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The adaptive significance of vertebral form in the pelvic regions of *Mabuya capensis* and *Acontias plumbeus* (Reptilia: Scincidae)

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Vertebral form in the pelvic regions of the terrestrial *Mabuya capensis* and the subterrestrial *Acontias plumbeus* reflect characteristics related to a combination of flexibility and strength. In *M. capensis* both the pre- and postsacral vertebrae become relatively shorter and broader towards the sacrum. This not only results in greater flexibility of the pelvic region but also provides a large bone area over which the forces generated during locomotion can be distributed. In *A. plumbeus* the precaudal and caudal vertebrae become relatively shorter and broader towards the precaudal–caudal transition giving its pelvic region attributes similar to that of *M. capensis*. The articular surfaces of the zygapophyses in *A. plumbeus* are larger and stretch further laterally than those of *M. capensis* probably allowing its vertebrae a greater degree of lateral movement. The condyles and therefore also the cotyles of *A. plumbeus* are broader and shorter (shallower) than those of *M. capensis* allowing the compressive forces generated during locomotion to be distributed over a larger bone area while also allowing the vertebrae more freedom of lateral movement. In both skinks the vertebrae have procoelous centra.

Werwelvorm in die bekkenwyke van die landbewonende *Mabuya capensis* en die ondergrondlewende *Acontias plumbeus* reflekteer eienskappe wat dui op 'n kombinasie van buigsaamheid en sterkte. In *M. capensis* word beide die pre- en postsakraalwerwels relatief breër en korter in die rigting van die sakrum. Dit lei nie alleen tot meer buigsaamheid van die bekkenwyk nie, maar verskaf ook 'n groter beenoppervlak waaroor die kragte wat tydens voortbeweing ontstaan, versprei kan word. In *A. plumbeus* word die prekoudaal- en koudaalwerwels korter en breër in die rigting van die prekoudaal- koudaaloorgang en dit gee aan sy bekkenwyk soortgelyke eienskappe as dié van *M. capensis*. Die artikulasievlakke van die sigapofises in *A. plumbeus* is groter en strek verder lateraal as dié van *M. capensis* en verskaf waarskynlik 'n groter mate van laterale beweging aan sy werwels. Die kondilusse en dus ook die kotilusse van *A. plumbeus* is breër en korter (vlakker) as dié van *M. capensis*. Dit verskaf 'n groter beenoppervlak waaroor die saamdrukkende kragte wat tydens voortbeweging ontstaan, versprei kan word, en laat ook 'n groter mate van laterale beweging toe. In albei akkedissoorte het die werwels prosele sentrums.

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Literature describing the structure of the vertebral columns of various lizards is quite common (El-Toubi 1938; Holder 1960; King 1964; Etheridge 1967), however in most papers very little is said about the adaptive significance of vertebral form. In this regard a valuable contribution was made by Johnson (1955) regarding the adaptive and phylogenetic significance of vertebral form in snakes. Troxell (1924) also looked at various vertebral dimensions in his analysis of the mechanics of crocodile vertebrae while Higgins (1923) commented briefly on the significance of the shape of the centra of the sacral vertebrae in *Alligator mississippiensis*.

M. capensis and *A. plumbeus* are examples of the two extreme body forms found in the family Scincidae, the former being a normal pentadactyl tetrapod and the latter being a limbless fossorial form. This paper deals with a morphometric analysis of the pelvic vertebrae of both forms of skink in an attempt to show how they are adapted to meet the demands of their specific mode of locomotion.

Materials and Methods

The vertebrae were prepared for measurement by allowing dermestid beetle larvae to eat the muscle tissue away. Measurements were taken with a graticule placed in the eyepiece of a stereo-microscope. Various measurements were made (Figure 1) and the data used to calculate certain indices for which linear regressions and histograms were constructed. As the data were used to calculate various indices the graticule measurements were not converted into SI units but simply given as graticule units (g.u.) in the tables. In *M. capensis* the last four presacral and the first four postsacral vertebrae of three specimens were examined, whereas in *A. plumbeus* the last four precaudal and the first four caudal vertebrae of two specimens were examined. The Student *t* test was used when comparing two means. A probability (p) smaller than 0,001 was described as highly significant, $p < 0,01$ as significant and $p > 0,01$ as not significant.

Results

Linear regressions were constructed to show how the length and width dimensions of the vertebrae change relative to each other through the pelvic region. In *A. plumbeus* vertebral length in the precaudal region decreased at a significantly faster rate ($p < 0,001$) than the increase in width towards the precaudal–caudal transition resulting in the precaudal vertebrae becoming relatively shorter and broader towards the transition (Figure 2, Table 1). In the caudal region both vertebral length and width increased towards the precaudal–caudal transition but width increased much faster than length ($p <$

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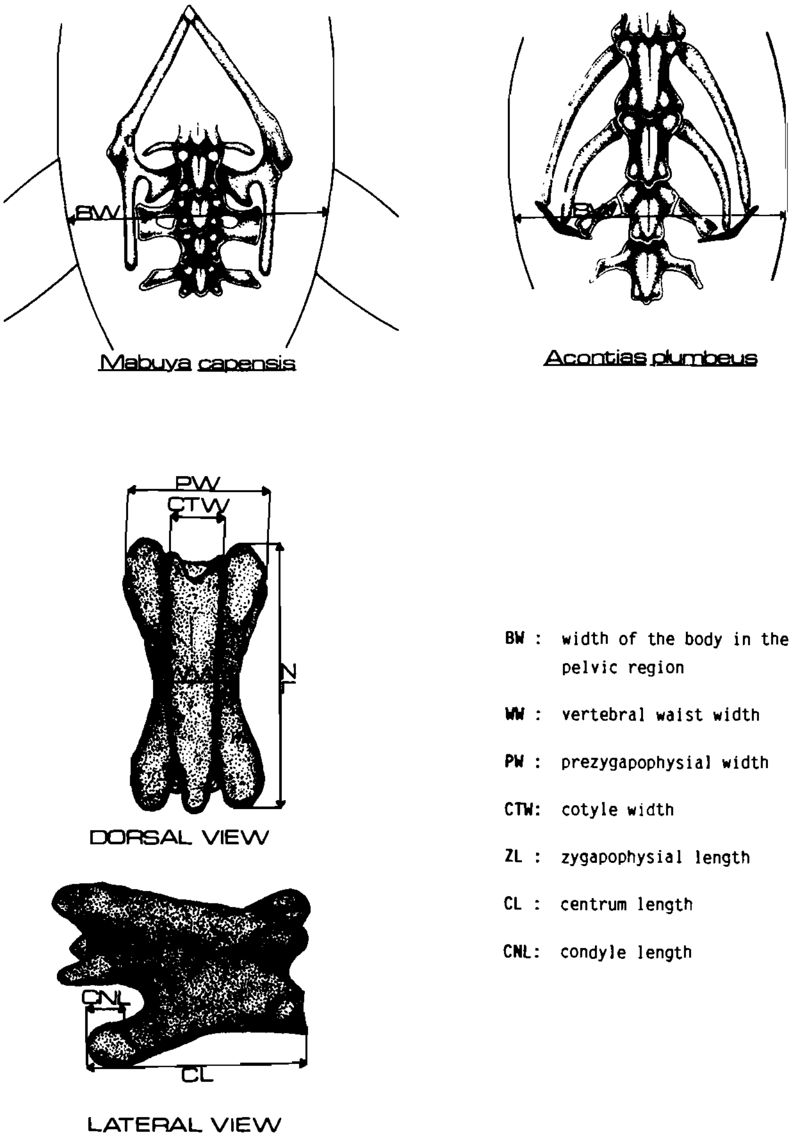

BW : width of the body in the pelvic region

WW : vertebral waist width

PW : prezygapophysial width

CTW: cotyle width

ZL : zygapophysial length

CL : centrum length

CNL: condyle length

Figure 1 The vertebral dimensions used for the calculation of various indices in *A. plumbeus* and *M. capensis*.

0,001) resulting in the caudal vertebrae also becoming relatively shorter and broader towards the transition. In *M. capensis* the width of the presacral vertebrae increased while their length decreased towards the sacrum (Figure 3, Table 2). The increase in width, however, occurred at a rate significantly faster ($p < 0{,}001$) than the decrease in length so that the vertebrae effectively became relatively shorter and broader towards the sacrum. The same held true for the postsacral vertebrae in which length decreased towards the sacrum while width increased at a much faster rate ($p < 0{,}001$).

The vertebrae in *M. capensis* were broader than those of *A. plumbeus* but their lengths showed little or no difference (Figure 4, Tables 1 and 2). Prezygapophysial width in *A. plumbeus* was greater than in *M. capensis* because the zygapophyses in *A. plumbeus* flared further laterally than in *M. capensis* (Figure 5, Tables 3 and 4). Cotyle width in *A. plumbeus* also exceeded that in *M. capensis* (Figure 5, Tables 3 and 4). The condyles in *A. plumbeus* were shorter than those of *M. capensis* (Figure 5, Tables 3 and 4) implying that their cotyles were also shallower than those of the latter.

Discussion

The functional demands imposed on the vertebral column in the pelvic regions of *A. plumbeus* and *M. capensis* by their respective environments appear to be related mainly to the improvement of its flexibility and strength. These requirements have been met by their pelvic vertebrae in ways which coincide in some respects but differ in others. *A. plumbeus* relies entirely on its axial skeleton and musculature to crawl through its dense subterrestrial habitat whereas *M. capensis* primarily uses its appendicular skeleton and musculature for locomotion. The axial system of *M. capensis* plays a more secondary role in locomotion than in *A. plumbeus*, facilitating greater stride length via backward and forward oscillation of the girdles. The primary functions of the axial skeleton of *M. capensis* are to keep the body suspended between the girdles and to protect the viscera.

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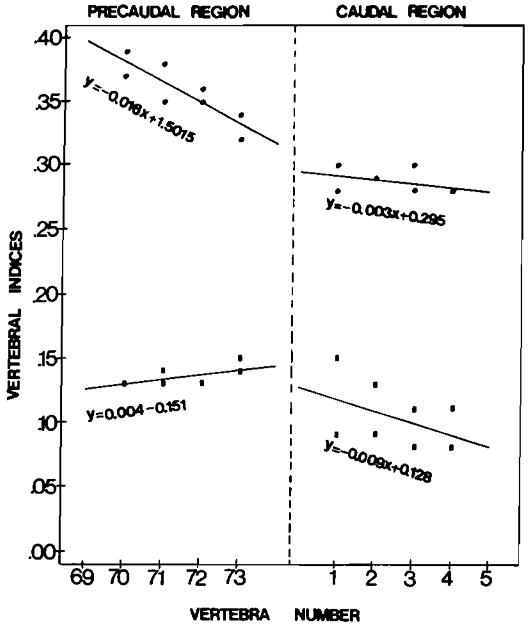

Figure 2 The relationship between the vertebral waist width (■) and zygapophysial length (●) indices in the pelvic region of *A. plumbeus*. The vertebrae of two specimens were measured and each point represents data from an individual vertebra. The dotted line represents the precaudal–caudal transition.

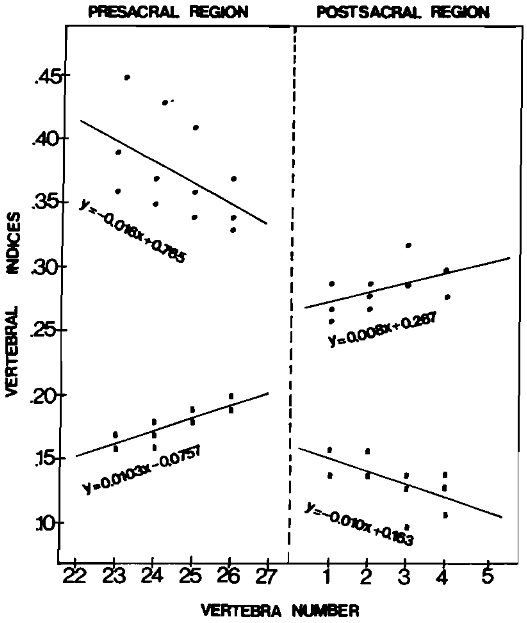

Figure 3 The relationship between the vertebral waist width (■) and zygapophysial length (●) indices in the pelvic region of *M. capensis*. The vertebra of three specimens were measured and each point represents data from an individual vertebra. The dotted line represents the sacrum.

Table 1 The vertebral waist width and zygapophysial length indices as calculated for the last four precaudal and the first four caudal vertebrae of two specimens of *A. plumbeus*

Region	Speci- men	Verte- brae	WW/BW	WW/BW Mean±*SD*	ZL/BW	ZL/BW Mean±*SD*
Precaudal	A	70	0,13	0,14±0,0070	0,39	0,36±0,0210
		71	0,14		0,38	
		72	0,13		0,36	
		73	0,14		0,34	
	B	70	0,13		0,37	
		71	0,13		0,35	
		72	0,13		0,35	
		73	0,15		0,32	
Caudal	A	1	0,15	0,11±0,0234	0,30	0,29±0,0083
		2	0,13		0,29	
		3	0,11		0,30	
		4	0,11		0,28	
	B	1	0,09		0,28	
		2	0,09		0,29	
		3	0,08		0,28	
		4	0,08		0,28	

Table 2 The vertebral waist width and zygapophysial length indices as calculated for the last four presacral and the first four postsacral vertebrae of three specimens of *M. capensis*

Region	Speci- men	Verte- brae	WW/BW	WW/BW Mean±*SD*	ZL/BW	ZL/BW Mean±*SD*
Presacral	A	23	0,16	0,18 ± 0,0129	0,44	0,37 ± 0,0332
		24	0,17		0,42	
		25	0,18		0,41	
		26	0,19		0,37	
	B	23	0,17		0,39	
		24	0,18		0,37	
		25	0,19		0,36	
		26	0,20		0,34	
	C	23	0,16		0,36	
		24	0,16		0,35	
		25	0,18		0,34	
		26	0,19		0,33	
Postsacral	A	1	0,16	0,14 ± 0,0179	0,29	0,29 ± 0,0154
		2	0,14		0,29	
		3	0,10		0,32	
		4	0,11		0,28	
	B	1	0,16		0,29	
		2	0,16		0,29	
		3	0,14		0,32	
		4	0,14		0,28	
	C	1	0,14		0,26	
		2	0,14		0,27	
		3	0,13		0,29	
		4	0,13		0,30	

A. plumbeus progresses forward mainly by means of lateral undulations whereby it throws its body into a series of horizontal travelling waves which sweep in a cranio-caudal direction. Each wave comprises a crest, an anterior arm and a posterior arm. This forms the basic unit of propulsion as the force generated in each wave crest results in the thrust of the arms against the

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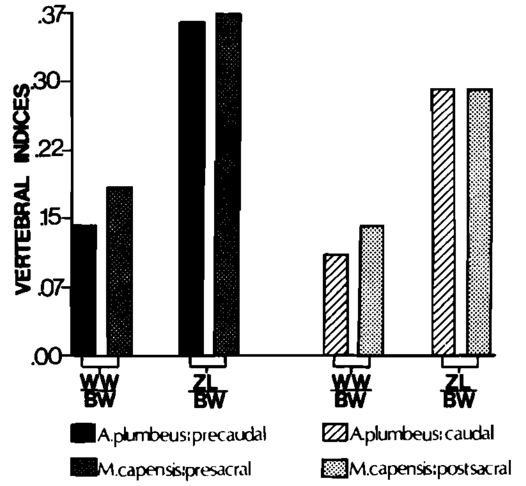

Figure 4 A comparison of the mean vertebral waist width and zygapophysial length indices in the pelvic regions of *A. plumbeus* (*n* = 8) and *M. capensis* (*n* = 12).

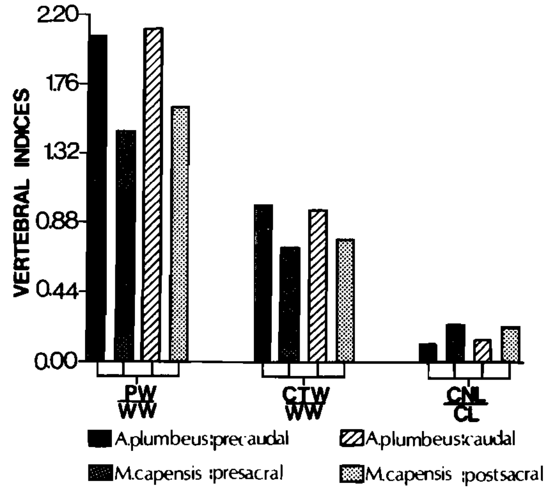

Figure 5 A comparison of the mean prezygapophysial width, cotyle width and condyle length indices in the pelvic regions of *A. plumbeus* (*n* = 8) and *M. capensis* (*n* = 12).

Table 3 The mean prezygapophysial width, cotyle width and condyle length indices as calculated for the last four precaudal and the first four caudal vertebrae of two specimens of *A. plumbeus*

	PW/WW	CTW/WW	CNI/WW	
Region	Mean ± *SD*	Mean ± *SD*	Mean ± *SD*	*n*
Precaudal	2,06 ± 0,1825	0,99 ± 0,1466	0,12 ± 0,0193	8
Caudal	2,11 ± 0,4110	0,96 ± 0,0647	0,15 ± 0,0482	

Table 4 The mean prezygapophysial width, cotyle width and condyle length indices as calculated for the last four presacral and the first four postsacral vertebrae of three specimens of *M. capensis*

	PW/WW	CTW/WW	CNI/CL	
Region	Mean ± *SD*	Mean ± *SD*	Mean ± *SD*	*n*
Presacral	1,46 ± 0,0592	0,72 ± 0,1815	0,24 ± 0,0390	12
Postsacral	1,61 ± 0,2280	0,78 ± 0,1356	0,23 ± 0,0390	

substrate which ultimately propels the body forward. The areas where the arms exert pressure on the substrate are referred to as points d'appui and the forces operating at these points (Figure 6) have been documented by Hildebrand (1974). For efficient lateral undulation it is essential to have a strong, flexible axial skeleton which facilitates the formation of travelling waves that effectively generate and transmit propulsive forces. The vertebrae of *A. plumbeus* are subjected to three major forces during locomotion. Firstly, there are the compressive forces generated when the epaxial muscles contract during wave formation. Secondly, there are the forces generated by the thrust of the wave arms against the points d'appui which reach the vertebrae via the ribs. Thirdly there are the compressive forces arising from the drilling of the body through the soil. To alleviate the impact of these forces, the vertebrae of *A. plumbeus* are relatively broad so that the forces are distributed over a relatively large bone area. The same holds true for the vertebral condyles and cotyles which are broad ellipses (Figure 5). The vertebrae of *A. plumbeus* are relatively short implying that a fairly large number can be accommodated per unit length. This means an increase in the number of joints per unit length and thus an increase in flexibility. Flexibility is further enhanced by the relatively shallow ball-and-socket joints formed between the short, broad condyles and shallow cotyles (Figure 5) which presumably allows them greater freedom of lateral movement. Dislocation of these joints is prevented by the tremendous hypertrophy of the epaxial muscles which hold the vertebrae in position (pers. obs.).

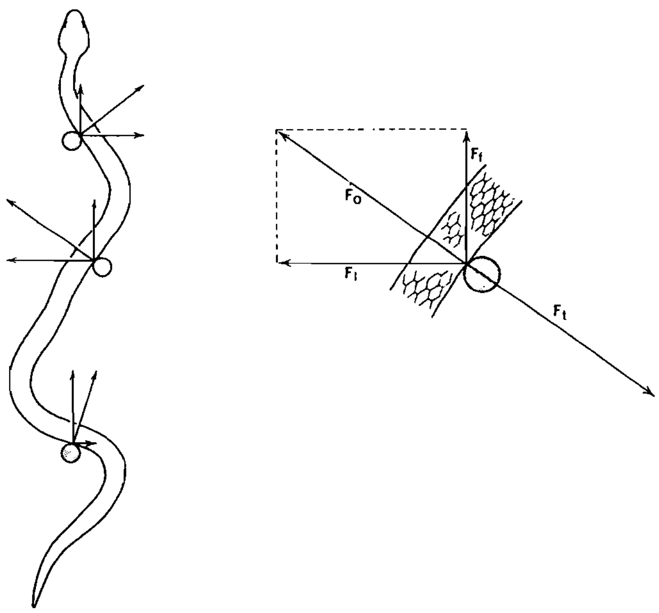

Figure 6 Diagram showing all the forces operating at a point d'appui. F_f : Component of F_o in the direction of motion of the lizard as a whole. F_t : Thrust of lizard against object. F_l : Lateral component of F_o. F_o : Reaction of object on lizard.

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Furthermore, the zygapophyses are broad and flare far laterally (Figure 5) thus facilitating firm but movable zygapophysial articulation.

From his analysis of vertebral form in snakes Johnson (1955) concluded that the anatomical features which are most subject to adaptive modification were zygapophysial length, body width and length, and condyle size. Arboreal snakes showed the highest degree of vertebral modification while the burrowing snakes in general had a reduced vertebral column. He found that in the vast majority of snakes, vertebral form did not reflect gross mode-of-life.

M. capensis dwells on the surface of the soil and its body is not subjected to the same environmental stresses as that of *A. plumbeus*. *M. capensis* is, however, forced to raise its trunk above the substrate during locomotion whereas the body of *A. plumbeus* is completely supported by the substrate. The sacrum, by its articulation with the ilium, serves as the posterior link between the axial and appendicular skeletons. This function obviously induces a certain amount of stress on the sacrum, especially during locomotion, and it can be expected that both the pre- and postsacral vertebrae close to it will be burdened with a substantial share of this stress.

To cope with the stress the vertebrae have undergone certain structural modifications the significance of which will perhaps be better understood if the forces inducing the stress are first mentioned. There are four major types of forces acting on the vertebral column of *M. capensis* during locomotion. Firstly, there is the force of gravity experienced when the body is suspended between the fore- and hindlimbs. Secondly, there are the compressive forces arising from the contraction of the epaxial musculature which bend the vertebral column. Thirdly, there are the distortional forces resulting from the alternate lifting of the hindlimbs and the backward and forward oscillation of the pelvic girdle. Finally, there is the force transmitted into the vertebral column when a hindlimb strikes the ground. The structure of the vertebral column in this region is thus a compromise between flexibility and strength. The former is important in facilitating a greater stride length while the latter enables the vertebral column to cope with the above-mentioned forces.

Flexibility of the vertebral column in the pelvic region of *M. capensis* is enhanced by an increase in the number of vertebrae, and therefore joints per unit length brought about by the decrease in length of pre- and postsacral vertebrae towards the sacrum. A strengthening of the vertebral column is reflected firstly by the rapid increase in width of successive vertebrae towards the sacrum shown by both the pre- and postsacral vertebrae (Figure 3) and secondly, by the deep ball-and-socket joints formed between their relatively long condyles and deep cotyles (Figure 5). The former adaptation implies that the impact of the compressive force and the impact of the force generated when the hindlimbs strike the ground is absorbed by a larger bone area which helps to reduce their effect. Furthermore, the fact that the vertebrae in *M. capensis* are wider than those of *A. plumbeus* (Figure 4) probably points to a higher stress level experienced on the vertebrae.

Troxell (1924) suggests that the increase in size of the pre- and postsacral vertebrae toward the pelvis of crocodiles enables them to cope with the propulsive forces generated by the lashing of the tail during swimming as well as those resulting from the resistance offered by the water to the animal's progression. Both these forces increase in magnitude towards the sacrum. Etheridge (1967) examined the tails of a number of limbed lizards and also demonstrated that the proximal postsacral vertebrae are short and broad compared with the distal ones which are long and narrow.

The functional significance of vertebral structure in the pelvic region of *M. capensis* and *A. plumbeus* can thus be explained with reference to their respective modes of locomotion. The higher degree of flexibility shown by the pelvic region of *A. plumbeus* compared with that of *M. capensis* can be attributed to the fact that its mode of locomotion is completely axial. The larger bone area and firmer articulation of the vertebrae in *M. capensis*, on the other hand, suggest that its pelvic region experiences more stressful forces during locomotion.

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