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Original article

Effects of diet on the systematic utility of the tortoise carapace

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Abstract.—The main character used in identifying species of Chelonia is the carapace. The taxonomy of several terrestrial tortoise genera remains highly disputed, due in part to a limited knowledge of the limits of variation in many populations. For taxa where substantial captive populations are maintained and play an important role in conservation, there is a need to ensure correct identification. The use of the carapace in identification has sometimes been criticised due to potential problems of distortion caused by captive diets. I studied the effects of diet on two species; *Testudo ibera* and *Dipsochelys dussumieri*. I confirmed previous findings that low calcium - phosphorus ratios cause scute pyramiding and that extreme calcium deprivation results in metabolic bone disease. However, even though poor diets result in bone resorption, deposition at points of stress and abnormal fusion patterns, they do not comprimise the taxonomically useful characters of scute proportions, coloration and depressions and they have no impact on the plastron. Such carapace characters and those of the plastron in particular, remain of value in systematics. My study highlights the need for careful examination of the value of taxonomic characters.

Key words.—Chelonia, diet, calcium deprivation, *Dipsochelys*, metabolic bone disease, *Testudo*, Chelonian systematics.

The skeleton of the Chelonia is unique among terapods in having an external covering of dermal armour in the form of the characteristic turtle carapace and plastron. The dermal component is a relatively late forming tissue and is not ossified during embryology. Accordingly, the carapace may be strongly influenced by the external environment whilst the internal skeleton is largely determined by embryological processes within the protection of the egg.

The carapace is the most obvious external feature of chelonians and is especially important in taxonomy. All turtle and tortoise species have distinctive carapace morphologies although many species show an overlap of characters and may be difficult to identify to species with certainty. This problem of overlap is further complicated by a high degree of individual variation in some species and a reported susceptibility to distortion due to environmental effects (Medica *et al*. 1975; Jackson *et al*. 1976; Arnold 1979; Kirsche 1984; Lambert 1986; Lambert *et al*. 1988; Highfield 1994). These environmental effects are reported to be dietary protein levels and the ratio between dietary calcium and phosphorus, and levels of exposure to ultraviolet light. Protein excess and low calcium:phosphorus ratios are reported to lead to the development of pyramidal shaped scutes (Medica *et al*. 1975; Jackson *et al*. 1976; Kirsche 1984) and, in extreme cases, 'metabolic bone disease' (Highfield 1994). This latter condition is manifest as abnormal carapace morphology, thick, spongy bone, with progression to kidney failure and death. UV light deprivation is also reported to cause these

Table 1. Number of individual *Testudo ibera* and *Dipsochelys dussumieri* examined under various dietary conditions.

Hatchling diet (< 5 years)	'Adult' diet (> 5 years)	*N* *T. ibera*	*D. dussumieri*
balanced	balanced	155	257
balanced	phosphorous rich	12	12
balanced	protein rich	8	2
phosphorus rich	balanced	25	21
protein rich	balanced	8	5
phosphorus rich	phosphorous rich	32	57
Total		240	354

symptoms (Kirsche 1984; Highfield 1994) although the precise relationship between these factors and the reported conditions has not been determined or quantified. Carapace distortion has been reported to be particularly significant in the tortoise genera *Testudo* and *Dipsochelys*.

Testudo is a circum-Mediterranean genus of largely arid-adapted tortoises containing a highly disputed number of species. Most authors accept five species in the genus (e.g., Ernst & Barbour 1989) although the most recent and most thorough revision identifies 21 species (Perälä 2002a,b,c) (including three species in *Agrionemys* which is usually considered a subgenus of *Testudo*; Ernst *et al*. 2000) on the basis of carapace colour, shape and size patterns. Carapace colour, shape and size have been reported to be strongly influenced by environmental factors.

Dipsochelys includes the Aldabra Giant Tortoise, *D. dussumieri*, and two Seychelles species, *D. hololissa* and *D. arnoldi*, recently reported to be surviving only in captivity (Gerlach & Canning 1998). These species differ in carapace shape and scute proportions, variations which have been suggested to be the result of captive diets (Arnold 1979). Determining the precise effects of environmental (especially captive diet) influences on the morphology is particularly important in these genera as large captive populations are maintained and play an important role in conservation efforts for several taxa. The present study investigates dietary effects in order to evaluate the conflicting claims that diet has a major influence on the chelonian carapace (Lambert 1986; Arnold 1979) or is of limited significance (Gerlach & Canning 1998; Gerlach 2004).

MATERIALS AND METHODS

The morphology of captive bred or captive reared (from hatchling size) tortoises of both genera was studied using data supplied by private tortoise keepers. These comprised 240 British captive bred and reared *Testudo* (*T. ibera sensu* Perälä 2002a,b,c) and 354 Seychelles captive bred and reared *Dipsochelys dussumieri*. The diets of some of these tortoises were changed during rearing (Table 1). All tortoises were 10-15 years old when measured.

For each tortoise, the length of all carapace and plastron scutes were measured as well as the carapace straight length, curved length, width, height at the centres of vertebrals 1-4, costal height (vertical height to the top of the costals at the mid point) and plastron length. In addition, two measures of the most frequently reported distortions were used; the degree of pyramiding of the 3rd vertebral scute (scute height / scute width) and carapace slope (carapace height at the 3rd vertebral scute / height at the 1st vertebral).

Information on dietary composition was provided by tortoise keepers and the approximate proportions of the reportedly key elements calcium and phosphorus (Lambert *et al*. 1988; Highfield 1994; Barrows 2001) obtained from references on nutrition (Schils & Smeets 2001). Records were also kept on vitamin D3 supplementation and the availability of natural or artificial ultra violet light exposure; all important features in calcium metabolism (Barrows 2001; Martin & Rodan 2002).

Table 2. Factor loadings of principal components of variation for *Testudo ibera* and *Dipsochelys dussumieri*.

	T. ibera		*D. dussumieri*	
Character	PC1	PC2	PC1	PC2
Eigenvalue	7.856	4.182	7.788	5.068
% of variation	60.426	32.162	54.630	36.204
Costal height	0.814	0.049	0.822	-0.058
Height of vert. 1	0.764	-0.982	0.319	0.794
Height of vert. 3	0.928	-0.560	0.741	0.373
Height of vert. 4	0.876	-0.470	0.429	0.452
Height of vert. 2	0.833	-0.295	0.527	0.684
Costal 1	0.297	0.741	0.444	-0.445
Costal 2	0.278	0.773	0.212	-0.495
Vertebral 2	0.304	0.433	0.654	-0.449
Vertebral 3	0.143	0.330	-0.408	-0.151
Vertebral 4	0.110	0.272	-0.562	0.497
Plastron	0.159	-0.268	-0.037	-0.288
Anal	0.090	0.353	0.446	-0.174
Anal notch	-0.188	0.437	-0.622	0.248

A wide range of skeletal material was examined for both species, but for most specimens no dietary data are available. Comparisons were made between tortoises showing typical carapace morphologies and those exhibiting pyramiding or distortion. These comprised 20 normal, five pyramidal and five distorted *T. ibera*, and 163 normal, one pyramidal and one distorted *D. dussumieri*.

Analysis of morphology was carried out using principal component analysis for each genus. As the dietary data provide only approximate values, regression statistics were not appropriate but graphical representation of the dietary influence on carapace shape provided an indication of distortion patterns.

Results

Tortoises consuming a wide range of dietary values were recorded, ranging from those eating relatively balanced diets with high calcium levels to extremes of high protein content, to an extreme of a purely meat based diet. None of the tortoises studied here received any vitamin D3 supplementation. All the *T. ibera* studied received lower UV light levels than would probably be natural in the species' wild range. However all the individuals studied were given access to natural UV light for much of the year. As UV exposure levels were similar for the different captive groups, difference in UV could be discounted as a cause of morphological differences in the tortoises examined.

In the case of *D. dussumieri*, all tortoises experienced natural light with the exception of two 15 year-old individuals kept in the dark from hatching, and the specimens in one collection where juveniles were housed in a dark building for their first three years. These tortoises received a natural diet and all deviation from the normal morphology can be attributed to the lack of UV exposure. The tortoises reared in the dark for 3 years had a normal carapace curvature (vertebral 3 the highest point of the carapace, with vertebrals 2 and 4 being 5-10% lower) but were all strongly pyramidal (vertebral height/width = 0.4-0.5). Those reared to maturity in the dark were highly distorted, with a carapace slope of 0.5 (Fig. 1).

The principal components analysis (Fig. 2) fails to provide clear separation of the morphology of tortoises raised under different diet types. For both *Testudo* and *Dipsochelys*, tortoises raised on protein-rich diets are separated from those on phosphorus-rich ones by the second principal component, which is dominated by the height of the first vertebral in both taxa (Table 2). This indicates that the pattern of distortion caused by the dietary differences is the same in both genera. The reported general carapace distortion and pyramiding is apparent in the samples of both genera with phosphorus-rich diets being associated with highly pronounced scute pyramiding, whilst in protein rich diets, pyramiding is limited but carapace slope is increased (Fig. 3). For *T. ibera* calcium:phosphorus ratios of less than 1.8 induce

Table 3. Post-cranial skeleton dimensions (selected bones) for *Testudo ibera* and *Dipsochelys dussumieri*.

	T. ibera			*D. dussumieri*		
	normal	pyramidal	distorted	normal	pyramidal	distorted
Humerus diameter/length	0.11-0.14	0.13-0.15	0.15-0.16	0.13-0.14	0.17	0.17
Ilium diameter/length	0.19-0.23	0.20-0.25	0.26-0.28	0.22-0.24	0.27	0.28
Femur diameter/length	0.10-0.13	0.14-0.17	0.16-0.19	0.11-0.13	0.16	0.18

pyramiding and carapace sloping, with severe distortion at ratios of less than 1.5. *D. dussumieri* has a higher calcium requirement with ratios having to remain above 2 to prevent pyramiding and sloping.

Comparisons of the skeletons of pyramidal or distorted tortoises and those with normal morphologies failed to identify any significant effects of carapace morphology on the internal skeleton except for bone dimensions (Table 3) and surface texture (Fig. 4). Cranial suture arrangements, foramina and processes used in taxonomy (Gerlach & Canning 1998; Gerlach 2001) did not vary between the carapace forms. Similarly postcranial skeleton did not vary in bone proportions. Both skeletons with pyramidal and distorted carapaces had relatively thick bones (Table 4) and a distinctly rugose surface texture in comparison to the more slender, smooth bones of skeletons with normal carapaces. Long bones become relative broad, probably to compensate for their reduced bone density and weakened structure, whilst the bones of the carapace become thickened with a spongy consistency. The increased surface rugosity reflects this reduced bone density with the internal honeycombed nature of the bone influencing the outer surface.

DISCUSSION

The present study confirms earlier reports that inappropriate diets can cause morphological abnormalities in tortoises. Specifically low calcium - phosphorus ratios (as a result of phosphorus rich diets or calcium deprivation in excessively high protein diets) results in scute pyramiding and excess protein can cause the extreme carapace deformation manifest in cases of ‘metabolic bone disease’ (nutritional

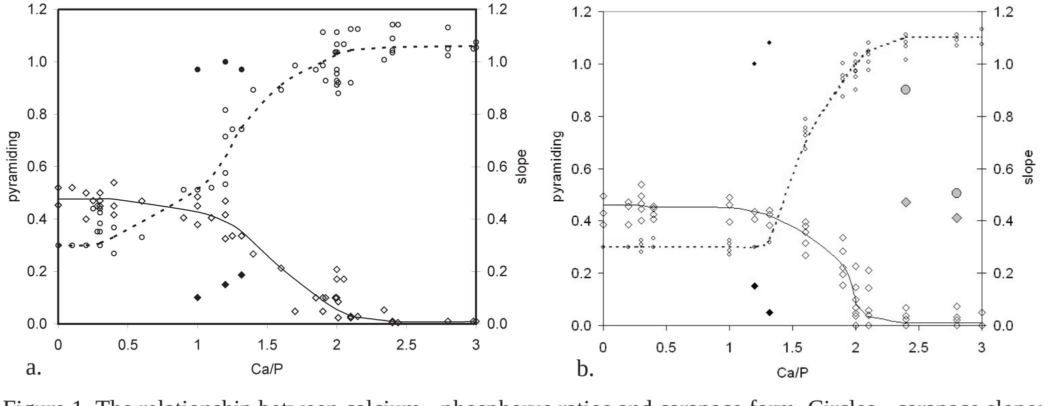

Figure 1. The relationship between calcium - phosphorus ratios and carapace form. Circles - carapace slope; Diamonds - level of scute pyramiding; Open symbols - animals reared on a single diet; Black symbols - animals transferred onto low calcium diets; Shaded symbols - animals with a natural diet but no UV exposure. a. *Testudo ibera*; b. *Dipsochelys dussumieri*.

Table 4. Protein (dry weight), calcium and phosphorus composition of main diet types for *Testudo ibera* and *Dipsochelys dussumieri* (wild *D. dussumieri* data from Gerlach 2004).

	Location	Diet type	Protein %	Ca/P
T. ibera	captive	Balanced	4.3-9.2	1.52-2.65
		protein rich	16.8-21.1	1.1-1.30
		phosphorus rich	6.8-7.3	0.78-0.99
D. dussumieri	wild	Natural	10.3-17.0	3.01-4.27
	captive	Balanced/natural	10.9-13.5	2.03-3.03
		protein rich	9.8-10.2	1.07-1.28
		phosphorus rich	7.6-8.7	0.60

secondary hyperparathyroidism). These distortions can also be caused by a lack of ultra violet light exposure in the absence of dietary problems; in hatchlings UV deprivation may cause pyramiding whilst long term deprivation results in severe metabolic bone disease. All these factors of calcium, phosphorus and UV levels combine in the process of calcium metabolism which is an essential process in skeleton formation and modification. From the present study it is apparent that tortoise carapace distortion and pyramiding occurs in the first few years of development, with tortoises kept on a phosphorus rich or protein rich diet retaining a normal carapace shape if initially reared on a balanced diet.

Bone formation and remodelling have been studied extensively, particularly with reference to human pathologies and it is known that the process of bone resorption can lead to local weakening of the skeleton and corrective bone formation (Martin & Rodan 2002). A complex feedback process exists with an important mechanical component resulting from strain in the bone matrix stimulating or repressing the activity of bone forming osteoclasts and osteoblasts (Pavalko *et al*. 2003), this process is not uniform across the skeleton as the points of greatest stress are protected from resorption (Moschilde 1990). The net result is that bone is removed from areas of low stress and reformed at sites of high stress. When the calcium balance is disrupted due to dietary imbalance, pathologies affecting processes such as renal function or intestinal absorption, calcium is removed from bone (Moschilde 1990). Such calcium removal is exacerbated by high blood phosphate levels which sequesters the calcium by formation of relatively insoluble calcium phosphate (Frye 1992). Pyramiding of scutes in the absence of dietary problems has been

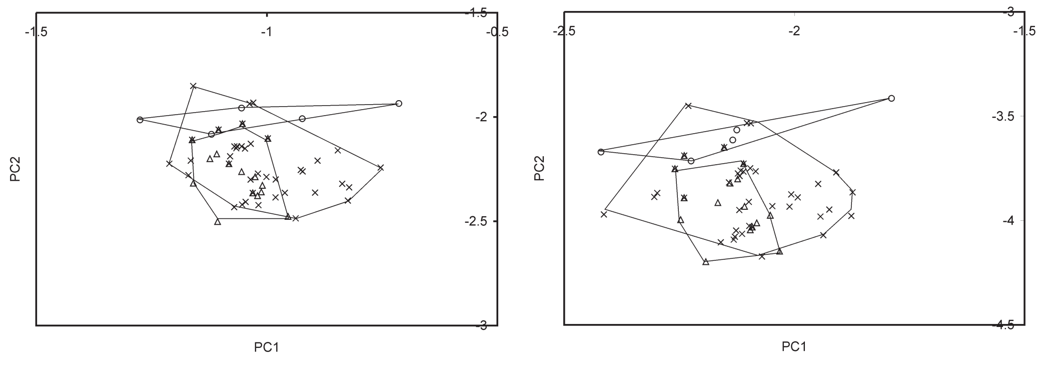

Figure. 2. Principal component analysis of tortoise morphology. a. *Testudo ibera*; b. *Dipsochelys dussumieri*.

reported as a result of endoparasitic diseases and abnormally low humidity levels (Häfeli & Zwart 2000; Wiesner & Iben 2003), both of which will have impacts on calcium metabolism through pathology and impaired digestion

In terms of the chelonian carapace, the weakened carapace resulting from calcium deprivation, phosphorous excess or UV deprivation leads to the deposition of fibrous, weakly structured bone in the areas of greatest stress. It has been reported that the areas of greatest stress lie at the centre of the vertebral scutes (Gerlach 2004) and bone deposition at these points creates the pyramidal scute morphology. With extreme calcium deprivation, the supporting skeleton is so weakened that early fusion of the neural bones occurs, resulting in constriction of the carapace with depression where the pelvis contacts the carapace. Accordingly, calcium deprivation results in pyramiding and extreme deprivation results in the carapace depression of typical metabolic bone disease.

Skeletal deformity as a result of calcium metabolism disruption is well known though mammalian pathology, especially of humans and domestic mammals. It is less well studied in other vertebrates, but is frequently reported in captive tortoises. This may be largely due to the unique chelonian feature of the dermal carapace manifesting bone distortions externally. The internal skeleton is rarely reported to be affected in tortoises, the exception being the shortening of the ilium in metabolic bone disease (Highfield 1994). The short, poorly ossified ilium fails to support the weakened carapace at the back of the carapace, resulting in a

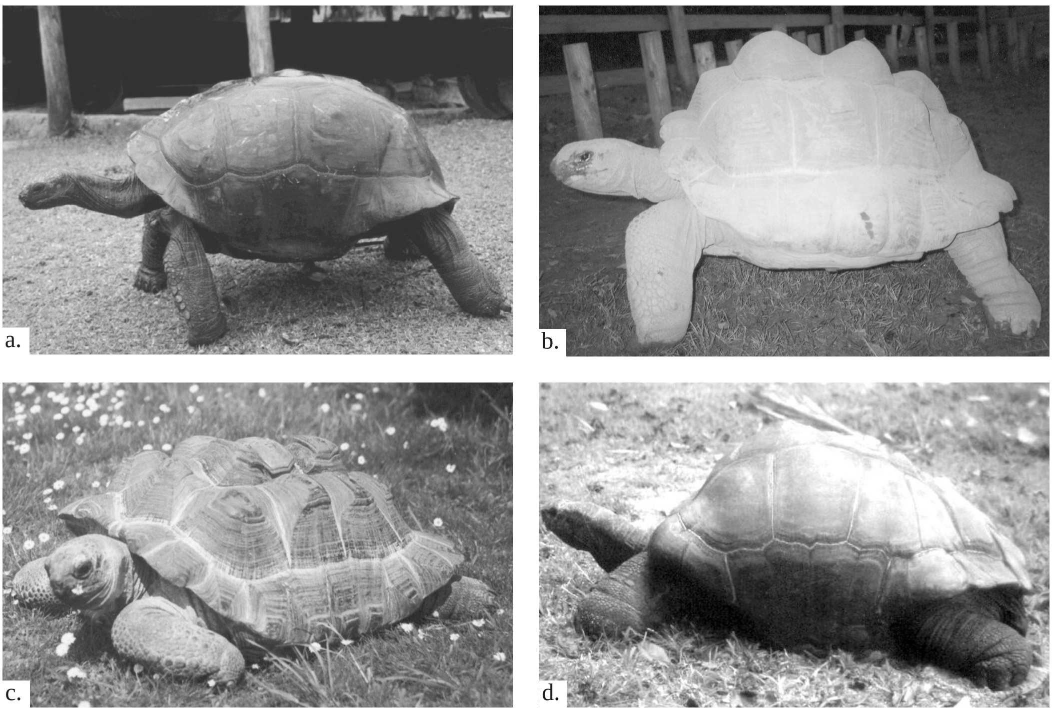

Figure. 3. Carapace morphology in *Dipsochelys*. a. Normal morphology of wild Aldabran *D. dussumieri;* b. Captive *D. dussumieri* with scute pyramiding due to phosphorus rich diet. c. Captive *D. dussumieri* with metabolic bone disease. d. Wild *D. hololissa* showing kyphosis despite natural diet.

characteristic sloping form (Highfield 1994). This is further exaggerated by kyphosis were extreme bone weakening is compensated for by early fusion of the 3rd and 4th neurals to resist the mechanical stress in the carapace. This constricts the central point of the carapace, resulting in a sloping, abnormal profile.

Kyphosis occurs in pathological captive bred tortoises with metabolic bone disease and wild turtles presumed to suffer unidentified metabolic pathologies (Lynn 1937; Nixon & Smith 1949; Ernst 1976; Plymale *et al*. 1978; Harding & Bloomer 1979; Wilhoft 1980; Rhodin *et al*. 1984; Stuart 1996; Saumure 2001). Skeletons of *T. ibera* and *D. dussumieri* with carapace morphology typical of severe metabolic bone disease have abnormally porous bones, with a reduced bone density and rough outer surfaces typical of bones undergoing calcium resorption (Moschilde 1990); no other abnormal features could be detected. This lack of significant variability or dietary induced change contrasts with a report of cranial variation in the soft-shelled turtle *Apalone ferox* (Dalrymple 1977). It should be noted that *A. ferox* is a highly specialised predator and may therefore be subject to different mechanical stresses compared to herbivorous tortoises. Calcium deficiency is not associated with any tortoise specimens of taxonomic importance, with the exception of the slightly pyramidal holotype of '*Testudo gouffei*' which is recognisable as an abnormal *D. dussumieri* (Gerlach & Canning 1998) with scute pyramiding (Fig. 3) and rugose bones resulting from bone resorption processes (Fig. 4).

The dietary impact on the carapace is not reflected in the plastron morphology as the plastron is not a stress bearing structure. Nor are scute proportions affected, except in cases of metabolic bone disease where early fusion of the underlying neural bones in kyphosis results in shortening of the associated scutes. There is some effect on coloration as the external layers of the carapace are composed of the keratinous epidermal scutes. These colorations are influenced by the structure of the proteins laid down in the epidermis and this different depositional processes resulting from diet and humidity, changes the depth of colour, but not pattern. Features of depressions on the scutes or notches between scutes are not connected to the mechanical processes in carapace formation and so are not affected by diet.

It is apparent from my study that features of the chelonian carapace can be affected by diet in the form of pyramiding or extreme metabolic bone disease, but that characters based on plastron morphology, scute proportions, and specif-

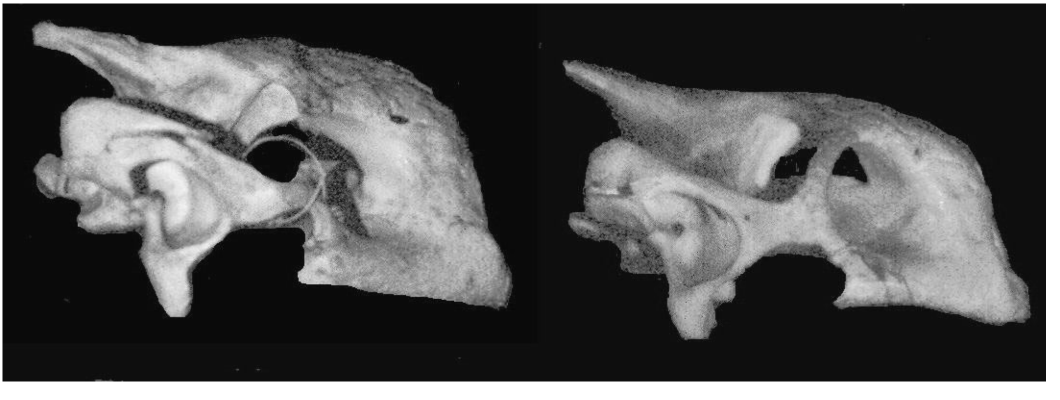

Figure. 4. Skulls of normal and pyramidal *Dipsochelys dussumieri*. Pyramidal (holotype of *Testudo gouffei*) on left and normal on right.

ic features of depressions or notches remain taxonomically useful. Individuals with distorted carapaces are easily identified and can be linked to captive diets or wild animals with pathological features of digestion or metabolism (Fig. 3).

For 250 years of chelonian taxonomy, species definitions have relied on the morphology of the carapace. Despite some confusion in certain taxa caused by the difficulties of identifying captive animals without provenance data, this reliance remains valid. The claims that taxonomic features of the external carapace may be caused by poor captive diets is supported by analysis of diet and morphology for characters such as carapace slope and the degree of pyramiding of the scutes. However, the taxonomic characters used in *Testudo* and *Dipsochelys* are not significantly affected by diet and recent revisions cannot be dismissed on this basis. Tortoise taxonomy has traditionally laid great emphasis on the rather variable characters of coloration and scute proportion without the use of sufficiently large sample sizes to determine the limits of variation. More emphasis on the less variable characters, especially of the plastron, may produce more robust taxonomies in the future. This would be of particular value for contentious genera such as *Testudo* and *Dipsochelys* among terrestrial tortoises, and for *Pelusios* in the aquatic terrapins. All taxonomic characters used in such revisions should be carefully examined and efforts made to avoid reliance on untested claims, either of their utility or their dependence on confounding environmental factors.

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