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The active venous pulse in the wing circulation of bats (Chiroptera). A contribution to comparative angiology

'I have not yet lost the dream that man's quest for the stars will come to find added guidance, and greater wisdom, in the lessons to be learned from the tiny, wonderfully adapted bodies of these fascinating, winged creatures of the night.'

*Frank C. Kallen**

'The vessels are the heart.'

J. W. Goethe

*F.C. Kallen, The Biology of Bats, vol. III, chapter 3 'The Cardiovascular Systems of Bats: Structure and Function', p. 466. Academic Press, New York 1977.

Introduction*

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The active venous pulse in the wing membrane of Chiroptera (bats and flying foxes) is an autonomous adaptation of peripheral circulation, and thus represents a very complex ecophysiological mechanism of survival. The phenomenon of the venous or auxiliary heart is of fundamental importance in comparative angiology as well as in the exploration of the peripheral circulation. Furthermore, intensified investigations of angiological problems are urgently needed at the present time.

Under such extreme physiological conditions as hibernation, periods of torpor, and active flight circulation in the wing membrane can only be maintained through multiple connections between haemodynamic regulation, integrative autonomic function, and nervous regulation. Multidisciplinary collaboration is needed in order to understand how the peripheral resistance in the duplicated wing membrane is overcome by venous peristalsis (venous hearts). An integrated review of the whole highly complex problem will be provided here by very brief discussions of individual aspects, such as morphological specialization of the vessels, natural stimuli, chemical and pharmacological internal environment, electrophysiology, automatism and conduction of excitation.

Comparative considerations

Besides the Chiroptera, no other animal group endowed with active flight developed a patagium, a wing membrane with a large surface and active rhythmic vasomotion. Only the extinct flying Saurians like *Pterodactylus* had bat-like cutaneous wing membranes which were vasculated, like those of bats, and probably were provided with an active venous pulse for the propulsion of blood. In contrast, no active vascular contractility is found in the parachute-like membrane stretched between hind- and forelegs of flying squirrel and flying makis and in other gliding animals, like the dragon lizard (*Draco volans*) and the gliding frog (*Racophorus*), no accessory mechanisms

*Dedicated to my friend and teacher Professor Alexander von Muralt, former Director of the Physiological Institute, Bern (Hallerianum) on the occasion of his 75th birthday. I succeeded in recording the first electrovenograms (Evg) in his institute.

Active venous pulse in the wing membrane of Microchiroptera. Comparative historical survey of the first research period (1852–1918)

Species	Patagium (wing membrane)	Vessel	Mechanical phenomena Rhythm	Frequency	Contraction – Dilatation	Structure Gross	Histology
Plecotus auritus, Vespertilio murinus, Barbastellus barbastellus	Plagiopatagium and Chiropatagium	Veins	Progressive constriction of vein caliber. Periodical changes in pulsation velocity. No tonic contractility of veins in addition to their rhythmical contracility.	10/min (7–13/min)	Rhythmical contractions and dilatations at times of minor extent. Supervening dilatations more rapid than contractions. During contraction venous blood flow is accelerated. Dilatation and contraction are correlated.	Sufficient and insufficient vein valves. Veins with single or double flaps. Walls of veins thicken during contraction. Retrograde blood flow if valves are incomplete. At each dilatation wall width is reduced to a 3rd or 6th of contraction width.	Valve structure: Reduplication of the clear innermost coat of the vein, a layer of fibrous tissue may be present. Veins have middle coat of circular muscle fibres. Fibres about 1/3600 inch wide, pale, grayish, semitransparent and granular (no transverse striations). Valves located close to entrance of a large branch vessel, but always distal to it.
	Chiropatagium	Arteries	Show tonic but no rhythmical contractility.	No pulsation.	Frequent great and abrupt constrictions.	No direct communication between arteries and veins (capillary system present). Equates muscular tissue of the lymphatic frog hearts with that of bat wing veins.	Muscle fibres of middle coat of arteries more transparent and more distinct. The fibres of the muscular coat of the veins lack cross striations.
Rhinolophus ferrum equinum	Chiropatagium	Veins	Finds no active venous pulse in lethargic bats (hibernation effect?).		Assumes neuroregulation of the venous pulse. Observation of galvanocaustic isolated triangular patagium piece proves the existence of the autonomous active venous pulse.		
Myotis myotis S.	Chiropatagium	Veins		8–10/min. Dependence of frequency on temperature.	Arrest of venous pulse in dilatation at high temperature. Following total separation of wing from body autorhythmicity continues for 4–5 min. After ligature of the vessel before amputation duration of active venous pulse is 10–15 min.		

T. Wh. Jones: Discovery that the veins of the bats wing (which are furnished with valves) are endowed with rhythmical contractility, and that the onward flow of blood is accelerated by each contraction, Phil. Trans. r. Soc., London, part I, 131 (1852).

T. Wh. Jones: Microscopical characters of the rhythmical contractile muscular coat of the veins web of the bats' wing, Proc. r. Soc., London, *16*, 342 (1868).

M. Schiff: Zur Ursache der rhythmischen Venenkontraktionen in der Fledermausflughaut, Arch. Physiol. *13*, 527 (1864).

H. Schiff: Untersuchungen zur Physiologie des Nervensystems, Pflügers Arch. Physiol. *1*, 181 (1955).

B. Luchsinger: Von den Venenherzen in der Flughaut der Fledermäuse, Pflügers Arch. Physiol. *26*, 445 (1881).

Natural stimuli Temperature	Pressure	Artificial stimuli External pressure	Electric	Innervation Anatomy and Physiology	Chemical milieu Chemical and Pharmacological Effects	Author and Remarks
10/min at room temperature.	After mechanical irritation veins contract and close but soon dilate wider than before. When pressure has been considerable, the vein becomes temporarily wholly obstructed by 'lymph deposit'.	Tonic contractions in response to external pressure. Strong pressure results in total obstruction by deposits.	Galvanic stimulation of vein produces rhythmic brisk contractions of the vein.	No tonic contraction following cutting of vein. Observed nerves running parallel to blood vessels.	Application of 'vinum opii' produced dilatation of all veins in the wing membrane.	**T. Wharton Jones** Discovery that the veins of the bat's wing (Microchiroptera) are endowed with rhythmical contractility. First clear description of the venous contractions. Observed more or less tonical contractility in arteries. Found deposit of a viscid-looking grayish granular lymph within the vessel at the site obstructing its channel and narrowing the stream of blood. On watching deposit was seen to detach and was carried away by bloodstream. Conclusion that the supplementary force of rhythmical contractility of veins, supported by the presence of valves, is called forth to promote the flow of blood in the wings, which, on account of their extent are, as regards their circulation, to a considerable degree, although not entirely, beyond the sphere of the heart's influence. The opinion that the muscle fibres of the veins had a different appearance than those of the arteries and somewhat resembled those of frog lymph hearts seems to have influenced Leydig's erroneous conclusion that the venous muscle coat bore suggestions of transverse striations.
				Venous pulse continues after cutting of the plexus brachialis. Denervation produces arrest in dilatation.		**M. Schiff** 1854/55 Initially assumes a central cause for the active venous pulse but later adopts Luchsinger's view of venous automaticity.
Infusion of Ringer's solution at room temperature activates pulse. Higher temperatures accelerate it. Cooling inhibits venous pulse.	Infusion of blood by aorta cannulation (20 h after death) produces normal rhythmical activity. Contractile frequency rises with increasing temperature (both in intact animal or in isolated wing membrane).		Application of tetanic electrical excitation produces acceleration of pulse rhythmicity (result of incidental direct stimulation of the venous musculature).	Normal active venous pulse after elimination of plexus brachialis. Elimination of sympathetic neuroplexus by application of ammonia has no influence on the active venous pulse.	Amylnitrate initially produces weakening of pulsation. On further treatment with amylnitrate pulse is accelerated and pulse amplitude increases.	**B. Luchsinger** 1881 Coins the term 'venous heart' (elementary heart). First experimental proof of peripheral local cause of rhythmical contractility. Demonstration of interior pressure as natural mechanical stimulus for the active venous pulse (stretch stimulus).

A. Karfunkel: Untersuchungen über die sogenannten Venenherzen der Fledermaus, Arch. Anat. Physiol. *I/II*, 538 (1905).
W. R. Hess: Untersuchungen über den Antrieb des Blutstroms durch aktive Gefässpulsationen, Pflügers Arch. Physiol. *173*, 243 (1918).

(Table continued on pages 1394/1395)

Species	Patagium (wing membrane)	Vessel	Mechanical phenomena Rhythm	Frequency	Contraction – Dilatation	Structure Gross	Histology
Vespertilio murinus	Chiropatagium and Plagiopatagium	Veins	Irregular rhythmicity under normal conditions.	6–15/min (room temperature). Pulsation series: 14, 12, 6, 6, 10, 13, 6, 6, 6, 7, 6, 8 (normal condition). Eight days following denervation. Pulsation series: 26, 25, 26, 31, 32, 32, 25, 28, 47, 29, 50, 57, 38, 51, 47, 55, 34, 25, 44, 47, 28/min.	Eventual onset of abnormal contractions in membranes prepared for observation. Artificial stimuli have special effect on the contractility phase.		Demonstrates (with the methods of Bielschowsky and Ramon y Cajal) the innervation of the walls of the arteries and veins (network). Histological evidence of a strong circular layer of smooth muscle fibres and of elastic fibres.
		Arteries	Observes tonic arterial contractions and continuous backward blood flow in them.				
Myotis myotis S., *Vespertilio murinus, Plecotus auritus*	Chiropatagium (between fingers II/III)	Veins	Pulse revolution time 3.62 sec. Pulse intervals are irregular.	16/min. Postulates that body size of bat determines its pulse frequency.	Systolic time 1.12 sec. Diastolic time 2.5 sec. Relation of systolic to diastolic vessel diameter 1:2.45 (1:2.65; 1:3.75). Demonstrates that propulsion of blood depends on pulse frequency as well as on pulse amplitude. In maximal diastole the trunk veins contain 58–73% of the blood.	Shows well-developed association of consecutive parts of vessels and stream-directing mechanism of peristaltic wave from periphery towards center. Valve location in the branch veins allows for alternating emptying of the neighbouring vessels, thus preventing the backflow of blood. Observed persistence of small venous lumen during maximal contraction.	

Natural stimuli Temperature	Pressure	Artificial stimuli External pressure	Electric	Innervation Anatomy and Physiology	Chemical milieu Chemical and Pharmacological Effects	Author and Remarks
Local response of venous wall to temperature stimuli.			Tetanisation of patagial nerves produces acceleration of autorhythmicity and stronger vein contractions. Postulates presence of ganglion cells in venous walls (unconfirmed).	Soon after denervation of the wing pulsation becomes slow. Innervation of the vein in the patagium controls function of the vein.	Adrenaline (0.01%) produces vein collabation. Adrenaline application (0.1% sol.) directly on exposed vein wall accelerates pulsation and increases contractility. Ether narcosis, initial effect: Acceleration of venous pulse. Deep ether narcosis: vein arrest in dilatation. Confirms Luchsinger's experiments for amylnitrate = blood flow increases in the veins, they respond with more frequent contractions which may initially be of greater amplitude than before.	**A. Karfunkel** 1905 Proof that the active venous pulse depends on direct local temperature. Eight days after denervation of the wing membrane the active venous pulse becomes normal on an autonomous base (myogenic automaticity). First clear description of active arterial rhythmicity. Confirms observations of Luchsinger that contraction of veins ceases upon loss of luminal pressure and becomes more frequent with increasing pressure.
Temperature influence remains uncertain.	Intravascular pressure is probably the main stimulus for amplitude regulation.					**W. R. Hess** 1918 Documents action of the venous pulse by means of microfilm. Understands the physiological mechanism of the peripheral heart (force of blood propulsion by an active peristaltic wave).

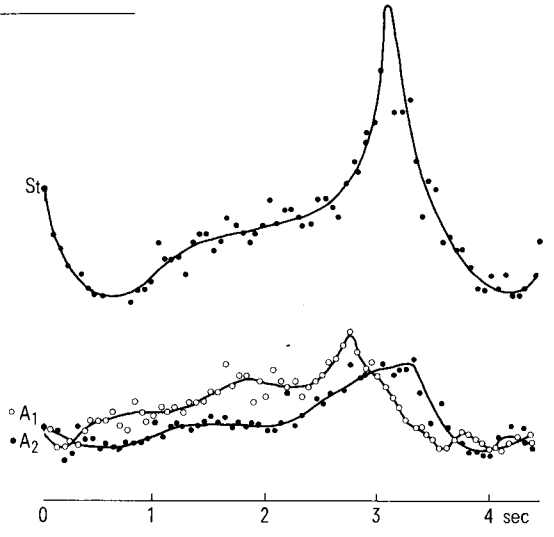

Diagram of active venous pulse (bats). Ordinate: changes of vessel diameter during 1 pulsation cycle. St, trunk vein; A_1 and A_2, vein branches; deepest point of the curve: beginning of the dilatation period.

have been found which would improve circulation. Only in the most highly organized invertebrates, the octopod cephalopods, is a real analogon observed in the peripheral circulation. The umbrella-like brachial membrane extended between the arms is highly vascularized by actively pulsating vessels which are controlled by the respiratory center. The vessels in the brachial membrane are correlated with respiration by the nervous system; both are synchronized by the inspiration center (Mislin[1]).

In contrast to Chiroptera, circulatory autonomy in octopods is not under autochthonous-myogenous but under neurogenous control. Type and variations in function of contractile vessels in peripheral circulation are independent of the organism's position in the systematic order, and are primarily dictated by functional, ecophysiological conditions.

First observations of the pulse-phenomenon

Active venous pulse was discovered by Thomas Wharton Jones (1851). He found that circulation in the chiropteran wing membrane extends over an extremely wide region and that the arterial pulse does not reach the peripheral capillary bed, so that an auxiliary circulatory mechanism becomes mandatory. With his discovery of the venous vasomotion in the bat's wing, he gives the first impetus to a comparative angiology, suggesting comparison of the activity between the 'venous hearts' and the lymphatic hearts. Let us recall that William Harvey discovered the closed blood circulation only with the help of comparative physiological methods. B. Luchsinger (1881) demonstrated experimentally that this special venous mechanism consists of an 'autonomous venous pulse' or, as he called it, an 'auxiliary heart'. In 1918 W.R. Hess investigated the haemodynamics of wing membrane veins, especially the functional connection between vascular persistalsis and closing mechanism of the venous valves. Later on, several other haemodynamic peculiarities of the wing membrane were discovered, mechanisms which can change the resistance in the peripheral vascular bed: arterio-venous anastomoses of the thumb (J. Hyrtl), v. cephalica with dilatating muscle (m. propatagilalis proprio), a non-pulsating propatagium vein which regulates drainage towards the thumb (S. Schumacher), parallel arteries in legs and arms (O. Grosser), spontaneous periodic changes of the arterial diameter in the wing membrane (1-4/min)* and contractile lymph vessels in the chiropatagium (60-80/min). Our knowledge of the peripheral vascular association in these transport systems is at the present time still incomplete. On the other hand, the physiology of the pulsating patagium veins has been rather thoroughly investigated. The table 'Active venous pulse in the wing membrane of Microchiroptera' may be primarily of historical interest, but it also shows the basis for the continuing interest in the phenomenon of spontaneous vessel activity (table, pages 1392-1395).

Our own experiments are based on these historical results, in particular on those by B. Luchsinger, who was the first to experiment with isolated wings. The decision to embark on an investigation of the physiological properties of active veins arose for me, a comparative physiologist, from the wish to understand the mechanism which produces automatic rhythmic activity, which is still not known. It was clear that the simplest method of studying the action of physiological stimuli was to remove the vessel from the wing membrane and to develop different isolated vein preparations: 3 different types of preparations were employed in order to demonstrate the characteristics typical of the auxiliary hearts: the 'little venous sac' preparation, the 'venous tube' preparation, and the 'three veins' preparation. All observations were filmed and recorded photoelectrically.

The venous sac-preparation is especially suitable for the determination of the localized effects of temperature and pressure stimuli and for the recording of the Evg of single contractile units. The venous tube-preparation is used mainly for measurement of the propagation velocity of the excitation wave and for the study of reversal of the excitation wave. The three-veins-preparation serves to follow the specific direction of the conduction wave as it moves from segment to segment of the vein wall and it is used also for studies of coordination within this associated vessel complex (maximal isolated veins).

1. The venous sac-preparation

An isolated 1-3-mm-long piece of wing membrane vein is ligatured to a cannula so as to form a blind sac. With increasing internal pressure from 0 respectively 1 cm H_2O to 14 cm H_2O, the pulse frequency of the venous sac rises continuously. Once contractions are initiated they may continue even if luminal pressure is set equal to that of the surrounding medium. Over the entire biokinetic temperature range (2-45 °C), pulse frequency is a simple exponential function of 1/T. Vant'Hoff's temperature coefficient Q_{10} is approximately 2. The veins in the intact animal respond to internal pressures ranging from 5 to 25 cm H_2O. In the venous sac-preparation (maximal isolated veins) we found at approximately 6 mm Hg responses between 0 and 20 °C, and at 9 mm Hg responses between 20 and 45 °C. The venous sac exhibits a relatively high sensitivity to oxygen deficiency and respiratory poisons, thus demonstrating the dependence of venous activity on continuous oxidative metabolism. These results lead to the assumption that pulse frequency is based upon a comparatively simple metabolic process. Pulse frequency seems to be directly proportional to the rate of these chemical reactions. In

*For the comparison of autorhythmicity between the veins and arteries of the wing membrane, we were successful in giving experimental proof that on direct respiration (central CO_2 effect by alveolar CO_2 concentration) the arteries of the intact unanaesthetized animal react by autonomic innervation with vasoconstriction, while the veins were not influenced by this central stimulus: Myogenic nature of pacemaker activity (Mislin[2]).

addition to pressure and temperature as natural stimuli, L-arginine (5–20 µg/ml) was found in this preparation to be a myotropic factor of the venous heart. Arginine induced an increase in frequency, amplitude and tone. These observations definitely establish the existence of a myotropic humoral stimulus for the venous heart. Vein sac preparations retained contractility for up to 8–10 days.

2. The venous tube-preparation

The little venous sac, the venous tube and the isolated piece of membrane vein alike are able to induce of themselves the necessary stimuli for vasomotion. This was best observed in a venous tube of 4–6 mm length. Under favorable conditions, tonic and rhythmic-phasic activities are performed.

Distally and proximally the venous tube is ligated to cannulas. In this way the isolated vein can be perfused in both directions and becomes very suitable for checking the spontaneous occurrence of peristalsis and antiperistalsis. Rather strong dilatation stimuli of short duration induce antiperistalsis. Weak dilatation stimuli are almost always followed by a decrease of the diameter of the vein. Dilatation may also lead to delay and summation of stimuli. The manifestations interpreted as generation of excitation and excitation conduction are not identical with the waves of muscular contraction. This emerges clearly from the fact that action currents (Evg) can be recorded also from a venous tube preparation showing no visible contraction at the stimulated spot or in the whole venous tube or anywhere else.

The venous tube preparation typically keeps a constant direction of excitation conduction during the entire experiment. Up to 3 recording electrodes are aspirated on the preparation. Increasing the distance between electrodes results in a tendency toward faster conduction of excitation. Small pressure differences are without any influence on excitation conduction. With constant distance between 2 recording electrodes (ca 2 mm) pressure differences placed centrally or peripherally in the venous tube do not induce any significant changes in excitation conduction. On the other hand, conduction slows down with unilateral distal or proximal pressure decrease. Changes in static pressure had no effect in either of the isolated preparations, but conduction speed decreased when the gradient was established byowering pressure at either end of the venous tube. With increasing distance between electrodes on the venous tube conduction velocity tends to go up irrespectively of the direction in which excitation is propagated. In *Myotis,* with electrode distances similar to those in *Pteropus*, we found that spike travel was preponderantly (but not always) toward the heart. This resembles the venous tube, where the spike proceeded in a constant direction for a given experiment, although the direction could change from preparation to preparation. Average conduction speeds (21.6 vs 21.5 mm/sec) were the same in both directions. In this preparation only, conduction speed tended to rise as distance between the electrodes was increased.

3. The three veins-preparation

The complex of symmetrically dichotomous veins is isolated from the chiropatagium in the angle between fingers. This complex consists of a main vessel and 2 venous branches all 3 of which are cannulated. The preparation can be perfused in 2 directions: from the left branch to the main vessel or from the right branch to the main vessel. The tightly closing valves at the passage from branches to main vessel prevent perfusion from main vessel to branches. Increasing internal pressure in the main segment remains without any hydrostatic influence on the branches. For this reason, we can be certain that the induction of reactive venous contractions must be due to excitation conduction in the muscular wall. Highly localized pressure stimuli, involving very small groups of muscle fibres can be applied to this preparation and we can thereby produce highly localized contractions which can be visually observed and recorded by photoelectrical techniques. Experiments with varying pressure showed that excitation can be conducted in the venous wall from main vessel to branches and vice versa, and also from branch to branch. Excitation conduction is possible in distal, proximal, and lateral direction. In addition we could show in this preparation that propagated excitation is a consequence of direct passive contraction in the distal hydrostatically uncoupled part of the veins, and that contractility and conductibility in the venous wall are physiologically separate manifestations. The preparation demonstrates further that, although each venous section has its own inherent frequency, a synchronization over the entire preparation takes place by excitation conduction.

In the stationary three veins-preparation, it is possible by increasing pressure in the vein stem to activate simultaneously the pulse in both venous branches and so to demonstrate a transference of the stimulus from the stem to the branches. Furthermore with increasing pressure in one branch, it was possible by transference of the stimulus to the un-filled 2nd branch to synchronize the pulse to the higher frequency of the stimulated vein. Experiments on longlasting pulsing three vein-preparations showed that an intravascular stretch stimulus in the actively pulsating stem vessel can raise the pulse frequency in both venous branches from 10 to 20 and 15 to 45/min. The latent period for the transference effect is markedly reduced in the pulsating vessel preparation. Besides the synchronisation of the frequency, a general pulse dissociation is often also seen, in spite of ubiquitous equal inner pressure. In this case the venous stem and the two branches show a pulsation frequency of their own which may last for some time and which is not always influenced by the pressure stimulus. On the other hand, an agreement of frequencies of all associated veins can last a long time in spite of local differences in pressure.

Experiments concerned with propagation of excitation and velocity of conduction in the venous wall reveal a striking variability of the excitatory state in adjacent sections of the vein. Thus for peripheral association and coordination of dichotomously branched venous sections, the possibility of tonus control through nervous structures has to be taken into account. Vasomotor nerves have definitely been demonstrated to be responsible for the regulation of arterial diameter, but they have no direct influence on the active venous pulse. The vein's own innervation seems to be solely responsible for tone regulation in these wing membrane vessels.

The functional potencies of the isolated wing membrane vein are often influenced simultaneously and unidirectionally by the same conditions of the interior medium (temperature, oxygen content, adequate Ringer solution or bovine serum). They therefore appear to depend on a common underlying mechanism. It should be added however, that responses to the ionic composition of the medium, for instance, could only be obtained with veins exhibiting a special functional disposition. Only under such conditions was a systolic effect of calcium and a diastolic effect of potassium observed. In potassium-free Ringer solution, the vein contracted until the open lumen disappeared completely, whereas in calcium-free Ringer the vessel was maximally dilated.

Summing up these results we can say that besides the natural stimuli (pressure, temperature, and humoral factors) we must realize that conduction of excitation, effects of propagation and variations in the excitability of associated venous segments also take part in the functional organization of venous peristalsis. The myogenous organization of the pulsation mechanism is the result of the interaction of all of these factors. The venous heart, in contrast to the heart proper, can be tetanized; a definite refractory state does not exist. We conclude that in the smooth venous muscle the contractile elements are neither simultaneously excited nor do they contract at the same time. Additional stimuli are effective at every phase of the pulsation. During the entire systole excitability is not diminished; with the onset of diastole, often even during the beginning of the diastolic pause, excitability disappears completely: this represents an additional constructive-functional difference between the venous heart and the heart proper. A comparison of the autorhythmic mechanism of the actively pulsating veins of the bat wing with the portal vein in bats, mice, rats and lower vertebrates and also with the contractile lymph vessels, will lead to a more soundly based comparative angiology. The self-regulation of the vascular apparatus to be discussed in the following papers may provide an impetus for further fruitful research.

Acknowledgment. I should like to express my thank to my coworkers H. Huggel and R. Schipp for carrying on the experimental work on the ideas which I had planned.

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Overview of circulation in the wing membrane

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In meeting the profound metabolic demands involved in achieving true flight, bats have been successful in specializing their otherwise typical mammalian cardiovascular system rather than having to modify its basic organization. The remarkable efficiency of this system may well be reflected, for example, in the fact that all bats at rest, whether of a hibernating species or not, tend toward what in most other mammals would amount to a functional bradycardia. The problems involved in maintaining adequate circulation and homeostasis in a bat wing in particular must be such as to call upon a maximal number of specializations to maintain a successfully operating system. Unlike birds, bats must maintain nutrient support to living tissue in the outermost boundaries of their flight surfaces. At the same time, they must avoid such complications as excessive capillary pressure and tissue edema in all areas of this extensive wing, whether the animal is at rest or in flight. Moreover, in addition to locomotion, the wing subserves other important needs of the animal such as thermoregulation, during which dramatically sudden engorgement of wing vessels can take place throughout the entire extent of the patagial membranes.

As far as is known, the properties of the capillary beds and tissue spaces themselves are typical of any mam-