Turtles on the Brink in Madagascar: Proceedings of Two Workshops on the Status, Conservation, and Biology of Malagasy Tortoises and Freshwater Turtles
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Madagascar: Island Continent of Tortoises Great and Small

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Abstract. – Most areas of the thousand-mile-long island of Madagascar do not have tortoises, and there is very little overlap in the ranges of the handful of species still found there today. True giant tortoises have been extinct there since early human times. The surviving tortoise species in Madagascar are notable for their extraordinary beauty, their slow growth and longevity, and the heavy human impact that is now pushing all towards extinction.

Key Words. – Reptilia, Testudines, Testudinidae, body size, shell, extinction, Madagascar

The thousand-mile long island of Madagascar, partly within the tropics and partly temperate, was a biological paradise for millions of years before humans arrived from Asia and Africa about 2000 years ago. This halcyon fauna included extraordinary creatures, among them the elephant birds (three species of *Aepyornis* and three of *Mullerornis*); three species of *Hippopotamus*; an array of lemur genera and species that ranged from the diminutive mouse lemur (*Microcebus*) to some as large as bears (*Megaladapis, Archaeoindris,* and *Palaeopropithecus*); and, not forgetting the spectacular array of amphibians and reptiles, almost all endemic to the island. There are thought to be about 300 amphibian species, only two thirds of them named, and 346 reptile species, all but 35 endemic to the island.

Since the arrival of humans, overexploitation of the extraordinary endemic fauna and unsustainable agricultural practices, have systematically reduced that fauna from the top down. The large lemurs are gone, although we are left with some of medium size, including the wonderful and totally bizarre aye-aye (*Daubentonia*), and many small ones. The colossal elephant bird, *Aepyornis maximus*, is now recognized as having been exterminated just a millennium ago, with its formidable eggshells still a prestigious commodity for treasure seekers in the deserts in the extreme south of the island; and, one of the largest tortoise species in the world, *Dipsochelys grandidieri*, became extinct about 1200 years ago. This huge tortoise, with its depressed and extremely thick carapace, is known from about a dozen subfossil shells, mostly now in the Paris Museum (Fig. 1), and many fragments, found scattered over the southwestern quarter of the island and into the highlands. It was partially sympatric with another large tortoise species, *Dipsochelys abrupta*, which in sharp contrast to *grandidieri* was characterized by a very high, domed carapace (Fig. 2). The strongly depressed shell of *D. grandidieri* gave rise to the original name that Grandidier himself gave to this tortoise, namely *Emys gigantea*. *Emys* is the generic name for the European pond turtles, and in earlier days it encompassed all freshwater chelonians; in this case, Grandidier wrongly assumed that a chelonian species with such a flat shell must be aquatic.

The question arises as to why *D. grandidieri* was not only very large (carapace length up to 125 cm), but also very thick-shelled (up to about 40 mm in the marginal areas). The specimen collection at the Chelonian Research Institute includes complete shells of two large tortoise species, *Chelonoidis nigra duncanensis* (from the Galápagos Islands) and *C. denticulata* (from continental South America) of identical length, but the latter weighs five times as much as the former. Some giant tortoises, especially the extinct species of the Mascarene Islands and also the recently extinct *C. n. abingdonii* in the Galapagos, had very thin shells. Hatchling tortoises of any kind are small enough to be swallowed whole by even small and medium-size predators. But the force behind the differences in shell thickness between the small island tortoises and the Madagascar giant may lie in the absence of large predators on the oceanic islands with, or formerly with, large tortoises, and their presence on Madagascar itself, with its spectacular megafauna (before the arrival of humans). In such a case, a thick carapace may indeed have provided some protection, at least in sub-adult and adult specimens, from predators such as the fossa (also called "foos"), a mammal appearing to the layman as being somewhere between a felid and a canid, as well as other predators now entirely extinct. It has been noted that the few mammalian carnivore species known from Madagascar are "derived from a single common ancestor that colonized Madagascar only once, sometime in the past" (Yoder and Flynn 2003). It is also important to realize that very large tortoises were widespread in Pleistocene times from the Bahamas, several Caribbean Islands, Florida, Spain, and through Europe to India and Asia, as far east as Java. Such large tortoises may have once been the norm throughout much of the world, not just on certain remote islands, until they were restricted to small islands by the spread of humanity over all the continents.

Perhaps the giant birds of Madagascar's past produced some predatory forms that may have been dangerous to

Figure 1. *Dipsochelys grandidieri* shell in the Paris Museum, collected at Etseré, Madagascar. Photo by Peter C.H. Pritchard.

young tortoises, just as Great Ground Hornbills today are serious predators of Leopard Tortoises up to at least half-grown in size in Botswana and South Africa, and ravens in the California deserts, their populations swollen by access to tourist trash, are constant predators upon hatchling desert tortoises.

One may assume that *D. grandidieri* had ancestors in East Africa, the passive ocean crossing to Madagascar being an entirely feasible one, especially when Madagascar was closer to the continent than it is today. In this case, the massive carapace, of adult tortoises at least, might well have deterred predation by the classic carnivores that remain in East Africa today – lions, hyenas, cheetahs, leopards, hunting dogs, etc., and their ancestors and forebears, and perhaps the remarkable armor, while no longer essential, was at least not a hindrance to survival in Madagascar.

An interesting specialized morphological feature, the remarkable upward expansion of the nasal opening at the front of the skull of *D. grandidieri*, must have been an adaptation for "snorting" water from very shallow and otherwise inaccessible rain puddles, in places and at times where rain could be a very limiting and indeed a limited commodity. On its own, this statement about behavior in an extinct species would appear to be rank speculation, but there is evidence that this is not the case. The Aldabra tortoise (variously known as either *Dipsochelys dussumieri* or *Aldabrachelys gigantea*), and the closest relative to *grandidieri*, survives and indeed flourishes on its isolated atoll not far from northern Madagascar and has the ability to secure a drink during hard times in exactly this fashion. *Dipsochelys grandidieri's* ancestors came from the west, but its descendants went north, or perished; the relationship between the extinct giants of Madagascar and the surviving large tortoises of Aldabra has now been confirmed by genetic comparison (Palkovacs et al. 2002). Genetic analysis has also indicated that the tortoises formerly found on the northern tier of the Western Indian Ocean Islands that bear the species names *ponderosa, gouffei, daudinii, arnoldi, sumeirei, hololissa, dussumieri,* etc. cannot readily be distinguished genetically from the Aldabra tortoise (Palkovacs et al. 2003). However, full genomic analysis of all the various forms has not been carried out, and morphological evidence suggests that at least some morphotypes (*arnoldi* and *hololissa*) may be genetically distinct (Gerlach 2011). Some factor has resulted in tortoises throughout this far-flung chain of islands having sufficient genetic contact by occasional passive flotation that they failed to speciate even though a number of them seem to be easily distinguished by the human eye. In contrast, the tortoises of the islands of the Mascarenes (i.e., Reunion, Rodrigues, and Mauritius), all now extinct, had diversified and speciated substantially before their extinction by the beginning of the 19th century. Curiously, *grandidieri* and *abrupta* shared at least one feature with the Mascarene tortoises that was not present in the surviving tortoises from Aldabra etc., namely the absence of an anal notch.

Novel techniques can generate new insights into extinct animal species, especially with sub-fossil material in caves or other sites that offer natural protection from humidity, sun, and rainfall. Not long ago one needed to carry flasks of liquid nitrogen to field-preserve DNA samples; today, we are learning about the DNA sequences of animals that have been dead for 1000 years or more. Moreover, the large keratinous scutes that cover the carapace and plastron of turtles and tortoises may reveal data about the natural diet of both living and extinct species. Examining stable isotopes of the elements that are present in the scutes (e.g., carbon and nitrogen), as well as in the bones, may offer different isotope ratios for herbivorous animals that forage in different ecosystems and at different times. Such dietary items will, to different degrees, become laid down in characteristic ways in the hard tissues of the browsers and grazers in question, and may even allow identification of different diets at different stages of ontogeny.

Such techniques have yielded findings relevant to the two extinct giant tortoise species of Madagascar. It is of great interest that there is a major geographic overlap between the territories occupied by these two species, *abrupta* having the wider apparent range in central, southwest, and southern Madagascar. The usual assumption is that giant tortoise species, being generalized feeders and tolerant of many habitat types, do not usually show sympatry. This is the case with the various taxa of Galapagos tortoises, and even with the smaller tortoises of North America, no two species are found together. One of the few exceptions to this

Figure 2. Variation in star-shaped shell pattern in *Pyxis arachnoides*. Photo by Peter C.H. Pritchard.

rule is the case of the extinct giant tortoises of the island of Rodrigues in the Mascarenes, where tortoise specimens found included the rather large and strongly saddle-backed *Cylindraspis vosmaeri* and the smaller, dome-shelled species *C. peltastes*. The island is very small, and the two tortoise species were apparently sympatric, judging by locations of subfossil remains, yet it is not apparent why or how the two forms were able to evolve their contrasting morphotypes. If Galapagos tortoises are anything to go by, the long-necked, relatively large *vosmaeri* may be based upon male specimens, and the smaller, domed tortoises (*peltastes*) may have been the females. Possibly, too, the sub-fossil material may have accumulated over a relatively long span of time, perhaps spanning the duration of occupancy of two tortoise species in the same place, but not at the same time.

Nicholas Arnold at the Natural History Museum (London) was able to determine the "order of events" of arrival and evolution of tortoises in the Mascarenes by examining both DNA of subfossil tortoises and also that of individual museum tortoises (London, Paris, and Vienna) that had been collected with external scutes intact from the islands before the resident species became extinct. The conclusion was that the ancestral *Cylindraspis* (presumably a gravid female) first arrived on Mauritius, where it speciated into two taxa (*C. triserrata* and *C. inepta*), the latter then giving rise to a propagule on Rodrigues, where it speciated into *vosmaeri* and *peltastes*, and another propagule from the same lineage colonizing Reunion to produce *C. indica*. Reunion is the largest of the islands and the most intensively volcanic and there may have been earlier tortoise colonizations there, of which all traces disappeared when the fauna of the island was overwhelmed by lava flows.

On Madagascar itself, the parallels to the tortoise situation in the Mascarenes and even the Galápagos are striking. Stable isotope analysis has indicated that the heavy, flat *grandidieri* was a grazer, probably in open, herbaceous habitats, including wetlands; whereas *abrupta* was a browser in more closed habitats and may have coexisted with humans for more than 1300 years. They were not strikingly different in size, but *grandidieri* reached 125 cm CL and *abrupta* only 115 cm. Both taxa have parallels with the Galápagos tortoises that still survive: the Galápagos equivalent of *grandidieri* is the very large, strikingly flattened *Chelonoidis n. guentheri* found in certain areas of Sierra Negra on southern Isabela Island and the adults normally show erosion and pitting of the carapace that would seem to be evidence of a wet habitat favoring erosive keratin fungi. Elsewhere on Isabela, tortoises, especially adult females, are often of the more domed *abrupta* form.

With the giants long gone, we are left with tortoises of merely medium size in Madagascar (*Astrochelys yniphora* and *A. radiata*), or small size (*Pyxis arachnoides* ssp. and *Pyxis planicauda)*. This size breakdown also occurs in southern Africa, where the medium-sized Leopard Tortoise (*Stigmochelys pardalis*) coexists with the Angulate Tortoise (*Chersina angulata*), and in different places with the various small species of the genera *Homopus* and *Psammobates*.

Many of these smaller tortoises have a characteristic, although variable, pattern on the carapace, by which the design on each scute looks (more or less) like a star (Fig. 2). On the continent, this occurs, with considerable variation, throughout the genus *Psammobates*. In Madagascar, *A. radiata* is famed for its beautiful, starred carapace, a

Figure 3. *Pyxis planicauda* in the Kirindy Forest, western Madagascar. Photo by Peter C.H. Pritchard.

feature shared with the genus *Pyxis*, as well as the various forms of *Psammobates*.

Two subspecies of the genus *Pyxis* (*P. arachnoides arachnoides* and *P. a. oblonga*) are remarkable for having an anterior plastral-hinged flap. Perhaps even more remarkable is that the third subspecies *P. a. brygooi*, separated from the other subspecies by the Onilahy River, and with a profoundly discontinuous range, lacks plastral kinesis. Moreover, the function of the flap in the first two of these subspecies is unclear. Plastral kinesis is quite common among chelonians, and takes many forms. In kinosternids, there are often, but not always, two lines of kinesis and the plastron may be large enough to close the shell openings completely, or it may be much too small for this. In the American box turtles, there is a powerful hinge across the middle of the plastron, allowing elevation of both fore and hind plastral lobes, whereas in other species (e.g., the Asian *Cyclemys dentata*) the hinge is not strong, and may not even be functional. Most *Pelusios* species (African side-neck turtles) have a well-developed kinetic anterior plastral lobe with the unusual feature of the anterior plastral buttresses being modified into "levers" with muscle attachments for elevation of the anterior lobe, although in one species (*P. broadleyi*) there is no kinesis. In the Spiny Turtle from Asia (*Heosemys spinosa*), the adult female has functional posterior plastral kinesis (perhaps to facilitate laying the startlingly large egg), whereas the entire shell of the adult male is completely rigid.

In tortoises, plastral kinesis, if it exists at all, is usually manifested by a slight flexion of the posterior plastral lobe, probably to assist oviposition. But the kinesis in *Pyxis* lies across the base of the anterior lobe, and instead of being forceful, is rather loose and floppy. In the unrelated *Staurotypus*, a kinosternid turtle from Central America, there is a rather limp anterior plastral hinge, but the anterior lobe is very small and its function seems to be to allow this large-headed and predatory turtle to lower the front of the plastron passively when the head is retracted and the jaws opened widely in a threat gesture. Among Madagascar tortoises, it has been suggested that the anterior plastral hinge, being found only in the two subspecies that live in the driest part of coastal Madagascar, is associated with resistance to dehydration. Another possibility is that, because the front edge of the anterior lobe is the thickest part of the plastron, it may serve to protect the retracted head from certain predators. Also, noting that these tortoises, although burrow builders, are able to push their way into fine sand during times of extreme heat, this may help the tortoise from getting sand pushed into the nose and mouth when they retreat underground. The plastral hinge is located between the humeral and the pectoral scutes, and this would normally be on a line that would traverse the entoplastral bone, but, as the tortoise matures, a realignment of the anterior plastral elements takes place, so that the humeral/pectoral junction becomes perfectly transverse, with the reduced entoplastron entirely within the anterior moveable part of the plastron.

It is curious that Siebenrock (1906), working with no fewer than 630 Vienna Museum specimens of *Pyxis* of all ages from close to Tulear, did not notice that the specimens from north of Tulear itself were different from those to the south, and it was not until 1972 that Vuillemin and Domergue examined a specimen from near Lake Ihotry that had the carapace of a typical *Pyxis*, but had an entirely rigid anterior plastral lobe. They named it *Pyxoides brygooi*, but the taxon was reduced to subspecific rank (*Pyxis arachnoides brygooi*) by Bour (1979).

One might seek to establish a relationship between the continental and island species of comparable size, such as leopard tortoises and radiated tortoises; or between the diminutive star tortoises of South Africa and those of the genus *Pyxis* in Madagascar. But this is not the case. DNA analysis indicates that the various tortoises of Madagascar are more closely related to each other than to any continental tortoises, despite their wide size range. The star pattern has in fact originated quite frequently in the evolution of turtles and tortoises, and today there are star tortoises in northwestern and southern India, Sri Lanka, southern Africa, and Myanmar, as well as in Madagascar, and the pattern even shows up in non-testudinid turtles such as the Florida and ornate box turtles of the genus *Terrapene*. One assumes that it is relatively easy to code genetically, as the rays of the stars elongate passively as each scute undergoes peripheral expansion. The pattern is also significantly advantageous in the field; most star tortoises live in relatively arid habitats, in which they often retreat into tussocks of dry grass, a medium in which they become almost invisible.

There is little sympatry among the tortoises of Madagascar, although there was more in the past. No other tortoise comes close to *A. yniphora* in its minuscule range in northwestern Madagascar, and the Flat-tailed Tortoise, *P. planicauda*, is isolated in a tiny area known as the Menabe Region, 40 km north of the city of Morondava, on the mid-western coast (Fig. 3).

The range of *A. radiata* incorporates a considerable stretch of coastal terrain in southern Madagascar, once extending inland as far as 50 km, and at least formerly reaching as far as, or beyond, Tulear on the southwest coast, and Tolagnaro on the southeast coast. Different parts of this range are shared, or were shared, with one or another of the subspecies of *P. arachnoides*, namely *P. a. oblonga* in the southeast, *P. a. arachnoides* in the south, and *P. a. brygooi* in the southwest. All *Pyxis* taxa are much smaller than adult *A. radiata*, and they are confined much more closely to the coastal area, especially in places with good sand dune development, than is *radiata*. The range of *brygooi* is very disjunct, and there are only three centers of distribution, one being very small.

There are a fair number of situations in which related chelonian species are able to coexist by having a significant size difference between the adults – they can avoid damaging competition by using different types of retreats, eating different plant species, and so on. Furthermore, it is possible that the very different carapace patterns may help avoid cross-mating attempts, especially between male *Pyxis* and juvenile *A. radiata*. *Astrochelys radiata* is remarkably variable in pattern, both as hatchlings and juveniles, and especially so as adults. The typical pattern of animals half grown or beyond consists of a yellow or golden center to each of the vertebral and costal scutes, from which yellow bands, increasing in width the further they get from the areolae, extend in all directions on the vertebral scutes and mostly in a downward direction on the costal scutes, and upwards on the marginal scutes (Fig. 4). However, variation is rampant and in some individuals, mostly old ones, the pattern imitates the South American *Chelonoidis carbonaria* in just showing yellow areolar blotches, without any radiations (Fig. 5). Large numbers of *A. radiata* are kept in captivity on the island of Reunion, and in one case a live hybrid tortoise (*radiata*/*carbonaria*) was produced in one of these facilities. In other cases, older tortoises may show a broad proliferation of the yellow areas of the carapace, sometimes with complete elimination of the shell pattern with age.

The shell pattern of *P. arachnoides* differs from that of *A. radiata* in having a single black blotch on each of the lateral marginals (two on each anterior marginal), and with a bold yellow band separating costal from marginal scutes on each side. The costal radiations extend anteriorly and posteriorly, but not downwards. The yellow areas expand, and black ones recede, with age, and the oldest individuals may have a plain brown or yellowish carapace. The plastron is usually immaculate, but in the subspecies *oblonga*, there are variable black blotches on the sides of the pectoral and abdominal scutes.

Most of Madagascar lacks tortoises, but the spectacular *A. radiata* still survives – and in some places flourishes – in the extreme south and southeast of the island. Its historic range encompasses about 21,000 square kilometers, but shrinks every year, as local people continue to consume this most beautiful of all tortoises, and others are caught for illegal trade or export. The remaining tortoises of Madagascar include the largest one, the very rare Angonoka, *A. yniphora*,

Figure 4. Radiating lines on shell of typical young adult *Astrochelys radiata*. Photo by Peter C.H. Pritchard.

Figure 5. Near-obliteration of radiating lines on shell of very old *Astrochelys radiata*. Photo by Peter C.H. Pritchard.

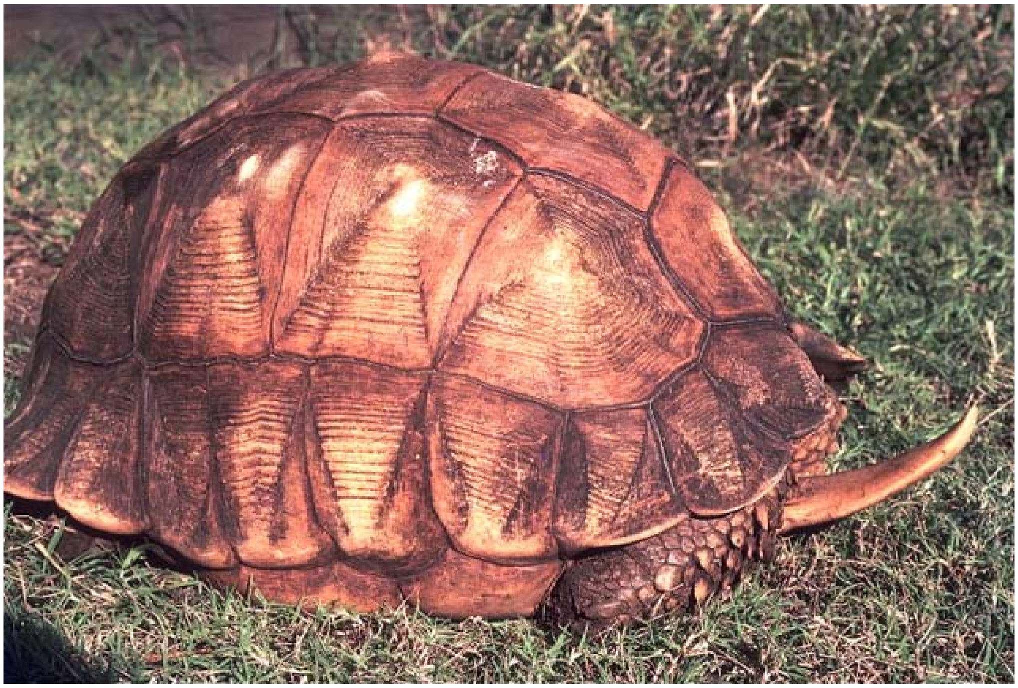

Figure 6. Old male *Astrochelys yniphora* with prominent gular "ploughshare" strut. Photo by Peter C.H. Pritchard.

confined to a minuscule area in the northwest, the small species *P. arachnoides* (all three subspecies) in southern coastal areas, and the extremely localized *P. planicauda* near Morondava in the west. All of these tortoise species tolerate extremely high field temperatures, and their habit of remaining immobile for long periods during the hot season may result in their growth annuli being very narrow, but also remaining distinct and unabraded for decades after the hatchling stage. Adult *A. radiata* typically show up to about twenty broad growth annuli on each scute, after which growth is sharply curtailed and annuli are bunched together and too narrow to count, as asymptotic size is approached. The smaller species (*Pyxis*) also tend to retain growth annuli that can be counted quite easily on the scutes of both carapace and plastron, and in the extreme case (*P. planicauda*), examination of the intact areolae on the shell scutes indicates that the adults are only about twice the length of the hatchlings; annulus counts indicate that the tortoises took about 15–16 years before annuli became too narrow to count and growth presumably stopped. The hatchlings of *planicauda* are in fact remarkably large, and the typical clutch consists of just a single egg. I once had responsibility of caring for several dozen adult *planicauda*, and kept them in an outdoor enclosure with a layer of dead leaves several inches thick. The tortoises were amazingly still almost all the time, with heads extended above the leaf litter, and remaining immobile and (seemingly) totally alert for many hours at a time. When rain fell they would thrust head and neck deep into the leaf litter, apparently seeking the moisture below the surface.

The Radiated Tortoise, *A. radiata*, is durable in captivity and may be the most long-lived of all chelonians, with two individuals of this species (one raised in Bundaberg, Australia, the other in Tonga) having reached ages well into their second century. One of these, known as Tui Malila, lived for a great many years on the island of Tonga, where it was kept, at large most of the time, in the Royal Gardens. Oral history insisted that this tortoise was presented to the King of Tonga by Captain Cook in 1773, or 1777, and it died on 19 May 1966 (possibly 189 years old) after which the preserved animal was kept for a while in the lobby of the International Date Line Hotel before being transferred permanently to the Tonga National Museum. The specimen indeed appears to be of great age, with no trace of the radiating carapace markings typical of the species, and with one side of the shell badly damaged and also scorched by a grass fire in the palace grounds. It is said to have been totally blind in its latter years and had to be fed by hand.

Another Radiated Tortoise that lived a very long time was known by the name of Torty. This animal was brought to Australia as a hatchling from Madagascar by John Powe in 1847, and resided with succeeding generations of the Powe family, living in Sydney, Gladstone, and finally Bundaberg. In 1964, the last of the Powe family, being in ill health, donated the tortoise to the Queen Alexandra Park Zoo, where it was still alive in 1981 (about 134 years old). Several years later I visited Bundaberg with the intention of filming Torty, but was sorry to hear that she had died recently, and even more unfortunately, the deceased animal was not preserved or kept.

The smaller tortoises of Madagascar do not share the resilience of *radiata*, and are very difficult to keep alive in captivity, although a few specialists have been able to breed *Pyxis*. The situation is paralleled by that of South Africa, where the larger tortoises (*Stigmochelys pardalis* and *Chersina angulata*) are relatively robust in captivity, whereas the dwarf tortoises of the genera *Psammobates* and *Homopus* are very hard to maintain, or breed. The difference probably lies in the fact that the miniature species in both areas are ecological specialists, with ecosystems, diets, and temperature and humidity preferences that are hard to replicate in captivity.

The final species, the Angonoka, *A. yniphora*, is a unique and spectacular animal, the largest surviving Madagascar tortoise, with the highest domed carapace of any tortoise, and although now considered to be a congener of *A. radiata*, it is so distinctive that one could possibly justify a separate genus for this species, and this was indeed proposed by Le et al. (2006), who Latinized the local vernacular for the species, i.e., *Angonoka*. When young, the species is yellow with bold black borders to the dorsal scutes, whereas the carapace of older animals becomes uniformly golden. The domed carapace has a remarkable structure, in that the scutes are extremely thickened except around the periphery of each, and the bulbous undersides of the scutes fit into shallow concavities in the bony carapace, the latter being extremely thin. The only other tortoise that shows this osteological feature is *Manouria impressa*, from Southeast Asia.

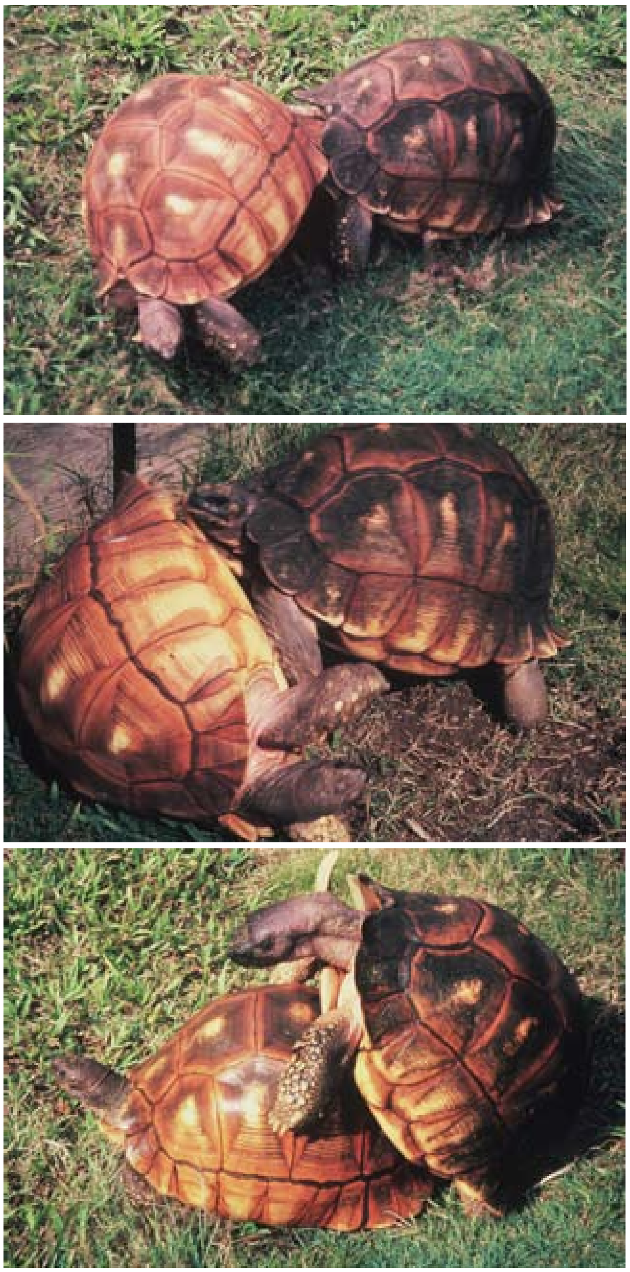

Figure 7. Male *Astrochelys yniphora* using his gular strut in courtship to hook, overturn, and successfully mate with a female. Photo sequence at the Honolulu Zoo by Sean McKeown.

The most conspicuously unique feature of *yniphora* is the great development of the gular area of the plastron, the gular scutes being fused into a single, rigid unit, which in adult males extends forward 10 cm or more as a gular strut from the anterior plastron, akin to a "ploughshare" (Fig. 6). It always shows very distinct growth annuli, and follows a gently rising curve, and would seem to be a lifelong inconvenience to the animal, forced to spend its life looking at its own ploughshare and forced to reach out sideways with its head and neck at a sharp angle to be able to feed. With misguided mercy, local tribal people have been known to sometimes cut off the ploughshare structure in order to make it easier for the tortoise to feed, but unfortunately this action would severely jeopardize the ability, at least of the male tortoises, to prevail in courtship and combat (Fig. 7; see description of courtship in McKeown et al. 1982), thus removing the individual from the ranks of successful breeders. Few other tortoises have this feature, but the much smaller *Chersina angulata*, plentiful in South Africa, shows a very similar development, although with its gular strut extending straight forward rather than curving progressively upwards. In both species, the gular strut of the female is much smaller than that of the male.

Madagascar is a nation, and an island – even a continent – with a tragic level of habitat destruction and a population of twenty million people, the vast majority of whom suffer from extreme poverty. The pressure upon edible fauna is thus extreme. Tortoises of all kinds have the problem of being highly esteemed for food, and so slow moving that, once spotted, can be picked up with ease and taken home – or to market. Vulnerability is different for each of the Madagascar tortoise species. The range of the *angonoka* in the northeast around Baly Bay, where it is limited to bamboo habitats, has probably always been very limited, and predation by both local people and visiting Arabs, as well as imported African pigs, has a long history. In recent years, there has been successful captive breeding of the angonoka, especially at the Durrell Wildlife Conservation Trust facility at Ampijoroa, and this has resulted in some successful releases of captive-raised specimens. Consumption by local people no longer seems to be the main problem. However, the great size and spectacular appearance of the angonoka, and its extreme rarity, have resulted in avaricious animal dealers and keepers in several European and Asian countries being prepared to pay enormous sums for living specimens, to a degree that the species itself is now critically threatened. At one point, a thief broke into the breeding facility at Ampijoroa and was able to escape with a significant part of the entire colony, including both juveniles and adults. The future of the species is thus highly uncertain, but captive breeding – behind high walls and with well-armed guards – will be a significant part of it.

The situation with the Radiated Tortoise, the *sokake* (*A. radiata*), in southern Madagascar is somewhat different, but is also somewhat dire. In pre-human times, there is evidence that the species once extended as far north as Ambato and Ankevo, and shared the ecosystems of the Morombe area with the *kapidolo* (*P. planicauda*). However, subsequent human pressure reduced the range to the level of Tulear and, on the eastern side of the island, to Tolagnaro. The sheer beauty of this tortoise has made it sought after by hobbyists, animal dealers, and many others. This category of consumers includes individuals who at least want their tortoises to survive and prosper (and possibly even to breed), but the pressure on radiated tortoises for food has been unrestrained and frightening in its scale. Relatively recently, a new form of exploitation has appeared, wherein tortoise shells are found with evidence of the carapace having been broken open on one side with a hammer or a rock – proof positive that the tortoise had been killed for its liver. Only a few years ago, Lewis (1995) made an estimate that, in the reduced area still well-populated by tortoises between Tsimanampetsotsa and Cap Sainte Marie, there was an estimated total population of between 12 to 54 million tortoises. Just a few years later, Leuteritz (2002) agreed with Lewis' estimate of the remaining radiated tortoise range, but indicated that the current population had been massively harvested for both food and the pet trade, yet he was still able to calculate an estimate of about 2522 tortoises/sq km in the southern part of the range.

Today, the massive consumption continues, and the numbers get lower and lower. One can find slaughtered *radiata* shells on every garbage dump in southern Madagascar, and one notable dump near Tulear had no fewer than 495 adult shells. There are still many live tortoises in captive colonies provided by confiscated animals, and the species breeds freely in a number of American collections. There are still thousands, mostly kept in captivity, on the island of Reunion, but the trend line for *radiata* in the wild is not optimistic.

Résumé

La majorité du territoire de l'île de Madagascar, longue d'un millier de milles, ne possède pas de tortues, et les aires de répartition des quelques espèces encore présentes de nos jours se chevauchent très peu. Les véritables tortues géantes s'y sont éteintes peu après l'arrivée de l'homme. Les espèces actuelles de tortues de Madagascar sont connues pour leur beauté extraordinaire, leur lente croissance et leur longévité, ainsi que pour l'impact massif des activités humaines sur elles qui les pousse toutes vers l'extinction.

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