MORPHOMETRICS OF THE PANCAKE TORTOISE
(MALACOCHERSUS TORNIERI) IN TANZANIA

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ABSTRACT
Observations were made of the morphometrics of captive pancake tortoise (Malacocephalus tornieri) in June 1995. Carapace length ranges for immature tortoises and adult males and females were 50-115, 123-160 and 129-171 mm respectively. The respective carapace widths were 45-90, 97-130, and 92-129 and 97-130 mm. Carapace height ranges were 15-29, 25-40 and 117-159 mm, respectively, while plastron length ranges were 45-110, 108-150 and 117-159 mm. The relationships between carapace length and width (males: \( y = 13.763 + 0.639x \); females: \( y = 17.302 + 0.639x \)) and height (males: \( y = 6.851 + 0.170x \); females: \( y = 17.274 + 0.170x \)) were isometric and sexually dimorphic in adults. The relationship between carapace length (x) and plastron length (y) was also isometric (\( y = 20.438 + 0.790x \)) but not sexually dimorphic in adults. The respective mass ranges for immature tortoises, adult males and females were 20-200, 200-500 and 240-580 g. The relationship between mass (x in g) and carapace length (y in mm) were strongly allometric (males: \( y = 32.026x^{0.261} \); females: \( y = 26.188x^{0.261} \)) and not sexually dimorphic in adults. That in immature tortoises was \( y = 16.482x^{0.363} \).

INTRODUCTION
Malacocephalus is a monotypic genus represented by a single species, the pancake tortoise (Malacocephalus tornieri) and endemic to East Africa. The species is known only from Tanzania and Kenya, with a patchy distribution extending from central Kenya to southern Tanzania (Loveridge & Williams 1957, Broadley 1989). In Tanzania, the species’ range extends eastward from south of Lake Victoria to central Tanzania and southward into Ruaha National Park (Loveridge & Williams 1957, Broadley 1989). The species’ preferred habitat is reported to be patches of small rocky outcrops and
kopjes primarily within the Somalia-Masai Floristic Region (White 1983), a largely semi desert area extending into northern and central Tanzania in the form of extensive Acacia-Commiphora deciduous bushland and thicket (Broadley & Howell 1991).

*Malacochersus tornieri* is unique among the testudinids in having a thin, dorso-ventrally flattened, flexible and fenestrated shell, that allows the plastron to move in and out as the animal breathes (Procter 1922, Loveridge & Williams 1957). The oddly shaped shell appears to be an adaptation for squeezing into and sheltering in narrow crevices found in the rocky outcrops and kopjes (Broadley 1989, Moll & Klemens 1996). Although juveniles of other testudinids possess similar fenestrations in their bones, they fill in as the tortoise grows, leaving the shell solid and inflexible; this apparently does not occur in *M. tornieri* (Loveridge & Williams 1957). Also, the reduction in body mass of the thin shell may facilitate escape from predation as the pancake tortoise appears to rely on speed to reach security of the crevice when threatened, rather than retreating into its shell as in other tortoises (Ireland & Gans 1972). Despite their bizarre shape, there is scanty information on the biology of *M. tornieri*. Klemens and Moll (1995) assessed the effects of commercial exploitation on *M. tornieri*, showing that trade was the only major threat to the survival of Tanzanian populations. Moll and Klemens (1996) examined the ecology of the species and tabulated measurements of size characters for Tanzanian populations. However, details on the morphometrics of the species are lacking. The present study examined the relationship between the various morphometric characters and whether these relationships were sexually dimorphic.

**METHODS**

Observations on captive pancake tortoises were made at three tortoise farms licensed by the Wildlife Division to breed animals for the export trade (Kabigumila 1995). A total of 213 animals comprising the breeding stock (n = 119) and immature tortoises (n = 92) were studied. All of the breeding stock had been captured from Kondoa in central Tanzania. For each tortoise, records were made of the midline straight-line lengths of the carapace and plastron, maximum width of the carapace and height, body mass and sex (Lambert 1993). Since the shell is very flexible, care was taken not to squeeze it when measuring the height of the carapace. Sex was determined using external characters: adult males could be identified by their longer and
thicker tails relative to the females and by their smaller overall size. Some individuals were sexually indeterminate. Most such tortoises were immature animals with a carapace length less than 90 mm (Moll & Klemens 1996).

Tortoises were categorised into adults and immature animals using carapace length as an index of age (Andrews 1983, Kabigumila 2000). Sexual maturity is reached at 90-100 mm and 130-140 mm in males and females, respectively (Moll & Klemens 1996).

Regression techniques were used to examine the relationships between the various morphometric characters. Analysis of covariance (F) was used to compare the regression lines, followed by the multiple comparisons test, q (Zar 1996). A Mann-Whitney U test (Zar 1996) was used to examine variation in morphometric characters between the sexes. Where appropriate, the 95% confidence limits for means are given. All probabilities are two-tailed and the results are recorded as significant at P<0.05.

**RESULTS**

**Body size**

Comparison of body size between immature tortoises (n = 94), adult males (n = 43) and females (n = 76) is shown in Table 1. The respective carapace length ranges were 50-115, 123-160 and 129-171 mm. Carapace width and height ranged from 45-130 mm and 15-45 mm, respectively, while plastron length ranged from 45-159 mm. There was a significant difference in carapace width and height between the sexes with females being wider and more domed than males by a factor of 1.03 and 1.05, respectively (Mann-Whitney U Test: width, d = 2.320, P = 0.020; height, d = 2.658, P = 0.008, n₁ = 76, n₂ = 43). However, no significant difference in carapace and plastron length was detected between the sexes (Mann-Whitney U Test: carapace length: d = 0.208, P>0.05; plastron length, d = 0.891, P>0.05).

The relationship between carapace length (x) and other dimensions (width, height and plastron length) (y) was isometric and highly significant in both adult and immature tortoises. In the relationship of carapace length with width, no significant difference in slope was detected between immature tortoises, males and females (F₂,20₅ = 0.005, P>0.05) (Fig. 1), and the common slope was 0.639. However, comparison between the intercepts showed a significant difference (F₂,20₇ = 11.388, P<0.001), with females (17.302) differing from males (13.763) (q = 67.80, P<0.001). No significant
difference was detected between immature animals (15.871) and males (q = 1.795, P>0.05) or females (q=2.242, P>0.05). The respective isometric equations were:

Males: \( y = 13.763+0.639x \) (r = 0.830, P<0.001),
Females: \( y = 17.302+0.639x \) (r = 0.764, P<0.001) and
Immature tortoises: \( y = 15.871+0.639x \) (r = 0.957, P<0.001)

**Table 1. Comparison of morphometric characters in the pancake tortoise (*Malacochersus tornieri*) from Tanzania. The difference between the sexes in adult tortoises was tested by the Mann-Whitney U Test**

<table>
<thead>
<tr>
<th>Sex/Age Class</th>
<th>Carapace length (mm)</th>
<th>Carapace width (mm)</th>
<th>Carapace height (mm)</th>
<th>Plastron length (mm)</th>
<th>Body Mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immature (n = 92)</td>
<td>Range = 50-115</td>
<td>45-90</td>
<td>15-29</td>
<td>45-110</td>
<td>0.02-0.20</td>
</tr>
<tr>
<td></td>
<td>Mean = 71.3 –2.6</td>
<td>61.8 –1.8</td>
<td>22.0 –0.6</td>
<td>66.2 –2.5</td>
<td>0.06–0.01</td>
</tr>
<tr>
<td>Adult female (n = 76)</td>
<td>Range = 129-171</td>
<td>97-130</td>
<td>30-45</td>
<td>117-159</td>
<td>0.24-0.58</td>
</tr>
<tr>
<td></td>
<td>Mean = 147.7 –2.1</td>
<td>111.3 –1.6</td>
<td>36.8 –0.8</td>
<td>137.8 –1.8</td>
<td>0.41–0.01</td>
</tr>
<tr>
<td>Adult male (n = 43)</td>
<td>Range = 123-160</td>
<td>92-119</td>
<td>25-40</td>
<td>108-150</td>
<td>0.20-0.50</td>
</tr>
<tr>
<td></td>
<td>Mean = 147.5 –2.9</td>
<td>107.6 –2.2</td>
<td>35.1 –1.0</td>
<td>135.7 –2.7</td>
<td>0.37–0.02</td>
</tr>
</tbody>
</table>

Mann-Whitney U Test

- d = 0.208
- P = 0.020
- P = 0.008
- P = 0.007

**ns = not significant**
Fig. 1: Relationships of carapace length with width in the pancake tortoise (*Malacochersus tornieri*) for immature tortoises, adult males and females from Tanzania.

In the relationship between carapace length and height (Fig. 2) there was no significant difference in slopes between immature tortoises, males, and females (*F*<sub>2,205</sub> = 1.000, *P* > 0.05) and the common slope was 0.170. However, comparison between the intercepts showed a significant difference (*F*<sub>2,207</sub> = 6.236, 0.003 > *P* > 0.001), with males (6.851) differing from females (17.274) (*q* = 8.072, *P* < 0.005). No significant difference was detected between immature animals (8.959) and males (*q* = 0.132, *P* > 0.05) or females (*q* = 1.894, *P* > 0.05).

The respective isometric equations were:

Males: \( y = 6.851 + 0.170x \) (r = 0.562, *P* < 0.001),
Females: \( y = 17.274 + 0.170x \) (r = 0.375, *P* < 0.001) and
Immature tortoises: \( y = 8.959 + 0.170 \) (r = 0.751, *P* < 0.001).
Fig. 2: Relationship of carapace length with height in the pancake tortoise (*Malacochersus tornieri*) for immature tortoises, adult males and females from Tanzania

The relationship between carapace length and plastron length (Fig. 3) showed a significant difference between the slopes ($F_{2,205} = 7.418$, $P<0.001$), with immature tortoises (0.937) differing from females (0.760) ($q = 6.067$, $P<0.001$) and males ($q = 6.070$, $P<0.001$). The difference between the sexes was not significant ($q = 1.421$, $P>0.05$). The respective isometric equations were:

Males: $y = 11.763+0.841x$ ($r = 0.874$, $P<0.001$),
Females: $y = 25.485+0.760x$ ($r = 0.897$, $P<0.001$) and
Immature tortoises: $y = -0.652+0.937x$ ($r = 0.987$, $P<0.001$).
Table 2. Allometric relationship of carapace length (CL) (y) (mm) to body mass (x) (g) in tortoises. Size ranges of animals measured are also shown

<table>
<thead>
<tr>
<th>Species</th>
<th>Relationship</th>
<th>Body size (range)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CL (mm)</td>
<td>Body mass (g)</td>
</tr>
<tr>
<td>Malacochersus tornieri</td>
<td>$y = 31.046x^{0.261}$</td>
<td>123-171</td>
<td>0.20-0.58</td>
</tr>
<tr>
<td></td>
<td>(n=119)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kinixys spekii</td>
<td>$y = 33.806x^{0.239}$</td>
<td>141-208</td>
<td>0.50-2.00</td>
</tr>
<tr>
<td>Northern Tanzania</td>
<td>(n=60)**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testudo graeca</td>
<td>$y = 16.630x^{0.340}$</td>
<td>151-218</td>
<td>0.78-1.95</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>(n=58)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testudo graeca</td>
<td>$y = 21.430x^{0.300}$</td>
<td>Not given</td>
<td>0.078-2.38</td>
</tr>
<tr>
<td></td>
<td>(n=28)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testudo hermanni</td>
<td>$y = 11.870x^{0.380}$</td>
<td>Not given</td>
<td>0.796-2.20</td>
</tr>
<tr>
<td></td>
<td>(n=9)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geochelone pardalis,</td>
<td>$y = 17.575x^{0.333}$</td>
<td>200-492</td>
<td>1.5-19.5</td>
</tr>
<tr>
<td>Northern Tanzania</td>
<td>(n=141)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geochelone pardalis,</td>
<td>$y = 14.822x^{0.350}$</td>
<td>78-386</td>
<td>0.11-11.1</td>
</tr>
<tr>
<td>Eastern Zambia</td>
<td>(n=48)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geochelone pardalis,</td>
<td>$y = 10.486x^{0.399}$</td>
<td>169-654</td>
<td>1.06-31.9</td>
</tr>
<tr>
<td>Hargeisa</td>
<td>(n=6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geochelone sulcata,</td>
<td>$y = 12.643x^{0.363}$</td>
<td>183-797</td>
<td>1.90-93.0</td>
</tr>
<tr>
<td>Mali</td>
<td>(n=58)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geochelone sulcata,</td>
<td>$y = 13.357x^{0.361}$</td>
<td>240-630</td>
<td>3.50-42.6</td>
</tr>
<tr>
<td>Sudan</td>
<td>(n=8)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Legend
* = Captive animals
** = Data pooled for all tortoises
= Data pooled for adult tortoises
+= Calculated from Wilson’s (1966) data
Fig. 3: Relationships of carapace length with plastron length in the pancake tortoise (*Malacochersus tornieri*) for immature tortoises, adult males and females from Tanzania

**Body mass**

The respective mass ranges for immature tortoises, adult males and females were 20-200, 200-500 and 240-580 g, respectively (Table 1). There was a significant difference in body mass between the sexes with females being heavier than males by a factor of 1.1 (Mann-Whitney U Test: d = 2.714, P = 0.007). The relationship between mass (x in g) and carapace length (y in mm) was strongly allometric in both adult and immature tortoises (Fig. 4). Comparison of exponents showed a significant difference ($F_{2,205} = 131.4$, $P<<0.001$), with immature tortoises (0.363) differing from males (0.258) ($q = 3.730$, $0.01>P>0.005$) and females (0.288) ($q = 3.750$, $0.01>P>0.005$). However, no significant difference was detected between the sexes ($q = 1.500$, $P>0.05$) and the common slope was 0.261. The respective allometric equations were:

- **Males:** $y = 32.026x^{0.261}$ ($r = 0.770$, $P<0.001$),
- **Females:** $y = 26.188x^{0.261}$ ($r = 0.857$, $P<0.001$) and
Immature tortoises: $y = 16.482x^{0.363}$ ($r = 0.830$, $P<0.001$).

![Graph showing relationships of carapace length (mm) with body mass (g) in the pancake tortoise (Malacocephalus tornieri) for immature tortoises, adult males and females from Tanzania.]

**DISCUSSION**

Observations on the morphometrics of *Malacocephalus tornieri* were obtained from captive animals which may not be representative, because it is often difficult to confirm their provenance, and factors that may influence their present behaviour, or condition. With such variables, it is often difficult to extrapolate information from captive to wild animals. It is very important to know the area where the specimens came from due to variation in morphology and ecology, characteristic of tortoises (Swingland & Klemens 1989). Therefore, the present data should be interpreted with caution, and used only as an approximate guide to the morphometrics of the species.
Body size
Size dimensions recorded in the present study are comparable to those reported for the species in the wild in Tanzania (Moll & Klemens 1996). Carapace width and height differed significantly between the sexes, which was also shown by the respective relationships with carapace length. Adult females were marginally wider and deeper in the carapace than males suggesting that the two characters were sexually dimorphic. The wider and deeper form of females is probably related to egg production. M. tornieri usually produces one elongate egg measuring 47-50 mm long and 25-31 mm wide, which is comparatively large relative to the size and flatness of the shell.

No significant difference in either carapace or plastron length, or in the relationship between the two characters was detected between the sexes, indicating that the two characters were not sexually dimorphic. This is in contrast to Moll and Klemens’ (1996) animals, in which carapace length was sexually dimorphic, probably due to the limited sample size of adult animals (females: n = 22; males: n = 18). The relationship of carapace and plastron length varied between adults and immature tortoises, suggesting that as shown previously for other testudinids (Bourn & Coe 1978, Lambert 1982, 1993, 1995, Kabigumila 1998), changes in ontogenic shape occur with growth in M. tornieri. As mentioned earlier, the shell of M. tornieri is very flat and flexible and can be depressed within a certain limit, allowing the tortoise to squeeze into very small crevices. It appears that this unique ability is perfected as the animals grow, thus causing changes in shell profile. This may partly explain why immature tortoises, particularly hatchlings do not resemble adults in shape: immature tortoises are somewhat more domed than adults are, and can easily be confused with the Hermann’s tortoise (Testudo hermanni) (Highfield 1994).

The isometric relationship between carapace length and other dimensions has also been recorded in the spurred tortoise (Geochelone sulcata) (Lambert 1993), leopard tortoise (Geochelone pardalis) (Lambert 1995, Kabigumila 1998), spur-thighed tortoise (T. graeca) (Lambert 1982) and T. hermanni (Meek 1985). However, in contrast to M. tornieri and G. pardalis, the relationship between carapace and plastron length in other species varied significantly between the sexes, suggesting that plastron length was sexually dimorphic. Males are larger than females, with well-developed gular scutes in G. sulcata (Pritchard 1979, Lambert 1993), but smaller, with prominent
and acute anal scutes in Testudo graeca (Lambert 1982) and T. hermanni (Meek 1985).

**Body mass**

Records of body mass obtained in the present study lie within the range reported for natural M. tornieri populations in Tanzania (Moll & Klemens 1996). The relationship of carapace length to body mass was strongly allometric, suggesting that body mass increases exponentially with growth in M. tornieri. The exponent value did not differ significantly between the sexes indicating that the pattern of growth is similar. However, comparison between the age classes showed a significantly lower value for adults, suggesting a relatively greater increase in body mass in relation to increases in carapace length. Allometric growth is well documented for the angulate tortoise (Chersina angulata) (Branch 1984), G. sulcata (Cloudsley-Thompson 1970, Lambert 1993), G. pardalis (Lambert 1995, Kabigumila 1998), Texas tortoise (Gopherus berlandieri) (Bury & Smith 1986), T. graeca (Lambert 1982), T. hermanni (Meek 1982) and the Namaqualand speckled tortoise (Homopus signatus) (Bayoff 1995).

Allowing for the confidence limits, the exponent value for adult animals in the present study (0.261 –0.036) is lower than the 0.33 value required for geometric similarity, i.e. the value required for retention of body shape as the animal grows (Gould 1966, 1971, Meek 1982, Iverson 1984). In contrast, the exponent value for immature animals (0.363 –0.022) though slightly higher than 0.33, lies within the range of values for other testudinids (0.300-0.399, Table 2). The depressed and flexible shell characteristic of adult animals may explain this.

**CONCLUSION**

Sexual size dimorphism is less pronounced in M. tornieri than in G. pardalis (Kabigumila 1998, Lambert 1995), but comparable to other smaller sub-Saharan Africa testudinids in which females are the larger sex, such as the Speke's hinge-back tortoise (Kinixys speki) (Kabigumila 1995), and Bell's hinge-back tortoise (Kinixys belliana) (Broadley 1989). M. tornieri females were marginally larger than males, presumably because significant sexual size dimorphism would be maladaptive as the maximum size attained is constrained by the rigid habitat requirements of the species.
A study examining the allometric growth curves for wild *M. tornieri* would provide useful information for comparison with captive tortoises, since differences in diet, food availability and possibly seasonal fluctuations in climate, may produce fluctuations in body mass and the overall health of an individual.

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