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MORPHOMETRIC ANALYSIS OF *MANIS TRICUSPIS* (PHOLIDOTA-MAMMALIA) FROM SOUTH-WESTERN NIGERIA.

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ABSTRACT

Lengths of the head, body and other body parts of live-trapped white-bellied pangolins, *Manis tricuspis* (Rafinesque) from the forests in south-western Nigeria, were measured and the age-class and sex-related differences in dimensions analysed. Relative growth between head and body length (HBL) or total body length (TBL) as the reference dimension (X), and other body parts (Y) was studied using ratios, and allometric equations of the form, $Y = bX^a$. Age-classes differed in all body dimensions and some morphometric ratios. Six growth fields were identified some of which are related. With increase in HBL, growth of head dimensions decreased (negative allometry, $a < 1$), locomotor structures, the tongue and gastro-intestinal length maintained a constant growth ratio (isometry, $a = 1$) and the trunk and trunk scale grew at a faster rate (positive allometry, $a > 1$). An anterior-posterior growth gradient from the head to the tail was evident.

KEYWORDS: Body parts, growth field/gradient, *Manis tricuspis*, morphometry, relative growth.

INTRODUCTION

The white-bellied pangolin, *Manis tricuspis* (Rafinesque) is one of the three representatives of the Manidae (Pholidota- Mammalia) in West Africa (Cansdale, 1947; Booth, 1960). It is semi-arboreal and more widely distributed than the other species, *M. tetradactyla and M. gigantea* (Sodeinde and Adedipe, 1994). White-bellied pangolins are highly specialised with their entire structure being adapted to the requirements of a diet of soil-inhabiting insects and to arboreal life (Cansdale, 1947; Hayman, 1954; Doran and Allbrook, 1973).

Pangolins are covered by tough, spirally arranged overlapping scales which protect the whole dorsum as well as the outside of the legs and both surfaces of the broad flattened tail. The head is earless with tiny thick-lidded eyes to ward off ants attacking the head (Hayman, 1954). The manus and pes have large powerful recurved claws for breaking open ant and termite nests and the long cylindrical tongue is used in probing holes and collecting crawling insects (Hayman, 1954; Sikes, 1966; Doran and Allbrook, 1973).
The muscles controlling the tongue are greatly developed and extend well back into the body cavity. The long truly prehensile tail of *M. tricuspis* is used in locomotion and feeding (Cansdale, 1947; Kingdon, 1971) and is about 3/5th of the total body length (Sikes, 1966).

Despite these specialised adaptations, body growth patterns in pangolins and their functional significance given their form have not received commensurate attention. Functional and adaptive significance of relative growth have been studied in other relatively less specialised species (Gould, 1966; Goldstein, 1972; Dodson, 1975; Werns and Howland, 1976; Montague, 1984; Tanaka, 1984; Swartz, 1989). Pagés (1970) observed that adaptations involving body weight, tail proportions and the forms of body extremities exist among arboreal and ground-living pangolins but did not investigate the relationships.
The objective of this study was to study age-sex related differences in size and the growth relationships between the body parts of white-bellied pangolins procured from the forests of south-western Nigeria. The relationship between growth patterns and function of body parts was explored.

MATERIALS AND METHODS

The pangolins analysed were collected

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discontinuously between 1989 and 1997 from the forests in south-western Nigeria located at Agọ-Iwọye, Omo via Ijebu-Ode, Ejinrin and Ondọ. Each pangolin was weighed to the nearest 0.1g on a portable scale and the body dimensions were measured to the nearest mm using a tape rule.

Measurements taken for morphometric analysis (Tables 1 & 4) include: (1) the body: - total body length (TBL), head and body length (HBL), snout-cranial platform or head length (HEL), girth at mid-trunk region (MTG) and tail girth at the junction with the trunk (TAG); (2) the limbs: - lengths of the middle and distal segments; (3) trunk scale: - length of scales removed from the mid-dorsum (TSL); (4) organs: - lengths of the gastro-intestinal tract segments and of the oral and xiphisternal portions of the tongue complex. The xiphisternal portion consists of muscular sheaths surrounding the tongue, xiphoid extensions and specialised muscles.

Simple ratios between some body parts were calculated to show growth relationships. Relative growth between the head and body (X) as the reference dimension, and other body parts (Y); and between total body length (X) and body parts along the anterior-posterior axis of the body (Y) was examined. For these analyses log-transformed morphometric data were employed in deriving Bartlett's best-fit allometric equations of the form $Y = bX^a$, where a, the allometric coefficient, is the ratio of the geometric growth rates of X and Y (Simpson *et al.*, 1960).
The HBL and TBL satisfied the criteria for selecting X (Dodson, 1975). These criteria are that X should: (i) correspond to some intuitive concept of size, (ii) be the measurement with the greatest absolute magnitude or range of size and (iii) constrain a significant number of allometric coefficients to fall on both sides of 1.00.

To determine whether X and Y grow isometrically ($a = 1$) maintaining a constant ratio of sizes, or allometrically ($a \neq 1$) with a constantly changing ratio, the null hypothesis

Table 1. Means (±SE) and ranges of body weight (kg) and dimensions (mm) of external body structures of *M. tricuspis* age classes.

Body dimension	Juveniles (n = 2)	Subadults (n = 8)	Adults (n = 11)	Range
Body weight (BW)	0.13±0.01[c]	0.97±0.14[b]	1.36±0.16[a]	0.12-1.61
Total body length (TBL)	351±21[b]	771±40[a]	963±11[a]	330-984
Head & body length (HBL)	175±5[c]	319±18[b]	428±9[a]	170-445
Trunk length (TRL)	111±3[c]	225±14[b]	338±9[a]	108-352
Trunk girth (MTG)	78±1[c]	127±3[b]	165±20[a]	77-204
Tail length (TAL)	177±17[c]	453±22[b]	535±14[a]	160-560
Tail girth (TAG)	63±3[c]	142±6[b]	155±10[a]	60-170
Trunk scale length (TSL)	8±0[c]	34±2[b]	44±3[a]	8-50
Head length (HEL)	64±2[b]	93±5[a]	91±3[a]	62-110
Head width (HEW)	46±3[b]	62±2[a]	64±4[a]	44-70
Interocular distance(HIO)	30±0[b]	40±2[a]	44±1[a]	30-49
Hand width (HAW)	13±2[c]	26±1[b]	32±1[a]	11-35
Foot width (FOW)	14±2[c]	30±1[b]	37±4[a]	12-45
Radius/Ulna length (RUL)	23±1[c]	54±2[b]	62±5[a]	22-68
Tibia/fibula length (TFL)	32±2[b]	74±6[a]	83±5[a]	30-90
Ear slit length (ESL)	3.1±0.1[c]	6.5±0.6[ab]	7.8±0.4[a]	3.0-8.5

Means along each row with the same superscript are not different ($P > 0.05$)

Table 2. Mean quotients (± SE) some related body parameters of *M. tricuspis* age classes.

Morphometric ratio	Juveniles	Subadults	Adults[1]
Head length: TBL	0.18 ± 0.01^{a}	0.12 ± 0.01^{b}	0.09 ± 0.01^{c} [2]
Head length: TRL	0.57 ± 0.01^{a}	0.41 ± 0.01^{b}	0.27 ± 0.01^{c}
Head length: HEW	1.40 ± 0.01^{a}	1.51 ± 0.12^{a}	1.42 ± 0.11^{a}
Trunk length: MTG	1.43 ± 0.03^{c}	1.77 ± 0.09^{b}	2.11 ± 0.26^{a}
Tail length: HBL	1.02 ± 0.02^{c}	1.44 ± 0.04^{a}	1.35 ± 0.07^{b}
Tail girth: TAL	0.36 ± 0.02^{a}	0.31 ± 0.01^{b}	0.29 ± 0.01^{c}
Foot width: HAW	1.12 ± 0.03^{a}	1.12 ± 0.02^{a}	1.14 ± 0.05^{a}

[1] Number for each age-class is the same as in Table1
[2] Means along each row with the same superscript are not different ($P > 0.05$)

of no significant difference between each allometric coefficient and the isometric constant, 1, was tested. This test employs a Student's t-test criterion (Steel and Torrie, 1980). Body parts in the same growth field (growing at the same proportionate rate) were determined by comparing the 95% confidence intervals on allometric coefficients.

Pair-wise and multiple comparisons between pangolin sexes and age-classes were by means of t-tests and one-way analysis of variance. Means for multiple comparisons were separated using Duncan's New Multiple Range Test. Tests were conducted at the 5% significance level.

RESULTS

Morphometry

Body measurement by age-classes

Dimensions of body structures are shown in Table 1. Adults had higher values than sub-adults in ten of the 16 dimensions measured. These include HBL, TAL and TSL. The age-classes differed in only five of the seven quotients (Table 2). Juveniles had higher HEL: TBL, HEL: TRL and TAG: TAL quotients than sub-adults whose values were higher than of adults.

Dimensions of the gastro-intestinal segments

Lengths of the segments of the gastro-intestinal tract are shown in Table 3. The small intestine made up the greatest proportion of the GIT length and the stomach, the shortest although its luminar diameter was about six-fold that of the intestine. Quotients of the parts relative to HBL did not differ between age-classes.

Dimensions by gender

Adult males had longer heads than females but did not differ from females in dimensions of other structures and their morphometric ratios (Table 4).

Relative growth

The range of HBL was wide (Table1). The allometric coefficients ranged between 0.35 and 1.75 and the negative ($a < 1.0$) and positive coefficients ($a > 1.0$) were about equally distributed on either side of the isometric ones ($a = 1$) (Table 5A).
Six growth fields were delineated based on the grouping of allometric coefficients according to confidence intervals (Table 5A). These consisted of two from the negatively allometric, two from the isometric and two from the positively allometric with some overlaps between fields. All head dimensions showed negative allometric growth and growth of the tongue proper was slightly negatively allometric. The xiphisternal portion of the tongue, limb and tail elements all showed isometric growth. Positive allometric growth characterised the trunk and trunk scales.

Trunk girth (Group 3, Table 5A) was also related to TAG, HAW, TFL and TBL in Group 4, and tail length was related to all attributes in Group 4. Relative to total body length (TBL), growth of HEL and HBL was negatively allometric (Table 5B), TAG and TRL were isometric and TAL and body weight showed positive allometric growth.

Table 3. Mean (±SE) body weight (kg), dimensions of body parts (mm) and morphometric quotients of mature male and female *M. tricuspis*.

Attribute	Male (n= 9)	Female (n= 8)	Range
Body weight	1.27 ± 0.06	1.02 ± 0.17	0.44 - 1.61
Total body length	807 ± 33	804 ± 58	669 - 984
Head & body length	392 ± 28	337 ± 27	275 - 445
Trunk length	289 ± 32	250 ± 27	188 - 352
Trunk girth	131 ± 4	144 ± 13	115 - 204
Tail girth	505 ± 8	468 ± 30	392 - 560
Trunk scale length	37 ± 3	38 ± 4	30 - 50
Head length	103 ± 5	87 ± 5*	82 - 110
Head width	61 ± 4	63 ± 2	53 – 70
Interocular distance	44 ± 2	40 ± 2	35 – 49
Hand width	29 ± 2	28 ± 2	22 – 35
Foot width	32 ± 1	32 ± 3	25 – 45
Radius/Ulna length	60 ± 3	55 ± 3	48 – 68
Tibia/fibula length	78 ± 3	76 ± 5	57 – 90
HEL:TBL	0.12 ± 0.01	0.11 ± 0.01	0.09 – 0.13
HEL:TRL	0.37 ± 0.05	0.36 ± 0.03	0.25 – 0.44
HEL:HEW	1.68 ± 0.20	1.38 ± 0.07	1.20 – 2.08
TRL:MTG	2.19 ± 0.18	1.73 ± 0.09	1.50 – 2.55
TAL:HBL	1.41 ± 0.03	1.42 ± 0.05	1.28 – 1.56
TAG:TAL	0.30 ± 0.02	0.31 ± 0.01	0.28 – 0.34
FOW:HAW	1.20 ± 0.03	1.14 ± 0.04	1.06 – 1.29

* significantly different ($P < 0.05$)

DISCUSSION

Morphometry

The ranges of body dimensions agree with earlier records of pangolins in this region (Rahm, 1956; Kingdon, 1971). Rahm (1956) reported a range of 300 - 410mm for HBL, 360 600mm for TAL and average trunk scale and intestinal lengths of 40mm and 2000mm respectively for sexually mature white-bellied pangolins. The general lack of disparity between the body dimensions of males and females implies that the species does not show sexual size dimorphism. Wittenberger (1981) observed that size dimorphism favouring males is known to evolve when larger size enhances male fighting prowess under conditions of intense intra-sexual selection. Although there is evidence of territoriality, such intense selection does not occur in *M. tricuspis* (Pagés, 1970).

Relative growth

Series of morphometric quotients give indication of proportional changes that occur in growing (different-sized) individuals of a species. A single allometric coefficient, however, replaces these series of ratios in conveying the sense of the change of a relationship during growth (Dodson, 1975). Quotients that do not differ between age-classes indicate relatively constant growth rate between the two parts. Quotients that increase with relative age indicate faster growth rate of the body part being compared to HBL (or the reference dimension) and those that decrease, show relatively slower growth

Table 4. Mean lengths and proportions (±SE mm) of the gastrointestinal (GIT) parts and tongue of *M. tricuspis* age-classes. Pooled proportions are shown in parentheses.

Attribute	Juvenile[a]	Subadult	Adult	Range
GIT length (GITL)	725	2278±60	2329±129	725-2495
GITL:TBL	2.20	2.90±0.09	2.58±0.05	(2.73)
GITL:HBL	4.26	7.27±0.49	5.45±0.41	(6.42)
Oesophagus Length (OEL)	55	105±5	130±8	55 – 145
OEL:GITL	0.08	0.05	0.06	(0.06)
Stomach length(STL)	30	72±5	77±2	30 – 90
STL:GITL	0.04	0.03	0.03	(0.03)
Small intestine Length (SIL)	390	1275±101	1233±39	390 – 1675
SIL:GITL	0.53	0.56	0.54	(0.55)
Large intestine Length (LIL)	200	616±85	875±36	200 – 921
LIL:GITL	0.28	0.30	0.31	(0.30)
Rectum Length (REL)	50	148±7	141±13	50 – 170
REL:GITL	0.07	0.06	0.06	(0.06)
Tongue length (oral)	41	125±8	126±17	41 – 150
Tongue length (xiphisternal)	67	148±9	194±8	67 – 210

[a] only the innards of one juvenile was available.

rate. These are synonymous to isometry, positive allometry and negative allometry respectively. Morphometric ratios of body parts relative to HBL for the three age-classes showed the same growth trend as indicated by the allometric coefficients.

Body parts showed an anterior-posterior growth gradient along the axis of the pangolin body from the head (negative) to the trunk (isometric) and to the tail (positive). The negative allometric growth that characterised the head of *M. tricuspis* does not indicate regression in head size but rather a slowing down in rate of growth of the head or a cessation of growth while other parts continued to grow. Increase in gape is associated with head enlargement in animals with jaws and is important in enabling animals capture bigger preys, as such animals grow bigger. Being edentate there is no compelling reason for progressive skull enlargement in pangolins.

Doran and Allbrook (1973) reported that jaw movements in *M. tricuspis* are limited and that masticatory muscles are almost totally absent. In contrast, they found that the tongue and the structures needed for its effective function as a food-gathering organ are well developed. The slightly allometric growth of the xiphisternum contrasts with the negative allometric growth of the tongue proper. This is an indication that the xiphisternal portion becomes relatively bigger during ontogeny as confirmed by their absolute sizes. Whereas sub-adults and adults had tongues that were about equal in length, the xiphisternum was much longer in adults. The intricately arranged muscles controlling the extension and retraction of the tongue are located in the xiphisternum (Sikes, 1966; Doran and Allbrook, 1973).

All locomotor structures (RUL, FOW, TFL, TAG, TAL) showed isometric growth with total body length and trunk girth. This close relationship we believe reflects the need for the structures to grow in direct proportion to body length and girth to ensure that adequate support is given the body at all growth stages. Reciprocals of the mean TAG: TAL quotients for the age-classes (2.8, 3.2, and 3.4 for juveniles, sub-adults and adults) show that the tail elongates faster than it thickens at the base as the animal gets bigger. This would

Table 5. Constants and coefficients of determination of the allometric growth relationship, $Y=bX^a$ between head and body length or total body length (X) and other attributes (Y) of *M. tricuspis* grouped according to growth relationships/affinities.

Attributes and groupings	b	a±95% C.I.	Sig.	R^2
A (Head and body length):				
1. Head width	1.80	0.35±0.23	***	0.56
Interocular distance	0.84	0.45±0.16	***	0.81
Head length	1.75	0.46±0.01	***	0.72
2. Tongue length (oral)	0.52	0.89±0.09	***	0.45
3. Trunk girth	0.90	0.77±0.27	ns	0.82
4. GIT length	6.59	0.99±0.66	ns	0.59
Tail girth	0.41	1.00±0.32	ns	0.85
Hand width	0.08	1.01±0.31	ns	0.86
Tibia/fibula length	0.19	1.02±0.45	ns	0.75
Foot width	0.08	1.04±0.30	ns	0.85
Radius/Ulna length	0.11	1.10±0.33	ns	0.86
Tongue length (xiphisternal)	0.37	1.07±0.26	ns	0.91
Total body length	1.52	1.12±0.50	ns	0.97
5. Tail length	0.60	1.23±0.29	ns	0.91
Trunk length	0.34	1.22±0.07	***	1.00
6. Trunk scale length	0.01	1.75±0.60	*	0.83
B (Total body length):				
1. Head length	1.82	0.42±0.17	***	0.78
2. Head and body length	0.78	0.86±0.12	*	0.98
Tail girth	0.24	0.92±0.16	ns	0.97
3. Trunk length	0.47	1.05±0.21	ns	0.95
Tail length	0.34	1.12±0.10	*	0.99
Body weight	0.03	2.36±0.46	***	0.97

Significance column indicates if **a** (allometry constant), is significantly different from 1.0 at $P<0.05$ (*) and $P<0.01$(***).

enhance the prehensibility of the tail which this pangolin uses as a climbing organ (Hildebrand, 1974).

Descriptions of movement in white-bellied pangolins do not indicate a disproportionate use of either the fore- or hind limbs compared with the tail. Sikes (1966) and Kingdon (1971) reported that the four limbs and tail are used to varying degrees depending on the type of movement. When climbing the tail takes the weight on lower branches as the clawed forelègs probe for a hold and the fore- and hind limbs are moved in pairs once one is found. When hunting on the ground the gait is quadrupedal while the gait is bipedal when ant and termite nests are being broken-open by the powerful claws on the forefeet. The hind legs bear the weight in the latter case and the tail is used as a counterpoise. The tail would be expected to show a stronger positive allometric growth in *M. tetradactyla, which* is a more arboreal species.

Although the trunk showed isometric growth, growth of trunk scales was positively allometric. The plausible explanation for this result is that trunk scales must grow faster than the trunk if they are to completely cover the areas they are to protect.

The white-bellied pangolin is insectivorous with the diet consisting of ants and termites (Cansdale 1947; Hayman 1954). The short length of the digestive tract and of segments of the tract relative to body length is characteristic of insectivores and other flesh-eaters (Hildebrand, 1974; Robbins, 1983). Young pangolins are precocial and start on a diet of insects early as they stay with the mother for only five months (Pagés, 1972). This might explain the lack of difference between age-classes in the relative proportions of the GIT segments, as the functional role of each part is likely to be similar among the age-classes.

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