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A quantitative analysis of the marked asymmetry existing between some muscle partners in the pelvic girdle of southern African species of the genus *Mabuya* (Reptilia: Scincidae)

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The pelvic girdle musculature of eleven of the eighteen southern African *Mabuya* species described by Branch (1988) was examined, using differences in mass to emphasize the marked asymmetry existing between partners of certain muscle pairs. The lighter muscles expressed as indices of their heavier partners gave a mean value of 0,38 ($n = 27$) with a range of 0,11 to 0,75. The mean value obtained for a symmetrical control pair was 0,95 ($n = 27$) with a range of 0,90 to 0,99. The arrangement of the asymmetric pairs was the same for all the species, irrespective of sex. The partners of a pair differed in size and the manner in which they originated on the pelvic girdle but showed agreement as far as their insertion on the head of the femur was concerned.

Die bekkenwykspiere van elf van die agtien Suider-Afrikaanse *Mabuya* spesies wat deur Branch (1988) beskryf is, is ondersoek. Verskille in massa is gebruik om die duidelike asimmetrie tussen paargenote van sekere spiere aan te dui. Die ligter spiere uitgedruk as indekse van hulle swaarder paargenote het gemiddelde waardes van 0,38 ($n = 27$) gelewer, met 'n meetgrens van 0,11 tot 0,75. Die gemiddelde waarde verkry vir 'n simmetriese kontrole-paar was 0,95 ($n = 27$) met 'n meetgrens van 0,90 tot 0,99. Die rangskikking van die asimmetriese pare was dieselfde vir al die spesies, ongeag die geslag. Die paargenote het verskil ten opsigte van hulle grootte en die wyse waarop hulle op die bekkengordel ontspring het, maar het ooreengestem sover dit hulle aanhegting aan die kop van die femur betref het.

The earliest documentation of the existence of marked asymmetry between certain muscle pairs of the lacertilian pelvic girdle appears to be that of Sukhanov (1957)*. *(This paper was not seen in its entirety as the author could only obtain a summary of it.) He found it to exist in genera of the families Gekkonidae, Lacertidae and Scincidae but not in genera of the families Agamidae and Iguanidae. A detailed description of the asymmetric condition in *Mabuya capensis* was given by Heideman (1987). Tiedeman & Tiedeman (1975) examined the pelvic girdle musculature of *Mabuya quinquetaeniata margaritifer* but did not mention anything about the existence of muscle asymmetry. This prompted the author to check and quantify its existence in this and other southern African species of the genus. The system used to identify and group the individual muscle pairs was that of Romer (1942).

Ten freshly collected specimens now in the collection of the University of Namibia and 17 preserved specimens obtained from the National Museum Bloemfontein, the Transvaal Museum and the Windhoek State Museum, were examined. In seven of the 11 species both males and females were dissected, in three only females were dissected and in the remaining one only a male specimen was examined. A list of all the voucher specimens is provided in Appendix 1. Dissections were carried out with the aid of a Vickers stereomicroscope using an Intralux 5000 Volpi cold light to prevent the muscles from drying out. The method for staining muscle fibres devised by Bock & Schear (1972) proved useful in the identification of individual muscles. The muscles were removed by cutting them loose at their origins on the pelvic girdle and at the point where they merged with their inserting tendons. In the fresh specimens the muscles were weighed immediately after their removal while those from the preserved specimens were first blotted with Whatman filter paper until no moisture showed on the paper and then weighed. Weighing was done with a Sartorius analytical balance with a lower limit of 0,1 mg. In the case of *Mabuya capensis* and *Mabuya varia* both viviparous and oviparous specimens were examined. The asymmetric condition in the oviparous specimens was checked without weighing the individual muscles.

The species all showed a pattern of muscle asymmetry similar to that described for *M. capensis* by Heideman (1987). In both sexes both the weakly and the well-developed muscles of each asymmetric pair originated in the same manner on the pelvic girdle. This was also the case in the oviparous *Mabuya capensis* and *Mabuya varia* specimens. The indices calculated from the mass values obtained for each asymmetric pair are given in Table 1. In some specimens the mass of certain muscles could not be

Table 1 Mean mass indicies of some of the pelvic girdle muscle pairs of eleven *Mabuya* species reflecting the marked asymmetry existing between certain pairs. In each case the lighter muscle was expressed as an index of its heavier partner. The following abbreviations are used in the table, M. pubo-ischio-femoralis internus II (M.p.i.f.i. II), M. pubo-ischio-femoralis internus IIIa (M.p.i.f.i. IIIa), M. pubo-ischio-femoralis internus IIIb (M.p.i.f.i. IIIb), M. pubo-ischio-femoralis externus IIIa (M.p.i.f.e. IIIa) and M. pubo-ischio-femoralis externus IV (M.p.i.f.e. IV)

Species	Sex	*n*	M.p.i.f.i.II Mean ± *SD*	M.p.i.f.i.IIIa Mean ± *SD*	M.p.i.f.i.IIIb Mean ± *SD*	M.p.i.f.e.IIIa Mean ± *SD*	M.p.i.f.e.IV Mean ± *SD*
Mabuya acutilabris	M	1	0,93	0,13	0,33	0,11	0,40
	F	1	0,90	0,15	0,20	0,13	0,52
Mabuya binotata	M	1	0,97	0,35	0,37	0,26	0,36
	F	1	0,98	0,19	0,39	0,34	0,36
Mabuya capensis	M	3	0,95	0,26	0,25	0,45	0,53
			± 0,004	± 0,037	± 0,025	± 0,160	± 0,037
	F	2	0,97	0,26	0,17	0,36	0,51
			± 0,015	± 0,125	± 0,105	± 0,070	± 0,040
Mabuya hoeschi	M	1	0,93	0,20	0,40	0,61	0,74
Mabuya occidentalis	F	1	0,99	0,16	0,37	0,46	0,64
Mabuya quinquetaeniata margaritifer	M	1	0,96	0,31	0,65	0,28	0,30
	F	1	0,95	0,36	0,75	0,36	0,31
*Mabuya spilogaster**	M	4	0,96	0,20	0,34	0,29	0,61
			± 0,028	± 0,075	± 0,100	± 0,028	± 0,045
	F	3	0,96	0,21	0,37	0,25	0,69
			± 0,017	± 0,029	± 0,117	± 0,107	± 0,107
*Mabuya striata**	M	2	0,91	0,29	0,44	0,50	0,60
			± 0,005	± 0,250	± 0,060	± 0,015	± 0,135
	F	1	0,95	0,11	0,38	0,59	0,68
Mabuya s. sulcata	M	1	0,98	0,16	0,19	0,44	0,51
	F	1	0,92	0,23	0,47	0,56	0,75
Mabuya varia	F	1	0,93	0,47	0,40	0,55	0,48
Mabuya v. variegata	F	1	0,90	-	-	-	0,54

* Freshly collected specimens.

determined as it fell outside the lower limit of the balance used. These are indicated by a dash in the table. No consistent differences were found between the male and female indices. The marked asymmetry was found in the M. pubo-ischio-femoralis internus IIIa, the M. pubo-ischio-femoralis internus IIIb, the M. pubo-ischio-femoralis externus IIIa and the M. pubo-ischio-femoralis externus IV. The first two belong to the dorsal group and the last two to the ventral group of pelvic girdle muscles (Romer 1942). The M. pubo-ischio-femoralis internus II of the dorsal group served as the symmetrical control pair in each specimen. The asymmetric pairs were arranged sensibly with the number of weakly and of well-developed muscles originating on the right side of the pelvic girdle equalling the number of weakly and of well-developed ones originating on the left side.

The table of data confirms the existence of marked asymmetry between partners of certain pelvic girdle muscle pairs in southern African species of the genus *Mabuya* which resulted in a complex, intertwined muscle pattern. However, there seems to be a number of differences between the findings of this investigation and those of Sukhanov (1957) whose survey of the pelvic girdle musculature of five lacertilian families included a *Mabuya** species. *(Specific name and locality not given in summary of paper at author's disposal.) He found the M. pubo-ischio-femoralis internus of the latter to comprise four parts whereas in this study the M. pubo-ischio-femoralis internus was found to have only three parts with the third part further subdivided into three parts. The M. pubo-ischio-femoralis externus had four parts in the southern African species with the third part further subdivided into two parts. Sukhanov reports only three parts for this muscle in his article. The condition found in the southern African species coincides with that described for *M. quinquetaeniata margaritifer* by Tiedeman & Tiedeman (1975). Marked asymmetry was found between certain pairs of both the internal and external M. pubo-ischio-femoralis but Sukhanov mentions asymmetry in the internal M. pubo-ischio-femoralis only. He also refers to the asymmetric pairs differing in their manner of insertion while the asymmetric pairs in the southern African species differed only in the way they originated on the pelvic girdle but coincided with respect to their manner of insertion on the head of the femur. These are major differences and reasonable explanations for their existence are not easily put fowward.

An obvious question regarding the asymmetric muscle condition in some lacertilian pelvic girdles would be of

what functional value it is to these lizards. Sukhanov (1957) mentioned that although the function of the muscle intertwining is not clear, it may serve as a means of reinforcing them. However, he did not elaborate on the possible reasons for this type of complex reinforcement. He also suggested that the Agamidae and Iguanidae with their simple muscle pattern may form an evolutionary line separate from the Gekkonidae, Lacertidae and Scincidae with their complex muscle pattern. His hypothesis is, however, based on the conditions found in a small number of representatives of each family which permits only tentative conclusions to be made. The asymmetric condition may allow a wider range of movements of the hindlimbs but exactly what these are and why they are required by these lizards is not clear, there not being any obvious difference between their mode of locomotion and that of the families with the symmetrical condition. A detailed study of the locomotor process and its underlying muscle mechanics in the two groups could therefore prove useful in casting light on the reasons for the difference in muscle pattern between them. The possibility of the condition being a proto-adaptation to the reduction and eventual loss of the pelvic girdle and hindlimbs, a phenomenon which is quite common in the Scincidae, is also refuted by its occurrence in the Gekkonidae and Lacertidae for which the phenomenon has not as yet been reported. The difficulty in explaining the functional significance of the condition could perhaps be resolved by accepting that it does not represent a specific adaptation but simply the result of a selectively neutral mutation(s) which became fixed in the ancestral group of the Gekkonidae, Lacertidae and Scincidae as a result of stochastic processes such as random genetic drift and inbreeding.

To conclude, the seemingly wide occurrence of the asymmetric condition does suggest that lacertilian ancestral stock may have diverged into separate evolutionary lines based on the structure of the pelvic girdle musculature. As for explaining how the peculiar condition could have arisen, the explanation referring to selective neutrality seems to be the most plausible of those put forward.

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Appendix 1 List of voucher specimens dissected during the investigation. The following abbreviations are used in the list: NMB (National Museum, Bloemfontein), SMWN or SM-R (State Museum, Windhoek), TM (Transvaal Museum, Pretoria) and UNB (University of Namibia, Windhoek)

Species	Reference number	Sex	Locality
M. acutilabris	SMWN 5846	M	Otjovasondo (Outjo)
	SMWN 5851	F	Orupembe (Kaokoland)
M. binotata	TM 63139	M	Kaokoland
	TM 52818	F	Spaarwater (Damaraland)
M. capensis	SMWN 1961	M	Alte Feste (Windhoek)
	NMB 5559	M	Florisbad (Brandfort)
	UNB 8856	M	Augustineum (Windhoek)
	SMWN 6020	F	Namutoni (Etosha)
	NMB 5200	F	Magdalen (Bloemfontein)
	TM 47176*	F	Pretoria
M. hoeschi	SMWN 3209	M	Swakopmund
M. occidentalis	SMWN 5651	F	Damaraland
M. q. margaritifer	TM 29188	M	unknown
	TM 29185	F	unknown
M. spilogaster	UNB 48856	M	Windhoek
	UNB 58856	M	Windhoek
	UNB 88856	M	Windhoek
	UNB 98856	M	Windhoek
	UNB 128856	F	Windhoek
	UNB 78856	F	Windhoek
	UNB 68856	F	Windhoek
M. striata	UNB 18856	M	Koës
	UMB 38856	M	Koës
	UNB 288	F	Koës
M. s. sulcata	SM-R 4699	M	Windhoek
	TM 32425	F	Otjinungua (Kaokoland)
M. varia	TM 27536	F	unknown
	TM 67117*	F	Gazankulu
M. v. variegata	SMWN 3225b	F	Kuiseb River

* Oviparous specimens in which the asymmetric condition was checked without the muscle pairs being weighed.