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The Evolutionary Ecology of the African Pancake Tortoise *Malacochersus tornieri* (Siebenrock 1903): A Review and Synthesis Based Upon Current Knowledge

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ABSTRACT.– The pancake tortoise *Malacochersus tornieri* (Siebenrock 1903) of East Africa is morphologically, behaviourally and ecologically unique among extant land tortoises of the family Testudinidae. Recent studies suggest it shares a common ancestor with the *Indotestudo – Testudo* group, but the selective pressures and evolutionary pathway that produced the single extant species, *Malacochersus tornieri,* are poorly understood. We propose that intense predation pressure and competition initiated the process of change from an ancestral, generalized tortoise form by driving *Malacochersus* into rocky areas and subsequently rock crevices, where predation and competition were reduced. This change in habitat led to rapid changes in morphology, ecology, and behaviour in order to better adapt to the crevice environment, and to enhance its safety within from predators. These changes in turn led to strict limits to the extent and duration of out-of-crevice activity. The changes in morphology also allowed greater mobility, agility, and speed to enhance safety when tortoises left their crevices to forage, mate, defecate, or colonize new habitats. Padlopers, an extant clade of small, southern African tortoises may provide insight into the pancake tortoise's ancestral evolution toward its modern form, lifestyle, and reproductive characteristics. Both the pancake tortoise and padlopers also inexplicably display an unusually large amount of anomalous variation in scute and/or shell characteristics.

KEY WORDS: East Africa, crevice fauna, competition, tortoise predation, tortoise evolution

INTRODUCTION

The pancake tortoise, *Malacochersus tornieri* (Siebenrock 1903) is the only extant species of its genus, and it is morphologically, behaviourally and ecologically the most unique, and distinctive extant member of the land tortoises of the family Testudinidae (Fig. 1). Mautner et al. (2017) provided a concise summary of efforts to understand the evolutionary origins of the pancake tortoise. They described the earliest attempts using morphological characters (i.e., Loveridge and Williams 1957; Crumly 1984; Gaffney and Meylan 1988) and later attempts using molecular techniques (i.e., Le et al. 2006; Parham et al. 2006; Fritz and Bininda-Emonds 2007). The consensus opinion based mainly on the studies of Le *et al* 2006 and Fritz and Bininda 2007 is that *Malacochersus* is derived from the *Indotestudo – Testudo – Malacochersus* clade. This view has recently been generally supported by Kehlmaier et al. (2019). Unfortunately, there is no known fossil record for *Malacochersus* at this time; therefore, a significant time and knowledge gap exists between the origin of the pancake tortoise ancestor(s) and the unique extant form present in East Africa today.

FIGURE 1. Pancake tortoise, *Malacochersus tornieri*, captive specimen from East Africa. Note extreme dorso-ventral flattening, a characteristic of this crevice-dwelling species. Photo by F.J. Obst

Malacochersus has a wide, but disjunct distribution in suitable habitats (i.e., crevice-rich rocky hillsides and kopjes [Fig. 2A]) across East Africa with naturally occurring populations known from Kenya, Tanzania and (marginally) Zambia (Moll D. and Klemens 1996; Mwaya et al. 2018a). It spends most of its time in rock crevices with suitable dimensions and structural characteristics where it can tightly wedge itself between crevice walls and ceilings (Fig. 2B). It's extremely dorso–ventrally flattened, thin shell and scutes, and extensive skeletal fenestration enhance this capability. Additionally, it has the ability to inflate itself slightly, or brace itself against the crevice ceiling to wedge itself even more tightly when threatened within the crevice (Moll D. and Klemens 1996; Mwaya et al. 2018a). More detailed, basic morphological studies related to these capabilities include those of Siebenrock (1904), Procter (1922), Loveridge and Williams (1957), Pritchard (1979, 2007), Ernst and Barbour (1989), Lovich and Ernst (1989); and Mautner et al. (2017). When emergence is necessary to forage, seek mates, defecate and colonize new habitats, or when rapid return to the crevice is required to escape or avoid dangerous situations (e.g., predation, trampling, unfavourable environmental conditions) these tortoises can move swiftly, turn over quickly if they fall on their backs, and climb rocks in an almost lizard-like manner. These behaviours may be facilitated by morphological changes that have lightened the shell (Kabigumila 2002), and have been further enhanced by greater suppleness in the wrists and ankles than seen in most testudinids (see also Procter 1922; Honegger 1968; Ireland and Gans 1972; Wilke 1984; Moll D. and Klemens 1996; Wood and MacKay 1997; Kabigumila 2002; Malonza 2003; Schmidt 2006; Mwaya et al. 2018a).

The objectives of this paper are to elucidate a plausible evolutionary scenario

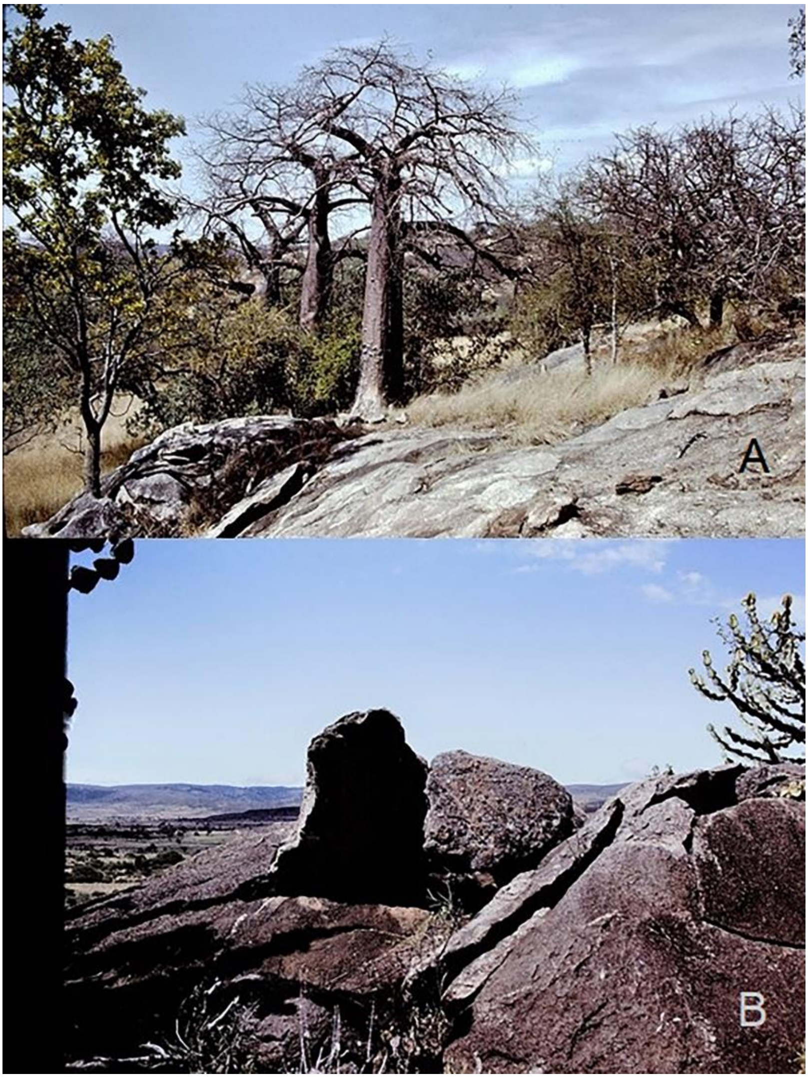

FIGURE 2. Pancake tortoise macrohabitat in northern Tanzania's Yaedachini Game Reserve (2A), and microhabitat near Mbulu, Tanzania (2B). A pair of pancake tortoises (not visible) are present in the diagonal crevice in the rock at the right foreground of photo (2B). Photos by D. Moll

and relevant selective forces that may have been involved in shaping the unique morphology, behaviour and ecology of the extant pancake tortoise. The morphological, behavioural and ecological characteristics of the southern African padloper tortoises (genera *Homopus* and *Chersobius*, Family Testudinidae) will also be briefly discussed as they may provide insight into some of the evolutionary stages undergone by the pancake tortoise's ancestors. Reproductive characteristics, as well as scute and shell anomalies in the pancake tortoise and padlopers are also briefly discussed.

MATERIALS AND METHODS

Literature search

The methodology of Brown et al. (2008) was employed to obtain a maximum number of relevant references concerning the subject matter of this paper. Searches employing numerous combinations of search words, and the search engines Google, Google Scholar (Advanced Scholar Search), and JSTOR Advanced Search were conducted. We also used traditional library-based searches of paper sources at Illinois State University's Milner Library, and DM's and LEB's personal herpetological and paleontological libraries to obtain pertinent references. Detailed field notes by one of us (DM) concerning his 1992 Tanzanian field studies of the pancake tortoise's ecology were also consulted and cited in this paper.

Scientific names follow those designated by the Turtle Taxonomy Working Group (2017). No original DNA sequencing was conducted in our research related to the preparation of this manuscript. However, DNA sequence registration information and DNA sequencing methodology employed are provided in the papers by Parham et al. (2006), Le et al. (2006), Fritz and Bininda-Emonds (2007), and Kehlmaier et al. (2019) that we referred to in our Results and Discussion section.

RESULTS AND DISCUSSION

Into the crevice: selective pressures and morphological change

We envision the earliest ancestral *Malacochersus* to be a small to medium-sized tortoise with a typical hard-shelled testudinid morphology (e.g., similar to extant *Indotestudo* or *Testudo* or *Homopus* tortoises). Considering both fossil and molecular evidence, Le et al. (2006), Parham et al. (2006), Fritz and Bininda-Emonds (2007), and Kehlmaier et al. (2019) suggested *Malacochersus* was derived from the *Indotestudo – Testudo – Malacochersus* group of species within the Testudinidae. Available evidence suggests this group originated in the Palearctic Region (i.e., Eurasia) as recently as the late Miocene (~5-15 myo). An invasion of Africa by members of this group, perhaps via land bridge(s) present in the late Miocene (Rögl 1999), occurred somewhat later. This is much younger than the oldest known African tortoises (e.g., *Gigantochersina ammon* at 35.4-35.6 myo – Holroyd and Parham 2003). Parham et al. (2006) point out that the clade containing the ancestral pancake tortoise; therefore, must have invaded Africa after other tortoises, including the diverse and widespread *Geochelone* complex were already well established on the continent.

The ancestral *Malacochersus* that arose within this clade would probably have been a habitat generalist and would have been distributed across a variety of habitats which provided suitable foods (mainly vegetation), shelter from environmental stresses, suitable reproductive sites, and at least some protection from predators. We assume predator diversity and predation pressure would have been important selective forces on prey species in ancient Africa as they are today. A diverse array of mammalian, avian (probably underestimated in importance) and reptilian predators would have preyed on tortoises of all ages and sizes along with their eggs much as they do today (Moll D. and Klemens 1996; Mwaya et al. 2018a). Interspecific competition with already established tortoises and other vertebrate herbivores would also have been an important selective force.

Parham et al. (2006) suggested that given the great length of time that tortoises were present in the Ethiopian Region before the group containing the ancestor(s) of *Malacochersus* colonized there, it is likely that one or more radiations may have occurred before their arrival (e.g., the evolution of the diverse *Geochelone* complex-Hofmeyr et al. [2016]). If so, the niches available for newly arriving, herbivorous tortoises would likely have been limited, and competition for resources could have been intense.

The generalized ancestral *Malacochersus* would likely have been more vulnerable to predation and competition pressure in some habitats than in others, depending on ecological factors referred to above, and the diversity and effectiveness of potential tortoise predators and competitors present. Habitats that reduced the tortoises' effectiveness in defense and niche use against resident predators and competitors would result in lower population sizes, or perhaps even extirpation, while habitats that more effectively supported and protected resident tortoises would provide refugia from predators and competitors.

We suggest that tortoises inhabiting rocky habitats were able to benefit from greater opportunities for shelter, crypsis, and protection from predators and competitors compared to tortoises in other habitat types. An ability to shift in diet to low-growing plants associated with rocky areas (as utilized by extant pancake tortoises [Moll and Klemens 1996; Mwaya 2009; Mwaya et al. 2018a]) would have helped in adapting to the new niche. As a result, the tortoise populations in these rocky habitats were able to survive and thrive while those in other habitats did not.

Presumably, tortoises in rocky habitats would have begun using rock crevices, caves, rock slabs, and other semi-enclosed rock structures for shelter and protection from predators, and from inclement weather and other unfavourable environmental conditions outside. Loehr (2002) stated that the characteristic thin shell and large fenestrae of pancake tortoises could just as well have been "a reduction of unnecessary investment in shell, replaced by protection by rocks" rather than necessarily being an adaptation which allowed them to inflate themselves in rock crevices to avoid being pulled out by predators. We agree that the protection afforded by the rock crevice allowed the luxury of shell reduction and softening to proceed, but we envision a more complex series of specific adaptive morphological and behavioural changes occurring at this stage. We do not think the reduction and change in shell structure was just the result of random atrophy (and which may be analogous to the reduction in wing structure leading to flightlessness in island-colonizing birds and insects freed from predation [Carlquist 1965]). In the case of the pancake tortoise the extensive fenestration and thinning of the scutes and underlying bone led to greater flexibility and even slight inflation capability while still maintaining specific sturdier areas (especially its hard, ossified vertebral/neural section at the dorsal rear location of the carapace [Fig. 1]) for protection from predators and for bracing against the crevice ceiling (see below for a more detailed description of morphological and behavioural adaptations for crevice life).

We suggest the hard-shelled pancake tortoise ancestor(s) began entering rock shelters (e.g., caves, fissures, larger crevices, etc.) mainly for protection from predators and other external threats. This behaviour was effective against larger mammalian and avian predators, but it left the pancake tortoise ancestor vulnerable to agile small and medium-sized mammalian predators such as herpestids (e.g., mongooses), viverrids (e.g., genets and civets) and also reptilian predators (e.g., varanid lizards). These predators still prey on pancake tortoises, and other tortoises in East Africa today, and routinely enter crevices in search of prey (Moll D. and Klemens 1996, Moll D. pers. obs.; Mwaya et al. 2018a). This type of predation served as a strong selective force precisely guiding profound, specific behavioural and morphological changes that promoted the utilization of ever-smaller and narrower crevices. Utilization of these new habitats could be considered analogous to the first attempts to take to the air by bird-like, maniraptoran theropod dinosaurs (i.e., entering a new adaptive zone). Once the utilization of the new zone was initiated, a cascade of adaptations that better adapt the organisms to the new niche would occur. Modifications in morphology, behaviour and ecology occurred which changed the tortoise into a form possessing the characteristics of, and eventually becoming, the extant pancake tortoise, *Malacochersus tornieri*.

The proposed, critical, formative processes influencing the ancestral pancake tortoise's evolution can be summarized in the following event sequence: 1) dispersal from Palearctic origins into the Ethiopian Biogeographic Region by the pancake tortoise ancestor(s) ~5 – 15 myo in the late Miocene, 2) the selective pressures of predation and competition led to the utilization of rocky habitats for shelter and protection, by the ancestral pancake tortoise, 3) the continued selective pressure of smaller to medium-sized predators (e.g., mongooses) led to the pancake tortoises' use of increasingly smaller and narrower crevices, 4) changes in morphology continued to better adapt the pancake tortoises' ancestral form to these new specialized habitats, and 5) associated changes in ecology and behavior continued in the ancestral pancake tortoise's lineage until the extant form evolved.

Parham et al. (2006) researched the phylogeny of a number of species of tortoises (including *M. tornieri*) using mitochondrial genome sequences. Their results implied a higher mtDNA rate of evolution for *M. tornieri* than the other tortoises examined. This may be associated with the rapid effects of natural selection on behaviour and morphology, which must have been progressing at essentially the same time, and would have enhanced the adaptive value of each trait in a positive feedback loop. The Parham et al. (2006) and Omland (1997) studies (see below) also suggested that the changes could have taken place very rapidly, perhaps in just a few generations.

The processes described above represent evolutionary stages we envision where crevice selection became very specific, and was based upon the requirements for maximum protection (according to Moll and Klemens 1996: where the crevice ceiling is <5 cm above the floor and where, preferably, this crevice section is somewhat removed from the crevice entrance). Indeed, if suitable crevices are not present or very scarce in a particular kopje or rock outcrop, pancake tortoises are unlikely to be found there (Moll D. and Klemens 1996; Mwaya et al. 2018a). Crevice dimension preferences are very precise, and this is because the unique behaviours of wedging, bracing, and inflating, accomplished in different ways depending upon the configuration of the crevice, are apparently very important in preventing dislodgement of resident tortoises by potential predators (Moll D. and Klemens

1996). Morphological specializations are also involved in wedging effectively (i.e., part of the suite of unique morphological changes characterizing pancake tortoises, and especially, affecting their shell structure [see references concerning morphological studies cited in the Introduction]). Briefly, the main morphological modifications for crevice life in conjunction with those behaviours referred to below as inflation and bracing include: 1) the shell is dorso-ventrally flattened (Fig. 1), so that the tortoise can more easily squeeze into narrow crevices, 2) the plastron and carapace are soft and widely fenestrated to facilitate compression, 3) the scutes on the shell are thin facilitating flexion and compression, and 4) the bones of the shell are connected by thin flexible cartilage, again enhancing the flexion and compression of the shell. These shell characteristics collectively allow the tortoise to mold its body into the contours of the crevice (i.e., simple wedging) and enhance its capacity to resist dislodgement. When crevice dimensions and configurations allow, bracing and/or inflation may be employed also to provide even more effective mechanisms to avoid dislodgement.

The presence of a solid hump of scute and underlying bone on the dorsal rear of the carapace (Fig. 1), allows a threatened tortoise to brace itself tightly against the ceiling of the crevice. This is accomplished by extending and straightening the hind legs in order to thrust the hump into the rock ceiling. As pancake tortoises often wedge themselves into crevices with their posterior shell facing toward the crevice entrance (Moll, D. pers. obs.), the hardened rear of their carapace may also physically shield them from injury by intruding predators. Inflation is caused by retracting the limbs, and head into the shell while the tortoise inhales and holds its breath. This behaviour results in the expansion of a large underlying plastral fontanelle (Fig. 3), and produces a slightly larger body circumference for the tortoise in the crevice, again enhancing the capability for tighter wedging (Moll D. and Klemens 1996).

Leaving the crevice

The benefits of shell reduction and greater thinness are obvious in a crevice-dwelling tortoise with the ecological and behavioural specializations of *Malacochersus*, but they also come at significant cost. Emergence from the crevice is much more perilous than it was previously due to the reduced protection provided by the greatly modified shell. Predators outside the crevice are the main concern, but there may be other dangers as well. Trampling by hooved, mammalian herbivores has not yet been documented by observation to our knowledge, but *Malacochersus* lives in areas known for large herbivore herds and the great size and sharp hooves of individuals composing some of these herds pose a threat (Mwaya et al. 2018a). One of us (DM) has observed large herds of African buffalo (*Sincerus caffer*) foraging just outside rock crevices containing pancake tortoises in Tarangire National Park, Tanzania. Excessive heat experienced while foraging or in other outside activity could also be dangerous to pancake tortoises or their ancestors that wandered too far from the crevice with its often more moderate and/or stable internal environment (Honegger 1968; Wilke 1984; Moll D. and Klemens 1996; Schmidt 2006).

Although time spent within the relative safety of the crevice is considerable in the extant pancake tortoise (and presumably its immediate ancestor[s]) certain out-of-crevice activities are essential for survival and reproduction within the species, such as foraging, seeking mates and mating, nesting

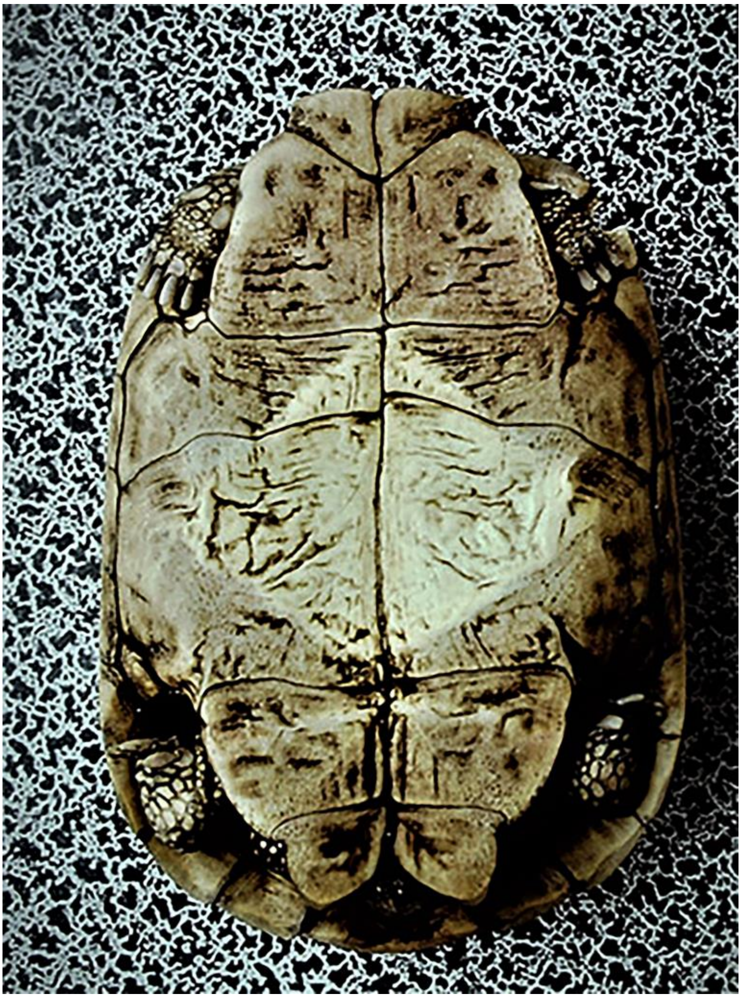

FIGURE 3. Adult pancake tortoise showing the large light-coloured area of the plastron covering the central fenestrated area in the underlying bony layer. Photo by D. Moll

and oviposition, basking, and defecating. One of us (DM) has observed and collected considerable amounts of pancake tortoise scat outside crevices and inside, near the entrances, but little within the crevices themselves. All of these activities have been observed outside crevices, but some may occur within as well – the ability to observe activity inside a crevice is obviously limited. Moll D. and Klemens (1996) and Mwaya et al. (2018a) suggested male pancake tortoises may move overland to reside with females in crevices for a time, but whether mating occurs there is unknown. The social behaviour of pancake tortoises remains largely unstudied (Moll D. and Klemens 1996; Mwaya et al. 2018a). Single eggs have been observed within crevices in the wild and in captive conditions (Loehr 2002; Schmidt 2006; Mwaya et al. 2018a), but the normal method of oviposition is usually the standard chelonian method of digging a shallow hole, laying an egg in it and burying the (usually single egg) clutch (Mwaya et al. 2018a). Oviposition in the crevice would initially seem to be a favourable and safer way to reproduce, but pancake tortoises often share their crevices with a variety of reptilian and other usually commensal residents (Moll D. and Klemens 1996; Mwaya et al. 2018a). The regular movements of pancake tortoises and the other crevice dwellers could damage the egg(s) inside and some of the crevice dwellers could possibly also eat some (e.g., varanid lizards). In addition, the crevices usually have a rock floor so burying the egg(s) would be impossible. Exposure to the crevice environment over the long incubation period could also be detrimental to egg development. As *Malacochersus* is a TSD species (i.e., has temperature-dependent sex determination [Ewert et al. 2004]) the normal population sex ratio of eggs could be disrupted if too many individuals oviposit within crevices, rather than in outdoor substrates in a more normal chelonian manner.

The solution to the problems imposed by outside activity of extant pancake tortoises (and presumably their immediate ancestor[s]) is to prolong their stay in their crevices as long as possible before emergence. Once outside they curtail the time spent engaging in outside activities by limiting the distance traveled from the nearest suitable crevice (Moll D. and Klemens 1996; Branch 2012; Mwaya et al. 2018a).

Observations of foraging pancake tortoises (by Njalale A. *in* [Moll D. and Klemens 1996] and *in* Mwaya et al. ([2018a]) suggest that most activity occurs near the crevice entrance, is of relatively short duration (although some individuals may be immobile outside for a longer period of time), and may occur throughout the day. Branch (2012) observed that ~50% of the pancake tortoise's movements he observed are between crevices on the same rock outcrop although considerable movement between outcrops may sometimes occur. Mwaya (2002) also noted occasional longer movements between crevices, especially by males. During these forays, including the periods of immobility, the plain horn colour (usually in older individuals) and "sunburst" carapacial scute patterns and varied carapacial colours displayed in other individuals may serve a cryptic function for both juveniles and adults (Fig. 4A, B). It is notable also that the diurnal activity patterns displayed by tortoises engaging in external activities contrast with the predominantly nocturnal activity of their main mammalian predators, the herpestids and viverrids. To our knowledge, there are no recorded observations of pancake tortoises active outside their crevices at night. However, the potential for nocturnal movements by *Malacochersus* has not been thoroughly investigated. Moll D. and Klemens (1996) counted at least seven mutilated pancake tortoise carcasses in close proximity to crevices (within 2 meters) in Tarangire National Park, Tanzania. The three freshest carcasses were discovered in early morning surveys, and clearly displayed wounds resembling those made by mammalian teeth (Moll D. unpubl. field notes). Mwaya R. (unpubl. observ.) also found several predated pancake tortoises outside of crevices in Tarangire National Park, but the predators involved, and distance from crevices, are unknown. No tortoises or other signs of predation were observed, despite intensive searches at more distant locations (i.e., beyond several meters from crevices

FIGURE 4. Adult pancake tortoises displaying cryptic colouration against backgrounds of lighter coloured rock (4A) and black rock with orange lichens (4B). Photos by D. Moll

[Moll D. unpubl. field notes]). Pancake tortoises may have been surprised and pulled from their crevices during the night and consumed just outside before dawn. A few dead tortoises (i.e., four in ~two months of fieldwork) were found within crevices, but they displayed no signs of predation (Moll D. unpubl. field notes). Avian diurnal predators known to prey upon small tortoises and other reptiles, such as secretary birds (*Sagittarius serpentarius*), ground hornbills (*Bucorvus leadbeateri*), white-necked ravens (*Corvus albicollis*) and pied crows (*Corvus albus*) would still be a threat to both juvenile and adult pancake tortoises outside the crevices during the day, perhaps reduced by the cryptic behavior and colour patterns mentioned above (Uys 1966;

Fincham and Lambrechts 2014; Mwaya et al. 2018a). However, diurnal activity by pancake tortoises probably minimizes the occurrence of predation by the smaller mammals that are so effective at night.

Whether reduction in dietary diversity (i.e., confined to plants present in rocky habitats) and greater restriction in movements occurred in ancestral forms as shell reduction was occurring is unknown, but such behavioural and ecological changes seem plausible.

One other possible reason for outside movement would be the occasional need to find and colonize new suitable habitat. Suitable habitat in Tanzania, and presumably other locations within the range of the pancake tortoise (or ancestor[s]), consists of rock outcrops or kopjes often composed of exfoliating gneiss with numerous crevices of suitable structure and dimensions. Habitats may degrade in quality over time and become crevice-less mounds of rubble (Moll D. and Klemens 1996). Under such conditions resident tortoises may have to move and negotiate longer distances to colonize more distant (>several kilometers) habitats that meet their requirements. Similarly, hatchlings and juveniles inhabit crevices like those used by adults. However, they often use shallower crevices, and may find shelter nearer to crevice entrances than adults (Moll D. and Klemens 1996). They also may need to find and colonize new habitat as they mature and grow. Suitable crevices are usually limited and presumably fully occupied even in good macrohabitats (whether overcrowding before dispersal leads to the sharing of a single crevice by multiple individuals as observed by Moll D. and Klemens [1996] and Mwaya et al. [2018a] is unknown). No observations of very long distance dispersal events are known to us, but we assume they must happen occasionally. The widespread, but disjunct range of *M. tornieri* in East Africa suggests it must occur.

Padloper parallels

Our understanding of the evolutionary pathway of *Malacochersus tornieri* is obviously hampered by the lack of a fossil record that could potentially fill in some of the gaps in our knowledge between the pancake tortoises' ancestral origins and the single extant species of today's East Africa. However, another clade of extant testudinids and one fossil form, rather distantly related to *Malacochersus*, collectively called padlopers (genera *Homopus* and *Chersobius* [see Hofmeyr et al. (2016)]), may provide some insight into *Malacochersus*' evolutionary history.

There are five extant padloper species *H. areolatus, H. femoralis, C. boulengeri, C. signatus* and *C. solus* from South Africa and Namibia (Boycott and Bourquin 2000; Branch 2012) (Table 1). The fossil species is *Homopus fenestratus* from South Africa (Cooper and Broadley 1990; Branch 2012). These small tortoises are represented by two rather generalized species (genus *Homopus*), both morphologically and ecologically, while the remaining three extant species and single fossil species display greater morphological and ecological specialization (the latter, presumed in the extinct species *H. fenestratus*). The extant *Homopus* tortoises have a more typical tortoise body form with a moderately domed, solid carapace, deeper than that of *Chersobius* (Fig. 5 A, B; Table 1), and they live in more diverse and varied habitats (Boycott and Bourquin 2000; Branch 2012). The *Chersobius* tortoises have distinctly dorso-ventrally flattened carapaces, are very small (Fig. 5 B; Table 1), and live in rocky habitats where rock slabs and crevices are typically used for

TABLE 1. Selected ecological and morphological characteristics of the pancake tortoise, *Malacochersus tornieri* and extant padloper tortoises (genera *Homopus* and *Chersobius*). Data from Boycott and Bourquin 2000, Branch 2012 & Mwaya et al. 2018a. Quantitative values may vary geographically.

Name	**Habitat/Lifestyle**	**Normal Egg Clutch Size; Egg Shape**	**Carapace Length; Larger Adults (cm)**		**Carapace Height (cm)**		**Fenestration present**
			Female	**Male**	**Female**	**Male**	
M. tornieri	rocky hillsides, kopjes; crevice dweller	1, elongate	17.8	17.0	4.0	3.6	Yes
H. femoralis	grasslands of mountain plateaus; morphological generalist, habits poorly known	1-3, ovate	15.39	13.7	7.0	6.0	No
H. areolatus	mainly moist coastal regions with a variety of vegetation types; generalist	1-3, elongate to ovate	12.0	10.0	6.0	5.0	No
C. boulengeri	rocky ridges and outcrops in the Great Karoo succulent veld and desert grassland; rock dweller	1, elongate	11.0	9.0	5.0	4.0	No
C. signatus signatus	semi-desert rocky terrain; rock dweller	1, elongate	10.6	8.75	4.32	3.34	No
C. signatus cafer	rocky terrain and rock outcrops in arid vegetation and bushveld in northeast; wetter heathlands and bushveld in South; rock dweller	1, elongate	9.5	8.0	4.0	3.0	No
C. solus	rocky semi-desert, low scrub succulent veld, short grassland with rocky outdrops; rock dweller	1, elongate	11.0	9.0	3.0-4.0 (sexes unspecified)		Yes

cover. *Chersobius solus* is distinctly fenestrated well into adulthood, as is the single known fossil form (carapacially in the former, plastrally in the latter). We suggest that padlopers display morphological and ecological features that may be similar to those exhibited by ancestral *Malacochersus'* at various stages in the pancake tortoise's evolutionary trajectory. This progression from generalist ancestor(s) toward a more specialized form may also have culminated in the unique, modern pancake tortoise morphology. These comparisons can only be taken so far; however, as padlopers never attained the extreme levels of specialization in morphology, behaviour and ecology that are observed in the extant pancake tortoise. Schmidt (2006) suggested this difference could be due to the greater intensity of predation pressure in Tanzania, where more predators are present than in southern Africa. This may also help to explain the presence of several extant padloper species while *Malacochersus* is represented by a single extant species. Nevertheless, the general evolutionary pattern seen in padlopers

FIGURE 5. A morphologically generalized padloper species (*Homopus femoralis*) (Fig. 5A) and a flattened, rock-dwelling specialist (*Chersobius signatus*) (Fig. 5B) are portrayed. Photos by Victor Loehr (5A) and Arie van der Meijden (5B)

may be instructive in envisioning the transitional process and intermediate forms that may have been present during the evolution of the extant pancake tortoise.

Other similarities between the pancake tortoise and the smaller rock dwelling padlopers are the normal production of a single egg per clutch (Moll D. and Klemens 1996; Boycott and Bourquin 2000; Branch 2012; Mwaya et al. 2018a; Table 1), and the unusual prevalence of scute and/or skeletal anomalies in both groups.

Enigmatic reproductive patterns and scute and bone anomalies in the pancake tortoise and padlopers

Mautner et al. (2017) stated that "comparing shell height of tortoises with reproductive (number of eggs in a clutch) and ecological factors (natural habitat preference) did not reveal clear trends." They also pointed out that "the *Indotestudo – Testudo – Malacochersus* clade is, with the exception of *M. tornieri*, neither particularly flat nor high domed."

These observations concerning the nature of the relationships between shell height, ecological factors, and reproductive characteristics within tortoises may result from the diluting effect of considering too many forms collectively. In larger clades with their varying ecological requirements and the influences of many poorly recognized selective forces trends may be obscured. Moll E.O. (1979) stated that between the extreme chelonian reproductive patterns lie a wide range of intermediates that employ certain advantages of each pattern, and are undoubtedly influenced by many other selective forces which may not be realized yet. However, these difficulties of interpretation may not be a problem with particular, specialized species in very specific habitats. This seems to be the case with the flattened, crevice-dwelling pancake tortoise and the flattened-rock dwelling padlopers.

Moll E.O. and Legler (1971) associated small clutches with morphological and ecological specialization in chelonians, and Moll E.O. (1979) listed pancake tortoises and padlopers among the smallest and most specialized of extant forms. Single or very small clutches of relatively large eggs are characteristic of many small, often tropical species (e.g., Dobzhansky 1950; MacArthur and Wilson 1967), and this is true of the south temperate rock-dwelling padlopers, as well. In the pancake tortoise and rock-dwelling padlopers it may be that the need for movement through small spaces, sheltering in crevices and under rocks, and rapid movement in and outside of rock shelters may, in addition to the small, flattened body shape, collectively provide strong selective pressure to forego large clutches in favor of one relatively large, elongated egg. The larger egg would increase the food supply for the developing embryo, produce a larger offspring with greater likelihood of survival, limit predation loss, and reduce the burden of carrying a large clutch (Dobzhansky 1950; MacArthur and Wilson 1967; Lack 1968; Moll E.O. 1979). It may also be considered an extension of parental care in the oviduct. The normally elongated or ovate single egg would reduce weight and energy expenditure during the periodic activity required for foraging, escape behaviour, and movements to find mates or new habitats, while not disrupting the flattened carapacial shell profile required for shelter in crevices or under rock slabs. Other ecological niches filled by chelonians also require flattened shapes and lightened shells (e.g., aquatic, trionychid softshelled turtles), but the similar, interconnected triumvirate of adult morphology, clutch size, and egg shape in these rock-dwelling species suggests a highly evolved set of interconnected traits for successfully existing and reproducing in these particular habitats.

In reference to Mautner's et al. (2017) morphological observations of the *Indotestudo – Testudo – Malacochersus* clade, it does not seem particularly relevant to us to consider all the clade members collectively in reference to their shell shape and reproductive patterns. The morphologically more "normal" members of the clade, and therefore, presumably more ecologically generalized, would also be presumed to reproduce more normally (e.g., more eggs in a clutch, variability in egg shapes and sizes depending on their ecology and habitat type, etc.). The ecologically most specialized member of the clade, *Malacochersus*, would be expected to be the most distinctive morphologically and reproductively, as is the case.

Another unusual characteristic observed in the pancake tortoise, and also to some extent in the rock-dwelling padlopers is the great variability in the external scutes, and/or in the underlying bones. In the pancake tortoise the level of variation is greater than in any other extant chelonian (see Mautner et al. 2017 for a review of literature related to this subject). A number of reasons for these anomalies have been proposed including: 1) environmental pollutants, 2) desiccation of eggs during development and incubation, 3) incubation temperatures, 4) genetic defects, or 5) consequences of accidents or trauma during the embryonic stage. Mautner et al. (2017) suggested the anomalies observed in *M. tornieri* may be related to its unique lifestyle, but do not provide more specific information.

Parham et al. (2006) observed that "*M. tornieri* displays a more rapid rate of sequence evolution compared to other members of its clade," and that its "elevated rate of mitochondrial evolution coincides with its other unusual genomic characteristics." Some researchers have also noted that molecular and morphological evolutionary rates are often correlated (e.g., Omland 1997), as seems to be the case in *M. tornieri*, but possible underlying mechanisms remain obscure (e.g., Bromham et al. 2002; Marko and Moran 2002). Parham et al. (2006) suggest these phenomena may be due to "a relaxation of selection on the mt genome, a less accurate replication or repair mechanism, or an environment conducive to mutagenesis." It is interesting to note that both the rock crevice-dwelling pancake tortoise and the padlopers all share the trait of unusual prevalence of skeletal and/or scute anomalies as well as the capacity for undergoing more significant morphological changes (Parham et al. 2006; Loehr 2016; Mautner et al. 2017). Although no evidence exists of mutagenic properties in such habitats, this similarity in *M. tornieri* and three of the padlopers that dwell in rocky habitats with similar characteristics seems worthy of further investigation. Current evidence from Branch (2007) and Loehr (2016) suggests that scute anomalies may be particularly prevalent in the rock dwelling padlopers (e.g., in 44% of *Chersobius signatus* examined by Loehr), but Mautner et al. (2017) pointed out that quantitative data from other species for comparison are still few. As we have only a sample of one extant species of pancake tortoise and five extant padlopers (and one poorly preserved fossil) to observe, it is impossible to evaluate when in the evolutionary history of these groups a propensity for higher levels of scute and skeletal anomalies may have developed (or why).

CONCLUSIONS

We have endeavored to compose a plausible overview of the evolutionary ecology of the pancake tortoise, *Malacochersus tornieri*, based upon original data from our own fieldwork in combination with a comprehensive review and synthesis of other published sources of relevant information. We consider our contribution to be the first of its kind concerning the pancake tortoise, but unavoidably a preliminary effort in many respects. Although we believe the anatomical, molecular and ecological data we incorporated to support our predictions are the best available, our analysis must still be considered tentative and unavoidably speculative in some aspects.

It is glaringly obvious that a major impediment to a more reliable understanding of the evolutionary ecology of the pancake tortoise is the absence of a fossil record for this unique species. A close second would be the still superficial knowledge of the ecology of this tortoise in the present, and even less so during its evolutionary past. We believe our predictions concerning the origins of the pancake tortoises' paleoecology, morphological change and current ecological and behavioural characteristics are logical and valid given the evidence available, but they are clearly falsifiable – a requirement of any valid scientific hypothesis. The discovery of a fossil in the wrong time period, or geographic location or even its fossil matrix could and should alter or negate the current hypothesis. We have been questioned by some colleagues whether the data are currently inadequate to present a useful synopsis of the evolutionary ecology of the pancake tortoise, but we disagree. We do agree that modifications in the scenario that we present here may be necessary, and even welcomed as new data become available, but this is how science progresses. We see our contribution as an early but necessary step in the process.

Conservation concerns

The unique morphology, behaviour and ecology of the pancake tortoise have successfully equipped it to survive and even thrive into, and through, the Holocene. In more recent times, its unique appearance has promoted significant interest among tortoise collectors, however, and it has become a popular animal in the commercial exotic animal trade, both legal and illegal (Klemens and Moll D. 1995; Mwaya et al. 2018a; Mwaya et al. 2018b). One of the few chelonians lucky enough to escape being used as a significant human food source, or harmed by domestic or feral animals in any serious way, its populations have been decimated in many locations, and its habitat degraded by commercial collecting. Its long-term survival now depends on immediate action to control commercial collection and export of this unusual animal (Mwaya et al. 2018a; Mwaya et al. 2018b). It is ironic that the same unique adaptations that greatly contributed to its survival over such a long span of time could become the cause of its extinction in the modern world.

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