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* Notes on the Blood System of the Marsupialia

By

JOSEPH PEARSON

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The following notes were made in the course of a study of the comparative anatomy of the Marsupialia. The heart and great vessels have been reserved for a future paper.

In all thirty-three specimens belonging to the following thirteen species have been dissected:—

Dasyurus viverrinus (Native Cat).
Sarcophilus harrisii (Tasmanian Devil).
Isoodon obesulus affinis (Short-nosed Bandicoot).
Perameles gunnii (Tasmanian striped Bandicoot).
Petaurus breviceps (Lesser Flying Phalanger).
Pseudocheirus convolutus (Ring-tailed Phalanger).
Trichosurus vulpecula fuliginosus (Brush-tailed Phalanger).
Phascolomys ursinus (Island Wombat).
Phascolomys ursinus tasmaniensis (Tasmanian Wombat).
Bettongia cuniculus (Tasmanian Bettong).
Potorous tridactylus apicalis (Long-nosed Rat Kangaroo).
Thylogale billardierii (Rufous Wallaby).
Macropus tasmaniensis (Forester Kangaroo).

1. ARTERIES ARISING FROM THE BASE OF THE AORTA

There is as much variation in the origin of these arteries in the Marsupials as there is throughout the entire Mammalia, and all stages exist from what may be regarded as a primitive condition to be found in *Phascolarctos*, in which the subclavians and common carotids of both sides arise independently, to the highly specialized condition found in *Petaurus breviceps* in which the four subsidiary arteries arise from the aorta through the medium of a common vessel.

In the following summary I have brought together the results of my own observations together with those of other workers.

A. Four Arteries arising independently from the Aorta

This condition has been described by Sonntag (1921a) in *Phascolarctos cinereus* (Fig. 1).

B. Three Arteries arising from the Aorta

(*a*) Right subclavian and right common carotid connected with the aorta by the right innominate artery.

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* This work has been carried out under the auspices of the Biological Survey of Tasmania. Most of the specimens which provided material for the present study were obtained by the Biological Survey.

Bettongia cuniculus (Pearson) (Fig. 3); *Phascolarctos cinereus* (Forbes, 1881; Sonntag, 1921b); *Petaurus breviceps* (Sonntag, 1921b); *Phascolomys ursinus* (Forbes, 1881; Sonntag, 1921b; Pearson).

In *Phascolomys* I have found one case in which the right subclavian arose so close to the base of the right common carotid artery (Fig. 2) that it was difficult to say whether this case belongs to Group A or is an intermediate condition between Group A and Group B (*a*).

(*b*) The right subclavian artery arising independently, the two common carotids arising from an innominate.

Dasyurus viverrinus (Cunningham, 1882; Sonntag, 1921b; Pearson). See Fig. 4.

C. Two Arteries arising from the Aorta

(*a*) An innominate from which are given off the right subclavian and the right and left common carotids, the left subclavian arising separately.

(1) The innominate short, with the right subclavian arising near the junction of the innominate with the aorta (Fig. 5).

Sarcophilus (Pearson), *Dendrolagus* (Parsons, 1903) and *Notoryctes* (Sweet, 1904).

(2) The innominate of medium length, with all three arteries arising from the innominate at the same level (Fig. 7).

Macropus (Sonntag, 1921b; Pearson); *Spilocuscus nudicaudatus* (Cunningham, 1882); *Phascolarctos* (Forbes, 1881; Sonntag, 1921b); *Dendrolagus* (Sonntag, 1921b); *Thylogale billardierii* (Pearson).

(3) The innominate long, with the right subclavian given off some distance from the base, behind the origins of the right and left common carotids.

Isoodon obesulus affinis (Pearson) Fig. 6; *Thylacinus* (Cunningham, 1882); *Trichosurus vulpecula fuliginosus* (Cunningham, 1882; Sonntag, 1921b; Pearson); *Didelphys cancrivora* (Sonntag, 1921b); *Petaurus australis* (Sonntag, 1921b).

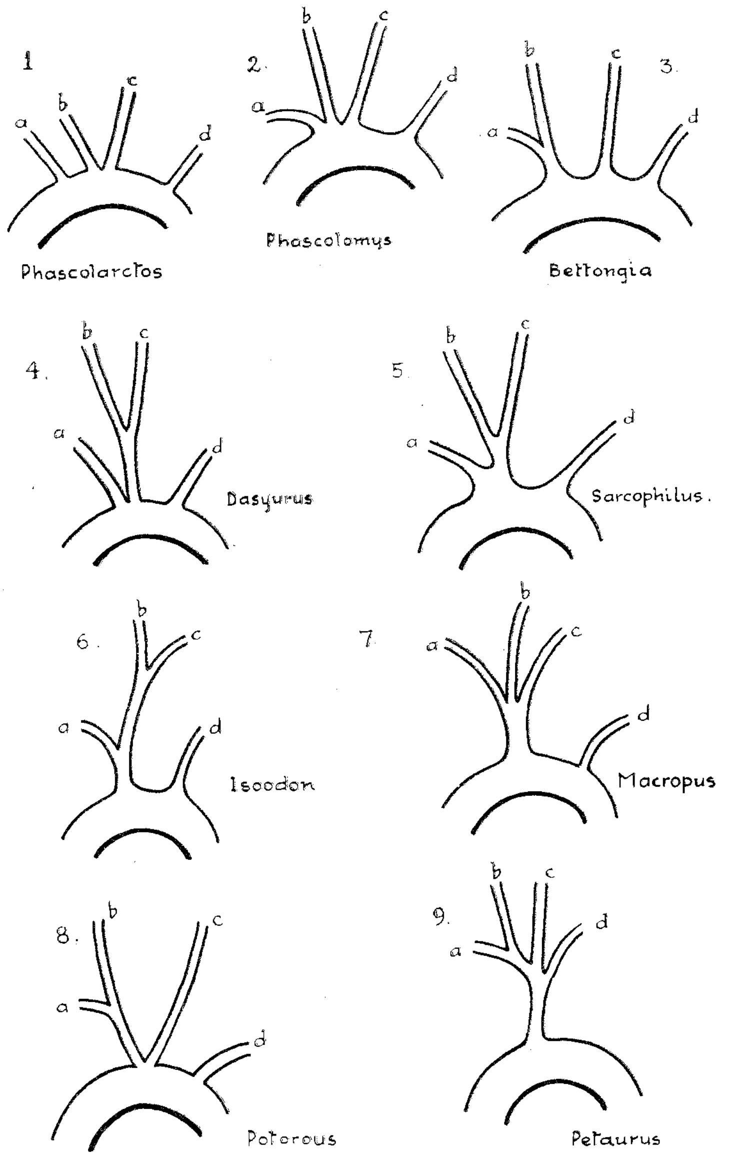
(*b*) The right and left common carotids arising together from the aorta, the right subclavian arising from the right carotid. The left subclavian arising separately from the aorta.

Potorous tridactylus apicalis (Pearson, Fig. 8).

D. One Artery arising from the Aorta

So far as I am aware this highly specialized condition is found only in *Petaurus breviceps* (Forbes, 1881; Pearson); (Fig. 9).

Parsons (1902) made a survey of the arrangement of the branches of the mammalian aortic arch, and he was able to show that there was considerable variation in these branches throughout the mammalian series. A careful study of his paper leads one to the conclusion that the method of branching of the vessels arising from the aortic arch is not correlated with the affinities of the various members of the group. From the analysis which has been given above it is obvious that the disposition of the branches of the aortic arch is of no value in determining the relationships and probable evolution of the various members of the Marsupialia. There is, in fact, just as much variation in the arrangement of these arteries within the single order Marsupialia as there is in the whole of the Mammalia.



ARRANGEMENT OF THE ARTERIES ARISING FROM THE BASE OF THE AORTA IN THE MARSUPIALIA

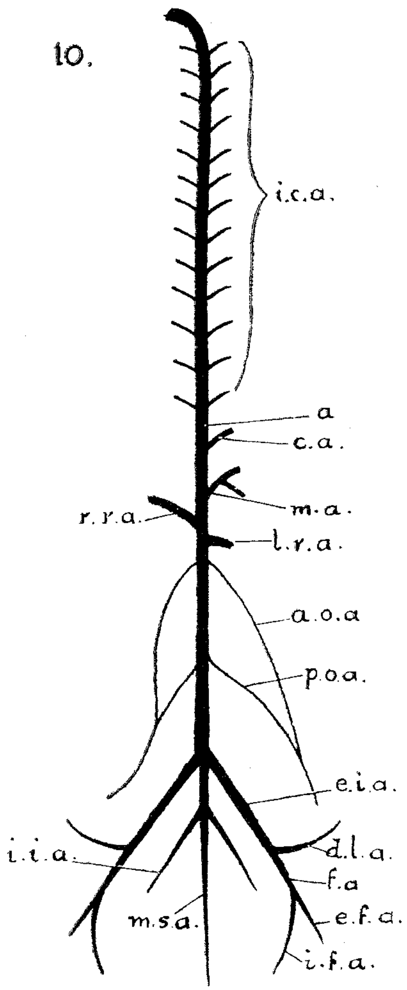
FIG. 1.—*Phascolarctos cinereus* (after Sonntag); FIG. 2—*Phascolomys ursinis*; FIG. 3—*Bettongia cuniculus*; FIG. 4—*Dasyurus viverrinus*; FIG. 5—*Sarcophilus harrissi*; FIG. 6—*Isoodon obesulus affinis*; FIG. 7—*Macropus tasmaniensis*; FIG. 8—*Potorous tridactylus apicalis*; FIG. 9—*Petaurus breviceps*.

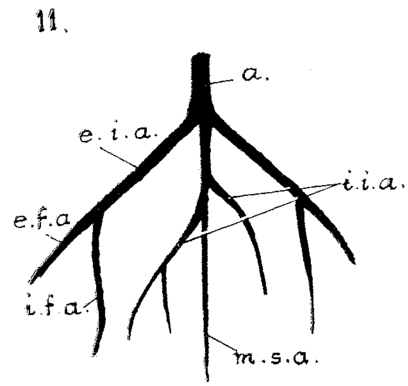
a, right subclavian artery; *b*, right common carotid artery; *c*, left common carotid artery; *d*, left subclavian artery.

2. Posterior Arteries

After giving rise to the arteries which have been dealt with above, the aorta makes a sudden turn to the left and runs immediately below the vertebral column to the posterior end of the body. In its anterior region the aorta gives off a series of paired intercostal arteries, each of which lies in an intercostal space immediately behind the corresponding intercostal vein (Fig. 10).

A short distance behind the diaphragm the coeliac artery gives off branches to the liver, pancreas, stomach and duodenum. Immediately behind the coeliac artery the mesenteric artery arises, generally near the level of the right renal





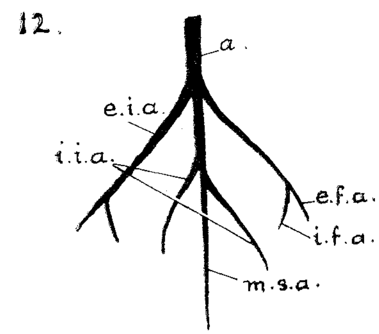


Fig. 10—Dorsal aorta and its branches in the Marsupialia ; Fig. 11—Posterior arteries in *Phascolomys* ; Fig. 12—Posterior arteries in *Trichosurus*.

a, aorta ; *a.o.a.*, anterior ovarian artery ; *c.a.*, coeliac artery ; *d.l.a.*, dorso-lumbar artery ; *e.i.a.*, external iliac artery ; *i.c.a.*, intercostal arteries ; *e.f.a.*, external femoral artery ; *f.a.*, femoral artery ; *i.f.a.*, internal femoral artery ; *i.i.a.*, internal iliac artery ; *i.l.a.*, ilio-lumbar artery ; *l.r.a.*, left renal artery ; *m.a.*, mesenteric artery ; *m.s.a.*, median sacral artery ; *p.o.a.*, posterior ovarian artery ; *r.r.a.*, right renal artery.

artery. The mesenteric artery divides almost immediately into the anterior mesenteric artery, which supplies the main parts of the intestine and spleen, and the posterior mesenteric artery, which supplies the rectum. This arrangement differs from that in the Monodelphia where the anterior and posterior mesenteric arteries usually arise separately from the aorta.

The spermatic (or ovarian) arteries consist of an anterior pair of vessels which arise from the aorta immediately behind the renal arteries, and a posterior pair which arise from the aorta about half way between the origin of the left renal artery and the point at which the aorta divides posteriorly into the two external iliac arteries. The anterior and posterior spermatics join and supply the reproductive organs. The two external iliac arteries arise from the posterior end of the aorta and immediately behind their point of origin a median artery is given off from which the two internal iliac arteries and the median sacral artery arise. This arrangement differs from that generally found in the higher Mammalia in which the external and internal iliac arteries arise from a common iliac artery. Each external iliac artery passes down the hind limb of its own side and divides into the external and internal femoral arteries. The internal iliac arteries supply blood to the pelvic regions and the bladder. The median sacral artery is continued into the tail as the caudal artery. The right and left internal iliacs are not always given off at the same level (Figs. 11 and 12).

3. Anterior Venae Cavae

According to Forbes (1881) and Sonntag (1921b) and confirmed by my own dissections, *Petaurus breviceps* has a single anterior vena cava formed by the junction of the right and left innominate veins, a condition frequently found in the higher mammalia. With this single exception all marsupials which have been dissected have two anterior venae cavae, right and left respectively. Fig 13 gives the arrangement of the tributaries of the right anterior vena cava in *Phascolomys ursinus*, and, with minor variations, this arrangement holds good for all marsupials. In all cases the external jugular vein is the largest vessel returning blood from the head to the heart. The anterior jugular (thyroid) vein, which receives blood from the larynx and thyroid gland, and is connected with the sub-maxillary vein, is generally larger than the internal jugular vein, which runs alongside the common carotid artery. In *Dasyurus viverrinus*, however, the internal jugular is larger than the anterior jugular vein.

Each external jugular vein is made up of five principal branches, namely, the sub-maxillary vein, the anterior facial (external maxillary) vein, the posterior facial (internal maxillary) vein, the post-auricular, and the cephalic, which arises from the radial side of the fore limb.

The sub-maxillary vein runs transversely and receives blood from the sub-maxillary glands and from the region between the rami of the mandibles. It runs across the ventral and inner side of the masseter muscle (Fig. 14). The anterior facial vein passes across the ventral face of the masseter muscle and joins the posterior facial vein, which passes through the substance of the parotid gland. The common vein thus formed almost immediately receives the sub-maxillary vein on its inner and the post-auricular vein, from behind the ear, on the outer side. The above veins form the external jugular, which passes backward ventral to the insertion of the sterno-mastoid muscle and runs on the outer side of this muscle. It then receives the cephalic vein on its outer side and the anterior jugular vein and the internal jugular vein on its inner side. Immediately posterior to the junction of these veins the common vein thus formed receives the subclavian vein from the fore limb to form the anterior vena cava which passes backwards and opens into the right auricle (Figs. 14 and 15). On its way the anterior vena cava may receive a number of smaller veins such as the sternal (internal mammary) vein, the vein which receives the anterior intercostal veins, and the azygos vein.

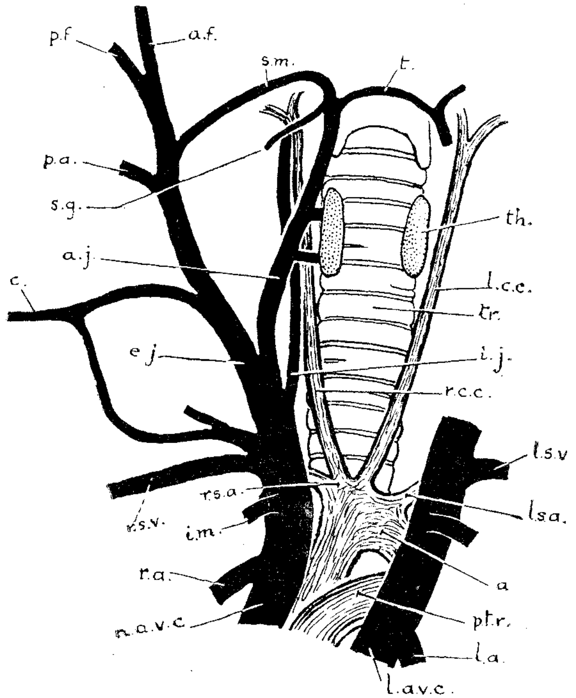


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FIG. 13—Blood system of neck region in *Phascolomys*.

a., base of aorta; *a.f.*, anterior facial vein; *a.j.*, anterior jugular vein; *c.*, cephalic vein; *e.j.*, external jugular vein; *i.j.*, internal jugular vein; *i.m.*, internal mammary (sternal) vein; *l.a.*, left azygos vein; *l.a.v.c.*, left anterior vena cava; *l.c.c.*, left common carotid artery; *l.s.a.*, left subclavian artery; *l.s.v.*, left subclavian vein; *p.a.*, post-auricular vein; *p.f.*, posterior facial vein; *p.tr.*, pulmonary trunk; *r.a.*, right azygos vein; *r.a.v.c*, right anterior vena cava; *r.c.c.*, right common carotid artery; *r.s.a.*, right subclavian artery; *r.s.v.*, right subclavian vein; *s.g.*, vein from submaxillary gland; *s.m.*, submaxillary vein; *t.*, transverse vein; *th.*, thyroid gland; *tr.*, trachea.

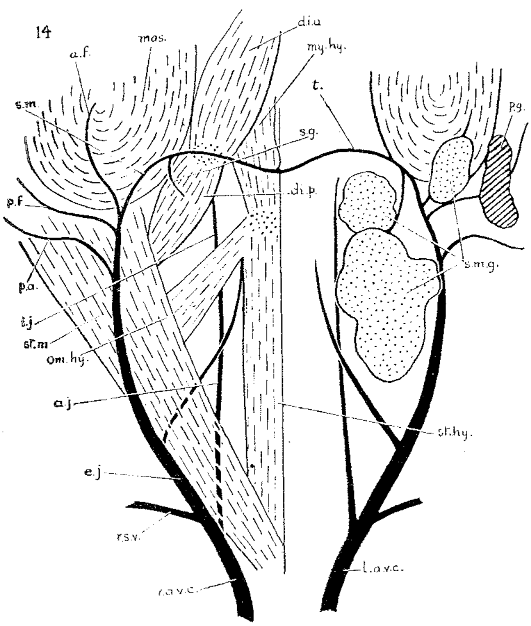
4. THE AZYGOS SYSTEM

Among the important vessels returning blood to the heart from the posterior region of the body are the postcardinals, two veins which usually form an important constituent of the renal portal system of the more primitive vertebrates and which make an early appearance in the development of the Mammalia. Originally the blood from the posterior region of the body enters the heart by way of these vessels, but after the formation of the posterior vena cava, a relatively new vessel, the postcardinals gradually lose their importance and ultimately become cut off from direct contact with the posterior region of the body.

It is usually agreed that the azygos veins of the Mammalia are vestiges of the anterior portion of the post-cardinal veins. McClure (1906) showed clearly that in the case of the American marsupial *Didelphys* the azygos veins and the postcardinals are present at the same time in an 8 mm. embryo. In this genus the azygos veins are apparently formed by the anastomosis of a series of lateral offshoots of the postcardinals, and the two sets of veins remain connected for some time by a series of transverse vessels. Ultimately the postcardinals disappear and the left azygos grows considerably, while the right either disappears altogether or remains as an insignificant vessel, receiving veins from not more than five intercostal spaces.

Beddard (1907) describes an interesting condition in the newly-born South American rodent *Myopotamus*. In the thoracic region there were two vessels connected with the right precaval and one with the left precaval. In Beddard's opinion these represent a right and left postcardinal and a single right azygos.

It would appear that the homology and origin of the azygos veins vary in different mammals. Beddard suggests that the true azygos is always a single vein and that when right and left vessels are present they are either two postcardinals or a single azygos and one persistent postcardinal. This, however, is not borne out by McClure's investigations into the venous system of *Didelphys*, and the investigations of other workers show that there is apparently no hard and fast rule for the development of the azygos veins, but that in most cases they are either the actual vestiges of the postcardinal or are derivatives of them. The problem of the homology of this system of veins presents many difficulties, and it is probable that the development of the azygos system is not uniform throughout the Mammalia.



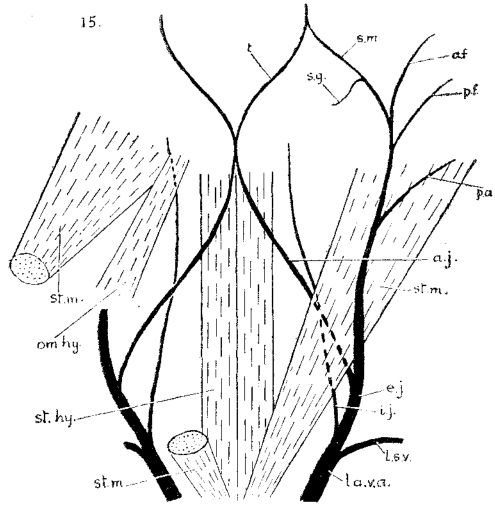


FIG. 14—*Dasyurus viverrinus*. Veins of the neck. On the right side the submaxillary and parotid glands have been removed. On the left side the muscles are not shown: FIG. 15—*Sarcophilus harrisii*. Veins of the neck. On the right side the sterno-mastoid muscle has been cut.

di.a., digastric muscle (anterior part); *di.p.*, digastric muscle (posterior part); *mas.*, masseter muscle; *my.hy.*, mylo-hyoid muscle; *om.hy.*, omo-hyoid muscle; *p.g.*, parotid gland; *s.m.g.*, sub-maxillary glands; *st.hy.*, sterno-hyoid muscle; *st.m.*, sterno-mastoid muscle. (Other references as in fig. 13.)

The azygos veins are variable in the Mammalia, and occur either as paired vessels returning blood from the intercostal spaces to the anterior venae cavae, as in many Marsupials, Rodents, Insectivores and Artiodactyles, or as a single vessel returning blood from the intercostal spaces of both sides, the right azygos in some Marsupials, Carnivora, Edentates, Lemurs and Primates, and the left in some Marsupials, Rodents and Artiodactyles (Beddard, 1907, p. 222).

Within the Order Marsupialia, the azygos veins show a great variety of arrangement. Milne-Edwards characterized the group as having two azygos veins equally developed and the great comparative anatomist, Richard Owen (1841), concurred in stating that the azygos veins in the Marsupialia 'retain their original separation and symmetry.' It would be more correct to say, however, that although the azygos system in the marsupials is based upon the essential plan of the primitive posterior cardinals, more often than not the original symmetry has been lost and all conditions may be found from the double azygos of *Phascolomys* to the condition found in *Didelphys* where the right azygos is usually absent.

With the exception of *Phascolomys,* which has 15 pairs of ribs, most marsupials have 13 pairs, and the intercostal veins run immediately posterior to the ribs alongside and anterior to the corresponding intercostal artery. Generally speaking, the azygos system is linked up with all the intercostal veins except the first two or three pairs. Usually the left azygos enters the left precava slightly posterior to the level of the entry of the right azygos into the righ precava. The oesophageal vein enters either the right or left azygos vein (Fig. 16).

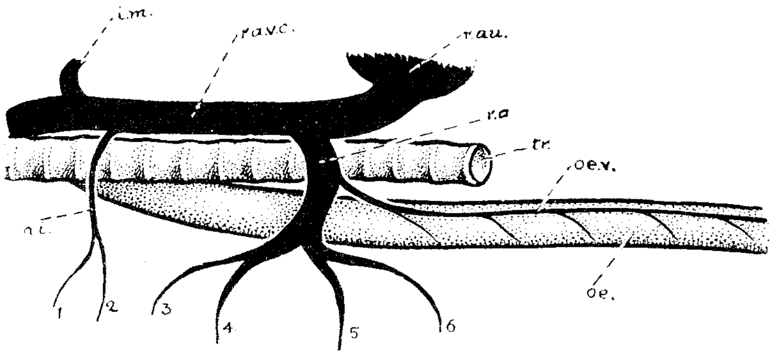


FIG. 16—*Sarcophilus harrisii.* Lateral view of azygos vein of right side (the complete system is seen in fig. 26).

a.i., right anterior intercostal vein receiving the veins from the 1st and 2nd intercostal spaces; *i.m.*, internal mammary (sternal) vein; *oe.*, oesophagus; *oe.v.*, oesophageal vein; *r.a.*, right azygos vein; *r.au.*, right auricle; *r.a.v.c.*, right anterior vena cava; *tr.*, trachea.

In the marsupials, the azygos system is rarely connected with the veins of the first two intercostal spaces.* The arrangement of these anterior intercostal veins would appear to vary considerably in different forms. In *Didelphys* McClure (1903) has shown that the blood from the first two intercostal spaces is collected by the superficial superior intercostal veins which open into the anterior venae cavae. He has also shown that these veins anastomose with the deep superior intercostal veins and as Beddard (1907) has pointed out, these latter veins may, in some cases, be the sole means by which the contents of the first two intercostal veins are returned to the heart. There is still a further possibility. The right and left sternal (internal mammary) veins receive blood from the

* In figs. 17-27 which deal with the azygos system the first two pairs of intercostal veins are not shown.

ventral portion of the intercostal spaces and open into the anterior vena cava and possibly in some cases this may be the only means by which the blood from the anterior intercostals is returned to the heart. Very rarely the anterior intercostals actually open into the azygos. In some marsupials which I have dissected it has been difficult to trace the two anterior intercostal veins and occasionally these vessels enter the anterior vena cava by a common vein which does not appear to have any relation to the vessels mentioned above.

For instance, in *Thylacinus* Cunningham (1882) showed that the first three intercostal veins of the right side open into the right anterior vena cava by a single vein which is distinct from the azygos. Similarly on the left side where there is no azygos the first three intercostal veins open into the left anterior vena cava by a single vessel. I have found a comparable state of things in *Sarcophilus*. Here the blood from the first two intercostal spaces opens into the anterior vena cava of each side by a single vein which is not connected with the azygos veins (Fig. 16) which in this form are present on both sides. A similar arrangement has also been noted by me in *Perameles gunnii*. The veins receiving the anterior intercostals in the above instances do not appear to be either the superficial or deep superior intercostals.

McClure (1903) and Beddard (1907) have summarized the findings of previous observers with regard to the disposition of the azygos system in Marsupials.

McClure considers that the azygos system may be arranged in three different ways, viz.,

1. Right and left azygos veins equally developed.
2. Right azygos vein only developed.
3. Left azygos vein only developed.

This statement of the case is misleading, as it suggests a clear cut separation into three distinct types, a distinction which does not exist, and no allowance is made for intermediate types between 1 and 2 and between 1 and 3. If a sufficiently large number of specimens of each marsupial species were examined I do not think that there are many (if any) species in which traces of both right and left azygos veins are not sometimes present.

Beddard's interpretation is more satisfactory in this respect as he includes these intermediate types and recognizes five different arrangements of the azygos system, viz.,

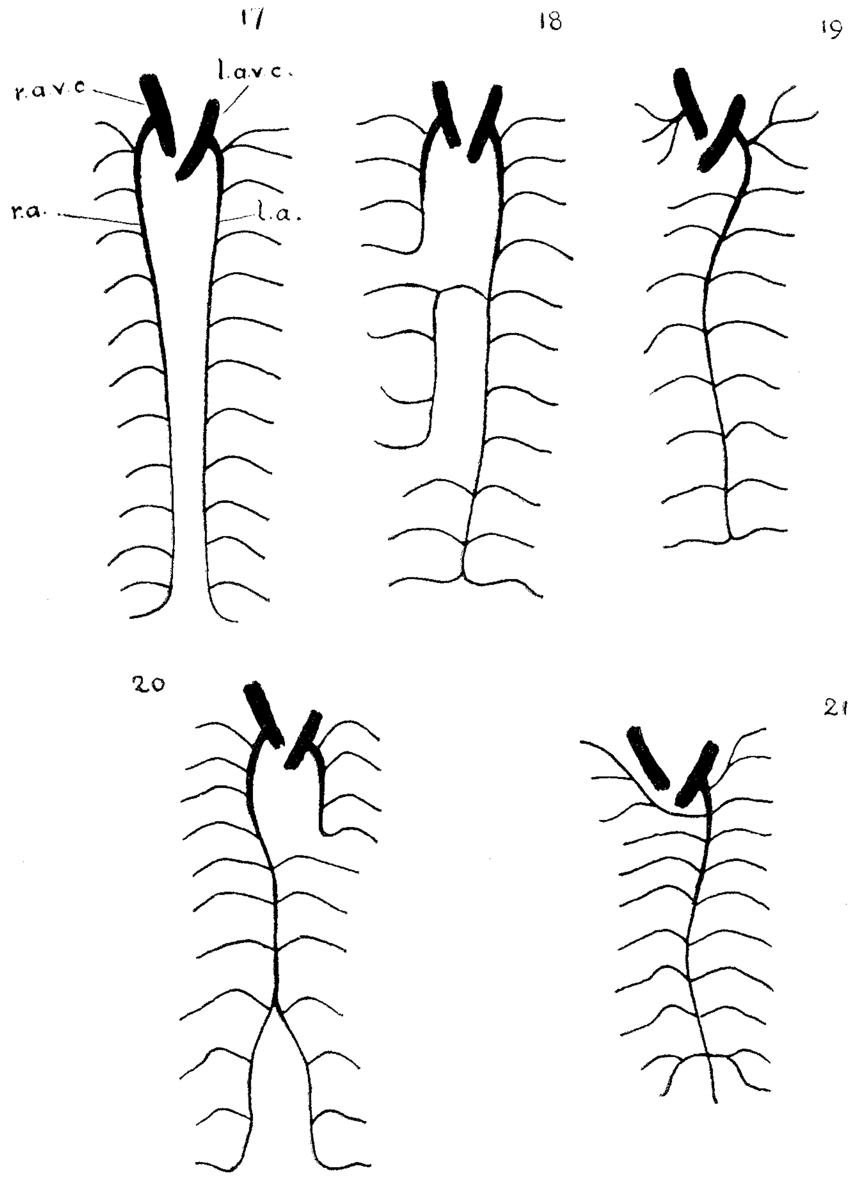
1. Right and left azygos, equal or nearly equal.
2. Large right azygos, small left azygos.
3. Azygos on right side only.
4. Large left azygos, small right azygos.
5. Azygos on left side only.

But even Beddard's classification does not meet all cases, although it may be regarded as being sufficiently true as a general statement of the case.

The following is a statement of the results of dissections of the azygos system in the course of the present investigations. If these are added to Beddard's list, a fairly complete knowledge of the arrangement of the azygos system in the Marsupials can be obtained:—

1. Right and left Azygos Veins equally developed

Here the intercostals of each side drain into the azygos of the same side. I have found this arrangement consistent in six specimens of *Phascolomys ursinus* which I have examined (Fig 17). Forbes (1881), however, gives a case in which the right azygos of *Phascolomys* was extremely small and most of the intercostal veins opened into the left. There was, however, a small connexion between the posterior intercostal vein opening into the right azygos and the anterior intercostal of the right side which opened into the left azygos and this connexion probably indicated a relic of the right azygos.



TYPES OF AZYGOS SYSTEM IN THE MARSUPIALIA

FIG. 17—*Phascolomys*; FIG. 18—*Potorous*; FIG. 19—*Pseudocheirus*; FIG. 20—*Thylogale*; FIG. 21—*Isoodon*.

l.a., left azygos vein; *l.a.v.c.*, left anterior vena cava; *r.a.*, right azygos vein; *r.a.v.c.*, right anterior vena cava. (The lettering in fig. 17 applies to all five figures.)

In a specimen of *Bettongia cuniculus* which I dissected both right and left azygos veins were fully developed though the right was thinner than the left.

Out of three specimens of *Sarcophilus harrisii* examined by me one came under the present category (Fig. 25) though in the others the right azygos was poorly developed.

2. **Left Azygos well developed. Right Azygos relatively small**

In this category the left azygos receives not only the left intercostal veins but also the posterior intercostal veins of the right side (Figs. 18, 19).

In one example of *Dasyurus viverrinus* the right azygos was almost as long as the left and only the three posterior intercostals of the right side drained into the left azygos (Fig. 22.)

In specimens of the following species I found the right azygos small and draining only two to four intercostal spaces.

Dasyurus viverrinus (Figs. 23, 24).
Perameles gunnii.
Potorous tridactylus apicalis (Fig. 18).
Sarcophilus harrisii (Figs. 26, 27).
Trichosurus vulpecula fuliginosus.
Pseudocheirus convolutor (Fig. 19).

3. **Left Azygos well developed. Right Azygos absent.**

Here the intercostal veins of both sides drain into the left azygos.
Isoodon obesulus affinis (Fig. 21).

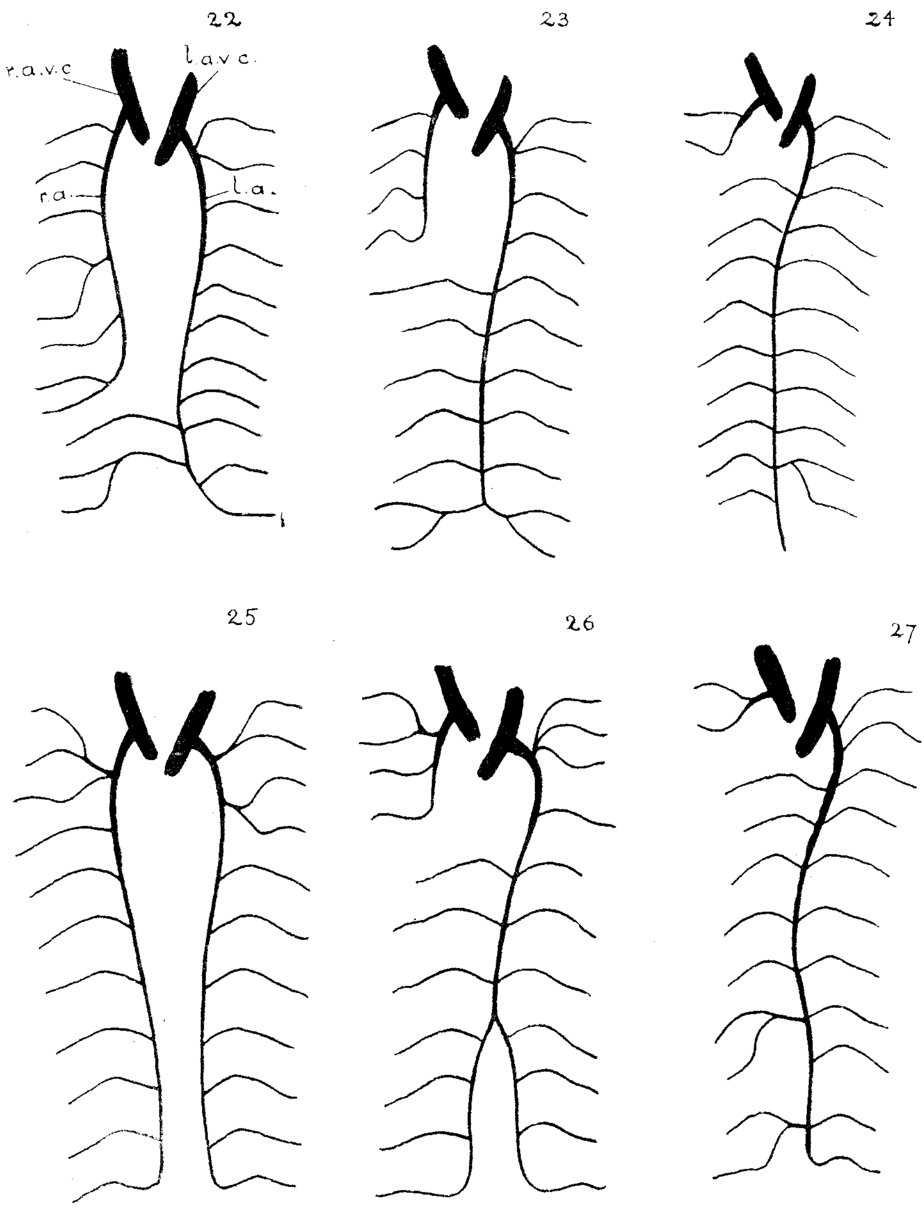
4. **Right Azygos well developed. Left Azygos with few intercostals**

This is a rare and exceptional condition in the Marsupials. It has been recorded by Cunningham (1882) in *Thylacinus* and by Parsons (1896) and Beddard (1895, 1907) in some of the Macropodinae. I have found it in *Thylogale billardierii* (Fig. 20).

It is clear from the above lists that there is considerable variability in the disposition of the azygos system in the Marsupials. Not only do related species show differences, but even within the limits of a single species there may be almost every type of arrangement. For example, in *Dasyurus viverrinus* Beddard (1907) has given a case which had equal right and left azygos veins, and in the course of the present investigation dissections of this species have shown that usually the left azygos predominates and that the right azygos may vary from having two intercostal veins to as many as eight (Figs. 22, 23, 24). Cunningham (1882) and Beddard (1907) have recorded instances in which the right azygos was entirely wanting in this species. Again in *Sarcophilus* I have found a considerable variation in the arrangement of the azygos system from two complete azygos veins to a condition in which the right azygos vein is reduced and receives only two intercostal veins while the left azygos is predominant (Figs 25, 26, 27). In *Thylacinus* there appears to be considerable variation as Cunningham (1882) found the left azygos absent. On the other hand Beddard (1907) stated that the left azygos predominates and the right azygos supplies only four intercostal spaces.

Having regard to this wide range of variability it would be unwise to attach too much importance to the azygos system as a basis of classification or as a means of indicating relationships. Beddard (1907) was inclined to regard this system as indicating relationships and affinities though he added the qualification that this indication was given only in a general way.

The condition in which both azygos veins are equally well developed may be regarded as primitive, nevertheless *Didelphys*, which, according to Bensley (1903) represents the nearest living approach to a primitive marsupial type, shows



VARIATION IN THE ARRANGEMENT OF THE AZYGOS SYSTEM

FIGS. 22-24—*Dasyurus viverrinus.* FIGS. 25-27—*Sarcophilus harrisii.*

(The lettering in fig. 22 applies to all six figures. References as in figs. 17-20.)

a very highly specialized condition in usually having no vestige of the right azygos. On the other hand, the wombat and some of the kangaroos sometimes show the primitive arrangement, though these animals are regarded as being highly specialized marsupials. A careful examination of McClure's and Beddard's lists, together with those cases which are given in the present paper, shows that the azygos veins in the marsupials give no reliable indication of the affinities of the various members of the order. I cannot agree, therefore, with Beddard (1907. p. 219) when he says that 'the division of the marsupials into Diprotodont and Polyprotodont is justified by the condition of the azygos veins,' and I do not think there is much in his contention that 'in the Diprotodont division there is a much greater tendency for the two azygos veins to persist than among the Polyprotodonts'. As I have shown above *Sarcophilus* and *Dasyurus* (both Polyprotodonts) show all stages between a complete double system of azygos veins and a predominant left azygos vein. The fact is that in the Marsupialia the azygos system is of little value in determining relationships.

McClure (1903) was of opinion that the single azygos is the rule in marsupials and that when the right and left are present this condition may be regarded as a variation. My own investigations do not confirm this. On the contrary I consider that the double azygos is typical of the marsupials, though frequently one, generally the left, is much more highly developed than the other, as for example, in *Trichosurus vulpecula fuliginosus* where the right azygos is very small and receives blood from only three intercostal spaces, or in *Thylogale billardierii* where the right azygos predominates. Milne-Edwards and Owen erred in the opposite direction in stating that the two azygos veins in the marsupials were equally developed and symmetrical.

Our present knowledge of the arrangement of the azygos system in the Marsupials may be stated as follows—normally, right and left azygos veins are present, usually, however, one is larger than the other, and in such cases it is more common to find the left azygos vein the predominant one. The arrangement of the azygos system is not always constant even within the limits of a single species, and a comparison of the arrangement of this system in different species of marsupials rarely helps in assessing the relationships of the members of the group.

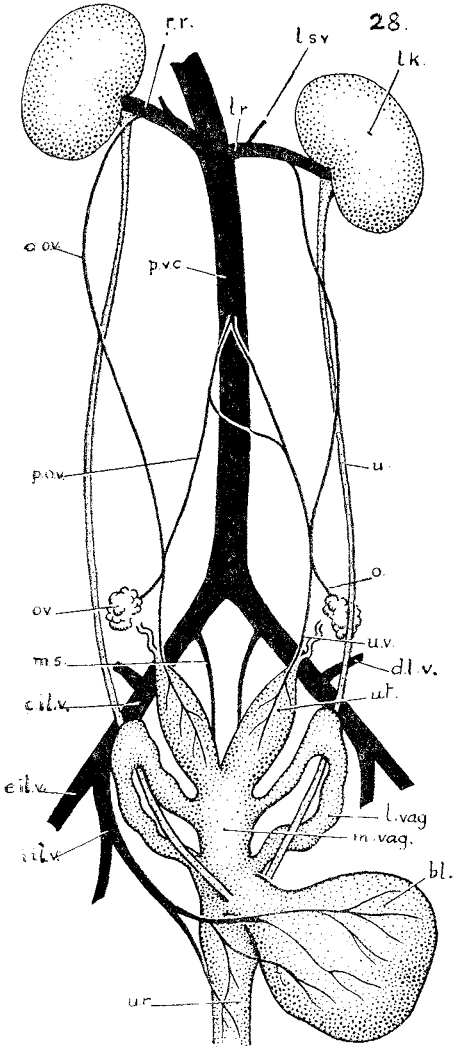
5. The Posterior Veins.

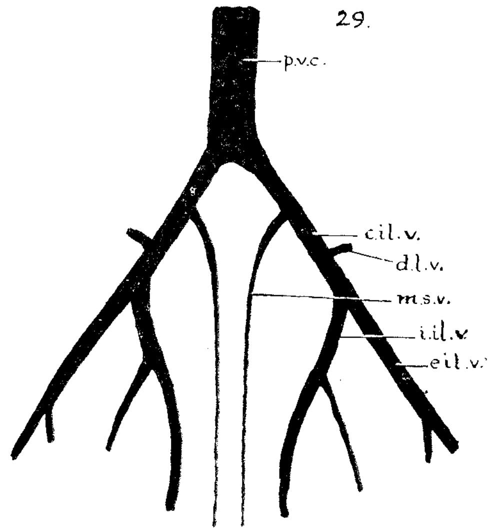
The posterior vena cava receives the blood from the posterior region of the body and alimentary canal, and returns it to the right auricle. As in the higher mammals the veins from the alimentary canal unite into the hepatic portal vein which breaks up in the liver. From the liver the blood is collected by the hepatic veins which enter the posterior vena cava.

Posterior to this the posterior vena cava receives blood from the hind limbs, the pelvic region, the reproductive organs, kidneys and lumbar region. It is important to note that the marsupials differ from the higher mammals in the manner in which the posterior vena cava lies completely ventral to the aorta. The only exception to this rule would appear to be *Schoinobates volans* (= *Petaurus taguanoides*) in which, according to Hochstetter, the aorta lies ventral to the posterior vena cava as is the case in the higher mammalia.

Beddard (1909) has discussed at some length the arrangement of the spermatic (or ovarian) veins in Marsupials which show considerable variation. The essential arrangement is shown in *Thylogale* (Fig. 28) and *Sarcophilus* (Fig. 31) where the ovarian vein from each ovary receives the uterine vein. About the level of the beginning of the posterior vena cava each ovarian vein divides into an inner posterior ovarian vein, which joins the posterior vena cava with its fellow from the other side, and an outer anterior ovarian vein which enters the renal vein.

McClure (1903) has dealt very fully with the numerous variations which are to be found in the arrangement of the posterior tributaries of the posterior vena cava in *Didelphys*.





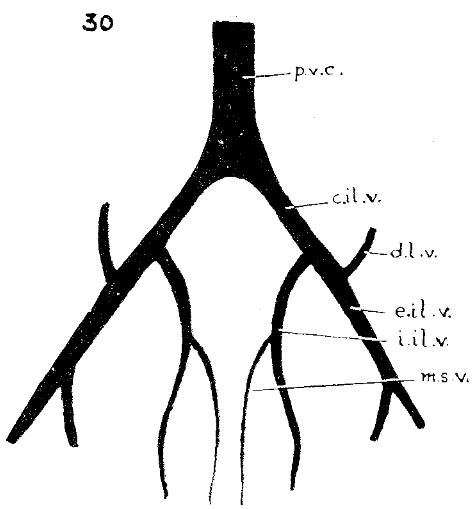


FIG. 28—*Thylogale billardierii.* Veins of the urogenital system connected with the posterior vena cava. FIG. 29—*Dasyurus viverrinus.* Posterior veins. FIG. 30—*Phascolomys ursinus.* Posterior veins.

a.o., anterior ovarian vein; *bl.*, bladder; *c.il.v.*, common iliac vein; *d.l.v.*, dorso-lumbar vein; *e.il.v.*, external iliac vein; *i.il.v.*, internal iliac vein; *l.k.*, left kidney; *l.r.v.*, left renal vein; *l.s.v.*, left suprarenal vein; *l. vag.*, lateral vaginal canal; *m.s.v.*, median sacral vein; *m. vag.*, median vagina; *o.*, ovarian vein; *ov.*, ovary; *p.o.*, posterior ovarian vein; *p.v.c.*, posterior vena cava; *r.r.v.*, right renal vein; *u.*, ureter; *ur.*, urethra; *u.t.*, uterus, *u.v.*, uterine vein.

In the course of the present investigation it has been found that there are two main plans upon which the affluents of the posterior vena cava are formed.

(1) The internal Iliac Veins remain distinct from the Median Sacral (Caudal) Veins

This condition is found in *Thylogale billardierii* (Fig. 28), *Sarcophilus harrisii* (Fig. 31), *Perameles gunnii,* and *Dasyurus viverrinus.*

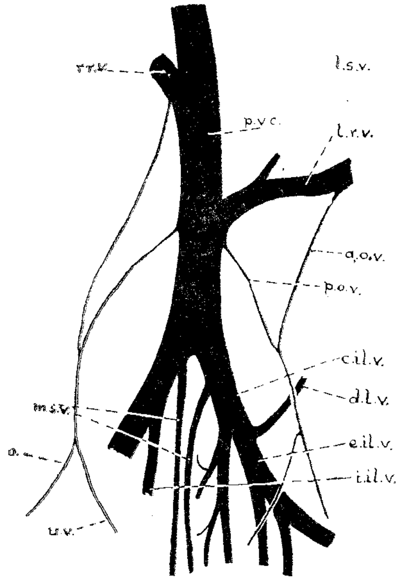


FIG. 31—*Sarcophilus harrisii*—posterior vena cava and its branches.
(References as in figs. 28-30.)

In this type the two median sacral veins start in the tail and run along the ventral side of the sacrum, one on each side of the median sacral artery and finally open into the common iliac vein. Each internal iliac vein returning blood from the bladder and pelvic region joins with the external iliac (femoral) vein of its own side to form the common iliac vein which joins with a similar vein of the opposite side to form the posterior vena cava (Fig. 29).

(2) The Median Sacral Veins join the Internal Iliacs

This condition is found in *Phascolomys ursinus* and *Trichosurus vulpecula fuliginosus.*

Here the two median sacral veins run forward on either side of the median sacral artery and each opens into the internal iliac vein of its own side. The internal iliac vein then joins the external iliac vein to form the common iliac vein. The two common iliac veins unite to form the posterior vena cava (Fig. 30).

If the posterior veins are as variable in other marsupials as they are in *Didelphys* it is not likely that the two types given above may be found in the same species.

SUMMARY

One of the objects of the investigation was to ascertain if the arrangement of the blood system in the Marsupialia threw any light upon the vexed question of the relationships of the major divisions of the group as well as upon the affinities of the group as a whole.

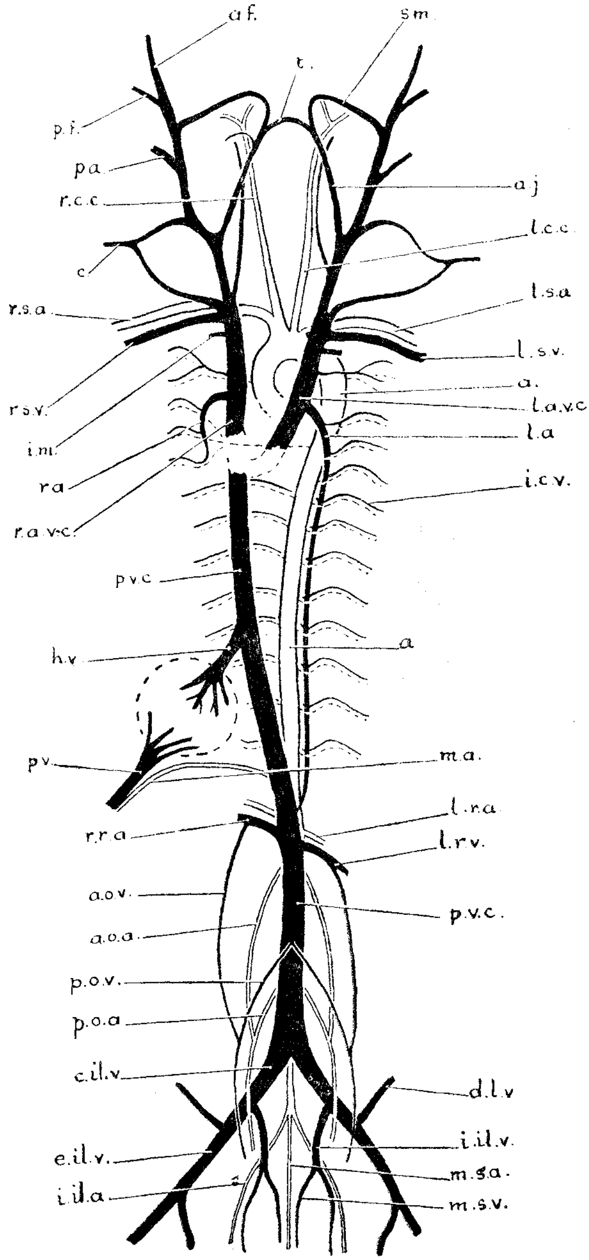


FIG. 32—Generalized diagram of blood system of a marsupial. (The veins are shown black, the arteries as double lines. The intercostal arteries are shown as dotted lines.)

h.v. = hepatic vein; *p.v.* = portal vein; *i.c.v.* = intercostal vein.

(Other references as in previous figures.)

Parsons (1902) has analyzed the arrangement of the branches of the aortic arch throughout the Mammalia and has shown that it is very variable, and, further, has made it clear that no specific arrangement characterizes any particular Order of Mammals. This same variability is to be seen within the Marsupialia which, incidentally, contains all the variations instanced by Parsons for the whole of the Mammalia.

With one exception (*Petaurus breviceps*) the marsupials retain the right and left anterior venae cavae derived from the primitive anterior cardinal veins, a character which they share with many Monodelphids.

Beddard (1907) made a comprehensive analysis of the azygos system in the Mammalia in which the system shows considerable variation. McClure (1903), Beddard (1907), and the present writer have shown that this system is very variable within the Marsupialia and in the present paper evidence has been submitted to show that considerable variation may exist even within the limits of a single species. Broadly speaking, the marsupial azygos system may be regarded as being more primitive than that of the higher mammals, because it shows more consistently than in the latter the presence of the primitive right and left branches, though usually the left is more highly developed than the right. Occasionally one side may be missing altogether, but I regard this as being abnormal.

The analysis given in this paper makes it clear that the blood system of the marsupials differs in no fundamental respect from that of the Monodelphia, where considerable variation is to be found.

For what it is worth the evidence of the marsupial blood system points to the fact that the Didelphia and Monodelphia have arisen from a common stock in which there were two anterior venae cavae and two azygos veins.

With the exception of Fig. 1 all the illustrations are original and were redrawn for publication by Capt. D. Colbron Pearse of the Tasmanian Museum and Art Gallery.

References

BEDDARD, F. E., 1895.—On the visceral anatomy and Brain of *Dendrolagus bennetti*. *Proc. Zool. Soc.*, 1895, pp. 131-137.

——————, 1907.—On the Azygos veins in the Mammalia. *Proc. Zool. Soc.* 1907, pp. 181-223.

——————, 1909.—On the Postcaval vein and its branches in certain Mammals. *Proc. Zool. Soc.* 1909, pp. 496-526.

BENSLEY, B. A., 1903.—On the Evolution of the Australian Marsupialia with remarks on the relationships of the Marsupials in general. *Trans. Linn. Soc. Lond.* (2), IX, Part 3, pp. 83-217.

CUNNINGHAM, D. J., 1882.—Report on some points in the Anatomy of the Thylacine (*Thylacinus cynocephalus*), Cuscus (*Phalangista maculata*), and Phascogale (*Phascogale calura*). *Zoological Reports of the voyage of H.M.S. "Challenger"*, vol. 5, Part XVI.

FORBES, W. A., 1881.—On some points in the anatomy of the Koala. *Proc. Zool. Soc.* 1881, pp. 180-195.

MCCLURE, C. F. W., 1903.—A Contribution to the Anatomy and Development of the venous system of Didelphys marsupialis (L), Part I, Anatomy. *Amer. Journ. Anat.*, vol. 2, n. 3, pp. 371-404.

——————, 1906.—Part II, Development. *Amer. Journ. Anat.*, vol. 5, n. 2, pp. 163-226.

OWEN, R., 1841.—Marsupialia from the *Cyclopaedia of Anatomy and Physiology*.

PARSONS, F. G., 1896.—On the anatomy of *Petrogale xanthopus* compared with that of other Kangaroos. *Proc. Zool. Soc.*, 1896, pp. 683-714.

————, 1902.—On the arrangement of the branches of the mammalian aortic arch. *Journ. Anat. and Physiology*, XXXVI, pp. 389-399.

————, 1903.—On the Anatomy of the Pig-footed Bandicoot (*Chaeropus castanotis*). *Journ. Linn. Soc. Lond.* (Zool.) 29, no. 188, pp. 64-80.

SONNTAG, C. F., 1921a.—Comparative anatomy of the Koala (*Phascolarctos cinereus*) and Vulpine Phalanger (*Trichosurus vulpecula*). *Proc. Zool. Soc.*, 1921, pp. 547-577.

————, 1921b.—Contribution to the visceral Anatomy and Myology of the Marsupialia. *Proc. Zool. Soc.*, 1921, pp. 851-882.

SWEET, G., 1904.—Contribution to our knowledge of the Anatomy of *Notoryctes typhlops* Stirling. *Proc. R.S. Vict.*, 17, pp. 76-111.