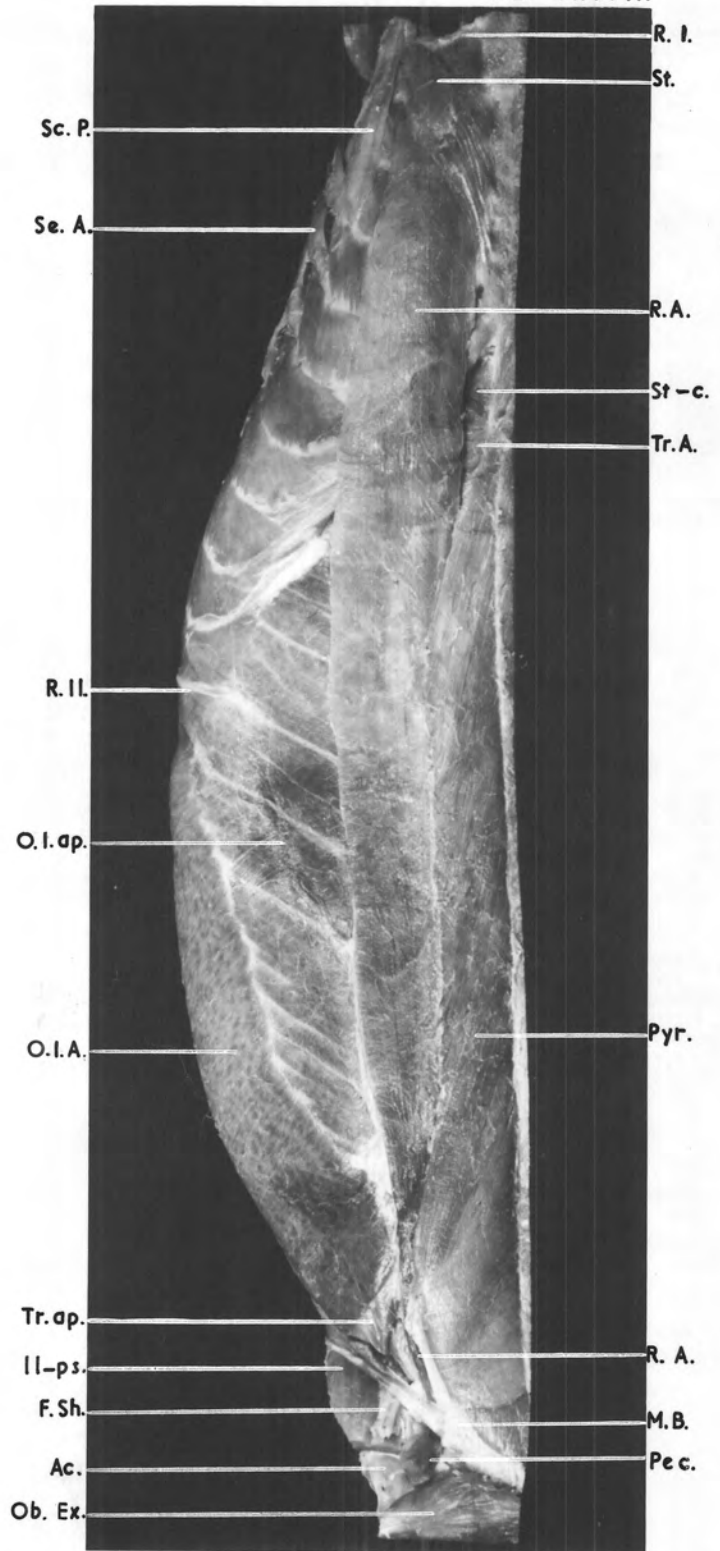
Carlsson's (1914) account of the muscle in T. vulpecula differs from mine in taking the origin cranially to the third rib and caudally to the anterior superior iliac spine: she found only four intersections in it.

The number of ribs from which this muscle arises differs somewhat in other marsupials reported, the first digitation usually coming from the third, fourth or fifth rib. Haughton (1866) gives the origin as extending as far as the second rib in M. giganteus.

The nerve supply of the external oblique in Trichosurus is derived from the ventral rami of the spinal nerves from the fourth thoracic to the third lumbar.

Plate XXVII (cf. fig. 41). Ventral view of trunk. The fore-limb with most of its attaching muscles and the obliquus externus abdominis are removed, and the hind-limb is disarticulated at the hip. $\times \frac{2}{3}$.

- Ac. - Acetabulum.
- F.Sh. - Femoral sheath.
- Il-ps. - Ilio-psoas.
- M.B. - Marsupial bone.
- Ob.Ex. - Obturator externus.
- O.I.A. - Obliquus internus abdominis.
- O.I.ap. - Aponeurosis of obliquus internus abdominis.
- Pec. - Deep head of pectineus.
- Pyr. - Pyramidalis.
- R.A. - Rectus abdominis.
- R.1. - First rib and costal cartilage.
- R.11. - Eleventh rib and costal cartilage.
- Sc.P. - Scalenus posterior.
- Se.A. - Serratus anterior.
- St. - Sternalis.
- St-c. - Sterno-costalis.
- Tr.A. - Transversus abdominis.
- Tr.ap. - Aponeurosis of transversus abdominis.



Obliquus Internus Abdominis (fig. 41; pl. XXVII) arises from the thoraco-lumbar fascia and from the edge of the "ilio-gluteal fascia": in some other marsupials reported this latter part of the origin is stated as coming from the lateral part of the inguinal ligament but I feel that in Trichosurus it is rather from the fascia mentioned, although the two are very adherent here. Owen (1839-1847, 1868) gives this part of the origin from an aponeurotic band passing from the anterior superior iliac spine to the acetabulum (which probably corresponds to the edge of my "ilio-gluteal fascia") - not from the inguinal ligament. The muscle fibres extend as far as the rectus in the caudal fourth of the abdomen but further cranially the line of transition from muscle to aponeurosis runs cranio-laterally towards the eleventh costal cartilage and then turns slightly medially again for a short distance; the fibres run cranio-medially and a small portion of the muscle is visible through the lateral part of the superficial inguinal ring. The muscle is inserted into the last three costal cartilages and, through its aponeurosis, into the whole length of the linea alba; the aponeurosis is so adherent to that of the transversus, however, especially in the caudal part of the abdominal wall, that the muscle might almost be said to have its insertion into the transversus aponeurosis. Where the aponeurosis lies on the muscular part of the transversus it is extremely thin, medially it passes mainly deep to the rectus abdominis but in the caudal part of the abdomen also gives off a superficial sheet to help form the ventral sheath of the rectus.

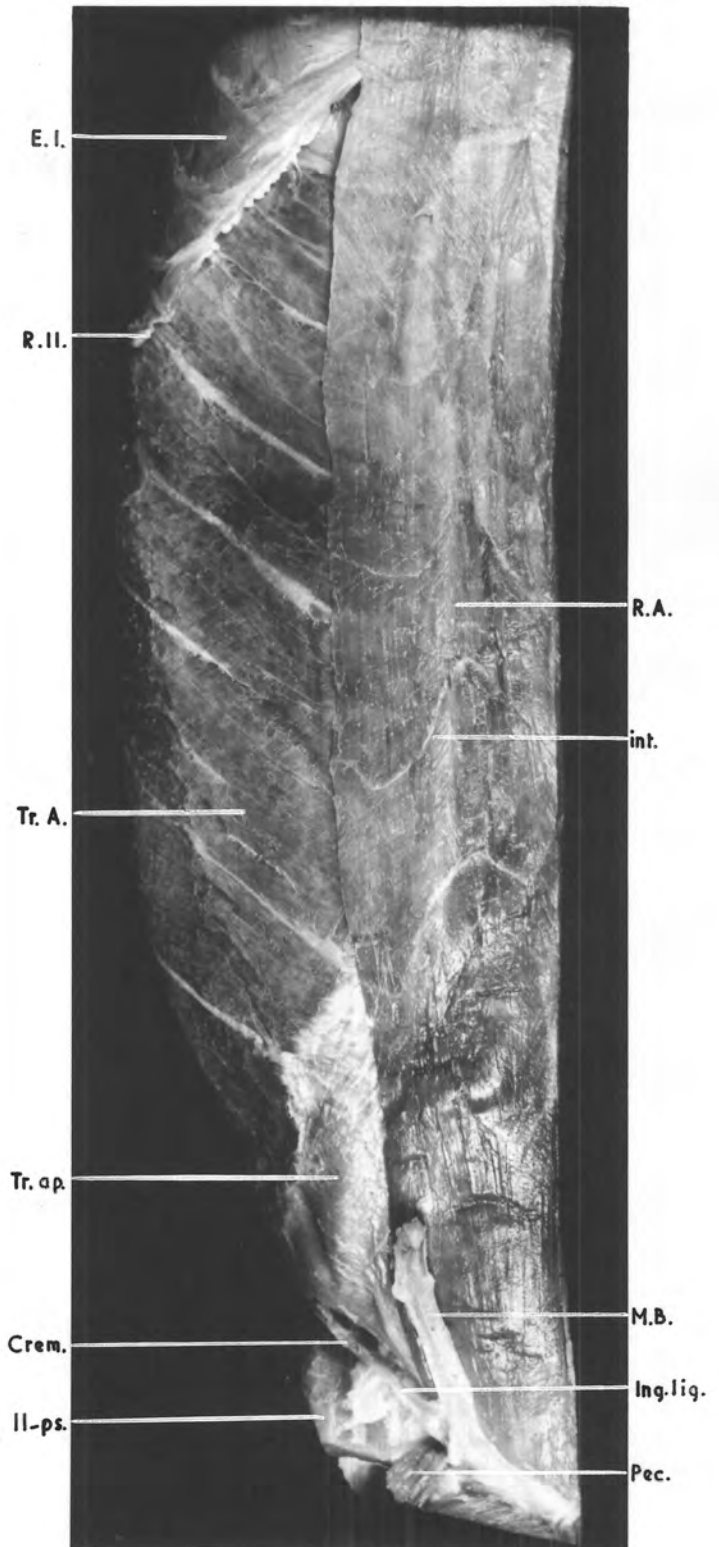
The muscle seems to differ little in extent in other marsupials reported. Some degree of fusion with the transversus has been reported in some - in Choer. castanotis (Parsons, 1905) they are inseparable, in Did. virginiana (Coues, 1872) and Pet. xanthopus (Parsons, 1896) they have a common aponeurosis, and in Phasc. cinereus (Macalister, 1872b) they are separable only with great difficulty; in the last species Young (1882) describes four or five tendinous intersections in serial continuity with the ribs.

Its innervation is derived from the last two thoracic and the first three lumbar nerves.

Transversus Abdominis (fig. 42; pl. XXVIII) has its origin from the last seven costal cartilages (i.e. 7 to 13 inclusive) - this attachment being to the inner surfaces about a centimetre cranial to the costal margin and consisting of slips that interdigitate with those of the diaphragm - and from the thoraco-lumbar fascia as far as the anterior superior iliac spine. In the cranial half of the abdominal wall the muscle fibres extend deep to the rectus, the most cranial ones reaching right to the linea alba; further caudally the line of transition to aponeurosis runs out towards the mid-inguinal region. Owen (1859-1847, 1868) says the line of musculo-aponeurotic junction is the same as that of the internal oblique but this was not so in my specimens. There is insertion to the whole length of the linea alba, which overlaps the xiphoid cartilage at the cranial end. The nerves from the seventh thoracic to the third lumbar were seen to contribute to its innervation.

Plate XXVIII (cf. fig. 42). Ventral view of abdominal wall. The hind-limb is disarticulated at the hip, and the obliquus externus abdominis, obliquus internus abdominis and the pyramidalis are removed. Slightly enlarged.

- Crem. - Cremaster (cut off).
- E.I. - External intercostal.
- Il-ps. - Ilio-psoas.
- Ing.lig. - Inguinal ligament.
- int. - One of the tendinous intersections in the rectus abdominis.
- M.B. - Marsupial bone.
- Pec. - Deep head of pectineus.
- R.A. - Rectus abdominis.
- R.11. - Tip of cartilage on eleventh rib.
- Tr.A. - Transversus abdominis.
- Tr.ap. - Aponeurosis of transversus abdominis.



Here again, apart from differences in the position of the line of musculo-aponeurotic transition, there seems little difference in the muscle in most other marsupials reported, though from the accounts of Osgood (1921) and Haughton (1866) there is considerably less costal origin in Caenolestes and M. giganteus respectively. Cremaster arises by a short flat tendon from the anterior superior iliac spine deep to the caudal part of the internal oblique and continuous with, but easily separable from, the caudal border of the transversus. In the male it accompanies the spermatic cord, gradually spreading out to partly surround it, and is inserted into the proximal part of the tunica vaginalis testis. In the female the muscle is just as large as in the male, here it is inserted into the mammary gland tissue deep to the lateral border of the marsupium. This account agrees substantially with that of Owen (1859-1847, 1868) and the insertions given here appear to be standard for marsupials, though Leche (1874-1900) found some fibres crossing the midline to the other side in a female Myrmecobius, and Katz (1882) figures the two muscles fusing together in the scrotum before insertion in a male Das. viverrinus. Katz (1882) notes that the marsupial cremaster is part of the transversus abdominis.

The muscle is supplied by the genito-femoral nerve.

Intercostales Externi (figs. 46, 47, 48; pls. XXX, XXXI) are twelve in number since there are thirteen ribs; the first five stop nearly three centimetres short of the sternum ventrally, the sixth one reaches nearly to the ventral end of its intercostal space, the last

six reach quite to the end. The last four are peculiar, the main or ventral part of the muscle stops three centimetres short of the vertebral column dorsally, this making the last one less than one centimetre wide; then after a gap of one to two centimetres there is a thinner more oblique part which I take to be part of the external intercostal also. If this is so all the external intercostals reach to the heads of the ribs dorsally and their dorsal portions are covered by the erector spinae. Through the gaps in the last four muscles the slips of the serratus posterior inferior pass to their insertion.

Intercostales Interni (figs. 45, 48) fill the whole of each intercostal space except for a centimetre or so on the average at the vertebral end, this interval being smaller in the cranial spaces and increasing as we pass caudally; in the last intercostal space the interval suddenly increases to about three centimetres. In Did. virginiana (Coues, 1872) these muscles occupy the whole length of each intercostal space.

Intercostales Intimi are defined from the internal intercostals only by the presence of the intercostal nerves and vessels which separate them. The more cranial ones are found only in the dorsal fourth of their intercostal spaces; further caudally they expand to occupy about half of the length of the spaces. They are inseparable from the subcostal muscles which lie internal to the dorsal parts of the intercostales intimi.

Each intercostal muscle is supplied by the corresponding

intercostal nerve.

Subcostales are found in relation with only the most dorsal parts of the thoracic wall, but they are present from its cranial to its caudal end. Each one forms a slip from a half to one centimetre wide with fibres extending dorso-caudally for two segments, the cranial ones being rather thicker and narrower than those situated more caudally. Consecutive muscles are separated by a narrow interval through which some of the intercostalis intimus can be seen. The first subcostal arises from the first rib and is inserted into the third, the insertion extending, as do the others, as far as the head of the rib; the last one passes from the twelfth rib to the fascia on the ventral surface of the erector spinae caudal to the thirteenth, so there are twelve of these muscles in all.

Sterno-costalis (*Triangularis Sterni*) (fig. 45) arises from the sides of the fourth and fifth segments of the sternum and the narrow section of the xiphoid; its fibres run cranio-laterally, the cranial ones most obliquely, the more caudal ones almost transversely. It is inserted into the lateral ends of the costal cartilages from the second to the sixth and into the fascia of the intervening intercostal spaces. The muscle is composed of five slips, only the caudal one of which is completely separate, the others being fused along their edges, especially medially. The first slip extends from the fourth sternal segment to the second costal cartilage and the fascia of the second space, the second from the fourth and fifth segments to the third cartilage and some of the fascia of the third

Figure 43 (cf. pl. XXIX). Abdominal surface of diaphragm. $\times \frac{2}{3}$.

Figure 44. Ventral aspect of quadratus lumborum, iliacus and psoas muscles. $\times 1$.

Figure 45. Internal aspect of ventral thoracic wall to show sterno-costalis. $\times \frac{2}{3}$.

Ao.	- Aortic opening in diaphragm.
C.C.7.	- Seventh costal cartilage.
C.M.	- Line of costal margin.
C.T.	- Central tendon of diaphragm.
Er.Sp.	- Erector spinae.
I-co.	- Infra-coccygeus on dorsal pelvic wall.
Il.	- Iliacus.
Il-co.	- Ilio-coccygeus.
In.I.	- Internal intercostals.
I.V.C.	- Vena caval opening in diaphragm.
L1, L2, etc.	- Levels of lumbar vertebral bodies.
Oes.	- Oesophageal opening in diaphragm.
o.T-l.f.	- Origin of quadratus lumborum from thoraco-lumbar fascia.
Pec.	- Deep head of pectineus.
Ps.ma.l.	- Lateral part of psoas major.
Ps.ma.m.	- Medial part of psoas major.
Ps.mi.	- Psoas minor.
Pub.	- Pubis.
Q.L.	- Quadratus lumborum.
R.Cr.	- Right crus of diaphragm.
R.Cr.t.	- Tendinous part of right crus of diaphragm.
R.2,3,4, etc.	- Ribs.
S1.	- Level of first sacral vertebral body.
St1, St2, etc.	- Segments of sternum.
T10, T11, etc.	- Levels of thoracic vertebral bodies.
Xi.	- Xiphoid.
Xi.C.	- Xiphoid cartilage.
Xi.sl.	- Slip of diaphragm arising from xiphoid.

Fig. 43.

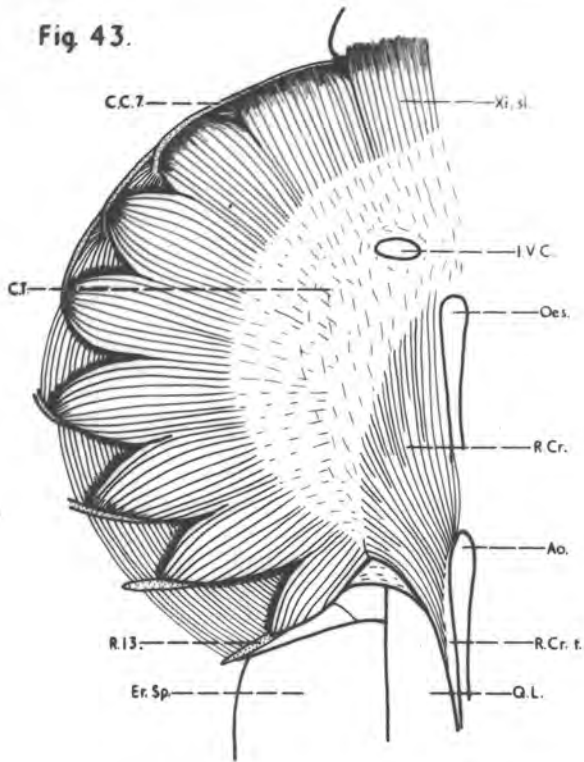


Fig. 44.

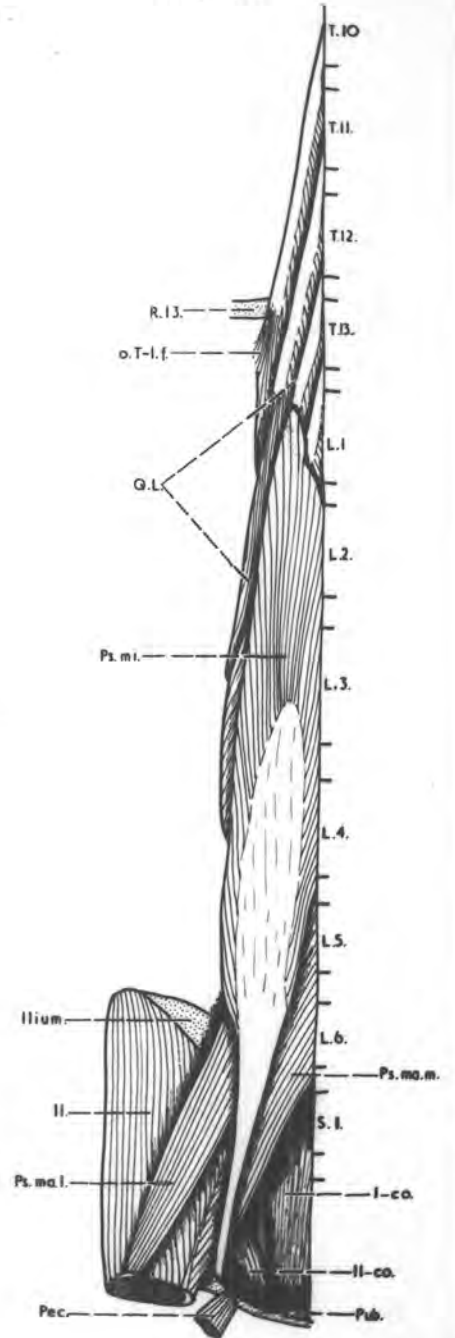


Fig. 45.

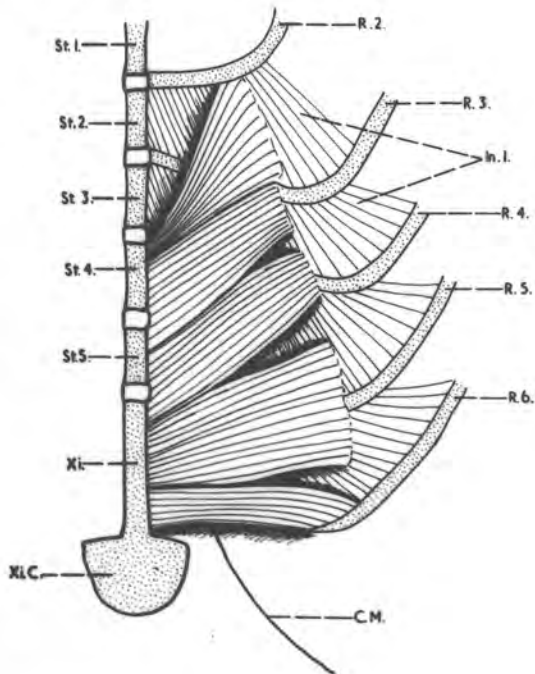
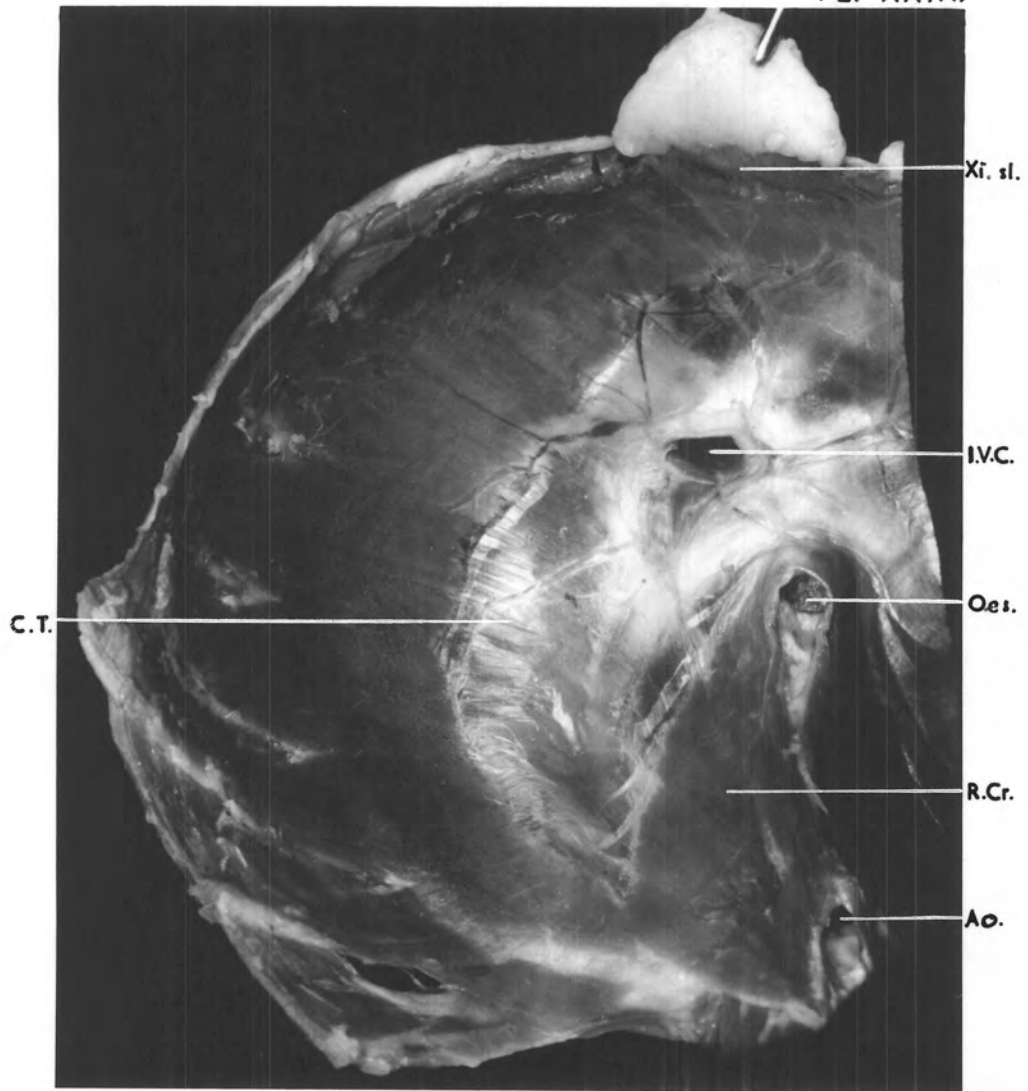


Plate XXIX (cf. fig. 43). Abdominal surface of diaphragm. $x1\frac{1}{8}$.

- Ao. - Aortic opening.
- C.T. - Central tendon.
- I.V.C. - Vena caval opening.
- Oes. - Oesophageal opening.
- R.Cr. - Right crus.
- Xi.sl. - Origin from xiphoid.



space, the third from the fifth sternal segment and the base of the xiphoid to the fourth cartilage and the fascia of the third space, the fourth from the xiphoid to the fifth cartilage and the fascia of both adjacent spaces, and the fifth and last slip goes from the xiphoid to the sixth costal cartilage.

A similar insertion extending from the second cartilage to the sixth has also been reported for Did. virginiana (Coues, 1872) and Chir. variegatus (Sidebotham, 1885) in both of which the origin extends further cranially on the sternum, and in the former case does not touch the xiphoid. In Phase. cinereus (Young, 1882) also there is no origin from the xiphoid and the insertion extends from the third cartilage to the sixth.

The muscle is supplied by the ventral branches of the intercostal nerves from the second to the sixth.

5). Muscles in the dorsal wall and roof of the abdomen.

Diaphragm (fig. 43; pl. XXIX) has an extensive origin from the xiphoid, the last seven costal cartilages and the lumbar vertebrae. The fibres from the vertebral part of the origin just touch, but are separate from, those of the costal; the two groups are connected by an arcuate ligament from which no muscle fibres arise. The xiphoid origin consists of one single slip continuous across the midline and joined on either side to the costal origins which consist of eight slips from the seven costal cartilages, the seventh cartilage giving rise to two slips separated by the origin of the first digitation of the transversus abdominis. The two crura make up the vertebral

origin, the right extending to the caudal part of the second lumbar vertebra, the left to the disc between the first and second, though in one animal (No. 2) they reached nearly one vertebra further. The origin of each crus is partly fleshy and partly tendinous, the tendinous part of each occupying its medial border and giving off muscle fibres from its lateral side: the two tendinous edges meet in the midline over the aorta at the level of the disc between the last two thoracic vertebrae. The most cranial fibres of the two crura bound the oesophageal opening as seen from the abdominal surface of the diaphragm; this opening thus appears to lie between the two crura and is at the level of the caudal part of the tenth thoracic vertebra in the median plane. When viewed from the thoracic surface, however, the tendinous part of the right crus is seen to give off some fibres from the medial side of its cranial end that run towards the left and bound the left side of the oesophageal opening which therefore really lies in the right crus. The vena caval opening lies to the right of the median plane at the level of the ninth thoracic vertebra in the large thin crescentic central tendon that provides the insertion of all the fleshy fibres of the muscle.

The diaphragm is supplied as usual by the phrenic nerve; it may also receive fibres from the caudal intercostal nerves but no branches of any size could be found coming from this source.

In Did. virginiana Coues (1872) describes the oesophageal opening as lying between the decussated fibres of the crura so that it is bounded on the right by fibres of the left crus and vice

versa. Young (1882) gives this same opening in Phasc. cinereus as lying between the crura and almost behind the diaphragm like the aorta; while Boardman (1941) says it is in the right crus in M. robustus.

Quadratus Lumborum (fig. 44) lies on the ventral aspects of the lumbar transverse processes and the last ribs, its ventral surface being in turn partly covered by the psoas muscles (mainly the minor). It arises from the ventral surface of the sacro-iliac joint and the adjacent part of the ilium, from all the lumbar transverse processes, the thirteenth rib and the fascia on the ventral aspect of the erector spinae just caudal to the last mentioned bone. The general direction of the fibres is cranially and medially; fibres in the more dorsal part of the muscle are inserted into all the lumbar transverse processes, some of the most dorsal ones connecting consecutive transverse processes and probably representing the lumbar intertransverse muscles. Most of the more ventral part of the muscle divides into seven parts each of which is inserted by a small flattened tendon into a vertebral body and also by fleshy fibres into the vertebra next caudally, this fleshy insertion being covered by the tendon of the next part of the muscle coming to that vertebra. These tendons give the muscle insertion into the vertebrae from the tenth thoracic to the third lumbar inclusive and the fleshy insertion of the seventh part gives attachment to the fourth lumbar also. The last two of these seven parts just described are small and caudal to them the ventral part of the muscle

has insertion into the sides of the fifth and sixth lumbar vertebral bodies, this portion of the muscle not being divided into definite subdivisions nor provided with the clearly defined tendons of the more cranial portion. In one animal (No. 4) the part of the muscle from the ilium and sacro-iliac joint was inserted entirely into the sixth lumbar transverse process and the muscle began anew from there. The tendons attaching to the vertebral bodies give part origin to the psoas minor muscle.

Young (1882) and Sonntag (1922) indicate that this muscle is practically non-existent in Phase. cinereus; in Caenolestes (Osgood, 1921) it does not extend as far caudally as the ilium. Haughton (1866), in his account of M. vallabiensis, and Coues (1872), in his description of Did. virginiana, both place the muscle, rather oddly, dorsal to the lumbar transverse (or costal) processes; while Carlsson (1914) and Parsons (1896) say that the muscle is united with the erector spinae in Dend. dorianus and Pet. xanthopus respectively. Apparently the muscle varies a good deal amongst marsupials though there are not many adequate accounts upon which to judge.

The quadratus lumborum in Trichosurus is supplied by the ventral rami of the spinal nerves from the twelfth or thirteenth thoracic to the third lumbar.

4). Dorsal thoracic muscles.

Serratus Posterior Superior (figs. 46, 47; pls. XXX, XXXI), also called "serratus dorsalis cranialis" (Boardman, 1941) and "serratus

Figure 46 (cf. pl. XXX). Dorsal aspect of trunk after the removal of trapezius and latissimus dorsi. $\times \frac{2}{3}$.

Figure 47 (cf. pl. XXXI). Dorsal aspect of trunk showing serrati posteriores. The fore-limb with all its muscles and the oblique muscles of the abdomen are removed. $\times \frac{2}{3}$.

Figure 48. Levatores costarum from the dorso-lateral aspect after the removal of the erector spinae etc. $\times \frac{2}{3}$.

E.I.	- External intercostal.
E.I.d.	- Dorsal part of external intercostal.
E.I.v.	- Ventral part of external intercostal.
Il.Cr.	- Iliac crest.
In.I.	- Internal intercostal.
In-sp.	- Infraspinatus.
Lat.D.o.	- Line of origin of latissimus dorsi from thoraco-lumbar fascia.
L.C.7&8.	- Seventh and eighth levatores costarum.
O.E.A.	- Obliquus externus abdominis.
O.I.A.	- Obliquus internus abdominis.
Rh.	- Rhomboid.
R.1,2,8,13.	- Ribs.
Sart.	- Sartorius.
Se.A.	- Serratus anterior.
Se.P.I.	- Serratus posterior inferior.
Se.P.S.	- Serratus posterior superior.
T-l.f.	- Thoraco-lumbar fascia.
T.maj.	- Teres major.
Tr.A.	- Transversus abdominis.
T.1.sp.	- First thoracic vertebral spine.
T.12.sp.	- Twelfth thoracic vertebral spine.

Fig. 46.

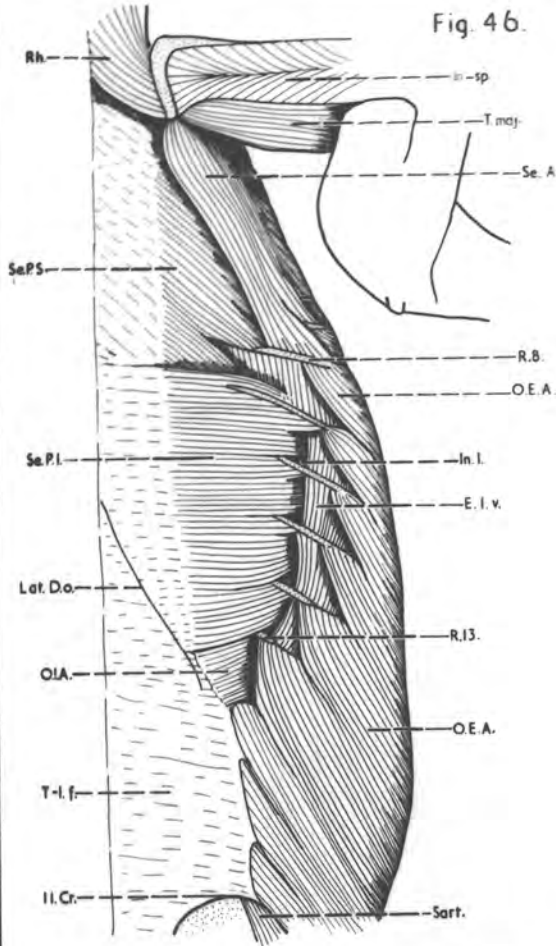


Fig. 47.

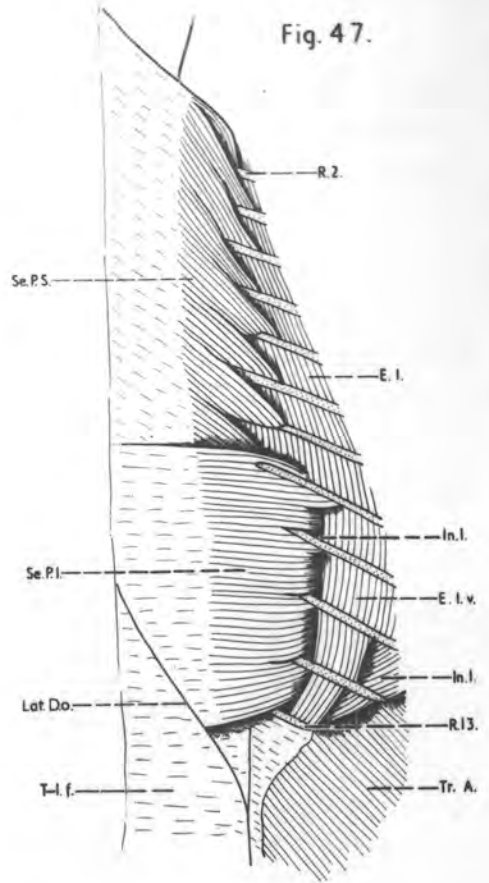


Fig. 48.

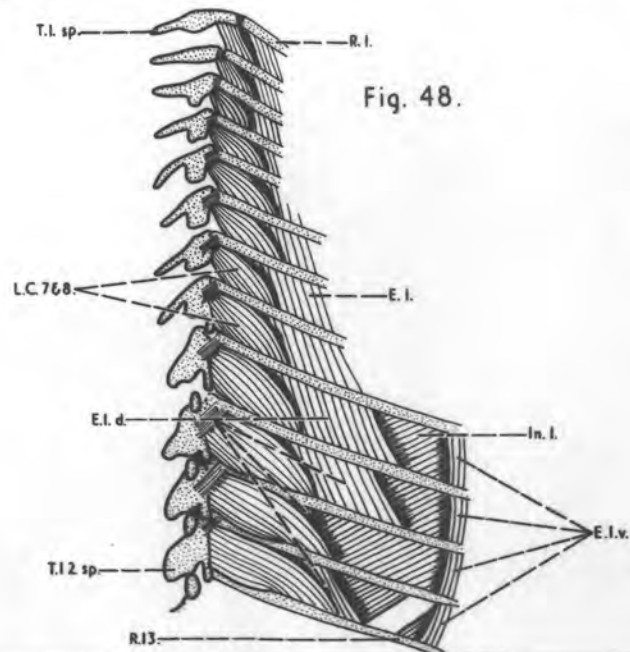


Plate XXX (cf. fig. 46). Dorsal view of muscles of trunk.

Trapezius and latissimus dorsi are removed. Slightly enlarged.

- E.I. - External intercostal (ventral part).
- Il.Gr. - Iliac crest.
- O.E.A. - Obliquus externus abdominis.
- O.I.A. - Obliquus internus abdominis.
- Rh. - Rhomboid.
- Se.A. - Serratus anterior.
- Se.P.I. - Serratus posterior inferior.
- Se.P.S. - Serratus posterior superior.
- T-l.f. - Thoraco-lumbar fascia.
- T.maj. - Teres major.

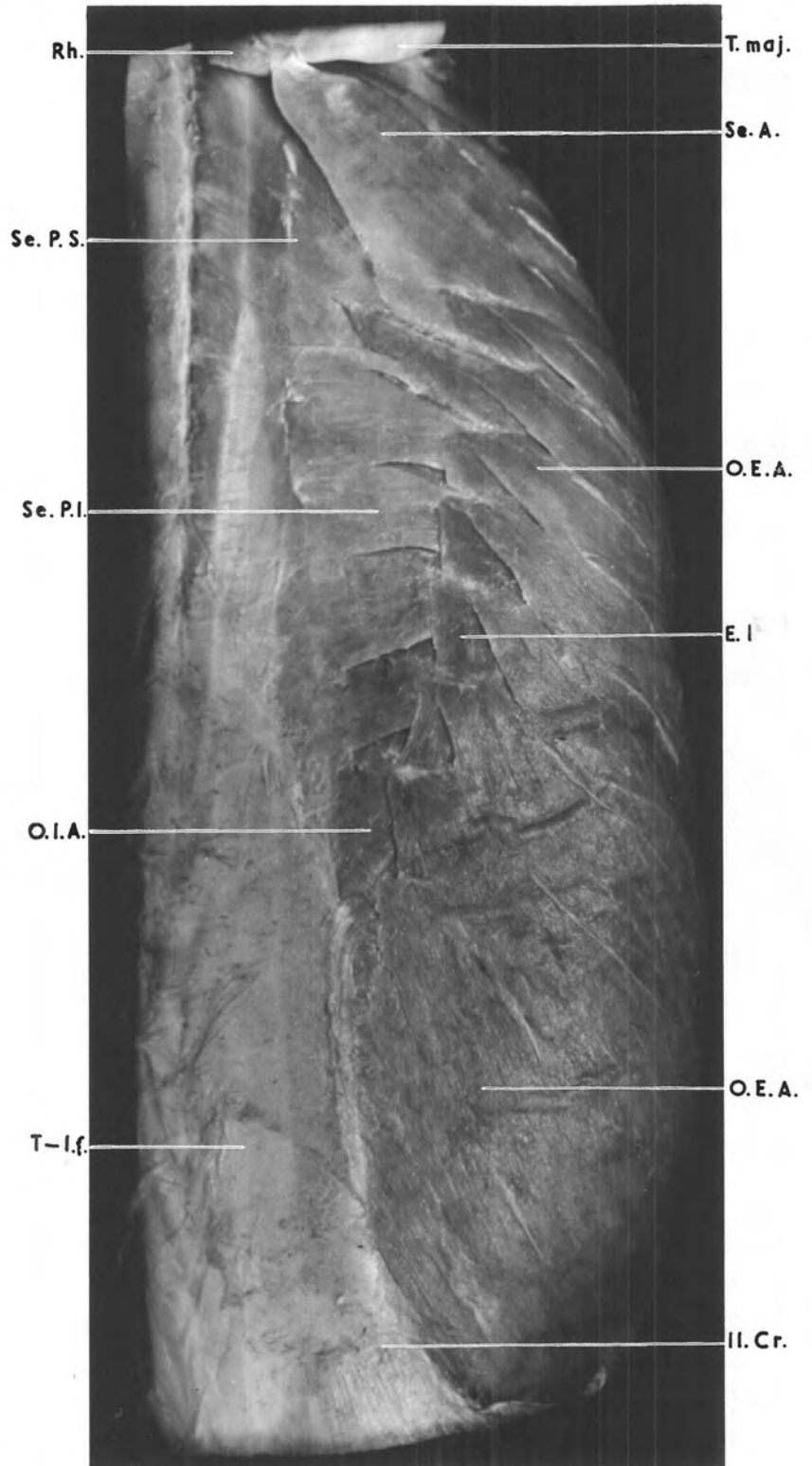
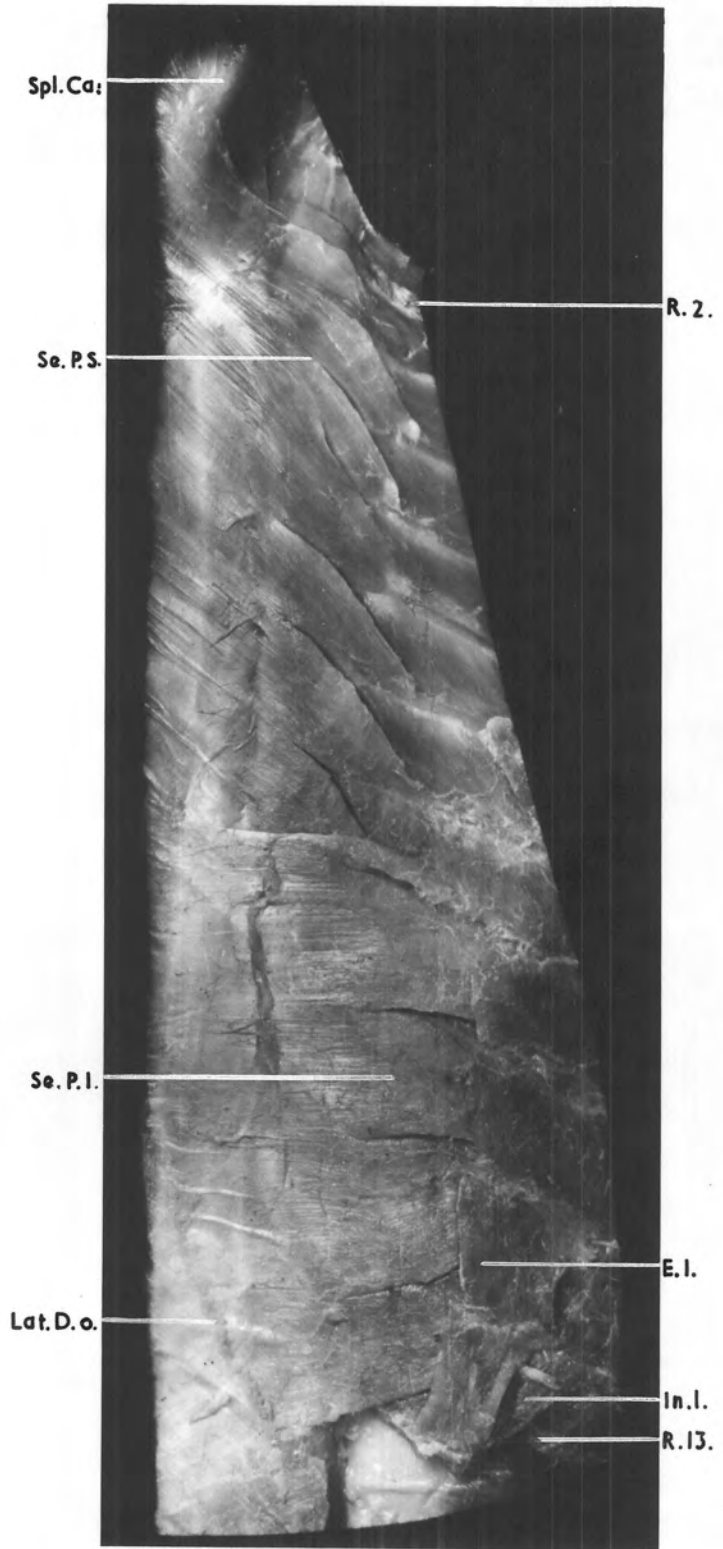


Plate XXXI (of. fig. 47). Dorsal view of trunk to show serrati
posteriores. The fore-limb with all its connecting muscles
and the abdominal muscles are removed. $\times 1\frac{1}{2}$.

- E.I. - External intercostal (ventral part).
In.I. - Internal intercostal.
Lat.D.o. - Line of origin of latissimus dorsi from
thoraco-lumbar fascia.
R.2. - Second rib.
R.13. - Thirteenth rib.
Se.P.I. - Serratus posterior inferior.
Se.P.S. - Serratus posterior superior.
Spl.Ca. - Splenius capitis.



thoracis" (Windle and Parsons, 1897a), arises by a thin aponeurosis from rather less than the caudal half of the ligamentum nuchae and the thoracic spines from the first to the eighth, this aponeurosis virtually forming part of the thoraco-lumbar fascia. The muscle fibres, which come from the aponeurosis near the lateral border of the erector spinae, form ten digitations that are inserted into the ribs from the second to the eleventh inclusive; the fibres of this muscle are parallel to those of the external intercostals which they overlap.

Serratus Posterior Inferior (figs. 46, 47; pls. XXX, XXXI) - "serratus dorsalis caudalis" (Boardman, 1941), "serratus lumbalis" (Windle and Parsons, 1897a) - also takes origin from an aponeurosis incorporated in the thoraco-lumbar fascia through which it is attached to the spines from the eighth thoracic to the first lumbar. The muscle fibres arise near the lateral border of the erector spinae and form separate digitations passing to the ninth, tenth, eleventh and twelfth ribs and also to the fascia of the eighth intercostal space (in one animal reaching to the eighth rib). This muscle therefore overlaps the caudal portion of the serratus posterior superior to a considerable extent. The major parts of the digitations attaching to the ribs run deep to the ventral parts of the external intercostal muscles in the last four spaces: as noted previously these four intercostals each consist of two parts, the dorsal part lying deep to the serratus posterior inferior many of whose fibres pass through the gap that separates the two parts. The

fibres of this muscle run more transversely than those of the serratus superior, and the inferior is continuous caudally with the internal oblique muscle of the abdomen.

The serratus posterior superior is supplied by the intercostal nerves from the first to the ninth, the inferior by those from the ninth to the twelfth; the ninth intercostal nerve gives separate branches to the two muscles.

The marsupials reported show considerable variation in the ribs that provide insertion for these two serrate muscles; some overlap in the insertions of the two is evident in the descriptions of MacCormick (1887) for Das. viverrinus, Boardman (1941) for M. robustus, Heighway (1939) for Hyps. moschatus and Sidebotham (1885) for Chir. variegatus. Macalister (1870) does not distinguish the two entities in his account of Phasc. wombata and S. ursinus, while in Phasc. cinereus (Macalister, 1870; Young, 1882) they are distinguished only by the different direction of their fibres. According to Parsons (1896) only the anterior is present in Pet. xanthopus. Levatores Costarum (fig. 48). There are twelve of these, increasing in size from the cranial ones to the caudal, as occurs in Did. virginiana according to Coues (1872). The cranial ones take origin from the caudal borders of the respective transverse processes and to a slight extent from the pedicles; further caudally the origins are mostly from the sides of the vertebral bodies and the anapophyses, and in each of the last six also from a fibrous band

connecting the base of the anapophysis to the preceding rib and from that rib itself. They are inserted into the dorsal parts of all the ribs except the first and, in the case of the cranial ones particularly, are difficult to separate from the external intercostals: the caudal five have some insertion also into the fascia over the external intercostal muscles. Part origin from the next rib has also been mentioned for some of these muscles in Did. virginiana by Coues (1872); Young (1882) notes that they are continuous with the external intercostals in Phasc. cinereus.

These muscles are supplied by the corresponding intercostal nerves.

(d). Deep dorsal muscles of the neck and trunk.

Erector Spinae (fig. 49). Caudally this muscle mass begins partly as a continuation of the levator caudae lateralis and partly by an extensive origin from the iliac crest and the cranial end of the iliac fossa. It passes cranially having connection to all the lumbar transverse processes and metapophyses and also deriving new fibres from aponeuroses on its medial-superficial and lateral aspects which connect it respectively to the spines and to anapophyses and metapophyses. Further cranially, in the thoracic region, it has attachment to the spines, anapophyses, transverse processes and ribs.

The ilio-costo-cervicalis separates off from the lateral side of the main mass at the level of the eleventh rib and from there on takes further origin from the ribs from the tenth to the second; it

Figure 49. Dorsal aspect of erector spinae and neck muscles after the removal of the limb-girdle musculature and the serrati posteriores. $x\frac{1}{2}$.

Figure 50. Muscles on the dorsal aspect of the neck after the removal of trapezius, rhomboid, splenius, biventer cervicis, erector spinae and longissimus capitis. $x1$.

Figure 51. Muscles of suboccipital triangle. The semispinalis is removed in addition to those mentioned with fig. 50. $x1$.

Ap.or.	- Aponeurotic part of origin of biventer cervicis.
Bi.Ce.	- Biventer cervicis.
Bi.Ce.o.	- Biventer cervicis of opposite side.
Ce.lam.	- Laminae of cervical vertebrae.
Cl-m.	- Cleido-mastoid (displaced).
Er.Sp.	- Erector spinae.
Il.	- Iliacus.
Il-co-ce.	- Ilio-costo-cervicalis.
Il-co-ce.ce.	- Probable representative of ilio-costo-cervicalis in the neck.
Il-co-ce.d.	- Deep slips of ilio-costo-cervicalis.
Int-sp.	- Interspinales.
Is.	- Longissimus.
Is.C.	- Longissimus capitis.
Mu.	- Multifidus.
N.Cr.	- Nuchal crest.
O.C.I.	- Obliquus capitis inferior.
O.C.S.	- Obliquus capitis superior.
O-t.	- Omo-trachelien (displaced).
R.C.P.M.	- Rectus capitis posterior major.
R.1,3,4,15.	- Ribs.
Sc.	- Part of scalenus.
Spi.	- Spinalis.
Spi.C.	- Probable spinalis cervicis.
S-sp.C.	- Semispinalis capitis.
S-sp.ce.	- Semispinalis cervicis.
St-m.	- Sterno-mastoid (displaced).
Te.	- Temporalis.
T.p.1,2,3.	- First three thoracic transverse processes.
T.1.sp.	- Spine of first thoracic vertebra.

Fig. 49.

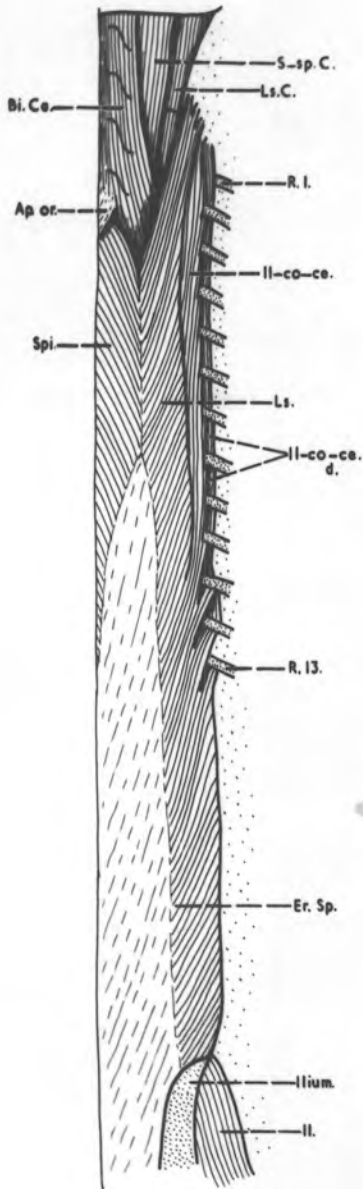


Fig. 50.

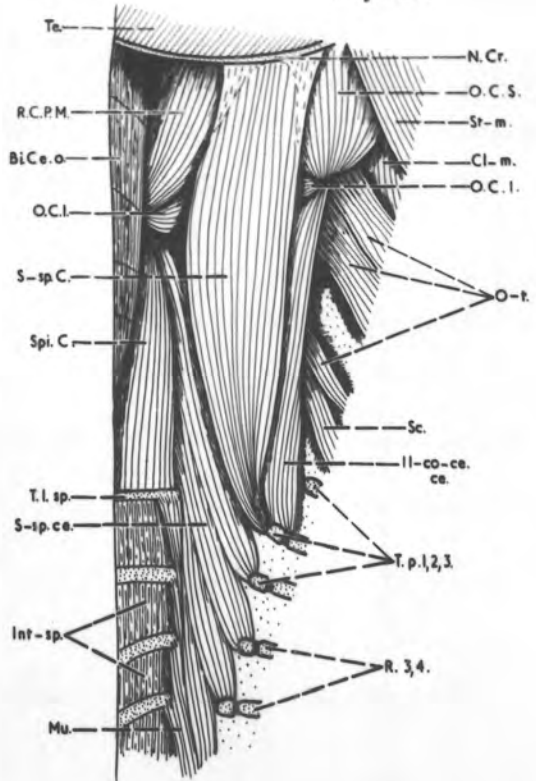
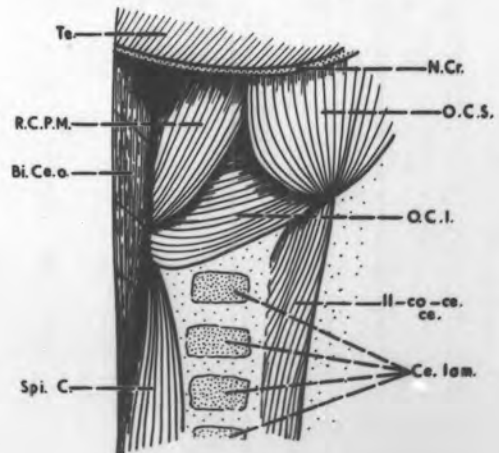


Fig. 51.



is inserted into these same nine ribs and also to the transverse process of the last cervical vertebra which is the cranial limit of its extent. On one side of one animal (No. 2) this muscle column was inserted wholly into the tenth rib and began anew from there. Deep to the main part of the ilio-costo-cervicalis, and in most cases just visible at its lateral border, are slips of muscle connecting one rib to the next in the first eleven intercostal spaces; these slips are supplied, like the main mass, by the dorsal rami of the spinal nerves, so I take them to be part of the ilio-costo-cervicalis. Slips similar to these have been described for M. robustus by Boardman (1941) who associates them with the external intercostals. The lateral part of the main erector spinae mass in the caudal part of the thoracic region attaching to the last three ribs before it divides up into columns should probably be considered as part of the ilio-costo-cervicalis also.

In the neck, lying partly medial to the cranial end of the main ilio-costo-cervicalis column, is another muscle that may be the representative of the ilio-costo-cervicalis in this region. It arises from the articular processes of the last four cervical and the transverse processes of the first two thoracic vertebrae and runs cranially to be inserted into the caudal border of the transverse process of the atlas.

The spinalis is apparently represented mainly in the medial side of the main erector spinae mass which is inserted into the spines from the second lumbar onwards; it does not separate from the

longissimus until the level of the third thoracic spine and its insertion extends as far as the spine of the first thoracic vertebra.

Adjacent to the midline of the neck is a muscle arising from the cranial border of the spine of the first thoracic vertebra and the spine of the last cervical, and passing to the caudal end of the spine of the axis and the spines of the next four vertebrae. This muscle is probably the spinalis cervicis, or possibly is related to the interspinales. Osgood (1921) mentions a somewhat similar muscle in Caenolestes and the opossum which he regards as representative of the interspinales.

The central part of the erector spinae, after the ilio-costocervicalis and the spinalis have separated off, continues as the definitive longissimus which extends far enough to gain insertion into the last four cervical transverse processes.

Longissimus Capitis (Trachelo-mastoid) (fig. 49) arises on the medial side of the rest of the longissimus from the transverse process of the third thoracic vertebra and passes to an insertion on the lateral part of the base of the mastoid process. At about its middle it has a thin aponeurotic intersection. Carlsson (1914) gives the origin of this muscle from the posterior cervical vertebrae.

In other marsupials reported the longissimus capitis has a much more extensive origin than that found here, usually coming from several of the posterior cervical and anterior thoracic vertebrae. A tendinous intersection has also been noted in Caenolestes (Osgood,

1921) and Chir. variegatus (Sidebotham, 1885); Parsons (1896) found two intersections in Pet. xanthopus.

Multifidus. In the thoracic and anterior lumbar regions the multifidus is represented by fibres passing cranio-medially to the vertebral spines from tendinous origins on the metapophyses and transverse processes, which fibres are not separable from the deep part of the erector spinae. Caudal to the mid-lumbar region the multifidus is large and forms a distinct muscle, the levator caudae medialis. In the neck it is completely fused with the semispinalis cervicis - which is not surprising as these two muscles, according to Howell (1956), belong to the same fundamental group and differ only in the length of their fibres.

Rotatores were not noted. Howell (1956) points out that these muscles are basically only short deep fibres of the multifidus system.

Intertransversarii. These muscles were not specifically sought; it has been noted that they may be represented in the lumbar region by some of the dorsal fibres in the quadratus lumborum, and some fibres of the scalenus medius connecting transverse processes have also been described which may be related to the intertransversarii in the neck. They are obvious in the tail where they form the abductor caudae medialis (q.v.).

Interspinales are obvious in the thoracic region where the spines are long, here they cover both sides of the interspinous ligaments for the full length of the spines. A possible representative in the

neck is discussed with the spinalis. They were not noted in other regions.

Splenius Capitis (figs. 22, 23; pl. XV) arises from nearly the whole length of the ligamentum nuchae and from the first three thoracic spines through an aponeurosis that forms part of the thoraco-lumbar fascia. It passes cranio-laterally to be inserted into the lateral end of the nuchal crest and the side of the mastoid process as far as its tip, the insertion being through a short wide aponeurosis. Carlsson (1914) also gives some insertion to cervical vertebrae representing the splenius cervicis; such was certainly not present in any of the material I examined.

The origin of the splenius given for other marsupials reported in the literature does not vary very much in longitudinal extent from that given here, the cervical origin, however, is given in many cases from the vertebral spines instead of the nuchal ligament as is the case in Trichosurus. There is no cervical insertion in Did. virginiana (Coues, 1872) or Myrmecobius (Leche, 1874-1900), nor is any mentioned by Heighway (1959) for Hyps. moschatus, by Osgood (1921) for Caenolestes or by Sidebotham (1885) for Chir. variegatus; it is present, however, in several others reported, viz. Phasc. cinereus (Macalister, 1872b; Young, 1882), Phasc. wombata, S. ursinus (Macalister, 1870), Pet. xanthopus (Parsons, 1896), Dend. dorianus, Pet. penicillata and A. rufescens (Carlsson, 1914).

The splenius is supplied, in Trichosurus, by the dorsal rami of the anterior cervical nerves.

Biventer Cervicis (fig. 49) is closely related to, but quite separate from, the semispinalis capitis which lies lateral and partly deep to it. It arises from the transverse processes of the third to sixth thoracic vertebrae (or in one case the second to fifth), and also from the first two thoracic spines by a small aponeurosis that lies superficial to the cranial end of the spinalis. From here it passes cranially to be inserted into the medial part of the nuchal crest for nearly two centimetres. The muscle appears typically to possess four tendinous intersections, though in one specimen (No. 2) only one could be found: Carlsson (1914) found four in Dend. dorianus but none in T. vulpecula. Coues (1872) found a partial intersection in Did. virginiana, while Osgood (1921) noted at least one in Caenolestes, and Leche (1874-1900) found six in Myrmecobius (where the muscle is fused with the semispinalis capitis). I have found no mention of an origin from the vertebral spines in any other marsupial.

The biventer cervicis is supplied from the dorsal rami of the first five or six cervical nerves.

Semispinalis Capitis (Complexus) (figs. 49, 50) takes origin from the caudal articular processes of the last five cervical, and the transverse processes of the first two thoracic vertebrae; it passes to an insertion into the lateral half of the nuchal crest, the insertion being aponeurotic at the edges while in the middle the fleshy fibres reach almost to the bone. It has a tendinous inscription visible only on the deep surface.

The origin of this muscle varies somewhat in other marsupials reported, the nearest to that found here being in Hyps. moschatus (Heighway, 1939) and Did. virginiana (Coues, 1872). An intersection was noted in the muscle in Chir. variegatus by Sidebotham (1885) and in Caenolestes by Osgood (1921), while Macalister (1870) found several in S. ursinus.

The muscle is supplied by the dorsal rami of the first five or six cervical nerves.

Semispinalis Cervicis (fig. 50) is a continuation of that deep part of the erector spinae that represents the multifidus. It arises from the last four cervical vertebrae at the junction of the articular processes with the laminae, and from the first six thoracic transverse processes; its insertion is on the caudal end of the spine of the axis and the spines of the next four vertebrae.

Suboccipital Muscles.

Rectus Capitis Posterior Major (figs. 50, 51) arises from the whole length of the spine of the axis and passes cranially and a little laterally to its insertion on the base of the skull in an area just below the medial part of the nuchal crest. It is not divided into the two layers that Windle and Parsons (1897a) call the recti capitis dorsales superficialis et medius, though these two layers are present in M. rufus (Windle and Parsons, 1897b), Pet. xanthopus (Parsons, 1896) and Phase. cinereus (Young, 1882), but not, however, in Hyps. moschatus (Heighway, 1939). Leche (1874-1900) gives some additional origin for this muscle from the atlas in Myrmecobius,

while Coues (1872) extends the origin to the third cervical vertebra as well as the second in Did. virginiana.

Rectus Capitis Posterior Minor is a small muscle passing from the cranial border of the dorsal arch of the atlas to an area on the skull just dorsal to the foramen magnum and ventro-medial to the insertion of the major. It lies deep to the major and qualifies well for the name that Windle and Parsons (1897a) would give it - rectus capitis dorsalis profundus.

Obliquus Capitis Inferior (figs. 50, 51), or, as Windle and Parsons (1897a) would have it, obliquus colli, is a larger muscle than the rectus capitis posterior major deep to which it arises from the whole length of the lateral surface of the spine of the axis. It is inserted into the dorsal aspect of the transverse process of the atlas towards the tip. In Phasc. cinereus (Young, 1862) the origin of this muscle extends caudally to the fourth cervical spine, and in Didelphys (Coues, 1872; Osgood, 1921) to the fifth.

Obliquus Capitis Superior (figs. 50, 51) is the largest of the suboccipital muscles and radiates from its rather small origin on the tip and half of the cranial border of the transverse process of the atlas to an extensive fleshy insertion into the dorsal surface of the mastoid process deep to the sterno-mastoid, splenius capitis and longissimus capitis. The muscle is with difficulty separable into dorso-medial and ventro-lateral parts; Young (1862) notes that the muscle is double in Phasc. cinereus also.

All the suboccipital muscles are supplied by the dorsal ramus of

the first cervical nerve.

(e). Muscles of the tail.

Pubo-coccygeus has a linear fleshy origin from the inner surface of the pubis, the line extending from the middle of the symphysis to the ilio-pectineal eminence. The muscle runs medially and dorsally and a little caudally around the side of the rectum and urethra, the fibres converging somewhat to be inserted into the hypapophyses (chevron bones) of the fifth and sixth caudal vertebrae. The hypapophyses of this species are small individual bones closely related to the intervertebral disc cranial to the vertebra to which they belong as well as to the cranial end of the vertebra itself.

As is the case with the other muscles of the tail, there are very few accounts of the pubo-coccygeus of other marsupials in the literature with which comparison can be made, and most of the reports that do occur are rather sketchy anyway.

Ilio-coccygeus (fig. 44) arises mainly cranial to the pubo-coccygeus, but also to a small extent dorsal to it in the region of the ilio-pectineal eminence where the obturator nerve runs between the two; from here the origin runs cranially on the pelvic surface of the ilium to the sacro-iliac joint where a few fibres are derived from the transverse process of the first sacral vertebra. This muscle runs much more caudally than the pubo-coccygeus and so crosses the dorsal surface of the latter where the ilio-coccygeus gives rise to four or five small tendons. These pass towards the midline as they run caudally, crossing over the flexors of the tail from lateral to

medial side, and being inserted into the hypapophyses of the caudal vertebrae. Where there are five tendons they attach to these bones from the sixth to the tenth inclusive, where there are only four they are inserted either to the first four or the last four of this same series of five. The fibres arising nearest the sacrum give rise to the tendon inserted most distally, those arising more ventrally (i.e. nearer the origin of the pubo-coccygeus) provide the more proximally inserted tendons.

The muscle described by Osgood (1921) for Caenolestes appears to be very similar to this.

Ischio-coccygeus (figs. 53, 54) is the most dorsally placed of these pelvi-caudal muscles and arises from about a centimetre of the dorsum of the ischium in the region of the ischial spine, the origin of the caudal fibres being in relation with the origin of the superior gemellus. The muscle fans out to be inserted into the transverse processes of the caudal vertebrae from the second to the sixth inclusive.

In other marsupials reported this muscle usually attaches to the transverse processes of several of the proximal caudal vertebrae, the nearest to the extent of insertion found here being in Chir. variegatus where Sidebotham (1885) gives the insertion of the "coccygeus" to the first six, and in Did. virginiana (Coues, 1872) where the muscle attaches to the first five or six.

Heighway (1959) gives the name "abductor caudae lateralis" as an alternative to the name given here, while the muscle that Parsons

(1896) describes as the "abductor caudae externus" in Pet. xanthopus also appears to be the ischio-coccygeus. In Trichosurus, however, as in Caenolestes (Osgood, 1921), there is another muscle that seems to have a better claim to the name "abductor caudae lateralis".

Recto-coccygeus is a small slip of muscle arising in the midline of the dorsal surface of the rectum and passing caudally, unpaired, to be inserted into the sixth caudal hypapophysis. Coues (1872) describes the muscle in Did. virginiana attaching to the second or third caudal vertebra or both, while van den Broek (1910) reports that he did not find the muscle in the Macropodinae that he examined.

Flexor Caudae Medialis (Infra-coccygeus) (fig. 44) has a fleshy origin from the ventral surfaces of the bodies of the two sacral and the first caudal vertebrae, the intervening discs and the second caudal disc; in one animal the origin reached the second caudal vertebra as well. Long thin tendons, usually eight in number, arise from the muscle belly and their insertions into the hypapophyses continue the series begun by the tendons of the ilio-coccygeus to about the seventeenth caudal vertebra. As in the case of the other tail muscles that produce long tendons of insertion (ilio-coccygeus, flexor caudae lateralis, levator caudae lateralis) the fleshy part of the muscle is partly divisible into separate bellies each of which gives rise to one of the tendons. The slips are arranged in a dorso-ventral sequence, the most ventrally arising tendon being the first to end.

The muscle seems to vary widely in the few accounts given for

other marsupials, none of which at all closely resembles the description I have given here. Perhaps the nearest is Caenolestes (Osgood, 1921).

Flexor Caudae Lateralis (Sacro-coccygeus) lies lateral to, and at first slightly overlapped by, the flexor caudae medialis. It arises from the first sacral to the fifteenth caudal vertebrae. Where it is adjacent to the origin of the flexor caudae medialis it arises from the ventral aspects of the transverse processes, further distally beyond that muscle's origin it attaches to the bodies as well. The fleshy part of the muscle gives way to long thin tendons that are inserted into the caudal transverse processes from the ninth or tenth to the end of the tail.

Flexor Caudae Profundus extends from the disc between the first two caudal vertebrae almost to the end of the tail; it consists of fibres passing only one or two segments so is really a series of short muscles fused together. The fibres arise from the bodies and hypapophyses and are inserted into the hypapophyses situated more caudally. It lies adjacent to the midline and is at first overlapped from the lateral side by the flexor caudae medialis whose tendons cross it before insertion; further caudally beyond the origin of the flexor caudae lateralis the tendons of the latter come to lie on its superficial surface and it comes into close relation laterally with the slips of the abductor caudae medialis.

Abductor Caudae Medialis (Intertransversarii Caudae). As far as the fourth caudal transverse process these muscles simply extend from

one vertebra to the next in the manner of ordinary intertransverse muscles. From there on each consists of a medial part similarly connecting consecutive transverse processes, and a lateral part which runs two segments and overlaps the dorsal aspect of the next member of the series; after about the fifth these lateral parts are inserted through the deep fascia rather than directly into the transverse processes themselves. They extend to within two or three vertebrae of the end of the tail. I have not found these long lateral parts described for any other marsupial. The muscles similarly end a few segments short of the end of the tail in Hyps. moschatus (Heighway, 1959) and Dend. dorianus (Carlson, 1914).

Abductor Caudae Lateralis (figs. 53, 54; pl. XXXIII) lies lateral to the levator caudae lateralis and is the most lateral muscle seen on the dorsal aspect of the tail. It arises from the dorsum of the ilium near the sacro-iliac joint and from the sacral and first eight or nine caudal transverse processes, and is inserted by short tendons into the first ten or eleven caudal transverse processes. The muscle is partly divisible into two portions, a medial which comprises the ilio-sacral origin and the insertion into the first three caudal vertebrae, and a lateral with origin from the caudal transverse processes and from an aponeurosis on the lateral surface of the medial part and which produces the more caudal tendons of insertion. The tendons from the medial part become evident on its profundo-medial surface, those from the lateral on its superficio-lateral aspect.

The only other accounts I have found of a muscle that appears to correspond to this in another marsupial are those by Osgood (1921) who describes an "abductor caudae externus" in Caenolestes, and by Sidebotham (1885) who describes under the name "agitator caudae" in Chir. variegatus a muscle that sounds as if it may represent this - it seems to resemble Osgood's abductor caudae externus very closely.

Levator Caudae Lateralis (Extensor Caudae Lateralis, Externus) occupies the interval between the transverse processes and the metapophyses and is continuous with the erector spinae of the trunk, a point noted by Heighway (1939) in Hyps. moschatus and suggested for mammals in general by Howell (1936). It arises by tendinous slips from the metapophyses from the second lumbar vertebra to about the seventeenth caudal, though the last four or so of these contribute only a few fibres each. It is inserted through very long thin tendons into the metapophyses of the caudal vertebrae from the seventh to the end of the tail. The first tendons arise from the superficial surface of the muscle and run to the medial side where they embed themselves in the dense fascia between levator caudae lateralis and medialis before finally piercing the fascia to be inserted in relation with the fleshy part of the latter muscle; from about the tenth tendon onwards they come off from the lateral side and then run in the fascia covering the lateralis and the inter-accessory slips of the levator caudae medialis.

This muscle appears to be much more constant amongst the various marsupials reported than most of the other tail muscles, though some

authors give either its origin or its insertion to transverse processes instead of metapophyses.

Levator Caudae Medialis (*Extensor Caudae Medialis, Internus*) is, as noted in other marsupials by Heighway (1939) and Osgood (1921) and for mammals generally by Howell (1936), apparently a continuation into the tail of the multifidus and lies in the interval between the metapophyses and the dorsal midline. It appears to begin as a distinct muscle as far cranially as the anterior lumbar region but, I suppose, should only be called "levator caudae medialis" caudal to the sacrum. It consists of fibres that pass from the spines caudo-laterally to the metapophyses a variable number of segments further caudally: in the lumbar region the fibres pass up to five segments, at the base of the tail two or three, further into the tail only two. Closely associated with this muscle are slips connecting consecutive metapophyses to one another; these are the interaccessorii mentioned by Carlsson (1914). At first they are deep to the levator medialis, towards the tip of the tail they are lateral to it and covered by the tendons of the levator lateralis. Beyond about the twentieth caudal vertebra the slips of the levator medialis and those of the interaccessorii become inseparable, apparently being formed mainly by the fibres of the latter. They stop about three or four segments from the end of the tail, although Carlsson (1914) says that the interaccessorii stop ten vertebrae from the end of the tail.

The levators and abductors of the tail are supplied by the dorsal rami of the spinal nerves which in the tail form a dorsal nerve cord

running in the substance of the levator caudae lateralis. The pelvi-caudal muscles and the flexors receive their innervation from the ventral rami of the two sacral and six caudal nerves, the first group mainly from the second sacral nerve, the second largely through a ventral longitudinal nerve cord that begins as a branch of the second sacral and receives contributions from all the caudal nerves.

(f). Muscles of the perineum.

Sphincter Cloacae consists of fibres passing circularly around the perineal orifices and covering over the crura, bulbs and glands of the region. A considerable slip takes origin from the crus penis (or clitoridis) and runs dorsally over the bulb of the corpus spongiosum of the corresponding side to blend with the main circular part of the sphincter dorso-lateral to the anus. This apparently corresponds to the part of the sphincter that van den Broek (1910) describes attaching to the corpus cavernosum in Phascolumys, but which he says is connected to the pubic ramus in Didelphys, Dasyurus and Phascogale as well as the Phalangeridae he studied which included T. vulpecula (and, incidentally, Ph. vulpina which he apparently takes to be a separate species). Here, however, I found the muscle attached to the pelvis only indirectly through a broad aponeurotic band that binds the crus penis (or clitoridis) to the ischio-pubic ramus. Young (1879) says that none of the fibres has any attachment to the pelvis in Phasc. cinereus.

The muscle described as the sphincter cloacae in Did. virginiana

by Coues (1872) is, as he himself says, a sphincter of the rectum; the muscle that he calls the sphincter ani corresponds to the sphincter cloacae as interpreted here.

Retractor Penis is a long band of muscle with a mainly tendinous origin from the ventral surfaces of the two sacral vertebrae (in No. 5 it arose from the first caudal body and the sacro-caudal disc). It passes ventrally and caudally past the side of the rectum and is inserted into the base of the glans. The corresponding muscle in the female (retractor clitoridis) is about the same size and has the same origin; as it passes the rectum some fibres come off its dorsal border to blend with the longitudinal coat of the rectum, and it finally ends in the side wall of the cloaca beside the clitoris.

This muscle is practically identical with that described for a number of other marsupials - Hyps. moschatus (Heighway, 1939), Thyl. cynocephalus, Ph. maculata (Cunningham, 1832), Phasc. cinereus (Young, 1879) and the various marsupials examined by van den Broek (1910): Coues (1872) gives an origin sometimes as far cranially as the last lumbar vertebra in Did. virginiana. These accounts deal only with the muscle in the male, I have found no mention of fibres joining the rectum such as I found in the female of T. vulpecula.

Levator Penis is a small slip of muscle commencing from the bulb of the corpus cavernosum and running medially to become tendinous and meet its fellow, the two being inserted into the dorsum of the penis deep to and in common with the suspensory ligament after they have run for some distance towards the glans. The corresponding muscle

in the female (*levator clitoridis*) arises from the *crus clitoridis* and appears to end on the front of the urethra deep to the symphysis pubis. The muscle described here for the male seems to have the typical marsupial arrangement, it closely resembles that figured for *Didelphys* by van den Broek (1910): Cunningham (1882) gives the origin in *Thyl. cynocephalus* from the *tuber ischii*, while Coues (1872) gives part origin from the ischial ramus in *Did. virginiana* and Heighway (1959) gives the origin from the pubis in *Hyps. moschatus*.

Ischio-cavernosus forms a thick muscular covering for the enlarged end or bulb of the *crus penis* and has no external attachment. No homologous muscle was found in the female. Absence of any bony attachment seems to be the rule for this muscle in marsupials, connection with the ischium has been found, however, in *Hyps. moschatus* (Heighway, 1959), *Thyl. cynocephalus* (Cunningham, 1882) and *Phascologomys* (van den Broek, 1910).

Bulbo-spongiosus, like the above, forms a thick covering for the corresponding bulb of the *corpus spongiosum* and has no bony attachment. The muscle was not found in the female. None of the accounts I have seen of the muscle in other marsupials mentions any attachment to bone.

The perineal muscles are all supplied by the pudendal nerve.

(g). Muscles of the hind-limb and girdle.

1). Ventral pelvic muscles.

Psoas Minor (fig. 44) is a large muscle arising from the tendons of

insertion of the quadratus lumborum into the last two thoracic and the first two lumbar vertebrae, and also directly from the bodies of the first four lumbar vertebrae and the intervening discs. It ends in a strong flattened tendon that is inserted into the lateral part of the ilio-pectineal eminence.

The psoas minor is usually a large muscle in marsupials, in most cases larger than the major; the extent and position of its origin vary considerably, the most extensive reported being from the last three thoracic and first six lumbar vertebrae in Chir. variegatus (Sidebotham, 1885). The insertion, on the other hand, is constant.

In Trichosurus the psoas minor receives its nerves of supply from the ventral rami of the first four lumbar nerves; Parsons (1896) gives the second to the fifth for the psoas in general in Pet. xanthopus.

Psoas Major (fig. 44) consists of two fairly distinct parts separated by the femoral nerve. The medial part is somewhat the larger and arises from the bodies of the last two lumbar and the first sacral vertebrae (in one animal - No. 4 - there was some origin from the fourth lumbar as well), its origin being a caudal continuation of that of the psoas minor: it runs caudally medial to the iliacus and forms the main ilio-psoas tendon into the lateral side of which many of the fibres of the iliacus are inserted and which finally attaches to the tip and back of the lesser trochanter of the femur. The lateral part arises from the bodies of the last three lumbar vertebrae and runs across the ventral surface of the

iliacus towards its lateral side, becoming separated from the medial part by a narrow triangular interval. It forms the lateral aponeurotic portion of the combined ilio-psoas insertion which attaches anteriorly and distally in relation to the rest of the insertion, the portion of the attachment derived from the lateral part of the psoas reaching lowest of all. Carlsson (1914) gives the origin of the psoas major from the last lumbar vertebra only, as in Dend. dorianus.

The origin given here seems to correspond fairly closely in longitudinal extent with that given for most of the other marsupials reported, the nearest being Ph. maculata (Cunningham, 1882), Pet. penicillata (Carlsson, 1914), Did. virginiana (Coues, 1872) and Gaenolestes (Osgood, 1921). In N. typhlops (Thompson and Hillier, 1905), Hyps. moschatus (Heighway, 1939), and Phasc. wombata and S. ursinus (Macalister, 1870) the origin is much more extensive and reaches the caudal thoracic vertebrae.

Cunningham's (1882) account of the muscle in Thyl. cynocephalus provides the only other mention I have found of a psoas major consisting of two parts; from his report the two portions seem something like the two I found in Trichosurus but the posterior part, which I take to correspond to my medial, is inserted independently of the iliacus. MacCormick (1887) mentions three parts to the psoas major in Das. viverrinus.

The psoas major in T. vulpecula is supplied by the fourth and fifth lumbar nerves as well as several branches from the femoral

nerve.

Iliacus (fig. 44) has a fleshy origin from the whole of the iliac fossa except for a small area at the cranial end where the origin of the erector spinae encroaches from the iliac crest, and to a slight extent from the fascia that separates it from the gluteal muscles beyond the ventral border of the ilium - a layer I have called the "ilio-gluteal fascia". The iliacus is inserted in the region of the lesser trochanter of the femur, partly through the tendinous insertions of the two parts of the psoas major and partly by fleshy fibres in between these. It is supplied by the femoral nerve.

Part origin from the layer corresponding to my "ilio-gluteal fascia" has also been described for Hyps. moschatus (Heighway, 1939) and Das. viverrinus (MacCormick, 1887). Macalister (1872b) describes the muscle as bipartite in Phasc. cinereus.

2). Muscles of the gluteal region.

Agitator Caudae (Femoro-coccygeus) (fig. 52; pl. XXXII) arises from the continuation of the thoraco-lumbar fascia into the tail opposite the second to fifth caudal vertebrae, and also by a deeper origin that lies ventral to the abductor caudae lateralis and springs from the second, third and fourth caudal transverse processes. It is inserted into the dorsal aspect of the femur from the base of the greater trochanter to a point more than two thirds of the way to the genicular end. The cranial border of the muscle is separable only with some difficulty from the gluteus maximus. It is supplied by the inferior gluteal nerve.

Imperfect separation of the agitator caudae from the gluteus maximus is a common feature of marsupials. Some accounts of this muscle do not make it clear whether or not both superficial and deep origins are present as described here, they appear to be so in Ph. maculata and Thyl. cynocephalus (Cunningham, 1882); the deep origin is definitely absent in Das. viverrinus (MacCormick, 1887). Windle and Parsons (1897b) describe in M. rufus a deep origin for part of the gluteus maximus from the anterior caudal transverse processes which may be the same structure as I have described since they do not mention a separate agitator caudae.

Thompson and Hillier (1905) describe for N. typhlops, under the name "femoro-coccygeus", a muscle arising from the ischium and passing to the patella that I feel may well be the quadratus femoris which they say is absent. The muscle that Sidebotham (1885) calls "agitator caudae" in Chir. variegatus appears to correspond to the muscle I have described as the abductor caudae lateralis, the real agitator caudae probably being included in the gluteus maximus.

Windle and Parsons (1897a) favour the name "caudo-femoralis" for this muscle, and Parsons (1905) uses this name for it in his account of Choer. castanotis. Heighway (1959), Carlsson (1914) and Leche (1874-1900) use this name, however, as an alternative to "ischio-femoralis", and the same apparently applies to Osgood (1921) and Thompson and Hillier (1905).

Parsons (1905) gives the nerve supply from the superior gluteal nerve in Choer. castanotis.

Figure 52 (cf. pl. XXXII). Dorso-lateral aspect of gluteal region and thigh. $\times \frac{7}{8}$.

Figure 53 (cf. pl. XXXIII). Gluteal region and proximal part of thigh after the removal of most of the superficial part of gluteus maximus, agitator caudae, gluteus medius, biceps femoris, semitendinosus and sartorius. $\times \frac{7}{8}$.

Figure 54. Gluteal region and proximal part of thigh after the removal of the same muscles as in figure 53 and the reflection of piriformis, ischio-femoralis and the vertebral origin of biceps femoris. $\times \frac{7}{8}$.

Ab.W.	- Abdominal wall.
A.C.L.	- Abductor caudae lateralis.
Ag.C.	- Agitator caudae.
Ag.C.d.	- Deep origin of agitator caudae.
Bi.Ca.	- Caudal (vertebral) origin of biceps femoris.
Bi.Ca.l.	- Lateral division of caudal head of biceps femoris.
Bi.Is.	- Ischial head of biceps femoris.
Cl.	- Cloaca.
Ge.S.	- Gemellus superior.
Gl.f.	- Gluteal fascia.
Gl.max.	- Gluteus maximus.
Gl.max.d.	- Deep part of gluteus maximus.
Gl.max.s.	- Insertion of superficial part of gluteus maximus.
Gl.med.d.	- Insertion of deep part of gluteus medius.
Gl.med.f.o.	- Area of origin of gluteus medius from the fascia on levator caudae lateralis.
Gl. med.s.	- Insertion of superficial part of gluteus medius.
Gl.min.	- Gluteus minimus.
I-G.f.	- "Ilio-gluteal fascia".
Il-co.	- Ilio-coccygeus.
Il-ps.	- Ilio-psoas.
Int.	- Tendinous intersection common to caudal head of biceps femoris and semitendinosus.
Is-co.	- Ischio-coccygeus.
Is-f.	- Ischio-femoralis.
Ob.In.	- Obturator internus.
Ob.In.&Ge.I.	- Obturator internus and gemellus inferior.
Pir.	- Piriformis.
P-s-m.	- Preseminembranosus.
Q.F.	- Quadratus femoris.
R.F.	- Rectus femoris.
Sart.	- Sartorius.
Sart.m.	- Thin medial part of sartorius.
S-m.	- Semimembranosus.
S-t.	- Origin of semitendinosus.
V.Lat.	- Vastus lateralis.

Fig. 52.

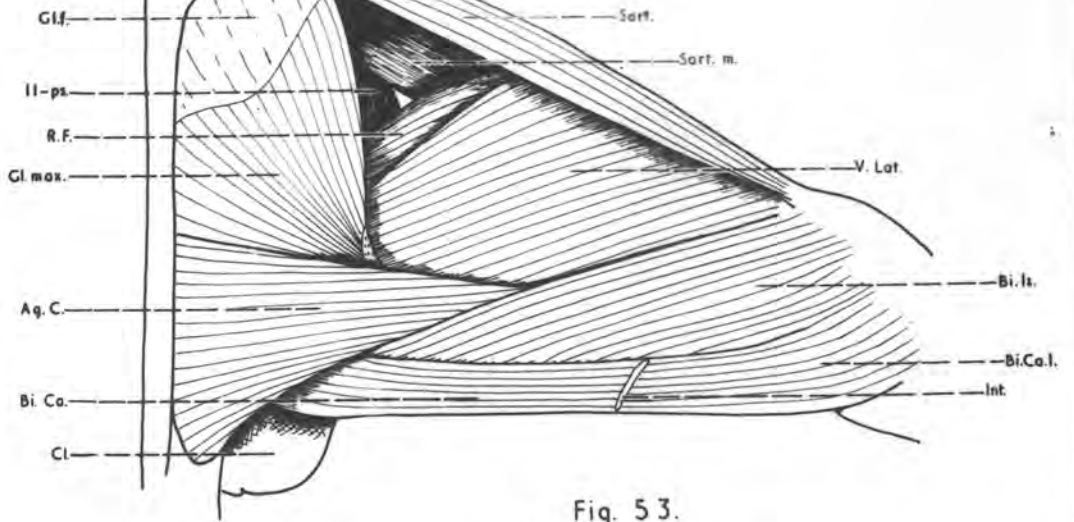


Fig. 53.

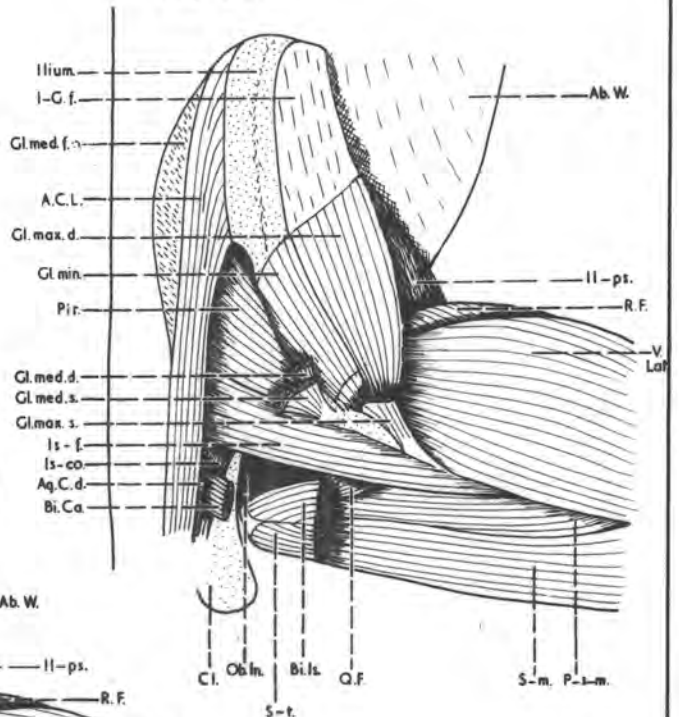


Fig. 54.

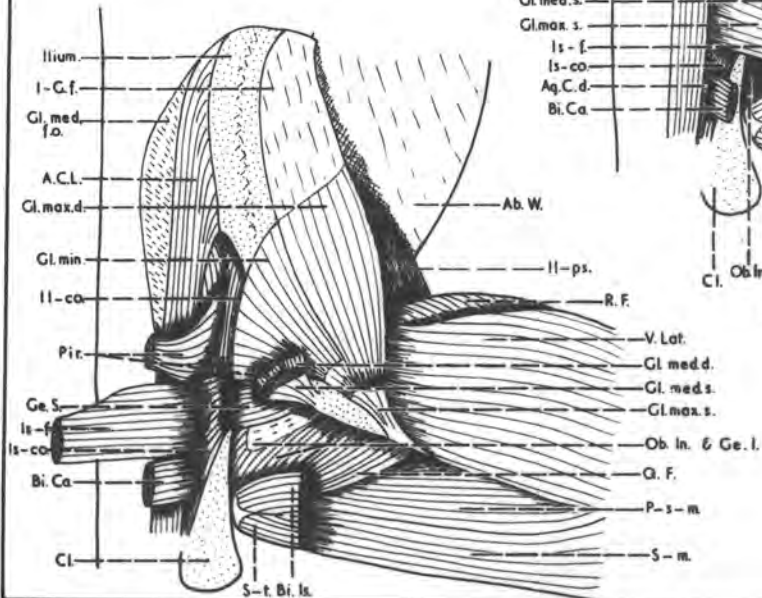
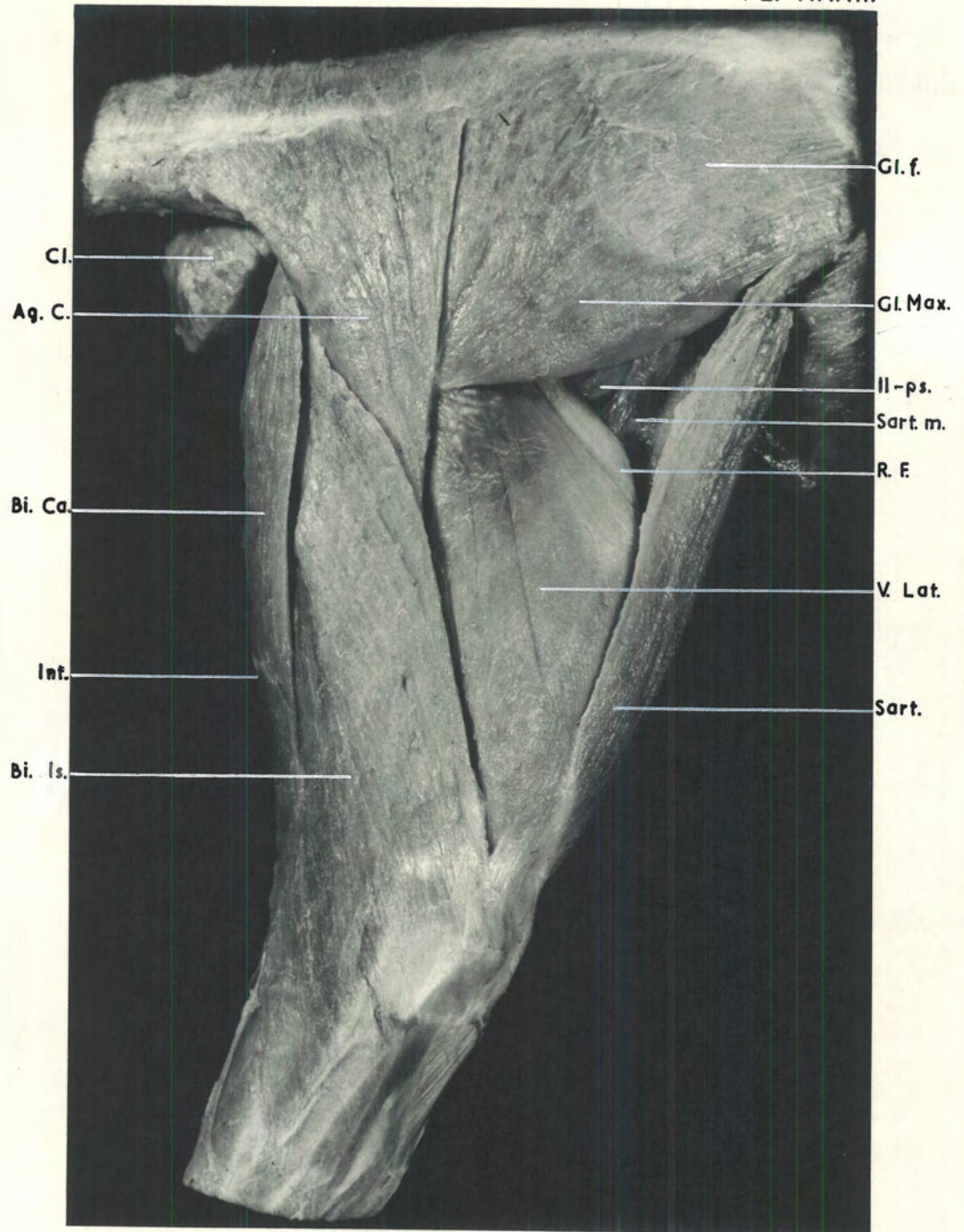


Plate XXXII (cf. fig. 52). Dorso-lateral view of gluteal
region and thigh. $\times 1\frac{1}{4}$.

- Ag.C. - Agitator caudae.
- Bi.Ca. - Caudal (vertebral) head of biceps femoris.
- Bi.Is. - Ischial head of biceps femoris.
- Cl. - Cloaca.
- Gl.f. - Gluteal fascia.
- Gl.Max. - Gluteus maximus (superficial part).
- Il-ps. - Ilio-psoas.
- Int. - Tendinous intersection common to caudal
head of biceps femoris and semitendinosus.
- R.F. - Rectus femoris.
- Sart. - Sartorius.
- Sart.m. - Thin medial part of sartorius.
- V.lat. - Vastus lateralis.



Gluteus Maximus (Ecto-gluteus)(figs. 52, 53, 54; pls. XXXII, XXXIII) is a thin sheet of muscle in the same plane as the agitator caudae. It arises from the continuation of the thoraco-lumbar fascia in the proximal part of the tail, from the gluteal fascia over the gluteus medius and from the distal border of the "ilio-gluteal fascia" between the gluteus medius and the iliacus: this last part of the origin forms a deep portion of the muscle that is continuous with the main superficial part by a folding of the sheet around the lateral edge of the gluteus medius onto its deep surface. The deep part extends as far as the gluteus minimus. Most of the fibres of the "ilio-gluteal fascia" run in such a direction as to give it the appearance of being an aponeurosis of origin for this deep portion of the gluteus maximus from the ventral border of the ilium, an aponeurosis which then has the gluteus medius taking part origin from its outer surface, the iliacus from its inner surface and the sartorius from its free ventro-lateral edge. The muscle is inserted into the lateral and anterior aspects of the base of the greater trochanter of the femur, the insertion of the deep part reaching most anteriorly. The insertion is fused with that of the gluteus minimus.

The superficial part of the muscle is supplied by the inferior gluteal nerve; the deep portion and the fold around the edge of the gluteus medius derive their supply from the superior gluteal nerve and, I presume, represent the tensor fasciae latae.

Part origin from the gluteal fascia has also been described in

Ph. maculata (Cunningham, 1882), M. giganteus and M. vallabiensis (Haughton, 1866), Das. viverrinus (MacCormick, 1887) and Chir. variegatus (Sidebotham, 1885); in some marsupials there is some origin directly from the ilium, in others the origin is restricted to the vertebrae and thoraco-lumbar fascia.

Folding of the gluteus maximus around the edge of the medius to join the minimus occurs in Ph. maculata (Cunningham, 1882), Did. virginiana (Coues, 1872) and Chir. variegatus (Sidebotham, 1885). It seems possible that these authors have included the gluteus minimus in what I have called the deep part of the maximus, and have described the muscle corresponding to my gluteus minimus as the gluteus quartus. Whether or not this is so I can see no good reason for doing the same thing in Trichosurus and have accordingly not described any gluteus quartus.

Tensor fasciae latae is usually not present as a separate muscle in marsupials, being fused with the gluteus maximus: Carlsson (1914) says it is joined with the sartorius in Pet. penicillata, A. rufescens and T. vulpecula, but I cannot agree with this as I found no branch of the superior gluteal nerve to the sartorius; Parsons (1896) says the same for Pet. xanthopus but gives no supply from the superior gluteal nerve. Macalister (1872a) mentions a separate tensor fasciae latae in S. ursinus, as do Haughton (1866) and Alezais (1901) in Macropus.

Gluteus Medius (Meso-gluteus) is the largest of the gluteal muscles, and arises from the gluteal surface of the ilium, the septa

separating it from levator caudae lateralis and abductor caudae lateralis, the "ilio-gluteal fascia" and the deep surface of the gluteal fascia. The part from the ilium and the adjacent part of the "ilio-gluteal fascia" forms an incompletely separated deep section of the muscle which constitutes the middle area of the deep surface and is surrounded on three sides (i.e. all but the deep aspect) by the much larger superficial part. The two portions of the muscle become tendinous on their opposed surfaces and the tendinous layers fuse along their medial borders; the superficial part is inserted into the lateral aspect and the upper part of the posterior border of the greater trochanter, the deep part somewhat more anteriorly into the front part of the summit of the same trochanter. The nerve supply comes from the superior gluteal nerve.

Some degree of separation into deep and superficial parts occurs in this muscle in the majority of marsupials reported and was noted previously in Trichosurus by Carlsson (1914).

Gluteus Minimus (Ento-gluteus)(figs. 53, 54; pl. XXXIII). This small muscle is, as noted by Carlsson (1914), quite separate from the gluteus medius, and its caudal edge lies deep to the piriformis. Its origin continues the line of origin of the deep part of the gluteus maximus, thus it derives a few fibres from the "ilio-gluteal fascia" but has most of its origin from the hip-bone dorsal to the acetabulum and extending caudally as far as the ischial spine. It is inserted into the distal part of the front of the greater trochanter where its lateral edge is united with the gluteus

maximus.

Carlsson (1914) also mentions a small *gluteus quartus* (*scansorius*) for Trichosurus but gives no details.

Gluteus minimus is usually separate in the marsupials, though it is to a greater or lesser extent fused with the *gluteus medius* in Dendrolagus (Carlsson, 1914), Sarcophilus (Macalister, 1870) and Phascolomys (Macalister, 1870; Sonntag, 1922).

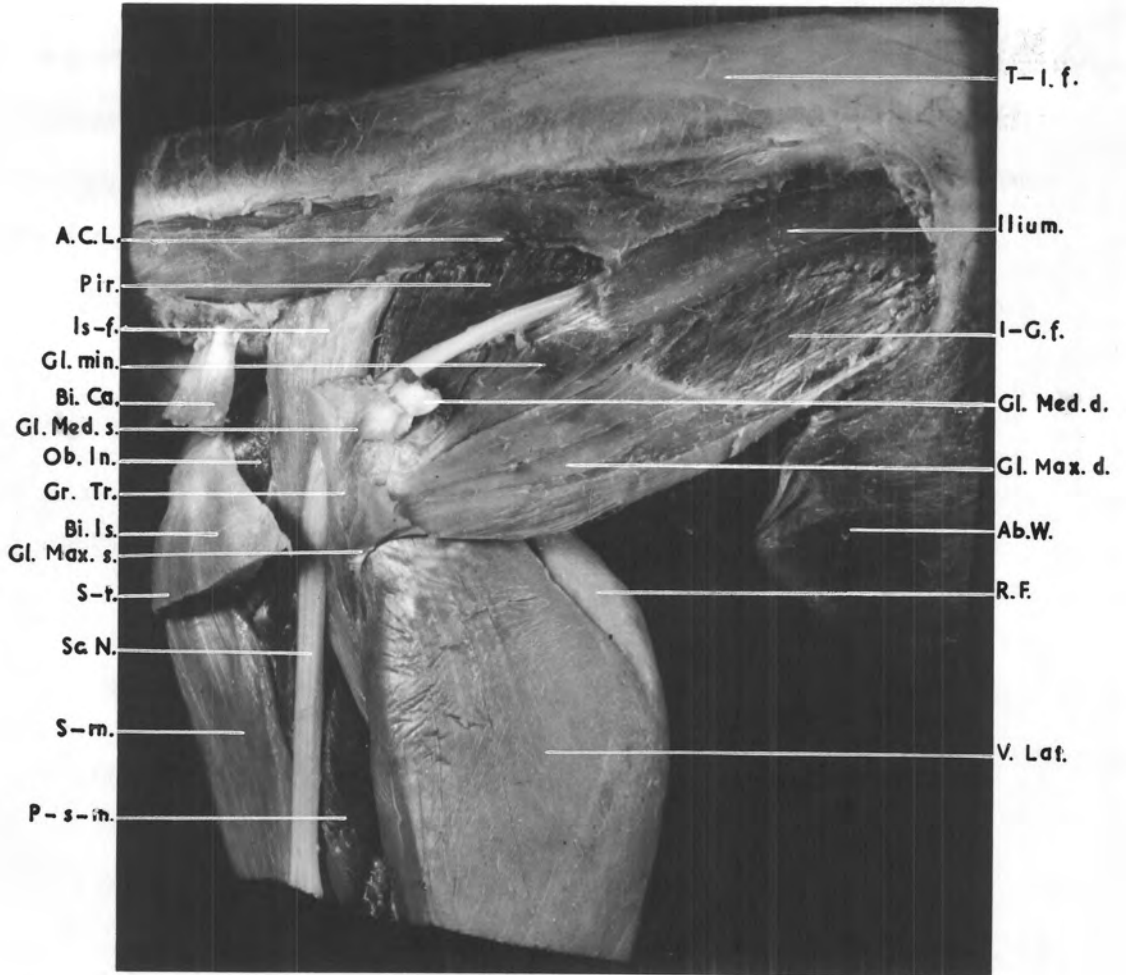
A *gluteus quartus* has been described for most of the marsupials reported in the literature.

As would be expected, the innervation of the *gluteus minimus* in Trichosurus is derived from the superior gluteal nerve. Ischio-femoralis (Caudo-femoralis) (fig. 53; pl. XXXIII) lies superficial to the obturator internus, the gemelli, the quadratus femoris and the presemimembranosus. It is covered by the agitator caudae and crossed by the sciatic nerve; in the same plane more caudally lies the vertebral origin of the biceps femoris and, just superficial to this, is the deep origin of the agitator caudae. It arises from the transverse processes of the first three caudal vertebrae and is inserted into the back of the femur from almost the tip of the greater trochanter to a point nearly half way down the shaft. The hamstring nerve lies deep to it and provides its innervation.

Carlsson (1914) gives the origin in T. vulpecula, as in Dend. dorianus, Pet. penicillata and A. rufescens, from the ramus and tuberosity of the ischium, saying that the muscle lies ventral to

Plate XXXIII (cf. fig. 53). Deep dissection of gluteal region and lateral side of thigh. Agitator caudae, the superficial part of gluteus maximus, gluteus medius and sartorius are largely removed and biceps femoris and semitendinosus are cut off close to their origins. $\times 1\frac{1}{2}$.

- | | |
|-----------|---|
| Ab.W. | - Abdominal wall. |
| A.C.L. | - Abductor caudae lateralis. |
| Bi.Ca. | - Caudal (vertebral) origin of biceps femoris. |
| Bi.Is. | - Ischial origin of biceps femoris. |
| Gl.Max.d. | - Deep part of gluteus maximus. |
| Gl.Max.s. | - Insertion of superficial part of gluteus maximus. |
| Gl.Med.d. | - Insertion of deep part of gluteus medius. |
| Gl.Med.s. | - Insertion of superficial part of gluteus medius. |
| Gl.min. | - Gluteus minimus. |
| Gr.Tr. | - Greater trochanter of femur. |
| I-G.f. | - "Ilio-gluteal fascia". |
| Is-f. | - Ischio-femoralis. |
| Ob.In. | - Obturator internus. |
| Pir. | - Piriformis. |
| P-s-m. | - Presemimembranosus. |
| R.F. | - Rectus femoris. |
| Sc.N. | - Sciatic nerve. |
| S-m. | - Semimembranosus. |
| S-t. | - Origin of semitendinosus. |
| T-l.f. | - Thoraco-lumbar fascia. |
| V.Lat. | - Vastus lateralis. |



A.C.L.

Pir.

Is-f.

Gl. min.

Bi. Ca.

Gl. Med. s.

Ob. In.

Gr. Tr.

Bi. Is.

Gl. Max. s.

S-r.

Sc. N.

S-m.

P-s-in.

T-l.f.

Ilium.

I-G.f.

Gl. Med. d.

Gl. Max. d.

Ab.W.

R.F.

V. Laf.

the sciatic nerve from a branch of which it is supplied. If it were not for the latter remarks one would wonder whether she was perhaps describing the quadratus femoris which she does not otherwise mention.

A vertebral origin for this muscle also occurs in Hyps. moschatus (Heighway, 1939) and Caenolestes (Osgood, 1921), while it arises from the ischium in M. rufus (Windle and Parsons, 1897b), Pet. xanthopus (Parsons, 1896) and N. typhlops (Thompson and Hillier, 1905). In Das. viverrinus (MacCormick, 1887) the origin is part vertebral and part ischial, while for Ph. maculata and Thyl. cynocephalus Cunningham (1882) gives it from the great sacro-sciatic ligament, and a similar origin to the last is given for Myrmecobius by Leche (1874-1900). In these same accounts the nerve supply is recorded as hamstring nerve in Petrogale and Macropus, great sciatic in Notoryctes and Myrmecobius.

Cunningham (1882) and Thompson and Hillier (1905) indicate that the muscle is subject to some confusion, sometimes being described as the quadratus femoris; one wonders whether perhaps on occasion the reverse may happen also.

Piriformis (fig. 53; pl. XXXIII) arises from the transverse processes and to a lesser extent from the sides of the bodies of the second sacral and first caudal vertebrae; its tendon of insertion appears first on the ventral surface and cranial edge and is finally attached to the medial part of the summit of the greater trochanter of the femur medial to the attachment of the deep part of the

gluteus medius, and to the medial side of the trochanter as far as the capsule of the hip joint. It appears to be supplied mainly, if not entirely, by the second sacral nerve. As seems to be the usual condition in marsupials the sciatic nerve runs on the dorsal surface of the piriformis, though in Hyps. moschatus Heighway (1939) found the nerve ventral to the muscle.

In the marsupials where the muscle has been described the origin varies somewhat, usually occupying one or more of the group of vertebrae formed by the sacral and first caudal; in Caenolestes Osgood (1921) gives some origin from the ilium. According to Macalister (1870) it is fused with the gluteus medius in Phalangista, as it is in N. typhlops (Thompson and Hillier, 1905). Obturator Internus (fig. 54) has an extensive origin from the inner surfaces of the body of the pubis, the pubic rami and the ischial ramus, the attachment not quite reaching the cranial border of the superior pubic ramus. There is no obturator membrane. The tendon of insertion develops on the surface of the muscle adjacent to the bone and turns sharply around the dorsal margin of the ischium where it is separated from the bone of the lesser sciatic notch by a large bursa; the bone is smooth here and accordingly the tendon is not grooved. The insertion is into the upper part of the trochanteric pit of the femur. The nerve of supply is derived from the lumbosacral plexus in company with the nerve to quadratus femoris.

Ridges which groove the tendon of obturator internus are present on the related surface of the ischium in Did. virginiana (Coues,

1872), Pet. xanthopus (Parsons, 1896) and Das. viverrinus (MacCormick, 1887), but not in Hyps. moschatus (Heighway, 1939), Ph. maculata or Thyl. cynocephalus (Cunningham, 1882). The muscle is said to be absent in N. typhlops (Thompson and Hillier, 1905), Phascolomys (Macalister, 1870; Sonntag, 1922) and Caenolestes (Osgood, 1921). In one paper (1870) Macalister says the muscle is absent in S. ursinus, in another (1872a) he reports finding a small slip representing it in that species.

Gemelli (fig. 54), as seems usual in marsupials, are relatively very large muscles. They arise from the dorsal surface of the ischium from a point in line with the caudal part of the acetabulum to the ischial tuberosity; they are fused with one another deep to the obturator internus tendon, a relationship that they maintain practically throughout, there being only a very slight superficial overlap of the cranial edge of the tendon by the superior gemellus. Most of the insertion is into the trochanteric pit of the femur, only a minority of the fibres attaching to the obturator internus tendon. The inferior gemellus also fuses with the obturator externus near its insertion. Both the gemelli are supplied by the nerve to quadratus femoris which runs through them as in Ph. maculata (Cunningham, 1882).

Quadratus Femoris (fig. 54) derives its fibres from the ischial tuberosity and from the tendon of origin of the presemimembranosus, and passes to an insertion into the lesser trochanter and a ridge that extends distally from it for rather less than a centimetre and

which should probably be considered as part of the trochanter.

This muscle is fairly typical of marsupials in general, the most similar insertion being that given for Das. viverrinus by MacCormick (1887). In a number of others the muscle attaches to the greater trochanter, while in Hypsiprymnodon (Heighway, 1939) and Macropus (Haughton, 1866) the insertion is half way down the back of the femur. In most cases the origin is from the ischium; Macalister (1872a) gives some vertebral origin in S. ursinus, but in an earlier report (1870) he indicated that the muscle was partly fused with the adductor magnus in that species, as he also noted in Phasc. cinereus (1872b) and as Cunningham (1882) reports for Thyl. cynocephalus. Sonntag (1922) and Young (1882) both give the origin in Phasc. cinereus from the great sciatic ligament; from the account of the latter author the muscle described could be the ischio-femoralis, and perhaps the same is the case in Macalister's later account of Sarcophilus. There is no quadratus femoris present in Phascologomys (Sonntag, 1922; Macalister, 1870) or Notoryctes (Thompson and Hillier, 1905).

This muscle receives a special nerve from the lumbo-sacral plexus, that arises with the nerve to obturator internus and the hamstring nerve. Leche (1874-1900) gives the supply from the obturator nerve in Myrmecobius and misquotes Cunningham (1882) as giving the same for Cuscus and Thylacinus.

5). Muscles of the thigh.

Sartorius (figs. 52, 55; pls. XXXII, XXXIV) takes origin from the

Figure 55 (cf. pl. XXXIV). Medial aspect of thigh. $x\frac{3}{4}$.

Figure 56 (cf. pl. XXXV). Medial aspect of thigh after the removal of sartorius and gracilis. $x\frac{3}{4}$.

- | | |
|-------------|---|
| Ab.W. | - Abdominal wall. |
| Ad.M. | - Adductor magnus. |
| Bi.m. | - Medial division of caudal (vertebral) head of biceps femoris. |
| Fl.T.&Gast. | - Flexor tibialis and gastrocnemius (medial head). |
| F.Sh. | - Femoral sheath. |
| G. | - Gracilis. |
| G.ap. | - Thin fascial part of gracilis insertion. |
| Gast. | - Gastrocnemius (medial head). |
| Il-ps. | - Ilio-psoas. |
| M.B. | - Marsupial bone. |
| M.lig. | - Medial ligament of knee. |
| Pat. | - Patella. |
| Pec. | - Superficial (long) head of pectineus. |
| Pop. | - Popliteus. |
| P.Sym. | - Pubic symphysis. |
| R.F. | - Rectus femoris. |
| Sart. | - Sartorius. |
| S-m. | - Semimembranosus. |
| S-t. | - Semitendinosus. |
| Ti.Tu. | - Tibial tubercle |
| V.Med. | - Vastus medialis. |

Fig. 55.

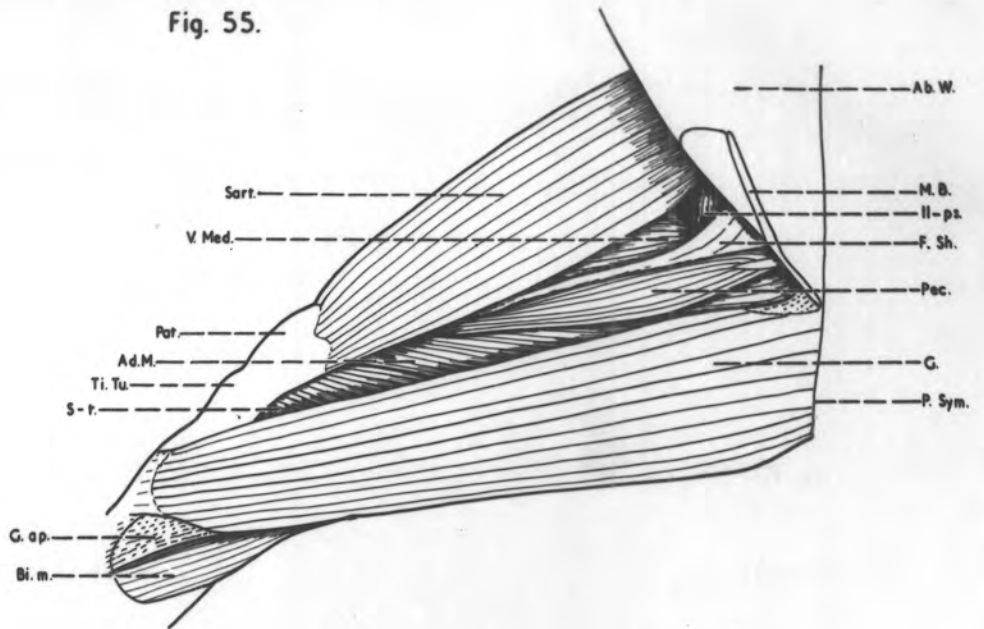


Fig. 56.

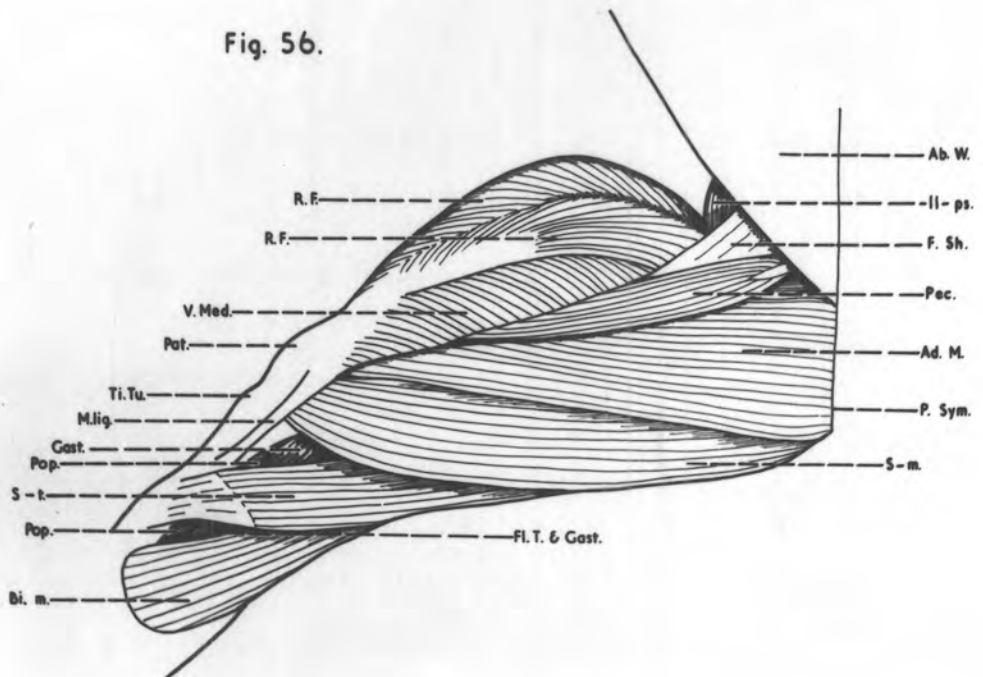
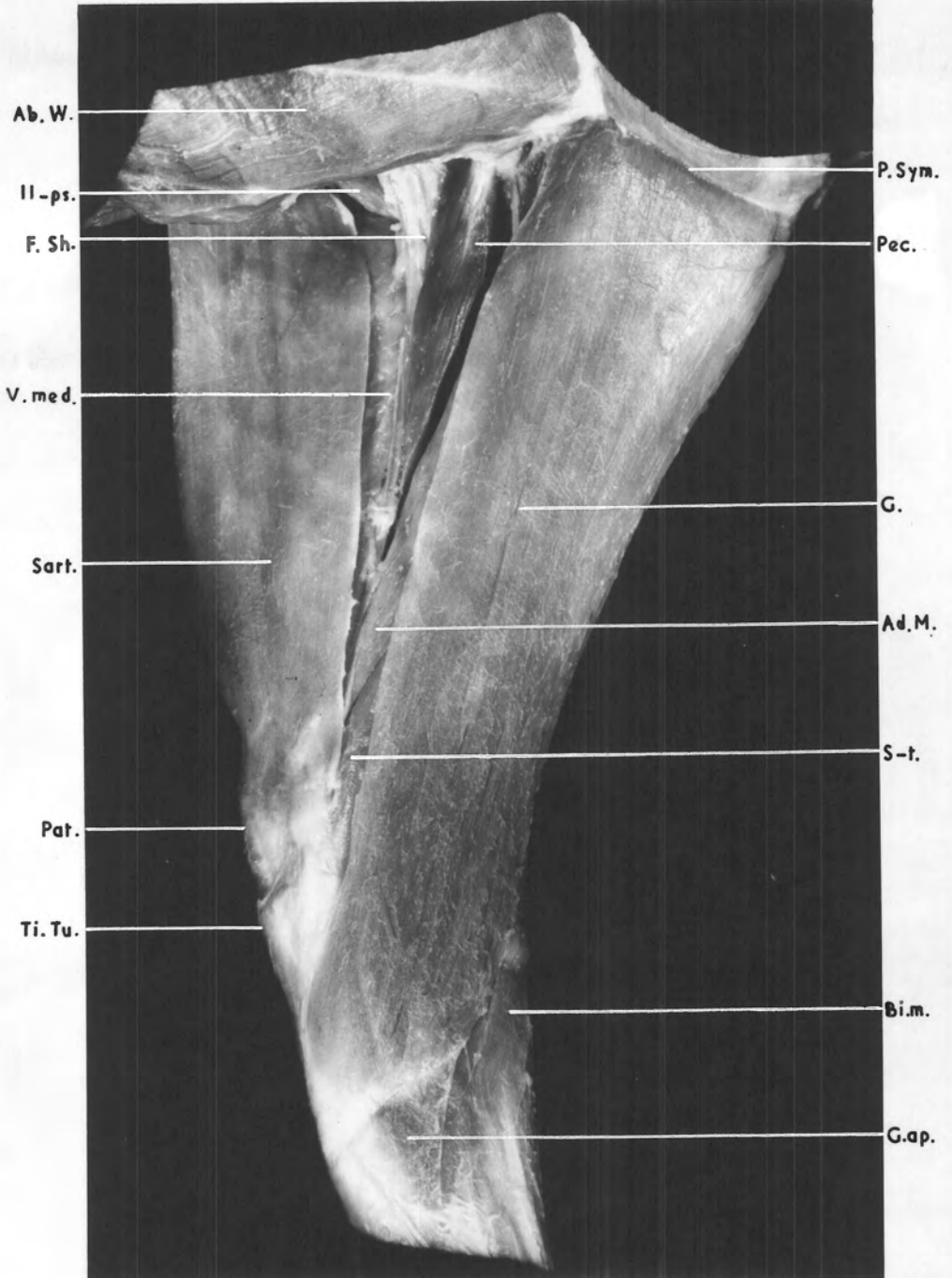


Plate XXXIV (cf. fig. 55). Superficial view of muscles of medial side of thigh. $\times 1\frac{1}{4}$.

- Ab.W. - Abdominal wall.
- Ad.M. - Adductor magnus.
- Bi.m. - Medial division of caudal (vertebral) head of biceps femoris.
- F.Sh. - Femoral sheath.
- G. - Gracilis.
- G.ap. - Thin fascial part of gracilis insertion.
- Il-ps. - Ilio-psoas.
- Pat. - Patella.
- Pec. - Superficial (long) head of pectineus.
- P.Sym. - Pubic symphysis.
- Sart. - Sartorius.
- S-t. - Semitendinosus.
- Ti.Tu. - Tibial tubercle.
- V.med. - Vastus medialis.



anterior superior iliac spine and the edge of the "ilio-gluteal fascia" where the latter is intimately bound to the lateral part of the inguinal ligament. The muscle is folded upon itself along the anterior border of the thigh so that it has a narrow but thick portion on the lateral aspect of the thigh and a thinner but much wider portion on the medial side of this segment of the limb; the lateral part is inserted into the superficial surface of the quadriceps tendon, the thinner medial part into the fascia on the medial side of, and extending slightly below, the knee. Thompson and Hillier (1905) say that the muscle is thin and ill-defined in Trichosurus, while Carlsson (1914) explains the fact that the muscle does not cover the saphenous nerve by reference to its small width: neither of these comments is applicable to the sartorius in the animals studied by me.

The attachments of this muscle vary very little in the published accounts I have seen for other marsupials, except in N. typhlops where Carlsson (1905) gives the origin from the marsupial bone and Thompson and Hillier (1905) describe it coming from the metapophysis of the fourth lumbar vertebra.

As noted by Cunningham (1881a, 1882) in Thyl. cynocephalus and Ph. maculata, so in T. vulpecula the sartorius is supplied by the femoral (anterior crural) nerve. Osgood (1921) gives the innervation in Caenolestes from the saphenous nerve.

Quadriceps Femoris (figs. 52, 56, 57; pls. XXXII, XXXV) consists of the usual parts, though the three vasti are fused into a single mass

of which the vastus lateralis forms the major portion, an arrangement that seems usual in marsupials.

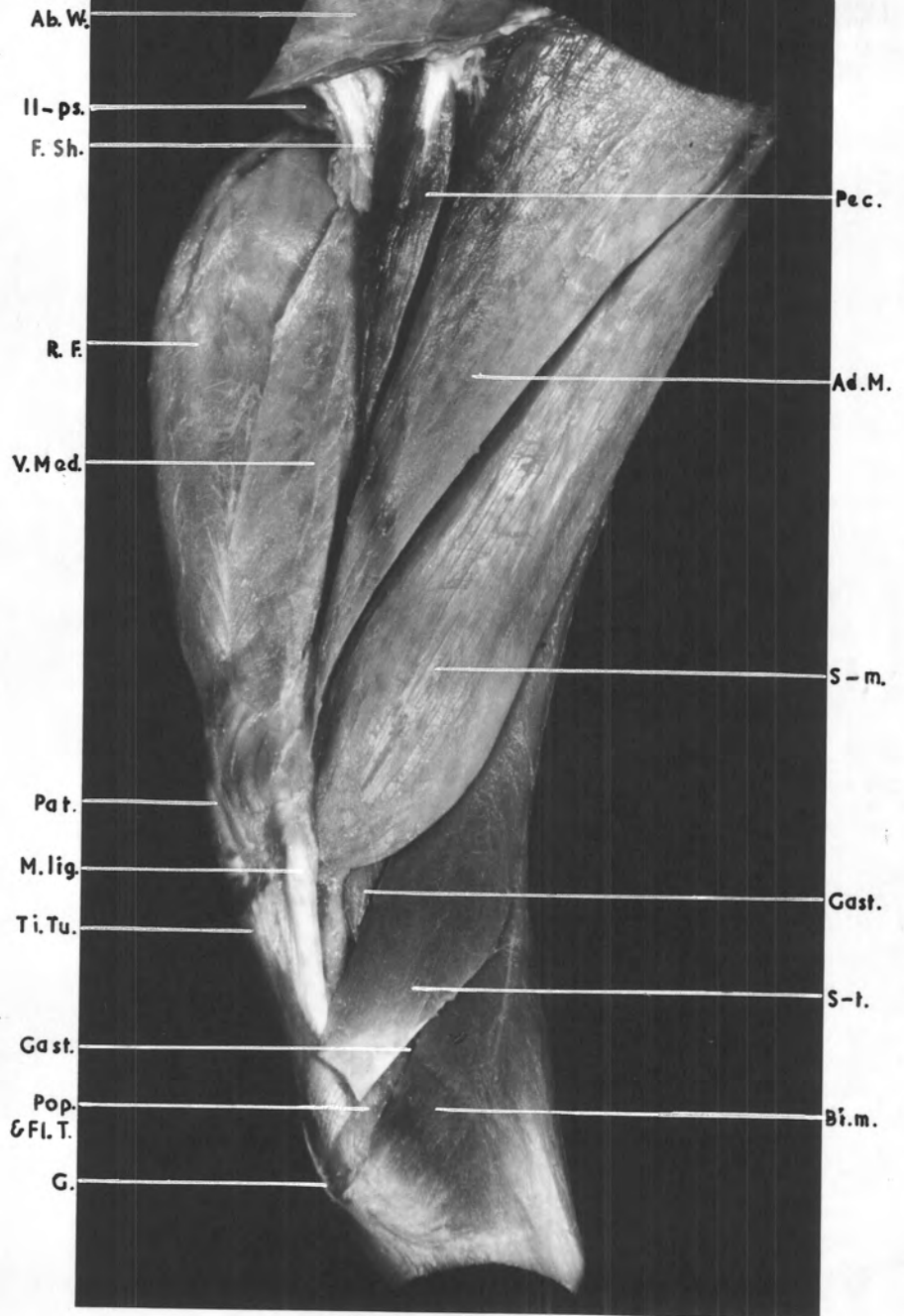
The rectus femoris arises from the capsule of the hip joint and from the ilium cranial and dorsal to the acetabulum. The main part of the origin is by tendon and represents the straight head while the more dorsal part, which is tendinous and fleshy and is separable with some difficulty from the rest for a short distance, apparently represents the reflected head.

As mentioned above, the vasti are inseparable, the medial arising from the femur above, in front of and below the lesser trochanter, from the linea aspera and from the proximal two thirds of the medial surface of the shaft. The lateral vastus arises from the front of the greater trochanter, the gluteal tuberosity, the linea aspera, the proximal half of the lateral supracondylar line and much of the lateral surface of the femur. The vastus intermedius continues this origin across the front of the bone, its origin stopping inferiorly about one and a half centimetres above the knee.

The tendons of the parts join together, that of the medial vastus remaining separate from the rectus longer than that of the lateral. The combined quadriceps tendon attaches partly to the top of the patella through which it extends onwards as the ligamentum patellae to the tubercle of the tibia, and partly, through expansions on the sides of the patella, to the condyles of the tibia, the medial ligament of the knee and the fascia of the leg.

Plate XXXV (of. fig. 56). Medial view of thigh after the removal
of sartorius and gracilis. $\times 1\frac{1}{4}$.

- | | |
|------------|--|
| Ab.W. | - Abdominal wall. |
| Ad.M. | - Adductor magnus. |
| Bi.m. | - Medial division of caudal (vertebral) head
of biceps femoris. |
| F.Sh. | - Femoral sheath. |
| G. | - Insertion of gracilis (cut). |
| Gast. | - Gastrocnemius (medial head). |
| Il-ps. | - Ilio-psoas. |
| M.lig. | - Medial ligament of knee. |
| Pat. | - Patella. |
| Pec. | - Superficial (long) head of pectineus. |
| Pop.&Fl.T. | - Popliteus and flexor tibialis. |
| R.F. | - Rectus femoris. |
| S-m. | - Semimembranosus. |
| S-t. | - Semitendinosus. |
| Ti.Tu. | - Tibial tubercle. |
| V.Med. | - Vastus medialis. |



Straight and reflected heads of the rectus femoris are present in Das. viverrinus (MacCormick, 1887), Thyl. cynocephalus, Ph. maculata (Cunningham, 1882), Ph. orientalis, Ps. peregrinus (Sonntag, 1922), Phasc. cinereus - which has no patella - (Young, 1882; Sonntag, 1922), Per. lagotis (Owen, 1859-1847, 1868) and N. typhlops (Thompson and Hillier, 1905). In some other marsupials the two heads are reported as united or the reflected head is not represented. Carlsson (1914) describes a head of origin of the rectus from the anterior superior iliac spine in Dend. dorianus, Pet. penicillata and A. rufescens, which she says is characteristic of some terrestrial Macropodidae; this probably corresponds to the extra head from the ventral border of the ilium given by Parsons (1896) for Pet. xanthopus.

The whole quadriceps is supplied by the femoral nerve, thus agreeing with the findings of Parsons (1896) and Cunningham (1881a, 1882) in the marsupials they studied (v.s.).

Biceps Femoris (figs. 52, 53, 55, 56; pls. XXXII, XXXIII, XXXIV, XXXV) is a complex muscle comprising two more or less distinct parts. The main or ischial part arises from the ischial tuberosity in common with the semitendinosus and, passing distally, spreads out somewhat to be inserted into the lateral side of the capsule of the knee and the fascia of the lateral side of the leg for about two centimetres, gaining through the fascia an indirect attachment to the anterior border of the tibia. The second (caudal or vertebral) part arises by a small tendinous origin from the transverse process

of the third caudal vertebra and runs down the thigh as a strong fleshy band that ends rather more than half way to the knee in a well marked tendinous intersection that is common to this part of the biceps and the semitendinosus: in one animal just prior to joining the intersection it gave a few fibres to the caudal border of the main ischial part of the muscle. The band issues again from the distal side of the intersection and soon divides into two slips or layers. The lateral passes to the lateral side of the leg and is inserted into the deep fascia for about two centimetres distal to and continuous with the ischial part; the medial goes to the medial side of the leg where it has an aponeurotic attachment to the anterior border of the tibia distal to the semitendinosus and partly overlapped by the gracilis. Carlsson (1914) includes this medial insertion as part of the semitendinosus.

A very similar arrangement of the biceps is present in Did. virginiana where Coues (1872) describes the vertebral part as a separate muscle, the "cruro-coccygeus", in Chir. variegatus (Sidebotham, 1885) in which the author gives the vertebral portion as part of the semitendinosus, and in Das. viverrinus (MacCormick, 1897) where the lateral insertion of the caudal head is very small and there is also present a bicipiti accessorius (of Haughton).

The muscle consists of similarly arranged parts, but without the presence of a tendinous intersection, in Ph. orientalis and Ps. peregrinus as described by Sonntag (1922) who, however, gives the ischial origin in common with the semimembranosus, in Caenolestes

where Osgood (1921), like Sidebotham above, includes the vertebral portion as part of the semitendinosus, and in Ph. maculata and Thyl. cynocephalus (Cunningham, 1882) in the latter of which a bicipiti accessorius is again present.

Some vertebral origin is also given for the muscle in Pet. penicillata by Carlsson (1914), Pet. xanthopus by Parsons (1896) and S. ursinus by Macalister (1870, 1872a) in the last of which there is again a bicipiti accessorius. For Phasc. cinereus Young (1882) gives only an ischial origin (as occurs in quite a lot of other marsupials), Macalister (1872b) gives the origin from the sacrum, while Sonntag (1922) gives it from the ischial tuberosity and caudal vertebrae. Thompson and Hillier (1905) describe a bicipiti accessorius (temuissimus) in N. typhlops arising from the ischium unlike the others mentioned here where it springs from the caudal vertebrae. In Choer. castanotis Parsons (1905) gives some vertebral origin and lateral crural insertion for the semitendinosus that could possibly represent some of the vertebral section of the biceps.

So far as I can determine a femoral (short) head of origin has not been described for a marsupial. If the view of Howell (1956) - that the short head found in man is a degeneration of the caudo-femoralis - is correct then this is not surprising.

The biceps in Trichosurus is supplied by the hamstring nerve; a branch of the sciatic nerve also sends twigs towards the divisions of the caudal head just above the popliteal fossa but I believe these all pass between to become cutaneous. Cunningham (1881a,

1882) gives additional supply from the pudendal (pudic) and the external saphenous nerves in Thyl. cynocephalus, and from the musculo-cutaneous and external saphenous in Ph. maculata, as well as the supply from the hamstring nerve.

Semitendinosus (figs. 53, 54, 56; pls. XXXIII, XXXV) arises from the ischial tuberosity in common with the main origin of the biceps femoris and runs distally medial to the vertebral part of the biceps to which it is connected near the middle of the thigh where the two muscles share a common tendinous intersection. The muscle continues on towards the medial side of the leg where it is inserted through a flat tendon about a centimetre wide into a depression just medial to the anterior border of the tibia and just above the prominent tubercle found about one third of the way down this border. The insertion is covered by the gracilis. According to Carlsson (1914) this muscle arises independently of the biceps.

The semitendinosus also possesses an intersection in Did. virginiana (Coues, 1872), Chir. variegatus (Sidebotham, 1885), Das. viverrinus (MacCormick, 1887) and Hyps. moschatus (Heighway, 1939), but in the last mentioned it is not connected to the biceps.

The muscle is supplied by the hamstring nerve as in Pet. xanthopus (Parsons, 1896), Ph. maculata and Thyl. cynocephalus (Cunningham, 1881a, 1882).

Seminembranosus (figs. 53, 54, 56; pls. XXXIII, XXXV) has a linear origin from the whole length of the ischio-pubic arch, passes down the thigh as a thick muscle belly, and finally is inserted by a five

millimetre wide flattened tendon that runs deep to the cord-like medial ligament of the knee (as noted by Carlsson, 1914), and attaches to the medial side of the tibial tubercle. It too is supplied by the hamstring nerve as in the species mentioned above with the nerve supply of the semitendinosus.

The semimembranosus does not show very much variation amongst the marsupials reported in the literature: insertion by a tendon that passes deep to the medial ligament has been mentioned for Das. viverrinus (MacCormick, 1887), Thyl. cynocephalus, Ph. maculata (Gunningham, 1882), Ph. orientalis (Sonntag, 1922), Pet. xanthopus (Parsons, 1896), Pet. penicillata, A. rufescens, Dend. dorianus (Carlsson, 1914), Choer. castanotis (Parsons, 1905) and Caenolestes (Osgood, 1921).

Presemimembranosus (figs. 53, 54; pl. XXXIII) arises deep to the semimembranosus, and its origin is almost coextensive with the origin of that muscle but extends a little further at both ends, especially dorsally where its attachment to the ischial tuberosity is partly tendinous. This tendon also gives rise to some of the fibres of the quadratus femoris. The belly of the presemimembranosus lies in the thigh lateral to the adductor mass and ventral to the semimembranosus. It is inserted into the medial part of the popliteal surface of the femur a short distance above the condyles, the disto-medial part of the insertion being tendinous, the rest fleshy.

The muscle is supplied by the nerve to quadratus femoris which

ends in it. In his accounts of Ph. maculata and Thyl. cynocephalus Cunningham (1881a, 1882) describes this muscle as the adductor magnus, giving it the same innervation as stated here; as this author himself notes, however, it obviously represents only the hamstring part of the large adductor. Other authors also may have regarded this muscle as the whole adductor magnus as it is usually not mentioned with the hamstring muscles under the name presemimembranosus in accounts of marsupial myology. In some cases it may be incorporated with a true adductor component to form a composite muscle as in man, in which case it would reasonably be included with the adductors, but I have found no account of the innervation of the adductor magnus in a marsupial that would support this. Windle and Parsons (1897a) suggest the name "ischio-supracondyloideus" for this muscle.

Obturator Externus (figs. 40, 41, 42; pls. XXVI, XXVII) has a very extensive origin from the outer surface of the hip-bone, the attachment occupying all the circumference of the obturator foramen except adjacent to the acetabulum and covering all this outer surface of the body and rami of the pubis, the ramus of the ischium and reaching onto the body of the ischium. The tendon of insertion appears on the superficial surface and is inserted into the lower part of the trochanteric pit of the femur after uniting with the distal border of the inferior gemellus. It is supplied by the obturator nerve.

Unlike the obturator internus this muscle appears to be

constantly present in marsupials and shows few noteworthy features. According to Haughton (1866) the two obturator muscles have a common tendon in M. giganteus and M. vallabiensis; Macalister (1872a) describes a semi-detached slip of the externus in S. ursinus. Pectineus (figs. 40, 41, 42, 55, 56; pls. XXVI, XXVII, XXVIII, XXXIV, XXXV) consists of two completely separate parts. The long or superficial part has a partly tendinous origin from the medial end of the ilio-pectineal eminence and the angle of the marsupial bone and passes to an aponeurotic insertion to the middle third of the back of the femur, the aponeurosis fusing with this part of the adductor mass. The short or deep part, completely hidden by the superficial, arises by fleshy fibres from the medial part of the ilio-pectineal eminence and to a small extent from the ligaments connecting the marsupial bone to the pubis, but has no attachment to the marsupial bone itself. It is inserted into somewhat more than the proximal half of the line joining the lesser trochanter to the beginning of the linea aspera. Both parts are supplied by the accessory femoral nerve which arises in the lumbo-sacral plexus with the femoral nerve. In Thyl. cynocephalus (Cunningham, 1881a, 1882; Carlsson, 1905) and Ph. maculata (Cunningham, 1881a, 1882) the supply comes from the femoral (crural) nerve, as in Dend. dorianus where Carlsson (1914) gives some additional supply from the obturator as well.

The pectineus is frequently partly divided into two parts in marsupials, the complete separation noted here being previously

recorded by Thompson and Hillier (1905), and also occurring in Did. marsupialis, Thyl. cynocephalus (Carlsson, 1905), S. ursinus (Carlsson, 1905; Macalister, 1870) and Phasc. wombata (Macalister, 1870).

Adductor Mass (figs. 55, 56; pls. XXXIV, XXV). The single muscle mass representing the adductor muscles arises from the whole length of the symphysis pubis and from the cranial border of the body and superior ramus of the pubis nearly as far as the angle of the marsupial bone. The insertion is into the femur from a point between the lesser trochanter and the gluteal tuberosity down the linea aspera and the medial supracondylar line to the medial condyle, and also to the distal half of the popliteal surface and the lateral supracondylar line. The obturator nerve provides its innervation.

Cunningham (1882) takes the fact that none of the muscle lies superficial to the obturator nerve as evidence that the adductor longus is absent in Ph. maculata; using the same evidence here there is no adductor longus in Trichosurus either, as the nerve to the gracilis from the obturator nerve is entirely superficial to the adductor mass. In Dend. dorianus Carlsson (1914) mentions this superficial branch of the obturator nerve emerging between pectineus and the adductors, but she still describes an adductor longus. At first glance the long head of the pectineus might be taken as the adductor longus but its innervation from the accessory femoral nerve probably indicates its true morphology. The part of the mass

arising from the cranial border of the pubis and passing to the femur proximal to the attachment of the long head of the pectineus is partly separate from the rest, especially near the insertion, and apparently represents the adductor brevis, although there is no posterior branch of the obturator nerve running deep to it. The rest of the mass then represents the true adductor portion of the adductor magnus, the hamstring part being a separate muscle, the presemimembranosus.

Some degree of fusion of the adductor muscles is common in marsupials, but I have found no other account suggesting that the adductor longus is absent except that of Cunningham cited above. Usually the adductors arise from the pubis and ischium only, although attachment to the marsupial bone has been found in Thylacinus (Carlsson, 1905; Cunningham, 1882), Chironectes (Sidebotham, 1885), Macropus (Haughton, 1866), Petrogale (Parsons, 1896) and Phascolarctos (Macalister, 1872b). In most cases the os marsupiale attachment involves the longus only.

Gracilis (fig. 55; pl. XXXIV) is a broad and relatively thin sheet of muscle with an extensive origin from the whole length of the ventral surface of the pubic symphysis where it is superficial to the adductor magnus, from a few millimetres of the cranial border of the pubis by a small aponeurosis that just overlaps the adductor brevis, and from a similar amount of the inferior pubic ramus where it is superficial to the semimembranosus. In the middle part of the thigh the posterior edge of the muscle is adherent to the

corresponding edge of the vertebral head of the biceps superficial to the semitendinosus, and towards the knee the anterior border develops a fascial connection with the adjacent edge of the sartorius. It is inserted by a flat tendon into the anterior border of the tibia in the region of the prominent tubercle one third of the way down, and also distal to this by a thinner aponeurosis into the fascia of the medial side of the leg. It is supplied as usual by the obturator nerve.

The gracilis does not vary a great deal amongst marsupials, in a number some origin from the marsupial bone has been described, the nearest relatives to Trichosurus in this respect being Ph. orientalis and Ps. peregrinus (Somntag, 1922); Cunningham (1882), however, gives no epipubic attachment in Ph. maculata.

4). Muscles of antero-lateral region of leg and dorsum of foot.
Tibialis Anterior (fig. 58; pl. XXXVI) arises from the proximal half of the lateral surface of the tibia including the lateral condyle, from the corresponding part of the interosseous membrane, and to a small extent from the deep fascia and from the septum that separates it from the extensor digitorum longus and the peroneus brevis. Its tendon is inserted into the medial plantar aspect of the medial cuneiform bone, and, in one specimen, there was a small slip to the base of the first metatarsal; this slip was not found by Carlsson (1914), Thompson and Hillier (1905) or Bardeleben (1894) so insertion into the cuneiform only is probably the standard condition for this species. Like all the other muscles of the antero-lateral

Figure 57. Anterior aspect of quadriceps femoris. x1.

Figure 58 (cf. pl. XXXVI). Antero-lateral aspect of leg and foot showing extensor and peroneal muscle groups. x1.

Figure 59 (cf. pl. XXXVII). Antero-lateral aspect of leg and foot showing extensor and peroneal muscle groups after the removal of tibialis anterior and the extensor retinacula. x1.

E.D.B.	- Extensor digitorum brevis.
E.D.L.	- Extensor digitorum longus.
E.H.L.	- Extensor hallucis longus.
E.ret.	- Extensor retinacula.
Fab.	- Fabella.
F.D.L.	- Flexor digitorum longus.
Gst.l.	- Lateral head of gastrocnemius.
H.F.	- Head of fibula.
I-o.M.	- Interosseous membrane.
I-o.M.t.	- Thin part of interosseous membrane.
Lig.P.	- Ligamentum patellae.
L.lig.	- Lateral ligament of knee.
Pat.	- Patella.
Per.B.	- Peroneus brevis.
Per.L.	- Peroneus longus.
Per.Qa.	- Tendon of peroneus digiti quarti.
Per.Qi.	- Tendon of peroneus digiti quinti.
Per.ret.	- Peroneal retinacula.
Pop.	- Popliteus.
ref.	- Reflected head of rectus femoris.
R.F.	- Rectus femoris.
str.	- Straight head of rectus femoris.
T.A.	- Tibialis anterior.
Tib.	- Tibia.
Ti.Tu.	- Tibial tubercle.
V.Lat.	- Vastus lateralis.
V.Med.	- Vastus medialis.

Fig. 57.

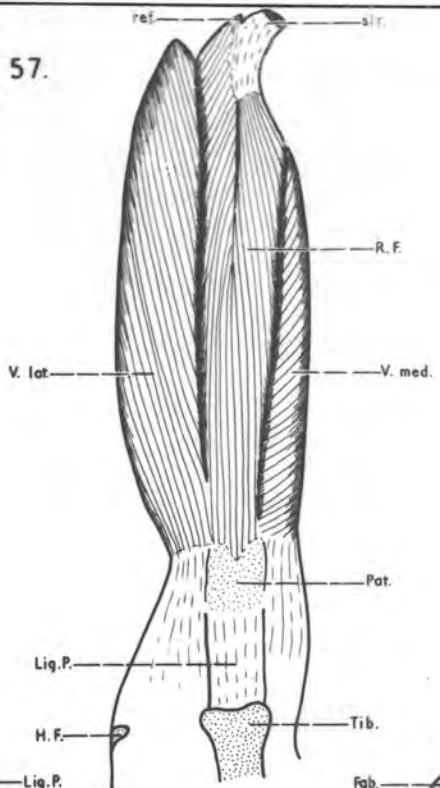


Fig. 58.

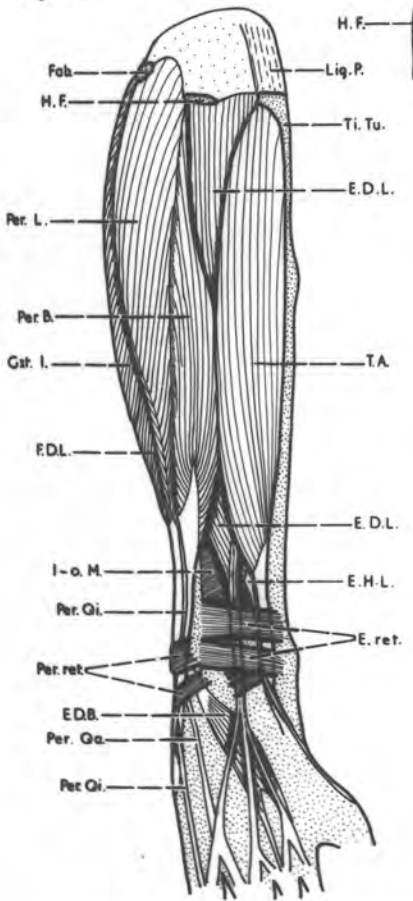


Fig. 59.

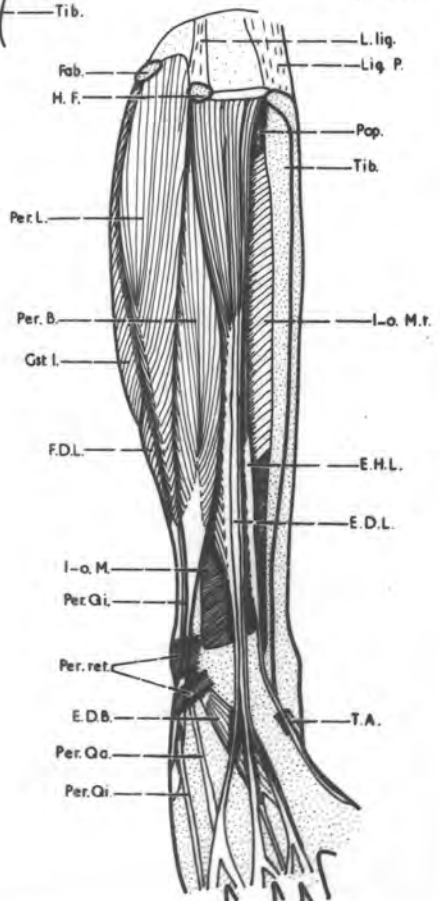


Plate XXXVI (cf. fig. 58). Antero-lateral view of leg showing
extensor and peroneal muscle groups. $\times 2\frac{1}{4}$.

- E.D.L. - Extensor digitorum longus.
- E.H.L. - Extensor hallucis longus.
- E.ret. - Extensor retinaculum.
- Fab. - Fabella.
- F.D.L. - Flexor digitorum longus.
- Gst.l. - Lateral head of gastrocnemius.
- H.F. - Head of fibula.
- I-o.M. - Interosseous membrane.
- Lig.P. - Ligamentum patellae.
- Per.B. - Peroneus brevis.
- Per.L. - Peroneus longus.
- Per.ret. - Peroneal retinaculum.
- T.A. - Tibialis anterior.
- Ti.Tu. - Tibial tubercle.

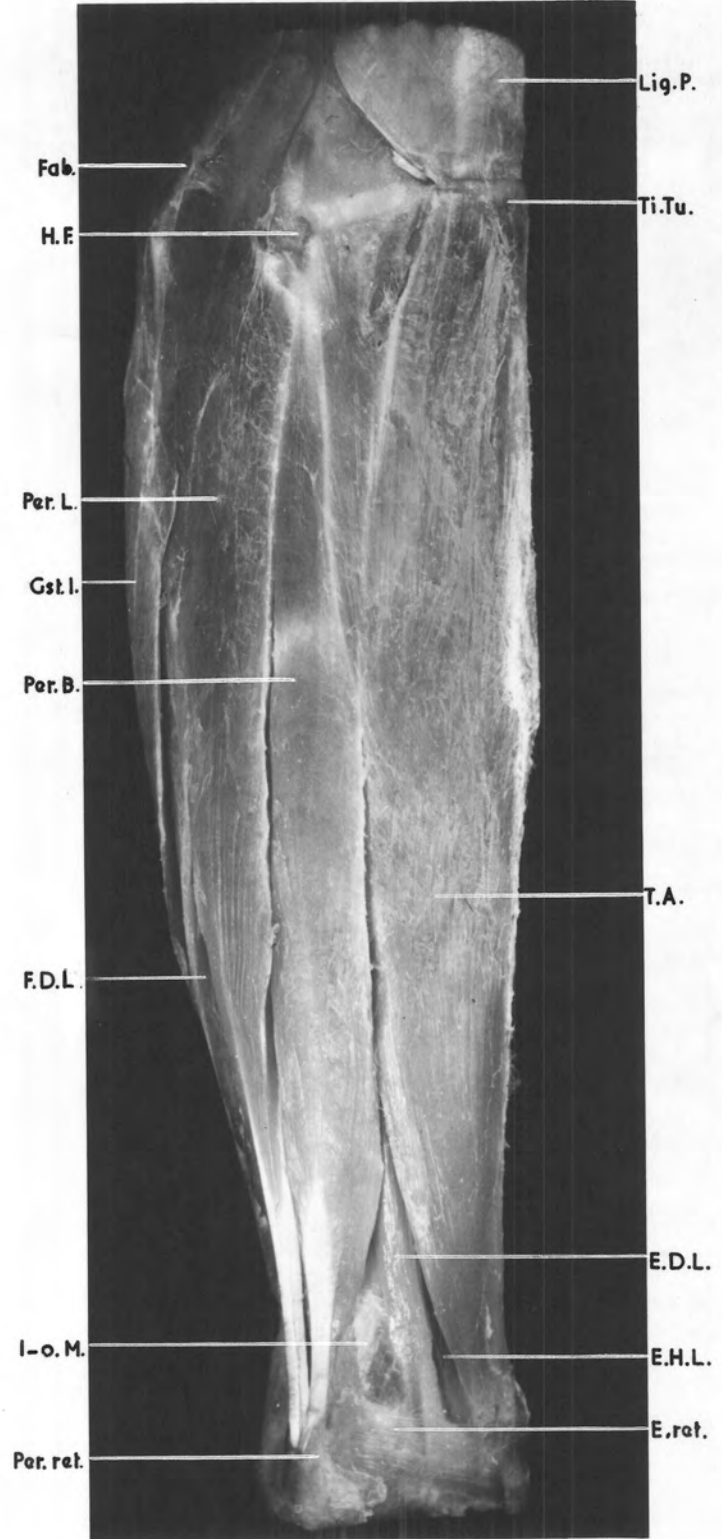
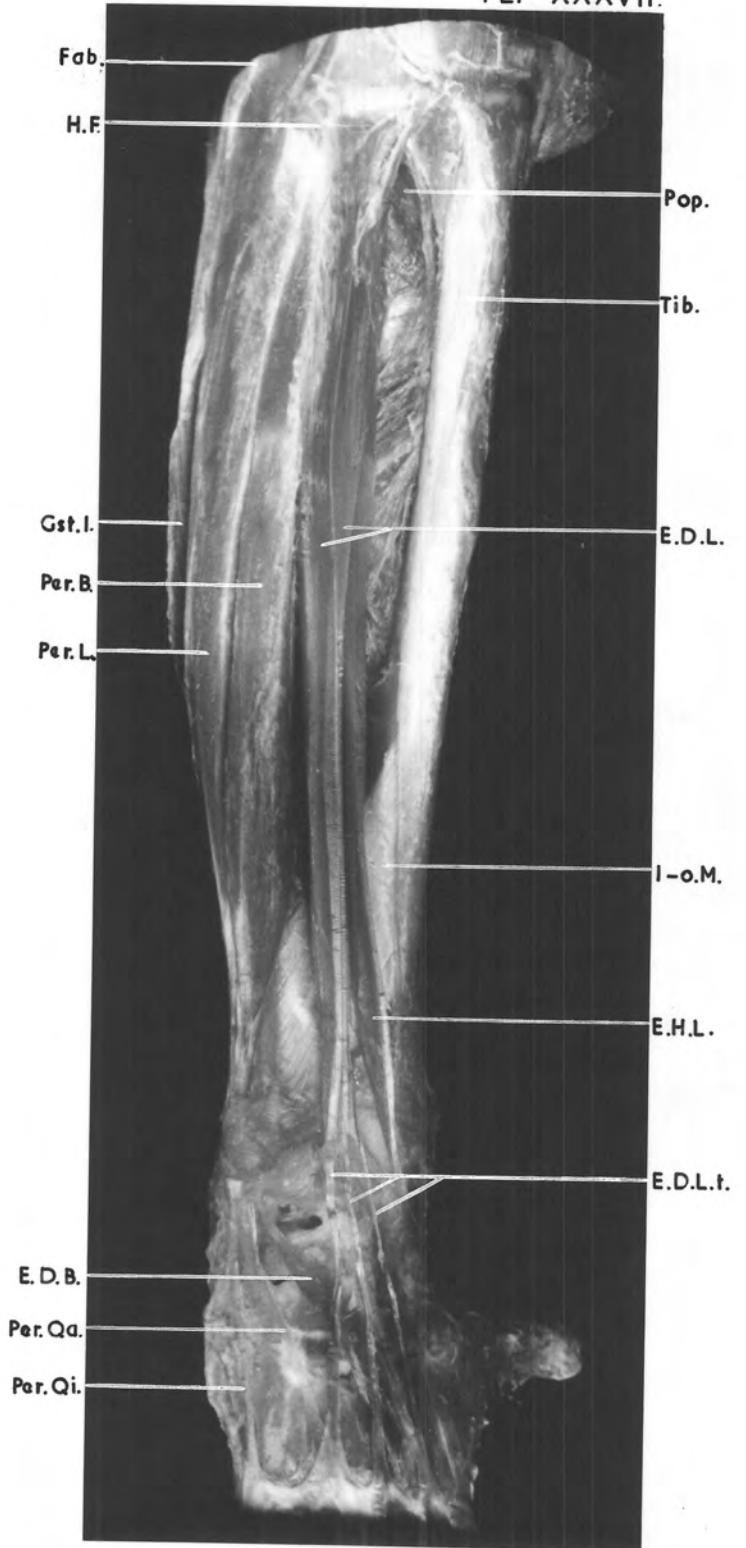


Plate XXXVII (cf. fig. 59). Antero-lateral view of leg and foot showing extensor and peroneal muscle groups after the removal of tibialis anterior and the extensor retinacula. $\times 1\frac{3}{4}$.

- E.D.B. - Extensor digitorum brevis.
- E.D.L. - Extensor digitorum longus.
- E.D.L.t. - Tendons of extensor digitorum longus.
- E.H.L. - Extensor hallucis longus.
- Fab. - Fabella.
- Gst.l. - Lateral head of gastrocnemius.
- H.F. - Head of fibula.
- I-c.M. - Interosseous membrane.
- Per.B. - Peroneus brevis.
- Per.L. - Peroneus longus.
- Per.Qa. - Peroneus digiti quarti tendon.
- Per.Qi. - Peroneus digiti quinti tendon.
- Pop. - Popliteus.
- Tib. - Tibia.



region of the leg the tibialis anterior is supplied by the continuation of the lateral popliteal nerve into the front of the leg where, since it gives off a large cutaneous branch to the leg and foot before this, we can probably regard it as the anterior tibial nerve - the cutaneous branch representing the musculo-cutaneous nerve. This is the way Cunningham (1881a, 1882) regards these nerves in the two species with which he dealt.

The medial cuneiform provides the insertion also in Ph. orientalis (Somntag, 1922), Phasc. cinereus (Young, 1882; Somntag, 1922), Hyps. moschatus (Heighway, 1939), Pet. xanthopus (Parsons, 1896), Dend. doriaemus (Carlsson, 1914), Phasc. wombata (Macalister, 1870), Das. viverrinus (MacCormick, 1887), Did. virginiana (Coues, 1872), Did. cancrivora (Frets, 1908) and Chir. variegatus (Sidebotham, 1835). The muscle also gives some of its attachment to the first metatarsal in Ph. maculata (Cunningham, 1882) and N. typhlops (Thompson and Hillier, 1905). In Caenolestes (Osgood, 1921) the tibialis anterior attaches to the same bones through two tendons; in other animals it is inserted into the second metatarsal as well, or into metatarsals only.

Extensor Digitorum Longus (figs. 58, 59; pls. XXXVI, XXXVII) arises from the proximal ends of the tibia and fibula and from an arch between them, and from the septum abutting peroneus brevis. The belly of the muscle is incompletely divided into three parts corresponding to the three tendons that arise from it. The smallest medial part is separate almost to its origin and is fleshy only in

the proximal one third of the leg, the middle part is joined to the lateral for a centimetre or so and remains fleshy to the middle of the leg, the largest lateral part possesses muscle fibres almost to the ankle. In the proximal third of the leg the belly of the large lateral part is superficial between the tibialis anterior and the peroneus brevis but in the middle of the leg the extensor digitorum longus is completely hidden between these two muscles. The lateral tendon passes to the fifth digit also having a large slip to the fourth, the middle goes to the fourth and gives a small slip to the third, while the medial tendon, which is the smallest, divides into two for the syndactylous second and third digits. These tendons form extensor expansions in a similar manner to those of the hand except that in the syndactylous digits there is less attachment to the middle phalanx. Carlsson (1914) also reports insertion of this muscle into the outer four toes, as is the case in most marsupials, the principal exceptions belonging to the Macropodidae in most of which only two toes are so provided.

The most similar arrangement to that given here which I have found in the literature is that described by Cunningham (1882) for Ph. maculata.

Extensor Hallucis Longus (figs. 58, 59; pls. XXXVI, XXXVII) arises from the head and proximal half of the shaft of the fibula and its tendon is inserted mainly into the base of the distal phalanx of the hallux, although the sides of the tendon are also adherent to the first phalanx. The tendon crosses that of the tibialis anterior at

the ankle and appears to be chondrified in the region of the metatarsal head.

In most marsupials possessing a hallux the muscle is inserted into this digit, though Sonntag (1922) gives the insertion to the first two digits in the phalanger and the opossum. Where the hallux is rudimentary or absent the muscle is either absent as in Choer. castanotis (Parsons, 1905), Thyl. cynocephalus (Cunningham, 1882) and Antechinomys (Alston, 1880), or moves its insertion to the rudimentary metatarsal as in Das. viverrinus (MacCormick, 1887) or to the syndactylous digits as in the typical Macropodidae. Leche (1874-1900) says it is incorporated in the tibialis anterior in Myrmecobius where he gives the insertion of that muscle to the tip of the rudimentary metatarsal.

Peroneus Longus (figs. 58, 59, 62; pls. XXXVI, XXXVII, XXXIX) arises from the head of the fibula, the lateral ligament of the knee, the fabella, the proximal half of the shaft of the fibula and the septa separating it from flexor digitorum longus and peroneus brevis. The fibular head attachment is split by the origin from the lateral ligament. The whole origin is divided into two parts by the anterior tibial nerve, one part comprising the fibres from the shaft of the fibula and the septum facing flexor digitorum longus, the other formed by the rest of the attachments mentioned above. The tendon takes its usual course across the sole of the foot and is inserted into the plantar surface of the first metatarsal bone - as noted by Bardeleben (1894). This insertion varies somewhat in marsupials

although it is always in the region of the medial cuneiform and the medial metatarsal bases. Simple insertion to the first metatarsal base, as found here, has been reported in Ph. maculata (Cunningham, 1882), Phasc. cinereus (Young, 1882), N. typhlops (Thompson and Hillier, 1905), Das. viverrinus (MacCormick, 1837), S. ursinus (Macalister, 1870) and Chir. variegatus (Sidebotham, 1885).

Peroneus Brevis (figs. 58, 59; pls. XXXVI, XXXVII) springs from the front of the head of the fibula and the septa separating it from extensor digitorum longus and peroneus longus. Its tendon passes behind the lateral malleolus with the other peroneal tendons. In the foot it bifurcates to transmit the tendon of the peroneus digiti quinti, reunites into a single tendon, receives a slip from the plantaris, and is finally inserted into the base of the first metatarsal and its tubercle, giving an expansion to the fascia over the abductor digiti minimi.

Peroneus Digiti Quinti (Peroneus Digiti Minimi, Peroneus Tertius) (figs. 58, 59; pl. XXXVII) takes its origin from the head of the fibula and the lateral ligament of the knee deep to the corresponding part of the peroneus longus, and slightly from the septum facing extensor digitorum longus. After passing behind the lateral malleolus the tendon perforates that of the peroneus brevis and is inserted into the fibular side of the extensor expansion of the fifth toe. Such perforation of the peroneus brevis tendon was noted in Trichosurus by Thompson and Hillier (1905), and has also been described in Caenolestes by Osgood (1921) and Hyps. moschatus

by Heighway (1939).

Peroneus Digiti Quarti (figs. 58, 59; pl. XXXVII) arises from the middle third of the shaft of the fibula in front of the peroneus longus, and its tendon passes behind the lateral malleolus still in front of the longus and medial to the brevis, finally being inserted into the lateral side of the extensor expansion of the fourth toe.

Extensor Digitorum Brevis (figs. 58, 59; pl. XXXVII). This muscle is confined to the foot, arising by a tiny tendon from a tubercle on the lateral surface of the calcaneum below the lateral malleolus. The tendon gives rise to a small muscle belly which in turn produces two tendons of insertion that join the extensor expansions of the syndactylous digits, an insertion agreeing with that given by Thompson and Hillier (1905). The muscle is supplied by the terminal part of the anterior tibial nerve. There is no extensor hallucis brevis.

The arrangement of the group of muscles formed by the peronei and the extensor digitorum brevis shows much variation in marsupials. The account given by Cunningham (1882) for Ph. maculata shows an arrangement almost identical with that found here in Trichosurus; the peroneal group consists of the same four muscles also in Hyps. moschatus (Heighway, 1939) and in the giant kangaroo, the phalanger, the opossum and the wallaby according to Macalister (1870). In some cases the peroneal group is increased by a shift of the origin of all or part of the extensor digitorum brevis up into the leg as occurs notably in the American marsupials - Caenolestes (Osgood,

1921), Chironectes (Sidebotham, 1885) and Didelphys (Coues, 1872; Frets, 1908) - and the Dasyuridae - Dasyurus (MacCormick, 1887), Sarcophilus (Macalister, 1870) and Thylacinus (Cunningham, 1882). According to Sonntag (1922) the same occurs in Phascolarctos. On the other hand the peronei may be reduced by the loss of the brevis, as in Petrogale (Carlsson, 1914; Parsons, 1896), Dendrolagus and Macropus (Carlsson, 1914), or of one or both of the quinti and quarti. An extensor hallucis brevis has been found in Dendrolagus (Carlsson, 1914), Caenolestes (Osgood, 1921) and Didelphys (Coues, 1872; Leche, 1874-1900; Frets, 1908).

5). Muscles of the flexor aspect of the leg.

Gastrocnemius (fig. 60; pl. XXXVIII). The medial head of this muscle is much the smaller. It arises from the proximal part of the back of the medial condyle of the femur and the capsule of the knee joint; the tendon of origin spreads out on the superficial surface of the muscle and gives rise to the fibres of the fleshy belly which ends one third of the way down the leg, the aponeurosis of insertion appearing on the deep surface. The lateral head, which remains muscular for three fourths of the leg, has a strong tendon of origin from the lateral condyle of the femur, the lower part of the lateral supracondylar line and the oblique posterior ligament of the knee. This tendon contains the fabella which articulates with the head of the fibula and marks the beginning of the fleshy part of the head. The lateral head also has origin from the expansion of the vastus lateralis on the outer side of the knee joint by an aponeurotic band,

Figure 60 (cf. pl. XXXVIII). Flexor muscle group of leg. x1.

Figure 61. Flexor muscle group of leg after the removal of gastrocnemius and plantaris. x1.

Figure 62 (cf. pl. XXIX). Flexor muscle group of leg after the removal of gastrocnemius, plantaris, flexor digitorum brevis and flexor digitorum longus. x1.

- Cal. - Posterior end of calcaneum.
- Fab. - Fabella.
- F.D.B. - Flexor digitorum brevis.
- F.D.L. - Flexor digitorum longus.
- F.F. - Fabellar facet on head of fibula.
- Fib. - Fibula.
- Fl.T. - Flexor tibialis.
- Gst.l. - Lateral head of gastrocnemius.
- Gst.m. - Medial head of gastrocnemius.
- M.lig. - Medial ligament of knee.
- Per.L. - Peroneus longus.
- Per.ret. - Superior peroneal retinaculum.
- Per.t. - Peroneal tendons on lateral malleolus.
- Pl.t. - Plantaris tendon.
- Pop. - Popliteus.
- Pop.d. - Distal part of popliteus ("pronator tibiae").
- sl.D5. - Slip of plantaris to digiti minimi.
- sl.H. - Slip of plantaris to hallux.
- sl.P.B. - Slip of plantaris to peroneus brevis tendon.
- T.Cal. - Tendo calcaneus.
- Tib. - Tibia.
- T.P. - Tibialis posterior.
- T.P.r. - Retinaculum over flexor tibialis and tibialis posterior.

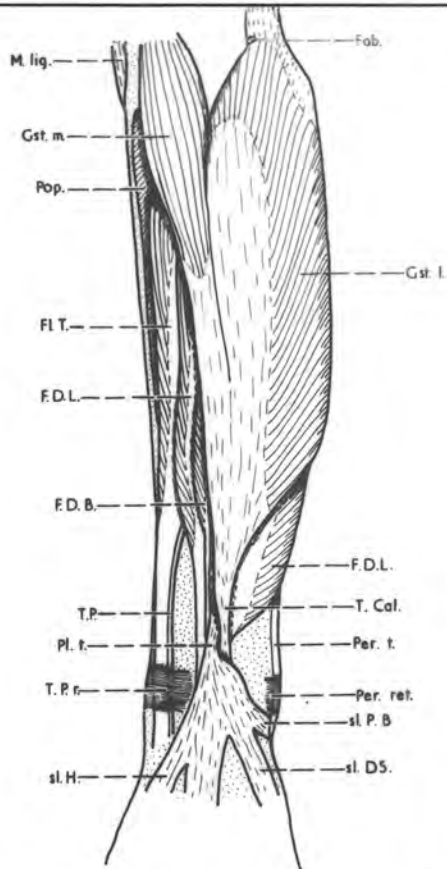


Fig. 60.

Fig. 61.

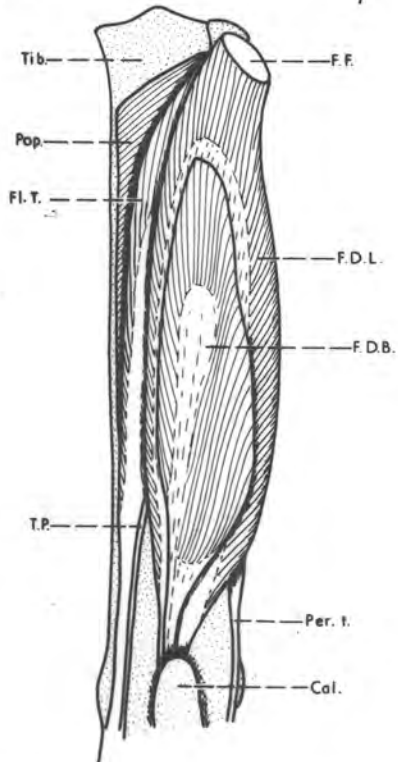


Fig. 62.

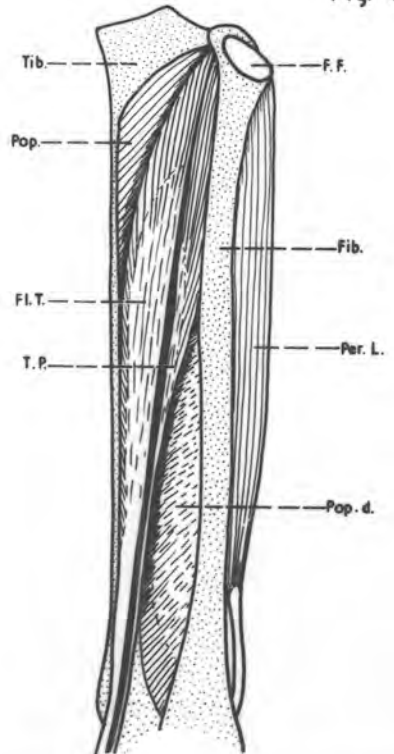


Plate XXXVIII (cf. fig. 60). Superficial view of flexor muscle
group of leg. x2.

- F.D.B. - Flexor digitorum brevis.
- F.D.L. - Flexor digitorum longus.
- Fl.T. - Flexor tibialis.
- Gst.l. - Lateral head of gastrocnemius.
- Gst.m. - Medial head of gastrocnemius.
- Per.t. - Peroneal tendons on lateral malleolus.
- Pl.t. - Plantaris tendon.
- Pop. - Popliteus.
- T.Cal. - Tendo calcaneus.
- T.p.r. - Retinaculum over flexor tibialis and
tibialis posterior.

Gst. m.

Pop.

Gst. l.

F. D. L.

Fl. T.

F. D. B.

T. p. r.

F. D. L.

T. Cal.

PL t.

Per. t.



and by a thinner aponeurosis from the deep fascia on the lateral side of the leg; this latter aponeurosis is pierced by the lateral popliteal nerve. The fibres of the lateral head from the knee region and the vastus expansion run nearly vertically and arise from an aponeurosis of origin that spreads out mainly on the deep surface; they end in the aponeurosis of insertion which begins on the superficial aspect and fuses by its medial edge with the rather thinner tendon of the medial head above the middle of the leg, there being no union of the fleshy bellies. The fibres from the deep fascia of the leg run a more oblique course, passing superficial to some of the vertical fibres and ending in the lateral side of their aponeurosis. From their relationship to the aponeuroses of origin and insertion, and to the oblique (superficial) fibres of the head I consider that the vertical fibres probably represent the soleus, which is otherwise not present; this view is exactly the opposite of that of Glaesmer (1908) in regard to this species where she suggests the oblique fibres represent the soleus, but it appears to be in accord with the ideas of Heighway (1959) concerning the comparable parts of the lateral head of the gastrocnemius in Hyps. moschatus.

The tendo calcaneus narrows as it approaches the posterior end of the calcaneum and the part of the tendon formed by the medial head crosses superficially over the lateral part and is inserted lateral to it, there being apparently some chondrification in the tendon near its insertion into the posterior end of the calcaneum. This twisting of the tendon has been reported for a number of other

marsupials, and was apparently first noted by Parsons (1894) who found it in the kangaroo as well as some placental mammals and pointed out that it also involves the plantaris and the long flexors of the toes.

The gastrocnemius is supplied by the medial popliteal nerve.

The degree of separation of the two heads of this muscle varies considerably in marsupials, sometimes they are present as two quite separate muscles. It appears that a distinct soleus muscle is usually not present.

Plantaris (fig. 60; pl. XXXVIII) springs from the fabella and is at first somewhat aponeurotic on its deep surface; it remains fused to the deep aspect of the lateral head of the gastrocnemius for a considerable distance. The muscle is fleshy almost to the ankle but its tendon of insertion begins higher up along its medial border and appears medial to the tendo calcaneus which it comes to overlie at the hind end of the calcaneum. At the heel the tendon spreads out to form a cap over this bony prominence, then continues into the sole broadening out further to produce two main slips with a thinner section between. The medial slip attaches to the hind end of the plantar sesamoid ("præhallux" of Bardeleben, 1894), continuing over this to some extent towards the base of the hallux, and also having some connection with the flexor retinaculum through which it gains attachment to the medial malleolus. The lateral slip attaches by its outer edge to the side of the calcaneus, then continues on to its principal insertion into the peroneus brevis tendon after this

has transmitted the tendon of the peroneus digiti quinti: it also has a lesser connection to the base of the fifth metatarsal bone. The central thinner part of the plantaris extends into the deep fascia of the sole which soon develops an intimate adherence to the skin. The nerve supply comes from the medial popliteal nerve.

Bardeleben (1894), Thompson and Hillier (1905), Glaesmer (1908) and Carlsson (1914) have all given some account of the plantaris muscle in Trichosurus, the most noteworthy difference in their descriptions being that none of them notes any attachment to the tendon of the peroneus brevis. In other respects their accounts, though less complete than that given here, are compatible, except that Carlsson mentions four slips going to the outer four toes.

In Choeropus (Parsons, 1905), Petrogale (Parsons, 1896), Macropus (Windle and Parsons, 1897b; Haughton, 1866) and Hypsiprymnodon (Heighway, 1939) the plantaris continues, at least in part, through the sole as tendons going to some of the toes; this is explained by considering that the tendons in the sole are the representatives of the flexor digitorum brevis.

The plantaris is absent in Phascologomys according to Macalister (1870) and Sonntag (1922), though Glaesmer (1910) describes one in a member of this genus.

Flexor Digitorum Brevis (figs. 60, 61, 65; pls. XXXVIII, XL) arises from the aponeurotic superficial aspect of the long flexor muscle in the middle two fourths of the leg or slightly lower. The muscle belly gives rise to three tendons that pass to the outer three toes;

the medial tendon is by far the smallest and may come from a partly separated portion of the muscle belly. These tendons are perforated in the usual way by those of the long flexor and attach after reunion of the bifurcated slips into the plantar surface of the second phalanx of the respective toe: opposite the base of the proximal phalanx strong vincula longa are given off which attach to the flexor sheath and to the base of the phalanx so that the main action of the tendons seems to be on the proximal rather than the middle phalanges. As noted by Glaesmer (1908), the muscle is supplied by a recurrent branch of the medial plantar nerve that runs up deep to the flexor retinaculum.

Bardeleben (1894), Glaesmer (1908) and Carlsson (1914) all give a fourth tendon from this muscle to the second toe in Trichosurus but I saw no example of this in my material. The last of these investigators found the origin at the level of the calcaneum in one of her animals, though it was high in the leg in the other. Bardeleben gives the insertion only to the proximal phalanx and the flexor sheath; he calls the muscle the "flexor digitorum sublimis" and regards it as the representative of the flexor tibialis, though others do not agree with him. Taylor and Bonney (1905) say that the flexor fibularis does not give rise to the superficial flexor in T. vulpecula but they do not say where the latter does arise. There is no superficial head of origin for this muscle in Trichosurus such as has been recorded for some species of Dasyurus and Didelphys (Glaesmer, 1908, 1910; MacCormick, 1887).

In nearly all marsupials where this muscle has been described it provides tendons for four toes; in Ph. maculata, however, Cunningham (1882) gives tendons for the outer three toes only, as does Bardeleben (1894) for Did. marsupialis. In Dend. dorianus Carlsson (1914) gives the muscle one tendon only - that to the fourth toe.

In Ph. maculata (Cunningham, 1882), Phascologmys (Glaesmer, 1910; Sonntag, 1922), Did. marsupialis (Glaesmer, 1910), Ph. orientalis and Ps. peregrinus (Sonntag, 1922) the flexor digitorum brevis separates off from the fleshy part of the longus (also having another origin in Did. marsupialis); this is also the case in Phasc. cinereus according to Young (1882). In most others it arises from the tendon of the long flexor either in the sole or in the distal part of the leg.

Cunningham (1881a, 1882) and Glaesmer (1908, 1910) noted the supply from the medial plantar nerve in a number of marsupials; in her later paper Glaesmer gives the supply in Phascologmys from the tibial nerve.

Flexor Digitorum Longus (Flexor Fibularis) (figs. 60, 61, 65; pls. XXXVIII, XL). This muscle is apparently the representative of the flexor hallucis longus, but in view of its insertion the name applied here, and by other authors, can, I feel, be tolerated. It arises from the head and proximal three fourths of the shaft of the fibula, the fascia on the popliteus and the septa separating it from the peroneus longus and the tibialis posterior. The muscle mass gives rise to a strong tendon that divides in the foot into four,

one each for the hallux and the fourth and fifth digits, and another that divides later into two for the syndactylous digits. The tendon for the hallux comes off first, almost at right angles to the main tendon, and just proximal to this point the tendon is folded down at each side to form a deep groove - almost a tunnel - for the tendons of the flexor digitorum brevis. Each of the tendons of the flexor longus is inserted into the plantar aspect of the base of the distal phalanx of one of the digits, in the case of the outer three after passing through the bifurcated brevis tendon. Bardeleben (1894), Taylor and Bonney (1905), Glaesmer (1908) and Carlsson (1914) all agree on the distribution of this muscle to all five digits.

The corresponding muscle also gives tendons to five digits in Ph. maculata (Cunningham, 1882), Phasc. cinereus (Macalister, 1872b; Young, 1882), Hyps. moschatus (Heighway, 1959), Chir. variegatus (Sidebotham, 1885) and three species of Didelphys reported by Glaesmer (1908, 1910). In other marsupials described there are only four tendons from the flexor fibularis, or in the case of Choer. castanotis (Parsons, 1905) only three. In Caenolestes (Osgood, 1921), Chir. variegatus (Sidebotham, 1885), Did. marsupialis, Didelphys crassicaudata, Per. obesula (Glaesmer, 1910), Choer. castanotis (Parsons, 1905) and Thyl. cynocephalus (Cunningham, 1882) the tendon joins some or all of the flexor tibialis tendon or the tendon that I take to represent it.

This muscle is supplied by the medial popliteal nerve as given for Ph. maculata by Cunningham (1881a, 1882); Glaesmer (1910) gives

essentially the same supply (tibial nerve) in Per. obesula.

There is no flexor digitorum accessorius (quadratus plantae) in T. vulpecula, this finding agreeing with Glaesmer (1908) who calls it "caro quadrata Sylvii".

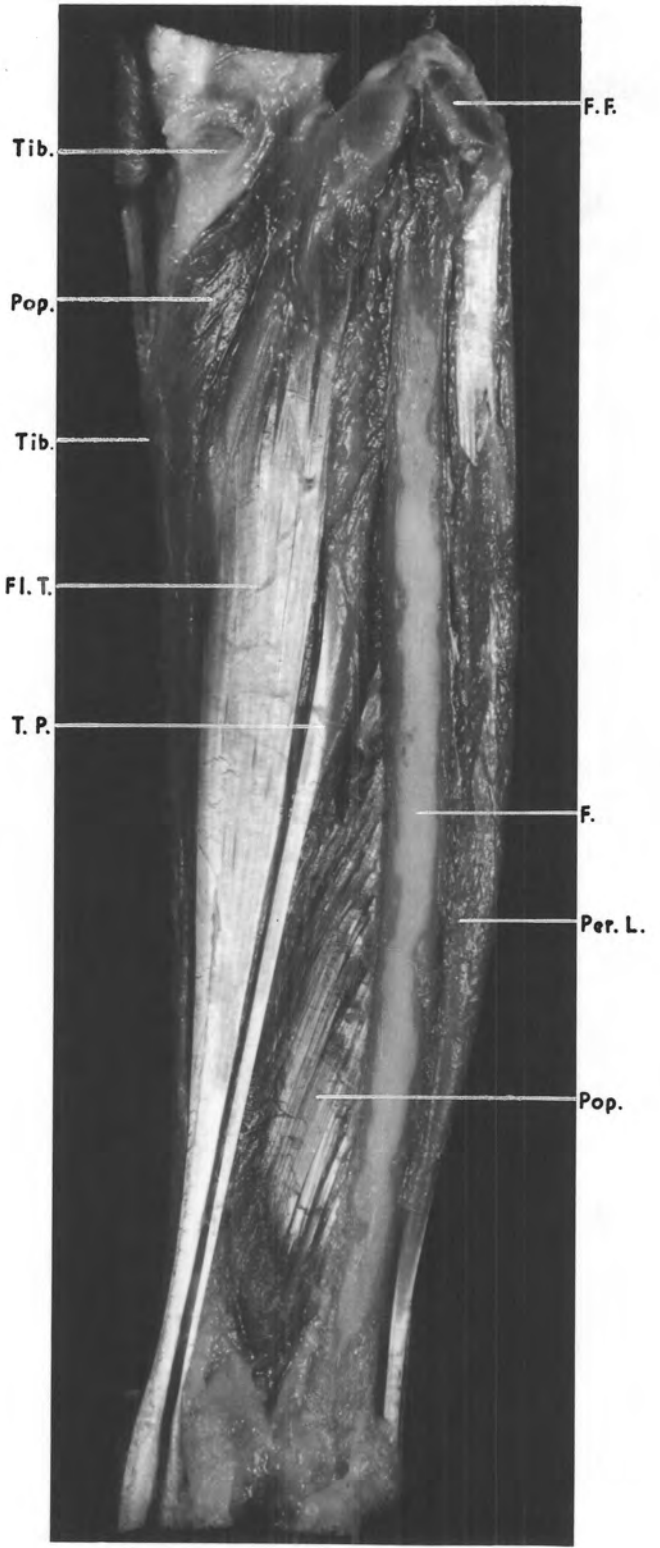
Flexor Tibialis (figs. 60, 61, 62; pls. XXXVIII, XXXIX), the representative of the flexor digitorum longus of man, arises from the head of the fibula and the popliteus fascia in the proximal half of the leg. Its tendon, which begins as an aponeurotic layer on the superficial surface of the muscle, lies medial to that of the tibialis posterior at the back of the medial malleolus and passes into the foot to be inserted into the plantar sesamoid and the medial cuneiform bone. Glaesmer (1908) gives in addition some origin from the proximal fourth of the tibia and from the interosseous membrane; this latter is also mentioned by Carlsson (1914), but to my mind the true interosseous membrane is excluded by the popliteus. Glaesmer (1908) notes the partial insertion to the medial cuneiform but Taylor and Bonney (1905) do not.

The flexor tibialis shows considerable variation in different marsupials: in some its tendon wholly or partly joins the flexor fibularis (q.v.), in Didelphys (Leche, 1874-1900) it joins the flexor brevis tendon at the base of the hallux, while in others it usually ends in the plantar fascia or sesamoid. Attachment to the medial cuneiform has also been noted in Hyps. moschatus by Heighway (1959) and Belideus by Leche (1874-1900). In quite a number of marsupials the muscle has not been described, in some cases

Plate XXXIX (cf. fig. 62). Deep muscles of flexor group of leg.

Gastrocnemius, plantaris, flexor digitorum brevis and flexor digitorum longus are removed. $\times 2\frac{1}{2}$.

- F. - Fibula.
- F.F. - Fabellar facet on head of fibula.
- Fl.T. - Flexor tibialis.
- Per.L. - Peroneus longus.
- Pop. - Popliteus.
- Tib. - Tibia.
- T.P. - Tibialis posterior.



apparently being included as part of the tibialis posterior; this is the case in Cunningham's (1832) account of Ph. maculata, and Owen's (1839-1847, 1868) of Ph. vulpina, and in view of the appearance and attachments of the muscle this is, I feel, not unreasonable. Leche (1874-1900) says the muscle is absent in Hypsiprymnus.

Like the tibialis posterior and the popliteus, the flexor tibialis is innervated from the medial popliteal nerve.

Tibialis Posterior (figs. 60, 61, 62; pl. XXXIX) is a very small muscle with its origin from the head and proximal third of the shaft of the fibula, the popliteus fascia and the septum separating it from the flexor digitorum longus. Its tendon lies lateral to the larger tendon of the flexor tibialis at the ankle and passes to an insertion into the navicular bone of the tarsus. Glaesmer (1908) found this tendon completely covered by that of the flexor tibialis at the ankle. Both Bardeleben (1894) and Young (1882) give the muscle a double tendon: I wonder whether possibly the flexor tibialis is included in the tibialis posterior in their descriptions, although Bardeleben does give the navicular as the insertion of both parts. Owen (1839-1847, 1868) definitely does include the flexor tibialis (as described here) as part of the tibialis posterior: he gives all the insertion to the cuneiforms - one to the medial, one to the intermediate. The muscle that Owen regards as representative of the flexor digitorum longus is that described here as the popliteus.

The navicular (scaphoid) is the usual insertion of this muscle

in marsupials; in some cases there is additional or even entire insertion into surrounding structures - medial cuneiform, sesamoid, metatarsal bases or even the astragalus. Heighway (1959) says the muscle is absent in Hyps. moschatus, as do Taylor and Bonney (1905) for Macropus melanops, Leche (1874-1900) for Hypsiprymnus and Glaesmer (1910) for two species of Didelphys; Glaesmer (1910) also says it is absent in Phascologomys but Macalister (1870) describes one in a member of that genus.

Popliteus (fig. 62; pl. XXXIX) has its origin from the head of the fibula just below the tibial facet, and from four fifths of the length of the shaft of the fibula. The part arising from the head of the bone is thicker and radiates to an insertion into the proximal third of the posterior surface of the tibia, overlapping to a small extent the thinner part which has an aponeurotic origin from the shaft of the fibula and is also rather aponeurotic on its posterior surface; this part is inserted into rather more than the distal two thirds of the length of the back of the tibia. The muscle thus comes to occupy the whole length of the interosseous space. I take the first part mentioned to represent the true popliteus (although it has no femoral attachment), the second part then corresponds to the so-called "pronator tibiae", an unfortunate name since, as pointed out by Young (1881), there is no true pronation and supination of the tibia in the hind-limb of marsupials. Only in the distal fourth or so of the leg is there a thick interosseous membrane on the anterior surface of this muscle. The slip

that Taylor and Bonney (1905) describe passing to the flexor tibialis was sought but not found. Carlsson (1914) indicates that there is some attachment to the femur but this was not present in my material, and has otherwise been reported only in Chir. variegatus (Sidebotham, 1885) and some of the Macropodidae - Dendrolagus (Carlsson, 1914), Petrogale (Carlsson, 1914; Parsons, 1896), Macropus and Hypsiprymnus (Taylor and Bonney, 1905). Glaesmer's mention (1908) of the muscle in Trichosurus appears to refer only to the proximal thick portion - the true popliteus.

In many marsupials this muscle does not occupy the whole length of the interosseous space. Others reported where the muscle does entirely or nearly entirely do so are Phasc. cinereus (Young, 1882), Hyps. moschatus (Heighway, 1959), Ph. maculata, Thyl. cynocephalus (Cunningham, 1882), Das. viverrinus (MacCormick, 1887), N. typhlops (Thompson and Hillier, 1905) and Did. virginiana, if we take Coues' (1872) "interosseus cruris" to correspond.

6). Intrinsic muscles of the sole of the foot.

Here again, as in the hand, I have, for the sake of convenience of description, used the basic grouping of Cunningham (1878c, 1882), modifying this in the light of other accounts of the morphology of the plantar musculature (McMurrich, 1907; Howell, 1936) to include the lumbrical muscles and to separate the abductors of the first and fifth toes from the interossei. McMurrich and Howell also include the flexor digitorum brevis with the intrinsic musculature but I have not grouped it so here.

Figure 63 (cf. pl. XL). Superficial muscles of sole. $\times 1\frac{1}{2}$.

Figure 64 (cf. pl. XLI). Musculature of sole after the removal of the long flexor tendons and lumbricals. $\times 1\frac{1}{2}$.

Figure 65 (cf. pl. XLII). Flexores breves of the foot after the removal of the long flexor tendons, lumbricals, adductors and the abductors of the hallux and fifth digit. $\times 1\frac{1}{2}$.

Figure 66 (cf. pl. XLIII). Interosseous muscles of the foot. All other muscles of the sole are removed. $\times 1\frac{1}{2}$.

Ab.D.M.B.	- Abductor digiti minimi brevis.
Ab.D.M.L.	- Abductor digiti minimi longus.
Ab.H.	- Abductor hallucis.
Ab.Mt.5.	- Abductor metatarsi digiti minimi.
Ad.H.	- Adductor hallucis.
Ad.tr.	- Transverse slip between 2nd and 4th digits.
Ad.5.	- Adductor digiti minimi.
Arch.	- Arch of insertion of interosseous muscle.
Cal.	- Posterior end of calcaneum.
F.B.H.	- Flexor hallucis brevis.
F.B.2,3,4.	- Flexores breves of middle three digits.
F.B.5.	- Flexor digiti minimi brevis.
F.D.B.t.	- Tendons of flexor digitorum brevis.
F.D.L.H.	- Tendon of flexor digitorum longus to hallux.
F.D.L.t.	- Main tendon of flexor digitorum longus to outer four digits.
Int.1,2,3,4.	- Interosseous muscles.
L.F.T.	- Long flexor tendons.
L.1,2,5.	- Lumbrical muscles.
Mt.2,3,4,5.	- Metatarsal bones.
Mt.5.Tu.	- Tuberosity of base of fifth metatarsal.
Op.D.M.	- Opponens digiti minimi.
r.	- Adductor raphe.
Ses.	- Plantar sesamoid.

Fig. 63.

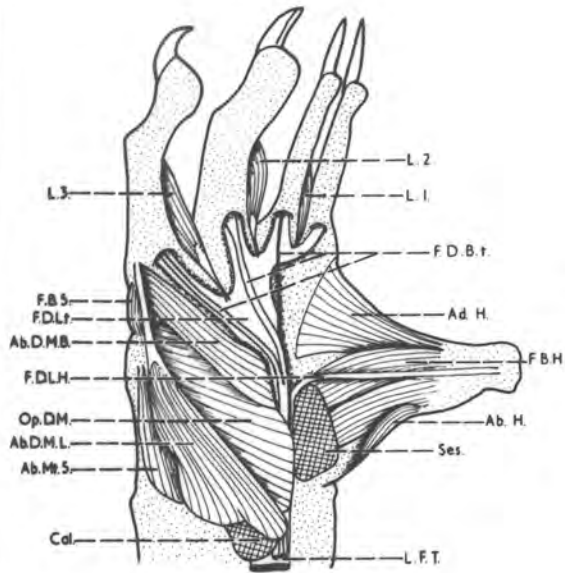


Fig. 64.

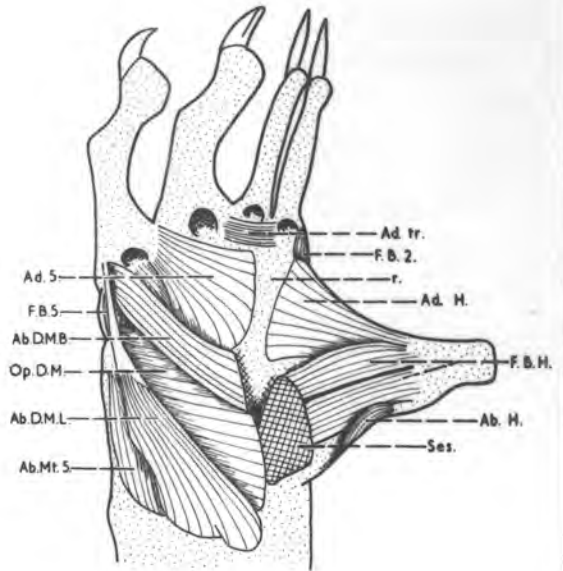


Fig. 65.

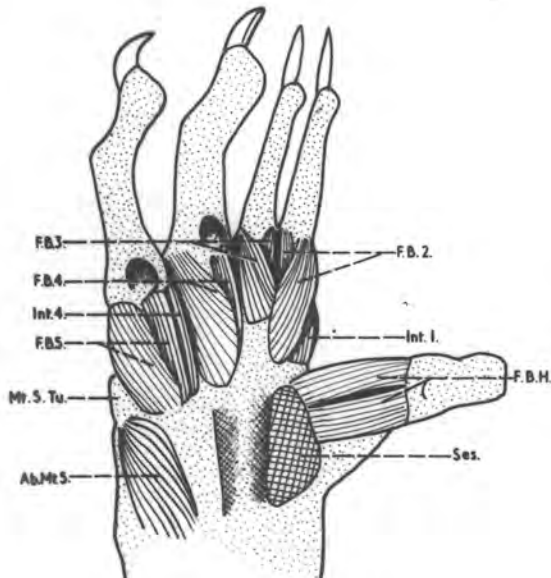


Fig. 66.

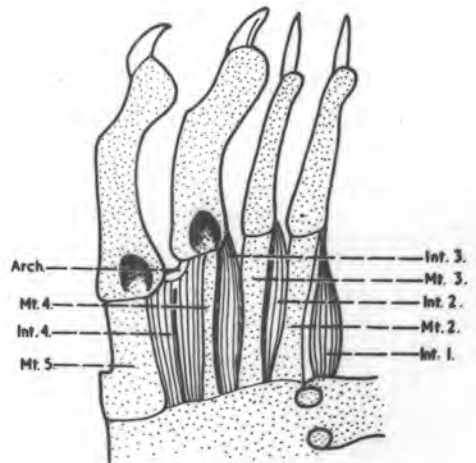
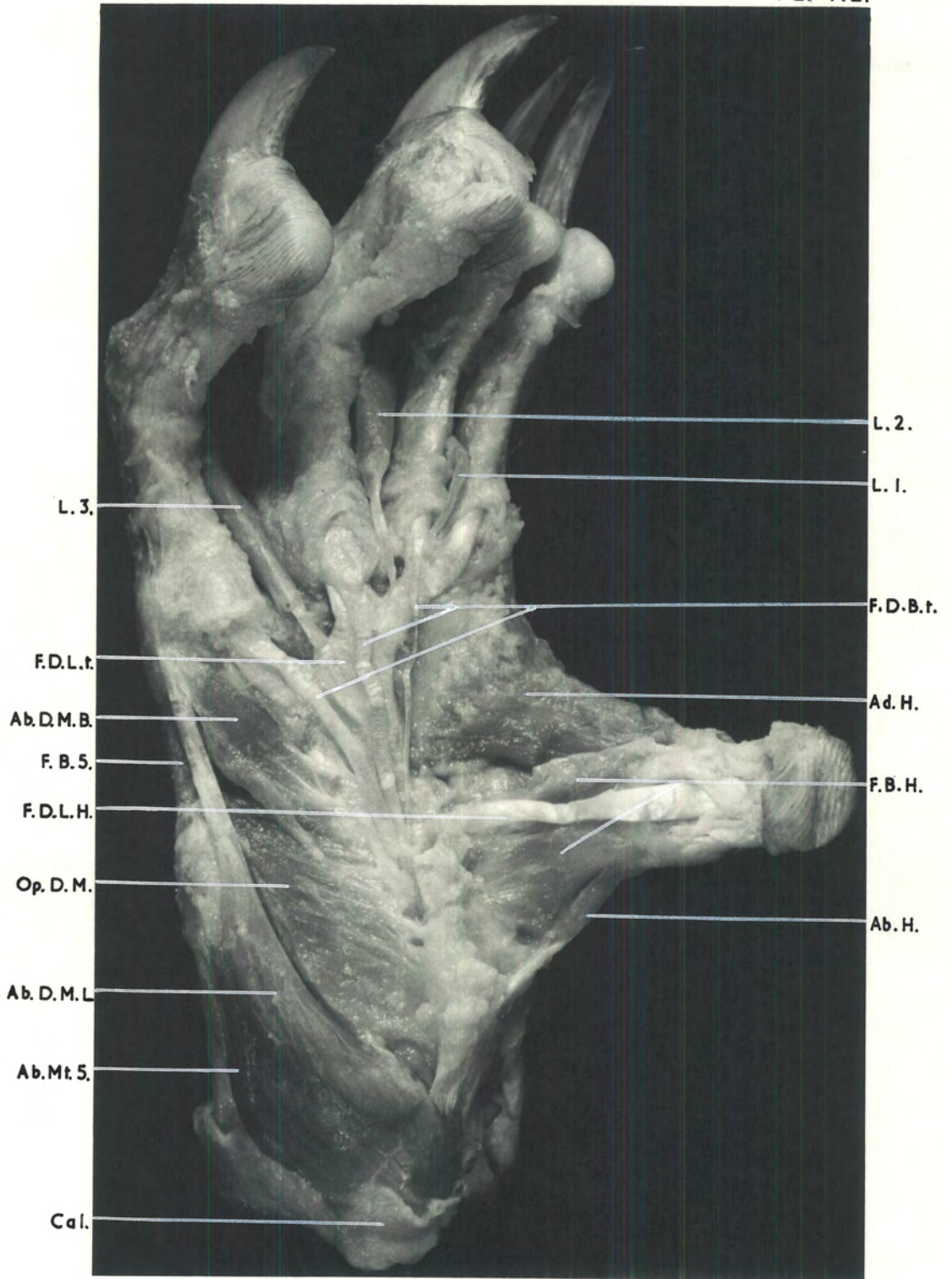


Plate XL (cf. fig. 65). Superficial muscles of sole. x3.

- Ab.D.M.B. - Abductor digiti minimi brevis.
- Ab.D.M.L. - Abductor digiti minimi longus.
- Ab.H. - Abductor hallucis.
- Ab.Mt.5. - Abductor metatarsi digiti minimi.
- Ad.H. - Adductor hallucis.
- Cal. - Posterior end of calcaneum.
- F.B.H. - Flexor hallucis brevis.
- F.B.5. - Flexor digiti minimi brevis.
- F.D.B.t. - Tendons of flexor digitorum brevis.
- F.D.L.H. - Tendon of flexor digitorum longus to
hallux.
- F.D.L.t. - Tendon of flexor digitorum longus to
other digits.
- L.1,2,3. - Lumbricals.
- Op.D.M. - Opponens digiti minimi.



Lumbricals (fig. 65; pl. XL). In the animals examined by me there were three of these muscles, the lateral two relatively large, the medial one very small - in fact practically non-existent in one specimen. The lateral two arise by small tendons from the clefts between the flexor longus tendons to the third, fourth and fifth digits; they are inserted into the tibial sides of the bases of the middle phalanges of the lateral two toes where they are also attached to the extensor expansions of these toes. The smaller medial one arises between the long flexor tendons to the syndactylous digits and is inserted into the fascia over the tibial side of the middle phalanx of the third toe. Bardeleben (1894) and Glaesmer (1908) found only two lumbricals in the foot in this species, Carlsson (1914) found two in one of her specimens, three in the other.

Different marsupials vary enormously in the number of lumbricals that they possess in their feet. N. typhlops (Thompson and Hillier, 1905) and Per. obesula (Glaesmer, 1910) have none; Choer. castanotis (Parsons, 1905) only one. The presence of two is characteristic of some of the Macropodidae - A. rufescens, M. giganteus, Pet. penicillata (Carlsson, 1914), Pet. xanthopus (Parsons, 1896). Three have been found in Dend. dorianus (Carlsson, 1914) and Phasc. cinereus (Macalister, 1872b), and four in Ph. maculata (Cunningham, 1882), Chir. variegatus (Sidebotham, 1885) and several species of Didelphys (Coues, 1872; Glaesmer, 1908, 1910; McMurrich, 1907). Larger numbers - six, seven, eight - have been reported for Did. marsupialis (Glaesmer, 1910), but seem more characteristic of the

Dasyuridae - Sarcophilus (Macalister, 1872a), Thylacinus (Cunningham, 1882) and Dasyurus (Glaesmer, 1908, 1910; MacCormick, 1887), in this last genus MacCormick actually describes fifteen, but says that only seven of them are proper lumbricals. Osgood (1921) found nine in Caenolestes.

As in the case of the corresponding muscles in the hand, the nerves to the lumbricals are extremely small and difficult to locate - particularly the superficial ones from the medial plantar nerve, but the supply appears to be as follows: the medial one is supplied by the medial plantar nerve, the lateral one by the lateral plantar and the middle one by both. Using notes from Cunningham, Brooks (1887) gives the supply to the tibial three from the medial plantar nerve in Ph. maculata.

Abductor Hallucis (figs. 63, 64; pls. XL, XLI) is a very small muscle arising from the extension of the plantaris tendon beyond the plantar sesamoid towards the hallux, and sometimes by a few fibres from the sesamoid itself. It is inserted into the medial side of the proximal phalanx of the hallux, and is supplied by the medial plantar nerve, as is the same muscle in Ph. maculata (Cunningham, 1881a, 1882).

Cunningham (1882) agrees that the muscle is poorly developed, but Carlsson (1914) says it is strong.

The abductor hallucis is absent in many of the Macropodidae, Dasyuridae and Peramelidae owing to the reduction of the hallux in these cases.

Abductor Metatarsi Digiti Minimi (figs. 63, 64, 65; pls. XL, XLI, XLII) springs from the middle third of the plantar surface of the calcaneum towards the lateral side, with some of the attachment lying deep to the long plantar ligament. The muscle is almost entirely fleshy and as it passes to its insertion into the proximal part of the tuberosity of the base of the fifth metatarsal it covers the peroneus longus tendon. Other reports of its presence cover Phascolarctos (Cunningham, 1882; Young, 1882), and numerous members of the group of American marsupials, Dasyuridae and Phalangerinae. Abductor Digiti Minimi Longus (figs. 63, 64; pls. XL, XLI) is fleshy only in its proximal half, the distal part being a small tendon. It arises from the posterior part of the plantar surface of the calcaneum, the middle part of the origin over and behind the long plantar ligament being fibrous: the tendon is inserted into the lateral side of the base of the proximal phalanx of the fifth digit and into the extensor expansion.

Abductor Digiti Minimi Brevis (figs. 63, 64; pls. XL, XLI) lies further forward than the last mentioned muscle; it has its origin from the plantar aponeurosis over the long flexor tendons distal to the plantar sesamoid, and passes distally and laterally to be inserted with the abductor digiti minimi longus.

Two abductors of the small toe, or an abductor with two parts, which probably (in some cases at least) correspond with the muscles described here have also been found in Caenolestes (Osgood, 1921), Chir. variegatus (Sidebotham, 1885), the opossum (McKerrie, 1907),

Das. viverrinus (Cunningham, 1882; MacCormick, 1887), one specimen of Thyl. cynocephalus, and in Ph. maculata (Cunningham, 1882).

Opponens Digiti Minimi (figs. 63, 64; pls. XL, XLI) is a muscle of considerable size arising from the lateral end of the plantar sesamoid and the lateral part of the plantar aponeurosis, its origin being fused with and partly deep to that of the abductor digiti minimi brevis. It is inserted into the base of the fifth metatarsal bone. The muscle is visible in the interval between the two abductors of the fifth toe and is to some extent joined with the short one.

The four muscles of the fifth digit just described are all supplied by the lateral plantar nerve.

Adductores (Contraahentes)(figs. 63, 64; pls. XL, XLI). Like the corresponding muscles of the hand these arise partly from the tarsal region and partly from a raphe which in this case is nearer to the line of the second digit than to the third. In the foot there are only two adductors.

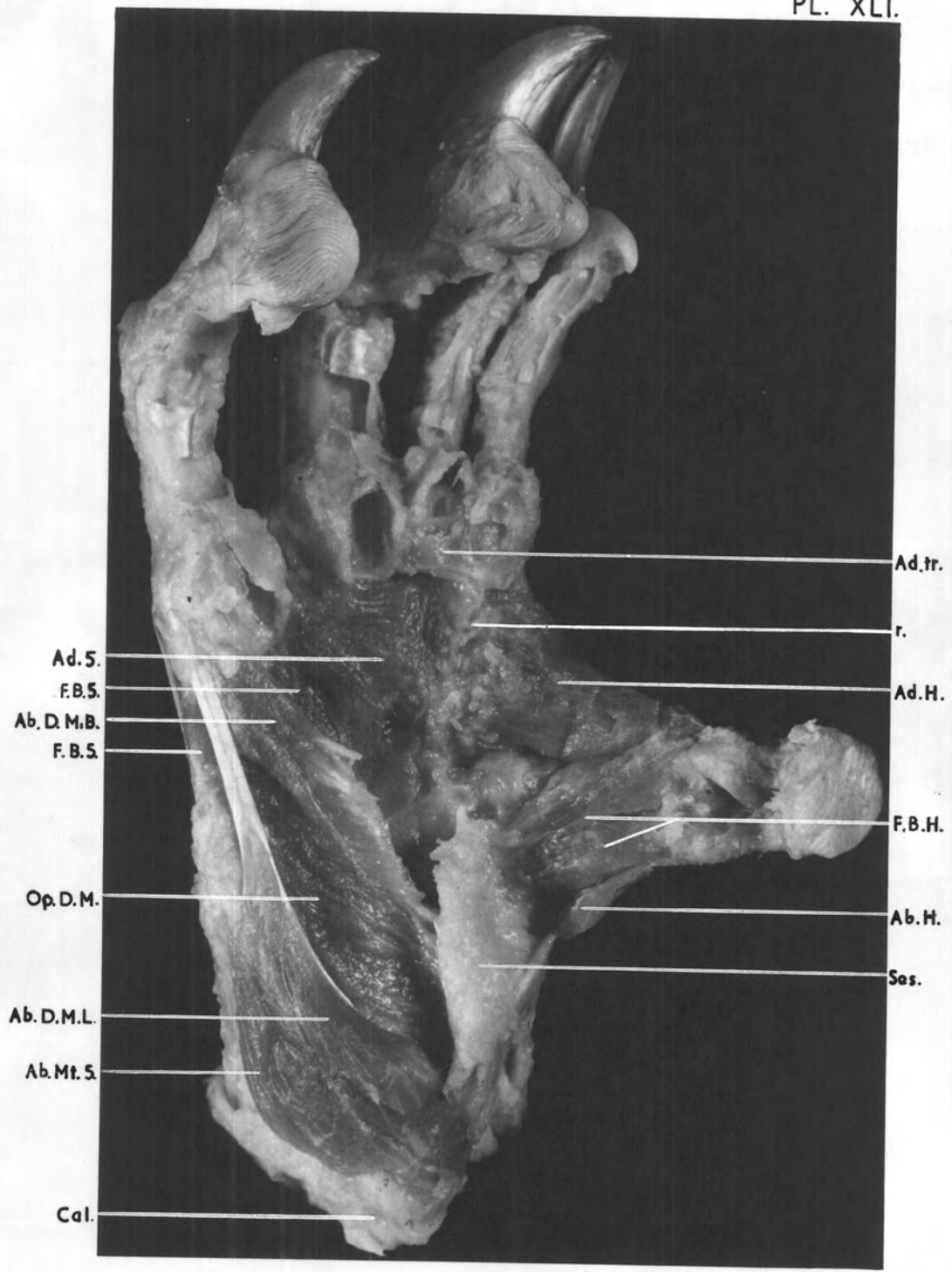
The adductor hallucis has its origin from the sheath of the peroneus longus tendon, from the tibial side of the raphe and to some extent from the deep surface of the plantar aponeurosis. It is inserted into the lateral side of the base of the first phalanx of the hallux and into the extensor expansion of this digit.

The adductor digiti minimi springs from the deep plantar fascia and from the fibular side of the raphe and is inserted into the medial side of the base of the proximal phalanx of the fifth toe and

Plate XLI (cf. fig. 64). View of sole showing adductor layer.

Long flexor tendons and lumbricals are removed. x3.

- Ab.D.M.B. - Abductor digiti minimi brevis.
- Ab.D.M.L. - Abductor digiti minimi longus.
- Ab.H. - Abductor hallucis.
- Ab.Mt.5. - Abductor metatarsi digiti minimi.
- Ad.H. - Adductor hallucis.
- Ad.tr. - Transverse slip between 2nd and 5th digits.
- Ad.5. - Adductor digiti minimi.
- Cal. - Posterior end of calcaneum.
- F.B.H. - Flexor hallucis brevis.
- F.B.5. - Flexor digiti minimi brevis.
- Op.D.M. - Opponens digiti minimi.
- r. - Adductor raphe.
- Ses. - Plantar sesamoid.



the corresponding extensor expansion.

Also belonging to the adductor sheet is a transverse slip of muscle passing from the base of the first phalanx of the second digit to the base of the same phalanx of the fourth, this slip is separate from the raphe and is reminiscent of a similar slip in the hand.

Bardeleben (1894) also gives an adductor to the second digit in this species, Carlsson (1914) says there are three but does not specify the toes concerned. Cunningham (1882) reports a third one to the second digit in one specimen, to the fourth in another. None of these authors describes the transverse slip mentioned above; the only similar slip described for any other marsupial is that which passes from the tibial side of the second toe to the fibular side of the third in Phasc. cinereus (Cunningham, 1882).

There are no adductor muscles in Choer. castanotis (Parsons, 1905) or N. typhlops (Thompson and Hillier, 1905); in Pet. penicillata, A. rufescens, M. giganteus (Carlsson, 1914), Pet. xanthopus (Parsons, 1896) and Hyps. moschatus (Heighway, 1939) there is only one - that of the fifth toe. In most other marsupials reported there are three or four; Carlsson (1914) describes six in Dend. dorianus but they all go to two toes. A raphe of origin is present also in Das. viverrinus (Cunningham, 1882; MacCormick, 1887), Phasc. cinereus, Ph. maculata (Cunningham, 1878c, 1882), Chir. variegatus (Sidebotham, 1885) and the opossum (McKerrieh, 1907).

The adductor sheet in T. vulpecula appears to be totally

supplied by the lateral plantar nerve as in Thyl. cynocephalus and Ph. maculata (Cunningham, 1881a, 1882). The medial plantar nerve gives branches that run in close proximity to the adductor hallucis and also the flexor brevis of the second toe and the first interosseous muscle but I think they are probably purely cutaneous.

Flexores Breves (fig. 65; pl. XLII) are five in number, one for each toe, and all divide so that each is inserted by two heads into the two sides of its particular toe; in the lateral three the lateral head is the larger, in the second one the medial head, while in the first (the flexor hallucis brevis) both heads are about the same size. The flexor hallucis brevis arises from the plantar sesamoid and the sheath of the peroneus longus tendon, the middle three flexors from the plantar ligaments of the appropriate tarso-metatarsal joints and also to a lesser extent from the adductor raphe, the fifth from the peroneus longus sheath (and through this from the crest of the cuboid bone) and also from a sesamoid on the medial side of the plantar aspect of the fifth metatarsal base. They are inserted into both sides of the bases of the proximal phalanges of the toes and to a variable extent into the extensor expansions; the second and third attach almost entirely to these expansions, while the first and the fibular head of the fifth are attached mainly if not entirely to bone. Carlsson (1914) and Cunningham (1882) both noted five of these muscles but the latter author gives only a fibular head for the flexor digiti minimi brevis.

Plate XLIII (cf. fig. 65). Flexores breves of foot. x4.

- Ab.Mt.5. - Abductor metatarsi digiti minimi.
F.B.H. - Flexor hallucis brevis.
F.B.2,3,4,5. - Flexores breves of other digits.
Int.1,4. - First and fourth interosseous muscles.
Mt.5.Tu. - Tuberosity of base of fifth metatarsal.

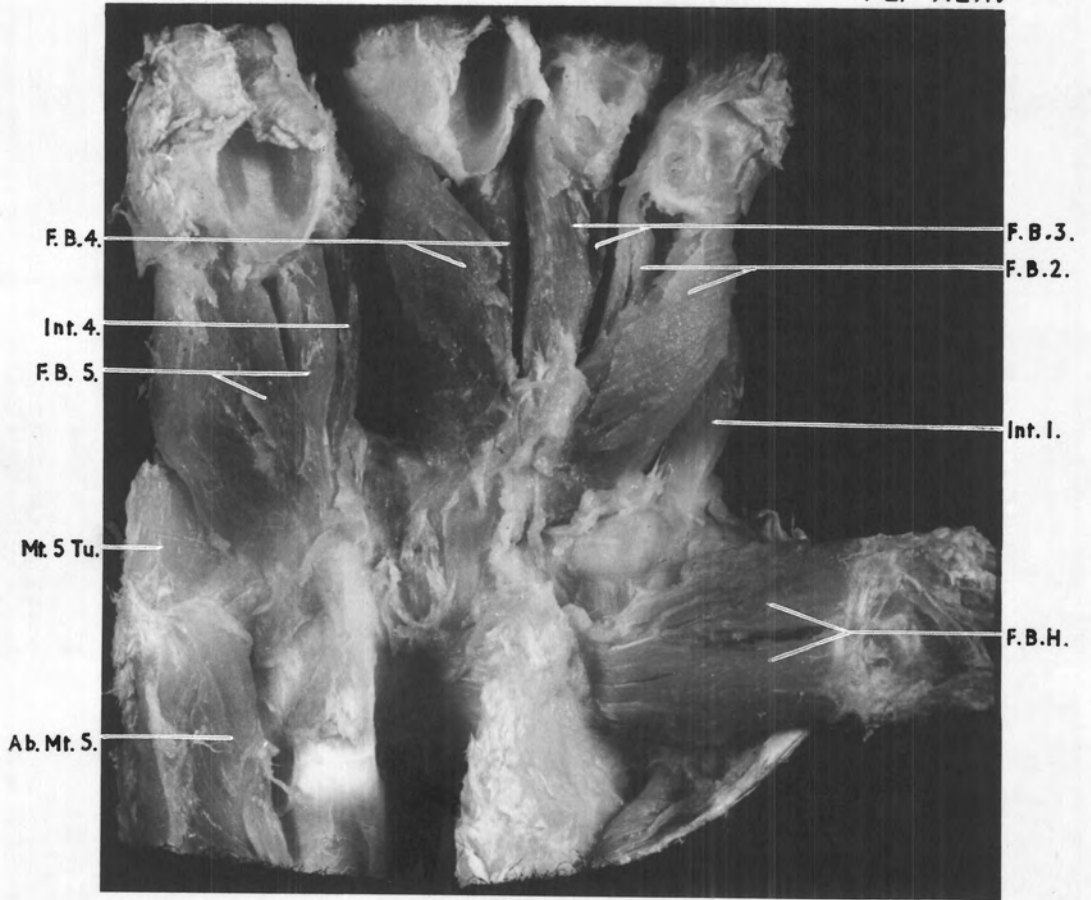


Plate XLIII (cf. fig. 66). Interosseous muscles of foot. All

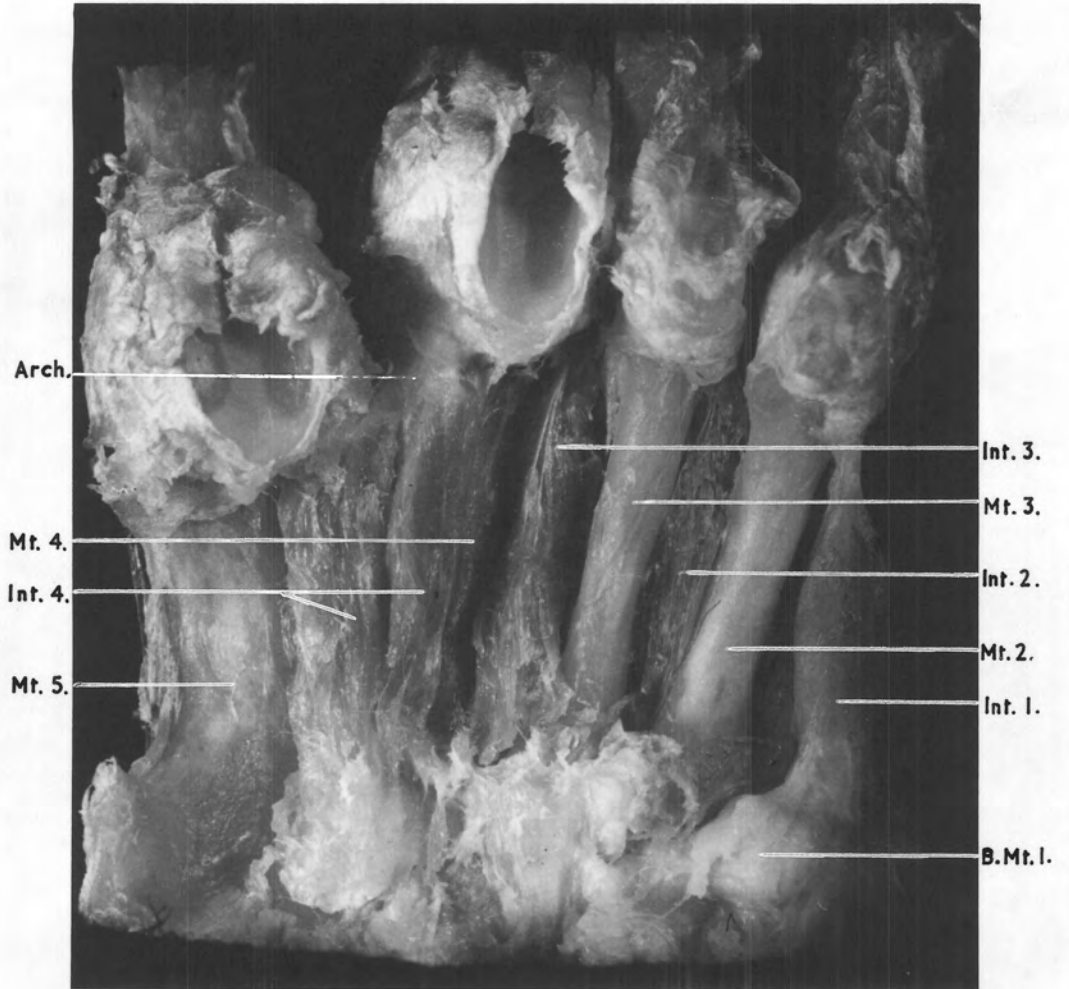
other muscles of the sole are removed. x5.

Arch. - Arch of insertion of fourth interosseous
muscle.

B.Mt.1. - Base of first metatarsal.

Int.1,2,3,4. - Interosseous muscles.

Mt.2,3,4,5. - Metatarsal bones.



The number of these muscles present in marsupials seems to be closely related to the number of toes, a rudimentary hallux having either a single small head or no muscle at all. Five muscles, all double headed, have been described for Caenolestes (Osgood, 1921), Chir. variegatus (Sidebotham, 1885) and Ph. maculata (Cunningham, 1878c, 1882). In Phasc. cinereus Cunningham (1882) and Young (1882) both note the absence of the fibular head of the fifth muscle which is apparently fused with the opponens; Macalister (1872b) mentions only the first in this species, he apparently includes the others with the interossei. In Petrogale (Carlsson, 1914; Parsons, 1896), Aepyprymus, Macropus and Dendrolagus (Carlsson, 1914) one double headed muscle serves both the syndactylous digits. Thompson and Hillier (1905) mention only those for the first and fifth digits in N. typhlops.

As noted by Cunningham (1882) the short flexor of the hallux is supplied from the medial plantar nerve, the others from the lateral plantar. He also gives the same innervation for Das. viverrinus, Phasc. calura (1882) and Ph. maculata (1881a, 1882). In Thyl. cynocephalus (1881a, 1882) he gives the supply to the four muscles present all from the lateral plantar nerve.

Interossei (fig. 66; pl. XLIII) are four in number and appear to be grouped around the midline of the fourth toe. The first arises from the fibular side of the base of the first metatarsal and passes to the tibial side of the base of the proximal phalanx of the second toe. The second takes origin from the fibular side of the base of

the second metatarsal and the dorsum of the intermediate cuneiform bone and is inserted into the base of the proximal phalanx and the extensor expansion on the tibial side of the third digit. The third comes from the dorsum of the lateral cuneiform and to a small extent from the base of the third metatarsal and goes to the tibial side of the fourth toe where it attaches mainly to the extensor expansion. The fourth is a much larger muscle and consists of two parts with the same attachments; it arises from the tibial side of the base of the fifth metatarsal and the adjacent fascia and also gets a few fibres from the fourth metatarsal, it is inserted partly into the base of the proximal phalanx of the fourth toe but mainly into a strong tendinous arch that joins this to the first phalanx of the fifth digit. There are similar, though much feebler, bands across the second and third interosseous spaces but they do not receive the insertion of any of the fibres of the corresponding interosseous muscles. Cunningham (1882) gives somewhat different origins for these muscles, he says the second is absent, apparently fused with the flexor brevis, and gives the third as bifurcating to be inserted into both the third and fourth toes; his account of the fourth, however, agrees with mine given here.

The most lateral of these muscles seems to fit the description of Campbell's (1939) "flexores digitorum minimi" in the hand, the muscles that he says are not true dorsal interossei. In Didelphys, however, whose foot he considers as typical of marsupials in general, he says that these muscles are not present in the foot and

that all the interossei are true dorsal interossei derived from the flexores breves.

The interossei are said to be absent in Choer. castanotis (Parsons, 1903) and N. typhlops (Thompson and Hillier, 1905), and Cunningham (1882) and Young (1882) both describe only one in Phasc. cinereus - to the second toe. A number of other marsupials have been reported with four and of these Ph. maculata (Cunningham, 1878c, 1882) and Caenolestes (Osgood, 1921) possess some that have attachment to both the adjacent digits. In Hyps. moschatus (Heighway, 1959) where there are only three two are attached to the opposite sides of the fourth toe suggesting a similarity to the grouping around this digit present in T. vulpecula.

I believe all the interossei are supplied by the lateral plantar nerve although, as in the case of the hand, I could not trace the small twigs through the short flexors as far as these muscles themselves. In Thyl. cynocephalus and Ph. maculata Cunningham (1878c, 1882) gives the supply to all from the lateral plantar nerve.

CONCLUSIONS.

As stated at the outset, the main aim of this investigation was to provide an account of the myology of Trichosurus vulpecula, indicate something of its innervation and to compare the findings with those reported for other marsupials: this, I hope, has been achieved in the foregoing pages. At this stage, however, there still remains to make some general comparisons between this species and other marsupials that have been described, based on a summation of the similarities and differences that have been noted in the case of the individual muscles and the plexuses. On this basis the musculature of Trichosurus resembles most closely that of the only other member of the Phalangerinae that has been adequately described, namely the genus now usually known as Spilocuscus, which has been reported in the literature under the generic names Phalangista, Phalanger and Cuscus. Next in order of similarity come such unrelated genera as the Polyprotodonts Dasyurus, Didelphys and Chironectes, whose musculature shows a greater resemblance to that of Trichosurus than does that of the more closely related but specialized Diprotodonts such as Phascolarctos and the Macropodidae. This latter fact is largely the result of the generalized nature of the muscular system in Trichosurus, for it has been noted that the majority of the muscles of Trichosurus show a condition that is more or less standard for a wide range of marsupials, or is about average for features where other types exhibit a range of variation. Some of the more specialized Polyprotodonts, as for example Notoryctes

and Choeropus, exhibit findings still more at variance with the condition in Trichosurus.

In the text some features were noted that appear to be unique in this species, or which at least are not commonly found amongst marsupials. Many of these may not be of great significance, and in some cases their apparent rarity may only be the result of an inadequacy of other accounts of the particular muscle concerned as a basis for comparison. In these features too there is a greater resemblance to the cuscus than to any other kind of marsupial.

Such features worthy of note are:-

- (i) the tendinous intersection in the genio-hyoid,
- (ii) the double nature of the thyro-hyoid,
- (iii) the tendinous intersection in the omo-hyoid,
- (iv) part origin of the omo-trachelien ventralis from the skull,
- (v) the presence of two parts to the coraco-brachialis,
- (vi) the double long head of the triceps,
- (vii) the insertion of the flexor carpi radialis into the scaphoid,
- (viii) the fibres of the extensor carpi radialis brevis derived from the supinator,
- (ix) the attachment of the extensor carpi ulnaris tendon to the middle three metacarpal bones as well as the fifth,
- (x) the transverse interphalangeal slips of the adductor sheet in the hand and foot,
- (xi) the extra hamate head of the flexor annularis brevis,

- (xii) the origin of fibres of the pyramidalis from the fascia on the rectus abdominis,
- (xiii) the absence of any origin of the rectus abdominis from the pubis,
- (xiv) the origin of fibres of the rectus abdominis from the linea alba,
- (xv) the presence of as many as eight tendinous intersections in the external oblique muscle of the abdomen,
- (xvi) the bipartite nature of the last four external intercostals,
- (xvii) the deep slips of the ilio-costo-cervicalis,
- (xviii) the small extent of origin of the longissimus capitis,
- (xix) the aponeurotic part of the origin of the biventer cervicis from the vertebral spines,
- (xx) the long lateral slips of the abductor caudae medialis,
- (xxi) the fibres of the retractor clitoridis passing to the rectum,
- (xxii) the bipartite nature of the psoas major,
- (xxiii) the absence of an adductor longus in the thigh,
- (xxiv) the insertion of the flexor digitorum brevis pedis to only three digits, and
- (xxv) the insertion of the flexor tibialis to the medial cuneiform bone.

The findings here described of the details of the musculature of Trichosurus vulpecula have many points of disagreement with the

reports of other investigators on this species, notably with those of Carlsson (1914) who dissected two specimens, one a young male of total length 38 cm., the other, which she claims to be an adult female, having a length of 45 cm.; these figures should be compared with an average length of 72 cm. for the three measured adults of my series.

In the case of the limb plexuses Trichosurus appears to show closest resemblance to Petrogale, with the cuscus next, the most noteworthy special features shown being the presence of an accessory femoral nerve and the "long nerve of the abdominal wall" going to the caudal part of the transversus abdominis.

The conclusions reached here are in keeping with the idea that Trichosurus vulpecula is a typical generalized member of the Phalangerinae and, more especially, of the Diprotodont group as a whole.

SUMMARY.

A full account is presented of the anatomy of the skeletal musculature of the marsupial Trichosurus vulpecula, its innervation is noted, and an outline of the brachial and lumbo-sacral plexuses is given, the findings reported being the results of a study involving five separate animals.

All discrepancies between the findings of this investigation and those previously reported for the species are noted, a comparison is made with the muscles described for other marsupials and the relatively few unusual features shown by this species are pointed out. From this comparison it is concluded that the musculature shows a fairly generalized pattern, and bears a closer resemblance, both in its overall structure and in the few uncommon features that it presents, to the cuscus than to any other marsupial that has been adequately described. The cuscus, now generally known by the generic name Spilocuscus, has been described in the literature as Phalangista, Phalanger and Cuscus, and is the only other member of the Phalangerinae for which an adequate account of the muscular system is available.

This work, apart from providing the most comprehensive description yet given of the musculature of any single marsupial species, furnishes additional evidence for the view that the vulpine phalanger is a typical Phalangerine of a basic generalized marsupial structure such as probably characterized the original Diprotodont stock.

REFERENCES.

- ABBIE, A.A. (1939a). A masticatory adaptation peculiar to some Diprotodont marsupials. Proc. zool. Soc. Lond. Ser. B, 109, pt. 2, 261-279.
- ABBIE, A.A. (1939b). The mandibular meniscus in monotremes and marsupials. Aust. J. Science. 2, 86-88.
- ADAMS, S.B., WHEELER, J.F.G. & EDGEWORTH, F.H. (1929). On the innervation of the platysma and the mandibulo-auricularis. J. Anat., Lond. 63, 242-252.
- ALEZAIS. (1901). Les muscles du membre postérieur du kangourou (Macropus bennetti). C. R. Soc. Biol. Paris. 1901. 971-972.
- ALSTON, E.R. (1880). On Antechinomys and its allies. Proc. zool. Soc. Lond. 1880. 454-461.
- BARDELEBEN, K. von (1894). On the bones and muscle of the mammalian hand and foot. Proc. zool. Soc. Lond. 1894. 354-376.
- BLIJVOET, W.F. (1908). Zur vergleichenden Morphologie des Musculus digastricus mandibulae bei den Säugetieren. Z. Morph. Anthr. 11, 249-316.
- BOARDMAN, W. (1941). On the anatomy and functional adaptation of the thorax and pectoral girdle in the wallaroo (Macropus robustus). J. Linn. Soc. N.S.W. 66, 349-387.
- BOAS, J.E.V. & PAULLI, S. (1908). Ueber den allgemeinen Plan der Gesichtsmuskulatur der Säugetiere. Anat. Anz. 33, 497-512.
- BROEK, A.J.P. van den (1910). Untersuchungen über den Bau der männlichen Geschlechtsorgane der Beuteltiere. Morph. Jb. 41,

347-436.

- BROOKS, H.St.J. (1887). Variations in the nerve-supply of the lumbrical muscles in the hand and foot, with some observations on the innervation of the perforating flexors. J. Anat., Lond. 21, 575-585.
- CAMPBELL, B. (1939). The comparative anatomy of the dorsal interosseous muscles. Anat. Rec. 73, 115-125.
- CARLSSON, A. (1905). Beiträge zur Anatomie der Marsupialregion bei den Beutelthieren. Zool. Jb. (Anat. u. Ont.). 18, 489-506.
- CARLSSON, A. (1914). Über Dendrolagus doriaemus. Zool. Jb. (Syst. Abt.). 36, 547-617.
- CORDS, E. (1922). Der M. mandibulo-auricularis. Anat. Anz. 56, 53-64.
- COUES, E. (1872). On the osteology and myology of Didelphys virginiana. Mem. Boston Soc. nat. Hist. 2, pt. 1, 41-149.
- CUNNINGHAM, D.J. (1878a). The nerves of the fore-limb of the thylacine (Thylacinus cynocephalus or harrisii) and cuscus (Phalangista maculata). J. Anat., Lond. 12, 427-433.
- CUNNINGHAM, D.J. (1878b). The intrinsic muscles of the hand of the thylacine (Thylacinus cynocephalus), cuscus (Phalangista maculata) and phascogale (Phascogale calura). J. Anat., Lond. 12, 134-444.
- CUNNINGHAM, D.J. (1878c). The intrinsic muscles of the mammalian foot. J. Anat., Lond. 15, 1-16.
- CUNNINGHAM, D.J. (1881a). The nerves of the hind-limb of the

- thylacine (Thylacinus harrisii or cynocephalus) and cuscus (Phalangista maculata). J. Anat., Lond. 15, 265-277.
- CUNNINGHAM, D.J. (1881b). The relation of nerve-supply to muscle-homology. J. Anat., Lond. 16, 1-9.
- CUNNINGHAM, D.J. (1882). Some points in the anatomy of the thylacine (Thylacinus cynocephalus), cuscus (Phalangista maculata) and phascogale (Phascogale calura), collected by H.M.S. Challenger, during the years 1875-1876; with an account of the comparative anatomy of the intrinsic muscles and nerves of the mammalian pes. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1875-1876. Zool. 5, 1-192.
- CUNNINGHAM, D.J. (1890). The value of nerve-supply in the determination of muscular homologies and anomalies. J. Anat., Lond. 25, 31-40.
- EDGEWORTH, F.H. (1935). The cranial muscles of vertebrates. Cambridge University Press.
- EDGEWORTH, F.H. (1957). The digastric muscle of Phalanger orientalis and maculatus. J. Anat., Lond. 71, 315-316.
- FRETS, G.P. (1908). Die Varietäten der Musculi peronaei beim Menschen und die Mm. peronaei bei den Säugetieren. Morph. Jb. 38, 135-193.
- GLAESMER, E. (1908). Untersuchung über die Flexorengruppe am Unterschenkel und Fuss der Säugetiere. Morph. Jb. 38, 36-90.
- GLAESMER, E. (1910). Die Beugemuskeln am Unterschenkel und Fuss bei

- den Marsupialia, Insectivora, Edentata, Prosimiae und Simiae.
Morph. Jb. 41, 149-536.
- GÖSSNITZ, W. von (1901). Beitrag zur Diaphragmafrage. Semon's
Zool. Forsch. 4, 205-262.
- GREGORY, W.K. (1910). The orders of mammals. Bull. Amer. Mus. nat.
Hist. 27, 1-524.
- HAINES, R.W. (1955). A consideration of the constancy of muscular
 nerve supply. J. Anat., Lond. 70, 53-55.
- HAINES, R.W. (1939). A revision of the extensor muscles of the
 forearm in tetrapods. J. Anat., Lond. 73, 211-255.
- HARRIS, W. (1939). The morphology of the brachial plexus. Oxford
 University Press.
- HAUGHTON, S. (1866). Notes on animal mechanics. No.IX. On the
 muscles of the marsupials. Proc. roy. Irish Acad. 1st ser., 9,
 469-487.
- HEIGHWAY, F.R. (1939). The anatomy of Hypsiprymnodon moschatus.
 M.D. thesis, University of Sydney.
- HOWELL, A.B. (1936). The phylogenetic arrangement of the muscular
 system. Anat. Rec. 66, 295-316.
- HOWELL, A.B. & STRAUS, W.L., Jr. (1931). The brachial flexor
 muscles in Primates. Proc. U.S. nat. Mus. 80, art. 13, 1-31.
- HUBER, E. (1924a). Zur Morphologie des M. auriculo-mandibularis der
 Säugetiere. Das Experiment als Unterstützung der
 morphologischen Muskelforschung. Anat. Anz. 58, 3-26.
- HUBER, E. (1924b). Über die Bedeutung der experimentellen Methode

- in der Facialisforschung, nebst Betrachtungen über die phylogenetische Entwicklung der Facialismuskulatur in der Vertebraten-Reihe. Anat. Anz. 58, 177-205.
- HUBER, E. (1925). Der M. mandibulo-auricularis der Säugetiere, nebst weiteren Beiträgen zur Erforschung der Phylogenese der Gesichtsmuskulatur. Morph. Jb. 55, 1-111.
- HUBER, E. (1930). Evolution of facial musculature and cutaneous field of trigeminus. Quart. Rev. Biol. 5, 133-188, 389-437.
- HUBER, E. & HUGHSON, W. (1926). Experimental studies on the voluntary motor innervation of the facial musculature. J. Comp. Neurol. 42, 115-163.
- KAJAVA, Y. (1910). Die kurzen Muskeln und die langen Beugemuskeln der Säugetierhand. Anat. Hefte (1. Abt.). 42, 1-194.
- KATZ, O. (1882). Zur Kenntnis der Bauchdecke und der mit ihr verknüpften Organe bei den Beuteltieren. Z. wiss. Zool. 56, 611-670.
- KOHLBRUGGE, J.H.F. (1898). Die Homotypie des Halses und Rumpfes. Eine vergleichende Untersuchung der Hals- und Brustnerven und ihrer Muskeln, mit einem Anhang über den N. facialis. Arch. Anat. Entw-Gesch. 1898. 199-262.
- LANGWORTHY, O.R. (1932). The panniculus carnosus and pouch musculature of the opossum, a marsupial. J. Mammal. 13, 241-251.
- LECHE, W. (1874-1900). In Bronn's Klassen und Ordnungen des Tier-Reichs. 6.

- LIGHTOLLER, G.H.S. (1939). Probable homologues. A study of the comparative anatomy of the mandibular and hyoid arches and their musculature. Trans. zool. Soc. Lond. 24, pt. 5, 349-444.
- LUBOSCH, W. (1908). Das Kiefergelenk der Edentaten und Marsupialier. Semon's Zool. Forsch. 4, 519-556.
- MACALISTER, A. (1868). On the homologies of the flexor muscles of the vertebrate limb. J. Anat., Lond. 2, 283-289.
- MACALISTER, A. (1870). On the myology of the wombat (Phascologomys wombata) and the Tasmanian devil (Sarcophilus ursinus). Ann. Mag. nat. Hist. 4th ser., 5, 153-175.
- MACALISTER, A. (1872a). Further observations on the myology of Sarcophilus ursinus. Ann. Mag. nat. Hist. 4th ser., 10, 17-20.
- MACALISTER, A. (1872b). The muscular anatomy of the koala (Phascolarctos cinereus). Ann. Mag. nat. Hist. 4th ser., 10, 127-134.
- MACCORMICK, A. (1887). The myology of the limbs of Dasyurus viverrinus. J. Anat., Lond. 21, 103-137, 199-226.
- McMURRICH, J.P. (1903). The phylogeny of the palmar musculature. Amer. J. Anat. 2, 463-500.
- McMURRICH, J.P. (1907). The phylogeny of the plantar musculature. Amer. J. Anat. 6, 407-437.
- MILLER, R.A. (1954). Comparative studies upon the morphology and distribution of the brachial plexus. Amer. J. Anat. 54, 143-175.
- OSGOOD, W.H. (1921). A monographic study of the American marsupial,

- Caenolestes. Field Mus. nat. Hist., Chic. Zool. 14, 5-156.
- OWEN, R. (1839-1847). In Todd's Cyclopaedia of anatomy and physiology. 3. Longman, Brown, Green, Longmans and Roberts; London.
- OWEN, R. (1868). On the anatomy of vertebrates. 5. Longmans, Green, and Co., London.
- PATERSON, A.M. (1887). The limb plexuses of mammals. J. Anat., Lond. 21, 611-634.
- PARSONS, F.G. (1894). On the morphology of the tendo-Achillis. J. Anat., Lond. 28, 414-418.
- PARSONS, F.G. (1896). On the anatomy of Petrogale xanthopus, compared with that of other kangaroos. Proc. zool. Soc. Lond. 1896. 683-714.
- PARSONS, F.G. (1905). On the anatomy of the pig-footed bandicoot (Choeropus castanotis). J. Linn. Soc. (Zool.). 29, 64-80.
- SIDEBOTHAM, E.J. (1885). On the myology of the water-opossum. Proc. zool. Soc. Lond. 1885. 6-22.
- SMITH, W.K. (1931). The motor innervation of the superficial facial and superficial cervical musculature of mammals. Anat. Rec. 50, 353-355.
- SONNTAG, C.F. (1921a). The comparative anatomy of the koala (Phascolarctos cinereus) and the vulpine phalanger (Trichosurus vulpecula). Proc. zool. Soc. Lond. 1921. 547-577.
- SONNTAG, C.F. (1921b). Contributions to the visceral anatomy and myology of the Marsupialia. Proc. zool. Soc. Lond. 1921.

- 851-882.
- SONNTAG, C.F. (1922). On the myology and classification of the wombat, koala, and phalangers. Proc. zool. Soc. Lond. 1922. 836-896.
- STRAUS, W.L., Jr. (1942). The homologies of the forearm flexors: Urodeles, Lizards, Mammals. Amer. J. Anat. 70, 281-316.
- STRAUS, W.L., Jr. (1946). The pattern of the intrinsic palmar musculature. Biol. Bull. Wood's Hole. 91, 255.
- TAYLOR, G. & BONNEY, V. (1905). On the homology and morphology of the popliteus muscle: a contribution to comparative myology. J. Anat., Lond. 40, 34-50.
- THOMPSON, P. & HILLIER, W.T. (1905). The myology of the hind limb of the marsupial mole (Notoryctes typhlops). J. Anat., Lond. 59, 308-351.
- TOBLER, L. (1902). Der Achselbogen des Menschen, ein Rudiment des Panniculus carnosus der Mammalier. Morph. Jb. 30, 453-507.
- TODD, T.W. (1912). The hinder end of the brachial plexus in man and mammals. Anat. Anz. 42, 129-144.
- WILSON, J.T. (1894). On the myology of Notoryctes typhlops, with comparative notes. Trans. roy. Soc. S. Aust. 18, 3-74.
- WINDLE, B.C.A. (1890). The flexors of the digits of the hand. J. Anat., Lond. 24, 72-84.
- WINDLE, B.C.A. & PARSONS, F.G. (1897a). On some points in comparative myological nomenclature. J. Anat., Lond. 31, 522-529.

- WINDLE, B.C.A. & PARSONS, F.G. (1897b). On the anatomy of Macropus rufus. J. Anat., Lond. 52, 119-134.
- YOUNG, A.H. (1879). On the male generative organs of the koala (Phascolarctos cinereus). J. Anat., Lond. 13, 305-317.
- YOUNG, A.H. (1880). The intrinsic muscles of the marsupial hand. J. Anat., Lond. 14, 149-165.
- YOUNG, A.H. (1881). On the so-called movements of pronation and supination in the hind-limb of certain marsupials. J. Anat., Lond. 15, 392-394.
- YOUNG, A.H. (1882). The muscular anatomy of the koala (Phascolarctos cinereus), with additional notes. J. Anat., Lond. 16, 217-242.