springs showed much greater stiffness. In the cases of both the L- and T-hairs, the stiffness in this plane was about 4 times greater in the long hairs and about 8 times greater in the short ones than in the plane of best mobility. Except for the orientation of the plane of best mobility, L- and T-hairs have the same mechanical properties: these include the length-stiffness relation and the spring anisotropy. The orientation of the plane of best mobility depends upon positional information at the time of differentiation from an epidermal mother cell [17]. The information is translated into the alignment of the tormogen cell which secretes the anisotropic spring diaphragm.

The amount of L-L stiffnesses measured in the filiform hairs of crickets within 1 h after imaginal ecdysis ('New' in the figure) showed no difference when compared with the results for older animals. The springs seem to be functional from the time just after ecdysis. No further tanning seems to be necessary to establish the mechanical sensitivity of the cercal filiform hairs, whereas the body wall cuticle must be tanned for a couple of hours to achieve full strength.

The thoracal filiform hairs of *Barathra* caterpillars regain their maximal sensitivity within a few minutes of ecdysis [18]. During ecdysis, when the cuticular structures of hair sensilla are replaced, the hairs suffer a loss of sensitivity to air-motion. It is crucial for all cuticular mechanoreceptors that this blind period should be as short as possible. Although the recovery of sensitivity after ecdyses has not yet been studied in the cercal sensory afferents, we have at least found that the mechanical parts are functional just after ecdysis.

The directionality of hair mobility under an oscillating air current shows a figure of eight [15]. The ratio between amplitudes with respect to the plane of best mobility and those which are perpendicular to it agree well with the polarization of spring stiffness which we have found here. The directional mobility of cricket sensilla in response to air fluctuation is a direct reflection of the polarizing spring.

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Functional similarities in the mechanical design of the aorta in lower vertebrates and mammals

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Summary. The mechanical properties of the aorta from the toad *Bufo marinus*, the lizard *Gekko gecko* and the garter snake *Thamnophis radix* were compared to those of the rat, by inflation of vessel segments in vitro. The arteries of the lower vertebrates, like those of mammals, were compliant, higly resilient, and non-linearly elastic. The elastic modulus of the artery wall was similar in the lower vertebrates and mammals, at their respective mean physiological pressures. We conclude that the aorta in each of these animals is suitably designed to function effectively as an elastic pulse smoothing component in the circulation; differences in the pressure wave transmission characteristics of lower vertebrates and mammals do not result from dissimilarities in arterial elastic properties, but from substantial differences in heart rate of these two groups.
Key words. Aorta; elasticity; mechanical properties; Windkessel.

Arterial elasticity is an important determinant of haemodynamics in animals. The major arteries act as an elastic reservoir, storing blood transiently during systolic ejection, and providing flow to the periphery during diastole. In this way the elastic recoil of the artery wall converts the pulsatile output of the heart into a smoother flow in the peripheral circulation [1]. The elastic compliance of the arterial tree also reduces the pressure pulse and hydraulic impedance, and directly influences the speed of pressure wave transmission in the system.

In mammals the artery wall exhibits non-linear elasticity. This means that the vessel is compliant at low pressures,

but becomes much stiffer and less distensible with increasing pressure. The non-linear behaviour results from the combined effect of two connective tissue proteins found within the arterial wall. Elastin is highly extensible and rubber-like, while collagen is 1000 times stiffer and relatively inextensible. The ratio of collagen to elastin provides a comparative index of wall stiffness at physiological pressures in different arteries [2], but the total quantity and structural arrangement of the connective tissues are also important in determining the artery mechanical properties [3]. Within the tunica media, elastin fibres are organized in concentric lamellae which are interconnected by smaller fibrils. Collagen fibres are found between elastin lamellae and in the adventitial layer [4]. Roach and Burton [5] showed that the compliance of the artery wall at low physiological pressures was associated with the extensibility of elastin, while the much greater stiffness at high pressures was provided by collagen. Apparently, as distending pressure is increased through the physiological range, the elastin becomes fully loaded and collagen fibres are recruited, producing the observed non-linear properties [6].

Studies on the mechanical properties of mammalian arteries are numerous, and models of this circulation have been described in detail [1]. In contrast, there is very little information available on the elastic properties of arteries of animals from the lower vertebrate groups, particularly reptiles and amphibians. This is surprising, considering the importance of arterial elasticity to circulatory physiology, and that major differences exist between the circulatory systems of mammals and those in lower vertebrates. Blood pressures and heart rates have been measured in many poikilotherms, including the toad *Bufo marinus* [7, 8], the frog *Rana catesbeiana* and *R. pipiens* [9, 10], the salamander *Salamandra salamandra* [9], the cod *Gadus morhua* [11], the turtle *Pseudemys scripta* and *Testudo graeca* [12], the lizard *Tiliqua rugosa* [7], and the garter snake *Thamnophis radix* [13]. These studies all showed that, compared to mammals, poikilotherms have relatively low heart rates and low blood pressures, but they did not provide direct measurements of the elastic properties of the arteries. In one study by B. M. Learoyd, however, (unpublished results cited by Satchell [14]) arterial elasticity was quantified in the shark *Odontapsis arenarius* and *Carcharodon carcharias*. The ventral and dorsal aorta both had non-linear properties, but the former was about four times more compliant at any pressure. A strong correlation between the proportion of collagen and elastin, and the elastic modulus was found [14].

The simplest haemodynamic model is the two-element Windkessel. This consists of a single elastic reservoir (the compliant aorta) which feeds a non-compliant peripheral resistance. Each pressure pulse is assumed to be transmitted instantaneously throughout the Windkessel, and its effects are completely diminished before the next pulse occurs. Although this model cannot account for the complex wave transmission characteristics of the mammalian arterial system, which result primarily from the interaction of reflected waves [15], it has been shown to apply very well to poikilothermic vertebrates such as the frog [10] and turtle [16]. In these animals, unlike the situation in mammals, no amplification or distortion of the pressure waveform occurs as it travels away from the heart, suggesting that reflected waves are unimportant. Likewise, in the dorsal aorta of the shark, pressure pulses are transmitted with no apparent reflection effects [14]. These studies all suggest that the arterial systems of lower vertebrates have some elastic behaviour. In this investigation we present quantitative data on the elastic properties of the aortae from two reptile and one amphibian species, and show that they have strong structural and functional similarities with mammals. Thus, the arterial wall of these lower vertebrates is appropriately designed to function effectively as an elastic component in the circulatory system.

Materials and methods

The mechanical properties of aortae from the toad, *Bufo marinus*, the lizard, *Gekko gecko*, the garter snake, *Thamnophis radix*, as well as the rat (Sprague-Dawley strain) were studied by inflation of vessel segments in vitro. The toads and lizards were killed with a lethal injection of MS-222 (Sandoz, 1:1000, 1 ml/100 g b. wt). The rats were killed by cervical dislocation and the snakes by decapitation. The entire length of the dorsal aorta distal to the aortic arches was removed from each animal and stored in saline at 4 °C. Experiments were performed in a saline-filled chamber at room temperature within 24 h of death. Aortic segments (approximately 5 cm long) were cannulated, stretched and held at their in vivo length, and slow inflation-deflation cycles (lasting 1–2 min) were performed using a variable speed pump. Conditioning cycles (usually 2–3) were run until the pressure-volume (P-V) curves were stable and reproducible. Pressure was recorded by a strain gauge transducer and external diameter was measured simultaneously using a video dimension analyzer (Instrumentation for Physiology and Medicine, model 303) as described by Fung [17]. These data were collected on-line, and successive cycles were signal-averaged, by a PDP 11/23 lab computer (Digital Equipment Corp.) which was also used for further calculations of artery wall stress (σ), strain (ε), and incremental elastic modulus ($\mathbf{E}$) at pressure intervals of 0.5 kPa, as described by Milnor [15].

Circumferential wall stress (σ) is defined as:

$$\sigma = \mathbf{Pr/h} \qquad (1)$$

where $\mathbf{P}$ is the pressure, $\mathbf{r}$ is the internal radius, and $\mathbf{h}$ is the wall thickness. Circumferential wall strain (ε) at the mid-wall radius is calculated as:

$$\varepsilon = \Delta \bar{\mathbf{R}}/\bar{\mathbf{R}}(0) \qquad (2)$$

where $\bar{\mathbf{R}} = (\mathbf{R} + \mathbf{r})/2$, $\mathbf{R}$ is the external radius and $\bar{\mathbf{R}}(0)$ is

the unpressurized mid-wall radius. The incremental elastic modulus is a measure of the vessel stiffness which, at constant length, can be derived as:

$$\mathbf{E} = (0.75)(1 + \varepsilon)\,\Delta\sigma/\Delta\varepsilon \qquad (3)$$

The unstressed wall thickness was measured from frozen-cut sections of each vessel segment after inflation tests by using a microscope digital micrometer (Wild-Leitz MMS235). By assuming that the artery wall volume is constant, and knowing the initial dimensions, **h** and **r** can be calculated from **R** at each pressure interval[18]. Luminal volume was calculated from internal radius, and volume changes were expressed relative to the initial volume ($\Delta V/Vo$). Pressure wave velocity was calculated at mean physiological pressure, using the corresponding values of **h** and **R**, according to McDonald[1] as:

$$\mathbf{C} = (\mathbf{Eh}/2\varrho\,\mathbf{R})^{1/2} \qquad (4)$$

where ϱ is the density of the blood. In the tetrapod species, the length of the arterial tree (**L**) was measured from the heart to the abdominal bifurcation, presumably the major reflecting site. Since the snake aorta has no comparable bifurcation, **L** was arbitrarily chosen as the distance from the heart to the end of the abdominal aorta at the level of the cloaca. Pulse transit times were calculated as **L**/**C**.

For histological examination, fresh vessel segments were fixed and processed according to standard methods[19]. Transverse sections were stained for elastin with Verhoeff's technique and for collagen with picro-ponceau.

Results and discussion

Upon removal from the animal, the aorta of each species studied showed longitudinal elastic recoil of approximately 30%. If vessel segments were inflated untethered, each would lengthen with increasing pressure, up to a maximum value which occurred at about the mean blood pressure for that species, and was equal to the original in vivo length. With further increases in pressure, no significant lengthening was observed. We held each vessel tethered to the in vivo length while recording inflation data. Typical pressure-volume (P-V) curves are shown in figure 1 for inflation cycles from preconditioned vessel segments of the toad, lizard, snake, and rat. These plots show that the lower vertebrate aortae have essentially the same mechanical behaviour as that of the mammals, i.e. the increasing slope of each inflation curve indicates that there is non-linear elasticity, with high compliance at low pressures, but a sharp decrease in distensibility at pressures above the physiological range. When arteries are subjected to cyclic loading, the relationship between pressure and volume is different in the loading portion (energy input) than in the unloading portion (elastic energy recovery) of the cycle. The area within the P-V loop indicates the mechanical hysteresis, that proportion of energy absorbed which is lost through viscous processes during an inflation-deflation cycle. Hysteresis values were relatively low in all cases, ranging from 17–25% for artery segments from the toad, lizard, and snake, and somewhat lower (8%) for the rat aorta. These results demonstrate that all the vessels are highly resilient, and that a large proportion of the strain energy input during systolic inflation of the vessel will be recovered by elastic recoil in diastolic deflation. Thus, the aortae of these poikilotherms, like those of mammals, exhibit the necessary mechanical behaviour to function effectively as elastic pulse smoothing components in their respective circulatory systems.

Inflation data from the various aortae were quantified by Eqns 1–3, in order to make comparisons of their mechanical characteristics. A close resemblance in the material properties of the artery wall of the poikilotherms and the mammal is seen in figure 2, where the incremental modulus of elasticity is plotted as a function of circumferential strain. In all cases, the inherent non-linear elasticity results in an increase in stiffness with extension, particularly above strains of about 0.6 in the rat and 0.7 in the others. This kind of mechanical behaviour is typical of biological materials which are composites[20, 21].

When we consider the elastic modulus as a function of pressure (fig. 3), a clear difference is evinced between the properties of the lower vertebrate aortae and that of the rat, i.e. the curve for the latter is shifted far to the right of the others. This occurs because the physiological blood pressure range is much higher in mammals than in these lower vertebrates (11 vs 3 to 4.4 kPa, respectively). In order to make a functional comparison of the mechanical behaviour of these aortae, the data are plotted again in figure 4, with pressures normalized to the mean blood pressure for each species. The results now show a striking similarity between the two groups in terms of the physiological significance of their aortic elasticity. In each animal the elastic modulus of the aorta is low at low relative pressures, rises to around 0.3–0.5 MPa at the mean blood pressure, and increases sharply at higher pressures. These characteristics ensure that the vessel is compliant in the physiological range, where it acts as a pulse smoothing mechanism, but is stiffened to prevent aneurysms or rupture at elevated pressures[5, 15, 20, 22]. Thus we may conclude that, at their respective physiological pressures, the aortae of the lower vertebrates have the same functional mechanical properties as that of mammals.

The compliance of blood vessels at low pressures can be attributed to the extensibility of the elastic fibres within the vessel wall. The increased stiffness at high pressures is due to the reinforcing effect of collagen fibres[6]. In the lower vertebrates, collagen and elastin are arranged in layers within the artery wall much like the mammalian aorta (fig. 5), but the elastin lamellae of the former appear thinner and less well ordered. Minor variations in artery wall structure among the toad, lizard and snake, as

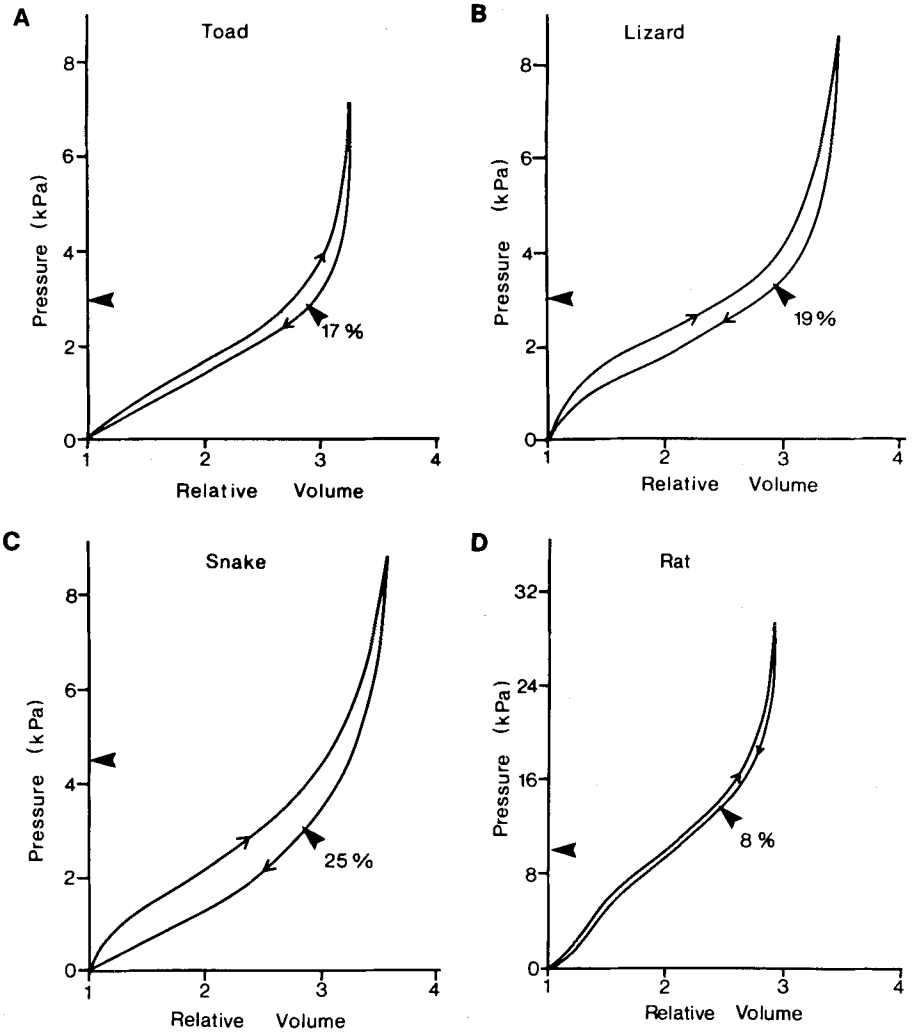

Figure 1. Pressure-volume (P-V) curves for an inflation-deflation cycle on aortic segments for *A*) toad, *B*) lizard, *C*) snake, and *D*) rat. Luminal volume changes were calculated from external radius measurements and normalized by the unpressurized volume. The mean physiological pressure for each animal is indicated by an arrow on the pressure axis. Values for mechanical hysteresis are shown beside each P-V loop. These curves represent a stable response in the pressure-volume curve, which was obtained after 2 to 3 cycles for each aorta.

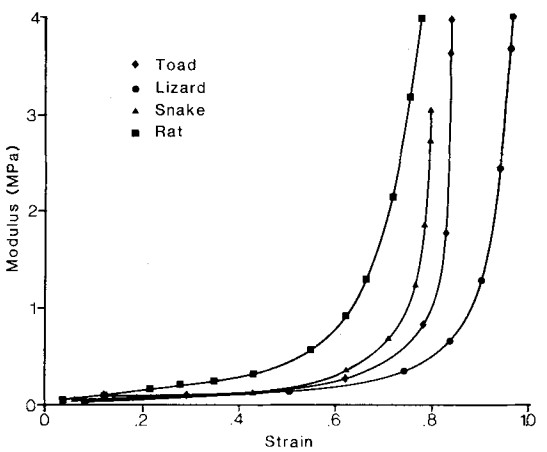

Figure 2. A quantitative comparison of the artery wall material properties in different species. Incremental elastic modulus, calculated from inflation data, is plotted as a function of circumferential strain.

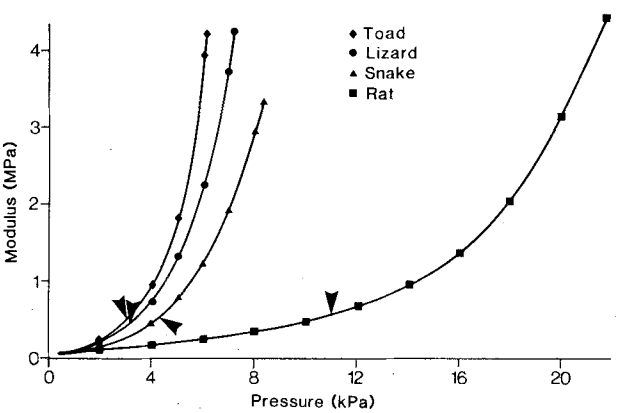

Figure 3. The incremental elastic modulus of the aorta plotted against inflation pressure for the toad, lizard, snake, and rat. Arrows indicate mean physiological pressure for each species. (For the garter snake, this is taken from Burggren[13]; others are our measurements).

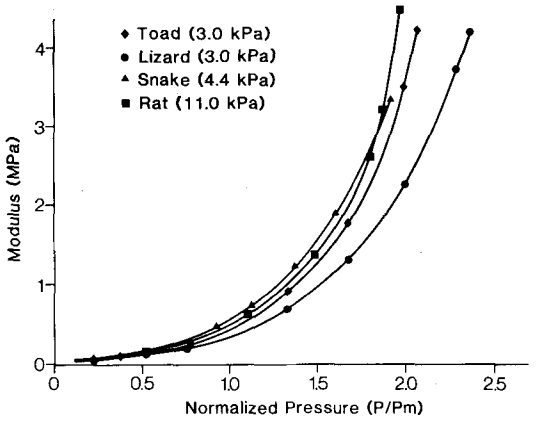

Figure 4. Functional mechanical properties of the vertebrate aortae. The elastic modulus data of fig. 3 are plotted on a pressure scale which is normalized to the mean blood pressure (P_m) for each species.

seen in figure 5A–C may be related to the slight differences in their mechanical properties shown in figures 2 and 3. For example, the snake artery is more compliant and has a greater number of elastin layers than that of the toad.

In general, there appears to be relatively less elastin and more collagen in the artery wall of these lower vertebrates than in the mammalian aorta. This may explain, in part, why the aortic stiffness is greater at all pressures in the poikilotherms than in the mammal (fig. 3). Further, the relatively thinner aortic wall of the toad, lizard and snake, compared to that of the rat, (h/R ratio; table 1) will experience a higher circumferential stress at

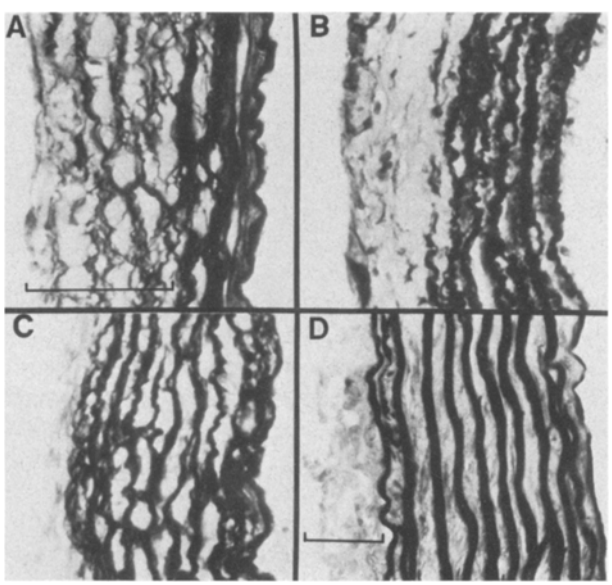

Figure 5. Light micrographs showing elastin lamellae (positively stained) in transverse sections of the artery wall in *A*) toad, *B*) lizard, *C*) snake, *D*) rat. The luminal side for each is on the right. Collagen occurs predominantly in the outer adventitia of the lizard and snake aortae, while it is present between the elastin layers throughout the wall in the toad aorta. The scale for (*A*), (*B*), and (*C*) is indicated by a 60-μm bar in (*A*). The scale for (*D*) is indicated by a 50-μm bar in (*D*).

Table 1. Structural properties of vertebrate aortae

	Toad	Lizard	Snake	Rat
External radius **R**[a] (mm)	0.9	0.6	0.7	1.1
Relative wall thickness[a] (**h/R**)	0.11	0.14	0.12	0.20
Mean blood pressure (kPa)	3.0	3.0	4.4	11.0
Average number of lamellae	6	6	10	11
Tension per lamella[b] (Pa · m)	0.54	0.33	0.36	1.2

[a] untethered at zero pressure; [b] at mean blood pressure; (tension = P · r).

any pressure, according to Eqn 1. The variance in aortic elasticity of the two taxa, illustrated in figure 3, may also result from differences in the artery wall microstructure and connective tissue mechanical properties which have not been fully elucidated.

One structural feature which differs among the aortae shown in figure 5 is the thickness and number of elastin lamellae. In mammals there is a linear relation between the total circumferential tension (T = P · r) at physiological pressure, and the number of lamellar units in the wall, such that the tension per layer is nearly constant in all species[23]. In the rat there is an average of 11 lamellae, 5–7 μm thick, each supporting a tension of 1.2 Pa · m (table 1). In the aorta of the toad, lizard and snake the elastin layers are thinner (2–3 μm) and less regularly arranged. Taking averages of 6 for the toad and lizard, and 10 for the snake we calculated the tension per layer as only 0.54, 0.33, and 0.36 Pa · m, respectively (table 1). These results suggest that the elastic lamellar unit of the aorta is structurally and perhaps mechanically different in the lower vertebrates than in mammals. We are currently investigating this phenomenon further.

Pressure wave transmission properties of the aortae from the vertebrate species used in this study are compared in table 2. The pressure wave velocity is highly dependent on the elastic modulus of the aorta (Eqn 4), which is similar for the toad, lizard, snake and rat, at their respective mean blood pressures (fig. 4, table 2). Therefore, the wave velocities for these species are also close, ranging from 220 to 400 cm s^{-1}, and the pulse transit times (i.e. the time for the pressure wave to travel through the arterial tree to the major reflection site) all fall between 30 and 90 ms (table 2). Due to the relatively low heart rates of the toad, lizard, and snake, the pulse transit time is a negligible fraction of the cardiac cycle, whereas in the

Table 2. Pressure wave transmission properties of vertebrate aortae

	Toad	Lizard	Snake	Rat
Elastic modulus[a] (MPa)	0.33	0.30	0.51	0.5
Pressure wave velocity[a] (cm s^{-1})	220	220	330	410
Heart rate (min^{-1})[b]	37	35	30	300
Length of arterial tree (cm)	11	7	32	17
Pulse transit time (s)	0.05	0.03	0.09	0.04
Transit time as % of cardiac cycle	3	2	5	24
Propagation effects	none seen,	.....	Windkessel	transmission line system

[a] at mean blood pressure; [b] at 22 °C in poikilotherms.

rat, the transit time is about 24% of the cycle, or 5–12 times greater than in the poikilotherms. In these low heart rate animals, each pressure wave will be reflected within the aorta 20–50 times before the next cardiac contraction begins. Considering that wave amplitude decreases with each reflection, and that energy losses occur due to hysteresis of the artery wall and blood viscosity[1], each pulse will be almost completely attenuated before the next wave occurs. Therefore, there will be no significant interaction between successive pressure waves; no wave propagation effects, such as pulse amplification, distortion and impedance oscillations will occur, and the arterial systems of these animals should function as simple Windkessels. Indeed, haemodynamic studies of the turtle[16], frog[10], and python snake[24] demonstrate that this is the case for lower vertebrates. In contrast, the much higher heart rate in mammals compared to poikilotherms creates a complex transmission line system in which the interaction of reflected waves with successive pulses produces significant wave propagation effects that are absent from the simpler Windkessel[1,15]. Thus, it is heart rate, rather than differences in the vessel elasticity, which is the major factor determining whether the aorta acts like a Windkessel, as in poikilotherms, or like a transmission line as in mammals. Although the circulatory systems of the toad, lizard, and snake may be described by a much simpler haemodynamic model than can be applied to mammals, the aortae of these lower vertebrates have mechanical design features which are functionally similar to those of mammals.

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A first report of relative movements within the hyoid apparatus during feeding in *Anolis equestris* (Reptilia: Iguanidae)

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Summary. The movements of the hyoid apparatus of *Anolis equestris*, during mechanical reduction of prey, have been studied by cinefluoroscopy. In the SO and FO stages, ceratobranchials I move forward faster than the ceratohyals. Muscle stimulation experiments show that contractions of the m. ceratohyoideus and m. mandibulohyoideus I produce this movement. The other hyoid and extrinsic muscles of the tongue may be divided into protractors and retractors. In the FC-SC stage, the tongue-hyoid complex moves backward. The movements of ceratobranchials II follow those of the other elements after a short delay.
Key words. Lizards; feeding; mechanical reduction; hyoid apparatus; tongue.

The tongue-hyoid complex of early tetrapods seems to have been used in several distinct activities: feeding, drinking, flicking and display. Feeding consists of cyclic movements of the complex co-ordinated with jaw cycles[1–3]. A model of the tongue movement during feeding of a generalized tetrapod has been constructed on the basis of some earlier studies of amphibians and reptiles[3]. In lizards, the wide variation of tongue morphology[4] and its adaptation to their diets have been clearly demonstrated[5]. Only a few studies have presented the movements of the hyoid and the tongue during food manipulation. Dorso-ventral and antero-posterior movements of the whole hyoid-tongue complex have been reported in *Chameleo dilepis*[6], *Ctenosaura similis* and *Tupinambis*