OBSERVATIONS ON THE ANATOMY OF THE TAIL IN THE VERVET MONKEY, *CERCOPITHECUS*, WHICH BEAR ON THERMOREGULATORY FUNCTION IN THE ORGAN (PRIMATA : CERCOPITHECIDAE)

P G WRIGHT

Department of General Physiology, University of the Witwatersrand, Johannesburg.

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ABSTRACT

A long tail is characteristic of the Family Cercopithecidae but apart from a limited contribution to postural adjustment no other function seems obvious.

The tail has a large proportion of skin which contributes significantly to the total body surface area. Because it has a widely adjustable blood flow rate and appears specially adapted for low flow rates under cool conditions a thermoregulatory function is ascribed to it.

The structural arrangement of the blood vessels favours heat loss mechanisms but this may be disadvantageous under cold conditions. A system of venae comitantes affecting the upper portion of the arterial supply, which could function as a counter-current heat trap, is described.

The origin of the caudal nerves and the continuation of the sympathetic chain into the fourth post-sacral vertebral segment is described.

INTRODUCTION

A very long tail is characteristic of all guenons and in his division of *Simia* Linnaeus (1758) reserved the name *Cercopithecus* for the long-tailed species (Osman Hill 1966: 209). The observations of Hongo & Luck (1953) and of Wright (1959) on blood flow in the tail of the vervet monkey (*Cercopithecus pygerythrus*) led to the conclusion that one of the main functions of the tail was to act as a highly adjustable radiator in the temperature control of the animal.

Studies thus far have been concerned with autonomic nervous function and the control of blood flow (Wright 1964), but it is apparent that there is a number of anatomical features relevant to a thermoregulatory function of this organ which have not been described and which are not mentioned in otherwise detailed anatomical considerations of this species (Osman Hill 1966).

The observations reported here have all been made in specimens of *C.pygerythrus* from central Uganda or from the Transvaal but observations made on single specimens of *C.neglectus*, *C.ascanius*, *C.albogularis* and *Erythrocebus patas*, suggest that these features may be common to the Family Cercopithecidae.

MATERIALS AND METHODS

The animals used in this study were mainly adult vervets of both sexes, varying between 2 and 5 kg body mass, which had been used for blood flow studies.

Specimens were dissected fresh or after perfusion with 5% formol-saline. In a number of cases the circulation was cleared of blood by perfusion with warm 0,9% NaCl solution. Arterial vessels were then injected with red latex via the abdominal aorta, and the veins with blue latex via cannulae in the preipheral ends of the lateral caudal veins. These preparations were then either dissected fresh, preserved with formol-saline, or cleared in 10% NaOH solution and preserved in glycerol.

The valves in the lateral and central veins were identified by retrograde injection of methylene blue, dissolved in 0,9% NaCl solution, down a lateral vein via a cannula in the central end. Dissection followed to locate the distribution of dye and then the vein was recannulated below the uppermost valve. This procedure was repeated sequentially down the length of the tail.

For descriptive clarity the terms coccygeal and caudal have not been used and all vertebral segments beyond the third sacral have been called postsacral (pS) in conformity with Osman Hill (1966).

ANGIOLOGY (Figures 1,2)

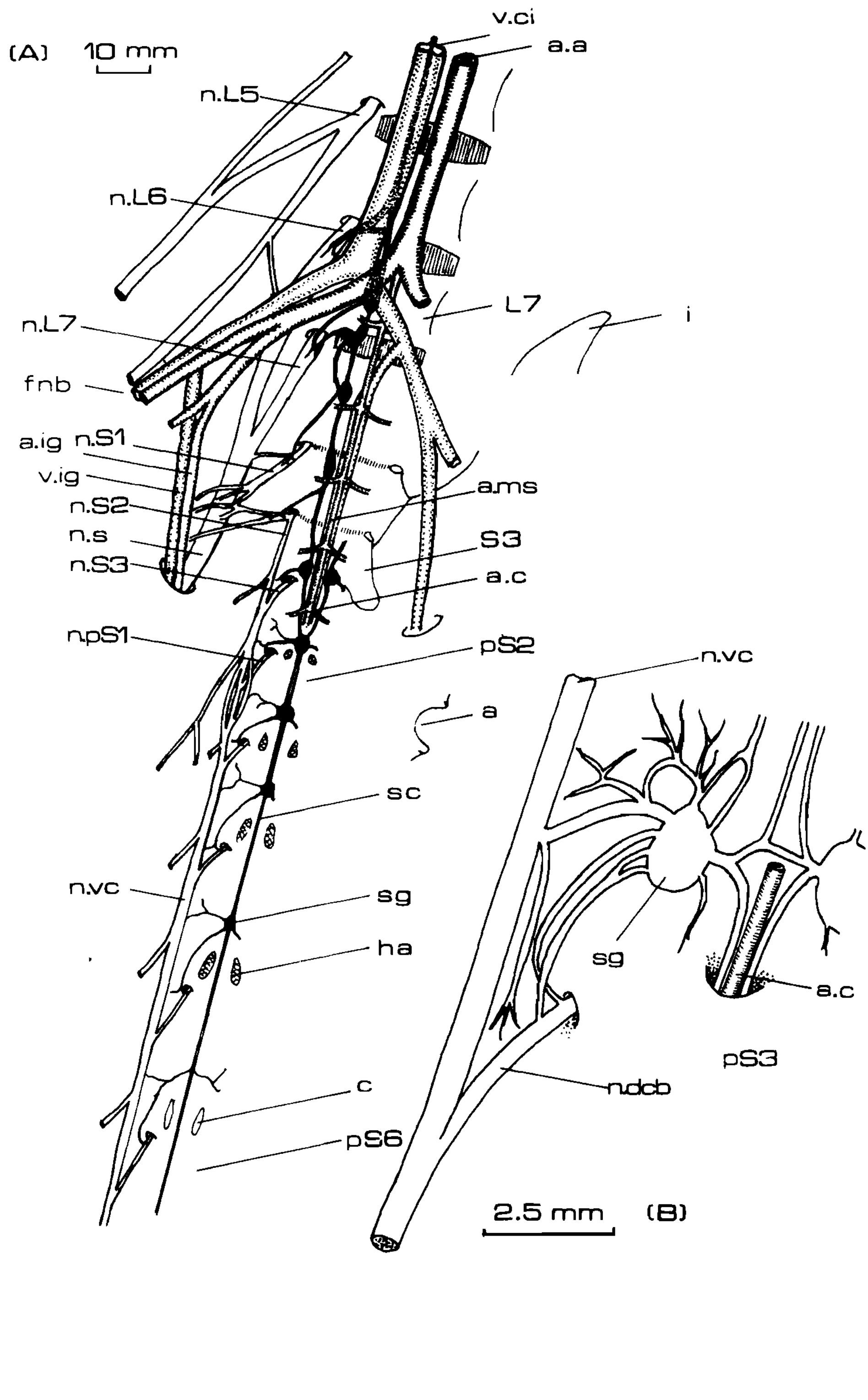
Blood is supplied to the tail by the caudal artery which is a direct continuation of the median sacral artery which arises dorsally from the aortic bifurcation. Initially a small dorsal branch supplies the lumbar vertebrae but the main vessel runs superficially along the ventral surface of the sacrum to pass through the haemal arches of the upper five post-sacral vertebrae. So far it is deep within the tail tissues but in the sixth post-sacral segment it moves ventrally to run superficially beneath the skin and between the chevron-bone remnants of the remaining twenty-or-so articulations. Small dorsal branches supply the joints and bone, and at the proximal third of each vertebral segment a major dorsal branch arises. This immediately bifurcates (occasionally both branches arise close together directly from the caudal artery) and the branches pass either side of the vertebra to supply the muscles, nerve and other tissues and the skin of the upper side of the tail. Three small ventral branches of the main artery supply the skin of the lower side of the tail in each segment. There is an arcuate system of vessels from which arise many branches to supply the tissues of the dermal papillae.

FIGURE 1

A. The vascular and nerve supply to the tail of *C. pygerythrus* (ventral aspect). Structures are omitted where necessary for clarity. The scale is approximately correct except that the sympathetic ganglia are slightly exaggerated.

B. Part of an unfused pair of ganglia at postsacral 3.

For abbreviations see p. 483.


(A) 10 mm
v.ci
a.a
n.L5
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n.L7
L7
i
fnb
a.ig
n.S1
v.ig
a.ms
n.S2
n.s
S3
n.S3
a.c
n.pS1
pS2
a
sc
n.vc
sg
ha
c
pS6
n.vc
sg
a.c
pS3
n.dcb
2.5 mm (B)

Venous drainage is provided by two large muscular-walled veins, which lie dorsolaterally, and by a small median vein which lies for the most part dorsally beneath the caudal artery. Halfway along each vertebral segment there is a major branch of each dorsolateral vein and the two branches unite to join the median vein. These two communicating veins receive most of the drainage from the muscle and other deep tissues, while three or four superficial branches drain the skin directly into the dorsolateral veins in each segment.

Three superficial branches drain the ventral skin into the median vein and there are connections between superficial branches in dorsal and ventral areas. Each dorsolateral vein runs superficially beneath the skin to join the inferior gluteal vein and enter the pelvis through the greater sciatic foramen. The inferior gluteal veins runs as venae comitantes to the gluteal arteries, a distance of about 10 cm in an adult vervet.

The median vein is small along most of its course but above the last haemal arch (postsacral 5/6) it becomes larger and duplicates, with branches forming a substantial plexus around and close to the caudal and median sacral arteries. The branches unite and join one or other common iliac vein asymmetrically; usually the junction is with the left common iliac vein. Occasionally the branches do not join but both enter the common iliac vein asymmetrically. From the last haemal arch to the origin of the median artery and veins these vessels are closely associated for a distance of about 20 cm in an adult animal.

Venous branches draining the erector spinae muscle and dorsal skin enter through the lower two sacral foramina and divide, supplying a small branch which joins the inferior gluteal vessels.

Valves occur in the deep venous branches just before they join the communicating veins in each segment, and in both dorsolateral veins and the medial vein immediately peripheral to their junctions with the communicating veins.

Two main lymph vessels accompany the medial vessels but the first lymph gland is just within the pelvic cavity.

The glomeruli caudales (Figure 2)
Halfway along the tail there is an interesting addition to the vascular pattern so far described. In the tenth post-sacral segment (15/20 specimens) or the eleventh postsacral segment (5/20 specimens) glomus-type arteriovenous structures appear and are then present in each segment to the tail end. In the middle region of each vertebral segment usually one large and two (sometimes three) smaller structures are to be found arising from a superficial skin branch of the caudal artery, or from one of the two main segmental branches close to its origin. The normal small artery divides into numerous smaller convoluted vessels having a modified structure, which reunite to become an efferent vessel which joins the median vein usually via a vein draining the skin. In hundreds of dissections this pattern has invariably been found; there is never any connection of this nature between the artery and the dorsolateral veins.

The vascular structures are encapsulated with connective tissue so they are recognizable as discrete organs, and each glomus receives a discrete nerve filament from the segmental branches of the dorsal caudal nerves. The nerve supplies both myelinated and nonmyelinated fibres and there are profuse nerve endings in relation with the modified vessels of the organ.

INNERVATION

Spinal nerves (Figures 1,3)

The structures of the tail are innervated *via* two substantial ventral nerves and two smaller dorsal nerves lying deep between the caudal muscles on each side. The larger ventral nerves arise by longitudinal connections between the ventral branches of S2, S3, pS1, pS2, pS3, pS4 nerves and a small branch of the dorsal nerve in the fifth postsacral segment which has no separate origin from the cauda equina. The dorsal nerves arise by longitudinal connections between the dorsal branches of pS1, pS2, pS3 and pS4 nerves. Each dorsal nerve branches before it joins the collector nerve and the branch goes through to join the ventral nerve. The dorsal root ganglia are displaced so that the ganglia of the fourth postsacral nerves lie within the canal of the second postsacral vertebra, the third postsacral nerve ganglia within the first postsacral vertebra, with the remainder in close sequence so that the ganglia of the first sacral nerves are within the seventh lumbar vertebra.

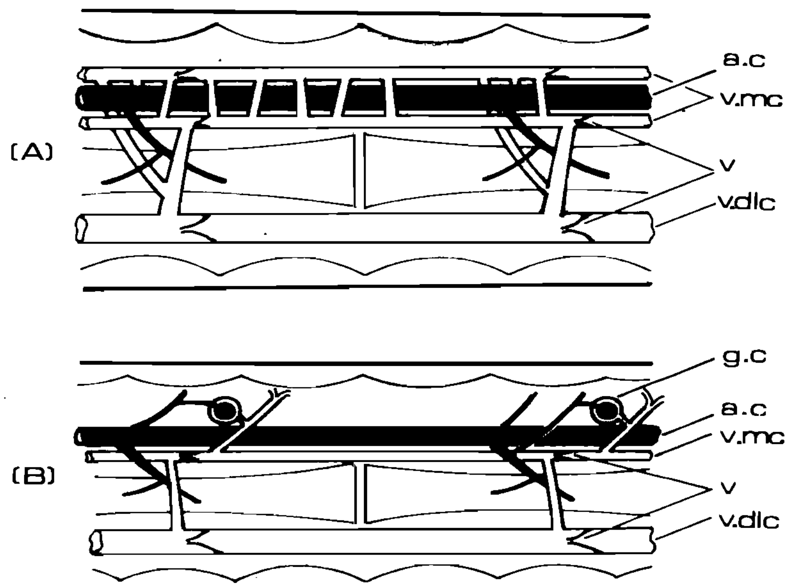

FIGURE 2

Diagram of vascular arrangement anterior and posterior to the ninth postsacral vertebral segment in *C. pygerythrus*. (A) p S1 - p S8, (B) p S9 - p S26.

Two possible arterial supplies to the glomus caudalis are shown. Ventral surface above, dorsal below.

For abbreviations see p. 483.

Autonomic nerves (Figures 1,3)
Zuckerman (1938) reported that 'there are usually four sacral ganglia, the fourth being the ganglion impar, which may be situated on the first of the caudal vertebrae'. Commenting on the variability in arrangement he also said that the number may be reduced to three with the third as the ganglion impar. These observations were in respect of the rhesus monkey (*Macaca mulatta*), but in five specimens of *Cercopithecus* he found no difference in arrangement. Osman Hill (1966:359-63) reported similarly for both families. Giordano-Lanza & Donnorso (1964) in their study of *C. aethiops sabeus* reported the same arrangement as Zuckerman.

In the present study apart from the arrangement described by Zuckerman, Giordano-Lanzo & Donnorso and Osman Hill, three further fused pairs of ganglia have been found in each of ten dissections. They lie deep to the medial caudal vessels midway along the second, third and fourth postsacral vertebrae. The ganglia are more or less saddle-shaped depending upon the degree of 'fusion' of the pairs, except that in five instances no 'fusion' had occurred and the two ganglia remained discreet.

Irrespective of the amount of ganglionic fusion the pre-ganglionic nerves remained separate between successive ganglia. From each ganglion (or half-ganglion) one nerve continued with the medial vessels whilst other postganglionic nerves supplied the tissues directly. Still further postganglionic branches joined the ventral caudal nerve trunk and the penetrating branch connecting the ventral and dorsal caudal nerves in each segment.

No study has been made of the caudal limits of emergence of the white rami communicates; the levels described by Zuckerman (1938), Kuntz (1933) and Trumble (1934) were decided on grounds of colour, consistency and disposition, not on histological or physiological examination.

DISCUSSION

The tail appears to be an organ used to some extent for balance in posture and locomotion. Several authors have described the tail positions characteristic of various *Cercopithecus* species (Osman Hill 1966: 372-74), but as the tail is not prehensile its usefulness would appear to be limited. However, in the longtailed monkeys it appears to comprise a significant proportion of the total skin and of the body surface area (Wright in press) so that it can be expected to contribute significantly to thermoregulation. Functional studies have indicated that it is well adapted for this purpose (Hongo & Luck 1953; Wright 1959, 1964, 1976). The structure and behaviour of the prominent dorsolateral veins have indicated their suitability to meet conditions of low blood flow under cool conditions.

In many species it is usual to find a system of venae comitantes supporting thermoregulation in the skin (Schmidt-Nielsen 1963). In *Cercopithecus* the dorsolateral caudal veins run superficially along the whole of the tail and flank into the sciatic foramina and are only then related to the gluteal arteries. This provides a short distance only for thermal exchange and the arterial blood is not supplied to the tail. Only the small median caudal

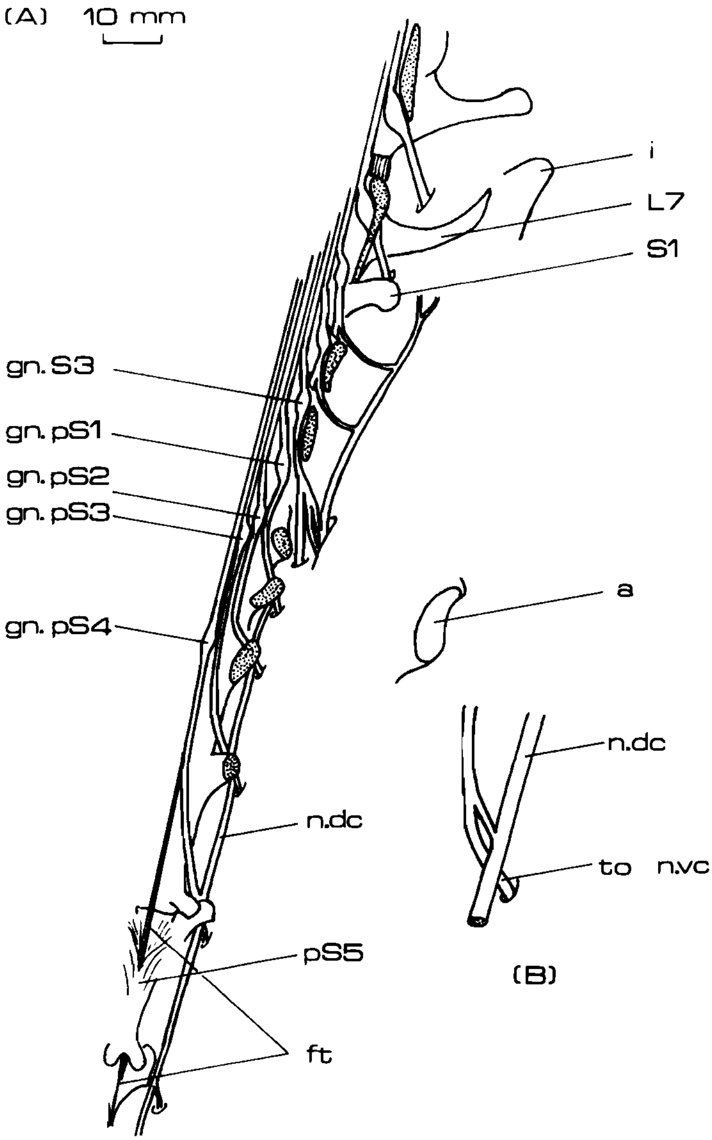

FIGURE 3

A. The origin of the caudal nerves in *C. pygerythrus* (dorsal aspect). Structures are omitted where necessary for clarity.

B. Connections to dorsal and ventral caudal nerves obscured in (A) by lateral vertebral processes.

For abbreviations see p. 483.

vein is related to the caudal artery but above the sixth postsacral vertebra it assumes the nature of a plexus around the caudal and median sacral arteries. While it is still not large in cross-section compared with the two dorsolateral veins, its relationship will allow it to exchange heat with the caudal arterial inflow to the tail. The balance of blood flow between the four vessels will then determine the effectiveness of such a counter-current heat exchange system.

The structure of the glomus-type arteriovenous anastomoses was originally reported by Von Schumacher (1907) in *M. mulatta* and, while suggestions as to their function have been made, little experimental evidence has yet been adduced to support these suggestions. Further investigations are in progress (King & Wright 1976; Wormald & Wright 1976).

SUMMARY

The arterial and venous vasculature of the tail of *Cercopithecus* has been described in detail. The aspects relevant to a thermoregulatory function of the organ have been stressed.

The origin of the dorsal and ventral caudal nerves has been described.

The arrangement of the sympathetic nerve supply to the tail has been reviewed and the extension of the chain for three ganglia beyond the ganglion impar has been described.

It is suggested that the caudal circulation may make a significant contribution to thermoregulation and, in particular that a counter-current heat exchange system is possible above the level of the sixth postsacral segment.

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LIST OF ABBREVIATIONS

a = acetabulum
a.a = abdominal aorta
a.c = caudal artery
a.ig = inferior gluteal artery
a.ms = median sacral artery
c = chevron bone
fnb = femoral neuro-vascular bundle
ft = filum terminale
g.c = glomus caudalis
gn.pS1, 2, 3, 4 = dorsal root ganglion of postsacral nerve
gn.S3 = dorsal root ganglion of sacral nerve
ha = haemal arch
i = iliac crest
L7 = lumbar vertebra
n.dc = dorsal caudal nerve
n.dcb = dorsal caudal nerve branch
n.L5, 6, 7 = lumbar nerve
n.s = sciatic nerve
n.S1, 2, 3 = sacral nerve
n.vc = ventral caudal nerve
pS2, 5, 6 = postsacral vertebra
sc = sympathetic chain
sg = sympathetic ganglion
S1, 3 = sacral vertebra
v = valve
v.ci = inferior vena cava
v.dlc = dorso-lateral caudal vein
v.ig = inferior gluteal vein
v.mc = median caudal vein